

Spatial–temporal variation of *Achirus* larvae (Actinopterygii: Achiridae) in mangrove, beach and reef habitats in north-eastern Brazil

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The genus Achirus is made up of demersal fish that have a close relationship with the substrate and exhibit peculiar aspects during their larval stage. The aim of the present study was to determine whether the abundance of Achirus larvae differed among a set of habitats in the estuary of the Formoso River in the State of Pernambuco (north-eastern Brazil). Sampling was performed monthly between April 2009 and March 2010, and comprised horizontal hauls with plankton net during the day and night in mangrove, beach and reef habitats. Fish larvae were sorted, identified, measured and larval stage recorded. Density and body length values were used in a non-parametric analysis of variance for the determination of variations between seasons, habitats and diel periods. A total of 204 larvae were collected, with an average density of 2.1 larvae.100 m⁻³. Density was greater in the nocturnal samplings, with no differences found between habitats. The larvae occurred in the yolk-sac to post-flexion stage, with pre-flexion the most abundant stage (78%). Size segregation was observed. Larger larvae were captured at night and in the mangrove. The smallest larvae were caught on the reef, with length increasing toward the mangrove. The results indicate that Achirus larvae come from deeper regions near reefs, where spawning probably occurs, and perform ontogenetic migration towards the shallow waters of mangrove, where they settle.

Keywords: coastal habitats, larvae, flatfish, tropical

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INTRODUCTION

The family Achiridae is made up of species of small fish that mainly inhabit coastal zones of tropical and subtropical seas (Munroe, 2002). Like other representatives of the Pleuronectiformes, the group is known to exhibit peculiar life history aspects, especially during the early stages of development, with a pronounced metamorphosis in comparison to other teleosts and a movement from a pelagic to benthic habitat (Geffen *et al.*, 2007). The plankton larvae initially have a symmetrical, laterally compressed body, with the subsequent migration of the left eye, a change in the position of the gut and an increase in the pigmentation on the eyed side (Richards, 2006). Achiridae larvae also have a deep body, large gut, a peculiar cephalic bulge and large eyes and maxilla (Ahlstrom *et al.*, 1984).

Following the complete metamorphosis of the planktonic larva, the organism passes to the juvenile phase and settles on the nursery habitat (Van der Veer & Leggett, 2005). The change to this habitat is influenced by behavioural patterns that begin in the larval stage, such as vertical migrations

synchronized with the tide, which can lead to either retention or export to more favourable environments for larval development (Bailey *et al.*, 2005). The attributes of the habitat, such as the type of substrate and structural complexity, also influence distribution patterns (Moles & Norcross, 1995), settlement (Walsh *et al.*, 1999) and feeding habits (Florin & Lavados, 2010) in the early phases of Pleuronectiformes. Also, the survival and dispersion of these organisms is reported to be affected by hydrographic conditions (Yamashita *et al.*, 2001).

The genus *Achirus* (Lacépède) encompasses four species described on the Brazilian coast: *A. achirus* (Linnaeus, 1758), *A. declivis* Chabanaud, 1940, *A. lineatus* (Linnaeus, 1758) (Menezes *et al.*, 2003) and *A. mucuri* Ramos, Ramos & Lopes, 2009 (Ramos *et al.*, 2009). However, only *A. lineatus* has been characterized with regard to its larval development (Richards, 2006), which is valuable information for the identification and differentiation of individuals collected in this phase. The scarcity of studies describing the different larval stages hinders the identification of larvae in plankton samples and leaves a gap in the knowledge on the ecological aspects of these larvae, such as their abundance and spatial–temporal distribution.

In different estuaries along the Brazilian coast, Achiridae larvae account for a significant proportion of the ichthyoplankton community (Barletta-Bergan *et al.*, 2002; Bonecker *et al.*, 2007; Sarpedonti *et al.*, 2008). However, no studies have yet recorded data and focused on the larval ecology of

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these individuals. Moreover, ichthyoplankton surveys on Brazilian coastal ecosystems have mainly been carried out in estuarine areas with muddy bottoms associated with mangroves (e.g. Mafalda Jr *et al.*, 2008), and there is less information about fish larvae on reef (Nonaka *et al.*, 2000) and beach (Godefroid *et al.*, 1999) habitats.

