The queen snapper (*Etelis oculatus*) is among the deepest dwelling species of the family Lutjanidae, and the only Atlantic species of *Etelis*. Its distribution covers the tropical western Atlantic Ocean, from North Carolina to the eastern tip of Brazil, at depths of 130 to 450 m (Allen, 1985).

Although it reaches a large size and presents no risk of ciguatoxicity (Lorance1), the species is exploited by only a few fisheries in the Caribbean. Most often it is only a minor part of the catch of line fisheries that focus on the whole community of deep snappers, or on more abundant species such as vermilion snapper (*Rhomboplites aurorubens*) or silk snapper (*Lutjanus vivanus*) (e.g., in Venezuela: Mendoza and Larez, 1996). In a few cases, however, *E. oculatus* is specifically sought by fishermen; for example, in Saint-Lucia within a traditional fishery operating during the months when migratory pelagics are not fished (Murray et al., 1992), or in Bermuda where it has been caught irregularly (pulse fishery) since the ban on potfishing (Luckhurst, 1996). Commercial exploitation is only beginning in the French West Indies, but is much more developed in Barbados (Prescod et al., 1996) and Puerto Rico (Matos-Caraballo, 2000). Exploitation of the queen snapper is poorly documented, and very few detailed catch statistics are available; in all cases, the amounts landed in each country are small (probably not exceeding a few tens of tons per year), but the potential production of these resources has never been estimated.

Owing to the depth of its habitat and to the relatively small economic importance of the fisheries for queen snapper on the local scale, very little is known about the biology of *E. oculatus*. It is generally cited in species checklists or in general descriptions of deepwater fisheries. Very few studies actually have focused on the species itself (Murray, 1989; Murray and Charles, 1991; Murray et al., 1992; Murray and Moore, 1992; Murray and Neilson, 2002).

The objective of this study is to present new information about the biology of *E. oculatus*, obtained from fishing experiments undertaken since the 1980s in the French West Indies (Martinique, Guadeloupe, Saint-Barthélemy, and the French part of Saint-Martin), Dominica and Saint-Lucia, and from a study conducted in the late 1990s on the artisanal and semi-industrial fisheries off the Caribbean coast of Honduras.

### Material and methods

#### Areas studied

The data were collected from various research projects (Fig. 1 and Table 1):

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1) On the French parts of the wide shelf shared by St-Martin, St Barthélemy, and Anguilla (abbreviated as SMSBA shelf in the text), exploratory fishing experiments were conducted to assess the fishing potential and the risk of ciguatoxicity (Lorance2). The deep slopes of the bank (200–300 m) were fished in 1986–87, using bottom longlines, trammel nets, and secondarily bottom gill nets.

2) In Martinique, exploratory fishing experiments were conducted in 1986–87 on various parts of the shelf slope (100–300 m), and some observations were made in 1982 and 1988–91, mainly with gill nets and trammel nets (Guillou3).

3) In Saint-Lucia, observations were made in 1987 on the commercial fishery, and fishing experiments were conducted in 1992 with longlines (Guillou4).

4) In Dominica, fishing experiments were conducted in 1992 with longlines and gill nets.

5) In Guadeloupe, experiments were conducted in 2001 with gill nets in the range 200–400 m (Diaz et al., in press); some small *Etelis* were also caught with 10-mm-mesh traps used for a survey of deep crustacean resources.

6) In the Bay Islands, off the Caribbean coast of Honduras, a fisheries survey was conducted in 1999–2000 as part of a coastal zone management project (Berthou et al.5). This artisanal fishery uses mainly handlines to catch snappers and groupers on the shelf, but a fraction of the fishing effort is directed towards the deepwater snappers on the shelf slopes.

7) In Honduras, the landings of the semi-industrial fishing fleet based in Roatán (Bay Islands) were studied, through catch statistics of the export firms and by sampling in the collecting centers (de Rodellec6). These fleets target snappers and groupers over the entire Caribbean shelf of Honduras, and fish with handlines.

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Table 1

Summary of sample sizes and depth ranges of queen snapper (*Etelis oculatus*) by area and fishing gear, in exploratory or commercial fishing operations (SMSBA = Saint Martin-Saint Barthélemy-Anguilla).

