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Changes in population structure of the white grouper *Epinephelus aeneus* as a result of long-term overexploitation in Senegalese waters

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In Senegal, a significant decrease in catches indicates that many demersal fish stocks are being overexploited. The white grouper *Epinephelus aeneus*, locally known as the 'thiof', is exploited by both small-scale and industrial fisheries. A 28-year database of *E. aeneus* catches along the Senegalese coast provided by the Centre for Oceanographic Research of Dakar-Thiaroye, and size at maturity measured in Dakar (Senegal) from monthly samples in 2010, were used to analyse changes in population structure in the area over the past 37 years. Catches from the northern fishing areas were lower than those from the southern fishing areas, and decreased steadily during the period (Kolmogorov–Smirnov test, $D = 0.243$, $p = 0.0002$). The individual mean weight of catches decreased from 1974 to 2010 (linear regression, $r^2 = 0.40$, $n = 37$) and only 60% of the individuals were mature. The calculated sizes at maturity were 49 cm total length (TL) for females and 55 cm for males, and the optimal length of capture for a sustainable fishery was 96 cm, but only 0.03% of *E. aeneus* caught reached this length. Most of the catch consisted of juveniles; the larger reproductive individuals had disappeared. The number of individuals caught decreased significantly between 1974 and 2010 (1974–1983, $r^2 = 0.98$, $n = 74\ 674$; 1984–1993, $r^2 = 0.95$, $n = 96\ 696$; 1994–2003, $r^2 = 0.93$, $n = 12\ 619$; 2004–2010, $r^2 = 0.91$, $n = 12\ 887$), whereas the length range remained the same (10–110 cm TL). Biological indicators clearly showed that *E. aeneus* stocks in Senegal are overexploited and the species is now endangered. Immediate active management of fishing pressure is needed, therefore, to maintain *E. aeneus* populations in the area. Our results suggest a minimum size of <50 cm should be introduced and that fishing effort should be reduced.

Keywords: biological indicators, fishing pressure, length at maturity, size spectrum, West Africa

Introduction

The Mauritanian-Senegalese upwelling area is known to be the richest fishing ground in West Africa (Cury and Roy 1988). Senegal has a continental shelf of about 196 000 km^2 and a coastline of 718 km, with waters that are rich in fishing resources given their particular hydrodynamics (Faure 2000) and their favourable geomorphology and climate (Roy 1992). Fish are exploited by both industrial and small-scale fisheries and are important in the area for food security, the local economy and employment (Camara 2008). However, these resources are subject to very high levels of exploitation and this, coupled with degradation of environmental conditions, has led to a decrease in fisheries production, with some fish species becoming rare (CSE and CERPOD 1996). For several decades Senegalese small-scale, or artisanal, fisheries have been affected by significant changes: the fleet doubled in size from about 6 400 fishing canoes in 1985 to 12 600 in 2005 (Thiao 2009), and it continues to expand. The report by the Fishing Committee for the Central and Eastern Atlantic (COPACE 2003) considered pelagic species moderately exploited but demersal species fully or overexploited. Among the highly exploited species, the white grouper *Epinephelus aeneus* (Geoffroy Saint-Hilaire 1817) is considered to be overexploited in most Atlantic areas and is listed as Endangered on the International Union for Conservation of Nature (IUCN) Red List (Thierry et al. 2008). The species is found throughout the southern Mediterranean and along the western coast of Africa, from Gibraltar (Spain) to the southern coast of Angola. Adults live on rocky, muddy or sandy bottoms in depths of 20–200 m, whereas juveniles are captured in coastal lagoons and estuaries (Bruslé 1982). It is a voracious predator that eats fish, cephalopods and shellfish (Fisher et al. 1981). In Senegal, *E. aeneus*, locally known as 'thiof', is the most exploited of the seven groupers (Bruslé 1985) and is also the most popular for the main traditional dish in the area ('Ceebu jën', literally 'rice and fish'). Senegalese catches of *E. aeneus* decreased because fishing effort continued to increase after 1971 (Barry et al. 2004). The annual number of fishing trips by canoes increased from about 150 000 to 210 000 between 1981 and 1999, and the annual number of days at sea in the industrial sector increased from 8 000 to 17 500 between 1997 and 1999.

