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## Structure and dynamics of demersal fish assemblages over three decades (1985–2012) of increasing fishing pressure in Guinea

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In a context of growing fishing pressures and recommendations for an ecosystem approach to fisheries, there is a need to monitor changes in fish communities over time. In this study, we analysed data from scientific trawl surveys carried out on the continental shelf off Guinea between 1985 and 2012. We performed factorial analyses and calculated biodiversity indices to characterise the changes in the structure and composition of fish communities that occurred over the 28-year period in this area, particularly given intensive fishing activities. We show that, over the study period, fish communities on the Guinean shelf were structured primarily according to spatial factors, with temporal changes being less pronounced than expected. However, a temporal analysis of biodiversity indices and species dominance showed that the intensification of fishing had significant effects on the general ecological features of the fish assemblages under study. There was a decrease in fish density and in mean trophic level. In addition, there were changes in species dominance, whereby large, slow-growing species with high commercial value were gradually replaced by smaller, fast-growing species of lesser commercial interest. These results from field observations are in line with some conclusions from previous modelling studies in the same geographical area, and provide further support for the hypothesis of a progressive 'ecosystem effect of fishing' occurring in Guinean waters.

Keywords: biodiversity, ecosystem indicators, fishing impact, historical data, marine ecology, trawling surveys

#### Introduction

In the light of growing fishing pressure, assessing the state of harvested marine ecosystems and monitoring their changes over time are currently of utmost importance (Garcia 2004; Shin et al. 2010a). Despite awareness of this urgency and the recognised necessity of a so-called 'ecosystem approach to fisheries' (UN 1992), the current management of living marine resources, including fish populations targeted by fisheries, continues to be based primarily on monospecific analyses (Pitcher and Cheung 2013). However, there is a primary need for an overall and multispecific understanding of the dynamics of the community to which fished populations belong. On a basic level, this type of analysis is the logical first step towards understanding the impact of fishing on the marine ecosystem as a whole. On a practical level, a multispecific approach is particularly appropriate for assessing the impact of fisheries and ecosystem health, because there are abundant historical data on fish, one of the most harvested and studied groups of marine fauna. Therefore, examining fish community structure and dynamics is a suitable and generalisable approach for stock assessment working groups that are periodically set up to support decision-management in many fisheries worldwide. Hence the multispecific fish community-based analysis that we propose here can effectively complement the monospecific stock assessment modelling approach, which is often the only approach routinely carried out in the scientific assessment of many fisheries, particularly those in developing countries (Jouffre et al. 2004a; Pitcher and Cheung 2013).

In this context, the Guinean continental shelf represents an interesting case study for analysing the impact of fishing on the marine ecosystem: (i) the current marine fisheries operating there are highly developed, with large and diversified catches and varied fishing techniques, both artisanal and industrial; and (ii) there are abundant scientific data on bottom trawling in this area and they cover a relatively long period (i.e. from surveys carried out using the same protocol more or less annually for more than 30 years).

The dataset we analysed contains a large number of taxonomic groups and offers a particularly rich source of information for analysing the impact of fishing on the functional structure and multispecific composition of fish communities. Furthermore, the dataset covers a long period with contrasting patterns in fishing intensity; although

fisheries resources on the Guinean continental shelf have been exploited for decades, the fishing sector only began to develop in an industrial sense in this area in the 1980s (Domain et al. 1999). Off Guinea, and in particular in its coastal zone where demersal fish communities are located (Domain et al. 1999), a growing number of stocks have transitioned from low fishing pressure to overfished status within a short period of time (Sidibé 2003; Gascuel et al. 2009; Belhabib et al. 2012). Moreover, illegal, unreported and unregulated (IUU) fishing affects several developing countries, including Guinea (MRAG-DFID 2005; Agnew et al. 2009), with more than 60% of Guinean industrial fishing vessels estimated to practise IUU fishing in 2001 (Boto et al. 2009). According to data collected by the Food and Agriculture Organisation (FAO), commercial catches from the Guinean exclusive economic zone (EEZ) nearly doubled during the period 1993-2003 (FAO 2007), following the intense development of artisanal and industrial boat fleets operating in Guinea. A revised estimate of Guinean fisheries statistics indicates landings of 47 509 tonnes (t) in 1993 compared with 223 024 t in 2010, an increase of more than 300% (Belhabib et al. 2012). Correspondingly, a national survey of the artisanal fishery fleet indicated that the number of fishing canoes almost doubled, from 3 636 in 2001 (CNSHB 2002) to 6 025 in 2009 (ONP/FAO 2009). This rapid and continuous growth in fisheries over the past three decades is likely to have modified the functional and taxonomic structure of fish communities in the area. However, most studies conducted to date on fisheries resources in Guinea have focused on strictly monospecific approaches (e.g. Sidibé et al. 2004).

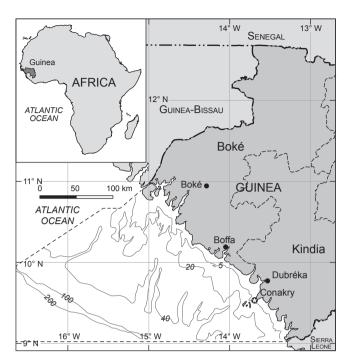
In this study we used complementary datasets: scientific trawl surveys (species abundance data) and artisanal and industrial fisheries data (to quantify fishing pressure) to analyse the multispecific dynamics of demersal fish communities in Guinea over the past three decades. We aimed to describe the major spatio-temporal patterns of these communities and monitor some taxonomic and/or functional indicators over time to reveal any potential impact that fishing might have had on them.

#### Material and methods

#### Geographical setting

The study focuses on the ecosystem of the Guinean continental shelf, located on the south-western border of the West African Craton. Guinea, a country on the West African coast, has a particularly large maritime domain (Domain et al. 1999; Sidibé et al. 2004), with a surface area of about 43 000 km² (Pezennec 1999) (Figure 1). The location and its environment (i.e. the largest continental shelf of the central eastern Atlantic, dense coastal hydrographic network, muddy and sandy mud seabed sediments, mature mangroves) support a diverse and abundant coastal marine fauna (Pezennec 1999).

The local climate oscillates between a cold, dry season from November to April (characterised by upwelling in the northwest) and a hot, wet season from May to October (characterised by high precipitation). There are large interannual fluctuations in precipitation of up to 1 m (Pezennec 1999), which might affect the biological productivity of the



**Figure 1:** Geographical setting and bathymetry (m) of the Guinean exclusive economic zone (EEZ), delimited by a polygon inscribed between 13°30′ W and 17°00′ W and 9°03′ N and 10°50′ N. The Guinean maritime border with Guinea-Bissau to the north is perpendicular to the coastline, whereas the Sierra Leone border follows the line of latitude

environment and the availability of exploitable fish owing to the importance of precipitation in influencing the high terrigenous inputs that contribute to the coastal marine environment in Guinea (Domain 1980; Sidibé 2003).

The coastal fish community is represented by two relatively different ecological communities (Domain et al. 1999; Sidibé 2003):

- the Sciaenidae community, dominated by members of the Sciaenidae, which has a nearshore distribution. This community lives in warm, brackish waters down to 15 m depth. Its high biomass is associated with the local abundance of muddy sediments, giving rise to ecologically rich seabeds; and
- the Sparidae community, which has an offshore distribution ranging from 20 to 60 m depth. The species in this community frequent colder, saltier waters, and their densities are low.