<table>
<thead>
<tr>
<th>Area</th>
<th>Trammel nets (exploratory)</th>
<th>Gill nets (exploratory)</th>
<th>Lines (exploratory)</th>
<th>Lines (commercial)</th>
<th>Depth range (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Martinique</td>
<td>300</td>
<td>209</td>
<td>6</td>
<td></td>
<td>140−300</td>
</tr>
<tr>
<td>SMSBA shelf</td>
<td>249</td>
<td>406</td>
<td>230−430</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saint-Lucia</td>
<td>34</td>
<td>394</td>
<td>210−290</td>
<td></td>
<td>210−290</td>
</tr>
<tr>
<td>Dominica</td>
<td>191</td>
<td>20</td>
<td>180−300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Guadeloupe</td>
<td>1133</td>
<td>195−410</td>
<td>195−410</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bay Islands</td>
<td></td>
<td>794</td>
<td>unknown</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Honduran shelf</td>
<td></td>
<td>3948</td>
<td>unknown</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fishing gears used

In all islands but Guadeloupe, gill nets had mesh sizes of 65 mm (knot to knot) and a stretched height of 6.4 m. In Guadeloupe, mesh was 60 mm and height was 4 m; in addition, the nets were given more slack than in Martinique to increase their efficiency, and thus caught a wider size range of fish.

Trammel nets had mesh sizes of 40 mm (knot to knot) on the central panel and 200 mm on the outer panels, and were 2 m high. All nets (trammel nets and gill nets) were set overnight (15 to 20 hours of fishing time) in units of 200 or 300 m.

Three types of longlines were used in the fishing experiments. Vertical longlines were derived from those used by fishermen in the Lesser Antilles and had about 20 hooks on 40 cm-long secondary lines. Pole longlines were adapted from a technique used in Florida and Puerto-Rico: poles about 2 m long are fastened to the main line lying on the bottom, each having 12 to 25 hooks on very short secondary lines (20 to 30 cm). Reinforced longlines are horizontal longlines whose main line is heavier, in order to fish on very rough grounds. All longlines were hauled after 30 to 45 minutes fishing. For the analysis, no distinction was made between samples of these three types of longlines. Various kinds of longlines are used in the small-scale queen snapper fishery in Saint-Lucia. Handlines used in the artisanal and semi-industrial Honduran fisheries are either mono- or multifilament, and bear one or several hooks. No detailed observations were made on the size of hooks or on the bait used in the commercial queen snapper fisheries.

Data collected

None of these studies was specifically designed for the study of *E. oculatus*, and therefore the nature and amount of available information (sampling coverage though time, space, and depth) for this species were variable. Species identification (Allen, 1985; Anderson, 1987) could be done reliably in the field for adults and juveniles, but had to be confirmed under the microscope for the smallest individuals (less than 10 cm). Fish length was the only information recordable from professional landings (St-Lucia, Honduras); fishing experiments yielded more detailed data, by order of decreasing frequency: length (fork length FL, total length TL, or both; unless specified, all lengths mentioned in the text are fork lengths), weight, and sexual stage, and occasionally a few additional observations (such as unusual number or length of fin rays). Sexual stages were identified by using the macroscopic scale defined by Barnabé (1973) and were coded as follows: 1 (immature, without identifiable sex), 2 (immature, of identifiable sex), 3 (mature), 4 (prespawning), 5 (spawning), 6 (postspawning), and 7 (resting). Depth was recorded only in the fishing experiments; for gillnet and trammel-net stations, it was measured at each end of the net, and the depth used in the analysis was the average of these two values.

Length-frequency analysis

In most cases, length-frequency analysis was strongly hindered by gear selectivity and sample sizes. We attempted to estimate $L_\infty$ and $Z/K$ with the method of Wetherall et al. (1987) applied to the sample of the semi-industrial Honduran fishery. All other samples were unsuitable for length-frequency analysis because of severe violations of one or several assumptions, principally regarding constant catchability above the full selection length, which was obviously not the case for the three gears used in the fishing experiments.

Results

Depth distribution

During the fishing experiments, *E. oculatus* of marketable size (i.e., larger than about 20 cm) were caught
between 140 and 430 m. In Martinique, the trammel nets were set between 100 and 300 m but did not catch any E. oculatus in the shallowest part of this range. In Guadeloupe, gill nets were set down to 410 m, but the deepest catch of queen snapper was 340 m. No E. oculatus were caught in shallower (<80 m) fishing experiments with any of the gears used (traps, gill nets, trammel nets, and longlines) on the SMSBA shelf. According to some local fishermen, however, queen snappers can be caught from about 100 m down to 550 m (Lorance²).

