The behaviour and ecology of social organization in a Caribbean surgeonfish

By

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Abstract

I studied the behaviour and ecology of social organization in a Caribbean surgeonfish, the blue tang (*Acanthurus coeruleus*). In chapter 1, I identify and describe the social modes exhibited by adult blue tangs and include the first description of adult territoriality in this species. Adults in the population were either territorial or non-territorial. Non-territorial fish formed schools and wandered, while territorial fish never schooled but sometimes wandered from their territory. In chapter 2, I explore potential determinants of the variation in the social organization in an attempt to explain the coexistence of the territorial and non-territorial modes. I examine the distribution of territorial, schooling and wandering tangs in relation to life history stage, habitat, time of day, competitor density, food abundance and population density. Life history stage, density of competitor damselfishes and conspecific population density appear to be key determinants of this social organization.

Résumé

J'ai étudié l'organisation sociale (comportement et écologie) du chirurgien bleu (*Acanthurus coeruleus*), un poisson corallien des Caraïbes. Dans le premier chapitre, j'identifie et je décris les diffèrentes formes d'organisation sociale des adultes, incluant la première description de la forme territoriale chez les adultes chirurgiens bleus. Les adultes dans la population étaient, soit territoriaux soit non-territoriaux. Les individus non-territoriaux se trouvaient en banc et passaient souvent en mode ambulant, tandis que les individus territoriaux ne se trouvaient jamais en banc, mais se trouvaient en mode ambulant quand ils quittaient leur territoire temporairement. Dans le deuxième chapitre, j'examine des déterminants potentiels de variation dans l'organisation sociale afin de tenter d'expliquer la coexistence des formes territoriales et non-territoriales. J'examine la distribution des individus territoriaux, en banc et en mode ambulant, relativement à l'étape du développement, l'habitat, l'heure de la journée, la densité de leurs concurrents, l'abondance de nourriture, et la densité de la population. L'étape du développement, la densité des desmoiselles concurrents, et la densité de la population d'adultes chirurgiens bleus semblent être des déterminants importants de cette organisation sociale.

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Preface

All data were collected and analyzed by I. Morgan. Preliminary work on focal observations was done with the help of field assistants M. Nadon and V. Binette. M. Nadon also helped in trapping and tagging. Dr. D.L. Kramer contributed to the design of the field study and the interpretation of the results and provided many suggestions for revision. Chapter 1 and chapter 2 are being prepared as two manuscripts and will be submitted for publication with Dr. D.L. Kramer as co-author. Because of this, the chapters are written in the third person plural. All other sections of the thesis are written in the first person singular.

This thesis is presented in accordance with the regulations of the Faculty of Graduate Studies and Research regarding thesis format, as presented in the Guidelines for Thesis Preparation:

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.

If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: A Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a review of the literature, a final conclusion and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers."

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General Introduction

Intraspecific variation in the social systems of vertebrates, specifically coral reef fishes, is common (Lott 1991, Shapiro 1991). Many species in the surgeonfish family (Acanthuridae) exhibit intraspecific variation in their social systems (Barlow 1974, Robertson et al. 1979, Montgomery et al. 1989). Despite this, potential reasons for the variation have not been specifically studied (but see Barlow 1974), and of the described surgeonfish social systems, few studies have focused on Caribbean surgeonfishes (Foster 1985, Reinthal & Lewis 1986). This thesis is a detailed study of the variation in the social organization of the blue tang surgeonfish (*Acanthurus coeruleus*) on the inshore fringing reefs of Barbados, West Indies.

The blue tang is a conspicuous and locally abundant member of Caribbean coral reef fish assemblages. The juvenile blue tang is yellow and territorial (Bell & Kramer 2000). The adult blue colour is attained between settlement and 7 months (unpublished data, Foster 1985). In Barbados, like in other Caribbean locations, adult blue tangs form large schools or behave as non-aggressive, solitary wanderers (Alevizon 1976, Foster 1985, Reinthal & Lewis 1986). In a preliminary study I encountered territorial adult tangs, a mode not previously described in the adults of this species (see Foster 1985 for anecdotal observation). Initial surveys of the study site revealed that individuals in the schooling, wandering and territorial social modes occurred in four ecologically different habitat zones on one fringing reef.

On a patch reef in Panama, schooling tangs achieved higher bite rates and received less harassment from damselfish then wandering tangs, and when damselfish were removed from an area, wandering tangs achieved bite rates similar to those of schooling individuals (Robertson et al. 1976, Foster 1985). It has thus been proposed that blue tangs school to gain access to the defended high quality algal resources in damselfish territories (Robertson et al. 1976, Foster 1985). Reinthal & Lewis (1986) found that wandering tangs were cleaned more often than schooling individuals and therefore proposed that tangs wander from schools to visit cleaning stations. Each of these studies was done in one ecologically homogeneous reef habitat or zone, despite the presence of tangs in most fringing reef zones (Lawson et al. 1999).

In Chapter 1, I identify and describe all of the distinct adult social modes on South Bellairs Reef. I tag individuals to determine the distinctness of each of the described modes. In keeping with previous studies, for individuals in each mode, I record bite rate, harassment rate by damselfishes and the rate of visits to cleaning stations (Robertson et al. 1976, Foster 1985, Reinthal & Lewis 1986). I also include measures of mobility. Unlike previous studies, I collect these data in each of the four ecologically different fringing reef zones at my study site. By doing so, I am able to compare the behaviours of different social modes in different environments. This allows me to examine relative differences between modes within a habitat zone and consider the results in the context of the proposed functions of each mode.

In Chapter 2, I examine the distribution of each of the modes described in Chapter 1 in the four fringing reef zones. The main study takes place on one reef, but I also determine the distribution on three other reefs. I predict that the distribution of the wandering and schooling social modes will be consistent with their proposed functions. The main objective of the chapter is to attempt to identify potential demographic, ecological and social determinants of the variation in the tang social organization. Specifically, I examine the role of life history stage, food abundance, damselfish density and population density in the occurrence and coexistence of the multiple social modes. In particular, I was interested in the occurrence of the territorial mode, a seemingly rare behaviour in the adults of this species. Although juvenile territoriality has been recognized (Foster 1985, Bell & Kramer 2000), the actual ontogeny of social organization has not been documented and, in this Chapter therefore, I include information on the density and distribution of all size classes.

Overall, these chapters provide a broad description of blue tang social organization and evidence for potential determinants of social organization in this common and abundant member of Caribbean coral reef fish communities.

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Chapter 1

The social system of adult blue tangs (*Acanthurus coeruleus*) on a fringing reef, Barbados, West Indies

1.1Abstract

Adult blue tangs on a fringing reef in Barbados exhibit three social modes. Fish in the territorial mode, not previously described in adults of this species, restricted their diurnal activity to a small area that overlapped the areas used by other territorial fish. They actively chased conspecifics and were chased by tangs and other species. They swam more slowly and fed at higher rates than other modes. Fish in the schooling mode moved over wide areas in compact, polarized groups of conspecifics, congeners and other species, often numbering 50-300 individuals. They were not aggressive and were attacked by damselfishes and territorial conspecifics. They swam rapidly and fed at intermediate rates. Fish in the wanderer mode showed neither aggression nor association with other individuals. They swam rapidly, well above the substrate, fed little, received more aggression and visited cleaning stations more often then other modes. Individuals in all three modes were found in all four main habitat types of our study reef, although schools in the back reef were transient. Behaviour of fish in a given mode depended on habitat-type. Territorial fish in the spurs and grooves zone fed less, displaced farther and were chased more often by damselfishes than those in other zones. Schooling individuals behaved similarly across zones but swam faster in the crest. In the back reef zone, wanderers fed more, moved less and did not visit cleaning stations. Observations of transitions between modes and of tagged fish indicated that individuals were consistently either territorial or non-territorial. Non-territorial fish formed schools and both territorial and non-territorial fish wandered. Wandering allowed fish in either mode to visit cleaning stations and alternative feeding sites.

1.2 Introduction

The surgeonfishes (Acanthuridae) are a diverse and widespread family in which all member species are obligate reef fish (Choat & Bellwood 1991). To date 6 genera have been characterized with a total of 72 recognized species, 4 of which are found in the Caribbean (all in the genus *Acanthurus*) (Nelson 1994). Three of these four species are common throughout the Caribbean Sea and are generally locally abundant. However, most studies of acanthurid social systems have been done on Indo-Pacific and Red Sea surgeonfishes (Barlow 1974b, Robertson et al. 1979, Montgomery et al. 1989). Surgeonfishes show considerable variation in social organization, with the adults found either in small to large schools, as solitary wanderers, in dominance hierarchies, or in territorial systems (Hiatt & Strasburg 1960, Jones 1968, Barlow 1974a, b, Robertson et al. 1979, Robertson & Gaines 1986, Montgomery et al. 1989, Craig 1996). In many Indo-Pacific species, intraspecific variation in social behaviour at different times or in different places has been reported (Barlow 1974a, Vine 1974, Robertson et al. 1979, Hourigan 1986, Craig 1996).

In the Caribbean, adult blue tangs (*A. coeruleus*) commonly form mixed-species schools (Foster 1985a). Schooling behaviour is thought to facilitate access to defended high quality algal resources in damselfish territories (Robertson et al. 1976, Foster 1985a). Non-territorial solitary individuals, which switch between schooling and solitary behaviour have also been described (Reinthal & Lewis 1986). In addition, Foster (1985a) recognized that a few individuals in her focal adult population were territorial, and Colin (1977) mentioned temporary male territoriality during spawning. Juveniles are solitary and territorial (Bell & Kramer 2000). Adult territoriality, however, has never been studied in detail.

Although blue tangs can occur in all fringing reef zones (Lawson et al.1999) and can move between these zones (Chapter 2), previous studies examined only patch reef habitat (Foster 1985a,b) or the spurs and grooves zone of fringing reefs (Reinthal & Lewis 1986). Reef zones are very different from each other in a variety of physical and biological variables (Lewis 1960). Whether individual fish respond behaviourally to these differences, has not been explored in surgeonfishes (although see Choat & Bellwood 1985).

The present study is a detailed account of the intraspecific variation of the social modes exhibited by adult blue tangs. The specific goals of the study were 1) to identify all social modes of adult blue tangs on one fringing reef, 2) to quantify behavioural differences between social modes, 3) to determine whether the behaviours varied among reef zones, and 4) to examine the temporal stability of the identified modes. Chapter 2 examines the densities of these different social modes in these reef zones and relates their distribution to potential determinants of their social organization.

1.3 Natural History and Study Site

1.3.1 Study species

Blue tangs are diurnal, obligate coral reef fish found at depths of 1-25 m (Humann 1999). They are labriform swimmers (Lindsey 1978), using pectoral fins for routine movements and the caudal fin for burst swimming. Adults are considered relatively mobile (Chapman & Kramer 2000). Juveniles settle from the plankton at a total length (TL) of 3.1-3.4 cm (modified from Foster 1985a), and the largest recorded adult size is 39.0 cm (TL) (Figueiredo & Menezes 2000). Juvenile blue tangs are bright yellow and defend small territories against juvenile conspecifics and juvenile congeners (Foster 1985, Bell & Kramer 2000). The adult blue colour is usually attained 1-7 months after settlement (Foster 1985a) at 6-8 cm (TL) (Bell & Kramer 2000). Blue tangs feed mostly on benthic algae (Clavijo 1974), although they seem to supplement their diet with animal material during seasons when algal resources are scarce (e.g. dry season, Duarte & Acero 1988). Sexes have no known external morphological differences. Sexual maturation has not been well studied but is believed to occur at a minimum of 11 cm fork length (FL) for males and 13 cm (FL) for females (Reeson 1975).

1.3.2 Study site

The study was conducted from the Bellairs Research Institute of McGill University, in Barbados, West Indies on an inshore fringing reef called South Bellairs Reef (Lewis & Oxenford 1996). This reef is protected by the Barbados Marine Reserve (BMR). With the exception of cast netting for clupeids, all harvesting of coral, invertebrates and fishes is prohibited in the BMR (St. Hill 1987). The reef extends 215 m offshore and has a total surface area of 3.47 ha (Lewis 2002). South Bellairs has typical Caribbean fringing reef zonation (described by Lewis & Oxenford 1996), with a back reef, a reef crest and a spurs and grooves zone (see Figure 2.1, Chapter 2). The back reef begins several metres from shore and the depth ranges from 0.5-1.5 m. The back reef has low coral cover, low habitat complexity, high turbulence, and the substrate is largely composed of rock and dead coral rubble covered in turf algae. The crest has higher habitat complexity and coral cover than the back reef. At high tide, the depth ranges from 1 to 3 m; at low tide, the highest crest pinnacles are sometimes exposed. The spurs and grooves zone is the most seaward and deepest zone (3-8 m) with the highest live coral cover. In addition to the three typical fringing reef zones, South Bellairs also has a unique fourth zone, which we refer to as the 'flat'. It appears to have been part of the crest and spurs and grooves zones that have subsequently coalesced into a 'plateau'. It is similar to the back reef in its topography, but deeper (1.5-3 m). Coral cover is relatively low, but fire coral (*Millepora sp.*), mustard hill coral (*Porites astreoides*) and branching, encrusting and fan gorgonians are present. The majority of the substrate consists of dead coral rock covered in turf algae and therefore fits the definition of a shallow 'Gorgonian-dominated pavement or hardground' (National Park Service 1994).

1.4 Methods

1.4.1 Social mode descriptions and focal observations

To classify the social modes of all adult individuals for focal observation, we used operational definitions based on a preliminary study of 30 haphazardly chosen adults followed for 5-100 min between 10:30-15:00 (June 18-June 30, 2001). All individuals appeared to fall into one of three social modes: territorial, schooling and wandering. Territorial individuals displayed aggression and persisted in an area when chased by other fish. Schooling individuals swam in a polarized fashion with at least 10 fishes (tangs or other species). Wanderers stopped foraging and swam away when attacked by other fish (both conspecifics and heterospecifics). We divided the population into five FL size classes: 1) <12 cm, 2) 12-14.5 cm, 3) 15-17.5 cm, 4) 18-22.5 cm and 5) >22.5 cm. Size class 5 was rare, and size class 1 was likely to be sexually immature. Both size classes were therefore excluded from the focal observations.

We performed focal observations between July 8 and October 29, 2001 on each social mode in each zone where they were found. All data presented here were recorded by I.M. while snorkelling or using SCUBA. Quantitative behavioural data were recorded between 10:00 and 14:30 (peak foraging time of adult tangs according to Reinthal & Lewis 1986). The observer followed 8-13 individuals of size class 2, 3 or 4 per social mode (territorial, schooling, wanderer) in each zone (spurs, flat, crest, back) (total n=121). Territorial fish were haphazardly chosen and, in order to prevent concentrated sampling in one area, care was taken to not watch neighbouring fish. For the territorial fish sampled, we placed a small marked stone at the centre of their territories in order to prevent re-sampling that individual. Schools were dispersed over a large area and often difficult to locate. Therefore, the observer performed the focals on the first school seen in the zone, with the individual focal haphazardly chosen within the school. The position of the tang within the school changed often; thus there was no danger in over-sampling a section of a school. Wandering individuals in the spurs, flat and crest were often difficult to locate; therefore, the first wanderer observed upon entering the zone was followed. Although some schooling and wandering fish focals were tagged, ensuring that we did not re-sample the schooling and wandering individuals was more of a challenge than with territorial fish. However, the population of wandering and schooling tangs on South Bellairs Reef at midday is estimated to be 552 and 370 tangs, respectively (Chapter 2). Thus, the chance of sampling one individual more than once is low.

For the data to be used in the analysis, we set a pre-determined target of no less that 15 min and no more than 30 min of observation time. The focal was stopped if an individual left the designated zone, switched social modes or was lost in deeper water before the 15-min criterion. Although large schools were regularly observed in the back reef, the school or individuals in the school always spent less than the required 15 minutes schooling in this zone (see Chapter 2 for further detail). Therefore, we have no focal observations on schooling tangs in this zone. If the observer lost visual contact with a schooling focal individual (due to confusion with other members of the school) a composite individual was used (as in Foster 1985a). Immediately after losing visual contact, another individual was chosen and the focal continued. This new individual was of the same approximate size, exhibiting the same type of behaviour and found in the same general area of the school as the previous focal individual. Composite focals (n=6) were based on two or three individuals. All focal observations on territorial individuals (n=48) lasted 30 min. Focal observations on schooling individuals (n=29) and on wandering individuals (n=44) averaged 25.6 ± 5.4 (SD) min and 25.3 ± 6.0 min, respectively.

We determined the size and species composition of schools by conducting daily surveys in each of the zones of South Bellairs Reef for the study reported in Chapter 2. When schools were encountered during a survey, we counted all tangs and heterospecifics participating in the school (Chapter 2). We present the results of the midday size and species composition surveys here.

For each focal fish, a plastic slate was used to record 1) foraging rate on substrate, 2) aggression received from other fish, 3) time to perform 50 pectoral fin beats (as a measure of swimming speed), 4) horizontal displacement distance, 5) visits to cleaning stations, and 6) chases or other aggressive acts directed toward other fish. For territorial individuals, forays from the territory and the presence of other individuals using the same area (cohabitants) were also recorded. Forays were temporary departures at least 5 m from the area the fish was seen defending and were not included in the total focal time. Foraging rate was determined by recording the number of bites taken in the first 5 min and in the last 5 min of the focal. To calculate the bite rate per minute, we took the mean of these two measures and divided it by five. Displacement was determined by placing a marked surface buoy at the location of the start of the focal and measuring the straight-line distance to the buoy at the end of the focal. Switches between social modes were recorded during all attempted focal observations, whether or not the 15-min criterion was met, to provide a measure of short-term temporal stability of social mode. Data were not collected on the individual when it had switched out of a mode, but data collection was resumed if the individual returned to the original mode. The time spent out of the mode was not included in the final focal time.

In May 2003 we returned to the study site and measured the area used by territorial tangs. We estimated area by watching 17 territorial adults (9 in the crest, 8 in the flat) for 20 min. During this time we noted the farthest points visited by the tang and marked them with white coral stones. We measured the longest length of the territory and the distances between these points. On a slate, we drew the positions of all the right (90°) triangles within the area bound by the edges. We measured the three sides of the triangles and using these measurements, we mathematically verified that the angles were indeed 90 degrees. Using these measurements, we calculated the total territory area.

In order to convert the pectoral fin rate into swimming speed, regression models were derived from an independent data set. On days when there was no current and surge was low, the observer haphazardly chose a tang, placed a stone where the observation began, and followed the tang, counting the number of pectoral fin beats until the tang changed direction. Time, number of pectoral fin beats and distance traveled (a straight line) were recorded. Data were gathered on 11 individuals of size class 2 and 19 fish of size classes 3 and 4. Linear regressions relating swimming speed to pectoral fin beat rate were calculated. Size class 2: Y= 0.254X ($p<0.0005$); size class 3/4: Y= 0.289X ($p<0.0005$) where Y is swimming speed (m sec^{-1}) and X is pectoral fin beat rate (beat sec^{-1}). The intercept was not significantly different from zero in either case (see Appendix A for further details).

1.4.2 Tagging study

We captured 42 adult tangs (3 fish in May and 39 fish in October-November 2001) using dip nets on sleeping individuals in the early evening or by means of modified Antillean fish traps. Individuals over 12 cm were tagged in the musculature under the dorsal fin using plastic, multi-coloured anchor tags (Floy Tag®) to permit recognition without re-capture. The observer recorded tagged individuals whenever seen, noting zone and social mode.

