

Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species

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Synopsis

Territorial behaviour is a conspicuous determinant of social organisation in many reef fishes including parrotfishes. Most parrotfish studies in the Caribbean have focused on the species *Scarus iserti* and *Sparisoma viride* over limited ranges of reef habitat. By contrast, our study has included all common parrotfishes in Belize (*Sc. iserti*, *Sp. viride*, *Sparisoma aurofrenatum*, *Sparisoma chrysopterum*, and *Sparisoma rubripinne*) at three sites with different physical and biotic conditions and a wide range of fish densities. Density in *Sc. iserti* was strongly positively correlated to substrate rugosity. In contrast, densities of *Sp. chrysopterum* and *Sp. rubripinne* were unrelated to rugosity and territories were large. Territory size was smallest in *Sc. iserti* (mean areas at the three sites ranged from 41 to 120 m²) and largest in *Sp. rubripinne* (ranged from 168 to 1400 m²). All species except *Sp. chrysopterum* exhibited significantly larger territories where density was low as suggested by territory theory. Territory size decreased rapidly with increasing density of competitors. Patterns of harem size differed between two groups of parrotfishes. (1) *Sc. iserti*, *Sp. viride*, and *Sp. aurofrenatum* exhibited an expected positive correlation with territory size. (2) Harem size was smaller in *Sp. rubripinne* and *Sp. chrysopterum*, and showed no spatial pattern. Aggression in *Sp. viride* and *Sc. iserti* was directed entirely towards intraspecifics and positively density dependent. Interspecific interactions accounted for only 10% of observations and were recorded exclusively whilst following *Sp. chrysopterum*, *Sp. rubripinne*, and, to a lesser extent, *Sp. aurofrenatum*. A meta analysis of species interactions suggested that intraspecific interactions were most common where overall fish density was greatest and conversely, interspecific interactions occurred more often at lower densities. This may suggest that the economic defensibility of territories is largely confined to intraspecifics where density is greatest. Most (62%) of the interspecific interactions comprised *Sp. rubripinne* chasing the smaller species *Sp. chrysopterum*, suggesting that territorial behaviour has at least some non-reproductive origin and may therefore be associated with either food or shelter. It is feasible that at such low population densities, it is economically feasible for *Sp. rubripinne* to defend against intraspecifics and *Sp. chrysopterum*. Social behaviour in *Sp. chrysopterum* and *Sp. rubripinne*, and to a lesser extent *Sp. aurofrenatum*, differs to that of *Sc. iserti* and *Sp. viride* which conform to existing theories of social behaviour in reef fish.

Introduction

Territorial behaviour is a conspicuous element of social organisation in many reef fishes. Most studies of territoriality in reef fish have focused on damselfishes (family Pomacentridae), many of which defend a home range against conspecifics and heterospecifics (Sale 1971, Thresher 1976, Brawley & Adey 1977,

Kaufman 1977, Ebersole 1980, Warner & Hoffman 1980, Jones & Norman 1986, Itzkowitz & Slocum 1995, Letourneur 2000). Relatively few studies (e.g. Ogden & Buckman 1973, van Rooij et al. 1996a) have addressed territoriality in parrotfishes (Scaridae) which are sequential hermaphrodites with three colour phases: brightly coloured terminal (adult) males, drab intermediate (adult) males and females, and juveniles

(Barlow 1975). The terminal-phase (TP) male usually defends a territory and is associated with a harem of intermediate females with whom mating takes place daily (van Rooij et al. 1996c).

The concept of economic defensibility (Brown 1964) is widely used to explain territorial behaviour. It predicts the development of territorial behaviour if the benefits derived from exclusivity of access to a particular resource are greater than the costs of defending it. As competition increases (for example, as a result of higher population densities of competitors), territory size decreases until territoriality is abandoned altogether (Davies & Houston 1984, Norman & Jones 1984). For example, studies of the parrotfish *Sparisoma viride* in Bonaire, Western Atlantic (van Rooij et al. 1996b), revealed an inverse relationship between population size and territory size. Further, smaller territories contained fewer harem females, possibly because of reduced availability of resources within such territories (van Rooij et al. 1996b).

Defended resources within parrotfish territories include mates and spawning sites. Evidence for the latter includes the predominance of spawning in deeper areas (where territories occur) rather than in shallow areas dominated by non-territorial, multi-male, group fish (van Rooij et al. 1996c). Food is also likely to be a defended resource although its importance relative to spawning success in determining territoriality is unclear. van Rooij et al. (1996a) suggested that food is a defended resource because (i) territoriality occurs throughout the day (i.e. not just during the 1–2 h spawning period), (ii) non-spawning group fish (multiple males) exclude conspecifics from their home ranges, (iii) food resources are of higher quality in territories (Bruggemann et al. 1994b), and (iv) food may be a seasonal limiting resource affecting fish condition (see van Rooij et al. 1995). However, van Rooij et al. (1996a) also found great overlap in vertical distribution and substrate use by *Sp. viride* and other scarids which did not reconcile with the apparent absence of interspecific aggression. They suggested that intraspecific aggression arises because it is not economically possible to defend resources against all potential competitors (see also Robertson & Polunin 1981). As such, it is best to defend against individuals with the most similar resource requirements (conspecifics). There may also be a community-wide advantage to partitioning territory defence between conspecific individuals.

Eleven parrotfish species are found on Caribbean coral reefs but territoriality and social behaviour have only been studied in six of these, mostly *Sp. viride*

(Barlow 1975, Robertson & Warner 1978, Hanley 1984, Bruggemann et al. 1994b, van Rooij et al. 1996a, Overholtzer & Motta 1999), *Scarus iserti* (Buckman & Ogden 1973, Clifton 1989, 1990), and, to a lesser extent, *Sparisoma aurofrenatum* (Barlow 1975, Dubin 1981, Clavijo 1982, Muñoz 1996). Few studies have considered interspecific parrotfish interactions, although available evidence suggests that adult aggression is mostly directed towards conspecifics (Barlow 1975, van Rooij et al. 1996a).

This study investigated the social biology of parrotfishes among species and sites with different physical and biotic conditions. It constitutes the first direct comparison of territory and harem sizes between the common parrotfish species *Sc. iserti*, *Sp. viride*, *Sp. aurofrenatum*, *Sparisoma chrysopterum*, and *Sparisoma rubripinne*. As far as we are aware, this is also the first investigation of parrotfish aggression at multiple densities. Specific hypotheses were: (i) territoriality occurs in all common parrotfish species, (ii) territory size is smallest where the local density of conspecifics is greatest, (iii) more harem females occupy larger territories, and (iv) aggression is entirely intraspecific and most frequent where conspecific density is highest.