**Depth-size relationship**

No clear relationship between depth and average size of fish was found in the fishing experiments (Fig. 2). This is not unexpected given the selectivity of some gears (gill nets) and the small sample sizes in most depth strata outside the main fishing range (250–300 m); 70% of the 456 fish caught by longlines were in the 290 m depth stratum, and five or fewer fish were caught in most of the other strata.

A different picture emerges from the analysis of the professional fisheries of Honduras. Multivariate analysis (principal component analysis followed by hierarchical classification) applied to the landings by species revealed the two different categories of fish caught by the two types of semi-industrial vessels operating from Roatán (de Rodellec), the shelf-operating fleet and the slope-operating fleet. The first category of fish were dominated by shallow species such as Ocyurus chrysurus (59.8%), Lutjanus analis (7.8%), and several grunts (Haemulidae), whereas E. oculatus accounted for only 2.2%. On the other hand, the second category comprised mainly deep snappers: L. vivanus (39.6%), E. oculatus (22.4%), R. aurorubens (6.9%) or L. buccanella (1.9%). The two divisions of the fleet independently exploit the continental shelf and the deep slope. Although actual depth of fishing operations is unknown, the shelf-operating fleet probably catches E. oculatus in the deepest part of its working area (i.e., at the shallowest part of the species’ bathymetric range), whereas the slope-operating fleet exploits the main habitat of the deepwater snappers. The size structures of Etelis catches (Fig. 3, A and B) strongly indicate that only the fish up to 45–50 cm live on the shelf or its edge, whereas individuals of all sizes, and particularly the largest ones, inhabit the shelf slope.

A similar observation was made for the island of Roatán, where the artisanal fleet is the least developed of the archipelago: fishermen using small (<6 m) and often (57%) nonpowered canoes fish quite close to the shore and catch a large diversity of coastal reef fishes, a large proportion of which are juveniles. Etelis oculatus is rarely caught by these small-scale fishermen but is so only as individuals smaller than 50 cm, sometimes as small as 16 cm (Fig. 3C).

**Habitat of early juveniles**

Some observations were made on very small (smaller than 10 cm) individuals of E. oculatus. Off Guadeloupe, a few of them were entangled in gill nets at 300 m depth (Fig. 3D); on the same island, previous exploratory fishing operations with small-mesh traps caught six juveniles ranging from 5.5 to 7 cm FL at 490 m depth; off Dominica, one small individual (8.5 cm TL) was found in the stomach of a predator caught at a depth greater than 200 m (see below). In spite of the general tendency of increasing size with depth found for the larger individuals, these observations show that the habitat of early postsettlement juveniles is not restricted to the shallowest part of the species depth range.

**Morphometric relationships**

The main morphometric relations were computed from the fish sampled in commercial or scientific fishing operations in the Lesser Antilles (Martinique, Saint-Lucia, SMSBA shelf). Because the differences between relations for males and females were insignificant, only global equations are given (Table 2).

**Maximum size and weight**

The largest individual caught was 90 cm FL in the Lesser Antilles (Guadeloupe) and 86 cm in Honduras, and the maximum weight recorded was 6280 g, in the Lesser Antilles; fish were not weighed individually in Honduras.

**Sex-related length differences**

When sex was recorded, the largest fish were always female, and no male was found above 70 cm. The difference between size-structure of male and female catches
was particularly clear for trammel nets (Fig. 3, E and F): the mode corresponding to fish gilled in the small-mesh central panel had similar characteristics for both sexes (range 25–45 cm and peak at 36 cm), as opposed to the diffuse mode for fish >45 or 50 cm (predominantly females) entangled in the large-mesh outer panels. With many fewer fish ($n=23$ for both sexes), the longline samples showed a similar difference between sizes of males (maximum 55 cm, mean 43.8 cm) and females (maximum 71 cm, mean 51.8 cm). In Guadeloupe, the sex of fish was not determined, but the existence of two modes in the overall size structure of gillnet catches (Fig. 3D) could possibly be related to this sex-related length difference.

