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Social organization and sexual pattern in the Mediterranean parrotfish *Sparisoma cretense* (Teleostei: Scaridae)

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Abstract We examined the social organization and reproductive pattern of a population of *Sparisoma cretense* L. at Lampedusa Island (Italy). During the breeding season (July to September) individuals occur either in territorial or in non-territorial groups, which quantitatively differ with respect to use of space, sex-ratio and sexual activity. Territorial groups consist of one male plus one to three females, whereas in non-territorial groups as many as 54 fish share a common area. Among non-territorial groups, variations, in both sex-ratio and behavior, suggest they could represent either feeding aggregations or reproductive aggregations. Spawning, always in pairs, occurs daily in a short period of time before dusk and has been observed only in territorial groups. Group spawning has never been observed, but another alternative mating tactic, streaking on pair spawning, was recorded. In the non-breeding season fish do not aggregate in organized social units. Histological examination of gonads showed that adults are larger than 12 cm total length. Females have an asynchronous ovary, typical of species spawning several times during the breeding season. Males show secondary testes, indicating that their gonads develop ovaries as juveniles, which are later re-differentiated into functional testes. Histological and demographic data seem to indicate that, as in other species of this genus, prematurational sex-change occurs. The sexual pattern appears to be essentially gonochoristic, but the potential for sex-change is not excluded.

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Introduction

Parrotfishes display a very diverse array of social organization and reproductive patterns, often within a single species (Robertson and Warner 1978; Thresher 1984) . They range from monochromatic, strictly monandric protogynous species, in which males are permanently territorial, to dichromatic, functionally diandric protogynous (true diandric and monandric with prematurational sex-change) species, in which males hold only temporary reproductive territories. Different types of social organization within the same species, as described for *Scarus iserti* (=*croicensis*) (Ogden and Buckman 1973; Barlow 1975; Colin 1978) and *Sparisoma viride* (van Rooij et al. 1996), in which adults live either in multi-male groups or in one-male groups, suggest a flexibility of the scarid socio-sexual system. Changes in the system may be due to environmental factors such as availability and competition for spawning sites, population density, food resources, water temperature, etc. Because of this diversity, parrotfishes represent a source of comparative data with which to organize information and to test hypotheses concerning the functional significance of interspecific and/or intraspecific differences in reproductive patterns. Additional information on reproductive ecology, such as activity pattern, density, sex-ratios, location and duration of spawning activity, social organization and mating behavior, could provide a framework for better understanding the range and the evolution of reproductive patterns in this group of fishes.

The scarid *Sparisoma cretense* L. (subfamily: Sparisomatinae), the only Mediterranean species and one of the few temperate species of this family (Schultz 1969; Thresher 1984), is a parrotfish of particular interest because its social organization and reproductive pattern could shed light on the influence of seasonal variations in the complexity of scarid social organization.

Sparisoma cretense is a daytime feeder, grazing on algae and *Posidonia oceanica*. It scrapes algae and small invertebrates from the substrate with its fused, beak-like

jaw. Some aspects of the reproductive biology of *S. cretense* have been studied by Papaconstantinou and Petrakis (1986), Gonzales and Lozano (1992) and Gonzales (1993). The breeding season occurs between July and August. A sexual dichromatism is present with the male showing a grey-brown coloration while the female is generally reddish with a large grey spot on the rear part of the head and a yellow spot on the upper part of the caudal peduncle (Tortonese 1971). Male and female size ranges largely overlap, and the species is considered to exhibit a gonochoric sexual pattern, with females reaching sexual maturity earlier than males (Gonzales and Lozano 1992). Despite these observations detailed information on the social organization, reproductive activity during the course of the breeding season, spawning behavior and gonad morphology of *S. cretense* is lacking.

The aim of the present study was to describe the social organization of *Sparisoma cretense* in Lampedusa, an island in south Italy, to address its reproductive biology through: (1) identification of spawning sites; (2) determination of timing and duration of spawning activity; (3) spawning behavior; (4) determination of spawning frequencies; (5) evaluation of population density, size composition and adult sex-ratios; and (6) evaluation of the sexual pattern.