Materials and methods

Study sites

Field studies were carried out at three sites on the windward forereef of Glovers Atoll, Belize, Western Atlantic (16°44' N, 87°50' W). The structural complexity (rugosity) and fish density were greatest at Long Cay, intermediate at Middle Cay and lowest at South West Cays. To simplify interpretation of the results, these sites are subsequently named site H (i.e. high density), site M (medium density), and site L (low density). Sites H and M each covered an area of ca. 2200 m² whereas site L was larger, at ca. 10 000 m² (1 ha). Rugosity was measured by laying a 2 m chain (segment length 3 mm) over the substrate surface and measuring the linear horizontal distance between the start and end of the chain with a survey tape. Rugosity was calculated as the ratio of chain length to horizontal distance and 15 replicate measurements were made per site. Site H had a mean rugosity of 1.97 (standard error, SE 0.10) and was dominated by dead colonies of the star coral, *Montastraea annularis* (34.2%), and dead colonies of the branching coral, *Acropora cervicornis* (31.5%), largely due to Hurricane Mitch which

Table 1. Mean biomasses (g) of terminal and intermediate-phase parrotfish involved in aggressive interactions.

Sexual phase	Parrotfish species				
	<i>Sp. aurofrenatum</i>	<i>Sp. rubripinne</i>	<i>Sp. chrysopterum</i>	<i>Sp. viride</i>	<i>Sc. iserti</i>
Terminal	152.3 (5.3)	668.9 (35.5)	383.8 (32.3)	642.9 (18.6)	33.0 (2.8)
Intermediate	47.9 (15.6)	224.9 (32.9)	137.2 (16.0)	169.3 (16.6)	7.2 (0.9)

Standard errors are shown in parentheses.

struck the atoll in October 1998 (Mumby 1999). Total live coral cover was 9.0% (determined from map of entire site rather than sub-sampling). Site M was dominated by *Acropora*-derived rubble (54.9%) and living *M. annularis* (9.2%). Total live coral cover was 11.2% and rugosity was 1.42 (SE 0.09). Live coral cover was lowest at site L (<1%) which mainly consisted of a pavement carbonate terrace dominated by gorgonians and rugosity was 1.12 (SE 0.05). All three sites lie within a fishery-exclusion zone so anthropogenic disturbance to fishes was minimal. All surveys were undertaken between depths of 6–11 m.

The density, fork length, and sexual phase of parrotfishes were recorded using a minimum of fifteen 30 m × 2 m transects orientated randomly at each site.¹ Accuracy of fork-length estimates were tested using model fish until 90% of observations were within 2 cm. Fork lengths were converted to biomass using length-mass relationships for Caribbean fishes.²

Study species

Territory size, harem size, and aggressive interactions were recorded for TP males of *Sc. iserti*, *Sp. aurofrenatum*, *Sp. chrysopterum*, *Sp. rubripinne*, and *Sp. viride*. A total of 111 individuals were studied in June and July 2000 (25 *Sc. iserti*, 27 *Sp. viride*, 25 *Sp. aurofrenatum*, 17 *Sp. chrysopterum*, 17 *Sp. rubripinne*). To prevent bias due to diurnal changes in behaviour, studies of each species at each site were split as evenly as possible between morning (8:00–10:00 h),

noon (11:00–13:00 h), and afternoon (14:00–16:00 h) and conducted in random order (e.g. nine *Sp. viride* were sampled at site M, comprising three individuals for each time of day). The mean biomass of each species and sexual phase are given in Table 1.

Territory size

Territories were not delineated purely using the locations of aggressive interactions (Reese 1978) for two reasons. First, rather than using Noble's (1939) restrictive definition of a territory as a defended area, we followed Kaufman's (1983) inclusive definition in that a territory holder has priority of access to resources in some fixed area and that this dominance be achieved through social interactions. Under this definition, overt aggressive behaviour in defence of the area is not a prerequisite for territoriality; territories may be maintained through mutual avoidance. Secondly the frequency of aggressive encounters was too low to allow the boundaries of territories to be mapped (see also Gronell 1980, Pressley 1981). Consequently, territories were delineated from positional observations taken at regular intervals (Norman & Jones 1984) of 1–2 min and locations of aggressive interactions. To determine position while monitoring fish behaviour and mapping individuals' territories, each study area was marked at regular intervals (ca. 20 m) using inverted, coded, plastic cups suspended 1 m above the substratum. Each position was recorded as a distance and direction (left or right) to at least two markers. This method was preferred over the physical marking of positions using small coloured weights (Nursall 1974, 1977, Reese 1978, Hixon & Brostoff 1996) as this might affect fish behaviour, and is more time consuming. Both surveyor's ability to estimate the distance between fish and markers was tested using flagged bolts placed at various distances from markers. Following 30 min practice, the combined mean error was 11 cm and estimated and measured distances did not differ significantly (paired t-test, $p = 0.54$, $n = 23$). Individual fish were not tagged

¹ Ginsburg, R.N., P. Kramer, J. Lang, P.F. Sale & R.S. Steneck. 1998. Atlantic and Gulf reef assessment (AGRA); revised rapid assessment protocol. University of Miami, Miami. 13 pp. The technique recommends a minimum of 10 transects but 15 were used in this study.

² Bohnsack, J.A. & D.E. Harper. 1988. Length-weight relationships of selected marine reef fishes from the southeastern U.S. and the Caribbean. Technical Memorandum 215, NOAA, National Marine Fisheries Service, South East Fisheries Center, Miami. 37 pp.

as Larson (1980) found that fish were shy of divers for approximately a week after tagging and therefore it is preferable to identify fish without tagging during short-term studies.³ TP males showed clear territory boundaries and individual fish could be attributed to distinct areas of reef without difficulty (thus avoiding pseudoreplication). Groups of TP males were rarely observed at the depths surveyed and did not complicate the study. At all three sites, all five studied species readily habituated to the presence of a diver, allowing behavioural observation at close range (up to 3 m but not within 1 m) without creating any apparent reaction in the subject (Reese 1978). Preliminary observations of *Sp. viride* for 60 min periods indicated that individuals swam a repeated pattern (territory) every 5–15 min. Therefore, an observation time of 20 min was used for individuals of all species which was comparable to 15 min used by van Rooij et al. (1996b) and 10 min by Tolimieri (1998). It was also found to be appropriate for species with larger territory sizes (i.e. each fish repeatedly moved along the perimeter of its territory).

The spatial relationship between markers was established using triangulation to at least three other markers (accuracy of measurements <0.2 m). The spatial distribution of reef habitats was then mapped *in situ* and digitised into a Geographic Information System (GIS). Territory borders were established by digitising the most distant locations of each fish on the GIS. Points were joined with straight lines unless territory borders were observed to follow specific features of the benthos which had been mapped in detail. Patches of rubble, sand gullies, and drop-offs usually formed part of the territory. Thus a territory was defined as the area of the polygon that could be constructed by lines connecting some or all of the points at which position recordings had been made (adapted from the convex polygon method, Schoener 1981). The precision (ratio of standard error to mean, expressed as a percentage) of territory areas was calculated at the intermediate-density site (M) by randomly selecting a fish of each species and re-surveying it at a different time and on a different day. Precision was high in having a mean value of 2.6% across species and a range of 0.2% (*Sp. aurofrenatum*) to 7.8% (*Sp. viride*).

