Environmental and Physical Factors Affecting the Diversity and Distribution of the Ichthyoplankton in an "Inverse Estuary", the Sine Saloum (Senegal)

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I seem to have been only like a boy playing on the seashore, and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.

- Isaac Newton

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Abstract

Estuarine mangrove ecosystems are considered essential nursery grounds and feeding areas for the early life stages of many fish species, often including commercially important ones. Particularly, climate change is expected to affect and have a substantial impact on mangrove estuaries, through processes including changes in precipitation, increased temperature, and changing patterns of ocean and estuarine circulation. As a result, the inversion of the salinity gradient in several estuaries throughout the dry tropics is either underway or can be expected in the near future. Such modifications of these important estuarine environments are cause of concern because spawning and nursery grounds of fishes have requisite environmental and physical attributes. Thus, there is a strong scientific consensus that related pressing contemporary research questions regarding the early life history of fishes in these transformed estuaries should be addressed.

Located in Senegal, West Africa, the Sine Saloum system is representative of estuaries where the salinity gradient has been inverted due to climatic changes in the region. Given the high overall salinity and the resulting mangrove degradation that is taking place there, its potential role (compared to "classic estuary") as a recruitment and nursery area for fish larvae is far to be clear. Thus, the Sine Saloum estuary is a natural and excellent choice to study how these climatic environmental transformations are affecting the ichthyoplankton community. The aim of this thesis is to gain knowledge on the environmental and physical factors affecting the Sine Saloum ichthyoplankton diversity and distribution.

The survival of fish larvae is known to be influenced by complex interactions between environmental changes and tropho- and hydrodynamic processes. Consequently, I first analysed the spatial and seasonal distribution of the fish larval assemblages related to environmental parameters. Second, a field experiment measuring simultaneously vertical current profiles and larval transport were conducted to investigate the effectiveness of larval fishes in regulating transport in and out of the estuary. Lastly, stable isotope analysis was used to evaluate the contribution of the sea surface microlayer (SML) to the diet of larval and juvenile African halfbeaks (*Hyporamphus picarti*), one of the dominant species in the system.

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The summarised key findings of the thesis are:

A total of 41 taxa representing 24 families and 34 genera were sampled in the estuary, which is lower than that of other tropical estuaries, providing evidences that high salinity environment may harbour a less diverse ichthyoplankton fauna. Additionally, the distributional pattern of fish larvae revealed that the total abundance and the richness in the estuary decreased from the lower to the upstream areas with salinity and water temperature as the variables that best explained the spatial and temporal differences observed. Larval fish assemblages also showed a clear vertical structure corresponding to three distinct water strata.

The circulation at the entrance of the Sine Saloum estuary was characterized by the existence of a longitudinal gravitational circulation with vertical shear and net near-surface inflow into the estuarine system. This is of critical importance in the context of fish recruitment because it offers a natural path into (resp. out of) the estuarine system for organisms that would be able to maintain themselves in the upper (resp. lower) part of the water column. The distribution of the fish larvae taxa that were examined revealed depth range preferences that did not change in time, independent from tide conditions, and were consistent with the use of these pathways. From a behavioural perspective, this mechanism can be viewed as simpler than selective tidal stream transport in that it does not require the organisms to synchronise their vertical migrations with the phase of the tidal currents.

By obtaining statistically distinct $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures for the SML, its presence at the entrance of the Sine Saloum estuary was confirmed. The organisms contained in the SML presented an important food source for *H. picarti* larvae and juveniles, contributing to more than 70 % of their diets. These results underline the importance of the SML and the role of this estuary as a spawning and nursery habitat for *H. picarti*.

In conclusion, despite the environmental transformation that has taken place in the Sine Saloum estuary, the collective information gathered in this thesis indicated that some the prevailing environmental and physical conditions resulted in a reduction of the ichthyofauna diversity, but nevertheless allowed the maintenance of the estuary's role as an important recruitment and nursery habitat. Furthermore, it contributes to our understanding about the potential development of other, currently less disturbed mangrove estuarine systems in West Africa and around the world.

Zusammenfassung

Mangrovenökosysteme entlang tropischer Küsten sind wichtige Aufwuchs- und Nahrungsgebiete für frühe Entwicklungsstadien vieler, auch kommerziell wichtiger, Fischarten. Diese Ökosysteme sind von verschiedenen Auswirkungen des globalen Klimawandels betroffen, wie zum Beispiel Veränderungen der Niederschlagsmenge in den Einzugsgebieten, erhöhte Temperaturen und sich verändernde Muster der Ozean- und Ästuarzirkulation. Eine Folge dieser Klimaveränderungen kann die Umkehrung oder Inversion des typischen Salzgehaltsgradienten in einem Ästuar sein, was einen ansteigenden Salzgehalt mit zunehmender Entfernung von der Küste bzw. Mündung bedeutet. Dieser Prozess ist in vielen Ästuaren der trockenen Tropen entweder schon im Gange oder kann in naher Zukunft erwartet werden. Diese einschneidenden Veränderungen der hydrologischen Bedingungen in den Flussmündungssystemen sind ein Anlass zur Besorgnis, da damit wichtige ökologische und physikalische Eigenschaften der Laich- und Aufzuchtgebiete von Fischen verändert werden. Daher besteht ein dringender Forschungsbedarf, die Konsequenzen dieser Umweltveränderungen für den Fortplanzungserfolg von Fischarten, deren frühe Lebensstadien auf ästuarine Habitate angewiesen sind, zu untersuchen.

Das Sine Saloum System im westafrikanischen Senegal repräsentiert ein solches Ästuar, in dem der Salzgehaltsgradient aufgrund von Klimaveränderungen in der Region umgekehrt wurde.. Der hohe Salzgehalt hat eine Degradation des lokalen Mangrovenwaldes zur Folge und es ist unklar, welchen Effekt dies auf dessen Qualität als Rekrutierungs- und Aufzuchthabitat für die Fischarten hat. Somit stellt das Sine Saloum Ästuar ein natürliches Laboratorium dar, welches hervorragend geeignet ist, den Einfluss der beschriebenen Umweltveränderungen auf das Vorkommen von Fischlarven und die Zusammensetzung der Ichthyoplanktongemeinschaft zu untersuchen.

Das Überleben von Fischlarven wird durch komplexe Wechselwirkungen verschiedener Umweltbedingungen bestimmt, wobei trophodynamische und hydrologische Prozesse von besonderer Relevanz sind. In dieser Arbeit wurde daher zuerst die räumliche und saisonale Verteilung von Fischlarven im Sine Saloum System und die Beziehung von Fischlarvenabundanz zu verschiedenen Umweltfaktoren untersucht. Der zweite Teil der vorliegenden Arbeit beschreibt ein Feldexperiment, in dem untersucht wurde inwiefern Fischlarven ihren Transport in und aus dem Ästuar in das angrenzende Küstenmeer beeinflussen können. Dafür wurden gleichzeitig sowohl vertikale Strömungsprofile als auch die Position und Abundanz von Fischlarven in

verschiedenen Wassertiefen bestimmt, um Larventransportraten abschätzen zu können. Im dritten Teil der Dissertation wurde mittels stabiler Isotopenanalyse die Bedeutung der Oberflächenfilms für die Ernährung von larvalen und juvenilen Stadien des Afrikanischen Halbschnabelhechts (Hyporamphus picarti), der eine der dominierenden Arten im Sine Saloum System ist.

Die wichtigsten Ergebnisse dieser Arbeit können wie folgt dargestellt werden:

Insgesamt wurden Larvenstadien von 41 Fischtaxa im Sine Saloum Ästuar gefunden, die 24 Familien und 34 Gattungen repräsentieren. Diese Zahlen sind deutlich geringer als in anderen tropischen Ästuaren mit einem normalem Salinitätsgradienten und lassen darauf schließen, dass eine Umgebung mit hohem Salzgehalt eine weniger vielfältige Ichthyoplanktonfauna beherbergt. Zusätzlich zeigte das räumliche Verteilungsmuster der Fischlarven, dass sowohl die Anzahl als auch der Artenreichtum von Fischlarven im Ästuar vom Mündungsgebiet hin zu den Oberläufen abnahmen, wobei Salzgehalt und Wassertemperatur die beiden Umweltparameter mit dem höchsten Einfluss auf die beobachteten Unterschiede darstellten. Außerdem konnte eine klare vertikale Strukturierung der Fischlarvengemeinschaft in drei unterschiedliche Zonen beobachtet werden.

Die Wasserzirkulation an der Mündung des Sine Saloum Systems war durch einen longitudinalen Gravitationskreislauf mit vertikaler Scherung gekennzeichnet,. Oberflächennah wurde ein Nettowasserzufluss in das Ästuar gemessen, in tieferen Wasserschichten wurde dagegen ein Nettowassserabfluss gemessen. Diese Umkehrung der Strömungsrichtung innerhalb der Wassersäule stellt einen Transportweg für Fischlarven in das und aus dem Ästuar dar, in dem sie ihre vertikale Position entsprechend anpassen. Die vertikale Verteilung der untersuchten Fischlarven ergab unterschiedliche Tiefenpräferenzen für verschiedene Taxa, welche jedoch zeitlich stabil und unabhängig von den Gezeiten waren. Aus verhaltensbiologischer Sicht kann aus dieser Beobachtung geschlossen werden, dass im Sine Saloum Ästuar ein vereinfachter und energetisch vorteilhafter Transportmechanismus für Fischlarven in und aus dem System besteht. Es entfällt die Notwendigkeit auf eine mit dem Gezeitenstrom synchronisierte Vertikalwanderung, wie sie anderen Ästuaren gefunden wird.

Die wichtige Rolle von Plankton des Oberflächenfilms als Nahrungsquelle für Larven und Jungfische des Afrikanischen Halbschnabelhechts (*H. picarti*) konnte durch die Untersuchungen der δ^{13}C- und δ^{15}N Isotopensignatur nachgewiesen werden. Durch die Anwendung dieser

Technik konnte gezeigt werden, dass im Sine Saloum Ästuar eine Oberflächenfilm existiert, deren spezifische Planktonorganismen mehr als 70% der Nahrungszusammensetzung bei den Jugendstadien von *H. picarti* ausmachten. Dieses Ergebnis unterstreicht die Bedeutung der Oberflächenfilms und die Rolle der ästuariner Mündungsgebiete als Brut- und Aufzuchtgebiet für *H. picarti*.

Zusammenfassend konnte die vorliegende Arbeit zeigen, dass die geänderten ökologischen- und physikalischen Bedingungen im Sine Saloum Ästuar zwar zu einer Verringerung des Artenreichtums der Ichthyoplanktonfauna führten, das Flussmündungungsgebiet aber weiterhin ein wichtiges Rekrutierungs- und Aufzuchtgebiet für viele Fischarten darstellt. Weiterhin erlauben die Ergebnisse dieser Arbeit eine bessere Abschätzung, welche Auswirkungen der Wandel weiterer mangrovengesäumter Flussmündungssysteme zu einem inversen Ästuar auf die betroffene Fischfauna haben kann. Ein Prozess der bei anhaltendem klimatischen Wandel weiteren Ästuaren in Westafrika und in der restlichen tropischen Hemisphäre droht.

General Introduction

Early life stages of fishes and recruitment hypotheses

The main goal of ecology is to describe the distribution and abundance of living organisms and how the distribution and abundance are affected by interactions between the organisms and their environments (Krebs, 2009). We generally think of the ecological position of the adults, but in animals, such as fishes with complex and varied life histories, the position of the eggs, larvae, and juveniles may be very different from that of the adults. Accordingly, the ecological requirements of these early life stages are in most cases different from those of the mature and more developed individuals, but like the adults, they operate at all of the levels of ecological organization: the organismal, population, and ecosystem levels (Cushing, 1996; Reynolds, 2001). Thus, knowledge specific to the early life stages is important for a sound understanding of the biology, ecology, and evolution of fishes.

Many have made the link between recruitment and the rates of survival during the early life of marine fishes (Houde, 2002). It is during their early life phases that fishes are most vulnerable to environmental problems (Miller and Kendall, 2009), thus they must survive this critical period (**Fig. 1**), or at least a few must survive and be recruited to sustain populations through time (Rothschild, 2000). Accordingly, recruitment is viewed as one of the key processes in the life cycle of a fish for maintaining the population, and its variability is commonly understood as driven by complex interactions between physiological, tropho- and hydrodynamic processes, and environmental changes that are acting throughout pre-recruit life from the egg to the juvenile phase (Houde, 1987, 2008; Lehodey et al., 2006).

Recruitment hypotheses have emphasized alternative views about the relative importance of different ecological processes that act on different life history stages. As early as 1914, Hjort proposed two major factors that could increase larval mortality. First, a lack of prey items during a "critical period" within which the larvae must feed or die ("Critical Period Hypothesis") and second, larvae could be dispersed by advective currents to unfavourable areas where they may not grow or would not be recruited to the adult population and would perish ("Offshore Transport Hypothesis"). Complementary, the "Aberrant Drift", "Stable Ocean", and "Optimal Window" hypotheses stressed the effects of hydrodynamic conditions on larval and juvenile stages, whereby recruitment is determined by retention on, or transport to, favourable nursery areas (Begg and Marteinsdottir, 2002; Hjort, 1914) or favourable hydrological conditions

for foraging (Cury and Roy, 1989; Lasker, 1975). Attempting to unite all of the previous mentioned hypotheses, one recently emerging concept that appears to have substantial explanatory power is that of 'Ocean Triad Hypothesis'. A series of comparative studies of the climatology and geography of known preferred spawning areas (Bakun, 1990, 1996; Bakun and Parrish, 1991; Cury and Roy, 1989; Parrish et al., 1983) have served to identify three major groups of physical processes that combine to yield favourable recruitment habitat for coastal pelagic fishes and also many other types of fishes: (1) nutrient enrichment (upwelling, mixing, etc.), (2) concentration of larval food (convergence, frontal formation, water column stability), and (3) processes favouring retention within (or drift toward) appropriate habitats.

The central idea behind these recruitment hypotheses is that survival and mortality rates during early life phases determine its strength, thereby affecting the size of the adult population. Also, recurrent to all these hypotheses are the need for optimal environmental conditions, appropriate larval transport, and feeding success. A suitable environment during the fishes' early life phases is therefore critically important in population terms, and an understanding of how different conditions associated with these processes influence larval survival is a prerequisite for assessing long-term variations and sustainability of fish populations and stocks. Consequently, the research on the early life history of fishes (particularly the larval stage) should be wide-ranging, with the aim of identifying the mechanisms by which factors such as environmental conditions, larval transport, and feeding success can influence larval abundance, distribution, and survival.
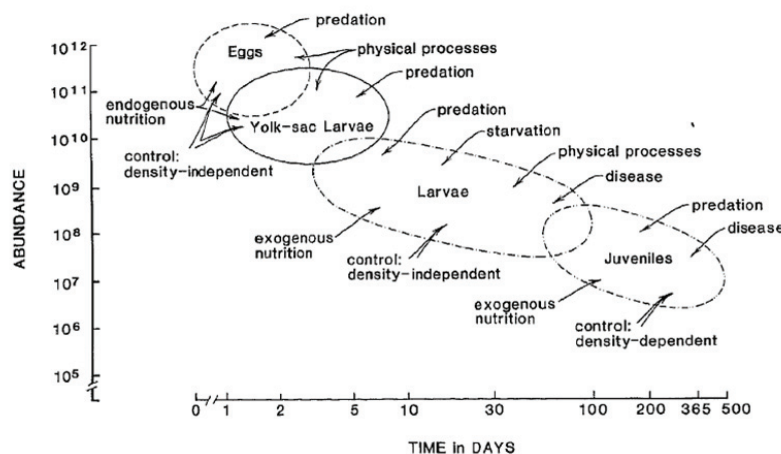

Fig. 1. A conceptualization of the recruitment process in fishes including the sources of nutrition, probable sources of mortality, and hypothesized mechanisms of control for four early life history stages. Log_{10} scales are used on both axes (taken from Houde, 1987).

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Environmental conditions (abiotic factors)

Many environmental factors probably affect survival of fishes' early life stages and their dynamics can be influenced by both regional and basin-wide environmental fluctuations (Boeing and Duffy-Anderson, 2008; Doyle et al., 2009; Hsieh et al., 2005). Two of the most potent abiotic factors in the early life stages of marine fishes are temperature and salinity (Kinne, 1963). Several studies have demonstrated that temperature and salinity played a defining role in structuring larval fish assemblages (e.g. Harris and Cyrus, 2000; Strydom et al., 2003). Temperature, which changes the rate of metabolism of eggs and larvae, might affect production of their prey, and can change currents that transport eggs and larvae to or away from suitable nursery grounds. As an example, Beaugrand et al. (2003) analysed monthly data collected during 1958–99 to show that *Gadus morhua* (Atlantic cod) recruitment in the North Sea was related to temperature-dependent processes. With regards to salinity, laboratory experiments have investigated its influence on egg and larval development and although the tolerance of larvae to salinity appears to be highly species specific, and may change during ontogeny, many of these studies could demonstrate a detrimental effect of elevated salinities. For example, Fielder et al. (2005) showed that growth of snapper larvae was significantly reduced at the high salinity of 45 PSU. Moreover, salinity can affect yolk utilization, larval growth, and survival by influencing the amount of energy needed for osmoregulation (Howell et al., 1998). Salinity also affects the buoyancy of eggs and larvae and this can impact on the ability of larvae to get to a suitable position in the water column for finding food or/and for being transported by favourable currents (Battaglene and Talbot, 1993; Hadley et al., 1987). In addition, high salinities are known to cause important shifts in zooplankton communities (Anton-Pardo and Armengol, 2012; Jensen et al., 2010), with the associated trophic interaction affecting the fish larvae and juveniles consuming them.

Larval transport

In marine fishes, the coupling between adult population size and the physical processes that control transport of larvae is expected to be strong. This is because, many inshore marine fishes in temperate and tropical environments spawn offshore but their larvae or juveniles use shallow habitats such as bays, mangroves, and other estuarine regions as nurseries (Beck et al., 2001). In these cases, the larval transport phenomenon has three main components: (1) movement towards shore, (2) location of and movement into nursery areas, and (3) retention in nursery areas (Boehlert and Mundy, 1988; Miller and Kendall, 2009; Norcross and Shaw, 1984) (**Fig 2**). Consequently, the survival of the larvae are bound to effective transport to recruitment and nursery areas and are an important feature of their life history having a significant effect on the successful recruitment to the adult populations (Roughgarden et al., 1988). This is because disrupting connectivity could lead to impeding a population to access resources (e.g. nursery area with favourable environmental conditions and adequate access to food sources), which diminishes the resilience of that population (Gawarkiewicz et al., 2007) and affect the whole ecosystem (Mumby and Hastings, 2008).
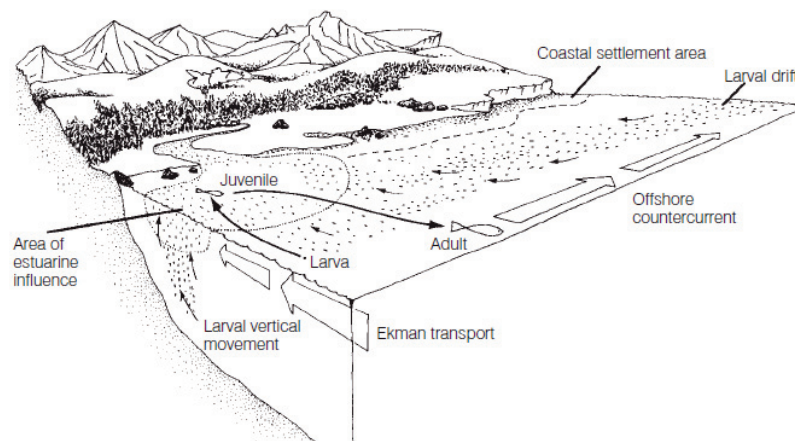

Fig. 2. The general sequence of movement of marine larvae from offshore to inshore nursery grounds (taken from Boehlert and Mundy, 1988).

Feeding condition

Inadequate food has been found, in the worst cases, to directly lead to starvation, and in the best cases, to slow growth and thereby increasing predation leading to high mortality rates. As mentioned earlier, one of the principal agents of recruitment regulation is hypothesized to be food-mediated mortality occurring during the larval stages. Indeed, starvation have long been considered a major cause in larval mortality (Hjort, 1914, 1926) and accordingly, food production in the sea and other coastal ecosystems, larval feeding behaviour, and nutrition have been the objects of a large amount of research to understand larval survival (Grote et al., 2012; Lehman, 2004; Munk and Kiorboe, 1985; Primo et al., 2017). In a situation of limited food resources, the competition for prey can negatively influence growth rates and recruitment success according to the "Stage Duration Hypothesis" (Houde, 2008, 1987) where well-fed and fast-growing larvae require less time to transit stages that are the most vulnerable to predators. The production of larval food is usually dependent on conditions such as temperature, salinity, oxygen, and nutrient levels, and is often associated with conditions fostering high productivity (Cushing, 1996). Consequently, larvae and juveniles rely on the production of particular kinds and amounts of food for their survival. To be in a location that provides high quality feeding is thus of vital importance for the larvae and juveniles.

Shifting climatic condition of fish larvae environments

Facing severe environmental degradation of coastal marine ecosystems due to climate change (IPCC, 2014), there is a strong scientific consensus that new pressing contemporary questions in early life history research should be addressed. Many studies have documented modifications in adult marine and coastal fish distributions and linked these to climate change (e.g. Jung et al., 2014; Shackell et al., 2014). For example, it has been shown that climate change can have deleterious effects on fishes by affecting individuals, populations and communities through changes of extremes in environmental factors, such as elevated water temperature, low dissolved oxygen or high salinity (Moyle and Cech, 2004; Rijnsdorp et al., 2009). However, for many coastal marine ecosystems there is a dearth of information on early life history characteristics of their constituent fish populations and their specific connections to new

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prevailing climatic and environmental conditions. This inhibits the development of meaningful ecological frameworks for predicting population responses to these environmental changes. Therefore, there is a need to better understand the implications of these environmental transformations on fish early life survival, abundance, and distribution. This is particularly important in the context of the potential impacts of global climate change on fish populations, especially in high latitudes that are experiencing some of the most rapid and severe changes (IPCC, 2008, 2014).

Mangrove estuaries and climate change

Particularly, climate change is expected to affect and have a substantial impact on mangrove ecosystems (Ellison, 2015), through processes including sea level rise, changing ocean currents, increased temperature, and changes in precipitation (Mckee et al., 2012). This is relevant and an additional cause of concern as mangroves are known to provide food and refuge for larval and juvenile fishes, where they occur at higher densities, avoid predation more successfully, or grow faster than in a different habitat (Laegdsgaard and Johnson, 2001; Verweij et al., 2006; Nagelkerken et al., 2008). For these reasons, mangrove estuarine systems are considered as "nurseries"; an established and ubiquitous concept accepted by scientists, conservation groups, fisheries managers, and the general public (Beck et al., 2001). It is now well documented that the use of mangrove estuarine areas by larvae and juveniles is a critical phase of the life history of many marine fishes, including many commercially valuable species (Barletta et al., 1998, 2005; Brehmer et al., 2006; Haedrich, 1983; Pauly, 1988). Notably, these groups of commercially important species (e.g. classified as estuarine-dependent) are often the base for economic valuation of mangroves (Nagelkerken et al., 2008). In addition, several authors have reported that there is a positive correlation between fisheries landings and the size of mangrove habitat in an estuary (Aburto-Oropeza et al., 2008; Carrasquilla-henao and Juanes, 2016; Lee, 2004; Manson et al., 2015; Meynecke et al., 2007). If that holds true, additional mangrove degradation and loss as a result of climate change will impact the early life stages of fishes and consequently have the potential to lead to a reduction of fisheries production in coastal waters. Yet, these mangrove systems that are important nursery habitats continue to decline and

in some cases alarmingly fast (Alongi, 2002; FAO, 2007; Giri et al., 2011; Polidoro et al., 2010; Valiela et al., 2001). The forecast is grim as it is anticipated that an additional 25 % of mangrove forests in developing countries could be lost by 2025 (Mcleod and Salm, 2006), making them one the most threatened tropical ecosystems (Feka, 2015).

Warming is expected to be linked to changes in rainfall (Jones et al., 2002), which can adversely affect the supply of water for mangrove ecosystems. The IPCC (2014) predicts an increase in hydrological extreme events, and these are typically defined as floods (associated with extremes in rainfall) and droughts (associated with a lack of precipitation and often extremely high temperatures that contribute to drying). Indeed, drought events have generally increased throughout the 20th century (Dai et al., 2004; Trenberth et al., 2007), as measured by the Palmer drought severity index (PDSI), and it is expected that this tendency will continue in the coming decades (IPCC, 2008, 2014). Increased heating leads to greater evaporation and thus surface drying, thereby increasing the frequency, intensity, and duration of drought events (Trenberth, 2011); resulting in significant decline in freshwater inflows and an increase of the evaporation rates in mangrove estuarine systems (U.S. DOE., 2012). The lack of precipitations and freshwater inflows can lead to insufficient flushing of soils and sediments (Ellison, 2015), thereby increasing the degree of salt stress faced by mangroves and associated fauna. Under a reduction of precipitation scenario, mangrove estuarine waters would experience elevated temperature, saltwater intrusion resulting in high overall salinity (Pagès and Citeau, 1990), thereby decreasing overall mangrove cover and productivity (Ball and Pidsley, 1995) to finally lead to a reduction of the geographic area where mangroves grow (Wilson, 2017). As larvae normally found in these estuarine areas could be subject, for example, to salinities above their tolerance limit, these transformed habitats may no longer provide quality nurseries and are likely to have negative impacts in larval survival, abundance, and distribution. For fishes, these changing environmental conditions might not meet the specificity of habitat requirements of their early life stages and pose problems affecting connectivity, recruitment, and population growth rates.

As a region of importance for mangroves, the West African coast is hosting about 12 % (20,410 km^2) of the world's mangroves (Feka and Ajonina, 2011). These mangroves cover 15 % of the 8492 km of the West-Central African coastal zone (UNEP, 2007) stretching from the west coast of Mauritania through the Gulf of Guinea countries down to Angola, covering some 19 countries with over 300 million people depending directly and indirectly on their ecological

services (e.g. fisheries) (**Fig. 3**). In the region, these estuarine ecosystems have been particularly subjected to enormous pressures and threats (climate change leading to reduced precipitation and anthropogenic use) within the last past decades with great losses (**Fig. 4**); a decline by more than 25 % of the western African mangroves had been observed over the past 35 years (UNEP, 2007). Therefore, many mangrove habitats may face severe degradation if climate change continues at the predicted rates. Given the link between fish reproduction success and mangrove systems, the observed degradation and loss due to climate change and direct human impacts negates the availability of nursery habitat, increases vulnerability of fish populations using them, and subsequently decreases their sustainability. As a consequence, significant environmental, economic, and social costs for human societies are expected.

Fig. 3. Map of the mangrove distributions (in green) along the West African Coast (taken from UNEP, 2007)
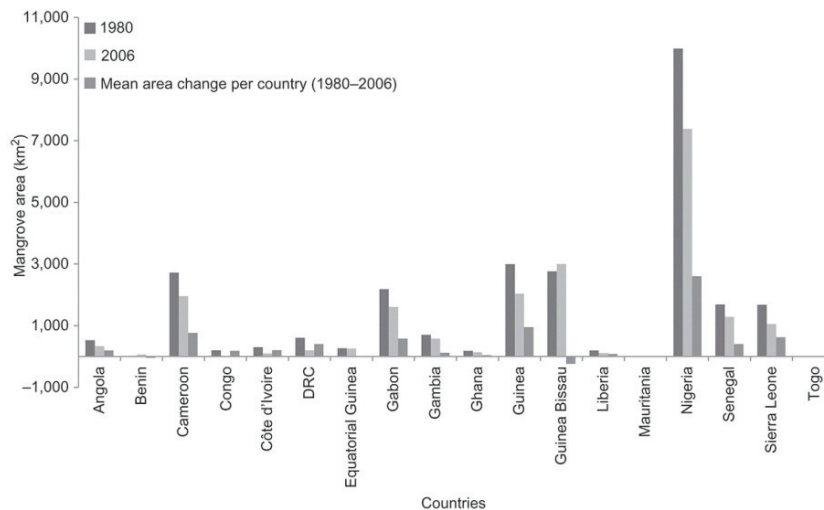
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Fig.4. Status of mangrove forests in West-Central Africa; including mean area change per country (1980–2006). Negative values indicate a gain in mangrove area (taken from Feka and Ajonina, 2011; and orginally compiled from UNEP-WCMC, 2007).

Study system – The Sine Saloum estuary

Situated along the West African semi-arid coastline, the Sine Saloum estuary (**Fig. 5**) differs significantly from its southern and wetter tropical counterparts in one major respect. The Sine Saloum is an "inverse estuary" (Pagès and Citeau, 1990; Pritchard, 1967), where water salinity is higher than that of seawater and increases monotonically with distance from the sea. This estuarine system became permanently inverted in the late sixties mostly due to an increasing lack of freshwater inflow (Barusseau et al., 1985; Pagès and Citeau, 1990), a direct consequence of the prolonged drought (known as the Sahelian drought) that has affected the entire Sahel region (Nicholson, 2005; Nicholson et al., 2000). The annual rainfall has been decreasing in this region, first slowly until 1961, and then more drastically in recent decades (Pagès & Citeau, 1990). Between 1931-61 and 1961-85, the average annual rainfall fell from 893 to 636 mm in Foundiougne (29 % reduction), from 796 to 612 mm in Kaolack (23 % decrease) and from 810 to 582 mm in Fatick (28 % deficit) (Diop-Gueye, 1991). Compare to the pre-Sahel drought conditions, the five-month wet season is now reduced to a three/four-month period, and across the watershed the average annual rainfall is now only about 650 mm (Doumouya et al., 2016), which correspond to an annual deficit of ~10 billion m^3 of freshwater inflow into the system. For comparison purpose, the Gambia River estuary (situated only about

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50 km south of the Sine Saloum system) receives an average annual precipitation of 1500 mm (Villanueva, 2015), more than two times what the Sine Saloum gets. Consequently, freshwater inflows have fallen sharply and no river of significant size currently flows into the Sine Saloum estuary. For example, the already low flow of the Nema-Ba River, a tributary of the estuary, which was 0.29 m^3 s^{-1} in 1976, was only 0.03 m^3 s^{-1} in 1981 (Diop, 1990). Indeed, in contrast to "classical estuary", it is the combined effects of reduced freshwater inputs, extended dry seasons with intense evaporation, and a low gradient of the slope in the lower estuary that have resulted in the inversion of the salinity gradient and the hypersalinization of the upstream areas of the system.

The hydrographic system of the Sine Saloum estuary (~850 km^2) is made up of three main branches (**Fig.5**): the Saloum (~110 km long; maximum depth 25 m), the Diomboss (~30 km; $\leq$ 10 m), and the Bandiala (~18 km; $\leq$ 10 m). As a result, the salinity difference between upstream and downstream is strong at the end of the dry season for the Saloum branch (e.g. 75 in 1942, 62 in 1960, 90 in 1983, and 84 in 1993), but for the Diomboss and Bandiala branches it remains low (Maximum recorded 5) (Diouf, 1996; Panfili et al., 2004). These main branches are surrounded and interconnected by a very dense network of channels of different sizes (locally named "bolongs"). The vegetative cover of the Sine Saloum is characterized by the presence of mangroves dominated by Rhizophora and Avicennia species. With the exception of the remaining patchy mangrove vegetation found in the "Lagune de la Somone", along the Senegal River Delta, and the relics of the Mauritanian coast, the Sine-Saloum is home to the most northerly mangroves in West Africa. Furthermore, the Sine Saloum system exhibit a quite uncommon example of a mangrove system with little freshwater input except by direct rain or by ground water (Pagès and Citeau, 1990). Affected by the regional climatic changes and following the increase of the salinity and the resulting soil acidification, an important proportion of the mangrove cover has been replaced by huge, flat, bare, salt-saturated areas locally called "tannes". In the southern part of the Sine Saloum, the mangrove is very extensive. It occupies almost the entire space between the "bolons". The mangroves are high (7 to 11 m) along the tidal channels and especially in their downstream parts (**Fig. 6a**). The central portion is characterized by an increase in "tannes" and a lower and shorter (2-8 m) mangrove cover than in the south (**Fig. 6b**). The mangroves of the upstream parts of the "bolons" of this zone often have a more degraded appearance. The north of the estuarine complex is occupied by a much degraded mangrove (generally less than 4 m) that

eventually disappears upstream of the Saloum and being completely replaced by "tannes" (**Fig. 6c and d**).
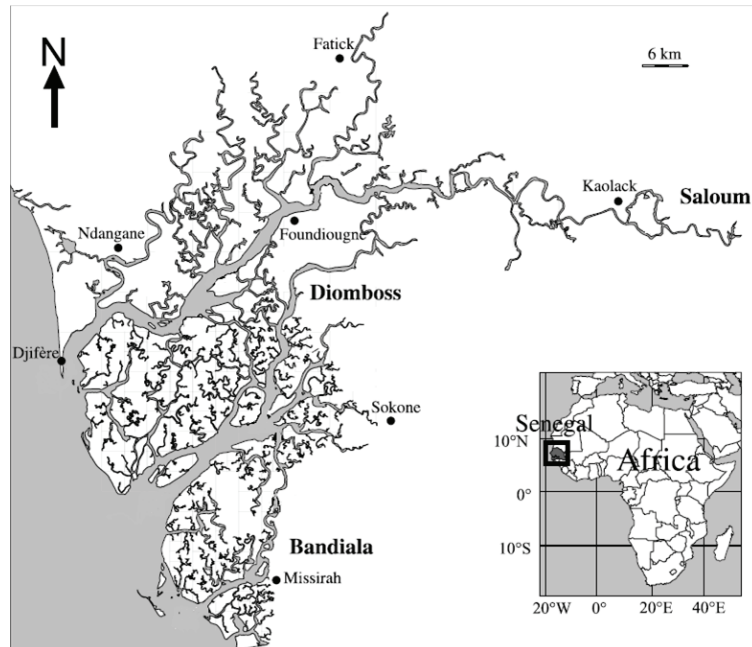

Fig. 5. The Sine Saloum estuary

The Saloum region economy is essentially based on fishing, mangrove exploitation, and more recently tourism (Mbow et al., 2008). The Sine Saloum is of great concern in terms of conservation and management because of the traditional and well developed fishing activities taken place there. The adult fish community has been well studied in the past decades (e.g.Diouf, 1996; Sadio et al., 2015; Simier et al., 2004) and a total of 114 species of fish belonging to 52 families have been recorded in the estuary of the Sine Saloum. In the absence of flooding, only small-scale seasonal variations of fish assemblages were observed, resulting from the migration of some species between the continental shelf and the estuary (Simier et al., 2004). Fish assemblages are characterized by the almost complete absence of freshwater species, while the number of marine species is proportionally high for an estuarine system. The three main branches are dominated in both numbers and biomass by a small number of species belonging to the families of Clupeidae (*Sardinella maderensis, Ethmalosa fimbriata*), Pristigasteridae (*Ilisha africana*), Gerreidae (*Gerres nigri*), Carangidae (*Chloroscombrus chrysurus*), Mulgilidae

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(*Liza grandisquamis*), and Cichlidae (*Sarotherodon melanotheron, Tilapia guineensis*). These fishes are vital subsistence resources for coastal communities across the country and the ecological and economic importance of the estuary has led the state of Senegal and the international community to take steps to protect the biodiversity of this site. The whole estuarine system has been classified as a "Reserve of Biosphere of UNESCO" in 1981, designated Senegal's third Ramsar Wetland of International Importance in 1984, and has recently been listed as an UNESCO world heritage site in 2011. The Sine Saloum estuary is located within the Senegalo-Mauritanian East border upwelling system, considered one of the most productive and economically important fishing zones in the world, and is also part of the West African Marine Ecoregion (WWF, 2017).
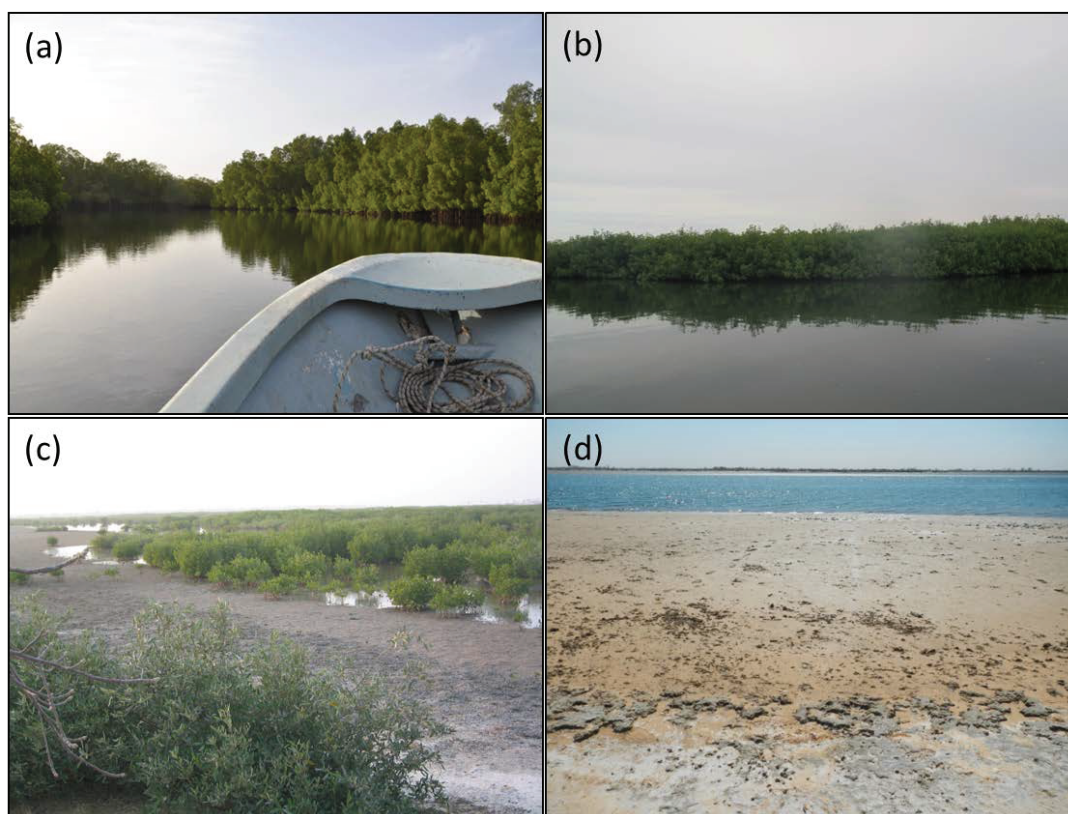
Fig. 6. Variations of the mangrove cover in the Sine Saloum estuary. Mangroves cover almost the entire southern portion of the system and progressively diminish in the north. (a) The south-western area is characterized by dense and tall mangroves, (b) which become shorter in the central zone, (c) thin out in the north-eastern area and (d) totally disappear in the upstream Saloum, replaced by huge, flat, salt saturated intertidal areas "tannes".

