

**SPAWNING BEHAVIOUR OF THE STOPLIGHT  
PARROTFISH *SPARISOMA VIRIDE* Bonnaterre, ON  
BONAIRE AND SABA (NETHERLANDS ANTILLES).**

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Vakgroep Mariene Zoölogie  
Begeleiding:  
Dr. J.J. Videler  
Drs. J.M. van Rooij

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Master thesis Y.A.M. van Etten  
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Department of Marine Zoology, University of Groningen, Haren, the Netherlands  
with help of Dr. J.J. Videler and Drs. J.M. van Rooij

Rijksuniversiteit Groningen  
Bibliotheek Biologisch Centrum  
Kerklaan 30 — Postbus 14  
9750 AA HAREN

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## ABSTRACT

The reproductive behaviour of the stoplight parrotfish, *Sparisoma viride* Bonnaterre, was studied on two Caribbean islands of the Netherlands Antilles. In the northwest of Bonaire, the *S. viride* population living on the reef off Karpata exists of group fishes sharing a common home range in the shallowest parts of the reef and harem fishes occupying most of the rest of the reef. Group fishes were not seen spawning in their feeding area, but some may spawn during about one hour daily close after sunrise on the reef slope at a depth of ca. 40 m. Harem fishes mate consistently in the early morning in their territories. Harem males may spawn up to 12 times daily and can have extraharem matings. Harem females spawn once or twice with the harem male, but additionally may mate at a deep spawning site. In the late afternoon the harem fishes may spawn again for a shorter period and at a lower frequency.

In the southwest of Bonaire, the *S. viride* population living on Tori's reef consists of only harem individuals. The fishes mate exclusively in their territories during about one hour daily in the mid afternoon. Females spawn once or twice a day, while the harem males may spawn up to 6 times daily. Differences in the daily timing of spawning between these reefs are probably related to the different times of the day at which local currents are favourable for larval retention.

In the northwest of Saba, the *S. viride* population living in Well's bay exists of nonharem wandering fishes who spawn at a very low level in July. Seasonal spawning during the cooler months of the year is suggested. Differences in the timing of spawning might indicate tidal tracking.

The variety in socio-sexual system at the three study sites suggests an adaptation to local variation in resources. Significant differences in the spawning behaviour of the fishes at the different localities are probably the result of the plastic nature of this behaviour varying under different environmental conditions.

## 1 INTRODUCTION

Coral reefs along the coast of many Caribbean islands are rich and very diverse benthic communities. They are structurally extremely vulnerable because they are continuously threatened to be overgrown by fast growing epilithic algae. Parrotfishes, as part of the herbivore guild, play an important role in preventing overgrowth by algae (Wanders, 1977; Randall, 1961b) and thus prevent the degradation of the coral reef. Additionally, the grazing behaviour of parrotfishes may create space for the settlement of juvenile corals (Bak & Engel, 1979).

Coral reefs are restricted to shallow waters and mutually isolated by deep oligotrophic oceans. This geographic isolation enhances the vulnerability of coral reefs. It complicates the exchange of genetic material between populations and increases the chance of major losses due to offshore drift (Young & Chia, 1987).

Parrotfishes produce planctonic eggs and larvae (Randall & Randall, 1963; Reeson, 1983). It was generally believed that planktonic stages serve long range dispersal. However, hard evidence for this hypothesis is lacking and there is increasing evidence that long range dispersal is more often exception than rule (Young & Chia, 1987). Johannes (1978) describes the timing of reproductive behaviour of coral reef fishes in relation to occurrence of circular currents and suggests larval retention as a possible function of the specific timing of spawning.

Oceanic islands lying in major current systems (sometimes caused by persistent trade winds) often have downstream eddies (Emery, 1972). In an optimal scenario, pelagic eggs could join such an eddy if spawning took place at the right location and time. These eggs are taken out into the ocean at first but the mass of water in which they are trapped returns later on (Sale, 1970). The eggs of parrotfish hatch at sea after some 24 hours (Koltes, 1993) and the larvae will be able to swim by the time the water mass reaches the reef again.

If this is the case, genetic isolation between populations on island coral reefs can be very important. *Sparisoma viride* populates the isolated coral reefs of the Netherlands Antilles. Morphological differences between individuals of this species from different islands have never been demonstrated. In the case of local isolation and lack of genetic exchange among populations a moderate or strong genetic differentiation may be present. As we observe no differences on the morphological level, genetic differences could be expressed on the behavioural level.

The analysis of how an animal or species budgets its time into various behavioural activities is an important approach to the study of behavioural strategies. The time-budgets of animals are constrained by social and environmental factors (Hanley, 1984). Kroon (1991) showed that the social status of *S. viride* affected the time spent on high swimming and interactions with conspecifics because territorial males have to inspect and defend their territory. Time-budgets were also shown to vary in this species according to the size and life-phase of individuals (Hanley, 1984). Thus, by considering the time utilization of *S. viride* during the spawning period, differences in time budgets of different populations may be found to be related to differences in their social and mating system.

The behaviour and social structure of *S. viride* is found to vary between different locations in the Caribbean (Kraan, 1993) and even varied within a single population (Kok, 1988; van Veghel, 1989; Kroon, 1991).

Part of the variability in social and mating (socio-sexual) systems can be explained by the complexity and variability of resource (food, shelter, mating sites) distribution within and among coral reefs (Shapiro, 1991). Fishes can be expected to adapt social behaviour and discrete features of their socio-sexual system to these local variations (Robertson & Hoffman, 1977). For example, spawning sites are probably selected, at least in part, on the basis of how pelagic eggs and larvae are influenced by local water movement at those sites (Johannes, 1978; Shapiro *et al.*, 1988). Consequently, the location of suitable spawning sites will vary widely from one reef to another as the reefs vary in factors influencing local water movement (size, shape, exposure to wind, current, and waves). Variations in the degree of separation between foraging and spawning sites will force the fishes to vary the extent to which they do or do not migrate out of foraging zones to spawn (Shapiro, 1991).

Another part of the explanation for socio-sexual system variation derives from variability in time, place, and rate of recruitment of pelagic juveniles onto reefs. Variable recruitment and mortality rates will create large variations in local population density, which may, in turn, influence spatial and behavioural aspects of social and mating systems (Shapiro, 1991).

The intra- or intersite variation in the socio-sexual system of *S. viride* can be the result of the presence of several behavioural genotypes within the population. However, it is also possible that behaviour is sufficiently plastic to produce these variations under different environmental conditions (Shapiro, 1991).

The purpose of this study was to investigate the spawning behaviour of populations of *Sparisoma viride* on two islands of the Netherlands Antilles. As the reproductive behaviour on Bonaire is already well studied (Zuidema, 1989; Kroon, 1991), Bonaire serves as a starting-point. The situation on Bonaire (part of the Leeward Islands of the Netherlands Antilles) will serve as a benchmark for the comparison between the islands Bonaire and Saba (part of the Windward Islands of the Netherlands Antilles).

One expects small behavioural differences between animals from different parts of the same island. Thus, the *S. viride* population spawning along the north-west coast of Bonaire will probably behave similar compared to that spawning along the south-west coast. As the geographic distance between the islands Bonaire and Saba is approximately 900 km, the *S. viride* populations living on these islands may be genetically isolated. Thus, differences in spawning behaviour between animals from these islands are expected to be larger. However, variations in reproductive behaviour between locations and within populations can also be the result of adaptations to locally different environmental conditions.

To determine the differences in spawning behaviour of *Sparisoma viride* populations on two locations on Bonaire, and on one location on Saba, the following questions were examined for each of these locations:

- 1] What is the daily timing of spawning ?
- 2] Where are spawning sites situated ?
- 3] What is the frequency of spawning per day for each of the social categories ?
- 4] Which fish participate in the reproductive process ?
- 5] What are the time-budgets of the spawning populations ?

To determine the effect of local conditions on the socio-sexual system, the following questions were examined for each of the locations:

- 6] What is the density of the three life-phases of *Sparisoma viride* ?
- 7] What are the substrate characteristics, in terms of substrate cover ?



## 2 MATERIAL AND METHODS

### 2.1 STUDY SITE

Field studies were conducted while snorkelling and scuba diving along parts of the reefs from the Caribbean islands Bonaire and Saba (figure 1). Bonaire, Curaçao and Aruba, form the Leeward Islands of the Netherlands Antilles. Saba, together with St. Maarten and St. Eustachius, is part of the Windward Islands of the Netherlands Antilles. The distance between Bonaire (12°N, 68°W) and Saba (17°N, 63°W) is approximately 900 km.

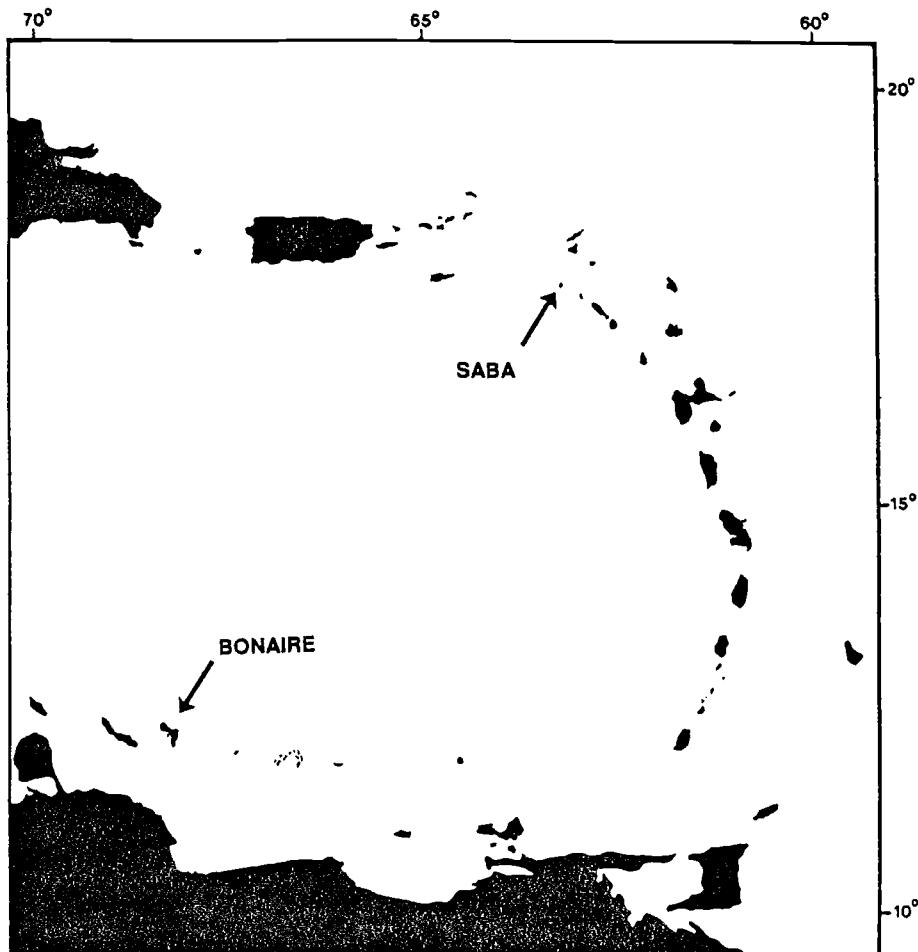


Figure 1: The position of Bonaire and Saba in the Caribbean (Baker *et al.*, 1977).

On Bonaire two study sites were chosen on the leeward side of the island. One is the fringing reef off the ecological center Karpata in the northwest of Bonaire, the other is the fringing reef off the dive site Tori's reef situated in the southwest of Bonaire (figure 2). The field work took place from May '92 till July '92. On Saba, one study site was chosen on the leeward side of the island named Well's bay (figure 3). The field work took place from July '92 till September '92.

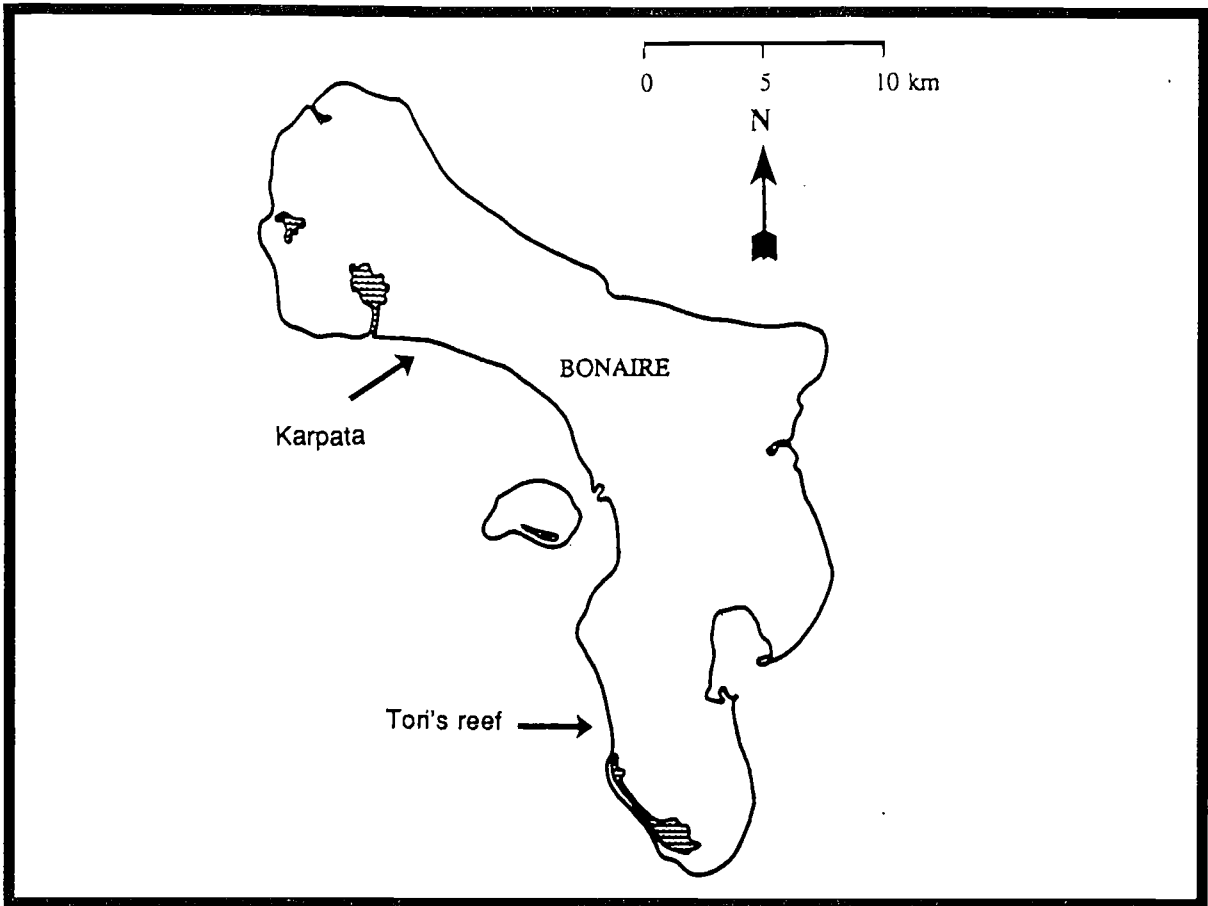


Figure 2: Location of the study sites Karpata and Tori's reef on Bonaire.

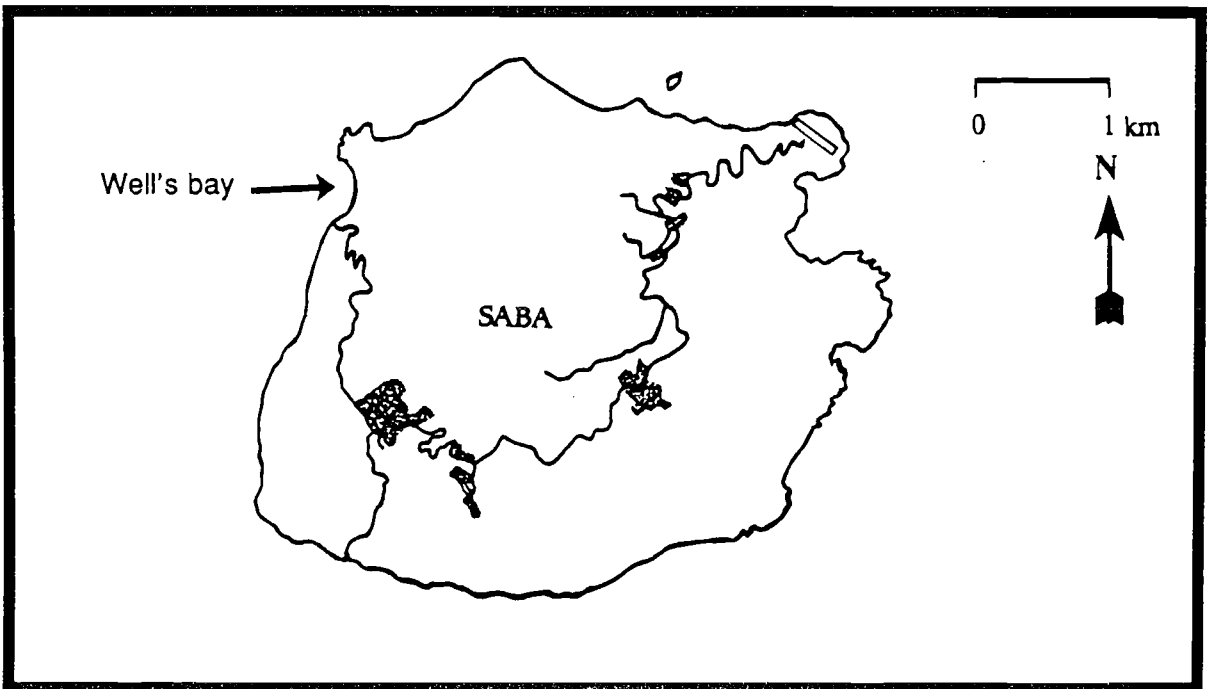


Figure 3: The location of the study site Well's bay on Saba.

