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High plasticity in habitat use of *Lycengraulis grossidens* (Clupeiformes, Engraulididae)

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A B S T R A C T

In this study, we analyzed the Sr:Ca and Ba:Ca ratios of the otoliths of 139 *Lycengraulis grossidens* individuals sampled along the southwestern Atlantic Ocean, including two freshwater areas, to describe patterns of habitat use and their latitudinal organization. Otolith sections were analyzed by laser ablation inductively coupled plasma mass spectrometry along core-to-edge transects. Otolith edge analysis revealed significant differences in Sr:Ca and Ba:Ca ratios between fish from freshwater habitats and those from estuarine/marine habitats, indicating that these ratios may be used to describe habitat use patterns. Lifetime transects of Sr:Ca and Ba:Ca indicate at least four distinct habitat use patterns: freshwater residents, estuarine/marine residents, and two distinct diadromous/nomadic types. Most individuals (88.6%) sampled at northern latitudes in sheltered marine bays and the coastal ocean were estuarine/marine residents, whereas at southern latitudes, most individuals were diadromous (72.5%). We also identified landlocked populations in the Uruguay River and in Mirim Lagoon. These results suggest that *L. grossidens* exhibits flexible habitat use strategies and may use freshwater, estuarine and marine environments throughout their lifetime.

1. Introduction

Intraspecific variation in migratory behavior of fishes has increasingly been documented worldwide (Secor, 2010). There is a variety of behaviors that may be related to the ability of fish to survive in alternative habitats as compelled by reproduction, feeding, searching for refuge against predators, avoidance of intraspecific competition and may also give increased resilience for the population as a whole in the face of environmental perturbations (see Kerr et al., 2010; Chapman et al., 2011a, 2012).

The term "partial migration" was proposed to describe the migratory behavior in which some fish within a population remain at their natal area while others migrate (Jonsson and Jonsson, 1993; Secor, 2010). Many species that were once regarded as classical migrants, such as trout *Salmo trutta* (anadromous), eels *Anguilla* spp. (catadromous) and mullets *Mugil cephalus* (catadromous), may currently be classified as partial migrants (Bohlin et al., 2001; Daverat et al., 2006; Wang et al., 2010). As the number of studies of fish migration increases, it appears that partial migrations may be the rule rather than the exception for many migratory fish species (Chapman et al., 2011a, 2012). In addition, intraspecific variation in the migratory behavior of many species previously recognized as diadromous (i.e., they move between salt- and freshwater habitats) has been increasingly reported in recent years (Limburg et al., 2001a,b; Daverat et al., 2011; Magath et al., 2013; Tulp et al., 2013).

As both migratory and non-migratory individuals may be found in the same population, the concept of migratory species is changing from the more restricted idea of obligatory movements across large distances (Myers, 1949; McDowall, 2001) towards a more flexible concept that includes the full gradient of behaviors from full residency to full migration.

One interesting example of the huge conceptual confusion surrounding migratory characterization is illustrated by the engraulid

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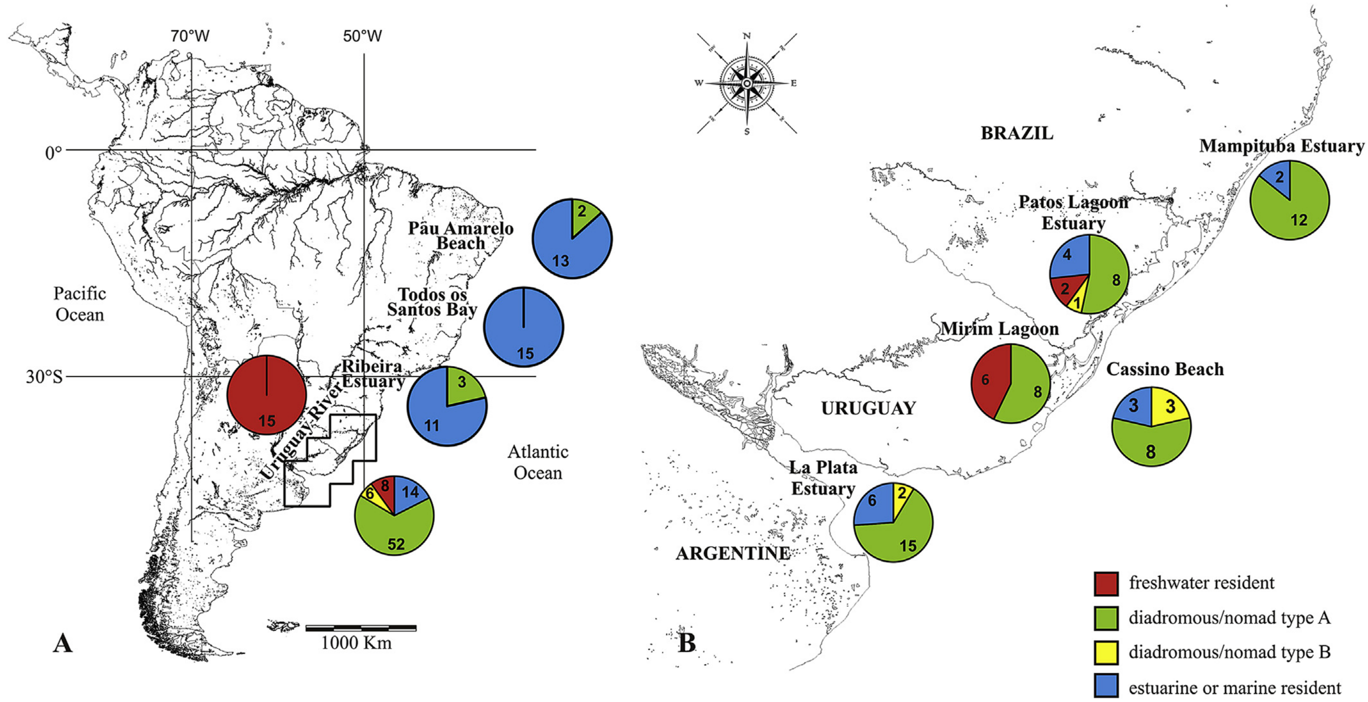

