Socio-behavioural context of reproduction in the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain)*

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SUMMARY: The evolution of social structures and reproductive behaviours leading to actual spawning in the Mediterranean dusky grouper, *Epinephelus marginatus*, was studied in the Medes Islands Marine Reserve on the Spanish coast (NW Mediterranean) from February 1995 to October 1996. Density, size, sex, colour patterns, relation the bottom, swimming activity and site occupation were monitored by visual census surveys at monthly and daily scales. The main observed socio-behavioural trends were in part comparable with some patterns reported in tropical groupers, although differences exist, which might in part be related to the temperate conditions of the northern Mediterranean sea. The density of dusky groupers in the area was low in winter, and maximal in summer, from late June to late August (up to 8-fold increase); numbers risen in spring, before the beginning of reproductive activities which led to spawning by mid August, and dropped rapidly afterwards. During this long reproductive period (about 2 months), dominant males (recognized by their highly specific colour pattern) established territories in which they displayed aggressively towards neighbouring males and numerous smaller females (the species is protogynous); the observed sex-ratio was approximately 1:7 (sexually active males versus adult females). Territoriality of males is the base of the social structuration of the reproductive population; in addition, behaviours typical of the pre-spawning period include repeated evening gathering of females in open water, and the appearance of specific colours patterns. This overall socio-behavioural pattern changed in the evenings when spawning was observed (16th - 21st of August), the males patrolling a reduced territory in which females would come to mate; spawning behaviour itself was described in Zabala et al. (1997). The complex socio-behavioural structure leading to reproduction in the Dusky Grouper should be considered in fishery management, since it could hardly develop under strong human pressure. In this respect, the contribution of Marine protected areas is determinant for the reproductive success of this species in the NW Mediterranean basin.

Key words: Grouper, *Epinephelus marginatus*, colour patterns, social structure, reproduction, marine reserves, Mediterranean Sea.

RESUMEN: CONTEXTO SOCIO-COMPORTAMENTAL DE LA REPRODUCCIÓN DEL MEROS *EPINEPHELUS MARGINATUS* (LOWE, 1834) (PISES, SERRANIDAE) EN LA RESERVA MARINA DE LAS ISLAS MEDES (MEDITERRÁNEO NOROCCIDENTAL, ESPAÑA). - La evolución de las estructuras sociales y del comportamiento reproductor que conduce a la faena del meros *Epinephelus marginatus*, fueron estudiados en la Reserva Marina de las Islas Medes (costas españolas; Mediterráneo noroccidental) entre Febrero de

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INTRODUCTION

The tropical groupers, fishes from the Epinepheline tribe of the Serranidae family, studied until now use to exhibit a complex and socially structured reproductive behaviour, together with specific ephemeral colour patterns (Colin et al., 1987; Gilmore and Jones, 1992; Tucker et al., 1993; Baehr et al., 1994; Sadovy et al., 1994; Samoilys and Squire, 1994; Donaldson, 1995a, b). Some of them engage every year in reproductive migrations towards aggregation sites, which proved to make them very sensitive to overexploitation at that time. This is why the knowledge of reproductive behavior is considered to be important in the management and conservation of groupers populations (Samoilys and Squire, 1994).

The dusky grouper Epinephelus marginatus (Lowe, 1834) is probably the most popular of littoral fishes along the Mediterranean coasts. Paradoxically, there are considerable gaps on the knowledge of its biology, social structures and behaviour. Thus, it is difficult to explain precisely the dramatic reduction of NW Mediterranean stocks in the past decades (for example, annual commercial catches along the Spanish coast were over 200 tons in the 70’s, but decreased to almost nothing in the 90’s; Gracia, 1996).

Marine protected areas are now the only places where groupers can be encountered in reasonably high densities. Moreover, the lack of juveniles and the dominance of very large individuals suggest that these populations are not self-recruiting, and are renewed by migratory movements of adult fishes (Chauvet, 1991; G.E.M., 1996). Recently, the finding of young groupers (less than 10 cm long) in the northern Mediterranean coasts of Spain and France (Harmelin and Robert, 1992; Lelong, 1993) brought the evidence that reproduction now occurs in the NW basin, although juveniles remain very few. But no direct observations of the spawning and reproductive behavior of this species has come yet to our notice.

Since 1990, we suspected that some reproductive activities of this species could take place in the Madea Islands Marine Reserve (NE Spain). During the course of a survey held in 1995 and 1996, we could observe the social and behavioural evolution of a group of dusky groupers, which led to reproduction. The actual spawning was witnessed, and spawning behaviour itself is the subject of another article (Zabala et al., 1997).

In this paper we focus on the social context of the reproductive behaviour of the dusky grouper: seasonal and daily changes of density, social structure, behaviour and colour patterns, territoriality and space occupation, sex-ratio and mating strategy. The results of this work may help in evaluating the requirements of the dusky grouper for its reproduction, and contribute to explain its poor reproductive success in the NW Mediterranean: they may also help in understanding why its populations decreased so abruptly, and how they could now recover.

MATERIAL AND METHODS

We provide here only a brief overview of the basic informations about the Madea Islands Marine Reserve and about the dusky grouper (for more detail, see Zabala et al., 1997).
Fig. 1. – **A.** Map of the Medes Islands marine Reserve with the area of study (rectangle); **B.** community and bathymetric map of the studied area showing the route of Transect 1 (around 200 x 10 m) designed for density analysis; **C.** detail of the studied area showing the route of the strip Transect 2 (around 100 x 10 m) and the scheme of zones used during the study of reproductive behavioural patterns; **D.** idealized section of the strip transect.
The site

Observations were carried out in the Medes Islands Marine Reserve (NE Spain, 3° 13’ E, 42° 3’ N). This little Reserve (about 90 Ha strictly protected), is composed of 7 islands and islets situated about 2 miles from the shore (Fig. 1A). It now shelters a dense population of *E. marginatus* (about 120 individuals in summer; García-Rubies and Zabala, 1994), most of which are concentrated in our study area, in the south-eastern end of the Reserve, where up to 65 individuals can be seen in a single census (Fig. 1B, C). Bottom topography in this small zone is a mix of different environments, including big boulders piling up between 5 and 20-25 m, and a deeper flat rocky platform with “coralligenous” concretions extending from 20 to 32 m (Fig. 1D).

