Review and consideration on habitat use, distribution and life history of *Lycengraulis grossidens* (Agassiz, 1829) (Actinopterygii, Clupeiformes, Engraulididae)

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Abstract: In this paper, we present a summary of the current knowledge of *Lycengraulis grossidens*, a widely distributed coastal fish that occurs from Belize to Argentina. This species is abundant in estuaries along the Southwest Atlantic Coast and is important for recreational fishing, and as bycatch of shrimp fisheries. We compiled data available on taxonomy, phylogeny, ecology, fisheries and organized conceptually the life cycle of the species according to modern estuarine-use classification. Our review showed that along its geographic distribution and inside some particular environments (i.e., estuaries and costal lagoons) the species have been classified in a variety of ways in order to describe the remarkable complexity of habitat use that varies from freshwater resident, anadromous, marine migrant, estuarine resident, marine stragglers, catadromous to semi-catadromous. We conclude that *L. grossidens* is able to reproduce either in freshwater or estuarine water and postulate that it has a high plasticity in habitat use and life history, with migratory and resident contingents in the same local population. There seems to be a latitudinal change in migratory behavior of this species along the South America Coast, prevailing anadromous or semi-anadromous pattern at higher latitudes and marine migrants at the tropical northeast coast of Brazil.
Keywords: *contingents, estuarine resident, anadromous, catadromous, freshwater resident, review.*

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Resumo: Neste trabalho é apresentada uma compilação do conhecimento atual de *Lycengraulis grossidens*, uma espécie de peixe amplamente distribuído pela costa oeste do Atlântico Sul, ocorrendo de Belize a Argentina. Esta espécie é abundante nos estuários e tem importância na pesca recreacional além de sofrer impacto da pesca do camarão. São revisados dados publicados sobre a taxonomia, filogenia, ecologia, pesca e ciclo de vida da espécie. Nossa revisão mostrou que, ao longo de sua distribuição, a espécie tem sido classificada de várias formas na tentativa de descrever seu uso do habitat, desde residentes de água doce, anádromos, marinhos migrantes, estuarinos residentes, catádromo e semi-catádromo. Conclui-se que a espécie é capaz de se reproduzir em água doce ou salgada, com uma alta plasticidade no uso do habitat e na sua história de vida, com componentes migrantes e residentes no mesmo local. Além disso, parece haver uma mudança no comportamento migratório da espécie em diferentes latitudes, mostrando um padrão anádromo ou semi-anádromo nas maiores latitudes e marinhos migrantes ao longo da costa tropical do Brasil.
Palavras-chave: *contingentes, estuarino residente, anádromo, catádromo, residente de água doce, revisão.*

Introduction

Engraulididae are usually found in schools, and many species are important fisheries resources, playing a relevant role as primary consumers (Berra 2007). Currently, sixteen genera of Engraulididae are recognized (Froese & Pauly 2011). Anchovies are primarily marine fishes, but in South America there are 12+ species that occur in major tropical rivers (Berra 2007, Bloom & Lovejoy 2012).

Different from other western Atlantic anchovies, the genus *Lycengraulis* has canine-like teeth, i.e., sharp and conical teeth of different sizes which are distinct from other Engraulididae that have filiform teeth (Whitehead et al. 1988). Currently, the genus comprises four species, one restricted to the western coast of the Americas (*Lycengraulis poeyi* (Kner & Steindachner, 1865)), and three inhabiting the east coast of the Neotropical region (*Lycengraulis grossidens* (Agassiz, 1829), *Lycengraulis batesii* (Günther, 1868) and *Lycengraulis limnichthys* (Schultz, 1949)). *Lycengraulis batesii* occurs to the west of Central and South Atlantic Ocean (Orinoco River, Manacacias River, rivers of the Guianas, and Amazon River) (Whitehead et al. 1988) and *L. limnichthys* inhabits Cartagena Bay and Maracaibo Bay, Venezuela (Nizinski & Munroe 2002). *Lycengraulis grossidens* is recognized to be widely distributed in the coastal zone from Belize to Argentina, including freshwater populations (Whitehead et al. 1988).

Lycengraulis grossidens can be characterized by a combination of characters as following: body fairly elongate and compressed, varying in depth 3.85-4.4 times in standard length (Schultz 1949, Whitehead et al. 1988). Snout pointed, projecting, a notch in the upper jaw, mouth large, maxillary ending below middle of pre-operculum (Jordan & Seale 1926) (Figure 1). Dorsal fin origin sits at midway between end of the caudal vertebra and the posterior margin of the eye, its longest ray scarcely equal to the base of the fin, being equal to head posterior of eye; origin of anal fin under ninth dorsal ray. Head 4.5 times in standard length. Eye a third more than snout, which is 4.7 of head. Cycloid scales that detach easily for its body. It presents four gill arches and a pseudobranquia (Jordan & Seale 1926, Fuster de Plaza & Boschi 1961). Species can reach up to 300 mm in total length (Carvalho-Filho 1999). Number of vertebras range from 42 to 48. Dorsal fin rays have 12-18, pectoral 13-17, ventral always have 7 and, anal range from 21-30. Number of gillrakers on upper anterior arch range from 11-20 and in lower 16-25 (Jordan & Seale 1926, Fuster de Plaza & Boschi 1961, Silva 2006). It has fusiform otolith, posterior margin lobed and anterior margin finished in notch, ventral margin dentate (Figure 2). Ventral height up to 3.15 and excisural notch up to 4.2 times the length of the otolith. Ventral height up to 1.75 times the length of the otolith. Rostrum and antirostrum present (Lemos et al. 1995). Comparison of the numeric characters reveals no sexual differences (Fuster de Plaza & Boschi 1961). Species can be distinguished for *Lycengraulis batesii* that possess less lower gillrakers (12 to 15), being the anterior 1 to 3 rudimentary in larger fish (Whitehead et al. 1988). *Lycengraulis limnichthys* has less vertebrates (39 to 42), and more lower gillrakers (19 to 23) (Whitehead et al. 1988, Nizinski & Munroe 2002).

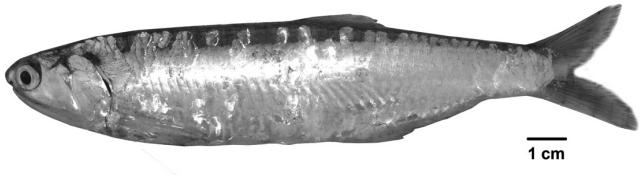

Figure 1. *Lycengraulis grossidens*, photograph taken of a live specimen at Solis Grande, Uruguay.

Lycengraulis grossidens is among the 10 most abundant species in the larger La Plata River, Patos Lagoon and Paranaguá Bay Estuaries (Spach et al. 2004, Oliveira 2008, Barletta et al. 2010, Vieira et al. 2010), and has economic importance for artisanal fisheries in Argentina, Uruguay and southern Brazil (Fuster de Plaza & Boschi 1961, Castello 1985, Spinetti et al. 2002, Ramos 2005).

This review is important because it brings a comparative vision of habitat use thought the latitudinal gradient of distribution of *L. grossidens*, raising new highlights on this context, and we focused our review and conclusions on habitat use and migration, since this is a controversial issue and crucial part of the life cycle of this species.

Material and Methods

More than a century of literature (since Evermann & Kendall 1906 to several authors at 2012) was extensively reviewed. Published papers used in this review were obtained from "Periódicos Capes" (http://www.periodicos.capes.gov.br/), Science direct (http://www.sciencedirect.com/) and Google Scholar (http://scholar.google.com.br/). We also included the Brazilian Digital Library of Theses and Dissertations (http://bdtd.ibict.br/) and "Plataforma Lattes" (http://lattes.cnpq.br/) for grey literature (unpublished theses, dissertations and monographs in Brazil). In addition, we obtained complementary material, which was not available online, by contacting researchers using electronic correspondence. Searches were conducted using the keyword "Lycengraulis" and the aim was to obtain current data available regarding phylogeny, distribution, diet, fisheries, growth, reproduction, and migration movements of *Lycengraulis grossidens*.

