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Coastal waters of a marine protected area of the Bijagós Archipelago, West Africa, shelter juvenile fishes of economic and ecological importance

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A B S T R A C T

In many marine ecosystems small pelagic fish exert a crucial role in controlling the dynamics of the community, mainly due to their high biomass at intermediate levels of the food web. These fish use coastal marine ecosystems as nursery areas, but also to forage and to avoid predation or competition. We studied spatial, seasonal, lunar and diel variations in a coastal fish community from a marine protected area of the Bijagós Archipelago, Guinea-Bissau. Fish were sampled with 46 beach seine net sessions in 2015 and 2016. A total of 35 fish species of 25 families were captured. Fish abundance varied between years and seasons, with a higher abundance in the dry season, but not by lunar tide. Nonetheless, the community composition was broadly similar over the seasons, among islands and between lunar tides. Clupeidae, Haemulidae and Gerreidae were the most abundant fish families. *Sardinella maderensis* highly dominated the captures throughout the year, with catches much higher than any other species. The differences in abundance between seasons and years may be related with movements to or from the shore due to feeding activity or to avoid predation, or else to differences in recruitment between years. There were no significant diel differences in species richness and diversity, although higher numbers of fish were captured during daytime. For most species the majority of individuals captured were immature, highlighting the importance of the archipelago as nursery area for several species. These small pelagics, and particularly *Sardinella maderensis*, represent the main prey for several marine predators. Thus, the conservation of such fish species may be key for the management of the Bijagós Archipelago.

1. Introduction

Small pelagic fish are essential to the functioning of marine ecosystems, connecting the lower and upper trophic levels in food webs worldwide (Rice, 1995; Bakun, 1996). Therefore, fluctuations in small pelagic populations may modify ecosystem structure and functioning (e.g. Cury et al., 2000; Shannon et al., 2000). Several small pelagics use coastal marine ecosystems in the near-shore as nursery grounds. Yet these ecosystems are among the most damaged by anthropogenic changes and one of the most vulnerable to future impacts of climate change (Barbier et al., 2011; Harley et al., 2006; Martínez et al., 2007; Sheaves et al., 2014).

Coastal marine ecosystems, due to their dynamic structure, exhibit fluctuations in abundance of different species and in the diversity of their communities (Gibson, 1993; Krumme, 2009). At a short temporal scale, this variability in the number of individuals may result from short-term movements among different habitats for feeding, reproducing or to avoid predation and competition and are often influenced by lunar, diel and tidal cycles (e.g. Ferreira et al., 2001; Hitt et al., 2011; Krumme, 2009). At a larger temporal scale, annual or seasonal migrations for feeding and spawning as well as the recruitment of young may also contribute to fluctuations in coastal marine communities (Gibson et al., 1993).

In the Eastern Central Atlantic region small pelagics are the most important group for fisheries, constituting almost 50% of the landings (Failler, 2014; FAO, 2018a). Most pelagic fish stocks are considered either fully exploited or overfished (FAO, 2018a). Moreover, this region is one of the most affected by illegal, unreported and unregulated fishing (Belhabib et al., 2015; Doumbouya et al., 2017; Intchama et al., 2018). Guinea-Bissau, located in the region, is strongly dependent on fisheries as one of its

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main economic activities (Lafrance, 1994; Campredon and Cuq, 2001; Belhabib et al., 2015). Fish is also the main animal protein source for the human population (Patsche et al., 2019). The Bijagós Archipelago, in particular, is recognized for its abundant fish resources and also considered as a nursery area for several fish species (Lafrance, 1994; Arkhipov et al., 2015; Campredon and Catry, 2016). The archipelago is free from industrial fishing, representing a refuge for several fish species that are strongly harvested in neighbouring countries (Polidoro et al., 2016). Fish communities at the Bijagós Archipelago are dominated by Clupeiformes and Perciformes (Lafrance, 1994; van der Veer et al., 1995). The archipelago possibly holds some resident populations since most common species are present throughout the year, although few studies have addressed the local coastal fish community and related seasonal variations (Lafrance, 1994; van der Veer et al., 1995).

The marine ecosystem of Guinea-Bissau is influenced by the tropical climate with two distinct seasons. The dry season (November to May) with close to zero precipitation (0.1 mm), is influenced by the Canary Current upwelling system and the rainy season (June to October), characterized by intense precipitation (median 400 mm/month) is influenced by the Guinean Current (Pennober, 1999; Valdés and Déniz-González, 2015; Republic of Guinea-Bissau, 2019). The effect of the currents along with the input of organic matter from rivers, results in a relatively high productivity in the marine coastal areas of Guinea-Bissau (Berrit and Rebert, 1977; Longhurst, 1983; Bakun, 1996; Tandstad et al., 2014).

The sea-surface temperature ranges from 26 to 30 °C and salinity from 36 to 30 ppt, in dry and rainy seasons, respectively (Lafrance, 1994) and the waters are mainly shallow usually not exceeding a depth of 20 m.

Here, we aimed to characterize the inshore pelagic fish community in a relatively undisturbed area of the Bijagós, part of a Marine Protected Area. Furthermore, we explored variations in species abundance between seasons (dry and rainy), lunar cycle (spring and neap tide), and diel periods (night and day) in the coastal fish community.

2. Material and methods

2.1. Study area and sampling

Fieldwork was carried out in the João Vieira and Poilão Marine National Park (JVPMNP) in the southeast of the Bijagós Archipelago (Fig. 1). The park covers 49,500 ha (of which only 5% are terrestrial) and comprises four main islands. The entire marine area of the JVPMNP is managed in regards to fishing activities, with two distinct zones. One of them representing 19% of its total area where fishing is totally banned, and another where some types of fishing nets, such as shark nets and all monofilament nets, are forbidden, and only fishermen of the local communities are allowed to operate (IBAP, 2007). Beach seine is not usually used for commercial or subsistence fishing in the park.

Our sampling was carried out using a beach seine 29.6 m in length and 1.70 m to 8.5 m in height (reaching the highest height in the central zone) with 1 cm mesh size. In the central area, it had an additional pyramid with a 1.5 m^2 base and 1 m in height with 0.5 cm mesh size (Fig. A.1).

Net setting started from the beach using a small boat to stretch the net perpendicular to shore, always keeping the two ropes from one end ashore secured by two people, until reaching approximately 35 m from the shoreline. In the farthest point from the shore the depth was on average 2.45 m. The net was then drawn towards the shore so as to form a semi-circumference. When the semi-circumference was formed, two to three people on each end pulled the ropes in order to completely pull the net out from the water. This process represents one haul. We always performed four consecutive hauls approximately ten metres apart from each other. We considered each group of four hauls as one session. All samples were collected at high tide, and those obtained in the same session were pooled.