Moderate to strong currents are common, and both their direction and strength can change repeatedly within a day, leading to sharp variations in water transparency, temperature and salinity. The mean water transparency ranges from 8.5 m in November and March to 26.5 m in August. Seasonal and interannual changes in water temperature have been documented for more than 20 years (Pascual *et al.*, 1995); the shallow waters reach the highest temperature (up to 25 °C) in August, and the lowest (down to 12 °C) in February-March. From May to August, shallow waters undergo a process of warming and thermo-haline stratification. The estival stratification enhances sinking of plankton and, together with a lowering of river outflows with low nutrient depletion, induces an increase in water transparency. Nevertheless, both temperature and transparency can change suddenly due to vertical shifts of the upper limit of the thermocline. Thus, groupers moving about at medium depths (15-20 m) may be exposed, sometimes within an hour, to temperature changes as high as 5 °C while visibility may double or lower by half.

Spawning (see Zabala *et al.*, 1997) occurred when the surface temperature reached its maximum of 25 °C in August, which also was the period of maximum water transparency.

The species

The dusky grouper *Epinephelus marginatus* (Lowe, 1834), was commonly cited in the past under the *nomen dubium* E. *gigas* (L.) or *E. gigas* (Brünich) (Heemstra, 1991). It is a protogynous hermaphrodite in which sex reversal seems to occur mainly when individuals are 14-17 years old and about 80-90 cm long (total length) (Bruslé and Bruslé, 1976; Bruslé, 1985; Chauvet, 1991; Gracia, 1996). Larger individuals, which are unquestionably males, can reach a maximum size of 120 cm, weight 40 kg, and be up to 50 years old. The first sexual maturity is reached when females are 5 years old and 40 to 50 cm long (Chauvet, 1988).

The reproductive season of *E. marginatus*, approximately known by dissection of mature individuals, ranges from June to August in the Western Mediterranean (Spartà, 1935; Barnabé, 1974; Bruslé and Bruslé, 1976; Bouain, 1980; Bouain and Saiu, 1983; Bruslé, 1985; Chauvet, 1988; Gracia, 1996).

Like other groupers, this species seems to display complex social and individual behavioural patterns, which we only begin to understand (Louisy, 1996). It is reputed to be sedentary, living more or less strictly associated with a permanent hole, though experiences of tagging (Chauvet and Francour, 1991) and visual identification by means of facial spots (unpublished data) showed that local movements, up to some miles in distance, occur commonly within a population. Larger migratory movements have never been proved but are probable, mainly for young individuals.

The groupers of Medes Islands

The change in behaviour of fishes, for example concerning preferred depths or reactions to divers, is one of the still poorly described effects of Mediterranean Marine Reserves (but see Harmelin *et al.*, 1995). Due to the high number of underwater visitors (diving in the Reserve is limited to 450 divers per day, but represents in fact about 65,000 dives a year), and to the permitted habit of feeding fishes, groupers of the Medes Islands Marine Reserve have lost their natural shyness and are strongly attracted by divers; it is not uncommon to see a group of divers surrounded by ten groupers or so looking for food. In a hand, this helps the observer to approach the fishes during reproductive activities, but it also complicates the interpretation of interactions and colour patterns.

In summer at least, groupers of the Medes Islands use to live out of their shelters. Most of them -even when territorial- wander widely and often swim in open water. If disturbed, they look for a shelter close-by, and rarely remain hidden in a fixed hole. When hungry, some individuals may follow divers for more than 200 m.
Methods

Underwater visual censuses (UVC) were undertaken following the strip transect method (Harmelin-Vivien et al., 1985). Each census was conducted by one trained observer, although different censuses were done by one of three persons. The observer adopted a fixed search pattern following a fixed route, in order to provide quantitative data on site preferences and changes in density, size structure and behaviour of groupers. Two different runs were chosen:

A) Transect 1 was designed to estimate changes in density in a year round scale. A closed route, about 200 m long and 10 m wide, running around two islets, was chosen to allow the observer to find easily his way, even when visibility was poor (Fig 1B). 22 UVC were repeated, roughly every two weeks, from February 1995 to January 1996 (with a gap during August 1995), and 4 times in August 1996 (to fill the gap). The route was swum in a set time of 40 min., and all the counts were made between 10:00 and 12:00 GMT.

B) Transect 2, a strip about 100 m long and 10 m wide, was chosen to cross areas of different depths and topographies, where groupers were previously observed to rest, feed and display reproductive interactions (Fig. 1D). It was divided in zones A to H (Fig. 1C). Censuses were repeated on this transect from May 1996 to September 1996, at different times of the day (about 6h, 13 h and 17h GMT), looking for daily and weekly changes in behaviour and activity. The route was swum in about 20 min.

When a grouper was encountered, the depth, zone, size, colour pattern and position relative to the bottom were quantified in discrete categories. Sizes (total lengths) were estimated at the nearest 5 cm, and arranged for most purposes in five classes (<40 cm, 41-60, 61-80, 81-100, >100); the observed sizes ranged from 35 to 120 cm TL. Colour patterns were recorded according to Louisy (1996), and numbered 1 to 8 (see Fig. 2). The depth of the encounter was estimated using a diving computer. The height of the fish above the bottom was estimated, and subsequently ranked in four discrete classes: 0) resting on the bottom or in a hole; 1) less than 2 m from the bottom; 2) 2 to 5 m above the bottom; 3) more than 5 m above the bottom.

After the censuses along the transects, and during additional dives, some of us spent a long time in behavioural observations. Despite the groupers’ “familiarity”, it appeared that a single observer behaving properly (i.e. looking “unconcerned”) would not interfer with the fishes. That was especially true when they were engaged in agonistic or reproductive behaviours. Thus, the very special context of the Reserve does not alter the descriptive value of the observations. Some results on colour patterns and agonistic behaviours not directly related with reproduction will be published later (Louisy and Zabala, unpublished data).

RESULTS

Our study showed that the actual spawning (see Zabala et al., 1997) is only the final event of a long term process engaged at least one and a half month earlier.

Size, colour patterns and sex

The direct examination of sex and gonad evolution being impossible (fishing prohibited in the Marine Reserve), we had to evaluate these parameters by observation of the free animals only. The relation existing logically between size and sex in the one hand, and between behaviour (especially colour patterns) and sex in the other, helped in determining the sex of a large majority of the observed individuals.