Two types of fishing methods coexist in this ecosystem. Traditional, artisanal fishing is practised from pirogues (wooden canoes), sometimes equipped with outboard motors (<50% of vessels have motors), with diverse fishing gear. This fishery targets the nearshore Sciaenidae community. Industrial fisheries use trawl gear and primarily cover offshore areas, although they can also target nearshore fish (Domain et al. 1999).

#### Data

We used two sources of data: species counts from scientific trawl surveys carried out on the continental shelf, and statistics from commercial catches and fishing effort recorded in the statistical bulletins of the Boussoura National Centre of Fisheries Sciences (CNSHB) available at www.cnshb.org.

#### Scientific trawl surveys

In all, data from 33 trawl surveys targeting demersal fish were used in this study, covering the period 1985–2012 (Appendix 1). No surveys were conducted in 1996, 1999, 2000, 2001, 2003, 2010 and 2011. For each survey, there are detailed data on the catches from multiple 30-min trawl hauls, or stations, carried out on the continental shelf (4–100 m depth and sometimes beyond) according to a standard protocol. Each haul is characterised by its coordinates (longitude and latitude), date, hydrological characteristics (temperature, salinity), the number of fish caught and the biomass of each sampled species. We chose to express abundance in terms of biomass density (kg km<sup>-2</sup>).

Only demersal fish species were considered, with the habitat as listed in www.fishbase.org. Pelagic fish caught during deployment or recovery of demersal trawls were not considered, nor were other taxonomic groups (non-fish species). The 50 most-frequently encountered demersal species (Appendix 2), representing 71% of the total fish biomass (pelagic and demersal species) in 1985–2012 (see full list of species in Appendix 3), were included in the analyses (hereafter referred to as the 'demersal fish community').

#### Fisheries statistics

The fisheries statistics used here to quantify the effects of fishing pressure include fishing effort and annual catches of both artisanal and industrial fleets for the period 1985–2012.

For the 18-year period 1995–2012, data on fishing effort were extracted from CNSHB surveys and comprise, in particular, the number of active pirogues/vessels on the Guinean continental shelf. For artisanal fishing, effort information was based on an exhaustive census of active pirogues. For industrial fishing, effort information was based on the number of registered commercial fishing vessels. The vessels were considered together as a fleet, with the exception of tuna-fishing vessels that spend little time in Guinean waters. For the earlier period 1985–1994, we used the nominal fishing effort as calculated by Gascuel et al. (2009) for both fisheries. The estimated values were interpolated from an initial value in 1985 that was determined empirically (assuming 1 000 pirogues in 1985).

For the period 1995–2012, estimates of annual catches both in artisanal and industrial fisheries were extracted from the CNSHB databases. For the period 1985–1994 we used estimates provided in Gascuel et al. (2009), where catches were derived from data on mean yield per vessel (industrial fishery) and mean yield per pirogue (artisanal fishery).

#### Data analysis

Changes occurring in the demersal fish communities on the Guinean continental shelf were analysed using factorial analyses and biodiversity indices. These methods are widely used in ecosystem approaches in fisheries studies to detect the impact of fishing on harvested marine ecosystems (e.g. Jouffre et al. 2004b, 2004c; Cury and Christensen 2005; Shin et al. 2010a, 2010b).

#### Factorial analyses

A principal component analysis (PCA) was used to obtain a summary of the organisation of demersal fish communities, and ascending hierarchical clustering (AHC) was used to classify samples using 'average linkage' as the criterion of aggregation based on a matrix of Euclidian distances of the individual PCA coordinates. This approach helps to facilitate the interpretation of PCA results and has already been applied to assess the ecology of fish communities in Portugal (Matono et al. 2012) and to model the spatiotemporal distribution of fish communities off West African coasts (Konan et al. 2006). PCA was applied to a 2 880 × 50 (samples  $\times$  species) matrix of  $\log(x + 1)$ -transformed fish abundances. This first analysis formed sample groups based both on their species abundance and composition. The typology of samples thus obtained (clusters) was represented on the same factorial plane as spatial (bathymetry, sediment characteristics) and temporal variables (year) to attempt to determine the major factors that structure fish assemblages on the Guinean continental shelf.

Another PCA was then used to characterise the major changes that occurred with respect to the dominant species. This PCA was carried out on the 20  $\times$  21-dominance matrix, constructed from the 20 most-abundant species during the 21-year period (1985–2012), and in which species are represented by their percentage of total biomass in the survey year.

All analyses were carried out using R 3.0.2 (R Development Core Team 2013).

#### **Biodiversity indices**

Five indices were calculated from the scientific trawl survey data: mean biomass density  $(D_m)$ , mean trophic level  $(TL_m)$ , the proportion of predator fish  $(P_{pred})$ , species richness (S), and Simpson's evenness index of diversity  $(E_{1-D})$  (Simpson 1949). Mean values of these indices were calculated for each year based on the  $50 \times 21$  (fish taxon  $\times$  year) matrix of mean density. Annual variations of these indices were compared using analysis of variance (ANOVA).

Mean biomass density is an index that is used frequently in ecology and provides a quantitative description of communities (Grall and Coic 2006). Mean annual biomass density (kg km<sup>-2</sup>) was calculated as follows:

$$D_m = \frac{1}{X \times A} \sum_{i=1}^{S} \frac{C}{N}$$

where C is the total catch per species (kg), N is the total number of sampled stations, A is the trawled surface per station (km²) and X is the proportion of fish caught in the net or trawl, i.e. the catchability coefficient (for calculating  $D_m$ , X was estimated at 0.5, which corresponds to a mean value used in previous studies on demersal fish and the type of fishing gear used in Guinea [see Domain et al. 1999]).

The mean trophic level  $(TL_m)$  is an index used to characterise the mean position of an individual of the study community (here, demersal fish) within the food chain of the study ecosystem. It is frequently used in marine ecology and, in particular, for monitoring fishery resources and heavily fished ecosystems. It is assumed to decrease

under the effect of fishing (Rochet and Rice 2005; Shin et al. 2010b). The mean trophic level was calculated for each year as follows:

$$\mathsf{TL}_{m} = \sum_{i=1}^{s} \frac{\mathsf{TL}_{\mathsf{sp.}\,i} \times D_{\mathsf{sp.}\,i}}{D_{\mathsf{total}}}$$

where  $\mathsf{TL}_{\mathsf{sp.}\,i}$  is the baseline trophic level for species i documented in www.fishbase.org,  $D_{\mathsf{sp.}\,i}$  is the density of species i and  $D_{\mathsf{total}}$  is total density.

The proportion of predator fish  $(P_{pred})$  is the ratio between the density of predator fish  $(D_{pred})$  and total fish density  $(D_{total})$ :

$$P_{\text{pred}} = \frac{D_{\text{pred}}}{D_{\text{total}}}$$

In this calculation, a species is considered a predator if it is referenced at a trophic level greater than or equal to  $3.25^{\circ}$  on www.fishbase.org. Although the index  $P_{\text{pred}}$  is conceptually strongly linked to  $TL_m$ , it was useful for this study, because it places an emphasis on the most sensitive part of fished communities. Therefore, this index is considered to be more relevant than  $TL_m$  for purposes of biodiversity conservation and preservation of the equilibrium in ecosystems. Both indices are often used in parallel in international monitoring programmes for marine ecosystems (www.indiseas.org).

