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Biology and ecology of sea catfish (Ariidae) of estuarine, lagoon and coastal ecosystems in West Africa

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Abstract :

The family Ariidae, sea catfish of the order Siluriformes, is widely distributed throughout the world, particularly in tropical and sub-tropical areas. The three species of Ariidae found on the coasts and estuaries of West Africa are the smoothmouth catfish Carlarius heudelotii (Valenciennes 1840), the rough-head catfish Carlarius latiscutatus (Günther 1864) and the Guinean sea catfish Carlarius parkii (Günther 1864). They have been increasingly exploited by artisanal and industrial coastal fisheries in recent decades, but there is still little information available on their ecology and biology. The aim of this study was to deepen our knowledge of these three West African Ariidae species, based on a dataset collected between 1980 and 2013 during experimental fishing programmes. They were carried out in Mauritania in the Banc d'Arguin National Park (PNBA), in Senegal in the Sine Saloum estuary including the Bamboung Marine Protected Area (MPA), in The Gambia in the Gambia estuary, in Guinea-Bissau in the Urok Islands MPA in the Bijagos archipelago, in Guinea in the Fatala estuary and Dangara inlet, and in Côte d'Ivoire in the Ebrié Lagoon. C. latiscutatus accounted for 65%, C. parkii for 29% and C. heudelotii for 6% of total number of Ariidae sampled. C. latiscutatus was abundant in the Sine Saloum and Gambia estuaries as well as in Guinea and Guinea-Bissau and was the only species present in the Ebrié Lagoon. C. parkii was in the majority in Mauritania. The three species were recorded in a salinity range of 0 to 50, a temperature range of 19 to 34 °C, in areas 1.7 to 15 m depth, and transparency ranging from 0.1 to 4 m (Secchi disk depth). C. heudelotii was present in less saline (25 vs. 32-34), less warm (27 vs. 29 °C) and less transparent (0.8 m vs. 1.6 m) waters than the two other species. The maximum sizes (453 mm, 614 mm, and 525 mm, for respectively, C. heudelotii, C. latiscutatus and C. parkii) were comparable to those recorded at sea. Length-weight relationships calculated for each species showed b coefficients greater than 3. Sex ratios were always in favour of females. The number of mature individuals and their smallest size at maturity were calculated per species, sex, and study area. A size of 27 to 28 cm at first maturity was estimated for females of C. latiscutatus. A few dozen records made it possible to describe fecundity and cases of oral incubation by females. The diet of the three species was composed of crustaceans, fish and mollusks, confirming their classification as generalist predators. Thanks to their high environmental tolerance, these sea catfish populations are able to occupy both the continental shelf and adjacent estuaries throughout their life cycle, with the exception of spawning, which generally takes place at sea.

Keywords : Ariidae, euryhalinity, marine catfish, tropical estuary, West Africa

Introduction

The family Ariidae, sea catfish of the order Siluriformes, is widely distributed throughout the world, particularly in tropical and sub-tropical areas (Marceniuk and Menezes, 2007). They are of marine origin, but many species enter estuaries, and some are confined to freshwater (Vreven and De Vos, 2007). In a review of diversity and conservation of Malaysian fishes, Ariidae have been reported in freshwater, marine and estuarine habitats (Chong *et al.*, 2010). In Papua New Guinea, they are an important component of the native freshwater ichthyofauna (Coates, 1991). Ariidae species are among the most abundant fishes in the Gulf of Mexico coastal zone (Yañez-Arancibia and Lara-Dominguez, 1988). They are predominant in density and biomass in the main channel of the Goiana estuary in north-east Brazil (Dantas *et al.*, 2010), and they are listed among the most ubiquitous families in a comparison between the fish assemblages of the Embley (north Australia) and Caeté (north Brazil) estuaries (Barletta and Blaber, 2007).

The Ariidae are characterised by three pairs of barbels, two closely spaced nostrils on either side of the head, short dorsal and anal fins, a forked caudal fin, and the presence of an adipose fin; their head is covered with bony plates (Daget, 1992; Vreven and De Vos, 2007). The West African species originally belonged to the genus *Arius* (Burgess, 1989; Daget, 1992; Fowler, 1936; Taylor, 1986, 1990) and were recently classified in a new genus, *Carlarius*, by Marceniuk (2003) who recognised them as a monophyletic lineage (Fricke *et al.*, 2020). The genus *Carlarius* differs from the genus *Arius* in that the lateral line does not bifurcate in the caudal region, reaching the upper lobe of the caudal fin and that the epi-occipital bone is exposed on the dorsal part of the skull (Marceniuk and Menezes, 2007).

The three species of Ariidae recorded on the coasts of West Africa (Acero and Betancur, 2016; Daget, 1992) are the smoothmouth catfish *Carlarius heudelotii* (Valenciennes 1840), the rough-head catfish *Carlarius latiscutatus* (Günther 1864) and the Guinean sea catfish

Carlarius parkii (Günther 1864). They occur mainly in coastal waters on muddy bottoms and regularly enter the brackish waters of estuaries and coastal lagoons (Conand *et al.*, 1995). A fourth species present in West Africa, the giant sea catfish *Carlarius gigas* (Boulanger 1911), is strictly confined to freshwater and has never been caught at sea (Daget, 1992).

In West African coastal environments, Ariidae are an important component of the demersal populations. They belong to the coastal Sciaenid community (Domain, 1980; Domain *et al.*, 1999; Longhurst, 1969), characteristic of soft bottoms from the coast to a depth of 20-30 m and of warm, potentially desalinated waters near estuaries. They are Marine-Estuarine species in the sense of Albaret (1999), i.e., highly euryhaline marine species that are abundant in estuarine and lagoon environments. Their distribution in these ecosystems is relatively widespread and permanent throughout the year; however, their reproduction takes place at sea. In the ecological guild proposed by Whitfield (2005) for fishes of Central and West African estuaries, *C. latiscutatus* and *C. parkii* belong to the category of marine migrants which generally reproduce at sea and whose juveniles and/or adults live in estuaries, while *C. heudelotii* is a marine straggler, of which only a small proportion of the population enters the estuary, generally near the mouth.

A number of recent works have highlighted the increasing importance of coastal Ariidae in the marine and estuarine fisheries of several West African countries. In Mauritania, all three species are fished in the EEZ, most notably *C. heudelotii*, which over the period 2000-2006 accounted for an average 3,378 t/year or 4.1% of the Mauritanian artisanal fisheries catch (Gascuel *et al.*, 2006). Particularly in the Banc d'Arguin National Park (PNBA), the landings of Ariidae have been increasing from 170 t in 2001 to 450 t in 2007, peaking at 674 t in 2005 (Correia *et al.*, 2020). In Senegal, Ariidae are one of the main coastal demersal resources, with a high export value, and the industrial Ariidae fishery, which started in 1977 with about 1,000 t/year, reached 8,892 t/year in 2014 (Diop *et al.*, 2017). In a recent study on the long-

term impact of fishing on Senegalese coastal demersal resources, which combined industrial and artisanal fishing CPUEs since the early 1970s and scientific trawl sampling surveys from 1986 to 2008, Ariidae came third in scientific fisheries and, of the 10 main demersal stocks studied, dominated by weight with 20% of CPUEs on average (Ba *et al.*, 2018). However, according to these authors, the trend has been towards a jagged decline since the 1980s and Ariidae are currently considered overexploited. On the Petite Côte of Senegal, Ariidae were among the main species fished between 2004 and 2013, mainly with set nets and longlines (Ndour *et al.*, 2016). In the Casamance estuary (Senegal), a study of by-catches of fixed shrimp gillnets in 2016 showed that *C. latiscutatus* was present in 23% of landings but accounted for only 0.44% of total catches, with individuals caught being either discarded or kept, depending on their size, and often smoked (Diadhiou *et al.*, 2018). In the Gambia estuary, in 2001-2002, Ariidae were one of the two taxa representing half of fish landings and accounted for 20% of catches by artisanal fisheries (Laë *et al.*, 2004). From 2005 onwards, their landings increased significantly, as a major by-catch of the bottom gillnet sole fishery in the Gambia estuary, and the stock assessment carried out in 2013 to estimate fishing mortality of *C. latiscutatus* and *C. parkii* led to recommendations to close the fishery from May to October, during their spawning period, and to increase mesh size for gillnets (Castro *et al.*, 2013). In Guinea-Bissau, a study carried out in the Bijagos archipelago between 2008 and 2010 showed that marine catfish accounted for 13% of the catches obtained by small-scale fisheries (Cross, 2015). In Guinea, the continental shelf is home to the largest Sciaenid community in the Gulf of Guinea and has enabled development of an important artisanal fishery sector but, having been competitively exploited by industrial trawler fishing, it showed signs of overexploitation in 1999 (Domain *et al.*, 1999). As a result of increasing fishing pressure from 1985 to 2012, Guinea's demersal assemblages thus suffered an overall decline and the large species (including Ariidae), which dominated Guinean artisanal and industrial

fisheries until the early 2000s, were gradually replaced by smaller species of lower commercial value (Camara *et al.*, 2016).

