Spatial patterns in reproductive traits of the temperate parrotfish Sparisoma cretense

3 authors:

Pedro Afonso
IMAR Institute of Marine Research / MARE Ma…

83 PUBLICATIONS   972 CITATIONS

SEE PROFILE

Telmo Morato
IMAR Azores & Marine and Environmental Re…

119 PUBLICATIONS   2,313 CITATIONS

SEE PROFILE

Ricardo Serrão Santos
University of the Azores

411 PUBLICATIONS   4,961 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project   MERCES - Marine Ecosystem Restoration in Changing European Seas View project

Project   Whale sharks and Azorean tuna fisherman, BFF? View project

Spatial patterns in reproductive traits of the temperate parrotfish *Sparisoma cretense*

Pedro Afonso [a,b,*], Telmo Morato [a], Ricardo Serrão Santos [a]

[a] *Department of Oceanography and Fisheries, University of the Azores, PT 9901-862 Horta, Portugal*
[b] *Department of Zoology/Hawai'i Institute of Marine Biology, University of Hawai'i at Manoa, 46-007 Lilipuna Road, Kane'ohe, HI 96744, USA*

Abstract

Reproductive biology and social behaviour of the parrotfish *Sparisoma cretense* was studied in the Azores Islands, northeast Atlantic, to characterize its spawning season and general reproductive biology in the region, to clarify the species mating system and associated spawning behaviours, and to evaluate the relationship between its reproductive traits and habitat features. *S. cretense* exhibits a dual mating system where males hold female harems within year-round territories or live in multi-male groups. Group behaviour predominates in smaller size classes, and territoriality in larger size classes. Males mature and become territorial earlier in life than females, and the best territories are held by larger males. The two behavioural modes are usually spatially segregated, with larger territorial fish preferring exposed and deeper reef ledges, and group fish occupying shallower, protected habitats. However, they frequently interact and overlap in space, especially during reproduction in the summer. Our findings indicate a highly competitive system and suggest that high quality spawning sites are important for the reproductive success of both types of fish. Patchiness of habitat along shorelines determines the relative distribution and equilibrium of territorial versus group fish. The complexity of this relationship between social structure and habitat might impact the populations' productivity, and could influence the success of marine protected areas for this species.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Reproductive biology; Mating system; Habitat; *Sparisoma cretense*; Marine reserves

1. Introduction

The efficacy of fishery marine reserves, areas set aside from fishing for fishery management purposes, relies on the reproductive output within the reserves to repopulate the fished areas (Russ, 2002). Additionally, an adequate reserve design should protect habitat essential for spawning whenever it is critical for a population's reproductive output (Kramer and Chapman, 1999). In cases of complex mating systems with alternative mating tactics and heterogeneous social structure, the behaviour of the different social components and their relationship with the habitat will influence this efficacy because this might imply differential contributions for the populations' potential productivity, and for its genetic diversity (Palumbi, 2001). Nevertheless, mating systems and their spatial dynamics has seldom been considered in the design of marine reserves.

Parrotfishes (family Scaridae) are typical components of tropical and subtropical shallow reefs worldwide, where they constitute a common target species of reef fisheries. They display a great diversity of mating systems and alternative mating tactics across and between species (Robertson and Warner, 1978; Thresher, 1984). Secondary males, i.e., males arising from sex reversal, are usually distinguishable from females by their different colour – terminal phase (TP) males, whereas primary, direct-developing males usually display the same colour as females – initial phase (IP) males. In many species primary and secondary males overlap in space and compete for habitat and mates, and display different mating strategies. Studies have also shown that local mating and social structure of parrotfish populations are both shaped and limited by habitat quality. For example, *Sparisoma* spp. of distinct social behaviours are spatially segregated by habitat type, and dominant territorial males compete for reef ledges where spawning opportunities are higher (Barlow, 1975; Van Rooij et al., 1996a,b).

* Corresponding author at: Department of Oceanography and Fisheries, University of the Azores, PT 9901-862 Horta, Portugal. Tel.: +351 292200400; fax: +351 292200411.

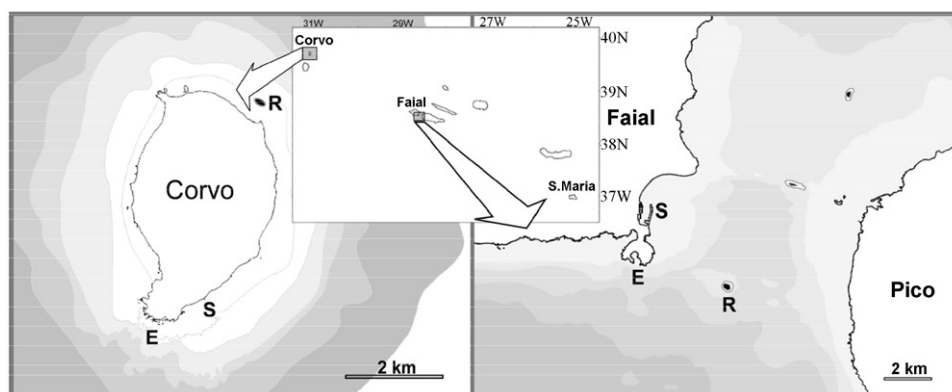*E-mail address:* afonso@notes.horta.uac.pt (P. Afonso).