Finally, changes in biodiversity were studied with two complementary indices widely used in ecology: species richness (S), which counts the number of species present in a given community (or a given sample), and Simpson's evenness index of diversity ( $E_{1-D}$ ), which estimates the evenness of abundance among the species in the community (Domalain et al. 2004; Grall and Coic 2006). Species richness is the number of species observed annually over all samples (trawl hauls), among the 50 fish species selected in this study. Simpson's evenness index expresses the dominance of one or more species when it approaches zero, or the evenness of the number of individuals among species when it approaches 1. It is calculated as follows:

$$E_{1-D} = \frac{1-D}{\left(1-\frac{1}{S}\right)}$$

where (1 - D) represents Simpson's diversity index (Simpson 1949). Simpson's diversity index is expressed as:

$$1-D=1-\left(\sum_{j=1}^{s}\left(P_{j}^{2}\right)\right)$$

where  $P_i$  is the relative abundance of species i in the sample.

#### Fishing pressure indices

Two indicators were used to characterise the fishing pressure that affects the fish in the community and to facilitate interpretation of changes in the biodiversity indices: nominal fishing effort (*F*) and a production index (PI) (Caddy et al. 1995). They were calculated from official CNSHB statistics for each year from 1985 to 2012. Nominal fishing effort expresses the total number of active pirogues (for artisanal fishing) or active vessels (for industrial fishing), i.e.

F(artisanal fishing) = number of pirogues F(industrial fishing) = number of industrial vessels

The PI expresses the production per surface area (Caddy et al. 1995) and is estimated using the annual value of catches divided by the fishing surface area. This index helps to interpret other results that pertain to the fish community. The fishing surface area was estimated at 15 000 km² for artisanal fishing and 29 000 km² for industrial fishing. The PI is a measure of what is extracted from the fish community by fishing activities. The larger the index, the more heavily the area is fished. It is expressed as follows:

$$PI = \frac{Total \ catch}{Fished \ area}$$

where 'Total catch' (kg) is the sum of all landings and discards.

#### Results

#### Characteristics of the whole fish community

Once the PCA was computed, we performed a clustering analysis (AHC) on the output of this analysis (i.e. coordinates of stations on the two first PCA axes) to better identify groups of stations. This clustering analysis identified four groups of stations (Figure 2). The species (Figure 3a) and samples (stations) (Figure 3b-d) projected on the first two PCA axes were clearly structured, with an inverted 'V' shape, characteristic of a Guttmann effect (Flament and Milland 2005) or an arch effect, which is generally associated with a gradient (Figure 3a). In other words, at the scale of the complete multiyear dataset, samples - positioned according to their species abundance and composition - were structured around a continuum with two extremes and all the intermediate situations. Figure 3b-d assist in interpreting this gradient. The centres of the four AHC groups were projected on the cloud of sample points (Figure 3b). Projections of bathymetric classes and seabed sediment showed similar patterns (Figure 3c, d, respectively). This observed gradient reflects high spatial structure (Figure 3a-d). Thus, samples taken from the shallowest depths with muddy seabed sediments were associated with coastal taxa (estuarine and nearshore Sciaenidae), which were primarily caught there. In the centre of the plots in Figure 3 are species associated with intermediate depths and fine-sand sediment. At the other end of the plots are the deepest samples, corresponding to coarse-sand sediments and Sparidae species that tend to occur offshore.

<sup>&</sup>lt;sup>1</sup>This value is the same as that used in the IndiSeas project (www.indiseas. org) as well as in the AWA (ecosystem Approach to the management of fisheries and the marine environment in West African waters) project in West Africa (http://www.spcsrp.org/AWA): its threshold is close to three and it excludes *Sardinella* spp. from the predator group, because they are generally described as forage species in the literature

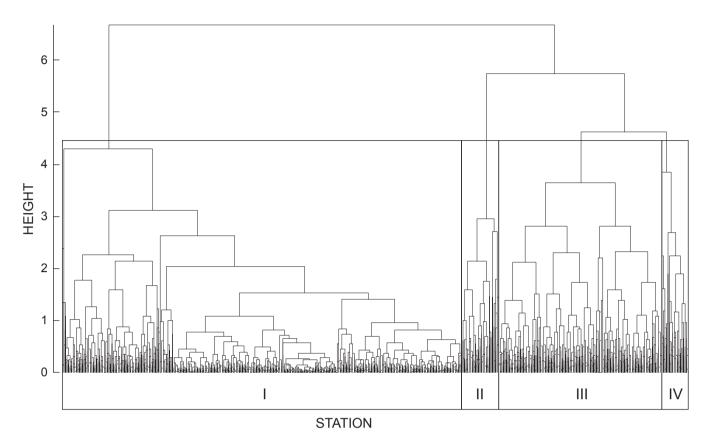


Figure 2: Ascending hierarchical classification (average linkage) of survey samples based on individual PCA coordinates of the first two PCA axes (Euclidean distance matrix). The four clusters formed a priori are shown on the x-axis

A temporal dimension can be added to this analysis (Figure 4) by projecting the cloud of sample points (as seen in Figure 3b-d) separately for each year (subclouds, with each panel corresponding to the samples from a given survey year). In each year, the same inverted-V pattern occurred, indicating that the gradient of species was expressed each year. Only 1994, and, more recently, 2007-2009 and 2012, were different and showed inverted-V patterns with truncated branches or reduced to only a few samples. In most cases, the global structure shown in Figure 3a was repeated clearly within a single survey year. Furthermore, projecting the centres of gravity of each year on the two-dimensional plot of all sample points did not show any coherent chronological pattern (Figure 3e). In particular, survey years were not positioned chronologically along the general inverted-V pattern. This absence of a temporal pattern confirms that the above-described gradient was primarily spatial in nature, rather than temporal.

#### Temporal changes in biodiversity indices

There was an overall decrease in annual mean density over time (Figure 5), with the ANOVA analysis showing a significant year effect (p < 0.001,  $r^2 = 0.5674$ ). Mean density decreased by more than 50% from 11 428 kg km<sup>-2</sup> in 1985 to only 4 261 kg km<sup>-2</sup> in 2012, with lowest densities in 1993, 2007 and 2008. A sharp drop followed the increase in fishing activities in 1985.

Temporal changes in mean biomass density did not reveal information about changes in relative species rank. Figure 6 illustrates the PCA on the dataset of the 20 dominant species (in terms of biomass), with the projection of species and years on the two-dimensional plot. The two principal axes account for 56% of the total variance. The first axis (42% of the variance) separates large nearshore species in the Sciaenidae community (Pseudotolithus elongatus, Pseudotolithus senegallus, Pseudotolithus senegalensis, Pentanemus quinquarius, Pomadasys jubelini, Arius latiscutatus, Carlarius heudelotti, Drepane africana) from large offshore species found in deeper waters (Pagellus bellottii, Pagrus caeruleostictus, Pseudupeneus prayensis) (Figure 6a). The second axis (14% of total variance) separates flatfish (Cynoglossus senegalensis, Trichiurus lepturus) from a species not targeted by commercial fisheries, Brachydeuterus auritus, a small fish with rapid growth. Figure 6b distinguishes four groups of years. In the lower right-hand corner is a group consisting of years 1985-1992. On the left, another group is formed by years 1993, 1994 and 2005. In the upper part of Figure 6b, a third group is made up of years from the period 1995-2004, with the exception of 2002, and the fourth group is composed of more-recent years (2006-2012) together with 2002. Species turnover mainly affects highly fished nearshore commercial species (P. elongatus, P. senegallus, P. senegalensis) that were replaced after 1992

