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Recruitment patterns of young-of-the-year mugilid fishes in a West African estuary impacted by climate change

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A B S T R A C T

With the persistence of the sub-Saharan drought since the 1970s, the Sine Saloum estuary (Senegal) – the second largest coastal Biosphere Reserve of West-Africa – has become an "inverse estuary" and hypersaline (salinity > 60) in its upstream part. A one-year survey was conducted from April 2007 to March 2008 at eight sites distributed along the salinity gradient, to investigate the recruitment patterns of young-of-the-year mugilids in such an impacted ecosystem. Fishes were sampled monthly with a conical net and a beach seine in salinities ranging from 31 to 104. Samples were identified to the species level. For the smallest individuals (<20 mm SL) a PCR–RFLP technique, developed on the mitochondrial 16S ribosomal RNA region, was used for identification. A total of 8438 juveniles belonging to six of the eight species of mugilids known for the tropical Eastern Atlantic were collected: *Mugil bananensis*, *Mugil cephalus*, *Mugil curema*, *Liza dumerili*, *Liza falcipinnis* and *Liza grandisquamis*. One species, *L. dumerili*, represented 89% of the total catch. Length–frequency distributions revealed that *M. cephalus* and *L. dumerili* preferentially recruited during the dry season whereas the recruitment of *M. curema*, *M. bananensis* and *L. falcipinnis* generally occurred during the wet season. Minimal size at recruitment ranged from 9 to 19 mm SL depending on the species, the smallest size being that of *L. dumerili*. Despite the general salinity increase in the estuary, most parts of the Sine Saloum were suitable for the juveniles. Only the hypersaline area in the uppermost part of the estuary presented very low fish abundance for all species. According to the species, small recruits (12–20 mm SL) were collected at salinities up to 47–78, suggesting that osmoregulatory capacities had been gained early during ontogenesis, possibly resulting from an adaptation of these populations to changing environmental conditions.

1. Introduction

There is a consensus that fish population abundance is positively correlated with the availability of habitats that promote growth and survival of early life stages (Gibson, 1994; Ross, 2003). The identification and evaluation of habitat quality for young stages has consequently become a central theme in fisheries science (NOAA, 2007; Valavanis, 2008). Estuaries have long been recognized as nursery areas, offering food and shelter for the larval and juvenile stages (Blaber and Blaber, 1980; Yanez-Arancibia et al., 1993; Whitfield, 1999). Within these complex nursery ecosystems, the identification of effective juvenile habitats is a major issue for conservation and management, where priorities must be set for limited funding and effort (Beck et al., 2001). Since growth and mortality rates are generally habitat-specific (Dahlgren and Eggleston, 2000) and rapid-growing juvenile fish often have a selective advantage over slower-growing conspecifics (Suthers, 1998; Vigliola and Meekan, 2002; Vigliola et al., 2007), fish are thought to select habitats according to trade-offs between predation risks and growth benefits (e.g. Krause et al., 1998). As a consequence, measurements of juvenile fish abundance and growth are often used as the principal indicators of juvenile habitat quality, such that high-quality nurseries are those where the abundance of juvenile fish is enhanced and fish growth optimized (Taylor et al., 2007).

Since the 1990s, annual landings of Senegalese coastal fisheries have stagnated at about 350,000 tons y^{-1} despite the increasing

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fishing effort (FAO, 2009). In order to limit a decline in fishery resources, the Senegalese government is promoting an ambitious management plan (Senhoury et al., 2007) based, partly, on a network of Marine Protected Areas (MPAs). The Sine Saloum estuarine system situated 100 km south of the capital, Dakar, was selected to contain several MPAs. This vast estuary of 180,000 ha is the second largest coastal Biosphere Reserve of West Africa (Campredon and Cuq, 2001). Furthermore, it is an uncommon example of estuarine ecosystem where the salinity gradient has been permanently inverted since the late 1960s due to an increasing rainfall shortage in the Sahelian region (Pagès and Citeau, 1990; Hulme, 1992; L'Hote et al., 2002; Tabutin and Schoumaker, 2004). Salinity in the upstream part of the Sine Saloum estuary is usually greater than 60 and can reach more than 130 at the end of the dry season (Simier et al., 2004). These are the hypersaline conditions according to Por's (1972) classification. Mangroves, which used to extend throughout the whole estuary in the 1960s, have been severely impacted by the salinity increase (Diatta et al., 1982). Despite this increasing degradation of potential juvenile habitats, very little is known on fish recruitment patterns in the Sine Saloum (but see Vidy, 2000). Yet, scientific information on early life stage history and juvenile habitat use is crucial for sound fishery management and the design of the MPAs network.

Mugilidae represent a particularly abundant fish family in West African estuaries. They often dominate fish landings and thus are considered as a major food and economic resource for local populations (Brulhet, 1975; Payne, 1976; Albaret and Legendre, 1985; Bernardon and Mohamed Vall, 2004). Mugilids include 62 species belonging to 14 genera distributed throughout the world in coastal fresh, estuarine and marine waters (Thomson, 1997). In the Sine Saloum estuary, seven mullet species are currently known (Thomson, 1997; Albaret, 2003; Trape et al., 2009): *Mugil bananensis*, *Mugil cephalus*, *Mugil curema*, *Liza bandialensis*, *Liza dumerili*, *Liza falcipinnis* and *Liza grandisquamis*. Given their remarkable osmoregulatory capacities at the adult stage, the distribution area of most of these species includes the hypersaline part of the estuary (Albaret, 2003; Panfili et al., 2006).

The biological features and early life histories of several Mugilidae species have been described for populations from other parts of the world (e.g. Chang and Tzeng, 2000; Chang et al., 2000; McDonough and Wenner, 2003; McDonough et al., 2003, 2005; Koutrakis, 2004). With a few exceptions, mullets remain in rivers and coastal lagoons during most of their life cycle and leave these areas to spawn at sea. After hatching, metamorphosis and a short period of growth, the juveniles start to recruit at 10–30 mm standard length (SL) into inshore coastal waters, primarily lagoons and estuaries (De Silva, 1980; Bruslé, 1981; Blaber, 1997). Once in these lagoons and estuarine systems, very little is known about juvenile habitat use. It is however generally agreed that young mullets spread throughout the shallow estuarine habitats but avoid deep waters (Blaber, 1987).

The present study focuses on the mugilid fish recruitment patterns in the Sine Saloum inverse estuary. We present the results from a one-year field study aimed at: 1) determining the temporal patterns in mullet recruitment on a monthly basis, 2) describing the spatial distribution patterns of juvenile mullets from the mouth to the uppermost part of the Sine Saloum and 3) testing the effect of some environmental factors, in particular the salinity gradient, on juvenile abundance. This work represents the first available information on recruitment and habitat use of juvenile fish from this family in both an inverse hypersaline estuary and in the West African region, allowing a better understanding of the consequences of decreasing rainfalls on the availability of suitable nurseries areas for mugilid species.