## 2.2 REEF DESCRIPTION

The reef at each study site was sub-divided into zones, based on substrata and depth ranges.

The two study sites on Bonaire were sub-divided into four zones.

### KARPATA (figure 4A)

1. Shallow reef (0.3-3m): this zone starts from an intertidal area (plateau) consisting of dead coral overgrown with algae. Somewhat deeper a small zone of large rubble and live coral (elkhorn coral) is found.

2. Sand/Rubble zone (3-4m): this zone is more like a limestone pavement with patches of fine rubble and sandy areas. Gorgonians and small boulders of brain coral also occur in this zone.

3. Drop off (4-11m): this zone yields a high diversity and density of live coral (mainly star coral, *Montastrea annularis*). Large sea fans and gorgonians grow inbetween. There are a few sandy areas and patches of fine rubble.

4. Reef slope (11-30m): this zone displays the highest coral diversity in the upper part. In the deeper regions red coralline algae become abundant. From 20 m on, sand grooves go down along the reef and corals have a flattened shape.

### TORI'S REEF (figure 4B)

1. Sand flat (1-5m): this zone exists entirely of white (coral) sand with rare patches of fine rubble.

2. Staghorn coral zone (5-7.5m): this zone contains a variety of hard and soft corals, but staghorn coral is most abundant.

3. Drop off (7.5-13m): this zone is dominated by star coral (*Montastrea annularis*) and staghorn coral is present in rare patches.

4. Reef slope (13-26.5m): this zone yields a high diversity and density of live coral. Below 26.5 m a large (33 m long) relatively flat sandy plain stretches out till it reaches a depth of 35m, where a second drop off starts.

The reef of the study site on Saba was sub-divided into three zones.

### WELL'S BAY (figure 4C)

1. Encrusted boulders zone (0-9m): this zone exists of basaltic rocks which are encrusted with a variety of hard corals, soft corals and sponges. In the shallow part big rocks (3 till 4 m high) are found, but the size of the boulders decreases with depth.

2. Soft coral zone (9-10.5m): this zone comprises many small encrusted basaltic boulders. On the sandy bottom patches of soft corals (sea fan, sea whips) and barrel sponges are common.

3. Sand flat (10.5-??m): this zone consists entirely of dark grey (volcanic) sand and slopes gradually to a drop-off further out.

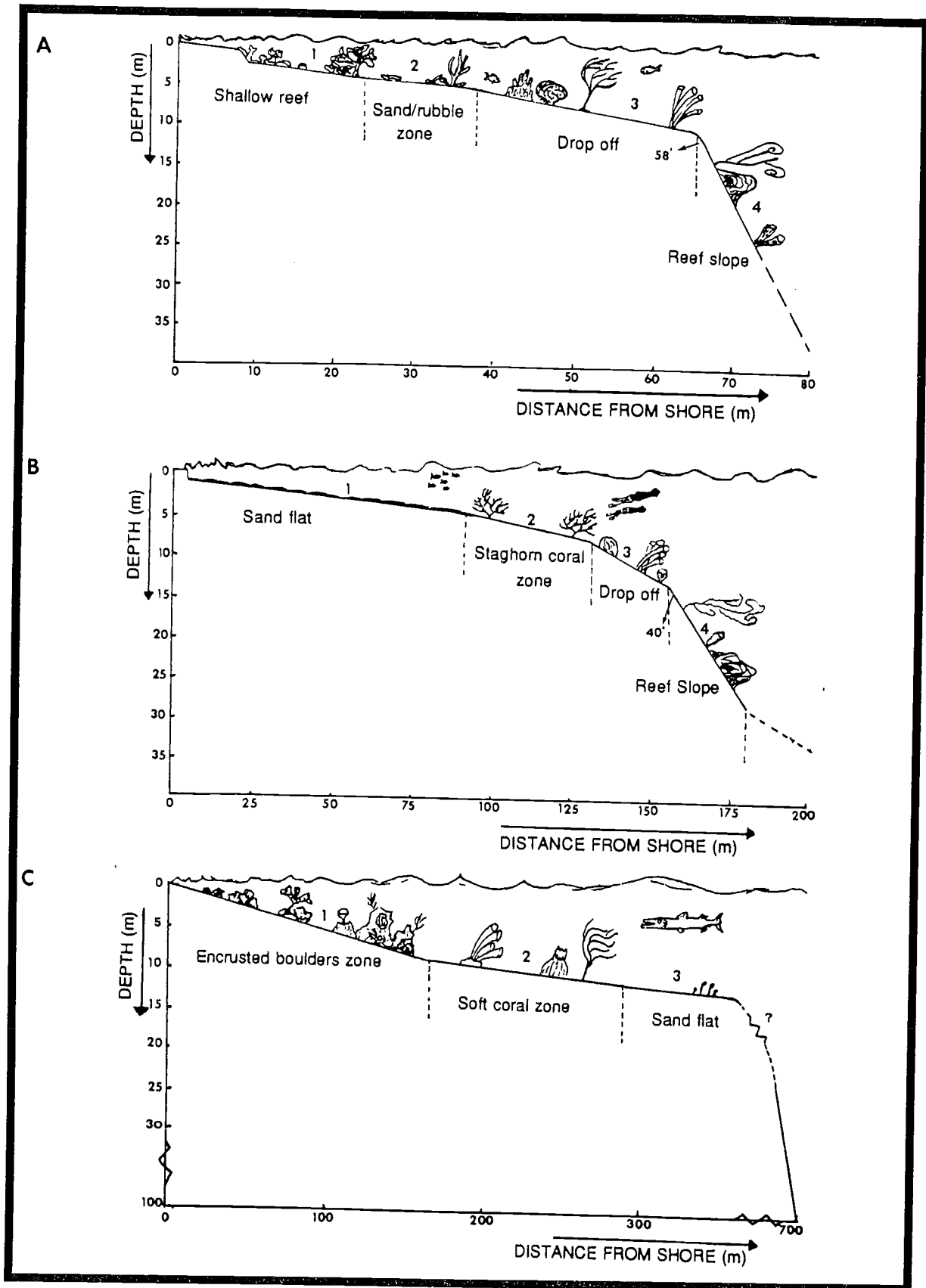


Figure 4: Schematic display of the reef zones of the three study sites. A= Karpata; B= Tori's reef; C= Well's bay. The position of the quadrats is indicated by numbers (Kraan, 1993).

## 2.3 STUDY ANIMAL

The stoplight parrotfish *Sparisoma viride* Bonnaterre (Scaridae) is a large reef herbivore (>500mm). It displays a scraping feeding habit: with the protruding beak it bites into the inorganic substratum selecting for both large turfs and sparse turfs on endolithic algae (van Oppen, 1990). The species is protogynous (Reinboth, 1968) and shows full sexual dichromatism, with the terminal male coloration being permanent (Robertson & Warner, 1978). Three life-history phases are recognized: juveniles, initial-phase and terminal-phase (figure 5). Juveniles are <160 mm standard length (Robertson & Warner, 1978). Initial-phase individuals are mainly female, while termphase fishes are all males (Hanley, 1984; Robertson & Warner, 1978).

The social system of the *S. viride* population may vary between different locations and may even vary within a single population. Kraan (1993) described the social structure of the *S. viride* populations living on the reefs of Karpata and Tori's reef and in Well's bay. Four social categories were distinguished among the fishes living on the reef off Karpata. At depths between 3 and ca. 20 m termphase males possess territoria that are actively defended against conspecifics. Some initial-phase females, called harem females, are nevertheless tolerated by the territorial male. On the shallowest parts of the reef (0.5-3 m) termphase and initial-phase fishes feed together in small groups and are referred to as group fishes. The groups are relatively stationary and maintain home ranges for longer periods. At Tori's reef, termphase males hold permanent feeding territories at depths between 5 and ca. 20 m and these also include some harem initial-phase females. At depths between 1 and 5 m there is an extensive sand flat where *S. viride* does not occur. In Well's bay, at depths between 1 and 10.5 m, the *S. viride* population consists of small groups of 4-7 fishes. The group structure is very loose, t.i., exchange of fishes between these groups takes place and individuals may leave the group for a while before returning to it. Territorial behaviour is not observed. As each group is not restricted to a certain home range and swim about in the whole bay ( $\pm 3.5 \text{ km}^2$ ), these group fishes are referred to as wandering individuals. From 10.5 m on, a sandy bottom gradually slopes down. *S. viride* does not live or feed in this habitat, but some termphases were seen in transit on occasion (Kraan, 1993).

Parrotfishes are strictly diurnal, foraging only during the day and sleeping at night. Twice a day they undertake migrations between their diurnal feeding areas and their nocturnal resting sites. *S. viride* tend to occupy the same sleeping site each night (Kroon, 1991). On Bonaire individuals spent from 77-96% of their diurnal time swimming close to the bottom and feeding (Kok, 1988; Kroon, 1991; Kraan, 1993). On Jamaica the stoplight parrotfishes spent from 84-97% of their diurnal time swimming, feeding and hovering (Hanley, 1984). Kraan (1993) also found that the time-budget of the stoplight parrotfish on Saba was greatly dominated by swimming and feeding (92-95%).

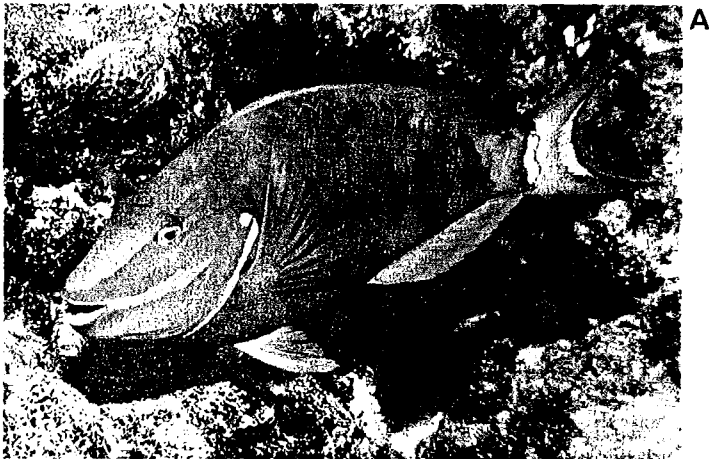


Figure 5: *Sparisoma viride*; A= terminal-phase male, B= initial-phase, C= juvenile (Humann, 1991).

## 2.4 POPULATION DENSITY

Population counts were conducted to determine the density of the three life-phases of *S. viride* at the three study sites. Quadrats (15 x 15 m) were established in every distinguished reef zone. To make accurate counts of juveniles, these quadrats were sub-divided into nine squares (5 x 5 m). Substratum descriptions were made of all quadrats by estimating the percentage covering of the different substrata.

The three life-phases were counted weekly in each quadrat, five times a day, over a period of one month. A visual census was carried out by slowly overswimming the quadrat hanging 1 to 2 meters above the bottom and counting the termphase, initial-phase and large juveniles (10-15 cm fork length) present in the quadrat. Scores were written on PVC slates. Hereafter, every square was scanned for small juveniles (<2-10 cm fork length). Since small juveniles are easily overlooked, every square was scanned by swimming a "S" close to the bottom. On average, a visual census of a quadrat lasted ca. 10 minutes, that is, 1 minute for counting the termphases, initial-phases and large juveniles, and 9 minutes for counting the small juveniles.

Visual censusing was performed at five different times during the day: 09.00h, 11.00h, 13.00h, 15.00h and 17.00h. This time period was chosen, because before 09.00h and after 17.30h the behaviour of *Sparisoma viride* is different. This is due either to spawning around sunset and/or sunrise or to migration of the fishes between their sleeping sites and their territoria /home ranges (Vaandrager, 1988; Kok, 1988). Each visual census of a quadrat was performed twice by two different observers. *S. viride* densities were standardized to individuals per 1000 m<sup>2</sup>.

The percentages substrate cover of the quadrats were converted into weighted averages of the substrate cover for each study site. The width of the reef zones (table 1), measured perpendicular to the coast being a relative measure of the surface area of the zones, was used to calculate the weighted averages. The width of the third zone of Well's bay was not measured as this sand flat gradually sloped down and was too extensive to be fully measured. For this reason, only the first two zones were used to calculate the weighed average of the substrate cover in Well's bay.

Table 1: The widths (m) of the reef zones of the three study sites.

	KARPATA	TORI'S REEF	WELL'S BAY
Width zone 1 (m)	12	89	169
Width zone 2 (m)	14	42	120
Width zone 3 (m)	27	27	?
Width zone 4 (m)	15	21	-

The same method was used to determine the weighted average of the population density of the three life-phases of *S. viride* at the three study sites.

## 2.5 OBSERVATIONS ON THE SPAWNING BEHAVIOUR

### 2.5.1 Determination of the daily timing of spawning

The time at which spawning by *Sparisoma viride* occurred was determined by observations from sunrise till sunset in shallow water. Two observers took turns every two hours. The spawning behaviour could easily be recognized, because videos of several pair spawnings were studied during the preparation of this study.

### 2.5.2 The activity of *Sparisoma viride* during the spawning period

The behaviour of adult terminal- and initial-phase individuals of *Sparisoma viride* was recorded during the spawning period, using an underwater eventrecorder (UWrec). The UWrec consists of a waterproof cylindrical PVC housing that contains a processor with 128K memory and 18 magnetic switch keys on top of the housing. Sixteen keys are functional for recording behaviour and numerous behavioural activities can be recorded by using these keys alone or in combination. By pressing one or several keys, the UWrec records what key(s) is(are) being pressed and at what time (in tenths of seconds accurate). The information is stored in a five byte record, which is called an event. Therefore, the 128K memory of the recorder can store more than 26,000 events. The events can be transferred to a diskfile for analysis using a PC.

As the social status of a fish is related to its spawning behaviour (Zuidema, 1989; Kroon, 1991), fishes from different social categories were studied. According to the description of the social structure of the *S. viride* populations at the three study sites given by Kraan (1993), the following social categories were examined:

#### KARPATA

1] Territorial termphase male (code KT)= termphase living in a territory, an area that is actively defended against conspecifics. Some conspecific initial-phase females are nevertheless tolerated by the terminal male.

2] Group termphase male (code KG)= termphase living in an area which comprises home-ranges of conspecifics. Thus some terminal- and initial-phase fish are tolerated.

3] Harem initial-phase female (code KV)= initial-phase living within the borders of the territory of a terminal-phase male.

#### TORI'S REEF

1] Territorial termphase male (code TT)

2] Harem initial-phase female (code TV)

#### WELL'S BAY

1] Wandering termphase male (code PG)= a terminal-phase male living in a large area which comprises several home-ranges of group fishes. Exchanges of fishes between the several groups are common.

2] Wandering initial-phase (code PV)



On Bonaire, territorial and group termphases could be followed twice as they were relatively site-attached and could easily be recognized by the distinct yellow spot at the base of the caudal fin. Initial-phase females could not be recognized individually. To enlarge the chance of observing the same initial-phase twice, the largest harem initial-phase (ca. 30 cm fork length) from a known territory was chosen to be studied. On Saba, the wandering terminal- and initial-phases could not be followed twice as the fishes swam around through the whole bay and were thus hard to locate. Fork lengths (FL) of the observed fishes were estimated to the nearest 5 cm. The number of harem initial-phase females present in the known territories during the day were estimated by counting them three times on different days during the non-spawning period.

Spawning observations commenced ca. 15 minutes before the expected spawning period started. The observation stopped ca. 30 minutes after the last spawning, except when the fish still displayed sexual related behaviour. When no sexual behaviour was displayed during the "expected" spawning period, the observation was continued for at least 60 minutes. On Bonaire, this was accomplished for almost all observations except for two protocols (KG3 observed on 01-05-1992 and KV3 observed on 06-05-1992). Thus, the time of monitoring different individuals with the UWrec on Bonaire ranged from 45 to 119 minutes. As most of the spawning activity of the observed fishes occurred in shallow water (<9m), the observer was not endangered by decompression problems. On Saba, the fishes were more difficult to keep up with, which often resulted in observation times less than 60 minutes. The time of monitoring different individuals with the UWrec on Saba ranged from 34 to 88 minutes.

The activities of different individuals in each of the social categories were recorded by two different observers during the spawning period using the UWrec. Some spawning records were made in pencil on PVC-slates while timing the pair spawnings with a water-proof stopwatch (table 2). Additional spawning observations at the deep spawning site of Karpata were made by hanging at a depth of 25 m and overlooking the spawning area. Notes were written on PVC-slates. Approximately 80 h were spent in observation.

Table 2: The number of individuals recorded with the UWrec per social category (SC); TT= territorial terminal-phase male, HI= harem initial-phase female, GT= group terminal-phase male, WT= wandering terminal-phase male, WI= wandering initial-phase; d= observation performed in duplo; t= observation performed twice on the largest harem female in the territory; \*= records made in pencil on PVC-slates (only frequencies).