Despite their importance in West African coastal fisheries, there is still little information available on the ecology and biology of these three Ariidae species (Correia *et al.*, 2020). Biometric size-age relationships were proposed for Guinean marine catfish by Conand *et al.* (1995), who highlighted their slow growth and therefore their high vulnerability to exploitation. According to these authors, the Ariidae would reach 40 to 42 cm at the age of 6 and the 80 cm individuals quite often caught by small-scale fisheries would be between 20 and 30 years old. In a recent study on the reproductive biology of Ariidae from two coastal bays of Guinea, Koivogui *et al.* (2020) concluded that they had only one breeding season, during which coastal fisheries should be restricted to preserve the ability of broodstock renewal. Concerning estuarine areas, some aspects of the biology of Ariidae among other fish species were studied in the Sine Saloum estuary (Ecoutin and Albaret, 2003; Faye *et al.*, 2012; Ndiaye *et al.*, 2015; Panfili *et al.*, 2006) and in the Gambia estuary (Ecoutin *et al.*, 2005a). Diop *et al.* (2017) compared the reproductive traits of *C. latiscutatus* inside and outside the Bamboung MPA (Sine Saloum, Senegal), and confirmed that the breeding season for this species lasts from March to July. Finally, the reproductive ecology and growth of *C. latiscutatus* and *C. parkii* in the PNBA were investigated by Correia *et al.* (2020), who proposed a short-term fishing closure in May and June, during their spawning period.

The aim of the present work is to consolidate our knowledge of the ecology and biology of the three West African species of Ariidae using a large dataset from experimental fishing programmes that covered several estuarine, lagoon and coastal ecosystems from Mauritania to Côte d'Ivoire between 1980 and 2013. We will (1) compare the distribution of abundance of the three species in these ecosystems, in order to highlight their coastal or estuarine affinities, (2) propose environmental trends for each species in terms of salinity, temperature, depth and

water transparency, in order to characterise their degree of tolerance to the variations of the water physical-chemical parameters, (3) describe the size structures for the three species and propose length-weight relationships and condition factors, (4) compute indicators of the reproductive status (sex ratio, size of the smallest mature individual, size at first maturity) of these species and (5) investigate the hypothesis that these catfishes are generalist predators using observations of their stomach content.

Materials and Methods

Data Collection

This work is based on a dataset that is part of the PPEAO information system (www.ppeao.ird.fr) on fish assemblages and artisanal fisheries in West African estuaries, lagoons, and reservoirs. The data were collected between 1980 and 2013 during experimental fishing programmes and surveys of artisanal fisheries. They concern the ecology and biology of fish species in these ecosystems and their exploitation by artisanal fishing. The data used for the present study came only from the experimental fishing programmes archived in PPEAO (Simier *et al.*, 2019).

Study area

From north to south (Figure 1), the data were collected in Mauritania in the Banc d'Arguin National Park (PNBA - Sadio, 2015), in Senegal in the Sine Saloum estuary (Diouf, 1996; Ecoutin *et al.*, 2010) including the Bamboung Marine Protected Area (Ecoutin *et al.*, 2014; Sadio *et al.*, 2015), in The Gambia in the Gambia estuary (Albaret *et al.*, 2004), in Guinea-Bissau in the Urok Islands Marine Protected Area located in the Bijagos archipelago (Sadio, 2015), in Guinea in the Fatala estuary and Dangara inlet (Baran, 1995), and finally in Côte d'Ivoire in the Ebrié Lagoon (Albaret, 1994).

Sampling methodology

A purse seine net (length 250 m, height 20 m, mesh size 14 mm) was used to sample fish populations in all the ecosystems studied, with the exception of the Urok Islands MPA in Guinea-Bissau, where batteries of surface and bottom gillnets of different mesh sizes (14, 25, 36, 50, 60 and 80 mm) were set overnight. The fish caught were identified by species and their abundance was quantified based on their number and weight. Individual measurements of fork length (to the nearest mm) and weight (to the nearest g), identification of the sex and the stage of maturity, as well as identification of stomach contents were also carried out. The main physical-chemical parameters of the aquatic environment were measured on each fish sampling occasion: depth of the bottom at the sampling location with a hand-sounder, water transparency with a Secchi disc of 30 cm in diameter, salinity with a refractometer and temperature of the surface water with a thermometer.

Data processing

The overall geographical distribution of the species is described using 390 fishing operations containing Ariidae. The proportion of fishing operations containing Ariidae and their ecological preferences were determined on the basis of 1,453 fishing operations (whether these contained Ariidae or not) belonging to the standardised sampling protocol representative of an ecosystem as a whole and in all seasons. The search for environmental preferences was limited to *C. latiscutatus* and *C. parkii* because too few data were available for *C. heudelotii*. A total number of 4,775 individuals of the family Ariidae were caught. Of these, 2,811 were the subject of biological records, at least the measurement of individual fork length (in mm). When more than 50 individuals of the same species were caught in the same fishing operation, random sub-sampling was carried out, and the size structures were extrapolated to all the individuals. The population structure was described by size frequency distributions and mean and maximum length in all three species. Of the 2,811 individuals measured, 1,866 were also weighed individually allowing the calculation of length-weight relationships,

globally and for each species. Linear regressions of log(W) vs. log(FL), where W is the total weight in g and FL is the fork length in mm, were calculated to obtain the length-weight relationship of the form $W = K*FL^b$ (Froese, 2006) where log(K) is the intercept and b is the slope of the log-log regression. Individuals considered as outliers in a first step which involved all the data, were discarded in a second regression to improve the quality of the fit. Out of 2,140 sexed individuals, sex ratios were calculated and evaluation of the stage of sexual maturity according to Albaret and Legendre (1985) made it possible to determine the number of mature individuals and the size of the smallest mature individual per species, per sex and per country. The size at first maturity (fork length at which 50% of the individuals are mature or FL50) could only be estimated for females of *C. latiscutatus* in the Sine Saloum and Gambia estuaries. This was done by logistic regression, after grouping the individuals into 1 cm size classes and calculating the percentage of mature individuals in each class. To complete the description of reproduction, 22 occasional records of fecundity (number of eggs in the gonads of mature females) and 27 records of oral incubation (presence of eggs or embryos in the mouth) were also considered. Finally, the feeding behaviour of the three species is described on the basis of 290 records of stomach contents. Statistical analyses and graphs were carried out with R software (R Core Team, 2020).

Ethical statement

The scientist in charge of data collection and fish manipulation holded the “University Diploma in Animal Experimentation, Level II Accreditation n° I-51UFRReims-S2-09 from the University of Reims Champagne-Ardennes” and the “Animal Experimentation School Diploma - Design and implementation of experimental procedures at the Laboratory of Animal Physiopathology and Functional Pharmacology at ONIRIS - Ecole Nationale Vétérinaire, Agroalimentaire et de l'Alimentation Nantes Atlantique”, which ensures that animal welfare was respected during the faunal surveys. No harsh practices or chemicals were

used to immobilise or kill the fish before handling. Measurement, weighing and observation of gonads and stomach contents were done after the fish were dead. No specimens were processed alive.