Objectives and Outline

As a consequence of the decline of numerous commercial fish populations, an ecosystem-based approach to fisheries management, which includes the assessment and protection of essential fish habitats, has emerged (Garcia et al., 2003). This doctoral thesis is part of the trilateral cooperation project Ecosystem approach to the management of fisheries and the marine environment in West African waters (AWA). This interdisciplinary research project aims at providing the scientific basis and requirements for setting up a strategic partnership capable of developing the vision of an ecosystem approach to fisheries in West African waters.

Given the high overall salinity and the mangrove degradation that is taking place in the Sine Saloum estuary, its potential role (compared to "classic estuary") as a recruitment and nursery area for fish larvae is far to be clear. Due to a globally changing climate, the inversion of the salinity gradient in several estuaries throughout the dry tropics is either underway or can be expected in the near future (Pagès and Citeau, 1990; Ridd and Stieglitz, 2002). Because spawning and nursery grounds of fishes have requisite environmental and physical attributes, early life-history stages must be considered when modifications of these environments are observed. For these reasons, the Sine Saloum estuary is a natural and excellent choice to study how these climatic environmental transformations are affecting the ichthyoplankton community. This thesis aims at gaining knowledge on the environmental and physical factors affecting the Sine Saloum ichthyoplankton diversity and distribution. For this, specific research topics are addressed in three separate chapters. **Chapter I** is a contribution to a better knowledge of the organization and dynamics of larval fish assemblages in high salinity environments and presents results of the first multispecies ichthyoplankton investigation in an inverse estuary. **Chapter II**, is a contribution to our understanding of the hydrography and the implications of physical dynamics upon the potential pathways for larval fish transport between low-flow estuaries and coastal waters in seasonally arid climates. Presented here are the first current measurements that simultaneously look at the estuarine physics (including circulation) and larval transport in an inverse estuary. **Chapter III**, is a contribution to an initial understanding of the dietary importance of the sea surface microlayer (SML) for larval or juvenile fish development. Stable isotope composition of the SML was for the first time quantified and allowed the application of Bayesian stable isotope mixing model to calculate its contribution to the diet of larval and juvenile African halfbeaks (*H. picarti*). The combined information in those three chapters allowed the recognition of

valuable patterns and processes acting on the early life stages of fishes in this ecologically and economically important mangrove estuary, but also contributes to knowledge about the potential development of other, currently less disturbed mangrove estuarine systems in West Africa and around the world. These chapters are followed by a synoptic discussion that is summoning up the main results of this thesis, connecting the aforementioned studies, and discussing additional aspects. Finally, highlights of emerging questions and potential future research lines are proposed.

Chapter I

"Composition and structure of the larval fish community related to environmental parameters in a tropical estuary impacted by climate change"

Hans Sloterdijk, Patrice Brehmer, Oumar Sadio, Hanno Müller, Julian Döring, Werner Ekau
(Accepted in Estuarine Coastal and Shelf Science)

Climate changes that include the reduction of the average annual precipitation in parts of the dry tropics have resulted in the inversion of the salinity gradient of a number of estuaries. In these so called "inverse estuaries", several studies on adult fish assemblages have been undertaken during the last decades. However, to have a comprehensive picture of how these environmental transformations are affecting the diversity, abundance, and distribution of the ichthyofauna, early life stages of fish must be included and consequently, **Chapter I** is a contribution to a better knowledge of the organization and dynamics of larval fish assemblages in high salinity environments and presents results of the first multispecies ichthyoplankton investigation in an inverse estuary, the Sine Saloum system. The aims were (1) to describe the composition and structure of the larval fish community, and (2) to analyse the influence that abiotic factors, in particular salinity, have on the distribution of fish larvae in this ecosystem. Using neuston and ring trawl nets, larval fishes were sampled at locations distributed along a salinity and distance-to-the-sea gradient during four field campaigns covering an annual cycle.

Chapter II

"On the larval fish transport in and out of the Sine-Saloum estuary"

Hans Sloterdijk, Xavier Capet, Patrice Brehmer, Werner Ekau
(Submitted in Estuaries and Coast)

For several species of marine fishes, recruitment to adult population requires successful early life transport from open ocean spawning regions to estuarine nursery habitats. **Chapter II**, is a contribution to our understanding of the hydrography and the implications of physical dynamics upon the potential pathways for larval fish transport at the interface of an inverse estuary connected to the North Atlantic Ocean. First, the flow structure at the entrance of the Saloum branch of the Sine-Saloum estuary is characterized. Second, the movement of fish larvae in and out of the estuary is described by looking at the variation in the larval fish densities and transport rates as related to phase of the tide, time of the day, and location within the entrance of the Saloum river branch. Finally, the focus is on the physical and the possible impact of larval behaviour by which larval fishes are transported between the shelf and the estuarine areas. The survey extended over two full semidiurnal tidal cycles and included simultaneous measurements of larval density, transport, and current velocity (ADCPs).

Contribution of the authors: H. Sloterdijk designed the study and conducted the field sampling. H. Sloterdijk conducted the DNA work on the fish larvae. H. Sloterdijk and X. Capet analysed the data and wrote the manuscript. W. Ekau and P. Brehmer advised on data analysis and commented on the manuscript.

Chapter III

"The importance of the sea surface microlayer as a feeding source for larval and juvenile *Hyporamphus picarti* in the Sine Saloum estuary: stable isotope analysis"

Hans Sloterdijk, Werner Ekau

(Submitted in Marine Ecology Progress Series)

Unexplored in terms of its potential as an important contributor of the nursery value of a habitat for fish larvae and juveniles, the sea surface microlayer (SML) represents a unique physical and chemical environment quite different from that of the underlying waters. As an important first step towards a better understanding of its function and derived dietary importance for organisms such as larval and juvenile *Hyporhamphus picarti*, a species that nearly exclusively lives in the vicinity of SML, stable isotope analysis using diet-mixing model was used to look at the contribution of the SML to the diet of *H. picarti* larval and juvenile fish at the entrance of the Sine Saloum estuary, Senegal. Larvae and juveniles of this species are found in very high abundance in the Sine Saloum estuary and are exploited commercially throughout the West African coast. Because sampling the SML for isotope analysis was never done before, in **Chapter III**, stable isotopic signatures between the food sources are characterized, ontogenic shift in the isotopic signature of different size classes of the larvae and juveniles (the consumers) are looked at, and a Bayesian mixing model (SIAR) is used to estimate the proportion of the SML contributing to the larval and juvenile's diets.

Contribution of the authors: *H. Sloterdijk designed the study and conducted the field sampling. H. Sloterdijk prepared the samples and conducted the isotope analyses. H. Sloterdijk analysed data and wrote the manuscript. W. Ekau commented on the manuscript.*

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Publications

Chapter I

Composition and structure of the larval fish community related to environmental parameters in a tropical estuary impacted by climate change

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Abstract

Mangrove ecosystems have long been considered essential habitats and are commonly viewed and referred to as "nursery areas". They are highly sensitive to climate change, and environmental transformations in these ecosystems are expected. The Sine Saloum estuary is a case of a system affected by global climate change where reduced precipitation and temperature increase have resulted in an inversion of the salinity gradient. Within the estuary, the composition and structure of the larval fish community related to environmental parameters were investigated using neuston and ring trawl nets. Larval fishes were sampled at 16 stations distributed along a salinity and distance-to-the-sea gradient during four field campaigns (November 2013, February, June, and August 2014) covering an annual cycle. This is the first study documenting the spatial and temporal assemblages of fish larvae in an inverse estuary. The total of 41 taxa representing 24 families and 34 genus identified in this study was lower than that of other tropical estuaries. Clupeidae spp. was the dominant taxon, accounting for 28.9 % of the total number of fish larvae caught, followed by Gerreidae spp. (21.1 %), *Hyporamphus picarti* (18.8 %), *Diplodus bellottii* (8.9 %), *Hypleurochilus langi* (4.8 %), Mugilidae spp. (4.4 %), and Gobiidae sp.1 (3.5 %). A total of 20 taxa were recorded within the upper estuary region, whereas 29 and 37 taxa were observed in the middle and lower reaches, respectively. While larval fish were captured at all sites and during all seasons, abundances and richness decreased with increasing salinity. Larval fish assemblages also showed a clear vertical structure corresponding to three distinct water strata. Salinity, water temperature, and dissolved oxygen were the variables that best explained the spatial and temporal differences in larval fish assemblages. It is difficult to forecast the future situation for this system but so far, compared to other mangrove estuarine system, we have observed the loss of freshwater species in favour of species of marine origin. The information provided in the present study is a contribution to the knowledge of tropical biodiversity and modifications of the ichthyoplankton communities in the context of climate change and future green fund action.

1. Introduction

Estuarine and coastal ecosystems such as nearshore coral reefs, seagrass beds, salt marshes, lagoons, and mangrove forests are known to support numerous important functions (Beck et al., 2001). Providing a great deal of key ecosystem services, like coastal protection, water purification, carbon sequestration, fisheries, raw materials, and more recently tourism related activities; they influence human welfare both directly, through direct usage, and indirectly, via impacts on supporting and regulating services in other environments (Barbier et al., 2011; Brehmer et al., 2011; Costanza et al., 1997).

Amid these ecosystems, mangroves are among the most productive and biogeochemically active environments (Barbier et al., 2011). They have high primary and secondary productivity (Bouillon et al., 2008; Jennerjahn and Ittekkot, 2002) supporting a great abundance and diversity of ecologically and commercially important fishes and invertebrates (Primavera, 1998; Robertson and Duke, 1987). Many studies have shown that mangrove habitats can supply abundant and diverse food, and provide shelter for young fishes, where they occur at higher densities, avoid predation more successfully, and grow faster than in a different habitat (Laegdsgaard and Johnson, 2001; Verweij et al., 2006; Nagelkerken et al., 2008). Moreover, there is evidence that the hydrodynamic processes in mangrove areas enhance the entrapment of planktonic larvae (Chong et al., 1996). For these reasons, mangrove estuarine ecosystems have long been considered essential habitats and are commonly viewed and referred to as "nursery areas" (Manson et al., 2015; Faunce and Serafy, 2006; Field et al., 1998; Chong et al., 1990; Bell et al., 1984; Weinstein and Brooks, 1983). There is also an assumption that there is a positive correlation between the area of mangrove habitat in an estuary and fisheries landings (Carrasquilla-henao and Juanes, 2016; Manson et al., 2015; Aburto Oropeza et al., 2008; Meynecke et al., 2007; Lee, 2004). This paradigm predicts that changes in mangrove attributes, for instance mangrove loss or local disturbance, would then lead to a reduction in, or a massive loss of fisheries production in coastal waters. Strengthening this view, several authors have emphasized the importance of estuaries for marine fisheries by demonstrating that a large part of the landings around the world is made up of species that spend part of their lives in estuarine waters (Barletta et al., 2005, 1998; Brehmer et al., 2006; Pauly, 1988). Moreover, groups of commercially important species classified as estuarine-dependent are often the base for economic valuation of mangroves (Nagelkerken et al., 2008).

These reasons are often invoked as grounds for the protection and conservation of mangrove estuarine ecosystems, and yet, these areas continue to decline, and in some cases worryingly fast (Polidoro et al., 2010; FAO, 2007; Alongi, 2002; Valiela et al., 2001). Throughout history, estuaries have played a critical role in human development. However, anthropogenic threats have made the estuaries one of the most degraded ecosystems on earth (Edgar et al., 2000). The impacts come from a long list that includes coastal development, dredging, filing and draining of wetlands, hardening of shorelines with riprap or concrete, upstream dams and diversions that alter freshwater inflow, land-based pollution, and overfishing (Lotze et al., 2006). More recently, the effects of climate change such as sea-level rise, an increase in the number, duration, and intensity of tropical storms, and longer periods of drought in some regions are now recognized as important stressors threatening estuarine ecosystem functioning (Scavia et al., 2002). Accordingly, local and national conservation plans stress the need to get more information on such ecosystem.

Located in Senegal, West Africa, the Sine-Saloum estuary has been affected by climate change and direct human disturbances, and consequently has undergone significant environmental transformations (Mbow et al., 2008; Xenopoulos et al., 2005). This estuarine system became permanently inverted in the late sixties due to the increasing lack of freshwater inflow (Barusseau et al., 1985; Pagès and Citeau, 1990), a direct consequence of the prolonged drought (known as the Sahelian drought) that has affected the entire Sahel region (Nicholson, 2005; Nicholson et al., 2000). Accordingly, salinity increases upstream and values throughout the system are usually greater than that of seawater. During the dry season (November to June), the difference between upstream and downstream could reach up to 90 (Diouf, 1996). What are currently unknown are the changes and impacts of this important environmental modification (inversion of the salinity gradient) in the Sine Saloum on its function as an essential habitat and important nursery area; both characteristics generally attributed to classics estuaries. Coupling this with indications that many arid regions are becoming drier as a result of climate change (IPCC, 2008, 2014), there is a need for managers and decision makers to understand and ultimately anticipate the gross effects of such natural and anthropogenic disturbances to these systems as they may further exacerbate the existing stresses on the food security and economy of these affected regions.

In the Sine Saloum estuary, several studies on adult fish assemblages have been undertaken during the last decades (Ecoutin et al., 2010; Simier et al., 2004; Vidy, 2000;

Diouf, 1996). Although many species could settle temporarily or permanently, few are dominant in terms of abundance and the ichthyofauna is dominated by a few species belonging to three main families: Clupeidae, Mugilidae, and Cichlidae (Simier et al., 2004; Diouf, 1996). The environmental conditions favour the establishment of a fish fauna mainly composed of species of marine origin and most of them are juvenile forms of species from the continental shelf (Simier et al., 2004). However, to have a comprehensive picture of the Sine Saloum estuary situation, early life stages of fish must be included and to our knowledge no study has been conducted and published on larval fish assemblages. This paper presents results of the first multispecies ichthyoplankton investigation in an inverse estuary, the Sine Saloum system. The aims were (1) to describe the composition and structure of the larval fish community, and (2) to analyse the influence that abiotic factors, in particular salinity, have on the distribution of fish larvae in this ecosystem. The present study is a contribution to a better knowledge of the organization and dynamics of larval fish assemblages in high salinity environments, particularly in inverse estuaries.

2. Material and methods

2.1. Study area: the Sine Saloum estuary

The Sine Saloum estuary (13°30' 14°30' N, 16°00'-16°80' W) is located in Senegal (West Africa) and covers an area of approximately 800 km^2 of open water (**Fig. 1**). It comprises three main branches/rivers (Saloum, Diomboss, and Bandiala) that are connected to each other by a vast network of small mangrove creeks locally named "bolong". The Saloum channel is 7 to 15 m deep; with maximum depth of 25 m, while the Diomboss and Bandiala have maximum water depth of 10 m (Saos and Pagès, 1985). Mangrove forests cover almost the entire southern portion of the system and progressively diminish in the North. Luxuriant in the Bandiala, patchy in the Diomboss and in the lower part of the Saloum, the mangrove fully disappears in the upstream Saloum (Simier et al., 2004; Trape et al., 2009). The region has a Sahelo-Sudanian climate (Köppen climate classification: BWh) and divides the year into two principal seasons: a single short rainy season from July to October and an extended dry season from November to June. The dry season can be further divided into two sub-seasons: "cool and dry" from November to March and "warm and dry" from April to June. Nowadays, as no river of significant size is flowing through the system, the Sine Saloum estuary does not receive freshwater inputs except by

local rainfall precipitation. Generally, in the system, salinity increases from downstream to upstream in all seasons. The difference between upstream and downstream is strong at the end of the dry season for the Saloum branch (75 in 1942, 62 in 1960, 90 in 1983, and 84 in 1993), but for the Diomboss and Bandiala branches it is still low (Maximum recorded 5) (Diouf, 1996; Panfili et al., 2004). During the year, the temperature of the water evolves in much the same way over the whole system with maximum reported values of about 32 °C between June and October and lowest reported between 21 to 22 °C between December and February (Diouf, 1996; Ecoutin et al., 2010; Saos and Pagès, 1985; Simier et al., 2004; Unesco, 1983). The whole system has been classified as a Reserve of Biosphere of United Nations Educational, Scientific and Cultural Organization (UNESCO) in 1981, designated as Senegal's third Ramsar Wetland of International Importance in 1984, and has been recently listed as an UNESCO world heritage site in 2011. The Sine Saloum estuary is located within the Senegalo-Mauritanian East border upwelling system, considered one of the most productive and economically important fishing zones in the world, and is also part of the West African Marine Ecoregion (WAMER) (WWF, 2017).
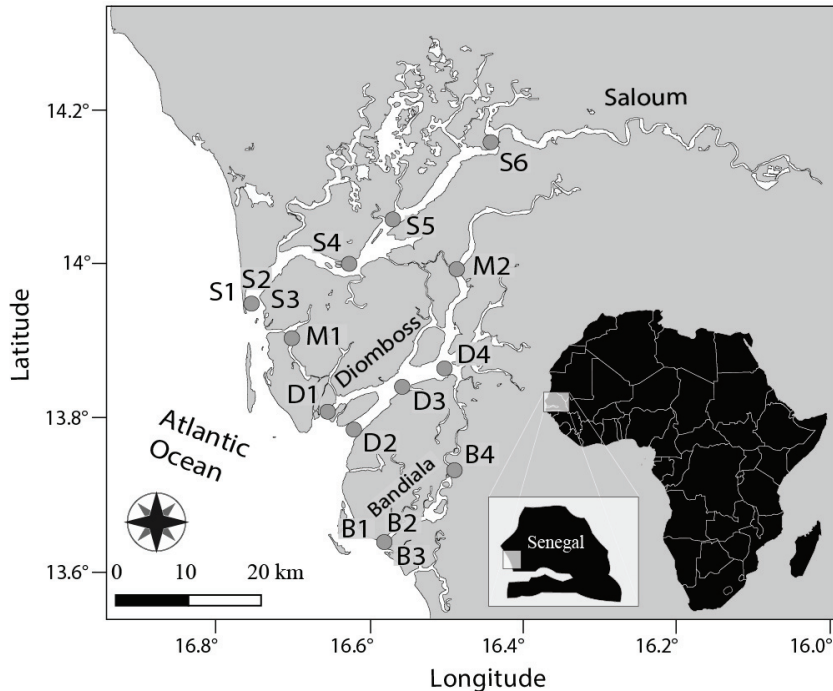

Fig. 1. Map of the Sine Saloum estuary and location of the 16 sampling sites.
(S: Saloum, D: Diomboss, B: Bandiala, M: Mangrove/Bolong)

2.2. Data collection

Based on the seasonality, four field campaigns were conducted covering an annual cycle: [1] November 2013 (end of the wet season) when the system has received its highest yearly amount of freshwater, [2] February 2014 (cool and dry season), [3] June 2014 (warm and dry season), and [4] August 2014 (wet season). In order to get representative samples, 16 sampling sites were selected for measurements of environmental parameters and for fish larvae sampling (**Fig. 1**). 14 were distributed within the three main branches (S1-6, D1-4, B1-4), along a salinity and distance-to-the-sea gradient, and two sites (M1-2) were selected in areas inside the inner mangrove (Bolong). Selected environmental parameters were measured using hand-held multi-parameter field instruments (WTW Multi 3430® and Lovibond-TurbiCheck®). Quantitative descriptors were water temperature (°C), salinity, dissolved oxygen (mg l^{-1}), turbidity (NTU), pH, and bottom depth (m). For each station, a vertical profile of these environmental variables was obtained by taking measurements starting at the surface with depth intervals of one meter until the bottom was reached. Although no quantitative measurements of the mangroves were made, observations made during sampling at each site allowed for a rough qualitative characterization of the extent of the mangrove cover. Mangrove cover categories included none, residual, patchy, luxuriant, and replicate those used by Simier et al., (2004).

For fish larvae sampling, two types of nets, both with mesh size of 500 μm were used: a paired neuston nets (opening 30x15 cm, 3 m long) stacked on top of each other (referred in the text to Neuston Top and Neuston Bottom) for collecting fish larvae at and near the surface and a ring trawl (ɶ 0.60 m, 3 m long) to collect fish larvae in the water column. Accordingly, 3 strata were sampled: surface (Neuston Top), near surface (Neuston Bottom), and mid-water (Ring Trawl). Both nets were custom made to be operated from an adapted catamaran (Hobie Cat 15®) deployed in a parallel route of a towing boat ensuring larval sampling well clear of its bow wave and wake. Each sample consisted of a 10-minute horizontal haul in the direction of the current at an average speed of 2-3 knots. All hauls were performed during daylight hours and sampling sites depths ranged from 4 to 15 m (**Appendix A.1.**). During the November sampling campaign, due to logistic reasons, only the ring trawl net was available and sampling was done only near the surface (referred later in the text as Ring Trawl Surface). The volume of water filtered was calculated using mechanical flow meters (Hydro-Bios®) attached to the centre of the nets so the number of larvae caught could be standardized into the number of larvae per

cubic meter (m^3) for abundance/density measurements. Samples were immediately preserved in 30 % alcohol/seawater and stored and cooled in an onboard electric coolbox. In the laboratory, fish larvae were sorted from the catches and gradually transferred to 50 % and 70 % alcohol.

Using the traditional morphological techniques, collected specimens were identified to the lowest possible taxon (Leis and Carson-Ewart, 2004; Moser, 1996; Richards, 2006; Tamoikine and Pandare, 1994). Due to the paucity of original descriptions and illustrations of fish larvae found in the literature covering the area of interest, especially the smaller individuals could not always be identified to the species level, but only to family or genus level.

Complementary to the morphological techniques, genetic identification of specimens, using DNA sequencing, was applied to selected samples. DNA barcoding was based on sequencing the commonly used barcode region, a ±600 base pair fragment of cytochrome c oxidase I (COI/COX) (Hebert et al., 2003; Aljanabi and Martinez, 1997). For amplification, the COI-primer pair FF2d + FR1d of Ivanova et al. (2007) was used. Samples that failed amplifying with this primer pair were amplified using the primer pair of Folmer et al. (1994). DNA was extracted (whole fish larvae) according to Aljanabi and Martinez (1997). All polymerase chain reaction (PCR) reactions were performed according to the protocols published with the primer pairs. Amplicons were sequenced using the PCR primers. Sequences were compared with the National Center for Biotechnology Information (NCBI) nucleotide collection database using BLAST (Altschul et al., 1990). Additionally, the BOLD Identification System was used (Ratnasingham and Hebert, 2007).

In order to identify selected specimens of the order Clupeiformes, we used the multiplex haplotype-specific PCR (MHS-PCR) method of Durand et al. (2010). Amplicons were separated on a 3 % agarose gel in TAE buffer for two hours at 120 V. Selected amplicons were sequenced to confirm MHS-PCR-based identification.

2.3. Data analysis

2.3.1. Analyses of larval fish data

In order to determine and compare the spatial and seasonal distribution of fish larvae within the Sine Saloum estuary, for each sampling site, integrated catches (Neuston Top, Neuston Bottom, and Ring Trawl) of larval fish were estimated and expressed as number of individuals

per 100 m^3. Since various transformations failed to normalize the data and stabilize the variance, nonparametric Kruskall-Wallis test was conducted to investigate whether the larval fish abundances differed among the sampling seasons.

Prior to multivariate analyses, all of which were carried out using routines in the **PRIMER** statistical package (PRIMER version 7.0.10, 2015; PRIMER-E Ltd, Plymouth, U.K.), standardized catch data (number of individuals per 100 m^3) were transformed to log (x+1) for all statistical analyses. The log (x+1) transformation balance the contribution of abundant species with consistently high counts against those of less common and rare species, ensuring that each taxonomic group contributed fairly evenly to each analysis, rather than a few abundant taxa in the samples dominating each analysis (Clarke, 1993; Field et al., 1982).

To assess if larval communities differed between positions in the water column (based on the type of net used: Neuston Top – Neuston Bottom – Ring Trawl – Ring Trawl Surface), a similarity matrix based on the Bray-Curtis similarity measure was generated, after which non-metric multidimensional scaling (nMDS) was used to graphically display a two-dimensional ordination plot of the inter-relationships among samples, based on the relative abundance of each taxonomic group (Clarke et al., 2014; Field et al., 1982). One-way Analysis of Similarities (ANOSIM), which is analogous to univariate analyses of variance, identified whether differences in assemblage groupings in the nMDS ordination were significant. The extent of any significant differences produced by this test were determined using the *R*-statistic value (Clarke, 1993; Clarke et al., 2014), which can range from +1, i.e. all samples within each nets are more similar to each other than to any of the samples from other nets, down to approximately zero, when average similarities within and between the nets are the same (i.e. the null hypothesis). When the pairwise comparison in the ANOSIM test detected a significant difference in larval fish compositions between the nets and across seasons, Similarity Percentages (SIMPER) was used to identify which species typified each of those nets in each season (Clarke, 1993; Clarke et al., 2014). If the relative density and composition of the larval fishes found in a particular pair of net types were found not to differ significantly, SIMPER was used to typify the collective fish larval composition of those two net types. Similarly, if the relative abundance and composition of the larval fishes found in a particular type of net (previously identified with ANOSIM) were found not to differ significantly between seasons, SIMPER was used to typify the collective fish larval composition of those two seasons. All SIMPER on species contributions used Bray-Curtis similarity matrices and a cut off for low contributions set at 85 %.

For each of the water stratum sampled (i.e. surface: Neuston Top; near surface: Neuston Bottom; mid-water: Ring Trawl), the RELATE procedure (Clarke et al., 2014) was used to test the significance of the relationships between the larval fish abundances of the taxa (larval fish resemblance matrix) and the environmental variables data (environmental resemblance matrix). The correlation between a larval fish matrix and the environmental matrix was considered significant if the associated p value was < 0.05. When a significant match was detected between a larval fish matrix and the environmental matrix, the BEST (BIOENV) procedure using all the possible combinations was used to determine which subset of environmental variables, provided the best correlation with the larval fish matrix. The resulted subset of environmental variables was thus considered to be most influential in distinguishing the larval fish assemblages at sites representing the different environmental conditions.

The individual relationships between the larval densities of the dominant taxa of the Neuston Top, Neuston Bottom, and Ring Trawl assemblages (SIMPER) and the environmental variables found to be the most influential (BIOENV) were explored to estimate the upper and lower limits where these individual taxa occurred.

3. Results

3.1. Environmental conditions

Throughout the Sine Saloum estuary, vertical profiles showed no stratifications. The water column was very well mixed as salinity, water temperature, dissolved oxygen, pH, and turbidity were nearly the same from top to bottom at any given place within each sampling season. The environmental characteristics of the 16 sampling sites are given in **Fig. 2** and **Table A.1.** The seasonal change of water temperature clearly showed an annual cycle (**Fig. 2a**) with a maximum in August (mean ± SD: 30.0 ± 0.34 °C) and a minimum in February (mean ± SD: 21.2 ± 0.56 °C). Through the annual cycle, the water temperature changed substantially in the same manner throughout the Sine Saloum estuary (**Fig. 2b**). Therefore, within each sampling season, there were only minor and negligible spatial differences (i.e. between sites) in water temperatures. With reference to salinity, seasonal values also showed an annual cycle (**Fig. 2c**). As for temperature, the highest values of salinity were recorded in August

(mean ± SD: 42.1 ± 5.28) but the lowest were recorded in November (mean ± SD: 29.6 ± 1.86) i.e. end of the wet season. As the dry season progressed (from November to June), there was a steady increase in the system's average salinity. However, at the end of the rainy season (November), a salinity gradient characteristic of classic estuaries was present with salinity values of the three main branches decreasing from downstream to upstream (**Fig. 2d**). Dissolved oxygen, highest in February (mean ± SD: 6.48 ± 0.30 mg l^{-1}) and lowest in August (mean ± SD: 5.21 ± 0.48 mg l^{-1}) presented values generally higher in sites situated close to the open ocean (**Fig. 2e-f**). Thus, an inverse relationship between dissolved oxygen and water temperature was observed (**Fig. 2a, e**). Seasonally, pH was highest in February (mean ± SD: 7.880 ± 0.118), a trend similar as what was observed for dissolved oxygen and opposite to water temperature. Turbidity (**Fig. 2i-j**) was low in all seasons and sites, ranging from 1.30 to 16.60 NTU. The turbidity was highest at the Bandiala mouth (B1, B2, and B3) with all values above 6 NTU obtained during February and June.

3.2. Abundance and taxonomic composition

During the study period, a total of 21 082 fish larvae were collected over 161 samples. 39 taxa were identified: 25 were assigned to species, 5 to genus, and 7 to family levels, while 2 remained unidentified. Overall, 24 families including 34 genera were represented. Clupeidae spp. was the dominant taxa, accounting for 28.9 % of the total number of fish larvae caught, followed by Gerreidae spp. (21.1 %), *Hyporamphus picarti* (18.8 %), *Diplodus bellottii* (8.9 %), *Hypleurochilus langi* (4.8 %), Mugilidae spp. (4.4 %), and Gobiidae sp.1 (3.5 %). These six taxa comprised 90 % of the total catch, the remaining 10 % being shared by the others 33 taxa. **Table 1** also provides the total number of individuals and additional information about each taxon collected in each net (water stratum). Markedly, when looking at the percentage contribution to the overall catch within each net, > 50 % of the total abundance of the separate net type could be accounted by a single taxon. *Hyporamphus picarti* accounted for 55.4 % of the Neuston Top, Gerreidae spp. 50.1 % of the Neuston Bottom, and Clupeidae spp. 60.7 % of the Ring Trawl total number of fish larvae caught (**Table 1**).
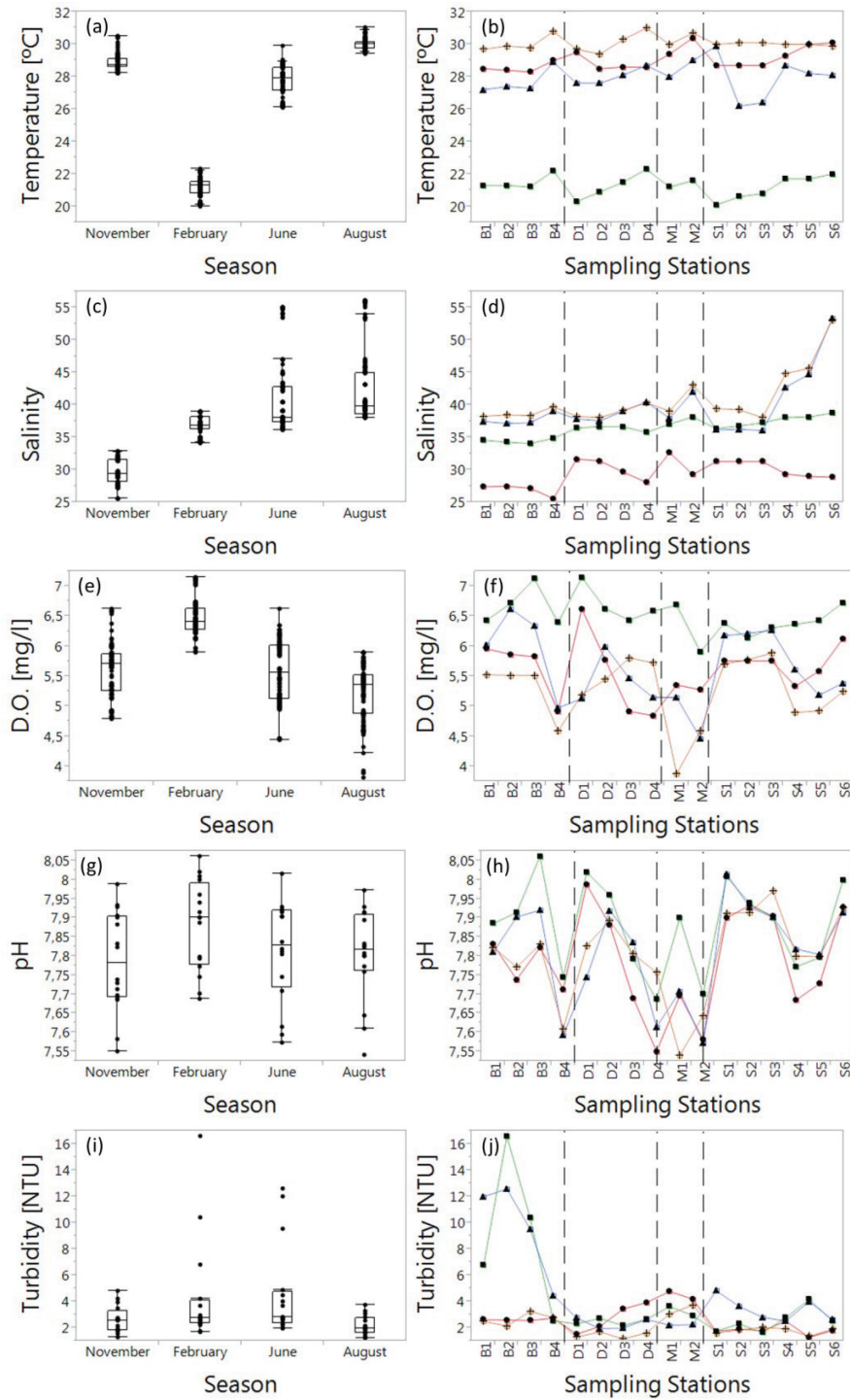
Fig. 2. (**Left Panel**) Box and whisker plots showing the seasonal variations in the main environmental parameters. The bottom and top edges of the boxes are located at the sample 25th and 75th percentiles. The centre horizontal line is drawn at the 50th percentile (median). The whiskers extend from the ends of the box to the outermost data point that falls within the distances computed as follows: 1st quartile - 1.5*(interquartile range) and 3rd quartile + 1.5*(interquartile range). Outliers are shown as data points outside the whiskers ranges and single points are single measurements. (**Right panel**) Spatial variation in surface values of the main environmental parameters. Dashed lines separate the different branches of the Sine Saloum.
(●, November; ■, February; ▲, June; +, August)

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Table 1

Rank by abundance (Rk), abundance (A), percentage contribution to the overall catch (%), and occurrence (O) of each larval fish species in samples collected in the Sine Saloum estuary. Abundance: total number of individuals. Occurrence: number of samples where the taxon was present. Neuston Top: Surface. Neuston Bottom: Near Surface. Ring Trawl: Water Column.

