

Reproductive seasonality of the fish fauna and limnoecology of semi-arid Brazilian reservoirs

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ABSTRACT

The native fish fauna commonly found in the drainage basins of rivers and reservoirs of Latin America, including those of the semi-arid Northeastern Brazil, are representatives of the Neotropical region. This work reports on the reproductive ecology of five commercially important and consumable native fish species, in relation to rainfall and hydrological variables of the semi-arid reservoirs in Brazil. Pluviometric precipitation, temperature, pH, dissolved oxygen and electrical conductivity of the water were registered, and maturation of fish gonads was assessed on a monthly basis. This region is characterized with short spells of rain interspersed with long dry season and rainfall seems to be the main environmental factor which modulates the timing of the spawning period of fish. Construction of reservoirs without adequate facilities for fish migration has an adverse impact on the migratory fish species which are of commercial and ecological importance to semi-arid Northeastern Brazil.

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Introduction

The Neotropical Region is one of the six major zoogeographical regions of the world which extends from Mexico to the southern most tip of South America. Brazil is an important part of this region which holds the largest biodiversity on the planet, accounting for around 13% of the total world biota (Queiroz et al. 2006). Although 90% of the country is located within the tropical zone, the climate of Brazil varies considerably from the Northern tropical zone to the temperate zones below the Tropic of Capricorn. Thus Brazil exhibits the equatorial, tropical, semi-arid, highland tropical and subtropical climatic regions. Semi-arid climate generally describes regions that receive low annual rainfall (250–500 mm) and the semi-arid region of Northeastern Brazil (“sertão”), considered as the area of drought polygon, is characterized by a network of seasonal rivers, with irregular and scanty rains (Andrade-Lima 1981). This region has distinctive scrub vegetation (“Caatinga”), consisting of xerophytic low thorny bushes adapted to the semi-arid climate and is recognized as a biodiversity hot-spot.

The hydrographic network of the semi-arid region is seasonal and modest when compared to other Brazilian regions. The main rivers are São Francisco and Parnaíba, which are perennial, besides other few mid-sized ones. These rivers have intermittent tributaries which flow to the Atlantic Ocean after crossing large areas of the semi-arid land. Construction of reservoirs of varied sizes in Northeastern Brazil resulted in benefits, such as public drinking water facilities, development of fish culture, irrigation, small industries and agricultural activities. However, the human activities also resulted in environmental impacts, leading to loss of biodiversity, degradation of water quality and loss of native riverine fish species (Agostinho et al. 1995; Henry 1999; Tundisi 2003).

The semi-arid freshwater ecosystems of northeast Brazil frequently encounter water level fluctuations because of recurrence of extended drought, irregular rainfalls, high temperatures and an elevated rate of water evaporation. The seasonality of the freshwater ecosystems of this region is defined by short spells of intense rainfall (March–July) coupled with an extended dry period throughout the rest of the year (Bouvy et al. 2000; Chellappa and Chellappa 2004).

Information regarding limnoecological aspects of native fish species is necessary for fish stock assessment, management controls and administration of fishery resources on a sustainable basis (Agostinho et al. 1995). Environmental factors influence the continental aquatic ecosystems by acting on the ecological processes

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of biological communities. The interaction of environment variables such as, temperature, rainfall and dissolved oxygen influences the periodicity of ecological events. The rainfall and consequent filling of reservoirs have demonstrated important correlations with the reproductive cycles of fish (Chellappa et al. 2003).

The fish species that occur in the freshwater ecosystems of semi-arid Northeastern Brazil are the result of evolutionary processes modulated by climatic factors and hydrological cycles of the region. However, human influence through environmental changes and the introduction of exotic species have modified the composition of the original ictiofauna. Although about 240 fish species pertaining to seven orders have been registered in this region, it is believed that this number could possibly be elevated if efforts are taken to compile the ictiofauna of the hydrographic basins of semi-arid Northeastern Brazil (Rosa et al. 2005).

Migratory fishes are an important component of Neotropical freshwater fisheries. Construction of reservoirs has imposed severe constraints on migratory fish species, as they block their migration. Such constraints result in fragmentation of fish populations, impairing both long and short distance migrations and blocking gene fluxes. The new environment formed after the construction of reservoir, presents lentic characteristics compared to the original lotic conditions of the river. This results in aquatic communities with significant changes of an unavoidable consequence, and also in the alteration in abundance and richness of species, with proliferation of some and reduction of others or even the elimination of some species (Agostinho et al. 2003).