Results

Spatial distribution

Ariidae were recorded in all the ecosystems sampled in West Africa, i.e., between 22°07N (PNBA in Mauritania) and 5°18N (Ebrié Lagoon in Côte d'Ivoire). Among the 4,775 individuals collected, 6% were *C. heudelotii*, 65% *C. latiscutatus* and 29% *C. parkii*. The proportion of purse seines containing at least one Ariidae of any species was 32% in Mauritania, 22% in Senegal and Guinea, 40% in The Gambia. It reached 97% in gillnet batteries in Guinea-Bissau. Table 1 lists the distribution of the three Ariidae species per ecosystem in terms of number of occurrences, numbers, and biomass. In the Banc d'Arguin National Park, the most abundant species was *C. parkii* (76% of Ariidae abundance), followed by *C. heudelotii* (23%) while *C. latiscutatus* was almost absent. In the Sine Saloum estuary (including Bamboung MPA), the Gambia estuary and the Urok Islands MPA, *C. latiscutatus* dominated (from 60% of Ariidae abundance in the Sine Saloum to 75% in the Urok Islands MPA), followed by *C. parkii*. *C. heudelotii* was rarely recorded (maximum 8.4% of Ariidae abundance in the Gambia estuary), if at all in the Urok Islands MPA. In Guinea, *C. parkii* was rarely present, and *C. latiscutatus* accounted for 60% of Ariidae abundance in the Fatala estuary, compared to only 14% in the Dangara inlet where *C. heudelotii* was dominant. In the Ebrié Lagoon, Ariidae were very rare, only six occurrences of *C. latiscutatus* were recorded and none for the other two species, so this ecosystem was subsequently disregarded.

Environmental trends

Salinity where Ariidae were recorded ranged from 2.5 to 43 with a median value of 25 for *C. heudelotii*, from 0 to 50 with a median of 31.9 for *C. latiscutatus*, and from 7 to 50 with a median of 34 for *C. parkii* (Figure 2A). The temperature range was 20.7 °C to 32 °C with a median of 27 °C for *C. heudelotii*, 22.5 °C to 34 °C with a median of 29 °C for *C. latiscutatus* and 19.3 °C to 34 °C with a median of 28.7 °C for *C. parkii* (Figure 2B). The bottom depth at the location of the fishing sites varied between 1.7 m and 15 m, with a median of around 6 m (Figure 2C). Ariidae were present in a range of transparency from 0.1 m to 4 m (Secchi disk depth), with a median value of 0.8 m for *C. heudelotii* versus 1.6 m for the other two species (Figure 2D). In the Gambia estuary, which was sampled over a distance of 220 km, *C. heudelotii*, *C. latiscutatus* and *C. parkii* were occasionally recorded up to 117 km, 140 km and 173 km from the mouth, respectively. In the Sine Saloum estuary, all three species were present up to 30 km from the mouth, but never in the following 110 km upstream.

The range of salinity with the highest occurrence of *C. latiscutatus* was 10 to 30, more particularly 15 to 20, where the species was present in 40% of fishing operations. *C. parkii* was preferentially found between 15 and 20 and between 30 and 35 (20 to 25% of operations). Neither species was recorded at a salinity higher than 50, while fishing operations occurred up to salinities of 134 in the inverse estuary of the Sine Saloum in Senegal. In terms of water surface temperature, the preferred range of *C. latiscutatus* was between 24 and 32 °C, where it was present in 20 to 30% of the fishing operations. Although samplings were made at temperatures as low as 16 °C, *C. latiscutatus* was never found below 22 °C, but was found at the highest temperatures encountered (32 °C). *C. parkii* was recorded from 19 °C and its preferential range was between 22 and 26 °C and between 30 and 32 °C, where it was present in 17% of the fishing operations. The depth range where *C. latiscutatus* and *C. parkii* were found in the highest occurrence was between 3 and 9 m (25 to 32% and 15 to 20% of the fishing operations respectively). The two species were only recorded at depths down to 15 m,

although samplings were conducted down to a depth of 20 m. In terms of transparency, *C. latiscutatus* was frequent between 0 and 2.5 m (more than 20% of operations) and the maximum occurrence was found between 0.5 and 1.0 m (32% of operations). The transparency preference for *C. parkii* was between 0.5 m and 1.5 m where the species was present in 20% of the fishing operations. The two species were never recorded when the transparency was higher than 4 m.

Size structure

Of the 2,811 individuals subjected to biological records, 8% were *C. heudelotii*, 60% *C. latiscutatus* and 32% *C. parkii*. In *C. heudelotii* (279 individuals), fork length ranged between 84 and 453 mm with an average of 193 mm (Table 2) and the main mode was between 120 and 180 mm, with a second, less marked mode between 220 and 280 mm (Figure 3). The length of the most abundant species, *C. latiscutatus* (3,136 individuals after extrapolation) ranged between 53 and 614 mm, with an average length of 302 mm and a well-marked mode between 280 and 340 mm. Finally, the size distribution of 1,401 individuals of *C. parkii*, whose lengths ranged between 72 and 525 mm with an average of 275 mm, was more widespread with no obvious mode. The smallest individuals (50 to 80 mm) were often found in the mouths of large individuals.

The maximum sizes of all three species were recorded in Senegal, i.e., 453 mm for *C. heudelotii*, 614 mm for *C. latiscutatus* and 525 mm for *C. parkii* (Table 3). *C. heudelotii* rarely exceeded 400 mm: apart from the maximum size, only one individual of 410 mm was caught in The Gambia. In *C. latiscutatus*, sizes of above 500 mm were measured 18 times in Senegal and Guinea-Bissau. In *C. parkii*, sizes larger than 500 mm were rare: apart from two individuals measuring 525 mm and 500 mm in Senegal, only one individual of 508 mm was recorded in Mauritania.

Length-weight relationships and condition factor

Despite the limited number of *C. heudelotii* (230 individuals measured but only 24 of them weighed), a good adjustment was obtained as for the other species (r=0.99). The allometry coefficient b was higher than 3 in all three species. The condition coefficient K (expressed in 10^{-5}) ranged from 0.417 for *C. latiscutatus* to 0.714 for *C. heudelotii*, via 0.627 for *C. parkii* (Table 4).

Reproduction

The distribution per species and sex showed that the sex ratio was always in favour of females whatever the species: 1.2 in *C. heudelotii*, 2.04 in *C. latiscutatus*, and 1.5 in *C. parkii* (Table 5). The proportion of immature individuals was much higher in *C. heudelotii* than in the other two species. In the smallest size classes (up to 24 cm for *C. latiscutatus* and 21 cm for *C. parkii*), the sex ratio was generally balanced, with the proportion of females increasing considerably above these sizes.

Of the 689 males, only 90 (13%) reached a stage of maturity corresponding to the beginning of sexual maturation (stage 3 on the scale of Albaret and Legendre, 1985). Most were *C. parkii* or *C. latiscutatus* (only 2 *C. heudelotii*). Of these, 37 individuals had reached maturity (stage 4), including 27 *C. parkii* and 10 *C. latiscutatus* caught in the Sine Saloum estuary. The smallest maturing male, a *C. parkii* caught in the Sine Saloum estuary, measured 239 mm (Table 6). In *C. latiscutatus*, the smallest maturing male was recorded in Guinea and measured 245 mm. In *C. heudelotii*, only two males were recorded at stage 3 or 4, both in Guinea, the smallest one measured 248 mm. Of the 1,245 females, 399 (32%) had begun sexual maturation. Of these, 236 were maturing (stage 3), 88 were mature (stage 4), 11 were in the spawning phase (stage 5) and 64 were at spent stage (stage 6). As with the males,

C. heudelotii was very rarely recorded at maturity (only 7 females at stage 3 or above). The smallest maturing *C. heudelotii* female was 280 mm long in Mauritania, the smallest maturing *C. latiscutatus* female was 225 mm long in The Gambia and the smallest maturing *C. parkii* female was 190 mm long in Senegal (Table 6).