The aim of the present study was to carry out the first description of the spatial–temporal distribution patterns of *Achirus* larvae at a tropical coastal system in north-eastern Brazil, including mangrove, beach and reef habitats. The following were the main points addressed: (1) does larval density differ between coastal habitats?; (2) are there size and larval stage segregation among these environments?; and (3) is there a correlation between density variations and abiotic variables? This study attempts to provide information that can support the understanding of seasonal and daily density patterns, as well as the influence of habitat characteristics on the distribution and settlement of these organisms.

MATERIALS AND METHODS

Study area

The present study was carried out in the lower region of the estuarine complex of the Formoso River, which is formed by the confluence of the Formoso, Passos, Ariquindá and Lemenho Rivers. The complex covers about 2724 hectares and is located in Rio Formoso municipality, 92 km from Recife, the state capital of Pernambuco (north-eastern Brazil). The estuary is divided into three different zones (upper, middle and lower), each one with particular biotic and abiotic characteristics (Lira *et al.*, 1979; Silva *et al.*, 2004; Paiva *et al.*, 2009). North-eastern Brazil has two distinct seasons—a rainy season from March to August and a dry season from September to February. The rainy season is accompanied by an increase in primary production, and can be characterized by eutrophic conditions in the estuary (Silva *et al.*, 2004).

Three distinct habitats were chosen for ichthyoplankton sampling—mangrove, beach and reef (Figure 1). Located within two Marine Protected Areas (MPAs: Costa dos Corais and Guadalupe), the habitats sampled cover a distance

of 6 km. A total of 185 fish species have been recorded in Costa dos Corais MPA (Ferreira & Cava, 2001), including *Achirus lineatus* and *A. declivis* among the Achiridae (Paiva *et al.*, 2009). The mangrove habitat, mainly composed of *Rhizophora mangle*, *Laguncularia racemosa*, *Avicennia schaueriana* and *A. germinans* (Nascimento-Filho *et al.*, 2007), is located on the left margin of the estuary, in a small creek known as Maria-Açu. This site represents a tidal channel flanked by mangrove plants, which provide significant structural complexity through its roots, with a substrate of fine mud rich in organic matter. On the right bank of the estuary is located Carneiros Beach, selected as the beach habitat. This site has a sandy substrate with patches of macroalgae and seagrass meadows, composed mainly of *Halodule wrightii*, and is considered an intermediate habitat. The meadows act as shelter for estuarine and reef fish recruits, functioning as a corridor between the other ecosystems (Pereira *et al.*, 2010). The reef habitat is located at the Formoso River mouth, forming part of a complex set of reef formations parallel to the coastline. Among the 105 fish species recorded in the Tamandaré reef, located offshore the Formoso River (Ferreira *et al.*, 1995), 40 were recorded in the adjacent estuary and have been considered to play a structuring role on the estuarine community (Paiva *et al.*, 2009).

Sampling

Sampling was carried out on a monthly basis between April 2009 and March 2010 during the day and at night, with triplicates in the three habitats studied, totalling 216 samples. In order to begin the nocturnal collections at dusk and operate under adequate navigation conditions, especially on the reefs, such collections were only performed during the low neap tide. The ichthyoplankton hauls were performed horizontally at the subsurface with 500 μm mesh plankton net. The net was hauled at a constant speed of approximately two knots for 10 minutes and the filtered volume was estimated with a flowmeter attached to the centre of the mouth of the net. Temperature ($^{\circ}\text{C}$), salinity, pH, dissolved oxygen ($\text{mg}\cdot\text{l}^{-1}$) and local depth (m) were measured at the surface during each haul, using portable monitors. No salinity data were collected in May 2009 or March 2010 and no oxygen

