

Cranial movements during suction feeding in teleost fishes: Are they modified to enhance suction production?

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Abstract

Suction is produced during prey capture by most teleost fishes. Here, we ask two questions about the functional basis of suction feeding. First, is there variation in the kinematic pattern produced by different species while suction feeding? Second, do species termed ‘suction specialists’ demonstrate similar modifications to their feeding behavior? We used 10 kinematic variables in a principal component analysis to identify axes of variation among 14 suction feeding teleost species (representing nine families and five orders within the Euteleostei) that demonstrate different feeding habits and habitats. MANOVA and Tukey post hoc tests were used to assess differences among species. Most species clustered together on the principal component axes, suggesting a generalized mechanism that facilitates unidirectional flow. Typically, only one species stood out as ‘extreme’ on each functional axis, and a species that stood out on one axis did not stand out on others. Only one species, the flatfish *Pleuronichthys verticalis*, an obligate benthic feeder, demonstrated modifications consistent with enhanced suction production. This species displayed a suite of changes that should enhance suction production, including large hyoid depression, large cranial rotation, and small gape. We suggest that suction performance may be greatest in such obligate benthic feeders because cranial morphology is highly modified and prey are captured from the substrate.

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Introduction

Suction feeding is the most common mechanism of prey capture in aquatic vertebrates, and probably was employed by the earliest gnathostomes (Lauder, 1985a; Moss, 1977). Suction feeding entails expanding the head and drawing the prey into the mouth along with some of the surrounding water. Because both the relative size and elusiveness of the prey can vary, the amount of

suction that is produced during feeding is expected to vary among species, and even within individuals of a species feeding on different prey types. Nonetheless, several studies have noted that the general patterns of movements, or kinematics, used by aquatic predators for capturing prey are remarkably conserved across a range of species, despite a variety of experimental prey types and feeding conditions (Bergert and Wainwright, 1997; Carroll and Wainwright, 2003; Gibb, 1997; Lauder, 1985b; Motta and Wilga, 2001).

Four phases of suction feeding were initially identified in bony fishes (Lauder, 1985a), and are now known to

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be present in elasmobranchs (e.g., Motta and Wilga, 2001), and some aquatic-feeding tetrapods (e.g., Lauder and Reilly, 1994). These are the ‘preparatory’ phase, the ‘expansive’ phase, the ‘compressive’ phase, and the ‘recovery’ phase. To produce suction, the oral or buccal cavity is first compressed during the preparatory phase, and then rapidly expanded, creating a flow of water into the buccal cavity, during the expansive phase. The rapid expansive phase is followed by the markedly slower compressive phase, where water is expelled from the opercular openings (or the mouth, if operculi are lacking), while the food item is retained in the oral jaws or buccal cavity. Finally, during the recovery phase, the elements of the head and jaws return to a relaxed, pre-feeding position. This cycle of events may be repeated cyclically to produce the flow of water necessary to transport prey into the esophagus (e.g., Gillis and Lauder, 1995).

Of central importance to suction production is the expansive phase. Both the overall change in buccal volume, and the velocity with which it occurs, affect the generation of flow into the mouth (Lauder, 1980a; van Leeuwen and Muller, 1984; Muller, 1987). Further, during the expansive phase, an anterior-to-posterior wave of expansion is generated by movement of the components of the head and jaws (Lauder, 1985a; Muller and Osse, 1984). That is, any given cranial element reaches the limit of its excursion slightly before the element immediately posterior to it. Thus, in the cranium of bony fishes (Fig. 1), the lower jaw reaches its maximal depression, then the neurocranium achieves maximum rotation, then the hyoid reaches maximum depression, and, lastly, the opercular region reaches its maximum expansion. The relative timing of the excursions of these individual elements creates unidirectional flow of water into the buccal cavity, and thereby generates ‘suction’ (Fig. 2; Ferry-Graham and Lauder, 2001). This wave-like expansive phase has also been observed in representatives from many of the major groups of aquatic-feeding vertebrates including elasmobranchs (e.g., Ferry-Graham, 1997), salamanders (e.g., Reilly, 1995), and turtles (e.g., Summers et al., 1998), underscoring its fundamental role in suction production for most aquatic-feeding vertebrates (although it is *not* seen in aquatic-feeding garter snakes that appear to generate no suction during forward strikes; Alfaro, 2002). Teleost fishes are perhaps the most derived vertebrates in this sense, having multiple mobile cranial elements (Figs. 1 and 2), and the capacity for rapid and extreme expansion (Liem, 1980).

Recent studies have attempted to correlate variations in cranial movements (or kinematics) during the expansive phase of prey capture with variations in suction pressure within individuals of a given teleost species (Svånback et al., 2002; Carroll et al., 2004). These studies reveal that the volume change of the

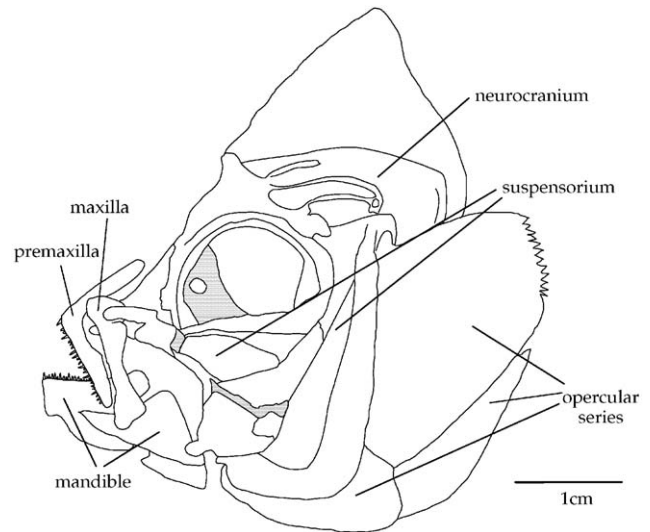


Fig. 1. Illustration of the cranium of a “typical” teleost, *Lepomis macrochirus* (after Gibb, 1997). Bones are shown as white elements; cartilages are shown as stippled elements. The cranium illustrated here possesses a protrusible premaxilla, which is present in all of the species chosen for this study. The neurocranium, or skull, houses the brain, and can be rotated dorsally relative to the axial skeleton. The oral, or anterior, jaws are comprised of the upper jaw (premaxilla and maxilla) and lower jaw (mandible). The suspensorium attaches the lower jaw to the cranium and the opercular series covers the gills. The hyoid (not shown) is medial to both the suspensorium and opercular series, and cannot be observed from a lateral view unless a fish is feeding. The buccal cavity is a medial space formed by the bones illustrated here.

buccal cavity during feeding is strongly correlated with the concomitant drop in buccal pressure, as would be expected based on simple physical principles. However, these studies were unable to pinpoint a specific kinematic variable, or even a coherent suite of variables, that explain variations in buccal expansion and resulting suction performance. For example, kinematic patterns of the oral jaws (gape), hyoid (depression), and suspensorium (abduction) all appear to play a role in determining suction production, but the relative contributions of each of these three parameters have not been defined, nor has the contribution of other cranial movements been ruled out (Svånback et al., 2002; Carroll et al., 2004). In fact, these cranial elements (the jaws, neurocranium, hyoid and opercular bones) must operate as an integrated structural complex (Sanford and Wainwright, 2002), which implies that an individual may change the amount of suction produced by manipulating the timing or maximal displacement of all four cranial elements at once.

As individuals of a species begin to specialize on a more elusive or otherwise challenging prey type, they may modify their ability to suction feed by modifying their prey-capture kinematics (as above), or by changing

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