Study site (time)	SC	Individuals observed during this study
Karpata (AM)	TT	KT1 d* KT2 d* KT3 d* KT4 d
	HI	KV1 t KV2 t KV3 t
	GT	KG1 d KG2 d KG3 d
Karpata (PM)	TT	KT1 KT2 KT3 KT4
Tori's reef	TT	TT1 d TT2 d TT3 d TT4 d
	HI	TV1 t TV2 t TV3 t TV4 t
Well's bay	WT	PG1 PG2 PG3 PG4 PG5
	WI	PV1 PV2 PV3 PV4 PV5 PV6 PV7 PV8 PV9

With the UWrec a continuous recording of behavioural components during a certain time period could be made. The behavioural components have been divided in two types: states and events. A state is the display of a certain type of behaviour during a measurable amount of time. An event is a phenomenon of very short duration that can occur during a state. Two states can never occur at the same time, so the start time of one state is the end time of the previous state.

Finbeat states, interaction states, and bite states, were recorded as bouts, consisting of a series of events. Every finbeat during swimming and interactions, and every bite, was recorded as a keystroke. A bout ended as soon as the fish displayed a different behaviour.

### ETHOGRAM OF SPARISOMA VIRIDE.

Behavioural categories related to reproduction:

State **high swim** (HiSwm): the displacement of the fish, while it is relatively high up in the water column, that is higher than all protruding obstacles within a radius of some two metres around the fish. This behaviour often precedes soliciting and courting.

State **solicite** (Solic): behaviour related to sexual display and refers to a fish signaling it's ready to spawn, without yet having established contact with one individual of the other sex (as far as evident to the observer). Such signals are zigzagging in the vertical plane (as mostly displayed by terminal-phase males) or an almost motionless hanging high in the water column, thereby occasionally spreading the median fins or slightly raising the head (as mostly displayed by initial-phase fish); it often precedes courting.

State **court**: behaviour always preceding (but not always followed by) a pair spawning. It can be recognized as the simultaneous and often synchronized movements of an initial-phase and a terminal-phase individual. It starts with an approach of the two individuals high in the water column, until the male swims directly above the initial-phase. After some synchronized zigzags in the horizontal plane, it may end in a sudden and very quick rush to a higher level in the water column, after which the pair spawning occurs.

Event **pair spawning** (PSpwn): After the very quick rush to a higher level in the water column, the terminal- and initial-phase individuals release their gametes, which is sometimes observed as a whitish cloud. Hereafter the terminal phase and the initial-phase immediately break up; pair spawning with or without a whitish cloud is recorded differently.

Behavioural categories not related to reproduction:

State **low swim** (LoSwm): the displacement of the fish, while it stays close to the bottom, following its relief at relatively constant distance.

State **interactions**: behaviour, by which the fish evidently responds to the occurrence or the behaviour of another fish. An interaction can either have a positive result (for instance chasing away of intruders) or a negative result (for instance being chased away) for the fish and is therefore recorded differently. The following interactions can be distinguished:

**interaction damselfish** (ldams)

**interaction terminal-phase** (lterm)

**interaction initial-phase** (linit)

**interaction remaining** (lothr)

State **bite dead coral** (Dbite): series of bites taken from dead coral.

State **bite living coral** (Lbite): series of bites taken from a living coral formation.

State **bite white spot** (Wspot): series of bites taken from a white spot, which is a conspicuous white grazing-scar in a living coral formation (mostly *Montastrea annularis*).

State **hanging** (Hang): the fish is hovering above the substratum, often with the head raised and the median fins spread out. This behaviour is often displayed when the fish is being cleaned.

State **laying** (Lay): the fish is resting with its ventral side on the substratum. This behaviour is always displayed by sleeping fish, but also by fish who are being cleaned by a cleaner shrimp.

Event **defecation** (Defec): the expelling of feces visible as a sandy cloud.

Event **yawning** (Yawn): the wide opening of the mouth without taking a bite.

Event **scrubbing** (Scrub): the fish scrubs one side along the substratum during a swimming motion.

Event **spitting** (Spit): ingested material is sometimes rejected again.

### 2.5.3 Data analysis and statistics.

All protocols obtained during the spawning period were reduced to one-hour sessions around the observed pair spawning(s) for analysis. When no pair spawnings had been observed, the one-hour protocols were synchronized with those of conspecifics who did spawn. As mentioned before, some protocols did not last 60 minutes and these were left out of the analysis.

The one-hour protocols of the different social categories were averaged. Average time percentages and standard deviations per hour of the behaviours low swimming, high swimming, biting (dead coral, live coral, and white-spot), and soliciting plus courting, were calculated. The average frequencies and standard deviations per hour of the events biting, defecating, and interactions with conspecifics (lterm and linit), were also calculated per social category.

To determine differences between the spawning behaviour of fishes at the different study sites, the time-budgets per social category during the spawning period were compared. For this purpose, the time percentages per behaviour per social category were tested using student's t test for unmatched samples ( $\alpha=0.05$ ). The same test was used to compare the frequencies of the events displayed during the spawning period. As the Student's t test requires the data to be normally distributed, the time percentages were transformed according to the arcsine-square root transformation (Martin & Bateson, 1986).

### 3 RESULTS

#### 3.1 SUBSTRATE DESCRIPTION OF THE THREE STUDY SITES

##### 3.1.1 Substrate cover of the reef zones at Karpata

Estimations of the percentage substrate cover of the different reef zones at Karpata showed that the shallow reef consisted for 83.3 % of dead coral (mainly large dead boulders of *Acropora palmata*) and for 13.9 % of small rubble (table 3). The sand/rubble zone is dominated by the substrata sand, dead coral, and rubble. The drop-off is mainly covered by star coral (25 %), but other corals may also be abundant. The reef slope consists mainly of dead coral (33.9 %) and star coral (31.1 %).

Table 4 shows the weighted average of the substrate cover of the reef off Karpata. It reveals that dead coral, star coral, sand, and rubble, are the main constituents of this reef.

##### 3.1.2 Substrate cover of the reef zones at Tori's reef

The first zone distinguished at Tori's reef comprises only sand, whereas in the second zone rubble (avg. 50 %) and staghorn coral (avg. 21.3 %) are the main components (table 3). The drop-off zone exists mainly of sand and rubble (53.3 %), while soft corals, dead coral and star coral make up 38.1 % of the substrate cover. The reef slope zone is dominated by dead coral (avg. 37.3 %), sand (22.1 %), star coral (avg. 15 %) and other corals (avg. 15 %).

Table 4 shows the weighted average of the substrate cover of Tori's reef. This reveals that sand takes up the highest percentage of cover (58.4 %) of this reef, which is caused by the extensive sand flat present at this site. The remaining zones on Tori's reef, where corals have developed, are dominated by rubble, dead coral, staghorn coral and star coral.

##### 3.1.3 Substrate cover of the reef zones in Well's bay

The average estimated percentages substrate cover of the three reef zones of Well's bay are shown in table 3. The encrusted boulders zone exists mainly of large basaltic boulders (avg. 67.2 %), while sand and other corals make up 9.8 % and 15 %, respectively, of the substrate cover. The soft coral zone is also composed of basaltic boulders and sand, but soft corals and brain coral are relatively more abundant in this zone. The third zone, an extensive sand flat, is totally made up of dark grey volcanic sand.

The weighted averages of the substrate cover of Well's bay (table 4) show that basaltic boulders (61.7 %) and volcanic sand (14.9 %) are the main components of the substrata covering the bay.

Table 3: The substrate description of the quadrats in the different reef zones of the three study sites. The percentages are the average of the estimated values of the substrate cover/unit surface area from two observers made of the nine squares that make up a quadrat. See also appendix A1-A3.

SUBSTRATE	KARPATA				TORI'S REEF				WELL'S BAY		
	QUADRAT				QUADRAT				QUADRAT		
	1	2	3	4	1	2	3	4	1	2	3
Sand	0	26.7	25.6	8.1	100	9.7	28.3	22.1	9.8	22.2	100
Dead coral	83.8	23	11.9	33.9	0	2.9	13.1	37.3	0	0	0
Rubble	13.9	38.4	9.6	0	0	50	25	0	0	0	0
Basaltic boulders	0	0	0	0	0	0	0	0	67.2	53.9	0
Star coral	0	4.7	25	31.1	0	7.6	10.9	15	2.3	2.6	0
Brain coral	0.6	1.4	6	8.7	0	2.3	1.8	3	2	6.8	0
Elkhorn coral	1.7	0	0	0	0	0	0	0	0	0	0
Staghorn coral	0	0	0.3	0	0	21.3	1.3	0	0	0	0
Other corals	0	5.1	13.4	11.7	0	2.4	6	12	15	4.2	0
Sponges	0	0	2.3	3.4	0	0.7	0.6	8	1.8	1.4	0
Soft corals	0	2.3	5.7	3	0	3.1	14.1	2.6	1.9	8.8	0

Table 4: The weighted average of the estimated percentages substrate cover/unit surface area of the three study sites Karpata, Tori's reef, and Well's bay.

SUBSTRATE	KARPATA	TORI'S REEF	WELL'S BAY
	% COVER	% COVER	% COVER
Sand	17.4	58.9	14.9
Dead coral	31.7	7.0	0.0
Rubble	14.2	15.5	0.0
Basaltic boulders	0.0	0.0	61.7
Star coral	17.8	5.2	2.4
Brain coral	4.7	1.2	5.0
Elkhorn coral	0.3	0.0	0.0
Staghorn coral	0.1	5.2	0.1
Other corals	9.0	2.9	9.5
Sponges	1.7	1.2	1.6
Soft corals	3.4	3.2	4.8

## 3.2 POPULATION DENSITY

### 3.2.1 Population density of *Sparisoma viride* on the reef off Karpata

Visual censuses show that the number of terminal- and initial-phase fishes decrease with depth (figure 6). However, the total number of juveniles (sizes <2 - 15 cm FL) reaches its maximum in the drop-off zone (31/1000 m<sup>2</sup>), whereas hardly any are found on the shallow reef.

Figure 9 shows the weighted average of the population density of the three study sites. For the reef of Karpata as a whole, the population density of terminal-phases, initial-phases and juveniles is 8/1000 m<sup>2</sup>, 5.6/1000 m<sup>2</sup>, and 20.8/1000 m<sup>2</sup>, respectively. Figure 6 shows that on the shallow reef of Karpata the color phase ratio (terminal-phase:initial-phase) is 2.3:1, while in the remaining three zones this ratio is 1:1. For the reef of Karpata as a whole, the color phase ratio of *Sparisoma viride* is 1.4:1 (figure 9).

### 3.2.2 Population density of *Sparisoma viride* at Tori's reef

Figure 7 shows the number of different life-phases of *Sparisoma viride* per 1000 m<sup>2</sup> in the different reef zones of Tori's reef. On the sand flat no stoplight parrotfishes were observed. In the other reef zones the density of both adult and juvenile fishes decrease with depth.

The weighted averages of the density of *S. viride* at Tori's reef are shown in figure 9. The density of terminal-phases, initial-phases and juveniles are 2.3/1000 m<sup>2</sup>, 4.9/1000 m<sup>2</sup>, and 12.7/1000 m<sup>2</sup> respectively. The color phase ratio (T:I) for the study site as a whole is 1:2.1 (figure 9).

### 3.2.3 Population density of *Sparisoma viride* in Well's bay

The number of adult stoplight parrotfishes per 1000 m<sup>2</sup> is extremely low in Well's bay, while the juveniles reach high densities (figure 8). The maximum juvenile density of 94/1000 m<sup>2</sup> is reached in the encrusted boulders zone. On the sand flat no *S. viride* are observed (figure 8).

The weighted average of the density of the different life-phases of *S. viride* in Well's bay is shown in figure 9. The density of terminal-phase males reaches 1.6/1000 m<sup>2</sup> and that of initial-phase fishes 1.1/1000 m<sup>2</sup>. The weighted average of the juvenile density is 63.4/1000 m<sup>2</sup>. The color phase ratio (T:I) of the adult fishes is 1.45:1 in Well's bay (figure 9).

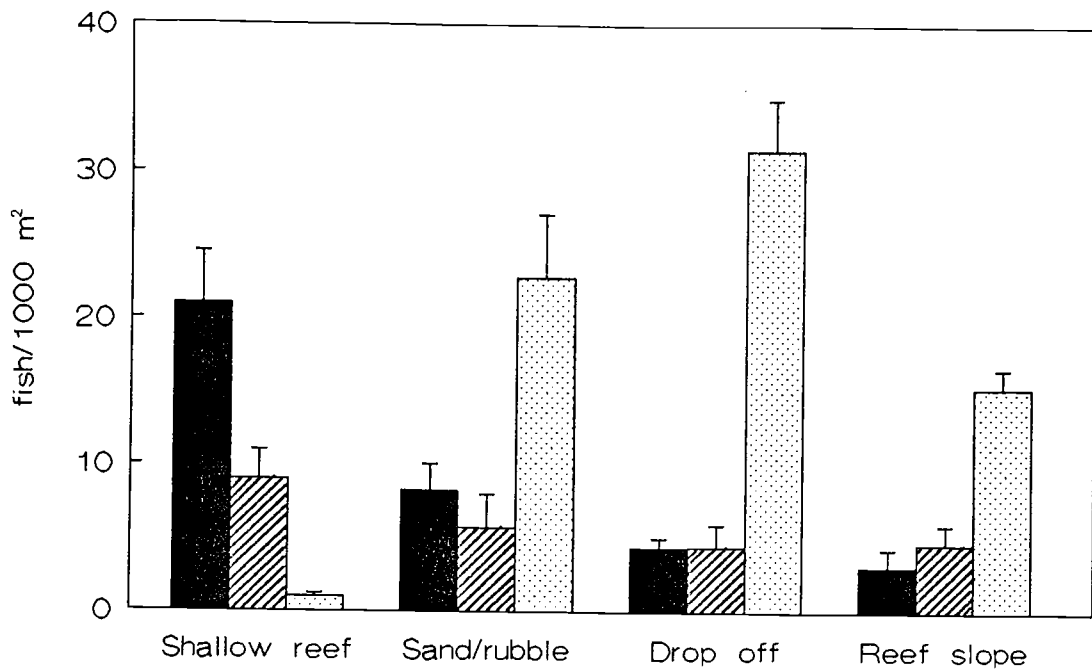


Figure 6: The average number of termphase males = , initial-phase fishes = , and juveniles = with standard deviation per 1000 m<sup>2</sup>, plotted against the different reef zones of Karpata (n=40). See also appendix A4.

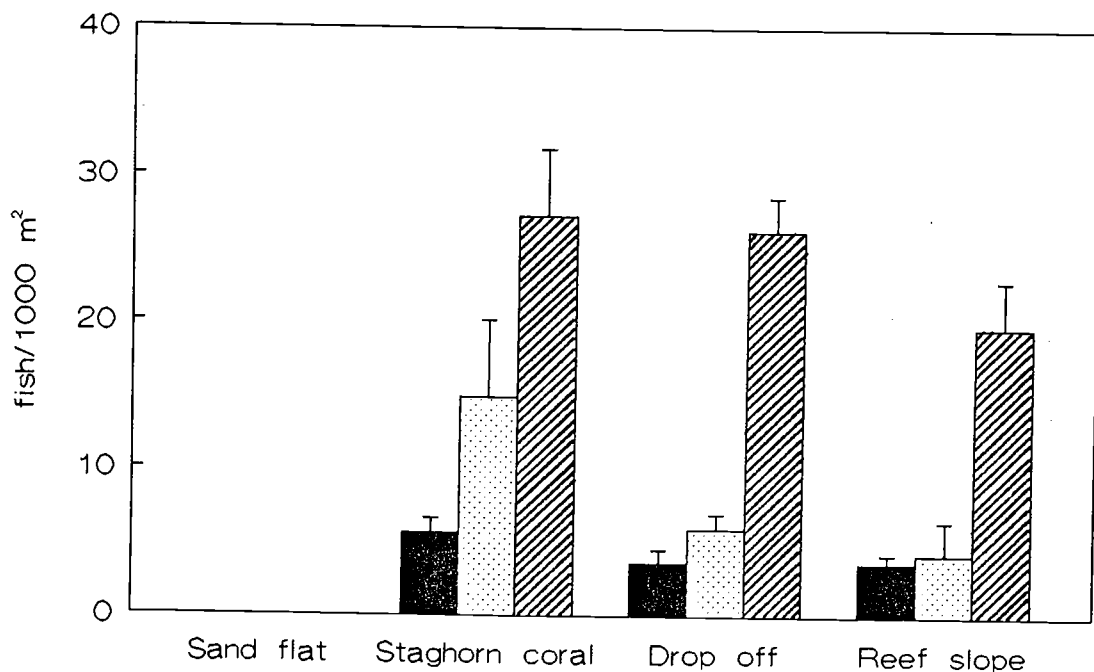


Figure 7: The average number of termphase males = , initial-phase fishes = , and juveniles = with standard deviation per 1000 m<sup>2</sup>, plotted against the different reef zones of Tori's reef (n=40). See also appendix A5.