**Growth and mortality**

The data collected in the various surveys did not allow any reliable analysis of the growth of *E. oculatus*. Because growth may be different for males and females, the length-frequency distributions of the large samples (where sex was not determined) from Honduras could not be processed rigorously to estimate life-history population parameters. However, in order to provide preliminary information on such a little known species, the regression method of Wetherall et al. (1987) was used in the modified version of FiSAT (Gayanilo et al., 1996) to estimate $L_\infty$ and $Z/K$. With a satisfactory fit of the regression line ($r=0.986$), the estimates were $L_\infty = 90.57$ cm and $Z/K = 3.73$. For the reason mentioned above (together with other weaknesses related to possible violations of the hypotheses underlying the regression
method), these estimates have to be seen only as indications that the asymptotic length of *E. oculatus* is quite large and that the Honduran population is moderately exploited (if $M = 2K$, as suggested by Ralston (1987) for snappers, then $Z/K = 3.73$ and $E = F/Z = 0.46$).

**Reproduction**

Macroscopic observations of gonads were recorded for 309 fish whose sex could be identified (118 males and 191 females); all stages of the reproductive cycle were observed, but only 20 individuals were in the prespawning to postspawning stages, and a single one was found to be in the process of spawning.

The smallest fish with developing gonads was 36 cm for females and 29 cm for males (Fig. 4). Although only part of the length range of males was adequately sampled (100 out of the 118 fish were smaller than 44 cm), it appears that the progressive build-up of the reproductive male population occurs between about 30 cm and 45 cm. The picture is clearer for females, whose sample size was larger and more evenly spread over the length range: above 54 cm, all females were found to be in a reproductive cycle. The maturing process therefore occurs at clearly lower sizes for males (30−45 cm) than for females (35−55 cm). Females in advanced reproductive stages (postspawning and resting stages) were observed across the length range, including the smallest adult sizes, those below 45 cm (Fig. 4).

A full analysis of the seasonality of reproduction is not possible because data were collected in only seven months, out of which only four (May, June, November, and December) yielded samples large enough for the analysis (21 to 72 females per month). No females were found to be spawning, but most of the pre- and postspawning stages (14 out of 17) were observed in November and December, and half of maturing females were fished during the last quarter of the year (Fig. 5). However, 74% of females at sexual rest (resting stage) were caught in May and June. Additional pieces of information confirm this pattern: the only spawning individual, a male, was observed in November (Dominica); females gonads in advanced stage of vitellogenesis were observed in September (Guadeloupe); no mature individual was found in Honduras in April−June. These observations show that an active spawning period occurs at the end of the year (even if all fish caught at this period were not close to the spawning phase), as opposed to late spring which is a period of sexual inactivity.

Such limited results leave open the overall interpretation of the annual reproductive cycle of *E. oculatus*. In particular, according to the fishermen working on the SMSBA shelf, the species could have an extended spawning season, lasting from November to April or May.

**Predators and prey**

No systematic observations were made on the trophic relationships of *E. oculatus*, but a few occasional recordings were made of its predators and prey. The only record of a predator was that of a beardfish (*Polymixia lowei*: Polymixiidae) measuring 40 cm TL containing a very small queen snapper (8.5 cm TL) and which was caught deeper than 200 m. This is the first record of such a food item for this beryciform fish whose diet had so far been reported to comprise cephalopods (Cervigon, 1991). The stomachs of *E. oculatus* that could be observed were most often empty; on a few occasions, unidentified squids were the only items present. This was the case for three fish (58 to 62 cm) caught at 430 m depth.

**Discussion**

*Etelis oculatus* was found on the upper part of the continental and insular slopes, from about 150 to 450 m; this observed range confirms previous indications (Allen, 1985), but the bathymetric distribution of the species could possibly extend beyond the maximum depth fished in these surveys. The presence of *E. oculatus* in shallower waters of the shelf seems possible, according to a statement that juveniles can be found in less than 30 m (Appeldoorn et al., 1987) and to the reported catch of one fish (size not recorded) at 59 m depth by a trawl survey off southeastern United States (Cuellar et al., 1996). However the present data, other fishery-independent surveys focusing on snappers (i.e., Marcano et al., 1996, down to 128 m), and most studies on Caribbean coastal fisheries strongly indicate that the species is very rare on the shelf itself.