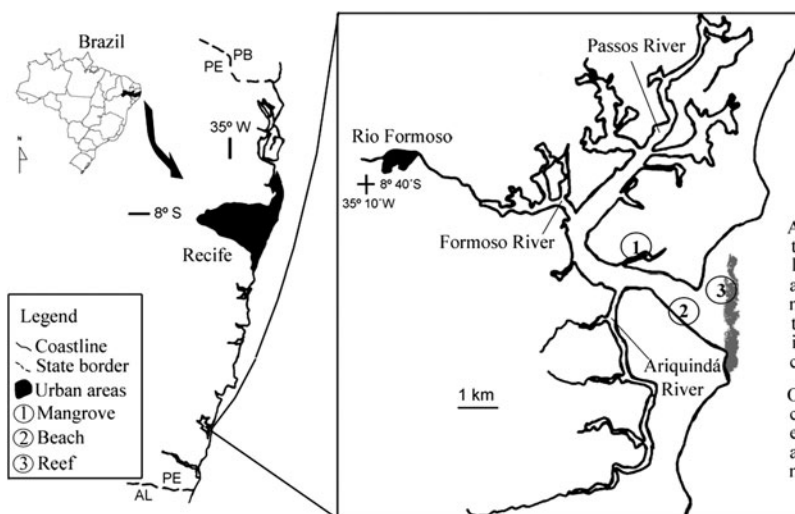


Fig. 1. Estuarine complex of the Formoso River, with indication of sampled mangrove, beach and reef areas.

data were collected in February or March 2010, as the necessary equipment was unavailable. Data on monthly rainfall at the Tamandaré station over the study period were from the databank of the Pernambuco Meteorology Laboratory.

Fixation of the samples was achieved with the addition of formalin solution buffered with calcium carbonate and diluted in seawater to a final concentration of 4%. In the laboratory, the material was sorted under a stereomicroscope, with the larvae identified, body length (BL) measured and larval development stage determined, based on Kendall *et al.* (1984). *Achirus* larvae were distinguished from other larvae of the family through the unique traits of the genus that distinguish it from *Trinectes*. These include the presence of an elongated third dorsal ray and a cephalic foramen in the intermediate and advanced stages as well as the absence of pigmentation in the early stages (yolk-sac and beginning of pre-flexion) (Ahlstrom *et al.*, 1984; Richards, 2006). The total number of larvae in each sample was determined and abundance values were converted into density values, expressed as larvae.100 m⁻³.

Data analysis

Density and BL values were considered in the analysis of spatial-temporal distribution. The fixed factors were habitat, period of the day and seasons. The data were standardized and transformed ($\log_{10} x + 1$) before statistical procedures. Variables normality was tested using the Kolmogorov-Smirnov-Lilliefors test (Zar, 1999) and homoscedasticity was determined using Bartlett's test. As the prerequisites for analysis of variance were not met, the variables were submitted to non-parametric tests: Mann-Whitney for the analysis of differences between periods of the day and seasons; and Kruskal-Wallis for the analysis of differences

among habitats. Results with P values < 0.05 were considered significant. The Scheffé's test was used as a *posteriori* analysis to determine what mean values were significantly different. Associations between environmental variables and larval density were determined using Spearman's non-parametric correlation test. This test was only considered as an exploratory analysis, as it is subject to generating results with random positive correlations.

RESULTS

Hydrographic conditions

The depth of the collection sites ranged from 0.8 to 14.9 m. The reef habitat was the deepest (mean depth: 6.0 ± 3.1 m) while the beach and mangrove habitats were shallower (mean depth: 1.95 ± 0.7 and 1.30 ± 0.5 , respectively). Mean temperature during the sampling period was 28.42°C . The lowest temperatures occurred between May and August (mean: 27.1°C) and the highest occurred in February and March (mean: 30.18°C). This parameter varied significantly only between seasons ($P < 0.0001$) and was higher in the dry season (mean: 29°C). No significant variation in temperature was found between periods of the day or habitats.

Mean salinity was 30.78, ranging from 26 in June to 36 in November. Salinity values were higher in the dry season ($P = 0.0049$) in the daytime samples ($P = 0.0294$) collected from the beach and reef habitats ($P < 0.0001$). Monthly distribution of mean precipitation was inversely correlated to salinity, with rainfall greater than 200 mm recorded between April and August (rainy season) (Figure 2).

