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High-Speed Cinematographic Evidence for Ultrafast Feeding in Antennariid Anglerfishes

Abstract. *Analyses by means of high-speed, light cinematography at 800 and 1000 frames per second have shown that members of the shallow-water anglerfish genus* Antennarius *are capable of producing an enormous suction pressure for prey capture by means of an extraordinarily rapid expansion of the buccal and opercular cavities. Prey is totally engulfed at speeds considerably greater than those recorded for any other fish. The structural adaptations responsible for this rapid prey engulfment provide anglerfishes with one of the fastest known vertebrate feeding mechanisms.*

Early comparative studies of the biomechanics of feeding in fishes were based solely on anatomical data (*1*). More recently, however, anatomical data have been integrated with functional data obtained through the use of living material and cinematographic and electromyographic techniques (*2*). The addition of these new techniques to anatomical analyses largely avoids the problems of extrapolating function from form and has provided a more accurate assessment of the role of individual bones, muscles, and ligamentous connections during feeding activity. In the past, cinematographic analyses have been limited to film speeds of 18 to 250 frames per second (*2a*). It has been suggested, however, that higher speeds in filming might reveal that single feeding events in fishes occur at greater speeds than previously believed (*2*). We report single feeding events in three species of shallow-water anglerfishes of the genus *Antennarius* filmed at speeds of 800 and 1000 frames per second, showing that mouth cavity (buccal and opercular cavities) expansion and subsequent prey capture take place at speeds that are more than four times greater than those described for fishes (*3*).

The Antennariidae, largest of the four families of the lophiiform suborder Antennarioidei, includes with few exceptions, shallow to moderately deep-water bottom dwellers with representatives in tropical and temperate waters of all major oceans and seas of the world (*4*). They are structurally and chromatically cryptic forms whose piscivorous