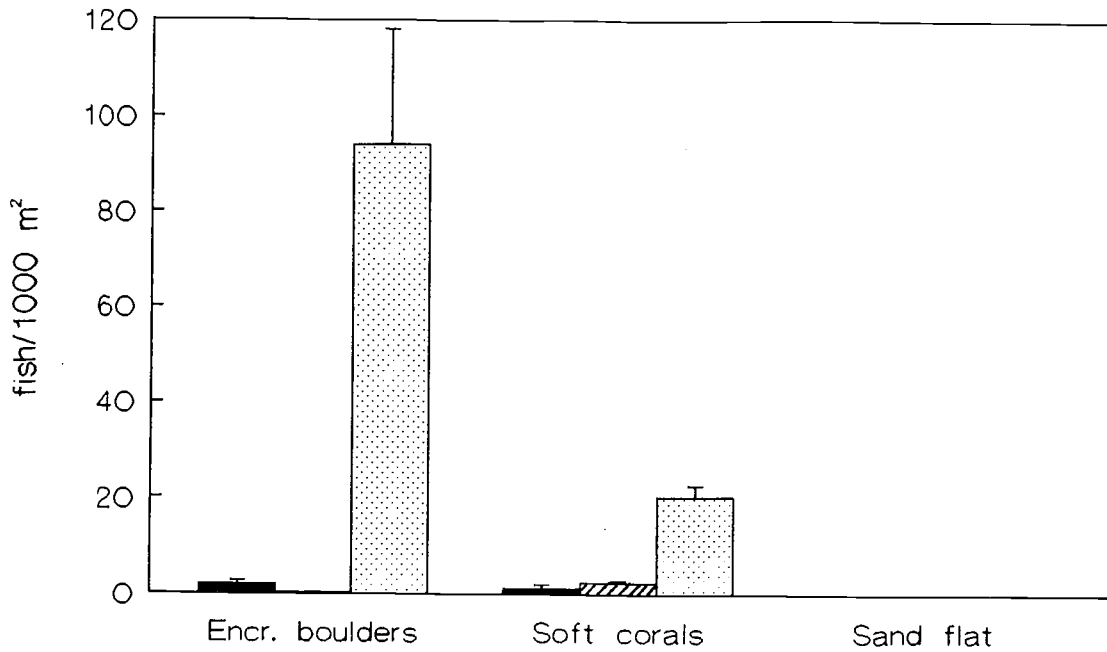


Figure 8: The average number of termphase males = , initial-phase fishes = , and juveniles = with standard deviation per 1000 m<sup>2</sup>, plotted against the different reef zones of Well's bay (n=40). See also appendix A6.

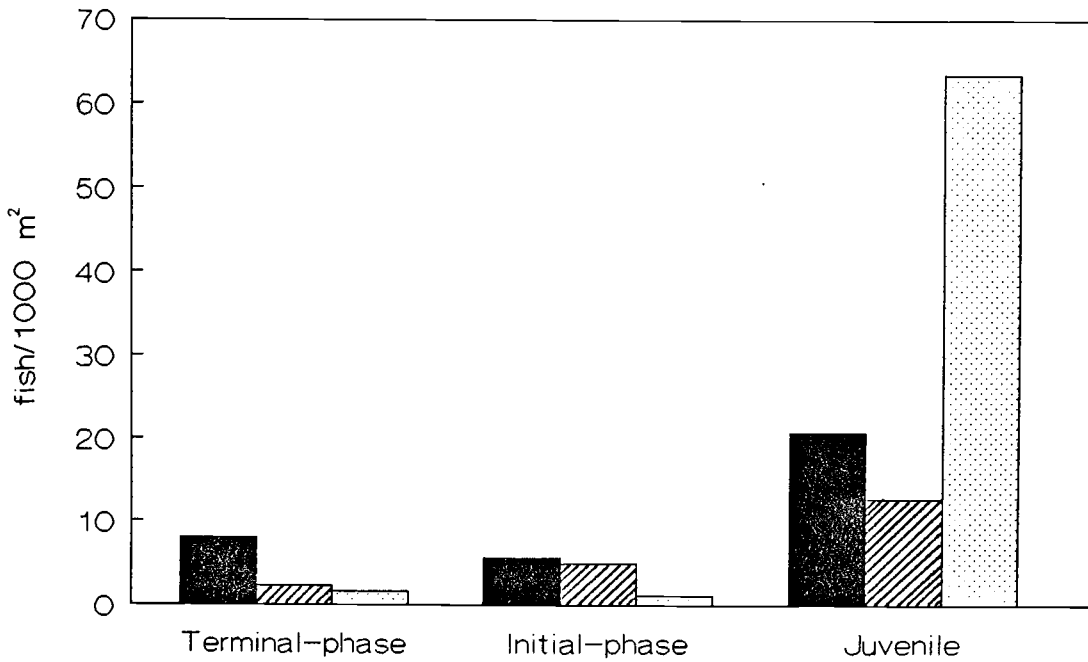


Figure 9: The weighted average of the number of terminal-phases, initial-phases and juveniles per 1000 m<sup>2</sup>, plotted against the three study sites. Karpata = , Tori's reef = , Well's bay = .

### 3.3 DAILY TIMING OF SPAWNING

The 12-hour observation of 27-03-1992 on the reef off Karpata (depth ca. 6m) revealed that sexual activity (courting and pair spawning) was displayed in the early morning from 07.15 h till 08.30 h and in the late afternoon from 17.30 h till 17.35 h. Recordings made hereafter during the months April and May showed that spawning by harem individuals consistently occurred in the early morning. The earliest spawning seen was at 07.07 h and the latest at 08.53 h (see appendix A7). Eighty-five pair spawnings involving territorial termphase males and (harem) initial-phase females were recorded during seventeen early morning observations with a total duration of 23 hours and 54 minutes (figure 10). On two days (13-05-1992 and 14-05-1992) territorial termphase males at Karpata were observed to determine the number of pair spawnings in the late afternoon. The first day the territorial termphase KT1 spawned twice and KT2 once (see appendix A7). The earliest spawning seen was at 17.20 h and the latest at 18.06 h (figure 10). Neighbouring fishes were also seen pair spawning during this time period. The second day no spawnings were observed by the territorial males KT3 and KT4. The absence of sexual activity was probably true for the entire population, as no neighbouring fishes were seen mating.

In the shallow waters of Tori's reef the 12-hour observation was made on 18-05-1992. Sexual activity by *S. viride* was observed in the mid afternoon from 14.45 h till 16.45 h. Recordings made hereafter in the months May and June showed that spawning by harem individuals occurred consistently in the mid afternoon. The earliest spawning seen was at 15.04 h and the latest at 16.47 h (see appendix A8). Forty-two pair spawnings involving harem termphase males and harem initial-phase females were recorded during sixteen mid afternoon observations with a total duration of 23 hours and 45 minutes (figure 10).

In Well's bay no sexual activity by *S. viride* was observed during the 12-hour observation of 06-07-1992. This suggested that mating, if it occurred at all, would probably not occur daily. After several observations during different parts of the day, the first pair spawning involving a termphase male and an initial-phase female was scored at 10.26 h (figure 10). However, the other fishes in the bay were not observed to spawn at this time. The following days, when observations were made during the same part of the day, no spawning activity was displayed by the study animals (see appendix A9). Seven days after the first spawning was scored, a single pair spawning was seen at 13.05 h (figure 10). Again no fishes in the surrounding area spawned at that time the same day, nor at that time in the following days. Five days after the second spawning was seen, a third one occurred in the early morning at 07.55 h (figure 10). The termphase male involved in this spawning mated with another female nearby several minutes later. Once again no spawning activity was observed the following days in the same time period (see appendix A9). Thus, in Well's bay the *S. viride* population did not spawn daily during the month July and timing of spawning was not consistent over a few days.

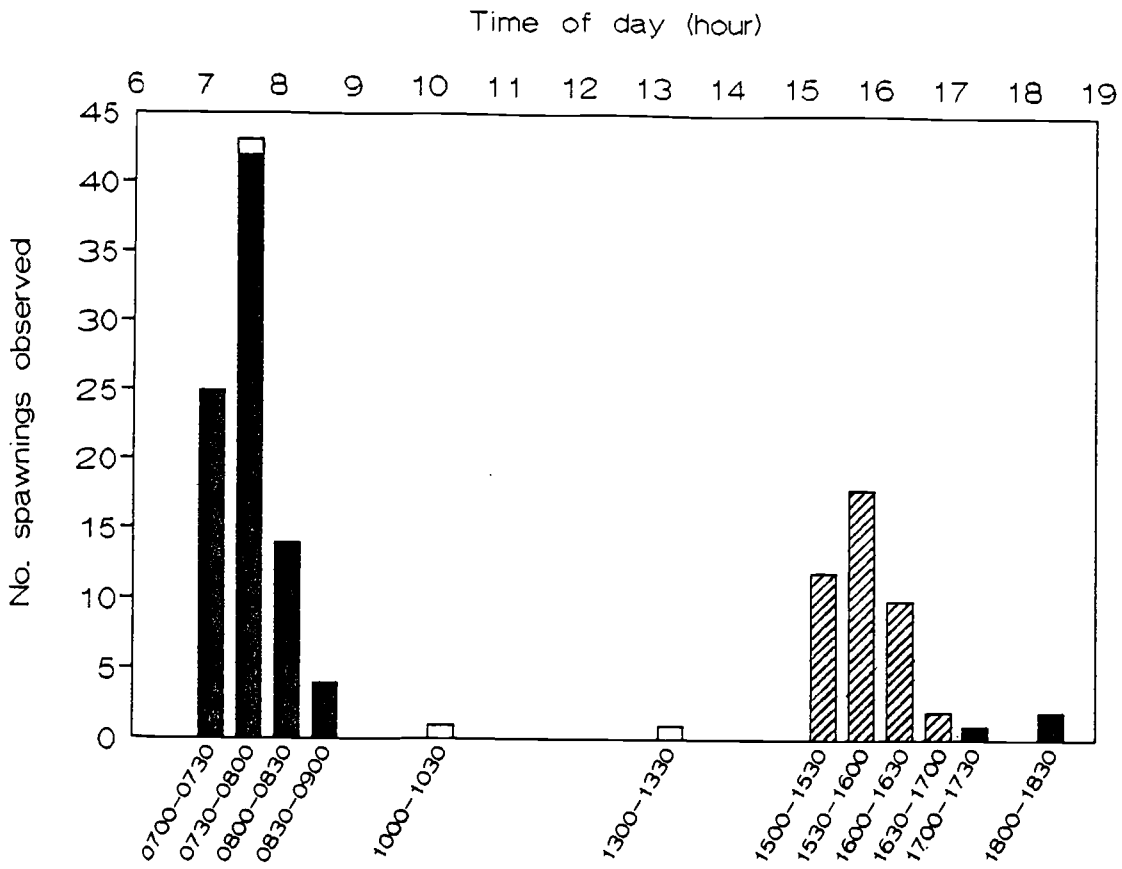





Figure 10: Daily timing of spawning by *Sparisoma viride* at the three study sites. The total number of pair spawnings observed during recordings are displayed per half-hour interval. Karpata = , Tori's reef = , Well's bay = .

### 3.4 LOCATION OF SPAWNING

At Karpata, the reef at depths between 3 till ca. 20 m is populated by terminal-phase males that hold permanent territories. The territories are defended against conspecifics and include a group of initial-phase females. During the early morning and the late afternoon spawning period these harem individuals mated in their territories. Termphase males living in groups on the shallow reef (0.5-3 m) were never observed spawning in their feeding area. On one occasion, a group initial-phase female was followed during the early morning spawning period. During the observation this female migrated to a deep spawning site, spawned there with a termphase male, returned to the shallower reef (ca. 7m), spawned again with an unknown territorial male, and finally swam to the shallow reef (<3 m) to join a group of feeding individuals. Thus, group females may spawn at a deep spawning site as well as within a harem males territory. Shortly after sunrise two known termphase group males were seen migrating to a deep spawning site (ca. 40 m), about 150 m away from their sleeping sites. However, these fishes were lost once the spawning site was reached so they were not actually seen spawning there. Many initial-phases were also seen migrating in small groups or alone to this deep spawning site after awakening, but it was unclear whether this were harem or group initial-phases.

At Tori's reef, the reef at depths between 5 and ca. 20 m is sub-divided into permanent territories with contiguous boundaries. The territories include a small group of females with whom the harem males mate during the mid afternoon spawning period.

In Well's bay, the wandering fishes swim about in the whole bay so spawning sites are probably not restricted to a certain home range. However, the three pair spawnings that were observed all took place in the soft coral zone about 200 m out of the coast where the water is ca. 10 m deep.

### 3.5 SPAWNING BEHAVIOUR OF *SPARISOMA VIRIDE*.

#### 3.5.1 Spawning mode and spawning rush

The common mode of spawning by *S. viride* on Bonaire and Saba is pair spawning. During this study 133 pair spawnings of *S. viride* were scored which all involved a terminal-phase male and an initial-phase female. Multimale spawning, as in group spawning and streaking, and sneaking of initial-phase males were never observed.

The stoplight parrotfish is a pelagic spawner, t.i., it produces pelagic eggs and releases them at the peak of an ascent made specifically for that purpose. The ascent usually starts while the fishes are swimming a few meters above the bottom, only sporadically starting off the bottom. At the apex of an upward rush the fishes flex their bodies sharply, thereby ejecting eggs and sperm considerably higher in the water column than the swimming level of the fishes when courting. The gametes may be visible as a whitish cloud for a couple of seconds. The female immediately returns to the bottom after the spawning and usually starts feeding. The male usually continues swimming high in the water column to wait for

other females to spawn with. At Karpata, after 58% of the observed spawnings a whitish cloud was visible, whereas at Tori's reef this occurred in 83% of the observed spawnings (see appendix A7 and A8). On Saba, all three spawnings resulted in a whitish cloud of gametes (see appendix A9).

During sexual activity no intensification of the termphase males color is observed. The initial-phase fishes gain a pale color when swimming high in the water column to join a termphase male or to start soliciting.

### 3.5.2 Spawning behaviour at the deep spawning site of Karpata

Around sunrise the parrotfishes awake and a part of the *S. viride* population migrates to a deep spawning site at first, before returning to their territories and home-ranges on the shallow reef where they spend the rest of the day. Most fish migrate at a depth of 10-13 m along the reef slope to the deep spawning site while swimming at a high speed. As the fishes have to pass through the territories of conspecifics, a lot of attacks by defending territory holders have to be endured.

Three early morning observations were made at the deep spawning site (24-05-1992, 04-06-1992, 08-06-1992). A few terminal-phase males characteristically arrive at the deep spawning site before the females ( $\pm 06.00$  h) and establish vigorously defended temporary spawning territories. The temporality of these territories was ascertained by the observation that in the afternoon the spawning site lacked the presence of these termphase males. Besides some termphase males were seen leaving the spawning site as the morning progressed. Two large termphase males ( $> 40$  cm FL) were observed establishing a territory at  $\pm 40$  m, while three males got hold of territories at a depth of about 25 m. Shortly after territorial boundaries have more or less stabilized, initial-phase fish begin arriving in small groups and roam about freely within and between the territories. Most initial-phases descend very deep, hereby passing the 25 m territories. Some initial-phases are being chased away (presumably the males), others are tolerated in the territories. The males spend all their time by actively trying to attract the passing females. They repeatedly swim 2 to 3 small rounds at a great speed which ends in a zigzagging movement upwards. When a female reacts positively to these sexual signals, short courting behaviour will follow which ends in a pair spawning. From  $\pm 06.30$  h till 07.15 h groups of initial-phase fish descend, return somewhere later, and are replaced by other groups. During this period ca. 30 pair spawnings take place between termphase males and initial-phase fish. After 07.15 h most initial-phase groups have left the spawning site and only some solitary initial-phases still descend into the deep. Despite the overwhelming numbers of initial-phases visiting the deep spawning site, no group spawning, nor sneaking or streaking, has been observed.

At a depth of 15 m a group of four terminal-phase males established a temporary home-range. The fishes spend a lot of time competing with termphase fishes of neighboring territoria. Regularly these group fishes were seen foraging in their home-range, but they were never observed in a pair spawning. At  $\pm 07.40$  h the group fishes left the site and swam to their home-range on the shallow reef.

### 3.5.3 Spawning behaviour on the shallow parts of the reef off Karpata

Around sunrise most territory holders presumably migrate from their sleeping sites to their territories directly after awakening. This was observed for one territorial male (KT2) that was followed. The harem initial-phase females will either do the same or migrate to the deep spawning site first. While observing the study area close after sunrise it was noted that most territory holders are usually present, but no or a few initial-phases could be scored in their territories. The number of group fishes (both termphase and initial-phase) present on the shallow reef during the first hour after sunrise is relatively low compared to the density of group fishes during the rest of the day.

On average, the territorial males spawned 7.4 times per morning, with a maximum of twelve and a minimum of two. Per morning the harem females mostly spawn once, but two of the six observed harem females spawned twice with the harem male (see appendix A7). The number of pair spawnings observed usually exceeded the estimated number of harem initial-phases present in the territory during the day (table 5). Accounting for the fact that harem females may spawn twice, this indicates that some harem termphase males may have both intra- and extraharem matings. Although no sneaking or streaking by initial-phase males has been observed, three observations were made of a territorial termphase male successfully "stealing" a spawning with a female who already had mated to the actively courting neighbouring territory owner. This behaviour only took place in an area close to their corresponding territory boundaries. The group fishes feeding on the shallow reef (<3 m) seem indifferent to the spawning activity of nearby harem individuals. No sexual activity has been observed among the termphase males living in groups (see appendix A7).

The frequency of late afternoon spawnings is low (avg. 1.5/afternoon; n=2) compared to that of early morning spawnings. Worth noticing about these afternoon matings is that the harem females seem to take the initiative in inducing a spawning in the termphase male. After the territorial males have spawned once or twice, they completely ignore the sexual signals of other females swimming high in the water column.