Fig. 1. Study sites in the Azores archipelago (reproductive biology) and within the islands of Corvo and Faial (mating system); shaded areas represent 50 m increment isobaths; R: offshore reef site, S: sheltered shore site and E: exposed shore site.

The parrotfish *Sparisoma cretense* (Linnaeus, 1758) is of particular interest in this context. It is the only parrotfish occurring in the whole Mediterranean and northeast Atlantic above 20°N, including the Macaronesian archipelagos of the Azores, Canary Islands and Madeira (Fig. 1). It is also one of the few secondary gonochorist (*sensu* Sadovy and Shapiro, 1987) species in the family; that is, males' testes always differentiate from immature ovaries, so mature males only exist as TP males (de Girolamo et al., 1999; Petrakis and Papaconstantinou, 1990; Gonzalez et al., 1993). In the Mediterranean, some males hold female harems during the reproductive season in higher quality territories located deeper, while others occupy shallower areas in multi-male groups (de Girolamo et al., 1999). Previous observations made by the authors seemed to indicate that this might also be the case for Azorean populations. Mediterranean territorial fish spawn in pairs, and group fish were only sporadically seen spawning as 'strikers', that is, males that would interfere in a pair spawning trying to fertilize the eggs (de Girolamo et al., 1999). It remains unclear: (1) whether group fish rely on group spawning or other alternative mating tactics as their main spawning behaviour and (2) what is the importance of spatial interaction and gamete exchange between the two social components. If populations of *S. cretense* are maintained by the reproductive output of haremic individuals, such output would then be governed by local availability of high quality habitat.

S. cretense is the target of important artisanal fisheries throughout the Macaronesian archipelagos, and it is also an important keystone species for the stability of benthic communities and resilience to trophic cascades (e.g. Tuya et al., 2004). Recent increase in the Azorean parrotfish fishery due to the opening of an export market increased the concerns of managers, given the sensitivity of this species to overexploitation that was shown in other regions (Tuya et al., 2006a,b). In fact, other sex-changing parrotfishes were shown to be highly sensitive to exploitation (e.g. Hawkins and Roberts, 2003), but non-sex-changing fishes might be particularly sensitive if they display complex social and mating systems (e.g. Rowe and Hutchings, 2003), as appears to be the case of *S. cretense*. These facts make it a priority target species for protection and management with networks of marine reserves. However, no information is available about the mating system of this species in Atlantic populations or

its reproduction in the Azores. Furthermore, the complex nature of its mating system and the interplay with habitat quality is not well understood.

This paper attempted to address these issues through a spatial analysis of reproductive traits of *S. cretense* in the Azores. Specific objectives were to: (1) characterize the spawning season and general reproductive biology in the Azores, (2) clarify the species' mating system and associated spawning behaviours, and (3) search for spatial patterns in the mating system at different scales in order to evaluate the relationship between reproductive traits and habitat.

2. Methods

2.1. Reproductive biology

The reproductive biology of *S. cretense* was studied on 645 individuals obtained from three different islands across the Azorean archipelago (Fig. 1). A total of 249 fish were caught in monthly collections in Faial Island between August 1997 and September 1998. Additional samples were taken on several occasions during the summers of 1997 and 1998 in the islands of Corvo ($N = 115$) and Santa Maria ($N = 204$), and the summer of 1999 in Faial ($N = 77$). Fish were caught by spearfishing. Equal numbers of the two sexes were taken at each site, based on the fishes' colouration, and approximately equal numbers were captured in each of three size categories—small (<22 cm), medium (23–34 cm) and large (>35 cm). Water temperature was continuously measured using underwater dataloggers (StowAway® TidbiT®) at 25 m depth.

Total length (L_T, cm), total weight (W_T, g), eviscerated weight (W_E, g) and gonad weight (W_G, g) were recorded. Individuals were sexed by visual examination of the gonads and were staged as immature (stage 0), resting (stage 1), developing (stage 2), ripe (stage 3), spawning (stage 4) or spent (stage 5) (adapted after González and Lozano, 1992). The sex of individuals smaller than 13 cm was unidentifiable. The colour morph of each fish was classified as immature, mottled brown, red or grey (see de Girolamo et al., 1999 for descriptions).

Differences in average length between sexes were tested by single-factor ANOVA (Zar, 1999). Length (L_{50}) at first maturity

was estimated by fitting the relative frequency of mature individuals, i.e., of macroscopic stages 1–5, over 1 cm L_T classes to a logistic curve using the Levenberg–Marquardt algorithm for solving non-linear least squares regression. Spawning season was determined by the monthly variation of macroscopic gonadal maturity stages and by variation of the mean gonado-somatic index (GSI), the ratio between W_G and W_E calculated for mature individuals.