Recent genetic studies showed distinct northern and southern populations of *E. aeneus* along the Senegalese coast, separated by the Cape Verde Peninsula but with some genetic exchange (JD Durand, IRD Montpellier, unpublished data). Further genetic investigations are needed to elucidate stock structure. Cury and Worms (1982) suggested that there is a seasonal migration of *E. aeneus* from Mauritania to Senegal to utilise increased productivity resulting from the onset of upwelling in Senegalese waters at the beginning of each year. Most epinephelids are protogynous hermaphrodites (Smith 1959, 1965, Moe 1969, Sadovy de Mitcheson and Liu 2008), but three species of groupers (*Cephalopholis furcifer*, *Epinephelus striatus* and *Mycteroperca rosacea*) are now recognised as functional gonochoric species, based on histological, demographic and mating system data (Sadovy and Colin 1995, Erisman et al. 2008). In Senegal, protogyny was reported in *E. aeneus* (Bruslé 1985) but the fish used in that assessment were reared in captivity or induced to undergo sex change. There is no record of natural sex change in *E. aeneus* which, in Senegalese waters, is not clearly hermaphrodite, males and females being present in all size classes (KD unpublished data).

The effects of fishing on fish assemblages can include selective removal of large individuals or reduction in the abundance of the most vulnerable species, usually of higher trophic levels. Hence fish biomass, species composition and size structure may change under fishing pressure (Bianchi et al. 2000). Changes in the size structure of fish communities may affect biology, genetics, biomass and interaction between species (Law 2000, Friedlander and DeMartini 2002, Shin et al. 2005, Woodward et al. 2005). Size spectrum is a key parameter for analysing exploited fish communities (Enin et al. 2004) and it can be used as an indicator to monitor stock sustainability. For example, the slopes of size spectra respond in a consistent way to changes in exploitation levels and provide indirect information on trends in fishing effort (Froese 2004).

This study focuses on changes in the size frequency distribution of *E. aeneus* catches over a long time-series (1974–2010) as an indicator of fishing pressure on the exploited population. We describe length at maturity of *E. aeneus* and analyse some fisheries indicators proposed by Froese (2004) as representative of stock structure. This study aims to establish a scientific basis for better management of local stocks of *E. aeneus*.

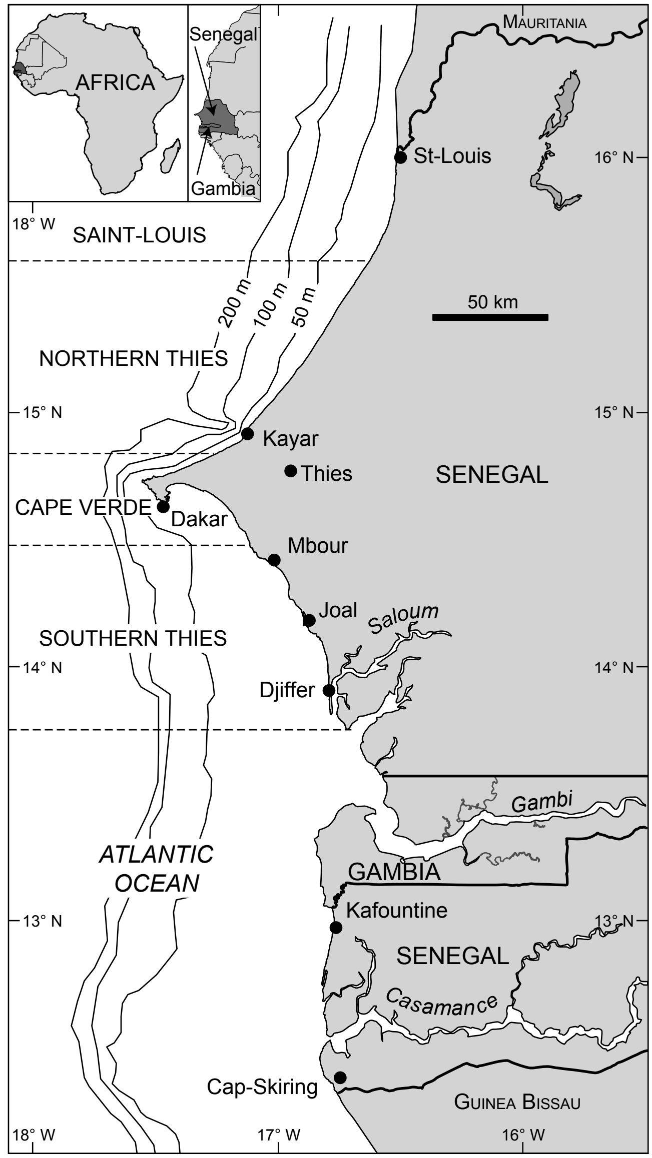

Figure 1: Map of the study area on the Senegalese coast showing the fishing areas