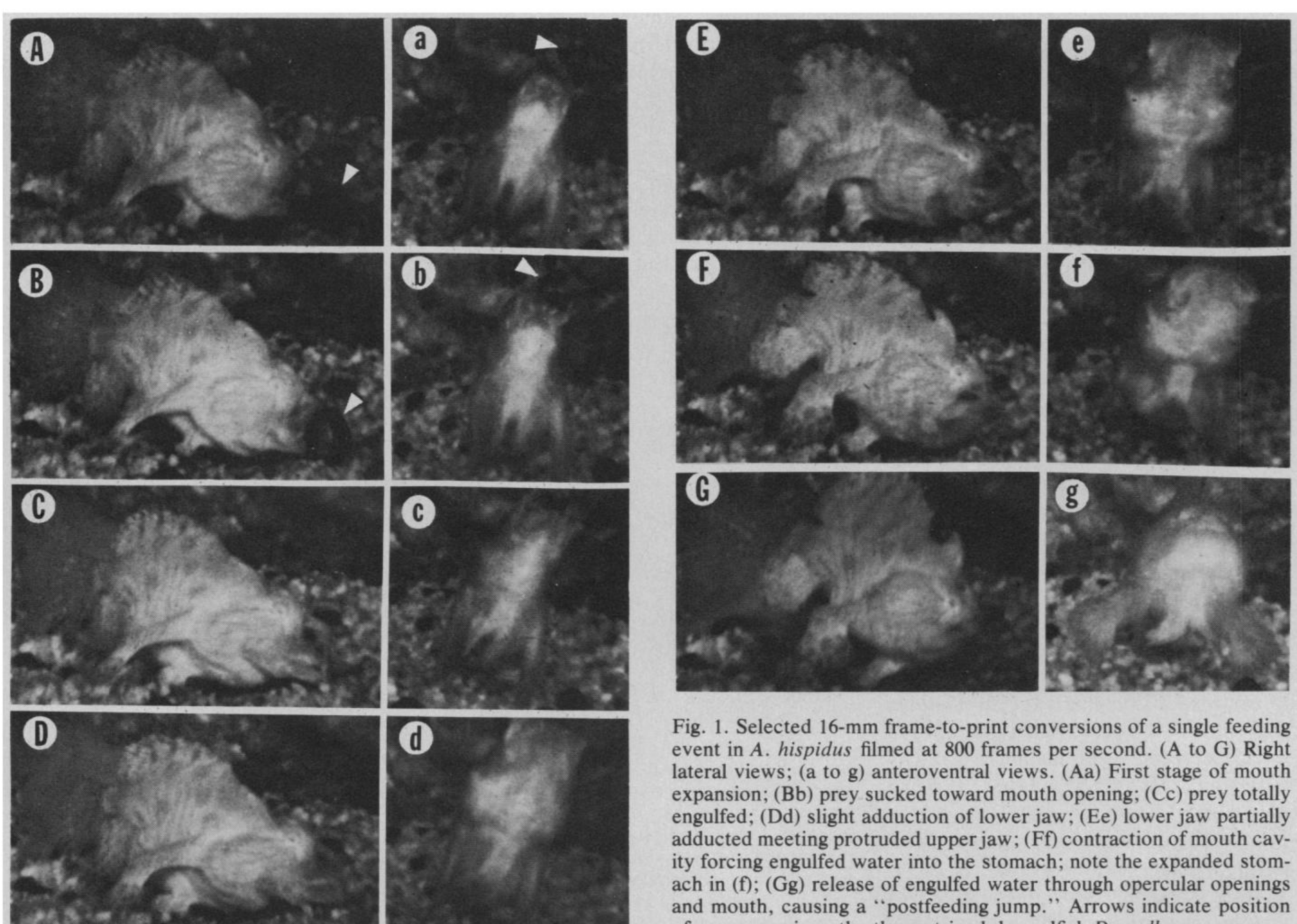

Fig. 1. Selected 16-mm frame-to-print conversions of a single feeding event in *A. hispidus* filmed at 800 frames per second. (A to G) Right lateral views; (a to g) anteroventral views. (Aa) First stage of mouth expansion; (Bb) prey sucked toward mouth opening; (Cc) prey totally engulfed; (Dd) slight adduction of lower jaw; (Ee) lower jaw partially adducted meeting protruded upper jaw; (Ff) contraction of mouth cavity forcing engulfed water into the stomach; note the expanded stomach in (f); (Gg) release of engulfed water through opercular openings and mouth, causing a "postfeeding jump." Arrows indicate position of prey organism, the three-striped damselfish *Dascyllus aruanus*.

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Table 1. Weights of paraffin casts made from closed and fully expanded oral cavities, volume expansion of oral cavities (weight of cast of fully expanded cavity to weight of cast of closed cavity), and speeds of prey engulfment for three species of *Antennarius*.

Species	Weight (g)		Volume expansion	Speed (msec)		
	Closed	Fully expanded		Trial 1	Trial 2	Trial 3
A. hispidus	2.3	29.9	12.8×	3.8	8.8	6.2
A. tridens	1.2	16.4	13.7×	6.2	7.5	5.0
A. phymatodes	2.1	25.4	12.1×	4.0*	10.0*	6.0*

*Determined by high-speed cinematography at 1000 frames per second, other values based on 800 frames per second.

feeding strategy consists of maintaining the immobile, inert appearance of a sponge or coralline algal–encrusted rock, while wriggling a highly conspicuous lure (*5*). They are well known for their ability to devour prey that is often considerably greater than their own body length.

Comprehensive anatomical analyses of the feeding mechanisms of *Antennarius hispidus* (Bloch and Schneider), *A. tridens* (Temminck and Schlegel), and *A. phymatodes* Bleeker were made, emphasizing the bones, muscles, and ligamentous connections of the jaws. These structural analyses were then integrated with functional data obtained through the use of living anglerfishes and 16-mm cinematographic equipment operated at speeds of 800 and 1000 frames per second (*6*). The functional data provided a time sequence that could be superimposed over the mechanical displacement of elements.