1.4.3 Data analysis

In order to ensure that the assumption of normality of parametric tests was not violated, we examined scatter plots of residuals and predicted values. The data were log10 transformed if the residuals showed consistent patterning or extreme variance. Levene's test for homogeneity-of-variances was done for each dependent variable. With normalized data, we performed fixed factor two-way ANOVAs in order to test the effects of social mode, zone and their interaction on each behavioural variable. We used a Type IV model in our ANOVA analyses because we were missing one treatment cell (back reef schools) (Milliken & Johnson 1984). With the exception of 'chases by blue tangs' and 'chases by ocean surgeonfish', all data met the assumption of normality following transformation. These variables were analyzed using a non-parametric test (Kruskal-Wallis) to test main effects. Because we had unequal and relatively small sample sizes per cell, some data sets had unequal variance. When we performed multiple comparisons with data of unequal variance, we used the Dunnett's T3 test; with data of equal variance, we used the GT2 test due to our unequal *n* (Day & Quinn 1989). Multiple comparisons for the interaction terms were done by contrasting means with a Bonferroni correction. Data analyses were done using SPSS 11.0.

1.5 Results

The five main variables (displacement rate, swimming speed, bite rate, visits to cleaning stations and aggression received) changed with social mode and with zone (Table 1.1). In all five of these cases the interaction term was also significant (Table 1.1) indicating that the differences between modes depended on zone (Table 1.2).

1.5.1 Territorial mode

Territorial blue tangs were the only social mode that exhibited aggression. Aggressive behaviour consisted almost exclusively of chases. One individual also directed tail beats toward conspecific wanderers (as described in *A. lineatus* by Nursall 1974). Territorial individuals chased intruders at a mean rate of 0.15 ± 0.01 chases min^{-1}, and this did not vary significantly with zone. Chases were directed primarily at adult conspecifics (120 of 203 chases), including wanderers (51.7 % of 120 chases) as well as overlapping (27.5 % of 120 chases) and non-overlapping (9.2 % of 120 chases) territorial individuals. Fewer chases were directed at juveniles (6.7 % of 120 chases) or schooling conspecifics (4.5 % of 120 chases). Some chases were also directed at ocean surgeonfish (*Acanthurus bahianus*) (32.0 % of 203 chases) and other species (8.9 % of 203 chases), including redlip blennies (*Ophioblennius atlanticus*), striped parrotfish (*Scarus croicensis*) and dusky damselfish (*Stegastes dorsopunicans*). Although rates of aggression by other individual tangs were not recorded separately, there appeared to be asymmetries in the rate of chasing between overlapping territorial individuals. When chasing wanderers, the front half of the body changed from blue to white most of the time (74.2% of 62 chases) in a display that appeared identical to the courting male colouration illustrated by DeLoach (1999). In contrast, most chases of schooling conspecifics (80% of 5 chases) involved a colour change in which the front half of the body turned very dark (almost black). When chasing other territorial individuals, colour changes occurred rarely (9.1 % of 44 chases), and these could be either the white front or black front pattern. Colour changes were never produced when chasing juvenile conspecifics or other species, except one case where a chase toward a dusky damselfish ended with a white front pattern.

Territorial individuals restricted most of their movements to relatively small areas and, while in their territory, remained close to the reef substrate. Territory areas averaged 6.7 ± 2.8 (SD) m^2 (range 1.7-12.1 m^2) and territory lengths averaged 3.8 ± 0.7 (SD) m. When chased by a damselfish, territorial individuals would ignore the attack, move a few centimetres or return the aggression, rather than continuing on in the same direction as did fish in the wandering and schooling modes. This is reflected in very small mean displacement distances (0.08 ± 0.01 m min^{-1}) as compared to the wanderers and schooling fish (2.40 ± 0.36 m min^{-1} and 1.92 ± 0.30 m min^{-1}, respectively; Figure 1.1, Table 1.2). Displacement rates of territorial fish differed among zones, being greatest in the spurs and grooves and lowest in the back reef (Figure 1.1). The space used by territorial fish was not exclusive but overlapped with the areas used by other adults (0.43 ± 0.08 overlapping individuals per home range), blue juveniles (0.48 ± 0.10 individuals) and yellow juveniles (0.17 ± 0.06 individuals), in addition to congeners and other species such as dusky and longfin damselfishes (*S. diencaeus*) and redlip blennies.

In addition to having lower displacement distances, territorial tangs also swam more slowly, averaging 0.10 ± 0.01 m sec^{-1}, only about half to one third of the speed of the other social modes (Figure 1.2, Table 1.2). This rate did not differ significantly among zones (Figure 1.2).

Foraging rates of territorial individuals were higher than those of other modes, except that territorial and schooling individuals did not differ significantly in the spurs (Figure 1.3, Table 1.2) and territorial and wandering individuals did not differ significantly in the back reef (Table 1.2). The foraging rates of the territorial individuals were highest in the flat and lowest in the spurs and grooves zone (Figure 1.3).

Tangs were cleaned by cleaner gobies (*Gobiosoma* spp.) and juvenile Spanish hogfish (*Bodianus rufus*) at traditional cleaning stations frequented mostly by other tangs. Some territorial individuals had cleaning stations within their territorial boundaries (which they did not defend against other clients), while others visited cleaning stations while on a foray. Territorial individuals did not differ from schooling individuals in their frequency of visits to cleaning stations, but they had far fewer cleaning station visits than wanderers in the crest and flat (Figure 1.4, Table 1.2). Cleaning station visits of territorial fish did not vary significantly among zones, though visits were rare on the flat and back reef.

Territorial tangs were attacked by damselfishes, other tangs, and ocean surgeonfish at a rate of about 0.40 ± 0.04 attacks min^{-1}. This is less than the amount of aggression received by wanderers in all zones except in the spurs and grooves but not different from that received by schooling tangs (Figure 1.5a, Table 1.2). Although overall attack rates towards territorial fish did not differ among zones, the source of aggression did. Chases by damselfishes were significantly more frequent in the spurs and grooves than in the flat and the back reef (Figure 1.5b). Chases by other blue tangs very rarely occurred (Figure 1.5c). Chases by ocean surgeonfish were not common overall, especially in the crest (Figure 1.5d). The observation that ocean surgeonfish chase blue tangs indicates a not yet described territorial mode in the adults of this species.

Eleven focal territorial individuals (23%) left their home ranges and began behaving like wanderers on 16 different occasions. These forays lasted between 52 sec and 11 min. During these forays, fish foraged on the substrate (twice) or in the water column (3 times), visited cleaning stations (3 times), joined a passing school for 1–2 min (3 times) or swam without any apparent additional activities (5 times).

Territorial individuals occupied the same home ranges on subsequent days. Four tagged and one untagged but recognizable individual were seen repeatedly in the same locations in the flat (n = 2) and crest (n = 3) until the tags fell out 6-180 days later (55 ± 72 (SD) days). However, home ranges were abandoned at night. Eight territorial individuals on the crest and flat observed at dusk all left their territories and moved toward deeper water between 18:15 and 18:35. Tagged territorial individuals were consistently seen on their home ranges by 6:00. The tagged individuals that had been captured for marking at dusk (n=3) were found in daytime home ranges 10 – 80 m from the point of evening capture.

Tagging also revealed seven individuals in the spurs and grooves that never displayed overt aggression but were consistently seen in the same small area in this zone (average time seen in area and tagged was 12 days, range 6-17 days). These individuals were also seen wandering and schooling over this period, at various times of the day. The wandering, schooling and non-aggressive 'territorial' behaviour exhibited by these individuals was not consistently related to the lunar cycle. When seen schooling, these individuals were usually in close proximity to their home range and all dropped out of the school when in their home range. On one occasion, one of these individuals was found schooling over 50 m away in the spurs and grooves. However, it left the school within 7 min and meandered back to its home range where it remained for the rest of the focal observation.

1.5.2 Schooling mode

Schooling blue tangs consistently moved together in a polarized fashion over the reef. Although in principle, two fish could form a school, the schools on South Bellairs consisted of at least 10 fishes (tangs plus other species) moving and foraging together, and the numbers were usually much greater (Figure 1.6). Schools most often included ocean surgeonfish and to a lesser extent doctorfish (*A. chirurgus*), Bermuda or yellow chubs (*Kyphosus sectatrix* or *incisor*), various parrotfishes *Scarus* spp. and *Sparisoma* spp., trumpetfish (*Aulostomus maculatus*), and yellow and spotted goatfish (*Mulloidichthys martinicus* and *Pseudupeneus maculatus*).

Schools were always seen in the crest zone and were rare in the flat. The absolute size and composition of the schools changed with zone (Figure 1.6) and with time of day (see Chapter 2). In mixed species schools in the flat and the crest, blue tangs were usually numerically the most abundant and found at the front of the group. In these zones, they were therefore the 'core' species, as defined by Itzkowitz (1977). Ocean surgeonfish were more often found at the back of the school, and the other species were interspersed throughout the group. In the crest, ocean surgeonfish tended to feed lower on the reef structure than blue tangs in the same school. Individuals, small groups and large groups often split from the main school and re-joined it as it moved. Although the schools had distinct edges, individuals moved freely within the school, frequently changing their position with respect to their neighbours. For example, in the crest, the zone with the largest number of tangs participating (Figure 1.6), tangs at the front of the school would feed at a patch while the rear members swam over them and assumed the front position. In the spurs and grooves and the flat, all members of the school fed in the same patch at the same time.

The situation in the back reef was slightly different from other zones. Ocean surgeonfish schools (mean 87.3 ± 67.4 (SD) ocean surgeonfish per school) were commonly seen in the back reef; although a few tangs (<12) were seen participating in these schools, their membership was sporadic. Schooling tangs in the deeper, more offshore section of the back reef, did not stay in the back reef and often swam deeper and into the flat zone. If such schools included ocean surgeonfish the species would separate, with the ocean surgeonfish moving towards the back reef and the tangs towards the flat. When seen schooling along the southern edge of the back reef, tangs would follow this edge and generally swim into deeper waters. If schooling tangs were seen in the transition zone between the crest and the back reef (*Diploria-Palythoa* zone, Chapter 2) the school would return to the crest within 10 minutes (and thus be a crest school). Although body colour varied among schooling individuals, there were no consistent colour changes. However, when crossing a large continuous sandy bottom, tangs became pale blue, returning to a darker blue upon reaching reef again.

During a half hour focal observation, schools in the crest and the spurs and grooves rarely left the zone in which they were first located, but individuals frequently dropped in and out of the school. At times, entire schools would cross over to a neighbouring reef (North Bellairs) either through a patch reef area connecting the two reefs (1 time) or by crossing a 30-60 m wide area of sand (3 times). Except for these brief sand zone crossings, schools were never seen to leave fringing reef habitat during the day.

Displacement distances of schooling fish were much greater than those of territorial fish. They averaged smaller displacements than wanderers, but these differences were statistically significant only in the spurs and grooves (Figure 1.1, Table 1.2). Swimming speeds of schooling fish (0.29 ± 0.02 m s^{-1}) were significantly higher than territorial fish, but not different from wanderers (Table 1.2). Schooling individuals swam fastest on the crest and slowest in the spurs and grooves (Figure 1.2) but their displacement rates between habitats did not differ significantly (Figure 1.1). Foraging rates of schooling individuals were lower than those of territorial fish on the flat and crest but not different in the spurs and grooves zone (Figure 1.3, Table 1.2). However, foraging rates of schooling individuals were similar in all zones (Figure 1.3). Individuals were rarely cleaned while in a school (Figure 1.4, Table 1.2). When it did occur, 4-8 tangs would stop at a cleaning station (usually under a coral overhang) to be cleaned by juvenile Spanish hogfish. These individuals would resume schooling once the rest of the school had passed. There was no effect of zone on the cleaning frequency in schooling tangs (Figure 1.4). The number of attacks received by schooling tangs was generally similar to that received by territorial fish, but less than that received by wanderers, although the difference was not statistically significant in the spurs and grooves (Table 1.2). Although damselfish aggression varied with zone, with the highest rates of aggression in the spurs and grooves and crest zones (Table 1.1), it generally did not differ among social modes (Figure 1.5b). However, schooling tangs in the spurs received significantly less aggression from damselfishes than territorial individuals did. Schooling fish also tended to receive less aggression from other tangs and ocean surgeonfish than wanderers did (Figure 1.5).

No schooling fish ever switched to the territorial mode during focal observations. However, switches from schooling to wandering were relatively frequent. A plot of the proportion of schooling fish selected for focal observations that were still schooling after a given period of time showed an average switch rate of 0.017 switches per individual per minute. After 30 min, 56% of focal individuals were still schooling. Although most of the individuals that left the school continued as wanderers for the remainder of the 30 min focal, four schooling individuals 'forayed', returning to a passing school 2.5-13 min after leaving. While on the 'foray', one individual swam to North Bellairs Reef by crossing the 30-60 m wide sandy area, one was cleaned, another foraged in the back reef and the last fed on plankton among schooling brown chromis (*Chromis multilineata*).

Nine tagged blue tangs that did not show territorial behaviour were observed at least twice. These tangs were seen either schooling or wandering 8-60 m away from the traps in which they had been caught originally. Four of these tangs were only ever seen schooling in the same general area of the same zone as they had been previously seen (2-9 days before). The five remaining tagged individuals were occasionally seen wandering. However, the majority of the observations of these fish (33 out of 40 re-sightings) occurred when they were schooling (over 4-15 days). For those that were seen wandering at least once (n=5), the zone in which they were seen wandering was the same as the zone in which they were seen schooling, but the location differed between observations.

1.5.3 Wanderer mode

Tangs in the wandering mode were distinguished by a lack of both aggression and association with other individuals. In general, they swam higher above the substrate than other modes, moved quickly, and did not persist in an area when chased. Wanderers often swam to North Bellairs Reef, either through an offshore patch reef area connecting the two reefs (9 times) or across the sandy area (1 time). Some wanderers left the fringing reef (7 times), swimming offshore over rubble substrate in the direction of a patch reef at 20 m depth.

Displacement distances of wanderers were higher than territorial fish and averaged more than schooling fish, although the difference was only significant in the spurs and grooves zone (Figure 1.1, Table 1.2). Swimming speeds were similar to those of schooling fish and considerably higher than territorial fish (Figure 1.2, Table 1.2). Wanderers fed sporadically between moves. Their foraging rates were lower than territorial fish in the spurs and grooves, flat and crest and lower than schooling fish in the spurs and grooves and crest (Figure 1.3, Table 1.2). Wanderers visited cleaning stations more often than other groups. Rates of cleaning station visits were higher than schooling fish in the crest and spurs and grooves and higher than territorial in the crest and flat (Figure 1.4, Table 1.2).

The wanderers in the spurs and grooves, flat and crest were not significantly different from one another for any behaviour. Wanderers in the back reef tended to be an exception to these trends. Their displacement, swimming speed, and cleaning visit rates were lower and their foraging rates were higher than in other zones (Figures 1.1-1.4). Furthermore, tangs in the back reef tended to form temporary aggregations. Individuals in these aggregations were always close to the substrate, constantly foraging, not swimming together, spaced 1-3 body lengths apart and scattered apart quickly upon disturbance (e.g. breaking waves, people wading through the area). There was neither cohesion nor aggression in these aggregations; all individuals that were observed moved independently of other individuals.

Wanderers were attacked least often in the spurs and grooves zone and most often in the flat (Figure 1.5a). Wanderers were attacked more often than other social modes in the flat, crest and back (Table 1.2). These differences appeared due mainly to aggression from blue tangs and ocean surgeonfish rather than from damselfishes (Figure 1.5).

A plot of the proportion of focal wanderers that were still wandering after a given period of time showed the average rate of switching to schooling as 0.024 switches per individual per minute with 22.5% remaining as wanderers after 30 min. This calculation was based on data from the spurs, flat and crest, which did not differ strongly from each another. Although wanderers in the back reef never switched to schooling in this zone, they may have left the zone to return to schools elsewhere. There were too few data to determine the rate at which wanderers switch to the territorial mode. There was no indication from the behaviour of wanderers whether they would become territorial or join a school.

Tagged individuals that were re-sighted more than twice were never only wandering. All were seen schooling at least once and none were seen to hold a territory.

1.5.4 Social mode and reproductive behaviour

Because we were unable to sex the fish in the field, the relationship between social mode and reproduction is unclear. Despite the overlap between some territorial individuals, no consistent pairing was evident. We performed focal observations on territorial individuals (n=6) and followed schools during full moon periods, the peak spawning time for blue tangs (Colin 1977). There was no evidence of pre-spawning activity on territories, and all observed territorial individuals left their territories at dusk. However, they remained on the reef where they joined small, unstable, wandering shoals until nightfall. It was not possible to determine whether the shoals were composed of either territorial or schooling fish or both. On two occasions, using SCUBA, we followed large schools of tangs and ocean surgeonfish as they left the fringing reef at dusk on the night of the full moon. It was not possible to establish whether territorial individuals were in the schools. The individuals swam offshore into deeper water (25 m) where they swam in a single file along a ledge. At one point, the school split and the majority of ocean surgeonfish swam north along the ledge while the blue tangs swam south. Some blue tangs were not participating in the single file migration. These individuals were exhibiting a high level of interaction in patch reefs along this ledge. The fish in the single file continued swimming offshore until nightfall when we lost sight of them.

1.6 Discussion

The territorial mode

Yellow-phase juvenile blue tangs are territorial (Bell & Kramer 2000) and it has been suggested that once they turn blue, juvenile tangs become more mobile (Foster 1985a) and presumably join the adult foraging schools. Although adult blue tangs have been recognized as occasionally territorial or at least aggressive (Foster 1985a), this mode has never been studied in detail. Our description of the territorial adult tangs on South Bellairs Reef is the first for an adult Caribbean surgeonfish.

According to Grant (1997), a fish is considered territorial if it responds aggressively to intruders in its home range. Adult blue tangs engaged in aggressive interactions mostly with conspecifics and congenerics. The overall attack rate against all intruders was 0.15 attacks min^{-1}. Previous work on territorial yellow juvenile blue tangs found an attack rate of 0.12 attacks min^{-1} (Bell & Kramer 2000), and studies on territorial Indo-Pacific surgeonfishes have found attack rates ranging from 0.17-2.5 attacks min^{-1} (Robertson et al. 1979, Choat & Bellwood 1985, Craig 1996). The average displacement of territorial individuals was 10-100 times less than the other two modes, and tagged individuals remained in the same small area for up to 6 months. Thus, some of the tangs in our study population meet Grant's (1997) criterion for territoriality.

Some individuals' territories overlapped with those of juvenile and territorial adult conspecifics. Maher & Lott (1995) included in their definition of territoriality the possibility for defense by a group of mutually tolerated individuals. All conspecific cohabitants chased intruders but did not actively exclude each other. However, aggressive displays between adult cohabitants were occasionally observed, indicating possible dominance relationships. Adult blue tang territories also overlapped with *Stegastes* damselfishes and blenny territories, much like the interspecific overlap in juvenile tangs (Bell & Kramer 2000, I. Morgan, unpublished observations). Spatial overlap between potential territorial food competitors is common in reef fishes (Smith & Tyler 1972), and cohabitation between surgeonfishes, blennies and damselfishes has been described in the Indo-Pacific (Robertson & Polunin 1981, Roberts 1985, Roberts 1987).