Materials and methods

Study area

The Exclusive Economic Zone (EEZ) of Senegal extends from 18°00′ N, 20°00′ W to 12°15′ N, 16°30′ W. The Cape Verde Peninsula is located between 14°30′ N and 15°00′ N and divides the EEZ into two areas with distinct topographic characteristics (Figure 1). In the northern part, the continental shelf is fairly narrow, with the edge oriented north–north-east. South of the peninsula, the continental shelf widens and the edge is oriented north–south.

Catch and fish samples

Details of the total weight of *E. aeneus* captured annually from 1974 to 2010 by small-scale and industrial fisheries in Senegalese waters were provided by the Centre for Oceanographic Research of Dakar-Thiaroye (CRODT). Data from small-scale fisheries were obtained through daily sampling of the catches taken by canoe (Ferraris et al. 1994). Sampling began in 1974 at the main landing harbours in Senegal. As the fishing industry developed, other catching areas developed and were also sampled. From 1981, samples were taken from the whole of the Senegalese coast. The coastal area was divided into four major fishing regions for *E. aeneus* (Figure 1; Saint-Louis, Northern Thies, Cape Verde and Southern Thies). Length distributions (sexes combined) were obtained from the catches of Senegalese small-scale fisheries from 1974 to 2010. These were used to estimate biological indicators (see below). Industrial fishery data for foreign trawlers were collected on board by inspectors. For each haul, the inspector recorded total catch, fishing time and related information (Barry et al. 2004). The trends of the total catches per year were tested using a Kolmogorov–Smirnov test.

Length at maturity
The Soumbédioune landing station (Cape Verde Peninsula, Dakar) was sampled monthly from January to December 2010 in order to calculate the length at maturity (L_{50}) at this location. This station is one of the main landing sites in the subregion and is the main landing port for *E. aeneus* on the peninsula. The samples were purchased from the fishery. For each individual the total length (TL) and weight (W) were measured. Maturity stages were classified from 1 (immature) to 5 (reproductively active) according to García-Díaz et al. (2002). Fish with gonads at stages 3 to 5 were considered to be sexually mature. Specimens collected from May to August were used for analysis, as the spawning period extends from late March to late August in coastal Senegalese waters.

The length at maturity (L_{50}) is the length at which 50% of the individuals are mature (≥ stage 3 of the maturity scale). This was estimated using the logistic function:

$$\%M = \frac{100}{1 + e^{(-a(L - L_{50}))}}$$

where %M is the percentage of mature fish per 50 mm length class, L is the mid-point of each length class and a and L_{50} are constants. The model was fitted using Statistica® and least squares (quasi-Newton method). Full maturity was reached when 90–100% of the individuals were sexually mature. The corresponding length (L_{90-100}) was also obtained using this logistic function.

Sex ratio
The size-specific sex ratio per 50 mm size class was calculated only at the Soumbédioune landing station (Cape Verde Peninsula, Dakar) during monthly sampling in 2010. Sex ratios at all other locations were assumed to be the same. Sex ratio was plotted against length and regression analysis was used to explore whether sex ratio varied predictably with length.

Fishery indicators
Three simple fishery indicators were calculated from the catch: (1) percentage of mature fish, (2) percentage of fish at optimal length and (3) percentage of mega-spawners. The percentage of mature fish (Froese 2004) was calculated using the estimated length at maturity (L_{50}) at the Soumbédioune landing station. The rationale for setting this as a minimum size would be to allow all fish to spawn at least once before they are caught, in order to rebuild and maintain spawning stocks. Optimal length was defined as the length at which fish should be caught to provide the maximum yield for maximum revenue. The optimal length is typically greater than L_{50} and is calculated using growth and mortality parameters (Froese and Binohlan 2000). An associated management objective would be for all fish caught to be within 10% of the optimal length (Froese 2004). The optimal length (L_{opt}) was calculated using the formula:

$$L_{opt} = L_{\infty} \times \frac{3}{3 + \frac{M}{K}}$$

where M is the natural mortality rate and L_{∞} and K are parameters of the von Bertalanffy growth function (VBGF). A value of $M = 0.3$ was taken from Sow et al. (2011). The growth parameters for the VBGF ($L_{\infty} = 2\ 020$ cm and $K = 0.005$) were calculated from a growth study of *E. aeneus* along the Senegalese coast, using otolith-derived age and corresponding length data collected monthly from January 2010 to December 2010 from the commercial catches of local fisheries (KD unpublished data).