Based on the records of occurrence from Fishbase (Froese & Pauly 2011) and from original publications, we constructed a distribution map using the program Diva-Gis (available in: http://www.diva-gis.org/). Whenever the data was available, latitudinal variations of species parameters were included. The meristic data are presented as follows: amplitude and the most often observed values in brackets.

In order to standardize the terms used for habitat use and migrations, we used the classification of estuarine-use functional groups proposed by Elliott et al. (2007) in addition to the freshwater component not observed in the original classification of Elliott et al. (2007).

Results

Our literature review were able to find a total of 93 published works on *L. grossidens* which was distributed into 64 papers, 15 books, 13 gray literature (thesis, dissertations, conference proceedings and, reports), and one website. Our survey period encompassed studies dated from 1906 to 2012. Most studies reviewed (43) are focused on studies related to ecology of fishes communities, 14

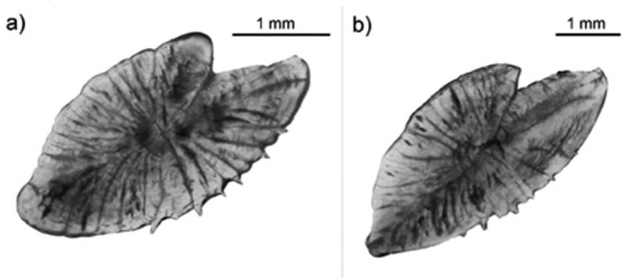

Figure 2. Photograph of sagitta otoliths of *Lycengraulis grossidens*, Iguape, SP: a) 129 mm total length (TL) individual and; b) 260 mm TL individual. Stereomicroscope Nikon SMZ 1500, with HR Plan Apo 1x WD54 lens coupled to digital camera Nikon Digita sight DS Fi1.

works deal specifically with the species of interest, 11 surveys were focused on by-catch of shrimp fisheries, and 25 surveys comprise others areas of knowledge.

1. Phylogenetic relationships

Grande & Nelson (1985) reviewed the entire family Engraulididae and divided into two clades: the first clade, the subfamily Coilinae, comprises six Indo-Pacific genera; and the second lineage, the subfamily Engraulinae comprises the Indo-Pacific marine genera *Encrasicholina* and *Stolephorus*, the worldwide, temperate-distributed genus *Engraulis*, and the so-called ''New World anchovies" that include the genera *Anchoa*, *Anchoviella*, *Anchovia*, *Cetengraulis*, *Jurengraulis*, *Lycengraulis* and *Pterengraulis*. These authors believed that taxonomic arrangement of the freshwater South American species were the result of multiple independent transitions from a marine environment.

The currently recognized molecular phylogenetics arrangement of New World anchovies suggest that fresh water South America species are the product of a single evolutionary transition from a marine to freshwater environment (Bloom & Lovejoy 2012). Thus, *L. grossidens* derived from freshwater lineages, where *Jurengraulis juruensis* was the basal lineages, the topology is fully resolved as follows: (*Jurengraulis*, (*Amazonsprattus*, (*Anchoviella*, (*Pterengraulis*, (*Lycengraulis batesii*, (*L. poeyi*, *L. grossidens*))))))) (Bloom & Lovejoy 2012).

2. Ecology

2.1. Species distribution

In freshwater and estuarine environments, the species have been recorded in Bela Vista (Prov. de Corrientes, AR), Rosário (Prov. de Santa Fé, AR), Negro River, Mar Chiquita and Buenos Aires (Prov. Buenos Aires, AR), Paraná River (until Itaipu Dam, AR), Uruguay River, Patos Lagoon, Peixe Lagoon, Tramandaí Lagoon (Rio Grande do Sul state, BR), Babitonga Bay (Santa Catarina state, BR), Paranaguá (Paraná state, BR), Iguape, Imbituba (São Paulo state, BR), Imboassica Lagoon (Rio de Janeiro state, BR), Vitória Bay, Doce River (Espírito Santo state, BR), Parnaíba River (Piauí state, BR), Negro River (Amazonas state, BR) and Orinoco and Maracaibo Rivers (Venezuela) (Evermann & Kendall 1906, Hildebrand 1943, Menezes 1950, Fuster de Plaza & Boschi 1961, Vieira et al. 1996, Benedito-Cecilio et al. 1997, Saint-Paul et al. 2000, Saad et al. 2002, Joyeux et al. 2004, Cervigón 2005, Ramos 2005, Bortoluzzi et al. 2006, Burns et al. 2006, Queiroz et al. 2006, Loebmann et al. 2008, Sánchez-Botero et al. 2008, Costa & Souza-Conceição 2009) (Figure 3).

In saltwater, the species have been recorded in Mar de Ajó, Mar del Plata, Necochea, Orense, Quequé Salado, Monte Hermoso, Bahía Blanca, and Carmem de Patagones, Argentina; Montevideo, Uruguay; Rio Grande (Rio Grande do Sul state; BR), Caravelas (Bahia state), Tamandaré, Itamaracá, Itapissuma (Pernambuco state), Cajueiro da Praia (Piauí state), Brazil; Guiana; French Guiana; Trinidad and Tobago; Venezuela; Colombia; Suriname and Belize (Schultz 1949, Fuster de Plaza & Boschi 1961, Valdez & Aguilera 1987, Whitehead et al. 1988, Albuquerque 1994, Santos et al. 1998, Kullender & Ferraris 2003, Cervigón 2005, Guedes et al. 2005, Silva 2006, Lira & Teixeira 2008, Santos et al. 2008, Mai et al. 2012) (Figure 3).

2.2. Population Structure

Based on morphological and meristic characteristics, the distribution of the species was divided into four distinct populations

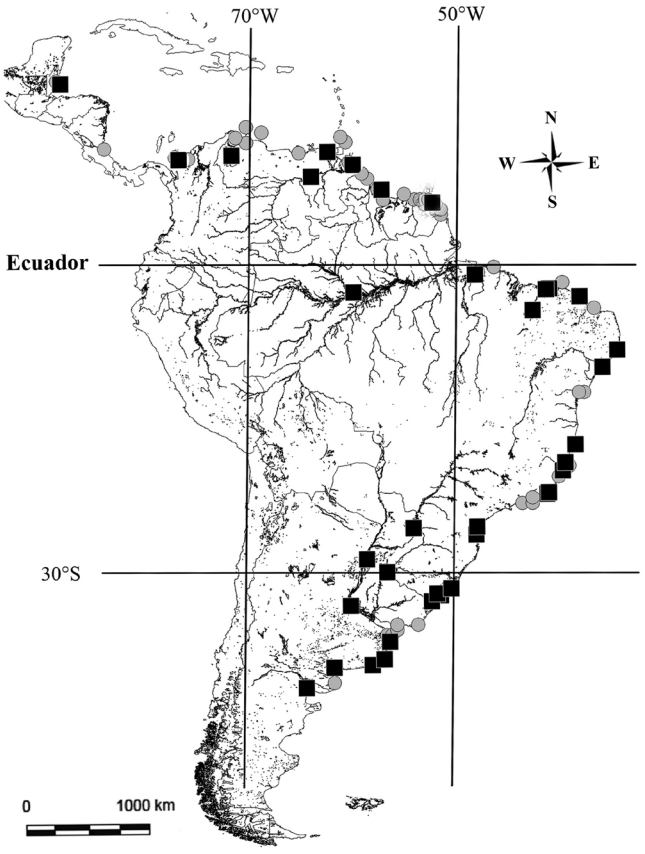

Figure 3. Distribution records of *Lycengraulis grossidens* plotted on a hydrographic map of Central and South America. Black squares showing locations of occurrence described in the literature reviewed, and gray circles are data available in Fishbase (Froese & Pauly 2011).

along the Brazilian Coast (Silva 2006): one from Pará, another from Ceará to Espírito Santo, the third between Rio de Janeiro and São Paulo, and the last one extended between the states of Santa Catarina and Rio Grande do Sul. Silva (2006) reports that the number of gillrakers was the meristic character that showed the clearest pattern of longitudinal variation, with values increasing with increasing latitude.