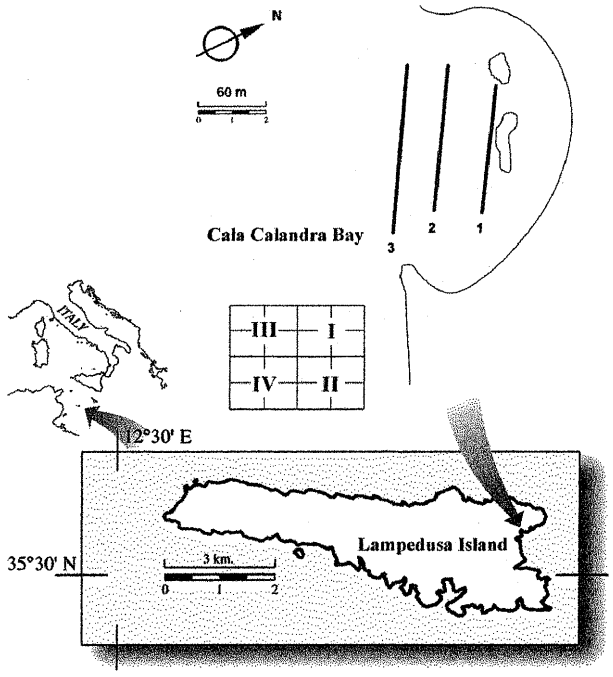

Fig. 1 Geographical setting of study site. Position of strip transects and grid area

Materials and methods

General setting

The study was conducted in Cala Calandra, a bay on the east coast of Lampedusa, Pelagie Islands (Italy) in July to September 1996, February 1997 and June to September 1997 (Fig. 1). Fishing pressure on *Sparisoma cretense* L. is negligible, and consequently observation at close range was possible using SCUBA gear. Records of general behavior, courtship and spawning were made by daily monitoring throughout observation periods ranging from 20 min to 2 h. Vertical distribution, abundance and size were quantified by visual census using both strip transects, in the shallower part of the bay, and a grid of 9600 m^2, in the deeper part (Fig. 1). The total effort exceeds 220 h of underwater observation, covering every part of the day. To check gonadal activity, fish were caught using handnets or, by local fishers, hooks.

Sparisoma cretense density, size and sex-ratio

Three strip transects, 20 m wide and ranging in length from 150 to 210 m , extending from 4.6 to 8.3 m depth, were laid down on the shallower, inner part of the bay (Fig. 1). A total of 17 counts, between 9:00 and 17:00 hrs outside the daily spawning period, was performed. A grid of 9600 m^2, divided in four 40 × 60 m rectangles, was roped off in the deeper, outer part of the bay (Fig. 1). Fish in the grid were censused five times, outside the spawning period, between 11:00 and 17:00 hrs. Density (ind. per 300 m^2) was calculated for the two different parts of the bay: the average density of the shallower part was calculated as the average of the three strip transects, while the density of the deeper part was calculated as the average of the whole grid.

Each fish counted was categorized by color pattern and estimated total length. Four color patterns were distinguished: (1) yellow head (YH), pale mottled grey body with the most anterior part of the head bright yellow; (2) mottled (M), a uniform mottled brown coloration; (3) red (R), red and grey body with a yellow spot on the caudal peduncle and (4) grey (G), a vivid grey body with opercular and jugular black stripes. Length estimation of fishes, performed by two divers, was validated periodically by comparing the estimated length underwater with the real length of the same individuals, caught with handnets (Wilcoxon test, Diver 1: $n = 9$, $Z = -1.272$, $p > 0.05$; Diver 2: $n = 8$, $Z = -1.687$, $p > 0.05$). The accuracy, defined as the closeness of a measured or computed value to its true value (Sokal and Rohlf 1995), was computed. It was calculated as *ac* (= estimated length/real length; St John et al. 1990), for the two divers performing size estimations and it appeared to be accurate (Diver 1: $ac = 1.050 \pm 0.023$ SE; Diver 2: $ac = 1.054 \pm 0.039$ SE).

Sex-ratio of adults was calculated as males/(males + females), considering male individuals to have G and females either M or R coloration. The reliability of ascribing M and R color patterns to females and G color pattern to males was supported by both the result of gonad histological analyses performed on 102 specimens and previous description of this species (Tortonese 1971).

Gonadal histology

Gonad development and morphology was studied by comparing the histological structure of gonads from 102 individuals. Small fish were collected in Cala Calandra by handnets while larger individuals were caught with hooks by local fishermen along the coast of the island. The total length (TL), to the nearest millimeter, of all specimens was measured, and the color pattern was categorized as previously described. These fish included 6 YH (3.7 to 6.8 cm TL), 10 M (7.2 to 12 cm TL), 56 R (12.6 to 34.2 cm TL) and 30 G (19.2 to 31.5 cm TL) specimens.

The trunk of specimens smaller than 10 cm SL was fixed in Dietrich's fixative (900 ml distilled water, 450 ml 95% ethanol, 140 ml 40% formaldehyde, 30 ml acetic acid) for 1 week, decalcified for 30 h in Fisher's calex solution, washed for 12 h in running freshwater, dehydrated in ethanol, embedded in paraplast, sectioned serially in 7-μm intervals, mounted on slides, and stained with hematoxylin and eosin. Gonads were excised from larger specimens and prepared in the same way, except they were not decalcified.