Table 1
Number of sessions (N) by season and lunar tide of the beach seine performed in the João Vieira from 2015 to 2016.

N	Season	Lunar tide
9	Dry	Neap
9		Spring
5	Rainy	Neap
4		Spring

In every haul, we counted and weighted (to the nearest 0.1 g) the total number of fishes by species. Furthermore, 50 random individuals from each species were measured (to the nearest 0.5 mm) and weighted. Rays (Chondrichthyes) were quickly measured on the beach and released alive and they were not weighted. Fishes were identified to the lowest possible taxonomic level following guides (Fischer et al., 1981; Schneider, 1990; Paugy et al., 2003). We were not able to identify all *Pomadasys* specimens to the species level (most probably *Pomadasys rogerii*, *Pomadasys perotaei* or *Pomadasys jubelini*; Lafrance, 1994; per obs), so we refer to them as *Pomadasys* sp. In the case of Mugilidae, individuals were identified to the genus or family level. Within the ones identified to the genus level, for most individuals we were able to identify four different groups, and we refer to them as *Mugil* sp.1, *Mugil* sp.2 (that are most probably *Mugil bananensis*, *Mugil cephalus* or *Mugil curema*; Lafrance, 1994; per obs), *Liza* sp.1 or *Liza* sp.2 (that are most probably *Chelon dumerili*, *Neochelon falcipinnis* or *Parachelon grandisquamis*; Lafrance, 1994; per obs).

2.2. Lunar and seasonal variation

Catches were carried out between February 2015 and September 2016. In order to explore the seasonal variation in the pelagic fish community we performed 27 sessions of beach seine in João Vieira Island in the study period (site 1, see Fig. 1). We always fished on three consecutive days, except for one occasion when only one day was sampled, and another one when only two days were sampled due to unsuitable weather and sea conditions (Table 1).

2.3. Spatial variation

In order to assess whether our main study site was representative of the whole marine park, and whether there was important spatial variation in the fish community, we sampled two different points of each of the three islands (João Vieira, Cavalos and Meio, Fig. 1) in six consecutive days in January 2016.

2.4. Diel variation — day/night

We explored diel variation in the pelagic fish community by performing eight catches during both day and night periods, in João Vieira (site 1, see Fig. 1), between January and March 2016.

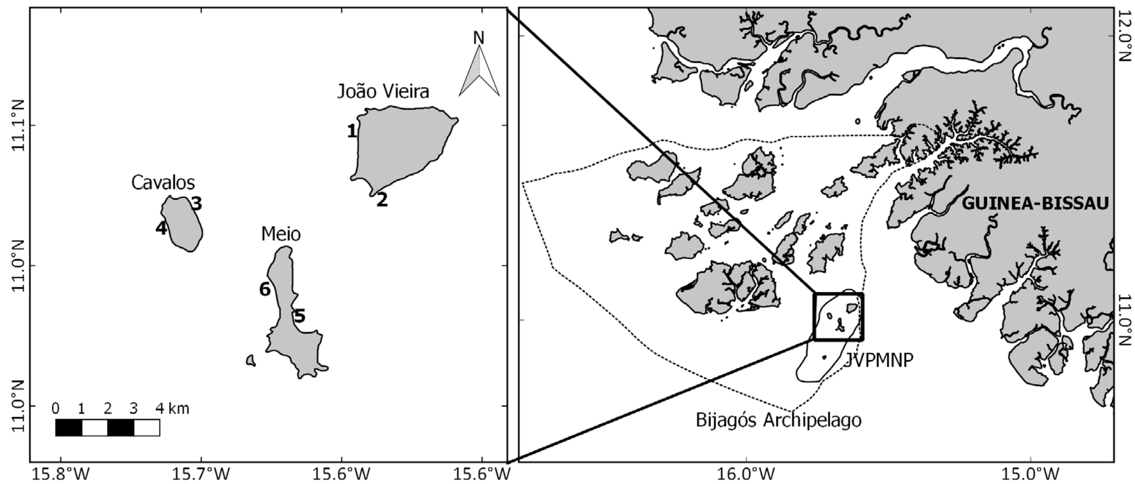

Fig. 1. Beach seine sampling location performed between 2015 and 2016, dash line delimitates Bijagós Archipelago, solid line delimitates João Vieira and Poilão Marine National Park (JVPMNP).

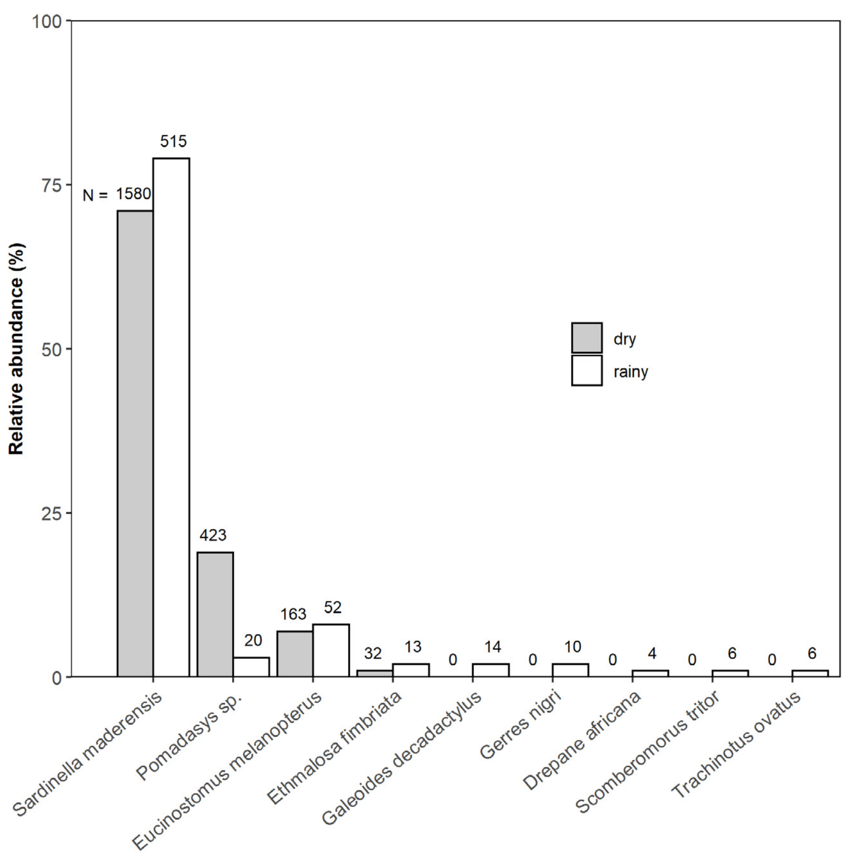

Fig. 2. Relative abundance (%) by species of the fishes captured during 19 sessions in the dry season and 9 sessions in the rainy season in João Vieira from 2015 and 2016, only species with relative abundance > 0% included; N — mean of the total number of individuals captured by session (complete information in Table A.2).

