Zoology 114 (2011) 340–347

Contents lists available at SciVerse ScienceDirect

Zoology

journal homepage: www.elsevier.de/zool

Jaw muscle fiber type distribution in Hawaiian gobioid stream fishes: histochemical correlations with feeding ecology and behavior

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ARTICLE INFO

Article history:
Received 14 September 2010
Received in revised form 22 February 2011
Accepted 14 May 2011

Keywords:
Muscle performance
Jaw opening performance
Feeding style
Fiber type
Gobiidae

ABSTRACT

Differences in fiber type distribution in the axial muscles of Hawaiian gobioid stream fishes have previously been linked to differences in locomotor performance, behavior, and diet across species. Using ATPase assays, we examined fiber types of the jaw opening sternohyoideus muscle across five species, as well as fiber types of three jaw closing muscles (adductor mandibulae A1, A2, and A3). The jaw muscles of some species of Hawaiian stream gobies contained substantial red fiber components. Some jaw muscles always had greater proportions of white muscle fibers than other jaw muscles, independent of species. In addition, comparing across species, the dietary generalists (*Awaous guamensis* and *Stenogobius hawaiiensis*) had a lower proportion of white muscle fibers in all jaw muscles than the dietary specialists (*Lentipes concolor*, *Sicyopterus stimpsoni*, and *Eleotris sandwicensis*). Among Hawaiian stream gobies, generalist diets may favor a wider range of muscle performance, provided by a mix of white and red muscle fibers, than is typical of dietary specialists, which may have a higher proportion of fast-twitch white fibers in jaw muscles to help meet the demands of rapid predatory strikes or feeding in fast-flowing habitats.

1. Introduction

The native ichthyofauna of Hawaiian streams consists of five amphidromous gobioid fishes. Although the taxonomic diversity of these species is limited, they exhibit diverse morphological and functional traits that can be associated with variations in their behavior and ecology (Kido, 1996a,b; Blob et al., 2006; Cediel et al., 2008; Maie et al., 2009a,b). For example, once larvae return to streams from the ocean, two of these amphidromous species (*Stenogobius hawaiiensis* and *Eleotris sandwicensis*) have ranges that are restricted to estuaries and lower stream reaches; however, juveniles from the remaining three species (*Lentipes concolor*, *Sicyopterus stimpsoni*, and *Awaous guamensis*) are able to climb waterfalls (frequently tens of meters high) and penetrate upstream habitats using prominent adhesive discs formed from fused pelvic fins (Fitzsimons et al., 1995; Nishimoto and Fitzsimons, 1999; Schoenfuss and Blob, 2003, 2007). Despite strong selective pressures imposed by the demands of waterfall climbing (Blob et al., 2008, 2010), two different functional strategies for performing this behavior have evolved in juveniles of these species (Schoenfuss and Blob, 2003; Blob et al., 2006). *L. concolor* and *A. guamensis* employ 'powerbursting', in which a rapid adduction of the pectoral fins is followed by quick axial undulations until the adhesive disc reattaches to the substrate; in contrast, *S. stimpsoni* use much slower 'inching' movements to climb, in which oral and pelvic adhesion alternate and axial undulation is limited. Correlated with the use of these different climbing strategies, juveniles of *S. stimpsoni* exhibit a much greater proportion of red muscle fibers in their axial muscles than the other climbing species, well-suited to their slower, more sustained locomotor behavior (Cediel et al., 2008).

Just as with locomotor behavior, variation in feeding behavior is also evident among amphidromous Hawaiian gobioids and may correlate with differences in the habitats of these species. For example, *L. concolor* penetrates the furthest upstream among Hawaiian stream fishes and lives in the fastest flowing water (Fitzsimons et al., 1995; Schoenfuss and Blob, 2007), feeding largely on items drifting by in the open water column (e.g., insect larvae) that are obtained with quick bursts of swimming from perches on the stream bottom (Kido, 1996b; Yamamoto and Tagawa, 2000; T. Maie, pers. obs.). In contrast, weaker-climbing *A. guamensis* are restricted to slower, lower reaches of streams and are more omnivorous than *L. concolor* (Kido, 1996b). Comparisons of feeding performance between adults of these species show that *A. guamensis* open their jaws more slowly (and thus have weaker suction-feeding performance) than *L. concolor*, a factor that may relate (and potentially contribute) to the restriction of *A. guamensis* to lower stream reaches with slower flow (Maie et al., 2009a). In contrast to

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doi:10.1016/j.zool.2011.05.005

Table 1
Hawaiian gobioid stream fishes collected for the present study on the Island of Hawai'i.

Species	N	Body mass (g)	Locality
Lentipes concolor	14	3.35 ± 0.36	Manoloa stream (5), Nanue stream (9)
Sicyopterus stimpsoni	17	4.90 ± 1.05	Nanue stream (12), Great Crack (5)
Awaous guamensis	10	6.06 ± 1.23	Hakalau stream (6), Waiakea Pond (4)
Stenogobius hawaiiensis	10	2.87 ± 0.47	Honoli'i stream (5), Waiakea Pond (5)
Eleotris sandwicensis	10	9.87 ± 2.95	Hakalau stream (5), Waiakea Pond (3), Richardson's Beach (2)

Body mass = mean ± S.E.M.; number in parentheses = number of individuals from particular locality.

locomotor behaviors, however, the functional basis for these differences in performance is less clear, as these species show differences in jaw opening performance despite possessing fairly similar jaw lever ratios (Maie et al., 2009a).