_E. marginatus_ being a protogynous hermaphrodite, the smallest individuals are undoubtedly females, while the largest are males (at least in a naturally balanced population). In the Medes Islands Marine Reserve, most groupers below 60-65 cm TL must be females, those longer than 95 cm being males with display a typical territorial activity. In this population, sex change seems to occur mainly between 65 and 95 cm TL, and probably more often in the 75-90 cm range of sizes: some 75 to 90 cm long individuals were obviously big females with “egg-swollen” bellies (one 75 cm female was seen spawning), and at least one 85 cm long individual displayed now and then a typical silver C.P. 6 (see below) together with the aggressive behaviour of males.

The dusky groupers show a variety of ephemeral colour patterns (C.P.), which can change within a split second. Most of them are illustrated in Fig. 2 (see also Louisy, 1996). The C.P. 1, 2 and 3 are probably shared by all classes of size and sex all the year long, and show no discriminant value (Fig. 3A). The smaller groupers (< 40 cm TL) were never seen with C.P. other than 1 and 2, and we assume they are immature fishes.
Fig. 2. – Colour patterns. 1, standard mottled; 1bis, cryptic mottled; 2, dark with three blotches; 3, uniformly dark; 4, light; 5, dark streaked light; 6, silver streaked; 7, basic male; 8, light male. (Illustration Copyright © Jordi Corbera)
A. YEAR ROUND COMMON COLOUR PATTERNS

1. est
2. aggressivity
3. perplexity?

1 bis

B. SEASONAL REPRODUCTIVE COLOUR PATTERNS

<table>
<thead>
<tr>
<th>TL (cm)</th>
<th>Dominant males</th>
<th>Big fishes (males?)</th>
<th>Immature and females</th>
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<tr>
<td>100</td>
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Fig. 3. – Colour patterns, size and sex. A. Common-colour patterns exhibited all-round the year; B. Estival evolution of main colour patterns related with reproduction (see Fig. 2 for more details).
Figure 3B summarizes the possible occurrence of the other colour patterns over the reproductive period, in groupers of different sizes.

During the reproductive season, the small groupers from 40 to 60 cm TL exhibited the light C.P. 4 more often than the common C.P. 1 and 2. Even if only a few of these individuals showed a clear egg-swollen condition, they represent the size class were the more spawnings were seen, and we assume they are mature females.

The dark streaked C.P. 5 could be exhibited by most groupers from 40 to 95 cm TL, especially in the evening. This C.P. was often shown by clearly egg-swollen individuals, i.e. gravid females, but also by larger ones (> 85 cm TL) with no sign of gravidity. In one occasion at least, one of these rather big groupers was seen to change from C.P. 5 (Fig. 4A) to C.P. 6 (Fig. 4B), typical of dominant males. Thus C.P. 5 cannot be assigned to a definite sex, although it is undoubtedly related with reproductive activity in some way.

During the reproductive season, the larger fishes, longer than 95 cm TL, used to exhibit the silver C.P. 6, a territorial colour pattern typical of dominant males. Most of them could change more or less temporarily to the basic male C.P. 7, mainly at the beginning and at the end of the reproductive season. By the end of September, all the dominant males
showed this C.P. for some time before they usually changed to the grey C.P. 8, which seemed related to physical and physiological exhaustion.

During spawning itself, males retained a bright silver C.P. 6, while females surprisingly displayed the standard C.P. 1 (Zabala et al., 1997). This last observation reinforces our idea that the meaning of C.P. 4 and 5 in the general reproductive context has a social nature.

Yearly changes in density and size structure

Fig. 5 shows the annual evolution of groupers density along the Transect 1 (year 1995, except data for August). Numbers were minimal in winter, from January to late March (about 0.2 individuals per 100 m²). A dramatic increase in density was observed from mid April to late June. In the studied zone especially, about 60-70 individuals (i.e. more than 1 individual per 100 m²) were observed permanently from June to mid September. After the reproductive peak of August, numbers decreased noticeably from September to mid October, but remained more or less stabilized from October to December, falling again around late December.

The size structure of the population also changed, although no clear pattern arises from the analysis (Fig. 6). Strong differences in the number of individuals observed at each season, and especially the too low number of groupers counted in winter, hinder any accurate analysis of these changes. Still, only small to medium-sized groupers could be observed in winter; large males able to compete for a territory (TL > 95 cm) appeared later, in early May. From June to late August, all the size classes were represented with a clear dominance of small (female) individuals. Groupers smaller than 23 cm TL were never found in the Medes Islands Marine Reserve during the study, nor since the start of the monitoring program in 1990.

Large males seem to remain in the Reserve at least up to December, but they disappear from censuses from January to May. Large individuals identified by diagnostic scar patterns were observed to return to the same zone. Thus, two big males at least (#1 and 6 in Fig. 7) are known to occupy the same area(s) each summer. For example, they were absent from January to May 1996, but were repeatedly sighted in zone A (Fig. 1C) from April to December 1995 and again from June to September 1996. From mid July to late August though, these two males could not be censused in zone A, but they were observed courting as dominant males (see below) in nearby areas D and E (Fig. 1C, 7), a habit reported each summer since 1994.

Monthly evolution of the reproductive behaviour

In order to study more accurately the evolution of density and behaviour of groupers during the reproductive season, UVC were also repeated along the Transect 2 from May to September 1996. Even if the

![Graph](image_url)
Fig. 6. – Size-frequency distributions of groupers censused in Transect 1 from February 1995 to January 1996. (*) August data came from year 1996.
watching effort was not evenly distributed throughout the period, we were able to detect changes in density, zonal distribution and position relative to the bottom, together with the appearance of specific colour patterns. These results are summarized in Table 1 (see also Fig. 3B).

In May, overall density in Transect 2 was low (about 0.6 ind./100 m² in the studied area), and most groupers concentrated in zone A (Fig. 1C), where many shelters were available. They often remained distant to divers, and usually sought shelter when disturbed. In the big holes, mixed groups of small, medium and large groupers could be observed, showing no clear signs of agonistic interactions. The dominant colour patterns were C.P. 1 and 2, with rarer occurrences of C.P. 3 and 4. No grouper was observed with a swollen abdomen.

