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The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups

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Synopsis

We present a detailed description of the social and mating system of the protogynous reef herbivore *Sparisoma viride* at the fringing reef of Bonaire (Netherlands Antilles). Initial phase (IP) fish and terminal phase (TP) males occur either in one- or in multi-male groups, which are compared quantitatively with respect to the use of space, size composition, social interactions and sexual activity. One-male groups consist of one TP male plus 1–14 IP females, whereas in multi-male groups up to 14 TP males and about twice as many IP fish share a common home range. The two social units further show marked differences in vertical distribution (one-male groups are restricted to depths between 3 and 22 m, multi-male groups mainly residing < 3 m), size composition (a larger proportion of small adults live in multi-male groups), size and stability of the range (larger in one-male groups) and sexual activity (daily spawning of one-male group members inside their normal home range; no activity in multi-male groups on the shallow reef). Sexual activity occurred daily, throughout the year, with no evidence for tidal tracking or major seasonal or lunar patterns. The one-male groups constitute less than 20% of the adult stock but control up to 77% of the inhabited reef. As a result they have access to higher-yield food patches and to suitable spawning sites inside their home range. Although members of both units appear to defend their common home range against intruding conspecifics, the degree of territoriality is clearly higher in one-male groups. We discuss the relative importance of food, shelter, mates and mating sites as defended resources and some life history implications. The complex social and mating system of *S. viride* shows much resemblance to that of another Caribbean scarid, *Scarus iserti*. This complexity seems to reflect the capacity of individuals to flexibly adapt their feeding, mating and life history styles to an unpredictable environment. We propose that *S. viride* is a good study animal to test adaptive explanations for its territorial organization and complex life history patterns.

Introduction

The social systems of parrotfish (Scaridae) are highly complex due to the occurrence of protogynous hermaphroditism, sexual dichromatism, alternative life history and mating styles, and considerable spatial variability (Choat & Robertson 1975, Robertson & Warner 1978, Thresher 1984, Shapiro 1991, Warner 1991). This complexity is well documented for a San Blas population of the striped parrotfish, *Scarus iserti* (= *S. croicensis*), in which three behavioural categories have been distinguished: territorial fish, stationary groups, and foraging schools (Ogden & Buckman 1973). Territories are shared by a single male and a number of females, are only defended against conspecifics, and appear to serve the dual function of feeding and spawning areas. All fish begin their life in stationary groups or foraging schools, between which they can move freely. Females move into territories while still small, but rejoin a foraging school or stationary group at the initiation of sex and colour change. Only the larger TP males become territorial again and attain relatively high reproductive success, pair spawning both with females from their own territory and with other females. Fish in foraging schools use a swamping technique to overcome the territorial defence of conspecifics and damselfish, allowing them to exploit the defended algal food (Buckman & Ogden 1973, Robertson et al. 1976, Warner & Downs 1977, Robertson & Warner 1978, Clifton 1989). *S. iserti* is diandric (sensu Warner & Robertson 1978), sex-changed TP males coexisting with gonochoristic males.

Much less is known about the social organization of other Caribbean parrotfish. As part of a larger project, addressing the trophodynamic role of one of the more common and larger (up to 40 cm) herbivores on the coral reef of Bonaire, we studied the social and mating system of the stoplight parrotfish, *Sparisoma viride*. In the course of our field work it became apparent that the social organization and behaviour of this monandric species are highly complex. We started to recognize patterns that suggested adaptive explanations for this complexity, which might explain some of the variability in our quantitative estimates of energy intake and allocation. To fit our data into an adaptive context, we needed basic data on its space use patterns, degree of territoriality, nature of the defended resources, and reproductive activity. The results of two relatively detailed studies at other reefs (Belize, Cardwell 1989, and Grand Turk, Koltes 1993), indicated that the social system of *S. viride* shows some resemblance to that of *Scarus iserti*. In both populations territorial (one-male) groups and non-territorial (multi-male) groups were found to co-occur, spawning appeared to be dominated by territorial males, and a harem-like mating system seemed to prevail, although the behaviour of females was not studied. We recognized the same pattern in our population and suspected that the difference between territorial and non-territorial (briefly: group) fish plays a crucial role in energy intake and allocation patterns.

The objective of this study is to give a detailed description of the social and mating system of the *S. viride* population in our study area. The main question we address is how real the difference between group and territorial fish actually is. To that end, we quantified in detail their: (a) spatial distribution and abundance, (b) size composition and sexual maturity, (c) size and exclusivity of range, (d) stability of range and status, (e) social interactions with conspecifics, and (f) reproductive activity. This study is largely descriptive, aimed at generating rather than testing adaptive hypotheses for the intraspecifc variability in behavioural traits. We will discuss the role of food, shelter and mating sites in explaining the differences between the two social units, as well as some life history implications.

Materials and methods

Study animal

Sparisoma viride is a daytime feeder, spending most of its active time grazing on dead coral substrates. It scrapes epilithic, crustose and endolithic algae from the carbonate substrates with its fused, beak-like jaw. Food selection, intake and absorption at our study site have been described in detail by Bruggemann et al. (1994a, b), while data on its growth are provided by van Rooij et al. (1995a).

Aspects of the life history of *S. viride* have been studied by Reinboth (1968), Robertson & Warner (1978), and Cardwell (1989). Three life phases are distinguished: juveniles (JU), initial phase (IP) and terminal phase (TP) adults. Fish in the IP colour pattern have a mottled brown body with white scales and red hues on belly and fins. TP males are more striking with an emerald green body, yellow spots on the opercula and the base of the tail, and purple or blue fin margins. The JU pattern resembles that of IP fish. After a pelagic larval period, JU settle on the reef as immature females. Sex and colour change may occur over a wide size range and are not necessarily coupled. As a result, some IP fish may be male although most (> 90% in all populations studied so far) are female, whereas TP fish are always male. The predominant mode of spawning is pair spawning of TP males with IP females. 'Streaking' (rushing in to join at the climax of a spawning pair) has been observed incidentally and is the mating style of IP males. From the low incidence of streaking (0.3% of 1110 observed matings) compared to that at another Bonaire location (14.1% of 71 matings), van Rooij et al. (1996b) inferred that IP males must be rare in our present study area. Eggs are released directly in the water column and inseminated externally without subsequent parental care.

General setting

The study was conducted on the fringing reef off Karpata ecological centre, on the leeward coast of Bonaire, Netherlands Antilles (12°13'N, 68°21'W), between April 1987 and November 1990. The entire reef of Bonaire is a marine park, where spearfishing has been banned since 1971 and anchoring since 1979. Fishing pressure on parrotfish is negligible and they can be observed at close range, using SCUBA or snorkel gear.

Records were made of the behaviour and movements of individually recognized and measured fish (3 JU, 40 IP and 45 TP), at time scales ranging from minutes to years, in a 100 m wide reef strip extending from the coast to 25 m depth (further referred to as the study area, encompassing 10 940 m^2).

Vertical distribution and abundance were quantified by visual censuses in 15 m wide quadrats, covering all five distinguished reef zones along the reef profile (see van Rooij et al. 1996a for description zones plus position quadrats).

The total effort exceeds 1575 h underwater observation, all year round and covering every part of the day. Permanent markers at 20 m intervals demarcated the 3.5, 7 and 16 m isobaths inside the study area to facilitate underwater orientation.

Recognition, measurement and capture of fish

TP individuals could be identified by the pattern of the yellow tail and opercular spots. IP fish could not be distinguished by natural markings and were tagged with nylon anchor tags in the dorsal musculature (Floy Manufacturing Company, Seattle, FD-67 or FD-67F tags, applied with a Mark II SS gun), which caused no visible injury. Most tags remained in position for 1–12 months. Adult fish were caught at night, using handnets and anaesthetic (quinaldine), and released early next morning. Their social status and behaviour towards the observer were not affected by this procedure. Fish were measured and tagged in less than 2 min, after anaesthesia in seawater containing 0.1 ml l^{-1} quinaldine. Fork length (FL, length from tip of closed mouth to end of median caudal finray) was measured to the nearest mm. To obtain an indication of sexual maturity, most fish were routinely checked for the presence of eggs or milt by gently squeezing the abdominal area. This was done the next morning, around the time of the daily spawning period. Between January 1989 and September 1990 the length of free-swimming territorial males was measured using stereo photography (accuracy ± 1 cm, van Rooij & Videler 1996) to minimize the level of disturbance.

To study group composition, two attempts were undertaken (in February and May 1990) to capture all adult *S. viride* from a part of the study area (referred to as the SE area, see Fig. 2) in the daytime by encirclement with a seine net (84 m long, 10 m deep, 5 cm stretched mesh). Fish caught this way were quite shy to divers the first few days after release but could be approached again after one or two weeks.

Use of space

Territorial (TTP) males

Approximate territory borders of TTP males were established by mapping the most distant grazing sites and the locations where conflicts with neighbouring males were observed. Unless a border followed some distinct feature in bottom topography (e.g. a spur or groove), straight lines were drawn through the most extreme locations. The borders were confirmed by checking the positions of the fish on successive sightings (2432 in total). Territories were coded according to their approximate depth range (roman numerals: II: 3–6 m, III: 6–10 m, IV: 10–22 m) and sequence along the isobaths (arabic numerals). Areas were measured from the map using a digitizing tablet. Throughout the study all mapped territories were checked at least monthly, but usually weekly, for the presence or a change of owners. A TTP male was considered to have left its territory if it was not found on three consecutive days or when consistently located somewhere else. The number of IP fish that were consistently present in each territory and not chased by the TTP males was counted five times (on separate days) in September 1988.

Group (GTP) males

Abundance and mobility of GTP males turned out to be too high to maintain a permanent record of all GTP in the study area. Therefore, the tailspot patterns of all TP males in a part of the study area (the SE area, encompassing 2400 m^2) were recorded between October 1989 and January 1990. All recognized GTP males were followed as long as they resided in the SE area. Until May 1990 the total number of TP fish (including males of unknown identity) residing in the SE area was counted weekly.

IP fish

Tagged IP fish, caught at night, were followed after their release the next morning to determine the location of their home range. At regular (usually weekly) intervals the entire study area (plus adjacent parts) was searched to check their presence, location and social status. IP fish residing in one-male groups will be referred to as territorial (TIP) and those in multi-male groups as group (GIP) fish (see Table 1 for a list of abbreviations). Some IP fish could still be recognized after tag loss and were provided with a new tag.

Size of foraging ranges

The extent of individual movement was quantified for fish in the SE area by mapping the range covered by a fish during three separate 15 min observation periods. These 15 min ranges were determined by marking the extreme positions of the grazing sites visited by a fish that was followed at a distance of about 4 m (after a 5 min habituation period). The positions were drawn on a scaled map and the areas of the resulting polygons were measured using a digitizing tablet. A pilot study indicated that the area covered by individuals after 15 min was ≥ 90% of that obtained after 60 min observation. However, there appeared to be shifts in the area of grazing activity in the course of a day. Therefore, individual 15 min ranges were determined in each of three daily periods (9:00–11:30, 11:30–14:00 and 14:00–16:00 h) within the same week. We defined the combined area of the three 15 min ranges (sum of the areas

Table 1. List of used abbreviations and symbols.