2.2. Social structure

The social structure and underlying mating system of the Azorean population of *S. cretense* was studied with underwater visual census (50 m × 5 m strip transects) during the summers of 2002 and 2004 around the islands of Faial and Corvo. During transects, individuals were sexed based on their colour dimorphism (e.g. Falcón et al., 1996; de Girolamo et al., 1999), and sized as one of four predefined classes: juvenile (<7 cm), small (7–22 cm), medium (23–34 cm), large (35–44 cm) and very large (>44 cm). The small size and cryptic behaviour of juveniles make them hard to count using this method, so quantitative data for this size class is not presented. The observer would also note the degree of association of the individuals and their agonistic behaviour towards conspecifics, so as to assign them to either the 'territorial' (haremic) or 'group' fish class. All transects were performed during spawning season, when territorial males are easily distinguishable by their aggressive behaviour towards group fish and other territorial males and by their constant patrolling behaviour. Males were assigned as territorial if they were isolated and displayed aggressive or patrolling behaviour, and group if they were seen swimming along with at least one other male. Females were assigned as territorial if they were seen isolated or swimming along with two or three other females only in the vicinity of a territorial male, and group otherwise. This set of diagnostic criteria was based on the detailed behavioural studies of de Girolamo et al. (1999) with a Mediterranean population that exhibited the same two social behaviours, and further ascertained with our own preliminary observations on some individuals. This allowed us to confirm that the two behavioural modes occurred in the Azorean population (at least during the spawning season) and that the criteria described could consistently be used in the diagnose. In general, this diagnose could be achieved within 30 s, but we could not identify the social mode of 82 fishes.

To test for the influence of habitat characteristics on the social and mating system, three different habitat types were surveyed in each of the two islands, totalling six sites: sheltered shoreline, neighbouring exposed shoreline, and offshore reef. Early work showed that the variability within habitat types is smaller that between different habitats types (Afonso, 2002), therefore the selected sites for each type can be considered as replicates. Only areas with substrate composed of boulder fields interspersed with rocky outcrops were chosen, as this is the species' preferred habitat (de Girolamo et al., 1999; Guidetti and Boero, 2002; Falcón et al., 1996; personal observation). Sites were sampled on every 10 m depth strata down to 40 m to detect any segregation of social type with depth, although the resulting design was not fully orthogonal because some strata were not available at some sites (e.g. shallow strata at offshore reefs and deeper strata at sheltered shorelines). Three to five randomly assigned replicates per plot (depth vs. site) were conducted.

Overall social structure was characterized by pooling all fishes of known social mode (*n* = 481) and determining the probability of fish pertaining to a given social status class (territorial or group fish) as a function of size class and sexes, which are fixed characteristics. This was based on the assumption that the possibility of pseudoreplication by multiple counts of individuals is negligible due to the random assignment of transects within habitat type and depth within every site. We used a log-linear model to analyze the resulting three-dimensional frequency table, treating social status as the response variable, and size and sex and the design variables (Zar, 1999).

Spatial differences in the social structure between sites were assessed with two-way crossed ANOVA on total abundance and biomass for each type versus sex combination, with island and habitat as fixed factors and using only data from intermediate depth strata common to all sites. Bonferroni-corrected pair-wise comparisons between levels were performed whenever ANOVA models were significant. All data were verified for normality (K–S tests) and homogeneity of variance and a square root transformation ($x + 0.5$) applied whenever needed to meet parametric assumptions.

2.3. Reproductive behaviour

Behavioural observations were carried out during 2003 and 2004 at the sites at Faial Island to clarify the mating behaviour associated with the different social modes and to ascertain the seasonality of territoriality. *S. cretense* is only active during daylight (personal observation), so observations were restricted to this period. General observations were made *ad libitum* on 35 dives and were timed so as to cover every daytime hour in the summer reproductive season and most daytime hours during the rest of the year. After the discovery of early morning spawning, the first two of hours of daylight were the subject of more intense observations in those sites.

3. Results

3.1. Reproductive biology

The fish caught in this study showed the same association between colour morphs and sex as fish from other geographic regions, that is, red livery for females and grey livery for males. The mottled livery only appeared in 10% of females of every maturity stage except spawning females and in 5.5% of males in resting condition but neither these nor any other fish showed any evidence of hermaphroditic transitional gonads.

Parrotfish caught in this study ranged in size from 3.1 cm to 52.2 cm L_T. Identifiable males ranged from 16.1 cm to 52.2 cm L_T, and identifiable females from 12.6 cm to 49.6 cm L_T. Males and females had similar length–frequency distributions with no clear separation in modal sizes (Fig. 2) but males dominated larger size classes (>47 cm L_T) whereas females dominated
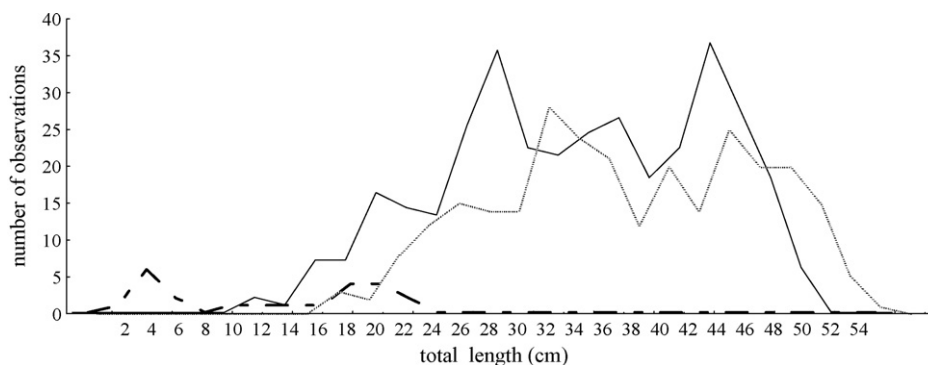
Fig. 2. Length–frequency distribution of *Sparisoma cretense* collected between 1997 and 1999 in the Azores: (solid line) males, (dotted line) females and (dashed line) indeterminate.

smaller size classes (<25 cm L_T). As a result, average length of males was significantly larger than that of females (36.2 cm vs. 34.4 cm L_T, ANOVA; $F = 7.07$; d.f. = 611; $p < 0.01$). We found 14 individuals of indeterminate sex ranging 3.1–23.4 cm.