There were only sufficient female *C. latiscutatus* individuals at the beginning of the sexual maturity process (stage ≥ 3) to allow the calculation of size at first maturity (FL50). In the Sine Saloum estuary in Senegal, FL50 was estimated at 28.12 ± 1.01 cm, for a sample of 214 individuals of which 121 were mature. In The Gambia, FL50 was estimated at 27.79 ± 0.54 cm for 66 individuals of which 26 were mature.

Fecundity was occasionally evaluated for female *C. latiscutatus* (n=6) and *C. parkii* (n=16) in the Sine Saloum and Gambia estuaries, from March to June, at the reproduction season. For *C. latiscutatus*, 13–20 eggs in the gonads were reported, i.e., an average of 16.2 ± 2.8 eggs per female. For *C. parkii*, fecundity ranged between 13 and 49 eggs with an average of 26.3 ± 10 eggs per female. In addition, cases of oral incubation of eggs or embryos by *C. latiscutatus* (n=8), *C. parkii* (n=19) and *C. heudelotii* (n=1) were recorded, at the same season, in the Sine Saloum and the Gambia estuaries. These were always females at spent stage, or sometimes in the spawning phase, varying in size from 250 to 495 mm. They carried in their mouths either eggs, embryos or young individuals less than 70 mm in size, sometimes with their yolk sac. For *C. parkii* (n=6) the number of eggs in the mouth ranged between 12 and 63 (30 ± 17.8).

Feeding behaviour

Stomach contents were identified in 290 individuals (Table 7). Among these, the great majority were *C. latiscutatus* (233 individuals), 55 *C. parkii* and only two *C. heudelotii*. The majority of these records were made in Guinea-Bissau and Senegal.

In 79% of the cases, only one type of content was identified; in 18% of cases there were two, and in only nine individuals, three to five different contents were identified in the same stomach. A total of 365 items were recorded. The most frequent was crab (37% of occurrences) such as *Callinectes sp.* and *Uca sp.*, followed by fish (23%), including pelagic fish such as *Sardinella maderensis* and *Ethmalosa fimbriata*, mollusks (13%), mainly bivalves, and shrimps (5%). In *C. latiscutatus* and *C. parkii*, the occurrence of fish was similar (22-24% of stomachs), whereas crabs were more frequently recorded in *C. latiscutatus* (40%) than in *C. parkii* (22%). Conversely, bivalves were more frequent in *C. parkii* (9%) than in *C. latiscutatus* (3%).

Discussion

Spatial distribution

This study highlighted the significant presence of the three coastal Ariidae species known in West Africa in several estuarine and very coastal areas from Mauritania to Côte d'Ivoire (i.e., between 22°N and 5°N). This is consistent with the distribution of these species along the West African coasts according to Acero and Betancur (2016), i.e., *C. heudelotii* from Cabo Blanco (Mauritania) to Gabon and potentially Angola, *C. latiscutatus* from northern Senegal to Namibia and *C. parkii* from Cabo Blanco (Mauritania) to Angola.

C. heudelotii was recorded in most of the areas studied here (except the Urok Islands and the Ebrié Lagoon) but generally in small numbers. It was abundant only in the Dangara inlet in Guinea and in the Banc d'Arguin National Park in Mauritania, both widely connected to the sea and without freshwater inputs. This is in adequacy with the classification of *C. heudelotii* by Whitfield (2005) as a marine straggler, category of which only a small proportion of the population enters the estuaries, generally near the mouth. *C. heudelotii*, commonly caught around 12-14 m on the Guinean continental shelf, is part of the coastal Sciaenid community,

grouping shallow-water species characteristic of sandy-muddy bottoms close to the coast, and rarely recorded at depths of more than 30 m (Conand *et al.*, 1995; Domain *et al.*, 1999). Thus, in the 1970s and 1980s, *C. heudelotii* was the main coastal species caught by the Senegalese artisanal fishing trawlers (Caverivière and Thiam, 1993). The two other species, *C. latiscutatus* and *C. parkii*, in the majority in the present study, are marine migrants according to Whitfield (2005), i.e. species which generally reproduce at sea and whose juveniles and/or adults live in estuaries. *C. latiscutatus* accounted for two-thirds of the total number of Ariidae in the estuaries of Sine Saloum and Gambia, as well as in the Urok Islands. *C. latiscutatus*, caught at sea in depths of between 8 and 14 m, was considered by Domain *et al.* (1999) to be a more coastal species than *C. heudelotii*. *C. parkii* accounted for almost one third of the total number of Ariidae in the present study. According to Domain *et al.* (1999), *C. parkii*, not abundant on the Guinean continental shelf, is characteristic of the estuarine Sciaenid community. In the present study, it made up three quarters of the abundances of Ariidae in the Banc d'Arguin National Park in Mauritania. *C. parkii* has occasionally been recorded on the Moroccan coast (Daget, 1986) and in the Mediterranean Sea (Golani and Ben-Tuvia, 1986; Golani and Sonin, 1996), where it was classified by CIESM (2002) as an 'alien' species (Kaimuddin *et al.*, 2016). Its dominance among the Ariidae in the Banc d'Arguin National Park tends to confirm that it is the most northerly of the three species.

Along the coast from Mauritania to Guinea, the Ariidae species account for a large proportion of the Sciaenid community (Caverivière *et al.*, 1988; Domain, 1980; Domain *et al.*, 1999). The wideness of the Senegalese-Mauritanian and Guinean shelves, 40 nm in front of the PNBA to 68 nm off Guinea-Bissau (Domain, 1977; Domain and Richer de Forges, 1985) could be a factor favouring the abundance of these very coastal demersal species living on muddy and sandy-muddy bottoms at shallow depths. Their significant presence reported in the present study in the estuaries of Senegal, Gambia, Guinea and the Bijagos archipelago

suggests that these ecosystems are a natural part of the habitat of coastal populations of Ariidae. In the Gambia estuary, the presence of Ariidae up to 173 km from the mouth attests to their wide use of estuaries, in agreement with data from small-scale fisheries reporting the frequent landing of Ariidae 187 km from the mouth of the Gambia estuary (Laë *et al.*, 2004). In the Casamance estuary, *C. latiscutatus* and *C. parkii* were recorded in landings up to 170 km and 93 km from the mouth, respectively (Kantoussan *et al.*, 2012). In the Ebrié Lagoon (Côte d'Ivoire), however, Ariidae were very rare, the only species occasionally encountered being *C. latiscutatus*. This could be related to their limited abundance along the coast in Côte d'Ivoire, where they are not among the main demersal species (Caverivière, 1982; Caverivière, 1993). The narrowness of the Ivorian continental shelf, only 10 nm off Abidjan (Martin, 1973), could be an unfavourable factor for the settlement of Ariidae populations off Côte d'Ivoire and therefore in the Ebrié Lagoon. Indeed, further south, opposite the Congo, where the continental shelf widens, Ariidae are among the dominant species of coastal settlement (Fontana, 1981). Another hypothesis concerning the limited abundance of Ariidae in the Ebrié Lagoon could be the competition with estuarine catfish of freshwater origin belonging to the family Claroteidae (*Chrysichthys maurus, Chrysichthys nigrodigitatus* and *Chrysichthys auratus)*, which are more regularly encountered and may occupy a similar ecological niche (Albaret, 1994; Ecoutin *et al.*, 2005b).