2. Materials and methods

2.1. Study area

The Sine Saloum estuary is located in Senegal, between 13°30′–14°30′N and 15°50′–16°50′W and encompasses approximately 80,000 ha of open water (Fig. 1). This large estuarine system comprises three main channels with – from North to South – the Saloum, the Diomboss and the Bandiala. The Saloum and the Diomboss are wide downstream (2 and 4 km at the mouth, respectively), deep (generally 10–15 m) whereas the Bandiala is narrower (800 m at the mouth) and shallower (generally 5–8 m). The area is strongly influenced by 0.5–1.6 m semidiurnal tides that reach the upstream Saloum with a delay of about seven hours at Kaolack. The channels are bordered by sandy/muddy tidal flats covered by discontinuous mangrove in the downstream part of the estuary. The mangrove, luxuriant in the Bandiala, patchy in the Diomboss and in the lower part of the Saloum, totally disappears in the upstream Saloum after the Foundiougne village (Simier et al., 2004).

The region has a Sahelo-Sudanian climate characterized by a dry winter season from November to June, and a wet summer season from July to October. At Kaolack, in the Northern part of the estuary, the average rainfall decreased from 821.4 ± 182.4 mm to 565.4 ± 125.2 mm for the 1947–1969 and 1970–2007 periods, respectively (Kaolack meteorological station, 1947–2007). At Toubakouta, in the Southern part of the estuary, rainfall decreased from 1093.7 ± 241.7 mm to 680.2 ± 174.7 mm for the same periods (Albergel and Pépin, 1995; Toubakouta meteorological station, 1993–2007). The freshwater supply to the estuary almost exclusively comes from summer rainfalls since no river of significant size is currently flowing. As a consequence, mean salinity shows a minimum at the end of the rainy season and progressively increases until the end of the dry season. In the Diomboss and the Bandiala, mean salinities are relatively homogenous due to the frequent renewal of waters and the presence of permanent localized groundwater in the Bandiala (Diouf, 1996). In contrast, the Saloum displays a marked and permanent salinity gradient between the downstream and upstream areas.

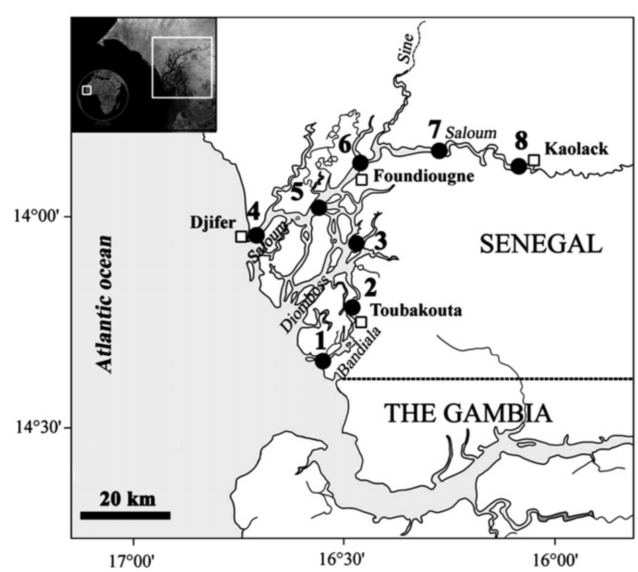

Fig. 1. Locations of the eight sampling sites (points) in the Bandiala channel (1–3) and the lower (4–5), middle (6) and upper (7–8) sections of the Saloum channel in the Sine Saloum inverse estuary (Senegal). White squares correspond to the main cities. (Source: 2009. Google)

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2.2. Field methods

Spatial and temporal recruitment patterns were studied from monthly collections of juvenile mullets that were conducted from April 2007 to March 2008 using a 10 × 2 m beach seine (5 mm mesh) and a conical ichthyoplankton net (500 μm mesh, 1 m diameter) in both the Saloum and Bandiala channels (Fig. 1). Eight sites spread over the two channels and spaced about twenty kilometers apart were sampled. The beach seine was towed parallel to the beach for a distance of 20 m during diurnal high tides, covering approximately 130 m^2. This collection technique was selected in our study as preliminary sampling campaigns and discussions with local fisherman indicated that juvenile mullets could best be captured with a beach seine along sandy/muddy beaches. The conical net sampling consisted of a 7 min surface haul during the nocturnal high tide in the opposite direction of the current at an average speed of 2.7 knots. Three replicate samples separated by few meters or several hundred meters were collected at each site for the seine and conical net hauls, respectively. All samples were collected by the same experienced team and were immediately preserved in 95% ethanol for genetic identification and length measurements. Each monthly collection was completed within eight consecutive days in order to have similar tidal conditions at each site. The water salinity and temperature were recorded immediately after the completion of the seine replicate hauls, at the surface, since no vertical stratification was observed. The mangrove state was estimated at each sampling sites. The luxuriant mangrove corresponded to the Bandiala (sites 1–3), the patchy mangrove to the lower Saloum (sites 4–5), the deteriorated mangrove to the middle Saloum (site 6), and no mangrove to the upper Saloum (sites 7–8).

2.3. Laboratory procedures and data analysis

All sampled mullets were counted and up to 100 individuals per haul were randomly sub sampled, identified and measured to the nearest mm standard length (SL). Fish larger than 20 mm SL were identified at the species level using a morphological key recently developed for West African Mugilidae juveniles (Trape et al., unpublished). PCR–RFLP analysis of the mitochondrial 16S RNA gene was used to identify juveniles smaller than 20 mm SL (Trape et al., 2009).

The recruitment patterns of juvenile mullets were first investigated by visual inspection of the length frequency distributions. At each site and for each species, fish from the seine replicate hauls were pooled and length–frequency distributions were constructed monthly from the observed size distributions in the sub samples and from the total number of individuals. The catch-per-unit-effort (CPUE) was then calculated to study spatial and temporal variations in juvenile abundance. At each site, for each month and for each species, the CPUE was calculated as the mean of the three replicate seine hauls and was expressed as the mean number of fish per seine haul. The catches from the conical nets were not included in the analyses since only very few specimens were collected with this method.

To describe the temporal variability in hydrological parameters and investigate the spatial occupation patterns of juvenile mullets, the sampling months were classified into hydrological seasons and sites in environmentally homogenous areas respectively. A hierarchical classification using the Ward method was carried out to classify (1) the 12 sampling months into salinity and temperature seasons, and (2) the 8 sites into environmental areas according to the values of three environmental parameters (salinity, temperature, and state of mangrove) across the 12 months. Nonparametric Kruskal–Wallis tests were performed to investigate whether salinity, temperature and CPUE differed among sites, hydrological seasons and environmental areas since various transformations failed to normalize the data and stabilize the variance. When significant differences were detected, multiple comparisons of means were performed using the Nemenyi test (Zar, 1999). Generalized Linear Models (GLMs, Gaussian error and identity link) were used to investigate the effect of environmental factors (salinity, temperature, distance to the mouth and state of mangrove) on juvenile abundance (log-transformed CPUE). Statistical analyses were performed only for species that were collected in sufficient numbers using the R software (R Development Core Team, 2007). Since the recruitment of juvenile mullets was strongly seasonal and consequently the CPUE highly variable temporally, GLMs were fitted during the peak of recruitment season of each species in order to enhance the power of the statistical analysis and limit type II errors.