³ Roberts, C.M. 1986. Methods for the study of fish territoriality. Report 19th Symp. Underwater Assoc. Natural History Museum, London. pp. 81–92.

Harem size

The total number of intermediate-phase female fish permitted within the territory by the TP male was recorded during, and immediately after, a survey of territory size. Mating activity was frequently observed but not quantified.

Aggression

A social (or aggressive) interaction can be defined as the response, excluding courtship and spawning, of the focal individual to another fish, resulting in the termination of the previous behavioural activity (van Rooij et al. 1996c). Aggression was manifest as either (i) one fish chasing another, often for tens of metres and usually involving a terminal male chasing intermediate males, (ii) two terminal males swimming parallel to one another at the border of their territories and with a visual display of fins (Randall & Randall 1963, Barlow 1975), or (iii) jaw fighting between TP *Sp. iserti* (Buckman & Ogden 1973). The locations of aggressive interactions were recorded whenever they were observed. For each interaction the species, size, and sexual phase (in the case of scarids) were recorded for both individuals. Whether the focal individual was being displaced or acting as aggressor was also noted.

Analyses

Aggressions at each site were summarised in species–species matrices. To compare matrices, the frequency of interactions was standardised for 10 fish per species per site arbitrarily. The Tau coefficient (Ma & Redmond 1995) was used to assess inter-site differences in the ratio of intraspecific to interspecific aggression. Tau coefficients are used to compare the frequency of values in the diagonal of a matrix (in this case, intraspecific interactions) to those occurring either side of the diagonal (i.e. interspecific interactions). In this case, the Tau coefficient represents the proportion of intraspecific interactions above that expected by chance alone, based on the distribution of all interactions in the matrix (i.e. Tau explicitly incorporates the species-level interactions). An advantage of using Tau coefficients is that their confidence intervals can be calculated, permitting testing of the null hypothesis that the ratio of intraspecific to interspecific interactions did not vary between sites. To examine whether the frequency of aggressive interactions was linearly related to the frequency of fish

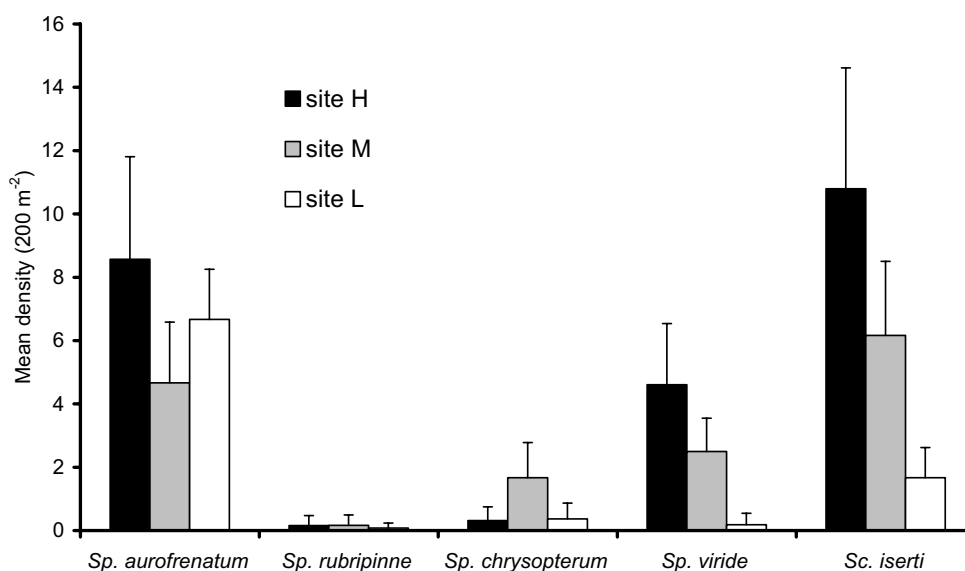


Figure 1. Mean densities of all parrotfish species surveyed during June 2000 at three sites. Error bars denote 95% confidence interval.

encounters (e.g. if aggression occurred every time a terminal male encountered an individual of species \times), the ratios of fish density between sites were used to calculate expected frequencies of aggression. The goodness-of-fit between observed and expected frequencies of aggression (scaled by fish density) were tested using Chi-square analysis (Sokal & Rohlf 1995).

The individual and interactive effects of species and site on territory size were tested using a general linear model, two-way crossed ANOVA.⁴ Species and site were treated as fixed factors, all data were normally distributed, and homogeneity of variances was improved using a log-transformation. To examine the additional influence of biomass, the analysis was repeated with biomass as a covariate. Pairwise multiple comparisons were conducted using Sidak simultaneous comparisons.³ Additional standard statistical methods (e.g. correlation, ANOVA) are not described here.

Results

Not all species showed the same trend in density between sites but, overall, *Sc. iserti* had the greatest density followed by *Sp. aurofrenatum*, *Sp. viride*, *Sp. chrysopteron*, and *Sp. rubripinne* (Figure 1).

⁴ Minitab. 1997. Minitab Users Guide. Minitab Inc., PRA, USA pp. 3-34-3-45.

Aggression

Overall, 90% of aggressive parrotfish encounters were intraspecific and the remaining 10% were interspecific. The relative proportions of intraspecific and interspecific aggression were similar at sites M and L (84% and 87% respectively), but a significantly ($p < 0.001$) larger proportion of intraspecific aggression occurred at site H (97%).

Species-level interactions are presented in a matrix for each site (Tables 2, 3, and 4). Pooling data from these tables to make an overall comparison of aggression among species (not shown), *Sc. iserti* was the most aggressive with intraspecific interactions accounting for 47% of all observations. Overall intraspecific aggression in the other four species was similar at 9% (*Sp. rubripinne*), 11% (*Sp. aurofrenatum*), and 12% (*Sp. chrysopteron* and *Sp. viride*) of all observations (the remaining 9% of observations were interspecific). Most (96%) intraspecific interactions involved the focal TP male chasing adults from the territory (i.e. only on 4% of occasions was the resident TP male chased within its own territory). Interspecific interactions were dominated by aggression between *Sp. rubripinne* and *Sp. chrysopteron* (6% of all observations). Of these interactions, *Sp. rubripinne* always chased the smaller *Sp. chrysopteron* (Table 1), accounting for 62% of all interspecific interactions. Other interspecific interactions accounted for $\leq 1\%$ of all observations although

Table 2. Matrix of intra- and interspecies aggression at site H.