A15	Area of 15-min range
FL	Fork length
IP	Initial phase
TP	Terminal phase
JU	Juvenile
GIP	Group IP
GTP	Group TP
TIP	Territorial IP
TTP	Territorial TP
?TP	TP of unknown social status
?IP	IP of unknown social status
MRT	Minimum residence time
NrIP	Mean number of IP fish tolerated inside a territory
% Sol	Percentage time that a territory is occupied by solitary (territorial) TP males
TkOv	Number of territory takeovers, converted to 3 year observation period
SpD	Spawnings per day; established by observation throughout the daily spawning period
Sp90	Spawnings per 90 min period; weighted average of all observations during spawning periods
Ep90	Excursions to deep spawning site per 90 min period; calculation as Sp90
Depth ranges:	
I	0–3 m
II	3–6 m
III	6–10 m
IV	10–25 m

minus the overlap) of a fish as its foraging range. Foraging ranges of TP males were determined in November 1989 and January 1990 (for all males in the SE area) and in May 1990 (only for males whose ranges had been determined before). The foraging ranges of all tagged IP fish in the SE area were determined in February and May 1990.

Exclusivity of range

Exclusivity of range was quantified by calculating two measures of space overlap for fish in the SE area: for TP males the percentage of their foraging range that was shared with one or more other TP males; for IP fish the proportion of their foraging range shared with the nearest TTP male.

Stability of range and status

Stability of range and status was measured in several ways: (a) Permanent records of presence, location and social status of all individually recognized fish allowed estimates of residence times and duration of social status. The observed residence times are minimum estimates (referred to as MRT), since both arrival and disappearance were witnessed for only a few individuals; (b) In the SE area, shifts in the location of an individual's foraging range could be quantified by measuring the amount of overlap between two successive foraging ranges. Foraging range overlap was expressed as the percentage of the combined area (summed area [ΣA] minus overlap [O]) of both foraging ranges ($100 \times O/[\Sigma A - O]$). As a result, it was not correlated with FL^2 ($r = -0.0301$, $n = 39$, $p = 0.428$) nor with the combined area ($r = -0.121$, $n = 39$, $p = 0.232$) and could be compared independently from fish or range size ; (c) To compare the average stability inside territories three indices were calculated: 1) the proportion of the total observation period that a territory was occupied by a solitary (i.e. territorial) TP male (% Sol), 2) the average MRT of all territorial males that resided in each territory throughout the study, and 3) the number of territory takeovers per 3 years (TkOv, calculated as the observed number of takeovers multiplied by 36 months and divided by the number of months that the territory was monitored). A takeover is defined as either the takeover of a territory by another TP male or by a group of TP males, or a change from group area to territory. Except for the SE area, changes in group composition of TP males inside group areas were not recorded.

Social interactions

Frequency of, and time expenditure on, social interactions were determined by continuous monitoring of the behaviour of focal animals in their natural habitat, using an underwater event recorder. Individually recognized fish were followed several times and on different days for 20–30 min periods (between 9:30 and 17:00 h; after 5 min habituation). A social interaction is defined as the response, other than courtship or spawning, of the focal animal to another fish, resulting in termination of the previous behaviour. We distinguished interactions with IP or JU *S. viride* from those with TP conspecifics. Interactions with other herbivores (scarids, pomacentrids and acanthurids) took up less than 1% of the time budget and are treated elsewhere (van Rooij et al. 1996a). To avoid complexity due to observer bias, only the protocols obtained by the first author between February and October 1990 (when considerable experience had been gained) were included in our analyses.

Reproductive activity

The timing of the daily spawning period was first established by two continuous observations from dawn til dusk in December 1987 and confirmed by subsequent observations of sexual activity. Spawning activity was recorded at least once a week from December 1987 to September 1990. The time and location of each spawning plus the identity of the partners were noted. To check for lunar synchronization, the sexual activity in four territories was recorded daily between 15 November and 16 December 1988. Because little was known about the tides on Bonaire, we installed two tidal gauges (one at the 'Salt pier' of the AKZO Solar Salt plant, 15 km south of our study site, the other at the 'Bopec pier' of an oil terminal, 3 km west of Karpata) and obtained continuous registrations between December 1988 (Salt pier) or December 1989 (Bopec pier) and September 1990. Furthermore, to get an idea of the current regime, 8 pilot measurements were carried out from the same two piers (water depth 8 and 35 m respectively) and from a raft, anchored above the drop off zone in our study area (depth 15 m). We used a mechanical flow velocity meter (torpedo type 'Ott C 31') to obtain 24 h depth profiles at different phases of the tidal cycle.

Two measures were obtained to estimate the reproductive activity of individuals. The first is the daily number of matings (SpD). It was determined by counting all matings of a single individual that was observed continuously throughout a spawning period. The fish was followed from 15 min before the expected start until at least 15 min after the last observed sexual activity of group members or conspecifics in adjacent home ranges. The second measure, spawning rate (Sp90), is based on all observed matings of an individual. It is calculated as the total number of matings per min observation time during spawning periods, and multiplied by the maximum duration of the spawning period (90 min). This provides an estimate of the average daily number of matings of individuals, including fish that were never followed throughout an entire spawning period. SpD was determined for a limited number of individuals, whereas Sp90 rates were obtained for most fish of known identity in the study area. Average rates for categories were calculated by weighting the rates of individual fish for the observation times on which they were based.

Sparisoma viride *abundance*

Three 15 × 15 m quadrats (extending from 2–4, 6–12 and 12–22 m depth) and two 15 × 10 m quadrats (extending from 0–2 and from 4–6 m depth) were roped off between 0 and 22 m depth. Each quadrat was subdivided in 5 × 5 m squares and represented a reef zone. A total of 26 counts were performed (3 in February, 4 in June, September and December 1989, 4 in March and June 1990, 3 in January 1992). No significant temporal variation in adult distribution or density was detected. Temporal variations in juvenile density and in adult size composition did occur and are treated elsewhere (Bruggemann et al. 1995, J.M. van Rooij & J.J. Videler unpublished data). Here we will only use the averages of all counts.

Fish were counted in 5 cm FL classes, except for the smallest juveniles that were divided in a 0–2 and a 2–5 cm class. All counts were performed between 9:30 and 17:00 h, outside the daily spawning period and dusk migrations. Further details on the census procedure are given in van Rooij et al. (1996b).

Densities (number ha^{-1}) were calculated for the five reef zones separately. Average density of the entire stock (referred to as the 0–20 m average) was calculated as the average of the five zones, weighted for the width of each zone.

Statistical analyses

The three major factors of interest in most comparisons are social status, life/colour phase, and depth at which fish reside, which could be confounded by size effects. Size was taken into account either by sudividing categories in size classes, or by using analysis of covariance (ANCOVA) with size as the covariate. The other three factors were not completely crossed (e.g. not all social categories occurred at all depths), so no 3-way designs could be used to test their effects. Instead, all categories were treated as levels of a single factor (*S. viride* category), which was tested in 1-way designs. In case of replicate measurements on the same individuals, categories were compared using nested designs (individuals nested within categories) or by using only the averages for individuals.

Of several models fitted (including a log-log fit), a linear relation between the size of the 15 min ranges and squared FL yielded the best fit, explaining 55.9% of the variance for IP fish ($n = 40$, $p < 0.001$) and 12.1% when both colour phases were pooled ($n = 156$, p . 0.001). Therefore, relative size of these ranges could be compared by ANCOVA, taking size differences into account. Most IP fish that were caught with the seine net in February 1990 behaved unusually shy towards the observer. In the first 2

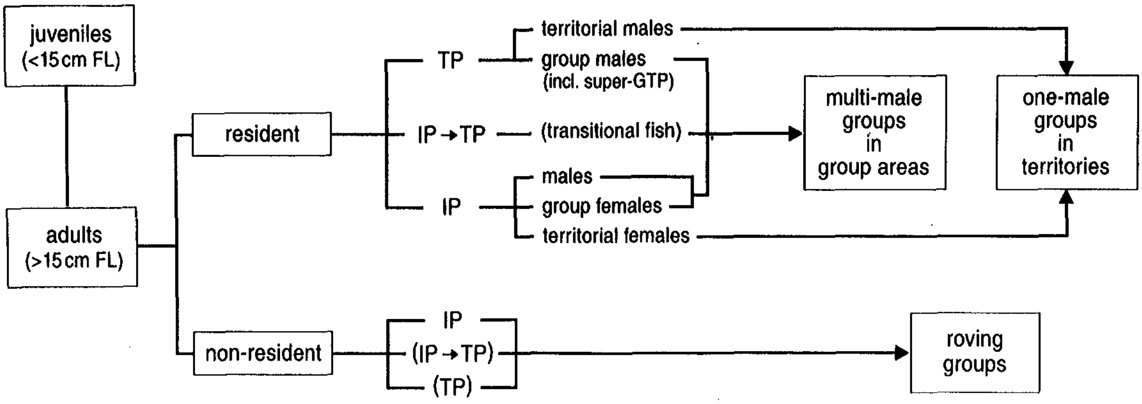

Fig. 1. Schematic overview of the categories that were distinguished in the study area.

weeks following capture and release, their 15 min ranges were much larger than two months later, when they behaved normally again ($F_{1,46} = 8.61$, $p = 0.005$). Such differences were not found for the TP males (who were not caught). Therefore, the data of the shy IP fish that were obtained in February were omitted from all analyses.

Percentages were normalized by angular transformation before applying parametric tests (Sokal & Rohlf 1981). Homogeneity of variance was checked by Cochrans C and Bartlett-Box F tests. Frequency distributions were compared by Pearson χ^2-tests of association, where classes were chosen such that expected frequencies were never less than 1 and in no more than 20% of the cases less than 5 (Sokal & Rohlf 1981). Significance of departure from independence in a cell was judged by comparing the residual with the Bonferroni error rate per comparison (α_{BPC}), using a familywise error rate of 0.05.

Most tests were performed with the computer package SPSS/PC+ (version 4.01). The outcome of a test was considered statistically significant if the 'Type I' error did not exceed 0.05.

Results

General description of the social system

The smallest (IP) fish observed to spawn were estimated to be 15–17 cm long. We therefore defined adult *Sparisoma viride* as fish larger than 15 cm FL. Adults have been categorized (Fig. 1) according to their degree of site attachment (residents vs. non-residents) and colour pattern (IP, TP and transitional). Resident adults are organized in either of two social units: in one-male or in multi-male groups of IP and TP conspecifics sharing a common home range. An obvious characteristic of the TP males in one-male groups is the active defence of their home range against TP conspecifics, throughout the day. These ranges are therefore referred to as territories and the adults residing in them as territorial fish (TTP and TIP), as opposed to the group fish (GTP and GIP) in multi-male groups that reside inside group areas (see Table 1 for abbreviations).