From May to June, censuses showed a progressive rise in density, parallel to a decrease in the mean length of the groupers, small females (40-55 cm TL) appearing later than larger individuals.

At the end of June, the density of groupers visually assessed in the transects reached its maximum (about 1.6 ind./100 m² in the studied area), and would stabilize until early September. Fishes were becoming more active, and could often be seen in open water (see Tab. 1C), hovering stationary against the current with a typical alternative movement of pectoral fins. Less fearful, and even attracted by divers, they rarely sheltered in a permanent hole, and were often encountered in zones B, D and F. Some females were seen displaying the light C.P. 4 and sometimes the dark streaked C.P. 5 (although in most instances vertical bars in the rear body were only diffuse, and C.P. would be quoted “4-5” during the censuses); a few of them showed a rounded abdomen. Some of the males displayed already C.P. 6 and 7.

| Table 1. - Seasonal evolution of some behavioural characteristics observed at midday and related with the prelude (June, July), the climax (August) and the end (September) of the reproductive activity of the Mediterranean Dusky Grouper at the Medes Islands Marine Reserve during summer 1995 and 1996. Pattern colours: 1, mottled; 2, dark with three blotches; 3, uniformly dark; 4, light; 5, dark streaked light; 6, silver streaked; 7, basic male; 8, light male. b. Abundances in zones A, B, D, G, and H (see Fig. 1C). c. Height above the bottom: 0, resting on the bottom or into a hole; 1, up to 2 meters above the bottom or below a roof; 2, between 2 and 3 meters above the bottom; 3, more than 5 meters above the bottom. N, number of records. n, number of censuses. |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  | A. Colour patterns (%) | 3 | 4 | 5 | 6 | 7 | 8 | N | n |
| June | avg. | 43.3 | 9.2 | 2.4 | 12.2 | 10.9 | 18.6 | 0 | 3.4 | 117 | 7 |
|      | std. | 11.7 | 7.4 | 5.8 | 7.6 | 10.0 | 10.9 | 0 | 5.4 | 157 | 6 |
| July | avg. | 34.0 | 5.3 | 0 | 20.1 | 25.4 | 15.2 | 0 | 0 | 0 | 186 | 6 |
|      | std. | 10.5 | 2.8 | 0 | 7.2 | 7.7 | 8.3 | 0 | 0 | 70 | 3 |
| August | avg. | 34.9 | 15.2 | 1.0 | 7.9 | 18.3 | 17.7 | 1.4 | 4.2 | 186 | 6 |
|      | std. | 4.2 | 13.3 | 1.5 | 9.4 | 11.9 | 8.4 | 3.1 | 5.7 | 70 | 3 |
| September | avg. | 39.1 | 7.0 | 2.3 | 13.3 | 1.1 | 0 | 12.2 | 0 | 0 | 15 | 2 |
|      | std. | 3.6 | 6.8 | 2.4 | 4.0 | 2.1 | 0 | 2.4 | 0 | 78 | 4 |

|  |  | B. Abundance in zones (%) |  
|---|---|---|---|---|---|---|---|---|---|
| A | B | C | D | E | F | G | N | n |
| June | avg. | 19.6 | 47.3 | 12.5 | 20.5 | 0 | 15 | 2 |
|      | std. | 5.4 | 9.8 | 12.5 | 8.0 | 0 | 78 | 4 |
| July | avg. | 14.7 | 31.3 | 38.2 | 10.5 | 5.2 | 114 | 5 |
|      | std. | 7.0 | 9.2 | 11.6 | 2.5 | 5.9 | 35 | 3 |
| August | avg. | 11.7 | 36.0 | 26.1 | 9.5 | 16.7 | 0 | 114 | 5 |
|      | std. | 4.5 | 10.9 | 6.7 | 6.0 | 13.1 | 0 | 72 | 4 |
| September | avg. | 30.1 | 12.6 | 30.4 | 7.0 | 5.0 | 0 | 48 | 3 |
|      | std. | 14.8 | 9.7 | 8.5 | 5.0 | 0 | 48 | 3 |

|  |  | C. Height above the bottom (%) |  
|---|---|---|---|---|---|---|---|---|---|
| 0 | 1 | 2 | 3 | N | n |
| June | avg. | 28.5 | 16.7 | 54.9 | 0 | 72 | 4 |
|      | std. | 3.0 | 7.1 | 9.7 | 0 | 97 | 4 |
| July | avg. | 11.5 | 40.6 | 48.0 | 0 | 57 | 3 |
|      | std. | 11.8 | 12.2 | 22.3 | 14.2 | 57 | 3 |
| August | avg. | 13.3 | 48.7 | 23.3 | 12.5 | 11.4 | 0 | 48 | 3 |
|      | std. | 9.4 | 20.5 | 8.9 | 0 | 48 | 3 |
By the middle of July, all groupers were very active, and would rarely shelter, rather resting on the bottom. Most of them congregated in the outer southern part of the studied area (zones B, D, F, G, H). At that time, all the described colour patterns (except perhaps C.P. 8) had been displayed. Small groupers (females) often exhibited the light C.P.4, but the most characteristic was the dark streaked C.P. 5, usually displayed by medium-sized individuals (60-90 cm TL), although small females could show it, especially in the evening (see below). This general behavioural pattern probably lasted until the first spawnings, although we unfortunately lack informations from 4th to 15th of August. Though part of the females (about 15 to 35%) had rounded bellies, especially the big ones, a majority did not obviously show an egg-swollen condition.

During the actual spawning days (spawnings observed between the 16th and the 21st of August), the general behaviour and spatial structure of the population seemed to remain about the same, except in the evening, when part of the females congregated in the males' courtship territories, then displaying essentially the standard C.P. 1 (see Zabala et al., 1997).

At the end of the reproductive season, the activity of territorial males lowered abruptly, the silver C.P. 6 more or less progressively shading to the basic male C.P. 7, and then to the grey C.P. 8. At that time, they appeared thin and weak, and became fearful. In the meantime, C.P. 5 also disappeared, and most individuals got back the common C.P. 1 and 2, while they moved to areas provided with shelters, especially in zone A. In 1996, these changes occurred suddenly in early September, just 2 weeks after the last spawning day; in 1995, they happened by mid October.