Gonads were classified in six categories. A gonad was called *undifferentiated* if it contained only primordial germ cells (gonia) and undifferentiated somatic cells, and no ovarian cavity. A gonad was called *oocytic* when it contained at least one oocyte at Stage 1 or 2 (Wallace and Selman 1981) but no ovarian cavity. An *ovary* was a gonad containing oocytes and an ovarian cavity. A gonad was in a *transitional* stage if it contained an ovarian cavity and both ovarian and testicular tissues, one of which was developing while the other was degenerating. A *primary testis* was a solid gonad consisting entirely of spermatogenetic tissue, while a *secondary testis* showed a membrane-lined central cavity (Sadovy and Shapiro 1987; Shapiro and Rasotto 1993).

Use of space

Territorial individuals

Approximate territory borders of individuals were established by mapping the most distant grazing sites and the locations where conflicts between neighboring G males were observed. Straight lines were drawn through the most extreme locations. The borders were confirmed by checking the position of the fish on successive sightings. Areas were measured using the software package AUTOCAD 14 (Genesis Computers, Padova, Italy). Throughout the study, 6 to 12 observations on mapped territories were performed, both outside and during the daily spawning period. The number of M, R and G individuals, present in each territory and tolerated by the resident G male, was estimated about six times on separate days during the study period.

Groups

The abundance and mobility of group individuals appeared too high to maintain a permanent record of all of them. Observations of their behavior, both outside and during the daily spawning period, were recorded between June and September 1996. The home range for five G males and four R females was estimated by marking the extreme positions of the grazing sites visited by a fish, in 20-min observation periods, and measuring the area of the resulting polygon with the same system utilized for estimation of territory area. A total of 240 observations on single individuals was performed, 120 on territorial and 120 on non-territorial individuals followed during 20-min observation periods.

Reproductive activity

The timing of the daily spawning period was established by two continuous observations from dawn to dusk in July 1996 and was confirmed by all subsequent observations of sexual activity. Spawning behavior and activity were recorded 86 times between July and September 1996 and 41 times between July and September 1997, through continuous observation, during the daily spawning period. From 15 to 16 observations were performed on six groups of territorial parrotfish. Fish were observed from 15 min before the expected start until at least 10 min after the last observed spawn. The time and location of each spawning, plus the color pattern type and the size of the partners, were noted.

Statistical analyses

All samples were independent and were tested for normality using the Kolmogorov–Smirnov test. If they were not normally distributed, they were square-root or log-transformed, and non-parametric tests were applied with variables that were still non-normally distributed after transformations. A significance level of $p = 0.05$ was used. Density data were processed separately for the total and for each color pattern using non-parametric tests, while correlation measures were computed using the Spearman correlation coefficient. For the deeper part of the bay, where data were normally distributed, we performed one-way analysis of variance (ANOVA) on density and sex-ratio. All tests were performed using the STATISTICA 5.0 (Statsoft Inc., Tulsa, Oklahoma and SPSS 4.0 for Windows package (SPSS Inc., Chicago).

Results

Gonadal morphology and color pattern

In all but the smallest undifferentiated specimens, the gonad was comprised of two lobes. In juveniles and adults, the two lobes were separated anteriorly and united posteriorly. The gonad was suspended from the coelomic wall by a short, thin mesogonium, running from anterior to posterior along the dorsal surface of each lobe.

Gonads of individuals smaller than 7 cm TL were either undifferentiated or oocytic (Table 1). The undifferentiated gonads developed as tiny buds in separate sheets of mesogonium. The oocytic gonads contained a few previtellogenic oocytes (Fig. 2.1); these lacked a surrounding layer of follicular cells. The cytoplasm of these oocytes was more basophilic than that of gonia and peripheral regions in the nuclei contained nucleoli.

In the ten individuals ranging from 7 to 12 cm TL (Table 1), the gonads were already differentiated as ovaries (Fig. 2.2, 2.3) with a well-developed, membrane-lined central cavity and ovigerous lamellae protruding into the cavity. Neither vitellogenic oocytes nor mature eggs were present. All individuals larger than 12 cm TL ($n = 86$) showed a sexually differentiated and ripe gonad. Ovaries ($n = 55$) contained oocytes at all stages of development (Fig. 2.4) from previtellogenic oocytes to mature, ovulated eggs and also post-ovulatory follicular sacs, indicating that deposition of eggs had recently taken place. Therefore they can be described as asynchronous ovaries, typical of species which spawn several times during the breeding season (Nagahama 1983). All testes ($n = 31$) showed a membrane-lined central cavity (Fig. 2.5) and a sperm duct located in the medial region of the organ, facing the dorsal mesentery. While the sperm duct was always full of sperm (Fig. 2.6), neither sperm nor spermatids were observed within the central

Table 1 *Sparisoma cretense*. Number and color pattern of specimens in four size classes (total length in cm), whose gonads were either undifferentiated (*U*), oocytic (*O*), transitional (*T*), primary testis (*PT*), secondary testis (*ST*) or ovary (*Ov*). Color patterns are also indicated: yellow head (*YH*), mottled (*M*), red (*R*), and grey (*G*)