3. Results

3.1. Environmental conditions

Salinity showed its highest and lowest mean values in June (56.6 ± 23.1 SD) and October (44.2 ± 12.8 SD), respectively (Fig. 2a). The hierarchical classification of the sampling months discriminated two main clusters: a first group including the months from August to December (wet season); a second group including the months from January to July (dry season). The mean salinity ± SD differed significantly between groups (Kruskal–Wallis test, $P < 0.001$) and was higher during the dry season (54.8 ± 2.2) than during the wet season (46.5 ± 3.1). A strong and highly significant salinity gradient occurred during both hydrological seasons (Fig. 2a and Kruskal–Wallis tests, $P < 0.001$). Post-hoc tests revealed no significant salinity differences between sites in the Bandiala, whereas in the Saloum, the mean salinity significantly increased throughout the middle and upper estuary during both seasons

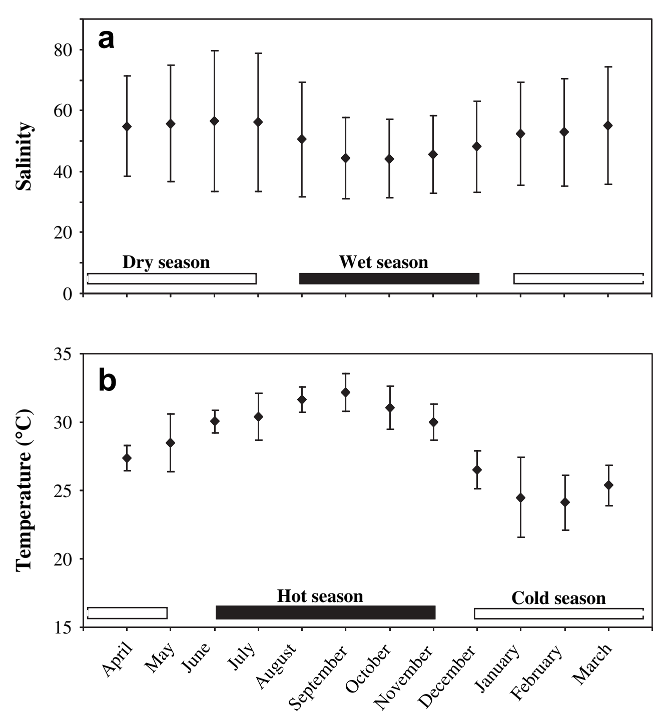

Fig. 2. Monthly temporal variations (mean ± SE) of salinity (a) and temperature (b) in the Sine Saloum estuary from April 2007 to March 2008. Salinity and temperature seasons established from Ward's hierarchical classification.

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(Fig. 3a). Salinity ranged from 31 to 40 in site 1 at the mouth of the Bandiala and from 65 to 104 in the uppermost site 8 of the Saloum channel.

Temperature showed it's lowest and highest mean values in February (24.1 °C ± 2.0) and September (32.2 °C ± 1.4), respectively (Fig. 2b). The hierarchical classification discriminated two main clusters: a first group including the months from December to May (cold season); a second group including the months from June to November (hot season). The mean temperature ± SD differed significantly between groups (Kruskal–Wallis test, $P < 0.001$) and was lower during the cold season (25.5 °C ± 1.6) than during the hot season (30.5 °C ± 1.5). Although mean temperatures showed a slight increase from the mouth to the upstream parts of the estuary (Fig. 3b), Kruskal–Wallis tests revealed no significant differences among sites during both seasons ($P > 0.05$). The highest and lowest temperatures were recorded in July (33.4 °C, site 8) and February (21.9 °C, site 4), respectively.

The hierarchical classification of the sampling sites based on environmental parameters (salinity, temperature, mangrove state) discriminated four main clusters (Fig. 3): a first group including sites 1–3 (Bandiala) corresponding to the Bandiala and characterized by relatively low salinities (mean 38.6), temperature (mean 27.7 °C) and a luxuriant mangrove; a second group including sites 4 and 5 (lower Saloum) corresponding to the lower part of the Saloum channel and characterized by relatively low salinities (mean 42.1), temperatures (mean 27.5 °C) and a patchy mangrove; a third "group" with site 6 (middle Saloum) corresponding to the middle part of the Saloum and characterized by intermediate salinities (mean 54.2), temperatures (mean 29.6 °C) and a deteriorated mangrove; and a fourth group with sites 7 and 8 (upper Saloum) corresponding to the hypersaline part of the Saloum and characterized by high salinities (mean 77.2), temperatures (mean 29.7 °C) and no mangrove.

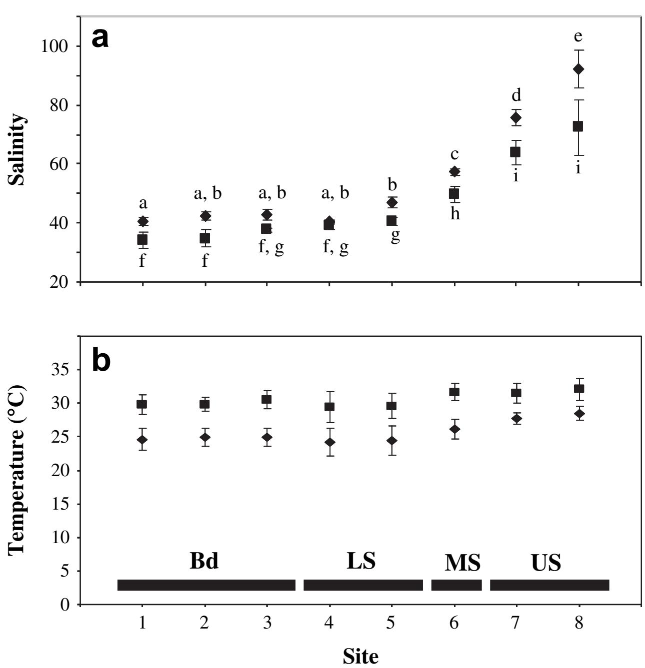

Fig. 3. Spatial variations (mean ± SE) of salinity (a) and temperature (b) in the Sine Saloum estuary from April 2007 to March 2008. Bandiala channel (Bd); lower (LS), middle (MS) and upper (US) sections of the Saloum. Lozenges correspond to dry/cold and squares to wet/hot seasons respectively. Means with different letters are significantly different at $P < 0.05$ (Nemenyi test).