All IP and TP fish that were individually recognized in our study area showed strong site attachment and were categorized as resident fish. They spent most of the day inside their home range, which they only left to sleep or to spawn at a deep spawning site (see below). Adult fish always slept at relatively sheltered sites between 6 and 16 m depth. Individuals were repeatedly found to use the same sleeping site and were never seen in a mucous cocoon (unlike some *Scarus vetula*, *S. iserti* and *S. taeniopteris* individuals). Besides resident fish, loosely organized schools of non-resident adults incidentally passed through the study area, alternately swimming and grazing. These fish are considered to represent a third social unit, referred to as roving groups. These groups mainly comprised IP fish but sometimes included a few fish with TP or transition-

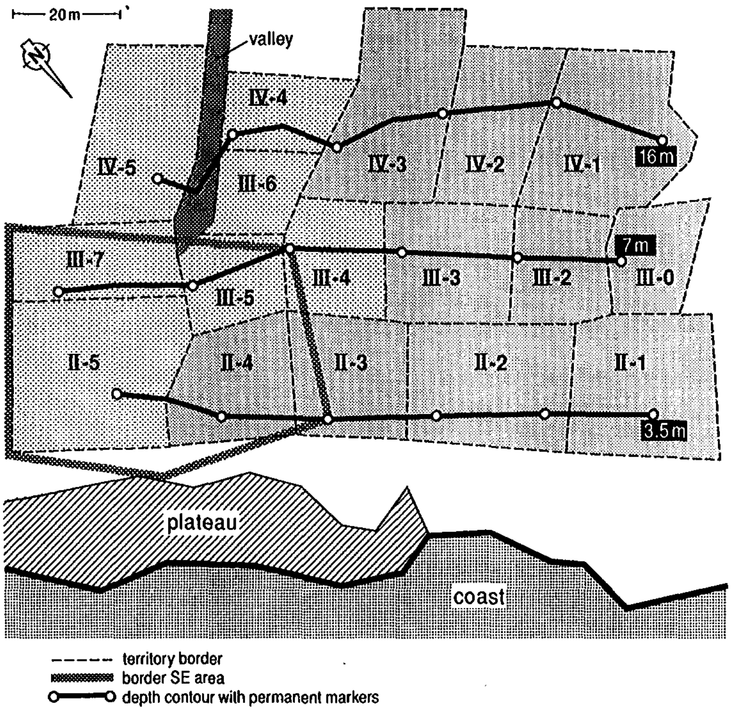

Fig. 2. Map of the study area (aerial view) with territory borders and codes, representing the situation in January 1988. Indicated are the three isobaths with permanent markers (at 20 m intervals), the SE area, an inaccessible shallow (. 0.3 m) plateau formed by dense stands of dead but erect *Acropora palmata*, and a sandy valley near IV–4 that was never occupied by TP fish. Dark shaded territories were permanently occupied by territorial males, while the lightly shaded territories were taken over by group males for some time during the study period. Group fish mainly resided in the shallow reef between the 3.5 m isobath and the coast (including the plateau).

al (IP → TP) colouration. Resident *Sparisoma viride* showed no aggression towards roving groups; some fish briefly joined one while it passed. Because of their rare occurrence, fish in such groups were not further studied.

Juveniles could not be studied in detail because they were difficult to catch and soon lost their tags. However, they showed a marked vertical distribution that deviated from that of adults. Whereas adult density peaked in the 0–2 m quadrat, JU were most abundant between 4 and 12 m depth. Three tagged JU (12–14 cm FL) were observed to freely move between and forage in different territories and group areas. They appeared to be ignored by the resident adults. JU are therefore treated as a separate category.

Adult fish with transitional colour pattern were occasionally observed inside group areas but never in territories. Repeated sightings of these fish indicate that complete transition from IP to TP colouration takes place within 3–5 weeks. Unless stated otherwise, transitional fish were categorized either as GIP or as GTP fish, depending on which pattern dominated.

As stated before, only a small proportion of the IP fish in our study area is assumed to be of male sex, as inferred from the rare occurrence of streaking behaviour. If resident, IP males probably reside inside group areas, since TTP males only seem to tolerate potential mates inside their territory. IP fish that were observed to spawn with a TP male are assumed to be females. The sex of IP fish that were not seen engaged in sexual activity and that did not release gametes upon examination remains unknown.

A few relatively large TP males temporarily defended a spawning site on the deeper (> 30 m) reef during the daily spawning period. Because of their

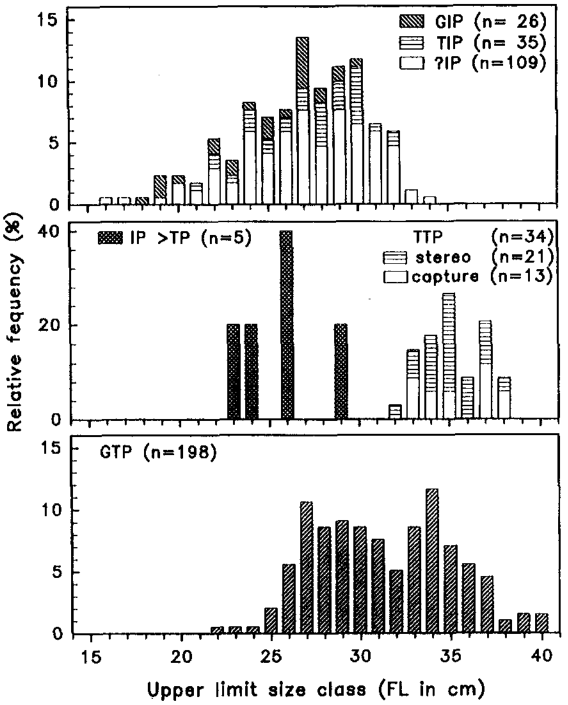

Fig. 3. Size composition of measured fish: initial phase adults (IP; social status indicated), transitionally coloured fish (IP → TP, all from group areas), territorial males (TTP; measuring method indicated) and group males (GTP). n: number of fish measured.

large size and high apparent spawning success they are referred to as 'super-GTP' (see below). However, outside the spawning period these males appear to reside inside group areas. Our observations are too incidental to justify their classification as a separate social category. Therefore, we consider these males to represent a special form of group males.

The results presented below are mainly restricted to resident adults. We will first describe the major characteristics of territorial fish (one-male groups) and then those of (multi-male) group fish before comparing the two social units. To facilitate comparison however, the data for both are summarized in the same figures and tables. Finally, to get more insight in the factors determining reproductive success, we will compare the major characteristics of all studied territories.

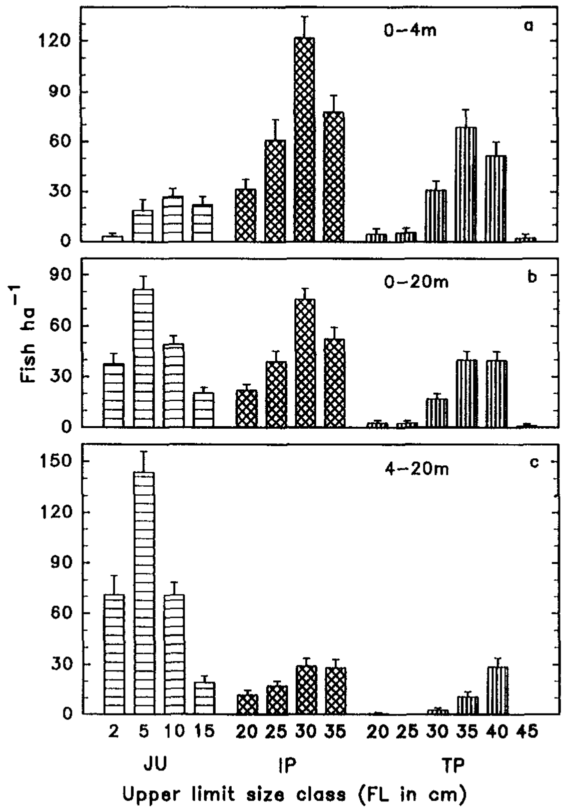

Fig. 4. Size composition of juvenile (JU) and adult life periods as obtained by visual census. Shown are the weighted average density (+ se) of size classes: a – in the shallowest two quadrats, representing the shallow group areas, b – over the entire reef (0–20 m), and c – in the territorial part of the reef (deepest three quadrats).

One-male groups

(a) Spatial distribution and abundance

Territories are restricted to depths > 3 m and, apart from a gap formed by a narrow sandy valley, all appeared to contiguous (Fig. 2). In January 1988, a maximum of 17 territories was found, comprising 77% (8450 m^2) of the entire study area. Territory size ranged from 240 to 820 m^2, the average in depth range III (358 m^2, n = 7) being significantly smaller than that in range II (620 m^2, n = 5) but not deviating significantly from that in range IV (570 m^2, n = 5) (ANCOVA: $F_{2,14}$ = 5.95, p = 0.014, followed by Tukey HSD test). The mean number of IP fish that was consistently counted inside territories (NrIP) varied from less than 1 (in III–50) to 14 (in II–80). On

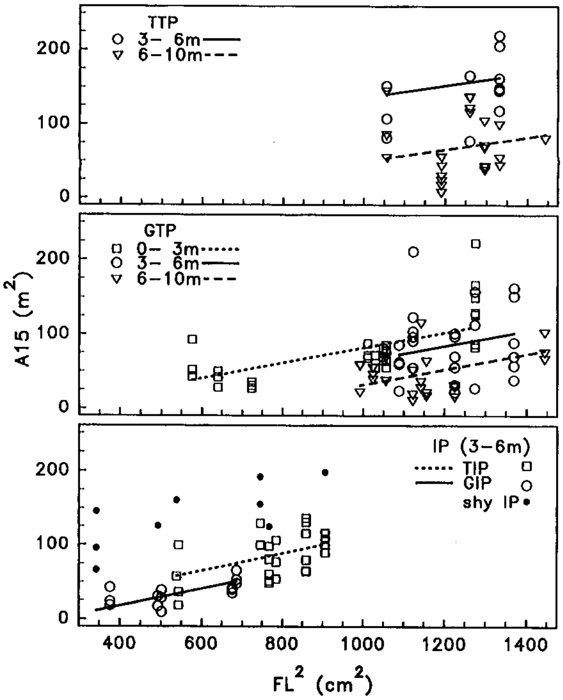

Fig. 5. Area of the 15 min ranges (A15) of group and territorial adults (subdivided according to colour phase and depth range) plotted against squared fork length. Lines in each figure are fitted with the common slope (equality of slopes tests indicating no significant differences). See Table 2 and text for outcome ANCOVA comparisons.

average the NrIP was significantly larger in range II (7.95) than in the other ranges (2.11 in III and 2.80 in IV; Kruskal-Wallis $\chi^2 = 43.8$, $p < 0.001$).

From these figures the average density in the territorial part of the reef can be calculated at 20 TTP and 81 TIP ha^{-1}. The average density obtained from all counts in the three deepest quadrats (between 4 and 22 m depth) amounts to 42.5 TP and 86.6 IP ha^{-1}. The difference between the two TP estimates is explained by invasions of the deeper reef by GTP males. A number of territories (indicated in Figure 2) were temporarily taken over by GTP males. Up to 21 GTP males simultaneously resided in up to 3 former territories, yielding a maximum TP density of 17 TTP and 25 GTP ha^{-1}. When summed, this compares well with the average TP density counted in the deeper (4–22 m) quadrats.

(b) Size composition and sexual maturity

Figure 3 shows the size composition of the adult fish that were actually measured, which do not necessarily represent an unbiased sample of the population. Figure 4 gives the length distribution of JU and adult fish as obtained from the visual censuses, yielding an unbiased sample but less accurate lengths. The measured TTP males ranged from 31.7–37.6 cm and TIP fish from 20.2–31.4 cm FL

Table 2. Outcome ANCOVA's (FL^2 as covariate) testing the effect of period of day, month and depth on A15 of adult categories.