3. Fisheries

Fisheries of *L. grossidens* have been recorded in Argentina and Uruguay (Fuster de Plaza & Boschi 1961, Spinetti et al. 2002, Baigún et al. 2003). At Maldonado (Uruguay), they are commercialized frozen and used as bait for recreational rod fishing (personal observation). Captures in the estuarine region of the Patos Lagoon by artisanal fishery, between 1974-1979, reached almost 9 ton/year (Castello 1985). Marques (1997) estimated that *L. grossidents* is bycatch of the shrimp fishery at the Patos Lagoon Estuary might have reached almost 30 ton/year. The species is also a component of the artisanal fisheries of the Casamento Lagoon, in the Patos Lagoon system, Rio Grande do Sul state - RS (Milani & Fontoura 2007). Rod, hook and line recreational fishing of this species is an important vocational tourist attraction in the estuarine area of the Tramandaí River, RS, Brazil, totalizing almost 1 ton/year (Ramos 2005).

Along the Brazilian Coast, the species has been recorded as bycatch of shrimp fishery in the south (Haimovici & Mendonça 1996, Vieira et al. 1996, Bail & Branco 2003, Branco & Verani

2006, Loebmann & Vieira 2006, Vianna & D'Incao 2006, Dumont & D'Incao 2011), and in the northeast (Albuquerque 1994, Santos et al. 1998, Santos et al. 2008).

4. Life history

4.1. Reproductive aspects

Lycengraulis grossidens is a split spawning species (Oliveira 2008) and has mean fecundity of 3,752 oocytes (minimum: 2,371, maximum: 6,847) (Oliveira 1997). The species spawns at austral spring and summer (Table 1). Reproductive activity was reported in freshwater (Paraná River, AR), approximately 800 km from the sea, and also in Uruguay River, BR, about 550 km from the sea (Mastrarrigo 1947, Fuster de Plaza & Boschi 1961, Oliveira 1997, Lepkoski et al. 2005). Reproductive activity was reported also in estuarine conditions in coastal lagoons and estuaries of southern Brazil (Ramos 2005, Oliveira 2008) (Table 1).

Information on length at first maturity was achieved only in the southern part of its distribution (below 30 °S), and revealed that sexual maturity occurs between 80 and 133 mm TL (Mastrarrigo 1947, Fuster de Plaza & Boschi 1961, Oliveira 1997, Ramos 2005) (details in Table 1).

4.2. Development and Growth

The eggs of *L. grossidens* are planktonic with an ovoid shape (eccentricity from 1.25 to 1.5), transparent, without oil drop, with vitellum divided between the alveoli and small periviteline space (Weiss & Krug 1977). Egg diameter ranges from 1.026 to 1.215 µm along the major axis, and from 756 to 945 µm along the minor axis, and egg volume ranges from 0.338 to 0.568 mm^3 (Weiss et al. 1976).

The newly hatched larva measures approximately 3 mm of total length (TL), is transparent and without any pigmentation, the vitellum has a granular aspect and the yolk-sack is oval-shaped, extending from the inferior part of the head to the middle of the body (Weiss & Krug 1977). The juvenile, at 40 mm TL, contains adult characteristics and growth changes from alometric to isometric. At this phase in the development, the body proportions, fin disposition, and rays are already definitive, the digestive system is complete, and the first scales are developed (Weiss & Krug 1977). The development time from egg to juvenile is not yet known.

Castello & Krug (1978) inferred the age of *L. grossidens* from the Patos Lagoon Estuary (Brazil) based on the reading of *sagitta* otolith rings. They suggest that individuals from 70-100 mm total length (TL) are one year old, 100-130 mm TL are two years old, and they analyzed only one individual measuring 210 mm TL, suggesting an age of three years. Goulart et al. (2007), using scales to infer ages of *L. grossidens* collected from the Uruguay River, assumed that individuals from 100 to 140 mm TL have one ring per year of age and they found individuals of up to three years old.

Goulart et al. (2007) proposed the von Bertalanffy growth function for each year of their study, were: for female length: $LT = 26(1\text{-}e^{0,266(t-(-2,19))})$ and $LT = 26(1\text{-}e^{0,59(t-(-0,12))})$; and for male length: $LT = 26(1\text{-}e^{0,12(t-(-0,69))})$ and $LT = 26(1\text{-}e^{0,42(t-(-0,69))})$.

4.3. Diet and feeding strategies

Lycengraulis grossidens presents a generalist feeding strategy (Ramos 2005) feeding mainly on Insecta, Crustacea, Mollusca, Polychaeta and, Osteichthyes (Froese & Pauly 2011). Although juveniles feed on invertebrates, feeding mainly on zooplankton, when they reaches approximately 140 mm, adults undergo a change in diet and become ichthyophagous (Ramos 2005, Oliveira 2008, details in Table 2).

5. Functional groups and habitat use

Lycengraulis grossidens inhabits marine, estuarine or freshwater environments (Whitehead et al. 1988, Barletta et al. 2010). Except for "freshwater species", several classifications of functional groups related to estuarine use have been proposed: anadromous, marine migrant, estuarine resident, marine stragglers, catadromous and semi-catadromous, and were standardized according to Elliott et al. (2007) in Table 3.

Studies performed in La Plata River (AR) and its tributaries classified *L. grossidens* as anadromous, reporting that the species, during the autumn and early winter, penetrates the "Río de la Plata" and other rivers of the La Plata basin to spawn in fresh water (Paraná River) in September and October, returning to the marine environment in November and December (Mastrarrigo 1947, Fuster de Plaza & Boschi 1961).

The presence of a large number of eggs and larvae and the absence of newly fertilized eggs in the estuarine region near Patos Lagoon, southern Brazil, led Weiss & Krug (1977) and Weiss (1981) to misleadingly hypothesize that *L. grossidens* spawn in coastal waters and behave as catadromous. Later, Ramos (2005), based on the abundance of juveniles and adults from bottom trawl and beach

Table 1. Reproductive aspects of *Lycengraulis grossidens*. L50 is the length where 50% of individuals were mature. References: 1 Oliveira (2008), 2 Oliveira (1997), 3 Ramos (2005), 4 Weiss (1981), 5 Mastrarrigo (1947), 6 Fuster de Plaza & Boschi (1961), and, 7 Lepkoski et al. (2005). – data not reported and * average length at which the peak of the first reproductive cycle is reached (Bervian & Fontoura 1994).

Localities	Reproductive peaks	Spawning site	L50 (total length)	Ref.
Paranaguá Bay, Paraná, Brazil	Spring	Spawning in estuaries	-	1
Itapeva and Quadros Lagoons, Rio Grande do Sul (RS), Brazil	October to January, with peak in December	Spawning in fresh water	80 mm*	2
Patos Lagoon, RS, Brazil	September to January, spawning is related to the increase in water temperature	Spawning in estuaries	112 mm to female and 133 mm to male	3
Patos Lagoon, RS, Brazil	-	Spawning in marine, salt water	-	4
Paraná River, Argentina	October to November, when the water reaches temperatures above 21°C	-	120 mm	5
Parana River, Argentina	October to November, when the water reaches temperatures between 20-24°C	Spawning in small streams, fresh water.	120 mm	6
Uruguay River, RS, Brazil	October to December, with peak in October	Spawning in fresh water	-	7

Table 2. Diet of *Lycengraulis grossidens* based on data available in the literature. N values represent the number of individuals analyzed in each study. References: 1 Lopes (1998), 2 Eskinazi (1972), 3 Lopes & Resende (2000), 4 Oliveira (1997), 5 Ramos (2005), 6 Mastrarrigo (1947), 7 Bortoluzzi et al. (2006) and, 8 Fuster de Plaza & Boschi (1961). – data not reported.

