

A review on habitat, diet and growth of the dusky grouper *Epinephelus marginatus* (Lowe, 1834)

*Bilan des connaissances sur l'habitat, l'alimentation et la croissance du mérou brun,
Epinephelus marginatus (Lowe, 1834)*

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Mots clés : mérou brun, *Epinephelus marginatus*, écologie, biologie.

ABSTRACT

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The dusky grouper (*Epinephelus marginatus*) inhabits almost exclusively coastal rocky bottoms (mostly <50 m depth). The preferred habitat of adults is characterized by large boulders which provide shelters for aggregating during the warm season, often in shallow waters in unfished areas. Juveniles occur within a narrower depth range (<15 m) and often display cryptic behaviour during the first year. Site fidelity is generally marked for old males and low for young females. Seasonal migrations involving a large part of the population seem to occur, as suggested by an apparent decrease in abundance in winter. However, there is no data on the habitats used during winter. Food categories used by *E. marginatus* change with the size of individuals. Juvenile dusky grouper consume first small crustaceans (amphipods, isopods, shrimps), and then essentially crabs. Individuals ranging from 20 cm to 60 cm TL feed equally on crabs and fish, and occasionally on molluscs when >30 cm TL. Preys of larger dusky grouper (>60 cm TL) are in order of importance cephalopods and fish. Size-weight relationships are known from 11 samples of different geographic origin (2 Atlantic and 9 Mediterranean sites). For a given individual size, the weight can double according to the site considered or the method used. Similarly, growth appears to have a marked site variability. The lowest growth rate has been recorded in Southern Tunisia and the highest rate in Western Algeria. The estimated age of the largest studied individuals (34 kg) was 36 yrs. However, *E. marginatus* is likely to live much longer as indicated by fished individuals weighing more than 50 kg. Special attention should be paid to the youngest stages for which ecological and biological data are scarce.

RÉSUMÉ

Harmelin J.-G., M. Harmelin-Vivien, 1999 - [Bilan des connaissances sur l'habitat, l'alimentation et la croissance du mérou brun, *Epinephelus marginatus* (Lowe, 1834)]. Mar. Life, 9 (2) : 11-20.

Le mérou brun (*Epinephelus marginatus*) fréquente presque exclusivement les fonds rocheux côtiers (<50 m), souvent à faible profondeur quand il n'est pas pêché. Les zones de gros blocs sont l'habitat préféré des adultes, de nombreux abris leur permettant de se rassembler pendant la période chaude. Les juvéniles vivent dans les 15 premiers mètres et semblent très cryptiques au cours de leur première année. La fidélité aux sites est grande pour les vieux mâles et généralement faible pour les jeunes femelles. Pour une grande partie de la population, il semble y avoir des mouvements saisonniers, mais l'habitat hivernal est mal connu. Le régime alimentaire de *E. marginatus* évolue avec sa taille. Les petits mérous consomment d'abord de petits crustacés (isopodes, amphipodes, crevettes), puis surtout des crabes. Entre 20 et 60 cm LT, ils se nourrissent à parts égales de crabes et de poissons, les mollusques n'apparaissant que dans le régime des individus de plus de 30 cm. Les plus gros mérous (>60 cm LT) capturent préférentiellement des mollusques céphalopodes puis des poissons. La relation taille-poids est connue dans 11 sites (2 en Atlantique, 9 en Méditerranée). Selon le site et la méthode employée (poids total ou éviscéré), le poids peut aller du simple au double pour un mérou de même taille. De la même façon, la croissance varie fortement d'un site à l'autre. La croissance la plus faible a été enregistrée chez des individus du sud tunisien et la plus forte dans l'ouest algérien. L'âge des plus gros individus étudiés (34 kg) a été estimé à 36 ans. Il est probable que *E. marginatus* puisse vivre beaucoup plus longtemps puisque des individus de plus de 50 kg ont été capturés. Une attention particulière doit être maintenant portée aux plus jeunes stades pour lesquels il n'existe que très peu de données.

INTRODUCTION

The dusky grouper, *Epinephelus marginatus* (Lowe, 1854) is one of the seven species of grouper recorded in the Mediterranean sea, which include two lessepsian migrants, *E. coioides* and *E. malabaricus* (Golani, 1996). *Epinephelus marginatus* has long been mistaken in the literature for the Haifa grouper, *E. haifensis* Ben-Tuvia, 1953 (Heemstra, 1991), under the names *E. guaza* or *E. gigas* (Bauchot, Pras, 1980; Bauchot, 1987). The geographical range of the dusky grouper includes the Mediterranean, the Eastern Atlantic from the Southern coasts of the British Isles to South Africa, and part of the coasts of Brazil (Heemstra, Randall, 1993). *Epinephelus marginatus*, like all grouper, is a protogynous hermaphrodite species. The first sexual maturity occurs at 5 yrs and sex reversal between 9 and 12 yrs (Chauvet, 1988; Heemstra, Randall, 1993). Since the first review on the biology of the dusky grouper written by Bruslé (1985), research on this fish species has developed in several Mediterranean countries, particularly thanks to the impetus given by the GEM (*Groupe d'Étude du Mérou*) founded in 1986. The present review was presented at the First International Symposium on the Mediterranean grouper (Embiez, France, 5-7/11/98) with the aim of identifying the major gaps concerning the habitat, feeding behaviour and growth of the dusky grouper.