The function of adult blue tang territoriality is not clear. In general, the resources defended in fish territories can include shelter and nest sites, mates, and food (Grant 1993). Adequate shelter sites appeared to be absent from territories in the flat, crest and back reef zones and territorial adults in these zones moved offshore at dusk. So, access to a night shelter site or to a daytime refuge from predation is not likely to be beneficial to holding a territory there. However, individuals in the spurs and grooves had access to shelter, and defence of a shelter site in this zone is a possibility for some territorial fish. We found no evidence that the territory was directly tied to reproduction. Blue tangs are broadcast group spawners (Colin 1977), so a nest site is not required. Some Indo-Pacific territorial surgeonfish live in pairs and spawn in their territory (*Zebrasoma scopas* and *A. leucosternon*, Robertson et al. 1979). Although some individuals overlapped home ranges with adult conspecifics (potential mates), 73% did not. Also, we observed territorial individuals leaving their territories on full moon nights, suggesting that pair spawning did not occur on territories and therefore the defence of a mate on the territory would not be of use. Nevertheless, large males can hold territories at group spawning sites (Colin 1977), and the similarity between the male courtship pattern (DeLoach 1999) and the aggressive colour change when attacking wandering conspecifics is intriguing.

Identifying the sex of the individuals in each of the different social modes is necessary for future work in this system.

The defence of food is a possible function of adult blue tang territoriality. Blue tangs are suspected to be food limited in Panama (Robertson 1991) and in Colombia, tangs supplement their diets with animal matter during seasons when algae is scarce (Duarte & Acero 1988). Therefore, competition for food may be high in certain places and/ or at certain times of the year and would presumably fluctuate with population densities of competitors. This might favour the defence of food. Although not all herbivores are consistently excluded from the home range, the small body sizes of some potential competitors (blennies, juvenile acanthurids) make their expulsion uneconomical (Wittenberger 1985, Roberts 1987). Because adult damselfish dominate blue tangs (Foster 1985b), they may be impossible to exclude.

Among territorial fish, bite rate, aggression from damselfishes and displacement rate were affected by zone, and swimming speed, total aggression received, and rate of cleaning station visits were not. Compared to the territorial fish in the flat, crest and back reef zones, the territorial fish in the spurs and grooves had the lowest bite rate and received the highest rate of aggression from damselfishes. The high density of damselfishes in the spurs and grooves zone (Chapter 2) could account for the higher rate of attack by damselfishes. This, coupled with the low algal cover in this zone (Chapter 2) could have contributed to the lower bite rate of territorial fish in the spurs and grooves zone.

Our tagging study identified individuals that remained in small, undefended stable home ranges. Such fish seemed relatively rare and their distribution was restricted to the spurs and grooves zone. These individuals were occasionally seen schooling but, unlike territorial fish, never displayed aggression towards passing conspecifics. Their home range was small, and the fish tended to remain near or in a structure which could have served as a shelter. This type of behaviour was not seen in wanderers or territorial fish in other zones, suggesting either a potential fourth social mode or a less aggressive variant of the territorial mode.

The schooling mode

Mixed species schools, ranging from 10 to more than 200 blue tangs were regularly observed on South Bellairs Reef. The schools were similar to schools of other surgeonfish species (Jones 1968, Vine 1974, Barlow 1974a,b, Hourigan 1986). Schools similar in form and apparent function have also been observed in parrotfishes (Ogden & Buckman 1973, Robertson et al. 1976) and African cichlids (Marsh & Ribbink 1986, Kohda & Takemon 1996). In each of these cases the schools, sometimes composed of two or more species, often split into smaller groups and then rejoin and feed in their competitors' territories.

The schools spent the day swimming over the reef, with individuals displacing up to 57 m in 25-30 min. The average swimming speed of schooling individuals was fastest in the crest and slowest in the spurs and grooves, where displacement also tended to be smallest. How fast and how far animals in a group move can be related to a variety of factors. Possibly, food density per feeding patch is higher in the spurs and grooves, leading to longer feeding bouts and consequently shorter foraging trips. Despite similar overall school sizes in the crest and spurs and grooves zones, schools in the crest contained a higher proportion of tangs (72%) than schools in the spurs and grooves

(49%). It may be that interspecific variation in mobility affects the movement of the group as in some primates (Cords 2000).

When schooling with other species, blue tangs and ocean surgeonfish were the most numerous, and, except in the back reef, blue tangs always led the school. Upon stopping at a food patch in the crest, the ocean surgeonfish fed more often in the sand and rubble areas whereas the tangs fed on the sides and tops of the pinnacles. However, the pattern was not common in the spurs and grooves zone and was not observed in the spurs and grooves zone in Belize (Reinthal & Lewis 1986). Blue tangs feed almost exclusively on algae whereas the ocean surgeonfish have a more diverse diet, including algae, detritus and micro-invertebrates (Duarte & Acero 1988). It is possible that in the crest, where tangs outnumber ocean surgeonfish, the fish position themselves to reduce competition for algae. This type of microhabitat partitioning during foraging in mixed-species groups has been documented in bird flocks (Austin & Smith 1972, Waite 1984).

Although schooling is often considered an anti-predator behaviour (Bertram 1978), there has been no indication to date that tangs school for this reason (Foster 1985a). There is, on the other hand, both experimental and observational evidence that acanthurids school to overwhelm the defences of territorial damselfishes and therefore gain access to high quality algae (Barlow 1974a, Robertson et al. 1976, Foster 1985a, Reinthal & Lewis 1986, Hourigan 1986). In a patch reef habitat in Panama (Foster 1985a) and in a spurs and grooves zone in Belize (Reinthal & Lewis 1986), the bite rate of schooling fish was higher than that of wanderers, and schooling fish received less harassment from damselfishes. At our study site, the average feeding bite rate of schooling fish exceeded that of wanderers in the spurs and grooves and crest zones, but not in the flat zone where the wanderers and schooling individuals achieved similar bite rates.

Schooling fish on South Bellairs Reef received fewer attacks from all competitors combined than did wanderers. Thus, schooling does seem to reduce the rate of attack from all territorial competitors, including conspecifics and congenerics. This would yield a case where conspecifics were exhibiting competing social modes resulting in density dependent social organization of the population. This situation has been noted in *A. nigrofuscus* where at low-intermediate densities all individuals hold territories, but at high densities only the full-grown adults hold territories while sub-adults school to access the resources in the adult territories (Barlow 1974a). However, contrary to previous work, the overall chase rates from damselfishes alone were not significantly different between the wandering and schooling individuals. Nonetheless, trends were suggestive. In the spurs and grooves zone, damselfishes tended to chase wanderers 25% more often than schooling fish. Because of small sample size and high variation, power to detect a difference was relatively low in our study. In addition, in Foster's (1985a,b) studies, damselfish densities were twice as high as the highest densities at South Bellairs Reef (Chapter 2) potentially resulting in higher attack rates on wanderers in Panama. Therefore, overall, our data tend to support the prevailing idea that blue tangs school to access defended food resources.

In contrast to territorial and wandering fish, in schooling individuals, only one variable, swimming speed, changed with zone. Given that damselfish densities and algal cover differ between zones (Chapter 2), this absence of an effect of zone in attack rate and bite rate indicates the effectiveness of schooling in diluting attacks from damselfishes.

The wandering mode

Our description of wanderers matches the solitary mode described by Reinthal & Lewis (1986) and the non-schooling tangs described by Lawson et al. (1999). Unlike observations on a neighbouring reef by Lawson et al. (1999), however, non-schooling blue tangs did not form loose groups of 2-3 individuals. The wandering blue tangs at our study site never associated with other fish. Other surgeonfish species with social organizations similar to the blue tang either have distinct wanderer individuals (Robertson et al. 1979) or individuals wander on forays from territories or schools (Vine 1974, Craig 1996). The wandering mode in blue tangs is also very similar to the description of the non-territorial or 'stationary' striped parrotfish (Ogden & Buckman 1973, Robertson et al. 1976).

Although mobility was high for wanderers, while on the fringing reef, movement of individuals appeared to be restricted to particular areas of the reef. The locations of re-sightings of tagged individuals indicated that non-territorial fish have very large but distinct home ranges or areas of high frequency of use.

Wandering blue tangs were cleaned more often than the schooling and territorial fish. This seems consistent with Reinthal & Lewis's (1986) conclusion that tangs wander in the spurs and grooves zone in order to gain access to cleaning stations. However, during most forays from schools or territories, individuals did not visit cleaning stations before returning to their respective mode. Furthermore, in the back reef, where wandering individuals were common, there were no traditional cleaning stations. We observed only one cleaning incident of a wanderer in the back reef and this lasted one-second and involved a juvenile wrasse. Our conclusion concerning the function of wandering is therefore tentative as our data show that blue tangs do wander to be cleaned but also that this is not their only purpose. We frequently followed wanderers and schooling fish, that left their school, swam to the back reef and began foraging. In the back reef, wandering individuals swim more slowly, displace shorter distances and forage at a higher rate than in the other zones. The back reef has low damselfish densities and high turf algal cover (Chapter 2). Perhaps wandering allows a blue tang to forage continuously, without having to expend the energy required to successfully forage as a non-territorial in the other zones (e.g. joining a school). Even so, due to its high sedimentation rates, the back reef may be a sub-optimal foraging habitat for tangs, which largely avoid sand when feeding, presumably because they digest by acidity (Lawson et al. 1999).

Distinctness of social modes

Territorial fish very rarely joined schools (only three observations of brief joining events) and tagged territorial fish were never seen participating in a school. We never saw a schooling fish become territorial during a focal observation or a previously schooling tagged individual become territorial some time later. Some territorial individuals left their territories on forays and assumed the wandering mode for 5-20 min. This behaviour has been observed with some regularity in other territorial surgeonfish species (Vine 1974, Robertson & Gaines 1986, Craig 1996). By comparison, we often saw schooling individuals leave schools and wander and very often we followed wandering individuals as they joined passing schools. The transition rates between modes suggest that in the spurs and grooves, crest and flat zones, individuals switch from wandering to schooling at a faster rate than from schooling to wandering. This situation would eventually lead to a larger proportion of individuals schooling than wandering in these habitats during the midday. This is consistent with our results from Chapter 2, where we found that the density of schooling individuals is highest at midday in the crest and to some extent in the spurs and grooves zones. Overall, we thus have evidence that adults are consistently either territorial or non-territorial. We frequently saw non-territorial fish school and wander and territorial individuals sometimes adopted the wandering mode while on a foray from their territory.

The situation in the adult blue tang closely parallels the social system of the striped parrotfish, where individuals are also either territorial or non-territorial (Ogden & Buckman 1973). Like in tangs, non-territorial parrotfish form foraging schools and wander and are chased by territorial conspecifics. Intra-site social variation of this kind has also been recognized in other surgeonfish species. Both Barlow (1974a) and Vine (1974) described surgeonfish populations (*A. triostegus* and *A. sohal*, respectively) in which aggressive or territorial and non-territorial modes are present. Both authors observed schooling, wandering and territorial behaviour. However, neither study included tagged individuals. Therefore these studies could not conclusively report that territorial and non-territorial fish were different individuals. Craig (1996), in his study of a population of *A. lineatus*, discovered that the territorial and non-territorial fish were different individuals. However, in that case, territorial fish were significantly larger than the non-territorial fish. Although we only directly measured tagged individuals, there was no indication from these data, or from our general observations, that territorial and non-territorial fish differed in size.

In conclusion, on South Bellairs Reef adult blue tangs are either territorial or non-territorial. Non-territorial fish are found in the schooling and wandering modes. To some extent, territorial fish adopt the wandering mode while on a foray from their territories. Wandering allows fish in either mode to visit cleaning stations and alternative feeding sites. The behaviour of individuals in each of the modes differs between zones. As a result, the relative differences in feeding success and escape from harassment depends on the interaction between zone and social mode.

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Table 1.1. Two-way fixed factor analysis of variance (Type IV model) testing the effect of social mode (territorial, wandering and schooling) and zone (back, crest, flat and spurs) on 6 behavioural variables.[1]

Behaviour	Source	df	F	P	R^2
Log$_{10}$ Displacement rate (m min^{-1})	Social mode	2	255.94	<0.0005	0.86
	Habitat	3	26.08	<0.0005	
	Social mode X Habitat	5	4.20	0.002	
	Error	100			
	Total	111			
Log$_{10}$ Swimming speed (m sec^{-1})	Social mode	2	66.18	<0.0005	0.62
	Habitat	3	4.58	0.005	
	Social mode X Habitat	5	2.52	0.034	
	Error	109			
	Total	120			
Bite rate	Social mode	2	28.68	<0.0005	0.47
	Habitat	3	9.92	<0.0005	
	Social mode X Habitat	5	3.27	0.009	
	Error	110			
	Total	121			
Number of visits to cleaning stations	Social mode	2	14.35	<0.0005	0.29
	Habitat	3	3.73	0.013	
	Social mode X Habitat	5	2.43	0.040	
	Error	108			
	Total	119			
Aggression received (from all sources)	Social mode	2	27.09	<0.0005	0.40
	Habitat	3	0.38	NS	
	Social mode X Habitat	5	3.23	0.009	
	Error	109			
	Total	120			
Aggression received from damselfishes	Social mode	2	0.29	NS	0.25
	Habitat	3	9.72	<0.0005	
	Social mode X Habitat	5	1.62	NS	
	Error	109			
	Total	120			

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[1] Displacement rate and swimming speed were log10 transformed. We were not able to achieve normality by transformation of the data on aggression received from ocean surgeonfish and from blue tangs. These variables were therefore not included.

Table 1.2. Significance levels from multiple pairwise comparisons between social modes in each zone for 5 behavioural variables. [1]

Zone	Spurs			Flat			Crest			Back		
Behaviour	T/Sch	T/W	Sch/W	T/Sch	T/W	Sch/W	T/Sch	T/W	Sch/W	T/Sch	T/W	Sch/W
Displacement rate (m min^{-1})	***	***	*	***	***	NS	***	***	NS	—	***	—
Swimming speed (m sec^{-1})	**	***	NS	***	***	NS	***	***	NS	—	***	—
Foraging Rate (bites min^{-1})	NS	**	*	**	***	NS	**	***	*	—	NS	—
Visits to cleaning stations (number of visits min^{-1})	NS	NS	*	NS	*	NS	NS	**	***	—	NS	—
Aggression received (from all sources) (attacks min^{-1})	NS	NS	NS	NS	***	***	NS	**	*	—	***	—

---

[1] T= territorial, Sch= schooling and W= wandering, NS = non significant (P>0.05), (--)= not applicable, (*)= p<0.05, (**)= p<0.01 and (***)= p<0.001

Figure 1.1. The average displacement rates (m min^{-1}) of individuals in each social mode in each of the four zones of South Bellairs Reef. Results of the multiple comparisons between zones within a social mode are reported. Shared letters indicate no significant differences between zones ($P>0.05$). Schooling tangs were transient in the back reef.

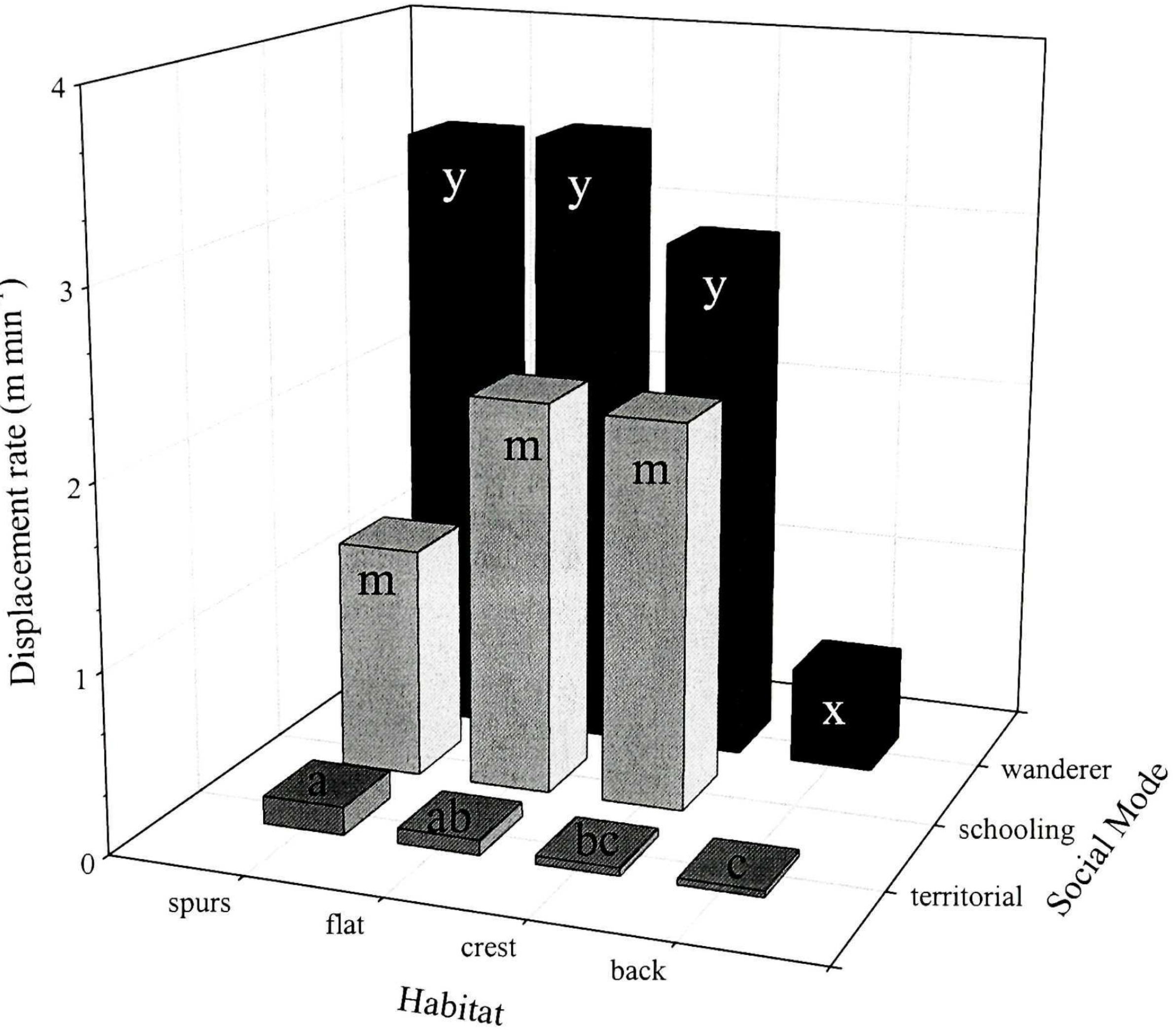

Displacement rate (m min^{-1})
0
1
2
3
4
y
y
y
x
m
m
m
a
ab
bc
c
spurs
flat
crest
back
Habitat
wanderer
schooling
territorial
Social Mode

Figure 1.2. The average swimming speed (m sec^{-1}) of individuals in each social mode in each of the four zones of South Bellairs Reef. Results of the multiple comparisons between zones within a social mode are reported. Shared letters indicate no significant differences between zones ($P>0.05$). Schooling tangs were transient in the back reef.