Localities	N	Empty	Diet / Items	Ref.
Itamaracá Island, Pernambuco (PE), Brazil	138	10.9%	Crustacea Peracarida Amphipoda, Isopoda and Tanaidacea; Decapoda Dendrobranchiata, and Pleocyamata Brachyura; Annelida Polychaeta, and Osteichthyes. Organic material and plants were considered incidental.	1
Canal de Santa Cruz, PE, Brazil	-	-	The most common Osteichthyes Gerreidae *Eucinostomus*, and Crustacea Decapoda *Penaeus*.	2
Itaparica Island, Bahia, Brazil	39	5.1%	Crustacea Peracarida Amphipoda; Decapoda Dendrobranchiata, and Pleocyamata Brachyura; and Osteichthyes. Organic material and plants were considered incidental.	3
Itapeva and Quadros Lagoons, Rio Grande do Sul (RS), Brazil	150	-	Crustacea Copepoda, Cladocera, Amphipoda, Palaemonidae, Isopoda; Teleostei; Diptera; Arachnida; Annelida; and seed.	4
Tramandaí River, RS, Brazil	1250	75.8%	Generalist / Algae; Nematoda; Annelida Polychaeta; Mollusca Gastropoda, and Bivalvia; Insecta; Crustacea Copepoda Calanoida, Cirripedia Cladocera, Amphipoda, Mysidacea, Decapoda Anoumura, Brachyura, and Macrura, Cumacea; Ostheichthys Mugilidae *Mugil* sp; and vegetables fragments.	5
Paraná, Uruguay and La Plata River	-	-	Osteichthyes, Crustacea Palaemoneidae and Insecta.	6
Uruguay River, Rio Grande do Sul, Brazil	589	52%	Ichthyophagous / Insecta Coleoptera, Hymenoptera Formicidae, Odonata Coenagrionidae, Trichoptera Hydropsychidae, Diptera Chironomidae, Lepdoptera; Crustacea Cladocera Sididae, Calanoida Diaptomidae Notodiaptomus; Osteichthyes Characidae *Astyanax bimaculatus*, *A. fasciatus*, *Apareiodon affinis*, *Characidium pterostictum*, *Salminus brasiliensis*, *Oligosarcus brevioris*, *Odontostilbe pequira*, *Bryconamericus stramineus*, Curimatidae *Cyphocharax voga*, Engraulididae *Lycengraulis grossidens*; sand, plants, seeds, eggs, gravels and, others invertebrates.	7
Bela Vista; Rosário; Mar del plata; Isla Trindade, Bahia Blanca; San Blas; Carmen de Patagones, río Negro, Argentine	700	60%	Carnivorous / Freshwater: Crustacea *Palaemonetes argentinus*, Pseudodiaplomus, Acantocyclops, Notodiaplomus, Isopodos, etc; Insecta Ephemenoptera, and Diptera; Osteichthyes Characidae *Astianax* sp, Clupeidae *Ramnogaster arcuata*, Pimelodidae *Luciopimelodus* sp, Atherinopsidae *Odontesthes bonariensis*. Salt water: Crustacea Brachyura, Copepode; Osteichthyes Clupeidae *R. arcuata*, and Engraulididae *Anchoa marinii*.	8

seine data in the Patos Lagoon and adjacent coastal areas classified *L. grossidens* as semi-catadromous *sensu* Elliott et al. (2007).

The classification of *L. grossidens* as catadromous or semi-catadromous, by Weiss & Krug (1977), Weiss (1981) and Ramos (2005) at Patos Lagoon Estuary may be due to errors in the interpretation of the species abundance in the lagoon and the adjacent coastal area. Considering the information provided by Weiss (1981), where it is reported that: (i) the highest frequencies of eggs are recorded within the estuary at high salinities and, (ii) that the greatest abundance of eggs occur in waters of low salinity (<5), and (iii) that eggs were not captured in the channel of the estuary, it would be more parsimonious to think that the spawning of *L. grossidens* occurs in low salinity environments, where the highest abundances were recorded, and after that the eggs were washed to the sea, which would explain their increased frequency, but no increasing in abundance in waters of higher salinities. This interpretation is corroborated by the data provided by Sinque & Muelbert (1998) who found that the greatest abundance of eggs of *L. grossidens* occurs on the surface of low salinity water that flows to the ocean, even with salty water intruding below.

Other authors studying the Patos Lagoon system classified the species as estuarine resident (Vieira et al. 2010), marine migrant, sub-category marine estuarine dependent *sensu* Elliott et al. (2007) (Chao et al. 1985, Garcia et al. 2003) or even freshwater resident in the limnic portion of the Patos Lagoon (Viamão), about 280 km from the sea (Lucena et al. 1994).

If we combine the data provided by Lucena et al. (1994) and information at the adjacent marine coast of Patos Lagoon (Cunha 1981), with the data analyzed by Ramos (2005) it is possible also to visualize an anadromous or semi-anadromous classification for *L. grossidens* in the Patos Lagoon. The species is absent in the sea during the winter (Cunha 1981), but occurs in the estuary and limnic portion of the Patos Lagoon (Ramos 2005). Adults are caught during the spring, both in the limnic and estuarine regions, which corresponds to the spawning period (September-January) (Ramos 2005).

The fact that the individual larger than the size of first maturation occurs year round in some parts of the La Plata River, the Patos Lagoon and Paranaguá Estuaries (Fuster de Plaza & Boschi, 1961, Lucena et al. 1994, Oliveira 2008, Vieira et al. 2010) could be attributable to part of the population that does not migrate. This would add a new hypothesis to the migratory behavior of the species: the existence of partial or facultative migration, where only part of the population adopts this migratory behavior as recently reported for other migratory species (Chapman et al. 2012).

5.1. Marine populations

There are records of *L. grossidens* fisheries between December and May along the Argentinean Coast (Fuster de Plaza & Boschi 1961). Along the coast of Uruguay, the species is abundant in marine

Table 3. Description of habitat use for *Lycengraulis grossidens* throughout its distribution according to the literature. The last column is a standardization of classification of estuarine-use functional groups following Elliott et al. (2007). References: 1 Krumme et al. (2004), 2 Vasconcelos-Filho & Oliveira (1999), 3 Reis-Filho et al. (2010), 4 Sánchez-Botero et al. (2008), 5 Vilar et al. (2011), 6 Costa & Souza-Conceição (2009), 7 Ramos (2005), 8 Lepkoski et al. (2005), 9 Chao et al. (1985), 10 Garcia et al. (2003), 11 Vieira et al. (2010), 12 Weiss et al. (1976), 13 Weiss (1981), 14 Mastrarrigo (1947) and, 15 Fuster de Plaza & Boschi, (1961). LAT/LONG = latitude/longitude.

Localities	LAT/LONG	Classification of habitat use proposed in the literature	Ref.	Standardization of classification of habitat use
Caeté Estuary, Brazil	0°/6° W	Marine migrant: utilize the estuary both as adults and juveniles, but spawn in the sea.	1	Marine migrant (MM)
Itamaracá, Brazil	7° S/34° W	Marine dependent: species found in estuary environment from juvenile to adult.	2	MM sub-category Marine estuarine dependent
Paraguaçu River Estuary, Brazil	12° S/38° W	Marine stragglers based on Elliott et al. (2007)	3	Marine straggler
Cabiúnas Lagoon, Brazil	22° S/41° W	Marine dependent: species spawn in the sea and use the coastal lagoons as a nursery for larvae and juveniles, or for adult permanence for long periods.	4	MM
Babitonga Bay, Brazil	26° S/48° W	Marine migrant: without explanation	5	MM
Babitonga Bay, Brazil	26° S/48° W	Estuarine resident: without explanation	6	Estuarine specie sub-category E. resident
Patos Lagoon and Tramandaí Estuaries, RS, Brazil	29° S/49° W and 32° S/52° W	Estuarine-catadromous: species born in the estuary, migrate to fresh water to grow and return to the estuary to breed.	7	Semi-catadromous
Uruguai River, Brazil	30° S/57° W	Freshwater species. This category is not in Elliott et al. (2007)	8	-
Patos Lagoon Estuary, RS, Brazil	32° S/52° W	Estuarine dependent marine fishes: those marine coastal spawners that utilize the estuarine environment as a post larval and juvenile nursery during the first years of their life cycles.	9	MM sub-category Marine estuarine dependent
Patos Lagoon Estuary, RS, Brazil	32° S/52° W	Estuarine dependent: marine or freshwater spawning species found predictably in large numbers in estuaries during certain periods of their life-cycle.	10	MM sub-category Marine estuarine dependent
Patos Lagoon Estuary, RS, Brazil	32° S/52° W	Estuarine resident: the species is found in the estuary year-round, either as juvenile or adult.	11	Estuarine species sub-category E. resident
Patos Lagoon Estuary, RS, Brazil	32° S/52° W	Catadromous: eggs found in the estuary and the absence of eggs in the early stages of development lead the author to believe that the species spawns on the coast.	12-13	Catadromous
Paraná and Prata Rivers, Argentina	34° S/58° W	Anadromous: Individuals migrate from estuary or adjacent marine region and spawn in Uruguay or Paraná Rivers, returning to the marine environment.	14-15	Anadromous

beach seine samples (Retta et al. 2006). In southern Brazil (Cassino Beach, RS), juveniles and larvae of the species are regularly found from September to May, being more abundant during the summer (Cunha 1981, Busoli & Muelbert 2003). The continuous record of *L. grossidens* as bycatch of shrimp fisheries in Rio Grande do Sul, Santa Catarina and São Paulo States certifies the presence of this species in the coastal zone of southern Brazil (see "Fishery" item). Although the species is frequently caught as adults in the coastal zone, there is no record of spawning in the marine environment, suggesting that the species use the marine habitat as a temporary or transitory environment. In the northeast of Brazil (Jaguaribe Beach, state of Pernambuco - PE), adults of *L. grossidens* are abundant in the coastal zone for most of the year, but absent in July, August and September (Santana & Severi 2009).