The majority of teleosts, including *Antennarius*, engulf prey by creating negative pressure (suction pressure) inside the mouth cavity (*7, 8*). This negative pressure is the result of a large volume increase produced by a rapid expansion of the mouth cavity. The mechanism by which oral expansion occurs in *Antennarius* does not appear to differ substantially from that used by most other teleosts (*8*). *Antennarius* is unusual, however, in that the amount of oral expansion during a single feeding event is considerably greater than that in most other teleosts (*9*). To determine the magnitude of oral expansion, we made casts by injecting liquid paraffin into the closed and fully expanded mouth cavities of freshly killed anglerfishes (*10*). Comparison of these casts revealed that the three species of *Antennarius* are capable of oral expansion that exceeds 12 times the volume of the closed cavity (Table 1). In contrast, using a similar wax-cast technique, Osse (*2*) found that the European perch, *Perca fluviatilis*, expands its mouth cavity approximately six times during a single feeding event.

More important than the actual volume increase of the mouth cavity during feeding is the speed at which this volume is increased. Analyses of high-speed films showing individual feeding sequences (*11*) revealed that *Antennarius hispidus* is capable of oral expansion and subsequent prey (*12*) engulfment in less than 4 msec (Figs. 1 and 2). Time sequences for total oral expansion in *A. hispidus*, *A. tridens*, and *A. phymatodes* were similar, with the average speed for all three species being approximately 6 msec (Table 1). These extremely rapid feeding sequences are unparalleled in other fishes so far examined. The ruff, *Gymnocephalus cernua*, expands its mouth cavity in approximately 250 msec (*13*), whereas the European perch requires 40 msec (*2*). Only rates recorded for the freshwater butterfly fish, *Pantodon buchholzi*, come near to what we have found in anglerfishes, yet these are still approximately four times slower (*3, 14*).

In anglerfishes the ability to engulf prey at ultrafast speeds may be a major component of a highly successful feeding strategy based on predator immobility and aggressive mimicry (*5*). This ability, furthermore, may not be confined to anglerfishes but may, instead be shared by a host of other, in some cases relatively unrelated, teleosts that utilize a similar mode of energy capture (*15*). An ultrafast feeding mechanism may, in fact, be a necessary prerequisite for the evolution of this kind of feeding. Since it is believed that aggressive mimicry devices used for the purposes of capturing prey are widespread among higher euteleosts (Acanthomorpha) (*16*), it seems that the evolution of ultrafast feeding mechanisms has been important in the proliferation of this largest and most morphologically diverse group of teleosts.

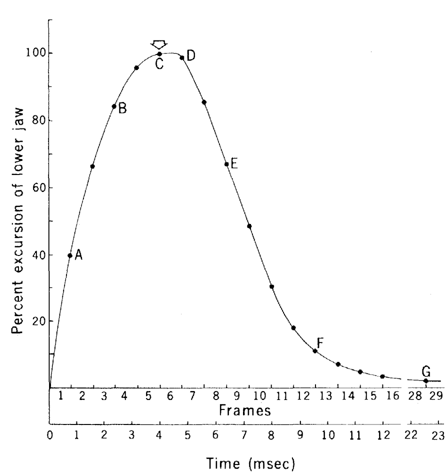

Fig. 2. Percent of excursion of lower jaw versus time (superimposed over cinematographic frames) of fastest single feeding event in *A. hispidus*. Letters indicate points on curve that correspond to individual cinematographic frame-to-print conversions shown in Fig. 1. Arrow indicates point at which prey organism is totally engulfed.

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10. Measurements of the magnitude of oral expansion were made on the same individuals that were used in the film sequences.
11. A Zeiss Moviscope, 16-mm film-editing machine was used to analyze nine individual feeding events (Table 1), three each for *A. hispidus* and *A. tridens* (film speed, 800 frames per second) and three for *A. phymatodes* (film speed, 1000 frames per second).
12. Natural prey organisms, several species of damselfishes of the genus *Dascyllus* (Pomacentridae), were used to feed anglerfishes while filming (Fig. 1).
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14. In contrast to other species mentioned, which all belong to highly evolved teleost groups, *Pantodon* is a primitive teleost, lacking fully protrusible jaws. Thus, a comparison of its feeding abilities with those of higher teleosts may be of limited significance.
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