**Daily changes related to reproductive activity**

During the period of main reproductive activity (about 15th of July to 21st of August), there was an evident daily evolution of colour patterns, zonal distribution and position related to the bottom. Due to a certain variability from day to day (depending probably on physical conditions: temperature, current, etc.), and to unevenly distributed records, the results presented in table 2 are not quite as clear as the overall impression retained by the observers.

### Table 2

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<td>0</td>
<td>7.9</td>
<td>18.0</td>
<td>17.1</td>
<td>1.4</td>
<td>4.2</td>
<td>186</td>
<td>6</td>
</tr>
<tr>
<td>Std.</td>
<td>4.2</td>
<td>13.3</td>
<td>0</td>
<td>9.4</td>
<td>11.9</td>
<td>8.4</td>
<td>3.1</td>
<td>5.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Abundance in zones (%)</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morning</td>
<td>13.1</td>
<td>26.2</td>
<td>38.6</td>
<td>6.5</td>
<td>15.5</td>
<td>83</td>
<td>3</td>
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<tr>
<td>Std.</td>
<td>2.3</td>
<td>4.5</td>
<td>13.7</td>
<td>5.1</td>
<td>13.2</td>
<td>109</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midday</td>
<td>13.0</td>
<td>37.8</td>
<td>27.9</td>
<td>11.7</td>
<td>9.7</td>
<td>108</td>
<td>5</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Std.</td>
<td>7.9</td>
<td>10.5</td>
<td>7.1</td>
<td>3.6</td>
<td>10.8</td>
<td>166</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Evening</td>
<td>5.0</td>
<td>15.6</td>
<td>24.1</td>
<td>17.6</td>
<td>37.7</td>
<td>153</td>
<td>3</td>
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<tr>
<td>Std.</td>
<td>3.4</td>
<td>13.8</td>
<td>8.0</td>
<td>6.9</td>
<td>15.3</td>
<td>79</td>
<td>3</td>
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<tr>
<td>C. Height above the bottom (%)</td>
<td></td>
<td></td>
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<tr>
<td>Morning</td>
<td>9.1</td>
<td>61.8</td>
<td>20.1</td>
<td>9.0</td>
<td>79</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Std.</td>
<td>8.3</td>
<td>3.4</td>
<td>9.4</td>
<td>12.7</td>
<td>173</td>
<td>10</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midday</td>
<td>22.6</td>
<td>24.4</td>
<td>51.0</td>
<td>2.0</td>
<td>6.0</td>
<td>242</td>
<td>10</td>
<td></td>
<td></td>
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<tr>
<td>Std.</td>
<td>2.2</td>
<td>9.5</td>
<td>13.4</td>
<td>6.0</td>
<td>19.3</td>
<td>18.4</td>
<td>10</td>
<td></td>
<td></td>
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Nevertheless, the general daily scheme in the studied area (zones shown in Fig. 1C) can be summarized as follows.

Early in the morning, most groupers concentrated in the pass (zone B), hovering against the current in shallow waters; some of them displayed the C.P. 4 and 5, and agonistic interactions occurred from time to time. Some smaller ones would rather be in the B-D area, quite close to the bottom, with usual C.P. 1 and 2. Later in the morning, a majority of groupers moved to zones G and I where divers would feed them. By midday and early in the afternoon, they were distributed all around the shallow zones provided with boulders (zones A, B, C, D, F), but remained rare in zones H and J. At that time, most of the small to medium-sized groupers would stay close to the bottom (mainly with C.P. 1), in the warm waters above the thermocline (5 to 15 m).

From late afternoon onwards, a significative part of them usually moved to the southern deeper zones H and J, closer to the males’ territories. They formed loose groups (3 to 15 individuals) facing the current in open water, remaining above the thermocline, often 5 to 10 m from the bottom. Some individuals (among the smaller) were in C.P. 4, but most of them exhibited the dark streaked C.P. 5, often turning into C.P. 2 during aggressive interaction (a curious aggressive “zebra” colour pattern also appeared from time to time: Louisy and Zabala, unpublished data).

The large territorial males spent most of the day patrolling their territory (usually under the thermocline) in silver C.P. 6, with periodic incursions into shallower waters, to display towards females.

**Sex ratio and number of reproductive units**

Figure 7 shows the location of males’ territories in an area encompassing a majority of the most suitable bottoms surrounding the Reserve: 13 males were found to be active during the six days when spawnings were observed (16th to 21st of August). In the same area the overall population is composed of about 120 groupers. Thus, there is about one active territorial male for 8 non-territorial individuals. But, according to the above criteria for sex estimation (size, colour pattern, swollen abdomen), we can state that non territorial “small” males represent about one (maximum two) individual out of ten. The actual “territorial males: adult females” ratio approximates then 1: 7, which is much less than the global sex-ratio of about 1: 2 determined by Bruslé and Bruslé (1976) in a Tunisian population.

Non territorial small males were not observed to take part in the spawnings; if this behaviour exists, it is likely to be marginal. In any case, the density of territorial big males seems to be the bottleneck for the reproductive capacity of the grouper population in the Medes Islands Marine Reserve.

**Territoriality of males**

Actual spawning was preceded by a long period of social interaction, of which males’ territoriality was the most conspicuous. During 2 to 3 months, this energy-consuming behaviour took a major part in the spatial and social structuration of the whole population.

The first reliable sign of territoriality was the appearance of the bright patches of silver C.P. 6. In 1996, that was first noted in the 22sd of June: this precocious display lasted only a few seconds before the grouper got frightened, and sheltered. By early July, most dominant males showed more or less per-
manently the silver C.P. 6, and were beginning to display aggressive territorial behaviour.

Territories were rather wide (reaching 100 m in their largest dimension), although variable in size. They could extend from 10 to about 30 m depth, but were preferably localized below 20 m, thus remaining most of the time under the upper limit of thermocline. The bottom was usually rather flat, at least in depth, but included some outstanding boulders serving as landmarks.

When in full activity (i.e. by the middle of July), males patrolled their territory tirelessly all the day long, in a very distinctive fast and “nervous” mode of swimming, usually no more than one meter above the bottom. Any encountered grouper was driven away, possible neighbouring males being especially attacked and chased, sometimes for more than 50 meters.

From time to time, territorial males made incursions into shallower zones were females used to stay, displaying towards encountered groupers, but not always chasing them. In these situation, males could display in different ways: frontal, lateral, with tail flapping, sometimes tilting the body (Louisy and Zabala, unpublished data).