In Mauritania, Senegal, The Gambia, and Guinea, 22 to 40% of fishing operations caught at least one Ariidae. This family appears to be very ubiquitous in West African estuaries but, in terms of numbers and biomass, it represents a small part of the fish assemblages (Baran, 1995). In the Banc d'Arguin in Mauritania, the Ariidae accounted for a very low percentage of the total numbers and biomass, with the exception of *C. parkii* representing 8 % of the biomass and 3.7 % within the PNBA (Sadio, 2015). In the Sine Saloum estuary, the fish communities were dominated by the small pelagic species *Sardinella maderensis*, *Ethmalosa*

fimbriata and *Ilisha africana* and the Ariidae were not abundant (Simier *et al.*, 2004). In the Bamboung MPA, however, the biomass of *C. latiscutatus* and *C. parkii* increased from year to year from the implementation of the fishing ban in 2003 to 2007: 11 to 572 kg and 9 to 195 kg respectively (Ecoutin *et al.*, 2014). In the same way, when comparing the fish assemblages in the Bamboung MPA to an unprotected neighbouring site, Sadio *et al.* (2015) showed that *C. latiscutatus* represented 24 % of the biomass in the MPA vs. only 0.5% in the unprotected site. In the Gambia estuary, the fish communities were largely dominated by the Sciaenidae *Pseudotolithus elongatus*, followed by the Clupeidae *Ethmalosa fimbriata*, *Ilisha africana* and *Sardinella maderensis*, while the three Ariidae species represented only 3.3 % of the biomass and 1.3 % of the numbers (Albaret *et al.*, 2004). In the Fatala estuary, the Ariidae accounted for less than 1 % of the numbers and biomass, except *C. parkii* with 2.3 % of the total biomass (Baran, 1995). All these fishing operations were carried out using a purse seine net, which is considered as more effective in sampling pelagic fish than demersal fish (Paugy and Lévêque, 1999). This purse seine net, however, was the same for all experimental fishing programmes, allowing reproducible sampling of fish assemblages, and was not very selective in its design (length 250 m, height 20 m, mesh size 14 mm) and the way it was used without any surface search for schools of fish (Albaret and Legendre, 1985; Albaret *et al.*, 2004). In addition, the water depth never exceeded 15 m, so the entire water column was sampled. In contrast, in the Urok Islands MPA in Guinea-Bissau, sampled using gillnets, *C. latiscutatus* and *C. parkii*, caught in almost all fishing operations, were also in the majority among the fish assemblages: respectively 30 % and 10 % of numbers and 34 % and 9 % of biomass (Sadio, 2015). Gillnets are indeed very selective for Ariidae which get easily meshed or hung due to the long erectile spines of their dorsal and pectoral fins.

Environmental trends

All three species were present in a wide range of salinity conditions, from freshwater to salty water, but never above 50. These results confirm, with a greater number of individuals, the outcomes of Panfili *et al.* (2006) for a sampling of the Sine Saloum and Gambia estuaries included in the present dataset. Ariidae, despite their euryhalinity, are not able to withstand extreme values of salinity such as those in the upstream part of the Sine Saloum estuary. The Sine Saloum has been affected by climate change in the decades before the 1990s, with a long period of drought resulting in a reversal of the salinity gradient and very high salinities (>100) in the upper estuary (Ecoutin *et al.*, 2010). The range of water temperatures where Ariidae were recorded was also wide, up to 34 °C, but never below 19 °C. All three species were caught in maximum water depths of 15 m and in a range of transparency from 0.1 m to 4 m. *C. latiscutatus* and *C. parkii* were recorded in very similar environmental conditions, while *C. heudelotii* tended to be present in less salty, slightly more turbid and slightly less warm waters. To our knowledge, no studies on the temperature or turbidity preferences of West African Ariidae have been published to date. Studies of other Ariidae species in various tropical estuarine ecosystems put forward the high eury-thermohaline capacity of these species and their Weberian apparatus acting as an amplifier of sounds and thus facilitating the detection of preys and predators in turbid environments. These particularities allows them to adapt to a large range of environments including turbid or low-salinity waters and to dominate fish assemblages in many tropical estuaries (Barletta and Blaber, 2007; Dantas *et al.*, 2010).

Size structure

In the estuarine ecosystems studied here, *C. heudelotii* was distinguished from the other two species by a narrower size range and an average length of only 19 cm (FL). This species rarely exceeded 40 cm (FL), and its maximum size recorded was 45 cm (53 cm TL), whereas according to Daget (1992) it can reach 76 cm (TL). *C. latiscutatus* and *C. parkii* reached

larger sizes, with average lengths of 30 and 27 cm and maximum lengths of 61 and 53 cm (73 and 60 cm TL), respectively, compared to 70 and 75 cm (TL) according to Daget (1992). In a comparative study of the reproductive traits of *C. latiscutatus* inside and outside the Bamboung MPA (Diop *et al.*, 2017), males averaged 390 mm (TL) inside the MPA and 380 mm (TL) outside, with maximum sizes of 609 and 525 mm (TL), while females averaged 424 mm (TL) inside the MPA and 402 mm (TL) outside, with maximum sizes of 750 and 674 mm (TL). Maximum sizes of 850 mm, 730 mm and 530 mm (TL) for *C. latiscutatus, C. heudelotii* and *C. parkii* respectively were measured at sea on the Guinean continental shelf (Conand *et al.*, 1995; Sidibé, 2003). In *C. parkii*, the maximum size in the estuary therefore seems to be slightly higher than at sea (60 cm vs. 53 cm TL).

Length-weight relationships and condition factor

The present study made it possible to propose length-weight relationships for each of the three species studied, based on large numbers of individuals, except for *C. heudelotii*. A global relationship for the three species was also calculated for the purpose of biomass estimates from fishing data where the three species are often grouped together. The allometry coefficient b was always higher than the theoretical value of 3, indicating a faster increase in weight than in size and thus a favourable environment for these species.

For *C. latiscutatus*, the parameters of the length-weight relationship we propose ($K=0.417*10^{-5}$ and $b=3.194$) can be compared to several other parameters for West Africa. The datasets used by Ecoutin and Albaret (2003) ($K=1.32*10^{-5}$ and $b=2.994$; n=80; FL range: 107–523 mm), and by Ecoutin *et al.* (2005a) ($K=0.486*10^{-5}$ and $b=3.166$; n=183; FL range: 87–347 mm) are included in the present study, but subsequent sampling in the Bamboung and Urok Islands MPAs brought the number of individuals measured to 1,201 and extended the size range (maximum length of 614 mm). In a recent study in the Sine Saloum estuary,

Ndiaye *et al.* (2015) found a=0.025 and b=2.54 (n=130; TL range: 20–28 cm) and in the PNBA (Mauritania), Correia *et al.* (2020) estimated a = 0.0026 and b=3.31 for male and female combined (n=346; TL range: 24.9–85.5 cm). These results cannot be directly compared with ours as they both concerned total lengths and Ndiaye *et al.* (2015) covered a very small size range. Finally, on the Guinean continental shelf, Sidibé (2003) obtained coefficients a=0.0117 (i.e., $K=1.027*10^{-5}$) and b=3.033 (n=1,789; FL range=12–50 cm). With the exception of the results of Ndiaye *et al.* (2015) and Correia *et al.* (2020), the different length-weight relationships proposed for *C. latiscutatus*, whether in estuaries or at sea, produced very similar results. Thus, the weight of a 300 mm individual (average fork length in our study) was estimated at 340 g based on the present study, 344 g according to Ecoutin *et al.* (2003), 338 g according to Ecoutin *et al.* (2005a) and 335 g according to Sidibé (2003).

Very few studies propose length-weight relationships for the other two species studied here: *C. parkii* ($K=0.627*10^{-5}$ and b=3.137) and *C. heudelotii* ($K=0.714*10^{-5}$ and b=3.111). A relationship ($K=0.506*10^{-5}$ and b=3.168; n=35; FL range=72–285 mm) was published for the first time for *C. parkii* by Ecoutin *et al.* (2005a) in the Gambia estuary. These parameters were close to those obtained here in a larger sample (591 individuals). For a 300 mm individual, the weight was estimated at 356 g and 370 g, respectively, by the two relationships. In the PNBA (Mauritania), Correia *et al.* (2020) proposed a=0.0064 and b=3.09 for C. parkii (n=345 – TL range 24.7– 66cm).