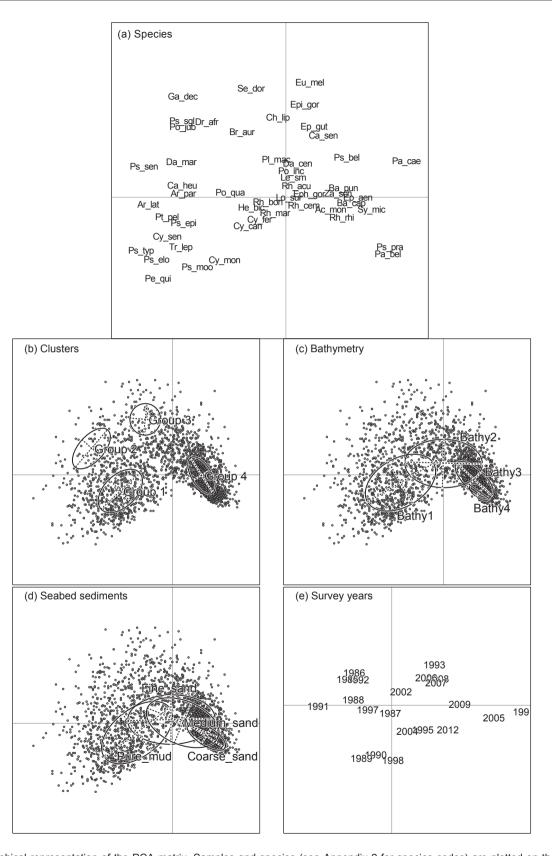


Figure 3: Graphical representation of the PCA matrix. Samples and species (see Appendix 2 for species codes) are plotted on the first two PCA axes with (a) projection of species; (b) projection of the samples (stations) and of the centres of gravity (inertia) of the four identified clusters of samples; (c) projection of the samples and of the centres of inertia of bathymetric classes (Bathy1 = 4–10 m, Bathy2 = 11–20 m, Bathy3 = 21–30 m, Bathy4 = 31–100 m); (d) projection of the samples and the centres of inertia of seabed sediments: pure\_mud (<63  $\mu$ m), fine\_sand (63–315  $\mu$ m), medium\_sand (315–500  $\mu$ m), coarse\_sand (500–2000  $\mu$ m); and (e) projection of the centres of inertia of survey years

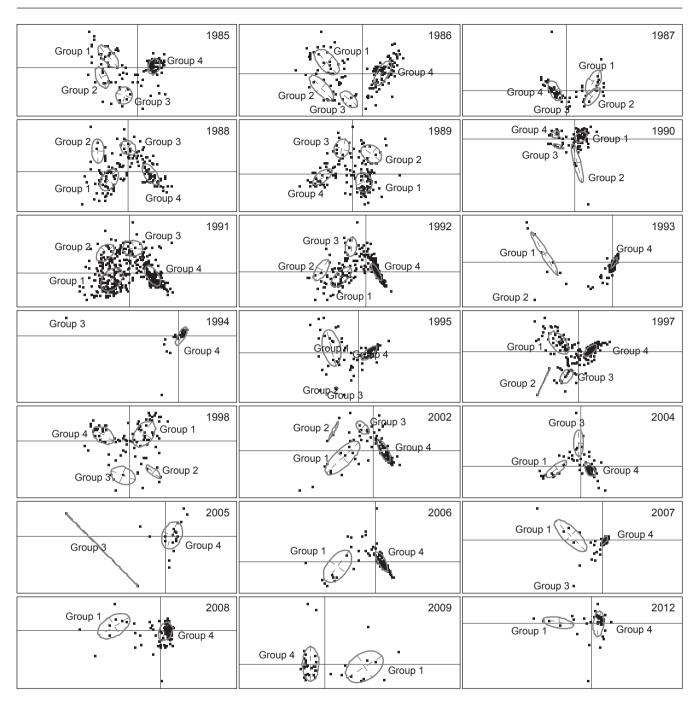


Figure 4: Plot of the samples on the first two PCA axes according to year (i.e. 21 subclouds), in chronological order

first by fisheries-targeted species from deeper waters until 2004 (*P. bellottii*, *P. caeruleostictus*) and, more recently, by a small species with rapid growth (*B. auritus*) that was not targeted initially, but that is increasingly present in catches (Figure 6a).

Most interannual changes observed from 1985 to 2012 on the various biodiversity indices showed decreases over this period (Figure 7). Species richness (Figure 7a) showed an overall decline from 49 species in 1985 to 42 species in 2012, but with some interannual variability that included two dramatic drops, one in 1994, with only 31 species, and one in 2005, with only 36 species. Sampling bias probably

explains these dramatic differences: few coastal stations were sampled in these two years.

Simpson's evenness index (Figure 7b) showed a fluctuating pattern with an overall downward trend, with the exception of the lowest value of 0.81 observed in 1994. There was a significant year-effect, although year accounted for little of the total variance in the dataset (ANOVA, p < 0.05;  $r^2 = 0.181$ ).

The mean trophic level (Figure 7c) showed a slight, but significant (p < 0.01; Kendall test score = -90,  $\tau = -0.429$ ), decrease over the study period, declining from 3.61 in 1985 to 3.55 in 2012, with a minimum value of 3.45 observed

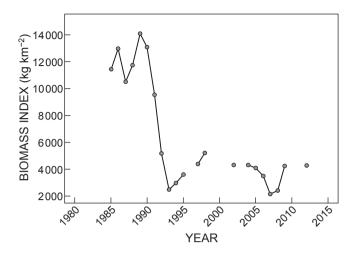
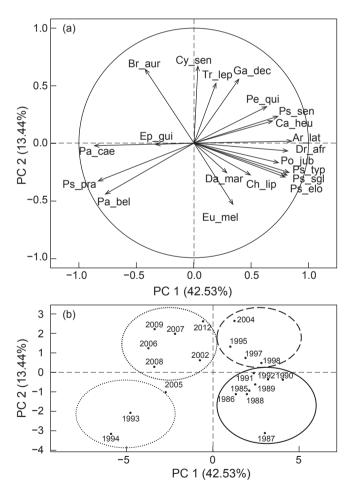


Figure 5: Annual change in the index of demersal fish biomass (gaps represent years when there were no scientific surveys)



**Figure 6:** PCA on species dominance reveals temporal change between 1985 and 2012: (a) variable factor map (species) and (b) individual factor map (years) projection on the first factorial plane (axes 1–2). For species codes see Appendix 2

in 2009. The overall pattern showed two phases, with relative stability in trophic level in the first decade of the study period (1985–1995), followed by a relatively marked decrease. The index for predator fish in catches showed a general decreasing trend over the study period, despite high interannual variability (Figure 7d).

