Zoology 119 (2016) 207–215

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

Functional morphology of gill ventilation of the goosefish, *Lophius americanus* (Lophiiformes: Lophiidae)

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ARTICLE INFO

Article history:
Received 2 September 2015
Received in revised form
13 November 2015
Accepted 27 January 2016
Available online 24 February 2016

Keywords:
Anglerfish
Gill opening
Branchiostegal ray
Crypsis
Ambush predator

ABSTRACT

The goosefish, *Lophius americanus*, is a dorso-ventrally compressed marine fish that spends most of its life sitting on the substrate waiting to ambush prey. Species in the genus *Lophius* have some of the slowest ventilatory cycles recorded in fishes, with a typical cycle lasting more than 90 s. They have a large gill chamber, supported by long branchiostegal rays and ending in a siphon-like gill opening positioned underneath and behind the base of the pectoral fin. Our goals were to characterize the kinematics of gill ventilation in *L. americanus* relative to those of more typical ray-finned fishes, address previous assertions about ventilation in this genus, and describe the anatomy of the gill opening. We found that phase 1 of ventilation (during which both the buccal and gill chamber are expanding) is greatly increased in duration relative to that of typical ray-finned fishes (ranging from 62 to 127 s), and during this phase, the branchiostegal rays are slowly expanding. This slow expansion is almost visually imperceptible, especially from a dorsal view. Despite this unusually long phase 1, the pattern of skeletal movements follows that of a typical actinopterygian, refuting previous assertions that *Lophius* does not use its jaws, suspensorium, and operculum during ventilation. When individuals were disturbed from the sediment, they tended to breathe more rapidly by decreasing the duration of phase 1 (to 18–30 s). Dissections of the gill opening revealed a previously undocumented dorsal extension of the adductor hyohyoideus muscle, which passes from between the branchiostegal rays, through the ventro-medial wall of the gill opening, and to the dorsal midline of the body. This morphology of the adductor hyohyoideus shares similarities with that of many Tetraodontiformes, and we suggest that it may be a synapomorphy for Lophiiformes + Tetraodontiformes. The specialized anatomy and function of the gill chamber of *Lophius* represents extreme modifications that provide insight into the potential limits of the actinopterygian gill ventilatory system.

1. Introduction

Active ventilation of the gills is a critical process for fishes, allowing them to exchange gases and ions with the environment and excrete some metabolic wastes. Because ventilation is an energetically expensive process for ray-finned fishes (Actinopterygii) that comprises 5–15% of the total metabolic budget (Cameron and Cech, 1970; Edwards, 1971; Farrell and Steffensen, 1987), fishes have evolved many adaptations for increased respiratory efficiency. These adaptations include maximizing surface area of the gill tissue, minimizing diffusion distance across the gill epithelium, and maximizing the oxygen partial pressure gradient between the blood and water (Hughes, 1966). The latter is achieved through a system of counter-current exchange in which blood in vessels of the gill lamellae flows in the opposite direction of oxygenated water (Hughes and Shelton, 1958). Establishing this unidirectional flow of water over the gills requires coordination of many cranial components. Given the diversity in cranial morphology and metabolic requirements among ray-finned fishes, we can expect to find a great variety of strategies for efficient pumping. However, functional variation in aquatic ventilatory pumps has received little attention.

Gill ventilation in most species of ray-finned fishes relies on changes in pressure driven by pumps in two chambers: the mouth (buccal chamber) and gill chamber. As shown in Fig. 1, these pumps alternate between suction (expansion to create negative pressure, drawing in water) and pressure (compression to create positive pressure, forcing out water; Hughes and Shelton, 1958; Hughes, 1960; Brainerd and Ferry-Graham, 2006). As defined by Hughes and

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http://dx.doi.org/10.1016/j.zool.2016.01.006
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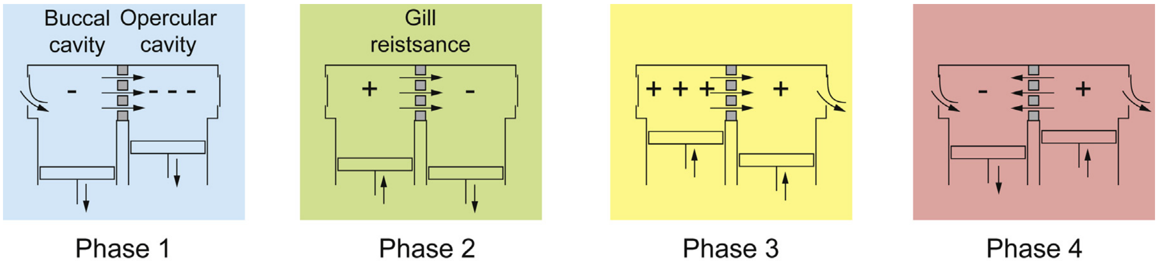

Fig. 1. Four phases of gill ventilation used by actinopterygians. During phase 1, both the buccal and gill chambers are expanding to produce negative pressure and take in water. During phase 2, the buccal chamber begins to compress. During phase 3, both chambers compress to produce positive pressure and force water out of the gill opening. During phase 4, the buccal chamber begins to expand, transitioning back to negative pressure to draw in water. Based on Brainerd and Ferry-Graham (2006), Summers and Ferry-Graham (2002), and Hughes (1960).