The rivers of Northeastern Brazil sustain some important migratory fish species that exhibit a potamodromous life history strategy (Rosa et al. 2005). Fish migration is generally triggered by climatic and hydrological cues and the stimulus for migration of the semi-arid fish species is the onset of the rainy period (Chellappa et al. 2003). The limnoecology and reproductive biology of the native fish has not been investigated, in spite of their important contribution towards ecology of reservoir ecosystems in the semi-arid northeast of Brazil.

This study examines the reproductive biology of commercially important and consumable native fish species of the semi-arid reservoirs in Brazil in relation to rainfall and hydrological variables, focusing on temporal patterns of gonadal development of the females, spawning season and strategy. An attempt is made to correlate the spawning season and spawning strategy exhibited by these fish species with rainfall, one of the environmental factors which modulate the spawning season in the tropical region (Chellappa et al. 2003; Souza et al. 2007).

Materials and methods

Study sites

The semi-arid region of Brazil contains the world's second highest density of reservoirs (>70,000 next to India), and is characterized by highly unpredictable and spatially heterogeneous rainfall (Bouvy et al. 2000). This region represents 11% of the Brazilian territory with 16 million inhabitants, and with nine administrative States. The three study sites Marechal Dutra, João Alves and Campo Grande Reservoirs are located in the State of Rio Grande do Norte of northeastern Brazil, which represents 52,797 km² (3.38%) of the Northeast area, with 3 million inhabitants (5.82%).

The first study site Marechal Dutra is an important reservoir for agriculture and fishery purposes, and is situated between latitudes 6°26'11"S and longitudes 36°36'17"W. This was constructed on the River Piranhas-Assu, has a maximum depth of 25 m, mean depth of 8.5 m, water storage capacity of 40 × 10⁶ m³

and a theoretical retention time of 1460 days. The River Piranhas-Assu originates in the southeastern State of Paraíba and flows north-northeast through Paraíba and Rio Grande do Norte States into the Atlantic Ocean.

The second study site João Alves Reservoir is situated between latitudes 06°41'56"S and longitudes of 36°37'76"W in the Municipality of Parelhas, State of Rio Grande do Norte. This reservoir was constructed in 1984 on the River Piranhas-Assu, has a maximum depth of 15 m, mean depth of 4.5 m, water storage capacity of 10 × 10⁶ m³ and a theoretical retention time of 780 days.

The third study site Campo Grande Reservoir is located in the Municipality of São Paulo do Potengi in the State of Rio Grande do Norte and is situated between latitudes 05°50'00"S and longitudes 37°45'00"W. This reservoir was constructed in 1984 by impounding the River Potengi, has a maximum depth of 24 m, mean depth of 5.2 m, water storage capacity of 34 × 10⁶ m³ and a theoretical retention time of 970 days.

Hydrological variables and rainfall

The values of temperature, pH, dissolved oxygen and electrical conductivity of the waters of all three reservoirs were registered between 9:00 and 10:00 h on a monthly basis over a period of one year, from August 2004 to July 2005, using portable equipment (Multiparameter kit). The mean monthly rainfall data of the region registered during the study period was obtained from the Meteorological Department of EMPARN (Empresa de Pesquisa Agropecuária do Rio Grande do Norte).

Fish sampling and analyses

From August 2004 to July 2005, fish samples from the three reservoirs were captured on a monthly basis, with the help of artisanal fishermen of the region. Fishing gear consisted of stationary nets and gillnets of different mesh sizes (6–10 cm).

Random sub-samples of fish were collected which came from a larger catch landed by fishermen. Fish were transported to the laboratory on ice, numbered and used for detailed morphometric and meristic analyses to check the taxonomical status of each species. Total body length of all fishes was measured (± 1 mm) and body mass recorded (± 1 g). Fish were dissected within a few hours of capture, gonads were removed, weighed (± 0.1 mg) and examined to separate the sex and assess the state of maturity.

The location and general aspects of the ovaries and testes were observed and stage of reproductive maturity determined using a macroscopic staging system (Vazzoler 1996; Mackie and Lewis 2001). Periodicity of gonadal development and reproductive activity were estimated by the gonadosomatic index (GSI) of the fish, which was calculated by dividing the wet weight of gonads (g) by its body weight (g) minus gonad weight (g) and multiplying by 100 (Wootton et al. 1978). The spawning season of fish was investigated using monthly variations of the mean GSI and the gonadal maturity stages of females. This study focused more on ovaries since their developmental stages were easier to distinguish than in testes, and because ovarian development usually defines the spawning season and number of offspring produced during spawning (De Martini and Fountain 1981).