		Category			
Factor		TTP	GTP	TIP	GIP
Multiway ANCOVA					
Period Day	F	0.83	0.05	0.59	1.06
	(df)	(2,21)	(2,53)	(2,19)	(2,7)
	p	0.450	0.955	0.562	0.397
Month	F	0.86	1.17	0.47	3.37
	(df)	(2,21)	(2,53)	(1,19)	(1,7)
	p	0.436	0.318	0.500	0.109
Depth	F	12.6	7.63		
	(df)	(1,21)	(2,53)		
	p	0.002	0.001		
Oneway ANCOVA					
Depth	F	27.85	11.0		
	(df)	(1,35)	(2,74)		
	p	0.000	0.000		

Multiway analyses: TP males = 3-way design including all 3 factors; IP fish = 2-way design testing period of day and month; no significant interaction terms. Oneway analyses: periods of day and months pooled. Abbreviations explained in Table 1.

(Fig. 3). This compares well with the census data, which indicate modal lengths of 30–40 cm for TTP and 20–35 cm for TIP (Fig. 4c; weighted average of the three deepest quadrats). On average the length of measured TTP males tended to decrease with depth (from 35.4 to 34.0 cm; $F_{2,20} = 2.36$, $p = 0.121$). cm FL.

Fifteen out of 23 examined TIP fish (65%) released eggs. These mature females were clearly larger (24.5–31.4 cm) than fish without eggs (22.0–23.2 cm FL). All 8 examined TTP males released milt.

(c) Size and exclusivity of range

The size of the 15 min ranges (further referred to as A15) of TTP males ranged from 8 to 219 m^2 and was not affected by the period of day or the month (Fig. 5a, Table 2). The effect of depth was significant however, A15 in depth range II being larger than in III. A15 of TIP fish (18–137 m^2, Fig. 5c) did not deviate from that of TTP males in the same depth range (ANCOVA, $F_{1,73} = 0.80$, $p = 0.375$). Foraging range size (69–360 m^2 for TTP males and 102–197 m^2 for TIP fish) showed the same trends as A15 (which were not tested because of their direct dependence on A15).

The foraging ranges of 4 TTP males residing in the SE area were mapped 11 times (those mapped in November 1989 are shown in Fig. 6a). In 7 cases there was zero and in 3 cases a small (< 5%) overlap with the ranges of other TP males. One male that had just settled in a former group area showed 19% overlap, which had decreased to zero one month later. Five of the 9 tagged IP fish from the SE area proved to reside inside a single territory (Fig. 6b). Their foraging ranges were mapped 9 times, in 8 of which they showed 80–100% overlap with that of the TTP male. The smallest overlap (64%) was found for the smallest IP fish (23 cm FL).

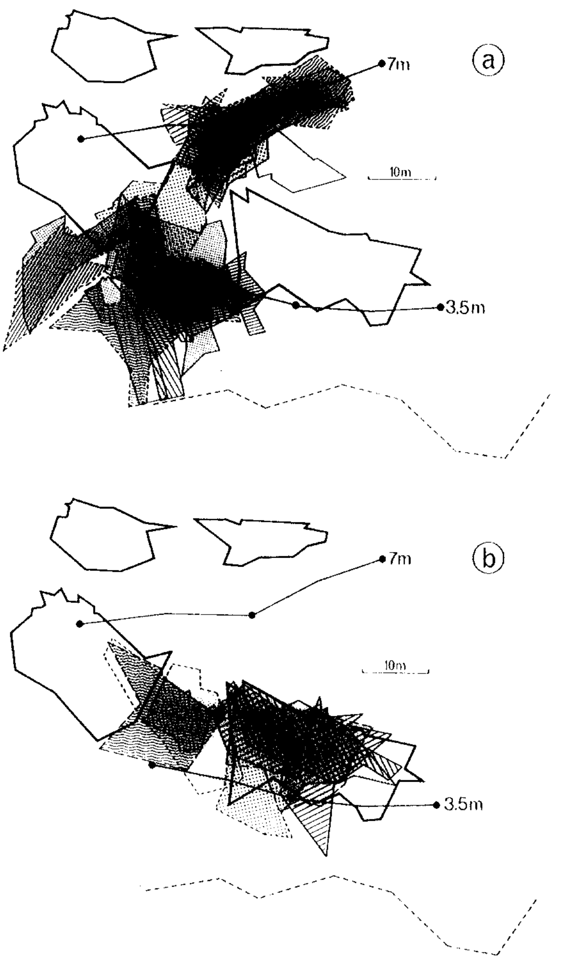

Fig. 6. a – foraging ranges of TP males in the SE area, as mapped in November 1989. Note the striking difference in overlap between group males (15 GTP, hatched areas) and territorial males (4 TTP, blank areas); b – foraging ranges of 8 IP fish (hatched areas) in the SE area, as mapped in February 1990, relative to the previously mapped ranges of 4 TTP males (blank areas). Note the large overlap of the ranges of 5 IP fish with that of one male (territory II–4 in Fig. 2).

(d) Stability of range and status

Between May 1987 and October 1990 a total of 32 TTP males and 25 takeovers (13 TTP → TTP, 5 TTP → GTP, 7 GTP→TTP) were recorded in the 17 mapped territories. The takeovers appeared to be randomly distributed in time (25 months with no change, 9 with 1 and 8 with 2 takeovers). Territories were always taken over within a day. Seventeen territory takeovers coincided with the departure of the TTP male. Twelve males were never seen again, but we do not know whether these died or were lost in the anonymity of the shallow group areas. Three males were resighted in a nearby group area and 1 male moved into an adjacent territory (from III–1 to IV–1), whose prior owner was occasionally resighted at depths > 25 m. One TTP male (from III–4) did not leave his territory (after 10 months of solitary

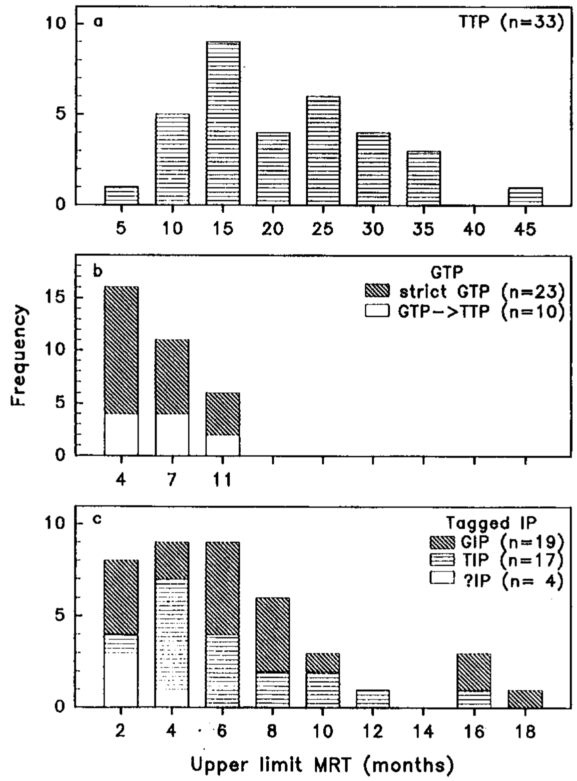

Fig. 7. Frequency distribution of the minimum residence times (MRT) of: a – territorial males, b – group males (including males that switched to territorial life), and c – tagged IP fish (status: territorial, group or unknown). For territorial (IP and TP) fish MRT refers to the residence inside a single territory; for the other categories the residence inside the SE area is shown. For GTP that switched to territorial life, only their residence as group male was taken into account. n: number of individuals.

residence) but tolerated up to 4 other TP males before disappearing 9 months later. Despite the takeovers, most territory borders remained quite stable throughout the study period; the mapped positions of successive TTP residents were always within the boundaries shown in Figure 2. The most striking changes were a division of one (into IV–4 and III–6) and a fusion of two other territories (III–2 and -3).

The minimum residence time (MRT) of TTP males ranged from 4 months to $3\frac{1}{2}$ years with the mode around 1 year and median at 17 months (Fig. 7a). IP fish could only be followed as long as they carried a tag. Twenty five out of 65 tagged IP fish had 'disappeared' within a week or were never re-sighted again. Seventeen of the other 40 IP fish were found in the same territory for periods up to 16 months (Fig. 7c). As established on a total of 282 localizations, only 1 TIP fish left its territory (III–5). It was localized 3 months later as a GTP male (still carrying its tag) in a shallow group area some 70 m to the Northwest. All 5 tagged TIP from II–4 stayed in this territory after disappearance of the first TTP male. Likewise, a tagged TIP from III–7 did not leave after a takeover by GTP males.

The overlap between individual TTP foraging ranges in different months was on average 42.0% (se ± 4.6%, n = 13) and was not significantly correlated with the time interval between successive determinations (r = 0.171, n = 13, p = 0.289). Tested in a 2-way ANOVA, neither depth nor period (comparing the overlap November–January, November–May and January–May) significantly affected the stability of the TTP ranges. TIP fish showed a somewhat but not significantly higher overlap (52.3 ± 1.9%, n = 5). No effect of depth or period could be determined for IP fish, since all resided in zone II and the interval between both determinations was about equal in all cases.

(e) Social interactions

Territorial fish actively keep other conspecifics, not belonging to their own one-male group, out of their territory. Territorial behaviour was never directed against other species. Territorial defence was most frequently observed for TTP males, as reflected in their relatively high time expenditure on interactions with (especially TP) conspecifics (Table 3). Furthermore, TTP males spent relatively much time swimming high in the water column, apparently controlling the territory borders, which occasionally resulted in vigorous chases of TP conspecifics. This behaviour was recorded as territory patrol and is not included in the time expenditure on interactions. On average it takes up 15–20% of their time budget, compared to < 5% for GTP and IP fish (J.M. van Rooij & J.J. Videler unpublished data). Defensive behaviour of TIP fish was observed rarely. However, aggressive chases of IP conspecifics were observed when captured fish were released outside their own home range and during the twilight periods when fish migrating to or from their sleeping sites passed through conspecific territories. TP fish were always chased by the TTP male, whereas IP fish were usually chased by a TIP fish, similar in size to the intruder. JU were ignored by adults.

Subtle interactions at grazing sites suggest a size-based hierarchy among group members, smaller fish always giving way to larger ones. This was particularly evident at conspicuous white grazing scars on live coral heads (mainly *Montastrea annularis*). Following an aggressive interaction or territory patrol, TTP males often took 1–3 bites from such scar, followed by other group members biting on the same scar, apparently in order of decreasing size. Average time expenditure of TTP males on interactions with conspecifics (group- and non group-members) is significantly higher than that of TIP fish and tends to decrease with depth (Table 3).

(f) Reproductive activity

The *S. viride* adults in our study area were observed to spawn daily, throughout the year. Virtually all sexual activity took place between 7:30 and 9:30 h, when the observed number of matings was much higher than expected from the somewhat higher observation intensity during that part of the day (χ^2_6 = 2493, $p < 0.001$, Fig. 8a). Occasionally (particularly at the deep spawning sites), mating started before 7:30. This involved 7.4% of all (1112) observed spawnings, whereas only 3.5% of the matings was observed at times later than 9:30 h. In all (148) instances that a focal animal was followed throughout the spawning period, all sexual activity in its home range occurred within a 90 min period.