	Total				Neuston Top				Neuston Bottom				Ring Trawl			
	Rk	A	%	O	Rk	A	%	O	Rk	A	%	O	Rk	A	%	O
Clupeidae spp.	1	5810	28.9	55	6	58	1.0	6	5	281	5.4	16	1	5471	60.7	33
Gerreidae spp.	2	4230	21.0	98	2	1204	20.5	26	1	2612	50.1	48	4	414	4.6	24
Hyporamphus picarti	3	3770	18.8	57	1	3253	55.4	34	4	489	9.4	18	21	28	0.3	5
Diplodus bellotti	4	1797	8.9	20	4	419	7.1	5	2	859	16.5	5	3	519	5.8	10
Hypleurochilus langi	5	956	4.8	94	5	257	4.4	30	3	617	11.8	39	14	82	0.9	25
Mugilidae spp.	6	887	4.4	72	3	563	9.6	32	6	162	3.1	24	8	162	1.8	16
Gobiidae sp.1	7	712	3.5	40	15	1	<0.1	1	7	37	0.7	7	2	674	7.5	32
Pseudotolithus sp.	8	352	1.8	7									5	352	3.9	7
Enneacampus sp.	9	293	1.5	45					14	12	0.2	5	6	281	3.1	40
Cynoglossus senegalensis	10	213	1.1	31					11	16	0.3	7	7	197	2.2	24
Synaptura cadenati	11	137	0.7	14					9	18	0.3	4	9	119	1.3	10
Gobiidae sp.4	12	113	0.6	9									10	113	1.3	9
Gobiidae sp.2	13	107	0.5	9					10	17	0.3	3	13	90	1.0	6
Bathygobius casamancus	14	97	0.5	16					25	1	<0.1	1	11	96	1.1	15
Chloroscombrus chrysurus	15	95	0.5	6	13	1	<0.1	1	22	1	<0.1	1	12	93	1.0	4
Atherina sp.	16	69	0.3	16	7	42	0.7	7	8	26	0.5	8	32	1	<0.1	1
Unknown 2	17	53	0.3	5					16	6	0.1	2	15	47	0.5	3
Trachurus trecae	18	49	0.2	9					12	16	0.3	5	19	33	0.4	4
Fodiator acutus	19	48	0.2	14	8	34	0.6	9	13	13	0.2	4	33	1	<0.1	1
Caranx rhonchus	20	47	0.2	6	14	1	<0.1	1	17	5	0.1	2	17	41	0.5	3
Synaptura lusitanica	21	43	0.2	5									16	43	0.5	5
Monodactylus sebae	22	38	0.2	20	17	1	<0.1	1	15	8	0.2	5	20	29	0.3	14
Trachinotus goreensis	23	36	0.2	10					18	3	0.1	2	18	33	0.4	8
Scombrus sp.	24	30	0.1	4	11	2	<0.1	1					22	28	0.3	3
Hemiramphus brasiliensis	25	29	0.1	7	9	27	0.5	6	21	2	<0.1	1				
Plectorhinchus macrolepis	26	20	0.1	6					27	1	<0.1	1	23	19	0.2	5
Hippocampus algiricus	27	13	0.1	9	16	1	<0.1	1					24	12	0.1	8
Stephanolepis hispicus	28	13	0.1	10	12	2	<0.1	2	19	3	0.1	2	26	8	0.1	6
Coryphoblennius gelerita	29	8	<0.1	5									25	8	0.1	5
Gobiidae sp.3	30	8	<0.1	4					20	2	<0.1	1	27	6	0.1	3
Ephippion guttifier	31	6	<0.1	3					23	1	<0.1	1	28	5	0.1	2
Ephippus goreensis	32	5	<0.1	2									29	5	0.1	2
Cheilopogon sp.	33	4	<0.1	2	10	3	0.1	1	24	1	<0.1	1				
Trachinotus teraia	34	3	<0.1	3									30	3	<0.1	3
Drepane africana	35	3	<0.1	1									31	3	<0.1	1
Polydactylus quadrifilis	36	1	<0.1	1					26	1	<0.1	1				
Sphyraena afra	37	1	<0.1	1									34	1	<0.1	1
Tylosurus crocodilus	38	1	<0.1	1	18	1	<0.1	1								
Unknown 1	39	1	<0.1	1									35	1	<0.1	1

Further identification of the larvae of Clupeidae, Gerreidae, and Mugilidae on a morphological basis was not possible inter alia due to the size of individuals, but DNA analyses performed on a random selection of specimens of these families indicated the presence of *Ethmalosa fimbriata*, *Sardinella maderensis*, and *Pellonulla leonensis* for the Clupeidae, *Gerres nigri* and *Eucinostomus melanopterus* for the Gerreidae, and *Liza dumerili* and *Liza grandisquamis* for the Mugilidae, bringing the total number of larval fish species recorded in this system to 43. Unidentified fish larvae that could not be assigned to any taxon (unknown 1 and 2) accounted for only < 0.01 % of the total number caught. In terms of bioecological categories, larval fish composition was dominated by estuarine forms of marine origin (35.7 %), followed by marine-estuarine species (28.6 %), marine species occasional to estuaries (14.3 %), marine species accessory in estuaries (14.3 %), and strictly estuarine species (2 %).

3.3. Spatial, temporal, and species richness distributions of larval fish abundances

Fish larvae were captured at all of the sampling sites and during all seasons. Larval abundances per sites (expressed as individuals per 100 m^3 and noted ind. 100 m^{-3}) and across seasons are shown in **Fig. 3**. The Kruskal-Wallis test showed that there was a statistically significant difference in fish larvae abundance between the different seasons, with $\chi^2(3) = 10.285$, $p = 0.02$, with a mean rank abundance (100 ind. m^{-3}) of 30.21 for November, 30.62 for February, 42.63 for June, and 22.38 for August. A maximum of 1631.47 ind. 100 m^{-3} was recorded at station S3 in June and a minimum of 2.27 ind. 100 m^{-3} was observed at station D3 in November. The seasonal maximum was obtained in June (mean ± SD: 357.2 ind. 100 m^{-3} ± 490.8) and the minimum in August (mean ± SD: 23.7 ind. 100 m^{-3} ± 21.3). Intermediate values of 59.3 ind. 100 m^{-3} ± 96.4 and 58.8 ind. 100 m^{-3} ± 77.9 were recorded in February and November, respectively. Despite these variations, an overall trend was evident across all seasons with the exception of August. The abundance in term of ind. 100 m^{-3} of larvae was pointedly higher in the lower estuary and declined with distance upstream. Fish larval richness (expressed as the total number of taxa) per sites and across seasons showed a similar trend, with decreasing richness with increasing distance from the open ocean (**Fig. 4**). A total of 20 taxa were recorded within the upper estuary region, whereas 29 and 37 taxa were observed in the middle and lower estuary regions, respectively. On

a seasonal base, 20 taxa were identified in November, 22 in February, 36 in June, and 24 in August. At the individual station level, a maximum of 25 taxa was observed at station B1 in June and a minimum of 2 taxa was observed at station D3 and S2 during the November campaign.

Fig. 3. Spatial distributions of larval fish abundances (ind. 100 m^{-3}) in the Sine Saloum System over the four sampling events. (a) November 2013, (b) February 2014), (c) June 2014, and (d) August 2014. Note: logarithmic (log) scaling of bubble sizes was used to respond to a few points that were much larger than the bulk of the data, allowing an all-encompassing visualisation of the large range of abundances values.
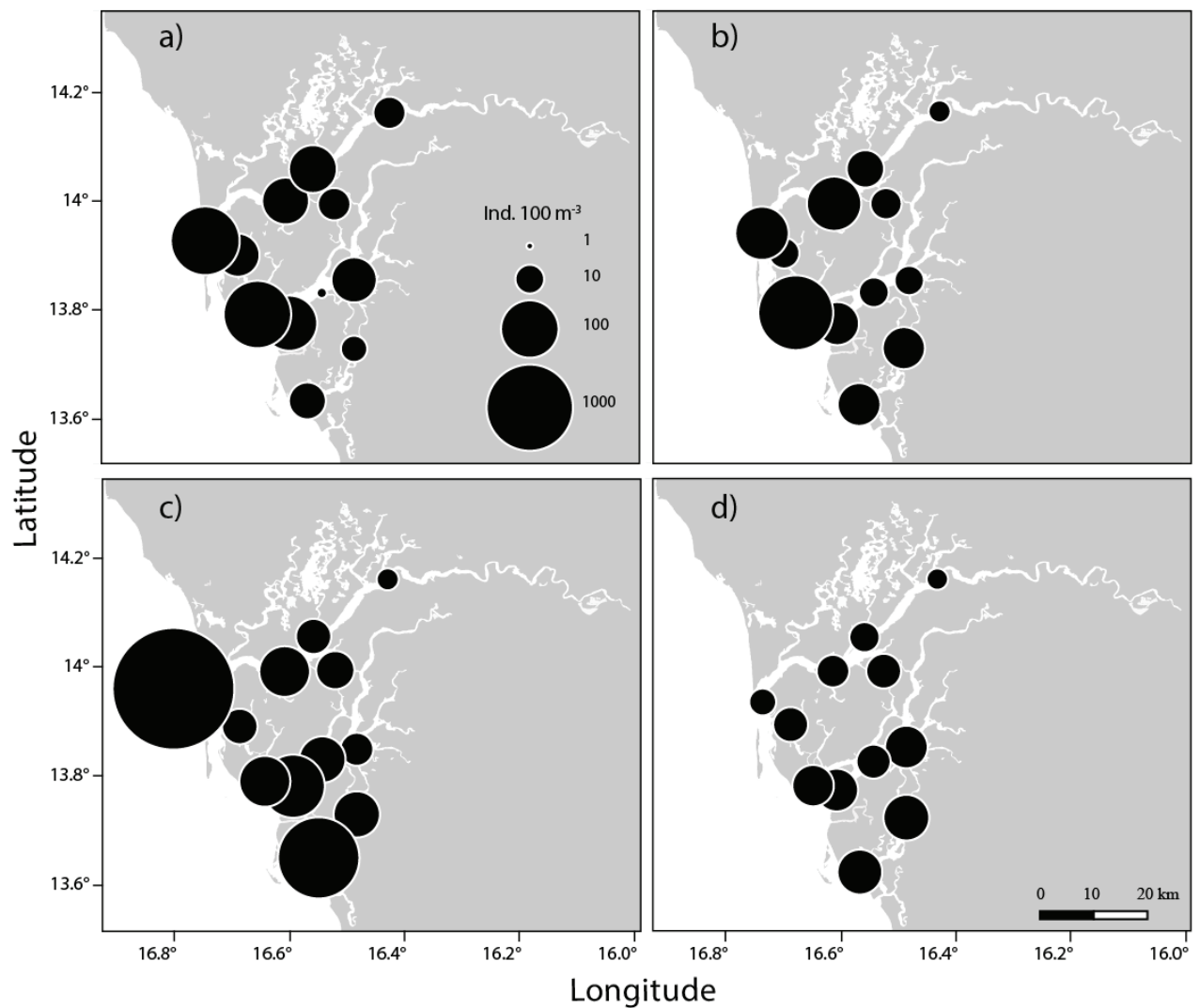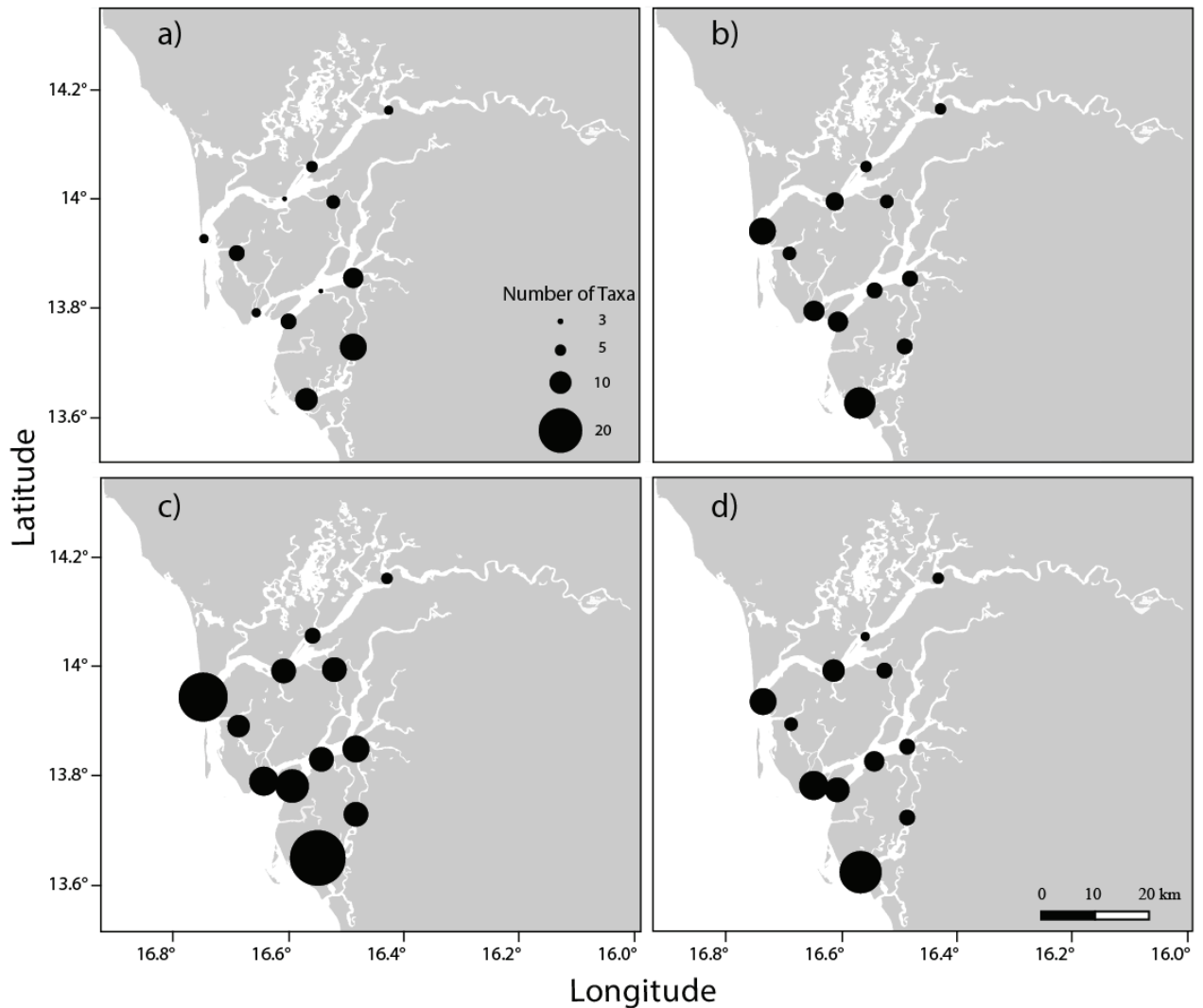
Fig. 4. Spatial distributions of larval fish richness (number of taxa) in the Sine Saloum System over the four sampling events. (a) November 2013, (b) February 2014), (c) June 2014, and (d) August 2014.

3.4 Vertical density and taxonomic composition of assemblages

When the densities (expressed as individuals per 100 m^3) of the various larval fish species in samples collected at each site in each net were subjected to an nMDS ordination, the samples showed a tendency to form groups on the basis of net type, in accordance to their positions in the water column (**Fig. 5**). Samples from the Ring Trawl net formed a discrete group that was located furthest from those representing the Neuston Top and Neuston Bottom nets. Samples from the

Ring Trawl Surface lay between those of the Neuston and Ring Trawl nets. A significant level ($p = 0.001$ %) and a value of R (= 0.38) for the one-way ANOSIM global test (99999 permutations) of nets Neuston Top, Neuston Bottom, Ring Trawl Surface, and Ring Trawl established that there were statistically significant differences in species composition and densities between these nets and the ANOSIM pairwise test results are presented in **Table 2**. The species composition and abundances between the nets were all significantly different from one another with the exception of the Neuston Bottom and Ring Trawl Surface. Species composition and abundances between these two nets were not distinguishable ($R = 0.04$, $p = 25.4$ %) from each other and consequently, the data from these two nets were combined and referred to Neuston Bottom prior to undertaking SIMPER.
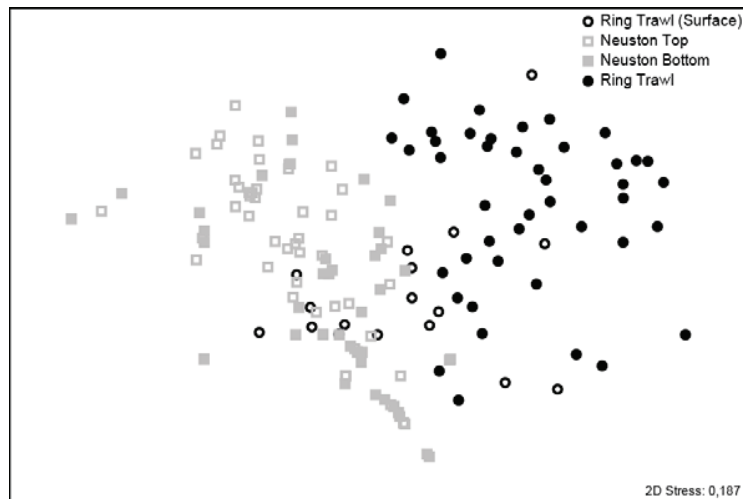
Fig. 5. Two-dimentional nMDS ordination showing larval fish assemblage structure in relation to the position in the water column.

Table 2
ANOSIM pairwise Tests for differences between net types

Net type Group	R Statistics	Significance Level %	Possible Permutation	Actual Permutations	Number Observed
Neuston Top, Ring Trawl	0.702	0.001	Very large	99999	0
Neuston Bottom, Ring Trawl	0.550	0.001	Very large	99999	0
Ring Trawl (Surface), Ring Trawl	0.338	0.001	Very large	99999	0
Ring Trawl (Surface), Neuston Top	0.303	0.003	Very large	99999	2
Neuston Top, Neuston Bottom	0.129	0.010	Very large	99999	10
(Ring Trawl Surface), Neuston Bottom	0.038	25.40	Very large	99999	25440

The taxa identified by SIMPER as those which typified the distinct larval fish assemblages in the three net types (water strata) are presented in **Table 3**. Since, for all the previously identified type of nets (ANOSIM), the relative density and composition of the larval fishes were found not to differ significantly between June and August, SIMPER was used to typify the collective fish larval composition of those two seasons. Some taxa characterized more than one assemblage. For example, Gerreidae spp. and *Hypleurochilus langi* were regularly abundant at all three water strata. In contrast, other taxa typified only one of the water strata, such as *Hyporamphus picarti* and Mugilidae spp., regularly abundant only in the Neuston Top (surface stratum) catches and *Enneacampus* sp., Gobiidae sp.1, Clupeidae spp., and *Cynoglossus senegalensis*, regularly abundant only in the Ring Trawl catches (mid-water stratum). The number of species, found near the surface, representing the Neuston Top and Neuston Bottom assemblages was lower compared to the Ring Trawl assemblages representing species more commonly found in the mid-water stratum.

Table 3
SIMPER similarity analysis of larval taxa within the different nets in each season

Net type	November (End of wet season)			February (Cool & Dry)			June & August (Warm & Dry)		
	Species	Contrib%	Cum.%	Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
Neuston T.				*Hyporamphus picarti*	46.70	46.70	Gerreidae spp.	48.69	48.69
				Mugilidae. spp.	30.32	77.01	*Hyporamphus picarti*	19.05	67.75
				Hypleurochilus langi	20.50	97.52	Mugilidae. spp.	15.16	82.91
							Hypleurochilus langi	14.64	97.55
Neuston B.	Gerreidae spp.	55.28	55.28	*Hypleurochilus langi*	51.95	51.55	Gerreidae spp.	83.70	83.70
	Hypleurochilus langi	19.56	74.85	*Hyporamphus picarti*	18.89	70.84	*Hypleurochilus langi*	9.98	93.68
	Mugilidae. spp.	8.96	83.81	Mugilidae. spp.	15.92	86.76			
	Clupeidae spp.	5.25	89.06						
Ring Trawl				*Enneacampus sp.*	46.04	46.04	Gobiidae sp.1	33.17	33.17
				Gerreidae spp.	19.77	65.81	*Enneacampus sp.*	24.44	57.61
				Clupeidae spp.	13.30	79.11	Clupeidae spp.	13.96	71.58
				Hypleurochilus langi	3.99	83.10	*Cynoglossus senegalensis*	6.18	77.76
				Hyppocampus algiricus	3.82	86.92	*Hypleurochilus langi*	5.11	82.86
							Gerreidae spp.	4.22	87.09

3.5 Density and composition of larval fish related to environmental parameters

RELATE procedure showed that, when the similarity matrices produced from the larval fish species assemblage data recorded at the various sites in each net were correlated with the distance matrices constructed from the data set of the measured environmental parameters of these same sites, the *Rho* values (ρ) were significant in each case ($p < 0.001$ %). The correlation was highest for the Neuston Top net (ρ = 0.38) and lowest for the Ring Trawl net (ρ = 0.26). In view of these significant relationships between the larval fish and environmental data, the BIOENV analyses (**Table 4**) suggested salinity, water temperature, and dissolved oxygen for the Neuston Top ($R = 0.34$) and Neuston Bottom ($R = 0.33$) assemblages. Ring trawl assemblage was best correlated with salinity and water temperature ($R = 0.33$). pH and turbidity were not recognized as significant variables and did not significantly contribute to explain the structure of the larval fish assemblages.

Table 4
Combinations of the 5 environmental variables yielding the best matches of biotic and abiotic similarity matrices for each net type, as measured by weighted Spearman rank correlation.

Net type	Environmental Parameters	Spearman correlation coefficient	Global test
Neuston T.	Salinity, water temperature, dissolved oxygen	0.335	P = 0.07%
Neuston B.	Salinity, water temperature, dissolved oxygen	0.334	P = 0.07%
Ring Trawl	Salinity, water temperature	0.360	P = 0.05%

Fig. 6 shows the individual relationships between the larval fish densities of the dominant taxa of the Neuston Top and Bottom assemblages and the environmental variables identified by the BIOENV analyses. No larvae of *Hyporamphus picarti*, Mugilidae spp., and *Hypleurochilus langi* were found at salinity above 45 and below salinity of 34. The highest densities were consistently obtained at salinity between 36 and 38. In regards to water temperature, all three taxa were found within the entire range encountered during the survey period and their densities were evenly spread across that range. No *H. picarti* larvae were found at dissolved oxygen concentrations lower than 5 mg l^{-1}, while Mugilidae spp. and *H. langi* were found at concentrations of dissolved oxygen of 4.5 mg l^{-1} or above. The highest densities were also consistently observed in association with high dissolved oxygen concentration. In the same way, **Fig. 7** shows the individual relationships between the larval fish densities of the dominant taxa of the Ring Trawl assemblages with those of the environmental variables identified by the BIOENV

analyses. Gerreidae spp. presented a narrow salinity range (from 35 to 41) where they were found, while Clupeidae and Gobiidae were collected at salinity up to 55. Gerreidae and Clupeidae were found throughout the entire water temperature range encountered during the survey period and their densities were evenly spread across that range, but Gobiidae spp. were not collected below 26 °C. Gerreidae were found within the entire range of dissolved oxygen concentration. The situation was similar for the Clupeidae spp. but had a lower limit of 4.3 mg l^{-1}. Gobiidae were observed at low dissolved oxygen concentrations down to 3.25 mg l^{-1} and up to 6.25 mg l^{-1}.

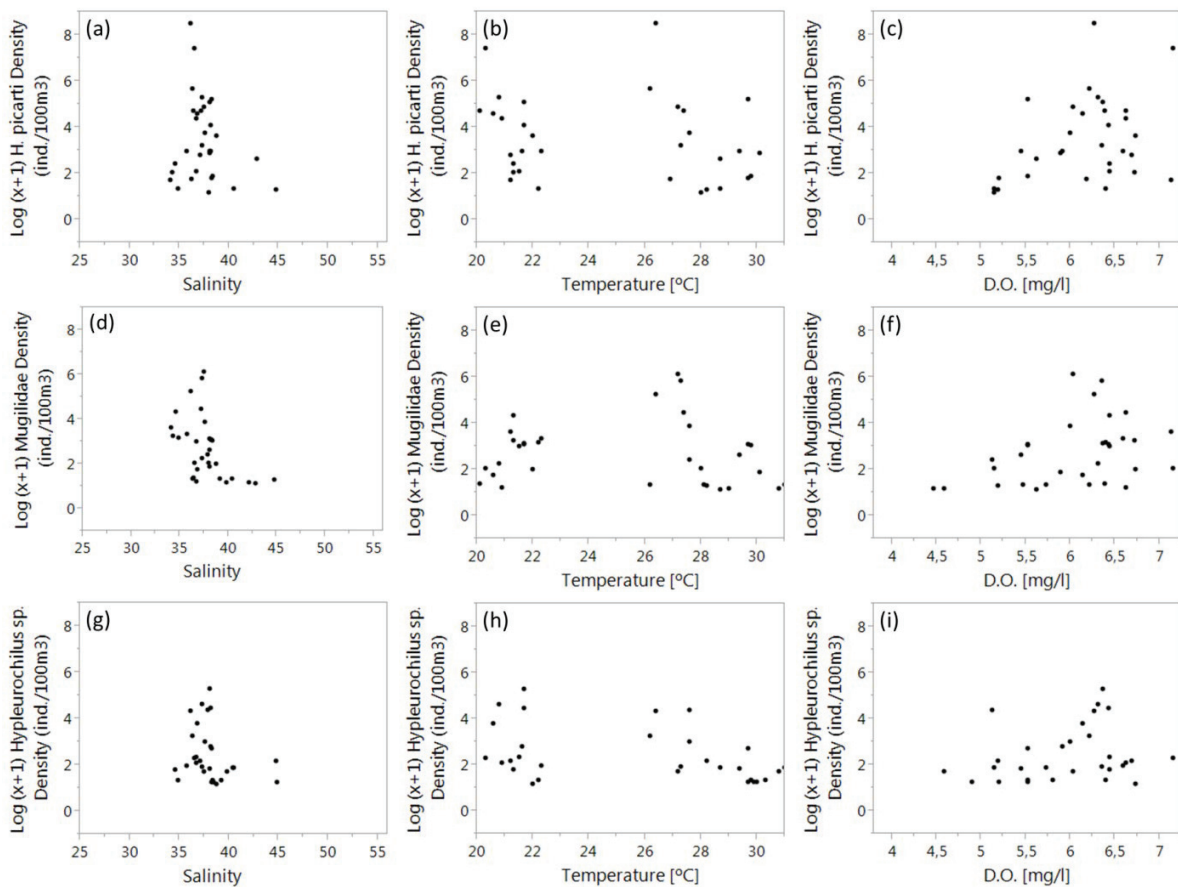**Fig. 6.** Relationships between larval fish density of the dominant taxa of the Neuston Top and Bottom assemblages and environmental variables – salinity, water temperature, and dissolved oxygen of (a-c) *Hyporamphus picarti*, (d-f) Mugilidae spp., and (g-i) *Hypleurochilus sp*. Note: The x-axis scales indicate the minimum and maximum values of each of the environmental parameter where the larvae were sampled.
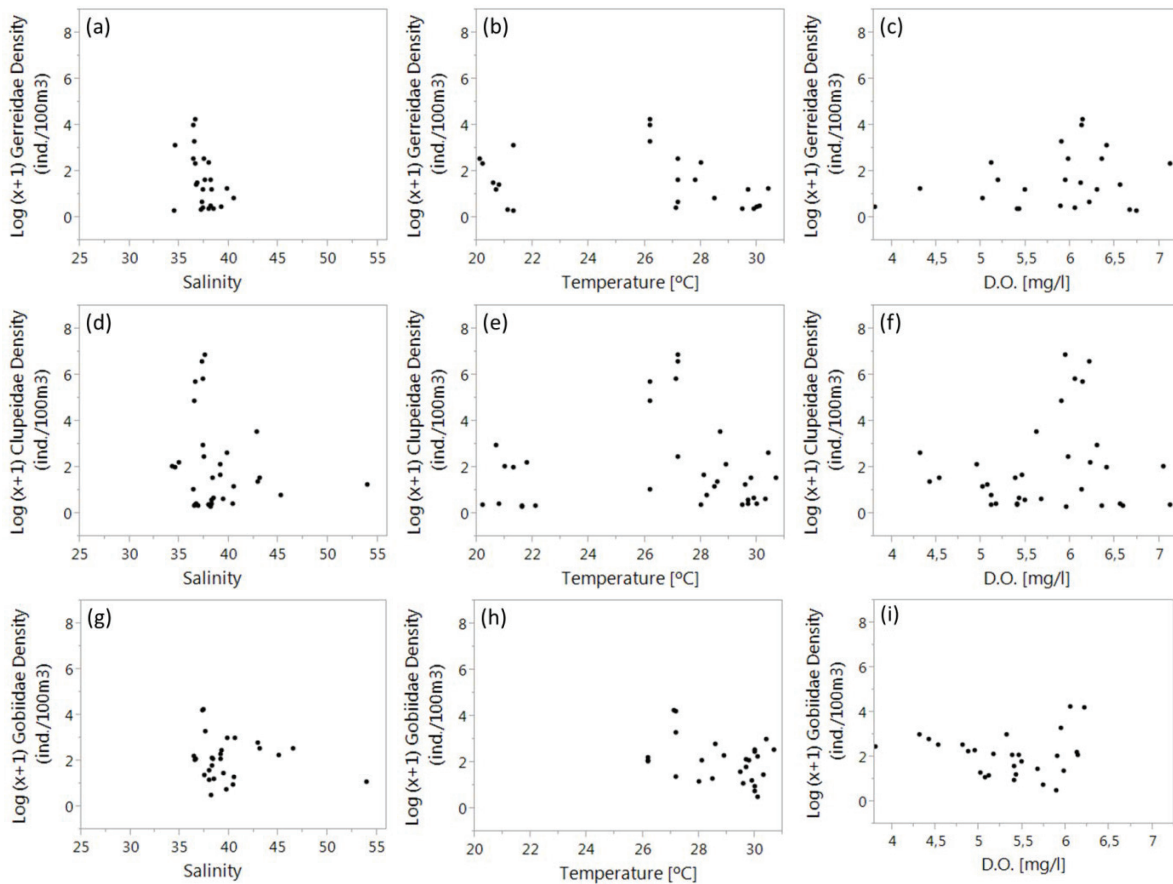
Fig. 7. Relationships between larval fish density of the dominant taxa of the Ring Trawl assemblage and environmental variables – salinity, water temperature, and dissolved oxygen of (a-c) Gerreidae spp., (d-f) Clupeidae spp., and (g-i) Gobiidae spp. Note: The x-axis scales indicate the minimum and maximum values of each of the environmental parameter where the larvae were sampled.

4. Discussion

The salinity regime of mangrove waterways can be influenced by interactions between catchment size, estuarine geomorphology, tidal range, and rainfall patterns (Wolansky, 1989). While tropical estuaries generally present higher salinities than temperate estuaries (Blaber, 2000), precipitation deficits combined with intense evaporation have particularly affected estuarine ecosystems of West Africa (Pagès and Citeau, 1990). In the Sine Saloum estuary, these climate changes have resulted in a high overall salinity and an inversion of the salinity gradient (**Fig. 2 and Table A1**). However, as indicated by our results, if precipitations are sufficiently high, at the end of the rainy season this inversion of the salinity gradient is no longer observed. Then, as the dry season is progressing, the characterising inverse salinity is gradually

re-established. Ecoutin et al., (2014), have also reported for the Sine Saloum estuary some intermediate areas having salinities below 35 during the rainy season (from July to October), while our results showed salinity below 35 throughout the entire system at the end of the rainy season (November 2013). To our knowledge, this is a situation that was not observed and reported in previous studies carried within the Sine Saloum estuary. Highly variable environments, where physical conditions such as salinity fluctuates regularly, are known to affect the reproduction of resident fish species (Blaber, 2000). During the study period, the biota of the Sine Saloum waterways was subjected to salinities ranging from 25.6 to 56.1 (**Table A1**). This is an outstanding feature of this environment as most tropical mangrove estuaries have salinity regimes ranging from 0 to 35 (Robertson and Blaber, 1992). In high-salinity environments, modification in the ichthyofauna biodiversity, species composition, and their seasonal dynamics have been reported (Vega Cendejas and Hernández De Santillana, 2004; Simier et al., 2004; Diouf, 1996; Albaret, 1987; Severin-Reyssac and Bertrand Richer de Forges, 1985). As a response to high salinity, low fish diversity and richness have been recognized. Until now, utilisations of these high-salinity environments by the early life stages of fishes and the associated changes in the ichthyoplankton composition remain very poorly studied. This knowledge is relevant and complementary to a better understanding of the quality of fish habitats (Brehmer et al., 2013; Mouillot et al., 2005), of the reproductive biology of fishes associated with estuaries (Blaber, 2000), as well as recruitment processes that help determine the nature of estuarine and coastal fish communities (Costa et al., 2002).

The larval fish community in the Sine Saloum estuary is comprised of a few species in large numbers and many rare species in low numbers. This is a common feature with those reported in many tropical estuarine larval fish assemblage studies (Barletta-Bergan et al., 2002; de Morais and de Morais, 1994; Tzeng and Wang, 1992; Yoklavich et al., 1992). Gobioid and Clupeoid larvae dominated the catches in most estuaries and the present study yielded comparable results. Despite these similarities, important differences were observed in the Sine Saloum estuary. As reported by Haedrich (1983), clupeids are less abundant at lower latitudes, where they are replaced by engraulids. The Sine Saloum estuary did not show a dominance of Engraulidae, instead Clupeidae comprised 28.9 % of the total catches. We can report a correspondence between dominance and occurrence of adult fishes in the Sine Saloum estuary; for instance, the dominance of Clupeids (80-88 %) is confirmed, by the results of the adult fish assemblages study of Simier et al., (2004) and fish sampling between 2003 and 2012 in

the Bamboung Marine Protected Area located within the Sine Saloum estuary (Sadio et al., 2015). In terms of bioecological categories, there is also a correspondence between the dominance and occurrence of a community essentially composed of species of marine origin with an unusually high contribution of marine species occasional in estuaries (14.3 %) and marine species accessory in estuaries (14.3 %). Since the salinity values throughout the system were usually greater than that of seawater, it may enhance the utilization of this system by the marine species occasional in estuaries and marine species accessory in estuaries. In an opposite manner, overall high salinities had a negative effect on species of freshwater origin as we noted their absence in all season.

The ichthyoplankton community's total number of families and species in the Sine Saloum estuary (24 families and 43 species) were lower than that of other tropical estuaries. For example, 68 families and 195 species were identified in the Pichavaram mangrove ecosystem of India (Krishnamurthy and Prince Jeyaseelan, 1981), 55 families and 105 species in the mangrove estuary of Tanshui River in Taiwan (Tzeng and Wang, 1992), 44 families and 85 species in the St Lucia Estuary in South Africa (Harris and Cyrus, 1995), 28 families and 63 species in the Caeté River Estuary in North Brazil (Barletta-Bergan et al., 2002), and 59 species in the Cayenne River Estuary in French Guiana (de Morais and de Morais, 1994). Taking into account the variations in sampling methods and efforts, differences in topography among systems, and the sparse and very uneven quality of literature on larval fish assemblages in West African estuaries, it is difficult to classify the situation in the Sine Saloum estuary and other estuaries in the region. A basic ichthyoplankton study in Guinean and Senegalese estuarine waters (Tamoikine and Pandare, 1994) reported 26, 7, 10, 19, 18, and 19 families in Conakry, Casamance, Sénégal, Fatala, Konkouré, and Tabounsou estuaries, respectively. Worthy of note, the Casamance estuary, also classified as an inverse estuary, had the lowest diversity at the family level (7), providing additional evidence that high salinity environment may harbour a less diverse ichthyoplankton fauna. For the Sine Saloum estuary, our study reports 24 families. Nevertheless, there are similarities in the taxonomic composition among the Sine Saloum estuary larval community with those described for other West African estuaries by Tamoikine and Pandaré (1994) with the most important groups including species representative of Carangidae, Clupeidae, Cynoglossidae, Gobiidae, Mugilidae, Scianidae, and Syngnathidae families.