Site H	<i>Sp. aurofrenatum</i>	<i>Sp. rubripinne</i>	<i>Sp. chrysopterum</i>	<i>Sp. viride</i>	<i>Sc. iserti</i>	Grand total
<i>Sp. aurofrenatum</i>	20.0		2.9			
<i>Sp. rubripinne</i>		8.0	1.4			
<i>Sp. chrysopterum</i>	1.0		1.4			
<i>Sp. viride</i>				21.0		
<i>Sc. iserti</i>					113.0	
Column total	21.0	8.0	5.7	21.0	113.0	168.7

Counts are standardised to represent 10 fish per species. Columns represent the fish that were followed. Rows represent the fish they interacted with. Boxed areas represent intraspecific interactions.

Table 3. Matrix of intra- and interspecies aggression at site M.

Site H	<i>Sp. aurofrenatum</i>	<i>Sp. rubripinne</i>	<i>Sp. chrysopterum</i>	<i>Sp. viride</i>	<i>Sc. iserti</i>	Grand total
<i>Sp. aurofrenatum</i>	8.9	1.3				
<i>Sp. rubripinne</i>	1.1	21.3	10.0			
<i>Sp. chrysopterum</i>		10.0	44.0			
<i>Sp. viride</i>				21.0		
<i>Sc. iserti</i>	4.4				45.6	
Column total	14.4	32.5	54.0	21.0	45.6	167.5

Counts are standardised to represent 10 fish per species. Columns represent the fish that were followed. Rows represent the fish they interacted with. Boxed areas represent intraspecific interactions.

Table 4. Matrix of intra- and interspecies aggression at site L.

Site L	<i>Sp. aurofrenatum</i>	<i>Sp. rubripinne</i>	<i>Sp. chrysopterum</i>	<i>Sp. viride</i>	<i>Sc. iserti</i>	Grand total
<i>Sp. aurofrenatum</i>	13.3					
<i>Sp. rubripinne</i>		5.0				
<i>Sp. chrysopterum</i>		2.5	1.4			
<i>Sp. viride</i>		5.0		4.3		
<i>Sc. iserti</i>					28.3	
Column total	13.3	12.5	1.4	4.3	28.3	59.9

Counts are standardised to represent 10 fish per species. Columns represent the fish that were followed. Rows represent the fish they interacted with. Boxed areas represent intraspecific interactions.

the next most-common interaction was *Sp. aurofrenatum* chasing the smaller *Sc. iserti* which constituted 12% of interspecific interactions.

Site-specific patterns of aggression differed between species. *Sp. rubripinne* and *Sp. chrysopterum* had the most similar patterns with greatest aggression at site M (Table 3) and lower aggression at sites H and L (Tables 2 and 4). Aggression was greatest at site H for *Sp. aurofrenatum* and *Sc. iserti*, but the pattern differed between sites M and L: similar aggression in the former species and a decline from site M to L in *Sc. iserti*.

Aggression in *Sp. viride* was similar at sites H and M and lower at site L.

A plot of mean intraspecific aggression versus density (Figure 2) reveals an overall positive and moderately strong correlation (Pearson $r = 0.67$, $p = 0.006$). Again, however, the pattern differed between species. Aggression only increased linearly with density in *Sp. aurofrenatum* and Chi-square analysis suggests that differences in density adequately explained patterns of aggression ($\chi^2 = 0.33$, $p > 0.05$). Chi-square analyses of aggression versus density

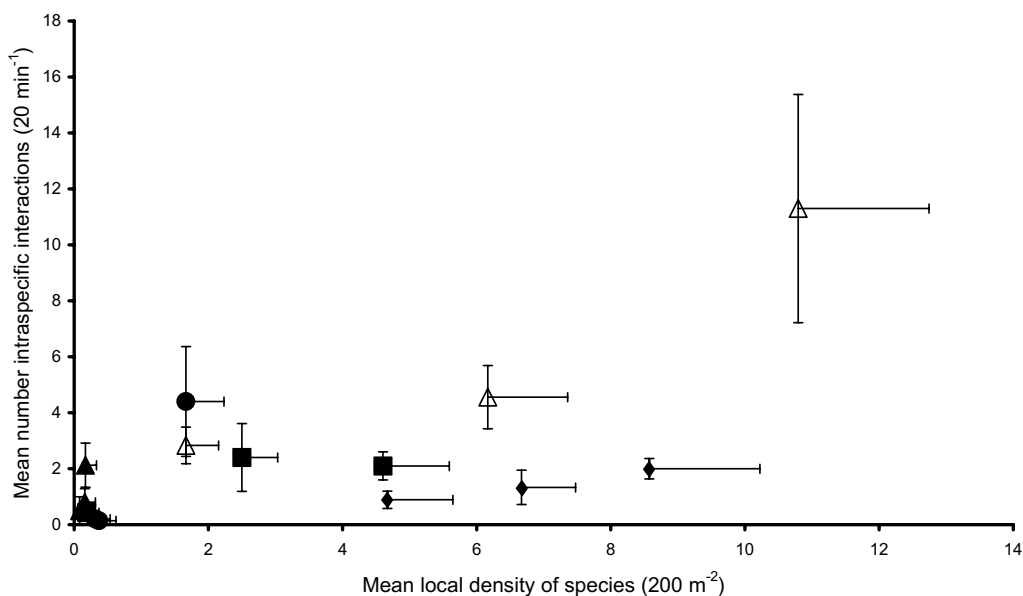


Figure 2. Relationship between intraspecific interactions and intraspecific density. Species represented by Δ = *Sc. iserti*, \blacksquare = *Sp. viride*, \bullet = *Sp. chrysopterus*, \blacktriangle = *Sp. rubripinne*, \blacklozenge = *Sp. aurofrenatum*. Error bars represent standard error.

for the three sites were significant ($p < 0.01$) in all other species indicating non-linear relationships. Minimum aggression occurred where density was lowest. Sharp increases in aggression with increasing density occurred in *Sc. iserti*, *Sp. chrysopterus*, *Sp. rubripinne*, and *Sp. viride*, but aggression reached an asymptote in the latter species. There were insufficient interspecific interactions to conduct Chi-square analyses, but a plot of mean interspecific interactions versus local density of interacting species (excluding intraspecifics) suggested that no simple relationships existed (Figure 3a). However, for *Sp. chrysopterus* and *Sp. rubripinne*, which had the most frequent interspecific interactions, the total number of aggressive encounters were positively related to the pooled density of both species (Figure 3b). Chi-square analyses suggested that observed aggression at site M was significantly greater than that expected from the relatively high density of these species at this site ($p < 0.05$).

Territory size

All five species formed territories at the depths surveyed (Figure 4). Territory size was smallest in *Sc. iserti* (mean areas 41, 49 and 120 m² at sites H, M, L respectively) and largest in *Sp. rubripinne* (330, 168, 1400 m²) except at site M where *Sp. chrysopterus* territories

were larger (324 m²). Thus, the general sequence of increasing territory size was *Sc. iserti*, *Sp. aurofrenatum*, *Sp. viride*, *Sp. chrysopterus*, and *Sp. rubripinne* (Figure 5).