3.2. Catch composition

A total of 8438 juvenile mullets belonging to six species were collected during the 12-month sampling period, including 39 individuals collected with plankton nets. A total of 999 individuals were identified using molecular markers, including all specimens smaller than 20 mm. Young-of-the-year mullets were captured in 57.7% of the seine hauls. Excluding the empty hauls, the number of mugilid species per sample ranged from 1 to 4, with an average value of 1.9 ± 1.0 SD species per seine haul. *Liza dumerili* was the most abundant species accounting for 89.0% of the total catch. It was followed by *Mugil curema* (4.2%), *Mugil bananensis* (4.0%), *Mugil cephalus* (1.7%), and *Liza falcipinnis* (1.1%). Only two specimens of *Liza grandisquamis* (12 and 15 mm SL) were collected during the study, in June and August, at sites 8 and 6 respectively.

3.3. Size distributions, temporal and spatial abundance patterns

3.3.1. Liza dumerili

Liza dumerili juveniles were consistently collected throughout the year at a size ranging from 9 to 93 mm SL (Fig. 4). Small individuals (<15 mm) occurred in the catches twice a year, in June and from October to January. The length–frequency distributions showed the progression of three distinct modes: a first one from April to July, a second one from June to October, and a third one from November to March, indicating the presence of three distinct cohorts. The first cohort probably recruited from November 2006 to January 2007 and the second one in June 2007. Both abruptly disappeared from our catches at a modal size of about 55 mm in July and November 2007, respectively. The third cohort recruited from November 2007 to January 2008 and reached a modal size of 30 mm SL at the end of the sampling period in March 2008. Although not significantly different (Kruskal–Wallis test), the mean CPUE were about three times higher during the dry season (44 individuals/seine haul), when the first and third cohorts occurred in the catches, than during the rainy season (15 individuals/seine haul) when the second cohort was collected. The greatest mean CPUE (79 individuals/seine haul) was recorded in June (Fig. 5) when fish from both the dry and wet season cohorts co-occurred in the catches (Fig. 4).

Juveniles occurred in all the sites except in site 8, the one most upstream (Fig. 6). The highest juvenile catches occurred in both channels at sites located close to the mouths of the Bandiala (site 1) and the Saloum (sites 4). Kruskal–Wallis test performed on the CPUE revealed a highly significant environmental area effect ($P < 0.001$). The mean CPUE ± SE were significantly higher in the Bandiala (30.7 ± 10.1 individuals/seine haul), the lower (69.6 ± 26.13 individuals/seine haul) and the middle Saloum (29.5 ± 10.6 individuals/seine haul), than in the upper Saloum (1.4 ± 0.8 individuals/seine haul). Although the difference was not significant, the mean CPUE in the Bandiala and middle Saloum were about twice as low than in the lower Saloum. Minimum adequate GLMs fitted on February to June CPUE data revealed a significant and negative relationship between CPUE and distance to the mouth in both the Saloum ($C = -0.073$, $P = 0.007$ on the log scale) and the Bandiala ($C = -0.039$, $P = 0.021$ on the log scale). The juveniles occurred in salinities ranging from 31 to 78 (Fig. 7). The smallest specimen collected in the upstream part of the estuary measured 12 mm and was collected in site 7 (upper Saloum), at a salinity of 78.

3.3.2. Mugil curema

Mugil curema juveniles were collected from April to November at a size ranging from 19 to 68 mm (Fig. 4). The recruitment of small individuals (<25 mm) occurred from June to November. The catches were very low from April to July and consisted of

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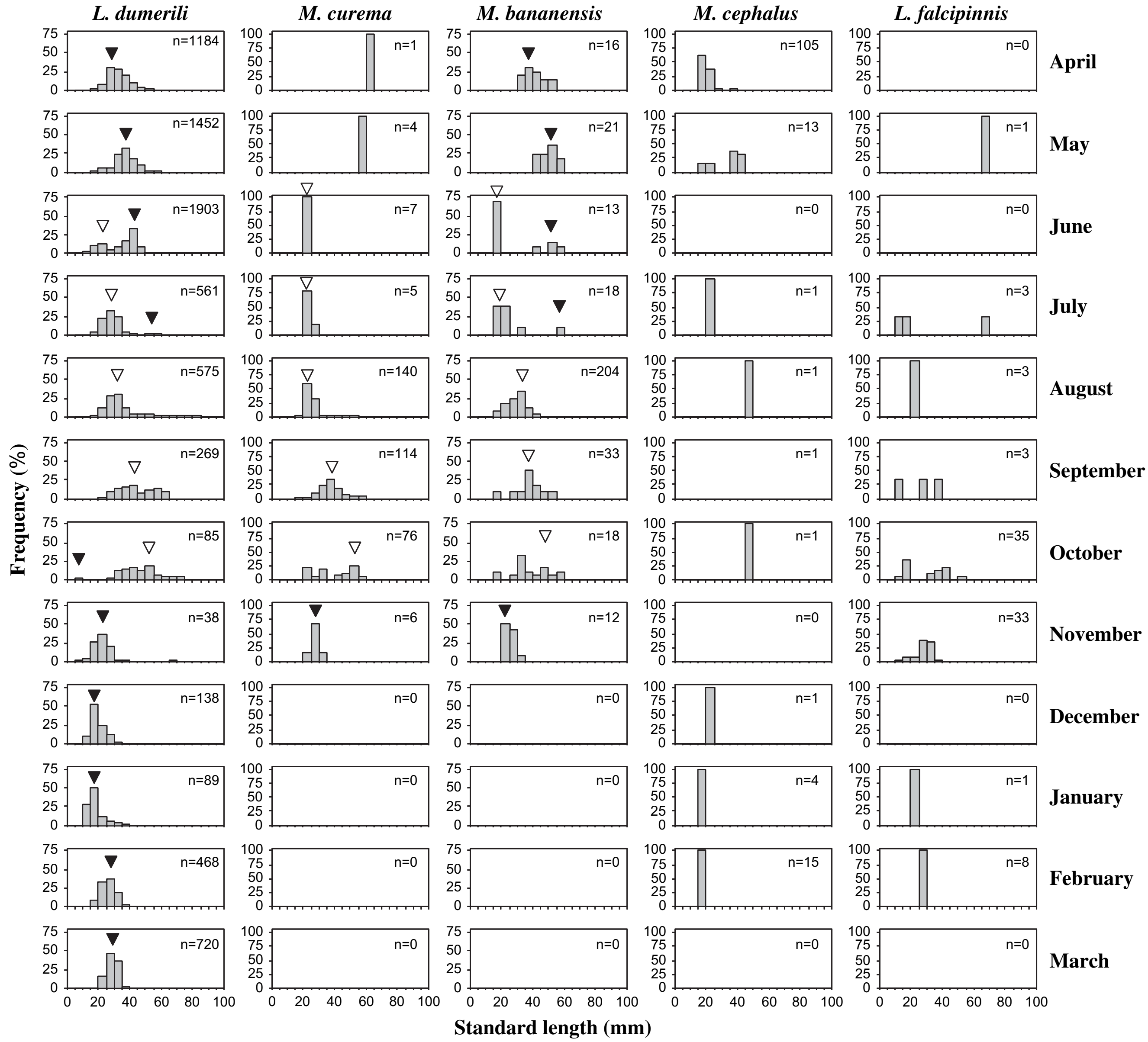

Fig. 4. Monthly length-frequency distributions (%) of the five juvenile mullet species collected from April 2007 to March 2008 in the Sine Saloum estuary. Arrowheads show identified cohorts. Note that the y-axes are scaled differently across species.