Table 2
Mean total length (TL) (mm) ± standard error by year and season for the most abundant species captured by beach seine in João Vieira, N — number of individuals measured.

Family	Species	2015				2016			
		Dry		Rainy		Dry		Rainy	
		N	TL (mm) ± SE	N	TL (mm) ± SE	N	TL (mm) ± SE	N	TL (mm) ± SE
Clupeidae	*Sardinella maderensis*	1920	59.08 ± 0.26	590	69.82 ± 0.62	872	68.13 ± 0.47	1309	60.96 ± 0.34
Gerreidae	*Eucinostomus melanopterus*	1072	78.01 ± 0.46	204	87.60 ± 1.50	380	68.82 ± 1.00	264	84.53 ± 1.58
Gerreidae	*Gerres nigri*	4	105.75 ± 8.73	30	109.17 ± 4.36	131	94.83 ± 4.23	64	110.13 ± 3.54
Haemulidae	*Pomadasys* sp.	1872	51.72 ± 0.36	30	84.93 ± 5.35	663	52.70 ± 0.51	130	35.54 ± 1.03

2.5. Data analysis

The abundance of fish corresponded to the total number of individuals captured in a session (four consecutive hauls), and the richness as the total number of species. For each species, we calculated the mean number and relative abundance of individuals caught per session. We further calculated, for each species, the mean total length and mean total mass of the individuals measured in João Vieira between February 2015 and September 2016 at site 1 (Fig. 1). To evaluate the diversity of the community, we calculated the Shannon–Wiener (H') diversity index and the Pielou's evenness index (J), (Brower and Zar, 1998) following the equations: H' $= -\sum$ pi $\log_e$ pi; J = H'/log(S); where *pi* is the proportion of species *i* in relation to the total number of species; J is the Pielou's evenness index. We tested for differences between lunar tides, islands and diel period in the diversity (Shannon–Wiener and Pielou's evenness) and richness using ANOVAs. The abundance of individuals was tested accounting for species on one hand, and for lunar tides/islands or diel period on the other, using two-way ANOVAs. Concerning seasonal variations, we tested the effect of season and year on diversity and richness using two-way ANOVAs, and tested the effect of species, season and year on the abundance of individuals using three-way ANOVAs. Statistical analyses were carried out using the software R (R Core Team, 2020).

3. Results

In total we captured 35 fish species from 25 families. The list of species with the respective threat status (IUCN, 2020) is in Table A.1.

3.1. Lunar and seasonal variation

Sardinella maderensis accounted for more than 70% of the total of individuals captured in the dry season and c. 80% in the rainy season (Fig. 2, Table A.2), followed by *Pomadasys* sp. (19% in dry season and 3% in rainy season) and *Eucinostomus melanopterus* (8% in dry season and 10% in rainy season). Total mean mass of individuals by species and by season is presented in Table A.3.

Concerning the variation between spring and neap tides, there were no differences in diversity (ANOVA: Shannon–Wiener diversity — $F_{1,25} = 0.28$, P = 0.60), in evenness (Pielou's evenness $F_{1,25} = 2.00 \times 10^{-3}$, P = 0.97), or in species richness (ANOVA: $F_{1,25} = 2.02$, P = 0.17). We tested for differences in the number of individuals captured among species and between spring and neap tides. There were significant differences in the abundance of individuals between species (two-way ANOVA $F_{30,239} = 5.62$, P < 0.001) but not by tide ($F_{1,239} = 1.33$, P = 0.25). Also, there was no significant interaction between species and tide ($F_{19,239} = 0.39$, P = 0.99). Therefore, data from neap and spring tides were pooled for subsequent analyses.

There were no effects of season or year in Shannon–Wiener diversity per session (two-way ANOVA: season: $F_{1,24} = 0.02$, P = 0.90; year: $F_{1,24} = 0.41$, P = 0.53), that presented a mean of 0.92 ± 0.01 (SE). There were also no significant effect of season or year differences in Pielou's evenness (two-way ANOVA: season: $F_{1,24} = 0.21$, P = 0.65; year: $F_{1,24} = 3.60$, P = 0.07), that presented a total mean of 0.40 ± 0.01 (SE). There was a significant effect of year and season on species richness (two-way ANOVA: season: $F_{1,24} = 5.06$, P = 0.03; year: $F_{1,24} = 14.66$, P < 0.001). The average species richness per session was 10.7 ± 0.1 (SE). We tested the effect of species, season and year on the abundance of individuals captured (three-way ANOVA). All variables had a significant effect on the abundance of individuals, however the species accounted for most of the variance (species: $F_{30,257}$ = 6.23, P < 2.0 x10^{-6}; season: $F_{1,257} = 8.44$, P < 0.01; year: $F_{1,257} = 9.31$, P < 0.01). We compared the total length between seasons and year for the three most captured families (Table 2; information on the total length and total mass of individuals of the remaining species are presented in Table A.4). We tested the effect of season (dry and rainy) and year (2015 and 2016) on total length of *Sardinella maderensis, Pomadasys* sp, *Eucinostomus melanopterus* and *Gerres nigri*. The total length of *Sardinella maderensis* was significantly higher in rainy season ($F_{1,4687} = 23.45$, P < 0.001) and in 2016 ($F_{1,4687} = 21.04$, P < 0.001). Conversely, *Pomadasys* sp. and *Eucinostomus melanopterus* were both significantly larger during dry season ($F_{1,2691} = 34.04$, P < 0.001; $F_{1,1916} = 109.13$, P < 0.001, respectively) and in 2015 ($F_{1,2691} = 4.51$, P = 0.03; $F_{1,1916} = 63.57$, P < 0.001, respectively). The size of *Gerres nigri* was larger during the rainy season ($F_{1,225} = 7.20$, P < 0.01), but no differences were found between years ($F_{1,225} = 0.01$, P = 0.91). There was a significant interaction between year and season on the total length of *Sardinella maderensis*, *Pomadasys* sp. and *Eucinostomus melanopterus* ($F_{1,4687} = 492.11$, P < 0.001; $F_{1,2691} = 258.60$, P < 0.001; $F_{1,1916} = 8.95$, P < 0.01 respectively), but no for *Gerres nigri* ($F_{1,225} = 0.28$, P = 0.60).

Table 3
Mean Shannon–Wiener diversity (H′), mean Pielou's evenness (J) diversity indexes and mean richness ± standard errors by island of the captures with beach seine in January 2016, N — number of sessions.