The results of this study have also shown that such ichthyoplankton sampling could be an effective means of determining and contributing on the knowledge of which species inhabit an

area because the plankton nets are in some ways less selective than various gears used to sample adult fishes. Small cryptic bottom fishes, not or rarely sampled as adults, have appeared in their larval forms relatively common in the plankton samples. Out of the 114 species reported in the Saloum by Diouf (1996), the 73 species reported by Simier et al., (2004), or the 85 species reported in Bamboung MPA by Ecoutin et al., (2014), the present study found ten species that were not previously reported by earlier studies assessing fish biodiversity in this system. Namely, *Atherina* sp., *Bathygobius casamancus*, *Ephippus goreensis.*, *Cheilopogon sp.*, *Coryphoblennius galerita*, *Enneacampus sp.*, *Hippocampus algiricus*, *Hypleurochilus langi, Hyporamphus picarti,* and *Trachinotus goreensis*. Including these additional species to the 114 previously reported by Diouf (1996), the total number of fish species known to be found in and using this system elevates to 124 species. There are a few resident and abundant species known to reproduce in the Sine Saloum system (Diouf, 1996) that nevertheless did not occur in the ichthyoplankton samples. Reproductive specializations such as brooding strategies, egg type, and spawning origin of adults can influence descriptions of larval fish community surveys. The most prominent examples of this study are the two nesting species of Cichlidae, *Sarotherodon melanotheron* (exhibiting mouth-brooding habit) and *Tilapia guineensis* (substrate brooder). Although relatively abundant in the Sine Saloum estuary, particularly in the upstream regions, the larvae are extremely scarce in the plankton and cannot be sampled effectively with the ichthyoplankton samplers used in this study.

The distributional pattern of fish larvae (**Fig. 3 and Fig. 4**) revealed that the total abundance and the richness in the estuary decreased from the lower to the upstream areas. This result contrasts with Barletta-Bergan et al. (2002), who reported high larval abundance in the most upstream sections of the Caeté River Estuary (North Brazil). Our results may indicate that, independently of the season, a relatively high number of fish larvae found in the Sine Saloum system originated from the surrounding coastal waters. This hypothesis is supported by the fact that in terms of bio-ecological categories (Albaret, 1999), the larval fish assemblages were greatly dominated by species of marine origin and that the freshwater species were totally absent. Past studies have shown that many coastal species often or always spawn in the ocean, but their larvae or early juveniles move to the estuary to spend their juvenile period (Tzeng and Wang, 1992; Gunderson et al., 1990). Elevated salinity could be in part responsible for the low densities and poor richness in the upstream regions. The lower estuary areas have much more stable salinities than the upper estuary areas which could in return enhance the

survival of eggs and larvae (Blaber et al., 1995). Whitfield (1999) suggested that species composition and abundance mostly respond to salinity changes because of osmoregulatory stress and/or disappearance of certain food resources, both plausible scenarios for the ichthyoplankton community in the Sine Saloum estuary.

Part of the process of discriminating sites and/or type of environments in multivariate studies is the ability to identify the species most responsible for the observed pattern (Field et al., 1982). Foremost, larval fish assemblages showed a clear vertical structure corresponding to their position in the water column (Neuston Top, Neuston Bottom, and Ring Trawl). Since the water column in the Sine Saloum estuary is extremely well mixed (no vertical stratification), the abiotic factors measured in this study could not be directly held responsible for the observed disparities between the different water stratum catches. We acknowledge that sampling was carried out only during day light hours, so diel vertical migration of certain species could not have been tested and accounted in this study. It is know that many species such as those of Clupeidae tend to stay close to the bottom during the day and migrate close to the surface during the night. Nevertheless, having sampled simultaneously the three different positions in the water column at random times and tidal phases, the catches were consistently and independently different and distinguishable between the Surface and the mid-water strata. Biological interactions such as trophic relationships (predator-prey), competition, and morphological adaptations must play an important part in defining and structuring these different communities (Leis, 1991). When assessing ichthyoplankton diversity and assemblages, the observed differences in vertical composition and structure of the larval fish community point to the practical and scientific importance of including neuston sampling.

The larval fish species found throughout the year such as *Hypleurochilus langi*, and *Hyporamphus picarti*, indicates that these species have protracted spawning strategies and are well adapted to the varying salinities. For the Gerreidae spp., Clupeidae spp., and Mugilidae spp., since these larvae could only be identified at the family level, it is not clear if at the species level, these have protracted spawning strategies. Their occurrence throughout the year might be an artefact of mixing and pooling the different species. Nevertheless, their occurrence over the seasons coincided with spawning activities observed by Panfili et al., (2004) in *Ethmalosa fimbriata* (Clupeidea), Trape et al., (2009) for mugilid fishes, and Diouf (1996) in Gerreidae species. These are part of a reduced group and are in accordance to the "resistance community" first identified in the inverse estuary of the Casamance River by Albaret (1987).

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Importantly, they are also part of the fish species most commonly targeted by the artisanal fisheries taking place in the Sine Saloum estuary. These dominant species of the larval fish community belonged to species able to adapt their eco-physiological abilities and some of their life history attributes (Albaret, 1987; Simier et al., 2004). This is consistent with the fact that most freshwater species are usually not capable of osmoregulating in salt water and consequently tend to be found in estuaries only when salinities decline to low levels during regular periods of heavy freshwater discharge (Potter and Hyndes, 1999), a situation that is no longer observed in the Sine Saloum estuary. The net assemblages did not differ much across seasons as they were mostly composed of the same taxa between the seasons (**Table 2**); a situation that might be explained by the fact that only a few species are capable of coping with the high salinities characterizing, for most of the year, the Sine Saloum estuary.

There are several abiotic factors that can produce negative or positive effects on the early life stages of fishes (Costa et al., 2002). Results of this study identified salinity, water temperature, and dissolved oxygen as the suite of best fitting environmental variables structuring the Neuston Top and Bottom larval assemblages, and salinity and water temperature for the Ring Trawl assemblage. These environmental parameters could have acted in a direct way via effect on the development rate, growth, and mortality of the larvae. Howbeit, water temperature and salinity, could have operated in an indirect way by having an influence on spawning induction. Moreover, faster growth at higher a temperature during the larval stage would reduce the time that larvae were exposed to predation. Coincidentally, the highest densities and diversity were observed in June, during the warm and dry season where the water temperature was high. Nevertheless, the results of our study are consistent with the hypothesis that abiotic factors as environmental stressors influence the spatial and temporal patterns in larval fish assemblages (Vega-Cendejas and Hernández De Santillana, 2004), which adjust constantly in response to changing seasons and especially the salinity gradients. With regards to salinity, both species composition and abundance have responded to salinity changes. Our analyses indicate that variations in salinity influenced the larval fish distribution patterns, which may generate favourable or tolerable conditions for a reduced community of suitably adapted species, but is unfavourable for most of the species. The inverse relationship that we found between salinity and both species richness and abundance has been previously discussed for the adult fish fauna. For example, Van der Elst et al., (1976) have shown that there is an inverse relationship between salinity and number of fish species at Lake St Lucia (South Africa). This is important because

most estuaries are subject to periods of freshwater flooding, whereas salinities seldom rise above sea water level, again a situation no longer observed in the Sine Saloum estuary and an increasingly likely scenario for other areas in the context of global warming (IPCC, 2014). Not only salinity, but also turbidity has been previously reported as an important factor associated with larval fish abundance (Harris et al., 2001; Harris and Cyrus, 2000). The present study did not identify such a relationship, knowing that water turbidity could be the fact of different element (e.g. sediment or phytoplankton). A factor not investigated in the present study and potentially correlated to salinity and distance to the sea is food availability (nature and/or abundance) as well as water quality (Brehmer et al., 2013). Additionally, our result did not show a particular higher larval concentration in the mangrove rich parts of the estuary. Relatively low concentrations were consistently found in sites with rich mangrove cover such as B4, D3, D4, M2, while high concentration where observed in sites where mangrove cover was poor such as sites S1, S2, and S3 (**Fig. 3 &Table A1**). This suggests that the presence of mangrove alone cannot provide optimal conditions for the fish larvae in the Sine Saloum estuary. Similarly, Vidy (2000), reported that good estuarine conditions alone are sufficient for good nursery function but mangrove alone is not.

The relative significance of each environmental parameter, in terms of larval densities, varied upon the different dominating taxa (**Fig. 6 & 7**). Importantly, it gave us a good indication of which taxa maybe more resilient to the environmental changes observe in the Sine Saloum. Highest densities situated at salinity between 37 and 38 were common to all of the dominating taxa, and can be an indication of their preferred spawning salinity. Generally, there were no larvae at salinities higher than 45. However, high salinity tolerance gives Clupeidae spp. and Gobiidae spp. (they are the only taxa found at salinities above 45) an adaptive advantage which is reflected by their high occurrence frequencies throughout the salinity range. This might be an important factor to insure high reproductive success within the system. Water temperature was identified as one of the best fitting environmental variable structuring larval assemblages, but when looking at its effect on the individual taxa, there were no evident trend. The larvae were found and densities were evenly spread across the range of temperature encountered during the survey periods. Gobiidea spp. were the exception with no larvae observed at water temperature below 26 °C. Unfortunately, limited information is available on dissolved oxygen concentration values (DO) and their influence of larval fish abundance and diversity (Costa et al., 2002). When DO concentrations are unfavourable, because of their lower swimming capacities, fish larvae are

surely less successful than adult at leaving areas with low DO concentrations. Exposure to low concentration can lead to reduced survival and reduced feeding rates (Bishai, 1962; Breitburg, 1994). *Hyporamphus picarti* and *Hypleurochilus langi* seem to be particularly sensible to DO concentration as no individuals were caught at DO < 5.1 mg l^{-1} (**Fig. 6c and f**). Breitburg (1994) reported that the most preferred dissolved oxygen zones for larvae should be those at dissolved DO concentration of 3 mg l^{-1} and above. The lowest DO concentration recorded was 3.8 mg l^{-1} and well above the value reported by Breitburg (1994). Hence, the role and impact of dissolved oxygen remain unclear even if it seems that larval densities are increasing with it. BIOENV analyses showed that DO is not acting alone but in combination with salinity and temperature. An alternative explanation is that DO will be indicator of high phytoplankton or algae presence (source of dissolved oxygen in this system), and correlated to the availability of prey fish larvae reported in high density.

5. Conclusion

This is the first study documenting the spatial and temporal fish larvae assemblages in an inverse estuary. The Sine Saloum is an example of a system where reduced precipitation, coastal erosion, and global temperature increase have resulted in major environmental transformations. Salinity, water temperature, and dissolved oxygen were the variables that best explained the spatial and temporal larval fish assemblages. It is difficult to forecast the future situation for this system but so far, compared to other mangrove estuarine system, we have observed the loss of freshwater species in favour of species of marine origin. Depending on the strength of marine and freshwater respective influences, other West African estuaries and their larval fish species are likely to be affected by global climate change and similar modifications of the ichthyofauna are to be expected. Monitoring these modifications deserves special attention because of the high ecological and socioeconomic values of these tropical mangrove systems. The nursery function is one of their main services they provide and protection of suitable areas, therefore, seems to be eminent to preserve the diverse fish assemblages and their key species. The information provided in this paper constitutes an important contribution to the knowledge of tropical biodiversity and to biological databases available for management of the ichthyofauna in the context of climate change and future green fund action.

Acknowledgments

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Description of the 16 sampling sites. Mean value, standard deviation (SD) and range are given for temperature (°C), salinity (PSU), dissolved oxygen (mg l^{-1}), pH, and turbidity (NTU).

Table A.1.
Description of the 16 sampling sites. Mean value, standard deviation (SD) and range are given for temperature (°C), salinity, dissolved oxygen (mg/l), and turbidity (NTU).

| Branch		Bandiala				Diomboss				Bolong		Saloum					
Site		B1	B2	B3	B4	D1	D2	D3	D4	M1	M2	S1	S2	S3	S4	S5	S6
Distance to the sea (km)		7	7	7	25	10	12	21	28	13	32	5	5	5	24	30	50
Mangrove		Luxuriant	Luxuriant	Luxuriant	Luxuriant	Luxuriant	Luxuriant	Patchy	Patchy	Luxuriant	Luxuriant	Residual	Residual	Residual	Patchy	Residual	None
Depth (m)		7	9	8	6	8	7	8	7	4	5	10	11	8	12	9	15
Temperature	Mean (±SD)	26.6 (3.3)	26.7 (3.3)	26.6 (3.4)	27.6 (3.4)	26.7 (3.8)	26.5 (3.4)	27.2 (3.4)	27.5 (3.2)	27.1 (3.7)	27.9 (3.8)	26.3 (3.9)	26.4 (3.6)	26.4 (3.6)	27.43 (3.4)	27.3 (3.5)	27.1 (3.3)
	Range	21.3-29.7	21.3-29.9	21.0-29.8	21.8-30.8	20.2-29.7	20.8-29.5	21.5-30.4	22.1-31.0	21.1-30.1	21.6-30.7	20.0-30.0	20.6-30.1	20.7-30.1	21.5-30.2	21.4-30.1	21.4-30.1
Salinity	Mean (±SD)	34.5 (4.3)	34.5 (4.3)	34.3 (4.4)	34.9 (5.8)	36.2 (4.3)	35.9 (2.7)	36.3 (3.9)	36.4 (5.2)	36.8 (2.5)	38.3 (5.6)	36.2 (3.1)	36.2 (3.0)	36.1 (2.8)	39.0 (6.1)	39.8 (7.2)	44.3 (11.2)
	Range	27.4-38.3	27.5- 38.5	27.2-38.5	25.6-39.9	31.7-38.3	31.4-38.1	29.7-39.5	28.1-40.6	32.7-39.2	29.3-43.1	31.3-40.8	31.3-40.3	31.3-39.6	29.4-45.9	29.0-47.1	28.8-56.1
Dissolved Oxygen	Mean (±SD)	5.94 (0.34)	6.03 (0.48)	6.13 (0.63)	5.19 (0.69)	6.00 (0.86)	5.93 (0.43)	5.61 (0.53)	5.49 (0.69)	5.26 (1.03)	5.06 (0.61)	5.86 (0.35)	5.89 (0.23)	6.01 (0.24)	5.46 (0.53)	5.40 (0.57)	6.63 (0.71)
	Range	5.47-6.45	5.38-6.74	5.35-7.13	4.21-6.40	5.13-7.15	5.40-6.63	4.90-6.44	4.79-6.65	3.81-6.69	4.43-5.96	5.27-6.39	5.33-6.22	5.65-6.31	4.88-6.37	4.66-6.43	4.59-6.73
pH	Mean (±SD)	7.838 (0.033)	7.832 (0.090)	7.910 (0.111)	7.665 (0.075)	7.895 (0.075)	7.914 (0.035)	7.782 (0.063)	7.653 (0.089)	7.712 (0.147)	7.625 (0.060)	7.959 (0.061)	7.929 (0.010)	7.920 (0.034)	7.770 (0.059)	7.783 (0.036)	7.943 (0.039)
	Range	7.811-7.886	7.739-7.915	7.823-8.062	7.593-7.744	7.745-8.020	7.882-7.960	7.691-7.837	7.551-7.837	7.541-7.758	7.573-7.701	7.900-8.016	7.915-7.939	7.901-7.971	7.686-7.819	7.729-7.805	7.914-8.000
Turbidity	Mean (±SD)	5.98 (4.47)	8.49 (7.24)	6.45 (4.10)	3.15 (0.90)	1.98 (0.68)	2.13 (0.44)	2.20 (0.94)	2.72 (0.95)	3.43 (1.08)	3.29 (0.86)	2.49 (1.57)	2.43 (0.83)	2.08 (0.52)	2.45 (0.36)	2.72 (1.60)	2.23 (0.43)
	Range	2.51-12.00	2.15-16.60	2.57-10.40	2.55-4.49	1.30-2.77	1.71-2.74	1.17-3.45	1.63-3.94	2.21-4.79	2.26-4.20	1.62-4.84	1.85-3.64	1.64-2.82	1.94-2.79	1.29-4.18	1.81-2.66

Appendix B.1.
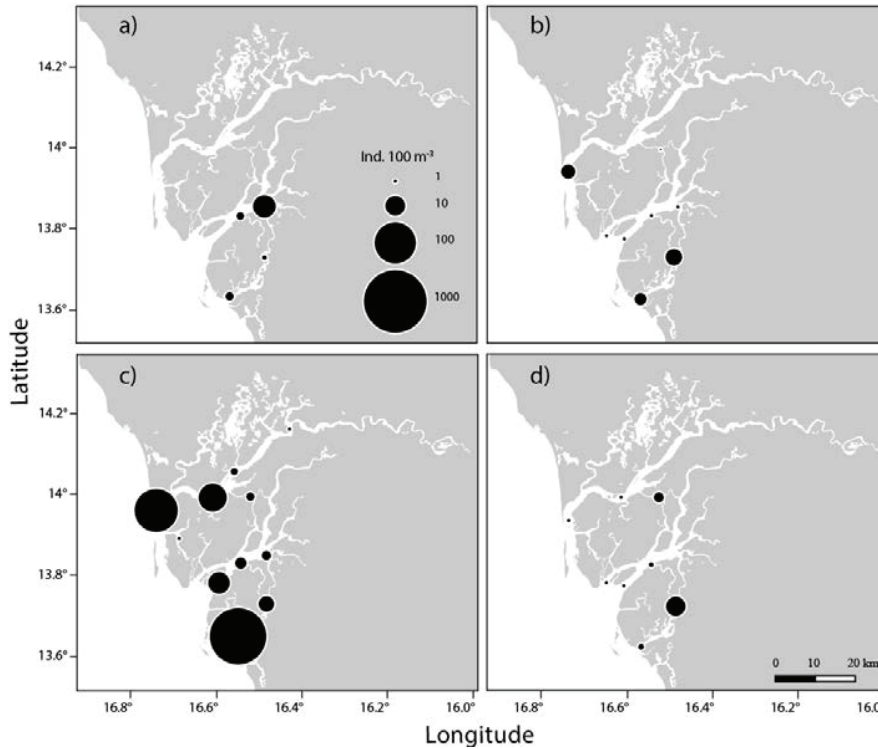
Appendix B.1. Spatial distributions of Clupeidae larvae abundances (ind. 100 m^{-3}) in the Sine Saloum System over the four sampling events. (a) November 2013, (b) February 2014), (c) June 2014, and (d) August 2014. Note: logarithmic (log) scaling of bubble sizes was used to respond to a few points that were much larger than the bulk of the data, allowing an all-encompassing visualisation of the large range of abundances values.
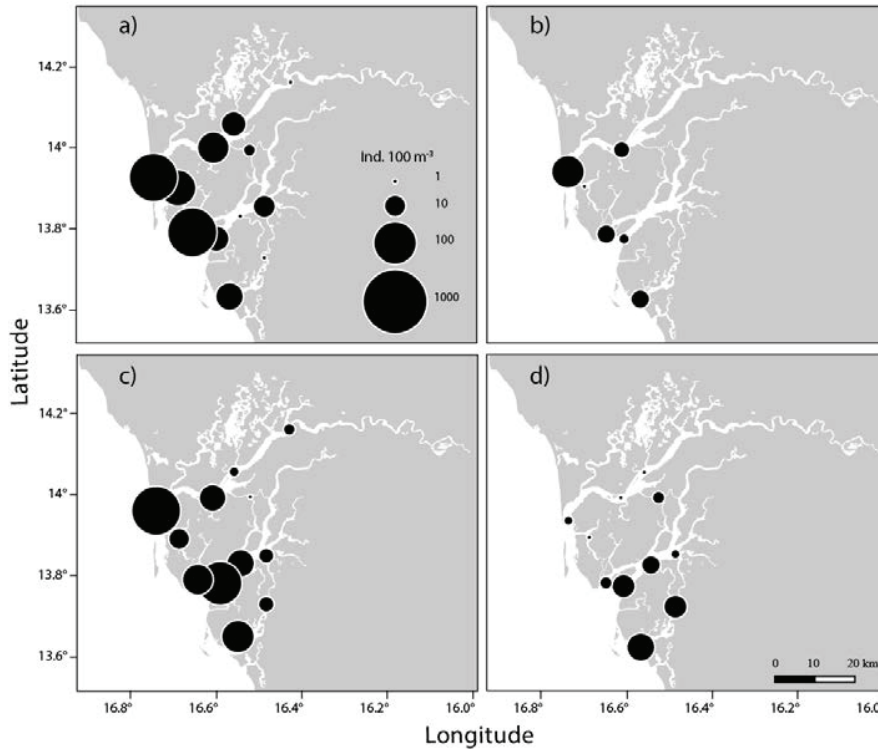
Appendix B.2. Spatial distributions of Gerreidae larvae abundances (ind. 100 m^{-3}) in the Sine Saloum System over the four sampling events. (a) November 2013, (b) February 2014), (c) June 2014, and (d) August 2014. Note: logarithmic (log) scaling of bubble sizes was used to respond to a few points that were much larger than the bulk of the data, allowing an all-encompassing visualisation of the large range of abundances values.

Appendix B.3.

Appendix B.3. Spatial distributions of *Hyporamphus picarti* larvae abundances (ind. 100 m^{-3}) in the Sine Saloum System over the four sampling events. (a) November 2013, (b) February 2014), (c) June 2014, and (d) August 2014. Note: logarithmic (log) scaling of bubble sizes was used to respond to a few points that were much larger than the bulk of the data, allowing an all-encompassing visualisation of the large range of abundances values.
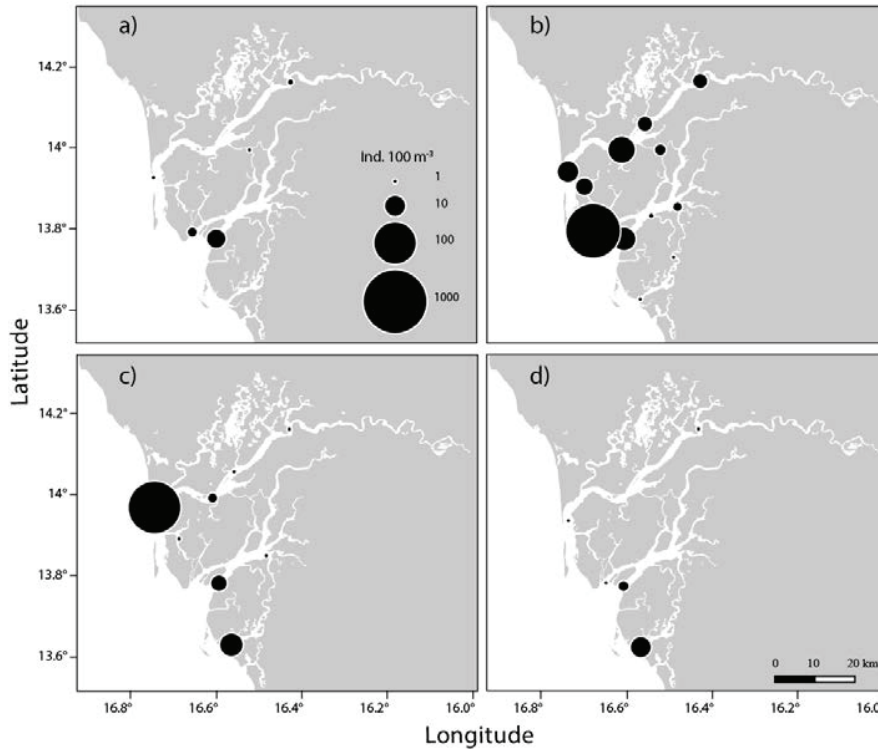
Appendix B.4.

Appendix B.4. Spatial distributions of Mugilidae larvae abundances (ind. 100 m^{-3}) in the Sine Saloum System over the four sampling events. (a) November 2013, (b) February 2014), (c) June 2014, and (d) August 2014. Note: logarithmic (log) scaling of bubble sizes was used to respond to a few points that were much larger than the bulk of the data, allowing an all-encompassing visualisation of the large range of abundances values.
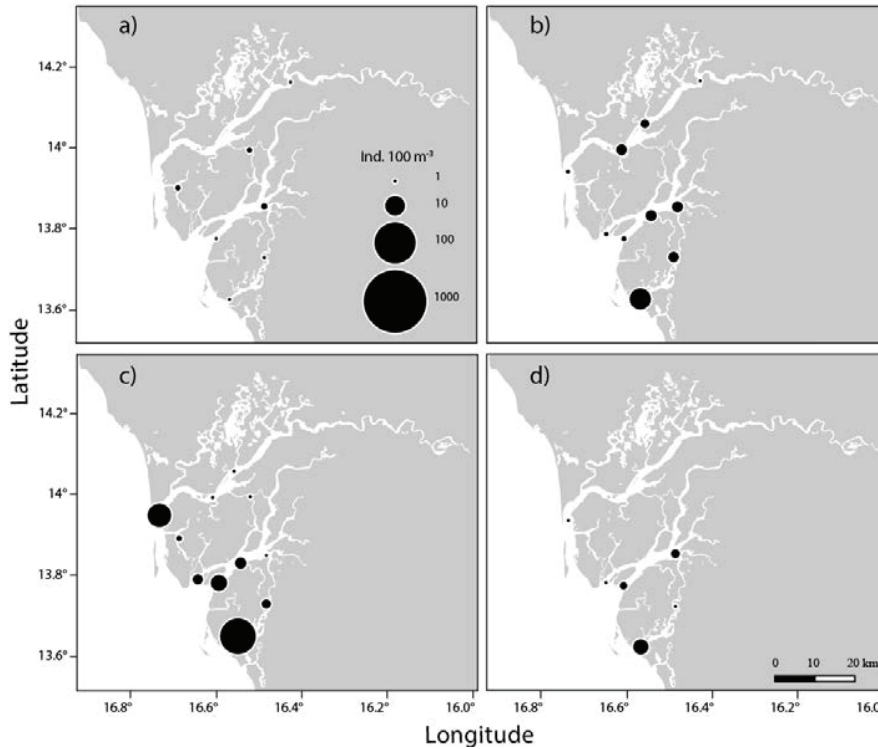
Appendix B.5.

Appendix B.5.1 On the left, the Diassanga, our towing boat and living and working platform while conducting fieldwork in the Sine Saloum estuary. On the right, the modified catamaran used for larval sampling.

Appendix B.5.2. This picture demonstrates the ability of the catamaran to sample in a parallel route of the towing boat ensuring larval sampling well clear of its bow and wake.

Chapter II

On the larval fish transport in and out of the Sine Saloum estuary

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Estuaries and Coasts

Abstract

The effectiveness of larval fishes in regulating transport between low-flow estuaries and coastal waters in seasonally arid climates is poorly known. In July 2014, a field experiment simultaneously measuring vertical current profiles (speed and direction) and larval transport was implemented during ~ 2.5 semi-diurnal tidal cycles at three locations situated at the entrance an important West African estuary, the Sine Saloum. We monitored four taxa: Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae; the selection was done due to their economic importance, contrasted life-cycle, and usage of the estuary environment. The physical conditions were characterised by a notable stratification in salinity, an up-estuary salinity gradient, and a tidal-averaged circulation that was vertically sheared and directed toward the mouth of the estuary near the surface. The "inverse estuary" conditions, due to higher salinity inside the estuary, provide natural pathways in and out of the estuary to fish larvae that are able to maintain themselves in a specific depth range. The distribution of fish larvae revealed depth range preferences that did not change in time, independent from the diel and tidal period, and were consistent with the use of these pathways by the organisms. In contrast, no support was found in favour of a selective tidal stream transport mechanism (STST). From a behavioural perspective, the proposed mechanism can be viewed as simpler than STST in that it does not require the organisms to synchronise their vertical migrations with the phase of the tidal currents. The prevalence of the gravitational circulation and the low energy cost for larvae to maintain themselves over a defined depth range vs the desired direction of mean displacement make the proposed larval transport mechanism potentially important most of the year.

1. Introduction

It is during their early life stages that fishes are particularly vulnerable to ecological and environmental related challenges. Underlining its significance for the fates of year classes (Hjort, 1926), the vast majority of species suffer high mortality during this period (May, 1974). Most marine fishes have non-swimming or weakly swimming pelagic early life stages, thus, fish larvae have locomotion capabilities that drastically differ from larger juvenile and adult fishes (Brehmer et al., 2011b). Accordingly, the distribution of larval fish is, at least, partially controlled by passive transport mechanisms (Norcross and Shaw, 1984), and the term "larval transport" was used to describe the movement of fish larvae in the marine environment (Pineda et al., 2007). At first, the transport of larvae in coastal areas is largely due to passive advection by oceanographic processes such as wind-driven circulations, convergence flows near river fronts and internal waves, tidal currents, net currents, river plumes, upwelling or downwelling currents, and eddies, which all can vary on a broad range of scales, from yearly, seasonally, daily, hourly, and down to a few minutes (Teodosio et al., 2016). Under unfavourable flow conditions, fish larvae might be transported to habitats less suitable for development, where they may fail to find appropriate amounts and types of planktonic prey (Hjort, 1926) or survive the prevailing abiotic conditions with respect to, for instance, temperature, salinity, dissolved oxygen, or UV-radiation (Miller and Kendall, 2009).

Many inshore marine fishes in temperate and tropical environments spawn offshore, but their larvae or juveniles use shallow habitats such as bays, mangroves, and other estuarine regions as nurseries (Beck et al., 2001) before moving and returning to the adult habitats; a life history pattern often observed in commercially and recreationally important fish species (Haedrich, 1983). Hence, larval transport has central implications for recruitment, as the maintenance of marine populations often depends on the completion of larval migration from the open ocean spawning regions to estuarine nursery habitats. Limitedly well understood, but a critical stage of this journey is ingress, retention, and movement between the coastal waters and an estuary (Churchill et al., 1999).

Most estuaries present special challenges to larval transport for marine taxa using them because their waters experience net seaward motion and current velocities frequently exceed larval swimming speeds (Boehlert and Mundy, 1988; Brehmer et al., 2011a; Forward Jr et al., 1999). Among fish species, different larval transport and resulting recruitment

problems related to estuarine use have been identified. First, some species are resident in estuaries throughout their life histories and their primary recruitment problem is to prevent the export of their early life stages from the estuary. Second, other species that visit estuaries periodically as adult for spawning face the same export problems as the residents. Finally, species that spawn offshore and subsequently enter estuarine systems as larvae or early juveniles, face the above-mentioned challenges of ingress to the estuarine nursery areas and prevention of export once they have entered. An important question, therefore, is how do such larvae, with their limited swimming capabilities, move in or out of these nursery areas? Theoretically, larval transport can be influenced by a number of elements of estuarine circulation. The dominant sources of water circulation in estuaries are tides, river flows, winds, non-tidal forcing from the coastal ocean, and topographically induced circulations (Norcross and Shaw, 1984). In most estuaries, the general pattern of circulation ("two-layer estuarine circulation") is an outflow near the surface that is partially balanced by a net inflow in the bottom layer (Dyer, 1997). Accordingly, movement of larvae into an estuary can also be modified, and feasibly controlled, by larval vertical behaviour. There has been a long history of investigating larval transport of fishes in stratified estuaries that experience substantial freshwater input and the most commonly cited behavioural mechanism leading to up-estuary movement by larvae is selective tidal stream transport (STST), in which larvae are up in the water column during rising tides and low in the water column during falling tides (Boehlert and Mundy, 1988; Forward Jr et al., 1999; Weinstein et al., 1980). STST has been the suggested mechanism for movement and retention within estuaries in several fish species such as young anguillid eels, herrings, shads, croakers, and plaice (e.g. Fukuda et al., 2016; McCleave and Kleckner, 1982; Tanaka et al., 1989; Weinstein et al., 1980). However, STST is constrained to certain hydrodynamic boundaries (Forward and Tankersley, 2001).

In arid climates, where rainfall is extremely low and insufficient to stratify estuaries during most of the year, the density of the water at the estuary's mouth is often similar to that in the ocean, and tidal diffusion rather than "two-layer estuarine circulation" may control exchange between the estuary and the open coast (Largier et al., 1997; Nidzieko and Monismith, 2013). However, excess evaporation over wide coastal or estuarine areas can also produce inverse salinity gradients pointing toward the head of the water body, partially stratified conditions, and a type of reverse thermohaline circulation with bottom outflow of salty water. This has been observed in many parts of the (sub)-tropics (Hetzel et al., 2013; Lavín et al., 1998;

Nunes Vaz et al., 1990). If present in the Sine Saloum, inverse estuary circulation is likely to affect larval transport and in particular exchanges with coastal waters.

This study is a contribution to our understanding of the hydrography and the implications of physical dynamics upon the potential pathways for larval fish transport at the interface of a tropical estuary connected to the North Atlantic Ocean. Over the past decades, the Sine Saloum estuary (Senegal) has been particularly affected by precipitation deficits, combined with intense evaporation. This has resulted in a more extreme and prevalent low-flow regime and increasing overall salinity (Mbow et al., 2008; Simier et al., 2004; Xenopoulos et al., 2005). What is currently unidentified is how these changes are affecting the physical and behavioural processes mediating larval transport between the estuarine waters and the open coast. These changes could affect fisheries locally and regionally, and the impacts have the potential of being damageable, especially in developing countries where the economic and social systems are greatly dependent upon their fisheries. The input of fish larvae is one of the factors that determine the importance of an estuary for many commercially important fish species. This study focused on a set of four fish taxa, namely the Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae, as they are the most common exploited families of fishes in the estuary. A better understanding of these physical and biological mechanisms will allow to assessing the impact of environmental changes.

2. Materials and Methods

In this study we first looked at the flow structure at the entrance of the Saloum branch of the Sine-Saloum estuary. Second, we focused on the movement of fish larvae in and out of the estuary by looking at the variation in the larval fish densities and transport as related to phase of the tide, time of the day, and location within the entrance of the Saloum river branch. Finally, the focus is on the physical and the possible impact of larval behaviour and other biological mechanisms by which larval fishes are transported between the shelf and the estuarine areas.