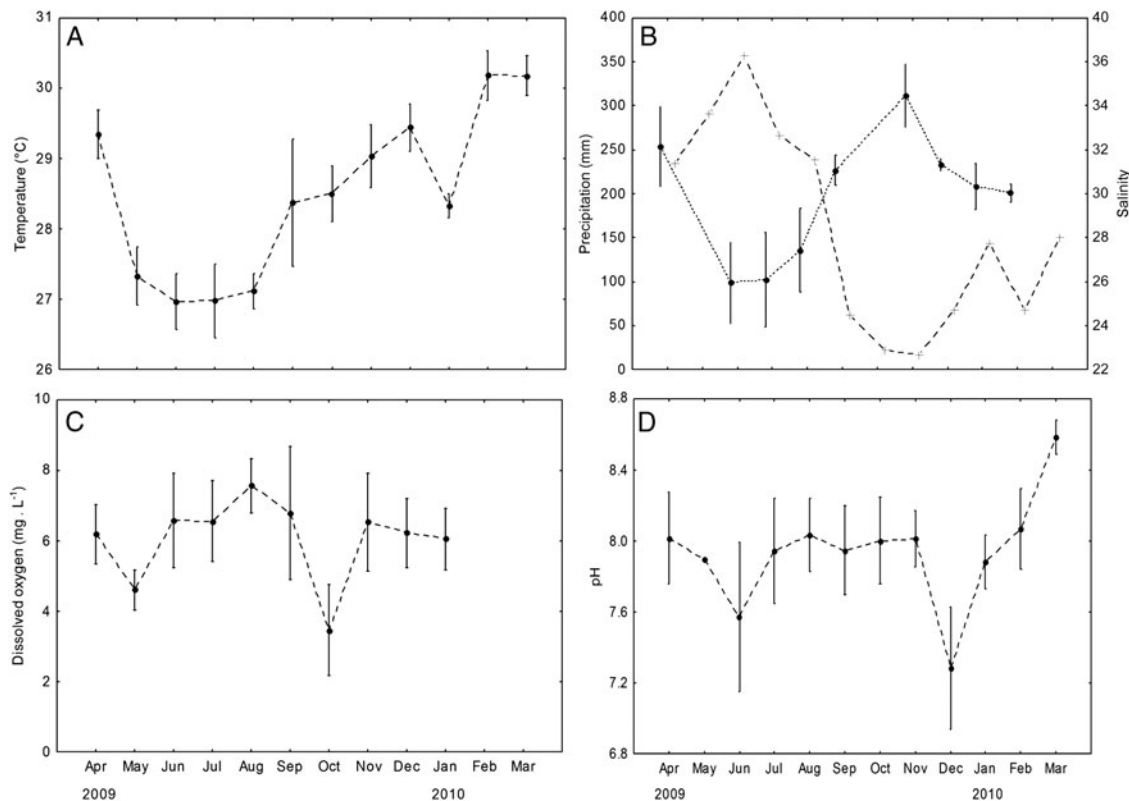


Fig. 2. Mean and standard deviation values for abiotic variables in different estuarine habitats of the Formoso River, Pernambuco, Brazil (— + —, precipitation).

The mean concentration of dissolved oxygen in the water was highest in August (7.58 mg.l^{-1}). Higher concentrations occurred during the day ($P = 0.0247$), with a mean value of 6.25 mg.l^{-1} . Between habitats, the lowest concentration was recorded in the mangrove samples, reaching 5.01 mg.l^{-1} , whereas the reef habitat had the highest values (mean: 6.82 mg.l^{-1} ; $P < 0.0001$).

The pH values ranged from 6.32 in December to 8.71 in March, with higher values occurring in the rainy season (mean: 7.97), although no statistically significant difference between seasons was found ($P = 0.1125$). The mangrove habitat had the lowest pH values (mean: 7.8) and the other habitats had mean values greater than 8.0 (Figure 2).