Island	N	H′	J	Richness
Cavalos	2	0.95 ± 0.05	0.39 ± 0.00	11.5 ± 1.5
Joao Vieira	2	0.93 ± 0.04	0.48 ± 0.02	7.0 ± 0.0
Meio	2	1.17 ± 0.12	0.57 ± 0.01	8.0 ± 2.0

3.2. Spatial variation

Sardinella maderensis and *Pomadasys* sp. accounted for more than 75% of the relative abundance in all three islands (Fig. 3, Table A.5). The diversity indexes and richness by island are presented in Table 3. We tested the effect of species and island on the abundance of individuals. There were significant differences in abundance of individuals of each species (two-way ANOVA $F_{19,99} = 9.15$, P < 0.001) but not between islands ($F_{2,99} = 2.00$, P = 0.14). There was also no significant interaction between species and islands, so the factor island was removed from these analyses (results not shown). Total mean mass of individuals by species and by island is presented in Table A.6.

3.3. Diel variation — day/night

Sardinella maderensis and *Pomadasys* sp. were the most abundant species during the daytime, while at night the most abundant groups were *Pomadasys* sp. and Mugilidae (Fig. 4, Table A.7).

The mean Shannon–Wiener diversity index was 1.21 ± 0.09 (SE) during daytime and 1.45 ± 0.14 (SE) during night-time, there were no differences between the two periods (ANOVA: Shannon–Wiener $F_{1,14} = 2.17$, P = 0.16). The mean species richness was 10.0 ± 1.1 (SE) during daytime and 8.75 ± 0.92 (SE) during night-time and did not differ significantly (ANOVA: $F_{1,14} = 0.73$, P = 0.41). The Pielou's evenness index, however, varied significantly ($F_{1,14} = 6.15$, P = 0.03), with a mean value of 0.54 ± 0.04 (SE) during the day and 0.68 ± 0.04 during the night period. We tested the effect of species and period in the abundance of individuals. There was a significant interaction between species and period (Two-way ANOVA: $F_{23,336} = 6.43$, P < 0.001), meaning that the relationship between periods and abundance is dependent on the species. There were significant differences in the total number of

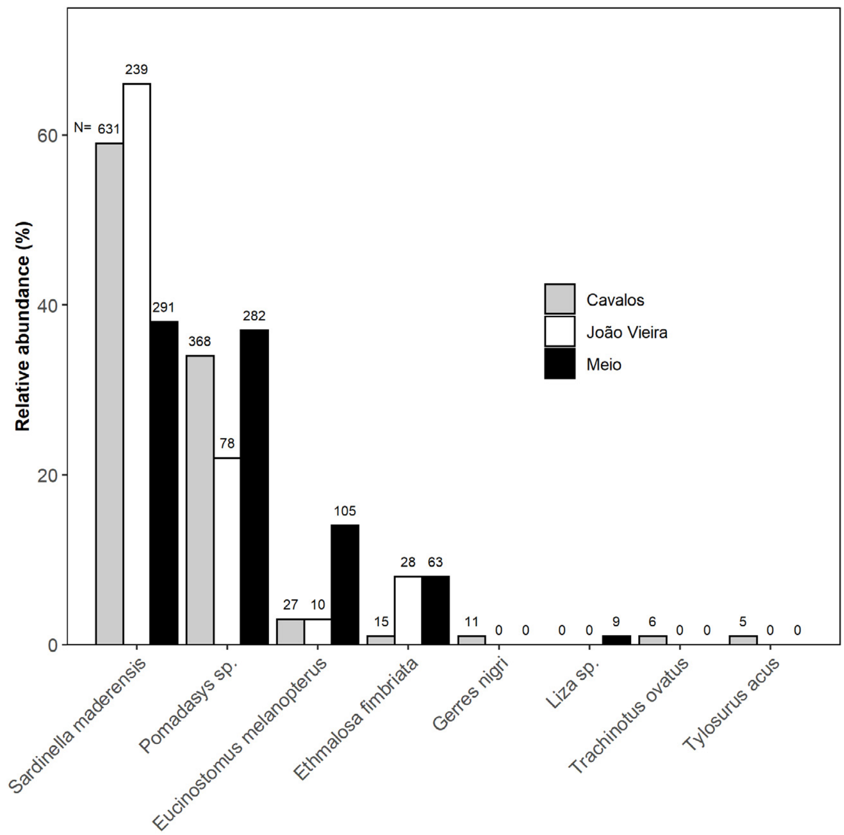

Fig. 3. Relative abundance (%) by species of the fishes captured by islands (Cavalos, João Vieira and Meio) during 6 consecutive days in January 2016, 2 sessions by island; only species with relative abundance > 0% included; N — mean of the total number of individuals captured by session (complete information in Table A.5).

individuals captured of each species ($F_{23,336} = 6.83$, $P < 0.001$), as well as between periods ($F_{1,336} = 18.34$, $P < 0.001$), with more individuals captured during the daytime except for a few species (Fig. 4, Table A.7). Total mean mass of individuals by species and by island is presented in Table A.8.

4. Discussion

This study showed that the coastal shallow water fish community of the Bijagós Archipelago is strongly dominated by species belonging to the Clupeidae, Haemulidae and Gerreidae families. In particular, *Sardinella maderensis* was by far the most numerous species with a relative abundance of over 70% throughout the seasons. There were also differences between day and night periods. During the night, most species were much less abundant inshore, except for Mugilidae, which was much more numerous. The fish species captured in this study are some of the most common coastal species in the Eastern Central Atlantic West Africa (Carpenter and DeAngelis, 2016; Polidoro et al., 2016).

4.1. Lunar and seasonal variation

The overall diversity was low when compared to other beach seine studies in West Africa (e.g. Aggrey-Fynn and Sackey-Mensah, 2012), mainly due to the much higher dominance of three species in our samples — *Sardinella maderensis*, *Pomadasys* sp. and *Eucinostomus melanopterus* (see Fig. 2, Table A.2). This is very clearly expressed in the very low values of equitability (<0.5). Most of the fish captured were immature individuals as assessed by their total length (Table 3 and Table A.4; Panfili et al., 2006; Froese and Pauly, 2020. This may be expected in shallow coastal areas, which can provide refuge from predation (Krumme, 2009). We found no differences in fish community composition between neap and spring tides. Such differences in tropical coastal ecosystems seem to be expected in heterogeneous shores, where spring tides give access to types of habitats that are not available during neap tides (Lubchenco et al., 1984; Krumme, 2009). The area sampled in our study was mostly composed of sandy bottoms and the habitat made available during spring tides is most likely not different from the one already available in neap tides, explaining the resemblance in fish community between the two (Castellanos-Galindo et al., 2010).