20–30 mm SL individuals, peaked in August (mean 6 individuals/ seine haul) and progressively decreased until December (Fig. 5). The length-frequency distributions showed the progression of a single major mode from August to October, indicating the presence of a single abundant cohort that mainly recruited in August and abruptly disappeared from the catches at a modal size of about 55 mm SL in October (Fig. 4). The collection of a few small individuals in November and larger specimens in April and May suggested that recruitment of a second cohort might occur, but of very low abundance.

The juveniles were absent in the hypersaline area of the estuary (Fig. 6). The highest catches occurred in sites 1 and 3 with mean values of 7 and 6 individuals/seine haul respectively. Although Kruskal–Wallis test revealed no significant differences in the mean CPUE between the four environmental areas ($P = 0.19$), mean CPUE were more than three times higher in the Bandiala (3.8 individuals/ seine haul) than in the lower area of the Saloum (1.1 individuals/ seine haul). GLM analysis performed on August and September CPUE data revealed no significant relationship between CPUE and environmental factors. The juveniles occurred in salinities ranging from 31 to 54 (Fig. 7). The smallest specimen collected in the upstream part of the estuary measured 21 mm and was collected in site 6 (middle Saloum), at a salinity of 47.

3.3.3. Mugil bananensis

Mugil bananensis juveniles were collected from April to November at a size ranging from 17 to 60 mm (Fig. 4). The recruitment of small individuals (<25 mm) occurred from June to November. The catches were low from April to July and mainly consisted of 15–35 mm individuals. A strong recruitment event occurred in August (mean 9 individuals/seine haul). The abundance however dramatically decreased in September and remained low until December after which no juveniles were collected (Fig. 5). The length–frequency distributions showed the progression of two

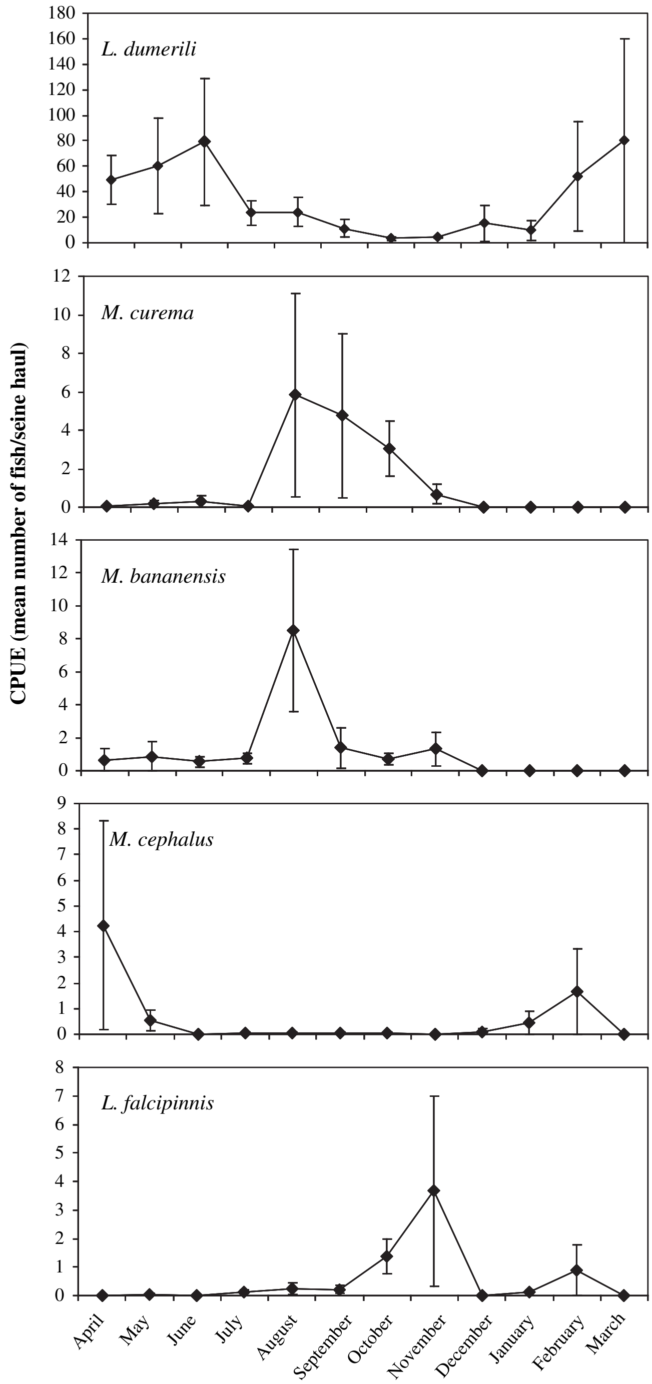

Fig. 5. Monthly mean CPUE (number of fish per seine haul ± SE) of the five mullet species in the Sine Saloum estuary.

distinct modes, a first one from April to July, and a second one from June to October, indicating the presence of two distinct cohorts (Fig. 4). The collection of a few small individuals in November suggested that recruitment of another cohort might occur. This later recruitment was probably responsible for the appearance in the estuary of the cohort that we collected from April to July.

Juveniles occurred in all sites investigated except in site 8, the one most upstream (Fig. 6). Kruskal–Wallis test revealed no significant differences in the mean CPUE between environmental areas ($P = 0.17$). However, some spatial occupation pattern existed within branch of the estuary. In the Saloum, the highest catches occurred in the middle part (site 6) in salinities ranging from 47 to 58, whereas in the Bandiala the highest catches occurred near the mouth in salinities ranging from 31 to 43. GLM analysis performed on August and September CPUE data revealed no significant relationship between the CPUE and environmental factors. Juveniles occurred in salinities ranging from 31 to 70 (Fig. 7). The smallest specimen collected in the upstream part the estuary measured 20 mm and was collected in site 6 (middle Saloum), at a salinity of 54.

3.3.4. Mugil cephalus

Mugil cephalus juveniles were collected almost throughout the year at a size ranging from 18 to 48 mm (Fig. 4). The recruitment of small individuals (<25 mm) occurred from December to May. A peak in catches occurred in April with a mean CPUE value of about 4 individuals/seine haul (Fig. 5). Isolated fish were caught in other months. No modal progression was observed in the length–frequency distributions.

