



Development and sexual dimorphism of the sonic system in deep sea neobythitine fishes: The upper continental slope



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ABSTRACT

The anatomy of sound production in continental-slope fishes has been ignored since the work of NB Marshall in the 1960s. Due to food scarcity at great depths, we hypothesize that sonic muscles will be reduced in deep-water neobythitine cusk-eels (family Ophidiidae). Here we describe and quantify dimensions of the swimbladder and sonic muscles of three species from the upper slope. They have four pairs of well-developed sonic muscles (two medial and two lateral) with origins on the skull and insertions on the medial swimbladder (medial pair) or on modified epineural ribs that attach to the lateral swimbladder (lateral pair). Despite minor differences, relatively similar swimbladder dimensions, muscle length and external morphology suggest a conservative body plan. However, there are major differences in sonic muscle mass: medial muscles are heavier in males and made of relatively small fibers (ca 10 μ m in diameter). Lateral muscles are generally larger in females and consist of larger fibers, as in epaxial trunk muscle. Muscle weight varies between species, and we suggest males produce advertisement calls that vary in amplitude and duration in different species. Due to differences in fiber size, we hypothesize that lateral muscles with larger fibers remain contracted during sound production, and medial muscles with smaller fibers will oscillate to drive swimbladder sound production.

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1. Introduction

Little is known about fish sound production in the deep sea, and early work on slope species by NB Marshall was based on anatomy, e.g. muscles attached to the swimbladder (Marshall, 1962, 1967). Recent passive-acoustic studies have concentrated on the continental shelf and upper slope (Mann and Jarvis, 2004; Rountree and Juanes, 2010; Rountree et al., 2012; Wall et al., 2012, 2013, 2014). A potential fish sound has been localized to about 700 m (Mann and Jarvis, 2004), but a long-term installation at similar depths failed to record definite fish sounds (Wall et al., 2014). The association of swimbladder muscles with sound production is so ubiquitous (Ladich and Fine, 2006) that sonic muscles can serve as a proxy for the ability to produce sound in lieu of direct observations (Fine and Parmentier, 2015). Owing to the low density of fishes and difficulties of recording on the continental slope, sonic anatomy will remain an important avenue for exploring this aspect of fish biology.

Fishes produce sounds via numerous independently-derived mechanisms (Ladich and Fine, 2006; Parmentier and Diogo, 2006;

Fine and Parmentier, 2015), the most common of which involves super-fast muscles that drive the swimbladder into vibration (Skoglund, 1961; Connaughton et al., 2000; Connaughton, 2004; Fine et al., 2001; Millot et al., 2011). In the toadfish, for instance courtship boat whistles with a 200 Hz fundamental frequency require 200 contractions per second from paired sonic muscles intrinsic to the swimbladder (Fine et al., 2001). Furthermore, these muscles can follow an electrical stimulus at 400 Hz without tetanizing. The swimbladder produces sounds as a forced rather than a resonant response (Fine, 2012; Fine and Parmentier, 2015).

Recently slow muscles have been found in carapid fishes (Parmentier et al., 2006b). Rather than completing a twitch in about 10 ms as in the toadfish (Skoglund, 1961; Fine et al., 2001), they require ca 500 ms for a twitch and tetanize at about 10 Hz. The carapid swimbladder can be divided into three regions: the anterior edge for sonic muscle attachment, followed by a stretchable fenestra, and then the remainder of the swimbladder, which is firmly attached to the vertebral column. Sonic muscles from the head pull the anterior swimbladder forward, and sounds are produced during rebound when the swimbladder snaps back to its resting position exciting vibrations of the bladder and the swimbladder plate, a specialized rib that sits over the fenestra. An

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intermediate condition has been found in unrelated glaucosomatid, pempherid and terapontid fishes (Mok et al., 2011; Parmentier et al., 2016) that shares parallels with slow muscle mechanisms, including head muscles that attach to the anterior swimbladder, a fenestra followed by firm attachments of the remainder of the bladder to the vertebral column. A glaucosomatid sound pulse has two parts: a weak but rapid pre-pulse indicative of a fast head muscle contraction and a second more intense part caused by rebound of the bladder via a stretched tendon, e.g. a slow type mechanism activated by a fast muscle (Mok et al., 2011).

The largely deep-sea family Ophidiidae, related to the carapids with slow muscles, includes two major subfamilies: the Ophidiinae and Neobythitinae (Nielsen et al., 1999). The Ophidiinae contains eight genera and about 40 species, and the more speciose Neobythitinae has 38 genera and about 160 species (Nielsen et al., 1999). Sounds have been recorded from only two shallow-water species, both in the Ophidiinae: the striped cusk-eel *Ophidion marginatum* (Mann et al., 1997; Sprague et al., 2001; Rountree and Bowers-Altman, 2002; Mooney et al., 2016) and *Ophidion rochei* (Kéver et al., 2014a, 2014b). Before the discovery of rebound following slow muscle contraction, the mechanism for generating courtship calls of the striped cusk-eel *O. marginatum* was unclear because their peak frequency is above 1 kHz (Mann et al., 1997; Sprague et al., 2001), too high to be produced by individual rapid muscle contractions. In slow systems muscle contraction determines the number of pulses but not the frequency in the pulse (Parmentier et al., 2010, 2016; Mok et al., 2011).