We found no large seasonal periodicity, although some more matings were observed in January and November and less in April than expected from our sampling effort during the daily spawning period in these months (χ^2_{11} = 72.3, $p < 0.001$, Fig. 8b). Likewise, we found no strong synchronization of sexual activity with the lunar phases, other than a slight (but significant) lower than expected activity around the last quarter (χ^2_3 = 13.1, $p < 0.005$, Fig. 8c).

Analysis of the tidal registrations showed that the tide is of the mixed type, with a diurnal pattern prevailing when the moon reached its maximum semimonthly declination (either north or south), and predominantly semidiurnal tides when the moon crossed the equator. No differences in time of low and high water were found between the two locations. The daily tidal range proved to depend much more on the moon's declination than on its phase. Maximum daily ranges (20–40 cm) always coinci-

Table 3. Average time expenditure categories on social interactions with TP or IP (including JU) conspecifics. Fish categorized according to life and colour phase, social status, and depth range (I–IV).

Category	% time expenditure (± se)			
Depth	TP	IP	n_{ind}	n_{prot}
JU				
III	0.00 ± 0.00	0.41 ± 0.26	2	12
TIP				
II	0.23 ± 0.04	0.82 ± 0.11	8	42
III	0.65 ± 0.24	0.26 ± 0.01	4	16
GIP				
I	0.20 ± 0.18	0.54 ± 0.49	4	5
II	0.34 ± 0.11	0.36 ± 0.09	6	33
TTP				
II	2.69 ± 0.70	1.53 ± 0.41	2	13
III + IV	1.57 ± 0.42	0.32 ± 0.08	3	17
GTP				
I	1.81 ± 0.42	0.62 ± 0.17	4	17
II	0.60 ± 0.17	0.49 ± 0.11	2	25

n_{ind} = number of individuals represented in each category; n_{prot} = total number of (20–30 min) protocols obtained for each category. Other abbreviations explained in Table 1.

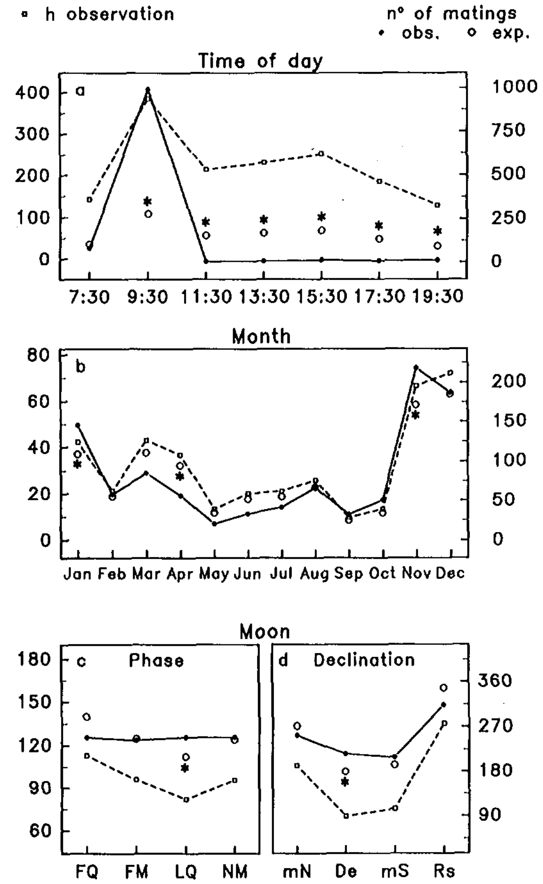

Fig. 8. Timing of the daily mating activity in relation to a – the time of day, b – month of the year, c – phase and d – declination of the moon. The frequency distribution of observed matings (black circles, 1112 in total) is plotted together with that of either total observation time [a: 1543 daytime hours, months and lunar periods pooled], or with that of the observations between 7:30 and 9:30 h [b, c, d: 385 h]. Data for all four years (1987–1990) pooled in all figures. Times shown on the abscissa in a are the upper limits of 2 h periods. Lunar periods = from 3 d before up to and including 3 d after date of corresponding phase [first quarter (FQ), full moon (FM), last quarter (LQ), new moon (NM)] or declination [maximum north (mN) or south (mS), or zero when crossing the equator on the descending (De) or rising (Rs) part of its path). Expected number of matings as calculated from a distribution proportional to that of observation time. Asterisks denote significance of the Pearson χ^2 residuals with a familywise error rate of 0.05.

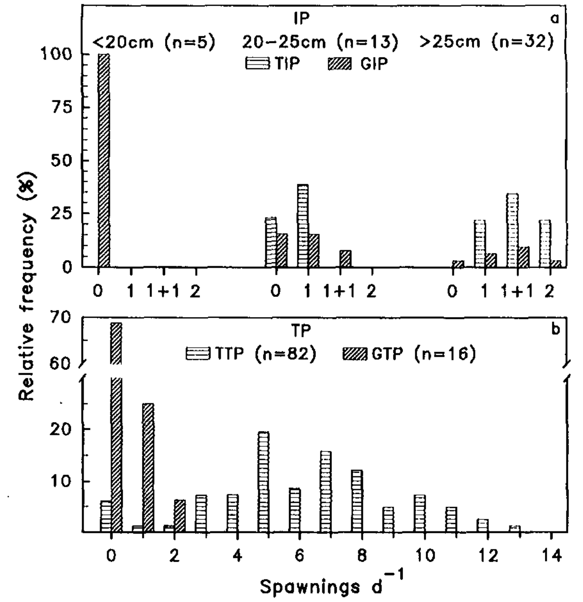

Fig. 9. Frequency distribution of daily number of spawnings (SpD) of: a – initial phase fish (11 territorial and 9 group fish, subdivided in three length classes), and b – terminal phase males (7 group and 12 territorial males). n: number of (90 min) spawning periods during which individuals were continuously observed.

ded with maximum declination and not necessarily with new and full moon. (Note that the periodicity of lunation involves a synodical month, i.e. 29.5 d, as opposed to the 27.3 d sidereal period of the declination cycle). Furthermore, our current measurements showed that the strongest currents (sub-surface peak values up to 27 cm s^{-1}) occurred at days with the largest tidal range. Therefore, we also subdivided our observations according to the moon's declination. Again, no clear synchronization was found, the only significant deviation being a slightly higher than expected activity around the days that the moon crossed the equator on its descent from north to south ($\chi^2_3 = 13.3$, $p < 0.005$, Fig. 8d).

The relatively constant time and (90 min maximum) duration of the daily spawning period allowed us to calculate Sp90 as a second (less laborious) quantitative estimate of daily spawning frequency, besides SpD. Furthermore, the lack of clear seasonal or lunar periodicity facilitated comparison of spawning rates of different categories, since all observations could simply be pooled. The spawning rates and frequencies presented below are all based on such pooled observations.

The main mating mode observed was pair spawning. Only 3 out of 1112 observed spawnings were interfered by a second IP fish (streaking; twice at a deep spawning site and once inside a territory). Group mating was never observed. TTP males exclusively spawned inside or at the border of their territory. No distinct mating sites were recognized, TTP males spawning throughout the territory, wherever an IP female would interact. During the spawning period TTP males spent relatively much time on territory patrol. Courtship and spawning behaviour are as described for other scarids (Thresher 1984), and involve slowly circling of fish high in the water column, brief upward rushes of the male, and a fast mating ascent (1–3 m high) at the top of which both partners release their gametes. Courtship did not always lead to a mating; sometimes the male broke off to chase an intruding TP conspecific or, more often, the female resumed grazing for no obvious reason. Females never spent more than a few minutes on courtship, much less than TTP males, whose grazing rates dropped significantly throughout the spawning period.

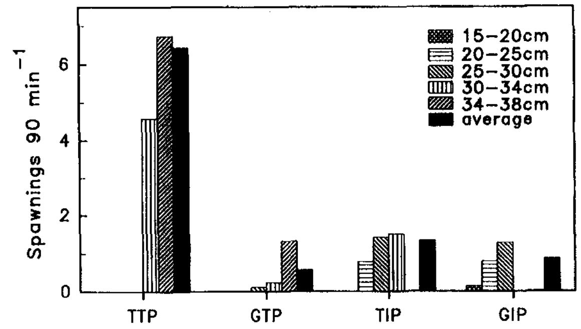

Fig. 10. Weighted average spawning rates (Sp90) of territorial and group terminal phase males and initial phase adults, subdivided in length classes (shaded bars) plus overall average for all sizes (solid bars). See Table 4 for the observation times on which the rates are based.

The daily number of matings was determined for 11 TIP females, most of which were followed several times and appeared to mate at least once a day (Fig. 9a). Nine larger (> 25 cm) TIP females regularly mated twice a day, first with a super-GTP at a deep spawning site and next with the TTP male inside

Table 4. Weighted average spawning rates (Sp90) for adult fish, categorized according to colour phase, social status, size class, and depth range (I–IV).

CATEG.	Sp90	n_{ind}	min	CATEG.	Sp90	n_{ind}	min
TIP				GIP			
20–25 cm				15–20 cm			
II	0.79	2 (0)	458 (0)	II	0.13	3 (2)	701 (346)
III	0.75	1 (0)	240 (0)	20–25 cm			
25–30 cm				I	0.00	2 (2)	26 (26)
II	1.42	6 (0)	1706 (0)	II	0.82	2 (1)	550 (65)
III	1.38	4 (0)	520 (0)	25–30 cm			
30–35cm				I	1.30	5 (2)	277 (124)
II	1.26	2 (0)	427 (0)	II	1.28	4 (0)	986 (0)
III	1.64	1 (0)	714 (0)				
TTP				GTP			
				25–30cm			
				I	0.25	2 (1)	354 (3)
				II	0.00	1 (1)	194 (194)
				III	0.00	2 (2)	259 (259)
30–34 cm				30–34 cm			
II	6.96	3 (1)	724 (12)	I	0.45	2 (0)	402 (0)
III	2.63	6 (2)	786 (226)	II	0.00	1 (1)	92 (92)
IV	3.44	4 (1)	183 (9)	III	0.00	7 (7)	304 (304)
34–38 cm				34–38cm			
II	7.95	7 (0)	4723 (0)	I	6.43	1 (0)	14 (0)
III	6.38	7 (1)	4232 (5)	II	1.28	3 (1)	701 (2)
IV	2.57	5 (0)	1017 (0)	III	0.88	4 (3)	102 (80)

n_{ind} = total number of individuals per category (in parentheses number of fish never observed to spawn); min = summed duration of observations on all n_{ind} fish (in parentheses observation time on inactive fish). Other abbreviations explained in Table 1.

their own territory. Some IP fish were lost out of sight while they swam to a deep spawning site and were observed to spawn inside their home range some time later. They probably also spawned at the deep site, so these cases are denoted 1+1 in the figure. Twelve TTP males were observed several times throughout a spawning period and mated up to 13 times a day inside their territory, 5–8 matings being quite common (Fig. 9b).

