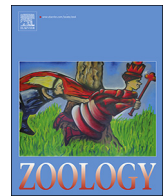




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Stealth breathing of the angelshark

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ABSTRACT

For benthic fishes, breathing motion (e.g., oral, pharyngeal, and branchial movements) can result in detection by both prey and predators. Here we investigate the respiratory behavior of the angelshark *Squatina japonica* (Pisces: Squatiniformes: Squatinidae) to reveal how benthic elasmobranchs minimize this risk of detection. Sonographic analyses showed that the angelshark does not utilize water-pumping in the oropharyngeal cavity during respiration. This behavior is in contrast with most benthic fishes, which use the rhythmical expansion/contraction of the oropharyngeal cavity as the main pump to generate the respiratory water current. In the angelshark, breathing motion is restricted to the gill flaps located on the ventral side of the body. We suspect that the gill flaps function as an active pump to eject water through the gill slits. This respiratory mode allows conspicuous breathing motion to be concealed under the body, thereby increasing crypsis capacity.

1. Introduction

Generation of a respiratory water current over the gills is essential for effective gas exchange across the gill surface in fish. Previous studies have shown that the majority of fish, including benthic elasmobranchs (sharks and batoids), achieve this function by buccal pumping (e.g., Brainerd and Ferry-Graham, 2006). Buccal pumping is a mechanism that utilizes rhythmical volume changes of the oropharyngeal cavity to generate a respiratory water current. As the oropharyngeal cavity expands, water is drawn in through the mouth and/or spiracles and forced over the gills by oropharyngeal compression, which involves closure of the mouth/spiracles and expansion of the parabronchial cavity (Hughes, 1960, 1965; Ferry-Graham, 1999; Brainerd and Ferry-Graham, 2006). Hitherto, this mechanism has only been documented for a small number of cartilaginous species, such as *Scyliorhinus canicula*, *Cephaloscyllium ventriosum*, *Raja clavata*, and *Leucoraja erinacea* (Hughes, 1960, 1965; Ferry-Graham, 1999; Summers and Ferry-Graham, 2001).

The present study aimed to investigate a newly observed respiratory behavior in the Japanese angelshark (*Squatina japonica*). The angelshark is a benthic specialist with a dorso-ventrally compressed, batoid-like body morphology (Compagno, 1984). One of the characteristics of its respiration system is its apparent lack of movement. A captive angelshark at Okinawa Churaumi Aquarium, Okinawa, Japan, has been observed to exhibit no respiratory motions that characterize buccal pumping (e.g., rhythmic movements of the mouth, spiracle valve, and

pharyngeal region) when resting on the bottom of the tank. This observation suggests that respiration in angelsharks does not employ buccal pumping. The ostensibly motionless respiration system of the angelshark was previously documented by Darbishire (1907), although technological limitations prevented an internal kinematical observation, thus prohibiting a detailed analysis on the breathing mechanism of the species.

The purpose of the present study was firstly to describe the internal and external respiratory behavior of the angelshark, and secondly to discuss the ecological significance of this species.

2. Materials and methods

2.1. Kinematics

Two captive Japanese angelsharks, specimen A and specimen B (51.5 cm and 96.0 cm total length (TL), respectively), were used for the kinematical observations. Both specimen A (male), and specimen B (female), were kept in a tank at Okinawa Churaumi Aquarium for more than a year before the experiment. Specimen A was transferred from the original tank to an acrylic aquarium (170 liters) one hour prior to the experiment. The sides and bottom of the aquarium were transparent, allowing for video monitoring of the fish's oral and opercular motions using two digital video cameras, Panasonic HC-W870 M (Panasonic Co., Osaka, Japan) and Sony DCR-SR220 (Sony Co., Tokyo, Japan).

Specimen B was transferred from the original tank to a portable

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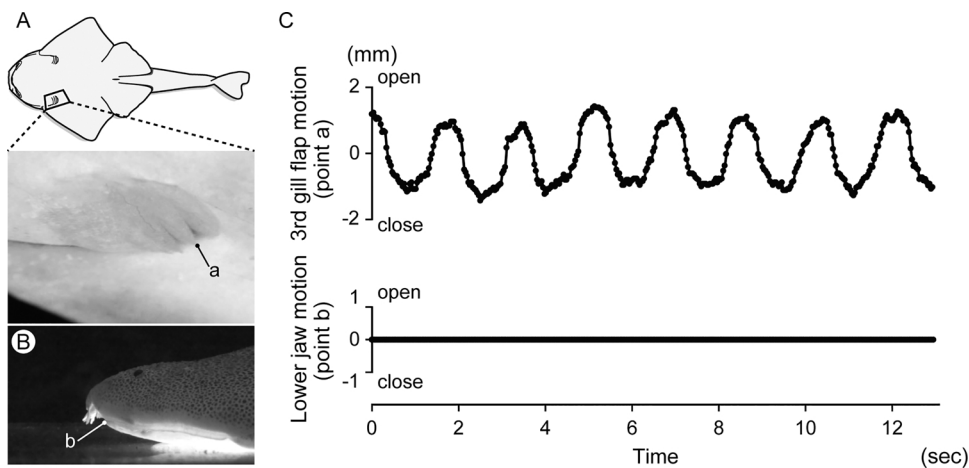