Results

Rainfall and hydrological variables

The mean monthly rainfall data during August 2004 to July 2005, indicate that the rainy period of the semi-arid region

Table 1

Mean annual values of hydrological variables of the reservoirs Marechal Dutra, João Alves and Campo Grande of northeastern Brazil during August 2004–July 2005.

Hydrological variables	Marechal Dutra	João Alves	Campo Grande
Temperature (°C)	28 ± 1.1	30 ± 1.2	30 ± 1.2
pH	8.4	8.6	8.2
Dissolved oxygen (mg L ⁻¹)	6.8 ± 2.1	6.2 ± 1.2	6.4 ± 1.1
Electrical conductivity (µs cm ⁻¹)	420 ± 220.4	920 ± 342.6	725 ± 246.2

correspond to a short spell of precipitation during the months of March–June, with a mean rainfall of 168 mm ± S.D. 74.52 mm. Occasional intense rains during March and April, with a peak of 512.6 mm, resulted in filling up of the reservoirs to the maximum capacity. The drought period occurred during the months of July–February, with a mean rainfall of 16.33 mm ± S.D. 10.40 mm. A striking variation in the rainfall pattern was observed during the dry and wet periods and there is a significant difference between the precipitation levels during these seasons ($t = 2.578$; $P = 0.0275$).

Mean annual values of hydrological variables of the three study sites are shown in Table 1. The mean values of water temperature showed slight variation ranging from 28 to 30 °C in all three reservoirs throughout the study period. The highest mean value of 31.1 ± 1.2 °C was registered during the dry period and the lowest mean value of 26.8 °C occurred during the rainy period. The pH values showed slight variations and were mostly alkaline throughout the study period. The highest value of 9.4 was registered during the dry period and the lowest value of 8.1 occurred during the rainy period. The monthly values of dissolved oxygen varied from 6.1 to 7.2 mg L⁻¹; however, a minimum value of 3.3 mg L⁻¹ was registered during the dry season. Elevated values of electrical conductivity were registered, which ranged from 1185 to 1451 µs cm⁻¹. With the intense rains lower values of 440–515 µs cm⁻¹ were registered.

Fish species

A total of 1274 fishes were collected and examined during the study period. Fish belonging to Osteichthyes consisted of 12 species, pertaining to 4 orders and 9 families. There was a dominance of species belonging to Characiformes and Perciformes. The native fish species of commercial importance in the three study reservoirs were mainly represented by the following species: Brazilian bocachico, *Prochilodus brevis* Steindachner, 1875; piau, *Leporinus piau* Fowler, 1941; red-eye piranha, *Serrasalmus rhombeus* (Linnaeus, 1766); sardinha, *Triporthus signatus* (Garman, 1890); traíra, *Hoplias malabaricus* (Bloch, 1794); toothless caracin, *Psectrogaster rhomboids* Eigenmann & Eigenmann, 1889; acará, *Cichlasoma orientale* Kullander, 1983; marble eel, *Synbranchus marmoratus* Bloch, 1795 and armoured catfish, *Hypostomus puitarum* (Starks, 1913). There were also fish species introduced from other Brazilian hydrographic basins, such as: oscar, *Astronotus ocellatus* (Agassiz, 1831); south American silver croaker, *Plagioscion squamosissimus* (Heckel, 1840) and tucunaré, *Cichla monoculus* Spix & Agassiz, 1831. The exotic Nile tilapia, *Oreochromis niloticus* was frequently present but was not considered in this study.