Shelton (1958), each ventilatory cycle begins with expansion of the buccal chamber, which draws water into the mouth. The gill chamber then expands, which draws water from the mouth over the gills. The buccal chamber then compresses to force water from the mouth over the gills. Finally, compression of the gill chamber forces water out of the gill opening. The gill tissues introduce resistance between the two chambers, limiting backflow during the transition from pressure back to suction. Changes in buccal chamber pressure are driven by movements of the jaw, suspensorium, and hyoid apparatus, and changes in gill chamber pressure are driven by the opercular bones (opercle, subopercle, and interopercle) and the branchiostegal apparatus (Liem, 1970). The relative timing of these movements and the resulting pressure changes vary considerably among taxa (Hughes, 1960), and there is substantial variation in the anatomy of the skeletal elements and musculature involved, particularly in the branchiostegal apparatus (McAllister, 1968). There is also significant morphological variation in the external openings of the buccal and gill chambers; for example, gill openings can be very large with a wide valve, or they can be restricted to a tiny aperture variably positioned on the head (McAllister, 1968; Farina et al., 2015).

The goosefish, *Lophius americanus*, is a commercially valuable marine fish common in waters off the northeastern coast of North America at depths ranging from just subtidal to over 900 m (Caruso, 2002; Richards et al., 2008). It is dorso-ventrally flattened, and its head is large for its body size (Fig. 2B). As in other anglerfishes (Lophiiformes) such as frogfishes, batfishes, and seadevils, it has an elongated first dorsal spine that has migrated to the front of the head where it supports a fleshy lure known as an esca. Species in the genus *Lophius* differ primarily in pectoral fin ray counts, shape of the esca, and dorsal spine length (Caruso, 1983). All are ambush predators that spend most of their adult life sitting on sandy, muddy, or rocky substrates, using their lure to attract fishes and other prey (Chadwick, 1929; Wilson, 1937; Gudger, 1945). When suction feeding, they rapidly expand the buccal cavity by means of hyoid and jaw depression, combined with a large degree of cranial elevation (Elshoud, 1986). When not feeding, they remain cryptic by matching skin colors to the substrate and using the pectoral fins to create recesses in the sediment (Wilson, 1937; Laurenson et al., 2004).

In his behavioral description of *Lophius piscatorius*, Wilson (1937) noted exceptionally slow ventilation, with individuals taking approximately 60–180 s to complete a single ventilatory cycle. Most other species of ray-finned fishes require 0.5–6 s to complete a ventilatory cycle (Hughes, 1960). The slow ventilation of *Lophius* is potentially related to low metabolic demands (evident from the low surface area of their gill lamellae; Hughes, 1966) and a need to remain cryptic as intermittent and opportunistic feeders (Armstrong et al., 1996; Laurenson and Priede, 2005; Fariña et al., 2008; Valentim et al., 2008). They increase their ventilatory rate immediately after feeding events (Wilson, 1937) or when they are disturbed from their sediment recesses. Their ventilatory anatomy

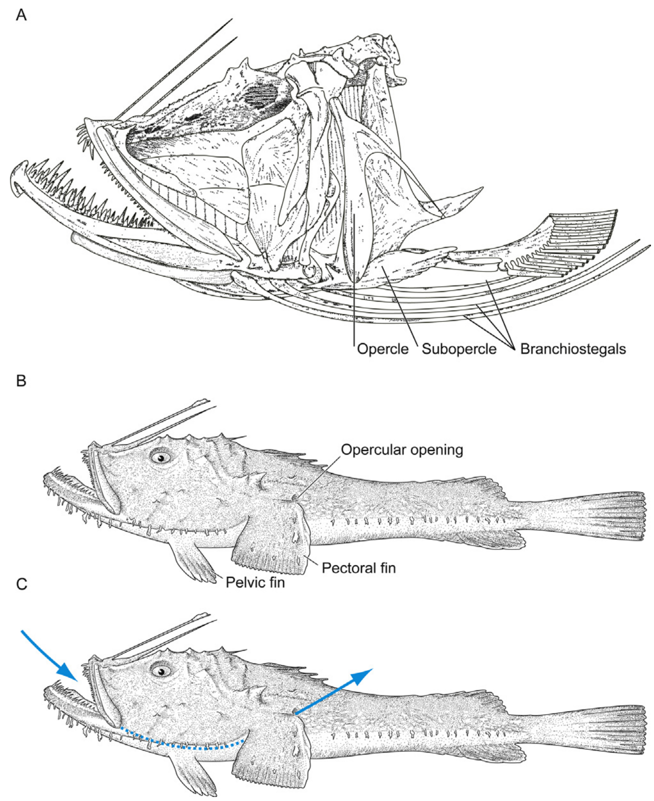

Fig. 2. Cranial skeletal and external anatomy of *Lophius*. (A) The large gill chamber consists of an L-shaped operculum and elongated branchiostegal rays that pass under the pectoral girdle. (B) The gill opening is located in the axillary region, posterior and ventral to the pectoral fins. (C) Water comes in through the mouth and passes over the gills to enter the large gill chamber. It then passes under the pectoral fin and out the gill opening. The illustration of cranial anatomy (A) is redrawn from Gregory (1933) and the illustration of external anatomy is modified from Liem et al. (2001).

consists of a large buccal cavity with a pronounced oral valve, an L-shaped operculum, six elongate branchiostegal rays, and a gill opening ventral and posterior to the pectoral fin (Fig. 2). As in other Lophiiformes, the gill opening is relatively small and siphon-like, forming a tube upon exhalation. The long branchiostegal rays and posterior position of the gill opening create a much larger gill chamber than is typical for actinopterygians.

L. americanus represents an extreme of fish ventilatory anatomy and function with its exceptionally slow ventilation and enormous gill chamber. It is therefore an important species to investigate when considering limits of the gill ventilation system of ray-finned fishes. Our first goal is to characterize the kinematics of gill ventilation in *L. americanus* and make comparisons to those of more typical ray-finned fishes. We also address some previous assertions