5.2. Estuarine Populations

At La Plata River (AR), *L. grossidens* is frequent and abundant in the riverine portion of the estuary, near the estuarine area (García et al. 2010). In the Patos Lagoon Estuary, the species occurs throughout the year (Buckup 1984, Chao et al. 1985, Ramos 2005, Vieira et al. 2010), and was among the ten most abundant species of shallow waters (Vieira et al. 2010), bottom trawl (Vieira 2006) and dominated the pelagic assemblage (Vieira & Castello 1997). At Patos Lagoon Estuary salinity appears to segregate different age cohorts of *L. grossidens*, with larvae preferring oligohaline waters for their development (Castello & Krug 1978), besides which the relative abundance of juveniles is higher in El Niño than La Niña years (Garcia et al. 2001).

In the Paranaguá Estuary (state of Paraná, Brazil) the species also occurs throughout the year (Oliveira 2008) and is the fifth most abundant species in beach seine catches (Spach et al. 2004). *Lycengraulis grossidens* was the seventh most abundant species in the Saco da Fazenda's Estuary (Itajaí – state of Santa Catarina, Brazil) (Barreiros et al. 2009). In Caeté Estuary (state of Pará, Brazil), the species has been recorded as the fourth and sixth most abundant in

number of larvae and adults, respectively (Barletta-Bergan et al. 2002, Krumme et al. 2004).

5.3. Freshwater Populations

Whilst there are some authors that pointed out that *L. grossidens* is able to migrate throughout the fishway systems in Salto Grande and Yacyreta reservoirs (Espinach Ros & Parodi 1997, Oldani et al. 2001, 2007), one landlocked population is described in the Uruguay River at more than 550 km from the sea, up to Salto Grande dam, where the species is captured year-round and has been able to reproduce (Lepkoski et al. 2005, Teixeira de Mello et al. 2011). There are also records of *L. grossidens* at least 1,500 km upstream the Paraná River, up to the Yacyreta dam (Benedito-Cecilio et al. 1997) and in the Amazonas River more than 1,300 km from the sea (Saint-Paul et al. 2000). Oliveira (1997) reported reproductive activity of the species in the Fortaleza Lagoon, RS, Brazil, which, during the study period, was fresh water and were isolated from the sea by a barrier. Reinforcing the idea that the species may remain in freshwater, *L. grossidens* has been reported year round at more than 300 km from the sea in the limnic portion of the Patos Lagoon (Lucena et al. 1994) and also in the Mirim Lagoon, RS, Brazil (Burns et al. 2006, Moura et al. 2012).

Final Conclusions and Future Research Directions

It is possible to identify some controversial information in the literature regarding habitat use, i.e. at least seven distinct classifications (marine migrant, marine stragglers, estuarine resident species, semi-catadromous, catadromous, anadromous and also freshwater habitant) have been proposed so far, and apparently *L. grossidens* has differences in its pattern of habitat use throughout its distribution, as suggested in the literature (see Table 3).

The patterns of habitat use seem to support a clinal use of the estuarine environment by *L. grossidens*. In lower latitudes *L. grossidens* has usually been described as marine migrant or marine straggler (Vasconcelos-Filho & Oliveira 1999, Krumme et al. 2004, Sánchez-Botero et al. 2008, Reis-Filho et al. 2010, Vilar et al. 2011), although spawning activities were never reported for lower or higher latitudes in the marine environment. In contrast, the species shows the proven ability to reproduce in both fresh water (Fuster de Plaza & Boschi 1961, Oliveira 1997, Lepkoski et al. 2005) and estuarine environments (Ramos 2005, Oliveira 2008). In higher latitudes, in Argentina, Uruguay and southern Brazil, the species seems to have a component with an anadromous or semi-anadromous behavior, i.e., some individuals spawn in fresh water or estuaries, migrating from marine or estuarine environment. Although other individuals of the same population seems to be resident in estuarine waters or even in fresh water (Fuster de Plaza & Boschi 1961, Lucena et al. 1994, Burns et al. 2006, Vieira et al. 2010). Thus, due to the number of possible patterns, the most parsimonious hypothesis is that this species has high plasticity in its habitat use for reproduction and that the species may be partial or facultative diadromous. Such intraspecific variation in migratory behavior is well known in different fish species and appears to be the rule rather than the exception (McDowall 2007, Chapman et al. 2012).

Although temperature could be considered as a factor to explain this latitudinal behavior, the magnitude of the estuarine systems along the western Atlantic Coast is also a good argument to explain the estuarine use. From the Amazon River (the largest river discharge in the world) to the south there are no significant freshwater discharges throughout the northeast and southeast Brazilian Coast. The freshwater influence starts to be important once more at Patos Lagoon and La Plata estuarine systems. The lack of saltwater spawning records and the increasing of estuarine related contingents at south of the distribution, in addition to the well know reported landlocked freshwater population suggest that *L. grossidens* has a freshwater origin.

Despite of large advances have been achieved with the molecular phylogenetics studies, and the publications of tools for application in population genetics as primers to microsatellite amplification (Lavoué et al. 2010, Bloom & Lovejoy 2012, Mai et al. 2013), population genetic studies are needed in order to know the degree of connectivity and gene flow between populations, as evidenced by the morphological investigations carried out along the Brazilian Coast by Silva (2006).

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References

ALBUQUERQUE, P.G.A. 1994. Recursos potenciais de peixes da fauna acompanhante a pesca de camarões da foz do rio São Francisco, Litoral Norte, Piaçabuçu, AL. Dissertação de Mestrado, Universidade Federal de Pernambuco, Recife.

BAIGÚN, C.R.M., SVERLIJ, S.B. & LÓPEZ, H.L. 2003. Recursos pesqueros y pesquerias del rio de La Plata interior y medio (margen Argentina). Freplata PNUD/GEF/RLA799/G31. www.freplata.org/documentos (último acesso em 26/05/2012).

BAIL, G.C. & BRANCO, J.O. 2003. Ocorrência, abundância e diversidade da ictiofauna na pesca do camarão sete-barbas, na região de Penha, SC. Notas Técn. Facimar 7:73-82.

BARLETTA-BERGAN, A., BARLETTA, M. & SAINT-PAUL, U. 2002. Structure and seasonal dynamics of larval fish in the Caeté River Estuary in North Brazil. Estuar. Coast. Shelf S. 54:193-206. http://dx.doi.org/10.1006/ecss.2001.0842

BARLETTA, M., JAUREGUIZAR, A.J., BAIGUN, C., FONTOURA, N.F., AGOSTINHO, A.A., ALMEIDA-VAL, V.M.F., VAL, A.L., TORRES, R.A., JIMENES-SEGURA, L.F., GIARRIZZO, T., FABRÉ, N.N., BATISTA, V.S., LASSO, C., TAPHORN, D.C., COSTA, M.F., CHAVES, P.T., VIEIRA, J.P. & CORRÊA, M.F.M. 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. J. Fish Biol. 76:2118-2176. http://dx.doi.org/10.1111/j.1095-8649.2010.02684.x

BARREIROS, J.P., BRANCO, J.O., FREITAS-JUNIOR, F.L. MACHADO, HOSTIM-SILVA, M. & VERANI, J.R. 2009. Space–time distribution of the ichthyofauna from saco da fazenda Estuary, Itajaí, Santa Catarina, Brazil. J. Coast. Res. 255:1114-1121. http://dx.doi.org/10.2112/08-1050.1

BENEDITO-CECILIO, E., AGOSTINHO, A.A., JULIO, H.F. & PAVANELLI, C.S. 1997. Length-weight relationship of fishes caught in the Itaipu reservoir. Rev. Bras. Zool. 14(1):1-14.