From the total number of fish collected, 492 specimens were used in this study. A total of 181 specimens of *H. puitarum* (60 males, 121 females), 43 specimens of *P. brevis* (26 males, 17 females), 152 specimens of *C. monoculus* (70 males, 82 females), 64 specimens of *L. piau* (30 males, 34 females) and 52 specimens of *C. orientale* (22 males, 30 females) were used for detailed

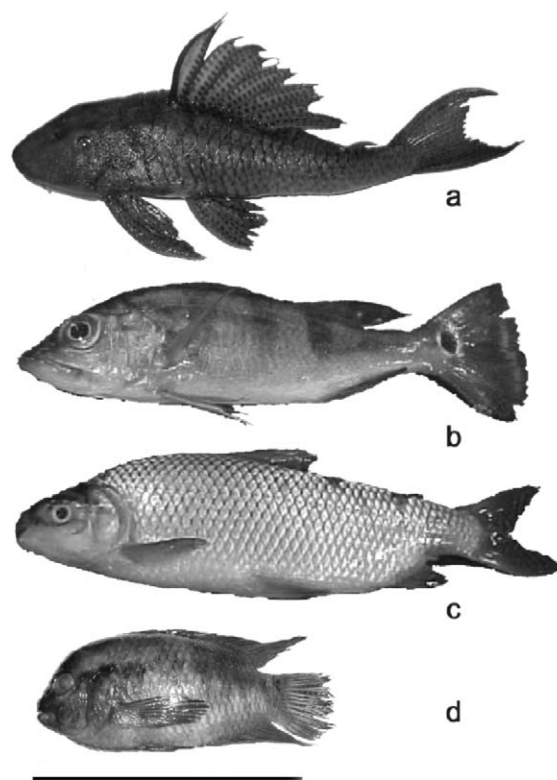


Fig. 1. Native fish species collected during the study: (a) *Hypostomus puitarum*; (b) *Cichla monoculus*; (c) *Prochilodus brevis*; (d) *Cichlasoma orientale*. (Scale bar = 150 mm.)

studies. Fig. 1 and Table 2 present the native fish species used in this study.

Total body lengths and body mass

The 121 female and 60 male specimens of *H. puitarum* ranged in total body length from 170 to 270 mm (mean 230.0 ± S.D. 62.8) and 192 to 280 mm (210.0 ± 20.7), respectively. The body mass of females ranged from 145 to 260 g (152.0 ± 43.3) and that of males from 80 to 290 g (154.1 ± 43.5). The amplitude of total body length of 17 females and 26 males of *P. brevis* varied from 230 to 300 mm (253.0 ± 36.4) and from 235 to 270 mm (260.0 ± 22.8), respectively. The body mass of *P. brevis* females were slightly heavier than the males, which ranged from 215 to 513 g (382.0 ± 87.5) and for males from 218.6 to 322.4 g (266.8 ± 25.7). The 70 males of *C. monoculus* were larger with 196–340 mm in total body length (260.0 ± 64.8) and heavier 98–450 g (320.0 ± 46.8) than the 82 females, 180–328 mm in total body length (230.0 ± 86.6) and 60–450 g in weight (280.0 ± 68.4). The amplitude of total body length of 34 females and 30 males of *L. piau* varied from 160 to 250 mm (220.2 ± 40.5), and body mass ranged from 45 to 270 g (168.8 ± 60.5). The amplitude total body length of 30 females and 22 males of *C. orientale* varied from 120 to 160 mm (140.4 ± 24.5), and body mass ranged from 78 to 105 g (96.2 ± 24.5).

Maturity stages of the ovary

Macroscopic observations of the ovarian developmental stages showed the immature, maturing, mature and partially spent stages for *C. monoculus*, *C. orientale* and *H. puitarum*. Whereas, the ovarian developmental stages of *P. brevis* and *L. piau* showed the immature, maturing, mature and totally spent stages.

Table 2

The native fish species captured from the semi-arid reservoirs of Brazil.

Order	Family	Species	Size range of fish (mm)
Characiformes	Prochilodontidae	<i>Prochilodus brevis</i> Steindachner, 1875	230–300
Characiformes	Anostomidae	<i>Leporinus piau</i> Fowler, 1941	160–250
Perciformes	Cichlidae	<i>Cichlasoma orientale</i> Kullander, 1983	120–160
Perciformes	Cichlidae	<i>Cichla monoculus</i> Spix & Agassiz, 1831	180–340
Siluriformes	Loricariidae	<i>Hypostomus pusalum</i> (Starks, 1913)	170–280

Type of spawning

Ovaries of mature females of *H. pusalum*, *C. monoculus* and *C. orientale* showed oocytes of varying sizes in different stages of development, which is characteristic of multiple spawners. These individuals spawn more than once within a breeding cycle. On the other hand, ovaries of mature females of *P. brevis* and *L. piau* showed mature oocytes of uniform size. These species show characteristic of total spawners.