Size (cm)	U	O	T	PT	ST	Ov
<7	2 YH	4 YH	–	–	–	–
7–12	–	–	–	–	–	10M
12–18	–	–	–	–	1R	12R
>18	–	–	–	–	30G	43R

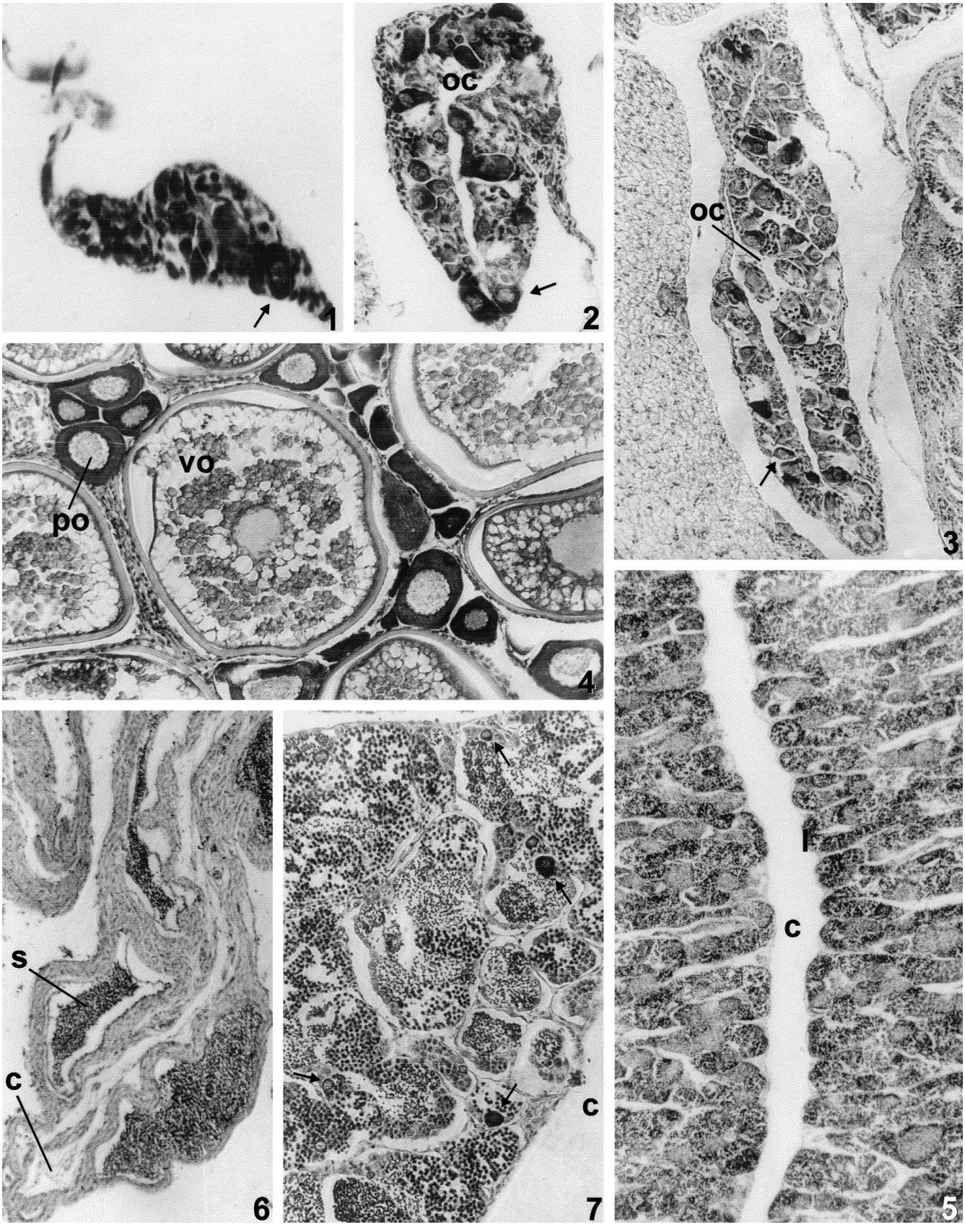
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Fig. 2 *Sparisoma cretense*. Gonad morphology. **2.1** Transversal section of an early oocytic gonad in a 6.8 cm specimen; previtellogenic oocytes (*arrow*) are spread among somatic cells (×400). **2.2** A fully differentiated ovary with previtellogenic oocytes (*arrow*) and ovarian cavity (*oc*) in a 7.3 cm specimen. (×300). **2.3** Ovary in a 10.6 cm specimen (×180). **2.4** Asynchronous ovary of a 27.4 cm ripe female with both vitellogenic (*vo*) and previtellogenic (*po*) oocytes (×300). **2.5** Secondary testis of a 25 cm ripe male. Testis is organized in lobules (*l*) and show an inner cavity (*c*). (×120). **2.6** Sperm duct of secondary testis: while the dorsal and ventral parts show sinuses full of sperm (*s*) a central empty cavity (*c*) is still present (×120). **2.7** Secondary testis with previtellogenic oocytes (*arrows*) in a 17.1 cm ripe male (×180)