BERRA, T.M. 2007. Freshwater fish distribution. University of Chicago Press, Chicago. http://dx.doi.org/10.7208/chicago/9780226044439.001.0001

BERVIAN, G. & FONTOURA, N.F. 1994. Dinâmica populacional da ictiofauna da lagoa Fortaleza, Cidreira, RS. III. *Corydoras paleotus* (Jenyns, 1842) (Teleostei, Callichtyidae). Biociencias 2:15-23.

BLOOM, D.D. & LOVEJOY, N.R. 2012. Molecular phylogenetics reveals a pattern of biome conservatism in New World anchovies (family Engraulidae). J. Evol. Biol. 25:701-715. http://dx.doi.org/10.1111/j.1420-9101.2012.02464.x

BORTOLUZZI T., ASCHENBRENNER, A.C., SILVEIRA, C.R., ROOS, D.C., LEPKOSKI, E.D., MARTINS, J.A., GOULART, M.G., QUEROL, E. & QUEROL, M.V. 2006. Hábito alimentar da sardinha prata, *Lycengraulis grossidens* (Spix and Agassiz, 1829), (Pisces, Engraulididae), Rio Uruguai médio, sudoeste do Rio Grande do Sul, Brasil. Biodivers. Pampeana 4:11-23.

BRANCO, J.O. & VERANI, J.R. 2006. Análise quali-quantitativa da ictiofauna acompanhante na pesca do camarão sete-barbas, na Armação do Itapocoroy, Penha, Santa Catarina. Rev. Bras. Zool. 23(2):381-391. http://dx.doi.org/10.1590/S0101-81752006000200011

BUCKUP, P.A. 1984. Distribuição e abundância de Engraulídeos (Osteichthyes, Clupeiformes) na região estuarial da Lagoa dos Patos, RS, Brasil. Tese de Doutorado, Universidade Federal do Rio Grande, Rio Grande.

BURNS, M.D.M., GARCIA, A.M., VIEIRA, J.P., BEMVENUTI, M.A., MARQUES, D.M.L. & CONDINI, M.V. 2006. Evidence of habitat fragmentation affecting fish movement between the Patos and Mirim coastal lagoons in southern Brazil. Neotrop. Ichthyol. 4(1):69-72. http://dx.doi.org/10.1590/S1679-62252006000100006

BUSOLI, R.O. & MUELBERT, J.H. 2003. Environmental factors and ichthyoplankton dynamics in the surf zone of Cassino sandy beach (32°10'S, 52°20'W). J. Coast. Res. 35:463-471.

CARVALHO-FILHO, A. 1999. Peixes: costa brasileira. Editora Melro, São Paulo.

CASTELLO, J.P. & KRUG, L.C. 1978. Distribution, growth and spawning groups of the manjuba (*Lycengraulis grossidens*) in the estuary of the Lagoa dos Patos, Rio Grande do Sul, Brazil. Atlântica 3:33-46.

CASTELLO, J.P. 1985. The ecology of consumers from dos Patos Lagoon estuary, Brazil. In Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecoystem Integration (A. Yanez-Arancibia, ed.). DR(R) UNAM Press, Mexico, p.383-406.

CERVIGÓN, F. 2005. La ictiofauna marina de Venezuela: una aproximación ecológica. Bol. Inst. Oceanogr. Venezuela 44(1):3-28.

CHAO, L.H., PEREIRA, L.E. & VIEIRA, J.P. 1985. Estuarine fish community of the dos Patos Lagoon, Brazil. A baseline study. In Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecoystem Integration (A. Yanez-Arancibia, ed.). DR(R) UNAM Press, Mexico, p.429-450.

CHAPMAN, B.B., SKOV, C., HULTHÉN, K., BRODERSEN, J., NILSSON, P.A., HANSSON, L.A. & BRÖNMARK, C. 2012. Partial migration in fishes: definitions, methodologies and taxonomic distribution. J. Fish Biol. 81(2):479-499. http://dx.doi.org/10.1111/j.1095-8649.2012.03349.x

COSTA, M.D.P. & SOUZA-CONCEIÇÃO, J.M. 2009. Composição e abundância de ovos e larvas de peixes na baía da Babitonga, Santa Catarina, Brasil. PanamJAS 4(3):372-382.

CUNHA, L.P.R. 1981. Variação sazonal da distribuição, abundancia e diversidade dos peixes na zona de arrebentação da praia do Cassino, R. S. - Brasil. Dissertação de Mestrado, Universidade Federal do Rio de Janeiro, Rio de Janeiro.

DUMONT, L.F.C. & D'INCAO, F. 2011. By-catch analysis of Argentinean prawn *Artemesia longinaris* (Decapoda: Penaeidae) in surrounding area of Patos Lagoon, southern Brazil: effects of different rainfall. JMBA 91(5):1059-1072.

ELLIOTT, M., WHITFIELD, A.K., POTTER, I.C., BLABER, S.J.M., CYRUS, D.P., NORDLIE, F.G. & HARRISON, T.D. 2007. The guild approach to categorizing estuarine fish assemblages: a global review. Fish Fish. 8:241-268. http://dx.doi.org/10.1111/j.1467-2679.2007.00253.x

ESKINAZI, A.M. 1972. Peixes do Canal de Santa Cruz, Pernambuco, Brasil. Trab. Ocean. UFPE 13:283-302.

ESPINACH ROS, A. & PARODI, C.R. 1997. Conservación de la fauna ictica en el embalse de Salto Grande. Publicacion de la comision administradora del Rio Uruguay y la comision tecnica mixta de Salto Grande, Montevideo.

EVERMANN, B.W. & KENDALL, W.C. 1906. Notes on a collection of fishes from Argentina, South America, with descriptions of three new species. Proc. US Nat. Mus. 31:67-108. http://dx.doi.org/10.5479/si.00963801.31-1482.67

FROESE, R. & PAULY, D. 2011. FishBase. www.fishbase.org.

FUSTER DE PLAZA, M.L. & BOSCHI, E.E. 1961. Areas de migracion y ecologia de la anchoa *Lycengraulis olidus* (Günther) en las aguas argentinas (Pisces, fam. Engraulididae). Fac. Cien. Exactas Naturales 1(3):127-183.

GARCIA, A.M., VIEIRA, J.P. & WINEMILLER, K.O. 2001. Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. J. Fish Biol. 59:1218-1238. http://dx.doi.org/10.1111/j.1095-8649.2001.tb00187.x

GARCIA, A.M., VIEIRA, J.P. & WINEMILLER, K.O. 2003. Effects of 1997–1998 El Niño on the dynamics of the shallow-water fish assemblage of the Patos Lagoon Estuary (Brazil). Estuar. Coast. Mar. Sci. 57(2003):489-500. http://dx.doi.org/10.1016/S0272-7714(02)00382-7

GARCÍA, M.L., JAUREGUIZAR, A.J. & PROTOGINO, L.C. 2010. From fresh water to the slope: fish community ecology in the Río de la Plata and the sea beyond. Lat. Am. J. Aquat. Res. 38(1):81-94. ry (Brazil). Estuar. Coast. Mar. Sci. 57(2003):489-500. http://dx.doi.org/10.3856/vol38-issue1-fulltext-8

GOULART, M.G., ASCHENBRENNER, A.D.C., BORTOLUZZI, T., SILVEIRA, C.D.R.D., LEPKOSKI, E.D., MARTINS, J.A., BRANDLI, E.D.S., ROOS, D.C., QUEROL, E. & QUEROL, M.V. 2007. Análise do crescimento de escamas de *Lycengraulis grossidens* (AGASSIZ, 1829), em populações da bacia do Rio Uruguai médio, Rio Grande do Sul. Biodivers. Pampeana 5(1):3-8.