Gonadosomatic index (GSI) and spawning season of fish

The mean monthly GSI of *H. pusalum* males ranged from 0.07 to 0.27 and that of females ranged from 0.66 to 10.6 during the study period. Temporal patterns of gonadal development of the females of *H. pusalum* showed that the ovaries were mature in February–April. In the months of May and June, the gonads were in spent condition, indicating that the reproductive season extends from February to June, with breeding occurring during May and June.

The mean monthly GSI of *P. brevis* males ranged from 1.5 to 6 and that of females ranged from 0.30 to 20.08. Both males and females had high GSI values prior to spawning season, and during October–December the males and females were sexually mature. In March, the males and females were in spent condition, indicating that spawning occurs during this month coinciding with the on set of rains.

The mean monthly GSI of *L. piau* ranged from 0.1 to 4.4 with high values in April and the spawning season began in February and extended up to May.

Sexually mature *C. monoculus* females and *C. orientale* females had GSI values as much as six times greater than in males. The mean GSI of mature males was 0.27 and the corresponding mean GSI of females was 1.86 showing an extended reproductive period with spawning occurring throughout the year.

Discussion

Although seasonal changes in temperature are minimal in tropical environments compared to higher latitudes, changes in rainfall regimes do cause some seasonality in most tropical ecosystems. In tropical freshwater environments, the rainfall variations are high-lightened among the environmental factors, since it aids in transport of nutrients, with consequent increase of their availability in the aquatic ecosystems (Lowe-McConnell 1987). With the onset of rainy season, there is an appreciable level of dissolved oxygen available to the organisms which stimulate the reproductive activity. In the semi-arid reservoirs precipitation also acts as a dilution factor resulting in low values of electrical conductivity. Chellappa et al. (2003) observed a correlation between the rainy season and low values of electrical conductivity in the reservoir waters.

The low levels of dissolved oxygen in the reservoir waters during the dry period is due to high utilization of oxygen for respiratory purposes of organisms and the decomposing organic material which is usually abundant in the tropical reservoirs (Chellappa and Costa 2003). During the drought season, low dissolved oxygen concentrations stimulate the morphological and physiological developmental mechanisms in some of the fish species of the family Loricariidae and Synbranchidae which have facultative respiratory mechanisms so that they can survive in low oxygen levels (Val 1996). The aquatic ecosystems with alkaline pH values are found in areas where there is a negative hydro balance, as in the reservoirs of Northeastern Brazil. During prolonged dry season, the pH values could be more than 9, and the declining trend in pH is related to the rainfall which characterizes the seasonality of the region.

Life history strategies result from natural selection for a species to produce the maximum number of young surviving to maturity under the conditions imposed by its biotopes (Lowe-McConnell 1987). Tropical fish species are very plastic and can allocate resources to reproduction according to rainfall regimes. Spawning seasons of semi-arid freshwater fish fauna are either restricted to rainy season as in the potamodromous *P. brevis*, or extended as in the cichlids, with spawning occurring during most part the year. Rainfall seems to be the main environmental factor which modulates the timing of the spawning period of most fish species.

Reservoirs are characteristic features of the Northeastern Brazilian river basins and consequently the impoundments pose a major problem for the migratory fish populations. Migratory fish populations depend on the extension of the river to complete their spawning but there are no provisions for fish passages enabling the migratory species to complete their life cycle. Thus the interruption of migratory routes is responsible for the slow disappearance of commercially important fish species as *P. brevis*. This impact has social and economic repercussions due to the dependence of fishermen and their families. Reservoir management policies related to stocking of fish fingerlings has not yielded good results and there is a reduction of migratory species in the reservoirs of Northeastern Brazil (Menescal et al. 2000).

Taylor et al (2006) investigated as to how the loss of a dominant migratory detritivorous fish species the flannel mouth characin, *P. mariae*, could alter ecosystem metabolism and organic carbon flow in an Andean river located in the Orinoco basin, which led to the degradation of the river. Tropical migratory fish species of Northeastern Brazil are almost all Characiformes. It could be considered that the construction of reservoirs without adequate fish passages had an adverse impact on the migratory fish species which are of commercial and ecological importance.