Seasonal variation in fish abundance was influenced by year and season. The interannual differences found in this study may be related to migrations to and from the coastal areas (Boely et al., 1978). Moreover, since fish recruitment is limited by food availability and spawning density, it is expected to fluctuate between years shaped by environmental conditions, influencing inshore abundance (Cury and Roy, 1989; Neill et al., 1994; Cury et al., 2000). The higher fish abundance found during the dry season can be related to a higher recruitment of juveniles during this season, which happens for several species in West Africa (e.g. *Sardinella maderensis*, Whitehead, 1985; Cury and Roy, 1989), or else, be related to migrations between adjacent inshore and offshore environments (Boely et al., 1978). Some species, including *Sardinella* spp, show seasonal migrations within their main areas of abundance in West Africa. These species move from Guinea-Bissau to Mauritania in May/June and the other way around in October/November; and also, from Angola to Congo during July/August and back in February/April (Boely et al., 1978; Fischer et al., 1981; Fréon, 1988; Cury and Fontana, 1988; Thiaw et al., 2017). Nonetheless, as only adults are expected to migrate and most of the individuals captured in this study were immatures, these movements should not have influenced our results. The

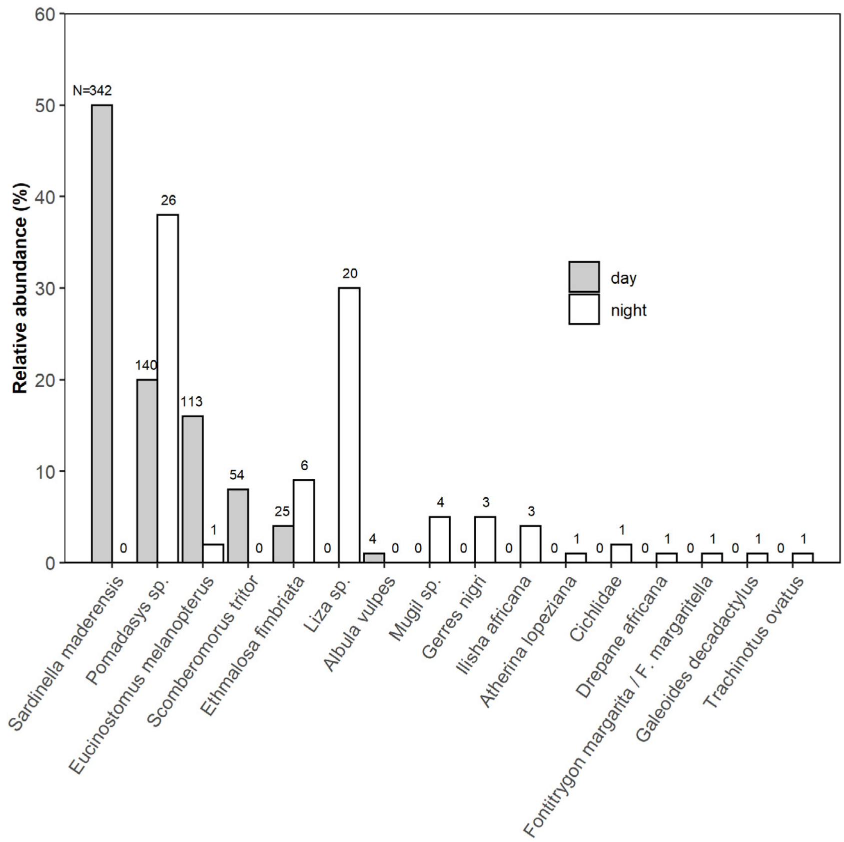

Fig. 4. Relative abundance (%) by species of the fishes captured by daytime (day, night) during 8 sessions in daytime and 8 sessions in night-time of beach seine in João Vieira Island in 2016 only species with relative abundance > 0% included; N — mean of the total number of individuals captured by session (complete information in Table A.7).

frequent capture of Chondrichthyes, particularly *Fontitrygon margarita/margaritella* and, to a lesser extent, *Glaucostegus cemiculus*, suggests that the Archipelago may be highly relevant for the conservation of this group, particularly since these species are listed as Endangered/Data Deficient, Critically Endangered by the IUCN, respectively. Chondrichthyes are declining rapidly worldwide and West Africa is among the priority geographic hotspots for their conservation (Dulvy et al., 2017). The Bijagós Archipelago may represent one of the most significant areas in West Africa for this fish group, holding large numbers of individuals (Tous et al., 1998; Campredon and Cuq, 2001).

4.2. Spatial variation

The fish community was overall similar among the three islands. *Sardinella maderensis* was the most abundant species in all islands (Fig. 3). Therefore, the results obtained from the beach seine performed in João Vieira from 2015 to 2016 may be representative of the composition and variations of the overall coastal fish community of the JVPMNP.

4.3. Diel variation — day/night

Species abundance and richness were generally higher during the daytime. However, Mugilidae was much more abundant at night, meaning that these individuals move nearer to shore during this period. Alongside Mugilidae, Haemulidae was also relatively abundant in night captures (Fig. 4). Due to the decrease in the dominant species, the values of equitability were significantly higher during the night, while keeping similar average diversities. The variation of fish behaviour along diel cycle differs between species and leads to differences in inshore catchability (Parsley et al., 1989). Therefore, some species are more prone to be captured during daytime and others during night-time (Parsley et al., 1989; Nash and Santos, 1998). The behavioural differences may be related to feeding activity (Torricelli et al., 1981), or to predation/competition (e.g. Hitt et al., 2011). The use of inshore shallow waters by small fish may reduce the risk of predation by subsurface predators but may increase the predation risk by aerial marine predators (e.g. Erwin, 1996; Krumme, 2009). Still, shallow waters may offer fewer foraging opportunities for some species. Thus, different strategies may be used by different species concerning the temporal use of these areas in order to achieve an equilibrium between low predation risk and foraging success (e.g. Erwin, 1996; Krumme, 2009). The relatively high abundance of Mugilidae and Haemulidae in night-time captures might be related with inshore movements for feeding, as for both species, night feeding activity has already been reported (Blaber, 1976; Torricelli et al., 1981; Nagelkerken et al., 2000; Dankwa et al., 2005; Krumme, 2009).

4.4. The importance of sardinella

The most abundant families, Clupeidae, Haemulidae and Gerreidae, are within the most captured in coastal areas of nearby countries (Aggrey-Fynn and Sackey-Mensah, 2012). The same fish families had already been reported as the most abundant in Guinea-Bissau in previous unpublished technical reports (Lafrance, 1994; Albaret et al., 2005), yet ours is the first detailed analysis of a coastal community in this country.

In our study area, *Sardinella maderensis* was the most abundant species in both seasons and around all the islands. This high abundance in the Bijagós Archipelago was not limited to the shore, as some experimental fisheries with a gillnet in deeper waters (up to 30 m) also showed *Sardinella maderensis* as the most abundant species (Table A.9).