The size at first maturity as determined by macroscopic evaluation of gonads was 24.16 cm for both sexes pooled ($n = 621$, $R = 0.99$) but males matured at smaller size than females (21.9 cm vs. 25.0 cm, Fig. 3). All males and females were mature at 33 cm and 34 cm L_T, respectively. Pooled L_{50} was 28.9 cm in Corvo, 27.0 cm in Faial and 24.1 cm in Santa Maria. Macroscopic evaluation of gonads showed a clear pattern of reproductive activity restricted to the summer. Ripe fish appeared first in June, spawning fish from July to September and spent fishes from August to October (Table 1). This was matched by the monthly evolution of GSI, which increased from June to August and then dropped until reaching its low, in November (Fig. 4). GSI associated closely with mean temperature. Maturation starts soon after the spring increase in temperature, and spawning lasts from around 20 °C until the fall temperature drop. Males were again more variable regarding when they became fully mature and ready to spawn. In summary, *S. cretense* spawns from mid-July to mid-September in the Azores. It is possible that some individuals extend their reproductive activity through October, given that this month was poorly sampled.
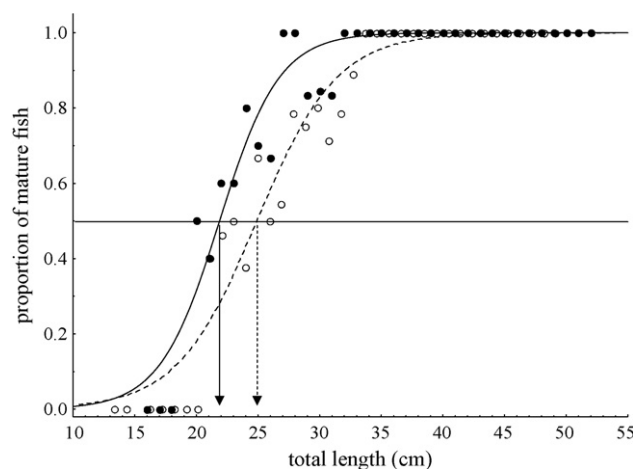

Fig. 3. Length at first maturity (L_{50}, arrows) for *S. cretense* collected between 1997 and 1999 in the Azores: (solid line/circles) males and (dashed line/open circles) females.

3.2. Social structure

Overall density of *S. cretense* was 7.4 ± 10.3 (mean $\pm$ S.D.) fishes per transect, ranging from 0 to 50 fish per transect ($n = 68$). Density of mature fish was 6.3 ± 9.2, ranging from 0 to 45 fish per transect (250 m^2). Difference in abundance between sexes

Table 1

Monthly percentage of macroscopic gonadal maturity stages per sex in mature *Sparisoma cretense* caught in the Azores between August 1997 and 1999

Maturity	Males						Females					
	1	2	3	4	5	*n*	1	2	3	4	5	*n*
January								100				1
February												–
March	97	3				34	67	33				60
April		100				1		100				1
May	84	16				19		100				17
June	12	88				17		56	44			18
July		8	92			25		20	56	24		25
August		9	47	36	9	47		13	47	34	6	70
September	11	6	18	44	21	66		48	15	23	13	52
October					100	2						–
November	100					2		100				1
December	92	8				13	7	93				14

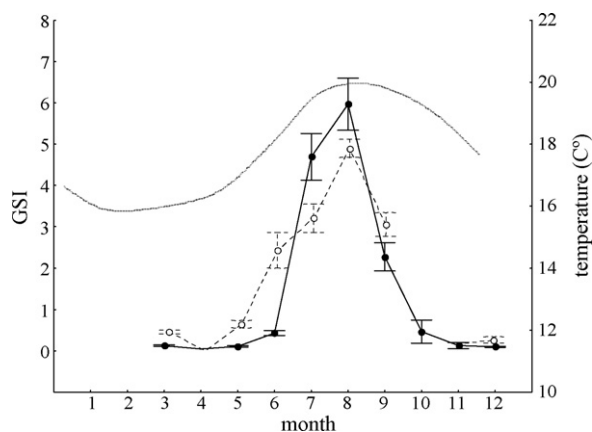1 = resting; 2 = developing; 3 = ripe; 4 = spawning and 5 = spent.