Across species, territory size was moderately correlated with biomass at each site (Pearson correlations, r , for sites H, M, L were 0.55 ($p = < 0.005$), 0.45 ($p = 0.005$), 0.45 ($p = 0.02$)). However, when biomass was added as a covariate in a two-way crossed ANOVA with site and species, it proved non-significant (Table 5). Therefore, whilst larger fish tend to have larger territories, this is a species-specific effect and biomass *per se* may not be the cause. Site, species, and their interaction exerted significant effects on territory size regardless of whether biomass was added as a covariate. Species explained the greatest proportion of variance (72.4%) followed by species/site interactions (16.2%). Thus, interspecific variation in territory size differed between sites.

Analysis of pairwise multiple comparisons (not shown, but see Figure 4) revealed that only *Sc. iserti* exhibited significant differences in territory size between sites H and M. Three species (*Sp. aurofrenatum*, *Sp. rubripinne*, and *Sc. iserti*) had significantly larger territories at site L than either of the higher rugosity sites ($p < 0.001$). *Sp. viride* territories were significantly different between the extremes of sites H

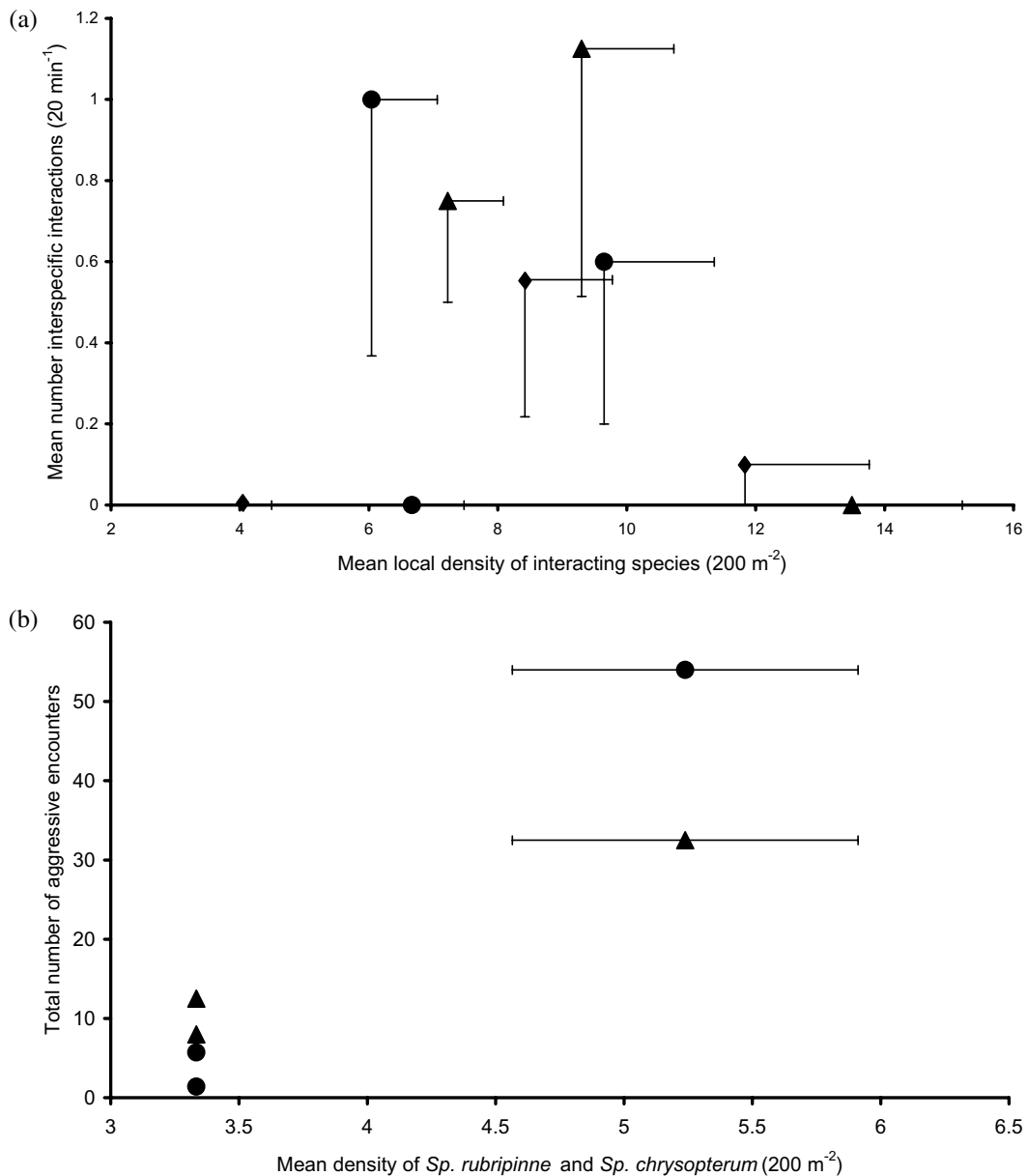


Figure 3. Interspecific aggressive interactions. a – Mean number of interspecific interactions versus mean local density of interacting heterospecific species. *Sp. viride* and *Sc. iserti* not shown because focal individuals only interacted with intraspecifics. Heterospecifics for *Sp. chrysopterum* (●) include *Sp. aurofrenatum* and *Sp. rubripinne*, for *Sp. rubripinne* (▲) include *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride*, and for *Sp. aurofrenatum* (◆) include all other species except *Sp. viride*. b – Total number of aggressive encounters in *Sp. rubripinne* (▲) and *Sp. chrysopterum* (●) versus combined density of *Sp. chrysopterum* and *Sp. rubripinne*.

and L, but territory sizes were intermediate (and indistinguishable) at site M. *Sp. chrysopterum* territories did not differ significantly between sites.