Table 5: The four observed territorial termphase males on Karpata (KT1-KT4) and the estimated number of harem initial-phase females present in their territories during the day. As 67% of the harem females spawn once and 33% spawn twice with the territorial males, the number of pair spawnings expected within the territory can be determined. TT= territorial terminal-phase; FL= fork length of territorial termphase; HI= harem initial-phase female; PS= pair spawning.

<b>KARPATA</b>				
TT	FL (cm)	No. HI estimated	No. PS expected	No. PS observed
KT1	35	5	5 - 6.7	5.0 ± 1.0
KT2	25	7	7 - 9.3	8.7 ± 1.5
KT3	35	5	5 - 6.7	4.3 ± 2.1
KT4	35	5	5 - 6.7	11.5 ± 0.7

#### 3.5.4 Spawning behaviour at Tori's reef

At depths between 5 and ca. 20 m the reef of Tori's reef is populated by harem individuals. All the termphase males seem to have occupied a territory, as there are no group fishes present. Sporadically, some wandering termphase fishes swarm by, causing some tumult among the harem groups.

On an average, the harem males spawned 4.1 times per afternoon, with a maximum of six and a minimum of three. The harem females normally spawn once a day with the harem male, but one of the eight observed harem females spawned twice with the same male (see appendix A8). The first spawning of this female was preceded by an intermittent spawning rush. Immediately hereafter the female continued swimming high in the water column and several minutes later the fishes spawned in the normal manner. Fifteen minutes after this spawning the female mated again with the same harem male (plus whitish cloud). The number of pair spawnings per territory usually corresponded with the estimated number of harem initial-phases present in the territory during the day (table 6). This indicates that the territorial males mate with their harem females exclusively.

Table 6: The four observed territorial termphase males on Tori's reef (TT1-TT4) and the estimated number of harem initial-phase females present in their territories during the day. As 87.5% of the harem females spawns once and 12.5% spawns twice with the territorial males, the number of pair spawnings expected within the territory can be determined. TT= territorial terminal-phase male; FL= fork length of territorial termphase; HI= harem initial-phase female; PS= pair spawning.

TORI'S REEF				
TT	FL (cm)	No. HI estimated	No. PS expected	No. PS observed
TT1	35	6	6 - 6.8	4.5 ± 2.1
TT2	30	5	5 - 5.6	5.0 ± 1.4
TT3	30	4	4 - 4.5	4.0 ± 0.0
TT4	30	3	3 - 3.4	3.0 ± 0.0

#### 3.5.5 Spawning behaviour in Well's bay

The wandering individuals of the *S. viride* population living in Well's bay spawn only sporadically during the month July. As only three pair spawnings of these fishes were observed, no substantial information can be given about their spawning behaviour.

### 3.6 THE TIME-BUDGET OF *S. VIRIDE* DURING THE SPAWNING PERIOD

On Bonaire, the time-budgets of territorial termphase males during the spawning period (figure 11) are greatly dominated by low swimming and biting (avg. 72% at both Karpata and Tori's reef). During the spawning period the territorial males living on the reef off Karpata spend significantly more time on the combined action of soliciting and courting (figure 11) than territorial males living at Tori's reef ( $P=0.049$ , unpaired t-test). Time spent on feeding by the males of Karpata is significantly less compared to the males of Tori's reef ( $P=8.89E-3$ , unpaired t-test). This is also reflected in the number of bites taken per hour (figure 12) which is significantly lower for territorial males of Karpata than that of territorial males of Tori's reef ( $P=3.86E-4$ , unpaired t-test). Accordingly, significantly less defecations take place during the spawning period on Karpata compared to Tori's reef ( $P=3.30E-3$ , unpaired t-test). Observations showed that four of the eight observed harem males at Tori's reef defecated during high swimming, whereas at Karpata this was observed for only two of the eight males. Frequencies of intra-group interactions (interactions between the territorial male and his harem females) and interactions with conspecific males (figure 12) do not differ between the territorial males living at Karpata and Tori's reef (all  $P>0.05$ , unpaired t-tests).

As group termphases on the reef off Karpata and wandering termphases in Well's bay were not seen spawning (appendix A7 and A9) during the numerous observations, no comparisons can be made between their time-budgets during the spawning period.

On Bonaire, the time-budgets of harem initial-phase females during the spawning period (figure 13) are also greatly dominated by low swimming and biting (avg. 85% at both Karpata and Tori's reef). No significant differences are found between the time-budgets of the harem initial-phase females at the two study sites (all  $P>0.05$ , unpaired t-tests). However, the number of bites taken per hour during the spawning period (figure 14) is significantly higher for harem females at Tori's reef compared to that of harem females at Karpata ( $P=0.01$ , unpaired t-test). Accordingly, the number of defecations per hour is also significantly higher at Tori's reef ( $P=1.04E-4$ , unpaired t-test). Observations showed that all harem females at Tori's reef defecated at least once (with an average of 3.9 times;  $n=8$ ) while swimming high in the water column and sexually displaying to a nearby male. Courting behaviour followed by a pair spawning was always preceded by a high swim-bout with one or more defecations. At the reef off Karpata defecations by females swimming high in the water column was never observed. Frequencies of intra-group interactions and interactions with conspecific initial-phases per hour (figure 14) are similar for harem females living at Karpata and Tori's reef (all  $P>0.05$ , unpaired t-tests).

On Saba, too few pair spawnings were observed following wandering initial-phase fishes to compose a time-budget of these fishes during the spawning period.



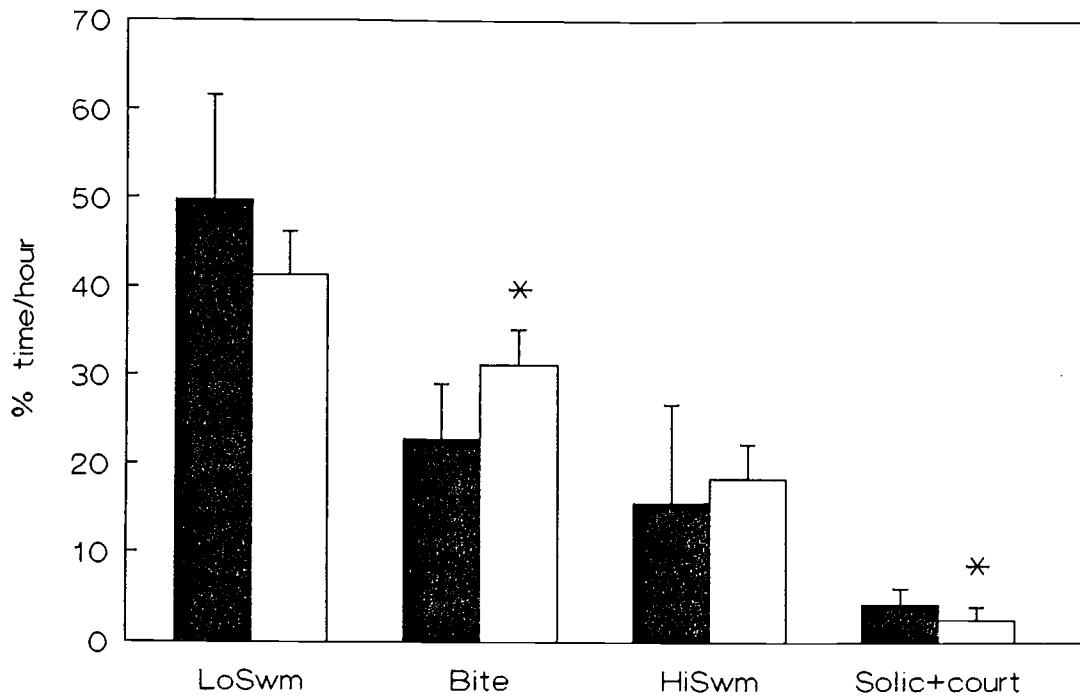


Figure 11: The time-budgets of four different behaviours displayed by territorial termphase males living at Karpata and Tori's reef during the spawning period. Behaviours are expressed as the percentage time per hour with standard deviation. See also appendix A10-A11. Karpata =  (n=8), Tori's reef =  (n=8). Significant differences are displayed by \*.

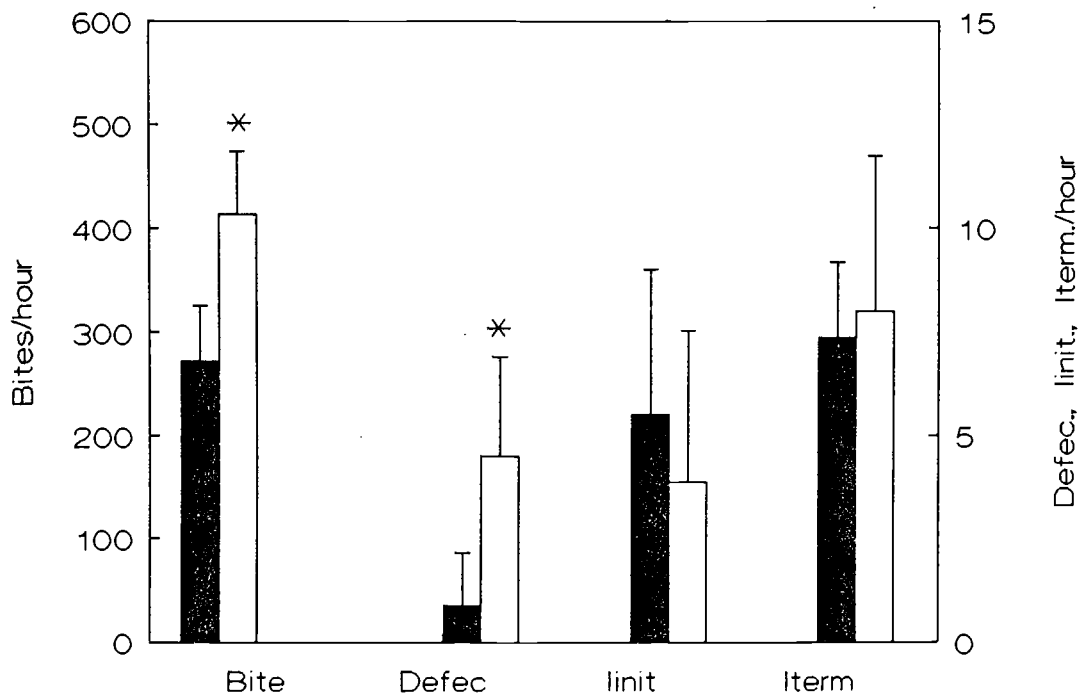


Figure 12: The frequencies per hour with standard deviation of four different behaviours displayed by territorial termphase males living at Karpata and Tori's reef during the spawning period. See also appendix A10-A11. Karpata =  (n=8), Tori's reef =  (n=8). Significant differences are displayed by \*.

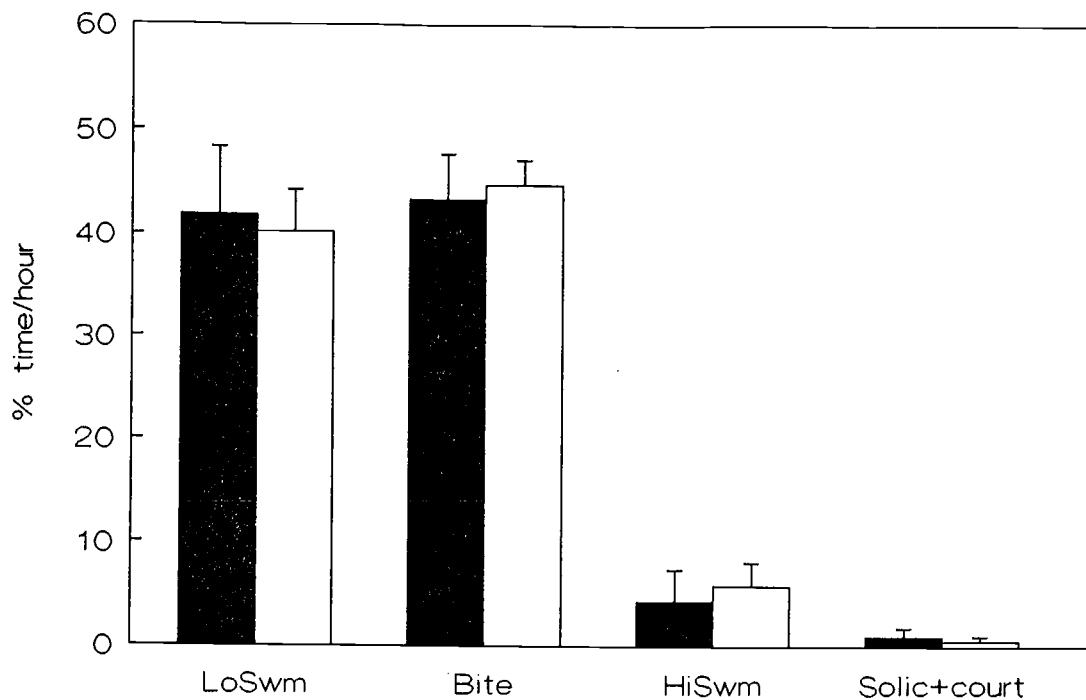


Figure 13: The time-budgets of four different behaviours displayed by harem initial-phase females at Karpata and Tori's reef during the spawning period. Behaviours are expressed as the percentage time per hour with standard deviation. See also appendix A12-A13. Karpata =  (n=5), Tori's reef =  (n=8). Significant differences are displayed by \*.

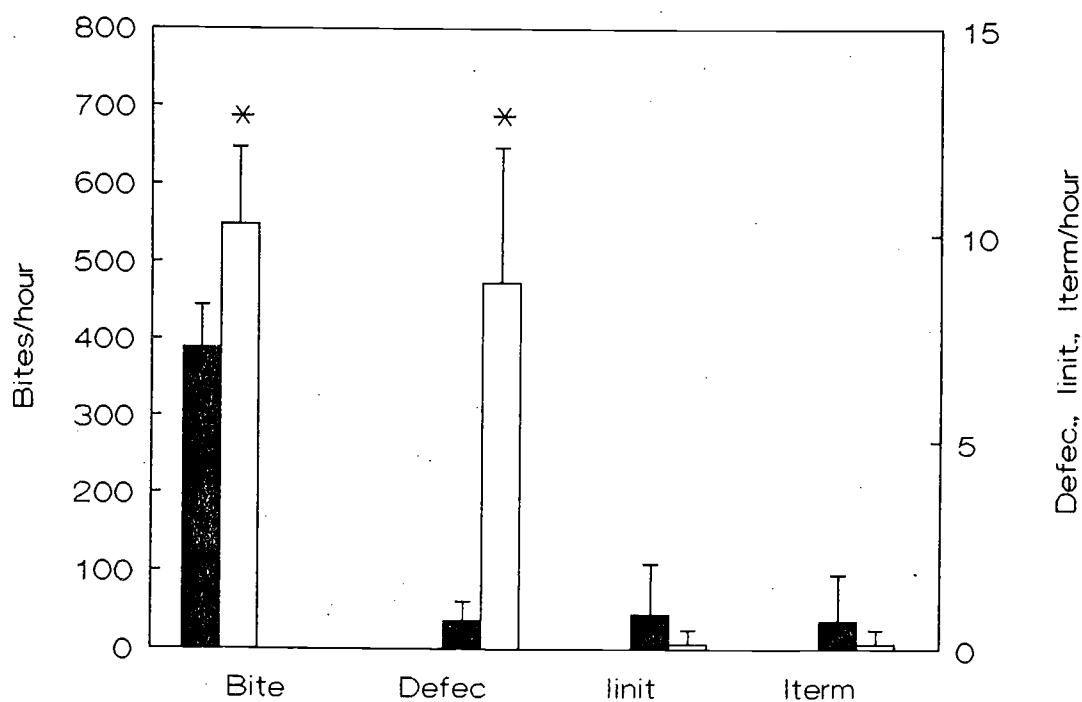


Figure 14: The frequencies per hour with standard deviation of four different behaviours displayed by harem initial-phase females at Karpata and Tori's reef during the spawning period. See also appendix A12-A13. Karpata =  (n=5), Tori's reef =  (n=8). Significant differences are displayed by \*.

## 4 CONCLUSIONS AND DISCUSSION

### 4.1 TIMING AND LOCATION OF SPAWNING OF *SPARISOMA VIRIDE*

#### 4.1.1 Daily timing of spawning

On Bonaire, the harem individuals of the *Sparisoma viride* population living at Karpata spawn consistently in the early morning (07.07-08.53 h) and occasionally in the late afternoon (17.20-18.06 h). Additionally, spawning of (mainly) group termphases and (harem) initial-phases at the deep spawning site of Karpata also occurs in the early morning but starts about one hour earlier (ca. 06.15-07.15 h). Zuidema (1989) and Kroon (1991) found similar spawning periods for this species living on the reef off Karpata. The harem individuals living at Tori's reef consistently spawn in the mid afternoon (14.45-16.47 h). Zuidema (1989) found a spawning period in this area that started around 13.00 h and continued till ca. 15.30 h. This difference might be caused by seasonal influences.

It has been proposed that adult biology may influence the evolution of diel reproductive patterns of reef fishes (Robertson, 1991). For example, diel spawning patterns of prey fishes may represent risk-minimizing responses to the diel feeding cycles of predatory fishes. Thresher (1984) suggested that most predatory fishes are least active during crepuscular periods so pelagic spawners could avoid high-risk periods by spawning at dusk. However, during this study *S. viride* was never observed spawning at dusk. As attempts by larger fishes to prey on spawning adults of *S. viride* were rare (personal observation), the daily timing of spawning is not likely to be influenced by the risk of predation during the spawning period. As reproductive output depends on food intake, daily spawning patterns could also represent adaptive responses that minimize feeding losses (Robertson, 1991). Feeding losses might be expected to have relatively strong effects on *S. viride* as it spawns frequently, spends much time feeding each day, and has an afternoon peak of feeding activity (Kroon, 1991). Thus, feeding costs might explain the early morning spawning period of the stoplight parrotfish at Karpata, but it does not explain the afternoon spawning period found at Tori's reef.

