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KINEMATICS AND POWER OUTPUT OF JET PROPULSION BY THE FROGFISH GENUS *ANTENNARIUS* (LOPHIIFORMES: ANTENNARIIDAE).—Jet propulsion is used as a means of aquatic locomotion by some soft-bodied invertebrates (Trueman, 1980), as well as fish (Breder, 1926; Wolf, 1963; Gradwell, 1971). Jet propulsion requires a body form which can: 1) allow a large mass of water to be forcibly expelled; and 2) expand after contraction to take in more water for additional thrust (Trueman, 1975). Pulsed water jets generate large thrust forces for a given mass of water expelled (Weihs, 1977).

Breder (1924, 1926) argued that the force of water exhaled from the gill openings in fish could be utilized for jet propulsion. Gradwell (1971) reported that banjo catfish (Aspredinidae) are able to locomote by jet propulsion using opercular exhalations. In the Antennariidae, *Histrio histrio* has been observed previously locomoting by jet propulsion (Wolf, 1963), and

Pietsch and Grobecker (1987) have reported jet propulsion by frogfish at velocities of 0.2–1.25 standard length/sec. Although the swimming speed and position of the fins were described in the frogfish, the energetic expenditure of jet propulsion by these fish was not considered.

Antennarius has a short, globose body form with a large mouth and oral cavity (Grobecker and Pietsch, 1979; Pietsch, 1984). In three species of *Antennarius* the oral cavity is capable of at least a 12 fold expansion (Grobecker and Pietsch, 1979). The opercular opening of *Antennarius* is restricted to a small, tube-like opening positioned posterior to the base of the pectoral fin (Pietsch, 1984). The constricted opercular openings and large oral cavity, in conjunction with pulsed water jets due to respiratory movements, can act effectively in jet propulsion (Pietsch and Grobecker, 1987). Additionally, the constricted apertures increase the effectiveness of the jet action by increasing its duration (Trueman, 1980).

Jet propulsion was observed on many occasions in three commercially obtained frogfish (standard lengths = 8.4, 9.1, 10.2 cm with a mean opercular diameter of 3.5 mm ± 0.6 SE). The frogfish used jet propulsion while swimming horizontally or when taking off from the bottom of a 42 liter aquarium. During jet propulsion, the pectoral fins were extended laterally from the body with the distal-fin rays abducted, the anteroventrally positioned pelvic fins were protracted with the distal-fin rays abducted, and the caudal fin was slightly abducted and held straight or laterally flexed. At no time during jet propulsion were fins or tail used in the generation of thrust as reported by Pietsch and Grobecker (1987). Although jet propulsion may have been used in conjunction with finned propulsion during rapid swimming by *Antennarius*, it could not be detected.

One of the frogfish (8.4 cm standard length), while horizontally jet propelling, was filmed at 50 frames/sec. Frame-by-frame analysis of the film was made with a stop-action projector.

The frogfish jet propelled at a velocity ranging from 2.3–2.7 cm/sec, which represented 0.27–0.32 standard length/sec. The jet action was generated by pulses of water forced through the constricted opercular openings during the normal respiratory cycle. Since the opercular openings are located at the posterior base of the pectoral fins, and are therefore located below the center of gravity of the fish, the pulsed expulsion of water from the openings produced a

rotation in the sagittal plane (pitch). The oscillations of the pitching movement were equal to the frequency of ventilatory pulsations. The frequency of the movements was 0.38 Hz. This represents a higher frequency than the ventilatory movements of resting fish (Hughes and Shelton, 1958; Hughes, 1960; Lauder, 1984), but was consistent with the rate of gill ventilation for exercising fish (Roberts, 1975) and jet propulsion by banjo catfish (Gradwell, 1971). Pietsch and Grobecker (1987) considered the biomechanics of jetting by frogfishes to be related to their respiratory movements.

Examination of pitching motion of the body showed the power and recovery phases of the jetting cycle as = 1.3 sec each. This is within the range of time for the period of water expulsion (1.2–2.1 sec) observed in *Histrio* (Wolf, 1963).

Jet propulsion at high velocities is considered to have a low efficiency compared to caudal fin propulsion (Alexander, 1977) and may thus be energetically costly to perform. A drag balance and water channel, described by Fish (1984), were used to determine the power output necessary to propel the fish. Each specimen was tested four times over a velocity range of 0.7–7.6 cm/sec. To remove variation due to differences in size and the test velocities of the three anglerfish, the power output was expressed as a function of the dimensionless Reynold's Number (R). Power output displayed a positive correlation with R according to the equation: Power Output (ergs/sec) = 0.00097 R^{1.63} (r = .993; df = 1; .05 < P < .1). For the anglerfish jet propelling at 2.7 cm/sec. (R = 2761.7) and frontal area of 51.0 cm², the estimated power output was 358.2 ergs/sec and the drag coefficient was 0.71. The lateral extension of the fins would be expected to increase the hydrodynamic drag experienced by the fish. However, the position of the pectoral fins was necessary to prevent restricting the opercular openings. Pietsch and Grobecker (1987) stated that the fins were used as hydrofoils to maintain stability while *Antennarius* was jet propelling.

The energetic cost, based on power output, and the drag coefficient are high compared to other fish utilizing finned propulsion (Webb, 1975; Blake, 1983). Jet propulsion may not be used extensively due to its high energy demands.

The occurrence of a jet mechanism in *Antennarius* and other antennariids, such as *Histrio*, may be more a consequence of feeding mode

than effective locomotion. *Antennarius*, which are benthic, use an energy-saving prey capture tactic in which they mimic sponges and encrusted rocks, attracting prey with a fleshy lure (Pietsch and Grobecker, 1978). The prey is then drawn into the mouth by negative pressure developed inside the large mouth cavity (Grobecker and Pietsch, 1979). The tactic of deceptive mimicry requires that body movement be kept to a minimum. By constricting the opercular apertures, and positioning them ventrally behind the maximum girth of the body, respiratory movements may go undetected.

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