During spawning events, males performed courtship activities within only a small area of their usual territory (30-50 by 7-10 m) centered on definite boulders, thus indicating where females should wait for mating (Zabala et al., 1997). The overall aggressive behaviour looked like usual, but turned into courtship in front of a receptive female.

After spawning, males remained in their territories for some time, progressively losing their reproductive colour pattern. They abandoned their territorial behaviour in early September (in 1996) to mid October (in 1995), until the next summer.

The case of big females

A few medium-large groupers (3 to 5 individuals in the studied area), between 75 and 90 cm TL, were seen with egg-swollen bellies since the beginning of July (Fig. 8). These big females were particular in their behaviour, and somehow in their colouration. They were very sedentary in shallow rocky areas (10-15 m depth) and evidently had a high dominance statute among the groupers usually frequenting the zone, showing aggressive behaviours which could be termed territorial. During most of the day, they remained close to the sea-bed (appearing then pinkish-grey rather than brown), often resting on the bottom as if they were feeling “heavy” (and then showing the usual resting C.P. 1 bis). In the evening, they alternated 5-15 min rests with periods of
hovering 1-2 m above the bottom, then changing to a uniformly whitish-grey colour pattern somewhat similar to C.P. 4; from time to time, they could be seen swimming in depth towards a territorial male which, after a reciprocal display, would usually drive them off. The hypothesis that these females were too big to take part in reproduction could be rejected, since one of them (75 cm TL) was seen actually spawning, while the others had recovered a normally thin belly after the spawning days.

DISCUSSION

Some reflections about the results

Size at sexual maturity and sex reversal

Chauvet (1988, 1991) states that females *E. marginatus* reach their first sexual maturity at a size of 40 cm, when 5 years old. The sizes of small mature females reported by various authors agree with this statement: 1.6 Kg, i.e. about 45 cm (Barnabé, 1974), 44 cm TL (Bouain et al., 1983). On the other hand, Bruslé and Bruslé (1976), studying Tunisian dusky groupers, found the first mature females to weight 3 to 5 Kg (i.e. about 55 to 65 cm TL). Our observations confirm that females only 50 cm long (TL) do spawn (see Tab. 2), and that smaller ones (40-45 cm long) at least join in the reproductive activity, displaying specific colour patterns (C.P. 4 and 5), and trying to mate with the territorial males during the spawning evenings.

Although sex change from female to male is achieved within a year for any given individual (i.e. between two consecutive reproductive seasons; Bruslé, 1985), the phenomenon is progressive when considered at the regional population scale: it occurs mostly in the 80-90 cm TL range of sizes, but precocious males weighing only 3 to 5 kg (i.e. 55-65 cm TL) may be encountered, and large groupers as heavy as 20 kg (i.e. about 100 cm TL) may still be females (Bruslé and Bruslé, 1976; Bruslé, 1985; Skaramuca et al., 1989).

However, this range of variability (established from fishery data) is probably much more restricted when local populations are considered. For instance, if sex reversal can be thought to take place mainly between 75 and 90 cm in the Medes Islands (see Results), it most probably happens earlier in the population of the Cerbere-Banyuls Marine Reserve (a mere 60 Km to the north), where dominant males are only 85 to 95 cm long, and where no "swollen" female larger than 70 cm TL could be identified (Louisy, personal observations).

Thus, the size at sex reversal seems to depend more upon the size and sex structure of each local population of dusky groupers than upon fixed physiological constraints. Such a social control of sex reversal has been hypothesized for various groupers: if large dominant males remain in the population, sex reversal within the spawning group may be inhibited (Shapiro, 1987; Gilmore and Jones, 1992; Shapiro et al., 1993; Shapiro et al., 1994). In our case, the patrolling behaviour of dominant males, which use to repeatedly show off amid other groupers of the area, may have a strong influence on the hormonal state of the females: this may stimulate gonadal maturation, and most likely also inhibit the tendency for sex reversal in large females (this hypothesis could well explain the special behaviour of the big females in the Medes Reserve). Our study thus brings a behavioural argument to support the above hypothesis.

From territorial activities to courtship

As mentioned above, the repeated encounters of territorial males with neighbouring females most certainly induce a reciprocal hormonal stimulation, eventually reaching a peak at the moment of actual spawning. But if the males expend such an impressive amount of energy in patrolling tirelessly, it is probably because these frequent interactions also help in mutual recognition, and teach females where to look for a mate when spawning time comes.

We noticed some differences in territorial behaviour between July and mid August (time of spawning), although we unfortunately could not observe the transitional period. The swimming speed of dominant males seems somewhat lowered in August, and their range of movement appears restricted to a small part of their former territories. In addition, whereas in July males were seen to look for females during their frequent runs in the shallows, it is the reverse in August, when the females choose to join in depth a sexually active male.

There are similarities between some of the territorial displays (mainly "tail flapping") and the first displays of courtship, but their development is different. In July, most displays of the male intend to impress females, by making itself stout and by exhibiting the bright silvery area of its front body; in the courtship however, the male assumes a leading
position, and rather holds its tail at the level of its mates, the flapping having then a direct effect on the females' lateral line.

Colour patterns and reproduction

The main colour patterns displayed by *E. marginatus* during the reproductive period were described by Louisy (1996); among them, the patterns named here silver C.P. 6, but also the light C.P. 4 and the dark streaked C.P. 5, were thought to play a part in reproduction. As we could observe during this study (see Zabala et al., 1997), the male indeed exhibits its territorial silver C.P. 6 at the moment of spawning, but the females surprisingly show then the most common standard C.P. 1. What is then the use of the other mentioned colour patterns?

The communicative function of these colour patterns, displayed more or less ephemerally in association with other behavioural features (postures and movements, but also position in the water column and swimming pattern), is evident according to our observations, but most of their meaning remains to be understood.

The light C.P. 4 was shown mainly by small to medium-sized adults (i.e. females) swimming more or less in open water, even when far from other groupers; it appeared early and disappeared late in the reproductive season. It is difficult to tell whether it is related to reproductive activity, to the social context, or simply to the tendency to swim further from the bottom during summer.