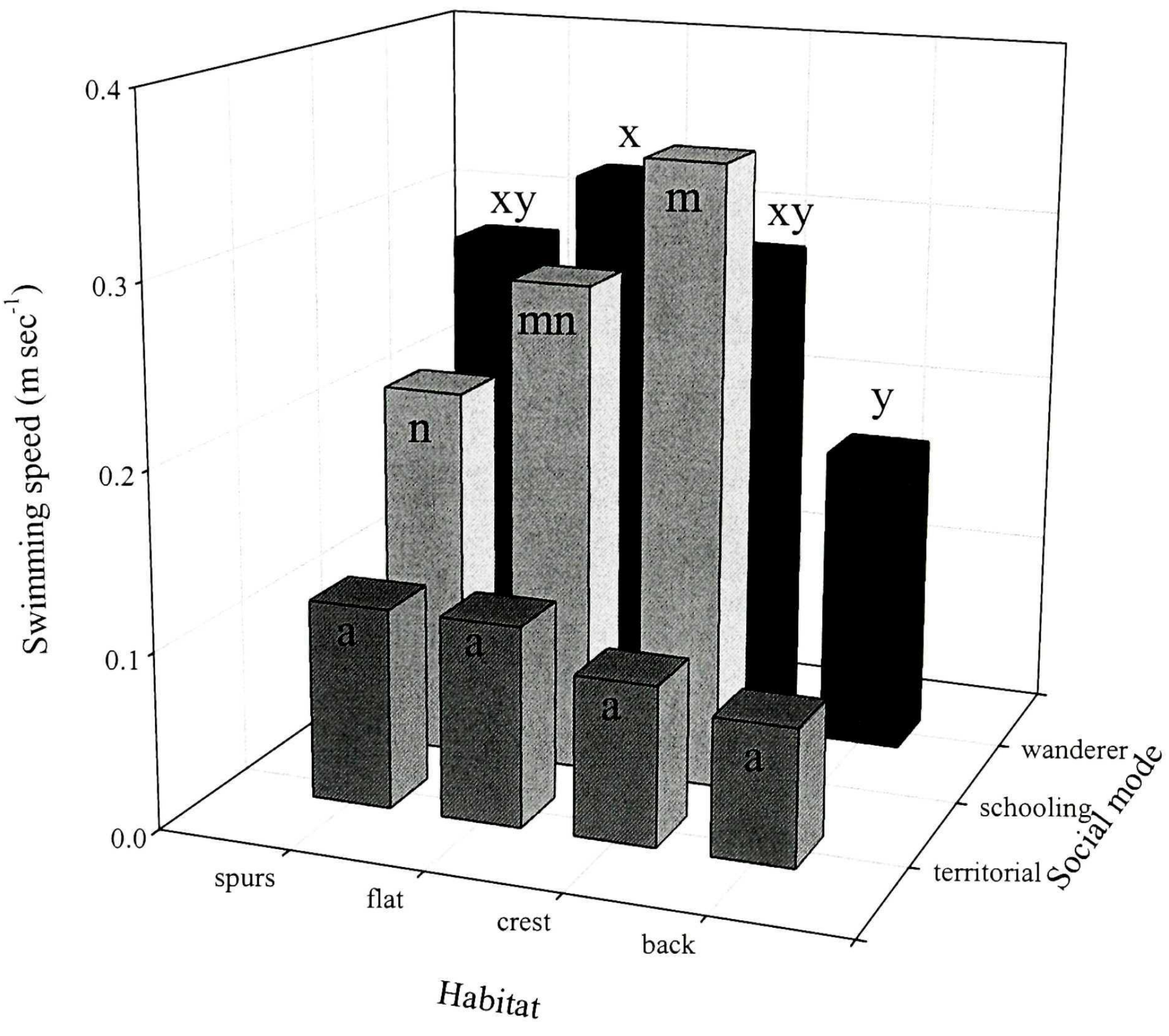

Swimming speed (m sec^{-1})
0.0
0.1
0.2
0.3
0.4
xy
x
m
xy
mn
n
y
a
a
a
a
spurs
flat
crest
back
Habitat
wanderer
schooling
territorial
Social mode

Figure 1.3. The average foraging rate (bites min^{-1}) of individuals in each social mode in each of the four zones of South Bellairs Reef. Results of the multiple comparisons between zones within a social mode are reported. Shared letters indicate no significant differences between zones ($P>0.05$). Schooling tangs were transient in the back reef. Note that to permit all values to be visualized, the sequence of social mode on the z-axis is inverted relative to Figures 1.1, 1.2, 1.4 and 1.5.

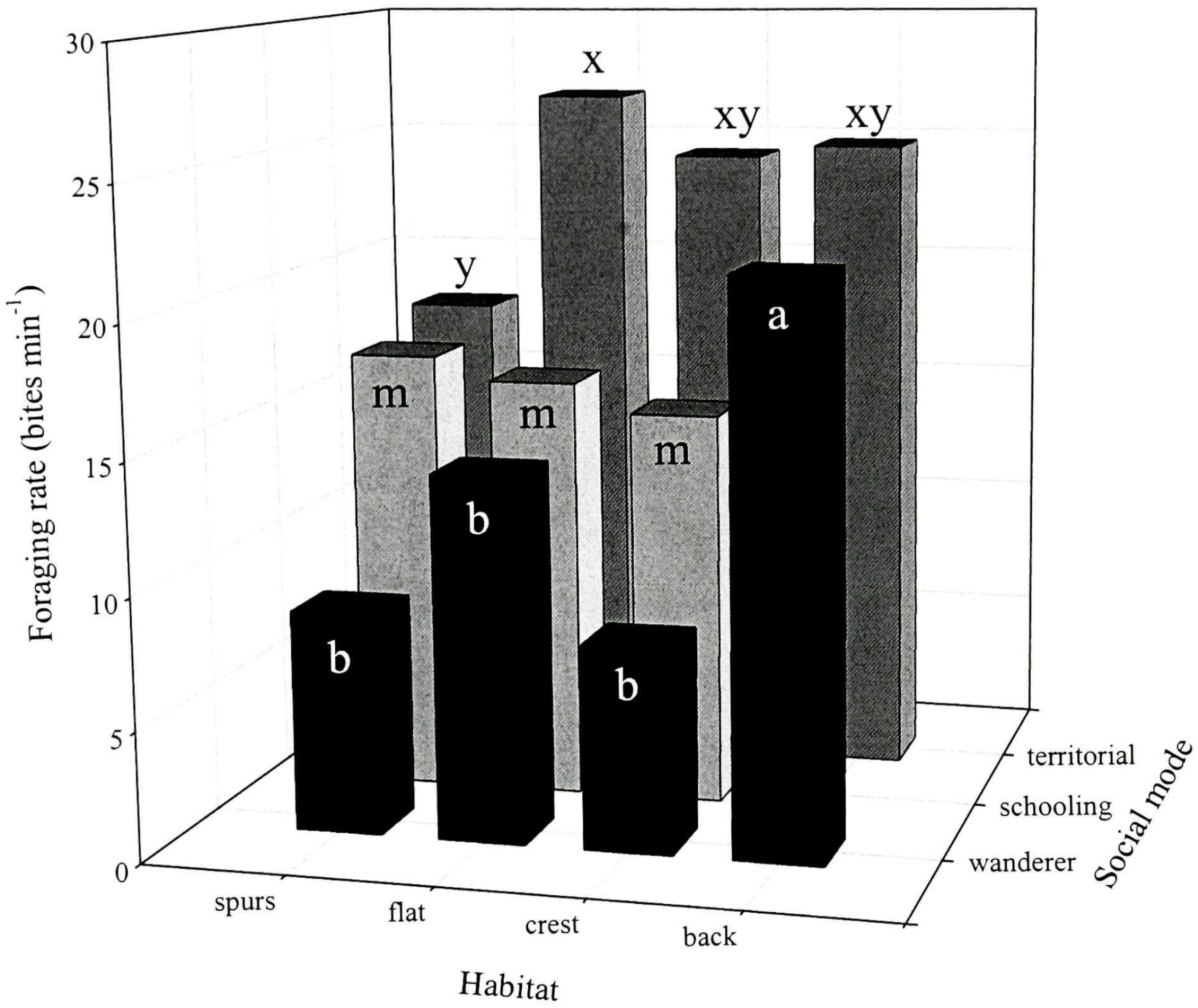

Foraging rate (bites min^{-1})
30
25
20
15
10
5
0
x
xy
xy
y
m
m
m
b
b
b
a
spurs
flat
crest
back
Habitat
territorial
schooling
wanderer
Social mode

Figure 1.4. The average number of visits to cleaning stations (visits min^{-1}) by individuals in each social mode in each of the four zones of South Bellairs Reef. Results of the multiple comparisons between zones within a social mode are reported. Shared letters indicate no significant differences between zones ($P>0.05$). Schooling tangs were transient in the back reef.

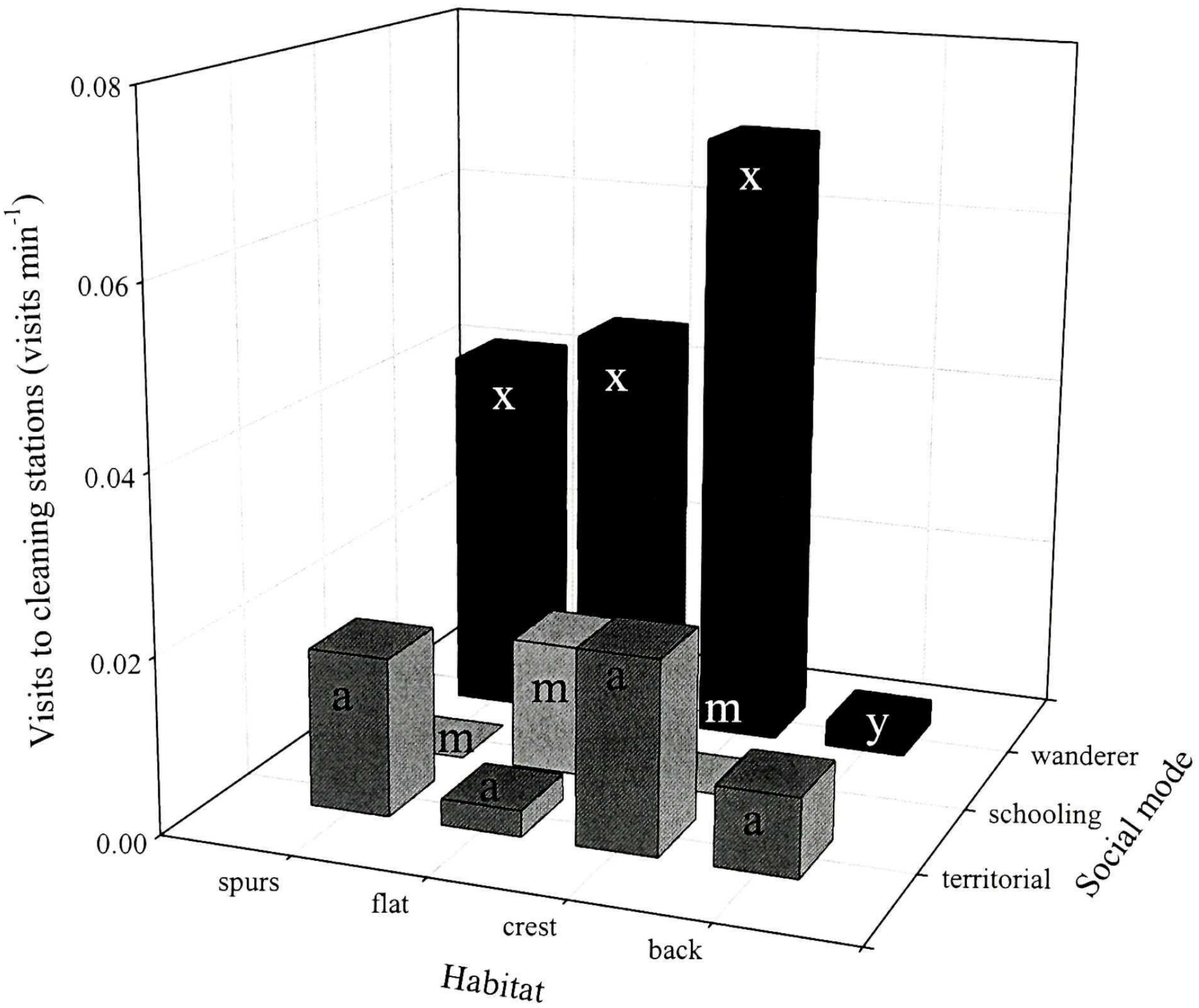

Visits to cleaning stations (visits min^{-1})
0.08
0.06
0.04
0.02
0.00
x
x
x
a
m
m
a
a
m
y
a
spurs
flat
crest
back
Habitat
wanderer
schooling
territorial
Social mode

Figure 1.5. The average amount of aggression received (attacks min^{-1}) by individuals in each social mode (territorial (T), schooling (Sch) and wanderer (W)) in each of the four zones of South Bellairs Reef; spurs and grooves (S&G), flat (F), crest (C) and back reef (B); a. Total aggression received, b. Chases received from *Stegastes* damselfishes, c. Chases received from territorial blue tangs, d. Chases received from aggressive ocean surgeonfish. Results of the multiple comparisons between zones within a social mode are reported for Figure 5a and 5b. Shared letters indicate no significant differences between zones ($P>0.05$). Multiple comparisons were not performed on the chases received from blue tangs and ocean surgeonfish because the data did not conform to the assumption of normality. Schooling tangs were transient in the back reef.

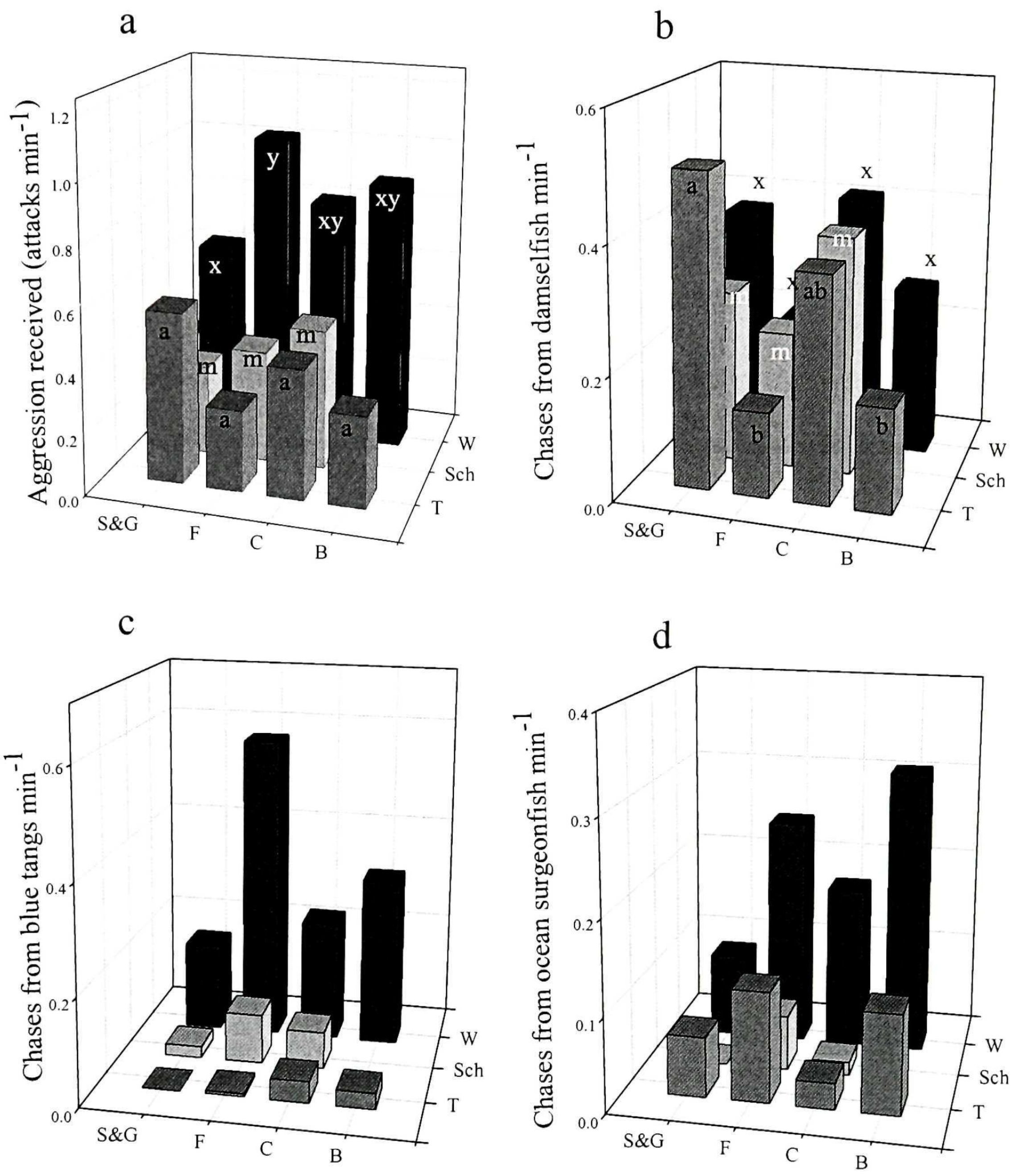
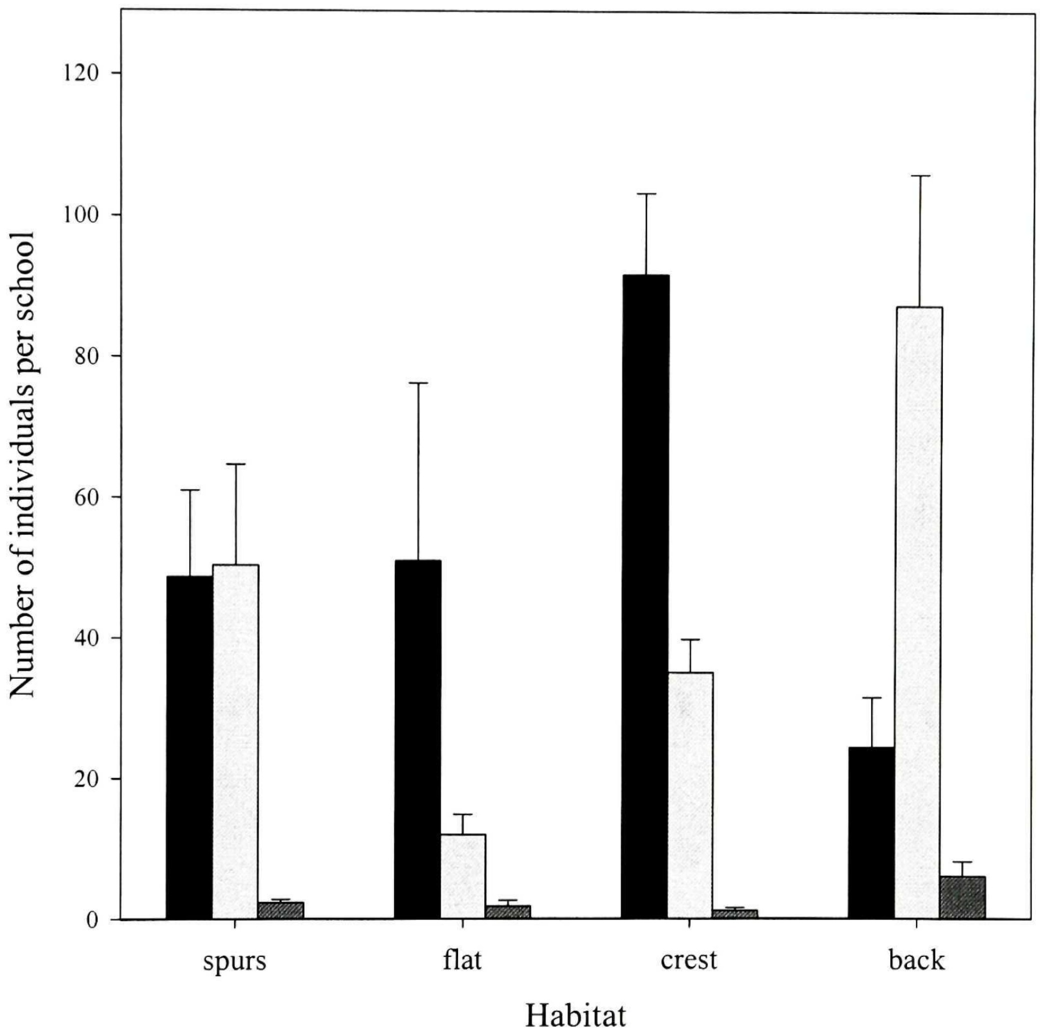

a
Aggression received (attacks min^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
1.2
S&G
F
C
B
W
Sch
T
a
m
m
m
a
a
a
x
y
xy
xy
b
Chases from damselfish min^{-1}
0.0
0.2
0.4
0.6
S&G
F
C
B
W
Sch
T
a
ab
b
b
m
m
m
x
x
x
x
c
Chases from blue tangs min^{-1}
0.0
0.2
0.4
0.6
S&G
F
C
B
W
Sch
T
d
Chases from ocean surgeonfish min^{-1}
0.0
0.1
0.2
0.3
0.4
S&G
F
C
B
W
Sch
T

Figure 1.6. The average number of individuals per school and the composition of schools containing at least one blue tang in the zones on South Bellairs Reef where blue tangs participate in schools. The black bars represent the number of blue tangs, the light gray bars represent the number of ocean surgeonfish and the dark gray bars represent the number of other species participating in the schools. Standard error bars are reported.