It is possible that differences in feeding performance among gobioid species, as well as differences in locomotor performance, might be correlated with differences in muscular fiber types. Myofibrillar ATP activity (i.e., glycolytic capacity or ATP hydrolytic capacity) can be viewed as reflecting muscular contractile velocity and capacity for force production (Bárány, 1967; Granzier et al., 1983; Saeki et al., 1987; Hoh, 2002; Ohnuki and Saeki, 2008). In fishes, muscle fibers with high mitochondria density, high vascularization, and low glycolytic capacity are referred to as red muscle fibers, which are suited for resisting fatigue at the expense of reduced contractile velocity and force (Burke et al., 1971, 1973; Johnston and Moon, 1980; Granzier et al., 1983). In contrast, muscle fibers with low mitochondria density and high glycolytic capacity are referred to as white muscle fibers, which generate fast and forceful twitches but have low endurance (Boddeke et al., 1959; Burke et al., 1971; Johnston and Moon, 1980; Granzier et al., 1983; Rome et al., 1988; Hoh, 2002; van Wessel et al., 2005). Although differences in red and white muscle fiber ratios in the propulsive musculature of Hawaiian gobioid fishes have been found to correlate with locomotor capacity (Cediel et al., 2008), fiber types of jaw musculature among these species have not yet been characterized in relation to physiological demands posed by their differing diets. Differences in jaw muscle fiber types have been observed in some cases across broad comparisons of other fish species with divergent feeding habits (e.g., cod with protrusible jaws compared to catfish and trout with non-protrusible jaws; Scapolo et al., 1989) and may contribute to functional differences observed among such species (Ono and Kaufman, 1983).

In the present study, we used histochemical approaches to compare the fiber types of muscles associated with feeding across Hawaiian gobioid fish species. Although the initial motivation for our work was to test for potential differences between the jaw opening muscles of *A. guamensis* and *L. concolor* as outlined above, the diversity of feeding habits among the other three amphidromous Hawaiian gobioids (Schoenfuss and Blob, 2007), as well as potential functional differences among subdivisions of jaw closing muscles (Maie et al., 2009b), led us to expand our comparisons to more broadly explore correlations between muscle histology and feeding function in this fish assemblage. With regard to feeding diversity, the climbing species, *S. stimpsoni*, is a highly specialized grazer on algal diatoms, cyclically scraping rocks with a highly protrusible premaxilla lined with tricuspid teeth (Kido, 1996b; Fitzsimons et al., 2003; Julius et al., 2005). Among the non-climbing species, *E. sandwicensis* is also highly specialized, but as a piscivore that feeds predominantly on juveniles of the other four amphidromous species as they enter streams from the ocean (Kido, 1996b; Maie et al., 2009b). In contrast, non-climbing *S. hawaiiensis* is a generalized detritivore, lacking strong teeth on their jaws but, instead, ingesting and filtering bottom sediments using their pharyngeal rakers (Kido, 1996b; Yamamoto and Tagawa, 2000; Schoenfuss and Blob, 2007; T. Maie, pers. obs.).

With regard to potential differences among the jaw closing muscles of these fishes, the adductor mandibulae complex is the primary jaw closing muscle of Hawaiian stream gobioids and is divided into A1, A2, and A3 muscle bundles in all five species we examined (e.g., Maie et al., 2009b). Our previous modeling of jaw closing function in these species based on lever mechanics predicted that A3 might be better suited for rapid jaw closing than A2 for all species (Maie et al., 2009b), but assumed the physiological properties of white fibers for all muscles and species considered (Westneat, 2003). If these muscles differ in their proportions of white and red fibers, the adjustments of model parameters required (Westneat, 2003) might either further reinforce our initial conclusions or act to counter them, depending on which muscle exhibited which proportions of fibers.

Based on the differences in diets reported for the five species of amphidromous Hawaiian gobioid fishes (Kido et al., 1993; Kido, 1996a,b) and previously measured differences in their feeding performance and jaw opening and closing muscles (Maie et al., 2009a,b), we predicted that the relative abundance of fiber types would vary among muscles in each species and for the same muscles between species. Our histochemical evaluations spanned all five species native to Hawaiian stream assemblages and sampled both jaw opening (sternohyoideus) and jaw closing (A1, A2, and A3) muscles, with the goal of refining the understanding of Hawaiian stream goby ecomorphology provided through our previous morphological and functional studies. Few studies have tested the functional significance of differences in fiber type composition of the jaw muscles in fishes relating to feeding function and ecology (e.g., Ono and Kaufman, 1983; Scapolo et al., 1989; Hernandez et al., 2005). Thus, through this study, we will help evaluate the importance of physiological properties of the jaw muscles for understanding the feeding habits, performance, and ecology of fishes.

2. Materials and methods

2.1. Specimen collection and muscle excision

Adult specimens from all five focus species ($N = 6–13$ per species) were captured from their native localities while snorkeling, using an o'pae net (i.e., prawn net). Collections were made on the Island of Hawai'i during the 2009 and 2010 field seasons (see Table 1 for stream localities). Collected fish were kept in aerated stream water at ambient temperature (18–22 °C), and housed at a research facility of the Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources (DAR) in Hilo, Hawai'i. After each fish was euthanized, the sternohyoideus and adductor mandibulae muscles (A1, A2, and A3) were excised (see Fig. 1 for the topology of these muscles), placed in 98% isopentyl alcohol (3-methyl 1-butanol; Alfa Aesar, Pelham, NH, USA), and stored in liquid nitrogen prior to being transferred to a shipping dewar for express transport to the Aquatic Toxicology Laboratory at St. Cloud State University (SCSU), Saint Cloud, MN, USA.