For *C. heudelotii*, a relationship (a=0.023 and b=2.65; n=104; TL range: 18.5–26 cm) was proposed by Ndiaye *et al.* (2015), but again in a very narrow size range. Parameters (a=0.025 and b=2.671; n=193) estimated for the Cross River Estuary, Nigeria (Etim, 2000) are available in Fishbase (Froese and Pauly, 2020). However, it is difficult to compare these results with ours, as the type of length and the size range were not given. For a 20 cm

individual, the latter relationship (Etim, 2000) estimates the weight at 74 g, while ours estimates it at 103 g.

Reproduction

In the present study, 13% of males and 32% of females, all species combined, had begun sexual maturation. Of the females, only 7% had reached maturity, 1% was in the spawning phase and 5% were at spent stage. This very low percentage of mature individuals is consistent with their classification as Marine-Estuarine species (abundant in estuaries, but do not breed there) by Albaret (1999) and with their classification as marine migrants (*C. latiscutatus* and *C. parkii*) and marine straggler (*C. heudelotii*) by Whitfield (2005). According to Diouf (1996), however, *C. parkii* can reproduce in estuaries, particularly in the cold dry season, whereas *C. latiscutatus* and *C. heudelotii* begin their sexual maturation in estuaries in the hot and dry season.

For *C. heudelotii,* the beginning of sexual maturity was recorded here in females measuring more than 28 cm (FL). The sex ratio for this species was fairly close to equilibrium, although it was calculated based on a small number of individuals because the proportion of undifferentiated individuals was almost 50%, consistent with the low average size (19 cm). For *C. latiscutatus* and *C. parkii,* the smallest mature individuals measured 22.5 cm and 19 cm respectively. In *C. latiscutatus,* females were in the majority overall, as pointed out by Diop *et al.* (2017): 70% females and 30% males inside and outside the Bamboung MPA. However, this bias was less marked in *C. latiscutatus* individuals under 24 cm in length, and in *C. parkii* individuals under 21 cm in length. This result should be linked to these of Sidibé (2003) for *C. latiscutatus* on the Guinean continental shelf, where the sex ratio was balanced up to 34 cm, and then increased in favour of females.

In females of *C. latiscutatus*, size at first maturity (FL50) was estimated to be 28 cm (33 cm in TL) in Senegal and The Gambia. Diop *et al.* (2017) reported higher values of TL50 in the Sine Saloum estuary: 40 cm in the Bamboung MPA and 42 cm outside. A FL50 of 40 cm was also proposed by Correia *et al.* (2020) for *C. latiscutatus* in the PNBA. However, our results are comparable to those of Sidibé (2003) and Domain *et al.* (1999), who reported a FL50 of 27.5 cm and 30 cm respectively for *C. latiscutatus* on the Guinean continental shelf.

Our records indicated an average fecundity of 16.2 ± 2.8 eggs per female for *C. latiscutatus*, which is less than the results of Diop *et al.* (2017), who reported 29 ± 14 eggs for this species in the Bamboung MPA and 22 ± 10 outside, and than those of Correia *et al.* (2020) in the PNBA with 45.3 ± 20.8 eggs. In *C. parkii*, fecundity was 26.2 ± 9.6 eggs on average, similar to the results of Correia *et al.* (2020): 25.9 ± 6.2.

In the present study, cases of oral incubation were recorded in a few *C. latiscutatus* and *C. parkii* females. Most, if not all, Ariidae are mouth incubators, a mode of reproduction rarely recorded in other catfish (Vreven and De Vos, 2007). Mouthbrooding catfishes are mainly estuarine or marine (Bruton, 1996). Males are generally reported to carry in their mouth relatively large fertilized eggs (e.g. 16 mm in diameter for *Galeichthys feliceps*) and hatched larvae up to 100 mm long (Bruton, 1996; Rimmer, 1985; Rimmer and Merrick, 1982; Tilney and Hecht, 1993). In a study of eggs and larvae mouthbreeding in *Genidens genidens* from Guaratuba bay (Brazil), Chaves (1994) reported that it was not possible to recognize the sex or degree of maturity of the adults carrying eggs, given the small volume of their gonads.

Feeding behaviour

In the specimens whose stomach content was investigated (80% *C. latiscutatus* and 19% *C. parkii*), the diet consisted mainly of crustaceans (crabs and shrimps), fish (including pelagic fish) and mollusks, which confirms the classification of West African coastal Ariidae as

generalist second-level predators. In the Sine Saloum estuary (Senegal), the diet of the three Ariidae was described by Diouf (1996) as being composed of fish and shrimps, plus crab and zooplankton for *C. latiscutatus* and *C. heudelotii*. In a feeding behaviour study of ten species of Bamboung MPA (Faye *et al.*, 2012), *C. latiscutatus* was characterised as a macro-carnivore, the volumetric proportions of its preys indicating that it was feeding half on fish (53%) and the rest on macro-crustaceans (17%), benthic invertebrates (15%) and mollusks (10%). Finally, in the Ebrié Lagoon (Côte d'Ivoire), the diet of *C. latiscutatus* consisted of juvenile fish, mollusks, shrimps, and crabs (Albaret, 1994).

The genus *Carlarius* is characterized by the absence of vomerine tooth plates and by well developed oval shaped accessory tooth plates (Marceniuk & Menezes, 2007). Palatal teeth for *C. latiscutatus* are in 2 paired patches (Acero & Betancur, 2016), which is comparable to other ariid catfishes from Australia, *Arius thalassinus* and *Arius bilineatus*, having two groups of three contiguous plates of palatine teeth on each side, meeting in the midline (Blaber *et al.*, 1994). The diet of *C. latiscutatus* was in fact very similar to the diet of these two Australian species, consisting of mainly fish and decapod Crustacea (crab and penaeid prawns). The palatal teeth of *C. parkii* are in two large patches separated by their own diameter or less, while those of *C. heudelotii* are absent or in one or two small patches very distant from each other (Marceniuk & Menezes, 2007). The palatal teeth of these two species look like those of *Arius* sp. 3 in Blaber *et al.* (2014), a primarily invertebrate feeder (alpheid shrimps, crab, polychaetes and molluscs), eating only a small proportion of fish. In the present study, bivalves were indeed more frequent in *C. parkii* than in *C. latiscutatus* but no information has been collected about the diet of *C. heudelotii*.

Conclusion

The analysis of this large dataset covering various types of estuarine, coastal and lagoon ecosystems in six West African countries has helped to consolidate knowledge on the biology of the three coastal Ariidae *C. heudelotii*, *C. latiscutatus* and *C. parkii*. Their regular presence has been attested in all ecosystems, the most abundant species being *C. latiscutatus*. It is likely that the abundance of coastal Ariidae, shallow-water demersal species, is favoured by the width of the continental shelf, including in the adjacent estuarine and lagoon ecosystems. Their high tolerance to environmental variations (salinity, temperature, turbidity) enables them to occupy estuarine environments as an extension of their coastal habitat, sometimes extending as far as significant distances from the river mouth. They thus move between the sea and the estuaries regardless of their age, as demonstrated by their wide range of sizes in estuaries, comparable to that in the coastal zone. However, *C. latiscutatus* and *C. parkii* undeniably have a stronger estuarine affinity than the more marine *C. heudelotii*. They spend their entire life cycle without distinguishing between the sea and estuaries, with the exception of spawning, which takes place at sea, after which they can quickly return to the estuaries, as shown by the presence of mature and mouthbrooding individuals in estuaries. It is therefore very likely that the same population is present in the sea and in the estuary. One hypothesis that could explain the occupation of estuaries by Ariidae could be of a trophic nature, as estuaries have a great wealth of potential prey, shellfish, crustaceans, or juveniles of other species. Comparative studies on their feeding behaviour at sea and in estuaries could enable this hypothesis to be tested.

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Figure 1. Map of West Africa with the countries and ecosystems studied.