The percentage of mega-spawners in the catch was calculated using the number of old individuals that were longer than L_{opt} plus 10% (Froese 2004). Maximising the number of large individuals in a population can improve reproduction, recruitment and survival (Birkeland and Dayton 2005). The management objective is to implement a fishing strategy that results in no mega-spawners being caught. Mega-spawners should constitute 30–40% of a healthy stock (Froese 2004).

Size spectrum analysis
The size spectrum of catches was analysed in three ways. First, a linear regression of the logarithm of the number of individuals in each length class in each period was calculated for the region of the spectrum where the number of individuals was decreasing. The slopes and intercepts were then compared using ANCOVA. Logarithmic transformation was used to normalise the length distribution and homogenise the variances (Stobberup et al. 2005). Second, the annual average total length was calculated. Third, the percentage of mature individuals, the percentage of fish at optimal length and the percentage of mega-spawners were calculated.

Results

Small-scale and industrial fishery catches of* E. aeneus *(1981–2008)
During the 28 years from 1981 to 2008 most of the catch of *E. aeneus* in Senegalese waters was taken by small-scale fisheries (Figure 2). At the beginning of the time-series (1981–1983), the catches were low, around 1 500 t. A peak was observed for both industrial (less than 1 000 t) and small-scale catches (close to 3 000 t) in 1984–1988. After this period, the catches of the small-scale fisheries declined (linear regression, $r^2 = 0.68$).

For each of the four landing regions, the catches varied in a similar way to the total catch of the small-scale fisheries (Figure 3). The largest catches were in the Cape Verde and Southern Thies areas but recently (since 2005) most of the catches came from the Southern Thies area and were negligible elsewhere. Catches in all landing regions decreased over the 28-year study period (Kolmogorov–Smirnov test, $D = 0.243$, $p = 0.0002$).

At the beginning of the 2000s, an analysis of the fishing methods used by small-scale fisheries indicated that motorised canoes using hooks and lines were the main fishing method, producing 70.5% of catches. Longlines

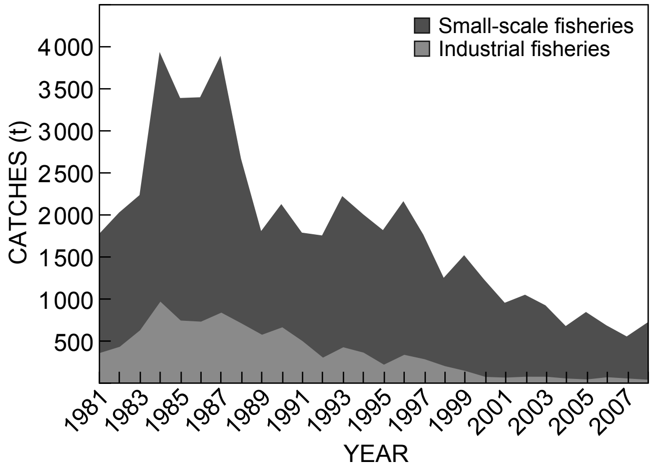

Figure 2: Total catches of *Epinephelus aeneus* by small-scale and industrial fisheries in Senegal between 1981 and 2008

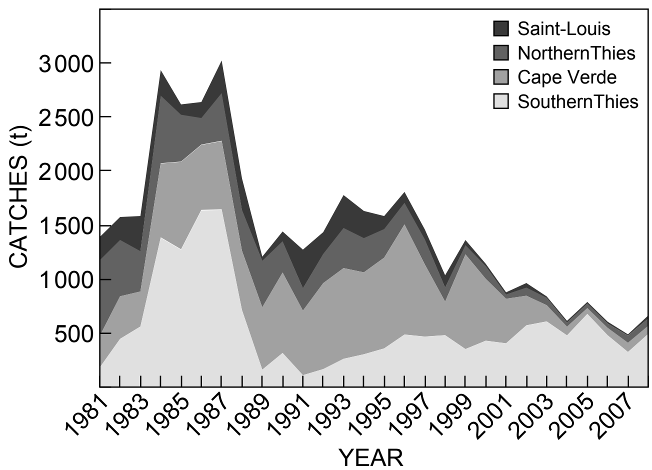

Figure 3: Total catches of *Epinephelus aeneus* by Senegalese small-scale fisheries for each catching area between 1981 and 2008

captured a further 15% and other types of fishing gear (set gillnet, seine, driftnet, cephalopod line, non-motorised canoe hook and line, trolling, underwater fishing) contributed 14% to the total catch.