Sardinella maderensis is mostly present in the continental shelf, wherein immature individuals are more dependent on coastal zones and adults usually distribute farther from the shore (Boely et al., 1978). Along its distribution range, restricted to the Atlantic Ocean, from south-eastern Spain to Angola (Carpenter and DeAngelis, 2016; Froese and Pauly, 2020), *Sardinella maderensis* presents two areas of major abundance: one from Mauritania to Guinea-Bissau, and another from Gabon to the north of Angola (Brainerd, 1991). Still, the dominance of this species in the fish communities studied here is striking and unreported for other West Africa coastal small pelagic communities (e.g. Aggrey-Fynn and Sackey-Mensah, 2012). Since the dominance of one or a few species of small pelagics in a marine ecosystem is an indicator of a wasp-waist structure (Bakun, 1996; Cury et al., 2000), our results suggest this type of ecosystem structure for the Bijagós Archipelago (see also Correia et al., 2019).

Sardinella maderensis first matures when its total length reaches about 170 mm (Boely, 1979; Youmbi et al., 1991). From the randomly measured individuals from the beach seine in João Vieira, only one presented more than 170 mm in total length, thereby possibly being a mature individual. All others were smaller in length and therefore immature, highlighting the importance of the Bijagós Archipelago as a nursery area for this species. The archipelago is located in one of the two main nursery areas identified for *Sardinella maderensis*: one in the north of Mauritania and the other ranging from the south of Senegal to the Bijagós Archipelago (Fréon, 1988; Brainerd, 1991).

Despite the Bijagós Archipelago showing high levels of abundance for *Sardinella maderensis* and great potential for recruitment, fishing pressure in West Africa, coupled with the high commercial value of the species (Valdés and Déniz-González, 2015; FAO, 2018b), have led to declines in its populations. The species is considered overfished in the region and is now classified as Vulnerable by the IUCN (FAO, 2018a; Polidoro et al., 2016; Corten et al., 2017).

Beyond its importance for fisheries, *Sardinella maderensis* has been shown to be the most frequent prey for several marine predators in the archipelago, such as seabirds and predatory fish (Correia et al., 2017, 2018, 2019). The fact that, in the Bijagós Archipelago, *Sardinella maderensis* is highly abundant and serves as the main link between plankton and marine predators, makes it a key species for the ecosystem. The correct management and conservation of nursery areas for this species should therefore be a priority to ensure a healthy ecosystem. The Bijagós Archipelago, by holding large numbers of immature *Sardinella maderensis,* certainly contributes for the maintenance of its offshore stocks (Sheaves et al., 2014). Moreover, as the archipelago still suffers less fishing pressure than its neighbouring waters (Campredon and Cuq, 2001), it represents a pivotal area for the conservation of *Sardinella maderensis*.

CRediT authorship contribution statement

Edna Correia: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing, Funding acquisition. **José Pedro Granadeiro:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Funding acquisition, Supervision. **Aissa Regalla:** Project administration, Funding acquisition. **Paulo Catry:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Funding acquisition, Project administration, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2021.101892.

References

Aggrey-Fynn, J., Sackey-Mensah, R., 2012. Species diversity and relative abundance of fisheries resources found in beach seine along the central coast of Ghana. West Afr. J. Appl. Ecol. 20, 1–9.
Albaret, J.-J., Simier, M., Sadio, O., 2005. Suivi biologique des peuplements de Poissons d'une aire protégée en zone de mangrove: le bolon de Bamboung (Sine Saloum, Sénégal), Rapport final.
Arkhipov, A.G., Mamedov, A.A., Simonova, T.A., Shnar, V.N., 2015. Species composition and features of ichthyoplankton distribution in the waters of Senegal and Guinea-Bissau. J. Ichthyol. 55, 346–354. http://dx.doi.org/10.1134/S0032945215030017.
Bakun, A., 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico.
Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81, 169–193. http://dx.doi.org/10.1890/10-1510.1.
Belhabib, D., Sumaila, U.R., Pauly, D., 2015. Feeding the poor: contribution of West African fisheries to employment and food security. Ocean Coast Manag. 111, 72–81. http://dx.doi.org/10.1016/j.ocecoaman.2015.04.010.
Berrit, G.R., Rebert, J.P., 1977. Océanographie physique et productivité primaire. In: G.R., Berrit (Ed.), Le milieu marin de la Guinée Bissau et ses ressources vivantes. ORSTOM, Pairs, pp. 1–60.
Blaber, S.J.M., 1976. The food and ecology of Mugilidae in the St. Lucia lake system. Biol. J. Linn. Soc. 8, 267–277.
Boely, T., 1979. Biologie Des Deux Espèces de Sardinelles (*Sardinella aurita* Valenciennes 1847 et *Sardinella maderensis* Lowe 1841) des côtes sénégalaises (Ph.D. thesis). Paris University VI.
Boely, T., Chabanne, J., Fréon, P., 1978. Schémas migratoires, aires de concentrations et périodes de reproduction des principales espéces de Poissons pélagiques côtiers dans la zone sénégalo-mauritanienne. COPACE/PACE 78 (IO), 63–70.
Brainerd, T.R., 1991. The sardinella fishery off the coast of West Africa: the case of a common property resource. In: Second Annual Conference of the International Association for the Study of Common Property (IASCP). University of Manitoba, Winnipeg, Canada, pp. 26–29.
Brower, J.E., Zar, J.H., 1998. Field and Laboratory Methods for General Ecology. McGraw-Hill, Boston, Massachusetts.
Campredon, P., Catry, P., 2016. Bijagos archipelago (guinea-bissau). In: Finlayson, C.M., Milton, G.R., Prentice, R., Davidson, N.C. (Eds.), The Wetland Book. II. Distribution, Description and Conservation. Springer, Dordrecht, pp. 276–284.

Campredon, P., Cuq, F., 2001. Artisanal fishing and coastal conservation in West Africa. J. Coast. Conser. 7, 91–100. http://dx.doi.org/10.1007/BF02742471.

Carpenter, K., DeAngelis, N., 2016. The Living Marine Resources of the Eastern Central Atlantic (Vol 2-4). FAO Species Identification Guide for Fishery Purposes. FAO, Rome.

Castellanos-Galindo, G.A., Krumme, U., Willis, T.J., 2010. Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). Mar. Ecol. Prog. Ser. 416, 241–254. http://dx.doi.org/10.3354/meps08768.

Correia, E., Granadeiro, J.P., Regalla, A., Dias, E., Almeida, A., Catry, P., 2017. Predatory pelagic fishes of the Bijagós Archipelago (Guinea-Bissau) show high overlap in diets dominated by sardinella. Afr. J. Mar. Sci. 39, 389–396. http://dx.doi.org/10.2989/1814232X.2017.1387605.