Fig. 4. Annual pattern of the gonosomatic index (GSI, $X \pm 1$ S.E.) for mature *S. cretense* in the Azores: (solid line/circles) males ($n = 243$); (dashed line/open circles) females ($n = 309$) and (dotted line) temperature.

was not statistically significant, whether considering all fish (3.6 ± 6.0 males vs. 3.7 ± 5.3 females; paired *t*-test, d.f. $= 68$, $p = 0.84$) or mature fish only (3.4 ± 5.8 vs. 3.0 ± 4.3; $p = 0.90$). Total density was higher in Faial Island than in Corvo Island (9.8 ± 14.2 vs. 5.5 ± 5.2), but this difference was not significant ($p = 0.09$).

Density of territorial and group fish per transect was nearly the same but variability was much higher among group fishes (2.5 ± 2.4 vs. 2.9 ± 8.7). Such dispersion reflects the behaviour of group fishes, which are constantly aggregating and disaggregating, and therefore the highly variable (2–30) number of individuals seen in a given group.

Fish from both sexes gradually switched from group to territorial behaviour as they increased in size, with the larger differences between behaviours in extreme classes (Fig. 5). All size classes showed higher proportion of group males than group females, again with the larger differences in the small and large size classes. As a result, size of a fish influenced its probability of belonging to a given social type (partial χ^2, d.f. $= 3$, $p < 0.01$) but sex alone did not (partial χ^2, d.f. $= 1$, $p < 0.80$), and the best fitting log-linear model to the frequency table include all second-order interactions (Pearson χ^2, $p = 0.07$).
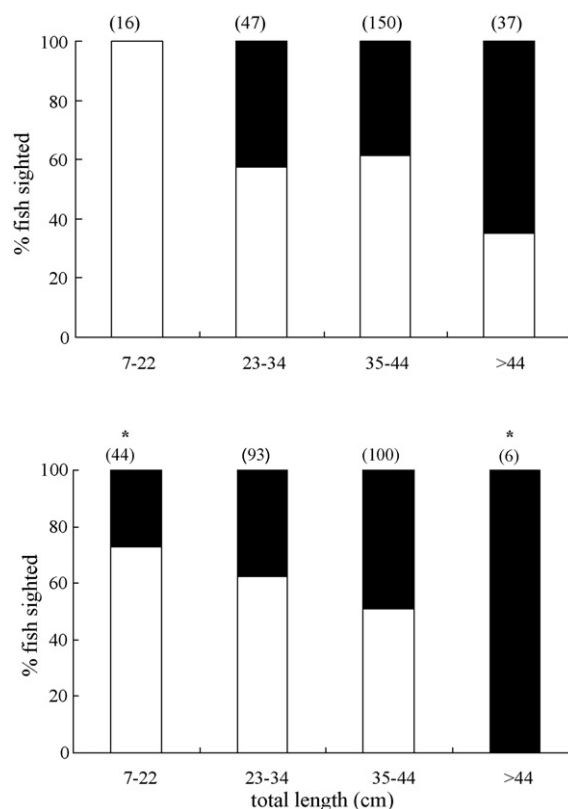

Fig. 5. Overall social structure of male (upper) and female (lower) *S. cretense* of different sizes in the Azores. (black bars) territorial fish and (white bars) group fish.

Both local and large-scale geography seemed to influence the sexual and social structure of *S. cretense*. Multivariate analysis of variance on the abundance of the four structural units altogether (sex vs. social type) showed that habitat type and island significantly explained the variability in the overall structure, whereas depth did not (Table 2). Habitat and island significantly explained the abundance of all units except territorial females. Abundance of group male and female were higher in Faial than in Corvo (Bonferroni post hoc comparisons: males $p < 0.01$ and females $p < 0.05$), and lower in offshore and exposed reef than in

Table 2
Output of multivariate (MANCOVA) and univariate (ANCOVA) analysis of covariance on the abundance of the sex/social units with habitat features

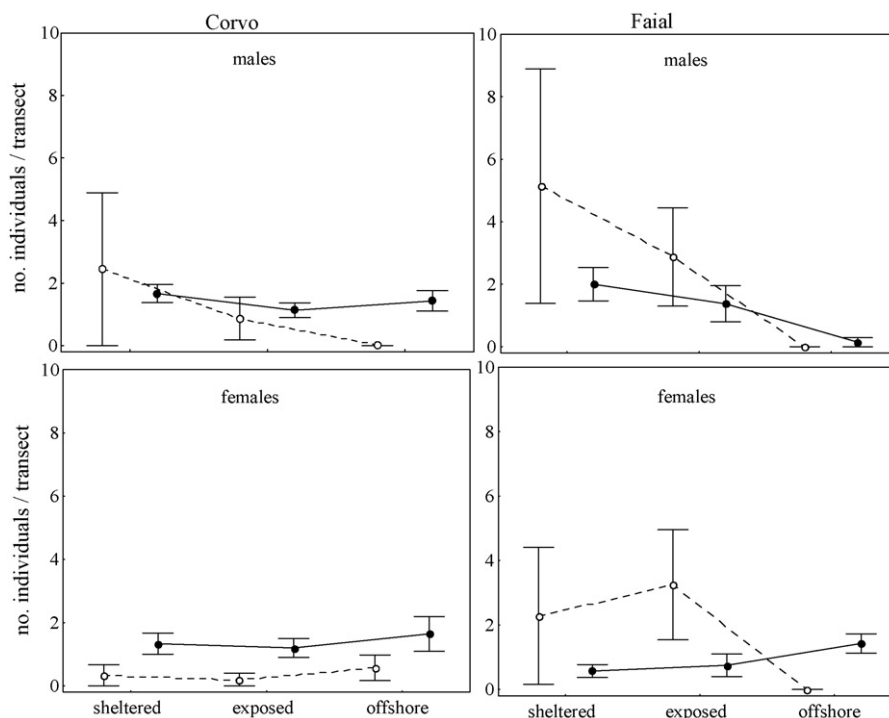|	ANCOVAs					MANCOVA		
	Effect d.f.	Territorial		Group		Effect d.f.	Error d.f.	*F*
		Male	Female	Male	Female			
		F	*F*	*F*	*F*			
Depth	1	0.12	0.02	2.35	0.69	4	58	0.72
Island	1	3.37	2.26	11.43[**]	5.48[*]	4	58	6.45[**]
Habitat	2	4.83[*]	1.51	9.07[**]	4.35[*]	8	116	3.19[**]
Island × habitat	2	2.42	0.41	6.70[**]	1.08	8	116	2.80[**]
Error d.f.		59	59	59	59			
R^2		0.22	0.12	0.43	0.24			
F		2.76[*]	1.39	7.6[**]	3.0[*]			