HABITAT

General features and sources of temporal variability

The dusky grouper is a necto-benthic species chiefly associated with coastal rocky bottoms and presenting a clear preference for shelter-rich sites. As for many fishes of the coastal zone, its depth range increases with age, first limited to the shallower waters of the infralittoral zone and afterwards extending across the whole continental shelf. The temporal variability of habitat frequentation is induced by three main types of factors: (i) ontogenetic changes, (ii) periodic movements, (iii) intraspecific interactions.

Ontogenetic changes

There is an age-related habitat shift, which is determined by the necessity of fulfilling several requirements: (i) a better match between habitat and fish size, (ii) the availability of food resources specific to the different age phases, (iii) the search for partners for constituting reproductive aggregations (Chauvet, Francour, 1989; Zabala *et al.*, 1997). The latter case concerns chiefly young females whose site fidelity appears to be limited.

The habitat of 0⁺ juveniles (on average < 13 cm TL, see below) is only known from very few records. Shallow waters (upper infralittoral) and the occurrence of small cavities allowing cryptic sheltering appear to be constant features of this habitat. However, by contrast with juveniles of other species

of the same general assemblage of coastal rocky bottoms, the habitat range of 0⁺ dusky grouper is not limited to a narrow depth range. They have been collected in tide pools at Pico, Azores (Azevedo *et al.*, 1995) and in the shallowest part (0-1 m depth) of rocky creeks of the Lavezzi Islands, Corsica (Bouchereau *et al.*, 1992; Bouchereau, Lam Hoaï, 1997), and of Brusç, Var, France (P. Lelong, personal communication). Juveniles of 3 to 10 cm TL were recorded in shallow-water *Zostera* and *Cymodocea* meadows at Castiglione, Algeria (Dieuzeide, Goëau-Brissonnière, 1951). However, 0⁺ juveniles were also collected deeper, a 2 cm long individual at 15 m depth in a cave near Toulon (Var, France) (Lelong, 1993; Louisy, 1996: figure 3), and a 1.5 cm individual in a *Posidonia* bed off Brusç at 10 m depth (P. Lelong, personal communication). Juveniles occurred in large numbers in 1990 in oyster-spat collectors (rolls of wire mesh) deployed at 12 m and 20 m depth on a sandy bottom at Maresme, near Barcelona (F.X. Llauro, personal communication).

The habitat of young individuals older than one year (13 to 40 cm TL) is also located in the upper infralittoral, generally at depths shallower than 15 m, as attested by several authors (e.g. Grange, Grange, 1991; Russino *et al.*, 1991; GEM, 1993; Coll *et al.*, 1995; Derbal, Kara, 1995; La Mesa, Vacchi, 1999; Vacchi *et al.*, 1999). Dusky grouper of this size may also be found in tide pools (Azores: Azevedo *et al.*, 1995; Provence: Louisy, 1996: figure 4). The preferred habitat comprises rocks covered with photophilic algae and providing cavities, like masses of medium-sized blocks and boulders.

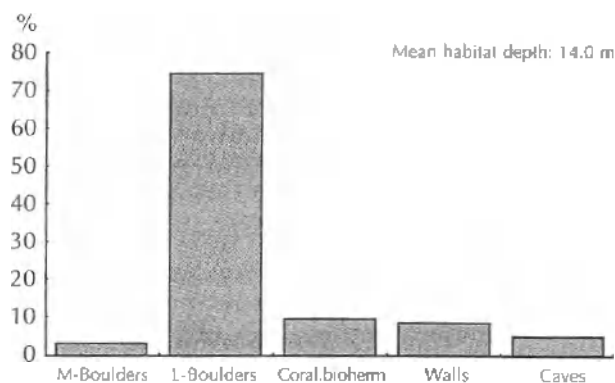


Figure 1 - Habitat distribution of *Epinephelus marginatus* at Medes Islands. Percentage of occurrence calculated on 75 specimens of 72.7 cm TL mean size (from Garcia i Rubies, Zabala i Limousin, 1993). M-Boulders: medium-sized blocks; L-Boulders: large-sized blocks; Coral.: coralligenous bioherm. / Habitat d'*Epinephelus marginatus* aux îles Medes. Pourcentage calculé sur 75 spécimens de taille moyenne = 72,7 cm TL (données de Garcia i Rubies, Zabala i Limousin, 1993). M-Boulders : blocs rocheux de taille moyenne ; L-Boulders : blocs rocheux de grande taille ; Coral : fonds coralligènes ; Walls : tombants ; Caves : grottes.