The dark streaked C.P. 5 was shown by the medium-sized to large adults and seems more directly related to the reproductive context although we observed no connection with the spawning itself. It may be shown by most females, but its sexual meaning is not quite clear, since one male was proved to display it. This colour pattern may be found in at least two variants (with light belly or dark belly) which may act as different signals, or express different underlying motivations (Louisy and Zabala, unpublished data). Still, C.P. 5 appears almost exclusively in social situations typical of the main reproductive activity, being especially dominant in the evening gathering of females in open water. Thus, it is certainly related -though in some still unexplained way- to reproductive activity.

Following the above conclusions, we consider the simultaneous appearance of silver C.P. 6 and dark streaked C.P. 5 in a given area to be a strong evidence of reproductive activity, though it does not ensure the success of spawning.

Some general questions

The main information emerging from our study is that the dusky grouper generally behaves as... a grouper: spawning occurs within a socially structured population, after an elaborate courtship involving a special colour pattern of the male, and polygyny is logically the rule for this protogynous species. Thus, the reproduction of *E. marginatus* shares at least a few common characteristics with that of most other studied groupers. Nevertheless, its reproductive behaviour and social structure are not really comparable to any of the known tropical species, and the discrepancies should be considered with regard to the typically temperate conditions in which the dusky grouper lives.

Two major reproductive "styles" have been described in tropical and subtropical groupers (Donaldson, 1995a). Most studied species make seasonal migrations towards definite sites where they aggregate in large numbers for reproduction (Smith, 1972; Colin et al., 1987; Colin, 1992; Gilmore and Jones, 1992; Tucker et al., 1993; Shapiro et al., 1993). Among them, group spawning seems to occur normally in *Epinephelus fasciatus* (Colin, 1992), which populations appear gonochoric, while the other species, considered protogynous hermaphrodites, use to spawn by pairs (Thresher, 1984; Shapiro et al., 1993; Samoilys and Squire, 1994). A second group of sedentary groupers (seemingly only *Cephalopholis* species) shows hermaphroditic structures in which both courtship and spawning preferably occur in single pairs (Donaldson, 1995a).

Are there seasonal migrations?

Seasonal changes in density are a common feature among the tropical groupers belonging to the first reproductive "style" mentioned above, in which migrations towards reproductive aggregation sites have been reported.

Seasonal changes in the abundance of *E. marginatus* in shallow rocky areas have been known by local fishermen for a long time. After Chauvet and Francour (1991), our results also confirm this popular knowledge: in the Medes Marine Reserve, the density of observed dusky groupers was high in summer, and very low in winter. The process leading to this variation remains poorly understood however (GEM, 1996).

Two hypothesis might explain these results. The first is that of a "wintering" phenomenon, the fishes
becoming more fearful and very sedentary within deep holes, where they lower their metabolism and remain invisible for most of the winter (G.E.M., 1996). Fig. 5, showing a strong parallelism between temperatures and observed densities, seems to support this “metabolic” explanation. It should also be noted that the low winter counts could partly ensue from methodological artifacts due to the poor water transparency and / or to the greater escape distance of groupers in winter.

On the other hand, considering the high summer densities of groupers in the Mekes Reserve, it seems unprobable that all of them could find shelter in the area. Moreover, all the individuals watched from February to late March were rather small groupers, showing an erratic swimming pattern and a tendency to shelter at random in any available hole. Rather than sedentary hibernant, they could be erratic individuals wandering along the coast (this hypothesis is consistent with the results of Chauvet and Francour (1991) in the Port-Cros National Park (France), showing by a tagging program that small to medium groupers could move out or into the studied zone between two consecutive summers). When they were first observed in April-May, large males, known to repeatedly occupy the same zones every year, behaved as if they would not “feel at home” and would often shelter in unusual holes, as could be expected from individuals just returning to the site. Thus, like in many tropical groupers, a part of the dusky grouper population most probably engages every spring and autumn in small scale migratory movements (at least). We do not know where they can go, but the migration pattern is likely to be of a “dispersal - gathering” type.

Is it a reproductive aggregation?

Reproductive “aggregations” have been reported in various tropical grouper species, the most documented being Epinephelus striatus (Smith, 1972; Colin et al. 1987; Colin, 1992; Tucker et al., 1993), E. guttatus (Colin et al. 1987; Shapiro et al., 1993) and Mycteroperca tigris (Sadovy et al., 1994) in the Western Atlantic, and Plectropomus leopardus (Samoilys and Squire, 1994) in the South Western Pacific. Aggregating behaviour was also reported in Epinephelus itajara, Mycteroperca bonaci and M. venenosus (see Sadovy et al., 1994).

The numbers of 24 to 32 groupers counted in summer in transect 2, correspond to about 12 to 16 fish.1000 m-2, which is far from the densities reached in typical aggregations of tropical groupers (Thresher, 1984; Shapiro, 1987; Colin, 1992; Samoilys and Squire, 1994). Still, this number represents a 5 to 8-fold increase compared with the minimum density observed in winter. There is undoubtedly a summer gathering of adult dusky groupers in the Medes Reserve, which is especially original by its duration (3 to 4 months), and the fact that it starts before the onset of reproductive activity (which lasts for about 2 months), and breaks up later.

This pattern differs from the typical spawning aggregations of tropical groupers, characterized by their short duration, and synchronous large scale migrations of both males and females. It rather recalls the situation observed for Mycteroperca microlepis and M. phenax in Florida (Gilmore and Jones, 1992), and probably for M. interstitialis (Bullock and Murphy, 1994), which display a hierarchical social structure in localized sites for months (fall to spring), seemingly with periods of higher population density; in these species, spawning seems to occur most of the year, with a peak in spring (data on gonadal state of captured fish). This apparent convergence (which would deserve deeper examination) could be linked to climatic conditions: rather subtropical than tropical, the climat of Florida might be closer to the temperate conditions in which dusky groupers live.

Is there a haremic structure?

Territorial males of E. marginatus are evidently polygynous, but are they haremic (i.e. do they control exclusively a group of females) ?

Not only the big males are territorial, but also probably big females; even the small females, although more mobile, seem to frequent preferential zones. Thus, a sexually active male might develop favoured contacts with a given set of females usually frequenting the neighbouring area. Supporting this hypothesis, males’ interactions with big sedentary females (but also with some smaller ones) showed a kind of “habitation” to each other along the pre-spawning period.