2.1. Study system: the Sine Saloum inverse estuary in West Africa

Situated in Senegal West Africa (13°30'-14°30' N, 16°00'-16°80' W), the Sine Saloum system (**Fig. 1a**) is representative of estuaries that receive, except from seasonal local rainfall, little or no freshwater input. Under intense evaporation, they have become in their entirety highly saline and in their upper reaches hypersaline. Between 1951 and 1980, the average yearly precipitation in the Sine Saloum estuary ranges from 880 mm in the southern part to 480 mm in the northernmost part (Dacosta, 1993). The overall average of 828 mm recorded in the fifties (Diaw et al., 1993), is now only about 500 mm, with rains concentrated over 3-4 months and surrounded by prolonged drought periods. This recorded change in the precipitation rate corresponds to a deficit of about 10 billion m^3 of freshwater input (Diouf, 1996). Classified as an inverse estuary (Pritchard, 1967), throughout the year, salinity ranges from 35 to 41 at the sea mouth and can reach over 130 in the upstream areas. This study was conducted at the mouth of the Saloum branch of the Sine Saloum estuary (**Fig. 1a**). The Saloum entrance connects the Atlantic Ocean to the estuarine areas, as an average depth of 10 m, and takes a south-north direction over approximately 3 kilometres (**Fig. 1b**). The west side of the entrance is bordered by a sand spit (Pointe de Sangomar) and the east side of the entrance by patchy mangrove cover. The average width on this reach is 1.5 km. Regional tides are semi-diurnal, having average tidal amplitude of about 1.20 m. The Saloum region is economically strongly based on fishing activities.
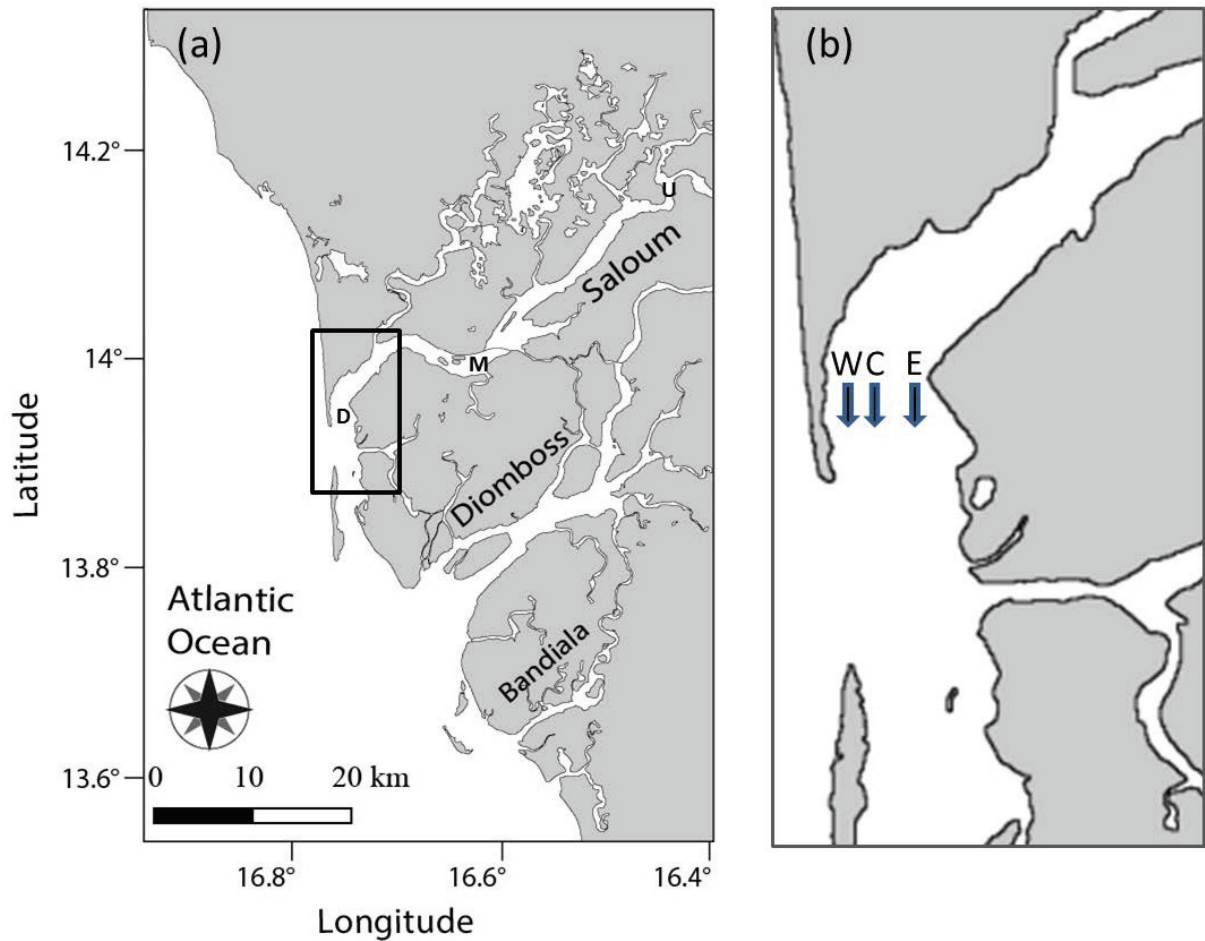
Fig. 1. (a) Location of the study system and the three sectors (U: Upstream, M: Midstream, D: Downstream). (b) Zoom showing the positions of the three sampling locations (W: West, C: Centre, E: East) in the Sine Saloum estuary (Senegal, West Africa).

2.2. Physical field sampling

2.2.1. Hydrodynamic data acquisition

Vertical current profiles (speed and direction) and bottom pressure were measured continuously during ~ 2.5 semi-diurnal tidal cycles at three locations situated at the entrance of the Saloum branch of the Sine Saloum estuary. Three upward-looking Acoustic Doppler Current Profilers (ADCPs) fastened to the base of aluminium frames were deployed and anchored on the sea floor (bottom mounted) with approximately uniform spacing across the channel's western and eastern flanks and near the centre; forming a transect line perpendicular to the entrance (**Fig. 1b**). These locations were named West, Centre, and East, and their GPS coordinates, depths, and

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observation periods, as well as instrument specifications and configuration parameters (bin size, blanking distance, and ensemble averaging) are provided in **Table 1**. As it is standard procedure for ADCP's data, near-surface data were discarded because of contamination from echoes scattered back from the sea surface (the depth above which data were considered non-usable was determined objectively; see Section 2.4.1). Near-bottom data are also not available because of the depth at which the instrument head was located (~ 0.5 m above ground) and the additional blanking distance. Consequently, the "West-Centre-East" deepest measurement cells were centred at respectively 1.15, 2 and 1.5 m above the sea floor. Deployment of ADCPs took place on 9 July 2014 for a period of ~ 30 hours starting at 09:00 UTC (Coordinated Universal Time) until 10 July 2014, 15:00 UTC the next day. Despite being part of the climatological monsoon season, no major rainfall had taken place in the months prior to our observational period, which was characterised by the absence of freshwater run-off in the Sine Saloum estuary. Thus, our observations are representative of the warm and dry conditions preceding the monsoon onset. It also followed the seasonal maximum larval abundances that was observed in a previous study (Sloterdijk et al., 2017). Tidal amplitude was close to average with a forecast tide coefficient of 72 (Pointe de Sangomar). Weather conditions were fair during the survey with winds systematically below 10 knots (personal observation).

Table 1

Details of ADCPs deployment positions (degrees and decimal minutes), depth in meters, observation periods (day/month/year), frequency in kilohertz of the ADCPs (F), bin size in meters (BS), blanking distance in meters (BD), ensemble averaging in seconds (EA). Depths are obtained using ADCP pressure measurement over an exact tidal cycle to which we remove pressure; a +0.5 m correction is then applied to account for the depth of the instrument head.

Stations	Position (DMM) Latitude / Longitude	Depth (m)	Observation Periods	F (kHz)	BS (m)	BD (m)	EA (s)
West	13° 56.708'N / 16° 45.628'W	8	09/07/2014 – 10/07/2014	1000	0.5	0.4	60
Centre	13° 56.764'N / 16° 45.114'W	13	09/07/2014 – 10/07/2014	400	1.0	1.0	60
East	13° 56.807'N / 16° 44.884'W	9	09/07/2014 – 10/07/2014	600	1.0	0.5	60

2.2.2. Physicochemical data acquisition

One shallow boat (R/V Diassanga, 10m, IRD) was used to sample the West (W), Centre (C), and East (E) locations. Salinity (PSU), water temperature (°C), and dissolved oxygen (mg l^{-1}) were measured using a hand held multi-parameter field instrument (WTW Multi 3430®). Vertical profiles of the physicochemical variables were obtained by taking measurements starting at the surface with depth intervals of one meter until the bottom was reached. Measurements of each location occurred at approximately 2-hour intervals and were coincident with larval sampling. Additionally, salinity measurements acquired during other field campaigns (Sloterdijk et al., 2017) (November 2013, February, June, and August 2014) at locations along the Saloum branch of the Sine Saloum estuary, were used in this study to assess bottom and surface longitudinal salinity differences between pre-established sectors (downstream, midstream, and upstream) as a function of season (**Fig. 1a**).

2.3. Fish larvae sampling

Fish larvae were actively sampled at each location at approximately 2-hour intervals. Two types of nets, both with mesh size of 500 μm were used: a paired neuston net (opening 30x15 cm, 3 m long) stacked on top of each other for collecting fish larvae at and near the surface, and a ring trawl (⌀ 0.60 m, 3 m long) to collect fish larvae in the water column. Accordingly, 3 strata were sampled and referred to: Surface (Neuston Top), Near Surface (Neuston Bottom), and Mid-Water (Ring Trawl). Both nets were custom made to be operated from an adapted catamaran (Hobie Cat 15®) deployed in a parallel route of a towing boat (R/V Diassanga) ensuring larval sampling well clear of its bow wave and wake. Each sample consisted of a 5-minute horizontal haul in the direction of the current at an average speed of 2-3 knots.

The volume of water filtered was calculated using mechanical flow meters (Hydro-Bios®) attached to the centre of the nets, so the number of larvae caught, when needed, could be standardized into the number of larvae per m^3 for density measurements. Samples were immediately preserved in 30 % alcohol/seawater and stored and cooled in an onboard electric coolbox. In the laboratory, fish larvae were sorted from the catches and gradually transferred to 50 and 70 % alcohol. In addition, standard length (SL) to the nearest 0.01 mm (measured from

the tip of the snout to the end of the notochord (Miller and Kendall, 2009)) was measured for all larvae at each sampling locations.

Using the traditional morphological techniques, collected specimens were identified to the lowest possible taxon using the following compendia: Leis and Carson-Ewart, 2004; Moser, 1996; Richards, 2006; Tamoikine and Pandare, 1994. Due to the paucity of original descriptions and illustrations of fish larvae found in the literature covering the area of interest, especially the smaller individuals could not always be identified to the species or genus level, but only to family level. Accordingly, a selection of the four most abundant taxa in the samples was made and further analysis in this study concentrated on Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae larvae. Complementary to the morphological techniques, genetic identification using DNA sequencing, was applied to representative individuals of the four pre-identified taxa to assist and confirm successful identification. For this, DNA barcoding was based on sequencing the commonly used barcode region, a ±600 base pair fragment of cytochrome c oxidase I (COI/COX) (Aljanabi and Martinez, 1997; Hebert et al., 2003). For amplification, the COI-primer pair FF2d + FR1d of Ivanova et al. (2007) was used. Samples that failed amplifying with this primer pair were amplified using the primer pair of Folmer et al. (1994). DNA was extracted (whole fish larvae) according to Aljanabi and Martinez (1997). All polymerase chain reactions (PCR) were performed according to the protocols published with the primer pairs. Amplicons were sequenced using the PCR primers. Sequences were compared with the National Center for Biotechnology Information (NCBI) nucleotide collection database using BLAST (Altschul et al., 1990). Additionally, the BOLD Identification System was used (Ratnasingham and Hebert, 2007).

2.4. Data analyses

2.4.1. ADCP's data processing

In a stratified estuary, we expect velocities (v) to differ between the surface and the bottom. This may have important implications because near-passive organisms such as eggs and larvae can modulate their lateral transport by simply modifying their position in the water column (e.g. through adjustments of their buoyancy or by vertical migration). To quantify this effect, we wish to compute the vertical velocity shear at the mooring locations using the equation:

$$\delta v(t) = v(surface) - v(bottom)$$

But because of ADCP limitations, none of these velocities are available and we instead computed $\delta v = v\left(n_{up}(t)\right) - v\left(n_{lo}(t)\right)$ where n_{up} and n_{lo} are respectively the indices of the upper most and lower most cells where valid ADCP currents are measured. n_{lo} is simply 1, i.e., the first available measurement cell whose centre is situated at a distance from the bottom equal to the blanking distance plus half the cell size. Differently, n_{up} depends on many factors including the tidal phase (which changes the position of the sea surface with respect to the bottom), and the surface wave field (which affects the reflection of ADCP signals). To determine n_{up} we used the following methodology. For all possible integers n we computed the RMS for the velocity difference between two consecutive cells:

$$RMS_{\delta v_n} = \sqrt{< \left(v(n_\zeta - n + 1) - v(n_\zeta - n)\right)^2 >}$$

where n_ζ is the index of the cell whose centre is the closest to the air-sea interface in the water and $<.>$ is the time averaging operator over a M$_2$ tidal cycle. $RMS_{\delta v_n}$ is remarkably constant in the subsurface and suddenly jumps to a significantly larger value (by a factor of three or more) when approaching the surface. Although this discontinuity may partly be physical, we use it to define n_{up} above which ADCP data are considered as possibly contaminated by side-lobe reflection and discarded. Corresponding n_{up} indices are respectively $n_\zeta - 4$, $n_\zeta - 3$, and $n_\zeta - 2$ for the West, Centre and East moorings (see **Fig. 2**; note that the western ADCP has a smaller bin size of 0.5 m so the West and East moorings have their upper most velocities at the same depth below the sea surface).

2.4.2. Larval densities related to location and tidal cycle

A series of two-sample t-tests assuming unequal variance were conducted to compare the densities (ind. m^{-3}) of Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae larvae in ebb and flood tide conditions at the West, Centre, and East locations. Ebb and flood conditions were determined using the meridional velocity (ebb when southward movement of water exiting the estuary; flood when northward movement of water entering the estuary). Larval concentrations

were transformed ($Log_{10}(x + 1)$) to meet the assumption of normality and goodness of fit was tested using Shapiro–Wilk test.

2.4.3. Vertical and length-frequency distribution of fish larvae

A two-way (factorial) analysis of variance (ANOVA) was conducted to compare the main effects of the depth and tide and their interaction effect on the larval transport at the different sampling locations. The larval transport (ind. m^{-3} s^{-1}) was calculated by multiplying the current velocity (from the ADCP moored at the sampling location; meters per second) by the larval density (number of larvae per cubic meter). The larval transport data were transformed ($Log_{10}(x + 1)$) to meet the assumption of normality and goodness of fit was tested using Shapiro–Wilk test.

Since various transformations failed to normalize the data and stabilize the variance, nonparametric Mann-Whitney test was conducted to investigate whether the larval fish sizes differed between those entering the estuary (flood condition) to those leaving the estuary (ebb condition).

3. Results

3.1. Physical conditions during the high resolution July measurements

Current measurements at the three locations are shown in **Fig. 2** and the time series of surface salinity in **Fig. 3**. Salinity temporal changes appear similar at all three moorings with salinity maxima that coincide with the reversal from ebb to flood (compare **Figs. 2** and **3**). This quadrature phase between v and salinity is consistent with the idea that the salinity field (increasing toward the head of the estuary, see **Fig. 4**) is repetitively moved past the moorings by the cyclic longitudinal barotropic flow. Integrating the tidal flow in time, we obtain longitudinal ebb/flood tidal excursions of 10-12 km. This and the temporal change of salinity, allow us to provide some estimates for the lateral salinity and density gradient present in the estuary in the vicinity of the moorings, which are 0.25 PSU km^{-1} (or 0.2 kg m^{-3} km^{-1}).

Stratification varies greatly over the full observational period. Surface to bottom salinity differences (not shown) range from 0 to 3 PSU but are frequently of the order of 0.5, which we take as a typical value for the three moorings. Combining this number with the one for the lateral salinity gradient provides us with an estimate for the isohaline slope of 0.5 %, e.g., quite similar to those found for the Shark Bay (Australia) inverse system in Hetzel et al. 2013; (their figure 2).

Close inspection of the ADCP measurements (**Fig. 2** lower panels) reveals the presence of positive vertical shear, i.e., near-surface (resp. near-bottom) waters exhibit more pronounced northward (resp. southward) velocities. This is confirmed by the examination of the time series of velocity measured at the lowest and highest valid ADCP bins (**Fig. 2** upper panels). Some spatio-temporal complexity is evident in the vertical shear (which is proportional to the separation distance between the red and blue curves). This is due to the variability of the turbulence induced by bottom friction (which varies greatly over a tidal cycle, but naturally favours positive shear during flood), of the turbulence induced by air-sea interactions, and also possibly due to pre-existing small scale heterogeneities in stratification produced remotely, e.g., transported from outside the estuary by the tidal flow. Lack of measurements in the surface and bottom layer prevents us from presenting full water column transport budgets, but vertical shear averaged over one tidal cycle is robustly positive at the West and Centre ADCPs, with a mean velocity difference between near-surface and near-bottom equal to 0.09 m s^{-1} (west) and 0.05 m s^{-1} (centre). These differences would presumably be even larger if we had access to velocities closer to the surface and bottom. At the East mooring, near-surface and near-bottom velocities differ most of the time but their averages over a tidal cycle remain within 0.01 m s^{-1} of each other. Averaging over all three mooring locations and assuming a near-zero net flow across our measurement section, these numbers imply the existence of a mean southward (resp. northward) flow with intensity of the order of 0.025 m s^{-1} near the bottom depth (resp. the surface). A slight volume imbalance is possible over a couple tidal cycles, but additional arguments are offered in the discussion section to support the significance of the flow vertical shear and its importance for the reproduction of fish.
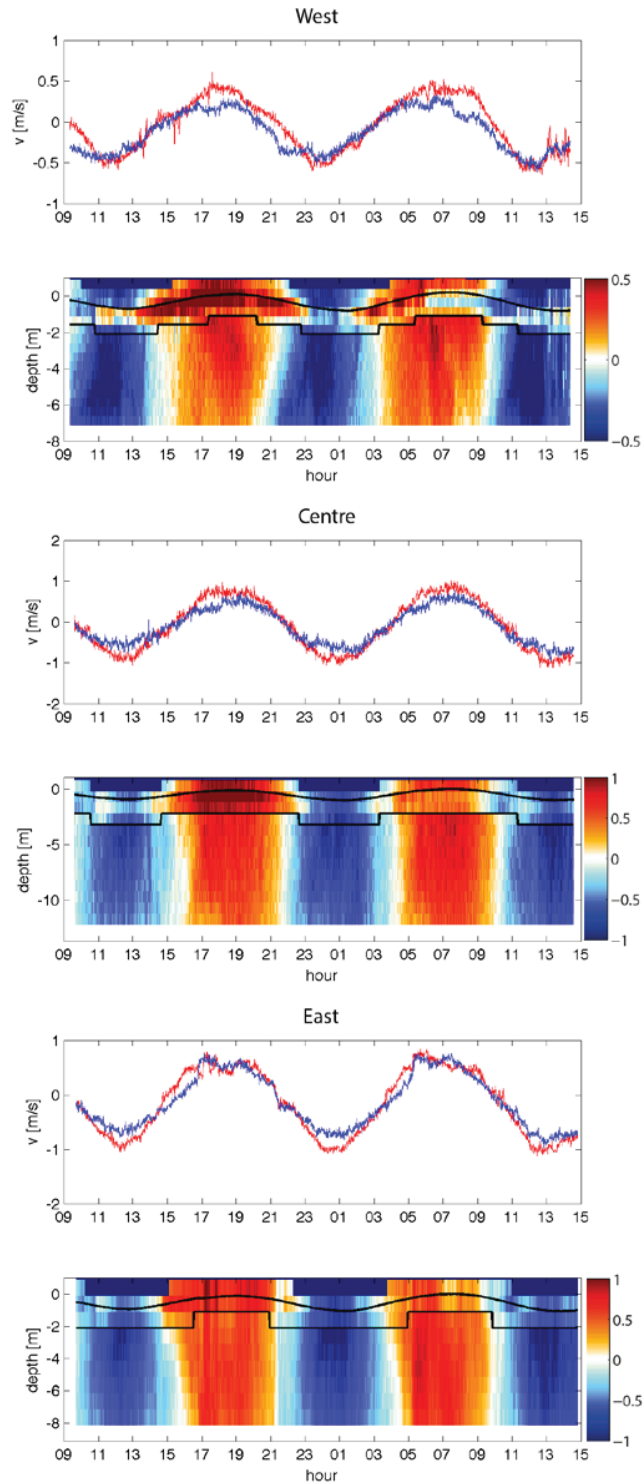
Fig. 2. Meridional velocity [m/s] measured from ADCPs at the western (upper), centre (middle) and eastern (lower) mooring locations. Time series of uppermost (red curve) and deepest (blue curve) valid velocities are shown in the upper panels. Complete depth-time diagrams for the entire deployment period are shown in the lower panels (in colour). The undulating black line represents the position of the air-sea interface. The step-like black line is situated at the top of the ADCP cell that is being used to compute near-surface to near-bottom velocity shear. This upper most valid cell is the shallowest one situated at least 2 m (ADCP: West, 1000 kHz and East, 600 kHz) or 3 m (ADCP: Centre, 400 kHz) below the free surface. Unit in [m/s] for the color bar legend of the lower panels.
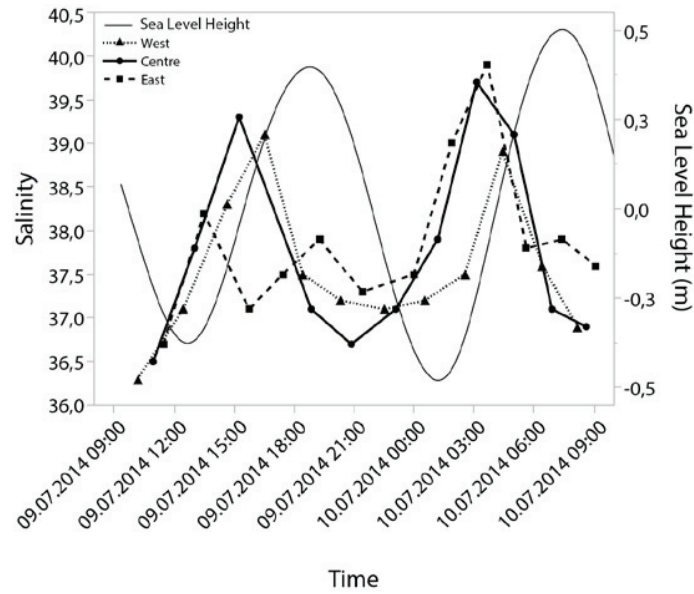
Fig. 3. Salinity profiles for the three stations at the head of the Saloum branch of the Sine Saloum estuary. Note the approximately quadrature phase between salinity and velocities, i.e., salinity maxima are obtained around 3PM and 3AM at the end of the ebb phase when waters reaching the moorings area are the ones that have the most estuarine characteristics possible (for a given tidal coefficient and excursion magnitude). Times are Coordinated Universal Time.
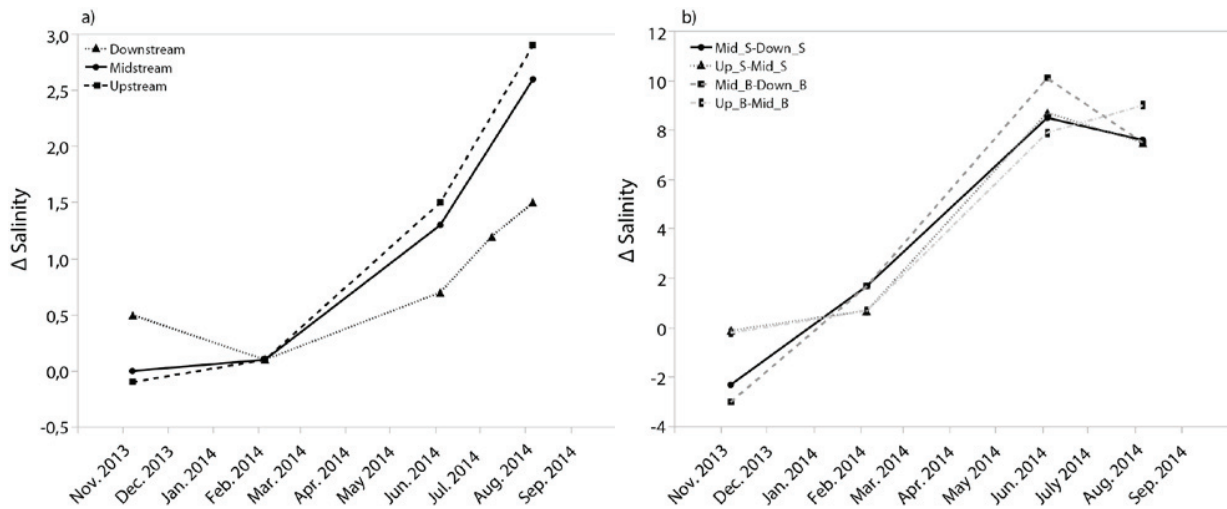
Fig. 4. November 2013 to August 2014 seasonal cycle for the (a) surface to bottom stratification due to salinity effects over the 3 different subareas referred to as downstream (Down), midstream (Mid) and upstream (Up) (see location in **Fig 1**), (b) lateral surface (S) and bottom (B) salinity contrasts between the Midstream and Downstream, or Upstream and Midstream.

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3.2. The Sine-Saloum thermohaline seasonal cycle

For the sampling periods other than the one in July 2014, no current measurements are available, but the nature of the estuarine circulation can be inferred from the analysis of the vertical stratification (**Fig. 4a**) and longitudinal salinity gradient (**Fig. 4b**) as a function of season. Bottom and surface longitudinal salinity differences are shown for the bottom and surface and also for two different sectors, between the lower and middle estuary, and between the middle and upper estuary (see **Fig. 1** for locations). Vertical stratification higher than 0.5 PSU was present in June, July and August at all locations. In November 2013, vertical stratification of similar magnitude was only found in the downstream area. This observation was corroborated by CTD profiles made 4 km north of the mooring area on 25 October and 13 November 2017 in ~12 m water depth, with observed surface to bottom salinity differences around 0.4 PSU (unpublished data). Horizontal contrasts of salinity shown in **Fig. 4b** reveal a noticeable shift in the lower part of the Saloum from classical estuary conditions in November 2013 (Mid-Down salinity values < 0 both at surface and bottom) to inverse estuary conditions (Mid-Down salinity values > 0, albeit only slightly so in February 2014). The time series of salinity contrasts in the upper Saloum differs in that no sign reversal is seen between November 2013 and February 2014. More data points would be needed to accurately characterise the seasonal cycle but the robust signs of vertical stratification of up-estuary salinity gradient and vertical stratification in **Fig. 4** are consistent with the dominance of "inverse estuary" conditions accompanied by gravitational sheared flow.

3.3. Larval densities related to location and tidal cycle

Densities (ind. m^{-3}) of Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae larvae collected during ebb and flood tide conditions at the West, Centre, and East locations are presented in **Fig. 5**. Visual trends were evident as for all taxa the densities were higher during flood conditions in almost all cases. To test if these visual trends could be interpreted correctly (i.e. there were statistical larval densities differences between tidal conditions), two-sample t-tests were conducted for each species at each of the three sampling locations.

Although visual differences in densities between ebb and flood conditions could be observed for Clupeidae larvae at all three stations (**Fig. 5a**), they were statistically not significant:

West: $t(5.7) = 0.07$, $p = 0.9496$; Centre: $t(6.6) = 0.78$, $p = 0.4616$; East: $t(8.7) = 1.29$, $p = 0.2316$. Therefore, no effects of tidal conditions could be statistically detected on the Clupeidae larval densities. Regarding the Cynoglossidae larvae, no differences in larval densities were observed at the West and East stations: West: $t(7.8) = 0.58$, $p = 0.5763$; East: $t(9) = -0.11$, $p = 0.9121$, but only at the Centre location a significant difference was found: Centre: $t(5) = 3.60$, $p = 0.0156$. This was expected, because at the Centre location, Cynoglossidae larvae were completely absent in the catches during ebb tide (**Fig. 5b**). Densities of Gerreidae larvae at the West and Centre locations were also visually higher (**Fig. 5c**) between the tidal cycles (ebb vs Flood), but again significant differences were only found for the East station (East: $t(6) = 4.61$, $p = 0.0037$; West: $t(7.5) = 0.12$, $p = 0.9039$; Centre: $t(9.8) = 2.02$, $p = 0.0721$.) where Gerreidae larvae were absent in the catches during ebb tide (**Fig. 5c**). Lastly, the Mugilidae larval densities (**Fig. 5d**), between the tidal conditions differed significantly for two locations, the Centre and East stations: Centre: $t(7.6) = 3.73$, $p = 0.0064$; East: $t(10) = 2.28$, $p = 0.0455$. At the West location, no significant differences between ebb and flood densities were detected: West: $t(9.9) = -0.75$, $p = 0.4726$. A detailed t-test score statistics is presented in **Table 2**.

3.4. Larval transport related to location and time of day

Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae larval transport (expressed as ind. m^{-3} s^{-1}) at the three locations and related to time of day for a ~ 24 h period are presented in **Fig. 6**. Clupeidae larval transport showed a similar trend between the three sampling locations (**Fig. 6a**). Maximum transport (0.34 ind. m^{-3} s^{-1}) occurred at the Centre location, followed by the West (0.16 ind. m^{-3} s^{-1}) and East (0.10 ind. m^{-3} s^{-1}) locations. For all three locations, highest transport numbers were obtained shortly after sunset between 19:00 and 21:00 UTC. Cynoglossidae larval transport did not show such a clear tendency to match between the locations (**Fig. 6b**), and maximum transport (0.03 ind. m^{-3} s^{-1}) occurred at the East location and shortly before sunset between 16:00 and 18:00 UTC. Almost equally high, transport of 0.028 ind. m^{-3} s^{-1} occurred at the Centre location but this time shortly after sunset between 19:00 and 21:00 UTC.

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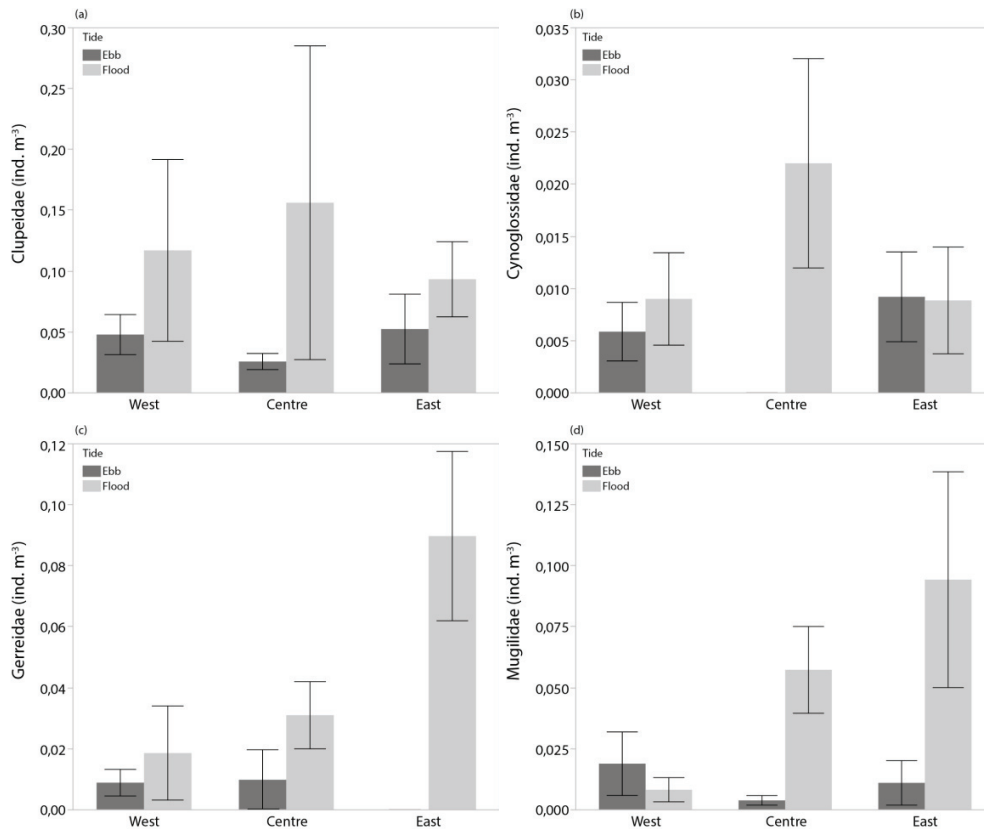
Fig. 5. Larval transport (ind. m^{-3}) of four taxa of fish larvae collected during ebb and flood tides at the West, Centre, and East stations located at the mouth of the Saloum branch of the Sine Saloum estuary. Each error bar is constructed using one standard error from the mean.

Table 2

Summary results of the two-sample t-tests for densities of the four taxa of fish larvae by tidal conditions at the three locations. Capital letters indicate significant differences with "A" being greater than "B". Non-significant is denoted with the abbreviation: ns. Mean expressed as ind. m^{-3}. SD = Standard deviation.

	Taxa	Ebb Mean (SD)	Flood Mean (SD)	Ebb	Flood	t value	p value
West							
	Clupeidae	0.753 (0.398)	0.777 (0.732)	ns	ns	0.07	0.9496
	Cynoglossidae	0.204 (0.255)	0.301 (0.301)	ns	ns	0.58	0.5763
	Gerreidae	0.293 (0.331)	0.320 (0.409)	ns	ns	0.12	0.9039
	Mugilidae	0.383 (0.406)	0.241 (0.252)	ns	ns	-0.75	0.4726
Centre							
	Clupeidae	0.665 (0.236)	0.867 (0.589)	ns	ns	0.78	0.4616
	Cynoglossidae	0 (0)	0.498 (0.339)	B	A	3.60	0.0156[*]
	Gerreidae	0.174 (0.425)	0.635 (0.366)	ns	ns	2.02	0.0721
	Mugilidae	0.180 (0.207)	0.856 (0.393)	B	A	3.73	0.0064[*]
East							
	Clupeidae	0.828 (0.305)	1.057 (0.303)	ns	ns	1.29	0.2316
	Cynoglossidae	0.295 (0.304)	0.275 (0.315)	ns	ns	-0.11	0.9121
	Gerreidae	0 (0)	0.972 (0.558)	B	A	4.61	0.0037[*]
	Mugilidae	0.241 (0.392)	0.902 (0.608)	B	A	2.28	0.0455[*]
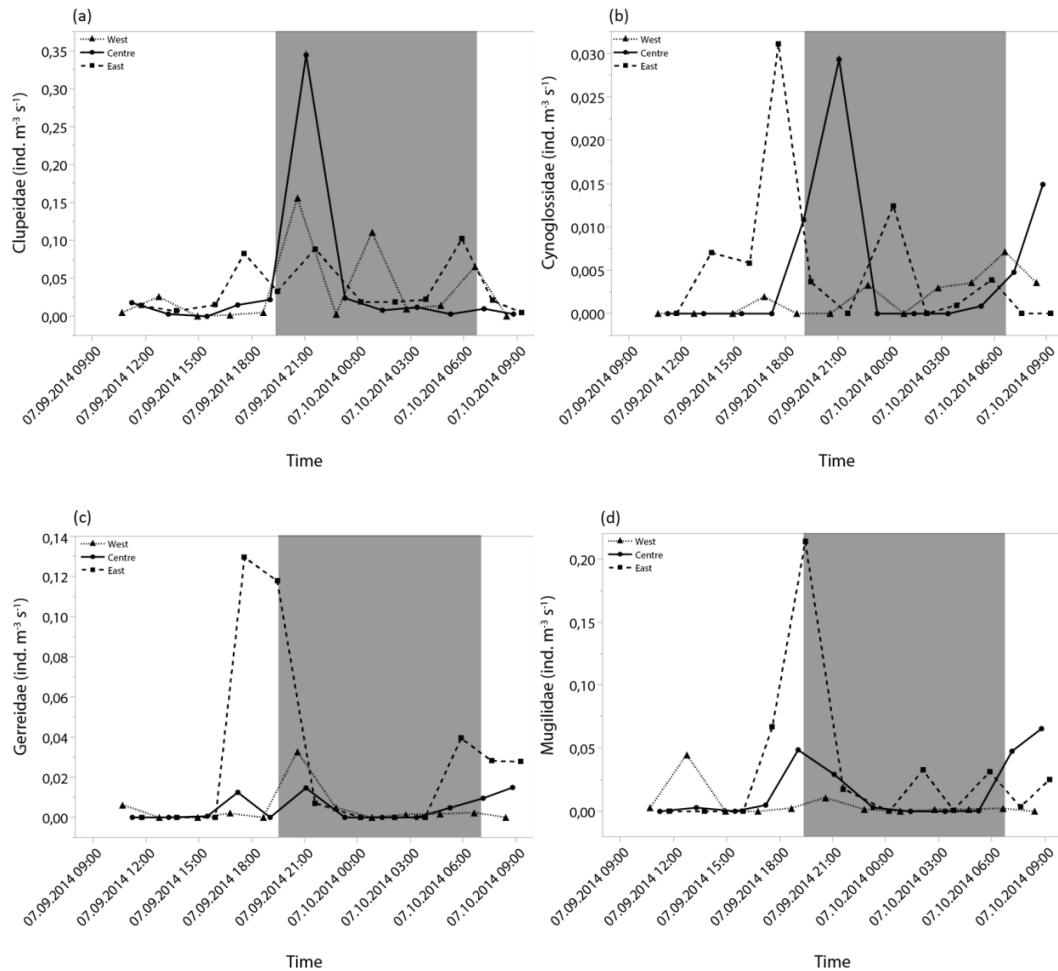
Fig. 6. Larval transport (ind. m^{-3} s^{-1}) of four taxa of fish larvae collected on a two-hour time interval frequency over the ~ 24 h sampling period at the West, Centre, and East locations with darkness hours shaded. Times are Coordinated Universal Time.