Adult dusky grouper have a much broader depth distribution, which ranges from the vicinity of the surface to the shelf break (250 m in Sicily and Calabria; Bolognari *et al.*, 1971; Bruslé, 1985). However, their frequency decreases considerably beneath 50 m depth. The preferred habitat consists in rocky bottoms with complex topography and offering numerous cryptic shelters, e.g. small caves and tunnels, crevices, cavities underneath blocks (Neill, 1967; Chauvet, 1991; Harmelin, Robert, 1992; Garcia i Rubies, Zabala i Limousin, 1993; Derbal, Kara, 1995). Around Medes Islands most dusky grouper (74.5%) dwell in areas with large boulders (Garcia i Rubies, Zabala i Limousin, 1993) while the rest of the population is associated with coralligenous bioherm, walls with steep slope, caves and tunnels, and medium-sized blocks (figure 1). The dusky grouper are scarcer when rocky bottoms and *Posidonia* patches are mixed (Derbal, Kara, 1995) and their frequency becomes very low when *Posidonia* beds are dominant (Bou-Ain *et al.*, 1983).

Because of the shallow-water distribution of the small- and medium-sized individuals, there is a positive relationship between the mean size of individuals and the depth at which they are encountered. This general trend is stronger in fished sites, particularly when impacted by spearfishing. Spearfishing tends to exclude adult individuals from shallow-water bottoms (Derbal, Kara, 1995; Coll *et al.*, 1999). In marine protected areas where protection has been effective for a long time, as in the national park of Port-Cros, France (founded in 1963), large grouper (90-110 cm TL) may be observed in shallow sites (< 15 m depth) when shelters are available (GEM, 1993, 1996; Harmelin, 1999). Recovering such natural behaviour patterns takes several years. It was not observed in the national park of Cabrera, Spain

after two years of protection (Coll *et al.*, 1995). In both the marine reserve of Medes Islands (Garcia-Rubies, Zabala, 1997, 1999) and the national park of Port-Cros (GEM, 1996; Harmelin, 1999), medium-sized individuals (i.e. mostly potentially reproductive females) have increased markedly in number since the late 90s and tend to spread into deep waters. A clear increase in the average habitat depth of small-medium (45-60 cm) and medium-large (65-85 cm) individuals was observed at Port-Cros between October 1993 and October 1996 (GEM, 1996), whereas no change was recorded for the smallest (20-40 cm) and the largest (90-110 cm) size classes (figure 2). This new pattern is assumed to result from the combined effects of protection and a general increase in the population dynamics of *E. marginatus* in the Northern parts of the Western Mediterranean, which entails reproduction events never recorded before (Lelong, 1993; Francour *et al.*, 1994; Zabala *et al.*, 1997; Harmelin, 1999).

Periodic habitat changes

Periodic movements of individuals comprise seasonal and daily habitat changes. These two types of cyclic movements are poorly documented, especially changes of habitat during winter. Population abundance in sites located at 0-50 m depth is maximum during the warm season and drops in winter (e.g. Bruslé, 1985; Chauvet, Francour, 1989; Chauvet *et al.*, 1991; Garcia i Rubies, Zabala i Limousin, 1993; Zabala *et al.*, 1997). These seasonal fluctuations in abundance, which mainly involve medium-sized individuals, may correspond to two types of behavioural relationships with the habitat (Zabala *et al.*, 1997): (i) wintering on the spot within cryptic shelters that lead the fish to be inaccessible to visual census; (ii) migration towards other sites, which can be located in deep water. Neither of these hypotheses is supported by direct observation. At Madeira, dusky grouper apparently reside permanently all year round at the same site (Waschkewitz, Wirtz, 1990). By contrast, in the same area some individuals of a group of *E. costae* (= *E. alexandrinus*) migrate seasonally. The departure and return to the same site of one of these individuals, easily identified by its xanthistic colour pattern, have been recorded during 8 consecutive years. In this case, reproduction seems to be the inducing factor as suggested by the timing of migration (summer) (Waschkewitz, Wirtz, 1990). The diel variability of habitat frequentation by the dusky grouper is also poorly known. This fish has been rarely observed at night but some information about its feeding behaviour indicates that it is mostly active during daytime and at dusk, but can also occasionally feed at night (see below). Therefore, it is likely that there is no noticeable nycthemeral habitat shift.