Fig. 1. Sample locations for *Lycengraulis grossidens* along the South American Coast. For each of the nine sampled regions, pie sectors are proportional to the relative contingents that were freshwater residents (red), estuarine or marine residents (blue) and diadromous/nomadic type A (green) and type B (yellow). A: Hydrological map of South America and B: Hydrological map of southern part of sample area. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Lycengraulis grossidens. This fish is widely distributed in the Atlantic Ocean from Belize to Argentina (Whitehead et al., 1988). It has been considered a marine fish (Bloom and Lovejoy, 2012) despite being one of the most abundant fish in estuaries of the southwestern Atlantic Coast and its occurrence in freshwater habitats (Barletta et al., 2010; Mai and Vieira, 2013). The patterns of habitat use and migration of *L. grossidens* remain unclear. For example, this species has been classified as anadromous (Mastrarrigo, 1947; Fuster de Plaza and Boschi, 1961), catadromous (Weiss et al., 1976), estuarine dependent (Chao et al., 1985), marine migrant (Krumme et al., 2004), estuarine resident (Vieira et al., 2010) and marine straggler (Reis-Filho et al., 2010). All of these classifications are based on patterns of fish abundance and reproduction across different habitats. In a recent review, Mai and Vieira (2013) recognized the intraspecific variation in the migratory behavior of *L. grossidens* and suggested that new inference tools are needed to understand their migratory patterns and movements along the southwestern Atlantic Ocean.

Fish movements have been studied using a variety of tools, such as mark and recapture, telemetry, and the analysis of trace elements in otoliths (Casselman, 1982); the latter has been widely used in recent years. Otoliths function as natural tags because some trace elements are incorporated in the substitution to Ca^{2+} into the otolith carbonatic matrix (Campana, 1999) in proportion to the element-to-Ca availability in the water. Strontium and barium are among the most studied otolith constituents and are expected to indicate the movements of a fish over its life span across a salinity gradient (Campana, 1999). While Sr:Ca ratios in the water usually increase with the transition from freshwater to marine waters, Ba:Ca ratios generally present the inverse pattern (Elsdon et al., 2008). These water chemical characteristics will subsequently be stored in the otoliths under a temporal organization. Otolith chemistry analysis presents advantages over other methods (e.g., mark and recapture, satellite transmitters), as each fish in a population is naturally-marked, with their otoliths potentially providing information over its lifetime (Campana, 1999; Elsdon and Gillanders, 2006; Secor, 2010).

In the present study, we asked two main questions: (1) As *Lycengraulis grossidens* occurs in fresh, estuarine and marine waters year-round and is frequently classified as migrant, does this species exhibit partial migratory behavior? (2) If so, is there a latitudinal organization of its migratory patterns along the southwestern Atlantic Ocean? We investigated these questions based on an intensive otolith chemistry dataset of *L. grossidens* collected over a broad latitudinal scale.

2. Materials and methods

Individual *Lycengraulis grossidens* ($n = 139$) were obtained from coastal and freshwater habitats of eastern South America from 7 to 36°S between 2010 and 2011 (Fig. 1). Environmental characteristics of each sampling site are described briefly in Table 1. All sampled specimens were measured for total length and weighed, and sagittal otoliths were extracted, cleaned and stored dry. The left otoliths were embedded in crystal polyester resin, and transverse sections were cut through the core using a low-speed, diamond-blade Isomet saw. Thin sections (0.4 mm) were mounted onto glass slides with cyanoacrylic glue. Prior to laser ablation inductively coupled plasma spectrometry analysis, otolith surfaces were polished with silicon carbide paper (no 8000), washed with ultrapure DI water (Milli-Q, Millipore, Bedford, USA), sonicated for 3 min, and rinsed three times with ultrapure water. The slides were then dried in a laminar flow cabinet before analysis.

2.1. Elemental analysis

Otolith transects were ablated from the core to the edge to encompass the entire fish life-history. Analytical measurements