TTP spawning rates are significantly affected by the depth at which they reside (size classes pooled: $\chi^2_2 = 50.5$, $p < 0.001$; Sp90 7.82, 5.79 and 2.70 respectively for depth range II, III and IV), as opposed to the rates of TIP females (Table 4). Sp90 of TTP males further increases with size (Fig. 10; depth ranges pooled: $\chi^2 = 11.7$, $p < 0.001$). For TIP females the differences between size classes are insignificant ($\chi^2_2 = 2.21$, $p > 0.25$). The average spawning rates of TTP and TIP fish (6.42 and 1.33) agree well with the averages, calculated from the daily number of matings (6.28 and 1.45), assuming that the 1+1 cases represent 2 matings.

TTP males mated daily with most of the TIP fish sharing their territory, but also readily mated with any other available IP fish (from adjacent areas or just passing by). This is confirmed by the fact that all 16 studied TIP females always mated with the resident TTP male (when observed to mate), whereas 4 of the 9 active GIP fish mated with a neighbouring TTP male.

Ten tagged TIP females were observed to visit one of two deep spawning areas (described below), always the same and not necessarily the most proximate one. TIP undertook on average 0.61 deep excursions per 90 min (Ep90, calculated as Sp90, see Table 4 for observation times). They were sometimes briefly chased by the TTP male on return in their territory. Seven out of 26 TTP males (from all depth ranges) that were observed for more than half an hour during the spawning period, were witnessed to undertake brief excursions to depths ≥30 m early in the spawning period. They usually swam rapidly to the IV–4 valley where they descended to greater depth, had some interactions with other TP males near a deep spawning site, and then quickly returned to their own territory. The TTP male from IV–3 went down directly from his own territory and was observed twice to court an IP fish at 40 m depth. TTP males attained an average excursion rate of 0.15 Ep90. For the depth ranges separately this rate is 0.17, 0.09 and 0.30 for II, III and IV respectively ($\chi^2_2 = 3.57$, $p < 0.20$).

Multi-male groups

(a) Spatial distribution and abundance

The shallower (< 3.5 m) reef parts are exclusively inhabited by multi-male groups (Fig. 2). Group fish were not restricted to the shallow reef however, since GTP males temporarily invaded certain territories. These were considered to represent group areas (and the resident IP fish as GIP) as long as they were occupied by GTP males. The average density of group fish on the shallow reef amounts to 164 GTP and 292 GIP ha^{-1} (weighted average of the counts in the two shallowest quadrats between 0 and 4 m depth). Exact size and composition of the multi-male groups is difficult to establish. Figure 6a suggests that 14 GTP males in the SE area are organized in 3 subgroups (of 2, 5 and 7 GTP), while the foraging range of the fifteenth male was divided between the two larger subgroups. However, these subgroups were not very stable (see below) and no aggression between males of different subgroups was observed. Because only a small proportion of the IP fish in the SE area could be tagged, the IP:TP ratio of this group remains unknown. The IP:TP ratios in the 0–2 m and in the 2–4 m quadrat obtained by visual census are 1.6 and 2.4 respectively (weighted average: 1.8). If we include the maximum number of GTP males invading the deeper reef the average ratio becomes 1.5.

(b) Size composition and sexual maturity

GTP males measured 21.7–39.5 cm and GIP 17.2–29.1 cm FL (Fig. 3). Note the (13–17 cm) large size overlap between IP and GTP fish (GTP of about 17 cm FL were occasionally observed but not caught), which suggests that fish may change colour over a wide size range. This is partly confirmed by the size range of 5 captured transitional fish (22.7–28.2 cm FL; fish as small as 15–17 cm FL were observed but not caught). The counts in the two shallowest quadrats (Fig. 4a) suggest that GIP > 30 cm and GTP < 20 cm are underrepresented in our captures, whereas 25–30 cm GTP males seem to be overrepresented.

Eleven out of 19 examined GIP fish (58%) released eggs. Mature GIP females were clearly larger (22.2–29.1 cm) than fish without eggs (16.7–21.6 cm FL). The majority (75%) of 134 examined GTP males released milt, and no size difference was found between GTP with and without milt and unexamined individuals ($\chi^2_{10} = 3.72$, $p = 0.959$; 6 size classes).

(c) Size and exclusivity of range

The only factor significantly affecting A15 is depth; A15 of GTP males (11–223 m^2) decreased at increasing depth (Table 2, Fig. 5b). A15 of GIP fish (9–66 m^2, Fig. 5c) did not deviate from that of GTP males in depth range II (ANCOVA, $F_{1,73} = 0.38$, $p = 0.541$). Again, foraging range size (44–394 m^2 for GTP and 63–90 m^2 for GIP fish) showed the same trends as A15.

The foraging ranges of 15 GTP males residing in the SE area (Fig. 6a) overlapped by 44–100% in 22 out of 23 cases. The range of one GTP male showed only 16% overlap but was at the border of the SE area, so the actual overlap (including males from outside the SE area) was probably higher. The foraging ranges of 3 tagged GIP fish (Fig. 6b) largely overlapped those of 5 GTP males, whereas the overlap with the nearest TTP male was much smaller (0–22%). The fourth tagged GIP fish (17.2 cm FL) had left the SE area after the first determination of its 15 min range.

(d) Stability of range and status

Between November 1989 and May 1990, the SE area was inhabited by 12–15 GTP males, 5 of which attempted to settle a territory. Four apparently succeeded, although only 2 managed to reach any spawning success within the next 10 months. Strikingly, the 4 new TTP males (33–35 cm FL) were not the largest members of their former group (which were estimated at 38–40 cm). Most individually recognized GTP males resided less than 7 months inside the SE area (Fig. 7b). Nineteen tagged GIP fish (187 localizations) were found for periods up to 18 months inside the study area. Four of these moved at least once to another foraging range. The smallest (17.2 cm FL, sexually inactive) GIP fish frequently changed between a multi-male group in II–5 and territory III–2, and finally appeared to settle in territorry II–4. Two other GIP fish (18.6 and 23.7 cm FL) changed one group area for another, as did a third (27.1 cm FL) that finally settled in a territory just NW of the study area.

The overlap between individual GTP foraging ranges mapped in successive months (mean ± se: 29.7 ± 5.3%, n = 19) showed a significant decrease in time ($r = -0.426$, $n = 19$, $p = 0.034$), indicating a progressive shift of position. Because many GTP males had disappeared in January or May, no effect of period could be determined in an ANOVA design; that of depth (in November–January) was insignificant. The stability of the foraging ranges of GIP fish was determined for two fish only and appeared to be relatively high (49.9 ± 18.9%).

(e) Social interactions

Although many GTP and GIP fish inside group areas tolerated each other, non-group members appeared to be kept out. This was obvious when captured fish were released outside their own home range and also during the twilight periods when non-group members passed through the group areas. As in one-male groups, defence was only directed against conspecifics and appeared to be shared among group members. Furthermore, subtle interactions about grazing sites also suggested a size-based dominance hierarchy; size appears to be more important than colour, since smaller GTP males were occasionally observed to withdraw on the approach of a larger GIP fish. In some of the deeper (> 2 m) group areas GTP males were observed to take bites from white grazing scars. Average time expenditure of GTP males on interactions with conspecifics is somewhat higher than that of GIP fish and tends to decrease with depth, but the differences are not significant (Table 3).

(f) Reproductive activity

Spawning of group fish was restricted to the deeper (> 2.5 m) parts of the reef. Despite the presence of potential mates (mature and large GTP males, see point b above) on the shallow reef, sexually active

GIP females always spawned in deeper water, either in territories or at one of the deep spawning sites. The three smallest (< 20 cm) GIP fish were never observed to spawn, whereas 4 large (> 25 cm) GIP regularly spawned twice a day (Fig. 9a), once at a deep spawning site and once inside or close to their normal home range. Only 1 large GIP (from depth range I) did not spawn on the one occasion that is was observed throughout the spawning period. All 7 GTP males that were followed hardly spawned at all (Fig. 9b). The smaller GTP males only spawned during a temporary absence of larger TP group members. The average spawning rate of group fish is not significantly affected by their residence depth (Table 4). Sp90 does increase with size however (Fig. 10; depth ranges pooled: $\chi^2 = 14.5$ and 7.89, $p < 0.001$ and 0.025 for GTP and GIP respectively). The mean mating rate of GTP males (0.56 Sp90) is significantly lower than that of GIP > 20 cm (1.13 Sp90; $\chi^2_1 = 4.71$, $p < 0.05$) and TIP females ($\chi^2_1 = 10.03$, $p < 0.005$). These rates agree well with the averages, calculated from the daily number of matings (0.38 and 1.17 SpD), assuming that the 1 + 1 cases represent 2 matings.

All mates of GTP males were GIP fish from their own group, although some males were occasionally observed to court TIP fish from adjacent territories. Four of the 9 active GIP females mated with a neighbouring TTP male. Four others mated with a (relatively large) TP group member, and the ninth (22.2 cm FL) spawned both with a GTP (on 4 days) and with a TTP male (once). All 5 larger GIP females that were observed to spawn on several days, always mated with the same male. However, when GIP females mated twice a day, there were always 2 TP males involved, their usual partner (2nd mating) and a super-GTP (1st mating).

No prolonged observations at deep spawning sites were carried out due to decompression limits to diving time. Most information was obtained when focal IP females undertook brief excursions to mate with a TP male at one of these sites. Additional data were collected by brief surveys of the deep reef during the spawning period. From our observations we inferred that: (1) Deep spawning sites are scarce and fiercely defended during the daily spawning period by relatively large TP males; One deep spawning area was located at the NW buttress bordering the IV–4 valley (see Fig. 2), where no more than 3 large TP males defended spawning sites at about 30, 40 and 50 m depth. A second deep spawning area was found at a buttress some 200 m NW of the first one (outside the study area). Small groups of TP males were frequently observed to hover in the IV–4 valley and were vigorously chased if they came too close. (2) The TP males at these sites attain much higher mating rates than TTP males (which is why we called them super-GTP); On all (44) early morning visits to the first deep spawning area sexual activity was observed to take place. Once a super-GTP was observed to mate 16 times in 10 min (Sp90: 144). The high success of super-GTP is further indicated by the fact that many IP fish were observed to queue at a deep spawning site, apparently waiting for their turn to spawn. (3) Outside the spawning period, super-GTP forage in shallow group areas and therefore represent a special (rare) type of GTP males; after 9:30 h the deep spawning areas were devoid of *S. viride*. Moreover, a super-GTP was once observed to migrate to a shallow group area (50 m SE of the study area) at the end of a spawning period.

Like TIP females, 4 tagged GIP females that visited a deep spawning area always went to the same area, not necessarily the most proximate one (on average 0.29 Ep90). Only the largest (37 cm FL) of 12 GTP males (– 30 min observed) was seen to make deep excursions, attaining a rate of 1.22 Ep90 (296 min observed). This male once behaved like a super-GTP, circling above a small area at 40 m depth, ± 35 m NW of the IV–4 valley, apparently to attract females. Five min later he returned to his group area without having spawned.

Comparison one- and multi-male groups

(a) Spatial distribution and abundance

Group and territorial fish clearly differ in their vertical distribution over the reef, one-male groups exclusively residing in the deeper and multi-male groups mainly in the shallower reef parts (Fig. 2). The 0–20 m average density amounts to 188 JU ha^{-1}, 189 IP ha^{-1} (22.9% residing in areas that are usually controlled by TTP males), and 103 TP ha^{-1} (8–10% of which are territorial).