GRANDE, L. & NELSON, G.J. 1985. Interrelationships of fossil and recent anchovies (Teleostei: Engrauloidea) and description of a new species from the Miocene of Cyprus. Am. Mus. Novit. 2826:1-16.

GUEDES, D.S., VASCONCELOS-FILHO, A.L. & MACEDO, R.M. 2005. Ictiofauna do infralitoral adjacente às margens do Canal de Santa Cruz - Itapissuma, Pernambuco. Bol. Técn. Cient. CEPENE 13(2):65-75.

HAIMOVICI, M. & MENDONÇA, J.T. 1996. Descartes da fauna acompanhante na pesca de arrasto e tangones dirigida a linguados e camarões na plataforma continental do sul do Brasil. Atlântida 18:161-177.

HILDEBRAND, S.F. 1943. A review of the american anchovies (Family Engraulididae). Bull. Bing. Ocean Collec. 8:1-165.

JORDAN, D.S. & SEALE, A. 1926. Review of the Engraulididae, with descriptions of new and rare species. Bull. Mus. Comp. Zool. 67: 355-418.

JOYEUX J.-C., PEREIRA, B.B. & ALMEIDA, H.G. 2004. The flood-tide ichthyoplanktonic community at the entrance into a Brazilian tropical estuary. J. Plankton Resour. 26(11):1277-1287. http://dx.doi.org/10.1093/plankt/fbh119

KRUMME, U., SAINT-PAUL, U. & ROSENTHAL, H. 2004. Tidal and diel changes in the structure of a nekton assemblage in small intertidal mangrove creeks in northern Brazil. Aquat. Living Resour. 17:215-229. http://dx.doi.org/10.1051/alr:2004019

KULLENDER, S.O. & FERRARIS, C.J. 2003. Family Engraulididae. In Check list of freshwater fishes of South and Central America (R.E. Reis, S.O. Kullender & C.J. Ferraris, eds.). Edipucrs, Porto Alegre, p.39-45.

LAVOUÉ, S., MIYA, M. & NISHIDA, M. 2010. Mitochondrial phylogenomics of anchovies (family Engraulididae) and recurrent origins of pronounced miniaturization in the order Clupeiformes. Mol. Phylogenet. Evol. 56:480-485. http://dx.doi.org/10.1016/j.ympev.2009.11.022

LEMOS, P.H.B., CORRÊA, M.F.M. & PINHEIRO, P.C. 1995. Catálogo de otólitos de Engraulididae (Clupeiformes-Osteichthyes) do litoral do Paraná, Brasil. Arq. Biol. Tecnol. 38(3):731-745.

LEPKOSKI, E.D., QUEROL, E., ASCHENBRENNER, A.C., BORTOLUZZI, T.P., MARTINS, J.A., ROOS, D.C., SILVEIRA, C.R., GOULART, M.G. & QUEROL, M.V.M. 2005. Biologia reprodutiva da sardinha prata *Lycengraulis grossidens* (Spix and Agassiz, 1829) na bacia do rio Uruguai médio, localidade de são marcos município de Uruguaiana região da fronteira oeste do estado do Rio Grande do Sul. In VII Congresso de Ecologia do Brasil, Caxambu, p.1-2.

LIRA, A.K.F. & TEIXEIRA, S.F. 2008. Ictiofauna da praia de Jaguaribe, Itamaracá, Pernambuco. Iheringia 98(4):475-480. http://dx.doi.org/10.1590/S0073-47212008000400010

LOEBMANN, D. & VIEIRA, J.P. 2006. O impacto da pesca do camarão-rosa *Farfantepenaeus paulensis* (Perez-Farfante) (Decapoda, Penaeidae) nas assembléias de peixes e siris do Parque Nacional da Lagoa do Peixe, Rio Grande do Sul, Brasil. Rev. Bras. Zool. 23(4):1016-1028. http://dx.doi.org/10.1590/S0101-81752006000400006

LOEBMANN, D., VIEIRA, J.P., BEMVENUTI, M.A., ASTARLOA, J.M.D., COUSSEAU, M.B. & FIGUEROA, D. 2008. Composition and relative abundance of fish species in two Coastal Lagoons in Austral South America: Peixe Lagoon (31ºS; 51ºW), Brazil, and Mar Chiquita Lagoon (37ºS; 57ºW), Argentin. Neotrop. Biol. Conserv. 3(1):28-33.

LOPES, P.R.D. 1998. Nota sobre a alimentação de *Lycengraulis grossidens* (Agassiz, 1829) (Osteichthyes, Clupeiforme, Engraulididae) na praia de Jagaribe (Ilha de Itamaracá), Pernambuco. Acta Biol. Leopondensia 20(2):243-249.

LOPES, P.R.D. & RESENDE, G. 2000. Nota sobre a alimentação de *Lycengraulis grossidens* (Agassiz, 1829) (Actinopterygii, Engraulididae) na praia de ponta da ilha (Ilha de Itaparica, Bahia). Acta Biol. Leopondensia 22(1):129-132.

LUCENA, C.A.S., JARDIM, A.S. & VIDAL, E.S. 1994. Ocorrência, distribuição e abundância de peixes na praia de Itapuã, Viamão, Rio Grande do Sul, Brasil. Comum. Mus. Ciênc. Tecnol. 7:3-27.

MAI, A.C.G., SILVA, T.F.A. & LEGAT, J.F.A. 2012. Assessment of the fish-weir fishery off the coast of Piauí State, Brazil. Arq. Ciên. Mar. 45(2):40-48.

MAI, A.C.G., VIEIRA, J.P., PLAVAN, A.A., NOBREGA, M.F., MORAES, L.E., RODRIGUES, F.L. & MARINS, L.F. 2013. Isolation and characterization of 18 microsatellites for *Lycengraulis grossidens* (Pisces: Clupeiformes). Conserv. Genet. Resourc. 5:15-18. http://dx.doi.org/10.1007/s12686-012-9718-2

MARQUES, W.M. 1997. Estimativa da rejeição da pesca do camarão-rosa *Pennaeus paulensis* com aviãozinho no estuário da Lagoa dos Patos (RS), Brasil. Dissertação de Mestrado, Universidade Federal do Rio Grande, Rio Grande.

MASTRARRIGO, V. 1947. La sardinha de la cuenca del Río de la Plata (*Lycengraulis olidus*) (Günther). Ministerio de Agricultura, Montevideo.

McDOWALL, R.M. 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. Fish Fish. 8:1-13. http://dx.doi.org/10.1111/j.1467-2979.2007.00232.x

MENEZES, R.S. 1950. Alimentação do peixe-cachorro, *Lycengraulis barbouri* Hildebrand, 1943, da bacia do Rio Parnaíba, Piauí (Actinopterygii, Engraulidae). Rev. Brasil. Biol. 10(3):285-293.

MILANI, P.C.C. & FONTOURA, N.F. 2007. Diagnóstico da pesca artesanal na lagoa do casamento, sistema nordeste da laguna dos patos: uma proposta de manejo. Biociências 15(1):82-125.

MOURA, P.M., VIEIRA, J.P., GARCIA, A.M. 2012. Fish abundance and species richness across an estuarine-freshwater ecosystem in the Neotropics. Hydrobiology 696:107-122. http://dx.doi.org/10.1007/s10750-012-1187-9

NIZINSKI, M.S. & T.A. MUNROE. 2002. Order Clupeiformes, Engraulididae. In The living marine resources of the Western Central Atlantic (K.E. Carpenter, ed.). Fao, Roma, p.764-794.

OLDANI, N., BAIGÚN, C., DELFINO, R. & RODRIGUEZ, R. 2001. Evaluación de los sistemas de transferencia para peces de la represa de Yacyretá. Natura Neotropicalis 32(2):87-101.

OLDANI, N., BAIGÚN, C., NESTLER, J.M. & GOODWIN, R.A. 2007. Is fish passage technology saving fish resources in the lower La Plata River basin? Neotrop. Ichthyol. 5(2):89-102. http://dx.doi.org/10.1590/S1679-62252007000200002

OLIVEIRA, A. 1997. Dinâmica populacional de *Lycengraulis grossidens*, Agassiz 1829 nas lagoas Itaperava e quadros, subsistema Norte de lagoas costeiras do Rio Grande do Sul, Brasil (Teleostei, Engraulididae). Dissertation, Pontificia Universidade Católica, Porto Alegre.