Diel spawning periods of pelagic spawners are also proposed to represent adaptations to larval requirements (Robertson, 1991). One hypothesis is that spawning is timed to reduce losses to mobile egg-predators. In this case, spawning in the afternoon or around dusk might be adaptive as diurnal egg-predators would be expected to be relatively satiated (Robertson, 1991). This egg-predation hypothesis might explain the afternoon spawning period of *S. viride* found at Tori's reef, but does not explain spawning in the early morning at Karpata. Predation on eggs by sergeant majors (*Abudefduf saxatilis*) immediately after release was observed in a few instances. However, the rapid up-down spawning rush might increase the difficulty with which egg-predators locate freshly spawned zygotes (Robertson & Hoffman, 1977), so actual rates of egg predation are probably too low to be of real significance. Johannes (1978) developed the hypothesis that the tidal regime is the primary factor controlling the daily spawning periodicity of reef fishes. He proposed that dispersal of planktonic propagules away from adult habitat is advantageous. Moreover, adults will facilitate dispersal and minimize predation

on propagules as they leave the reef by spawning at the stage of the tide most appropriate for dispersal, typically the beginning of ebb tide. If the eggs join an eddy, they will be transported off the reef at first, thereby avoiding predation by sessile filter-feeders (Young & Chia, 1987), and hatch offshore. A few days later the eddy will return to the reef where the larvae can settle on the home-reef and become juveniles. It is apparent, that *S. viride* populations spawn at different times of the day at different reefs on Bonaire. As phase eddies develop during certain stages of a tidal cycle on the lee of the reef (Black & Moran, 1991), it is possible that at one site the eddy develops earlier than at another site some distance away (Kingsford *et al.*, 1991). A combination of factors, like upwelling, tidal currents and trade winds, may also create locally different small-scale hydrographic conditions (Leis, 1982). It is possible that *S. viride* spawns during a time period that circular current patterns are most favourable for larval retention to the home-reef. At different localities of an island these favourable currents will occur on different times of the day for reasons mentioned before. Thus, spawning when currents are favourable for larval retention might explain the different times of day of spawning observed for *S. viride* populations living on the reef off Karpata (northwest Bonaire) and on Tori's reef (southwest Bonaire).

The initial-phase:juvenile ratio gives an indication of the rate of recruitment, as almost all females are thought to be sexually active. At Karpata this ratio is 1:3.7 and at Tori's reef 1:2.6. Recruitment rates might thus be somewhat higher on Karpata compared to Tori's reef. Given the hypothesis that larvae return to the home-reef, this could be a result of the higher spawning frequency of harem groups on Karpata (avg. 7.4/day) compared to that of harem groups on Tori's reef (avg. 4.1/day). However, it is also possible that the mortality rate of larvae settling on Tori's reef is higher than that of larvae settling on Karpata. This may be caused by high predation rates, low food-supply, competition, or other factors.

The spawning activities of both the *S. viride* population living on the reef off Karpata and on Tori's reef are synchronized. This may have several advantages, regardless of the time in which spawning takes place. One is that spawning synchronously could oversaturate active egg-predators (Robertson & Hoffman, 1977) and dilute the predation risk on the spawning adults. Another is that spawning can be accomplished quicker if all individuals are primed to spawn at a particular time (Colin & Clavijo, 1988). Moreover, more time can be spent on other activities, such as feeding, which might increase the number of gametes that can be produced (Colin & Clavijo, 1988).

On Saba, observations on the nonharem individuals living in Well's bay suggested that they do not spawn daily during the month July. Only three pair spawnings were observed which all occurred at different times of the day, ranging from 07.55 h till 13.05 h. Thus, timing of spawning is not constant over a few days and pair spawning seems not synchronized within the population. The reason for the fishes to spawn at different times of the day may be that the fishes can track the tide. As the time of peak height changes through the day, following this tide would permit the fishes to spawn in optimal current conditions almost daily. Spawning at ebb tides is thought to be adaptive to maximise dispersal of the eggs away from the reef with its potential predators (Johannes, 1978). However, it is unknown if the observed pair spawnings at Well's bay coincided with ebb tide or not.

The initial-phase:juvenile ratio in Well's bay is 1:57.6 which indicates a high rate of recruitment. Taking into account that adult fishes in Well's bay were only sporadically seen spawning, this high recruitment rate might indicate a supply of larvae from other regions. A possible resource for these larvae might be the Sababank. This "drowned" atoll is situated ca. 6-21 kilometers southwest of Saba (Wells, 1988) and its top is some 12 to 20 meters below sea-level (Zonneveld, 1977). When this shallow bank functions as a resource for larvae that disperse to the coast of Saba, then this could explain the high numbers of juveniles present in Well's bay. However, the existence of a spawning season might also explain this high juvenile density (see 4.1.2).

#### 4.1.2 Seasonal timing of spawning

Spawning of *Sparisoma viride* on Bonaire occurs year-round (Zuidema, 1989; Kroon, 1991; this study). This was also suggested for this species living in Panama (Robertson & Warner, 1978) and on Turks and Caicos Islands (Koltes, 1993).

On Saba, only some fishes spawned sporadically on the home reef in July. Therefore, it may be possible that the main breeding season was over, and that spawning only occurred at a low level. Colin and Clavijo (1988) suggested a spawning season for *S. viride* in southwestern Puerto Rico from October till April. Munro *et al.* (1973) suggested the breeding season of *S. viride* on Jamaica extends from October through May, based on fishes caught with active gonads. They believed that spawning is initiated when water temperatures drop below 28°C (to a minimum of about 26.5°C) and largely terminates when this temperature is exceeded. As Jamaica and Saba are situated on the same latitude, one might expect that spawning on Saba is also confined to the cooler months of the year (October-May). The existence of such a spawning season might explain the high number of juveniles found in Well's bay during this study. A recruitment peak would be expected ca. two months after the spawning season (Hunt von Herbing & Hunte, 1991), t.i., in July and August. As the population counts on Saba were conducted in July, this might explain the high juvenile density that was found in Well's bay.

#### 4.1.3 Spawning sites

The harem individuals of *S. viride* living at Karpata and Tori's reef spawn within their permanent feeding territories. This could be detrimental to the fishes, as moving to another area might be more favourable for egg dispersal. However, the male probably gains more by staying in his territory where food resources are favourable and where the male is guaranteed spawnings rather than moving elsewhere (Robertson & Hoffman, 1977). The harem females, living within the borders of a termphases territory, are assured of a fit male with whom they can mate daily (Barlow, 1975). Group fishes living in home ranges on the shallowest parts of the reef were never observed spawning in their feeding area. According to Shapiro *et al.* (1988) it would be a disadvantage for these fishes to spawn in their feeding area, because any eggs or larvae caught near the surf zone would be transported either up onto or over the reef crest. The only available spawning sites left for group fishes to spawn would be those that are not occupied by territorial

males, that is, the deep water sites. Thus, for mating the group fishes have to migrate to deep water. Many group fishes (both termphase and initial-phase) and harem females probably migrate to the deep spawning site at Karpata close after sunrise. This is assumed as their density on the reef during the first hour after sunrise was relatively low and increased as the morning progressed. Two known group termphases were actually seen migrating to the deep spawning site, but they were not observed spawning there. This is not surprising as only two or three males will be able to get hold of the limited number of available deep spawning sites at a depth of ca. 40 m.

Randall and Randall (1963) suggested that the areas where fishes concentrate their spawning activity are those that provide the best chance of eggs being carried off a reef and away of reef-based egg predators. Voltatina (1975) assumed that spawning at a deep site might be an adaptation to assure rapid offshore transportation of the eggs by an upwelling current caused by the offshore trade wind. It is questionable, however, whether the current system among the deep spawning site at Karpata could explain the choice of this spawning site rather than any other potential site on the deep reef. Other numerous non-spawning sites in the same area probably fell under the same current regime as the spawning site (Shapiro *et al.*, 1988). The deep spawning site at Karpata has been used daily for at least 3 years (van Rooij, personal communication). Thus, it is also possible that this site was originally chosen because of some favourable characteristics (for example, the site may be readily differentiated by fish from the surrounding areas for the benefit of fishes being able to quickly locating the site) and later on became traditional and learned by younger individuals from more experienced adults (Shapiro *et al.*, 1988).

## 4.2 SPAWNING BEHAVIOUR OF *SPARISOMA VIRIDE*

### 4.2.1 Spawning rush

All parrotfishes have evolved a spawning manner in which the gametes are released at the apex of an spawning rush. Randall (1961a) suggested that the sudden upward rush may facilitate the expulsion of eggs and sperm because of the expansion of the air bladder from the pressure change. Also the sharp flexing of the bodies of the spawning fish at the peak of the movement probably enhances the release of sex products. Thresher (1984) hypothesized that spawning ascents may be a means of releasing the gametes at a height above the reef that is sufficient for such eggs to achieve positive buoyancy before drifting within the reach of benthic filter-feeders. Furthermore, spawning ascents may be adaptive in that they result in the eggs being transported rapidly offshore, because there may be strong selection to place the eggs where there will be an area of high food concentrations upon hatching and subsequent first feeding (Thresher, 1984).

#### 4.2.2 Mode of spawning

During this study only spawnings which involved a terminal-phase male and an initial-phase female were scored. Thus, pair spawning seems to be the general spawning mode of *S. viride* on Bonaire and Saba. Parrotfishes do not have intromittent organs and fertilization is external (Reeson, 1983). Although external fertilization makes sneaking, streaking and group spawning possible (Warner *et al.*, 1975), these spawning modes were not observed at the three study sites. Spawning by individual pairs was also observed for *S. viride* in the Virgin Islands (Randall & Randall, 1963), Puerto Rico (Colin & Clavijo, 1988), and Panama (Robertson & Warner, 1978). Group spawning as a reproductive mode of the stoplight parrotfish has never been documented. Randall and Randall (1963) suggested that group spawning is related to the attainment of sexual maturity by males before the color change has been effected. If this is the case, initial-phase males must be rare or only transient in *S. viride* populations. Robertson & Warner (1978) found that 10.1 % of the initial-phase fish living near the San Blas Islands of Panama were males. However, no indications of successful sneaking and streaking by initial-phase males, or any group spawning which involved only initial-phase fishes, were seen (Robertson & Warner, 1978). Thus, even with one of the ten initial-phase fishes being a male, pair spawning between fishes of different color is the basic and most frequent reproductive pattern of *S. viride*.

#### 4.3 THE SOCIO-SEXUAL SYSTEM AND EFFECTS OF SUBSTRATE CHARACTERISTICS AND POPULATION DENSITY

At Tori's reef, with exception of the sand flat, the predictable availability of a limiting food resource in space and time probably has enabled this resource to be defended in feeding territories (Hixon, 1980). Robertson and Hoffman (1977) hypothesized that the continuing attachment of a female to a fixed and limiting resource, such as a foraging site, enables a larger male to exert behavioural control over her by aggressively dominating her. He can penalize the female if she is sexually uncooperative by reducing her access to that resource. A male can set up a harem by controlling a number of such females. The ability of a male to dominate a known group of females thus enables him to ensure that they mate exclusively with him. On the extensive sand flat no *S. viride* individuals are found. The absence of fishes in this zone is probably caused by the fact that the stoplight parrotfish does avoid feeding on algal turfs on sand (van Oppen, 1990) and by the absence of shelter sites. Thus, at Tori's reef all members of the *S. viride* population live in harems, and consequently there were no signs of any males employing a strategy of interference in the spawning activities of territorial males. The color phase ratio (terminal-phase:initial-phase) is 1:2.1. As expected for a reef occupied by harem groups, this ratio is favoured at the site of the initial-phases. However, this ratio is lower than suggested by the average number of harem females present in the territories that were observed. This indicates that during the visual counts the initial-phase fishes were more underestimated than the termphase fishes.

At Karpata, the deeper parts of the reef (>3m) are covered by large algal turfs and sparse turfs on endolithic algae, a food-supply favoured by *S. viride* because of its high energy content (van Oppen, 1990). The presence of these high quality food patches on the deeper parts of the reef allows this resource to be defended and thus harems have been developed. The high energetic yield of the food within the territory allows the male to spend less time feeding and use this "extra" time for defending his territory (Bruggemann, 1993). The harem male expresses his dominance by being aggressive to the females. Robertson & Hoffman (1977) assumed that during the spawning period harem females would be unable to leave the group to spawn elsewhere as the male could penalize a female by reducing her access to food within the territory. Indeed, no harem females were seen leaving the group during the spawning period during this study. However, harem females may take part in spawning migrations to a deep spawning site before the spawning period of the harem groups starts. This is assumed as harem females are largely absent in the territories during the first hour after sunrise. Thus, many harem females probably first spawn once at the deep spawning site shortly after awakening, and later spawn another time with the harem male in their feeding area. The harem male may also have extraharemic matings (table 5).

On the shallow reef of Karpata almost the entire substrate (ca. 98%) is suitable for grazing. In this zone sparse algal turfs on coral rubble and on crustose corallines are dominant. However, this food-supply is not favoured by the stoplight parrotfish because of its low energy profit per bite (Bruggemann, 1993). This uniformly distributed low energy food resource and the high number of *S. viride* in this zone indicate that holding and defending a territory in this zone would be both unprofitable and impossible. Thus, these individuals are forced to employ an alternative strategy: they form stationary feeding groups on the shallow reef. They consisted of up to 8 fishes of both color phases and a variety of sizes (Kraan, 1993). The females in these groups probably form a source of extraharemic mating for the harem males. Most of the time, however, these groups seem indifferent to the spawning activity of nearby territorial termphase males. Interference of group males in spawnings of harem groups is never observed. Probably, the strategy that is followed within this group is that both terminal-phase males and initial-phase fish channel their energy into growth until a reproductively profitable size is reached, either to become a harem female or a territory holder. Reproduction is not performed by these fishes. However, group termphases who already have grown to a size large enough to become a territorial male, probably channel their energy into spawning migrations to the deep spawning site. These males subsequently have to put a lot of energy into contesting for, and holding, the best spawning sites. The sites can only temporarily be defended, as the males have to return to their feeding area after the spawning period. These aspects have produced sexual competition in the form of a lek society. Given such an arrangement of the males, the females can increase their inclusive fitness by selecting the male that occupies the best site. That means the largest and strongest male (Barlow, 1975). Observations on the deep spawning site showed that the majority of initial-phase females visited the temporary territories at depths of 35-40 m. Indeed, males that had established territories that deep were very large (FL >40 cm). These observations may indicate that the deepest sites are the most favourable for spawning. The males are competing continuously to attract and induce spawning in females that pass their



territories. Sexual signals in males are well developed and there seems to be a low threshold of male responsiveness to females. By such behaviour, a male can maximize the number of females he attracts, encounters, and attempts to spawn with (Selander, 1972 in Robertson & Hoffman, 1977).

The color phase ratio at Karpata is 1.4:1. This ratio reflects the high density of group termphases present on the shallow reef. However, harem groups also form a great part of the *S. viride* population at Karpata as they inhabit the reef from 3 to a depth of ca. 20 m. Thus, one expects the color phase ratio to be in the advantage of initial-phase fishes. As this does not emerge from the visual counts, this could mean that the initial-phases were more underestimated than the termphases during the counts.

In Well's bay the *S. viride* population lacks every sign of territorial behaviour. The fishes were found dispersed singly throughout the bay ( $\pm 3.5 \text{ km}^2$ ) or in small, transient groups of up to 7 fishes of both color phases and of different sizes (Kraan, 1993). The general feeding pattern of the group fishes is to swim in small groups for some distance and then descend, feeding while spacing out and becoming relatively solitary, then ascend, reform the group, and move on. The main food resource (algae) will probably be sparse or patchy distributed, as only solitary individuals or small groups are expected to effectively exploit such a resource (Hanley, 1984).

The density of adult fishes in Well's bay is a factor 5 lower than that of adults living on the reefs Karpata and Tori's reef. On Bonaire, *S. viride* prefers to graze on both epilithic and endolithic algae growing on reef rock surfaces and in dead coral and coral rubble (van Oppen, 1990). On Saba no real coral reef has been developed, as the surf swept rocky shores are not favourable for reef development. Coral growth is mainly restricted to cobbly bottoms and the leeward side of boulders (Roos, 1971). Thus, boring algae which normally inhabit dead reef rock might not be able to inhabit basaltic rocks. In that case, endolithic algae might not be available for herbivores to feed upon on Saba. Well's bay might thus have a lower food-supply and subsequently a lower capacity to maintain large numbers of herbivores, such as *Sparisoma viride*.

Another explanation for the extremely low density of adult stoplight parrotfishes in Well's bay is the fact that *S. viride* is regularly spearfished by local inhabitants and fishermen on Saba. In consequence of this, the adult fishes will be kept at a low density. On Bonaire, spearfishing is forbidden since 1971 so populations can there reach their maximum density without human interference. The low numbers of adult stoplight parrotfishes in Well's bay might also be the result of both a low food-supply and spearfishing.