In Gerreidae larvae (**Fig. 6c**) highest transport (0.13 ind. m^{-3} s^{-1}) occurred at the East location followed by the West location (0.03 ind. m^{-3} s^{-1}) and Centre location (0.01 ind. m^{-3} s^{-1}). For the East location, highest transport were obtained shortly before sunset between 16:00 and 18:00 UTC, while the East and Centre locations got their highest transport rate was shortly after sunset between 19:00 and 21:00 UTC. Larval transport of Mugilidae larvae showed a similar trend between the West and Centre locations (**Fig. 6d**), with larval transport remaining low most of the ~ 24 h observation period. Highest density (0.21 ind. m^{-3} s^{-1}) occurred at the East location followed by the Centre (0.07 ind. m^{-3} s^{-1}) and West (0.05 ind. m^{-3} s^{-1}) locations. Highest densities were obtained for the East location shortly after sunset between 19:00 and 21:00 UTC, for the Centre location shortly after sunrise between 07:00 and 08:00 UTC, and for the West location in

the middle of the day at about 12:00 UTC. Overall, for the four taxa, a similar trend could be observed. Highest larval transport seems to be contained in a relatively short time window; shortly before the sunset and after sunset between 16:00 and 21:00 UTC. Also, Clupeidae showed highest larval transport measurements at the Centre location while the Cynoglossidae, Gerreidae, and Mugilidae showed highest larval transport measurements at the East location. Furthermore, what was observed, except for the Clupeidae, is a seemingly larval transport increase shortly after the sunrise.

3.5. Vertical distribution of fish larvae
3.5.1. Patterns and periodicity in larval vertical distribution

Larval transport fluctuations and changes in the vertical distribution of Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae fish larvae over the ~ 24 h sampling period can be seen in **Fig. 7**. None of the four taxa of fish larvae displayed apparent patterns of time or tide related vertical movement throughout the water column. In all locations, Clupeidae and Cynoglossidae larvae showed repeatedly higher larval transport in the Mid-Water stratum, while Mugilidae larvae, and to lesser extent Gerreidae larvae, showed consistently higher larval transport in the Surface stratum. For each of the four taxa, a two-way (factorial) analysis of variance was conducted on the influence of larval position in the water column and the tide condition, on the larval transport at the three sampling locations (**Table 3**). Larval position in the water column was labelled "depth" and included three levels (Surface, Near Surface, and Mid-Water), and tide condition consisted of two levels (ebb and flood). Across the taxa and location, not all effects (Tukey post-hoc test) were found to be significant and summary results are detailed in **Table 3** and **4**.

At all three locations, the larval position in the water column (depth) returned a significant effect on the larval transport of Clupeidae (West: $F_{(2,30)} = 8.80$, $p = 0.0010$; Centre: $F(2,30) = 20.77$, $p = 0.0001$; East: $F(2,30) = 13.51$, $p = 0.0001$). A post-hoc Tuckey test indicated that the mean larval transport score for the Mid-Water stratum was significantly higher than that of those of the Surface and Near Surface strata (Table 4). The same was observed for the Cynoglossidae larvae (West: $F_{(2,30)} = 9.90$, $p = 0.0005$; Centre: $F(2,30) = 7.74$, $p = 0.0020$; East: $F(2,30) = 9.84$, $p = 0.0005$). A post-hoc Tuckey test indicated that the mean larval transport score for the Mid-Water stratum was significantly higher than that of those of the Surface and

Near Surface strata (Table 4). Gerreidae larval transport seemed to be somehow more equally distributed in all three water strata as no effect of their position in the water column (depth) were detected and, therefore, did not show any statistically detectable preferences for one stratum over the other (West: $F_{(2,30)} = 0.47$, $p = 0.6324$; Centre: $F_{(2,30)} = 1.62$, $p = 0.2152$; East: $F_{(2,30)} = 2.87$, $p = 0.0724$). However, when looking at the number of individuals sample by water stratum (Appendix 1), Gerreidae larvae were constantly more abundant at the Surface stratum compared to the Near Surface and Mid-Water strata; indicating a preference of the Surface strata. Mugilidae larvae were almost exclusively located at the surface stratum at the Centre and East locations (Centre: $F_{(2,30)} = 18.48$, $p = < 0.0001$; East: $F_{(2,30)} = 3.99$, $p = 0.0291$) but as the West location's larval transport was mostly null throughout the ~ 24 h sampling period, no significant difference could be detected at that location (West: $F_{(2,30)} = 1.96$, $p = 0.1586$). Appendix 1 provides further evidence for the depth preference of all four taxa.

3.5.2. Length-frequency distribution of fish larvae

The length-frequency distributions of Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae larvae by tide condition (ebb and flood), depth (Surface, Near Surface, and Mid-Water strata), and location (East, Centre, and West stations) are shown in **Fig. 8**. In addition to the size distributions, the previously observed general patterns of vertical distribution of Clupeidae and Cynoglossidae larvae predominantly distributed in the Mid-Water stratum, Gerreidae larvae more evenly widespread across the three strata, and Mugilidae larvae essentially distributed at the Surface stratum, can be further and differently visualized. The four taxa of fish larvae length-frequency distributions, in term of the size range observed were quite homogenous across the three strata and locations (**Fig. 8**). The differences in the size distribution were minimal between samples categorized as ebb and flood conditions. Further, negligible differences in the size distribution between the locations and the positions in the water column were apparent and presented supporting evidences of strong depth preferences independent of the tidal condition and the location at the mouth of the Saloum branch of the Sine Saloum estuary. Therefore, there was no strong evidence of depth regulation. For all four taxa of fish larvae, larval size during ebb tide was no greater or smaller than larval size during flood tide. This indicates that larvae entering and

exiting the estuary are of similar size range and not from distinctly different cohort. **Table 5** reports on the Mann-Whitney U test p-values and on the size range of the four fish larvae taxa.
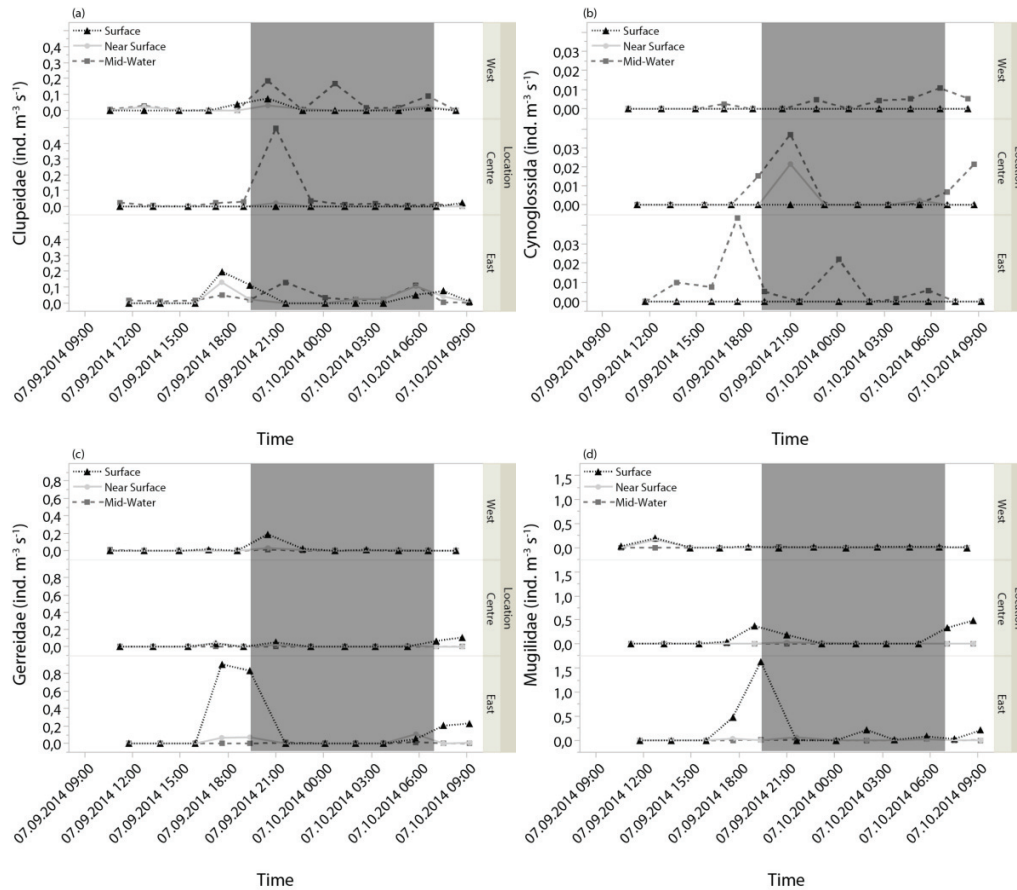

Fig. 7. Densities (ind. m^{-3} s^{-1}) of four taxa of fish larvae collected on a two-hour time interval frequency over the ~ 24 h sampling period at the West, Centre, and East locations, and for the three vertical sampling position in the water column. Darkness hours shaded and times are Coordinated Universal Time.

Table 3

Larval transport summary results from the two-way (factorial) analysis of variance and post-hoc connecting letter report for the four taxa of fish larvae collected at the surface, near-surface, and mid-water at the head of the Saloum branch of the Sine Saloum estuary. Non-significant results are abbreviated "ns", and capital letters indicate significant differences with "A" being greater than "B".

	Taxa	Depth (D)				Tide (T)			*D x T*
		p value	Surface	Near-Surface	Mid-Water	*p* value	Ebb	Flood	*p* value
West									
	Clupeidae	0.0010	B	B	A	ns	ns	ns	ns
	Cynoglossidae	0.0005	B	B	A	ns	ns	ns	ns
	Gerreidae	ns	ns	ns	ns	ns	ns	ns	ns
	Mugilidae	ns	ns	ns	ns	ns	ns	ns	ns
Centre									
	Clupeidae	0.0001	B	B	A	ns	ns	ns	ns
	Cynoglossidae	0.0020	B	AB	A	0.0008	B	A	0.0020
	Gerreidae	ns	ns	ns	ns	0.0299	B	A	ns
	Mugilidae	0.0001	A	B	B	0.0011	B	A	0.0001
East									
	Clupeidae	ns	ns	ns	ns	ns	ns	ns	ns
	Cynoglossidae	0.0005	B	B	A	ns	ns	ns	ns
	Gerreidae	ns	ns	ns	ns	0.0010	B	A	ns
	Mugilidae	0.0291	A	AB	B	0.0228	B	A	ns

Table 4
Results of Tukey's Post Hoc Multiple Comparisons for larval position in the water column.

|	Taxa	Mean Diff.	Std. Err. Diff.	Lower CL	Upper CL	*p* value
West						
	Clupeidae					
	Mid-Water – Surface	0.0323770	0.0170140	-0.009372	0.0741259	0.0238[*]
	Mid-Water – Near Surface	0.0349460	0.0170140	-0.006803	0.0766950	0.0153
	Near Surface – Surface	0.0025690	0.0170140	-0.039180	0.0443179	0.9875
	Cynoglossidae					
	Mid-Water – Surface	0.0027782	0.0008158	0.000776	0.0047801	0.0049[*]
	Mid-Water – Near Surface	0.0027782	0.0008158	0.000776	0.0047801	0.0049[*]
	Near Surface – Surface	0.0000000	0.0008158	-0.002002	0.0020019	1.0000
	Gerreidae					
	Mid-Water – Surface	0.0178396	0.0129114	-0.013842	0.0495216	0.3619
	Mid-Water – Near Surface	0.0021371	0.0129114	-0.029545	0.0338190	0.9850
	Near Surface – Surface	0.0157025	0.0129114	-0.015979	0.0473845	0.4522
	Mugilidae					
	Mid-Water – Surface	0.0124209	0.0170643	-0.029451	0.0542931	0.7488
	Mid-Water – Near Surface	0.0234178	0.0170643	-0.018454	0.0652900	0.3667
	Near Surface – Surface	0.0109969	0.0170643	-0.030875	0.0528691	0.7968
Centre						
	Clupeidae					
	Mid-Water – Surface	0.0531556	0.0327986	-0.027325	0.1336365	0.0413[*]
	Mid-Water – Near Surface	0.0531429	0.0327986	-0.027338	0.1336239	0.0415[*]
	Near Surface – Surface	0.0000126	0.0327986	-0.080468	0.0804936	1.0000
	Cynoglossidae					
	Mid-Water – Surface	0.2300352	0.0824502	0.027719	0.4323511	0.0230[*]
	Mid-Water – Near Surface	0.1798635	0.0824502	-0.022452	0.3821794	0.0893
	Near Surface – Surface	0.0501717	0.0824502	-0.152144	0.2524875	0.8165
	Gerreidae					
	Mid-Water – Surface	0.0219452	0.0091690	-0.000554	0.0444439	0.0571
	Mid-Water – Near Surface	0.0062059	0.0091690	-0.016293	0.0287046	0.7785
	Near Surface – Surface	0.0157393	0.0091690	-0.006759	0.0382380	0.2142
	Mugilidae					
	Mid-Water – Surface	0.1170195	0.0421444	0.013606	0.2204333	0.0238[*]
	Mid-Water – Near Surface	0.1142773	0.0421444	0.010864	0.2176911	0.0277[*]
	Near Surface – Surface	0.0027421	0.0421444	-0.100672	0.1061559	0.9977
East						
	Clupeidae					
	Mid-Water – Surface	0.0000501	0.0206713	-0.050673	0.0507733	1.0000
	Mid-Water – Near Surface	0.0072641	0.0206713	-0.043459	0.0579873	0.9343
	Near Surface – Surface	0.0072139	0.0206713	-0.043509	0.0579372	0.9352
	Cynoglossidae					
	Mid-Water – Surface	0.0079638	0.0030521	0.000475	0.0154530	0.0352[*]
	Mid-Water – Near Surface	0.0079638	0.0030521	0.000475	0.0154530	0.0352[*]
	Near Surface – Surface	0.0000000	0.0030521	-0.007489	0.0074892	1.0000
	Gerreidae					
	Mid-Water – Surface	0.1834352	0.0785744	-0.009370	0.3762406	0.0648
	Mid-Water – Near Surface	0.1647609	0.0785744	-0.028044	0.3575663	0.1060
	Near Surface – Surface	0.0186742	0.0785744	-0.174131	0.2114796	0.9694
	Mugilidae					
	Mid-Water – Surface	0.2174856	0.1107491	-0.054270	0.4892410	0.0372[*]
	Mid-Water – Near Surface	0.2113520	0.1107491	-0.060403	0.4831075	0.1522
	Near Surface – Surface	0.0061336	0.1107491	-0.265622	0.2778890	0.9535
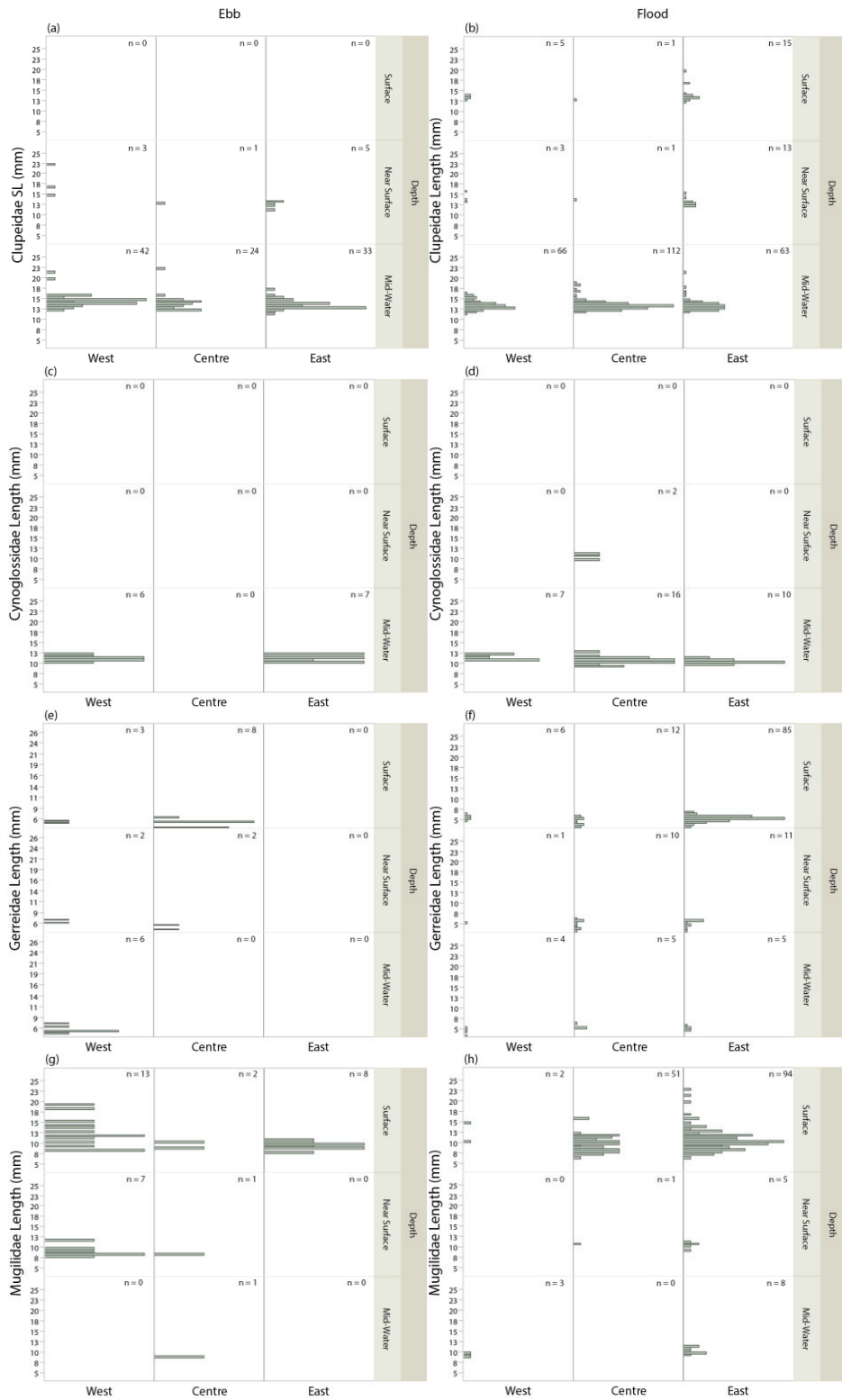
Fig. 8. Length-frequency distribution of fish larvae in three depth strata showing differences between ebb and flood tides samples. Length corresponds to standard length (i.e. measured from the tip of the snout to the end of the notochord).

Table 5
Size range in standard length (mm), standard length means (mm) with standard deviation (SD) of the four taxa of fish larvae collected during ebb and flood conditions, and p value statistic testing for differences in the standard length distribution between ebb and flood conditions.

Taxa	Ebb			Flood			Mann-Whitney U test
	Min.	Max.	Mean (SD)	Min.	Max.	Mean (SD)	*p*-value
Clupeidae	11.25	22.40	14.02 (1.82)	11.88	22.38	13.82 (1.71)	0.0815
Cynoglossidae	10.10	12.48	11.09 (0.61)	9.30	12.68	10.79 (0.83)	0.0614
Gerreidae	4.17	7.08	5.50 (0.76)	3.08	7.08	5.20 (0.67)	0.0679
Mugilidae	7.71	19.17	10.51 (2.75)	6.25	22.80	10.38 (2.43)	0.7286

4. Discussion

The use of estuarine nursery areas is an important phase of the life history of many marine organisms, including many commercially valuable fishes (Boehlert and Mundy, 1988; Haedrich, 1983). Diouf (1996) showed that for the Saloum, it is the downstream part that presents the most important reproductive activities. This is supported by the presence of high larval abundance in the most downstream sections of the Sine Saloum estuary (Sloterdijk et al., 2017), and the early life stages of Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae fishes were dominant in the larval community during this study. Their presence points to the possible importance of the connectivity between the nearshore coastal and estuarine habitats.

Precisely, sampling was designed to test whether fish larvae utilized tidal currents (ebb and flood) for their upstream or downstream transport in the estuary (**Fig. 5 and 6**), and if so, whether the larvae predominantly entered the estuary in a specific horizontal location (West, Centre, and East locations: see **Fig. 1**). For Clupeidae, Cynoglossidae, and Gerreidae, there were no dominating and clear patterns of changes in fish larvae densities (**Table 2**) and larval transport in relation to the tidal condition (**Table 3**). This means that despite some apparent visual differences (e.g. **Fig. 5**) and based on larval transport; in most cases the amount of larvae exiting the estuary during the ebb tide was roughly balanced by the amount of larvae entering the estuary during flood tide. Moreover, no significant change in the vertical position of the larvae was found (**Fig. 7**). With respect to the diurnal variations, a peak of abundance was observed at in the hours preceding the sunset and shortly after (**Fig. 6**), but the shortness of the experiment (~24 hours) did not allow us to observe if the pattern would have persist.

Accordingly, the most plausible interpretation consistent with these observations is that larvae are passively transported by the tidal current. In particular, no support is found in favour of

the selective tidal stream transport (STST) which requires some interplay between vertical migration and the alternating tidal currents. In that respect, our conclusions are similar to those reached by Roper (1986) at the entrance of the Whangateau Harbour, New Zealand where conditions were comparable to ours and no differences were found in the densities of ebb and flood tide catches of several species of fish larvae. This is in contrast with the findings of many other studies conducted in "classical estuaries" where higher catches of fish larvae were generally reported either during ebb or flood tides and characterised as ebb- or flood-tide transport depending upon which phase of the tide is used for transport (see Holt et al., 1989; Joyeux, 2001, 1999; Lyczkowski-shultz et al., 1990; Melville-Smith et al., 1981; Pattrick and Strydom, 2014; Teixeira Bonecker et al., 2009; Tzeng and Wang, 1997).

Compared to current speeds recorded in the Saloum entrance by the ADCPs (**Fig.2**), the swimming ability of fish larvae is, however, of minor importance, limiting their capability to influence their location by horizontal swimming. Therefore a mechanism alternative to STST is needed for fish larvae to be able to preferentially enter or exit the estuary. Based on observed currents and larval distributions, the alternative we hypothesise for larval transport into or out of the estuary results from interactions between vertically sheared low-frequency currents present in the estuary (i.e., ebb/flood tidal currents averaged out) and an appropriate positioning of the larvae in the water column. From a behavioural perspective, this mechanism can be viewed as simpler than STST in that it does not require the organisms to synchronise their vertical migrations with the phase of the tidal currents. The results section described the pieces of evidence, both physical and biological, that support the plausibility of our hypothesis. First, the ADCP data we presented provided circumstantial evidence for the existence of a longitudinal gravitational circulation in the Sine Saloum estuary, as in other inverse estuaries (Hetzel et al., 2013; Nidzieko and Monismith, 2013; Nunes Vaz et al., 1990). This type of vertically sheared circulation is of critical importance in the context of fish recruitment because it offers a natural path into (resp. out of) the estuarine system for organisms that would be able to maintain themselves in the upper (resp. lower) part of the water column. Second, the depth distribution of fish larvae we presented exhibit two distinct patterns that varied depending on the taxon. Clupeidae and Cynoglossidae larvae were almost exclusively distributed in the Mid-Water stratum (**Fig. 7a & b**); Mugilidae larvae were exclusively distributed in the Surface and Near Surface water strata (**Fig. 7d**); likewise, although a bit more broadly distributed in the three water strata, Gerreidae larvae had all their peak densities and highest larval transport in the Surface

stratum (**Fig. 7c**). Again, we stress that no significant changes in vertical distribution of the four taxa of fish larvae with the tidal phase were noticeable (**Table 3**) which rules out that STST type strategies were important for larval transport at the time of the experiment. On the other hand, maintenance into their preferred stratum plausibly led Clupeidae and Cynoglossidae (resp. Mugilidae) larvae to move toward the Saloum mouth and (resp. away from the Saloum mouth). The general transport tendency for Gerreidae larvae cannot be determined with great confidence given their more uniform distribution, but peaks in abundance were systematically close to the surface so their mean displacement may have been into the estuary. For all taxa, it is unclear, however, if the larvae actively maintained their position in the water column or if their specific buoyancy allows them to do so. If the latter is true, the proposed mechanism would be a very efficient and low cost way for fish larvae to move toward their nursery areas.

A caveat concerns the exact position of Clupeidae and Cynoglossidae larvae in the water column. Indeed, lack of vertical resolution in larval sampling does not allow us to distinguish larvae present in the water column away from the surface, where no or very weak gravitational flow is expected, from larvae present adjacent to the bottom where the strongest outflow resides. Another important limitation is that our ADCP and larval sampling data are only for the main Saloum entrance and cover ~ 2.5 tidal cycles during the very end of the warm/dry and low wind period, in July. Caution is thus needed in their interpretation, but less comprehensive observations of salinity (**Fig. 4**) and temperature made during other field experiments (Sloterdijk et al., 2017) taking place at different seasons and in several locations along the Saloum branch of the Sine Saloum estuary offer robust evidence that stratified conditions are prevalent in the estuary. Based on theoretical arguments as well as observations made in other inverse estuaries, we thus expect the vertically sheared gravitational circulation that permits the two-way larval transport between the estuary and the ocean to be a recurrent flow feature. Calm atmospheric conditions (as during the ADCP and larvae sampling period) and neap tides associated with weak oceanic turbulence favour the maintenance of some near-surface to bottom stratification and are generally linked with the presence of vertically sheared gravitational currents in estuaries (Hearn and Robson, 2002; Hetzel et al., 2015; Linden and Simpson, 1986). The only exception was found during the cold season (in Feb. 2014) when fully mixed temperature and salinity vertical profiles were encountered so that the gravitational circulation may not have been present (**Fig. 4a**). Winter conditions when winds are strongest and heat fluxes most prone to intense vertical mixing are expected to stop the gravitational circulation, albeit

perhaps intermittently depending on synoptic variability (e.g., upwelling events or relaxations; Ndoye et al., 2014). For the marine species taking advantage of the inverse estuary gravitational circulation to achieve larval transport in or out of the Saloum, the cold/dry winter season would thus be the one presenting, on average, particularly unfavourable recruitment conditions to be avoided. In the Sine Saloum estuary, Sloterdijk et al. (2017) observed that the seasonal abundance of the Clupeidae, Cynoglossidae, and Gerreidae larvae were lowest in February (winter season), which may be seen as indirect support in favour of this hypothesis. We note that winter reduction in larval abundance might be also due to other factors, for example, low temperatures.

The larval transport tendency we infer from their depth distribution is broadly consistent with the reproductive biology and ecology of several species representative of the Clupeidae, Cynoglossidae, Gerreidae, and Mugilidae, as described in many studies worldwide. For example, several species of adults and juveniles Clupeidae (such as *Ethmalosa fimbriata* and *Sardinalla* spp.) and Cynoglossidae (such as *Cynoglossus senegalensis*) found in the Saloum are abundantly found in the coastal waters outside the estuary and are known to enter estuaries to spawn, where the larvae mature before being gradually transported back toward the coastal environment (Albaret, 1999; Blaber, 2000; Charles-Dominique and Albaret, 2003). Conversely, Mugilidae fishes generally remain in rivers and coastal lagoons during most of their life cycle and leave these areas to spawn at sea (Chang et al., 2000; Koutrakis, 2004; McDonough et al., 2005, 2003; McDonough and Wenner, 2003; Trape et al., 2009). After hatching and a short period of growth, the larvae and juveniles start to recruit at 10–30mm SL into inshore coastal waters, primarily lagoons and estuaries (Blaber, 1997; De Silva and Silva, 1979). As for Gerreidae, most of the adult species occur in coastal system such as lagoon and estuaries bordered by mangroves but spawning occur at sea throughout the seasons with larvae and juveniles entering estuaries until they reach maturity (Blaber, 2000).

The stages of development at which fishes are present in inlets and estuaries may determine their ability to behaviourally alter their transport (Boehlert and Mundy, 1988). Consequently, our study also explored possible relationships between larvae length-frequency distributions, and tidal phase or water stratum of sampling. No significant differences in standard mean length of the four taxa of larvae caught on ebb and flood could be detected (**Table 5**). This indicates that at least within the sampling period, a group of larvae entering the Saloum branch on flood tide did not divide into one size group that was retained in the estuary and another size

group that was transported back toward the entrance of the Saloum during ebb tide, or vice versa. Statistical comparisons of the length-frequency distributions between the water strata were not possible due to the strong depth preferences found for the different taxa resulting in the absence or very low abundance in some of the water strata. In other words, no ontogenic behaviour favouring either estuarine ingress or egress could be detected. This being said, our hypothesis of larval transport without tidal vertical migration could be applicable to larvae of all size and development stage because sensory and behavioural abilities may not be needed, thereby removing the size-dependency associated with STST (Boehlert and Mundy, 1988).

5. Conclusion

The Sine-Saloum is categorized as an inverse estuary and its circulation dynamics suffers from vast knowledge gaps despite some recent progress in the description and understanding of the dynamics of other low-flow inverse estuaries (Largier et al., 1997; Nidzieko and Monismith, 2013; Nunes Vaz et al., 1990). To our knowledge, the ADCP data we presented for the period 9-10 July 2014 are the first current measurements in the area and we are not aware of any previous study measuring simultaneously the estuarine physics (including circulation) and larval transport. Our field experiment revealed that the circulation at the entrance of the Saloum branch of the Sine Saloum estuary was characterized by the existence of a longitudinal gravitational circulation with vertical shear and net near-surface inflow into the estuarine system. In the context of fish recruitment, the general pattern of larval transport into and out of the estuary appeared to have been tied to these characteristics of the flow. None of the taxa of fish larvae that were examined displayed apparent patterns of tide related vertical movement throughout the water column. Conversely, distribution of larvae showed clear and stable depth preferences, thereby allowing them to exploit the gravitational flow to either enter or exit the Saloum branch of the Sine Saloum estuary. The prevalence of the gravitational circulation and the low energy cost for larvae to maintain themselves over a defined depth range vs the desired direction of mean displacement make the proposed larval transport mechanism potentially important most of the year. Especially in the context of increasing pressure, e.g. overfishing and effect of climate change on fisheries in West Africa, the next step should focus on the acquisition of additional inter-seasonal and inter-annual data assessing the variability of the physical

environment and how these variations can modulate the effectiveness of this larval transport mechanism and recruitment success for species dependent upon larval migration into or out of the Saloum. Understanding the processes involved in establishing and modulating this connectivity is of central ecological importance and motivates the investigation of larval transport and its implications for larval survival (Norcross and Shaw, 1984).

Acknowledgements

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Appendix A

Rank by abundance (Rk), abundance (A), percentage contribution to the overall catch (%), and occurrence (O) of the four larval fish taxa in samples collected at the entrance of the Saloum branch of the Sine Saloum estuary. Abundance: total number of individuals. Occurrence: number of samples where the taxon was present. Surface: Neuston Top. Near Surface: Neuston Bottom. Mid-Water: Ring Trawl.

	Total				Surface				Near Surface				Mid-Water			
	Rk	A	%	O	Rk	A	%	O	Rk	A	%	O	Rk	A	%	O
3 Stations Combined																
Clupeidae	1	387	48.9	55/108	3	21	6.8	9/36	1	26	38.2	14/36	1	340	81.3	32/36
Cynoglossidae	4	48	6.1	20/108	4	0	0	0/36	3	2	3.0	2/36	2	46	4.0	18/36
Gerreidae	3	169	20.2	33/108	2	114	37.4	15/36	1	26	38.2	11/36	3	20	4.8	7/36
Mugilidae	2	196	24.8	33/108	1	170	55.8	21/36	2	14	20.6	6/36	4	12	2.9	6/36
West Station																
Clupeidae	1	119	66.5	17/36	3	5	17.2	3/12	2	6	37.5	5/12	1	108	80.6	9/12
Cynoglossidae	4	13	7.3	6/36	4	0	0	0/12	4	0	0	0/12	2	13	9.7	6/12
Gerreidae	3	22	12.2	10/36	2	9	31.0	4/12	3	3	18.7	3/12	3	10	7.5	3/12
Mugilidae	2	25	14.0	9/36	1	15	51.8	7/12	1	7	43.8	1/12	4	3	2.2	1/12
Centre Station																
Clupeidae	1	139	55.6	14/36	3	1	1.4	1/12	2	2	11.1	2/12	1	136	86.1	11/12
Cynoglossidae	4	18	7.2	7/36	4	0	0	0/12	2	2	11.1	2/12	2	16	10.1	5/12
Gerreidae	3	37	14.8	12/36	2	20	27.0	6/12	1	12	66.7	4/12	3	5	31.2	2/12
Mugilidae	2	56	22.4	10/36	1	53	71.6	7/12	2	2	11.1	2/12	4	1	0.6	1/12
East Station																
Clupeidae	1	129	35.6	24/36	3	15	7.4	5/12	1	18	52.9	7/12	1	16	76.2	12/12
Cynoglossidae	4	17	4.7	7/36	4	0	0	0/12	4	0	0	0/12	2	17	13.5	7/12
Gerreidae	3	101	27.9	11/36	2	85	42.1	5/12	2	11	32.4	4/12	4	5	4.0	2/12
Mugilidae	2	115	31.8	14/36	1	102	50.5	7/12	3	5	14.7	3/12	3	8	6.3	4/12

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Chapter III

The importance of the sea surface microlayer as a feeding source for larval and juvenile *Hyporamphus picarti* in the Sine Saloum estuary: stable isotope analysis

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Keywords: sea surface microlayer, fish larvae diet, nursery, stable isotopes, mixing model, Bayesian Inference

Abstract

West African tropical estuaries play an important role in the growth and survival of many commercially exploited fish species and enable the sustainability of considerable artisanal fishery yields. To be in a location that provides high quality feeding habitats is thus of vital importance for larval and juvenile fishes. Unexplored in terms of its potential as an important micro-habitat and food source for fish larvae and juveniles, the sea surface microlayer (SML) represents a unique physical and chemical environment quite different from that of the underlying waters. Here we present the first isotope data derived directly from the SML. At the entrance of the Sine Saloum estuary in Senegal, we have quantified the SML contribution to the diet of *Hyporhamphus picarti* larval and juvenile fish using two variants (δ^{13}C and δ^{15}N) of a multi-source Bayesian mixing model (SIAR). By obtaining statistically distinct δ^{13}C and δ^{15}N isotopic signatures for the SML, we first confirmed its presence at the entrance of the estuary. Second, we found that the SML presented an important food source for *H. picarti* larvae and juveniles, contributing to more than 70% of their diets. Our results underline the importance of the SML and the role of the Sine Saloum estuary as a spawning and nursery habitat for *H. picarti*. This is an important first step to a better understanding of the different roles of the SML providing insights and pushing the SML into a new and wider context that is relevant to fishery sciences and management.

1. Introduction

Recruitment variation in marine fishes can be enormous and consequently has major biological and economic implications for the management of industrial and artisanal fisheries (Leggett and Deblois, 1994). From the time when it became apparent that recruitment fluctuations were largely due to events occurring during early life history, the search for causes of larval and juvenile population fluctuations has occupied an important proportion of the fishery science (Miller and Kendall, 2009). The link between recruitment and abundance/survival during larval and juvenile life stages of marine fishes has since been sufficiently well documented to justify a continued interest in factors regulating survival and abundance during those stages. One of the principal agents of this regulation is hypothesized to be food-mediated mortality occurring during the larval stages. Indeed, starvation have long been considered a major cause in larval mortality (Hjort, 1914, 1926) and accordingly, food production in the sea and other coastal ecosystems, larval feeding behaviour, and nutrition have been the objects of a large amount of research to understand larval survival (Grote et al., 2012; Lehman, 2004; Munk and Kiorboe, 1985; Primo et al., 2017). It follows that inadequate food has commonly lead to starvation or slow larval and juvenile growth, and thereby indirectly increasing their vulnerability to predation and leading to high mortality rates. Consequently, larvae and juveniles rely on the production of particular kinds and amounts of food for their survival.