Density of larvae

A total of 204 *Achirus* larvae were collected, with a mean density of $2.1 \pm 4.92 \text{ larvae.100 m}^{-3}$ per haul. Density values were significantly different between months ($P = 0.0001$), with a maximum of $31.28 \text{ larvae.100 m}^{-3}$ in December 2009 and a minimum of $1.36 \text{ larvae.100 m}^{-3}$ in April 2010. Density also differed significantly between seasons and period of the day (Table 1). Mean density ranged from $0.83 \text{ larvae.100 m}^{-3}$ in the rainy season to $3.34 \text{ larvae.100 m}^{-3}$ in the dry season ($P < 0.0001$). The results of the Mann–Whitney test indicated significant differences between periods of the day ($P < 0.0001$), with mean larval abundance of $3.46 \text{ larvae.100 m}^{-3}$ in the nocturnal samples and $0.74 \text{ larvae.100 m}^{-3}$ in the daytime samples. No significant differences in total density values were detected between habitats ($P = 0.1478$), but a greater mean value was recorded in the reef ($3 \text{ larvae.100 m}^{-3}$), followed by the beach ($2.07 \text{ larvae.100 m}^{-3}$) and mangrove habitat ($1.23 \text{ larvae.100 m}^{-3}$). Among the hydrographic variables measured, larval density was only positively correlated to temperature ($r = 0.2$; $P < 0.05$) and salinity ($r = 0.2$; $P < 0.05$).

Larval stages and variations in length

All larval development stages of *Achirus* were found throughout the sampling period. Ten per cent were yolk-sac, 78% were in pre-flexion, 4% were in flexion and 8% were in post-flexion. The percentage participation of stages was similar among habitats, since the mean proportion of each stage did not differ significantly among them. In each habitat the stage proportion was uneven. In the mangrove ($P = 0.003$) the *post-hoc* test distinguished the post-flexion (33%) and pre-flexion (58%) stages as the most representative. On the

beach ($P = 0.001$) and reef ($P = 0.001$) habitats the mean proportion of pre-flexion larvae was 60 and 58%, respectively.

Analysis of variance revealed significant results regarding density per larval stage only for the pre-flexion and post-flexion stages (Table 1). The pre-flexion stage was more abundant in the dry season ($P < 0.0001$) during nocturnal collections ($P = 0.0005$) carried out in the reef and beach habitats ($P = 0.0430$). Significantly different values in post-flexion density were detected only between periods of the day ($P = 0.0086$), with greater mean values recorded during the nocturnal collections, whereas no differences were found between habitats or seasons (Table 1). However, there was a general tendency toward greater mean density of post-flexion larvae in the mangrove ($0.33 \text{ larvae.100 m}^{-3}$), whereas the lowest values were recorded in the reef habitat ($0.1 \text{ larvae.100 m}^{-3}$) (Figure 3).

Considering the peak density values in the different larval stages, the early stages (yolk-sac and pre-flexion) were more abundant in the reef habitat. There was a general increase in larvae during the nocturnal collections (Figure 3), although a high number of larvae in the pre-flexion stage was collected in the mangrove during the day ($P = 0.0322$). The flexion stage was distributed more evenly among the habitats, with peak density values in the nocturnal collections in the dry season and no differences between habitats. Greater density values of post-flexion larvae were found in the mangrove, with higher values in the dry season. On the mangrove and beach habitats, post-flexion larvae were caught exclusively during the nocturnal period.

Body length ranged from 1.4 to 4.5 mm (mean: $2.2 \pm 0.64 \text{ mm}$), with higher values found in the rainy season ($P = 0.0362$). Significant differences were found between periods of the day ($P = 0.0178$), with a mean value of 2.5 mm in the nocturnal samples versus 1.9 mm in the daytime samples. Significant differences were also found between habitats ($P = 0.0320$), with the largest sizes collected from the mangrove (Figure 4).

DISCUSSION

Ichthyoplankton in estuarine regions is dominated by estuary-dependent species, which find potential nursery areas in this ecosystem due to its favourable biotic and abiotic attributes (Reyier & Shenker, 2007). Many of these species, including Pleuronectiformes, are known to exhibit ontogenetic migration from spawning areas to estuaries (Bailey, 1997).

Table 1. Mean larval density and significance levels for non-parametric Kruskal–Wallis (habitat) and Mann–Whitney (period of day and season) analyses of variance of log densities of Achiridae collected between April 2009 and March 2010.