cavity. The testis internal structure consisted of seminiferous lobules, within the wall of which the various stages of spermatogenesis developed (Fig. 2.5). The testis is therefore of the unrestricted spermatogonial type (Grier 1993). Small previtellogenic oocytes lacking follicular cells were found among the seminiferous lobules in the testes of two specimens, 17.1 and 27.7 cm TL (Fig. 2.7). Because of the absence of both degenerating ovarian and testicular tissue and the presence of active spermatogenesis and of a central cavity not used for sperm storage and/or transport, these gonads were designated as a secondary testis, despite the presence of previtellogenic oocytes.

Juveniles with undifferentiated or oocytic gonad show a YH color pattern, while those with differentiated gonad are in M coloration (Table 1). Adults either show an R (female) or G (male) color pattern. The only exception observed to this rule was one of the two males with oocytes in their testes that showed an R color pattern (17.1 cm TL). During field observation it has often been recorded that R individuals can suddenly and briefly show an M color pattern, especially during aggressive interactions.

General description of the social organization

On the basis of spawning observation and histological analyses of the gonads we defined adults of *Sparisoma cretense* as fish larger than 12 cm TL. During the breeding season (July to September) adults are organized in either of two social units: territorial or non-territorial groups of conspecifics with R and G color patterns, sharing a common home range. A characteristic of territorial males is the active defense of their home range against male conspecifics throughout the day. These defended ranges are therefore referred to as a territory, and the adults residing in them as territorial fish, as opposed to fish of non-territorial groups that reside in an area but do not defend its border.

Territorial groups are composed of one male and a mean number of R females ranging from 1.2 to 3.7 ($n = 50$). Territorial defense is mostly maintained by the territorial male: it spends much time (78%, $n = 5$) swimming high in the water column, controlling territory borders; this occasionally resulted in vigorous chases of conspecific males. Fish number in non-territorial groups ranges from 6 to 54, but exact composition is difficult to establish because subgroups were not stable and individuals incidentally swimming and grazing in the study area were also present. Although most of the fish inside non-territorial group areas tolerated each other, subtle interactions over grazing sites and/or individual home ranges suggested a size-based hierarchy. Size appears to be more important than color, since smaller group-males were occasionally observed to withdraw on the approach of larger males. Both territorial and non-territorial adult fish slept in sheltered sites between 5 and 17 m depth and were never seen in a mucus cocoon. Juveniles (fish smaller than 12 cm TL) were observed to freely move between and forage in both territorial and non-territorial group areas, ignored by adults.

Outside the breeding season both territorial and non-territorial groups were not recognizable and only loosely organized schools of fish, comprising both males and females, were observed. Fish within a school show no aggression towards conspecifics and spend most of their time swimming (90%, $n = 16$) and grazing (3%, $n = 16$).

Spatial distribution, abundance, size composition and sex-ratio

These results are mainly restricted to adult fish during the breeding season. The shallower, inner part of the bay (< 8.3 m) was inhabited exclusively by a non-territorial group. Density and color pattern compositions, obtained from visual census, were not significantly different among the three sampled transects (Fig. 3; Kruskall–Wallis test, $n = 51$: total density, $\chi^2 = 1.65$, $p = 0.437$; R density, $\chi^2 = 1.34$, $p = 0.511$; G density, $\chi^2 = 1.26$, $p > 0.05$). No significant differences were observed

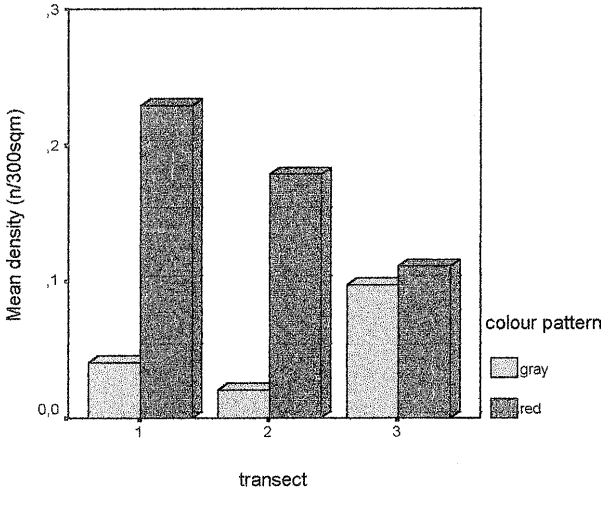

Fig. 3 *Sparisoma cretense*. Mean density and color pattern composition in transects of the shallower part of the bay. Density is calculated as number of individuals per 300 m^2