Number of individuals per school
120
100
80
60
40
20
0
spurs
flat
crest
back
Habitat

Having concluded that adult blue tangs are found in either the territorial or non-territorial mode (Chapter 1) I now examine their distribution and attempt to identify potential determinants of the variation in the social organization of the blue tang.

Chapter 2

Determinants of social organization in the blue tang (*Acanthurus coeruleus*) on a fringing reef in Barbados W.I.

2.1 Abstract

Individual blue tangs (*Acanthurus coeruleus*) are consistently either territorial or non-territorial. Non-territorial individuals school and wander and, to some extent, territorial fish adopt the wandering mode while on a foray. This study examines the distribution of the individuals in the territorial, schooling and wandering modes in relation to reef zone, time of day, size class, competitor density, food abundance, and population density. Individuals from all three social modes were found in all four fringing reef habitat zones at our site. Yellow juveniles were found primarily in more offshore reef zones, while adult densities peaked in shallower inshore reef zones. The density of territorial tangs did not change with time of day, but non-territorial tangs tended to wander more in the morning and to form schools more at midday. Small yellow-phase juveniles were always territorial and the incidence of territoriality decreased with increasing size, while schooling/wandering increased. Territorial tang density was negatively related to adult damselfish density. A higher proportion of tangs formed schools in reef zones with the highest densities of territorial damselfishes (spurs and grooves and crest). In the back reef and flat zones, where damselfish densities were very low, tangs rarely formed schools. Among fringing reefs, the incidence of territoriality increased with increasing population density. These data, together with quantitative observations of the behaviour of each mode in each reef zone (Chapter 1), suggests that life history stage, damselfish density and conspecific population density are important demographic, ecological and social determinants of blue tang social organization.

2.2 Introduction

Social organization or the social system of animals is the ultimate outcome of interactions between individuals (Hinde 1976). Intraspecific variation in social organization is widespread in vertebrates (Lott 1991) and has been recognized in various coral reef fishes including wrasses (Warner & Hoffman 1980), butterflyfish (Hourigan 1989, Colin 1989), parrotfish (Ogden & Buckman 1973) and grunts (Helfman et al. 1982). In general, variation in social organization is related to variation in the environment (Emlen & Oring 1977, Rubenstein & Wrangham 1986, Lott 1991, Shapiro 1991, Grant 1993, Maher & Lott 2000). Plasticity in social behaviour allows an animal to alter its strategy in response to the spatial and temporal variation in its environment (Lott 1991, Shapiro 1991, Warner 1997). The prevailing social system and its alternatives, therefore, are seen as outcomes of individual adaptive responses to developmental, ecological or social variables in their environment. The multiplicity and interactive nature of variables can lead to dynamic, complicated scenarios (Lott 1991), including the existence of multiple social patterns or modes within a single population.

If social modes are related to life history stage, then by necessity multiple social modes coexist in a population. Within a cohort of similarly sized individuals, however, the simultaneous occurrence of multiple social modes is more difficult to explain. While habitat heterogeneity may provide enough variation in relevant ecological determinants to drive the existence of simultaneous modes, it does not completely explain the coexistence of different modes within ecologically homogeneous patches. In this case, the social strategies of conspecifics may be important, because they could affect an individual's payoffs in alternative modes and thus drive the ultimate social organization of the population. Few studies of intraspecific variation in vertebrates have implicated the strategies of conspecifics as a determinant of a social system (Lott 1991).

The blue tang (*Acanthurus coeruleus*) is a common and locally abundant Caribbean herbivorous surgeonfish. Juveniles are bright yellow and settle from the plankton at 3.1-3.4 cm total length (TL) (modified from Foster 1985). The yellow-phase juveniles are solitary and territorial (Bell & Kramer 2000, I.M. unpublished data). At 1-7 months post-settlement (Foster 1985), the juveniles change to the adult blue colour. It has been assumed that once juveniles turn blue they become less territorial, more mobile and eventually begin to school with adults (Lawson et al. 1999). Previous work on adult blue tangs has described schooling and wandering social modes in adults (Robertson et al. 1976, Foster 1985, Reinthal & Lewis 1986), and we have identified territoriality as a distinct social mode in adult blue tangs (Chapter 1). Non-territorial adult blue tangs form small to large foraging schools (Alevizon 1976, Foster 1985, Chapter 1). Wandering individuals are thought to be schooling individuals temporarily away from the school (Reinthal & Lewis 1986, Chapter 1), and to some extent, territorial fish on a foray (Chapter 1). Our data from Chapter 1 suggest that territorial and non-territorial fish are different individuals in the same population. Individuals from each mode occur and interact in all four ecologically distinct zones of a single fringing reef. Therefore, two alternative modes (territorial and non-territorial) are maintained in our study population, and these coexist within a habitat type (reef zone). In this study, we examine which developmental, ecological and social determinants could contribute to the maintenance of both social modes.

Determinants of intraspecific social variation have not been specifically examined in surgeonfishes. In the blue tang, social mode appears to be partially associated with life history stage because juveniles are territorial (Foster 1985, Bell & Kramer 2000) and adults are both territorial and non-territorial. Shifting from a territorial to a schooling system sometimes occurs when food competitors are highly territorial (Lott 1991). The presence of territorial damselfishes has been implicated as a determinant of the schooling behaviour in various species of surgeonfishes, including the blue tang (Vine 1974, Barlow 1974a, Robertson et al. 1976, Montgomery 1981, Foster 1985, Hourigan 1986). In the case of adult blue tangs, there is experimental and observational evidence that schooling improves access to algae in damselfish territories (Robertson et al. 1976, Foster 1985, Reinthal & Lewis 1986). The benefits of territoriality, however, are unclear. Nor do we understand why schooling and territorial individuals can coexist in the same reef zones.

The specific goals of this study were to 1) document the ontogeny of social organization, 2) quantify the spatio-temporal distribution of each mode and size class among four zones of a fringing reef, and 3) to relate the distribution of each mode with potential ecological and social determinants within one reef and among several nearby reefs. Because of the suggested causal relationship between social mode and damselfish territoriality, we expected that more tangs would school in areas with higher damselfish densities. Since schooling entails more swimming to forage successfully (Chapter 1), we expected that tangs would not form schools in areas of low damselfish density where it was not needed to gain access to food. Finally, we examined the role of conspecific density in the coexistence of the territorial and non-territorial modes.

2.3 Study Site

Our study was conducted primarily on South Bellairs fringing reef in Holetown, Barbados, West Indies (Figure 2.1). South Bellairs Reef has a typical Caribbean fringing reef zonation with back reef, crest and spurs and grooves zones (Table 2.1; Lewis (1960) provides detailed descriptions). This particular reef has one additional zone, which we call the flat. This reef zone, which does not occur on typical Caribbean fringing reefs, matches the description of a shallow 'Gorgonian dominated pavement or hardground' (National Park Service 1994). The flat zone appears as though it was part of the crest and spurs and grooves zones that coalesced into a plateau. The habitat complexity, algal cover, depth, substrate composition and damselfish densities of each zone are detailed in Table 2.1 (see below for methods). The planimetric areas of the zones on South Bellairs Reef were directly estimated in the field by measuring the distance and angle between four points approximately surrounding the zone (Figure 2.1). The substrate of a fifth, unsurveyed reef zone (*Porites porites* zone) was composed of *Porites porites* (finger coral) rubble and occasional dead coral structures. Fishes of all species were rare in this zone, and occasional solitary adults were the only blue tangs seen swimming there.

The back reef is not homogeneous and can be divided into 3 sub-zones: 1) the shallow back reef is large and has a rock/coral rubble and sand as substrate, low rugosity, turf algae covering the substrate, and a depth range of 0.5-0.9 m. Because of the shallow depth, the water is generally turbid from sand in the water column; 2) the mid/deep back reef (transition zone to the flat) has a substrate similar to the shallow back reef except for the occasional large, dead or live coral heads and a depth range of 0.9-1.5 m; 3) The *Diploria—Palythoa* zone (described by Lewis 1960) (northwestern transition to the crest) is characterized by large colonies of brain coral (*D. clivosa*) and zooanthids (*P. mammillosa*). This area is shallow has high turf algae cover and is of higher complexity than the rest of the back reef. This habitat is not as rugose as the crest and is more turbulent due to exposure at low tide and breaking waves.

2.4 Methods

2.4.1 Distribution and density

In order to document the ontogeny of social organization, we divided the population into the following fork length size classes: yellow and blue small juveniles (2-6.5 cm), large juveniles (7-12 cm), adults (12.5-22.5 cm) and large adults (>22.5 cm). One observer, I.M., recorded all data between September and November 2001.

Non-schooling tangs

In order to determine the densities of territorial and wandering individuals we used 30 m by 6 m (180 m^2) transects. The transects were always laid parallel to the shoreline. Their locations within the spurs and grooves, flat and crest zones were chosen systematically such that they never overlapped. In order to test the effect of reef zone on distribution, 7-8 transects were performed per zone (total n=23). Each transect was repeated in the morning (6:00-7:45), midday (11:00-14:00) and afternoon (15:45-17:30). In order to minimize potential disturbance to the fish, the transect line was laid at least 1 hour prior to data collection and remained in place until the data collections for all times of day were completed.

The snorkeling observer swam along the transect line at a consistent speed and recorded all adults and large juveniles within the 6 m belt and whether they were in the wandering or territorial mode. Care was taken to observe both the water column and the substrate. We defined territorial tangs as those showing aggression and wandering tangs as those showing no aggression and easily chased away from an area by conspecifics and heterospecifics (see Chapter 1 for details). If an individual's social mode was not immediately apparent, the observer watched from 5 meters or more up to 30 seconds. This was enough time for an adequate categorization of social mode. The observer swam the transect a second time counting yellow and small blue juveniles which were more likely to be missed at the speed at which the observer first swam along the transect. Juvenile and adult tangs did not flee from snorkelers, so it is unlikely that they would be underestimated by this procedure.

For each transect, we collected ecological data on food abundance and competitor density, specifically percent algal cover, rugosity, and the densities of all species of damselfishes seen to harass tangs. Percent algal cover and the amount of substrate available for algal growth (rugosity) should correlate with food abundance. Percent algal cover included filamentous and turf algae but not coralline or macroalgae, the latter of which was relatively rare at our site. Rugosity, or substrate topographic complexity (Luckhurst & Luckhurst 1978), was measured by draping a 20 m chain over the substrate, along the transect line. Rugosity is the ratio of this 20 m length to the actual horizontal distance covered by the chain. The rugosity chain had pieces of flagging tape at 20 cm intervals. Mean algal cover was the percent of these flagging tapes that lay on filamentous or turf algae. Finally, we determined the density of adult and juvenile dusky damselfish (*Stegastes dorsopunicans*), longfin damselfish (*S. diencaeus*), bicolor damselfish (*S.*

partitus), and yellowtail damselfish (*Microspathodon chrysurus*) by swimming the first 25 m of the transect and counting the individuals within the 1 m on either side. Juvenile dusky, longfin and yellowtail damselfishes have a colour pattern that easily distinguishes them from adults. Bicolor damselfish juveniles and adults are the same colour and therefore, any individual less then half the average adult body length (5.5 cm (TL), Humann 1999) was considered to be a juvenile.

In the back reef, on transects with high densities, non-schooling individuals were continuously foraging and frequently moving between closely spaced foraging patches. Because of this apparently different feeding style, it was difficult to accurately determine the social mode. Therefore, social modes are estimated less precisely than in other reef zones, and only 5 transects were completed.

Schooling tangs

We defined schooling tangs as those moving synchronously with at least 10 other fish. Because schooling tangs are highly aggregated and quite mobile, we could not reliably estimate their densities using the same transects as for non-schooling tangs. Therefore, we employed a survey in which the observer began at a pre-designated, easily recognizable location (one for each zone) on the northern end of the reef. Then, at intervals of 10 m, the observer snorkelled back and forth across reef habitat, at an angle perpendicular to the 120-degree orientation of the reef. The interval was reduced to a minimum of 8 m if visibility was poor and abandoned if visibility was less than 8 m. Because the reef was too large to completely survey during a single session, we divided the effort such that all four zones, for each time of day, would be surveyed once in two days. On one day, we randomly chose two zones to survey for each time of day. On the following day, the remaining two zones for each time period were surveyed. In all, the observer performed 7-10 surveys per time of day, per zone (n total=108). Upon encountering a school, the time, the zone, the total number of adult tangs and heterospecifics, and the number of juveniles were recorded. Normally, schools of up to 50 individuals could be counted directly as they passed a given point. For larger schools, the volume occupied by about 50 individuals was used to estimate the total school size. Because there were fewer juveniles in the schools, their numbers are exact counts. If it appeared that a school was being double-counted because of its size, position, or the presence of a tagged individual, the second count was removed from the data set (4% of all school counts).

2.4.2 Multi-reef surveys

In order to judge whether territorial fish occurred on other reefs and the extent to which population density might influence the social organization of blue tangs, we surveyed three nearby fringing reefs: 1) Heron Bay Reef in recent publications (or Cunards 2 in Lewis (2002)), 2) North Bellairs Reef (or Bellairs 1) and 3) North Holetown Reef (or Sunset Crest 2). All except Heron Bay Reef are within the Barbados Marine Reserve. Using aerial photographs, Lewis (2002) estimated that the planimetric areas of Heron Bay, North Bellairs and North Holetown Reefs were 5.42, 1.58 and 1.10 hectares, respectively. Similar to the transects on South Bellairs Reef, transects to determine non-schooling tang densities were 6 m in width. However, the length of the transect was dictated by the width (parallel to the shoreline) of the reef or 125 m, whichever came first (range 27-125 m). Starting 10 m from shore, the observer snorkeled in a N-S direction, back and forth, at 15-20 m intervals. Because zones are stratified by depth and thus are generally homogeneous parallel to the shoreline, each transect crossed only one zone. Therefore, we were able to average the densities of non-schooling tangs by zone. We counted all individuals within the 6 m belt and recorded their social mode and size class. Transects were performed until the seaward tips of the reef in the spurs and grooves zone (Heron Bay, n=12 transects; North Bellairs, n=11 transects; and North Holetown, n=10 transects). We also performed one schooling survey across all zones, in the same fashion as on South Bellairs. Using aerial photographs of each of the three reefs provided by J. Lewis, we determined the relative proportion of the total area occupied by each of the reef zones and multiplied that proportion by the total area of the reef (from Lewis 2002). This gave an estimate of the planimetric area of each zone, which allowed for the calculation of schooling fish density per zone and overall population density. For each reef, the data were collected between 9:45-15:00 on a single day. No habitat data were collected. However, except for the lack of an equivalent to the flat zone, their topography and fish fauna were qualitatively similar to South Bellairs Reef. There was a small flow from a freshwater lagoon into the North Holetown back reef.

2.4.3 Data analysis.

In the analysis of the distribution of territorial and wandering modes on South Bellairs Reef, we met the assumption of normality and homogeneity of variance by log10 transformation of the data if the scatter plots of residuals and predicted values showed consistent patterning or extreme variance. In order to test the effect of time of day and of zone (spurs and grooves, flat, crest) on territorial and wanderer densities for each size class, a repeated measures ANOVA was performed. We contrasted means between times of day and reef zones using the Bonferroni method (Day & Quinn, 1989). Because we only completed 5 transects in the back reef, and the estimates are not as reliable as in the other zones, we did not include the back reef data in this analysis.

In our analysis of the relationships between tang densities and the ecological variables, we found that the ecological variables were significantly correlated with one another (Pearson correlation $P<0.05$, rugosity and percent algal cover; $r= -0.53$, rugosity and adult damselfish density $r= 0.85$, and percent algal cover and adult damselfish density $r= -0.55$). For this reason, we did not perform a multiple regression analysis but rather explored relationships between variables using simple linear regressions (Zar 1996). Because we tested many independent variables (10) for each dependent variable we performed a Bonferroni correction on the alpha value. We arcsine square root transformed the percent algal cover values (Zar 1996).

For each survey in each reef zone (including the back reef) we added together the number of tangs seen schooling. In order to calculate density per reef zone, we divided these counts by the planimetric area of each zone. The schooling data from South Bellairs Reef were highly skewed and neither log nor square root transformation achieved normality. The data were therefore rank transformed and a parametric test was applied to the rank transformed data (Potvin & Roff 1993). In order to test for the effect of reef zone and time of day on the density of schooling tangs we used a mixed-model ANOVA with zone as the main factor and time of day nested within zone as a random effect (Schwarz 2002). We performed post hoc tests on significant factors using Tukey's Honestly Significant Difference test (Tukey HSD).

Data analyses were done using SPSS 11.0 and JMPin 4.0.3.

2.5 Results

2.5.1 Effect of time of day and reef zone on the density of non-schooling individuals

Time of day did not strongly affect the densities of non-schooling individuals. The densities of territorial tangs did not change with time of day for any size class (Table 2.2). There were too few wandering small blue juveniles and large juveniles for statistical analysis of their distribution. The density of adult wanderers was affected by time of day (Table 2.2) with slightly but significantly higher density in the morning than at midday ($P=0.01$, Figure 2.2).

The density of territorial yellow juveniles did not differ significantly among the spurs, flat and crest zones (Table 2.2, Figure 2.3), although this class tended to be less abundant in the crest. Of the ecological variables recorded, yellow juvenile density was positively related only to the density of juvenile damselfish following Bonferroni correction ($R^2=0.477$, $P=0.001$). Territorial small blue juveniles did not differ significantly in density among zones, nor was their density significantly related to any recorded ecological variables. Territorial large juveniles showed a significant effect of zone, with more individuals in the flat than in the spurs ($P=0.024$, Table 2.2, Figure 2.3). Their density tended to be negatively related to adult damselfish density, but this was not statistically significant following Bonferroni correction. The separate analysis of the back reef indicated that there were fewer small juveniles as compared to the other three zones (Figure 2.3) while large juveniles were equally as abundant in the back reef as in the crest zone. Thus, there was a general trend for small yellow individuals to be more abundant on the spurs and less on the back reef and large blue individuals to show the reverse pattern with small blue individuals intermediate (Figure 2.3).