Correia, E., Granadeiro, J.P., Regalla, A., Monteiro, H., Catry, P., 2018. The diet of two opportunistic seabirds (Caspian and Royal Terns) confirms the importance of sardinella in West African coastal food webs. Mar. Biol. Res. 14, 961–972. http://dx.doi.org/10.1080/17451000.2019.1572193.

Correia, E., Granadeiro, J.P., Vanessa Mata, V.A., Regalla, A., Catry, P., 2019. Trophic interactions between migratory seabirds, predatory fishes and small pelagics in West Africa. Ecol. Prog. Ser. 622, 177–189. http://dx.doi.org/10.3354/meps13022.

Corten, A., Braham, C.B., Sadegh, A.S., 2017. The development of a fishmeal industry in Mauritania and its impact on the regional stocks of sardinella and other small pelagics in Northwest Africa. Fish. Res. 186, 328–336. http://dx.doi.org/10.1016/j.fishres.2016.10.009.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in wasp-waist ecosystems. ICES J. Mar. Sci. 57, 603–618. http://dx.doi.org/10.1006/jmsc.2000.0712.

Cury, P., Fontana, A., 1988. Compétition et stratégies démographiques comparées des deux espèces de sardinelles (*Sardinella aurita* et *Sardinella maderensis*) des côtes ouest-africaines. Aquat. Living Resour. 1, 165–180. http://dx.doi.org/10.1051/alr:1988018.

Cury, P., Roy, C., 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46, 670–680. http://dx.doi.org/10.1139/f89-086.

Dankwa, H.R., Blay, J., Yankson, K., 2005. Food and feeding habits of grey mullets (Pisces: Mugilidae) in two estuaries in Ghana. West Afr. J. Appl. Ichthyol. 8, 1–13. http://dx.doi.org/10.4314/wajae.v8i1.45786.

Doumbouya, A., Camara, O.T., Mamie, J., Intchama, J.F., Jarra, A., Ceesay, S., Guèye, A., Ndiaye, D., Beibou, E., Padilla, A., Belhabib, D., 2017. Assessing the effectiveness of monitoring control and surveillance of illegal fishing: the case of West Africa. Front. Mar. Sci. 4, 1–10. http://dx.doi.org/10.3389/fmars.2017.00050.

Dulvy, N.K., Simpfendorfer, C.A., Davidson, L.N.K., Fordham, S.V., Bräutigam, A., Sant, G., Welch, D.J., 2017. Challenges and priorities in shark and ray conservation. Curr. Biol. 27, R565–R572. http://dx.doi.org/10.1016/j.cub.2017.04.038.

Erwin, R.M., 1996. Dependence of waterbirds and shorebirds on shallow-water habitats in the mid-Atlantic coastal region: an ecological profile and management recommendations. Estuaries 19, 213–219. http://dx.doi.org/10.2307/1352226.

Failler, P., 2014. Climate variability and food security in Africa: the case of small pelagic fish in West Africa. J. Fish. Livest. Prod. 2, 122. http://dx.doi.org/10.4172/2332-2608.1000122.

FAO (Food and Agriculture Organization), 2018a. The State of World Fisheries and Aquaculture 2018. Meeting the sustainable development goals, Rome.

FAO (Food and Agriculture Organization), 2018b. Working Group on the Assessment of Small Pelagic Fish Off Northwest Africa. Nouadhibou, Mauritania, 22–27 2017. FAO Fisheries and Aquaculture. Report 1221.

Ferreira, C.E.L., Goncalves, J.E.A., Coutinho, R., 2001. Community structure of fishes and habitat complexity on a tropical rocky shore. Environ. Biol. Fishes 61, 353–369. http://dx.doi.org/10.1023/A:1011609617330.

Fischer, W., Bianchi, G., Scott, W.B., 1981. FAO species identification sheets for fishery purposes. Eastern Central Atlantic; fishery areas 34, 47 (in part). Canada Funds-in-Trust. Ottawa, Department of Fisheries and Oceans Canada, by arrangement with Food and Agriculture Organization of the United Nations.

Fréon, P., 1988. Réponses et adaptations des stocks des clupéidés d'Afrique del'Ouest à la variabilité du milieu et de l'exploitation. Analyse et réflexion à partir de l'exemple du Sénégal. Edition de l'ORSTOM, Coll. Etudes et Thèses, Paris.

Froese, R., Pauly, D. (Eds.), 2020. FishBase. World Wide Web electronic publication, URL: http://www.fishbase.org. (Accessed 15 March 2020).

Gibson, R.N., 1993. Intertidal teleosts: life in a fluctuating environment. In: T.J., Pitcher (Ed.), The Behaviour of Teleost Fishes, second ed. Chapman and Hall, London, pp. 513–536.

Gibson, R.N., Ansell, A.D., Robb, L., 1993. Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. Mar. Ecol. Progr. Ser. 98, 89–105. http://dx.doi.org/10.3354/meps098089.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241. http://dx.doi.org/10.1111/j.1461-0248.2005.00871.

Hitt, S., Pittman, S., Nemeth, R., 2011. Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. Mar. Ecol. Progr. Ser. 427, 275–291. http://dx.doi.org/10.3354/meps09093.

IBAP, 2007. Estratégia nacional para as áreas protegidas e a conservação da biodiversidade na Guiné-Bissau 2007-2011. Instituto da Biodiversidade e das Áreas Protegidas (IBAP), Bissau.

Intchama, J.F., Belhabib, D., Jumpe, R.J.T., 2018. Assessing Guinea Bissau's legal and illegal unreported and unregulated fisheries and the surveillance efforts to tackle them. Front. Mar. Sci. 5, 1–11.

IUCN, 2020. The IUCN red list of threatened species. Version 2020-1. https://www.iucnredlist.org. (Accessed 09 April 2020).

Krumme, U., 2009. Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken, I. (Ed.), Ecological Connectivity Among Tropical Coastal Ecosystems. Springer, Dordrecht, pp. 271–324.

Lafrance, S., 1994. Archipel des Bijagos ichtyofaune et éléments d'écologie marine. CIPA, Bissau.

Longhurst, A.R., 1983. Benthic-pelagic coupling and export of organic carbon from a tropical Atlantic continental shelf-Sierra Leone. Estuar. Coast. Shelf Sci. 17, 261–285. http://dx.doi.org/10.1016/0272-7714(83)90022-7.

Lubchenco, L., Menge, B.A., Garrity, S.D., Lubchenco, P.J., Ashkenas, L.R., Gaines, S.D., Emlet, R., Lucas, J., Strauss, S., 1984. Structure, persistence and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). J. Exp. Mar. Biol. Ecol. 78, 23–73. http://dx.doi.org/10.1016/0022-0981(84)90069-8.