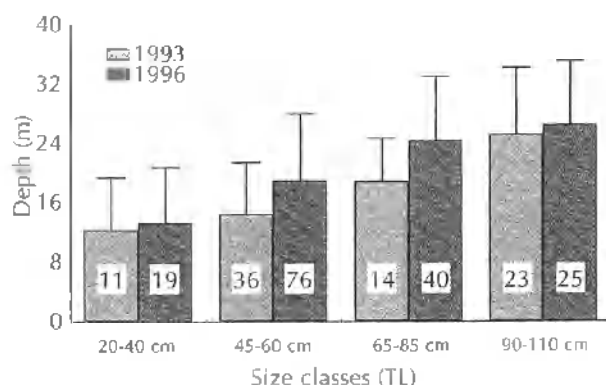


Figure 2 - Changes in depth distribution patterns of the various size classes of *Epinephelus marginatus* at Port-Cros between 1993 and 1996. Mean depth + standard deviation. Numerals within histograms: number of individuals observed. / Modification de la distribution bathymétrique des différentes classes de taille d'*Epinephelus marginatus* à Port-Cros entre 1993 et 1996. Profondeur moyenne + déviation standard. Le nombre d'individus observés est indiqué dans les barres de l'histogramme.

Movements induced by intraspecific interactions

The occurrence of large numbers of individuals coexisting closely in particular sites is commonly observed in unfished areas. These aggrega-

tions imply either neutral relationships between individuals or precise habitat sharing and territorial behaviour. Both patterns are observed among dusky grouper. Tracking experiments using hydroacoustic telemetry on medium-sized dusky grouper of Ustica Island, Italy (Lembo *et al.*, 1999) have demonstrated that these fishes displayed a marked site fidelity over several months. Territoriality is particularly evident for large dusky grouper, although several individuals may shelter in the same cavity, particularly between reproduction periods (Zabala *et al.*, 1997). Observations over several years in protected areas attest that some old individuals identified by particular scars or head spot design (Lelong, 1999) present a long-term sedentarity in their territory. The surface area of these territories can reach several thousand square meters for old males (Culioli, Quignard, 1999), which defend them actively and display agonistic behaviour against intruders (Neill, 1967; Chauvet, Francour, 1989; Zabala *et al.*, 1997). Site displacement of males, attested by marking experiments (Chauvet, Francour, 1989; Chauvet *et al.*, 1991), is likely to result from change in the dominance hierarchy between males, as suggested by *in situ* observations of aggressive behaviour among males of a structured group (Chauvet, Francour, 1989; Port-Cros; unpublished observations by A. Garcia-Rubies at Medes Islands).

These natural patterns of habitat sharing and site displacements are obviously disrupted by human interference, especially spearfishing, which is a major determinant of changes in behaviour patterns among dusky grouper and other target-species (Harmelin *et al.*, 1995; La Mesa, Vacchi, 1999).

FEEDING BEHAVIOUR

The dusky grouper is a carnivorous fish which feeds essentially on crustaceans, fish, and molluscs (Cadenat, 1954; Neill, 1967; Bouain, 1984; Smale, 1986). The most detailed information was given by Azevedo *et al.* (1995): 71 young individuals (47 with food items; 4-36 cm TL) from a tide pool of Pico, Azores Islands; Derbal, Kara (1996): 68 individuals (35 with food items; 16-98 cm TL) from Eastern Algeria; Barreiros, Santos (1998): 57 individuals (35 with food items; 60-138 cm TL) from Terceira, Azores Islands.

Diet variability with individual size

As in most carnivorous fishes, the diet of *E. marginatus* changes with the size of individuals. Indications of this size-related change are given by the stomach content analysis of young Azorean individuals made by Azevedo *et al.* (1995). The diet of 0⁺ specimens (4-7 cm TL) was dominated by crustaceans, both in number (amphipods, isopods and cumaceans) and in weight (shrimps and crabs). Polychaetes were occasional prey of these juveniles. In specimens of the size class 13-25 cm TL (1⁺/2⁺), crabs were clearly the dominant prey, both in number and in weight (N = 53.2%, W = 69.1%) and fishes, captured by about 30% of the specimens, now

reached the second rank (N = 19.4%, W = 22.8%). Fish species identified in stomach contents were: *Tripterygion delaisi*, *Thalassoma pavo*, *Gobius pagannellus*, *Chelon labrosus*, and smaller individuals of *E. marginatus*. Shrimps also held an important place in the diet of dusky grouper of this size class, whereas polychaetes, bivalves, gastropods and small crustaceans were only occasionally preyed upon. The only medium-sized specimen collected (36 cm TL) had fed on fish and crabs.