Compared to other species, *Sp. viride* had intermediate-sized territories (Figure 4) and the

greatest overlap in territory size with other species. Territory size was indistinguishable between *Sp. viride* and *Sp. aurofrenatum* at all sites. *Sc. iserti* territories increased in size from sites H to M to L and were indistinguishable in size to those of *Sp. viride* at

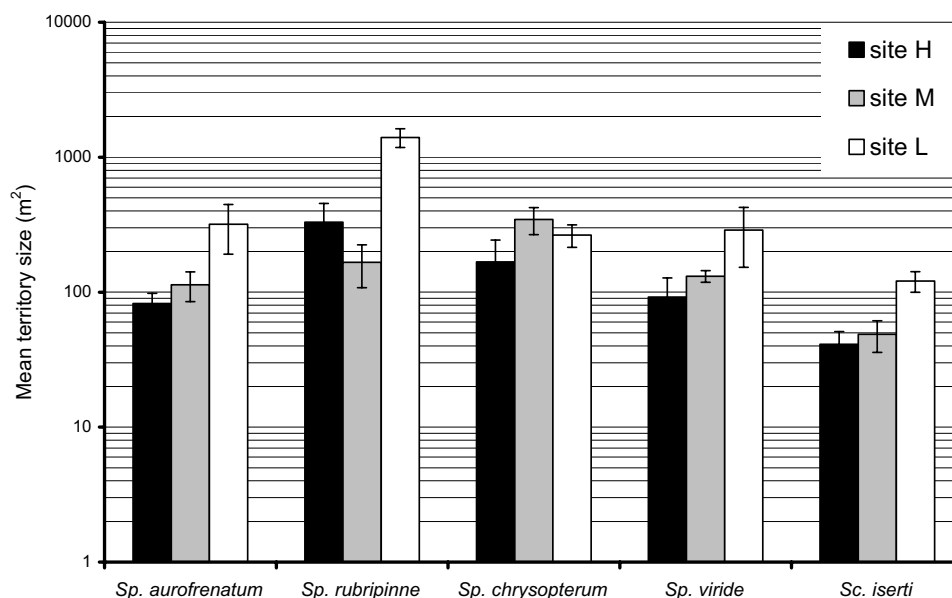


Figure 4. The effects of site and species on mean territory size. Error bars denote 95% confidence interval. Note logarithmic y-axis.

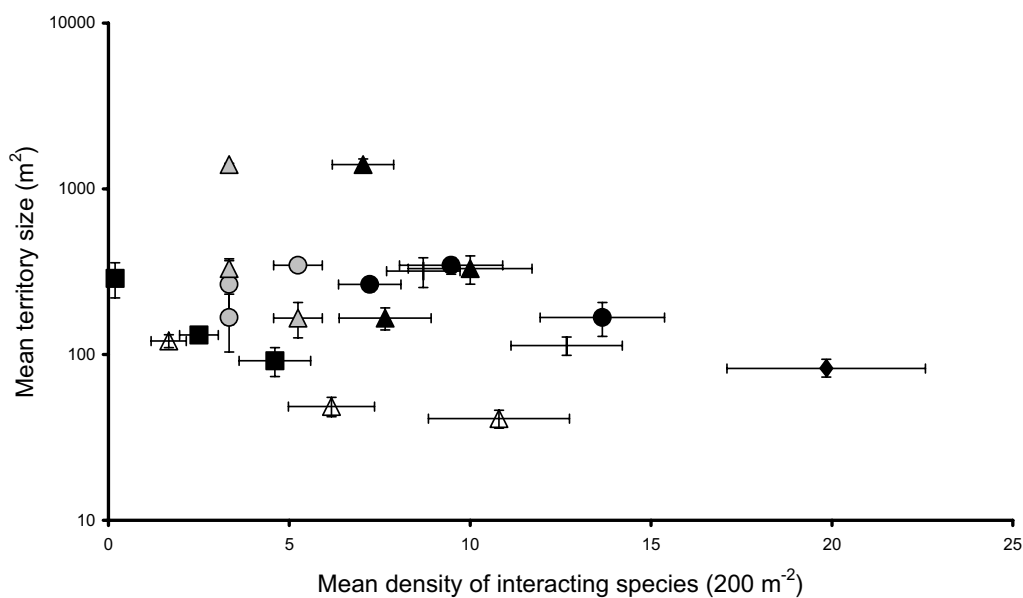


Figure 5. Overall effect of density of interacting species on territory size. Interacting species were intraspecifics for *Sp. viride* (■) and *Sc. iserti* (Δ). Intraspecifics and the following heterospecifics were included: *Sp. aurofrenatum* and *Sp. rubripinne* for *Sp. chrysopterum* (●), *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride* for *Sp. rubripinne* (▲) and all other species except *Sp. viride* for *Sp. aurofrenatum* (○). Shaded symbols represent combined density of *Sp. chrysopterum* and *Sp. rubripinne*.

site L because the latter species' territories showed less variation between sites. *Sp. rubripinne* and *Sp. chrysopterum* had similar-sized territories at the higher rugosity sites H and M but not at site L where

only *Sp. rubripinne* exhibited larger territories at the low rugosity, low density site.

Territory size in *Sp. viride*, *Sc. iserti*, *Sp. aurofrenatum*, and *Sp. chrysopterum* was inversely related

Table 5. Output of two-way crossed ANOVA on territory size with sites and species as factors.

	df	Seq SS	Adj SS	Adj MS	F	p	% var
Biomass (covariate)	1	18.20	0.05	0.05	0.32	0.574	
Site	2	24.75	20.27	10.13	56.91	0.000	5.1
Species	4	17.06	20.20	5.05	28.36	0.000	72.4
Site × species	8	8.71	8.71	1.08	6.11	0.000	16.2
Error	88	15.67	15.67	0.17			6.3
Total	103	84.41					

Parrotfish biomass was added as a covariate. The variance components (% var) are given for the case in which biomass was *excluded*.

Table 6. Output of two-way crossed ANOVA on harem size with sites and species as factors.

	df	Seq SS	Adj SS	Adj MS	F	p	% var
Site	2	29.0	20.8	10.4	10.8	0.000	43.5
Species	4	79.2	68.3	17.1	17.6	0.000	44.5
Site × species	8	31.9	31.9	3.9	4.1	0.000	9.5
Error	68	65.9	65.9	0.9			2.5
Total	82	206.1					

to the total density of interacting species, which, for the former two species, only comprised intraspecifics (Figure 5, see columns in Tables 2–4 for interacting species). A similar inverse relationship was found for *Sp. rubripinne* when only *Sp. chrysopteron* was included as an interspecific interactor.

Harem size

Overall, harem size significantly differed between sites and species and there was a small, but significant, interaction term (Table 6). Harem size did not vary significantly between sites in *Sp. rubripinne* and *Sp. chrysopteron* (Figure 6, multiple comparisons not significant). The remaining species, *Sp. aurofrenatum*, *Sp. viride*, and *Sc. iserti*, had significantly larger harems at site L than sites H and M (Figure 6, significance of Sidak multiple comparisons $p = 0.0018$, $p = 0.043$, $p = 0.002$ respectively). Harem size was also greater at site M than site H in *Sc. iserti* ($p = 0.001$). Further, harem and territory sizes were positively, moderately, and significantly correlated in *Sp. aurofrenatum*, *Sp. viride*, and *Sc. iserti* ($r = 0.63$, $p = 0.003$; $r = 0.45$, $p = 0.043$; $r = 0.52$, $p = 0.048$ respectively).