The size of one-male groups varies on average between 3 and 9 adults (IP:TP ratio 2–8), depending on depth. The 15 GTP males in the SE area probably belonged to a single group. Considering the 1.5–2.4 IP:TP ratios, it follows that the size of multimale groups is much larger.

(b) Size composition and sexual maturity

The most striking difference between TP males from both units is the much larger size range of GTP males. TP males < 30 cm and > 40 cm were only found in multi-male groups. Although there is a large size overlap, the smallest IP fish are GIP, whereas most larger IP fish are found in territories (comparison GIP, TIP and ?IP: $\chi^2_6 = 12.8, p = 0.046$). These differences are apparent both from the measurements (Fig. 3) and from the visual censuses (Fig. 4). The latter yielded significant between quadrat differences in the size composition of JU ($X^2_{12} = 63.85, p < 0.001$) and of TP males ($X^2_8 = 30.92$, $p < 0.001$), but not of IP fish ($X^2_{12} = 16.21, p = 0.182$).

Of the 124 IP fish that were checked for the presence of eggs, 50% released eggs with no significant differences between TIP and GIP fish ($\chi^2_2 = 3.824$, $p = 0.148$; 43.9% of the 82 ?IP fish had eggs). When all IP fish are pooled, those with eggs tend to be larger (comparison IP with and without eggs and unexamined IP: $\chi^2_{12} = 33.78$, $p < 0.001$). All TTP and most GTP males appeared to be sexually mature.

(c) Size and exclusivity of range

Comparison of A15 of the four adult categories (Fig. 5) in depth range II showed significant differences ($F_{3,73} = 9.99, p < 0.001$), the ranges of territorial fish being larger than those of group fish (contrast territorial vs. group: $F_{1,73} = 18.7$, $p < 0.001$), with no differences between IP and TP fish (contrast IP vs. TP: $F_{1,73} = 0.00$, $p = 0.962$). In depth range III the TTP ranges also tended to be larger than those of GTP males ($F_{1,46} = 3.13, p = 0.084$). Furthermore, the feeding ranges of territorial fish are more exclusive, not being shared by more than one TP male (Fig. 6). This is also apparent from the lower average adult density in the three deepest quadrats compared to that in the two shallowest quadrats (Fig. 4).

(d) Stability of range and status

Overall (data from all zones and periods pooled), the differences in foraging range overlap in successive months did not differ significantly between the four adult categories ($F_{3,35} = 2.565, p = 0.070$). However, the contrast between GTP males and the other three categories pooled ($F_{1,35} = 6.615$, $p = 0.015$) points to a smaller overlap for GTP males. Their lower stability is also apparent from their shorter MRT (Fig. 7) and from the progressive shift in the course of time. Furthermore, 5 GTP males were observed to settle a territory in the SE area during a 7 month period, compared to only 4 TTP males (in the entire study area) that switched to group life during 42 months. Range and status of GIP fish is also less stable than that of TIP fish, as indicated by their frequent shifts between different group areas and the settlement of some inside a territory. The only TIP fish that gave up territoriality was the one that changed into a TP male.

(e) Social interactions

No significant differences between categories were detected with respect to time expenditure on interactions with JU or IP conspecifics (nested ANOVA, $F_{8,26} = 1.92, p = 0.100$; individuals nested within categories: $F_{25,145} = 3.05$, $p < 0.001$), with damselfish (Kruskal-Wallis $\chi^2 = 14.5$, $n = 35$, $p = 0.070$) (Table 3). Time spent on interactions with TP *S. viride* differed between categories (ANOVA $F_{8,26} = 4.92$, $n = 35$ individual averages, $p < 0.001$), and is significantly higher for TTP males in depth range II than for JU, GIP in range I and TIP in range II (Tukey HSD). When only TTP and GTP males are compared in depth range II, the time expenditure of TTP males is also significantly higher (nested ANOVA, categories: $F_{1,2} = 19.4, p = 0.048$; individuals nested within categories: $F_{2,34} = 0.34, p = 0.587$).

Because we made no distinction between interactions with group or non-group members, the time spent on territory defence cannot be inferred from Table 3. However, the duration of interaction bouts reveals additional information, defensive acts generally lasting longer than interactions between group members. This is reflected in the frequency distribution of bout duration: only 3.5% of 201 recorded TP interaction bouts of GTP lasted longer than 10 s, compared to 44.3% of 79 bouts of TTP males. Long duration (> 10 s) interactions with IP fish were rare, comprising less than 1% of the bouts recorded for TIP, GIP and GTP (247, 90, and 122 bouts respectively) and 4.3% of the (115) bouts of TTP males.

(f) Reproductive activity

The overall average mating rates of the four adult categories (size classes and depth ranges pooled; Fig. 10) differ significantly ($\chi^2_3 = 414.7$, $p < 0.001$). TTP males clearly attain much higher rates than the other categories. The slightly higher average rate of TIP compared to GIP fish ($\chi^2_1 = 2.57$, $p > 0.10$) can be ascribed to their larger size, the differences between equal size classes being negligible. Comparison of the excursion rates to deep spawning sites shows that the rate of TIP fish is significantly higher than average ($\chi^2_3 = 26.5$, $p < 0.001$; only significant deviation: TIP: $p < \alpha_{BPC} = 0.013$).

Comparison between territories

Table 5 summarizes the sampling effort (months monitored and min observed during spawning periods) plus seven characteristics of all 17 monitored territories. The characteristics are: territory area (determined in January 88), mean length (FL) of the measured TTP males (those residing in the study area between January 1989 and September 1990), mean number of IP fish tolerated inside the territories (NrIP, determined in September 1988), the three stability indices (% Sol, average MRT and TkOv) and the (weighted) mean mating rate (Sp90). All pairwise correlations between these parameters are given in Table 6.

A significant positive correlation exists between FL, NrIP and Sp90. Apparently, larger males share their territory with more IP fish and attain higher mating rates. The fact that all 3 parameters tend to decrease on average with depth indicates that the most successful TTP males reside in the shallowest territories.

Table 5. Characteristics of the 17 monitored territories (mapped in Fig. 2).

Territory	Mo	Area	FL[a]	NrIP	% Sol	MRT[a]	TkOv	Sp90	min[a]
II–1	39	681	340^1	6.8	100	19.5^2	0.9	6.90	3092^2
II–2	36	671	348^1	4.2	100	18.0^2	1.0	8.68	591^2
II–3	36	460	363^1	7.4	100	18.0^2	1.0	9.00	520^2
II–4	36	462	365^1	13.4	100	18.0^2	1.0	9.17	1109^2
II–5	41	824	355^1	nd	51	10.5^2	1.8	9.33	135^2
III–1[b]	16	299	346^1	1.4	100	16.0^1	?	nd	0
III–2[c]	41	369	350^2	1.4	100	20.5^2	0.9	5.61	337^2
III–3[c]	42	510	354^2	1.4	100	21.0^2	0.9	6.08	454^2
III–4	40	374	336^1	0.6	78	15.5^2	1.8	2.74	328^2
III–5	41	291	352^2	3.0	44	9.0^2	2.6	7.47	807^3
III–6[d]	40	238	354^2	3.6	98	9.8^4	3.6	5.00	153^3
III–7	40	426	346^2	3.4	80	16.0^2	2.7	5.97	2939^2
IV–1	36	722	346^1	4.0	100	18.0^2	1.0	2.61	724^3
IV–2	42	482	340^2	2.4	100	21.0^2	0.9	2.66	169^2
IV–3	42	719	343^1	3.0	100	42.0^1	0.0	3.69	122^1
IV–4[d]	40	300	324^1	3.2	98	19.5^2	1.8	3.50	112^2
IV–5[b]	20	626	345^1	1.4	80	16.0^1	?	1.23	73^1

Mo = months monitored; Area in m^2; FL = mean FL (in mm) measured TTP; MRT = mean MRT all TTP; min = total observation time (in min) during spawning periods; other abbreviations explained in Table 1.

nd: no data.

[a] In superscript the number of TTP involved.

[b] Territories at border study area that were no longer monitored after departure first TTP, so TkOv unknown.

[c] Territories fused since 9th mo; min of TTP in fused territory equally divided over both.

[d] Territories originated from division IV–4 in 6th mo (before which no spawning observations).

There is no significant correlation between FL and territory area, not even when only the TTP present in January 1988 (whose territories were actually mapped) are considered (r = 0.192, n = 10, p = 0.595).

All three indices of temporal stability are correlated: the larger MRT, the larger % Sol and the lower TkOv. None of the indices differs significantly between depth ranges (1-way ANOVA's; % Sol: $F_{2,14} = 0.42$, $p = 0.66$; MRT: $F_{2,29} = 1.88$, $p = 0.17$; TkOv: $F_{2,12} = 2.956$, $p = 0.09$), although the stability tends to be lower in III and higher in IV. More strikingly, the stability is relatively low in the territories bordering valley IV–4 (III–7, III–6, III–5, IV–4 and IV–5), and to a less extent in 2 adjacent territories (II–5 and III–4).

The last significant correlation found is that between territory area and TkOv; stability, as measured by the latter index, appears to be greatest in the largest territories.

Discussion

By definition, the distinction between territories and group areas was based on group composition, which reflects differences in the degree of territoriality: the territorial behaviour of TTP males towards TP conspecifics results in one-male groups inside territories, as opposed to multi-male groups in group areas. It is a matter of definition whether either or both social units are considered to represent (intraspecific) group territories (see review by Kaufmann 1983, Davies & Houston 1984). However, we showed that the distinction is further justified by differences in:

- vertical distribution (territories restricted to depths > 3 m, group areas mainly < 3 m);
- size composition (larger proportion of smaller fish in group areas);
- size and exclusivity of the range (15 min ranges and foraging ranges of territorial fish larger and more exclusive);
- stability of the range (lower for group fish: GTP: shorter MRTs and larger foraging range shifts in

Table 6. Coefficients, (sample size), and two-tailed significance level for pairwise correlations between 7 characteristics of 17 monitored territories.

	Area	NrIP	% Sol	MRT	TkOv	Sp90
FL	0.0845	0.5371	–0.0818	–0.2265	0.0074	0.6681
	(17)	(16)	(17)	(17)	(15)	(16)
	0.747	0.032*	0.755	0.382	0.979	0.005**
Area		0.1586	–0.0320	0.3437	–0.5903	0.0906
		(16)	(17)	(17)	(15)	(16)
		0.557	0.903	0.177	0.021*	0.739
NrIP			0.2377	–0.0165	–0.1501	0.6536
			(16)	(16)	(14)	(15)
			0.375	0.952	0.608	0.008**
% Sol				0.5095	–0.4917	–0.1856
				(17)	(15)	(16)
				0.037*	0.063(*)	0.493
MRT					–0.7440	–0.3671
					(15)	(16)
					0.002**	0.317
TkOv						0.0351
						(15)
						0.901

Abbreviations as in Table 5.

*, ** 2-tailed significance at the 0.05 resp. 0.01 level

(*) 1-tailed significance at 0.05 level.

course of time; GIP: more frequent movements between different foraging ranges);
- sexual activity (daily in territories, never observed in shallow group areas).