In some way, this population structure recalls the territorial haremic social pattern observed in some Cephalopholis species (Shpigel and Fishelson, 1991; Donaldson, 1995a, 1995b), although the females’ territories (or home ranges) are mainly outside the male’s territory. But it seems that the diurnal movements of most females (see Results, Daily changes...) would allow them to get regularly alongside the territory of various males. Furthermore,
since the males’ sexual activity changes dramatically from one spawning evening to the next (Zabala et al., 1997), most females very probably mate with different males in different evenings.

Concerning these evenings when courtship and spawning occurred, the gathering of females in or around the reduced courtship territory of the male recalls the “clusters” described for Epinephelus guttatus by Shapiro et al. (1993). Being unable to estimate the mobility of females at the spawning time (and also from one evening to the next), we cannot tell if clustering actually exists in E. Marginatus. But if so, we can assert, in contrast with these authors, that it is definitely centered on the male’s territory and behaviour.

**Temperature, Marine Reserves and reproduction in the NW Mediterranean**

Our study (see also Zabala et al., 1997) gives the first known observation of actual spawning of the dusky grouper. It also provides the first positive evidence of the reproduction of this fish in the NW Mediterranean. But did this species reproduce in the area before?

Until recently, groupers were generally thought to reproduce south to a latitude of 41°5’ N, i.e., roughly a line Barcelona-Roma, the rather old individuals encountered northerly being supposed to have progressively migrated from meridional areas (Chauvet, 1991). More recent observations led to a change of this point of view.

In the Medes Islands Marine Reserve, the first clear signs of courtship were observed in 1995, but dominant males with their territorial colour pattern (C.P. 6) where regularly encountered at least since 1990, when summer routine censuses began. Sexual activity was observed in the Cerbère-Banyuls Marine Reserve (France) in 1995, and suspected for 1994 at least (Lousiy, 1996). Signs of reproductive behaviour were also observed in July 1995 in the Port-Cros National Parc (France) by M. Tillman (personal communication), and confirmed in 1996 (Charbonnel, 1996). Spawnings were also seemingly observed in the Lavezzi Marine Reserve (South of Corsica, France) in 1996 (J.P. Quignard, personal communication). Some records of juveniles (about one year old) in the NW Mediterranean suggest that reproduction could have occurred there since the late 80’s (Russino et al., 1991; Lelong, 1993).

Furthermore, observations of very young groupers about 2 cm long near Toulon (France) in 1991, 1992 and 1993 (Harmelin and Robert, 1992; Lelong, 1993 and personal communication) allow to postulate that reproduction took place in the area.

The main explanation given to these recent evidences of reproductive activity North to 41°5’ is a gradual rise in temperatures of the shallow waters, which could be measured (see for example Pascual et al., 1995), and seems to be corroborated by other biological indicators, like the Turkish Wrasse (Thalassoma pavo) which geographical distribution extended to the North (Lelong, 1993; Francour et al., 1995). The strength of this “thermic hypothesis” is such that the recent appearance of young groupers in the NW Mediterranean has itself been proposed to support this theory (Francour et al., 1995). In fact, as Lousiy (1996) already pointed out, temperature is certainly not the only parameter influencing groupers reproduction, and socio-behavioural factors also can prove to be very important.

As our study clearly showed, courtship and spawning of the dusky grouper ensue from a long and elaborate process involving a whole socially structured population. Thus, a minimal critical population size appears to be a fundamental requirement for reproduction, together with the peace necessary to develop reproductive behaviours. The scattered state of dusky groupers populations in the NW Mediterranean, following half a century of heavy fishing (especially spearfishing), evidently hinders reproduction, which would be difficult anyway, since most individuals stay below 30-50 m in depth, in waters cool enough to inhibit -at least partly gonadal maturation.

Marine Reserves constitute a noteworthy exception to this prevailing scheme: there, groupers are encountered in much higher density, and at shallower depths. In the Medes Islands, a clear evolution towards a greater density and a smaller average size (i.e. a higher number of females) was observed since 1990 (Garcia-Rubies and Zabala, 1994). The same trends could be assessed from censuses of groupers carried out in 1993 and 1996 in Port-Cros (G.E.M., 1994 and personal communication). More than density itself, the evolution of sex-ratio towards a greater proportion of females may explain the observation of reproductive activities in most marine protected areas in recent years. Furthermore, it seems that Marine Reserves can reinforce sex reversal inhibition by enhancing the survival of large dominant males, thus increasing the proportion of big, highly prolific females, and consequently the overall reproductive success (Gilmore and Jones 1992).
Groupers in general show a noticeable spawning plasticity, at least in captive individuals (Tucker, 1994), and *E. marginatus* might be able to reproduce within more scattered populations out of the protected areas but, according to their very small number, the quantitative impact of such events would be very low.

Thus, even if one supposes (logically) that water temperature is a strong limiting factor of dusky grouper’s reproduction (in that case, the rise in temperature would have triggered of the phenomenon), it is clear that no outstanding reproductive activity could have occurred without the Marine Reserves, shelters for large and well balanced populations: the preservation efforts had a major influence in this respect. It should be noticed however that the regular influx of young adult females in the Marine Reserves, which strongly improved the sexual balance of the populations, may well be linked to the progressive rise of water temperatures.

Management implications

In tropical areas, stocks of some groupers have been completely depleted through heavy harvesting of spawning aggregations in sites long known by fishermen (Colin, 1992; Samoilys and Squire, 1994). For this reason, the knowledge of their reproductive behaviour has been considered essential for management and conservation decisions.

The present study showed that the socio-behavioural context of reproduction in *Epinephelus marginatus*, although original in some traits, shows similarities with most other studied grouper species, and thus probably shares the same sensitivity to targeted fishing (the mere spearfishing of a few big males is enough to hinder the reproduction of a hundred groupers). Marine protected areas have shown already their positive role in permitting the actual reproduction of the dusky groupers in the NW Mediterranean, and it seems that protecting sites known as possible gathering and reproduction places is the only way to restore populations of this highly overexploited species.

Further research about social structures and reproductive behaviour would be of basic interest for fish biologists, but also for managers of coastal resources. Studies on the planktonic larval life of the dusky grouper would also be relevant to understand the dispersion and colonisation patterns of the species; and, together with studies on climatic parameters and reproduction itself, would permit a sustainable management of this most renowned fish of the Mediterranean heritage.

ACKNOWLEDGEMENTS

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