Length at maturity and length at 90–100% maturity

Of 97 sexed individuals in 2010, 21 mature females and five mature males were encountered. The size range of mature females was 45–75 cm and that of mature males 50–75 cm. The lengths at maturity (L_{50}) calculated for females and males were 49 and 55 cm respectively (Figure 4). The logistic function for females was used to estimate an L_{90-100} of 63 cm.

Sex ratio

The bulk of the catch sampled in 2010 consisted of females (Figure 5a), which was the case throughout the year. Sex was undetermined within the smallest size classes (10–15 cm). Size distributions of females (20–90 cm) and males (25–95 cm) were similar, and the mean size of females (55 cm) did not differ significantly from that of males (60 cm) (ANCOVA, $p = 0.052$). The minimum size was 22 and 24 cm for females and males respectively, and all individuals >95 cm TL were males.

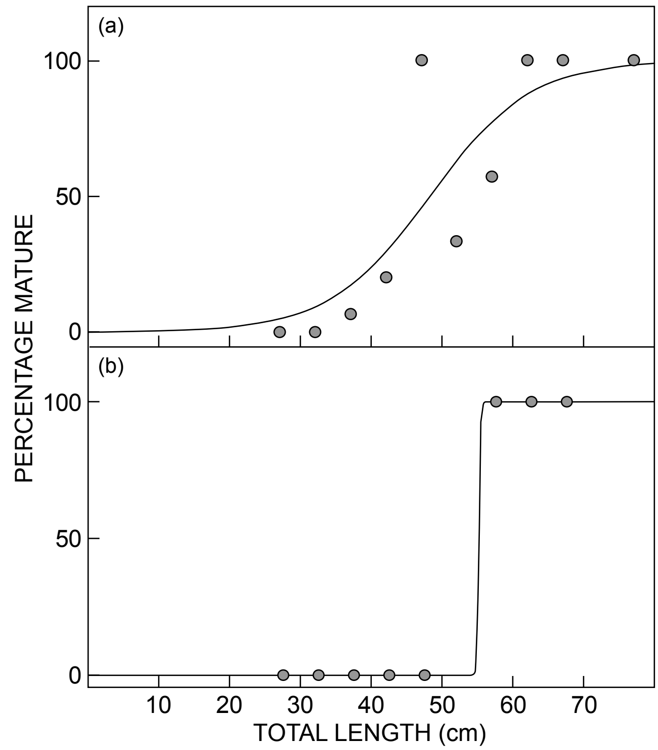

Figure 4: Logistic function estimated from the percentage of mature individuals per size class for (a) females and (b) males of *Epinephelus aeneus* in the Cape Verde Peninsula during the 2010 reproductive season

Size spectrum from 1974 to 2010

Size frequency distributions observed for each of the four periods (1974–1983, 1984–1993, 1994–2003 and 2004–2010) were bimodal with the same two peaks at approximately 50 and 80 cm, although the peaks were less marked for the two most recent periods (Figure 5b). The total number of fish measured per size class for the whole period declined significantly over the four periods, dropping from about 3 000 individuals for the larger of the modal size classes between 1974 and 1993 to 200 individuals for the period 2004–2010 (linear regression $r^2 = 0.40$). However, the length range landed along the Senegalese coast remained unchanged between 1974 and 2010 (ANOVA, $p = 0.058$). L_{opt} was 96 cm and, applying a 10% variance, the optimal length range was between 86.4 and 105.6 cm.