Catches were too low for statistical analysis of CPUE. However, a close inspection of the data revealed that *Mugil cephalus* juveniles were almost exclusively collected in the Saloum, the highest catches occurring near the mouth at site 4 (mean 6 individuals/seine haul) (Fig. 6). However, a peak in abundance at site 4 corresponded to a single day of high catches. The juveniles occurred in salinities ranging from 43 to 88 (Fig. 7). The smallest specimen collected in the upstream part of the estuary measured 20 mm and was collected at site 7 (upper Saloum) where the salinity was 77.

3.3.5. Liza falcipinnis

Liza falcipinnis juveniles were collected almost throughout the year at a size ranging from 15 to 68 mm (Fig. 4). The recruitment of small individuals (<25 mm) occurred from July to February. The catches were the largest in October and November and very low the rest of the year (mean 4 individuals/seine haul) (Fig. 5). No modal progression was observed in the length–frequency distributions.

The catches were too low for statistical analysis of CPUE. The distribution of *Liza falcipinnis* was relatively homogenous in space (Fig. 6). The highest catches occurred at site 6 (mean 1 individual/seine haul). The juveniles were collected in salinities ranging from 32 to 70 (Fig. 7). The smallest specimen collected in the upstream part of the estuary measured 20 mm and was collected at site 7 (upper Saloum) where the salinity was 70.

4. Discussion

4.1. Species composition

The recruitment patterns of Mugilidae in West African ecosystems had never been investigated before. The difficulty of identifying early juveniles is probably one of the causes for this lack of data for such an economically and ecologically important family. Molecular tools thus represent a good alternative for species identification when diagnostic morphological characters are unavailable (e.g. larvae of mullets) or difficult to define. To our knowledge, this is the first study documenting both the temporal and spatial recruitment patterns for Mugilidae using molecular markers.

Mullet juveniles belonging to six different species were collected in the Sine Saloum estuary during the 12-month sampling period. Eight Mugilidae species are known to occur along the West African coast between Southern Mauritania and Angola. *Mugil capurrii*, whose southern distribution limit is located along the North Senegalese coast (Thomson, 1997), has never been recorded in the Sine Saloum and was not observed in our study. The seven other West African Mugilidae species had been previously reported in the Sine Saloum estuary. However, *Liza*

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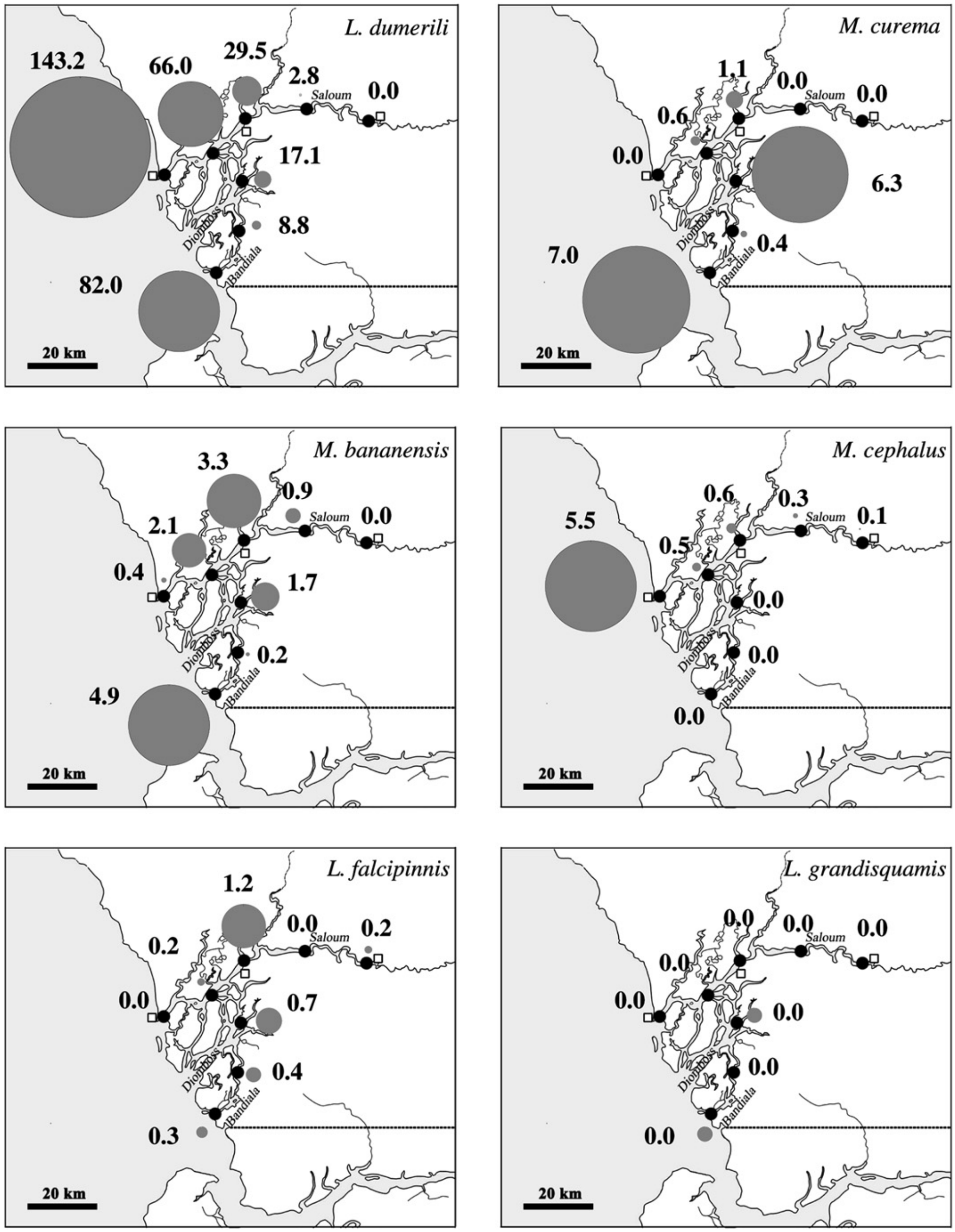

Fig. 6. Spatial distribution of catches in the Sine Saloum estuary for the six juvenile mullet species. Circle = mean catch per unit effort at each site. Note that scales are different across species.

bandialensis, a rare species only known from the nearby Sine Saloum and Gambia estuaries (Diouf, 1996), was not collected in the present study.

Our results indicated that *Liza dumerili* largely dominated the juvenile catches whereas *Liza grandisquamis* was the less abundant species. Previous purse seine studies on adult assemblages showed a similar dominance pattern for *L. dumerili* (Diouf, 1996; Simier et al., 2004). However, these studies also reported that adults of *L. grandisquamis* were relatively abundant. The selectivity of the sampling gears, weak recruitment for the studied year, and/or the existence of recruitment habitats non-explored by our study might explain the apparent discrepancy between juvenile and adult dominance in the catches for this species.