In summary, three different socio-sexual systems for *S. viride* were found at the three study sites. This suggests a basic flexibility of the scarid socio-sexual system that is shaped by factors as population density, availability of (and competition for) spawning sites, and the distribution in space and time of food and shelter sites (Thresher, 1984). Each type of socio-sexual system may be successful in a different habitat and may thus account for the continued success of many types of socio-sexual systems (Robertson & Warner, 1978).

#### 4.4 THE TIME-BUDGET OF *S. VIRIDE* DURING THE SPAWNING PERIOD

Comparing the time-budgets of territorial males during the spawning period, the time spent on the combined action of soliciting and courting differs significantly between Karpata and Tori's reef. On Karpata, territorial termphase males may spawn up to twelve times per morning (see appendix A7), as opposed to territorial males at Tori's reef that spawn with a maximal frequency of six per afternoon (see appendix A8). Thus, time spent on attracting the females and courting with them will subsequently be higher at Karpata. Time spent on biting differs significantly between Karpata and Tori's reef. This is probably due to the part of day at which spawning occurred. Kroon (1991) found that territorial males at Karpata spent significantly less time biting during the morning period (up to two hours after sunrise) compared to the afternoon and evening period (hour before sunset). Thus, the percentage time spent on biting is not related to the spawning period but to the time of day.

The number of male-female intra-group interactions at Tori's reef is  $3.9 \pm 3.7$  per hour during the spawning period (figure 15) and is not significantly different from that during the non-spawning period (Kraan, 1993;  $P=0.52$ , unpaired t-test). These interactions usually involve the male being aggressive to the females. The expression of the male dominance is important to each males sexual success, as it enables him to control numerous females and prevent any member of his harem from changing sex and reducing the size of his harem (Robertson, 1972). At Tori's reef the termphase males have small harems (avg. 4.5). Thus, the males can exert high levels of control over their females, which assures them that no extraharemic matings take place. Furthermore, as the harems are small, the loss of a single spawning is significant to the dominant male, and strong attempts to prevent them would be expected (Robertson & Warner, 1978). At Karpata, the frequency of male-female intragroup interactions during (figure 15) and outside (Kraan, 1993) the spawning period is similar to that found among harem-groups of Tori's reef. However, termphase males at Karpata have relatively large harems (maximum 7) and thus may not exert high levels of control over their females. This allows the females to have extraharemic matings. Van Rooij (personal communication) has seen harem females leave the harem to spawn elsewhere, but this never occurred during this study. The lack of high control over their harems may also have allowed for the successful "stealing" of harem females by neighbouring territory holders at Karpata. During the spawning period the number of interactions with conspecific males is also similar for territorial males at Karpata and Tori's reef. This might be surprising as at Karpata a large number of group termphase males are present a little away from the males territories. However, most of the time these males seem indifferent to the spawning activities of territorial males and interferences in spawnings of harem males were never observed.

During the daily spawning period both harem initial-phase females living at Karpata and Tori's reef normally spawn once with the harem male. Thus, it is not surprising that no significant differences were found between the time spent on sexual activities by harem females at Karpata and Tori's reef (figure 16). Moreover, the part of day in which spawning occurs has little effect on the time spent on non-reproductive activities by the harem females living at Karpata and Tori's reef.

Harem females at Tori's reef defecate significantly more frequent during the spawning period compared to harem females at Karpata (figure 17). This difference is probably related to the time of day of spawning. Harem females living at Tori's reef are actively feeding before the spawning period starts. Therefore, they will have full guts by the time spawning activities commence. Gut contents may be expelled during the upward spawning rush together with the gametes because of the expansion of the air bladder from the pressure change. To avoid the mixing of feces and gametes the females, and to a lesser extent the males at Tori's reef also, probably empty their guts before joining their mates in a spawning rush. As the females usually defecate during high swim bouts preceding the courting behaviour, the defecations may also have the additional function of a sexual signal towards the territorial male. Harem females living on the reef off Karpata probably had empty guts before their spawning activities in the early morning started, so their need of expelling their feces during high swim bouts preceding a spawning rush was absent.

In summary, all differences found between the time-budgets of harem individuals living at Karpata and Tori's reef can be explained by different environmental conditions, social factors, or time of day. Thus, the observed differences in the spawning behaviour of *S. viride* between different localities are unlikely to be a result of genetic differences between the populations.

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## APPENDIX

- Table A1-A3: Substrate description of the squares of the quadrats in the different reef zones of the three study sites.
- Table A4-A6: Population density of *Sparisoma viride* at the three study sites.
- Table A7-A9: Date and time of day of spawning of *Sparisoma viride* at the three study sites.
- Table A10-A15: Time percentages per hour (and their arcsine-square root transformed values) and frequencies per hour of different behaviours displayed by different social categories at the three study sites during the spawning period.



Table A1: Substrate description of the quadrats in the four reef zones of KARPATA. The values (%) are averaged estimates of the substrate cover/unit surface area from two observers.

KARPATA										
SUBSTRATE	THE SQUARES OF QUADRAT 1 IN THE SHALLOW REEF ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Dead coral	80	85	90	85	85	90	80	80	80	83.8
Rubble	20	15	9	15	14	10	14	13	15	13.9
Brain coral	-	-	1	-	1	-	1	2	-	0.6
Elkhorn coral	-	-	-	-	-	-	5	5	5	1.7
SUBSTRATE	THE SQUARES OF QUADRAT 2 IN THE SAND/RUBBLE ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	5	60	60	10	40	5	5	25	30	26.7
Dead coral	5	10	10	80	5	-	70	10	10	23
Rubble	85	20	20	1	40	75	-	45	50	38.4
Star coral	3	4	3	2	3	5	15	5	2	4.7
Brain coral	1	-	1	2	1	-	3	3	2	1.4
Other corals	-	5	5	4	9	10	6	6	1	5.1
Soft corals	1	1	1	1	2	5	1	5	4	2.3
SUBSTRATE	THE SQUARES OF QUADRAT 3 IN THE DROP OFF ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	40	25	15	50	5	15	40	10	30	25.6
Dead coral	10	4	5	10	15	20	20	15	10	11.9
Rubble	15	15	35	2	5	5	5	-	4	9.6
Star coral	15	30	10	15	40	25	20	40	30	25
Brain coral	5	3	3	10	8	5	5	10	5	6
Staghorn coral	1	1	-	-	-	1	-	-	-	0.3
Other corals	5	15	16	8	21	20	6	15	15	13.4
Sponges	2	2	1	1	2	5	2	5	1	2.3
Soft corals	7	5	15	4	4	4	2	5	5	5.7
SUBSTRATE	THE SQUARES OF QUADRAT 4 IN THE REEF SLOPE ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	5	15	5	10	10	5	15	5	3	8.1
Dead coral	20	10	20	30	32	30	58	50	55	33.9
Star coral	60	50	40	30	30	40	-	15	15	31.1
Brain coral	8	10	10	15	10	5	5	10	5	8.7
Other corals	4	13	16	10	10	17	5	15	15	11.7
Sponges	1	2	4	4	3	1	6	5	5	3.4
Soft corals	2	-	5	1	5	2	1	-	2	3

Table A2: Substrate description of the quadrats in the four reef zones of TORI'S REEF. The values (%) are averaged estimates of the substrate cover/unit surface area from two observers.

TORI'S REEF										
SUBSTRATE	THE SQUARES OF QUADRAT 1 ON THE SAND FLAT									
	1	2	3	4	5	6	7	8	9	
Sand	100	100	100	100	100	100	100	100	100	100
SUBSTRATE	THE SQUARES OF QUADRAT 2 IN THE STAGHORN CORAL ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	4	5	5	15	5	10	3	20	20	9.7
Dead coral	2	-	1	4	3	5	3	3	5	2.9
Rubble	80	70	45	60	60	40	30	25	40	50
Star coral	5	2	2	2	2	10	20	20	5	7.6
Brain coral	2	2	2	2	2	1	2	5	3	2.3
Staghorn coral	2	15	40	10	20	30	40	15	20	21.3
Other corals	1	2	2	2	2	1	1	10	1	2.4
Sponges	1	1	1	-	1	1	-	-	1	0.7
Soft corals	3	3	2	5	5	2	1	2	5	3.1
SUBSTRATE	THE SQUARES OF QUADRAT 3 IN THE DROP OFF ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	10	15	10	20	15	25	35	45	80	28.3
Dead coral	5	5	25	10	25	10	20	15	3	13.1
Rubble	35	45	20	30	25	30	20	10	10	25
Star coral	20	5	5	25	1	15	10	15	2	10.9
Brain coral	1	2	5	1	2	2	1	1	1	1.8
Staghorn coral	2	2	1	2	1	2	2	-	-	1.3
Other corals	7	5	9	7	10	5	1	9	1	6
Sponges	-	1	1	-	1	1	1	-	-	0.6
Soft corals	20	20	25	15	20	10	10	5	3	14.1
SUBSTRATE	THE SQUARES OF QUADRAT 4 IN THE REEF SLOPE ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	20	30	40	25	30	25	5	5	20	22.1
Dead coral	40	45	35	30	30	35	35	50	35	37.3
Star coral	20	10	5	15	15	15	40	10	5	15
Brain coral	2	3	2	2	3	6	1	3	5	3
Other corals	11	3	8	15	14	11	11	21	14	12
Sponges	5	4	5	10	5	5	8	10	20	8
Soft corals	2	5	5	3	3	3	-	1	1	2.6

Table A3: Substrate description of the quadrats in the three reef zones of WELL'S BAY. The values (%) are averaged estimates of the substrate cover/unit surface area from two observers.

<b>WELL'S BAY</b>										
SUBSTRATE	THE SQUARES OF QUADRAT 1 IN THE ENCRUSTED BOULDERS ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	10	5	13	15	5	20	5	10	5	9.8
Basaltic boulders	50	60	70	60	70	70	80	75	70	67.2
Star coral	1	4	1	1	4	1	3	1	5	2.3
Brain coral	5	4	2	1	2	1	1	1	1	2
Other corals	30	24	10	20	14	4	8	9	16	15
Sponges	3	2	1	1	3	1	1	2	2	1.8
Soft corals	1	1	3	2	2	3	2	2	1	1.9
SUBSTRATE	THE SQUARES OF QUADRAT 2 IN THE SOFT CORAL ZONE									
	1	2	3	4	5	6	7	8	9	Avg
Sand	40	20	15	15	40	30	10	20	10	22.2
Basaltic boulders	40	60	60	60	40	50	65	50	60	53.9
Star coral	3	2	1	3	2	2	4	4	2	2.6
Brain coral	5	5	4	5	6	6	10	10	10	6.8
Other corals	4	2	3	5	5	2	5	7	6	4.2
Sponges	1	1	2	2	1	2	1	1	2	1.4
Soft corals	7	10	15	10	6	8	5	8	10	8.8
SUBSTRATE	THE SQUARES OF QUADRAT 3 ON THE SAND FLAT									
	1	2	3	4	5	6	7	8	9	
Sand	100	100	100	100	100	100	100	100	100	100

Table A4: Population density of *Sparisoma viride* on the reef off KARPATA.

QUADRAT 1 (depth: 1-2.5 m)						
Date	12-05-1992	17-05-1992	24-05-1992	31-05-1992		
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	Avg.	Std.
Terminal-phase	16.0	19.6	25.3	23.1	21.0	3.55
Initial-phase	10.2	11.6	7.56	6.67	9.00	1.97
Juvenile (tot)	1.33	0.89	0.89	0.89	1.00	0.19
10-15 cm FL	1.33	0.89	0.89	0.89	1.00	0.19
5-10 cm FL	0.00	0.00	0.00	0.00	0.00	0.00
2-5 cm FL	0.00	0.00	0.00	0.00	0.00	0.00
<2 cm FL	0.00	0.00	0.00	0.00	0.00	0.00
QUADRAT 2 (depth: 3-5 m)						
Date	23-03-1992	30-03-1992	06-04-1992	13-04-1992		
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	Avg.	Std.
Terminal-phase	6.67	6.67	11.1	8.44	8.22	1.82
Initial-phase	1.78	6.22	7.11	7.56	5.67	2.30
Juvenile (tot)	18.7	24.4	21.3	26.7	22.8	4.30
10-15 cm FL	2.22	0.89	1.33	0.44	1.22	0.66
5-10 cm FL	4.89	11.1	6.22	12.0	8.56	3.05
2-5 cm FL	11.1	9.78	11.1	12.9	11.2	1.11
<2 cm FL	0.44	2.67	2.67	1.33	1.78	0.94
QUADRAT 3 (depth: 5-9 m)						
Date	23-03-1992	30-03-1992	06-04-1992	13-04-1992		
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	Avg.	Std.
Terminal-phase	3.56	4.00	4.44	5.33	4.33	0.66
Initial-phase	5.33	2.22	6.22	4.00	4.44	1.51
Juvenile (tot)	22.7	29.8	34.7	39.0	31.5	3.40
10-15 cm FL	2.67	1.33	4.00	3.92	2.98	1.09
5-10 cm FL	7.11	8.44	8.44	11.6	8.89	1.63
2-5 cm FL	9.33	14.2	12.9	13.3	12.4	1.86
<2 cm FL	3.56	5.78	9.33	10.2	7.22	2.68
QUADRAT 4 (depth: 9-21 m)						
Date	23-03-1992	30-03-1992	06-04-1992	13-04-1992		
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	Avg.	Std.
Terminal-phase	2.75	1.96	2.35	5.10	3.04	1.22
Initial-phase	3.14	4.31	4.31	6.67	4.61	1.28
Juvenile (tot)	12.2	15.7	11.4	22.0	15.3	1.34
10-15 cm FL	1.57	1.57	2.35	1.57	1.76	0.34
5-10 cm FL	4.31	4.71	3.14	3.14	3.82	0.70
2-5 cm FL	4.31	5.10	4.31	8.24	5.49	1.62
<2 cm FL	1.96	4.31	1.57	9.02	4.22	2.97

Table A5: Population density of *Sparisoma viride* at TORI'S REEF.

QUADRAT 1 (depth: 1.5-3 m)						
Date	02-05-1992	09-05-1992	15-05-1992	22-05-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	0	0	0	0	0	0
Initial-phase	0	0	0	0	0	0
Juvenile (tot)	0	0	0	0	0	0
10-15 cm FL	0	0	0	0	0	0
5-10 cm FL	0	0	0	0	0	0
2-5 cm FL	0	0	0	0	0	0
<2 cm FL	0	0	0	0	0	0
QUADRAT 2 (depth: 4-5 m)						
Date	02-05-1992	09-05-1992	15-05-1992	22-05-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	5.33	7.11	4.44	5.33	5.56	0.97
Initial-phase	11.6	11.6	12.1	24.0	14.8	5.32
Juveniles (tot)	25.8	30.2	25.4	27.6	27.2	4.64
10-15 cm FL	4.44	2.67	0.63	3.56	2.83	1.41
5-10 cm FL	11.6	13.3	12.1	8.89	11.5	1.62
2-5 cm FL	8.00	10.7	12.7	14.2	11.4	2.33
<2 cm FL	1.78	3.56	0.00	0.89	1.56	1.31
QUADRAT 3 (depth: 5-12 m)						
Date	02-05-1992	09-05-1992	15-05-1992	22-05-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	4.44	2.67	4.44	2.67	3.56	0.89
Initial-phase	5.33	5.33	7.62	5.33	5.90	0.99
Juveniles (tot)	30.2	28.4	22.9	23.1	26.2	2.28
10-15 cm FL	3.56	0.89	4.44	1.78	2.67	1.41
5-10 cm FL	14.2	8.89	5.71	5.33	8.54	3.56
2-5 cm FL	8.00	8.00	5.08	8.89	7.49	1.44
<2 cm FL	4.44	10.7	7.62	7.11	7.46	2.21
QUADRAT 4 (depth: 12-21 m)						
Date	02-05-1992	09-05-1992	15-05-1992	22-05-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	3.56	3.56	4.44	2.67	3.56	0.63
Initial-phase	3.56	8.00	2.67	2.67	4.22	2.21
Juveniles (tot)	21.3	17.8	18.7	20.4	19.6	3.24
10-15 cm FL	2.67	0.89	0.89	0.89	1.33	0.77
5-10 cm FL	4.44	1.78	0.89	5.33	3.11	1.83
2-5 cm FL	8.89	9.78	11.6	9.78	10.0	0.97
<2 cm FL	5.33	5.33	5.33	4.44	5.11	0.38

Table A6: Population density of *Sparisoma viride* in WELL'S BAY.

QUADRAT 1 (depth: 6 m)						
Date	01-07-1992	08-07-1992	15-07-1992	22-07-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	0.44	2.22	2.67	2.22	1.89	0.85
Initial-phase	0.44	0.44	0.00	0.00	0.22	0.22
Juveniles (tot)	68.4	79.1	104.4	124.0	94.0	24.2
10-15 cm FL	0.89	1.33	2.67	0.89	1.44	0.73
5-10 cm FL	0.00	1.33	3.11	3.56	2.00	1.42
2-5 cm FL	19.6	20.9	32.4	48.4	30.3	11.6
<2 cm FL	48.0	55.6	66.2	71.1	60.2	9.02
QUADRAT 2 (depth: 8-10 m)						
Date	01-07-1992	08-07-1992	15-07-1992	22-07-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	0.89	0.89	2.67	0.44	1.22	0.85
Initial-phase	2.22	3.11	2.67	1.78	2.44	0.50
Juveniles (tot)	15.1	12.9	20.0	33.3	20.3	2.33
10-15 cm FL	1.78	2.67	4.44	3.11	3.00	0.96
5-10 cm FL	0.00	1.33	3.11	5.78	2.56	2.16
2-5 cm FL	5.78	4.00	5.78	15.6	7.78	4.55
<2 cm FL	7.56	4.89	6.67	8.89	7.00	1.45
QUADRAT 3 (depth: 11 m)						
Date	01-07-1992	08-07-1992	15-07-1992	22-07-1992	Avg.	Std.
Density	n/1000 m <sup>2</sup>	n/000 m <sup>2</sup>	n/1000 m <sup>2</sup>	n/1000 m <sup>2</sup>		
Terminal-phase	0	0	0	0	0	0
Initial-phase	0	0	0	0	0	0
Juveniles (tot)	0	0	0	0	0	0
10-15 cm FL	0	0	0	0	0	0
5-10 cm FL	0	0	0	0	0	0
2-5 cm FL	0	0	0	0	0	0
<2 cm FL	0	0	0	0	0	0

Table A7: The date and time of day of spawning of harem and non-harem fishes at Karpata. Pair spawnings which were visible as a whitish cloud are noted by + , otherwise by -. SC= social category; TT= territorial terminal-phase male; HI= harem initial-phase female; GT= group terminal-phase male; FL= fork length.