Martínez, M.L., Intralawan, A., Vázquez, G., Pérez-Maqueo, O., Sutton, P., Landgrave, R., 2007. The coasts of our world: Ecological, economic and social importance. Ecol. Econ. 63, 254–272. http://dx.doi.org/10.1016/j.ecolecon.2006.10.022.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., de la Morinière, E.C., van der Velde, G., 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar Ecol Progr Ser 194, 55–64. http://dx.doi.org/10.3354/meps194055.

Nash, R.D.M., Santos, R.S., 1998. Seasonality in diel catch rate of small fishes in a shallow-water fish assemblage at Porto Pim Bay, Faial, Azores. Estuar. Coast. Shelf Sci. 47, 319–328. http://dx.doi.org/10.1006/ecss.1998.0362.

Neill, W.H., Miller, J.M., Veer, HW.van.der., Winemiller, K.O., 1994. Ecophysiology of marine fish recruitment: a conceptual framework for understanding interannual variability. J. Sea Res. 32, 135–152. http://dx.doi.org/10.1016/0077-7579(94)90037-X.

Panfili, J., Thior, D., Ecoutin, J.-M., Ndiaye, P., Albaret, J.J., 2006. Influence of salinity on the size at maturity for fish species reproducing in contrasting West African estuaries. J. Fish Biol. 69, 95–113. http://dx.doi.org/10.1111/j.1095-8649.2006.01069.x.

Parsley, M.J., Palmer, D.E., Burkhardt, R.W., 1989. Variation in capture efficiency of a beach seine for small fishes. Am. J. Fish Manag. 9, 239–244. http://dx.doi.org/10.1577/1548-8675(1989)009<0239:VICEOA>2.3.CO;2.

Patsche, C.B., Rudolf, F., Mendes, A.M.S., Cunha, I.Da., Gomes, V.F., Wejse, C., Jeppesen, C., 2019. Dietary intake in undernourished adults living in Guinea-Bissau; A cross-sectional study. BMC Nutr. 5, 1–8.

Paugy, D., Lévêque, C., Teugels, G.G., 2003. The Fresh and Brackish Water Fishes of West Africa. IRD Editions, Paris.

Pennober, G., 1999. Analyse spatiale de l'environnement côtier de l'archipel des Bijagós (Guinée Bissau) (BSc thesis). Université de Bretagne Occidentale, France.

Polidoro, B., Ralph, G., Strongin, K., Harvey, M., Carpenter, K., Adeofe, T.A., Arnold, R., Bannerman, P., Nguema, JN.B.B., Buchanan, J., Camara, K.M.A., Camara, Y.H., Cissoko, K., Collette, B.B., Comeros-Raynal, M.T., Bruyne, G.D., Diouf, M., Djiman, R., Ducrocq, M., Gon, O., Harold, A.S., Harwell, H., Hilton-Taylor, C., Hines, A., Hulley, P.A., Iwamoto, T., Knudsen, S., Lewembe, J.D.D., Linardich, C., Lindeman, K., Mbye, E.M., Mikolo, J.E., Monteiro, V., Mougoussi, J.B., Munroe, T., Beh, J.H.M., Nunoo, F.K.E., Pollock, C., Poss, S., Quartey, R., Russell, B., Sagna, A., Sayer, C., Sidibe, A., Smith-Vaniz, W., Stump, E., Sylla, M., Morais, L.T.D., Vié, J.C., Williams, A., 2016. Red List of Marine Bony Fishes of the Eastern Central Atlantic. IUCN (International Union for Conservation of Nature), Gland.

R Core Team, 2020. R: A language and environment for statistical computing. Austria: R Foundation for Statistical Computing. Available at https://www.R-project.org/. (Accessed 8 March 2020).

Republic of Guinea-Bissau, 2019. Guinea Bissau First Biennial Update Report to the United Nations Framework Convention on Climate Change. Republic of Guinea-Bissau, Bissau.

Rice, J., 1995. Food-web theory, marine food webs, and what climate change may do to northern marine fish populations. In: R.J., Beamish (Ed.), Climate Change and Northern Fish Populations. National Research Council of Canada, Ottawa, Ontario, pp. 516–568.

Schneider, W., 1990. FAO Species Identification Sheets for Fishery Purposes. Field Guide to the Commercial Marine Resources of the Gulf of Guinea. FAO, Rome.

Shannon, L.J., Cury, P., Jarre, A., 2000. Modelling effects of fishing in the Southern Benguela ecosystem. ICES J. Mar. Sci. 57, 720–722. http://dx.doi.org/10.1006/jmsc.2000.0716.

Sheaves, M., Baker, R., Nagelkerken, I., Connolly, R.M., 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuar. Coasts 38, 401–414. http://dx.doi.org/10.1007/s12237-014-9846-x.

Tandstad, M., Caramelo, A.M., Carocci, F., Carpenter, K., Sanciangco, J.C., 2014. Oceanography, geology, biogeography, and Fisheries of the Eastern Central Atlantic. In: Carpenter, K.E., De Angelis, N. (Eds.), The Living Marine Resources of the Eastern Central Atlantic. FAO, Rome, pp. 1–16.

Thiaw, M., Auger, P.A., Ngom, F., Brochier, T., Faye, S., Diankha, O., Brehmer, P., 2017. Effect of environmental conditions on the seasonal and inter-annual variability of small pelagic fish abundance off North-West Africa: The case of both Senegalese sardinella. Fish Oceanogr. 26, 583–601.

Torricelli, P., Tongiorgi, P., Almansi, P., 1981. Migration of grey mullet fry into the arno river: Seasonal appearance, daily activity, and feeding rhythms. Fish. Res. 1, 219–234. http://dx.doi.org/10.1016/0165-7836(81)90026-6.

Tous, P., Ducrocq, M., Bucal, D., Feron, E., 1998. Shark populations are possibly under serious threat in the Bijagos archipelago (Biosphere Reserve), Guinea Bissau. West Africa. Shark News 10, 4.

Valdés, L., Déniz-González, I., 2015. Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem. Intergovernmental Oceanographic Commission of UNESCO (IOC-UNESCO, Paris.

van der Veer, H.W., Adriaans, E.J., Bolle, L.J., Dankers, N., Malaba, L., Fonseca, D.A., Witte, JIJ., 1995. Ecological observations on juvenile flatfish in a tropical estuary: Arquipélago dos Bijagós, Guinea-Bissau. Neth. J. Sea Res. 34, 221–228. http://dx.doi.org/10.1016/0077-7579(95)90029-2.

Whitehead, PJP., 1985. FAO Species Catalogue. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Whitehead PJP FAO Fish. Synop. 125, 1–303, FAO, Rome.

Youmbi, J.T., Djama, T., Gabche, C., 1991. Reproductive patterns of *Sardinela maderensis* (Lowe, 1841) off Cameroon. J. Appl. Ichthyol. 7, 60–63. http://dx.doi.org/10.1111/j.1439-0426.1991.tb00595.x.