4.2. Temporal recruitment patterns

The recruitment of juveniles into estuarine nurseries is the result of complex interactions between spawning success, hydrodynamic processes, and pre-recruitment mortality. Temperature, salinity, food availability and hydrodynamic processes in estuarine and coastal waters have been identified as important factors affecting mugilid recruitment with an effect on both the reproductive strategy of the species and the survival of their early life stages (Blaber and Blaber, 1980; De Silva, 1980; Blaber, 1987; Vieira, 1991; Marin et al., 2003). In the Sine Saloum, the recruitment of juvenile mullets occurred throughout the year with distinct peaks in abundance differing between species (Fig. 8). The recruitment of

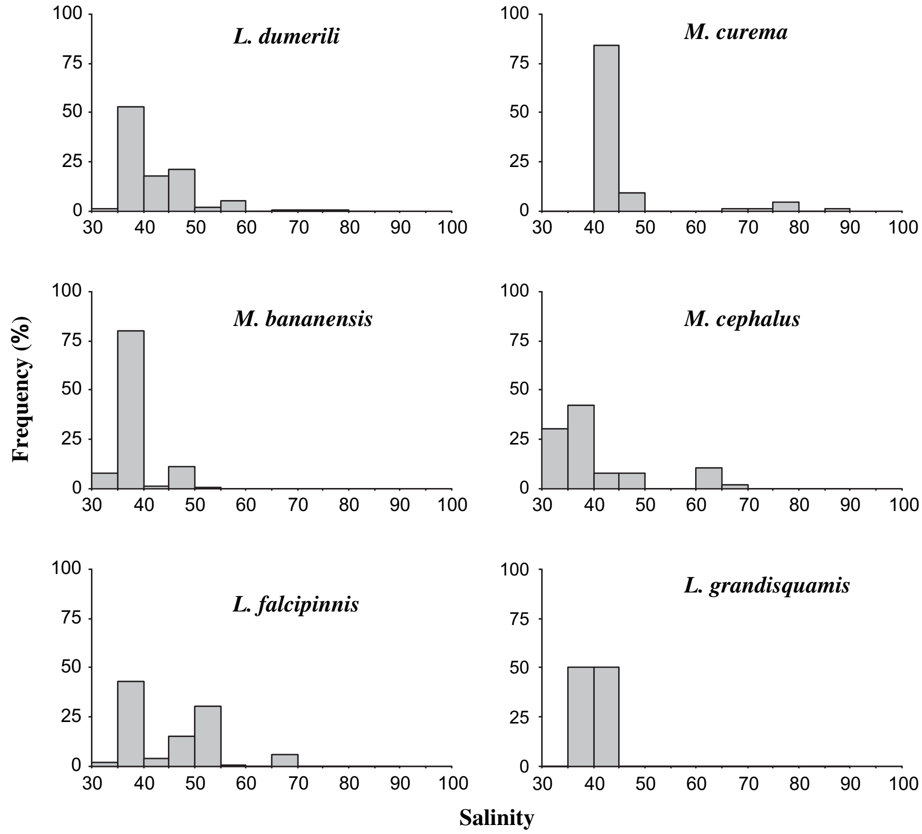

Fig. 7. Catch frequency distribution of the six mullet species in relation to salinity.

Liza dumerili occurred twice a year. A first minor cohort recruited in June, at the end of the cold dry season/beginning of the hot wet season, and a second major cohort occurring from November to January during the first half of the cold dry season. Other species only recruited once a year. *Mugil cephalus* preferentially recruited from December to May, during the cold dry season, whereas the recruitment of *Mugil bananensis*, *Mugil curema* and *Liza falcipinnis* mainly occurred from June/July to October/November, during the rainy season. For both *M. bananensis* and *M. curema* an abundant cohort recruited during the rainy season. For *M. bananensis* a second cohort occurring in our catches from April to July probably recruited at the beginning of the cold dry season. Only two recruits of *Liza grandisquamis* were collected during the study. These individuals were sampled in June and August respectively, suggesting that the recruitment for that species occurred at least at the end of the cold dry season and at the beginning of the hot wet season.

In temperate waters, the spawning activity of mullet species seems to be in a large part controlled by water temperature, each species having an optimal range of temperature for reproduction

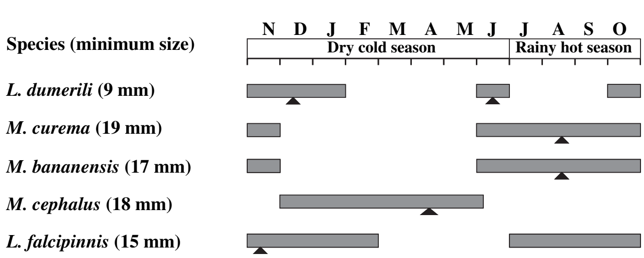

Fig. 8. Recruitment periods, abundance peaks (arrowheads) and minimum size at recruitment of Mugilidae species in the Sine Saloum estuary.

(Bruslé, 1981). Despite the geographical position of Senegal in the subtropical area, the seawater temperature shows a marked seasonal cycle due to a yearly seasonal upwelling from January to April (Wooster et al., 1976). Water temperatures which average 28.3 ± 0.3 °C from July to October progressively decrease to reach a minimum mean of 18.4 ± 0.1 °C in February (Rebert and Domain, 1977). The recruitment into the estuary for *Mugil curema* and *Mugil cephalus* started during the period of temperature increase and decrease, respectively. Similar patterns were observed in other parts of the world both for recruitment (Vieira, 1991; Chang and Tzeng, 2000; Chang et al., 2000) and spawning activity of *M. curema* and *M. cephalus* (e.g. Anderson, 1957, 1958; Ditty and Shaw, 1996; Chang et al., 2000; Bichy, 2004). It was experimentally shown that temperature was the primary factor determining the onset of vitellogenesis of *M. cephalus* (Kelley et al., 1991; Kuo, 1995). Although other factors may be involved in particular areas (e.g. meteorological tides in Mexico; Ibanez and Gutierrez, 2004), it appears likely that water temperature controls the spawning activity of these species not only in temperate regions but also in subtropical areas with high seasonal amplitude in water temperature, such as the Senegalese coast.

