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Ontogenetic changes in pharyngeal morphology correlate with a diet shift from arthropods to dreissenid mussels in round gobies (*Neogobius melanostomus*)

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ABSTRACT

The potential of predators to regulate populations of dreissenid mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis*) has been addressed since early in the dreissenid invasion of North America. Round gobies (*Neogobius melanostomus*) larger than approximately 60 mm have been shown to prey extensively on dreissenids, whereas smaller round gobies feed mainly on aquatic insects and crustaceans. We propose that ontogenetic changes in pharyngeal morphology may contribute to this diet shift in round gobies. Pharyngeals of 69 round gobies ranging from 31 to 164 mm total length were investigated using light microscopy and scanning electron microscopy. Areas of lower pharyngeals and pharyngobranchial 2 increased allometrically with fish length. Pharyngeals of round gobies smaller than 50 mm contained narrow (<0.1 mm diameter) papilliform teeth that are consistent with eating soft-bodied prey. By the time round gobies reached approximately 80 mm in length, pharyngeals contained larger diameter (0.3–0.5 mm) molariform teeth typical of those found in molluscivorous fish. Pharyngeal teeth of the largest round gobies also showed considerable wear. Although changes in pharyngeal morphology may contribute to the previously described diet shift in round gobies as they age, genetic and environmental factors both likely influence pharyngeal remodeling and therefore merit further investigation.

Introduction

The potential of North American predators, especially fish, to regulate populations of dreissenid mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis*) has been addressed since early in the dreissenid invasion. North American fish predators of dreissenids include at least 23 species belonging to 11 families (French, 1993; Kirk et al., 2001; Molloy et al., 1997). Molariform pharyngeal teeth such as those found in freshwater drum (*Aplodinotus grunniens*), copper and river redhorses (*Moxostoma hubbsi* and *Moxostoma carinatum*), and redear and pumpkinseed sunfish (*Lepomis microlophus* and *Lepomis gibbosus*) facilitate the crushing of dreissenids (French, 1993; Molloy et al., 1997).

Round gobies (*Neogobius melanostomus*) are predators of dreissenids in their native and invaded ranges, and dreissenids often dominate their diet (Andraso et al., 2011; Jude et al., 1995; Simonović et al., 2001). Round gobies have evolved anatomical and behavioral adaptations for preying on dreissenids while coevolving with them in the Ponto-Caspian region (Houghton and Janssen, in press). Like other teleost fishes, round gobies possess a pharyngeal feeding apparatus consisting of paired fifth ceratobranchials (lower pharyngeals) and paired second through fourth pharyngobranchials (upper pharyngeals) that aid the oral jaws in processing food (Helfman et al., 1997; Wainwright, 2005). Although teeth located on lower and upper pharyngeals of most percomorph fishes are relatively fine and conical (papilliform) and adapted to grasping prey during swallowing, broad (molariform) pharyngeal teeth appear to make round gobies adapted to consuming molluscs (Barel et al., 1977; French, 1993; Ghedotti et al., 1995; Houghton and Janssen, in press). That round gobies have been found to crush the majority of dreissenids they consume (Andraso et al., 2011) attests to the importance of pharyngeal teeth in their ability to prey on dreissenids.

Although round gobies larger than about 60 mm (total length, TL, unless otherwise noted) prey heavily on dreissenids, the diets of smaller individuals are typically composed of a variety of insects and crustaceans (Janssen and Jude, 2001; Jude et al., 1995). The age-related diet shift in round gobies may be related to ontogenetic changes in the pharyngeal feeding apparatus. Changes in pharyngeal morphology throughout life have been documented in other fish species and include hypertrophication of lower pharyngeals and replacement of papilliform teeth specialized for grasping prey with

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molariform teeth specialized for crushing prey (French, 1997; Hoogerhoud, 1986; Huysseune et al., 1994; Witte et al., 1990). The objective of this research was to use quantitative and qualitative analyses to determine if ontogenetic changes in pharyngeal morphology occur in round gobies collected from Lake Erie.

Methods

Round gobies were collected during the summers of 2008 and 2009 by angling and bottom trawl from the shipping channel that connects Presque Isle Bay (Erie, PA) to the main body of Lake Erie (N 42° 09.125′, W 80° 04.660′ to N 42° 09.230′, W 80° 04.369′). This is the same site used by Andraso et al. (2011) in a 2007 field study that described size-selective predation by round gobies on dreissenids. Upon capture, round gobies were euthanized with an overdose of MS-222 then fixed in 10% formaldehyde for approximately 2 weeks. After fixation, specimens were passed twice through 2-day washes of water before being stored in 70% ethanol. Gut contents of eight small (39–47 mm) round gobies collected by bottom trawl in 2009 were also identified.