Linear regressions of the logarithm of the number of individuals against length at the upper end of the distribution varied between periods (Figure 6). The slopes were identical for the periods 1974–1983 and 1984–1993 (ANCOVA, $p = 0.071$) but differed from those for the remaining two periods. The intercept decreased with each decade (ANCOVA, $p = 0.0003$): it was equal to 28.97 for the period 1974–1983 and dropped to 18.28 between 2004 and

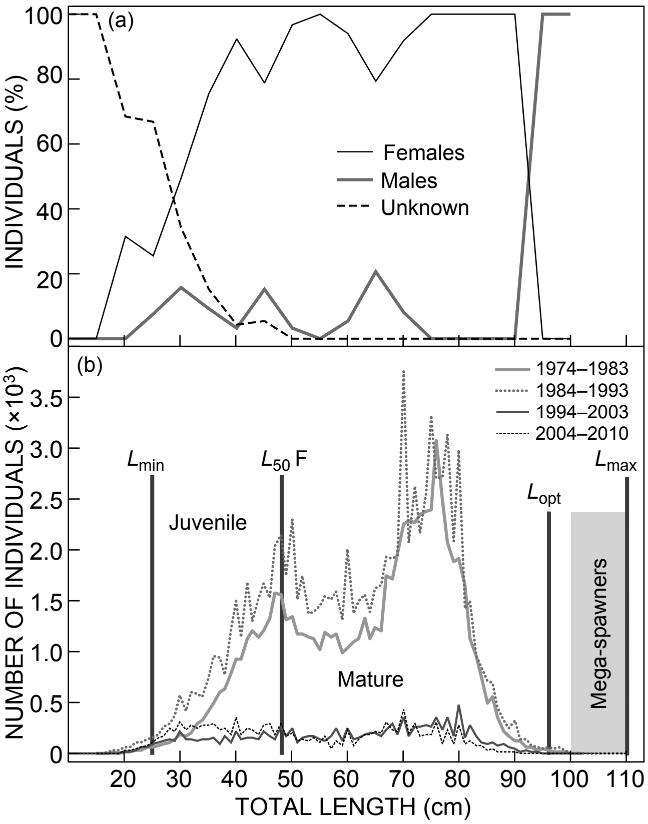

Figure 5: (a) Percentage of individuals of *Epinephelus aeneus* of each sex in Senegalese waters, in relation to length; (b) length frequencies of *E. aeneus* in small-scale fisheries for each 10-year period between 1974 and 2010. L_{min} = minimum size set by the Senegalese national code of fishing; L_{50}F = female length at maturity; L_{opt} = length associated with maximum sustainable yield; L_{max} = maximum size in the catch

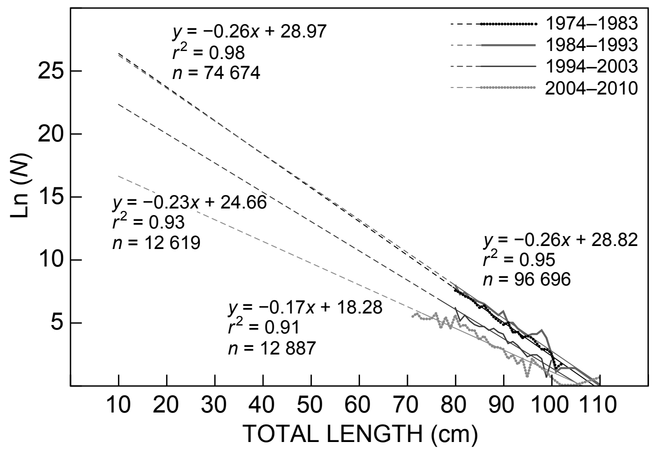

Figure 6: Linear regressions fitted to the log of the number of the larger size individuals against size classes of *Epinephelus aeneus* caught in small-scale fisheries in Senegal. Observed data shown are means per 1 cm size class. N = number of individuals for each size class; n = number of individuals measured

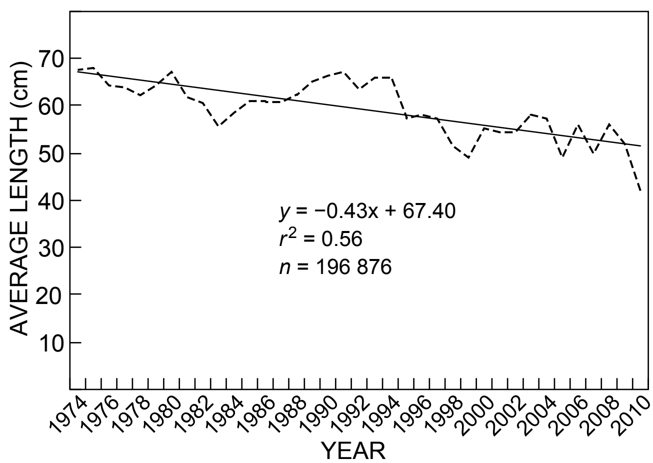

Figure 7: Average length (TL) of *Epinephelus aeneus* caught in small-scale fisheries in Senegal between 1974 and 2010

2010. The regressions indicated that numbers of individuals within the modal size classes decreased over time.

The average length of landed *E. aeneus* decreased significantly (linear regression, $r^2 = 0.66$), from 68 cm in 1974 to 42 cm in 2010 (Figure 7). The decrease in average length indicated a decline in the relative abundance of the larger individuals within the stock.