Estuaries are transitional zones of interaction between land and sea that present a very high level of productivity (Costanza et al., 1997). Because of some of their features, such as high salinity variations, low depths, warm waters, the presence of various and rich habitats, and high food availability; estuaries serve as nursery grounds for many marine fish species (Elliott et al., 2007; Franco et al., 2008; McLusky and Elliott, 2004). They provide critical habitats for species that are valued commercially, recreationally, and culturally. Larvae and juveniles aggregate in these areas where their fitness is enhanced, for example through better feeding conditions and optimal growth (Beck et al., 2001; Laegdsgaard and Johnson, 2001; Nagelkerken et al., 2008; Verweij et al., 2006). For instance, Deegan (1993) states that "estuarine fish faunas around the world are dominated in numbers and abundance by species which move into the estuary as larvae, accumulate biomass, and then move offshore." Clearly, they are important natural places, directly and indirectly providing goods and services that are economically and ecologically indispensable. First, the estuary as a whole was considered to be

the nursery, and only later the focus shifted to specific areas within the estuary. For example, areas of mangrove forests and seagrass meadows were often identified with higher nursery values because evidence suggested that they supported much greater densities of organisms than adjacent unvegetated substrates (Hutchings and Recher, 1974; Minello, 1999; Orth et al., 1984; Turner, 1977).

Unexplored in terms of its potential as an important nursery habitat for fish larvae and juveniles, the sea surface microlayer (SML) represents a unique physical and chemical environment quite different from that of the underlying waters. The SML is the boundary interface between the atmosphere and the water body and is generally defined as the uppermost millimetre of water where its physicochemical and biological properties are measurably distinct from the underlying waters (Cunliffe et al., 2013; Hardy, 1982; Wurl et al., 2017). Sea surface observations by optical imagery indicate that SMLs are a frequent phenomenon, covering large areas of coastal ecosystems and open oceans (John et al., 1984; Romano, 1996). The steep gradient of physicochemical properties across the atmosphere-water boundary concentrates a high amount of organic material in the SML, which attracts a variety of organisms of different sizes. Various microorganisms use this organic matter directly, resulting in planktonic communities in the upper 5 cm of the water column that are significantly different, both in composition and abundance, from those in the layers below (Hardy, 2005). Consequently, depending on the organism or ecological feature of interest, most processes at the SML occur over gradients of varying thickness. Our knowledge on the biology of the SML is still in its beginnings, but Zaitzev (2005) describes the SML and associated near surface layer (down to 5 cm) as an incubator or nursery for eggs and larvae for a wide range of aquatic organisms. Moreover, Sloterdijk et al. (2017) found in the Sine Saloum estuary (Senegal), a distinct larval fish assemblage and different abundances of larvae in the surface layer (down to 10 cm) from those of the underlying water. Yet, the empirical evidences in support of the role and value of the SML as a nursery habitat remain limited. In that sense, food availability and its dietary importance can influence the nursery value of habitats (in this case the SML) and might contribute to explain the very high abundance and distinct composition for certain larval and juvenile fish found in the vicinity of the SML. To the best of our knowledge, the dietary importance of the SML for larval or juvenile fish development has not been yet assessed.

Based on the adage that "you are what you eat", scientists have widely used stable isotopes analysis to quantify the contribution of multiple sources to a mixture, such as

proportions of food sources in an animal's diet (De Niro and Epstein, 1978; DeNiro and Epstein, 1980; Eggers, Jones, 2000; Layman et al., 2012; Phillips and Gregg, 2001; West et al., 2006). The stable isotope ratios of carbon ($^{13}C/^{12}C$, reported as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, reported as $\delta^{15}N$) in animal tissues reflect the isotopic signature of diet and can be used to determine the relative contributions of isotopically distinct food sources to an animal's diet (De Niro and Epstein, 1978; DeNiro and Epstein, 1980; Hobson, 1999; Post, 2002). In trophic interactions, as one species feeds on another one, the consumer tends to be isotopically heavier than its food source, a process called fractionation factor or trophic enrichment (Caut et al., 2009). Consequently, the ratio of stable isotopes of nitrogen ($\delta^{15}N$) can be used to estimate trophic position because the $\delta^{15}N$ of a consumer is typically enriched by 3–4 ‰ at each trophic level (DeNiro and Epstein, 1980). In contrast, the ratio of carbon isotopes ($\delta^{14}C$) changes little as carbon moves through food webs (Peterson and Fry, 1987) and, therefore, typically can be used to evaluate the ultimate sources of carbon for an organism when the isotopic signature of the sources are different. Based on this approach, through stable isotope analysis using diet-mixing model, we looked at the contribution of the SML to the diet of *Hyporhamphus picarti* larval and juvenile fish at the entrance of the Sine Saloum estuary, Senegal.

Our main objective was to gain initial insight into understanding the relative importance of the SML in supporting larval and juvenile African halfbeaks (*H. picarti*), a species that nearly exclusively lives in the SML. Larvae and juveniles of this species are found in very high abundance in the Sine Saloum estuary (our study population) (Sloterdijk et al., 2017) and are exploited commercially throughout the West African coast (Colette, 2016). For this, because sampling the SML for isotope analysis was never done before, we (1) looked if significant differences in stable isotopic signatures between the food sources, namely the sea surface microlayer (SML), the underlying water (UW), and the water column (WC) could be detected (see Materials and Methods section for a description of the water strata and sampling procedures); (2) we looked at ontogenic shift in the isotopic signature of different size classes of the larvae and juveniles (the consumers); (3) and we used a Bayesian mixing model (SIAR) to estimate the proportion of the SML contributing to the larval and juvenile's diet.

2. Materials and Methods

2.1. Study area

The study samples are all coming from the entrance of the Saloum branch (13°55' 13°57' N, 16°44'-16°45' W) of the Sine Saloum estuary, south of Dakar in Senegal (**Fig. 1b**). The estuary plays an important role in the growth and survival of many commercially exploited fish species and enables the sustainability of considerable artisanal fishery yields (Diaw et al., 1993; Diouf, 1996; Simier et al., 2004; Sloterdijk et al., 2017). The estuary has three main branches (Saloum, Diomboss, and Bandiala, from north to south), and a number of seawater channels of different sizes (locally named "bolongs") connecting in a complex manner (**Fig. 1a**). The main channel at the entrance of the Saloum (where the samples were collected) is 10 to 15 m deep (Sloterdijk et al., 2018). No river of significant size currently flows into the estuary. The absence of river inflow, the intense evaporation, and a low gradient in the lower estuary have resulted in seawater incursion, high overall salinity, and a positive upstream salinity gradient. Consequently, the Sine Saloum is classified as an inverse estuary (Pagès and Citeau, 1990; Pritchard, 1967), with salinity level at the mouth slightly higher than that of seawater, but up to 2-3 times higher in the uppermost upstream areas (Diouf, 1996; Simier et al., 2004; Sloterdijk et al., 2017). The region has a Sahelo-Sudanian type climate (Köppen climate classification: BWh) with a rainy season from July to October (where the summer rains provide the only freshwater supply) and a dry season from November to June. The dry season is divided into a cold season from November to March and a hot season from April to June. Mangroves cover almost the entire southern and south-eastern portion of the system and progressively diminish upstream. The main species are from three families: Rhizophoraceae, Verbenaceae, and Combretaceae. Diouf (1996) gave a complete description of climate and environmental conditions in the Sine Saloum estuary.
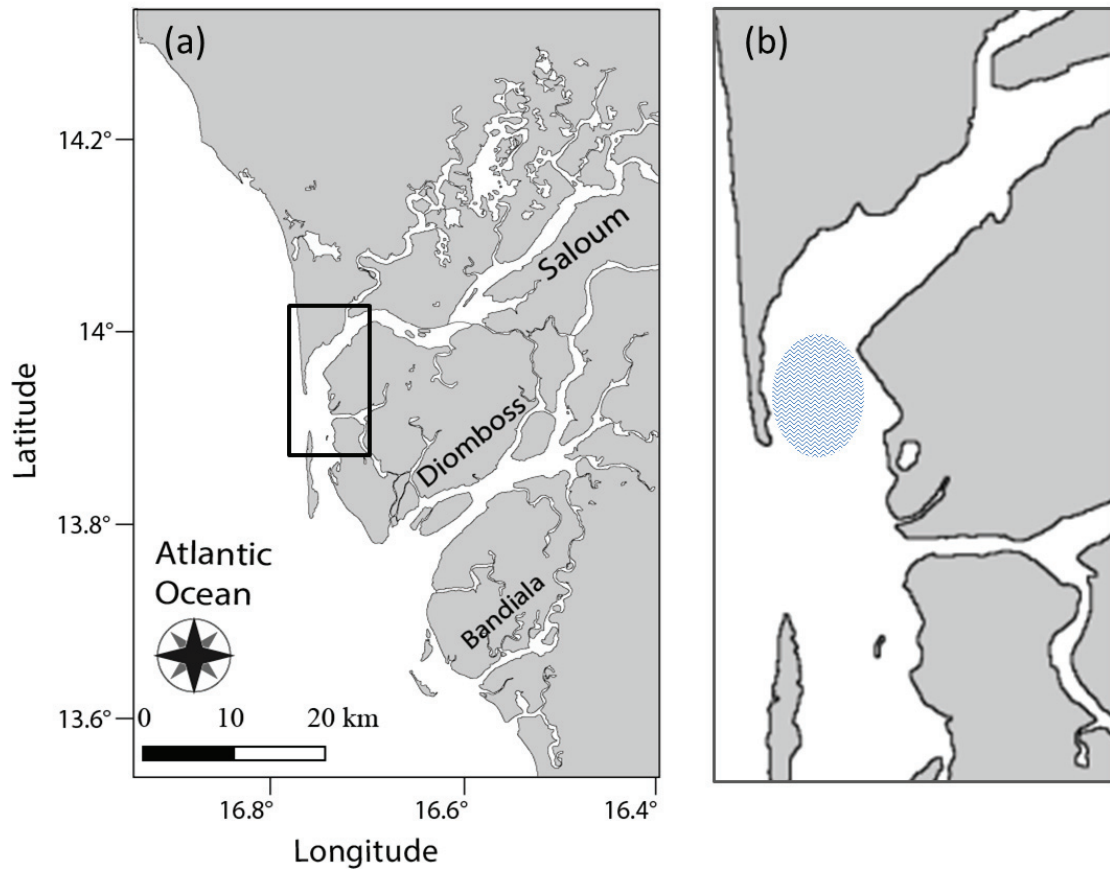
Fig. 1. (a) Location of the study system: Sine Saloum estuary; (b) Map showing the areas (zig zag pattern) where samples were collected.

2.2. Study species

The African halfbeak *Hyporhamphus picarti* (Valenciennes, 1847) is an Eastern Central Atlantic species known from Morocco and Dakar southward along the coast of the Gulf of Guinea to Luanda (Angola) and also from the southern shores of the Mediterranean Sea from Lebanon and Israel and west to Gibraltar (Colette, 2016). Their distributions are limited to inshore waters and they are known to frequently enter estuaries. All along the West African coast, they are exploited commercially and utilized fresh, dried, salted, smoked, and for fishmeal and oil (Bellemans et al., 1988). They are also important bait fish when fishing for marlins, swordfishes, and the like. Adults have an elongated body characterised by a greatly prolonged beak-like lower jaw, hence the name halfbeak. Literature on the biology and ecology of their early life stages is extremely scarce. A recent study has shown that *H. picarti* is the third most abundant species in

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the ichthyoplankton of the Sine Saloum estuary with an all year-round occurrence; peaking especially from February (cool and dry season) to June (warm and dry season) (Sloterdijk et al., 2017). Moreover, their vertical distribution is limited to the surface layer of the water; down to 25 cm, but almost exclusively concentrated in the upper 10 cm. Larvae are well developed at hatching with partially to fully pigmented eyes, an open mouth, fully flexed notochord, developing rays in the dorsal, anal, and caudal fins, and a small to moderate yolk sac (personal observation). During post-embryonic development, *H. picarti* larvae also undergo growth of their lower jaw length. These are thought to be adaptations to access the potential rich food source available in the SML.

2.3. Sample collection

Samples were collected early in the morning during periods of calm wind from the R/V Diassanga, a small experimental fishing/oceanographic vessel of the Institut de Recherche pour le Développement (IRD). Data collection occurred between the 5th and 10th of May 2014 during the warm and dry season shortly after the Harmattan, a season in the West African subcontinent that is characterized by a dry and dusty north-easterly trade wind (of the same name) which blows from the Sahara Desert over West Africa and into coastal and ocean areas. Saharan desert dusts are transported by these winds into the coastal waters providing pulses of nutrients, including iron, to surface waters. These dust depositions are known to be important sources of essential and limiting nutrients and metals to the ocean affecting the oceanic carbon uptake, phytoplankton growth, and productivity (Jickells et al., 2005). Moreover, recent reports also suggest that dust inputs may promote nitrogen fixation, by providing iron and other trace metals (Duarte et al., 2006; Mark Moore et al., 2009). Consequently, the sampling period was chosen accordingly as the SML might be enriched by these depositions, contributing to enhance their special productivity and their high quality food source. Moreover, conditions for a rapid *H. picarti* larval growth appear to be more favourable during this time of the year (Döring et al., 2017).

H. picarti larvae and juveniles were sampled using a custom made paired neuston net stacked on top of each other (opening 30x15 cm, 3 m long; mesh size of 500 μm) and operated from an adapted catamaran (Hobie Cat 15®) deployed in a parallel route of a towing boat

(R/V Diassanga) moving at an average speed of 2-3 knots. In the briefest time possible, larvae and juveniles were removed from the samples, kept in cryogenic vials, and frozen prior to preparation for stable isotope analysis. In the laboratory, unfrozen fish larvae and juveniles were first measured for standard length (SL) using the image analysis software ImageJ (National Institutes of Health of USA, available at www://sb.info.nih.gov/ij/download.html). Subsequently, larvae and juveniles were separated into one of five ontogenic categories based on larval size and attainment of juvenile characteristics: 5-6 mm, 7-8 mm, 9-10 mm, 11-13 mm, and juvenile individuals. Next, stomachs were removed from the fish and used separately for stable isotope analysis of stomach contents. The samples were then dried in a drying oven at 40 ºC for ~ 48 hours and grounded into a fine and homogeneous powder using a combusted mortar and pestle. Lastly, samples of larvae, juvenile, and stomach contents were weighed on a precision balance with a precision of 1 μg.

As proxies of possible food sources for *H. picarti* larvae and juveniles, we used collections of suspended particulate organic matter (SPOM) to obtain the isotopic signature of 3 distinct water strata, namely the sea surface microlayer (SML), the immediate and adjacent underlying water (UW) (2 cm below the SML), and water from the deeper water column (WC) (~ 5 m deep). SML water was collected using a glass plate (Cunliffe and Wurl, 2014; Harvey and Burzell, 1972). For this, a custom-made glass plate (20 x 20 cm by 4 mm thick) was gently plunged through the surface water and withdrawn vertically at a controlled rate of ~ 5 cm s^{-1}. Following sample withdrawal, excess water was allowed to drain for ~ 20 s by holding the plate vertically. The sample was then removed from both sides of the plate directly into a sampling vial (1 litre glass bottle) with a non-contaminating wiper (neoprene squeegee). Cunliffe et al. (2013) estimated that proper use of this technique allows to typically collecting the uppermost 20-150 μm of the surface. This procedure was repeated until the desired amount of sample was collected, i.e. until we obtained (after filtration, see below) filters with rich gold to green colour. For sampling the UW, we used a sterile syringe pump apparatus (Katznelson and Feng, 1998). The apparatus was constructed using 60 ml disposable syringe with Luer-Lok tip (Becton-Dickinson No.309663) and clear PVC Nalgene® flexible plastic tubing (diameter 3.2 mm; Nalge Nunc No.8000-1020). The end of the tubing was plunged at the desired depth (in this case 2 cm below the surface) and only then water was pumped. By doing so, we could get water samples at the desirable depth and avoid contamination by the SML. Once collected, the sample was pumped out into a sampling vial (1 litre glass bottle). As with the SML

method, this procedure was repeated until the desired amount of water was collected. To take samples within the WC, we used a Niskin-Type Plastic Water Sampler (Hydro-Bios® 5 l Model), a relatively simple device that can be opened at both ends. The open bottle was lowered into the water until the desirable depth (~ 5 m) was reached and then the bottle was closed by a weighted trigger that was sent down the cable from the surface.

SML, UW, and WC samples were filtered on pre-combusted (4 h at 450 °C) Whatman® glass microfiber filters (Grade GF/F) and were preserved by freezing them immediately. Afterwards, each filter was oven-dried (~ 48 h at 60 °C), weighed with a precision of 1 μg, and ground to a fine powder prior to isotope analysis.

2.4. Stable isotope analysis

Because of the small size of the individual fish larvae, $\delta^{13}C$ and $\delta^{15}N$ analyses were conducted on several individuals combined. For $\delta^{13}C$ analysis, sub-samples were placed in silver cups (Ag 5x12 mm). To remove non-dietary inorganic carbon contained in calcified structures (e.g. bones), chemical dissolution of the carbonates was done by adding 150 μl 1N HCL (hydrochloric acid) to the samples (Komada et al., 2008). Successively, the cups were placed in a fume hood overnight. Elemental values for carbon and nitrogen were determined with a Euro EA3000 Elemental Analyser. Samples for $\delta^{13}C$ and $\delta^{15}N$ were analysed with a Delta Plus isotope ratio mass spectrometer connected to the Carlo Erba Flash EA elemental analyser via a Finnigan ConFloII interface.

Ratios (R) of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per mil (‰) difference between the samples and international standards (Vienna PDB carbonate and N_2 in air, respectively) where:

$$\delta^{13}C \; or \; \delta^{15}N = \left(R_{sample}/R_{standard} - 1\right) \times 1000 \; (‰)$$

In addition to carbon and nitrogen isotopes from the same sample, continuous flow also reported % C and % N data. Isotope ratio mass spectrometry precision was ~ 0.1 ‰ for carbon and ~ 0.2 ‰ for nitrogen. Lipid extraction was not carried out on samples due to mean C : N ratios being much lower than 3.5 (Logan et al., 2008; Post et al., 2007).

δ^{13}C and δ^{15}N values from sources and consumers were tested for normality and data was analysed for differences between source types (SML, UW, WC), consumer's ontogenic stages (5-6 mm, 7-8 mm, 9-10 mm, 11-13 mm, juvenile), and stomach contents (larvae, juvenile) using JMP® Pro 12.2.1 (SAS Institute).

The diet compositions of *H. picarti* larvae and juveniles were modelled using Stable Isotope Analysis in R (SIAR), a Bayesian stable isotope mixing model that generates probability distributions for prey items based on their relationship with consumer tissue values (Parnell et al., 2010). SIAR models were generated using δ^{13}C and δ^{15}N values for the ontogenic stages (5-6 mm, 7-8 mm, 9-10 mm, 11-13 mm, juvenile), stomach contents (larvae, juvenile), and putative food sources (SML, UW, and WC), all sampled from the entrance of the Saloum branch of the Sine Saloum estuary. Since fractionation values could not be determined from literature sources, consumer's trophic fractionation of δ^{13}C and δ^{15}N were assumed and adjusted to be 1.5 ‰ for δ^{13}C and 3.5 ‰ for δ^{15}N (Cabana and Rasmussen, 1996; DeNiro and Epstein, 1980). No concentration dependence was used and the models were run for 500,000 iterations and the first 50,000 iterations were discarded. Credibility intervals (CI) of 0.95, 0.75 and 0.25 were computed and displayed on figures. Credibility intervals are used in Bayesian statistics to define the domain of a posteriori probability distribution used for interval estimation (e.g., if the 0.95 CI of a contribution value ranges from A to B, it means that there is a 95 % chance that the true contribution value lies between A and B).

3. Results

A total of 128 larvae and 14 Juveniles were used for the stable isotope analyses; ranging in size from 5.33 to 12.85 mm and 39.45 to 50.18 mm standard length, respectively.

3.1. Stable isotope signatures of composite food sources and consumers

Food sources δ^{13}C values ranged from -25.36 to -24.50 ‰ (SML), -23.89 to -23.05 ‰ (UW), -24.65 to -23.78 ‰ (WC) (**Fig. 2a**). We obtained significantly different δ^{13}C food source signatures (Kruskal–Wallis test, $X^2(2) = 15.68$, $p = 0.0004$) and comparisons for each pairs using Wilcoxon method indicated that the SML was isotopically distinct from the UW and the WC. As

a result, the SML was characterized by the most depleted mean (±SD) $\delta^{13}C$ value (-24.86 ±0.34 ‰), followed by the WC (-24.26 ±0.31 ‰), and the UW (-23.48 ±0.32 ‰) (**Fig. 4**). With reference to $\delta^{15}N$ values (**Fig. 2b)**, the SML ranged from 8.14 to 9.13 ‰, the UW from 6.81 to 7.23 ‰, and the WC from 6.93 to 7.71 ‰. $\delta^{15}N$ isotopic signature of the food sources were also statistically different (Kruskal–Wallis test, $X^2(2) = 14.32$, $p = 0.0008$) with the SML being characterized by the most enriched mean (±SD) $\delta^{15}N$ value (8.70 ±0.37 ‰), followed by the WC (7.24 ±0.27 ‰), and the UW (7.03 ±0.22 ‰) (**Fig. 4**). Thus, our results clearly indicate that the SML has its own carbon and nitrogen stable isotope ratios, providing indirect evidences for the presence of its own biological community that is significantly different, both in composition and abundance, from those in the layers below (UW and WC).

Fig. 2. Distribution of (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values obtained for the food sources.

When looking at the consumers, *H. picarti* larvae presented a narrow range of $\delta^{13}C$ values: 5-6 mm (-16.36 to -16.10 ‰), 7-8 mm (-16.52 to -16.41 ‰), 9-10 mm (-16.62 to -16.32 ‰), and 11-13 mm (-16.74 to -16.52 ‰) (**Fig. 3a**). Stomach content samples $\delta^{13}C$ values also showed a narrow range of -21.20 to -21.05 ‰ and -19.45 to -19.16 ‰ for the larvae and juveniles, respectively. Juvenile *H. picarti* $\delta^{13}C$ values were also small but broader than those of the larvae, ranging from -18.18 to -17.03 ‰. With regards to $\delta^{15}N$ values, larvae ranged from: 5-6 mm (11.79 to 12.26 ‰), 7-8 mm (10.18 to 10.22 ‰), 9-10 mm (10.19 to 10.29 ‰), and 11-13 mm (10.12 to 10.20 ‰); stomach content larvae (11.65 to 11.79 ‰) and stomach content juvenile (9.73 to 9.84 ‰); juvenile individuals

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(10.65 to 11.79 ‰) (**Fig. 3b**). The stable δ^{13}C and δ^{15}N mean (±SD) isotope ratios of the consumers were -16.24 ±0.09 ‰ and 12.05 ±0.17 ‰ for 5-6 mm larvae, -16.44 ±0.05 ‰ and 10.19 ±0.02 ‰ for 7-8 mm larvae, -16.55 ±0.13 ‰ and 10.22 ±0.04 ‰ for 9-10 mm larvae, -16.66 ±0.09 ‰ and 10.14 ±0.03 ‰ for 11-13 mm larvae, -17.62 ±0.36 ‰ and 11.23 ±0.36 ‰ for juveniles, -21.12 ±0.06 ‰ and 11.72 ±0.07 ‰ for stomach contents of larvae, -19.32 ±0.12 ‰ and 9.78 ±0.05 ‰ for stomach contents of juveniles, respectively (**Fig. 4**). We observed ontogenetic shifts in δ^{13}C and δ^{15}N values of *H. picarti* (δ^{13}C: $X^2(6) = 40.54$, $p < 0.0001$; δ^{15}N: $X^2(6) = 39.75$, $p < 0.0001$) and comparisons for each pairs using Wilcoxon method indicated that groups were isotopically distinct from one another with the exception of the larval groups 7-8, 9-10, and 11-13 mm, having similar isotopic signatures. Stomach contents of larvae presented the most depleted δ^{13}C values, followed by the stomach contents of juveniles, juvenile individuals, larvae 7-13 mm, and larvae 5-6mm (**Fig. 4**). Enriched δ^{15}N values were highest in larvae 5-6 mm, followed by larvae stomach content, juvenile individuals, larvae 7-13 mm, and stomach contents of juveniles (**Fig. 4**).
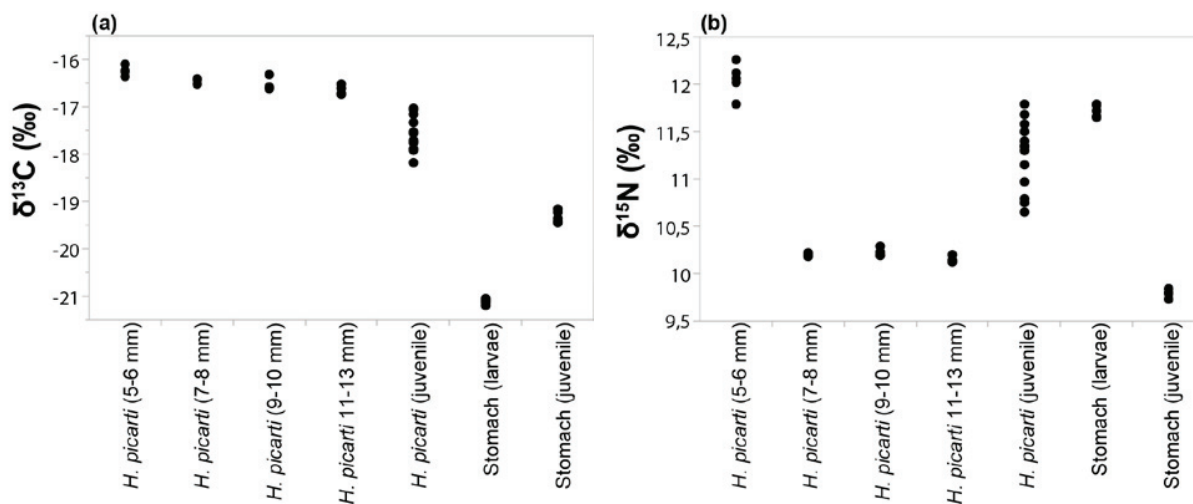

Fig. 3. Distribution of (a) δ^{13}C and (b) δ^{15}N values obtained for the consumers and stomach contents.
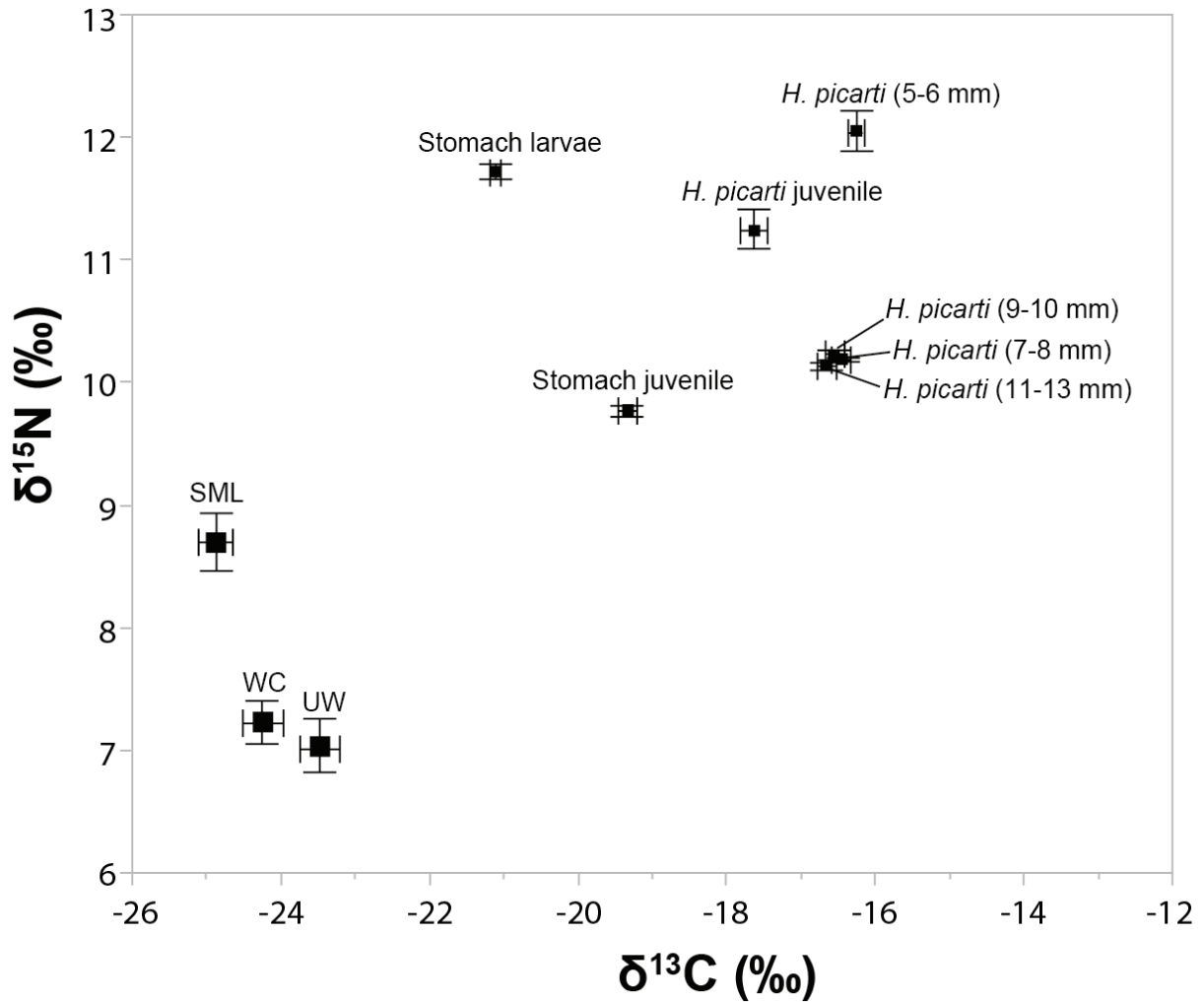
Fig. 4. Stable isotope signatures for the food sources and consumers at the entrance of the Saloum branch of the Sine Saloum estuary. Vertical and horizontal error bars are constructed using a 95 % confidence interval of the mean.

3.2. SIAR results

The food source contributions to *H. picarti* larvae and juveniles diets for the five size groups and for the stomach contents were calculated from stable isotope analysis using two variants ($\delta^{13}C$ and $\delta^{15}N$) of a multi-source Bayesian mixing model (SIAR). The model predicted that the SML comprised the largest diet contribution of the larvae and juveniles as well as their stomach contents, with low percentage contributions of the UW and WC (**Fig. 5**). Mixing model computations (mean ±SD) show relatively equal contributions of SML (38.59 ±1.9 %), UW (31.65 ±1.8 %), and WC (29.76 ±2.0 %) as food sources for the larvae 5-6 mm (**Fig. 5a**). We

then observed an increased and a clear domination of the SML as a contributor to the diet of larger larvae and juveniles. SML contributions were high and very similar for the ontogenic groups of larvae 7-8, 9-10, 11-13 mm; 74.44 ±1.6 %, 74.39 ±1.7 %, and 73.86 ±1.5 %, respectively (**Fig. 5b,c,d**). Similar values were obtained for the juveniles with SML contribution estimated at 69.84 ±2.2 % (**Fig. 5e**). SML contributions to the stomach contents of larvae and juveniles were 57.32 ±1.4 % and 59.08 ±1.2 %, respectively (**Fig. 5f,g**). A detailed summary of the model outputs including the 95 % credibility intervals values are presented in **Table 1**.
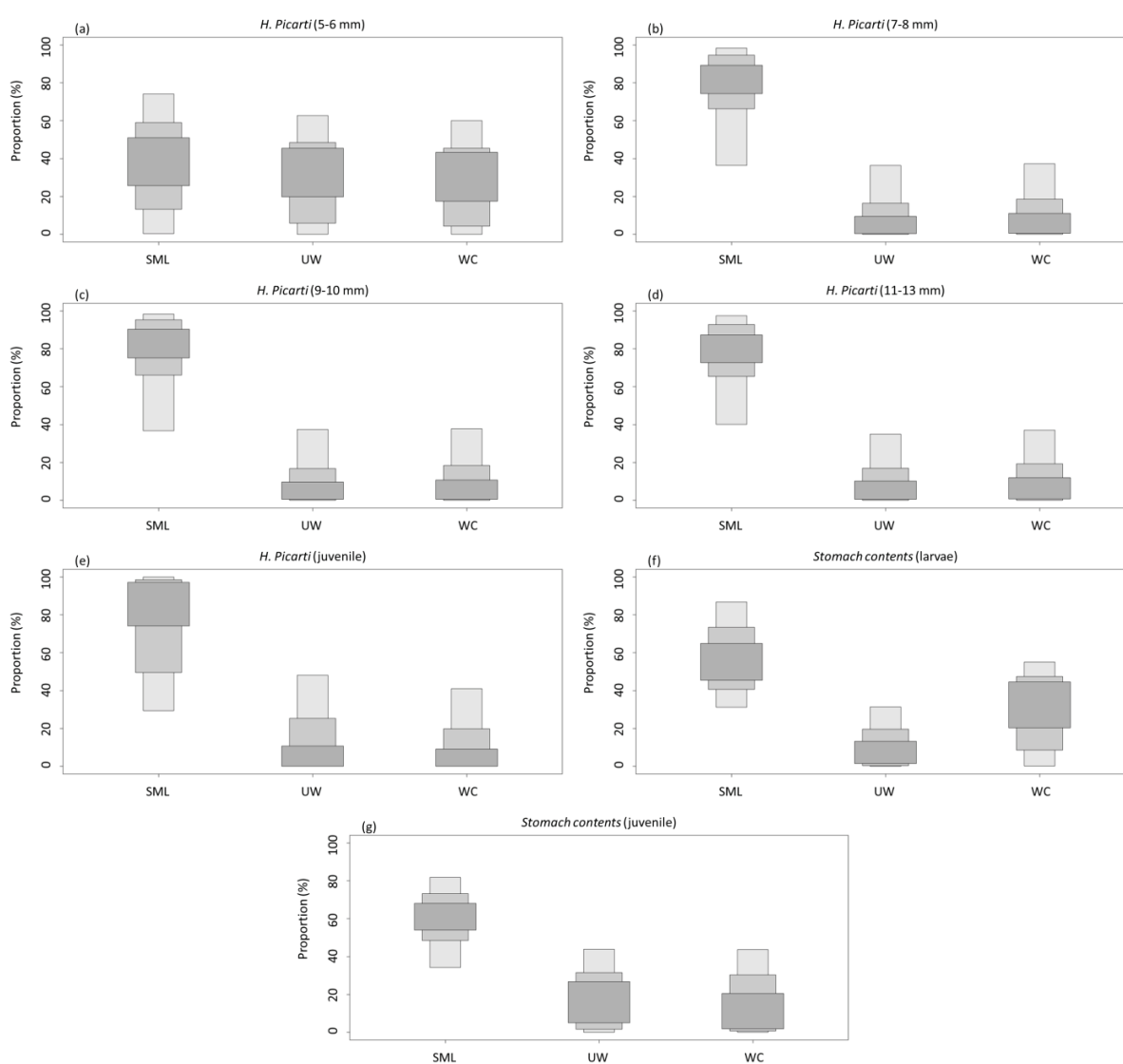

Fig. 5. Boxplot of the proportion (%) of potential food sources for each consumer size group (a: 5-6 mm, b: 7-8 mm, c: 9-10 mm, d: 11-13 mm, e: juvenile, f: stomach contents larvae, and g: stomach contents juvenile) *of Hyporamphus picarti* produced by the SIAR diet-mixing model. The food sources were SML: sea surface microlayer, UW: underlying water, and WC: water column. 0.95, 0.75, 0.25 credibility intervals are in dark grey, light grey, and white, respectively.