Figure 2. Distribution of occurrences of the 3 West African coastal Ariidae species according to surface salinity (A), temperature in °C (B), bottom depth in m (C) and water transparency in m (D).

Figure 3. Size frequency distribution (per 20 mm class) of *C. heudelotii* (A), *C. latiscutatus* (B) and *C. parkii* (C).

Table 1. Sampling effort (Number of fishing operations) and distribution of the three Ariidae species in the ecosystems studied: number of fishing operations where the species occurred (Occ); Abundance (Numbers); Biomass in kg (Weight).

Country	**Ecosystem**	**Number of fishing operations**	***C. heudelotii***			***C. latiscutatus***			***C. parkii***		
			Occ	Numbers	Weight	Occ	Numbers	Weight	Occ	Numbers	Weight
Mauritania	Banc d'Arguin National Park	79	6	73	9.14	2	2	8.70	18	246	58.36
Senegal	Sine Saloum estuary	479	6	9	1.88	47	157	46.77	32	94	23.70

	Bamboung MPA	426	3	3	2.41	11 1	2,124	1,11 9.77	69	842	387 .50
The Gambia	Gambia River estuary	215	16	56	10.1 6	77	496	64.4 5	37	115	10. 56
Guinea-Bissau	Urok Islands MPA	33	0	0	0	31	221	86.6 6	15	73	23. 43
Guinea	Fatala estuary	109	7	21	1.91	21	46	5.22	2	9	0.3 9
	Dangara Inlet	46	7	136	9.78	9	23	3.86	5	6	1.7 8
Côte d'Ivoire	Ebrié Lagoon	397	0	0	0	6	15	1.13	0	0	0

Table 2. Numbers after extrapolation, minimum and maximum length and mean length ± standard deviation per species.

Species	Numbers	Length range (mm)	Mean length (mm) ± SD
C. heudelotii	279	84 – 453	193.0 ± 66.9
C. latiscutatus	3,136	53 – 614	301.7 ± 82.8
C. parkii	1,401	72 – 525	274.7 ± 86.5

Table 3. Maximum length in mm and total number of individuals measured (in brackets) per species and country.

Country	***C. heudelotii***	***C. latiscutatus***	***C. parkii***
Mauritania	370 (73)	305 (2)	508 (144)
Senegal	453 (11)	614 (888)	525 (556)
The Gambia	410 (57)	366 (498)	343 (102)
Guinea-Bissau	-	557 (221)	450 (73)
Guinea	369 (89)	395 (57)	423 (15)

Table 4. Length-weight relationships in all ecosystems combined for the three Ariidae species pooled and per species. Numbers, allometry coefficient b (± standard deviation), condition coefficient K, correlation coefficient r, length and weight range.

Species	**Numbers**	**b ± SD**	**K (.10^{-5})**	**r**	**Length range (mm)**	**Weight range (g)**
Ariidae	1,830	3.159 ± 0.009	0.524	0.99	87 - 614	7 – 4,100
C. heudelotii	21	3.111 ± 0.064	0.714	0.99	155 – 453	49 – 1,386
C. latiscutatus	1,201	3.194 ± 0.010	0.417	0.99	87 – 614	7 – 4,100
C. parkii	591	3.137 ± 0.016	0.627	0.99	102 – 525	12 – 2,225

Table 5. Distribution per sex and species of the number of individuals subjected to sex determination.

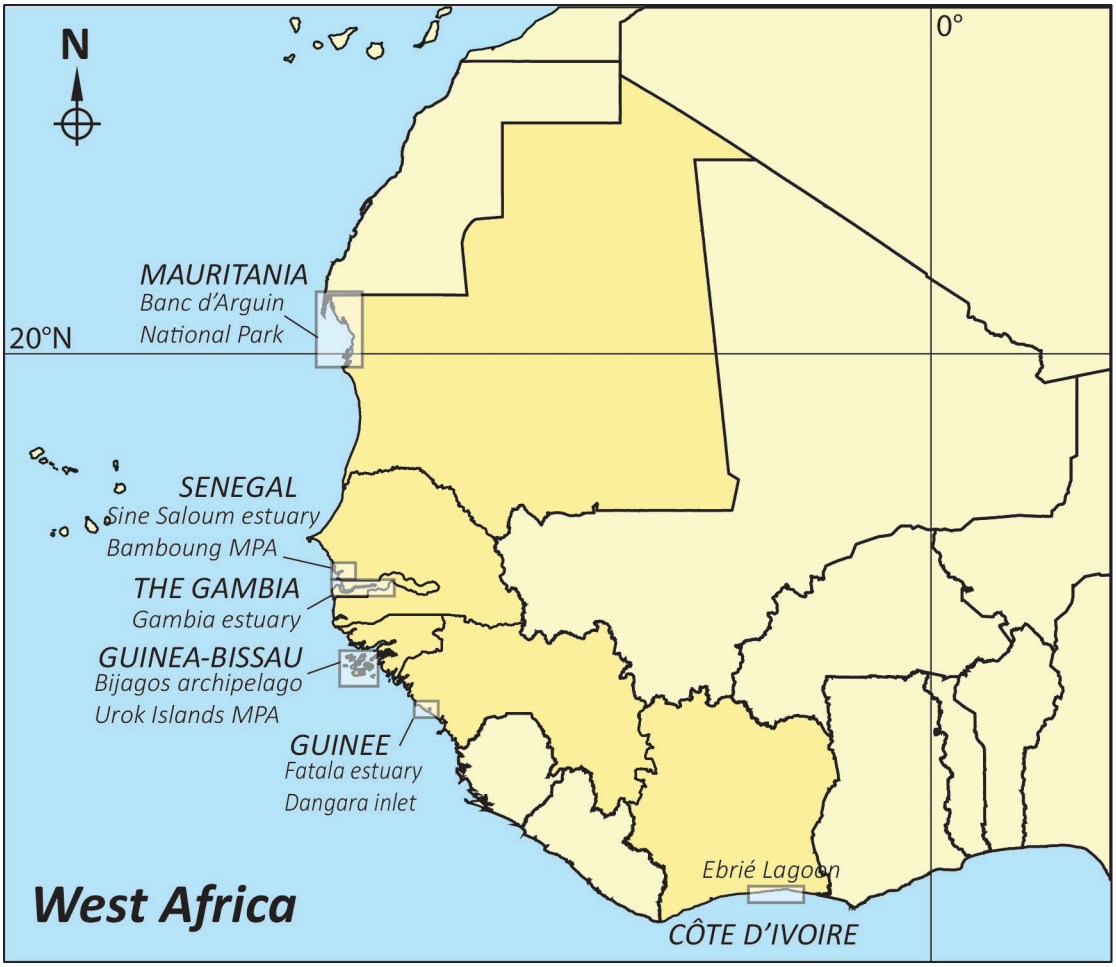
Sex	*C. heudelotii*	*C. latiscutatus*	*C. parkii*
Immature	73	66	67
Female	52	824	369
Male	43	404	242

Table 6. Fork length in mm of the smallest individual beginning its sexual maturation (stage ≥ 3) and number of mature individuals measured (in brackets), per country, species, and sex.

Country	***C. heudelotii***		***C. latiscutatus***		***C. parkii***	
	Male	Female	Male	Female	Male	Female
Mauritania	-	280 (4)	-	-	345 (1)	287 (9)
Senegal	-	312 (2)	254 (22)	230 (184)	239 (61)	190 (117)
The Gambia	-	410 (1)	-	225 (31)	-	213 (5)
Guinea-Bissau	-	-	-	290 (30)	-	291 (8)
Guinea	248 (2)	-	245 (8)	255 (4)	-	-

Table 7. Distribution of the number of individuals whose stomach content was investigated, per country and species.