[*] $p < 0.05$
[**] $p < 0.01$.

Fig. 6. Abundance ($X \pm$ S.E.) of male and female *S. cretense* as a function of the increasing degree of habitat hydrodynamic and oceanic exposure in the islands of Corvo and Faial: (black circles and solid line) territorial fish and (open circles and dashed line) group fish.

inshore reefs ($p < 0.01$, Fig. 6). Territorial males were affected by habitat only, due to lower abundance in the offshore reefs when compared to the inshore sheltered habitats ($p < 0.05$). Although depth did not play a major role when explaining total abundance, certainly reflecting the availability of strata in different habitats, it did influence the size structure of local populations, namely that of territorial fish. There was a general increase in size of territorial fish with depth for both sexes (Fig. 7).

3.3. Spawning behaviour

We saw parrotfish courting between July and September but spawning was only observed in August. We only saw spawning at dawn, always in the exposed reef of Faial.

Territorial males displayed to females frequently, within their territories and during the reproductive season. A male display consisted in circular swimming, usually taking place a few meters above an exposed reef ledge. Pair spawning, a vertical rush of the pair with simultaneous release of gametes in the water column (see de Girolamo et al., 1999 for descriptions), was observed twice between a male and a female from its harem. Sometimes territorial males engaged in group courtship in 'courtship arenas' in the water column, as described by de Girolamo et al. (1999), especially when group fish were around.

Group spawning was only witnessed once. The fish involved in group spawning were a female (ca. 25 cm) and 10 males (ca. 20–30 cm), apparently all group fish. The males actively pursued the female at very close distance, until the female darted vertically accompanied by several males and gametes were released in the water column. We never saw courtship within groups, but group males were occasionally seen engaging in the display

arenas together with territorial males, and group females were courted by territorial males. Territorial males frequently chased away other conspecifics when these would invade the male's territory. We did not see any fertilization stealing.
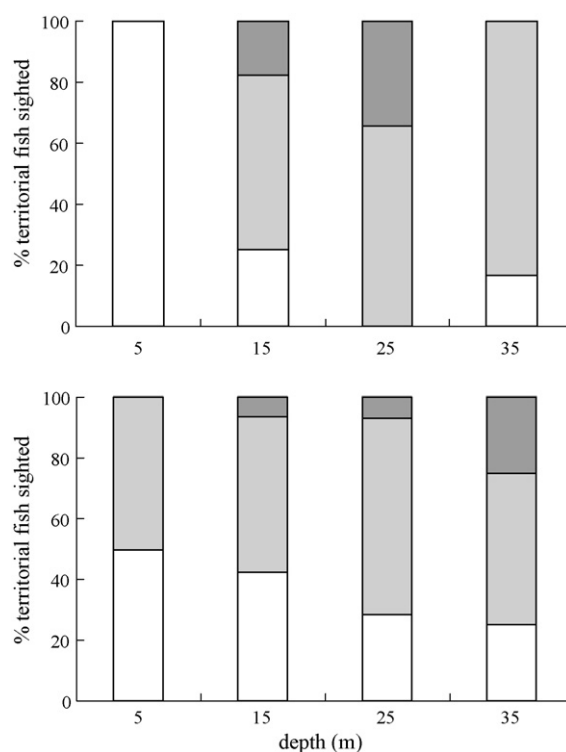

Fig. 7. Size structure of territorial male (upper) and female (lower) *S. cretense* per depth strata: (white) 23–34 cm total length, (light grey) 35–44 cm and (dark grey) >44 cm.