between data collected at different times of the day (Mann–Whitney test, $n = 51$: total density, $Z = -0.665$, $p > 0.05$; R density, $Z = -0.261$, $p > 0.05$; G density, $Z = -1.051$, $p > 0.05$). Average total density was 0.17 ± 0.07 R females and 0.05 ± 0.02 G males per 300 m^2. Sex-ratio was 0.243, demonstrating a prevalence of females in the composition of this non-territorial group. Size distribution obtained by visual census, ranged from 12 to 40 cm TL for all individuals; R females ranged from 12 to 30 cm TL and G males from 15 to 40 cm TL.

The outer part of the bay, ranging in depth from 8.3 to 17.8 m, was inhabited by both territorial and non-territorial groups. Territorial groups were restricted to depths >11.5 m, and their territories appeared to be contiguous (Fig. 4). Territory size ranged from 189 to 587 m^2 ($n = 7$) and was not affected by the period of day or the month. The home range of non-territorial individuals ($n = 9$) varied from 179 to 2020 m^2, while size of the area occupied by the whole group was highly variable, corresponding to group size.

The mean density in the whole censused area was 0.4 ± 0.1 fish per 300 m^2 for YH fish, 0.7 ± 0.1 for R fish and 1.4 ± 0.2 for G. Consequently a significant difference in the frequency of the three color patterns was present (ANOVA: $df = 2$, $F = 12.56$, $p < 0.001$), with G fish being more numerous than other color pattern individuals (Scheffé test). Depth did not affect YH fish distribution (Kruskal–Wallis test: $\chi^2 = 2.79$, $p > 0.05$), while in the deeper part of the grid area both R and G densities were lower (R, $\chi^2 = 9.48$, $p = 0.008$; G, $\chi^2 = 25.54$, $p < 0.001$). Comparing fish distribution and color pattern in the grid rectangles (Fig. 4), R fish were more abundant in Rectangle IV (ANOVA: $df = 3$ $F = 3.09$, $p < 0.05$), corresponding to the area occupied by territorial groups, with a mean density of 1.2 ± 0.3 individuals per 300 m^2. G fish were more dense in Rectangles I and II (ANOVA; $df = 3$, $F = 14.58$, $p < 0.001$), where non-territorial groups were resident, with a mean density of 4.2 ± 0.54 individuals per 300 m^2.

Sex-ratio strongly reflected the distribution of color pattern types (Fig. 5) varied from 0.29 in rectangles overlapping territorial groups to 0.72–0.73 in the others (ANOVA: $df = 3$, $F = 8.30$, $p < 0.001$). The non-territorial group present inside the grid was strongly male biased (sex-ratio 0.92).

Size distribution in the whole grid ranged from 4 to 42 cm TL, with YH fish ranging from 4 to 8 cm TL, R from 13 to 40 cm TL, and G from 17 to 42 cm TL. Territorial males ranged in size from 25 to 35 cm TL, while territorial females were 12 to 30 cm TL. The lengths of non-territorial males were between 15 and 40 cm TL, and females between 12 and 35 cm TL.

Reproductive activity

Sparisoma cretense was observed to spawn daily, throughout the beginning of July to the middle of September. Virtually all activity took place within a 50-min period at dusk. The main mode observed was pair spawning. Only 6 out of 250 observed spawnings events were disrupted by a second male (streaking). Group spawning was never observed. Male color pattern intensified during the daily spawning period, and black opercular stripes became extremely evident. Courtship and spawning behavior was quite similar to that described for other scarids (Thresher 1984). The male slowly circled the female, with fins fully spread, and performed brief upward rushes into the water column. If the female was ready she ascended slightly off the bottom, the male moved next to her with his head at the level of her pectoral fin and together the pair rushed upwards, rotating around and close to each other, in a