Sonic systems of the Ophidiinae are complex with atypical antagonistic muscle pairs (ventral, intermediate and dorsal muscles), and a number of adaptations that are not present in all species including a neural arch above the first vertebra that can pivot in the anteroposterior plane (the neural rocker), modified anterior ribs including the winglike process and swimbladder plate, a rocker bone (a bean-shaped bone protruding from the front of the swimbladder in some but not all species), a swimbladder with a fenestra, and in some cases a posterior ring encasing a membrane, a likely pressure-release system (Rose, 1961; Courtenay, 1971; Parmentier et al., 2006a; Fine et al., 2007; Nguyen et al., 2008, 2010; Kéver et al., 2012). Recent work has begun to explore the physiology and sounds of *O. rochei*, and surprisingly females appear to have fast sonic muscles (Kéver et al., 2014b).

Sounds have never been recorded from any species in the Neobythitinae due to their depths on the continental slope, and the sonic system has been described in a single species *Barathrodemus manatinus* collected between 1800 and 2600 m in the Bahamas (Carter and Musick, 1985; see also Marshall, 1967 and Howes, 1992). Its body is sexually dimorphic, and females have deeper more robust bodies than males. Carter and Musick describe a ventrolateral sonic muscle in males that originates on the ventrolateral surface of the prootic region of the skull, curves medially and inserts on the medial anterior swimbladder wall. Additionally, a ventromedial muscle from the ventromedial prootic inserts on wide ribs of the fourth vertebra. The authors comment that the ventromedial muscles are close to the swimbladder but apparently do not contact it. Females have only the ventromedial muscles and could be mute.

The sonic system of *B. manatinus* is simpler than any described in the sister subfamily Ophidiinae, which includes species that can live in shallow water near-shore (Nielsen et al., 1999). The effects of adaptation to deeper water that include reduced food (Gartner, 1997; Sutton et al., 2010) and increased hydrostatic pressure (Angel, 1997; Bochus and Seibel, 2016) are unknown. As the first part of an effort to investigate changes in the sonic system of neobythitines from shallow to great depths, we describe the sonic system and quantify growth and sexual dimorphism of three

relatively shallow-water species from the upper continental slope of Southern Taiwan. We hypothesize that upper slope species will have a more developed sonic system than ones from great depths (mid and lower slope).

2. Materials and methods

Three relatively shallow neobythitine species, *Hoplobrotula armata* (Temminck and Schlegel, 1846), *Neobythites longipes* (Smith and Radcliffe, 1913) and *N. unimaculatus* (Kamohara, 1938) (Fig. 1), were collected from the upper continental slope. *H. armata* occurs from 200 to 350 m, *N. longipes* from 300 to 480 m and *N. unimaculatus*, with a broader depth range, from 100 to 580 m (Masuda et al., 1984; Nielsen et al., 1999; Iwamoto and McCosker, 2014).

The specimens were purchased from the Overseas Chinese Market at the harbor in Donggang Township (120° 26'E, 22°28' N), Pingtung County, Taiwan. They were caught by bottom trawls at the fishing ground adjacent to the waters of Liueqi island (Township; 120°22'E, 22°22'N, located off the shore of Donggang Township). The fishing ground was on the upper continental slope around 200–300 m. Specimens were fixed in 10% formalin, measured for total length (TL) in cm and weighed in grams. Fish were dissected to determine sex and expose the swimbladders and sonic muscles whose origins and insertions were determined. Swimbladders were measured for length and width in mm at their widest point, and muscles were measured for length in mm while still attached in the fish. Muscles were removed, soaked in 0.9% NaCl for 5 min to insure uniform hydration and weighed in mg. Two to four medium and larger individuals from each species were placed in hot water to remove the tissues and expose the skeleton, which was further cleaned in 3% hydrogen peroxide.

Quantitative measurements from the swimbladder and sonic muscles were regressed against fish size (muscle and bladder weights against fish weight and linear dimensions against total length). Male and female regressions were compared with analysis of covariance (ANCOVA), and adjusted means were calculated using regressions for fish of 25 cm TL and 75 g. Regressions were compared between species using ANCOVA although for simplicity we show comparisons of percent muscle length (sonic muscle length index, SMLI) and weight (sonic muscle somatic index, SMSI), calculated respectively by dividing muscle length by fish TL and muscle weight by fish weight with quotients multiplied by 100. SMLI and SMSI for species and sexes were compared by ANOVA followed by Tukey's test.

Sonic and epaxial muscles from one male and one female of each species were sectioned at 10 µm on a cryostat and stained in methylene blue. We measured the diameter of 30 fibers from each muscle. Because some fibers exhibited a somewhat longitudinal orientation and the tendency of many sonic fibers to be slightly oval in cross section, we measured the minimum diameter of each fiber at its widest point.

3. Results

Hoplobrotula armata ranged from 14.7 to 29.9 cm TL and from 19.3 to 178.2 g and included 18 males and 15 females (Fig. 1). *Neobythites longipes* ranged from 18.7 to 30.1 cm TL and 30.8–148.1 g and included 11 males and 12 females. *Neobythites unimaculatus* ranged from 15.3 to 25.4 cm TL and 19.6–112.5 g and included 5 males and 8 females. Fish appeared monomorphic, and we were unable to distinguish sex externally in these species.

We will describe sonic morphology followed by quantitative treatments. Sexual dimorphism was determined qualitatively by examining morphology and quantitatively from regression

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