The same size-related diet shift was found for larger individuals from Eastern Algeria by Derbal, Kara (1996). Dusky grouper of 16-30 cm TL had ingested mostly fish (69.8% of prey weight), crabs (23.4% W), and more occasionally shrimps (1.6% W). However, crabs were the most frequent (present in 62.5% of stomachs) and numerous prey (N = 41.7%). Individuals of size class 30-60 cm TL had fed equally on fish (33.6% W), crabs (33.0% W), and molluscs (31.5% W). Crabs were still the most frequent and the most numerous prey while some isopods were occasionally ingested. The diet of individuals of 60-100 cm TL was dominated by molluscs (72.6% W) while fish and crabs decreased markedly in importance (respectively 18.8% and 6.5% W). In consequence of digestion, only one fish species has been identified (*Chromis chromis*). Crabs were represented by four brachyuran genera (*Scyllarides*, *Parthenope*, *Maja*, *Cancer*) and molluscs by two species (*Octopus vulgaris*, *Haliothis tuberculata*). The fragments of *Posidonia* and algae found in stomach contents had probably been accidentally ingested with animal prey. A similar feeding behaviour pattern was documented by Barreiros, Santos (1998) at Terceira, Azores Islands, who observed a size-related shift in food preferences. Fish were the dominant food of smaller individuals (60-90 cm TL), followed by molluscs (*Octopus vulgaris*) and crustaceans (*Scyllarides latus*, *Scyllarus arctus*). Larger individuals (90-138 cm TL) clearly preferred *Octopus vulgaris* to fish and crustaceans. According to Barreiros, Santos (1998), empty *Haliothis* shells in stomach contents may have been swallowed with *Octopus*.

Therefore, the diet of the dusky grouper comprises essentially (i) small crustaceans (amphipods, isopods, shrimps) during the first year (< 12 cm TL), (ii) crabs and fish when size ranges from 13 to 60 cm TL, and (iii) molluscs (chiefly cephalopods) and fish, when size exceeds 60 cm TL.

Feeding periodicity

All data on the feeding of *Epinephelus marginatus* correspond to fishes captured during daytime. Thus, it is impossible to infer any conclusion from those data about actual feeding rhythm. According to Neill (1967), the dusky grouper would appear to feed all day long, while Abel (1959, 1962) thinks that it is mainly active at crepuscular periods. Chafir, Guerrab (1992) have observed that trophic activity peaked between 5 h and 13 h. The occurrence of *Haliothis* among prey items (Cadenat, 1954; Neill, 1967;

Table I - Length-weight relationships and parameters of the Von Bertalanffy growth curve equation (L_{∞} , K , t_0) in the dusky grouper, *Epinephelus marginatus*. N= number of fish studied; W= total weight of fish; *W= eviscerated weight; TL= total length; ST= standard length; R= correlation coefficient of the length-weight relationship. / Relation taille-poids et paramètres de l'équation de la courbe de croissance de Von Bertalanffy (L_{∞} , K , t_0) pour le mérrou brun, *Epinephelus marginatus*. N = nombre de poissons étudiés ; W = poids total du poisson ; *W = poids éviscéré ; TL = longueur totale ; ST = longueur standard ; R = coefficient de corrélation de la relation taille-poids

Sites and authors	N	Length-weight relationship ($W=aL^b$)	R	Age range (years)	Size range (cm)	L_{∞}	K	t_0
SENEGAL (Franqueville, Fréon, 1976)	35	$W=0.00748TL^{3.221}$	0.999	?	35 - 103	?	?	?
AZORES (Azevedo <i>et al.</i> , 1995)	175	$W=0.0139TL^{3.085}$	0.998	0 ⁺ - 4	4 - 36	?	?	?
W. ALGERIA (Chalabi <i>et al.</i> , 1992)	60	$W=0.0243TL^{2.971}$?	1 - 8	25 - 90	177.43	0.073	-1.24
E. ALGERIA (Kara, Derbal, 1995)	33	$W=0.0081TL^{3.014}$	0.996	1 - 7	18 - 75	78.53	0.160	-0.73
N. TUNISIA (Bruslé, Prunus, 1980)	167	* $W=0.00783TL^{3.157}$	0.975	?	20 - 120?	?	?	?
NE. TUNISIA (Chauvet, 1988)	270	* $W=0.01256TL^{3.071}$	0.996	3 - 36	29 - 118	114.49	0.093	-0.75
S. TUNISIA (Bouain, 1984)	109	* $W=0.0195TL^{2.91}$?	1 - 19	18 - 95	197.79	0.025	-1.45
EGYPT (Rafail <i>et al.</i> , 1969)	251	$W=0.00692TL^{3.222}$?	1 - 7	20 - 80	80.00	0.112	-1.08
S. ITALY (Spedicato, Lembo, 1996)	96	$W=0.019046TL^{2.972}$	0.989	?	?	?	?	?
S. CORSICA - Lavezzi (Bouchereau <i>et al.</i> , 1999)	22	$W=0.125TL^{2.60}$	0.949	1 - 14	20 - 120	135.91	0.079	-0.80
BARCELONA (Castello Orvay <i>et al.</i> , 1992)	190	$W1=0.079SL^{2.551}$ $W2=0.046SL^{2.616}$ $W3=0.0285SL^{2.988}$	0.948 0.976 0.992	0 ⁺ 0 ⁺ 0 ⁺	5 - 11 5 - 11 5 - 11	?	?	?