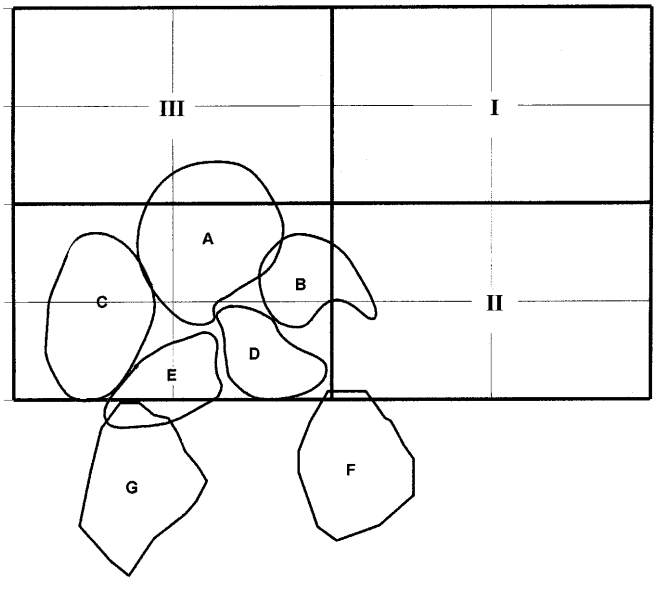

Fig. 4 *Sparisoma cretense*. Grid area divided in four rectangles. Territorial borders are marked. A, B, C, D and E territories were identified in 1995, G and F in 1996. Data for the male designated "B" were used only for correlation analysis

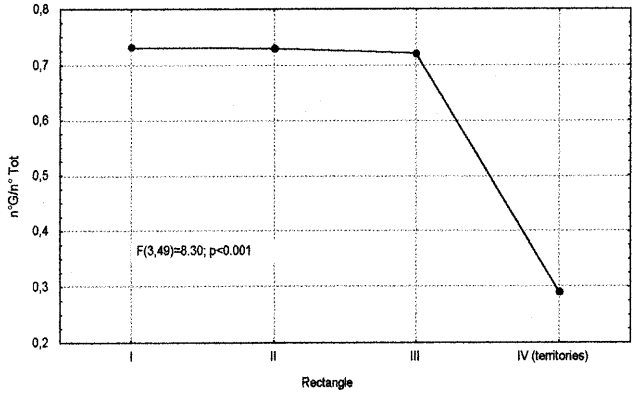

Fig. 5 *Sparisoma cretense*. Grid of sex-ratio calculated as males/(males + females), considering males to have G and females R (or M) coloration

fast spawning ascent. After a few meters of upward rush the fish suddenly reversed direction and returned to the bottom, usually leaving behind a visible cloud of gametes (Fig. 6). Females never spent more than a few minutes on courtship and resumed grazing immediately after spawning, while males stopped feeding throughout the spawning period. Courtship did not always lead to spawning; in fact courtship displays, such as the male upward rush or circling, were observed to be performed by several males of the non-territorial group resident in the grid area. However, spawning was recorded only in territorial groups. During the daily spawning period territorial males spent much time on territory patrol. They spawned mostly with females sharing their territories but also with other females, visiting or passing through. This was confirmed by both the fact that females of the non-territorial groups were observed to move during the spawning time into territory area and that 37, out of 128 times, the daily number of spawnings of territorial males exceeded the number of females resident in their territories. In fact, the daily number of spawnings, collected for seven males, ranged from 0 to 8, while the number of female residents in the same territories ranged between 1 and 3. Territorial male size was significant related to territory size ($n = 7$, Spearman's $R = 0.87$, $p < 0.05$), but no correlation appeared to be present between male size and number of territorial females ($n = 6$, Spearman's $R = 0.32$, $p > 0.05$).