	Habitats				Seasons			Periods		
	Mangrove	Beach	Reef	P^*	Dry	Rainy	P^{**}	Day	Night	P^{**}
Total	1.23 ± 3.53	2.06 ± 3.86	2.99 ± 6.65	0.217	3.34 ± 6.08	0.83 ± 2.85	<0.001	0.74 ± 2.85	3.46 ± 6.06	<0.001
Yolk-sac	0.03 ± 0.30	0.14 ± 0.57	0.36 ± 1.71	0.219	0.25 ± 1.40	0.10 ± 0.52	0.731	0.05 ± 0.33	0.30 ± 1.45	0.114
Pre-flexion	0.71 ± 3.33	1.62 ± 3.72	2.38 ± 6.10	0.043	2.68 ± 5.74	0.46 ± 2.60	<0.001	0.60 ± 2.77	2.55 ± 5.71	<0.001
Flexion	0.04 ± 0.38	0.10 ± 0.50	0.11 ± 0.43	0.268	0.13 ± 0.52	0.04 ± 0.33	0.089	0.05 ± 0.36	0.12 ± 0.50	0.095
Post-flexion	0.32 ± 1.12	0.19 ± 0.88	0.08 ± 0.42	0.518	0.22 ± 0.90	0.18 ± 0.81	0.783	0.03 ± 0.26	0.36 ± 1.16	0.008

P^* , Kruskal–Wallis test; P^{**} , Mann–Whitney test; SD, standard deviation.

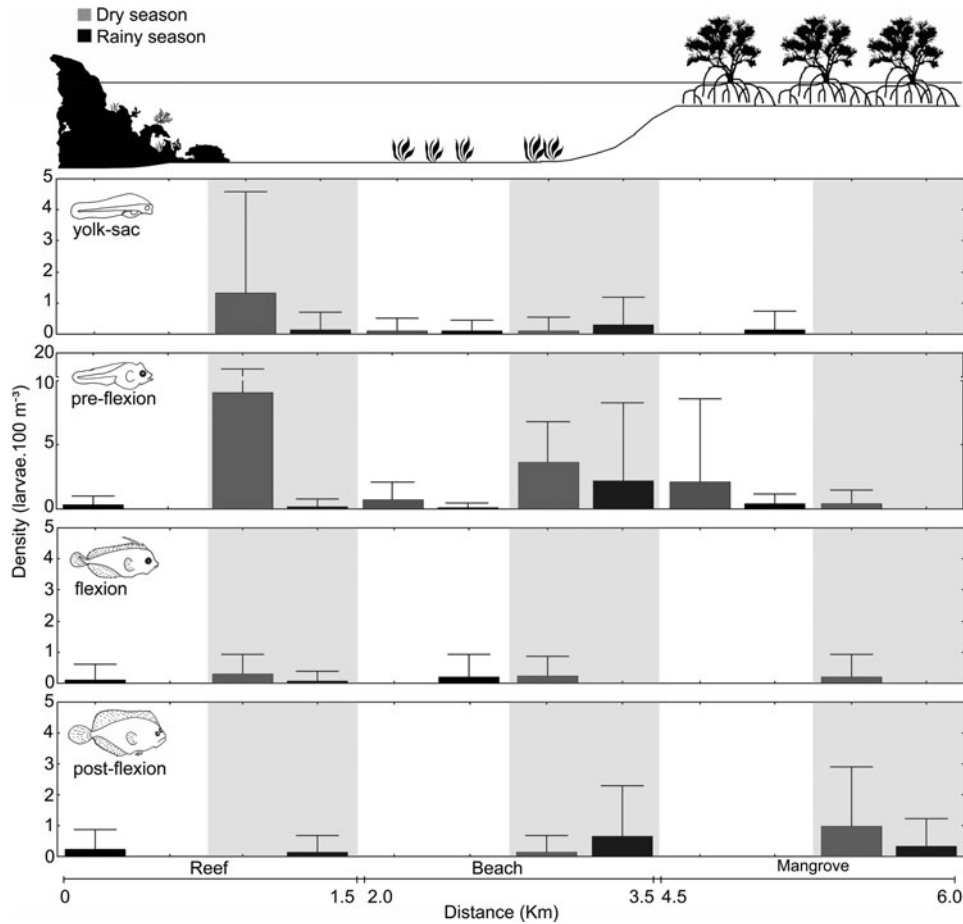


Fig. 3. Density of different larval stages of *Achirus* collected from different estuarine habitats of the Formoso River, Pernambuco, Brazil (shaded, nocturnal period; non-shaded, daytime).