OLIVEIRA, E.C. 2008. Ictiofauna da face norte da ilha rasa da cotinga, Baía de Paranaguá, Paraná: composição, estrutura da assembléia e reprodução. Dissertation, Universidade Federal do Paraná, Curitiba.

QUEIROZ, G.M.N., SPACH, H.L., SOBOLEWSKI-MORELOS, M., SANTOS, L.O. & SCHWARZ-JUNIOR, R. 2006. Caracterização da ictiofauna demersal de duas áreas do complexo estuarino de Paranaguá, Paraná, Brasil. Biociências 14(2):112-124.

RAMOS, L.A. 2005. Auto-ecologia de *Lycengraulis grossidens* (Agassiz, 1829) (Clupeiformes, Engraulididae) em estuários do Rio Grande do Sul e sua pesca na barra do rio Tramandaí, RS, Brasil. Tese de Doutorado, Universidade Federal de Rio Grande.

REIS-FILHO, J.A., NUNES, J.A.C.C. & FERREIRA, A. 2010. Estuarine ichthyofauna of the Paraguaçu River, Todos os Santos Bay, Bahia, Brazil. Biota Neotrop. 10(4):301-311. http://dx.doi.org/10.1590/S1676-06032010000400034

RETTA, S., MARTÍNEZ, G. & ERREA, A. 2006. Áreas de cría de peces en la costa Uruguaya. In Bases para la conservación y el manejo de la costa Uruguaya (R. Menafra, L. Rodríguez-Gallego, F. Scarabino & D. Conde, eds). Graphis, Montevideo, p.211-218.

SAAD, A.M., BEAUMORD, A.C. & CARAMASCHI, E.P. 2002. Effects of artificial canal openings on fish community structure of Imboassica coastal lagoon, Rio de Janeiro, Brazil. J. Coast. Res. 36:634-639.

SAINT-PAUL, U., ZUANON, J., CORREA, M.A.V., GARCÍA, M., FABRÉ, N.N., BERGER, U. & JUNK, W.J. 2000. Fish communities in central Amazonian white- and blackwater floodplains. Envir. Biol. Fish. 57: 235-250. http://dx.doi.org/10.1023/A:1007699130333

SÁNCHEZ-BOTERO, J.I., CARAMASCHI, E.P. & GARCEZ, D.S. 2008. Spatiotemporal variation in fish assemblage in a coastal lagoon without direct contact with the sea (Southeastern Brazil). J. Coast. Res. 24(4C):225-238. http://dx.doi.org/10.2112/06-0752.1

SANTANA, F.M.S. & SEVERI, W. 2009. Composição e estrutura da assembleia de peixes da zona de arrebentação da praia de Jaguaribe, Itamaracá (PE). Bioikos 23(1):3-17.

SANTOS, M.C.F., FREITAS, A.E.T.S. & SILVA, M.M. 1998. Composição da ictiofauna acompanhante da pesca de camarão em Tamandaré/PE e Pontal do Peba/AL. Bol. Técn. Cient. CEPENE 6(1):1-18.

SANTOS, M.C.F., ALMEIDA, L. & SILVA, C.G.M. 2008. Avaliação quali-quantitativa da ictiofauna acompanhante na pesca do camarão sete-barbas, *Xiphopenaeus kroyeri* (Heller, 1862) no município de Caravelas (Bahia - Brasil). Bol. Técn. Cient. CEPENE 16(1):99-107.

SCHULTZ, L.P. 1949. A further contribution to the ichthyology of Venezuela. Proc. US Nat. Mus. 99:1-211. http://dx.doi.org/10.5479/si.00963801.99-3235.1

SILVA, M.A. 2006. Variações morfo-merísticas da manjuba *Lycengraulis grossidens* (Agassiz, 1829) ao longo da costa brasileira. Tese de Doutorado, Universidade Federal Rural do Rio de Janeiro, Seropédica.

SINQUE, C. & MUELBERT, J.H. 1998. Ictioplancton. In Os ecossistemas costeiro e marinho do extremo sul do Brasil (U. Seeliger, C. Odebrecht & J.P. Castello, eds). Ecoscientia, Rio Grande, p.56-59.

SPACH, H.L., GODEFROID, R.S., SANTOS, C., SCHWARZ-JUNIOR, R. & QUEIROZ, G.M.L. 2004. Temporal variation in fish assemblage composition on a tidal flat. Braz. J. Ocean. 52(1):47-58.

SPINETTI, M., FOTI, R., RIESTRA, G. & FERNÁNDEZ, A. 2002. La actividad pesquera artesanal en el Río de la Plata: estructura y situación socioeconómica. In The Río de la Plata. Research for the management of the environment, the fisheries resources and fishery in the saline front (D. Vizziano, P. Puig, C. Mesones & G.J. Nagy, eds). UNESCO- ECOPLATA, Montevideo, p.235-272.

TEIXEIRA DE MELLO, F., GONZÁLEZ-BERGONZONI, I. & LOUREIRO, M. 2011. Peces de agua dulce del Uruguay. PPR-MGAP, Montevideo.

VASCONCELOS-FILHO, A.L. & OLIVEIRA, A.M.E. 1999. Composição e ecologia da ictiofauna do Canal de Santa Cruz (Itamaracá – PE, Brasil). Trab. Oceanogr. UFPE 27(1):101-113.

VALDEZ, J. & AGUILERA, O. 1987. Los peces del Golfo de Venezuela. Fondo editorial, Caracas.

VIANNA, M. & D'INCAO, F. 2006. Evaluation of by-catch reduction devices for use in the artisanal pink shrimp (*Farfantepenaeus paulensis*) fishery in Patos Lagoon, Brazil. Fish. Res. 81:331-336. http://dx.doi.org/10.1016/j.fishres.2006.06.011

VIEIRA, J.P., VASCONCELOS, M.C., SILVA, R.E. & FISHER L. 1996. A rejeição do camarão-rosa (*Penaeus paulensis*) no estuário da Lagoa dos Patos, RS, Brasil. Atlântica 18(1):123-142.

VIEIRA, J.P. & CASTELLO, J.P. 1997. Fish Fauna. In Subtropical Convergence Environments. The coast and sea in the Southwestern Atlantic. Subtropical Convergence Environments (U. Seeliger, C. Odebrecht & J.P. Castello, eds.). Spring-Verlag, New York, p.56-61.

VIEIRA, J.P. 2006. Ecological analogies between estuarine bottom trawl fish assemblages from Patos Lagoon (32S), Brazil, and York River (37N), USA. Rev. Brasil. Zool. 23(1):234-247.

VIEIRA, J.P., GARCIA, A.M. & MORAES, L. 2010. A assembléia de peixes. In Os ecossistemas costeiro e marinho do extremo sul do Brasil (U. Seeliger, C. Odebrecht & J.P. Castello, eds). Ecoscientia, Rio Grande, p.77-88.

VILAR, C.C., SPACH, H.L. & JOYEUX, J.C. 2011. Spatial and temporal changes in the fish assemblage of a subtropical estuary in Brazil: environmental effects. JMBA 91(3):635-648.

WEISS, G. 1981. Ictioplancton del estuario de Lagoa dos Patos, Brasil. Theses, Universidad Nacional De La Plata, Buenos Aires.

WEISS, G., SOUZA, J.A.F. & SANTOS, A. 1976. Contribuição ao conhecimento do Ictioplancton marinho de plataforma sul do Brasil. Atlântica 1(1):1-99.

WEISS, G. & KRUG, L.C. 1977. Características do desenvolvimento e metamorfose de *Lycengraulis olidus* (Engraulididae) e *Brevoortia pectinata* (Clupeidae) no estuário da lagoa dos Patos, Brasil. Atlântica 2(1):83-117.

WHITEHEAD, P.J.P., NELSON, G.J. & WONGRATANA, T. 1988. Clupeoid fishes of the world (Suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. FAO Fish Synopsis, Rome.

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