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Suction is kid's play: extremely fast suction in newborn seahorses

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Ongoing anatomical development typically results in a gradual maturation of the feeding movements from larval to adult fishes. Adult seahorses are known to capture prey by rotating their long-snouted head extremely quickly towards prey, followed by powerful suction. This type of suction is powered by elastic recoil and requires very precise coordination of the movements of the associated feeding structures, making it an all-or-none phenomenon. Here, we show that newborn *Hippocampus reidi* are able to successfully feed using an extremely rapid and powerful snout rotation combined with a high-volume suction, surpassing that observed in adult seahorses. An inverse dynamic analysis shows that an elastic recoil mechanism is also used to power head rotation in newborn *H. reidi*. This illustrates how extreme levels of performance in highly complex musculoskeletal systems can be present at birth given a delayed birth and rapid development of functionally important structures. The fact that the head skeleton of newborn seahorses is still largely cartilaginous may not be problematic because the hydrodynamic stress on the rotating snout appeared considerably lower than in adult syngnathids.

Keywords: prey capture; feeding; Syngnathidae; larvae; biomechanics

1. INTRODUCTION

Adult seahorses, and other syngnathid fishes such as pipefish and seadragons, are characterized by an unusual feeding strategy known as pivot feeding (de Lussanet & Muller 2007). To capture small crustaceans, they perform a rapid upward rotation of the head and snout, which brings the mouth quickly close to the prey (Muller 1987). Next, widening of their long snout generates a flow of water that draws the prey into the mouth. This process is astonishingly fast: adult seahorses capture prey in less than 5 ms after the start of the pivot movement. Recent studies

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(Van Wassenbergh *et al.* 2008) have demonstrated that the high speed of prey capture in adult syngnathids is generated by means of storage and release of elastic energy in the tendons of the muscles responsible for head rotation (i.e. *levator neurocranialis*, a derivative of the epaxial musculature).

Pivot feeding requires the integrated movement of the different components of the feeding system (neurocranium, hyoid, lower jaw and snout) to generate a successful feeding strike. If one of the components does not function properly or if the coordination is disrupted, prey capture by pivot feeding fails (Muller 1987). However, the early ontogenetic development of complex integrated musculoskeletal systems typically requires a period of differentiation, growth and maturation. Indeed, a gradual development and maturation of the coordination of the functional elements of the feeding system is typical for suction-feeding fishes, even after the onset of active feeding. For example, the lower jaw and hyoid move simultaneously for some time after the onset of active feeding in salmon (Coughlin 1991), cichlids (Otten 1982), cod and flounder (Hunt Von Herbing 2001). Suction performance only improves at a later stage, when the timing of the movement of these two elements can be adjusted owing to a newly formed anatomical linkage within the complex fish head (i.e. the operculum–lower jaw linkage; Otten 1982). Moreover, in some fishes, the contractile performance of the feeding muscles reaches adult levels only at later juvenile stages (Van Wassenbergh *et al.* 2007).

On the other hand, in analogy to what is found in other fishes with elaborate parental care, the brood pouch of male seahorses may allow the young to be 'born' at a later developmental stage. As this brood pouch functions as a placenta analogue where the embryos are provided nutrition by osmosis until complete disappearance of the yolk sac (Kornienko 2001), the feeding apparatus of newborn seahorses may show a relatively advanced developmental state compared with other fish larvae at birth.

Here, we studied whether, and how, a precisely coordinated, high-performance behaviour such as pivot feeding can be achieved in newborn syngnathid fishes. To do so, we investigated the morphology of the feeding apparatus, prey-capture kinematics, dynamics of cranial rotation and some hydrodynamic aspects of cranial rotation in newborn seahorses (*Hippocampus reidi*).

2. MATERIAL AND METHODS

Serial histological cross sections of the head of one specimen were made. Computer-generated three-dimensional reconstructions were made to visualize musculoskeletal topography based on the sections (see the electronic supplementary material for additional details).

Kinematic data were obtained from 11 high-speed videos of 0–3-day-old *H. reidi* recorded at 8000 frames per second. After manual digitization of specific anatomical landmarks (figure 2b) and reducing digitization noise, numerical differentiation yielded angular velocities and accelerations. The axis of neurocranial rotation was determined for each feeding sequence. Volume modelling of the head and buccal cavity was performed to estimate volume increase during suction based on video images of larval seahorses during feeding (see also the electronic supplementary material for additional details).