In tropical Brazilian estuaries, Achiridae larvae are frequent in ichthyoplankton samples and, in some cases, may figure among the most abundant taxa (Barletta-Bergan *et al.*, 2002; Barletta & Barletta-Bergan, 2009). Among the species of *Achirus* that occur on the Brazilian coast, only *A. lineatus* and *A. declivis* are recorded for the estuary of the Formoso River (Paiva *et al.*, 2009), although Araújo *et al.* (2004) also cite *A. achirus* for the north-eastern region of the country. The lack of information on the diagnostic characteristics of the larval forms of *Achirus* occurring in the studied area (Richards, 2006), render it difficult to affirm what exact species the present study addressed.

The occurrence of larvae throughout the year indicated that spawning activity was continuous in the estuarine complex of the Formoso River, with a likely peak in

December. In the estuary of the Caeté River (northern Brazil), *Achirus* also predominated in this month, which occurs in the dry season, with higher temperature and salinity values (Barletta & Barletta-Bergan, 2009). While there is little available information on the life cycle of Achiridae, fish from this family are known to exhibit more intensive spawning activity when the water temperature is above 20°C (Futch, 1970). Temperatures above this value were recorded in the present study, which may explain the occurrence of early-stage larvae in nearly every month. The only exception was June 2009, when there was a lower larval density, a month occurring in the rainy season.

High temperatures lead to an increase in growth rate, resulting in an increase in size at metamorphosis for some species (Geffen *et al.*, 2007), whereas high temperatures accelerate metamorphosis in other species, leading to a smaller size at metamorphosis and shorter larval period (Yamashita *et al.*, 2001). In any case, spawning in hotter seasons favours larval development and survival. Moreover, high salinity may also contribute to a greater density of larvae in the early stages. In species of sole which spawn in offshore waters and exhibit migration toward coastal areas in the larval phase, laboratory experiments have indicated that early-stage larvae do not tolerate low salinities, but pre-settlement larvae do (Burke *et al.*, 1995; Yamashita *et al.*, 2001). The data obtained for the studied area lend support to these observations, as the reef habitat, which is the furthest ecosystem from the coast, had

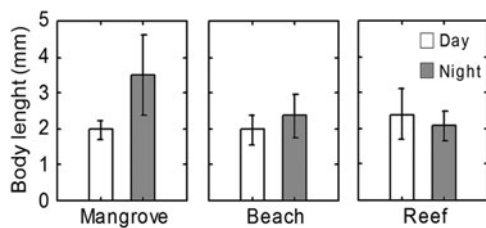


Fig. 4. Mean and standard deviation of body length values of *Achirus* larvae collected from different estuarine habitats of the Formoso River, Pernambuco, Brazil.

the greatest density of newly-hatched and pre-flexion larvae. This high occurrence prevailed in the dry season and the nocturnal period.

Under favourable hydrographic conditions, a synchrony is often reported to occur between the hatching of the larvae and the plankton production cycle, which increases the survival of the pelagic eggs and larvae (Rijnsdorp *et al.*, 1995). However, comparing the larval density data in the present study with peak primary production reported in studies by Silva *et al.* (2004, 2009) carried out in the same estuary, this synchrony is not apparent. Thus, plankton production may not be a limiting factor for these larvae in the area in question, likely due to the fact that it is a quite productive estuary (Silva *et al.*, 2009) and has a high amount of biomass throughout the year.

Larvae carry out vertical circadian migrations, concentrating at the surface at night and migrating to the bottom during the day. This behaviour is known for many fish larvae as a strategy for feeding and/or escaping from visual predators and may be associated with selective tidal stream transport (STST), which is a strategy for either exportation or retention through vertical migrations synchronized with the tide (Boehlert & Mundy, 1988). A number of studies have documented this behaviour, such as the retention of the larval forms of *Achirus* species, which migrate to deeper layers during the ebb tide (Aceves-Medina *et al.*, 2008) or are more abundant during the flood tide, suggesting transportation upstream (Barletta & Barletta-Bergan, 2009). The estuarine region of the Formoso River is an inlet, with considerable penetration of tide and often with a relatively low fluvial influence (Lira *et al.*, 1979), with no vertical salinity stratification, except in the innermost portions during the rainy season (Silva *et al.*, 2004). This condition stems from the strong influence of the ocean and may favour the retention of larvae in the water column in the estuarine zone. In this case, vertical migrations may be triggered mainly by the photoperiod rather than tidal variations. In the mangrove, larval density was not significantly influenced by the period of the day, although greater mean values were found in the daytime period. It is likely that the greater number of larvae captured in this environment was due to the turbidity of the water, greater in the mangrove area than the reef one (Silva *et al.*, 2009), which reduces visibility and, consequently, net evasion (Lemke & Ryer, 2006).