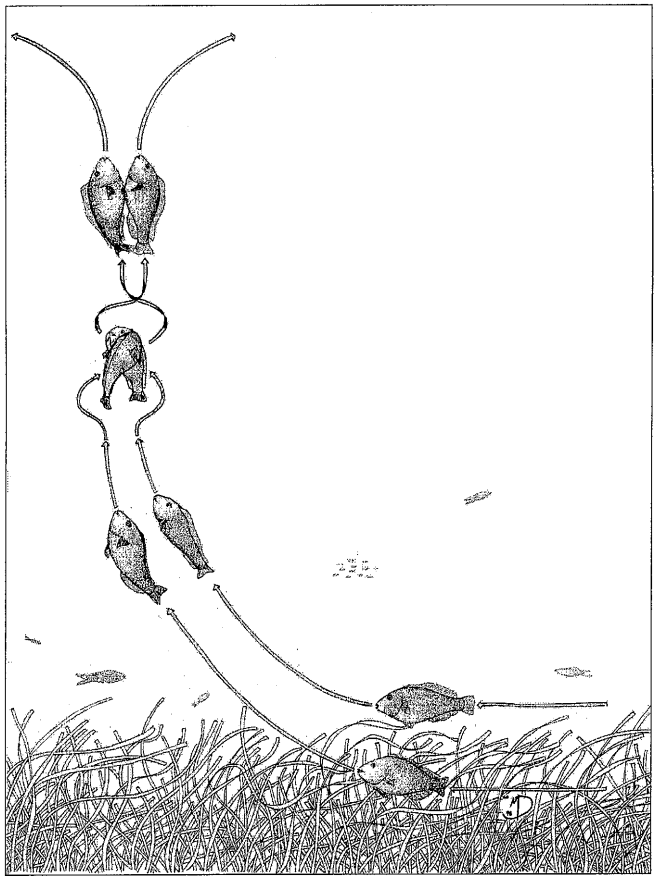

Fig. 6 *Sparisoma cretense*. Schematic drawing of spawning behavior

Discussion

Hermaphroditism is typically diagnosed by histological characteristics of the gonads, often supported by demography and by direct observation of adult sex-change in identified individuals (Sadovy and Shapiro 1987). Histological characteristics indicative of protogyny include a membrane-lined central cavity in testes, a remnant of the ovarian cavity from the previous female phase, and mature gonads undergoing sexual transition from female to male. In *Sparisoma cretense* males show a secondary testis, i.e. testis with a central cavity, and no transitional gonads have been observed. The observation of a secondary testis, sometimes with previtellogenic oocytes inside, in smaller mature males (those having the same age and size of females at first maturity; De Girolamo personal observations) strongly suggests the presence of a process of prematurational sex-change from immature females (Sadovy and Shapiro 1987). Those males arising from prematurational sex-change, showing morphological characteristics typical of hermaphroditic individuals, are actually functionally gonochoristic (Sadovy and Shapiro 1987). The development of a so-called "secondary gonochorism", with individuals spending their adult lives as males and having gonads definitely derived from ovaries, through a prematurational sex-change process, is a common feature of *Sparisoma* species (Robertson and Warner 1978). In the absence of transitional gonads, the presence of prematurational sex-change makes it difficult to infer whether functional sex-change occurs in adults. However, the observation of previtellogenic oocytes in the testis of a large male could indicate that a sex-change had recently taken place. In several species of protogynous fish (wrasses, parrotfishes and groupers; Robertson and Warner 1978; Warner and Robertson 1978; Sadovy and Colin 1995), it has been demonstrated that the degree of sex-change in the same species can be extremely variable, ranging from completely functional gonochoristic populations to pure protogynous ones. From the histological data of the present study, we suggest that *Sparisoma cretense* is essentially a gonochoristic species in which prematurational sex-change occurs. A potential for adult sex-change also is present. More information on gonad morphology of a larger number of individuals, belonging to different populations, is needed to clarify the sexual pattern.

With respect to reproduction, *Sparisoma cretenese* shows a well-defined breeding season during which, like tropical parrotfish (Thresher 1984), it spawns daily within a restricted period of time. Mating was observed only inside territories, almost always as pair spawning between a territorial male and either a territorial or a non-territorial female. The occurrence of a ripe male

with a female color pattern, together with the observation of pair spawning disrupted by a second male releasing sperm, suggests the presence of alternative male mating tactics in this species. Nevertheless, the streaking of territorial male spawnings, given its low percentage of occurrence (2.4% of the observed spawnings), is unlikely to represent the only mating tactics of non-territorial males. These males, at our study site, were more numerous than territorial males, and their sizes largely overlapped those of territorial males. Thus the possible occurrence of group spawning and/or non-territorial pair spawning needs to be investigated in order to fully understand the mating system of this species, especially since such behavior has been observed in other parrotfish (Robertson and Warner 1978; Thresher 1984)

More detailed information about female and male mating tactics, and the major factors influencing their choices would also shed light on the adaptive function of the complex social organization shown by this species during the breeding season. Indeed, from July to September, adults of *Sparisoma cretense* are organized either in territories or non-territorial groups. The distinction of these social units is justified by differences in: (1) vertical distribution (territories restricted to depths >11.5 m, non-territorial group areas <11.5 m); (2) sex-ratio (female biased in territories, either male or female biased in group areas); and (3) sexual activity (daily in territories, never observed in shallow group areas).

Differences can also be seen among non-territorial groups. The group observed in shallower water, in the innermost part of the bay, showed a strongly female-biased sex-ratio, and neither spawning nor courtship display were observed in the group. In their organization and behavior, this group resembled the foraging aggregations or schools described in other scarids, such as *Scarus iserti* (Robertson and Warner 1978; Clifton 1990) and *Sparisoma viride* (van Rooij et al. 1996) . During the daily spawning periods, females moved to the outer part of the bay where territorial groups were located (Rasotto personal observation). In contrast, the non-territorial group present in the outer part of the bay, near the territorial group areas, showed a sex-ratio strongly male biased, and courtship displays were extremely common. This group seems to represent "reproductive" aggregations such as the multi-male groups described in the stoplight parrotfish, *Sparisoma viride*, in which no group spawning was observed, although single large males of this species attained a high spawning frequency at deeper spawning sites (van Rooji et al. 1996).

The suggestion that the sexual pattern still maintains a potential for hermaphroditism, and the discovery of different social units in *Sparisoma cretense* add new information to previous classifications of parrotfish based solely on size and color pattern. New questions focused on the understanding of just which resources are important to be defended should be addressed in order to explain the difference in territoriality and life history traits of these fish.

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