A finite volume approach using the initial head volume reconstruction was used to calculate the moment of inertia of the rotating head. Additionally, we used computational fluid dynamics

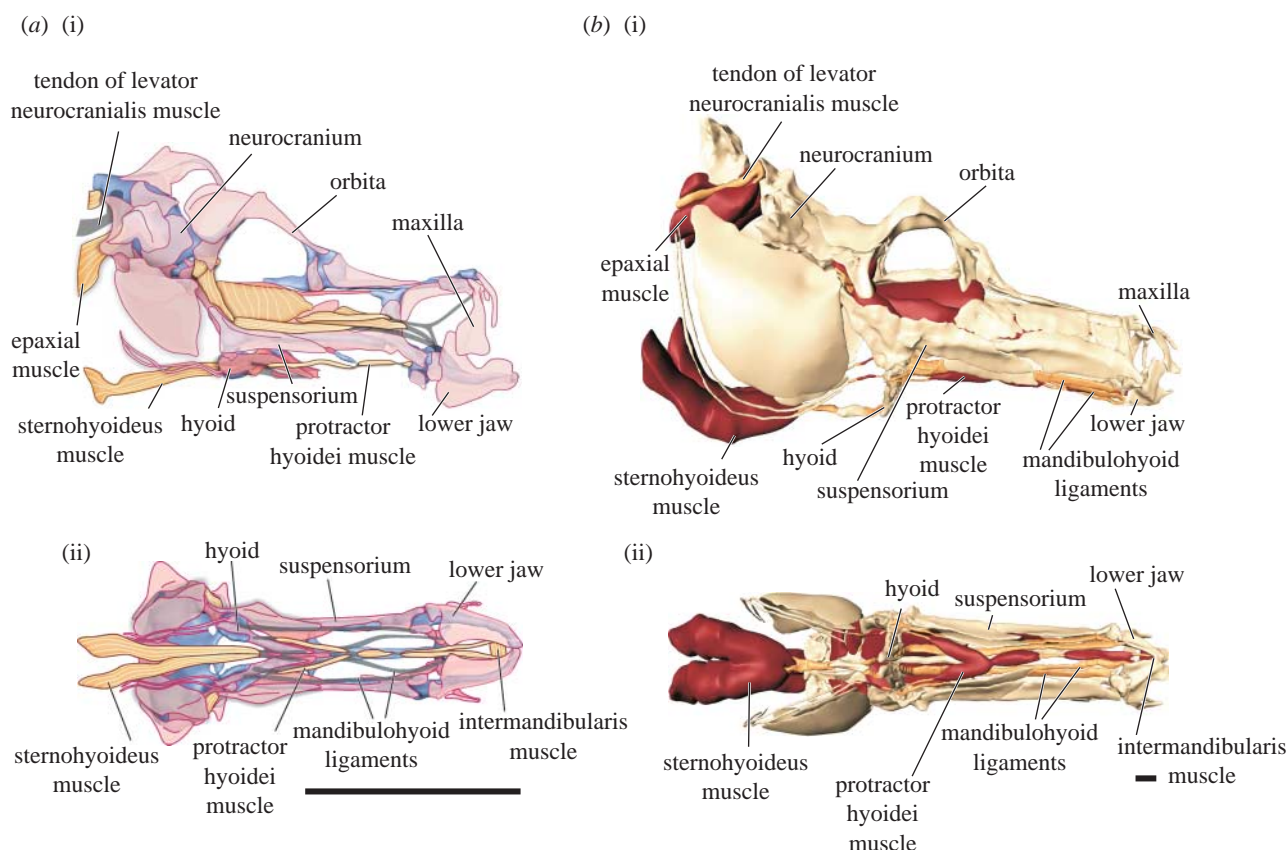


Figure 1. Three-dimensional reconstruction of the head skeleton and cranial muscles of (a) a newborn and (b) an adult *H. reidi* in (i) lateral view (after Roos *et al.* 2009) and (ii) ventral view. (a) Blue, cartilage; pink, bone; orange, muscle; grey, tendon. (b) Beige, bone; red, muscle; orange, tendon. Scale bars, 1 mm.

(CFD) to calculate the pressure loading on the snout, as well as the hydrodynamic torques resisting head rotation (see also the electronic supplementary material).

The power required from the epaxial muscles to accelerate the head was calculated by multiplying the angular acceleration of the head, its angular velocity and its moment of inertia. In doing so, we assume that the water-filled, neutrally buoyant head rotates as a rigid volume around a fixed axis of rotation, as determined from the recorded video images, without accounting for hydrodynamic effects. Additionally, the power required to overcome the hydrodynamic resistance was calculated by multiplying hydrodynamic torque (CFD result) by angular velocity. Muscle-mass-specific power requirement was calculated by dividing the power needed for the head movement by epaxial muscle mass. The latter was obtained from the volume reconstructions, assuming sea-water neutral buoyancy. This implies that the entire epaxial muscle complex, running from the head to the tip of the tail, is assumed to contribute to powering head rotation. Since probably only the anterior part of this muscle is active during pivot feeding, the reported mass-specific power output will be a conservative estimate.