Territorial adult densities showed an effect of reef zone (Table 2.2, Figure 2.2). Territorial adults occurred at higher densities in the crest (P=0.006) and in the flat (P<0.0005) and than in the spurs and grooves zone (Figure 2.2). Their density was negatively related to adult damselfish density (Figure 2.4, $R^2 = 0.540$, P<0.0005) and rugosity ($R^2 = 0.412$, P=0.001) and positively related to juvenile dusky damselfish density ($R^2 = 0.469$, P<0.0005). The separate analysis of the back reef suggested that territorial adult densities were somewhat higher than in the spurs and grooves zone but lower than the flat or the crest (Figure 2.2). The distribution of territorial adult individuals seemed to be clustered in the back reef. Territorial individuals were more common in the mid/deep back reef and the *Diploria—Palythoa* zone and rare or non-existent in the shallow back reef.

Wanderer densities did not significantly differ among the spurs, flat and crest zones. Following a Bonferroni correction, their densities were not significantly related to any ecological variables. On average, wanderer densities were about 4 times higher in the back reef than in other zones, but the variation between transects was high. This variation is likely due to the observed clustering of wanderers in the mid/deep back reef and the *Diploria - Palythoa* zone.

2.5.2. Effect of time of day and reef zone on the density of schooling individuals

Yellow juveniles were never seen schooling. Small blue juveniles sometimes formed schools with other small blue juveniles and sometimes schooled with adults. However, there were too few to statistically analyze their distribution. Large juveniles were only seen schooling with adults. There was no effect of reef zone on the density of large schooling juveniles. However, nested within reef zone, the density of large schooling juveniles differed with time of day (Table 2.2). Their densities peaked in the crest at midday (Tukey HSD $P<0.05$). The density of schooling adults was affected by both reef zone as a main effect and time of day nested within zone (Table 2.2). Adult densities were highest in the crest, and in this zone, they peaked at midday (Figure 2.2). It was not possible to statistically relate schooling fish density to habitat variables because schooling fish density was not recorded on the transects.

2.5.4. Effect of life history stage on social organization

We calculated the overall number of fish in each size class. For each mode, we multiplied the mean density of each size class in each zone by the planimetric area of the appropriate zone. This calculation yielded the number of fish per zone and could therefore be summed to a total number of individuals per size class. Overall, we estimated a total population of 203 small yellow juveniles, 277 small blue juveniles, 142 large blue juveniles and 1356 adult blue tangs on South Bellairs Reef. When all reef zones were combined, the proportion of territorial individuals decreased with increasing size class while the proportion of schooling and wandering individuals increased (Figure 2.5). This relationship of decreasing incidence of territoriality with increasing size was consistent within reef zones. The largest adults (>22.5 cm) were not included in Figure 2.5 because they were rare. However, we never observed a territorial individual larger than 22.5 cm.

2.5.5. Comparisons among reefs

The comparison between South Bellairs Reef and three nearby reefs showed considerable variation in the density of yellow and small blue juveniles (Figure 2.6). The additional reefs tended to have lower densities than South Bellairs, but this pattern was not consistent for all zones. The density of large juveniles on the three other reefs was negligible. Despite differences in absolute numbers, the qualitative trend for yellow juvenile density to be highest in the spurs and grooves zone, lower in the crest and nearly absent in the back reef held in all four cases. Similarly, all four reefs showed peak density of small blue juveniles in the crest and an increase in the density of this group in the back reef as compared to yellow juveniles. Variation in adult densities among reefs was considerably greater than the variation in juvenile densities (Figure 2.7). Heron Bay Reef, the only reef outside the BMR that was sampled, had particularly low densities. All four reefs showed the same qualitative trend for densities to be highest in the crest zone. However the relative density of adults in the spurs and grooves and back reef differed among the reefs.

The relative densities of the different social modes also differed among reefs (Figure 2.7). On Heron Bay Reef, all adults were in the wandering mode. No tangs were territorial, and no schooling tangs were seen in the Heron Bay survey. However, on previous visits a school had been noted, so it is possible that a school was present but missed in the survey. The other reefs all had territorial, schooling and wandering tangs. However, the density of territorial tangs on North Bellairs was very low as compared to South Bellairs and North Holetown Reefs. On the three reefs that had them, territorial tangs tended to occur at higher densities in the crest and back reef as compared to the spurs and grooves zone. The proportion of the adult population that was territorial was correlated with the total population density among the four reefs ($r = 0.975$, $P = 0.025$). Schooling tangs were most common in the crest on all three reefs with schools, but North Holetown also tended to show a high density of schooling individuals in the spurs and grooves zone, unlike the other two.

2.6 Discussion

On South Bellairs Reef, the distribution of social modes in the blue tang was strongly related to life history stage, moderately related to reef zone and ecological variables and weakly related or unrelated to time of day. Comparison among reefs suggested that population density also played a role in the appearance of the territorial mode. We will discuss each pattern in turn and then present a hypothesis to explain the appearance and maintenance of alternative social modes in one population.

Life history stage

On South Bellairs Reef, social organization was clearly related to life history stage. All yellow-phase juveniles were territorial. As size class increased, fewer fish held territories and a higher proportion schooled/wandered. This pattern is consistent with the assumption that blue tangs become more mobile as they grow (Lawson et al. 1999). Some surgeonfish species exhibit ontogenetic social development similar to the blue tang (*A. triostegus*, Barlow 1974b), while some show the opposite trend (*A. nigrofuscus*; Barlow 1974a, *A. lineatus*; Craig 1996). Unlike blue tangs, in some species of grunts and parrotfishes, the incidence of territoriality increases with increasing size (Warner & Downs 1977, Shapiro 1991). That individuals change the type of social unit as they grow is not unusual among coral reef fishes (Helfman 1978, Shapiro 1991). As a fish grows, its predation risk, diet, and /or reproductive status may change. Because social behaviour affects predation, foraging and reproductive success, one would expect the social behaviour to change with growth-related changes in predation risk, diet, and reproductive status.

Relationship between life history stage and zone

On South Bellairs Reef, the density of yellow-phase juveniles tended to peak in the most seaward zones while the density of the larger size classes generally increased shoreward. These distribution patterns resemble those found by Lawson et al. (1999) on North Bellairs Reef in 1997. Although juvenile surgeonfish have been rarely studied in detail, juvenile and adult habitat differences have been suggested in a number of surgeonfish species (Lieske & Myers 1994). Like blue tangs, sailfin tang juveniles (*Zebrasoma veliferum*) are found in offshore zones while the adults are more abundant in the shallow surge zone (Jones 1968). The adults and juveniles of the convict surgeonfish (*A. triostegus*, Sale 1969) and the sleek unicornfish (*Naso hexacanthus*, Hobson 1974) show the opposite trend. Ontogenetic habitat shifts are common in freshwater and marine fishes (Keast 1978, Helfman 1978, Lirman 1994, Light & Jones 1997, McCormick & Makey 1997). Because diet requirements, predation risk or level of competition often change with body size, an animal may need to change habitats in order to meet its needs as it grows (Werner & Gilliam 1984, Dahlgren & Eggleston 2000). In the case of blue tangs, for some individuals, the inshore shift is accompanied by a shift in foraging strategy (from all territorial to some schooling), suggesting that the habitat shift is associated with food procurement.

Relative to yellow-phase juveniles, blue juveniles of the same size tended to occur at higher densities in the crest and back reef zones. These distribution patterns could result from relocation of territories to more inshore sites with the colour change from yellow to blue. Although post-settlement movements can occur in juveniles (Frederick 1996), other explanations to the pattern must be considered. In blue tangs, colour change is not strictly size dependent (Appendix B). Therefore, it is possible that individuals which settle and survive in the more inshore zones turn blue sooner than those that settled in the deeper zones. Alternatively, colour change may be associated with age rather than with size, and therefore these patterns would suggest that the juveniles that settle inshore may grow at a slower rate than their offshore counterparts.

Effect of reef zone and microhabitat within a life history stage

The distribution of yellow juveniles was positively related to juvenile damselfish densities. Lawson et al. (1999) found that the variation in yellow juvenile tang distribution was related to algal cover, distance from shore and depth, but the proportion of variation explained was very low. The pattern in our data could result from tangs and damselfishes responding to the same habitat selection cues or from non-selective predation pressure on juveniles. Our data did not reveal any ecological variables related to the distribution of small blue juveniles. Lawson et al. (1999) found rugosity was an important habitat variable in explaining small blue juvenile distributions. However, as in yellow juveniles, the model fit was low. The large territorial blue juveniles, like territorial adults, tended to be negatively related to adult damselfish density. Overall, the juvenile distributions tended to be more highly correlated with the densities of other fish than with the habitat variables we measured. This could suggest that juvenile blue tangs respond more strongly to their immediate social environment rather than to their physical environment.

Territorial adults showed a strong negative relationship with adult damselfish density and a negative relationship with rugosity. Although damselfish density and rugosity are strongly correlated with one another, we suggest that the presence of the damselfishes is the key determinant of territoriality in the adult blue tang. In Hawaii, Hourigan (1986) studied the interaction between a functionally similar damselfish-surgeonfish species pair. He cleared an area of territorial damselfish and found that previously schooling surgeonfish (*A. triostegus*) stopped schooling and began defending territories in the cleared area. In Chapter 1, we found that the territorial tangs in the spurs and grooves had a lower bite rate and received more harassment from damselfishes than territorial tangs in the other reef zones. In the spurs and grooves zone, damselfish densities are highest and territorial tang densities are lowest. Overall, these observations are consistent with the suggestion that territoriality in adult blue tangs results from a relative lack of damselfishes in otherwise suitable habitat.

The formation of schools varied with zone. Previous work showed that tangs school to gain access to resources in damselfish territories (Robertson et al. 1976, Foster 1985). Thus, we expected that non-territorial tangs would school more often in zones with higher damselfish densities and would not form schools where damselfish densities are low. The crest and the spurs and grooves zones have the highest damselfish densities. The overall density of schooling tangs clearly peaked in the crest zone, and the proportions of tangs schooling in the crest and spurs and grooves zones were also high (54% and 36%, respectively). The smaller absolute density of schooling tangs in the spurs and grooves may be due to the lower algal cover and hence lower food abundance in this zone. Conversely, the flat and the back reef zones have the lowest damselfish densities. Schools were seen in the back reef and flat zones. However, blue tang schools did not stay in the back reef, and foraging non-territorial tangs did not form schools in this zone (Chapter 1). In the flat, both the density and percent (5%) of tangs schooling were low. This distribution in the flat zone is consistent with our data from chapter 1 where the individual payoffs in terms of bite rate were not different between wandering and schooling. In all, the distribution of schools by non-territorial fish is consistent with the proposed function of schooling.

Without including data from the back reef, neither zone nor ecological variables explained variation in the distribution of wanderers. In Chapter 1, we suggested that individuals wander for both feeding and cleaning benefits. Thus, the distribution of wanderers should be complex because tangs should wander in both zones favouring foraging opportunities and zones with cleaning stations. Wanderers achieved their highest bite rates in the back reef zone (Chapter 1), suggesting that the back reef provides non-territorial tangs with foraging opportunities outside of schools. Indeed, wanderer densities were highest in the back reef, a result consistent with their behaviour. Because the frequency of cleaning stations increases seaward (L. Whiteman, personal communication), cleaning stations should be most common in the spurs and grooves zone. Of the tangs in the spurs and grooves zone, a high proportion was wandering (45%), a result consistent with individuals seeking cleaning stations.

Overall, the distributions of the social modes in the adult blue tang show variation between reef zones and are partially related to the density of their dominant food competitor, damselfishes. Blue tangs form schools where damselfish densities are high and do not where damselfish densities are low. Barlow (1974a) and Hourigan (1986) recorded a similar distribution of schooling surgeonfish and their territorial competitors. Distribution did not seem to be strongly correlated to food abundance, as measured by the percent algal cover. However, we do not have a measure of algal quality between reef zones, and tangs have been shown to preferentially eat some (unidentified) algae over others (Reinthal & Lewis 1986). Therefore, the role of resource distribution as a determinant of tang density and social organization cannot be discounted.

Differences between reefs

Variation in the densities of juvenile and adult populations among the four surveyed reefs was high. The variation in juvenile densities between reefs could be attributed to the potential variation in larvae supply along the West coast of Barbados (Sponaugle & Cowan 1996) or to differential predation pressures on recruits. Despite the disparity in juvenile densities, however, distribution patterns among zones were remarkably similar. All else being equal, this could indicate that the distributions are a result of active habitat selection by recruiting juveniles.

Among the four reefs, densities of adults varied considerably. The reefs with the highest adult densities also had the highest juvenile densities and vice versa. Therefore, the differences in adult densities could have resulted from juvenile recruitment levels. Although not specifically targeted by fisherman, blue tangs frequently enter Antillean fish traps (personal observation, Chapter 1), a common fishing method in Barbados (Robichaud 1996). This could explain the very low adult density on Heron Bay, the only fished reef surveyed, although missing a large school by chance would have contributed to the low estimate. Because we observed adult blue tangs crossing between North and South Bellairs Reefs (Chapter 1), recruitment difference are less likely to explain the large differences in adult density between these reefs.

On all four reefs, adult densities consistently peaked in the crest. However, on North Holetown Reef, adults were more often found in the spurs and grooves than in the back reef, while on the other reefs, the opposite was true. Freshwater input to the back reef in North Holetown may have reduced tang activity in this zone or small tarpon (*Megalops atlanticus*) residing in the freshwater—saltwater interface may have increased predation risk in the back reef.

Adult social modes were also consistently distributed by zone. On the reefs with both territorial and non-territorial modes, fish formed schools in the crest and spurs and grooves zones, and territorial fish were most common in the crest zone. A study involving Red Sea surgeonfishes (*A. nigrofuscus* and *Ctenochaetus striatus*) with a social organization similar to the blue tang, reported that different social modes are found in different fringing reef zones (Bouchon-Navaro & Harmelin-Vivien 1981). In these surgeonfish, the proportion of individuals in schools peaked in the shallowest zone. Further offshore, this proportion gradually declined while the proportion of solitary fish increased.

We found that population density was significantly related to the proportion of territorial fish in the population. Although based on only four reefs, this result pattern suggests that conspecific density is a determinant in the blue tang social system. It is more common for animals to reduce territorial behaviour at high population densities (Kawanabe 1969, Cole & Noakes 1980, Ferron & Ouellet 1989), presumably due to increased intruder pressure and consequent uneconomical defence of the territory (Grant 1993, Chapman & Kramer 1996). Why the opposite trend occurs in tangs may be related to their adult schooling foraging strategy.

The adult blue tang population density may be higher now than in recent history. In 1983/84 an abundant herbivorous sea urchin (*Diadema antillarum*) experienced mass mortalities throughout the Caribbean (Lessios et al. 1984). This almost completely removed a potentially strong food competitor of blue tangs (Carpenter 1990, Robertson 1991). There is evidence that adult blue tang populations increased in Panama in the decade following this mass mortality event, despite little change in recruitment rates (Robertson 1991). Researchers who worked on South Bellairs Reef between 30 and 40 years ago do not recall seeing as many tang schools as there are now (J. Lewis personal communication). If, as our data suggest, high population densities do result in a shift in the social organization of adult blue tangs, the circumstantial evidence of recent increased tang abundances through a release of competition may have further implications for community structure. An increased number of tangs may put more pressure on the damselfish community through increased competition for algae (schooling) and even increased competition for space (territorial).

Time of day

There was a temporal component to the distribution of wandering and schooling tangs. Tangs tended to wander more often in the morning and less at midday while the densities of schooling tangs showed the opposite trend. This is consistent with the results presented in Chapter 1, which show that individuals switched frequently between these two modes. Tangs may wander more in the morning for a variety of reasons, the most basic being a search for others with whom to school (suggested by Reinthal & Lewis 1986). In addition, parasite loads are higher at dawn (Grutter & Hendrikz 1999) and visits to cleaning stations would be more valuable in the morning. Why most tangs join foraging schools at midday is not clear but may have to do with daily variations in nutritional value or palatability of algae (Polunin & Klumpp 1989).

Why alternative modes?

What allows coexistence of simultaneous alternative modes of adult tangs in the same habitat is not clear in this system. To some extent, this may be related to habitat heterogeneity within a zone. For example in the spurs and grooves and crest zones, there may be a few sites with sparse damselfish densities that permit tang territories. Another possibility is that a preferred social mode is density limited. For example, in some species when all available sites for territories are occupied, the remaining individuals may be forced to be non-territorial wanderers or live in groups (Brown 1969, Barlow 1974a). This scenario seems doubtful for tangs because it appears that schooling, not territoriality, is the preferred mode of adults. In addition, the increase in proportion of territorial individuals with increased population density among reefs makes such an explanation unlikely. Although schooling and wandering seem less likely than territoriality to show a saturation effect, density-dependence of schooling may occur. Tangs join schools in order to increase their foraging success in damselfish territories and should remain in the group if the success is valuable (Caraco 1979, Wolf 1987). However, an increase in conspecific density may contribute to lower per capita foraging success, for two reasons. Although the effectiveness of group foraging increases with an increasing number of school members (Foster 1985), because of passive competition between group members, feeding efficiency might be highest at a moderate size (Saino 1994). Some of the heterospecific schools at our study site were larger than Foster's largest schools and therefore may have reached a size where bite rates no longer increase with school size. Also, at higher overall population densities, the total amount of per capita algal resources in damselfish territories is lower. At higher consumer population densities, this finite resource could be diminished at a rate faster than its renewal time. Under this type of resource competition, the territorial and non-territorial modes may have equal payoffs, and developing individuals may be less likely to start and continue schooling when schools are large. In addition, non-territorial individuals would be expected to visit sub-optimal foraging habitats, like the back reef, in addition to participating in schools. The time spent as wanderers in these habitats should reflect the value of schooling in other zones. Similarly, at very high population densities, density dependence in territoriality could result from poorer quality territories or lead to more overlap between neighbours and hence reduce territoriality (Grant 1993).

Conclusion

In an attempt to synthesize these results, we present a hypothesis for what processes lead to the flexible social organization in the blue tang and may serve to explain the maintenance of the territorial and non-territorial modes in the ecologically homogeneous crest zone. Following settlement, a juvenile tang begins to defend a small territory against conspecific and congeneric juveniles (Bell & Kramer 2000). The purpose of the territory is unclear but may involve the defence of food and/or a nocturnal shelter (Bell & Kramer 2000). Juvenile territories usually overlap with adult damselfish territories (I.M. unpublished data), but the mechanisms by which the juvenile tangs avoid damselfish aggression are not obvious. Cohabitant damselfish may habituate to juvenile blue tangs. Habituation is a function of size and species, and as cohabitants increase in size, damselfish aggression towards them also increases (Harrington 1993). As the tang grows, its food and shelter size requirements also increase, necessitating the defence of a larger area, which would then overlap with more damselfish territories. At the same time, increased body size allows the fish to maintain the swimming speeds of schooling adults (Inoue 1970). Therefore, the concurrent increase in harassment rate and swimming abilities could prompt movement of the juvenile to a less hostile environment. The increased mobility could increase the encounter rate with conspecifics, including schooling adults. If the individuals experience reduced harassment from damselfish while schooling with conspecifics, they may remain in the school and eventually abandon their territory. Therefore, in zones with high densities of damselfishes (e.g., spurs and grooves zone), one would expect fewer territorial tangs. Likewise, in habitats where permanent residence is possible (e.g. flat zone with high algal cover and low sedimentation) and where damselfish densities are limited by lack of resources such as shelter and nest sites, tangs would not experience increased harassment with size and continue territoriality into adulthood. Although our distribution data from the flat and the spurs and grooves zone generally agree with this scenario, it does not completely explain the high density of territorial adult tangs in the crest zones of North Holetown and South Bellairs Reefs where the average density of damselfishes is also high. In this reef zone, our results concerning the role of population density may explain the coexistence of modes and suggest that the social organization of the adult blue tang is density dependent.