Nearly 90% of the larvae collected were in the yolk-sac and pre-flexion stages of development, with the latter accounting for 78% of the total. The predominance of larvae in the early stages is a common finding due to the direct relationship between the duration of larval period and mortality rate (Van der Veer & Leggett, 2005). Pre-flexion larvae were more abundant in the reef and beach habitats and at night. This corroborates the pattern observed by Able *et al.* (2006); these authors studied ichthyoplankton on the coast of the state of New Jersey (USA) and found that 77% of the pre-flexion larvae were collected from coastal sites and 90% of the post-flexion larvae were collected from the estuary. In the present study, most pre-flexion larvae were collected from the reef and beach environments, whereas post-flexion larvae were mainly collected from the mangrove. As larval development period is approximately one month for some species of *Achirus* (Ortiz-Galindo *et al.*, 1990; Flores-Coto *et al.*, 1992), no seasonal pattern (dry or rainy season) was related to the occurrence of different stages. However, a larger number of newly-hatched larvae arrived to the first ecosystem they inhabit (the reef) in the dry season. Salinity is lower during

the rainy season, which favours the survival of larger larvae (Yamashita *et al.*, 2001). The largest larvae caught in the estuarine complex of the Formoso River occurred in the rainy season, although at a lower density in comparison to the dry season.

With growth, fish larvae become less dependent on the currents, but may still benefit from the STST in the search for an appropriate habitat (Gibson, 1997). However, the change in habitat will only occur after the development of the structures necessary for survival. There is evidence to indicate that the period of the ontogenetic habitat shift is more related to body size than development phase (Fuiman, 1997), which do not always coincide. The gradual increase in the length of the larvae from the reef toward the mangrove is an indication of their migration from the spawning area to their likely settlement habitat. Among the habitats investigated, the reef had the greatest concentration of larvae, especially those in the early stages. It is likely that the hatching of these individuals occurs in deeper waters of the adjacent marine environment, with favourable currents allowing the eggs and larvae to drift towards the coast.

In the study area, the juvenile ichthyofauna occurring in the seagrass meadows off Carneiros Beach have been surveyed, but no Achiridae juveniles were found (Pereira *et al.*, 2010). Similarly, a survey carried out in an adjacent reef area found no specimens of this family (Ferreira *et al.*, 1995). Small juveniles of *Achirus lineatus* and *A. declivis* have been reported from the innermost areas associated with the mangroves (Paiva *et al.*, 2009), suggesting that these mangroves are a potential nursery for species of *Achirus*.

One may infer that migration between ecosystems and consequent population connectivity occurs during pelagic larval stages. The duration of the egg and larval stages must coincide with the transport period necessary to ensure metamorphosis (Van der Veer & Leggett, 2005). Thus, the pelagic larval stage of Pleuronectiformes is more critical to the survival of the individual than the juvenile and adult phases, as settlement in the benthic habitat occurs in specific nurseries (Gibson, 1997). The duration of the pelagic phase in some species of the family is rather short—generally not surpassing 30 days before the settlement of the individuals (Ortiz-Galindo *et al.*, 1990; Flores-Coto *et al.*, 1992). Moreover, many pelagic larvae of flatfish exhibit quite lethargic swimming, corresponding to only 1 BL.sec⁻¹ (Bailey *et al.*, 2005). This means that a larva in flexion, at approximately 3 mm length, is capable of travelling only 260 m in a day, which highlights the importance of vertical migrations for the optimization of larval transportation.

In conclusion, the three habitats investigated in the present study are used for the early phases of *Achirus*, but there was a tendency toward size segregation, indicating movement from the reef habitat (first post-hatching coastal site) to the mangrove (settlement site). The proximity of the habitats likely favoured this movement, resulting in connectivity between environments. Further studies addressing the settlement pattern and the reproduction of these fish in the region will help clarify issues related to their life cycle.

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