Change in the annual percentage indicators

Sixty percent of individuals caught overall were mature, with the highest proportion in 1974 (90%) and the lowest in 2010 (29%). A very small percentage of individuals (average for the whole period is close to 2%) reached L_{opt}, with the highest proportion in 1993 (6%). The trend associated with L_{opt} showed two phases: an increase from 1974 (0%) to 1993 (6%), followed by a marked decrease (Figure 8). The percentage of mega-spawners in the catch was very low (0.18%).

Discussion

Catches

Following Senegal's independence in 1960, Lourdelet (1966) highlighted the importance of the handline fishery targeting *E. aeneus* between Dakar and Saint-Louis. In the 1980s, despite its high price, *E. aeneus* was sold mainly locally, representing about 20% of the urban fish market (Chaboud and Kébé 1989). Between 1984 and 1987, *E. aeneus* catches by small-scale fisheries were very high, at around 3 000 t annually (Thiao et al. 2012, present study). These catches were above the maximum sustainable yield (MSY), which was evaluated at 3 630 t (Barry et al. 2004). During this period, the number of individuals that reached L_{opt} was high. Since then, catches have dropped, reaching their lowest level (500 t) in 2008. The studies of the FAO working group in 2006 also reported a decreasing trend in catches of white grouper during the period 2002–2006 (FAO 2006). The threat to *E. aeneus* comes from excessive fishing pressure during the past 20 years, the species being highly prized in the West African market and targeted by both small-scale and industrial fisheries (Heemstra and

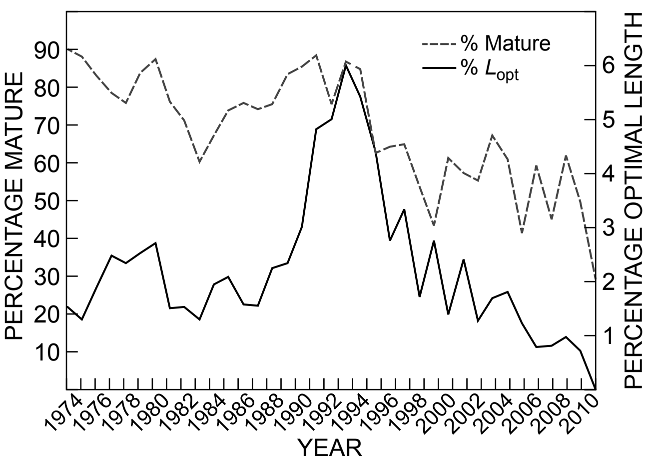

Figure 8: Percentages of mature *Epinephelus aeneus* and those at optimal length in the small-scale fisheries catch in Senegal between 1974 and 2010

Randall 1993, Thiao et al. 2012). Exploitation by small-scale fisheries is the main threat (Thiao et al. 2012, present study), due largely to the shallow-water habitat where the species is usually found. Until the early 1990s, industrial fisheries caught only relatively small quantities (about 400 t in 1981).

In the Ivory Coast area, Kouassi et al. (2010) showed that the exploitation level (E) of *E. aeneus* was 0.72, which was well above the maximum exploitation level (E_{max} = 0.42). This indicated that fishing pressure was very high and the stock in the Ivory Coast area seemed also to be overexploited.