Within the observed depth range, there is a tendency for the largest fish to be found in the deeper areas, as observed in the closely related Pacific species...
E. carbunculus and E. coruscans (Brouard and Grandperrin7), other deepwater lutjanids (Boardman and Weiler, 1980; Cuellar et al., 1996), and many reef fish species. The maximum size recorded for large samples (90 cm FL) is much greater than the 60 cm TL indicated by Allen (1985) but is consistent with other field observations, such as 94 cm TL in Saint-Lucia (Murray, 1989) or 100 cm TL in Venezuela (Cervigon, 1991).

No reliable growth estimate could be obtained because males and females showed very different size structures, and the only data suitable for length-frequency analysis were data for which the sexes had not been determined.

Important differences were found between sexes in terms of size structure and maturation size. Male E. oculatus attain a smaller length than females, and are much rarer above 45 cm. Sex-ratios skewed in favor of females in large size classes were observed in the most complete studies of snapper populations (Grimes, 1987), including Pacific deepwater snappers (Brouard and Grandperrin7), and probably result from a difference in growth and mortality between the sexes; in Cuba, for instance, females of most snapper species have been found to grow faster than males (Claro and Garcia-Arteaga, 2001). In the present study, sex-specific growth and mortality estimates were not available, but our interpretation seems likely because other possible causes could be ruled out, such as selectivity of nets (morphometric relationships are identical for both sexes) and fish behavior in relation to fishing gear (differences between sexes, however, were observed in trammel nets and lines whose catch mechanism is completely different). Different habitat preferences, which can lead to sex-related size structures in reef species (Garcia-Cagide et al., 2001), seem unlikely in our study because the deep slopes have fewer habitat gradients than the shallower reef environments and because no relation was found between depth and sex-ratio. A similar difference between males and females was found for reproductive size. Male snappers generally mature at a slightly smaller size than females, but sex does not appear as a significant factor of variation for relative length at first reproduction, as opposed to depth or continental or insular habitat (Grimes, 1987).

In the Lesser Antilles, E. oculatus spawns at the end of the year and has a period of sexual rest during from late spring through early summer. These results are not sufficient to establish the entire annual reproductive pattern, and even these partial findings cannot be applied to other parts of the Caribbean because snapper populations of continental and insular shelves generally show different seasonal patterns of reproduction (Grimes, 1987). This indication of a spawning period for E. oculatus in the cold season contrasts with the two eteline species (Aprion virens and E. coruscans) studied in Hawaii, which have a protracted spawning period extending through the summer (May or June through October or November) (Everson et al., 1989).

The data collected in these studies did not allow the analysis of the aggregation pattern of *E. oculatus*. In the Pacific, *E. coruscans* was found to form feeding aggregations near underwater promontories and these aggregations had important consequences for catchability (Ralston et al., 1986). For the deeper living alfonsinos (*Beryx* spp.) and orange roughy (*Hoplostethus atlanticus*), fisheries have shown their ability to quickly fish down aggregations once they are discovered (Lorance and Dupouy, 2001). Added to “K-selected” life-history strategies (high longevity, slow growth, late reproduction) and irregular recruitment, this aggregating behavior reinforces the vulnerability of deepwater species to overfishing (Koslow et al., 2000).

Recently gained knowledge about the exploitation of seamount and deep bank fish resources (Clark, 2001) cannot be applied directly to *E. oculatus* and the other slope-dwelling snappers which, although they are the deepest dwelling species of the family, are much closer in terms of demographic strategy to their shallow relatives (longevity 10−20 years; Manooch, 1987) than to these truly deep species (longevity 50 to more than 100 years; Koslow et al., 2000). However, less extreme life history traits do not protect deep snappers against overfishing, as shown by the example of *E. coruscans* and *E. carbunculus* in Hawaii (Simonds, 1995). The limited fishery data available on *E. oculatus* in the Caribbean do not seem to show evidence of a similar situation so far, but the stocks are being increasingly fished without much scientific basis (i.e., catch statistics) for management (Mahon, 1990; FAO, 1993). Regulation measures continue to be defined (Diaz et al., in press), but so far they are based only on conservative rules of thumb because of a lack of reliable biological information. To address this lack of information, future research on *E. oculatus* therefore should address, in particular, sex-specific growth, reproductive biology, and fine-scale distribution patterns.

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Literature cited