Fig. 1. Gill flap and jaw kinematics of the angelshark during respiration. A. Right-side gill regions of specimen A, showing the posterior-most point of the third gill flap (point a), which was used for kinematical analysis. B. Left lateral view of the head of specimen A showing the anterior tip of the lower jaw (point b). C. Displacement of points a and b over time.

container (500 liters). A transparent acrylic panel was set at a depth of 30 cm, upon which the fish was placed. A mirror was placed on the bottom of the container, which enabled observation of the ventral side of the fish. Video monitoring of the motion of the mouth, pharyngeal area, and gill flaps, was carried out using a digital video camera, Olympus Tough TG-4 (Olympus Imaging Co., Tokyo, Japan). In order to track the flow of water through the respiratory tract, a syringe was used to deliver water-diluted squid ink and cow milk adjacent to the mouth, spiracle, and gill slits of each specimen. During the experiments, the water temperature was maintained at 14 °C in keeping with that of the original tank.

Following video recording, still images were captured from the footage for specimen A using the movie editing software, KMplayer 2.9.4.1.1435 (Jelsoft Enterprises Ltd., Pangbourne, UK). The capture rate was 29 and 29.5 frames per second for mouth and gill flap motions, respectively. From each still image, coordinates of the distal-most point of the third gill flap (point a in Fig. 1) and anterior tip of the lower jaw (point b in Fig. 1) were acquired using ImageJ (US National Institutes of Health, Bethesda, MD, USA).

In addition to visual monitoring, sonographic experiments were carried out to observe internal movements in each fish during respiration. Each specimen was placed in a plastic tray with seawater and fitted with an ultrasonic transducer on the dorsal and ventral surfaces. We used ARIETTA Prologue (Hitachi-Aloka Medial Ltd., Tokyo, Japan) and FAZONE M (Fujifilm Co., Tokyo, Japan) sonographic diagnostic imaging systems for specimens A and B, respectively. Sonographic data were imported to ImageJ, and coordinates of the anterior-most point of the lower jaw (Meckel's cartilage; point a in Fig. 2) and the anterior-most point of the hyoid apparatus (basihyal cartilage; point b in Fig. 2) were obtained. In sonography, the outline of internal structures is sometimes vague, and thus the landmark collection from these structures involves some uncertainty. Therefore, the precision of our sampling method was estimated by calculating the standard deviation for 30 repeated coordinate samples for points a and b from the single still image captured from the ultrasound.

2.2. Anatomy

After the kinematical observations, specimens were euthanized with phenoxyethanol and placed in formalin for anatomical analysis. We calculated the relative gill flap length (r) using the equation:

$$r = L_{gf} / L_s$$

where L_s (length of the interbranchial septum) is defined as the linear distance between the gill-arch articulation and the distal margin of gill filaments; L_{gf} (length of gill flap) as the linear distance between the distal margin of gill filaments and the free margin of the gill slit

(Fig. 3A). Morphometric measurements were obtained using a hand caliper. For comparison, we also looked at the gills of five benthic/benthopelagic shark species: *Centrophorus moluccensis* (TL = 74 cm), *Cephaloscyllium umbratile* (TL = 84 cm) and *Orectolobus japonicus* (TL = 102 cm), *Proscyllium venustum* (TL = 66 cm), *Squalus cf. mitsukurii* (TL = 55 cm).

To obtain imagery of the angelshark's skeletal anatomy, we used computed tomography (CT) data. CT setting and specimen information can be found in Tomita et al. (2012). Three-dimensional reconstructions were prepared from CT-slices (1.25 mm interval) using DICOM editing software, AZE VirtualPlace (AZE Ltd., Tokyo, Japan).

The anatomical terminology follows that described by Shirai (1992).

3. Results

3.1. Kinematics

External observation of breathing motions in specimens A and B showed that their mouths remained stationary and slightly open (Movie S1 in the supplementary online Appendix). Spiracles also remained open during respiration. Gill flaps actively moved and gill slits rhythmically opened and closed (Movies S2 and S3 in the supplementary online Appendix). One or two pulse waves were continuously transmitted from the proximal to the distal portion of the gill flaps (Fig. 4; Movie S3 in the supplementary online Appendix). The average respiratory frequencies (\pm SD) were 57.4 (\pm 10.5, based on 7 times the measurement) min^{-1} and 51.7 (\pm 4.1, based on 6 times the measurement) min^{-1} for specimens A and B, respectively.

Flow visualization with water-diluted milk or squid ink showed that water was continuously taken in by both specimens through the mouth and spiracles and ejected through the gill slits. Upon expulsion, the water passed over the ventral side of the pectoral fin in a tail-ward direction and diffused into the surrounding water around the posterior margin of the pectoral fin.

Ultrasound footage for each specimen showed that the jaws (palatoquadrate and Meckel's cartilage) and hyoid apparatus (basihyal cartilage) were immobile during the experimental trials (Fig. 2; Movie S4 in the supplementary online Appendix), with jaw and hyoid cartilage coordinates remaining almost unchanged, barring minor fluctuations (Fig. 2D). These fluctuations were probably due to sampling error during landmark collection, because: 1) more than 95% of all points were between \pm 1 pixels (\pm 0.15 mm), a range much smaller than that found in other species with buccal pumping (e.g., > 10 pixels in a 70 cm TL neonate tiger shark, Tomita, unpublished data); and 2) the standard deviation of the fluctuations (0.82 and 0.76 pixels, in the lower jaw and hyoid cartilage, respectively) does not significantly

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