4. Discussion

4.1. The mating plasticity of S. cretense

S. cretense displays two contrasting social and mating behaviours, this being haremic territoriality or living in mixed-sex, loose groups (de Girolamo et al., 1999; this study). Multi-male group parrotfishes have been suggested to experience low reproductive success compared to territorial fish, including in *S. cretense* (de Girolamo et al., 1999) and *Sparisoma viride* (Van Rooij et al., 1996b). In this case, it would be adaptive for these fish to change tactic during their lifetime, as size has been shown to be advantageous for territory defence in other non-sex-changing fishes (e.g. Grant, 1997). Although individuals were not followed throughout their lifetime, the fact that territorial *S. cretense* are typically larger than group *S. cretense* is supportive of this hypothesis and of a competitive social system, where larger (and maybe more aggressive) males benefit more from territoriality. Group fish of *S. cretense*, which compose a considerable portion of the population, must show enough behavioural plasticity to switch their behavioural mode under favourable conditions. This has previously been shown in sex-changing scarids (Munoz and Warner, 2003) but not in non-sex-changing parrotfishes, and deserves further study.

Behavioural plasticity might also have physiological consequences. Sperm competition in group spawning or streaking is typically higher than in pair spawning and group males have to compensate this demand by producing higher quantities of sperm than territorial males (Marconato and Shapiro, 1996). This explains why we found large variability in relative gonad size of ripe males.

It is noteworthy that we observed so few spawning events in the Azores, considering that, at least the Lampedusa's population (de Girolamo et al., 1999), has been reported to spawn daily. However, in the Azores spawning was only observed at dawn, and earlier in the course of this study (2003). We made numerous observations at dawn afterwards, but did not succeed in spotting many spawning events, although we did observe courtship extensively. It is likely that the influence of the moon and/or tides on the spawning behaviour of Azorean populations of *S. cretense* explain why we saw few spawning events. However, this hypothesis could not be tested with our sampling protocol. This hypothesis deserves further investigation.

4.2. Effects of habitat on the local social structure

Territorial fishes preferred specific habitats in the Azores. Reef ledges located deeper and in areas more exposed to wave and current action are selected by larger, possibly experienced territorial males, whereas in sheltered, shallower habitats most territorial males are small. In this way, larger territorial males also gained access to larger females, which should assure higher reproductive output. We also observed this pattern in other islands. In the Mediterranean, territorial *S. cretense* also tend to live deeper and in areas of higher energy (de Girolamo et al., 1999). Therefore, it seems to be the rule that territorial males of *S. cretense* prefer this type of habitat, and its local availability must influence the distribution and abundance of territorial fish. Other studies with tropical parrotfishes reported similar habitat selection patterns whenever different social behaviours coexisted in the population (e.g. Van Rooij et al., 1996a). This behaviour might be widespread among parrotfishes.

Group fish appear competitively excluded by local territorial individuals from high-energy reef areas by local territorial individuals, but they still try to use these areas. Apparently, this is mostly for reproduction purposes (de Girolamo et al., 1999; this study). Group fishes were seen actively travelling to territorial areas during early morning reproductive events, presumably to take part in reproductive events. In this way group males increase opportunities to steal fertilizations (de Girolamo et al., 1999), and group females increase opportunities to mate with territorial males. Therefore, if spawning areas are within home range of group fish they can expect to increase their reproductive success. Furthermore, such mobility facilitates reconnaissance and evaluation of a possible change in tactic by taking over vacant territories. This partially explains why there are virtually no group fish in the offshore reefs.

4.3. Implications for management

A probable consequence of the spatial segregation of social units is that the fishery will be selective toward particular units. In the Macaronesian archipelagos, *S. cretense* is targeted mostly with gillnets in protected shores. Thus, one might expect group fishes to be selectively removed, given that this is their prime habitat. Territorial individuals apparently provide most of the population's reproductive potential, as indicated by their sexual activity and by their disproportionate contribution to larger size classes (de Girolamo et al., 1999; this study). For example, using the function of Gonzalez et al. (1993) for the Canary Islands, a very large (47 cm L_T) female (almost certainly territorial) would produce 3.8 million eggs, 25 times the output of a recently matured (25 cm) female (150,000 eggs), that will probably be a group female. Although this implies lower impact of gillnet fishing on the population's immediate fecundity, it can reduce the future population's fecundity if shortage of group fish reduces their capacity to replace local territorial population or affects the population's genetic diversity (see above).

The same rationale can be used to develop optimal designs of marine reserves for this species. Home range, migrations and larval dispersal patterns are potential determinants of a reserve's efficacy (Kramer and Chapman, 1999) and will affect decisions about how large and numerous reserves should be in a network (e.g. Halpern and Warner, 2003). However, if a population's reproductive potential is dependent on particular habitats, the inclusion of this essential habitat inside the reserves will largely determine the efficacy of the network to deliver larvae to adjacent fishing grounds, and ultimately control its self-sustaining capacity. Local populations of *S. cretense* appear dependent on high quality spawning sites for adequate reproductive output, but their longer term resilience and genetic diversity could also depend on the exchange of gametes between territorial and group fishes and, consequently, on the protection of adequate habitats for these fish as well.

5. Conclusions

The overall significant importance of this study is to show that *S. cretense* displays two types of mating tactics and associated behaviours, and that the social structure and the levels of sexual interference are labile and shaped by local habitat. Although our observations indicate limited home ranges, movement studies are desirable to test this possibility and to evaluate the degree of residency. This should be done taking in explicit consideration the hypothesis that territorial and group fish may differ in their spatial behaviour, and if they overlap in space during the spawning season.