3. RESULTS

Anatomical reconstruction of the head of a one-day-old *H. reidi* shows a predominantly cartilaginous cranial skeleton (figure 1). Bony elements are present, but are very thin and loosely distributed along the cartilaginous core (see also figure in the electronic supplementary material). The long tendons of the left and right neurocranial elevator muscles are clearly visible on serial sections of larval *H. reidi* (figure 1a).

Newborn *H. reidi* are capable of performing a coordinated pivot-feeding strike (figure 2a) during which they rotate their neurocranium over 40° in less than 2.5 ms (figure 2a,b). The velocity of head rotation exceeds $30\,000^\circ\text{ s}^{-1}$. The hyoid is

accelerated very early (between time = 0 and 0.5 ms), rotates over more than 90° (figure 2b) and reaches a velocity of $80\,000^\circ\text{ s}^{-1}$.

Volume modelling showed an initial mouth cavity volume of 0.10 mm^3 , which is approximately doubled during feeding, reaching $0.214 \pm 0.02\text{ mm}^3$ (mean \pm s.d.; figure 2c). A peak instantaneous power of 2381 W kg^{-1} is required from the approximately 0.046 mg of epaxial muscle to overcome the inertia of the head (at time = 1.0 ms). At this instant, CFD calculated an additional 1350 W kg^{-1} needed to overcome the hydrodynamic resistance. A peak pressure of 650 Pa was exerted by the water on the dorsal surface of the snout (figure 2d).

4. DISCUSSION

Even within the first day after being expelled from the male's brood pouch, *H. reidi* are capable of performing an extremely fast and powerful pivot-feeding strike (figure 1). Newborn *H. reidi* reach velocities of head rotation that are more than three times higher than that observed for adults (Roos *et al.* 2009). Furthermore, the small hyoid reaches an angular velocity that is even higher than the peak angular velocity of the swing of a mantis shrimp when breaking a snail (less than $57\,000^\circ\text{ s}^{-1}$; Patek *et al.* 2004), and is probably the fastest rotation ever observed in a prey-capture system. While mantis shrimp and seahorses are both equipped with an elastic recoil system to power their prey-capture movements, the smaller size (and thus lower rotational inertia) of the seahorse