Country	***C. heudelotii***	***C. latiscutatus***	***C. parkii***
Mauritania	0	0	6
Senegal	0	100	33
The Gambia	2	22	2
Guinea-Bissau	0	111	14



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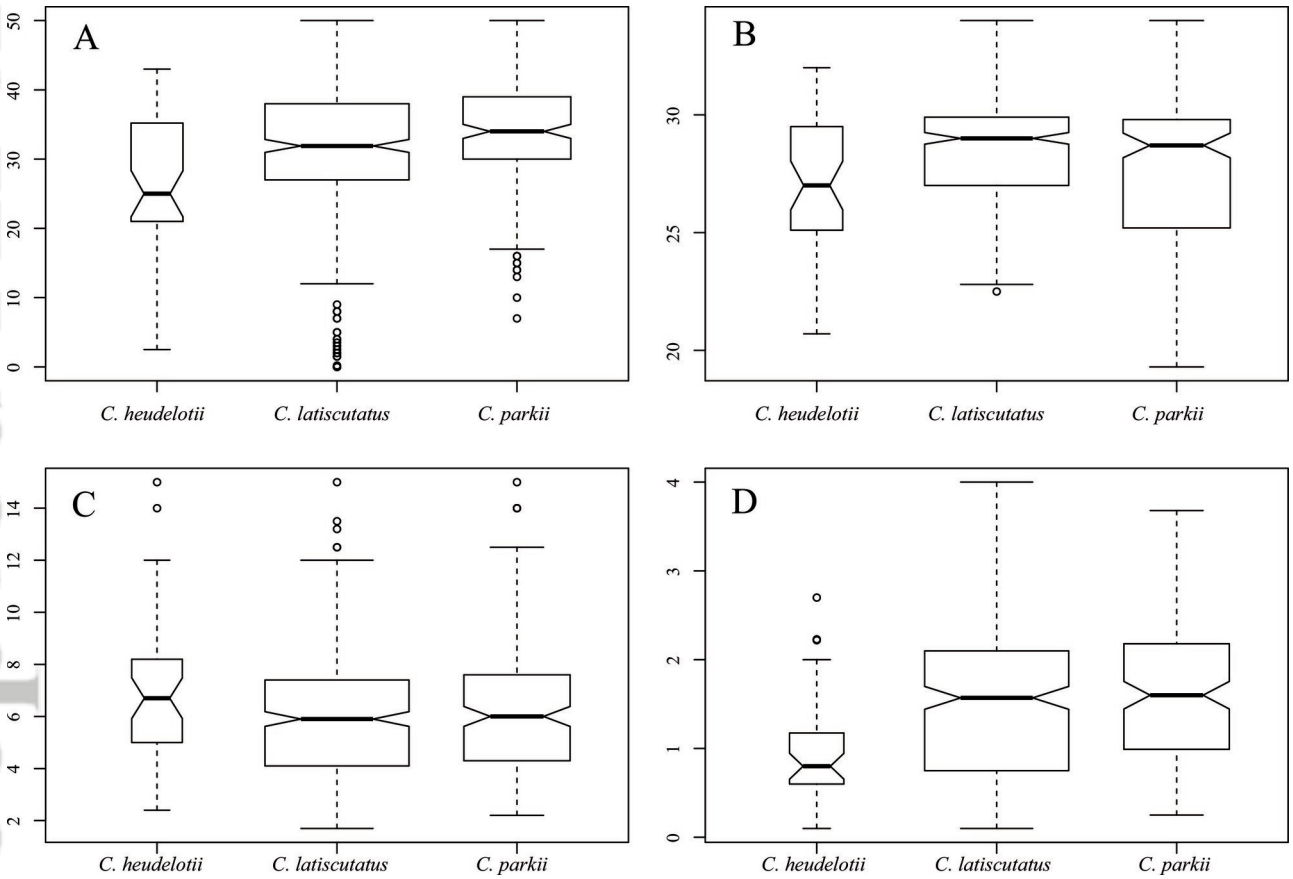

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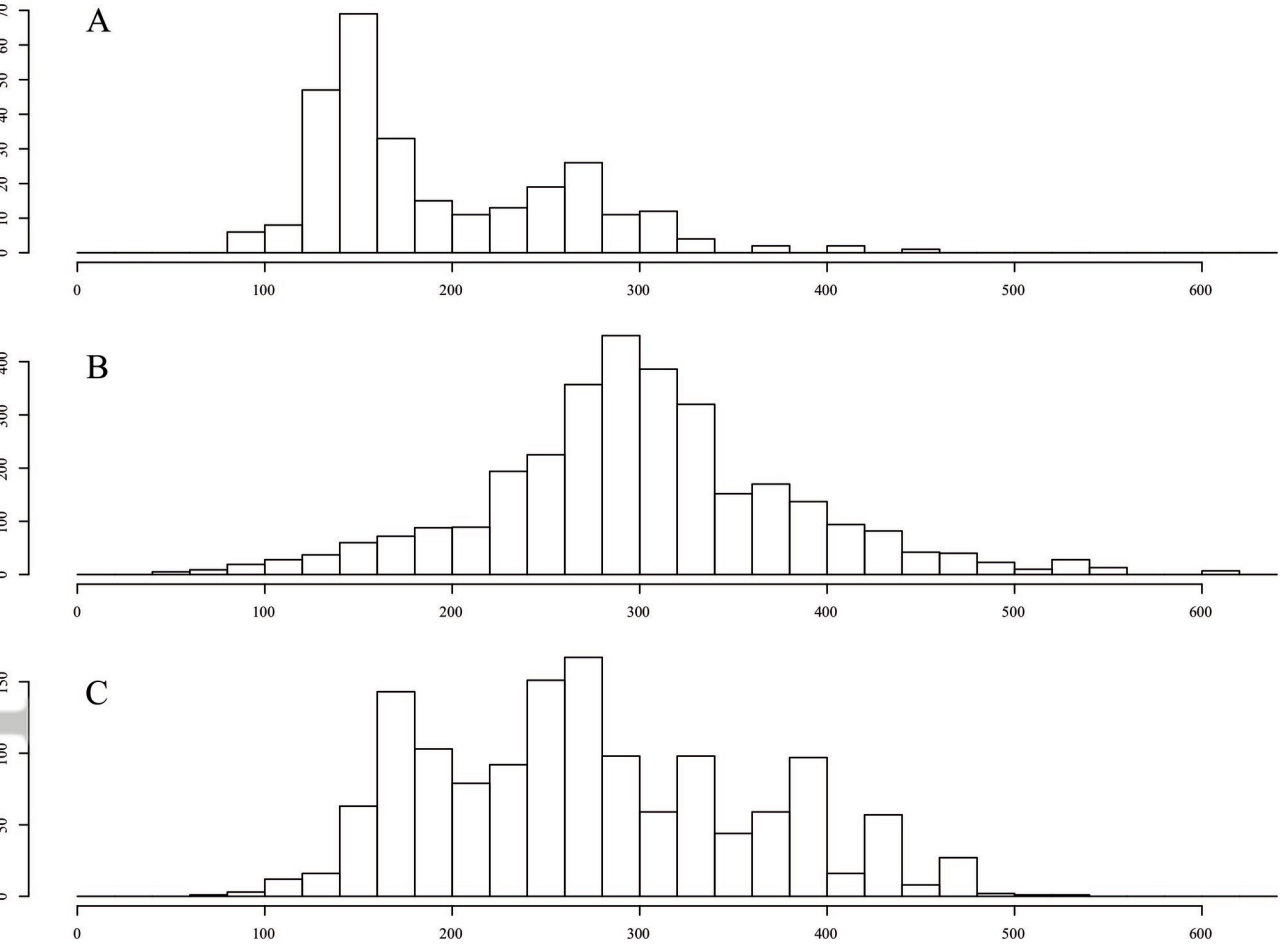

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Significance statement

Three species of sea catfish (Ariidae) are commonly fished on the coasts and estuaries of West Africa. Using a comprehensive dataset collected during experimental fishing surveys, we provide information about their environmental preferences, size structure, reproduction and feeding behaviour. Thanks to their high environmental tolerance, they are able to occupy both the continental shelf and adjacent estuaries throughout the year and throughout their life cycle, with the exception of spawning, which takes place at sea.