Length at maturity

Female *E. aeneus* in Senegal reached sexual maturity at 49 cm TL, a smaller size than the males (55 cm). In Tunisia, the length at maturity (sexes combined) was 46 cm TL (Bruslé 1982) and 40 cm SL (Bouain 1984). Since the rate of development (maturity stage, maturity size) is generally found to increase when temperatures become higher (Jobling 1995), this may explain the larger size in Senegalese waters. Temperatures in Senegalese coastal waters (a mean of 24 °C) are higher than those of Tunisian waters (13 °C) (Azaza and Kraïem 2007). Similarly, higher salinities in the Mediterranean (38.5) than in the Atlantic (34.7) (Azaza and Kraïem 2007) may explain the lower size at maturity off Tunisia. Conversely, however, higher exploitation rates in Senegalese waters might have been expected to lead to a reduced size at maturity but do not appear to have done so. A caveat is that the available sample size of mature animals in the present study was small (n = 26 individuals). Also, sizes at maturity were calculated for fish sampled in 2010 and the results were then assumed to apply to the entire period 1974–2010, which does not allow for possible density-dependent changes over time. In Senegal the minimum legal size at capture is 24 cm (Sow et al. 2011), which is considerably smaller than L_{50}. Hence the fish caught in Senegalese waters are mainly small and immature. In addition, $L_{90–100}$ in this study (63 cm) was estimated previously by Sow et al. (2011) to be 46 cm. It is therefore recommended that the legal minimum size be reviewed urgently.

Sex ratio

The sex of individuals ≤15 cm was not determined. Males and females were found in the same size range (20–95 cm) but males were less abundant than females. The similar size distribution and mean size of males and females suggested that *E. aeneus* in Senegalese waters is functionally gonochoric (i.e. the sexes are separate). Several studies, however, have contributed to the belief that all groupers are hermaphrodites (Borquez et al. 1988, Heemstra and Randall 1993). As with other marine fishes, sex change in groupers is influenced by social factors (Mackie 2003, Liu and Sadovy 2004) and protogyny might be expected in species or populations where large males are able to monopolise mating with females and exclude smaller males (Warner 1984). The fact that the largest individuals in the present study were male means that this possibility cannot be ruled out.

Size spectrum

Froese (2004) used three simple indicators (percentages of mature fish, fish of optimal length and mega-spawners in the catch) to show that the stock of *E. aeneus* was overexploited in Senegal. The percentage of mature fish decreased from almost 85% at the beginning of the 1990s to approximately 43% in 1999. Over the same period, the percentage of fish ≥ L_{opt} decreased from 5% to less than 0.2%. In the present study, most of the catch consisted of fish below L_{opt} (96 cm), as was also reported by Laurans et al. (2004) and Sow et al. (2011). The legal minimum size is 24 cm, which is half the length at maturity and which results in increased potential for overexploitation. Ideally, fish should be caught at a size greater than L_{opt}, but this does not seem feasible in the Senegalese context where, in some years, none of the catch was as large as L_{opt}. The percentage of mega-spawners (0.18%) was also much lower than the minimum required for sustainable fishing (30–40%). These observations confirm that the Senegalese stock of *E. aeneus* is severely overexploited.

The extent of overexploitation is alarming, particularly as the data presented do not take account of illegal fishing and there were no data from industrial fisheries because fishermen do not allow the catch to be handled. The scarcity of mega-spawners in catches is certainly the biggest threat to stock conservation because there is increasing evidence that old fish play an important role in the survival of a population. This is because (1) large females are much more fecund — the number of eggs increasing exponentially with length and weight in most species — and their eggs tend to be larger, thus increasing the potential survival of the larvae (Solemdal 1997, Trippel 1998); (2) reaching old age is usually a sign of overall individual fitness and thus these mega-spawners are reservoirs and distributors of desirable genes; and (3) high longevity and a prolonged reproductive phase can be viewed as natural safeguards against subsequent recruitment failure (Craig 1985, Beverton 1987). In other words, the percentage of mega-spawners in a stock can be viewed as a simple proxy for resilience against random events.

The slopes of the size spectra were similar during the two first periods (1974–1983 and 1984–1993) but decreased significantly between 1994 and 2003. Recently

(2004–2010), there has been a more marked decrease due to intense exploitation. The slope of the linear portion of the length distribution provides a direct index of the state of the fishery (Rice and Gislason 1996, Gislason and Rice 1998).

Conclusion

Indices of population status that were derived from the size structure of the catch of *E. aeneus* were assessed over a time period of nearly 40 years. A decrease in catch over time, coupled with information provided by the indices, indicated clearly the effect of fishing pressure on the stock. These results highlighted the need for better management of the species. Marine protected areas and/or seasonal protection during the reproductive season could be used to protect spawning aggregations. These measures could be used together effectively or combined with sales bans to aid enforcement. Marine protected areas could also be used to protect deep-water habitats. Given the increasing predominance of juvenile *E. aeneus* in landings, it would also be advisable to revise the current legal minimum size to 50 cm, the approximate size at maturity.

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