Where the local density of a species differed between sites (i.e. excluding *Sp. chrysopteron*), Chi-square analyses suggested that density and harem size were not

linearly related (null hypothesis rejected, $p < 0.001$, in each case). Where *Sp. viride* occurred at relatively low densities (site L, < 1 fish 200 m^{-2}), harem size was significantly greater than elsewhere (Figures 6 and 7). For comparative purposes, the data of van Rooij et al. (1996b) for *Sp. viride* in Bonaire are also plotted in Figure 7. The values of harem size were derived from the ratio of initial phase (IP) to TP fish (where IPs are sexually mature but not in terminal phase) and as the authors' point out, harem size was probably overestimated at the higher values (due to the presence of IP males) and underestimated at the lower values (due to the presence of group TPs). Estimates of density in the present study were from deeper parts of the reef (dominated by territoriality), whereas the van Rooij et al. (1996b) study encompassed a wider depth range. Given that the data from Bonaire should probably have a reduced range on both abscissa, the agreement with the current study is good. A similar inverse relationship between harem size and density was observed for *Sc. iserti* but not in *Sp. aurofrenatum* or *Sp. rubripinne* in this study.

Discussion

All of the species studied formed territories at all sites. Mean territory sizes of *Sp. aurofrenatum* at sites H and L (82 and 319 m^2 respectively) were similar to those recorded at Puerto Rico (88 m^2 , Clavijo 1982), Barbados (142–215 m^2 , Dubin 1981), and Florida (240 m^2 , Muñoz 1996). Territory sizes of *Sp. viride* were, however, smaller than those reported in Bonaire (91–289 m^2 in present study versus 300–529 m^2 in van Rooij et al. 1996b). Whether such geographic differences in territory size extend elsewhere is unknown. The territories of *Sc. iserti* in the present study (mid to deep forereef) were approximately four times larger

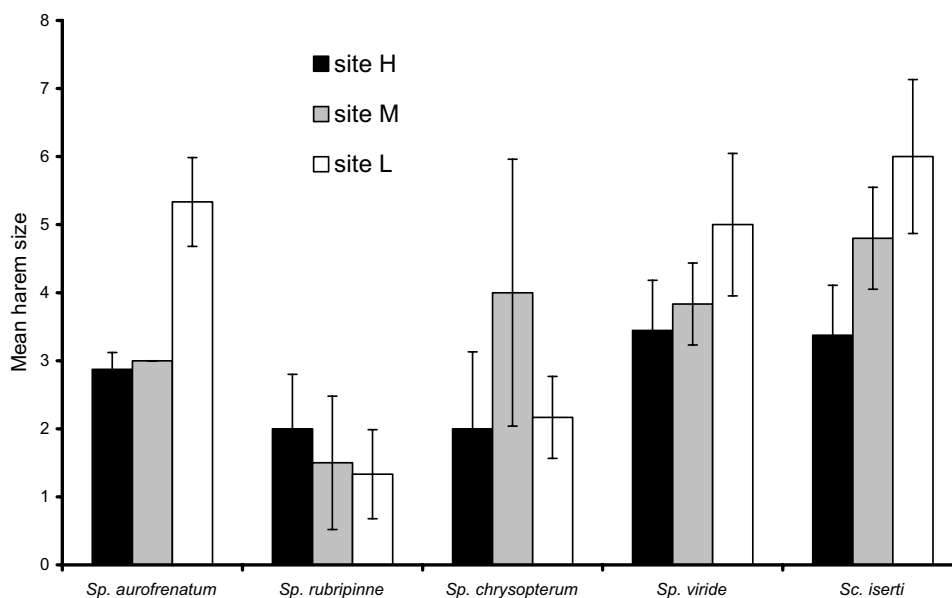


Figure 6. The effects of site and species on mean harem size. Error bars denote 95% confidence interval.

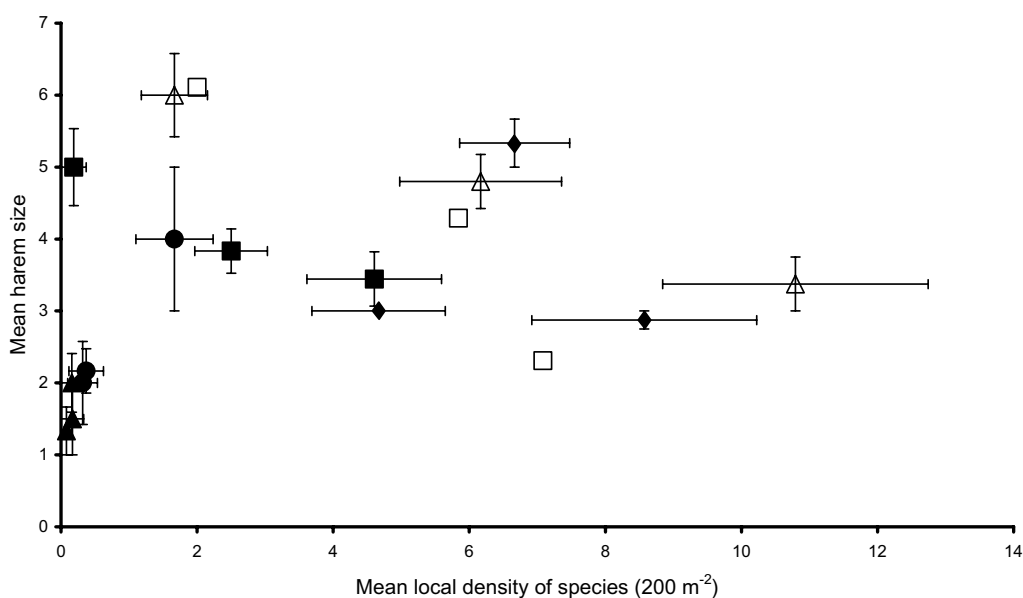


Figure 7. The effect of local density on the harem size of parrotfish species represented by Δ = *Sc. iserti*, \blacksquare = *Sp. viride*, \bullet = *Sp. chrysopteron*, \blacktriangle = *Sp. rubripinne*, \blacklozenge = *Sp. aurofrenatum*. Data for *Sp. viride* from van Rooij et al. (1996b) are superimposed as (\square). Error bars denote standard errors.

than those reported from shallow patch reefs in Panama (Buckman & Ogden 1973). Given that *Sc. iserti* density is usually greatest in shallow water and that density has a strong effect on territory size, this difference is not

surprising. For example, total *Sc. iserti* density at site H was 48 per 200 m² (SE 5.6) in shallow (4–5 m) water which was nearly double than in deeper water where the present study was conducted (27 per 200 m² SE 2.4).

The reasons for higher density in shallow water are not clear but probably involve greater algal productivity and topographic relief (shelter) in shallow areas and/or reduced exposure to predators which favour deeper areas (Lewis & Wainright 1985).