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References

- Agostinho, A.A., Matsuura, Y., Okada, E.K., Natakani, K., 1995. The catfish *Rhinelepis aspera* (Teleostei: Loricariidae) in the Guaira region of the Paraná River: an example of population estimation from catch-effort and tagging data when emigration and immigration are high. *Fish. Res.* 23, 333–344.
- Agostinho, A.A., Gomes, L.C., Suzuki, H.I., Júlio Jr., H.F., 2003. Migratory fishes of the Upper Paraná river basin, Brazil. In: Carolsfeld, Y., Harvey, B., Ross, C., Baer, A. (Eds.), *Migratory Fishes of South America: Biology, Fisheries and Conservation Status*. International Development Centre, Ottawa, pp. 19–98.
- Andrade-Lima, D., 1981. The caatingas dominium. *Revista Brasileira de Botânica* 4, 149–163.
- Bouvy, M., Falção, D., Marinho, M., Pagano, M., Moura, A., 2000. Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. *Aquat. Microb. Ecol.* 23, 13–27.
- Chellappa, N.T., Costa, M.A.M., 2003. Dominant and co-existing species of Cyanobacteria from a eutrophicated reservoir of Rio Grande Norte State, Brazil. *Acta Oecol.* 24, 3–10.
- Chellappa, S., Chellappa, N.T., 2004. Ecology and reproductive plasticity of the Amazonian cichlid fishes introduced to the freshwater ecosystems of the semi-arid Northeastern Brazil. In: Kaul, B.L. (Ed.), *Advances in Fish and Wildlife Ecology and Biology*, Vol. 3. Daya Publishing House, New Delhi, pp. 49–57.
- Chellappa, S., Câmara, M.R., Chellappa, N.T., Beveridge, M.C.M., Huntingford, F.A., 2003. Reproductive ecology of a Neotropical cichlid fish *Cichla monoculus* (Osteichthyes, Cichlidae). *Braz. J. Biol.* 63 (1), 17–26.
- De Martini, E.E., Fountain, R., 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. *Fish. Bull.* 79 (3), 547–559.
- Henry, R., 1999. *Ecologia de Reservatórios: Estrutura, função e aspectos sociais*. FAPESP, Botucatu, SP.
- Lowe-McConnell, R.H., 1987. *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, Cambridge.
- Mackie, M.C., Lewis, P.D., 2001. Assessment of gonad staging systems and other methods used in the study of the reproductive biology of the narrow-barred Spanish mackerel, *Scomberomorus commerson*, in Western Australia. *Fish. Res.* Report No. 136, 48 pp.
- Menescal, R.A., Oliveira, J.C.S., Campos, C.E.C., Araújo, A.S., Freire, A.G., 2000. Fish production in Marechal Dutra Reservoir, Acari, RN. *Revista de Ecologia Aquática Tropical* 10, 135–139.
- Queiroz, L.P., Rapini, A., Giulietti, A.M., 2006. Towards greater knowledge of the Brazilian Semi-arid Biodiversity. *Ministério da Ciência e Tecnologia, Brasília*, 142 pp.
- Rosa, R.S., Menezes, N.A., Britski, H.A., Costa, W.J.E.M., Groth, F., 2005. Diversidade, padrões de distribuição e conservação dos peixes da Caatinga. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (Eds.), *Ecologia e Conservação da Caatinga*. Editora UFPE, Recife, pp. 135–180.
- Souza, L.L.G., Chellappa, S., Gurgel, H.C.B., 2007. Biologia reprodutiva do peixe-donzela, *Stegastes fuscus* Cuvier, em arrecifes rochosos no nordeste do Brasil. *Rev. Bras. Zool.* 24 (2), 419–425.
- Taylor, B.W., Flecker, A.S., Hall Jr., R.O., 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* 313, 833–836.
- Tundisi, J.G., 2003. Água no Século XXI: Enfrentando a Escassez. RiMa, São Carlos.
- Val, A.L., 1996. Surviving low oxygen levels: lessons from fishes of the Amazon. In: Val, A.L., Almeida-Val, V.M.F., Randall, D.J. (Eds.), *Physiology and Biochemistry of the Fishes of the Amazon*. INPA, Manaus, pp. 59–73.
- Vazzoler, A.E.A.M., 1996. *Biologia de Reprodução de Peixes Teleosteos: Teoria e Prática*. EDUEM, Maringá, Brazil 169 p.
- Wootton, R.J., Evans, G.W., Mills, L.A., 1978. Annual cycle in female three-spined sticklebacks (*Gasterosteus aculeatus* L.) from an upland and lowland population. *J. Fish Biol.* 12, 331–343.