We have suggested life history stage, damselfish density and conspecific density as demographic, ecological and social determinants of the blue tang social organization. Plasticity in social behaviour is considered adaptive to animals that face variation in their spatial and temporal environments. That coral reef fishes show intraspecific variation in their social systems is not surprising as local adaptation to ecological factors is not realistic given the scale at which their pelagic offspring disperse (Warner 1997). In all probability, the offspring would settle in environments different from their parents' due to inter-reef variation in community and habitat (Shapiro 1991). The ability to alter their social strategy could allow developing tangs to face and maximize the variation in their ecological and social environments.

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Table 2.1: Description of South Bellairs fringing reef zones.

Zone	Depth range (m)	Rugosity (mean ratio)	Substrate	Live coral cover (mean percent ± SD)	Algae cover (mean percent ± SD)	Adult damselfish density (mean number of individuals per m^2 ± SD)
Back reef	0.5-1.5	Low (1.17)	Coral rock and rubble, sand	1.4 ± 2.1	87.0 ± 8.9	0.23 ± 0.16
Crest	1-3	High (1.52)	Dead coral rock	9.7 ± 8.4	78.1 ± 12.5	0.73 ± 0.15
Spurs and Grooves	3-8	High (1.66)	Dead coral rock	29.8 ± 3.2	47.1 ± 14.1	1.05 ± 0.22
Flat	1.5-3	Low (1.29)	Rubble, coral pavement	7.3 ± 3.3	72.9 ± 10.5	0.25 ± 0.14

Table 2.2. Results of repeated measures ANOVA analysis (for territorial and wanderer modes) and of a mixed model ANOVA with a nested factor (for schooling mode) testing the effects of zone and time of day (morning, midday and afternoon) on the density of blue tangs. The schooling analysis included the back reef.

Size Class	Social Mode	Model components	F	P
Yellow juvenile	Territorial	Time of day	2.36	NS
		Zone	0.57	NS
		Time of day X Zone	1.10	NS
Blue juvenile	Territorial	Time of day	0.25	NS
		Zone	0.41	NS
		Time of day X Zone	1.54	NS
Large juvenile (log10 transformed)	Territorial	Time of day	0.08	NS
		Zone	4.51	0.026
		Time of day X Zone	0.19	NS
Adult (log10 transformed)	Territorial	Time of day	2.12	NS
		Zone	15.90	<0.0005
		Time of day X Zone	1.90	NS
Adult	Wanderer	Time of day	5.50	0.008
		Zone	3.04	NS
		Time of day X Zone	2.38	NS
Large juvenile (rank transformed)	Schooling	Time of day (zone)	2.50	0.029
		Zone	1.46	NS
Adult (rank transformed)	Schooling	Time of day (zone)	3.32	0.002
		Zone	6.49	0.015

Figure 2.1. Diagram drawn from an aerial photograph showing South Bellairs Reef and the four studied zones and their planimetric areas.

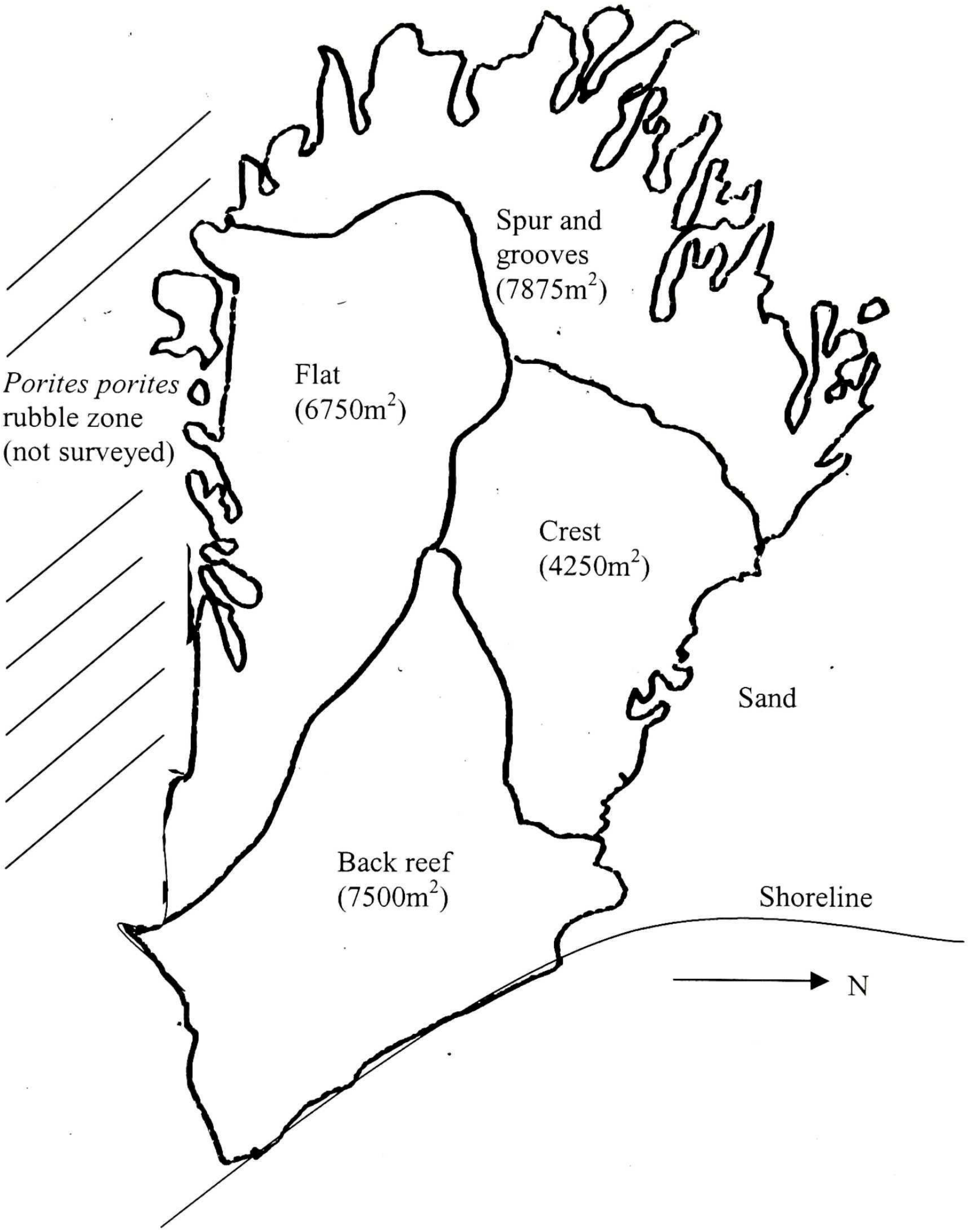
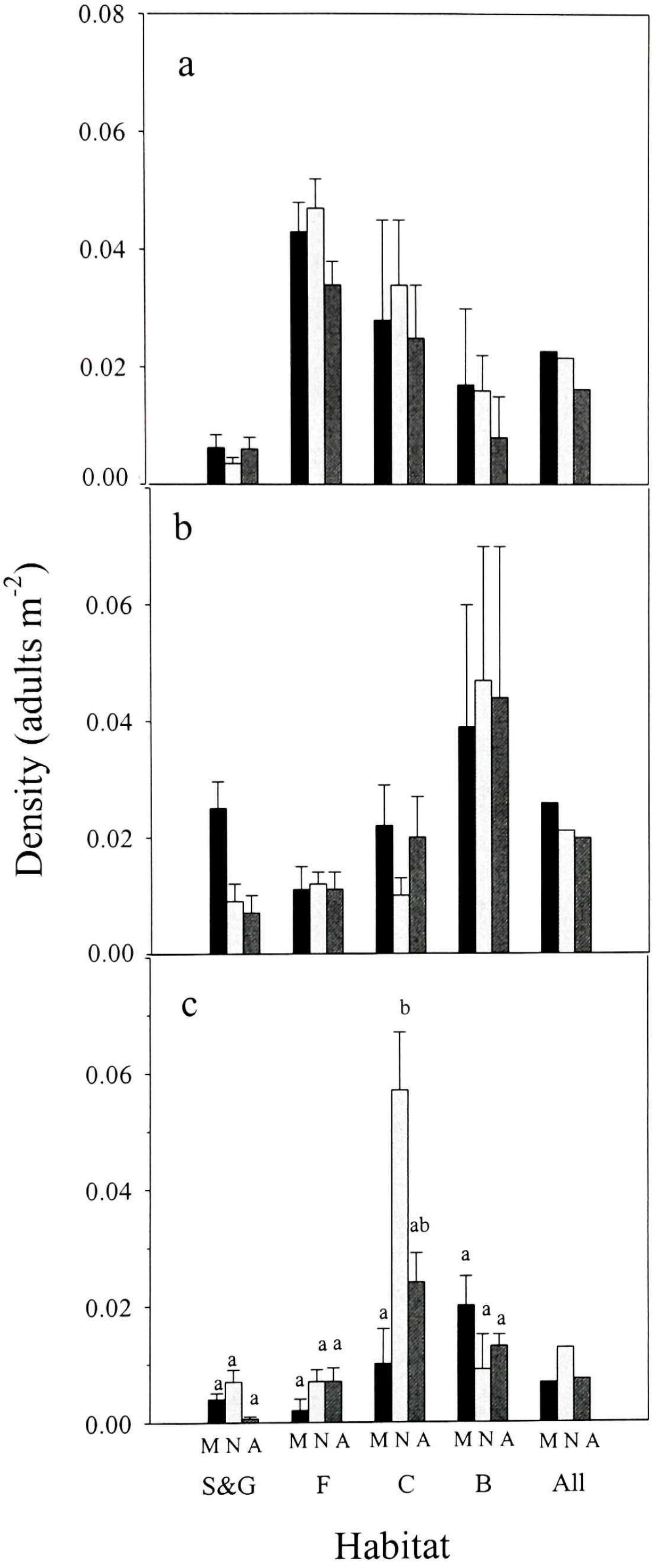

Spur and grooves (7875m²)
Porites porites rubble zone (not surveyed)
Flat (6750m²)
Crest (4250m²)
Sand
Back reef (7500m²)
Shoreline
N

Figure 2.2. Average densities (+ 1 S.E.) of adult tangs in the morning (M, black bars), midday (N, light gray bars) and afternoon (A, dark gray bars) in each of the four reef zones of South Bellairs Reef; spurs and grooves (S&G), flat (F), crest (C) and back reef (B), and the average over the entire reef (All); a. territorial individuals, b. wandering individuals and, c. schooling individuals. For territorial individuals, time of day had no significant effect. For wandering individuals, the higher density of wandering fish in the morning was significant only when data from all zones were combined (a contrast of means with Bonferroni correction, P=0.01). For schooling individuals, shared letters indicate no significant differences between times of day within the zone (Tukey's Honestly Significant test P>0.05).



Density (adults m^{-2})
0.00
0.02
0.04
0.06
0.08
a
b
c
b
ab
a
a
a
a
a
a
a
a
a
a
a
M N A
M N A
M N A
M N A
M N A
S&G
F
C
B
All
Habitat

Figure 2.3. Average densities of a. yellow juveniles, b. small blue juveniles, c. large juvenile blue tangs in each of the four reef zones of South Bellairs Reef; spurs and grooves (S&G), flat (F), crest (C) and back reef (B), and the average over the entire reef (All). For each size class, social mode is indicated by the colour of each bar: territorial (black), schooling (light gray) and wandering (dark gray). Standard errors could be presented only for yellow juveniles but not for the other classes because they were composed of more than one social mode.

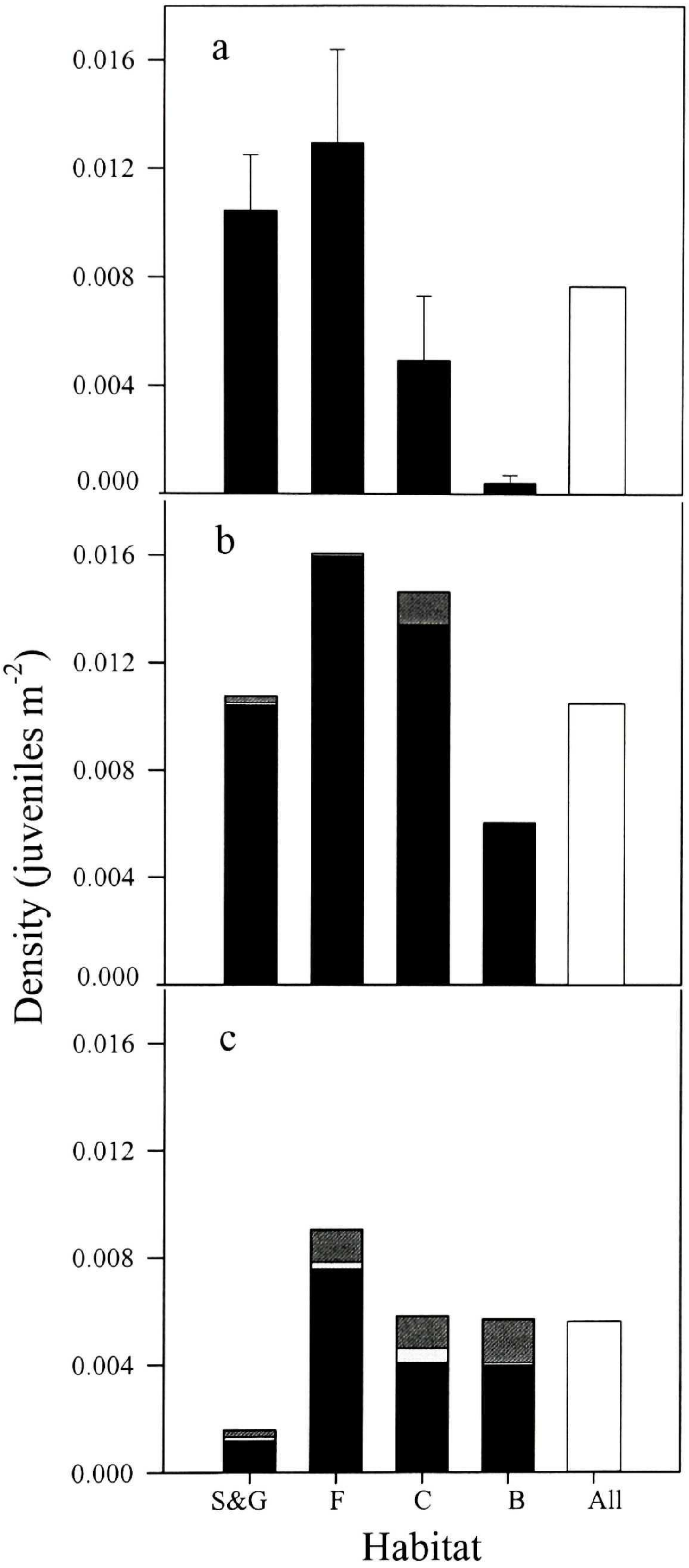

a
b
c
0.016
0.012
0.008
0.004
0.000
Density (juveniles m^{-2})
S&G
F
C
B
All
Habitat

Figure 2.4 The relationship between adult territorial tang density and adult damselfish density. Each point represents data from one transect. The data from the spurs are represented by the gray triangles, from the crest by the white squares, and from the flat by the black circles. The regression line is reported.

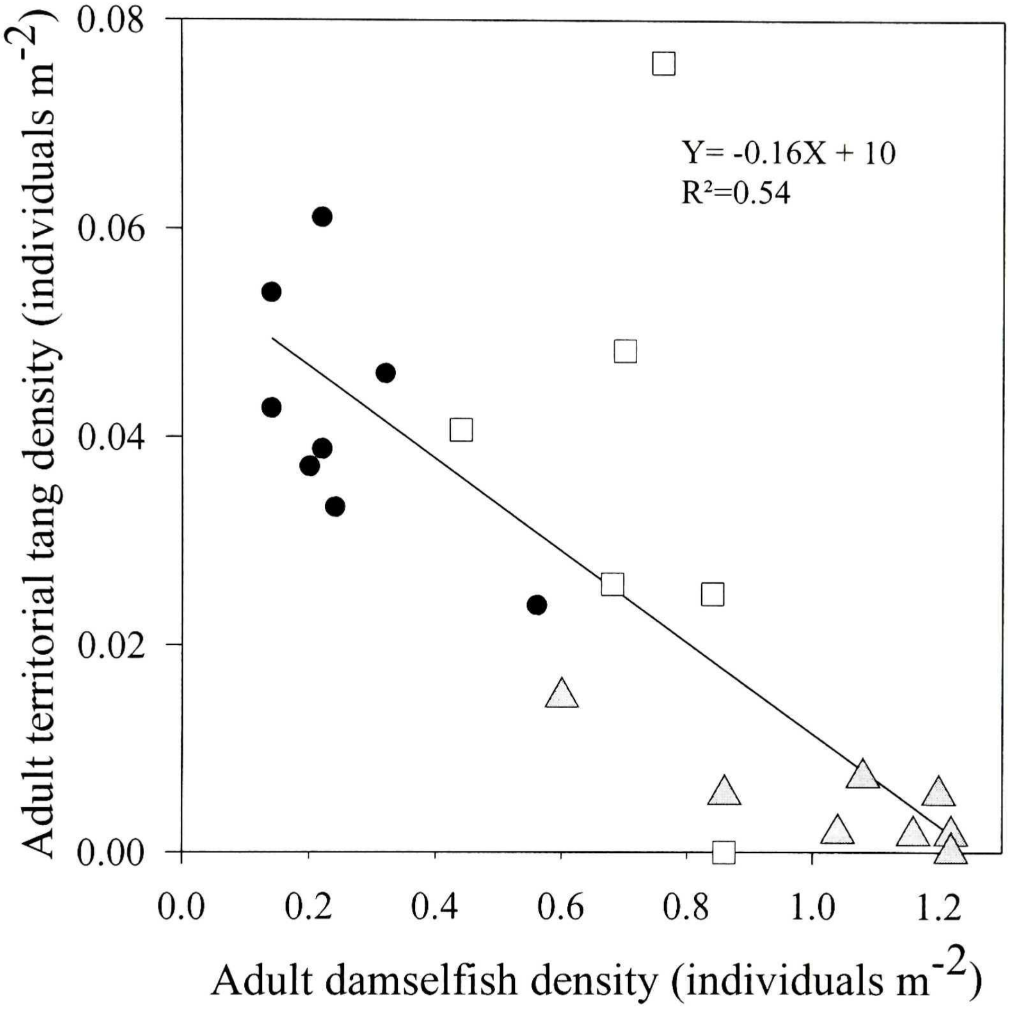

Y= -0.16X + 10
R²=0.54
0.08
0.06
0.04
0.02
0.00
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Adult territorial tang density (individuals m-2)
Adult damselfish density (individuals m-2)

Figure 2.5 The percentage of individuals in each size class exhibiting each social mode, territorial (black), schooling (light gray) and wandering (dark gray). Data were pooled over all of the four zones of South Bellairs Reef. Where there was a time of day effect, the midday values were used otherwise, for each transect, an average density over the three times of day was used.