Previous studies of parrotfish (e.g. van Rooij et al. 1996b, Tolimieri 1998) have suggested that rugosity and fish density are strongly positively correlated. The correlation probably exists because high rugosity sites provide better shelter for juveniles (i.e. enhancing post-settlement survival) and greater food availability (and possibly shelter) for adults. In the present study, only *Sc. iserti* showed tight correlations with rugosity. Given the small size of this species (33 g, Table 1), such correlation of density and rugosity might arise from a greater vulnerability to predation and therefore requirement for shelter. Furthermore, this species may favour high rugosity sites where food density is greater because it has a small foraging range (personal observation). In contrast, *Sp. chrysopterum* and *Sp. rubripinne* have large territories and their density appears to be unrelated to substrate rugosity (although the high abundance of gorgonians at site L may constitute high rugosity). The preference of *Sp. chrysopterum* for site M is not understood.

All species except *Sp. chrysopterum* exhibited significantly larger territories where population density was low at site L as suggested by territory theory (note that the density of *Sp. rubripinne* was particularly low at site L conferring very low statistical power, 10%, of detecting significant differences between sites). In each case, the inverse relationship between territory size and the density of interacting species (conspecifics plus relevant heterospecifics) appears to follow an exponential decay. In other words, territory size appears to decrease rapidly with increasing density of competitors. Further observations are required to confirm the precise shape of this relationship.

Patterns of harem size fell into two species groupings. In the first group, harem size in *Sc. iserti*, *Sp. viride*, and *Sp. aurofrenatum* exhibited the expected positive correlation with territory size. In the second group (*Sp. rubripinne* and *Sp. chrysopterum*), harem size was generally smaller and showed no clear spatial pattern. These latter species had low population densities and large territories and it is conceivable that a positive relationship between harem and territory size may not exist if spatial resources are not sufficiently limiting. In contrast, however, the overt aggression directed at *Sp. chrysopterum* by *Sp. rubripinne*

suggests that territorial behaviour has at least some non-reproductive origin and may therefore be associated with either food or shelter. Further, it is feasible that at such low population densities, it is economically feasible for *Sp. rubripinne* to defend against intraspecifics and *Sp. chrysopterum*. Further studies into resource utilisation by the two species will provide greater insight. For example, we hypothesise that interspecific competition between *Sp. rubripinne* and *Sp. chrysopterum* might arise because resource partitioning between these species is relatively limited. This hypothesis will be tested by comparing the feeding preferences between species.

Observations that *Sp. viride* and *Sc. iserti* direct aggression only towards intraspecifics (van Rooij et al. 1996a,c, Buckman & Ogden 1973) were confirmed in the present study at all three sites and densities. The absolute frequency of intraspecific interactions was, however, density dependent although more strongly in *Sc. iserti*. Such a strong density-dependent relationship may result from relatively high levels of intraspecific competition in *Sc. iserti* brought about by a high ratio of population density to territory size (0.26 versus 0.10, 0.05, and <0.001 in *Sp. aurofrenatum*, *Sp. viride*, and the remaining species respectively).

Interspecific interactions were recorded whilst following *Sp. chrysopterum*, *Sp. rubripinne*, and, to a lesser extent, *Sp. aurofrenatum*. At site H, where overall parrotfish density was greatest, the overall ratio of intraspecific to interspecific interactions was significantly greater than at sites M and L (analysis of Tau coefficient). Thus, a meta analysis of interactions suggests that intraspecific interactions were most common where overall density was greatest and that interspecific interactions occurred more often at lower densities. Whilst this relationship was not linear, it suggests that the economic defensibility of territories is largely confined to intraspecifics where density is greatest. The empirical data from *Sp. aurofrenatum* and *Sp. rubripinne* support this contention in that intraspecific aggression dominated at site H and interspecific aggression was most prevalent at the sites of lowest intraspecific density (sites M and L respectively). Unfortunately, species- and site-level statistical analyses of ratios cannot be undertaken because the total number of interspecific interactions was too low.

At the scale of parrotfish communities, intraspecific aggression dominates (84–97%) overt species interactions. However, the direction of interspecific relationships were highly asymmetric in that all

Sp. rubripinne/Sp. chrysopterum and *Sp. aurofrenatum/Sc. iserti* interactions were elicited by the former, larger species (t-tests of species' biomass, $p < 0.0001$). Why such species interact is unclear although the success of the larger species is not surprising (Davies & Houston 1984). Interspecific interactions do occur between some parrotfish species which suggests at least partial defence of non-reproductive resources and therefore future studies will examine whether some species (e.g. *Sp. viride* and *Sp. aurofrenatum*) evade interspecific aggression by mutual avoidance. Avoidance does not occur at the scale of territories because these overlap between all species (GIS interpretation, not shown). However, whilst individual TP males often swam around their territory several times during a 20 min observation period, feeding was confined to a small area of the territory during any given observation. Repeated observations of the same fish suggested that feeding sites differed throughout the day (personal observation, also noted by van Rooij et al. 1996c). Alternatively, interspecific aggression may be avoided by resource partitioning. Although feeding modes differ between parrotfish genera (Bellwood & Choat 1990), the degree of partitioning within genera is unclear. van Rooij et al. (1996a) found much overlap in substrate use between scarids whereas studies of parrotfishes on lagoonal patch reefs in Panama revealed significant partitioning among species (McAfee & Morgan 1996). Future work will examine resource use on forereefs.

Parrotfish usually dominate the biomass of herbivorous reef fish (Choat & Bellwood 1985, Horn 1989, Bruggemann et al. 1994a, van Rooij et al. 1996a) and, given the continued low abundance of the urchin *Diadema antillarum* on many Caribbean reefs (Lessios 1995), they dominate the entire herbivore guild in many parts of the region (Lewis & Wainwright 1985, Carpenter 1986, Lewis 1986, Morrison 1988). Not surprisingly, parrotfish may exert a profound effect on algal species distribution (Lewis 1986), phenotypic form (Lewis et al. 1987), diversity, and biomass (Brock 1979). Whilst parrotfish undoubtedly perform important functions on coral reefs, the vast majority of parrotfish biology has been derived from studies of *Sc. iserti* and *Sp. viride*. Overall, these species behave similarly and fairly predictably with respect to site rugosity and population density. Social behaviour in *Sp. chrysopterum* and *Sp. rubripinne*, and, to a lesser extent, *Sp. aurofrenatum* differs to that of *Sc. iserti* and *Sp. viride*. Thus, although feeding modes (scrapers

and excavators) have been categorised for parrotfish genera (Bellwood & Choat 1990), the overall ecological functions of parrotfish such as bioerosion and grazing of algal communities, which are affected by population density and social structure, cannot be categorised by genus. Similarly, the response of parrotfish to changes in resource availability (e.g. increased macroalgal cover following coral mortality) is likely to differ between species. Therefore attempts to model distribution and functions of parrotfish in reef systems may need a species-specific focus.

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