Ghafir, Guerrab, 1992; Derbal, Kara, 1996) may indicate that the dusky grouper feeds at least partially during crepuscular periods or at night as this gastropod is nocturnally active and remains cryptic during daytime.

With regard to the occurrence of seasonal variability in trophic activity, Chauvet (1991) indicates a peak in autumn, but without specifying the corresponding field data. Besides, the diet described by Derbal, Kara (1996) deals only with individuals captured during summer.

Thus, at present, there is no reliable data offering a basis for depicting precisely the nycthemeral and seasonal feeding rhythms of the dusky grouper.

GROWTH

The data presently available on size-weight relationships and on growth of *E. marginatus* are compiled in table I. These data are quite heterogeneous as the numbers of individuals considered, the types of measurement performed (total vs. standard length, total vs. eviscerated weight), as well as the size ranges taken into account are different or not known. The available size-weight relationships came

from 11 sites, two in the Atlantic and 9 in the Mediterranean. According to these data growth apparently varies tremendously between sites: the weight corresponding to a particular size can double from one site to another (figure 3). However, as the size-weight relationship varies markedly in the course of the life cycle and according to the environmental conditions, the season, and the individual physiological state, this parameter cannot be considered for comparing different populations.

In most studies, the age of individuals has been determined from the counting of annuli on scales collected beneath the pectoral fins. According to Bouain (1986) and Chauvet (1988) these rings are formed in June. The age determination combining the study of both scales and sagitta (the largest otolith) after burning has only been performed by Chauvet (1981, 1988). The parameters of the von Bertalanffy's growth equation (L , K , and t_0) have been calculated for samples from six Mediterranean sites (table I). The between-site differences observed for these parameters may result essentially from sampling bias. Calculations from samples lacking in large-sized individuals underestimate strongly the value of L , which otherwise has no real biological significance. Thus,

according to the available data the size of an individual dusky grouper at a given age can double from one site to another (figure 4). The lowest linear growth has been recorded for individuals from Southern Tunisia (Bouain, 1984) and from Egypt (Rafaïl *et al.*, 1969) while the highest growth rate has been observed for dusky grouper from Western Algeria (Chalabi *et al.*, 1992). Specimens from Southern Corsica also

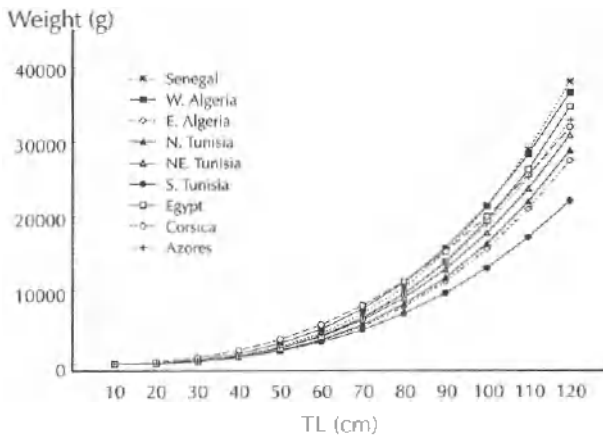


Figure 3 - Length-weight relationships in the dusky grouper *Epinephelus marginatus* according to different geographic locations. Data from Franqueville, Fréon, 1976 (Senegal); Chalabi *et al.*, 1992 (W. Algeria); Kara, Derbal, 1995 (E. Algeria); Bruslé, Prunus, 1980 (N. Tunisia); Chauvet, 1988 (NE. Tunisia); Bouain, 1984 (S. Tunisia); Rafaïl *et al.*, 1969 (Egypt); Bouchereau *et al.*, 1999 (Corsica); and Azevedo *et al.*, 1995 (Azores). / Relation taille-poids du mérrou brun, *Epinephelus marginatus* dans différentes zones géographiques. Données de Franqueville, Fréon, 1976 (Sénégal); Chalabi *et al.*, 1992 (W. Algérie); Kara, Derbal, 1995 (E. Algérie); Bruslé, Prunus, 1980 (N. Tunisie); Chauvet, 1988 (NE. Tunisie); Bouain, 1984 (S. Tunisie); Rafaïl *et al.*, 1969 (Égypte); Bouchereau *et al.*, 1999 (Corse); et Azevedo *et al.*, 1995 (Açores).