KARPATA			
SC	Fish (FL cm)	Date	Time (hour.minute.second)
TT	KT1 (35)	11-04-1992	07.28.36 + 07.33.10 - 07.33.24 + 07.37.26 +
		28-04-1992	07.25.32 + 07.26.21 + 07.33.54 + 07.34.11 + 07.35.54 +
		13-05-1992	07.29.18 - 07.29.37 + 07.51.17 - 07.51.27 - 08.06.54 + 08.21.27 + 18.06.26 + 18.06.54 +
	KT2 (25)	10-04-1992	07.24.30 - 07.24.47 + 07.26.29 + 07.33.25 - 07.34.19 - 07.35.34 + 07.38.30 - 07.54.19 - 08.01.44 -
		27-04-1992	07.11.54 - 07.12.21 + 07.13.05 + 07.13.29 + 07.18.34 + 07.28.03 + 07.28.56 + 07.29.09 + 07.48.19 - 07.48.59 +
		08-05-1992	07.23.13 + 07.24.12 + 07.25.03 + 07.30.54 + 08.03.21 + 08.03.32 - 08.26.22 +
		13-05-1992	17.20.20 +
	KT3 (35)	10-04-1992	07.07.30 + 07.16.41 + 07.30.56 + 07.42.39 + 07.53.40 - 08.09.53 +
		26-04-1992	08.06.01 + 08.13.08 +
		07-05-1992	08.25.51 + 08.26.40 + 08.32.56 + 08.38.06 + 08.52.55 +
		14-05-1992	No pair spawning in late afternoon
	KT4 (35)	07-05-1992	07.28.23 - 07.43.10 - 07.45.32 + 07.45.50 - 07.51.56 - 07.52.02 - 07.52.15 - 07.52.39 - 08.25.24 - 08.25.37 + 08.53.07 -
		12-05-1992	07.41.44 - 07.41.53 - 07.42.01 - 07.42.17 - 07.43.37 - 07.45.29 - 07.45.47 - 07.46.59 - 07.54.28 + 07.54.36 - 07.54.55 - 08.16.48 -
		14-05-1992	No pair spawning in late afternoon
	HI	KV1 (30)	06-05-1992
KV1 (25)		14-05-1992	07.41.38 +
KV2 (25)		05-05-1992	07.38.29 +
KV2 (30)		12-05-1992	07.16.21 +
KV3 (30)		06-05-1992	07.16.49 + 07.43.44 +
KV3 (30)		13-05-1992	07.22.07 +
GT	KG1 (30)	29-04-1992	No pair spawning in the early morning
		01-05-1992	No pair spawning in the early morning
	KG2 (25)	04-05-1992	No pair spawning in the early morning
		14-05-1992	No pair spawning in the early morning
	KG3 (35)	01-05-1992	No pair spawning in the early morning
		05-05-1992	No pair spawning in the early morning

Table A8: The date and time of day of spawning of harem fishes at Tori's reef. Pair spawnings which were visible as a whitish cloud are noted by + , otherwise by -. SC= social category; TT= territorial terminal-phase male; HI= harem initial-phase female; FL= fork length.

TORI'S REEF			
SC	Fish (FL cm)	Date	Time (hour.minute.second)
TT	TT1 (35)	26-05-1992	15.45.51 + 15.49.26 + 15.49.52 + 15.54.13 + 16.12.17 + 16.21.48 +
		02-06-1992	15.13.31 - 15.27.07 - 15.31.31 +
	TT2 (30)	21-05-1992	15.21.52 + 15.24.15 + 15.26.59 - 15.46.48 +
		01-06-1992	15.04.47 - 15.12.53 + 15.26.23 + 15.32.18 - 15.32.47 + 15.51.51 +
	TT3 (30)	26-05-1992	15.40.26 - 16.18.17 + 16.18.37 - 16.47.03 +
		02-06-1993	15.25.32 + 15.25.47 + 15.36.03 + 16.12.52 +
	TT4 (30)	22-05-1992	15.53.06 + 15.53.16 - 16.31.50 +
		01-06-1992	15.22.47 + 15.26.21 + 16.03.05 +
HI	TV1 (25)	27-05-1992	15.31.01 +
	TV1 (30)	03-06-1992	15.34.16 +
	TV2 (30)	27-05-1992	15.55.17 + 16.10.57 +
	TV2 (30)	03-06-1992	15.39.16 +
	TV3 (25)	28-05-1992	15.57.26 +
	TV3 (30)	04-06-1992	16.16.02 +
	TV4 (30)	28-05-1992	16.00.46 +
	TV4 (25)	04-06-1992	16.11.31 +



Table A9: The date and time of day of spawning of wandering fishes in Well's bay. Pair spawnings which were visible as a whitish cloud are noted by + , otherwise by -. SC= social category; WT= wandering terminal-phase male; WI= wandering initial-phase female; FL= fork length.

WELL'S BAY			
SC	Fish (FL cm)	Date	Time (hour.minute.second)
WT	PG1 (30)	13-07-1992	No pair spawning between 10.11.20 and 11.19.59
	PG2 (30)	16-07-1992	No pair spawning between 09.47.43 and 11.10.50
	PG3 (30)	20-07-1992	No pair spawning between 11.06.04 and 11.54.57
	PG4 (35)	23-07-1992	No pair spawning between 07.16.33 and 08.03.09
	PG5 (35)	23-07-1992	No pair spawning between 07.14.57 and 08.01.17
WI	PV1 (30)	09-07-1992	10.26.05 +
	PV2 (30)	14-07-1992	No pair spawning between 09.33.30 and 11.02.30
	PV3 (30)	16-07-1992	13.05.03 +
	PV4 (30)	20-07-1992	No pair spawning between 11.04.37 and 11.56.52
	PV5 (25)	20-07-1992	No pair spawning between 13.22.28 and 14.17.32
	PV6 (20)	20-07-1992	No pair spawning between 13.26.34 and 14.24.23
	PV7 (30)	21-07-1992	07.55.45 +
	PV8 (30)	21-07-1992	No pair spawning between 08.39.40 and 09.56.11
	PV9 (30)	23-07-1992	No pair spawning between 08.03.24 and 08.37.33

Table A10: The time percentages per hour (and their arcsine-square root transformed values) and the frequencies per hour of different behaviours displayed by territorial termphase males at Karpata during the morning and afternoon spawning period.

TIME % AND THE ARCSINE-SQUARE ROOT TRANSFORMED VALUES								
Fish	LOWSWIM		BITE		HIGHSWIM		SOLICITE AND COURT	
	Spawn (AM)	Spawn (PM)	Spawn (AM)	Spawn (PM)	Spawn (AM)	Spawn (PM)	Spawn (AM)	Spawn (PM)
KT1	46.51% 0.750453	22.02% 0.488406	34.45% 0.627275	51.31% 0.798455	8.60% 0.297632	1.46% 0.120940	2.91% 0.171458	0.49% 0.222950
KT1	31.24% 0.593079		30.51% 0.585172		16.92% 0.423878		4.25% 0.207713	
KT2	51.21% 0.797538	44.24% 0.727658	18.39% 0.443189	47.43% 0.759636	18.28% 0.441825	1.83% 0.135714	6.81% 0.263983	0.34% 0.185145
KT2	31.11% 0.591730		15.78% 0.408515		42.87% 0.713876		7.10% 0.269662	
KT3	56.16% 0.847110	58.47% 0.870531	22.82% 0.498064	33.44% 0.616628	12.73% 0.364880	0.17% 0.041175	2.65% 0.163429	0.00% 0
KT3	65.87% 0.946914		17.54% 0.432117		6.37% 0.255193		2.51% 0.158958	
KT4	58.68% 0.872617	36.79% 0.651670	24.14% 0.513629	45.17% 0.737045	6.65% 0.260823	0.11% 0.032494	2.60% 0.161952	0.00% 0
KT4	56.47% 0.850246		18.34% 0.442579		12.19% 0.356680		5.02% 0.226022	
AVG. STD.	49.66% 11.88%	40.38% 13.16%	22.75% 6.26%	44.34% 6.66%	15.58% 11.11%	0.89% 0.76%	4.23% 1.78%	0.21% 0.21%
FREQUENCY PER HOUR								
FISH	BITE		DEFECATE		INT. INITIAL		INT. TERMINAL	
	Spawn (AM)	Spawn (PM)	Spawn (AM)	Spawn (PM)	Spawn (AM)	Spawn (PM)	Spawn (AM)	Spawn (PM)
KT1	338 341	712	0 1	0	1 7	7	8 8	3
KT2	318 219	474	0 0	4	4 4	0	6 4	1
KT3	282 216	307	0 4	0	4 3	0	6 9	1
KT4	264 199	512	1 1	2	13 8	14	10 8	8
AVG. STD.	272.13 53.23	501.25 144.05	0.88 1.27	1.5 1.66	5.5 3.5	5.25 5.8	7.38 1.8	3.25 2.86

Table A11: The time percentages per hour (and their arcsine-square root transformed values) and the frequencies per hour of different behaviours displayed by territorial termphase males at Tori's reef during the afternoon spawning period.

FISH	TIME % AND THE ARCSINE-SQUARE ROOT TRANSFORMED VALUES			
	LOWSWIM	BITE	HIGHSWIM	SOLICITE AND COURT
	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)
TT1	32.24% 0.603792	30.29% 0.582787	20.13% 0.465277	3.22% 0.180483
TT1	38.08% 0.665044	33.89% 0.621360	22.05% 0.488808	0.64% 0.080015
TT2	45.19% 0.737240	29.83% 0.577759	13.03% 0.369316	5.52% 0.237090
TT2	43.75% 0.722762	23.20% 0.502585	24.73% 0.520417	1.91% 0.138687
TT3	38.57% 0.670044	38.37% 0.668017	18.66% 0.446728	3.09% 0.176589
TT3	44.55% 0.730761	31.84% 0.599536	15.67% 0.406989	3.04% 0.175381
TT4	48.66% 0.771979	31.59% 0.596909	13.25% 0.372564	1.21% 0.110019
TT4	39.11% 0.675601	30.28% 0.582726	19.06% 0.451734	1.03% 0.101691
AVG. STD.	41.27% 4.88%	31.16% 3.98%	18.32% 3.87%	2.46% 1.50%
FISH	FREQUENCIES PER HOUR			
	BITE	DEFECATE	INT. INITIAL	INT. TERMINAL
	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)
TT1	333 519	2 5	4 6	9 12
TT2	442 394	5 5	7 11	3 9
TT3	483 410	8 7	0 0	4 4
TT4	342 386	4 0	1 2	9 14
AVG. STD.	413.86 60.74	4.5 2.4	3.88 3.66	8 3.74

Table A12: The time percentages per hour (and their arcsine-square root transformed values) and the frequencies per hour of different behaviours displayed by harem initial-phase females at Karpata during the morning spawning period.

FISH	TIME % AND THE ARCSINE-SQUARE ROOT TRANSFORMED VALUES			
	LOWSWIM	BITE	HIGHSWIM	SOLICITE AND COURT
	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)
KV1	38.03% 0.664501	46.56% 0.751009	1.70% 0.130648	1.04% 0.102240
KV1	43.91% 0.724329	39.25% 0.677023	10.64% 0.332342	0.43% 0.065875
KV2	51.27% 0.798066	36.67% 0.650431	3.84% 0.197351	0.29% 0.053774
KV2	31.92% 0.600400	46.20% 0.747361	4.97% 0.224811	0.32% 0.056549
KV3	43.87% 0.723909	47.69% 0.762334	2.41% 0.155998	0.46% 0.068162
AVG. STD.	41.80% 6.48%	43.27% 4.45%	3.93% 3.39%	0.42% 0.31%
FISH	FREQUENCIES PER HOUR			
	BITE	DEFECATE	INT. INITIAL	INT. TERMINAL
	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)
KV1	360 365	1 0	0 0	1 0
KV2	347 499	1 1	2 3	0 0
KV3	369	0	0	0
AVG. STD.	388 55.99	0.6 0.49	1 1.26	0.2 0.4

Table A13: The time percentages per hour (and their arcsine-square root transformed values) and the frequencies per hour of different behaviours displayed by harem initial-phase females at Tori's reef during the afternoon spawning period.

FISH	TIME % AND THE ARCSINE-SQUARE ROOT TRANSFORMED VALUES			
	LOWSWIM	BITE	HIGHSWIM	SOLICITE AND COURT
	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)
TV1	40.84% 0.693266	42.60% 0.711153	3.88% 0.198144	0.26% 0.050848
TV1	40.89% 0.693633	45.22% 0.737519	8.39% 0.293846	0.20% 0.044424
TV2	46.19% 0.747305	43.00% 0.715195	4.69% 0.218333	1.30% 0.114143
TV2	39.00% 0.674462	40.35% 0.688260	7.66% 0.280448	1.14% 0.107053
TV3	41.29% 0.697868	48.51% 0.770479	4.15% 0.205221	0.15% 0.039096
TV3	31.40% 0.594786	45.78% 0.743125	8.34% 0.292893	0.45% 0.066924
TV4	38.93% 0.673721	47.12% 0.756604	7.24% 0.272515	0.55% 0.074042
TV4	42.97% 0.714858	44.64% 0.731683	2.31% 0.152522	0.17% 0.040836
AVG. STD.	40.19% 3.97%	44.65% 2.45%	5.83% 2.19%	0.53% 0.42%
FISH	FREQUENCIES PER HOUR			
	BITE	DEFECATE	INT. INITIAL	INT. TERMINAL
	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)	SPAWN (PM)
TV1	449 620	8 14	0 0	0 0
TV2	674 497	12 4	0 0	1 0
TV3	540 581	11 10	0 0	0 0
TV4	367 656	5 7	0 1	0 0
AVG. STD.	548 99.4	8.88 3.26	0.13 0.33	0.13 0.33

Table A14: The time percentages per hour (and their arcsine-square root transformed values) and the frequencies per hour of different behaviours displayed by wandering initial-phase females in Well's bay during the period a pair spawning was observed.

FISH	TIME % AND THE ARCSINE-SQUARE ROOT TRANSFORMED VALUES			
	LOWSWIM	BITE	HIGHSWIM	SOLICITE AND COURT
	SPAWN (AM-PM)	SPAWN (AM-PM)	SPAWN (AM-PM)	SPAWN (AM-PM)
PV3	80.63% 1.115007	11.15% 0.340455	1.93% 0.139294	0.39% 0.062177
PV7	74.78% 1.044699	20.08% 0.464584	0.40% 0.063507	0.12% 0.034567
PV1	56.40% 0.849546	19.60% 0.458628	10.15% 0.324196	0.14% 0.036901
AVG. STD.	70.60% 10.32%	16.94% 4.10%	4.16% 4.28%	0.21% 0.12%
FISH	FREQUENCIES PER HOUR			
	BITE	DEFECATE	INT. INITIAL	INT. TERMINAL
	SPAWN (AM-PM)	SPAWN (AM-PM)	SPAWN (AM-PM)	SPAWN (AM-PM)
PV3	116	10	0	0
PV7	209	7	0	0
PV1	214	17	0	0
AVG. STD.	179.67 45.07	11.33 4.19	0 0	0.33 0.47

Table A15: The time percentages per hour (and their arcsine-square root transformed values) and the frequencies per hour of different behaviours displayed by group termphase males at Karpata during the morning spawning period.

FISH	TIME % AND THE ARCSINE-SQUARE ROOT TRANSFORMED VALUES			
	LOWSWIM	BITE	HIGHSWIM	SOLICITE AND COURT
	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)
KG1	45.26% 0.737910	39.03% 0.674832	0.00% 0	0.00% 0
KG1	52.84% 0.813830	32.41% 0.605603	0.00% 0	0.00% 0
KG2	45.70% 0.742317	35.65% 0.639822	5.07% 0.227101	0.00% 0
KG2	63.32% 0.920220	29.91% 0.578699	0.51% 0.071747	0.00% 0
KG3	21.48% 0.481908	36.41% 0.647778	1.85% 0.136334	0.00% 0
AVG. STD.	45.72% 13.77%	34.68% 3.19%	1.24% 1.83%	0.00% 0.00%
FISH	FREQUENCIES PER HOUR			
	BITE	DEFECATE	INT. INITIAL	INT. TERMINAL
	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)	SPAWN (AM)
KG1	354 262	1 0	0 0	1 3
KG2	374 327	1 0	0 0	4 2
KG3	355	0	0	9
AVG. STD.	334.4 39.17	0.4 0.49	0 0	3.8 2.79