#### Temporal changes in fishing effort and production

An analysis of official fishery statistics showed that, in the artisanal fishery, the number of pirogues increased from 1 000 in 1985 to 3 636 in 2004, 6 025 in 2009 and 7 477 in 2012, a >600% increase in 28 years (Figure 8a). Concurrent with fishing effort, catches in the artisanal fisheries showed a continuous increase, with landings tripling from 30 000 t in 1985 to 90 000 t in 2012 (CNSHB statistical bulletins [data not shown]). In the industrial fisheries, fleet size increased from 48 vessels in 1985 to 166 vessels in the early 2000s and then gradually decreased after 2001, reaching 110 vessels in 2012 (Figure 8b). In parallel, catches increased, growing from 15 000 t in 1985 to more than 50 000 t in 2012 (CNSHB statistical bulletins [data not shown]). The temporal changes in the production index, PI, in both types of fishery over the study period show that the values of the index were three times higher in artisanal fisheries than in their industrial counterparts (Figure 8c, d). Different programmes for developing artisanal fishing have led to an increase in production for this type of fishery (Domain et al. 1999).

#### **Discussion**

#### Selection of 50 species

Only the 50 most-abundant demersal fish species present in the trawl surveys and representative of the whole continental shelf (4–100 m depth) over the period 1985 to 2012 were selected for PCA (hereafter referred to as 'the extensive dataset'<sup>2</sup>). This dataset was used to obtain an overall impression of the structure within the demersal fish community over three decades on the Guinean continental shelf.

Removing rare species from a dataset is a common practice in factorial analysis, because it helps reveal the major structuring factors and avoids random noise (sporadic variation observed in a few surveys) that can mask the effect of these factors. Previous multispecific analyses included similar choices (Jouffre and Domain 1999; Jouffre et al. 2004b), although those authors did not eliminate exactly the same species as in this study. Although they removed rare or unidentified species, they retained cephalopods and crustaceans.

#### Overall community structure - spatial structure

The extensive dataset of 50 species showed that the demersal fish community in Guinea is structured primarily in space, particularly with regard to depth. There was no clear temporal pattern over short or long time-scales. Although

<sup>&</sup>lt;sup>2</sup> As compared with the 'restricted' dataset used for species replacement analysis, which included only the 20 most-abundant species and aggregated data by year, ignoring the detail of individual samples, in contrast to the 'extensive' dataset

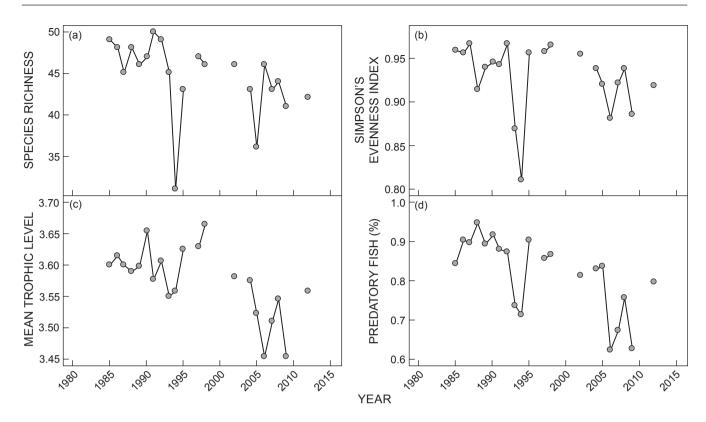


Figure 7: Temporal change in diversity indices of (a) species richness, (b) the Simpson's index of diversity (evenness), (c) mean trophic level and (d) the proportion of predatory fish (gaps represent years when there were no scientific surveys)

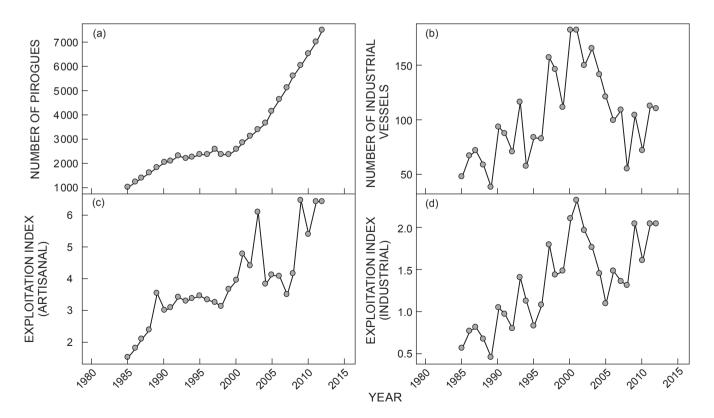


Figure 8: Annual variation in the nominal fishing effort for (a) artisanal fishing and (b) industrial fishing, and in the production index (kg km<sup>-2</sup>) for (c) artisanal and (d) industrial fisheries

our analysis was based on a longer time-series of surveys than previous analyses in the same area (Domain et al. 1999; Jouffre et al. 2004a, 2004b), our results highlight the dominance of spatial structuring and thereby corroborate the patterns observed previously over shorter time-series. Numerous studies from other regions also report similar findings (e.g. Gaertner 1997; Gaertner et al. 1998; Reiss et al. 2010). This type of spatial – and in particular bathymetric – structure seems to be the general case for fish (Jouffre et al. 2004b). In addition, the bathymetric structuring observed here concurs with general ecological gradients or ecological succession theory commonly considered in community ecology (Blondel 1985).

Therefore, despite the increasing fishing pressure over the 28-year study period, the fish assemblages were relatively stable over time, being structured mainly by environmental constraints with respect to spatial location. Although these results confirm multispecific analyses (Jouffre and Domain 1999; Jouffre et al. 2014b) on shorter time-series, they differ markedly from those of monospecific studies (Domain et al. 1999; Sidibé 2003; Gascuel et al. 2009) carried out during the same period, which conclude that fishing has a marked effect on the targeted study species. Below, we show that despite this apparent contradiction, the impact of fishing is also observed in a multispecific approach, but in different indicators.

#### A change in species dominance over time

As explained by Shin et al. (2005), fishing has indirect effects on population and community ecology. On the community scale, reduced predation and reduced inter- and intraspecific competition facilitate access to resources for small fish and improve their survival rate, and possibly their growth rate and time to reproductive maturity (Shin et al. 2005).

In our study, the PCA on species dominance (for the restricted dataset) showed a succession of dominantspecies replacements over time. Large-bodied fish that dominated in the early survey years were replaced gradually by smaller species, in particular B. auritus and T. lepturus. These successions in dominance indicated that species targeted by commercial fishing were replaced by species with low commercial value. Although previously noted, this taxon replacement was not as clear in previous studies based on shorter time-series than those used here (Lobry et al. 2003; Domalain et al. 2004). Overexploitation of large predators (rays and sharks) in Guinea has been reported in several studies (see Belhabib et al. 2012) as the cause of an overall decrease in fish size. This phenomenon of species replacement might have affected all of West Africa in the late 1980s, as indicated, for example, by the increase of Balistes capriscus and Balistes punctatus (Diallo et al. 2009) due to a drastic reduction in the stock of predators (large fish). Thus, in Guinea, increased fishing pressure appears to have led to a decrease in the number and weight of fish that dominated artisanal and industrial fisheries until the beginning of the 2000s, i.e. various grunts (Haemulidae), captain (Polynemidae), catfish (Ariidae) and barracuda (Sphyraenidae), etc. (Diallo et al. 2008). Our results on species replacement also corroborate the ecological interpretation of community dynamics (Frontier and Pichod-Viale 1991) and community dynamics theory (Huston 1995), which postulate that communities characterised by high disturbance and low productivity are dominated by r-selected strategists (small, fast-growing, short-lived species) that can tolerate disturbance. The community on the continental shelf thus appears to be disturbed. In the early years of the study period, there was a relatively stable community, comprising large species that experienced low fishing pressure. Then, with growing pressure, small, short-lived species became dominant. This shift in species has similarities with communities described in the Bay of Biscay by Blanchard (2001).