Although the latter three traits are affected by fish size and residence depth, we have shown that the differences cannot be exclusively ascribed to differences in size or vertical distribution. Moreover, although they make up less than 20% of the adult stock, territorial fish control up to 77% of the inhabitable reef. As a result they have access to less intensely grazed substrates and they do not have to leave their feeding range to spawn. The distinction between both social units is therefore useful, adding additional information to a classification of individuals based solely on size, life and colour phase and depth of the home range.

For a full understanding of the significance of this distinction two questions should be addressed. First, what resources are actually defended and explain the difference in the degree of territoriality between group and territorial fish? Secondly, what are the life history implications?

Resource defence

The distribution of shelter, mates, mating sites and food are major environmental parameters that may affect the social and mating system of animals (Emlen & Oring 1977, Warner 1980).

Shelter

Shelter is not likely to be the defended resource explaining the territorial behaviour of *S. viride*, since most adults from both units find shelter in the deeper reef, outside their home range (both to sleep and when persistently chased by a diver in the daytime). However, the vertical distribution of JU may well be related to the distribution of shelter. The zones where they abound typically provide plenty of small refuges (e.g. between the fine branches of corals like *Madracis* sp. and *Porites porites*). Due to their small size JU are potential prey for a wide array of predators and can be expected to suffer a higher predation risk than adults (Wootton 1990). We never observed predator attacks on adult *S. viride*, whereas twice an attack of trumpetfish, *Aulostomus maculatus* on a 2–5 cm JU was witnessed.

Mating sites

Mating sites certainly play a role in the temporary territorial behaviour of super-GTP at deep spawning sites. Although the (large and dominant) males may themselves be attractive to females, this does not explain why they spawn at the deep sites. The large TP male in territory III–5 that frequently left his territory outside the spawning period must have been highly dominant. Still, his mating rate (8.2 Sp90) was not higher than that of other TTP males. Apparently, some characteristic of the deep spawning sites must be attractive. Local hydrographic conditions are possibly favourable here, increasing the survival of the pelagic eggs, embryos and larvae (but see Shapiro et al. 1988).

Mates

No distinct mating sites were recognized inside the permanent territories and it is hard to tell whether the mates are defended by TTP males, or some resource attracting them, like food or mating sites. However, the lack of spawning activity in the shallow reef, despite the presence of sexually active fish, indicates that this part of the reef is not suitable for spawning. This may be due to the risk that eggs will be washed ashore. Alternatively, the necessity to perform a spawning ascent might force fish to spawn in deeper water. Randall & Randall (1963) suggested that the pressure drop and the resulting expansion of the air bladder facilitates gamete release during the ascent.

By defending mates or mating sites against other males, TP males obviously increase their spawning success. However, this does not explain the territorial behaviour of IP fish, nor the continued defence outside the spawning period. Furthermore, TTP males cannot prevent their females from spawning at a deep spawning site. If these sites are indeed favoured, why then do not TIP females exclusively spawn there? The dual female mating may reflect a bet-hedging tactic, related to the unpredictable fate of the eggs. Alternatively, females may have a spawning obligation towards the TTP male in order to get access to favourable food patches.

Food

The larger and more exclusive foraging ranges of territorial fish point to a lower *S. viride* grazing pressure inside territories than in group areas. This is confirmed by estimates based on the abundance of adults and suitable grazing substrates (van Rooij et al. 1996a). Indirect evidence of reduced grazing pressure inside territories is the four- to fivefold higher relative abundance (as % of suitable grazing substrates) of large algal turfs on the deeper reef (Table 3 in Bruggemann et al. 1994a). Assuming primary productivity is constant, a higher algal biomass points to reduced grazing pressure. Despite a lower foraging effort, territorial fish were found to assimilate higher amounts of food than group fish thanks to the exploitation of higher-yield food patches (Bruggemann et al. 1994b). If territorial life demands a higher investment in activities other than grazing, the availability of high-yield grazing sites may well be a prerequisite, without which territories are not economically defendable.

Resource sharing

Although territorial (and to a less extent group) adults defend their home range against conspecifics, they share their ranges with group members (and with many other herbivorous species). This requires an explanation.

Territory sharing can be expected when the tolerated individuals bring benefits that outweigh the costs (Davies & Houston 1984). From the male perspective, sharing of the high-yield food patches with female conspecifics is easily understood, since the latter pay with the most profitable currency: eggs. Furthermore, as in *Scarus iserti* (Clifton 1990, 1991), dominant TIP females may benefit from the presence of subordinates due to their help with territory defence and food detection.

The fact that *S. viride* territories are shared with other herbivores suggests that there is some degree of food partitioning. This subject is treated in more detail by van Rooij et al. (1996a).

Life history implications

Territorial life obviously offers some advantages. This can be inferred from the rapid takeover of vacated territories by TP males and from the lower stability of the ranges of group fish. For TP males the most obvious advantage is a guaranteed number of daily spawnings. For IP fish the access to high-quality food patches will be the main advantage. The best tactic for an individual therefore seems straightforward: settle inside a territory as early as possible (i.e. as a small IP) and stay there for the rest of your life. However, the life history of *S. viride* is actually more complicated due to the occurrence of sex change, alternative male mating styles, and differences in territory quality.

Sex change

A well known hypothesis explaining sex change is the 'size-advantage model' (Ghiselin 1969, Warner et al. 1975, Warner 1988). This model states that if the expected number of offspring differs between the sexes with size, an individual that changes sex at the right size will have more offspring than one that remains male or female. The largest females mate no more than twice a day, whereas large TP males can attain much higher mating rates. An individual can therefore clearly increase its lifetime reproductive success by changing sex. A TIP female that 'decides' to switch to the terminal phase will have to give up her territorial status. This is inferred from two observations: 1) territories were always immediately taken over by other TP males, and 2) fish with transitional colour were never residing inside territories. As a result all fish will start the terminal phase as a GTP male, and the territorial status will have to be acquired all over again. An interesting related phenomenon is the high abundance of relatively small (< 30 cm) GTP males. If these fish had remained IP females, they would have attained higher mating rates. As shown by Iwasa (1991), an extended nonreproductive period due to 'early sex change' can be adaptive if sexually active individuals suffer higher mortality or reduced growth rates. Evidence for faster growth of GTP males is presented by van Rooij et al. (1995a) and this topic is addressed in more detail by van Rooij & Videler (unpublished data).

Alternative male mating styles

Super-GTP spawning at the deep spawning sites seem to follow another mating tactic than TTP males. Their apparent high mating success explains two unexpected observations: 1) why some TTP males gave up their territorial status and moved to a group area, and 2) why invaded territories were not taken over by the largest and most dominant TP group members. Considering that TTP males hardly grow at all (van Rooij et al. 1995a), group life may be required to attain a size large enough to become a super-GTP. Another indication of the important role of the super-GTP style is the reduced temporal stability in the territories bordering the IV–4 valley, from where males may have better chances to acquire a deep spawning site. A third male mating style, that of streaking IP males, was rare in our study area and is not further considered here.

Territory quality

Not all TTP males are equally successful. The positive correlation between average spawning rate and the number of females residing in each territory indicates that TTP male success depends on the size of the 'harem'. However, comparison of the average TTP spawning rates and IP group sizes in the three depth ranges suggests that the males in range III obtain quite some 'extra-haremic' spawnings (Sp90: 7.8, 5.8 and 2.7; NrIP: 7.9, 2.1 and 2.8 in range II, III and IV respectively). Both male quality (reflected in size and dominance) and territory quality (reflected in food availability and quality, presence of favourable mating sites, or distance from the home range of group females) may determine the female choice where to spawn, and hence male success. Fish residing in poor quality territories may give up territoriality in order to try to find a place inside a better territory.

Timing of reproductive activity

The relatively constant daily time of spawning of *S. viride* at our study site contrasts sharply with reports from other reefs. Both at San Blas (Robertson & Warner 1978), Puerto Rico (Colin & Clavijo 1988), and Belize (Cardwell 1989) *S. viride* was observed to spawn throughout much of the day. Cardwell (1989) found that the spawning period closely followed the predicted time of high tide. When high tide occurred in the morning, spawning started maximally 1 h after the tidal peak, whereas it preceded high tide when occurring in the late afternoon. Colin & Bell (1991) observed a similar pattern for 13 scarid species at a reef situated in a major passage between the ocean and the lagoon of Enewetak Atoll. The daily timing of spawning in this passage with strong tidal currents (up to 1–2 m s^{-1}) began at or just after slack high water, when currents started to move out of the lagoon. Our current measurements indicated a much more complicated tidal current regime. The prevailing direction of the relatively slow current at Karpata was west (along shore) with several brief (< 10–20 min) standstills or 180° reversals that could not be clearly linked to a certain phase of the daily tidal cycle. Furthermore, strong vertical differences in speed, direction, and time of reversals were found at a scale of meters only. This is probably related to a relatively strong wind effect, the seaward tradewinds causing an offshore component in the upper layer that is compensated by a counter current at greater depth. Therefore, the most likely explanation for the lack of synchronization of spawning with the tide at our study site, is the low predictability and velocity of the tidal currents. However, the observation that *S. viride* spawns at different times of the day at other locations on the Bonaire reef (van Rooij et al. 1996b) suggests that there is some degree of daily timing. Whether this is related to the dispersal of embryos and larvae and/or to other factors (see Robertson et al. 1990 for an extensive discussion) remains to be investigated.

The lack of clear lunar periodicity, both with respect to phase and declination, could be ascribed to the same factors that explain the lack of tidal tracking. That is, in so far the lunar cycle is assumed to affect the dispersal of the planktonic propagules through its effect on currents. Since *S. viride* is an all-year round pelagic spawner (no parental care) and shows a strictly diurnal activity pattern, most other lunar effects that have been suggested to explain lunar reproductive cycles are not applicable (e.g. moonlight facilitation of adult migrations or egg guarding, synchronization of reproductive activity, Robertson et al. 1990).

The absence of important seasonal fluctuations in spawning activity might be ascribed to the relatively constant water temperature (maximum annual range 25.8–29.8° C, van Rooij et al. 1995b) and the small difference between dry and wet season. However, this does not mean that there is no seasonal effect at all. Both growth and condition were found to vary seasonally (van Rooij et al. 1995a, b). It is therefore possible that the number of eggs produced by females differs with the seasons as well.

Conclusions

About 23% of the IP and 10% of the TP adults in our *S. viride* stock reside in contiguous territories that cover up to 77% of the inhabited reef. Fish from both units show differences in use of space and reproductive activity that cannot be ascribed to differences in size or vertical distribution. Territorial life guarantees the males a spawning area plus a reliable number of mates, which in turn get access to high-yield food patches. Defence is shared between the TTP male and his 'harem' females and is mainly directed against (similarly sized) conspecifics. Although territorial life is beneficial both to TP and IP fish, life history considerations may cause individuals to give up territoriality: when changing from IP female to TP male, and when aiming at a better territory or at the super-GTP status.

The distinction between territorial and group adults in *S. viride* is similar to that in *Scarus iserti* and may be a basic feature of scarid social systems. The high complexity of scarid social systems seems to reflect the ability of individuals to flexibly adapt their feeding, mating and life history styles to local conditions. This seems highly adaptive considering the unpredictable fate of their pelagic larvae.

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