Acknowledgements

References

Afonso, P., 2002. Spatial patterns in the littoral fish community of the Azores. MS thesis, University of Coimbra, Coimbra, 104 pp.

Barlow, G.W., 1975. On the sociobiology of four Puerto Rican parrotfishes (Scaridae). Mar. Biol. 33, 281–293.

de Girolamo, M., Scaggiante, M., Rasotto, M.B., 1999. Social organization and sexual pattern in the Mediterranean parrotfish *Sparisoma cretense* (Teleostei: Scaridae). Mar. Biol. 135 (2), 353–360.

Falcón, J.M., Bortone, S.A., Brito, A., Bundrick, C.M., 1996. Structure and relationships within and between the littoral rock-substrate fish communities off four islands in the Canarian Archipelago. Mar. Biol. 125, 215–231.

González, J.A., Lozano, I.J., 1992. Determinación de curvas de madurez sexual en la veja, *Sparisoma (Euscarus) cretense* (L.) (Osteichthyes, Scaridae), de Canarias. Boln. Inst. Esp. Oceanogr. 8 (2), 271–297.

Gonzalez, J.A., Lozano, I.J., Hernandez-Cruz, C.M., 1993. Fecundity of *Sparisoma (Euscarus) cretense* (L.) (Osteichthyes, Scaridae) in the Canary Islands. Bol. Inst. Esp. Oceanogr. 9 (1), 123–131.

Guidetti, P., Boero, F., 2002. Spatio-temporal variability in abundance of the parrotfish, *Sparisoma cretense*, in SE Apulia (SE Italy, Mediterranean Sea). Ital. J. Zool. 69, 229–232.

Grant, J.W.A., 1997. Territoriality. In: Godin, J-G.J. (Ed.), Behavioral ecology of teleost fishes. Oxford University Press, pp. 81–103.

Halpern, B.S., Warner, R.R., 2003. Matching marine reserve design to reserve objectives. Proc. R. Soc. London Ser. B: Biol. Sci. 270 (1527), 1871–1878.

Hawkins, J.P., Roberts, C.M., 2003. Effects of fishing on sex-changing Caribbean parrotfishes. Biol. Conserv. 115, 213–226.

Kramer, D.L., Chapman, M.R., 1999. Implications of fish home range size and relocation for marine reserve function. Environ. Biol. Fish 55 (1–2), 65–79.

Marconato, A., Shapiro, D.Y., 1996. Sperm allocation, sperm production and fertilization rates in the bucktooth parrotfish. Anim. Behav. 52 (5), 971–980.

Munoz, R.C., Warner, R.R., 2003. Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. Environ. Biol. Fish 68, 307–319.

Palumbi, S.R., 2001. The Ecology of Marine Protected Areas. In: Bertness, M.D., Gaines, S.M., Hixon, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Sunderland, pp. 509–530.

Petrakis, G., Papaconstantinou, C., 1990. Biology of *Sparisoma cretense* in the Dodecanese (Greece). J. Appl. Ichthyol. 6 (1), 14–23.

Robertson, D.R., Warner, R.R., 1978. Sexual patterns in the labroid fishes of the western Caribbean. II. The parrotfishes (Scaridae). Smithsonian Control Zool. 255, 1–26.

Rowe, S., Hutchings, J.A., 2003. Mating systems and the conservation of commercially exploited marine fish. Trends Ecol. Evol. 18 (11), 567–572.

Russ, G.R., 2002. Yet Another Review of Marine Reserves as Reef Fishery Management Tools. In: Sale, P.F., (Ed.), The Ecology of Coral Reef Fishes pp. 421–443.

Sadovy, Y., Shapiro, D.Y., 2003. Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1987 (1), 136–156.

Thresher, R.E., 1984. Reproduction in Reef Fishes. T.F.H. Publ. Inc. Ltd., Neptune City, NY.

Tuya, F., Boyra, A., Sanchez-Jerez, P., Barbera, C., Haroun, R.J., 2004. Relationships among fishes, the long-spined sea urchin *Diadema antillarum* and algae throughout the Canarian Archipelago. Mar. Ecol. Prog. Ser. 278, 157–169.

Tuya, F., García-Diez, C., Espino, F., Haroun, R.J., 2006a. Assessment of the effectiveness of two marine reserves in the Canary Islands (eastern Atlantic). Cienc. Mar. 32 (3), 505–522.

Tuya, F., Ortega-Borges, L., Sanchez-Jerez, P., Haroun, R.J., 2006b. Effect of fishing pressure on the spatio-temporal variability of the parrotfish, *Sparisoma cretense* (Pisces: Scaridae), across the Canarian Archipelago (eastern Atlantic). Fish. Res. 77, 24–33.

Van Rooij, J.M., Kok, J.P., Videler, J.J., 1996a. Local variability in population structure and density of the protogynous reef herbivore *Sparisoma viride*. Environ. Biol. Fish. 47, 65–80.

Van Rooij, J.M., Kroon, F.J., Videler, J.J., 1996b. The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. Environ. Biol. Fish. 47, 353–378.

Zar, J.H., 1999. Biostatistical Analysis, 4th ed. Prentice Hall International Editions, New Jersey.