#### Overall decrease in abundance over time

The change in mean density (all species) showed a substantial overall decrease in the abundance of demersal fish in Guinea over the past three decades. This decrease in abundance is consistent with the results of a multispecies study based on a shorter time-series of yearly trawl surveys (Domain et al. 1999), and with those of a monospecific study involving the most-fished stocks in Guinea, i.e. the species with highest commercial value (Sidibé et al. 2004). Both studies attributed the decrease in abundance to fishing pressure. Similarly, we suggest that fishing is a causative factor in this decline in abundance, based on quantitative indicators that reflect the level and regularity of the intensification of fishing pressure over time.

Our results also corroborate those of Gascuel et al. (2009), based on Ecopath with Ecosim (EWE) modelling, that showed a very clear decrease in the biomass of the main groups of demersal fish between 1985 and 2006. According to this model, the total biomass of demersal fish in the Guinean ecosystem dropped from 500 000 t in 1985 to <200 000 t in 1995, a mean loss of 30 000 t per year (Gascuel et al. 2009). This decrease in density has also been demonstrated in a spatio-temporal simulation on the scale of the West Africa subregion (Christensen et al. 2002), in which the biomass of demersal fish and large pelagic fish in 2000 represented only one-thirteenth of their 1960 values. Our results show a decrease by a factor of three for the 1995–2012 period, in general agreement with results from previous modelling studies.

Trophic level and 'fishing down the marine food web' in Guinea Our results showed a mean decrease of 0.20 points in the trophic level of demersal fish in Guinea for the period 1985-2012 (Figure 7c). This trend supports that of Gascuel et al. (2009), who estimated (using the EWE model) a small, but significant, decrease in the mean trophic level of macroorganisms in the Guinean ecosystem, from 3.35 to 3.27 (not including the benthos or plankton) for the period 1985-2005. A decrease in the abundance of large fish that include apex predators represents a loss of the predation function in the ecosystem. Hence, a decrease in mean trophic level represents a loss of biodiversity, destabilising the ecosystem and making it more sensitive to environmental variability (Gascuel et al. 2009). A similar trend was reported by Shelton and Mangel (2011), who noted that targeting piscivorous species might lessen the pressure on their prey, which could result in an increase in biomass of prey species.

The decrease in trophic level observed in the current study encompassed a greater depth range than that observed by Laurans et al. (2004) in West Africa for the period 1985–2002, who reported a decrease of less than 0.1 for nearshore fish communities (depth <15 m), but no significant decrease at a larger scale (depth <30 m). Our study indicates a more pronounced decrease over the shelf as a whole (from the coast to 100 m depth), expressed particularly in the period following the study by Laurans et al. (2004).

The decrease in the mean trophic level of demersal fish communities in Guinea, although relatively moderate, is therefore confirmed by the current study based on direct observation (i.e. trawling surveys) of the whole shelf area. Furthermore, this result substantiates preliminary conclusions drawn from previous studies based on indirect observations (modelling) or involving only the nearshore area. This decrease appears to have been exacerbated over the past few years. This trend is compatible with the 'fishing down the marine food web' theory (Pauly et al. 1998), and appears to describe the changes on the Guinean continental shelf.

#### Species richness and Simpson's index of evenness

In terms of temporal change, there was a moderate decrease in species richness and Simpson's index of evenness as of 1993 (Figure 7a, b). The decline was amplified in 1994 (see below), but species numbers remained at comparable levels to those observed when fishing began in the 1980s. Hence, biodiversity did not appear to show a clear decreasing trend, or less marked than would be expected with regard to the general decrease in abundance. This pattern concurs with the studies of Lobry et al. (2003) and Domalain et al. (2004), in which the same indicators were used as in our study. These indicators yielded different results to those that combined taxonomic composition with functional characteristics, such as mean trophic level and the percentage of predators (Figure 7c, d). In our study, the decrease in these characteristics was more pronounced, suggesting that they are more sensitive to the effects of fishing.

#### Fishing effort and production index

Artisanal and industrial fisheries have collectively been exerting growing pressure on fish assemblages in Guinea since 1980. This increasing pressure was reported previously (Domain et al. 1999; Sidibé 2003; Gascuel et al. 2009) and attributed to the Guinean policy of promoting fishing as the key to 'sustainable development' (Kaczynski and Fluharty 2002; LPDPA 2009). Hence, the annual change in the production index illustrated here is not unexpected. because the fishing sector in Guinea has been affected by dramatic changes, with rapid and intensive development since deregulation in 1985. The production indices have tripled for both fisheries in less than 30 years. Sidibé (2003) estimated that the fleet of pirogues grew by 49% between 1989 and 1997, with a mean of 44% of pirogues equipped with a motor. Further, Gascuel et al. (2009) suggested that, in addition to the increase in the number of pirogues, an increase in fishing power (i.e. vessel efficiency) should be taken into account when considering the effective fishing effort exerted by artisanal and industrial fleets. Gascuel et al. (2009) estimated a 3% increase in fishing power per year for industrial fishing vessels, leading to a near-doubling of effective fishing effort for the industrial fleet over the period of their study (1985–1995). For the artisanal fleet, the increase in fishing power was estimated at 6.5% per year between 1985 and 1995, a period marked by motorisation for many pirogues, an increase in pirogue size and the development of onboard iceboxes, which allow fishers to go to sea for several days and consequently increase their fishing area. The FAO/COPACE (2009) report, based on the number of fishing days, attests to the large increase in fishing pressure exerted on nearshore species in Guinea over the past few decades.

The increase in fishing pressure should also be considered in the light of international fisheries agreements and the presence of foreign fleets that have been reported in Guinean waters for decades (Anon. 2006). Eastern European countries (Russia, Ukraine, the former Yugoslavia and Poland) and East Asian countries (Korea, Japan and China) accounted for the bulk of foreign industrial catches (68%) in the Guinean EEZ between 1950 and 1980 (Belhabib et al. 2012). After 1980, when Guinea declared its EEZ, foreign industrial catches were dominated by Western European countries, representing 50% of reconstructed catches, and by East Asian countries, accounting for 20% of the total foreign industrial catch from 1981 to 2010 (Belhabib et al. 2012).

#### Conclusions

Our study suggests that fishing pressure exerted on the continental shelf off Guinea over the past three decades has induced some changes in the demersal fish community in this area. Our results complement previous multispecific analyses (Jouffre and Domain 1999; Lobry et al. 2003; Domalain et al. 2004; Jouffre et al. 2004b, 2004c; Laurans et al. 2004), extending them and examining further the resilience of this ecosystem, which appears weaker than suggested by the previous studies that were based on shorter time-series of data. Finally, our results resolve the seeming contradiction among earlier multispecific and monospecific studies (Sidibé 2003; Sidibé et al. 2004), which covered concurrent time-periods, by demonstrating unequivocally that fishing has a pronounced effect on targeted fish resources and their ecosystem. In addition to the effects of fishing, the fish community of the continental shelf is subject to additional anthropogenic stressors (climate change, overpopulation of coastal regions, industrial pollution, etc.). These factors might potentially have an adverse effect on the ecological balance (through changes in migration, growth and reproduction) of this dynamic system. Therefore, as part of the sustainable management of fisheries resources, the governance of marine fishing must be improved by applying a horizontal approach, acquiring better knowledge of species inter-relationships and including a global consideration of coastal areas, at all scales, from local to international (Trouillet et al. 2011).