The interspecific differences in periods of recruitment for mullets in the Sine Saloum estuary could be the result of successive reproduction periods as observed for other mugilids (Bruslé, 1981). However, the temporal variability in water productivity (i.e. food availability) and oceanographic conditions along the Senegalese coasts (Domain, 1980) could induce differential mortalities in early oceanic life stages and thus have important consequences for recruitment. For example, the two cohorts of *Liza dumerili* which recruited into the estuary during the study, could be the result of (1) two spawning events of different intensities, assuming that the recruitment into the estuary accurately reflects the reproduction process, or (2) a single protracted spawning event, assuming that differential survival of the larvae over time created two distinct recruitment pulses. Interspecific differences in the duration of the oceanic phase may also affect the timing of recruitment into the estuary. For example, a shorter larval oceanic life for *L. dumerili* than for *Mugil bananensis* and *Muigl curema* could explain why the former species recruited earlier (June) than the latter two (August). This hypothesis is supported by a much smaller size at recruitment (and thus a younger age) for *L. dumerili* (9 mm SL) than for the two other species (17 and 19 mm SL for *M. bananensis* and *M. curema*, respectively) but assumes that there are no strong growth differences between species.

The minimal size at recruitment for Mugilidae in the inverse and hypersaline Sine Saloum estuary ranged from 9 to 19 mm SL according to the species. Similar sizes at recruitment have been reported in other parts of the world for mullets living in normal estuaries (e.g. De Silva, 1980; Vieira, 1991; Whitfield, 1994; Koutrakis, 2004). Despite its inverse functioning, the Sine Saloum estuary therefore seems still suitable for the early life stages of Mugilidae species. The apparent lack of salinity effect on mullet size at recruitment may result from an early acquisition of osmoregulatory capacities. Although experimental confirmation is needed, this hypothesis seems to be supported by the presence of numerous small recruits up to hypersaline waters (e.g. 12 mm SL at salinity of 78 for *Liza dumerili*, 20 mm at 77 for *Mugil cephalus*). Previous findings on *M. cephalus* from the East American coast (Florida) suggest that individuals smaller than 40 mm have poor osmoregulatory capacities in seawater (Nordlie et al., 1982). Cardona (2000) suggested that the osmoregulatory capacities of *M. cephalus* could differ according to populations. It is plausible that these differences could appear as soon as during the early juvenile stages, possibly resulting from local population adaptations to environmental conditions.

4.3. Spatial recruitment patterns

Early juvenile mullets were mainly concentrated from the mouth of the estuary to Foundiougne; where the mean salinities were always lower than 60. In the Saloum channel, two spatial patterns were observed. *Liza dumerili* and *Mugil cephalus* were mainly concentrated near the mouth, at a mean salinity of 39.8, whereas *Mugil bananensis*, *Mugil curema* and *Liza falcipinnis* mainly occurred in the middle part of the Saloum, at a mean salinity of 54.2. In the Bandiala, where mean salinities ranged from 37.9 to 40.8, juvenile mullets showed three spatial patterns: *M. bananensis* and *L. dumerili* were mainly concentrated near the mouth, *M. curema* both near the mouth and in the upper part of the channel, and *L. falcipinnis* in the middle part of the channel.

The distribution of estuarine fish is usually affected by complex interactions between salinity, temperature, turbidity, type of substratum, and vegetation (Blaber, 1997). Cardona (2000, 2006) showed that salinity was a key factor controlling the distribution of juvenile mullets (>80 mm) of five species in the Mediterranean estuaries of Minorca, each species being distributed along the salinity gradient according to its osmoregulatory capacities. In the present study, GLM analyses carried out for *Liza dumerili*, *Mugil bananensis* and *Mugil curema* failed to reveal significant salinity effects on CPUE suggesting that salinity was not the main factor controlling the distribution of early juveniles of these species in the Sine Saloum estuary. Similar results were observed for *Mugil cephalus* in Indo-Pacific estuaries, where in some areas individuals were mainly concentrated in high salinity sites (Marais and Baird, 1980; Silva and De Silva, 1981) and in others in oligo-mesohaline sites (Marais, 1981, 1983). According to Cardona (2000), this may be the result of differences in food availability rather than salinity preferences. For *L. dumerili* a significant negative effect of the distance to the mouth on CPUE was observed in both branches of the estuary. Other factors not investigated in the present study and potentially correlated with the distance to the mouth such as the food availability (nature and/or abundance), the sediment grading, the site accessibility could also be responsible for the observed distribution patterns (Blaber, 1976, Blaber and Whitfield, 1977; Bell et al., 1988).

The mangrove is a dominant feature of undisturbed tropical and subtropical estuaries around the globe. Whereas it is generally agreed that mangrove ecosystems absorb and transform nutrients and are inhabited by a variety of organisms, opinions vary as to the importance of the mangrove habitats for fishes and by extension for mangrove fisheries (Faunce and Serafy, 2006; Nagelkerken et al., 2008). Our results did not show a particularly higher juvenile abundance in the mangrove-rich parts of the estuary for mugilids species. Indeed, only the *Mugil curema* catches were higher in the Bandiala than in the lower part of the Saloum. Furthermore, both the interview of local fishermen and the results of two exploratory campaigns in October 2006 and April 2007 (Trape et al., unpublished results) indicated that mullets were rare in the mangrove tidal flat. This suggests that in the Sine Saloum estuary mangrove may not be an essential habitat for juvenile mullets and/or not increase the attractiveness of adjacent juvenile habitat for most mullet species.

It is well known that juveniles of a variety of taxa can display ontogenetic changes in habitat that are associated and/or caused by a variety of other changes such as changing diet or predation risk (Wootton, 1992). The abrupt disappearance of *Liza dumerili* from our catches in July and November at a modal size of about 55 mm and that of *Mugil curema* at a similar size in November is probably the result of a size-dependant change in habitat. Similar phenomena occurred in estuarine systems of the Greece coast for *Liza aurata* and *Liza ramada* at a modal size of 50–60 mm (Koutrakis, 2004) and in a coastal lagoon of Sri Lanka (De Silva and Silva, 1979) for *Mugil cephalus* at a size of about 30 mm. These juvenile habitat shifts are probably associated with changes in feeding ecology that occur between 30 and 55 mm for mullets (Albertini-Berhaut, 1974; De Silva, 1980; Bruslé, 1981; Blaber, 1997) and take place at a time when predation risk is reduced due to an increase in individual size and swimming capacities (Vigliola and Harmelin-Vivien, 2001). However, a complementary sampling using less selective sampling gears (e.g. trammel nets) would be necessary to confirm that individuals greater than 55 mm were really absent of the sampling area and not escaped of our sampling gear.

5. Conclusion

This is the first study documenting both the spatial and temporal recruitment patterns of juvenile Mugilidae using molecular markers. Despite a persistent sub-Saharan drought since the 1970s which has led to hypersaline conditions in the upper Sine Saloum estuary and considerably impacted the mangrove, most parts of the estuary seemed to be suitable for early juveniles Mugilidae of almost all West African species. Only the hypersaline area in the uppermost part of the estuary presented very low fish abundance. The presence of small recruits at salinities as high as 78 suggests that osmoregulatory capacities are gained early during ontogenesis, maybe resulting from an adaptation of these populations to changing environmental conditions.

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