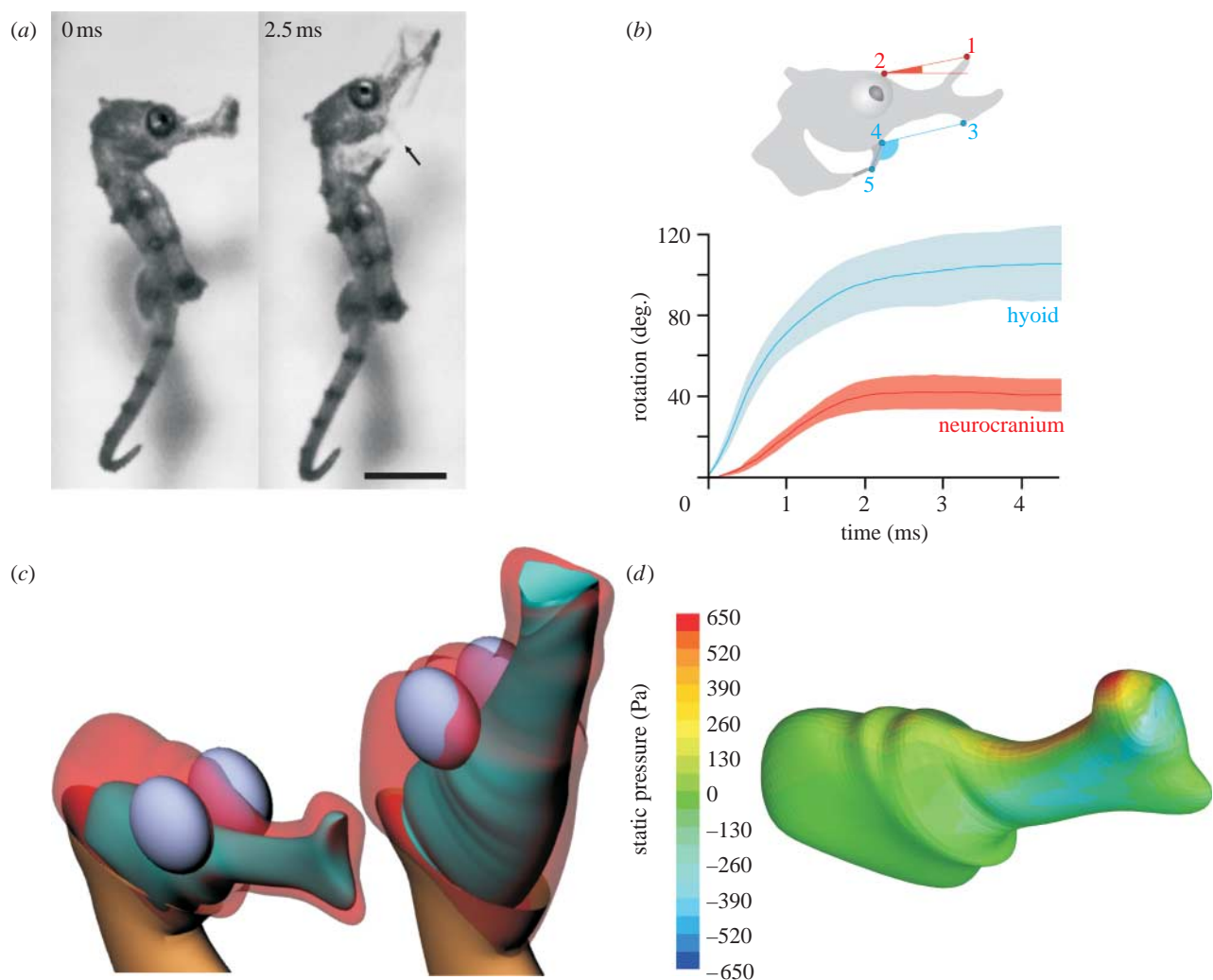


Figure 2. (a) High-speed video frames just before the start of feeding and at the completion of the suction event at 2.5 ms (arrow indicating hyoid tip). (b) Average kinematic profiles of rotation of the neurocranium (red, angle 1–2 horizontal) and the hyoid (blue, angle 3–4–5) during prey capture. Shaded areas denote \pm s.d. ($n=11$). The digitized landmarks are as follows: 1, tip of the snout posterior to the maxillae; 2, tip of the nose spine; 3, caudal tip of the processus retroarticularis; 4, hyoid joint at the interhyal; 5, distal tip of the ceratohyals. (c) Volume model of the expansion of the head (red) and mouth cavity (green). (d) Static pressure on the rotating head at the instant of peak pressure. Scale bar, 1 mm.

hyoid probably allows it to reach this exceptionally high rotational velocity.

These remarkably high speeds suggest that an elastic recoil mechanism of head rotation must be functional in newborn *H. reidi*. Estimates of muscle-mass-specific power requirement of head rotation can address this issue as the mechanical power output of muscle is limited (approx. 1100 W kg^{-1} ; Curtin *et al.* 2005). Our calculation showed peak instantaneous power requirements exceeding this value considerably, which suggests that a catapult-like mechanism, as described for adult pipefish, is already operational in newborn *H. reidi*.

Previous workers have suggested that the high rotational accelerations, torques and fluid pressures involved during pivot feeding demand a relatively advanced degree of ossification of the cranial skeletal components (Osse & Muller 1980). However, one-day-old *H. reidi* have a predominantly cartilaginous cranial skeleton (figure 1), which may have important consequences for their ability to withstand tensile and compressive stresses during feeding. Interestingly, CFD showed relatively low hydrodynamic pressures

on the dorsal surface of the snout (650 Pa; figure 2b) compared with adult pipefish (more than 2000 Pa; Van Wassenbergh & Aerts 2008). This indicates that, owing to their small size, the early developmental stages of syngnathids do not necessarily require the strong degree of ossification observed in adults because of a reduced hydrodynamic stress.

The observed doubling of the volume of the mouth cavity is significantly higher than what is observed for adults (less than 50% increase; G. Roos 2008, personal observation). Since this increase in volume is related to the amount of water being sucked into the mouth, newborn seahorses are capable of transporting a relatively large volume of water during feeding. Apparently, the cartilaginous head skeleton also manages to withstand the stresses occurring during such powerful suction. In this respect, the relatively short length of the snout in newborn seahorses compared with adults (Choo & Liew 2006) may be important to prevent buckling when high sub-ambient pressures are generated inside the snout during suction.

Our data show that whereas other fishes require a period of gradually improving their feeding

performance after hatching, seahorses give birth to young with a fully functional prey-capture system. The relatively late developmental stage of seahorses at 'birth' is reflected in a matured functionality of the feeding system compared with other fishes and highlights the crucial role of the brood pouch in male seahorses.

The feeding apparatus of fishes is potentially one of the most complex, integrated musculoskeletal systems in vertebrates, and consequently provides a unique opportunity to study the evolution and development of biomechanical design. In this respect, feeding in newborn *H. reidi* illustrates that increasing anatomical complexity during the pouch phase, resulting in an immediate high-performance system at birth, may help to overcome critical periods during early ontogeny.

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