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**Appendix 1:** Main characteristics of demersal surveys carried out on the continental shelf of Guinea between 1985 and 2012, with each survey represented by eight characters. The first two letters represent the name of the research vessel (AN = RS *Andre Nizery*, AT = RS *Antéa*, G\_AW = RS *Alawame*, GLC = RS *General Lansana Conte*). The first two digits represent the year of the survey and the last two digits denote the month; for surveys 28–33 the order is reversed. The last two letters refer to the type of survey (DM = demersal). The number of stations (Nb\_stations) represents the sampling effort

No.	Survey	Nb_stations	Year	Month	Min. depth (m)	Max. depth (m)
1	AN8503DM	81	1985	3	7	28
2	AN8510DM	80	1985	10	5	22
3	AN8603DM	90	1986	3	5	38
4	AN8610DM	80	1986	10	6	22
5	AN8711DM	79	1987	11	6	25
6	AN8804DM	88	1988	4	5	24
5	AN8809DM	90	1988	9	6	25
8	AN8909DM	75	1989	9	5	24
9	AN8911DM	76	1989	11	5	20
10	AN9004DM	25	1990	4	5	20
11	AN9007DM	65	1990	7	4	24
12	AN9101DM	65	1991	1	4	25
13	AN9103DM	80	1991	3	4	21
14	AN9106DM	80	1991	6	5	27
15	AN9109DM	80	1991	9	5	27
16	AN9111DM	69	1991	11	4	27
17	AN9201DM	80	1992	1	5	27
18	AN9204DM	80	1992	4	5	100
19	AN9210DM	164	1992	10	8	225
20	AN9302DM	159	1993	2	8	190
21	AN9305DM	156	1993	5	10	177
22	AN9405DM	57	1994	5	12	195
23	AN9502DM	96	1995	2	5	30
24	AT9703DM	110	1997	3	6	51
25	AT9709DM	95	1997	9	7	39
26	AT9809DM	91	1998	9	7	41
27	G_AW0209DM	120	2002	9	5	560
28	GLC1204DM	95	2004	12	4	43
29	GLC0406DM	109	2006	4	5	80
30	GLC1107DM	115	2007	11	4	55
31	GLC0308DM	121	2008	3	5	166
32	GLC0409DM	39	2009	4	6	42
33	GLC0112DM	44	2012	1	8	32

**Appendix 2:** List of the 50 demersal fish species selected for multivariate analyses. Each species was assigned a code consisting of the first two or three letters of the generic name followed by the first three letters of the specific name

Number	Species name	Code	Number	Species name	Code
1	Acanthurus monroviae	Ac_mon	26	Pagellus bellottii	Pa_bel
2	Arius latiscutatus	Ar_lat	27	Pagrus caeruleostictus	Pa_cae
3	Arius parkii	Ar_par	28	Pentanemus quinquarius	Pe_qui
4	Balistes capriscus	Ba_cap	29	Plectorhinchus macrolepis	Pl_mac
5	Balistes punctatus	Ba_pun	30	Polydactylus quadrifilis	Po_qua
6	Brachydeuterus auritus	Br_aur	31	Pomadasys incisus	Po_inc
7	Caranx senegallus	Ca_sen	32	Pomadasys jubelini	Po_jub
8	Carlarius heudelotii	Ca_heu	33	Psettodes belcheri	Ps_bel
9	Chaetodipterus lippei	Ch_lip	34	Pseudotolithus elongatus	Ps_elo
10	Cynoglossus canariensis	Cy_can	35	Pseudotolithus epipercus	Ps_epi
11	Cynoglossus monody	Cy_mon	36	Pseudotolithus moorii	Ps_moo
12	Cynoglossus senegalensis	Cy_sen	37	Pseudotolithus senegalensis	Ps_sen
13	Cynoponticus ferox	Cy_fer	38	Pseudotolithus senegallus	Ps_sgl
14	Dasyatis centroura	Da_cen	39	Pseudotolithus typus	Ps_typ
15	Dasyatis margarita	Da_mar	40	Pseudupeneus prayensis	Ps_pra
16	Drepane africana	Dr_afr	41	Pteroscion peli	Pt_pel
17	Ephippion guttifer	Ep_gut	42	Rhinobatos cemiculus	Rh_cem
18	Ephippus goreensis	Eph_gor	43	Rhinobatos rhinobatos	Rh_rhi
19	Epinephelus aeneus	Ep_aen	44	Rhinoptera bonasus	Rh_bon
20	Epinephelus goreensis	Epi_gor	45	Rhinoptera marginata	Rh_mar
21	Eucinostomus melanopterus	Eu_mel	46	Rhizoprionodon acutus	Rh_acu
22	Galeoides decadactylus	Ga_dec	47	Selene dorsalis	Se_dor
23	Hemicaranx bicolor	He_bic	48	Syacium micrurum	Sy_mic
24	Leptocharias smithii	Le_sm	49	Trichiurus lepturus	Tr_lep
25	Lobotes surinamensis	Lo_sur	50	Zanobatus schoenleinii	Za_sch

Appendix 3: List of fish species inventoried in trawl surveys carried out in the Guinean EEZ from 1985 to 2012

Number	Species name	Number	Species name
1	Ablennes hians	65	Chromis cadenati
2	Abudefduf hoefleri	66	Chromis limbata
3	Abudefduf saxatilis	67	Citharichthys stampflii
4	Acanthurus monroviae	68	Citharus linguatula
5	Albula vulpes	69	Conger conger
6	Alectis alexandrinus	70	Coris julis
7	Aluterus heudelotii	71	Cynoglossus browni
8	Aluterus schoepfii	72	Cynoglossus cadenati
9	Anguilla anguilla	73	Cynoglossus canariensis
10	Antennarius pardalis	74	Cynoglossus monody
11	Antennarius senegalensis	75	Cynoglossus senegalensis
12	Anthias anthias	76	Cynoponticus ferox
13	Antigonia capros	77	Dactylopterus volitans
14	Apogon imberbis	78	Dasyatis centroura
15	Ariomma bondi	79	Dasyatis hastata
16	Ariosoma balearicum	80	Dasyatis margarita
17	Arius gigas	81	Dasyatis marmorata
18	Arius latiscutatus	82	Dasyatis pastinaca
19	Arius parkii	83	Decapterus macarellus
20	Arnoglossus capensis	84	Decapterus punctatus
21	Arnoglossus imperialis	85	Decapterus tabl
22	Atractoscion aeguidens	86	Dentex barnardi
23	Aulopus cadenati	87	Dentex canariensis
24	Auxis thazard thazard	88	Dentex gibbosus
25	Balistes capriscus	89	Dentex macrophthalmus
26	Balistes punctatus	90	Dentex maroccanus
27	Balistes vetula	91	Dicologlossa cuneata
28	Batrachoides liberiensis	92	Dicologlossa hexophthalma
29	Bembrops heterurus	93	Diodon holocanthus
30	Blennius normani	94	Diodon hystrix
31	Bodianus scrofa	95	Diodon liturosus
32	Bodianus speciosus	96	Doratonotus megalepis
33	Boops boops	97	Drepane africana
34	Bothus podas	98	Echeneis naucrates
35	Brachydeuterus auritus	99	Elagatis bipinnulata
36	Branchiostegus semifasciatus	100	Elops lacerta
37	Brotula barbata	101	Enchelycore nigricans
38	Callanthias ruber	102	Engraulis encrasicolus
39	Campogramma glaycos	103	Ephippion guttifer
40	_ ,	104	Ephippion guiller Ephippus goreensis
41	Caranx crysos Caranx hippos	105	Epinephelus aeneus
42	Caranx rhonchus	106	· · ·
			Epinephelus fasciatus
43	Caranx senegallus	107	Epinephelus goreensis
44	Carcharhinus falciformis	108	Epinephelus marginatus
45	Carcharhinus leucas	109	Erythrocles monodi
46	Carcharhinus limbatus	110	Ethmalosa fimbriata
47	Carcharodon carcharias	111	Eucinostomus melanopterus
48	Carlarius heudelotii	112	Euthynnus alletteratus
49	Cephalopholis nigri	113	Fistularia petimba
50	Cephalopholis taeniops	114	Fistularia tabacaria
51	Chaetodipterus lippei	115	Galeocerdo cuvier
52	Chaetodon hoefleri	116	Galeoides decadactylus
53	Chaetodon robustus	117	Galeus polli
54	Chatrabus melanurus	118	Ginglymostoma cirratum
55	Cheilopogon furcatus	119	Gymnothorax afer
56	Chelidonichthys capensis	120	Gymnura altavela
57	Chelidonichthys gabonensis	121	Gymnura micrura
58	Chelidonichthys lucerna	122	Halobatrachus didactylus
59	Chilomycterus antennatus	123	Helicolenus dactylopterus dactylopterus
60	Chilomycterus reticulatus	124	Hemicaranx bicolor
61	Chilomycterus spinosus mauretanicus	125	Heteropriacanthus cruentatus
62	Chilomycterus spinosus spinosus	126	Hippocampus erectus
	Chlorophthalmus agassizi	127	Histrio histrio
63	Chiorophiliannus agassizi	121	1 113(110 1113(110