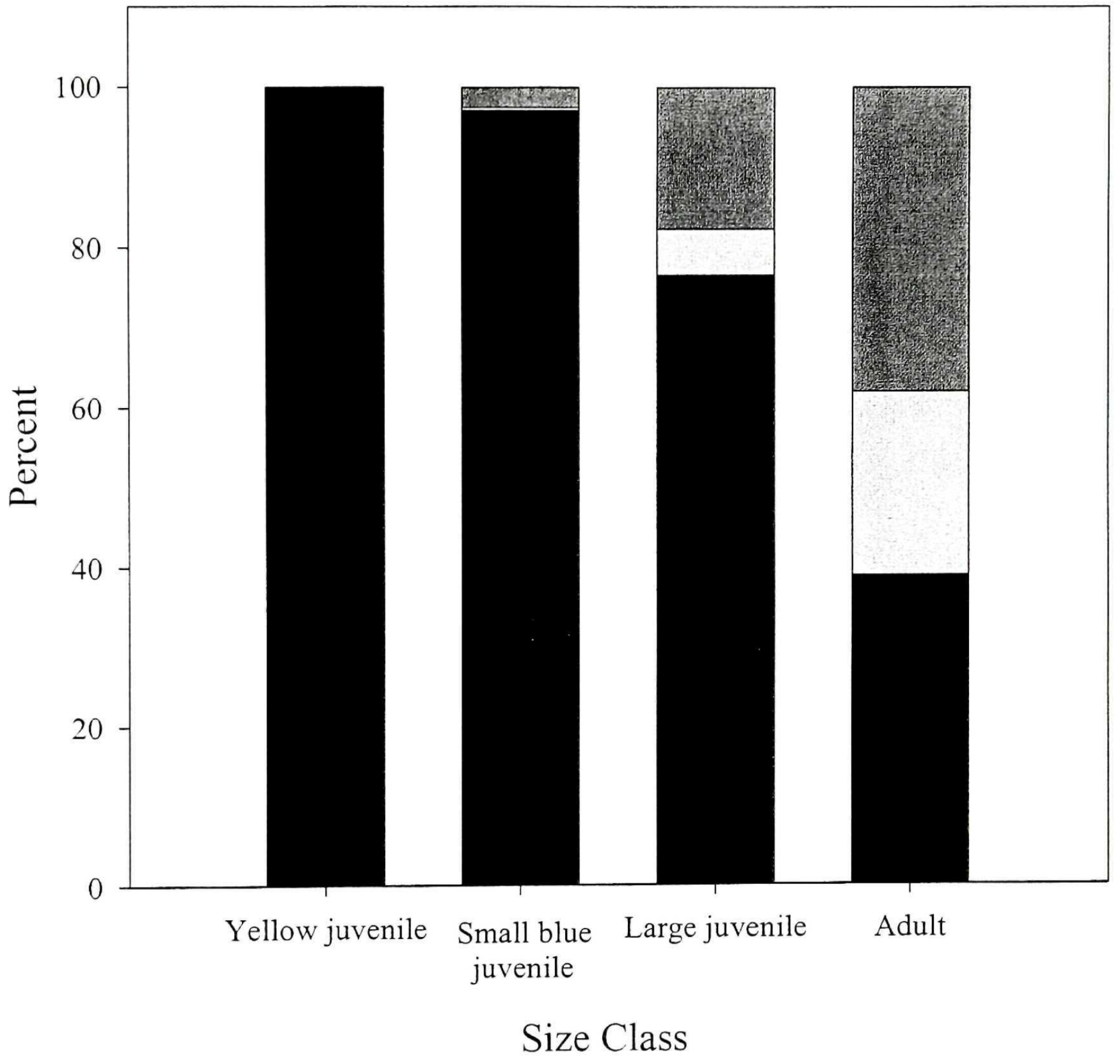

Percent
0
20
40
60
80
100
Yellow juvenile
Small blue juvenile
Large juvenile
Adult
Size Class

Figure 2.6. Average densities of yellow juveniles (black bars) and small blue juveniles (light gray bars) in each three zones (spurs, crest and back) on each of four reefs; a. Heron Bay, b. North Bellairs, c. South Bellairs, d. North Holetown. The data from the flat zone were not included in the South Bellairs Reef panel because this zone was absent from the other reefs. Standard error bars are reported. Note that the ordinate scales differ among reefs.

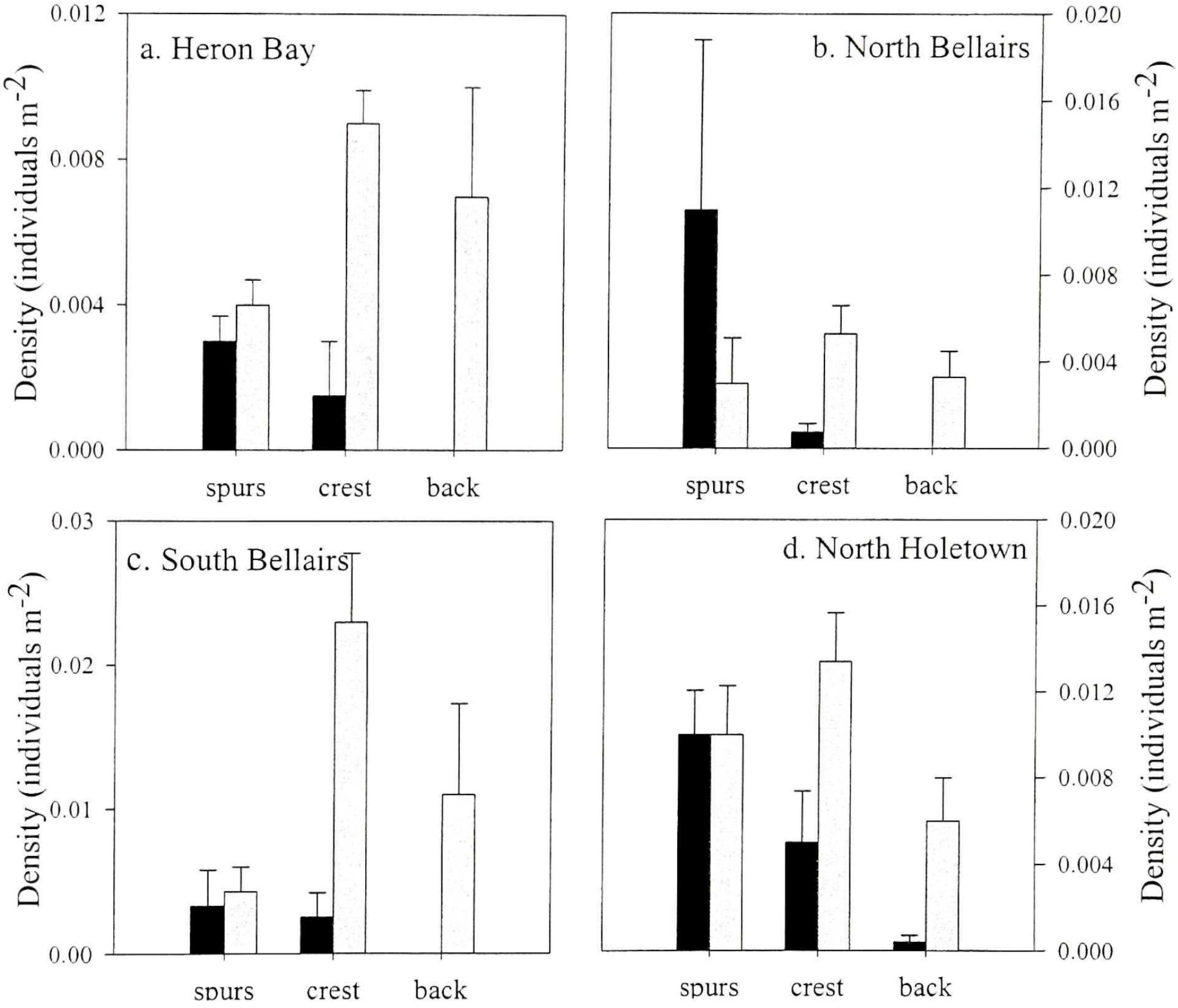
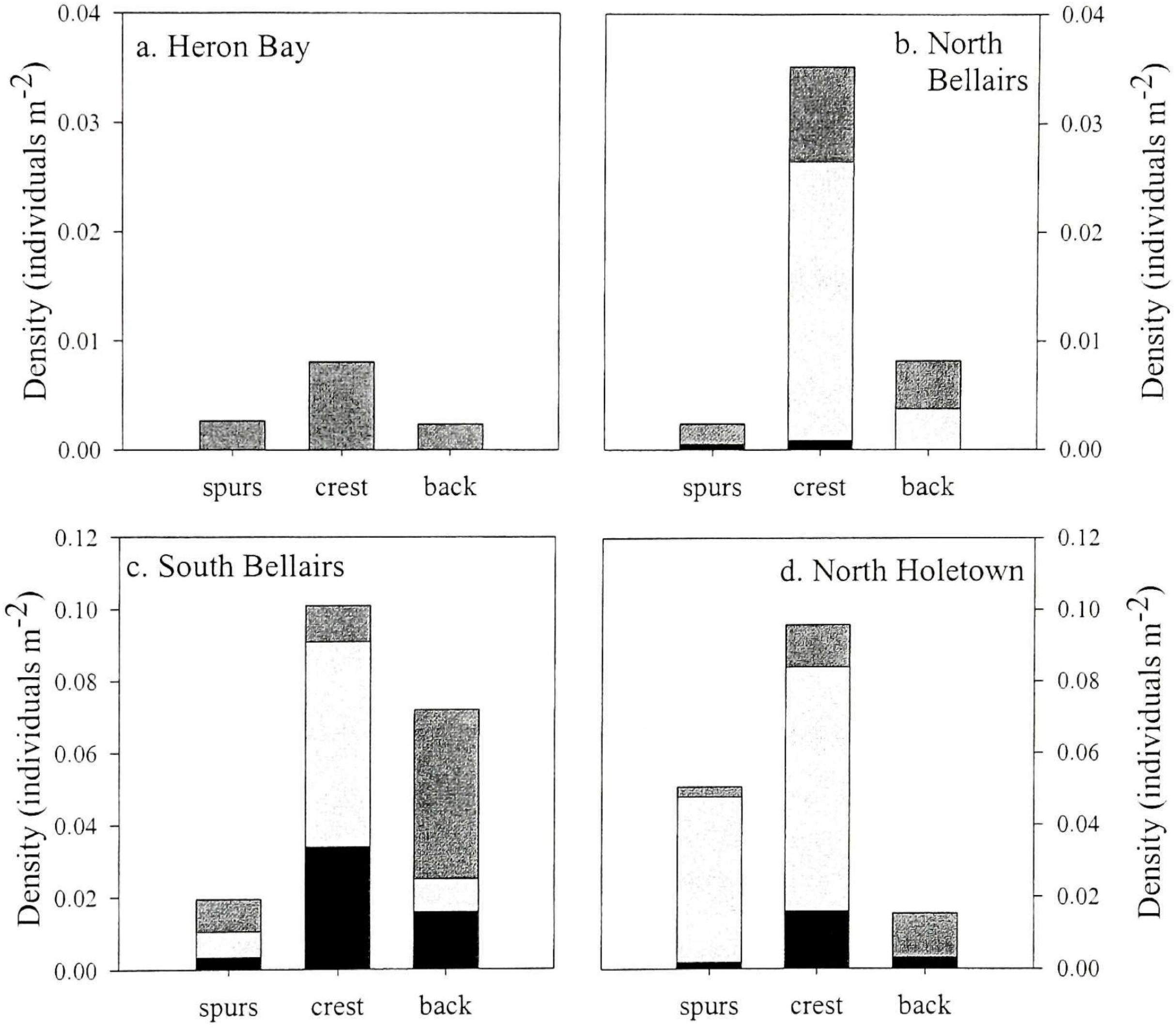

a. Heron Bay
b. North Bellairs
c. South Bellairs
d. North Holetown
Density (individuals m^{-2})
0.000
0.004
0.008
0.012
0.016
0.020
0.00
0.01
0.02
0.03
spurs
crest
back

Figure 2.7. Average densities of adult territorial (black), schooling (light gray) and wandering (dark gray) blue tangs in each zone (spurs, crest and back) on the four studied fringing reefs; a. Heron Bay, b. North Bellairs, c. South Bellairs, d. North Holetown. The flat zone data were not included in the South Bellairs Reef graph, because this zone was absent in the other reefs. Note that the ordinate scale differs between reefs.


a. Heron Bay
b. North Bellairs
c. South Bellairs
d. North Holetown
Density (individuals m-2)
0.00
0.01
0.02
0.03
0.04
0.00
0.02
0.04
0.06
0.08
0.10
0.12
spurs
crest
back

General Conclusion

These chapters have described the intraspecific variation in social behaviour exhibited by blue tangs. In Chapter 1, I have identified distinct territorial and non-territorial adults in one population. Non-territorial adults form schools and wander and territorial individuals sometimes adopt the wandering mode when on a foray. Because it is not technically feasible to tag and monitor all fish in the population, I was unable to determine if a distinct wandering mode (one that never schools) exists in the population. Based on my observations, however, if such a mode exists, it is rare.

Behaviour differed between modes, but these relative differences varied among reef zones. From the point of view of the individual, these relative differences may contribute to the social strategy adopted by a tang when in a particular reef zone, and consequently to the overall distribution of the modes over the reef. Consistent with this perspective, in Chapter 2, I found that the distribution of individuals in certain social modes varied with zone. Coupled with data from Chapter 1, the observation that non-territorial tangs school more often in zones of high damselfish densities support the prevailing hypothesis that tangs school to gain access to guarded resources (Robertson et al. 1976, Foster 1985). Based on their behaviour and overall distribution, I have also suggested that tangs not only wander to visit cleaning stations (Reinthal & Lewis 1986) but also to visit alternative foraging sites.

The main objective of Chapter 2 was to identify potential determinants of social organization in the blue tang. The ontogenetic development of social behaviour was clearly documented, with a decreasing proportion of territorial fish in the larger size classes. In addition, adult damselfish density emerged as a potentially important determinant of not only school formation by non-territorial tangs, but also of the occurrence of the adult territorial mode. Finally, a higher proportion of territorial adults existed in high-density populations. Although future work is necessary to further this finding, this result suggests that the social organization in blue tangs is density-dependent. I have presented a hypothesis integrating each of these potential determinants of social organization, underlining the interactions between their respective roles, but understanding the striking complexity of the social organization of this surgeonfish has only just begun.

Appendix A: The relationship between pectoral fin beat rate and swimming speed in the adult blue tang.

Introduction

In Chapter 1, I recorded the time it took a focal individual to beat its pectoral fins 50 times. The purpose of this measure was to quantify swimming speed (a component of mobility) and thus allow comparisons of mobility between social modes. In order to convert the pectoral fin beat rate (50 beats/ x seconds), a regression model was built. Because the focals involved two size classes (size class 2 and 3), two models were constructed in order to account for the potential effect of body size on swimming speed.

Methods

Data were gathered while snorkeling or using SCUBA during the month of November 2001. I haphazardly chose a tang to follow. A stone was placed where the observation and counts began, a timer was started and the tang was followed. I counted the number of pectoral fin beats until the tang changed direction. The timer was stopped and the distance between the end point (the point where the tang changed direction) and the start point (marked by the stone) was measured using a transect line. Time, number of pectoral fin beats and distance traveled were recorded. Care was taken to gather these data on days when there was no current and surge was low. Because these conditions were rare in November, sample sizes are relatively small. Data were gathered on 19 fish of size class 3 and 11 individuals of size class 2.

Analysis and Results

The dependent variable in this case is swimming speed (meters/s) and the independent variable is pectoral fin beat rate (# pectoral fin beats/s). Linear regressions were performed. The slopes were significantly different from zero but the constants were not. This result is biologically realistic and therefore the y intercept was set to 0. Final models are below:

Size class 3: $Y = 0.289X$ $P<0.0005$

Size class 2: $Y=0.254X$ $P<0.0005$

A general linear model revealed that there is no significant difference in slopes between the two size classes (interaction term $P=0.161$ with intercept set to 0). However, I continued with separate models in the analysis because each was the best fit for each size class. Data were analyzed with SPSS 10.1.

Converting the data

The calculated y gave us the average swimming speed, not necessarily the speed of the fish at all points in time (for the territorial individuals, swimming was in spurts between foraging areas). Although some focals were done on size class 4, time did not allow for data to be gathered for a separate model for this size class. Therefore, size class 4 individuals were treated as size class 3.

Appendix B: Juvenile survival

Introduction

Basic demographic data on coral reef fishes is rare relative to the amount gathered on temperate fish populations (Forrester et al. 2002). The survival rate of juvenile coral reef fishes is an important aspect in the study of local population dynamics and as such should be recorded whenever possible. In May 2001 a large recruitment event of ocean surgeonfish and of blue tangs occurred. The number of individuals seemed unusual and offered an opportunity to follow their survival. I focused my efforts on the blue tang because as juveniles, they are solitary and territorial (Bell & Kramer 2000) and therefore can be re-visited over a long period of time.

Methods

I delineated a haphazardly chosen 40m by 40m area in the spurs and grooves zone of North Bellairs Reef (Lewis 2002). Using a compass and small pieces of flagging tape I outlined the area and all of the 10m by 10m grid squares within it. A map was drawn of the area, after which I counted and recorded all of the yellow juvenile blue tangs in the grid. I used SCUBA gear for all surveys in order to ensure that I did not miss any juveniles that were under overhangs or otherwise hidden. I counted only the blue tangs less than 4.5cm in order to ensure I followed one cohort. There were no other larger juvenile blue tangs in the area and new recruits did not begin appearing at the site again until July (at which time the former cohort was clearly larger). For each individual, I performed a 5-minute focal observation and placed a flagged stone in the approximate centre of its home range. The locations of the markers were recorded on the map. Approximately every two weeks until October I revisited the site, visited each home range and counted the remaining juvenile tangs. In addition, I noted whether the resident tang had changed to the adult colour blue and estimated total length of some of the tangs. Due to the complexity of this particular area juvenile tangs were difficult to catch. Therefore while the fish was swimming freely, I estimated TL by visually aligning the fish with two recognizable structures on the reef and then measuring the distance between these structures. I ignored smaller blue tangs whose home ranges did not correspond to a marker stone because they were likely to be subsequent recruits. If a tang was missing from a home range, I could not determine whether it was due to a movement or to a death.

Results/ Discussion

Of the 64 juvenile tangs counted in late May, 8 remained in the last census taken in October indicating a 12.5% survival rate over a period of 136 days. More than 45% disappeared in the first week of the survey. Some of the missing blue tangs may have turned blue and joined schools or begun wandering. However, in Chapter 2, I recorded very few wandering blue juvenile tangs and even fewer schooling. Therefore, disappearance due to a change of social mode is unlikely in these early declines. Although the possibility of movements, exists and if ignored, can lead to overestimates of mortality (Frederick 1997), the early high disappearance rate is likely attributable to mortality due to predation or competition. Hunte & Cote (1989) found a correlation between the monthly percent mortality and density of recruits in red-lipped blennies on the same reef in Barbados. Also, Jones (1987) reported decreased survival in areas of high densities of simultaneous recruits. The recruitment of surgeonfishes was unusually large and simultaneous (within a few days). Therefore, the high mortality rate must be considered in this context.

Yellow juvenile tangs changed to the adult blue colour at a variety of sizes and the change did not seem to correspond with the expected change in social mode. Some of the new recruits from the first survey were blue, and all of the ensuing blue juveniles continued to hold and defend their territories (although I cannot account for the missing individuals). Overall however, over the course of the 5 months, there was an increase in the percentage of remaining juveniles that had changed colour. The mechanism of and reason for colour change has not yet been studied in this species. Measurements of sampled individuals revealed a growth rate of approximately 0.38 cm per month with individuals growing from 3.9 cm in May to 5.8 cm in October.

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Figure B-1. The number of remaining juvenile blue tangs on North Bellairs Reef 40 X 40 m grid over the time period of the survey (May 28th- October 11th 2001) (closed circles). The percentage of the remaining juveniles that have changed to the adult blue colour (open circles). X-axis is separated into 2-week intervals.