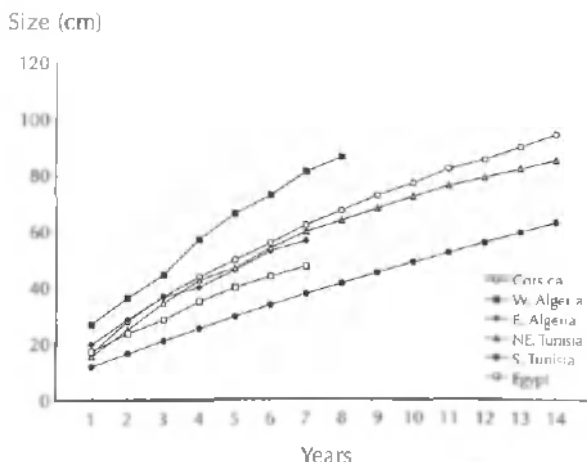


Figure 4 - Growth curve of *Epinephelus marginatus* in different regions of the Mediterranean Sea. Sources of data: see figure 3. / Courbe de croissance d'*Epinephelus marginatus* dans différentes régions de la Méditerranée. Sources des données: voir figure 3.

present a high linear growth rate (Bouchereau *et al.*, 1999), which exceeds slightly those of individuals from the Sicilian Strait (Chauvet, 1988) and from Eastern Algeria (Kara, Derbal, 1995).

The growth rate of *E. marginatus* is particularly high during the first year and decreases markedly thereafter. The average absolute increase of size (dTL, in cm) as a function of age has been calculated from five curves available for *E. marginatus* (figure 5). The growth rate decreases in average from 8 cm.yr⁻¹ to 4 cm.yr⁻¹ between the 2nd to the 10th year. At 25 years, the growth rate would be only 1 cm.yr⁻¹ (Chauvet, 1988). A decrease in growth has been recorded at five years old (age of first sexual maturity) by Chauvet (1988) for grouper in Tunisia. However, this phenomenon has not been observed in the other sites (Rafaïl *et al.*, 1969; Bouain, 1984; Chalabi *et al.*, 1992; Kara, Derbal, 1995). The age of the largest studied dusky grouper (118 cm TL, total weight = 34 kg, Tunisia) has been estimated as 36 years by Chauvet (1988). The heavier weight reached by some individuals (e.g. 54 kg for a specimen fished at Vis Island, Croatia, documentation from Komiza fisheries) suggests that the potential age the dusky grouper can reach is very great (>60 yrs?).

The wide range of variation observed for individuals younger than 8 yrs (cf. standard deviations: figure 5) reflect between-sites differences but also the high variability of individual size at a given age, as noticed by Bruslé (1985). Sizes ranging from 13 to 20 cm TL were found for individuals of class 1⁺ by Azevedo *et al.* (1995), and from 18 to 25 cm TL for those of class 2⁺. The mean size backcalculated for a one-year old individual (figure 5) is particularly overestimated as indicated by the few actual measurements available in the literature. According to Bouain's estimates (1984) in Tunisia, aquaculture

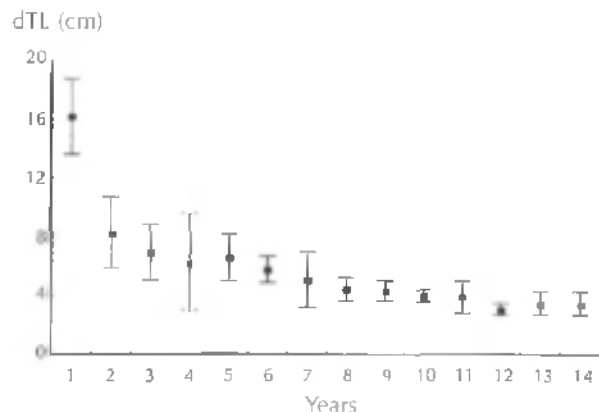


Figure 5 - Mean absolute increase in size (mean dTL in cm \pm standard deviation) in *Epinephelus marginatus* during the first 14 years of life (calculated from the growth curves of figure 4, excepted W. Africa). / Accroissement moyen de la taille d'*Epinephelus marginatus* (dTL moyen en cm \pm déviation standard) au cours des 14 premières années de vie (calculé à partir des courbes de croissance de la figure 4, exceptées celles d'Afrique de l'Ouest).

experiments of juveniles performed at Barcelona by Castello-Orvay *et al.* (1992), and ageing of young specimens collected in Azores Islands by Azevedo *et al.* (1995), the mean size of *E. marginatus* at one year would be around 11 cm SL (= 13 cm TL).