#### Appendix 3: (cont.)

Number	Species name	Number	Species name
29	Ilisha africana	193	Pomatomus saltatrix
30	Japonoconger africanus	194	Pontinus accraensis
31	Laemonema laureysi	195	Pontinus kuhlii
32	Lagocephalus laevigatus	196	Priacanthus arenatus
33	Lepidocybium flavobrunneum	197	Pristis pectinata
34	Lepidotrigla cadmani	198	Prognathodes marcellae
35	Lepidotrigla carolae	199	Prognichthys gibbifrons
36	Leptocharias smithii	200	Psettodes belcheri
137	Lethrinus atlanticus	201	Psettodes bennettii
138	Lichia amia	202	Pseudotolithus elongatus
39	Lithognathus olivieri	203	Pseudotolithus epipercus
40	Liza dumerili	204	Pseudotolithus moorii
41	Liza dullielli Liza falcipinnis	205	Pseudotolithus senegalensis
42	•	206	
	Liza grandisquamis	207	Pseudotolithus senegallus
43	Lobotes surinamensis		Pseudotolithus typus
44	Lophiodes kempi	208	Pseudupeneus prayensis
45	Lophius budegassa	209	Pteromylaeus bovinus
46	Lophius vaillanti	210	Pteroscion peli
47	Lutjanus agennes	211	Pterothrissus belloci
48	Lutjanus dentatus	212	Rachycentron canadum
49	Lutjanus endecacanthus	213	Raja miraletus
50	Lutjanus fulgens	214	Rhinobatos albomaculatus
51	Lutjanus goreensis	215	Rhinobatos cemiculus
52	Microchirus frechkopi	216	Rhinobatos irvinei
53	Miracorvina angolensis	217	Rhinobatos rhinobatos
54	Mobula mobular	218	Rhinoptera bonasus
55	Mobula rochebrunei	219	Rhinoptera marginata
56	Mobula thurstoni	220	Rhizoprionodon acutus
57	Monochirus hispidus	221	Rhynchobatus luebberti
58	•	222	-
	Monodactylus sebae		Rypticus saponaceus
59	Monolene microstoma	223	Sardinella aurita
160	Mugil bananensis	224	Sardinella maderensis
161	Mugil cephalus	225	Sardinella rouxi
162	Mugil curema	226	Sardinops sagax
163	Muraena robusta	227	Sargocentron hastatum
64	Mustelus mustelus	228	Sarpa salpa
65	Mycteroperca rubra	229	Saurida brasiliensis
66	Myrichthys pardalis	230	Scarus hoefleri
67	Mystriophis rostellatus	231	Scomber japonicus
68	Naucrates ductor	232	Scomberomorus tritor
69	Nicholsina usta usta	233	Scorpaena angolensis
70	Oblada melanura	234	Scorpaena laevis
71	Ophichthus ophis	235	Scorpaena maderensis
72	Orcynopsis unicolor	236	Scorpaena scrofa
73	Pachymetopon blochii	237	Scorpaena stephanica
74	Pagellus bellottii	238	Scorpaenodes insularis
75	Pagrus auriga	239	Selar crumenophthalmus
76	Pagrus auriga Pagrus caeruleostictus	240	Selene dorsalis
77	Pagrus pagrus	241	Seriola dumerili
78	Paragaleus pectoralis	242	Serranus accraensis
79	Parapristipoma octolineatum	243	Serranus cabrilla
80	Pegusa cadenati	244	Serranus sanctaehelenae
81	Pegusa lascaris	245	Solea senegalensis
82	Pegusa triophthalma	246	Solea solea
83	Pentanemus quinquarius	247	Solitas gruveli
84	Peristedion cataphractum	248	Sphoeroides pachygaster
85	Pisodonophis semicinctus	249	Sphoeroides splengeri
86	Plectorhinchus macrolepis	250	Sphyraena afra
87	Plectorhinchus mediterraneus	251	Sphyraena barracuda
188	Polydactylus quadrifilis	252	Sphyraena guachancho
189	Pomadasys incisus	253	Sphyraena sphyraena
90	Pomadasys incisus Pomadasys jubelini	254	Sphyrna lewini
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101			
191 192	Pomadasys perotaei Pomadasys rogerii	255 256	Sphyrna mokarran Spicara alta

#### Appendix 3: (cont.)

Number	Species name	Number	Species name
257	Squatina oculata	276	Trachinus armatus
258	Stephanolepis hispidus	277	Trachinus collignoni
259	Stromateus fiatola	278	Trachinus pellegrini
260	Syacium micrurum	279	Trachinus radiatus
261	Symphurus ligulatus	280	Trachurus trachurus
262	Synaptura cadenati	281	Trachurus trecae
263	Synaptura Iusitanica Iusitanica	282	Trichiurus lepturus
264	Synodus saurus	283	Trigla lyra
265	Synodus synodus	284	Trigloporus lastoviza
266	Thalassoma pavo	285	Trisopterus luscus
267	Thunnus obesus	286	Uranoscopus cadenati
268	Torpedo marmorata	287	Uranoscopus polli
269	Torpedo torpedo	288	Uraspis secunda
270	Trachinocephalus myops	289	Urogymnus asperrimus
271	Trachinotus goreensis	290	Vanstraelenia chirophthalma
272	Trachinotus maxillosus	291	Xyrichtys novacula
273	Trachinotus ovatus	292	Zanobatus schoenleinii
274	Trachinotus teraia	293	Zeus faber
275	Trachinus araneus		