Table 1.
Summary of the predicted diet compositions of *Hyporhamphus picarti* larvae and juveniles at the entrance of the Sine Saloum estuary derived from stable isotope analysis using two variants (δ^{13}C and δ^{15}N) of a multi-source Bayesian mixing model. Diet compositions were estimated using SIAR. Mean estimates with 95 % credibility intervals and modes are presented.

	Contribution			
	Low 95 (%)	High 95 (%)	Mode (%)	Mean ±SD (%)
***H. picarti* (5-6 mm)**				
SML	**0.06**	**74.32**	**38.63**	**38.59** ±1.9
UW	0.00	62.92	36.61	31.65 ±1.8
WC	0.00	59.71	33.11	29.76 ±2.0
***H. picarti* (7-8 mm)**				
SML	**38.80**	**98.16**	**81.54**	**74.44** ±1.6
UW	0.00	35.58	2.53	12.18 ±1.2
WC	0.00	37.58	2.71	13.39 ±1.2
***H. picarti* (9-10 mm)**				
SML	36.76	98.42	83.10	74.39 ±1.7
UW	0.00	37.34	0.44	12.39 ±1.2
WC	0.00	38.50	0.59	13.23 ±1.2
***H. picarti* (11-13 mm)**				
SML	40.12	97.47	81.10	73.86 ±1.5
UW	0.00	35.11	2.60	12.51 ±1.1
WC	0.00	36.82	2.52	13.63 ±1.1
***H. picarti* (juvenile)**				
SML	29.48	99.12	90.40	69.84 ±2.2
UW	0.00	48.10	0.77	16.58 ±1.6
WC	0.00	40.67	0.29	13.58 ±1.3
Stomach Contents (larvae)				
SML	30.83	86.28	52.29	57.32 ±1.4
UW	0.00	31.30	4.77	13.35 ±0.9
WC	0.01	55.02	4.75	29.33 ±1.6
Stomach Contents (juvenile)				
SML	35.03	81.70	60.90	59.08 ±1.2
UW	0.00	43.45	16.31	20.88 ±1.3
WC	0.00	42.99	5.28	20.03 ±1.3

4. Discussion

Here we present the first isotope data derived directly from the SML; an important first step towards a greater understanding of its function and derived dietary importance for organisms such as larval and juvenile fishes. We hypothesized that the SML serves as an important food source for *H. picarti* early life stages found at the entrance of the Saloum branch of the Sine Saloum estuary, and to our knowledge, no information existed on the carbon and nitrogen isotopic compositions of the SML and their fate in the associated food web. Representatively sampling the SML is still one of the largest practical challenges in related studies and a tedious task. This may partly explain the little attention and/or attempts towards assessing and quantifying its importance and potential as a food source. Only recently, representative and standardized procedures to sample the SML have been tested, accepted, and detailed by the scientific community (see e.g., Cunliffe and Wurl, 2014). In this study, we have used a glass plate sampler to collect SML samples, based on one of its advantage, as compared to other methods (for example, the mesh screen), of collecting a thinner SML fraction (i.e. 20-150 μm vs 150-400 μm) (Cunliffe and Wurl, 2014; Momzikoff et al., 2004). Therefore, it should have theoretically given a better representation of the biological composition of the SML (Wurl et al., 2017).

Reflecting the origins and biological compositions associated with each of the three water strata sampled in this study, $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures obtained for the SML (**Fig. 4**) were statistically different from those of the underlying water (UW) and those of the water column (WC). Indeed, the identification of these distinct isotopic signatures between the water strata (used as proxies of potential food sources) was crucial to the evaluation of their respective contributions to the larval and juvenile's diet. Consequently, $\delta^{13}C$ and $\delta^{15}N$ well discriminated the SML samples from those of the UW and WC, and these differences were strong evidences for confirming the presence of a SML at the entrance of the Saloum branch of the Sine Saloum estuary, and as mentioned earlier, concomitantly highlighted its distinct origin and biological composition. Although no direct quantitative measurements were made on the biological composition of the SML, qualitative observations of selected samples under a microscope revealed that the SML was characterized as being composed of a variety of micro-organisms such as aggregates of bacteria, protozoans, phytoneuston, micro-zooneuston (auto- and heterotrophic protists such as flagellates, dinoflagellates, ciliates, acantharids, radiolarians, foraminiferans, and metazoans such as copepod nauplii), and detrital matter with relative contributions (life in the

SML is dominated by organisms, which are collectively referred to as "neuston," whereas the term "plankton" is preferred and used for the organisms that inhabit the underlying water column). Therefore, in this study the SML had to be considered as a composite food source. The scientific literature on the biological communities of the SML have mostly focused on the diversity and abundance of "bacterioneuston" assemblages and showed that the species composition and activity can be very different compared to those of the underlying water column (for a review see Cunliffe et al., 2011). Another major biological component of SML is "phytoneuston", historically studied using microscopes (Hardy, 1982), and more recently through high-throughput sequencing (Taylor and Cunliffe, 2014). It has also been shown that "phytoneuston" composition differed from the phytoplankton composition of those in the adjacent underlying water and those of the remaining water column (e.g. Taylor and Cunliffe, 2014). Lastly, "micro-zooneuston" forms the third important biological component of the SML that has been described in the literature (Hardy, 1982). In that sense, by obtaining distinct isotopic signatures, our study is in good agreement with previous studies pointing out the unique and different biological composition of the SML. However, it is important to consider that there is still a large fraction of the living and non-living organic matter collected in the SML that remains to date unidentified, leaving some uncertainties about its total composition.

Among the water strata, the SML was characterized by the most depleted mean (±SD) $\delta^{13}C$ (-24.86 ±0.34 ‰) and also by the most enriched mean (±SD) $\delta^{15}N$ (8.70 ±0.37 ‰). We obtained for both a low standard deviation (SD), which indicates the narrow range of $\delta^{13}C$ and $\delta^{15}N$ values measured for the SML and attest of its well-defined isotopic composition. Direct comparisons of carbon and nitrogen isotopic SMLs' signatures were unfortunately not possible because: (1) we are not aware of other published studies looking at the isotopic composition of the SML and (2) the complicated nature of mixed samples such as SMLs, which comprised a complex mixture of living and non-living organic matter that can include bacteria, phytoneuston, micro-zooneuston, faecal pellets, and other organic detritus such as mangrove derived material (Engel et al., 2017). Consequently, tracing the origin of the SML is complex due to the many potential sources. However, indirect comparison were possible, for example, it is generally accepted that marine phytoplankton from tropical regions shows a $\delta^{13}C$ signal between -18 and -22 ‰ (Fontugne and Duplessy, 1981; Goericke and Fry, 1994), whereas estuarine phytoplankton may be more depleted in ^{13}C due to the uptake of isotopically light dissolved

inorganic carbon (DIC) resulting from the bacterial respiration of terrestrial detritus (Mook and Tan, 1991). Our δ^{13}C values obtained for the SML were generally more depleted than those reported from typical tropical marine phytoplankton, which is not completely unexpected considering the estuarine nature of the Sine Saloum (geographical situation) and the mixed biological composition of the SML. We conclude that because of its relatively depleted values, terrestrial detritus (presumably including mangrove-derived material), dust inputs (possibly Saharan dust), and its mix biological composition are likely to have influenced, directly and indirectly, the isotopic values of the fraction of suspended biological matter that we were able to detect in the SML. Despite our efforts, we were unable to find other sources of information regarding the relative isotopic compositions specific to elements of the microbial loop. Nevertheless, the δ^{13}C composition and qualitative microscopic observations of the SML were still indicative that a variety of organisms contributed to the observed values and that phytoneuston and micro-zooneuston contributions were likely important.

Mean (±SD) δ^{15}N of the SML (8.70 ±0.37 ‰) was higher than those of the UW (7.03 ±0.22 ‰) and WC (7.24 ±0.27 ‰) (**Fig. 4**). Taking an average trophic-level increase in δ^{15}N of 3.5 ‰ for first level consumers (Cabana and Rasmussen, 1996; DeNiro and Epstein, 1980), the observed differences (~ 2 ‰) between δ^{15}N values of the SML and those of the UW and WC were small and did not span one average trophic level. Therefore, these differences could not be completely explained by position dissimilarity in their respective average trophic levels. Variations in δ^{15}N are difficult to resolve for the three water strata because small organisms tend to have fast nitrogen turnovers that often translate in some δ^{15}N variability (Cabana and Rasmussen, 1996; Paasche and Kristiansen, 1982). Moreover, since the biological composition and the environmental conditions in the SML (e.g. higher solar irradiation, greater temperature variability, and its boundary interface between air and water) are different than those of the rest of the water column, δ^{15}N higher values might have been influenced by a number of factors and processes: (1) the source of organic matter and the phytoneuston/plankton specific species composition (Fontugne and Duplessy, 1981; Goericke and Fry, 1994); (2) δ^{15}N uptake by organisms is influenced by their growth rates, and in return, growth rates are affected by factors such as the amounts of sunlight, the water temperature, and the nutrient concentrations (Jones and Stewart, 1969; Laws, 2013), all of which can vary based on its position in the water column; (3) the isotopic composition of the locally available dissolved inorganic nitrogen (Hadas et al., 2009; Owens, 1987); (4) the SML microbial composition differs from the rest of the

water column (Cunliffe et al., 2013) and might have some consequences on the nitrogen cycle (namely nitrogen fixation, nitrification, and denitrification), which in return impacts isotopic fractionation during microbial nitrogen transformation and assimilation by other micro-organism (Owens, 1987); (5) Saharan dust enrichment of the SML might have an effect on the $\delta^{15}N$ as land derived nutrients have been shown to increase $\delta^{15}N$ values (Gritcan et al., 2016; Moore and Suthers, 2005).

Regarding the different *H. picarti* ontogenic groups, the carbon stable isotope ratios ($\delta^{13}C$) showed little differences (**Fig. 4**), giving the first indications that the carbon sources were similar across the whole size range. Especially, the larvae of size 7-8, 9-10, and 11-13 mm clustered together and their values did not differ significantly. We obtained mean (±SD) values that were lowest for juveniles (-17.62 ±1.6 ‰), intermediate for larvae 7-13 mm (-16.55 ±0.13 ‰) and highest for larvae 5-6 mm (-16.24 ±0.09 ‰). Therefore, we did not observed a clear length-dependent shift in $\delta^{13}C$, reinforcing the idea that the larvae continued to feed predominantly on the same food source during their development. Nevertheless, the slightly depleted $\delta^{13}C$ values of the juveniles may indicate the beginning of a change in their food selection or may reflect (giving their older age) a seasonal change of the SML biological composition (Michener and Kaufman, 2007).

When comparing the $\delta^{15}N$ signatures between the ontogenic groups (**Fig. 3b & 4**), larvae of 5-6 mm showed the most enriched values with a mean (±SD) of 12.05 ±0.17 ‰. Because the ratio of stable nitrogen isotopes ($\delta^{15}N$) tends to increase with trophic level (DeNiro and Epstein, 1980; Peterson and Fry, 1987), it might seem counterintuitive to have, among the ontogenic groups, the smallest larvae associated with the highest trophic level. However, these identified specific isotopic differentiations may be explained by a transgenerational transmission of isotopes from the spawning stock to the newly hatched larvae. Even if *H. picarti* newly hatched larvae (5-6 mm) begin consuming the same resource as the older larvae (7-8, 9-10, and 11-13 mm), isotopic composition of their tissues will reflect a mixture of food isotope ratios and isotope ratios at birth, until their tissues turnover and equilibrate to the isotopic composition of their food resource (Pilgrim, 2007). This is because at birth, their tissues are built from maternal resources transmitted in the yolk sac rather than food resources of their immediate environment. Consequently, our results suggest that when evaluating ontogenic shifts in isotopic composition of consumer tissues within the context of a dietary analysis, the isotopic starting point of consumers in the population should always be taken

in context (maternal transmission) and consideration (García et al., 2017). In this case, the observed changes in the δ^{15}N isotopic composition of older larvae relative to the newly hatched larvae (5-6 mm) should not be automatically interpreted as a shift in their resource use, but most likely as a combination of maternal effect and yolk sac absorption. If it is the case, it highlights the biological importance of maternal transmission and may be fundamental for larval survival of *H. picarti* larvae as it transfers nutritional and immunological conditions to the larvae (Green and McCormick, 2005; Marteinsdottir and Steinarsson, 1998; Perez and Fuiman, 2015; Swain and Nayak, 2009).

The isotopic analyses of carbon and nitrogen presented here (**Fig. 5** and **Table 1**) suggested interesting features regarding the importance of the SML as a food source for *H. picarti* larvae and juveniles in the Sine Saloum estuary; a key component for the nursery assessment of this habitat. Although direct evaluation of the contribution of each habitat to adult recruitment is necessary to identify the real nursery value (Beck et al., 2001), our overall results indicate that the SML potentially holds an important contribution to the nursery value of the Sine Saloum for species such as *H. picarti*. This is because the results from our stable isotope measures of *H. picarti* larvae, juveniles, stomach contents, and their potential food sources were applied to the trophic SIAR model and showed substantial contributions of the SML to the diet of larval ontogenic stages 7-8, 9-10, 11-13 mm larvae and juveniles (**Fig. 5** and **Table 1**), contributing on average (±SD) for 74.44 ±1.6 %, 74.39 ±1.7 %, 73.86 ±1.5 %, and 69.84 ±2.2 % of their diets, respectively. These outcomes are good indications that the organisms present in the SML were likely the main energy sources for larvae of size 7-13 mm and juveniles. For the newly hatched larvae (5-6 mm), the situation was not as clear. The SML was to a lesser degree contributing to their diet as the model estimated that they obtained their nutrition more or less evenly from all sources, obtaining on average (±SD) 38.59 ±1.9 %, 31.65 ±1.8 %, and 29.76 ±2.0 % of their nutrition from biological organisms and materials found in the SML, UW, and WC, respectively. It is unclear if the 5-6 mm larvae were indeed feeding on different organisms than the larger larvae and juveniles or if the isotopic composition of their tissues reflected a mixture of food isotope ratios and isotope ratios at birth. Halfbeaks hatch between 4.8-11 mm (Colette et al., 1984) and until their tissues turnover and equilibrate to the isotopic composition of their food resource (García et al., 2017; Pilgrim, 2007), it is possible to obtain values that reflect the retention of a maternal signal rather than clear differences in resource utilisation among the larval ontogenic groups. On one hand, stomach contents of larvae had

intermediate contribution from the SML with an average (±SD) of 57.32 ±1.4 % (**Table 1**), but unfortunately, as the stomach content of 5-13 mm larvae were pooled together prior to the analyses, these estimations could not provide clear or supporting information exclusive to the 5-6 mm larvae. In *H. picarti* juveniles, muscle isotopic turnover rates (i.e. the speed at which this tissue reaches a new isotopic signature equilibrium after a shift to an isotopically distinct diet) are not known and can possibly exceed one month (Carseldine and Tibbetts, 2005; Tieszen et al., 1983). Likewise, we cannot exclude that the isotopic signatures of the juvenile individuals might still partly reflect the ones acquired during their larval life and consequently might overestimate (or alternatively underestimate) the juvenile exploitation of the SML (69.84 ±2.2 %). However, the size range of juveniles used in this study (39.45 to 50.18 mm standard length), their preference for the surface, and their morphology (elongated lower jaws and heavy pigmentation) all points to the utilisation of the SML. So despite the general categorization of adult *H. picarti* as bottom feeder (Colette, 2016), the SIAR model outputs and their larvae and juveniles showed feeding behaviours (by their position in the water column) that are consistent with the idea that they used the rich food source found within the SML. Though, it is not clear yet in exactly what proportion of detritus, bacteria, phytoneuston, or zooneuston were *H. picarti* larvae and juveniles' diets composed of. The literature on the diets of halfbeak larvae is scarce and to the best of our knowledge absent for *H. picarti*. To compare with a close relative, the main food items of the larvae *Hyporhamphus sajori* are reported in a few Japanese studies. Oya et al., (2002) reported that *H. sajori* larvae smaller than 30 mm fed mainly on copepod nauplii and copepodid and larger individuals on copepod and cladocera. Wada and Kuwahara (1994) described their diets mostly composed of the copepod *Euterpina acutifrons*, and cladocera such as *Penilia avirostris*, *E. tergestina*, and *Podon polyphemoides*. Lastly, Yamamoto and Nishioka (1947) reported that the larvae took small crustaceans, especially copepodite and nauplii of copepods, and mollusca larvae. We note that these studies were relying solely on gut content analysis, and because small micro-organisms (e.g. heterotrophic protists) are rapidly digested, it is possible that the contribution of these smaller organisms to the diet and growth of the larvae were underestimated. Heterotrophic protists are part of the microbial loop, which is driven by the recycling of dissolved organic matter by bacteria and the consumption of bacteria and pico/nano size phytoplankton by microheterotrophs. For example, protists can be primary or secondary consumers in the microbial loop, preying on autotrophic and heterotrophic flagellates as well as on cyanobacteria and bacteria. If *H. picarti* larval fish indeed consumed heterotrophic protists

present in the SML during at least part of their ontogeny, they would have effectively been feeding at a higher trophic level than larvae feeding solely on copepod nauplii and copepodites, which feed primarily on phytoplankton, although they may also rely on microzooplankton when phytoplankton are less abundant (Turner, 2004). This may explain the relatively high values of $\delta^{15}N$ obtained for the larvae and for their stomach contents (**Fig. 4**). Although, we recognize that in the case of *H. picarti*, for exact quantifications and to better elucidate their diet compositions, combining traditional stomach content analysis and stable isotope analysis would be required.

With the presence of *H. picarti larvae* in the Sine Saloum estuary throughout all seasons of the year (Sloterdijk et al., 2017), it is possible that SML conditions prevail most the year; a situation that would offers advantageous feeding conditions for species able to exploit this enriched micro habitat. It also seems that *H. picarti* is only using the system during its early life stages as none of the previous studies assessing the ichthyofauna biodiversity in the system have been recording the presence of adults (Diouf, 1996; Ecoutin et al., 2014; Faye et al., 2011; Sadio et al., 2015; Simier et al., 2004), reinforcing the importance of the estuary as a nursery ground for this species. Although other environmental parameters surely have important influences on the early population dynamic of this species (Döring et al., 2017), we suggest that the presence of the SML benefits *H. picarti* larval and juvenile development and survival and is likely to positively influence their growth rate.

Lastly, concerning the model assumptions, even if the commonly assumed values of 3.5 ‰ ($\delta^{15}N$) and 1.5 ‰ ($\delta^{13}C$) approximated the mean fractionation that we would normally expect, the exact variability in fractionation could not have been considered (due to the nature of the SML and because data are completely absent from SML alike samples) and consequently, it is not known how much error the observed variation imparts to our quantitative stable isotope model outputs. Although not presented here, sensitivity analyses of the SIAR model showed, however, that shifts (±1.5 ‰ for $\delta^{15}N$ and ±0.5 ‰ for $\delta^{13}C$) in the trophic fractionation factors did not markedly change the outcome of the model. While sensitivities in models such as the present one must be considered and choosing the correct isotopic fractionation is important in diet reconstruction (Bond and Diamond, 2011), the resiliency of our SIAR model to shifts in fractionation factors points to and reinforce our confidence concerning the importance of the SML to the diet of *H. picarti* larvae and juveniles at the entrance of the Saloum branch of the Sine Saloum estuary. The model is similar in principle to IsoSource (Phillips and Gregg, 2003) but allows all sources of uncertainty such as in the sources or trophic fractionation values to be

propagated through the model to return a true probability distribution of estimated dietary proportions of mass-balanced solutions (**Table 1**) from a nominated set of possible contributions (Phillips and Gregg, 2003). Moreover, Parnell et al. (2010) argued that this approach based on Bayesian inference is also able to avoid the limitations linked to variability within sources and among samples. Thus, our SIAR estimates of the dietary composition of *H. picarti* are likely robust, even if the system was undetermined as it is likely that some of the potential sources were missing.

5. Conclusion

Recent studies now indicate that the SML covers the ocean and coastal areas to a significant extent, and evidence shows that it is an aggregate-enriched biofilm environment with distinct biological communities. In this paper, by obtaining statistically distinct $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures for the SML, we confirmed its presence at the entrance of the Sine Saloum estuary (Senegal). Subsequently, we have evaluated its contribution to the diet of *Hyporhamphus picarti* larval and juvenile fish, by use of a Bayesian stable isotope mixing model (SIAR). Overall, we found that the SML presented an important food source for *H. picarti* larvae and juveniles, contributing to more than 70% of their diets. Our results underline the importance of the SML and the role of the Sine Saloum estuary as a spawning and nursery habitat for *H. picarti*. This study is a contribution to a better understanding of the different roles of the SML. Moreover, it provides insights and pushes the SML into a new and wider context that is relevant to fishery sciences and management.

Acknowledgements

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Synoptic Discussion

For several decades, the rainfall deficit experienced by the Sahelian zone has strongly disturbed the West African estuarine ecosystems and in particular the Sine Saloum estuary in Senegal. The most obvious changes of the environment are unquestionably the inversion of the salinity gradient, the hypersalinization of the upstream zones, and the associated mangrove degradation. Underlying these peculiarities, a key question motivated and served as a common thread in this thesis: **have these environmental changes affected the estuary's ecological function of nursery for fishes?** By looking at components such as the larval diversity and community structure, transport of larvae in and out of the system, and feeding value of the sea surface microlayer, this thesis gain knowledge on a variety of important and complementary environmental/physical factors influencing the diversity and distribution of the ichthyoplankton; thereby the nursery quality of this estuary for fishes. Importantly, knowledge gain in this thesis is not only relevant in the West African regional context, but also throughout the dry tropics as it is expected that such transformations are on their way or will be in the near future for several estuaries (Pagès and Citeau, 1990; Ridd and Stieglitz, 2002). In that sense, the Sine Saloum served as a case study for understanding and estimating future changes in estuaries vulnerable to similar environmental transformations.

At the beginning of this thesis, published literature about larval fishes in the Sine Saloum estuary was practically non-existent and consisted of one paper on the molecular identification of larvae of the order Clupeiformes (Durand et al., 2010). Considering the economic and ecological importance of this estuarine system, the difficulty of identifying fish larvae is probably one of the causes for this lack of data. Indeed, studies of the abundance and diversity of fish larvae were completely lacking, thus what was first needed was baseline information on the utilization of the inverse estuary by early life stages of fishes; and a comparative approach with other tropical mangrove estuaries has been adopted. In this thesis, I have reported three features of the Sine Saloum larval fish community structure that are common to what is reported in many comparable studies in "undisturbed" tropical mangrove estuaries: (1) the larval fish community is comprised of a few species in large numbers and many rare species in low numbers, (2) Clupeoid and Gobioid larvae are one of the most abundant taxa in the catches, and (3) salinity, water temperature, and dissolved oxygen were important factors associated with larval fish abundance and diversity. (e.g. Barletta-Bergan et al., 2002; de Morais and de Morais, 1994;

Tzeng and Wang, 1992; Yoklavich et al., 1992). However, other aspects of the larval fish community structure differed considerably and I have identified five important differences with other tropical mangrove estuaries: (1) the ichthyoplankton community's total number of families and species in the Sine Saloum estuary (24 families and 43 species) is significantly lower, (2) fish larval richness is decreasing with increasing distance from the open ocean, (3) the abundance of larvae is pointedly higher in the lower estuary and declined with distance upstream, (4) in terms of bioecological categories, the larval community is essentially composed of species of marine origin and characterized by the complete absence of species of freshwater origin, and (5) larval fish assemblages do not differ much throughout the year as they are mostly composed of the same taxa between the seasons.

Despite some recent progress in the description and understanding of the dynamics of other low-flow inverse estuaries (Largier et al., 1997; Nidzieko and Monismith, 2013; Nunes Vaz et al., 1990), no comprehensive measurements on the Sine-Saloum circulation dynamics were available prior to this thesis. Moreover, this thesis has presented the first study measuring simultaneously the estuarine physics (including circulation) and larval transport in an inverse estuary. There has been a long history of investigating larval transport by fishes in "classic estuaries" that experience substantial freshwater inputs year-round, where rates and directions of larval transport are mediated by depth preferences of larvae and the timing, duration, and amplitude of their vertical migrations (e.g. Fukuda et al., 2016; Gibson, 2003; Kunze et al., 2013; McCleave and Kleckner, 1982; Morgan, 2006). Again adopting a comparative approach with what was observed in "classic estuaries"; for the period where the measurements were made, I have identified major differences concerning the physical and behavioural processes mediating larval transport between the estuarine waters and the open coast: (1) the Sine Saloum circulation at the entrance of the Saloum branch is characterized by the presence of a longitudinal gravitational circulation with positive vertical shear, i.e., near-surface (resp. near-bottom) waters exhibit more pronounced inflow (resp. outflow) velocities, and (2) none of the taxa of fish larvae that were examined have displayed apparent patterns of tide related vertical movement throughout the water column, and their distributions have shown clear and stable depth preferences. Therefore, no support was found in favour of a selective tidal stream transport mechanism (Boehlert and Mundy, 1988) and in the context of successful recruitment, an alternative mechanism is needed for fish larvae to be able to preferentially enter or exit the inverse estuary. Based on the observed currents and larval distributions, I propose that suitable

larval transport into or out of the estuary results from interactions between the longitudinal gravitational circulation with positive vertical shear currents and an appropriate positioning of the larvae in the water column. I have demonstrated that the vertically sheared circulation offers a natural path into (resp. out of) the estuarine system for organisms that are able to maintain themselves in the upper (resp. lower) part of the water column and have shown that different taxa are remaining in a specific position of the water column leading to a directional transport into the estuarine waters (ingress) or out of the estuary (egress). From a behavioural perspective it can be viewed as simpler than selective tidal stream transport in that it does not require the organisms to synchronise their vertical migrations with the phase of the tidal currents.

Unexplored in terms of its potential as an important contributor of the nursery value of a habitat for fish larvae and juveniles, the sea surface microlayer (SML) represents a unique physical and chemical environment quite different from that of the underlying waters (Wurl et al., 2017). As an important first step towards a better understanding of its function and derived dietary importance for organisms such as larval and juvenile *Hyporhamphus picarti*, in this thesis I have presented the first isotope data derived directly from the SML and showed: (1) the presence of a well-defined SML at the entrance of the estuary, and (2) that microorganisms contained in the SML are the major food source for *H. picarti* throughout the larval and juvenile stages, contributing to more than 70 % of their diets.

Based on the above mentioned findings, I have demonstrated that compared to undisturbed tropical mangrove estuaries, the Sine Saloum has undergone clear modifications that are reflected in the structure of the ichthyoplankton community and in the estuarine circulation. However, a holistic view of the overall results still gives arguments for the presence of circumstantial environmental and physical factors that contribute to the overall nursery value of the Sine Saloum estuary for local fishes. There are a number of key considerations on the variables that should be accounted when accessing the nursery value of an area and Beck et al., (2001) proposed that the term nursery implies a special place for early life stages of marine organisms where functions and processes such as density, connectivity between early life stages and adults habitats, and growth are enhanced over those in adjoining habitat types. Based on this premise, these three aspects were highlighted in the results of this thesis and serves as arguments in support of the attribution of some nursery values of the Sine Saloum estuary: (*density*) larval densities were high throughout the year in the lower part of the estuary, (*connectivity*) the circulation dynamic at the mouth of the Saloum branch offers a natural pathway in and out of the

estuary, and (*growth*) the presence of the sea surface microlayer provides a rich food source that is likely to enhance growth for species able to exploit it such as the very abundant *Hyporhamphus picarti*. Ideally, these specific ecological processes operating in the Sine Saloum estuary would be compared with other estuaries in the region to assess and quantified their respective contribution to adult recruitment. However, at the moment direct comparisons of these aspects are difficult due to the general absence of data and the lack similar studies in West African estuaries. In that sense, I propose that because of the variety of estuary types and lagoons (Albaret, 1999, 1987), West Africa is a privileged setting for studying these processes on the early life stages of fishes.

The preservation of the nursery function of the Sine Saloum is strongly influenced by the environmental and physical factors acting on the diversity and distribution of its early life stages of fishes and salinity is an important limiting factor for fish larvae in the system. In high-salinity environments, a reduction of the adult ichthyofauna biodiversity and modifications of species composition have already been reported (Vega Cendejas and Hernández De Santillana, 2004; Simier et al., 2004; Diouf, 1996; Albaret, 1987; Severin-Reyssac and Bertrand Richer de Forges, 1985). Thus, in environments subjected to significant stress such as the high salinity in the case of the Sine Saloum, a very severe selection of species should be expected and this thesis shows that these reduction and modifications are also reflected in the diversity and distribution of the ichthyoplankton, and that larval assemblages are not distributed randomly in the system. In the lower part of the Sine-Saloum, moderate salinities allow the development of a relatively species rich and abundant ichthyoplankton. On the other hand, high salinity conditions have drastically limited the number of species and the abundance of larval fishes. Accordingly, in the Sine Saloum, fish larvae that are the most abundant throughout the year and present in most areas are composed of a small selection of species belonging to families such as Clupeidae, Gerreidae, Hemiramphidae, Mugilidae, and Cynoglossidae. A likely key to their success, they belong to species able to adapt their eco-physiological abilities (Potter and Hyndes, 1999) and some of their life history attributes (Albaret, 1987; Simier et al., 2004). These are part of a reduced group and are in accordance to the "resistance community" first identified in the inverse estuary of the Casamance River by Albaret (1987). So although the diversity is relatively low in this system, these species are able to tolerate the high salinity conditions and may benefit from the absence of strong interspecific competition (Larkin, 1956), enabling them to thrive in great numbers. Moreover, Diouf, (1996) claimed that the abundance of juveniles made up about 85 %

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of the Sine Saloum fish population with relatively strong year-round reproductive activities for representative of the above mentioned families. These are also part of the most common families of fishes in West African estuaries (Albaret, 1999; Haedrich, 1983) and are also targeted by the artisanal fisheries (Campredon and Cuq, 2001). This can be seen as an encouraging sign for the development of other estuaries where similar elevated salinities are predicted in the near future (Ridd and Stieglitz, 2002), thus mitigating the negative impacts of such environmental transformations.

The mangrove is a dominant feature of undisturbed tropical and subtropical estuaries around the globe (FAO, 2003). Whereas it is generally agreed that mangrove ecosystems absorb and transform nutrients and are inhabited by a variety of organisms, and although there is a general scientific consensus that mangroves are important nursery areas, to this day, opinions vary as to the exact importance of the mangrove habitats for fishes and by extension for mangrove fisheries (Faunce and Serafy, 2006; Nagelkerken et al., 2008). The results presented in this thesis did not show a particularly higher larval abundance in the mangrove-rich parts of the estuary. For example, relatively low concentrations were consistently found in sites with rich mangrove cover, while high concentrations where observed in sites where mangrove cover was poor such as at the entrance of the Saloum branch. This suggests that the presence of mangrove alone cannot provide optimal conditions for the fish larvae in the Sine Saloum estuary. Similarly, Vidy (2000), reported that good estuarine conditions alone are sufficient for good nursery function but mangrove alone is not.

This thesis, by describing indirect effects of climate change on the environmental and physical factors affecting the diversity and distribution of larval fishes in the Sine Saloum estuary, may give insights to the effect of regional climate change in other inverse estuaries along the West African coast and throughout the world. Its relevance comes from the situation that considerable decrease in water runoff in some major rivers of West Africa have already resulted in the intensification of seawater intrusion processes for other estuaries such as the Senegal and the Casamance rivers (Mikhailov and Isupova, 2008), but also globally, water bodies that exhibit inverse estuarine characteristics across a variety of scales and times are becoming more and more common and examples include: northern Gulf of California, Mexico (Lavín et al., 1998); Laguna San Ignacio, Mexico (Winant and Gutiérrez de Velasco, 2003); Spencer Gulf, Australia (Nunes-Vaz, 2012); and Shark Bay, Australia (Hetzel et al., 2015). It is difficult to forecast the future situation and to quantify the amplitude of changes for other estuarine systems, but with a certain

degree of confidence it is likely that their larval fish communities will face similar shifts in their diversity and abundance. However, to a certain extent, oceanographic information at relatively fine spatial scales is probably of critical importance because of the known role of the oceanographic structure in shaping populations and assemblages of adjacent coastal ecosystem (Woodson et al., 2012). The Sine Saloum estuary is located within the Senegalo-Mauritanian East border upwelling system, considered one of the most productive coastal waters in the world. Various studies have established that upwelling-driven nutrient supply is the key factor regulating chlorophyll concentration and primary production off NW Africa (Auger et al., 2016; Lathuilière et al., 2008; Messié and Chavez, 2015; Ohde and Siegel, 2010). So the Sine Saloum may benefit from the high productivity of its coastal waters, a situation that might help to compensate or buffer the effect of some of the degradation taking place in the estuary. This might not be the case for other estuaries in a different geographical context, for example situated next to less productive and poorer coastal waters. Even if we do not have a clear understanding of the roles of geographical location of the estuaries in community resiliency and stability, the results of this thesis may be broadly applicable to coastal upwelling systems along the western margins of continent and in arid climates where small, shallow, low-flow estuaries are common (Largier, 2002). Thus, the validity and the predictive power of this thesis could be reinforced by continuing similar studies in other inverse estuaries and at other times.

The fast rate of global change raises questions about the consequences for biodiversity in terms of species diversity, distributions, and community structures (Walther et al., 2002). In the context of climatic change and the resulting environmental transformations that have been taking place in the Sine Saloum estuary, knowledge of local adaptation and adaptive potential of natural populations is becoming increasingly relevant. Divergent natural selection due to transformation of the environment is expected to promote adaptive evolutionary responses (Kawecki and Ebert, 2004). In the dominant larval fishes identified in this thesis, adaptation to salinity conditions is probably of high importance throughout pre-recruit life from the egg to the juvenile phase. The concern is that other species have been negatively affected by increasing salinity without the capacity to adapt. In that sense, salinity-related adaptability in traits related to early life history are expected to be particularly important in the dominant larval fishes found in inverse estuaries. For future research, I propose to investigate populations of species of Clupeidae, Gerreidae, Mugilidae, and Cynoglossidae for evidence of adaptations in early life-history traits to their local environments, especially salinity regimes. For this, detailed and

comparative studies on the physiological and ecological traits of the early life stages of these species are missing and should be carried. This could be achieved with studies looking at their trophic ecology, nutritional condition, and daily growth rates focusing on the associated environmental conditions. Moreover, metabolic rates to estimate minimal energy requirements and the response of respiration rates to high salinity concentrations can help to better determine salinity tolerance of larval and juvenile key species (Hettler, 1976; Ismael and Moreira, 1997). However, it should be noted that adaptive responses to climate change in traits related to phenology, such as spawning time differences, may be at least as important as adaptability in early life-history traits, and a comprehensive assessment of the evolutionary potential of populations should ideally include both types of traits. Lastly, in 'inverse estuary' systems the longitudinal density gradient, and thus density-driven circulation, seems to be often weaker than in classic estuaries with freshwater input (Largier, 2010). Although not addressed in this thesis, given the additional anthropogenic pressure and intense use of estuaries, this can be an additional cause of concern as it can increase their vulnerability to ecological problems such as accumulation of pollutants. Therefore, pollutant related studies in inverse estuaries should be justified and implemented in the near future.

Particularly important in the context of the potential impacts of global climate change on fish populations, especially in high latitudes that are experiencing some of the most rapid and severe changes, I hope that the information contained in this thesis helps to address the dearth of information on early life history characteristics and their specific connections to new prevailing climatic and environmental conditions, and hopefully contributes to the development of meaningful ecological frameworks for predicting population responses to these environmental changes.

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In loving memory of my Mom,
Carole Bois Sloterdijk
❤️

Eidesstattliche Erklärung

Gemäß §6 der Promotionsordnung der Universität Bremen für die mathematischen, natur- und ingenieurwissenschaftlichen Fachbereiche vom 14. März 2007 versichere ich, dass die vorliegende Arbeit mit dem Titel,

„Environmental and Physical Factors Affecting the Diversity and Distribution of the Ichthyoplankton in an "Inverse Estuary", the Sine Saloum (Senegal)"

1. Ohne unerlaubte, fremde Hilfe angefertigt habe,
2. Keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutz habe,
3. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Ebenfalls erkläre ich hiermit, dass es sich bei den vor mir abgegebenen Arbeiten um drei identische Exemplare handelt.

Universität Bremen

Bremen, Juni 2018

Hans Sloterdijk