DISCUSSION AND PERSPECTIVES

Habitat

The precise characteristics of the habitat of juvenile dusky grouper are still poorly known. A better knowledge of the depth at which settlement occurs and of the physical and biotic characteristics of the nursery sites should make it possible to estimate the variability in time and space of recruitment intensity. Concerning the habitat of juveniles, issues of major interest for the management of the dusky grouper populations are: (i) Does the geographical distribution of settlement sites present any relationship with the location of adult aggregations? Precise knowledge of the duration of the pelagic larval stage and of the coastal circulation would be necessary to answer this question. (ii) What anthropogenic perturbations particularly act on post-settlement mortality? Among these perturbations, one has to take into account habitat modifications induced by pollution and its secondary effects, particularly on macrophyte cover, but also the impact of line fishing on juveniles. (iii) Is it possible to enhance the recruitment intensity through habitat management, e.g. specifically designed artificial reefs? The discovery in the Barcelona region of many juveniles of *E. marginatus* in immersed structures designed for collecting oyster spat may provide useful indications on the feasibility of such management measures. In Virgin Islands, Beets, Hixon (1994) have noted a higher recruitment success for Nassau grouper (*E. striatus*) on small artificial reefs than on natural substrates.

An unresolved question concerning the habitat ecology of subadults and females is their site fidelity. Is site fidelity dependent on the distance between nursery areas and localities where males aggregate? The marked differences in population abundance and structure between warm and cold season raise the problem of the location of part of the population in winter. Does it correspond to a vertical migration towards deep-water sites poorly accessible to direct observation? Or do grouper stay on the spot permanently hidden in holes? This cryptic behaviour and apparent decline in abundance have been observed in winter among fish on rocky bottoms in the Northern Adriatic (Kotrschal, Reynolds, 1982) and in summer in Provence when wind-induced upwellings cause abrupt temperature drops (unpublished personal observations). Periodic observations of the behaviour of a significant number of individuals during the period preceding the minimum in water temperature should be informative. The use of hydroacoustic tracking could produce results if migration is not too sudden, but would be inefficient if the grouper stay hidden beneath rocks.

Feeding

The available data on the feeding behaviour of *E. marginatus* indicate that the dominant food categories consist in small crustaceans for juveniles, crabs and fish for medium-sized individuals, and in cephalopod mollusks and fish for large grouper. A similar ontogenetic shift has been observed in several species of tropical grouper (Harmelin-Vivien, Bouchon, 1976; Brulé, Rodriguez Canche, 1993; Brulé *et al.*, 1994). However, as the diet of the dusky grouper has been documented only from few specimens, there is no information on its regional variability and on the daily and seasonal feeding rhythms. All studies on the feeding habits of this grouper were performed on specimens collected during daytime. Some prey found in stomach contents suggest that the dusky grouper feeds at least partially during crepuscular periods or at night. On the coral reefs of Madagascar, most grouper species feed in the daytime as well as at night on the same food categories (Harmelin-Vivien, Bouchon, 1976) with only changes in their relative proportions: fish are the most frequent prey during the day, and crabs and cephalopods at night. Other authors have observed a peak in feeding activity at crepuscular periods in other tropical grouper species (Parrish, 1987; Sluka, Sullivan, 1996). Therefore, the feeding behaviour of the dusky grouper needs to be better documented.

Growth

The growth of *E. marginatus* has been studied only in some Mediterranean sites, mainly along the coast of Algeria (Chalabi *et al.*, 1992; Kara, Derbal, 1995), of Tunisia (Brulé, Prunus, 1980; Bouain, 1984; Chauvet, 1988), and Egypt (Rafail *et al.*, 1969). Only one recent study deals with individuals from Northern Mediterranean (Corsica: Bouchereau *et al.*, 1999). Several aspects concerning the growth of *E. marginatus* remain poorly documented. There is a particular need for reliable information on size-age relationships within the whole size range of this species. The time of formation of annuli and the reliability of their reading remain uncertain. The possibility of determining the age of individuals from otoliths, at least for younger specimens, has not been fully evaluated. Moreover, the ageing of large dusky grouper is problematic, as for every long-lived species (Crabtree, 1998). It would be interesting to know whether the technique of otolith weight could be used for determining the age structure of the dusky grouper populations as was done for the Australian coral trout, *Plectropomus leopardus* (Russ *et al.*, 1998). The growth rate of *E. marginatus* during its larval stage and the first years of its benthic life is unknown, as is the duration of the planktonic larval stage.

Some results on the growth rate of this species from different regions are conflicting and it is not clear whether the differences observed result from study protocols or reflect actual geographical differences (e.g. differences in productivity, or in prey availability). Thus, it would be useful to perform a

more thorough assessment of links that may exist between geography and growth rate. This study should encompass comparisons between northern and southern populations in the western and eastern basins of the Mediterranean, western and eastern populations along the coasts of Maghreb, and in the eastern Atlantic, between populations from West Africa and those from South Africa.

In conclusion, despite the fact that the dusky grouper is an emblematic species in the Mediterranean, where it has been fished since pre-historic times (Desse, Desse-Berset, 1999), many aspects of its biology and ecology remain poorly known, particularly concerning larvae and juveniles. A better knowledge of this species should help towards understanding the changes observed in the northern populations over the past decade (Chauvet, Francour, 1989; Harmelin, Robert, 1992; Francour et al., 1994; Zabala et al., 1997).

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