Total length and sex of each fish were recorded before lower and upper pharyngeals were removed. Pharyngeals were digested in trypsin, bone-stained, and cleared in glycerol as described by Helland (2009). Briefly, the method involved placing structures in 1% (178 mM) potassium hydroxide for 1 day, clearing initially in 0.2% (0.086 mM) buffered porcine trypsin at 37 °C for 1–3 days (dependent on round goby length), bone staining in 1% (178 mM) potassium hydroxide to which alizarin red S was added at a final concentration of about 0.001% (0.03 mM) for 12–24 h, destaining in 1% (178 mM) potassium hydroxide for 1 day, and clearing finally in glycerol.

After clearing in glycerol for at least 10 days, pharyngeals were photographed in glycerol using a stereomicroscope with an integrated digital camera (Leica EZ4D). Several measurements of lower and upper pharyngeals of each specimen were made using image analysis software (ImageTool version 3.0, University of Texas Health Science Center). Length (LPL) and width (LPW) of the lower pharyngeals (Fig. 1a) were measured and used to calculate the LPL:LPW ratio for each round goby (Barel et al., 1977). Areal measurements included the area of the lower pharyngeals; vacant area bounded by the caudal border of the lower pharyngeals and a horizontal line extending between its rami; and areas of left pharyngobranchials 2–4 (Fig. 1b). Replacement teeth emerging through soft tissue of the lower pharyngeals and left pharyngobranchial 3, two of the primary force-bearing structures involved in mollusc crushing (Lauder, 1983; Wainwright, 1989), were counted. The diameter of the largest tooth on the lower pharyngeals was also measured for each round goby.

Upper and lower pharyngeals of several specimens were rinsed of glycerol in water, dehydrated in 95% ethanol, dried, and used for additional microscopic analyses. Images of upper and lower pharyngeals of representative lengths of round gobies were captured with a

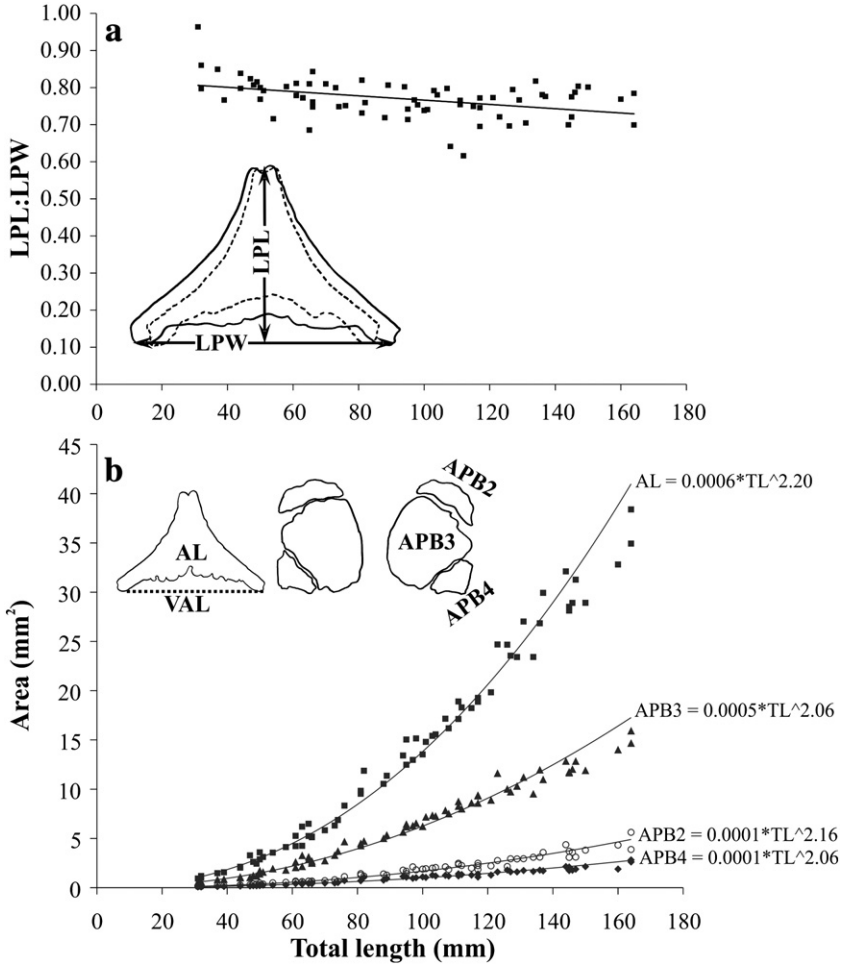

Fig. 1. a.) Ratio of length (LPL) to width (LPW) of lower pharyngeals as a function of body length for 69 round gobies collected from Presque Isle Bay, Lake Erie. Inset: superimposed outlines of lower pharyngeals of 32 mm (dashed line) and 164 mm (solid line) round gobies drawn to the same length. b.) Relationships between areas of pharyngeal structures and body length. Inset: outlines of lower (left) and upper (middle and right) pharyngeals of a round goby. Rostral is up. AL = area of lower pharyngeals (composed of paired ceratobranchial 5); VAL = vacant area behind lower pharyngeals (bounded by caudal margin of lower pharyngeals and dotted line connecting their rami); APB2, APB3, APB4 = areas of left pharyngobranchials 2–4.