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Center of mass motion in swimming fish: effects of speed and locomotor mode during undulatory propulsion

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ABSTRACT

Studies of center of mass (COM) motion are fundamental to understanding the dynamics of animal movement, and have been carried out extensively for terrestrial and aerial locomotion. But despite a large amount of literature describing different body movement patterns in fishes, analyses of how the center of mass moves during undulatory propulsion are not available. These data would be valuable for understanding the dynamics of different body movement patterns and the effect of differing body shapes on locomotor force production. In the present study, we analyzed the magnitude and frequency components of COM motion in three dimensions (x : surge, y : sway, z : heave) in three fish species (eel, bluegill sunfish, and clown knifefish) swimming with four locomotor modes at three speeds using high-speed video, and used an image cross-correlation technique to estimate COM motion, thus enabling untethered and unrestrained locomotion. Anguilliform swimming by eels shows reduced COM surge oscillation magnitude relative to carangiform swimming, but not compared to knifefish using a gymnotiform locomotor style. Labriform swimming (bluegill at 0.5 body lengths/s) displays reduced COM sway oscillation relative to swimming in a carangiform style at higher speeds. Oscillation frequency of the COM in the surge direction occurs at twice the tail beat frequency for carangiform and anguilliform swimming, but at the same frequency as the tail beat for gymnotiform locomotion in clown knifefish. Scaling analysis of COM heave oscillation for terrestrial locomotion suggests that COM heave motion scales with positive allometry, and that fish have relatively low COM oscillations for their body size.

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1. Introduction

As a representation of the total forces exerted on an animal, center of mass (COM) movement provides important information on locomotor dynamics and can be used to calculate energy expenditure, efficiency, and the effect of ground reaction forces on limbs (Biewener, 1989; Ortega and Farley, 2005). In horses, humans, and other terrestrial animals, COM movement is used to compare work done over different gaits (Blickhan and Full, 1987; Pfau et al., 2006; Kuo, 2007; Biknevicius et al., 2013). It is also used to describe the effect of limbs on whole body movements, especially where the limbs comprise a significant portion of the body's mass (Abourachid et al., 2011; Walter and Carrier, 2011). COM oscillation patterns are even used as a "locomotor signature" to identify pathological gaits or evolutionary trends (e.g., Clemente et al., 2008; Minetti et al., 2011).

Despite the breadth of research that has been done on terrestrial and aerial COM movement during animal locomotion and its importance in understanding animal dynamics, almost nothing is known about COM movement in fishes during undulatory locomotion. This is especially surprising given the extensive descriptive literature defining and comparing body kinematic patterns in fishes, with the accompanying proliferation of terminology to describe body motions. Anguilliform (eel-like), carangiform (jack-like), labriform (wrasse-like), and gymnotiform (knifefish-like) are just a few of the terms used to describe fish swimming patterns (Webb, 1975; Sfakiotakis et al., 1999; Shadwick and Lauder, 2006). These terms are meant to reflect broad kinematic differences among fish species and generally how thrust is generated during locomotion by the body and fins. But how differing body movement patterns affect COM motion remains unknown, and the effects of changing swimming speed on COM oscillation amplitude in fishes with different body shapes are likewise not yet understood. Due to differences in locomotor media and in the use of limbs on land compared to thrust generation using body deformation in the water, amplitudes and frequencies of COM oscillation could differ substantially between aquatic and terrestrial animals.

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The limited data from steadily rectilinearly swimming fishes in which COM oscillations have been experimentally measured includes quantification of COM motion data during pectoral fin locomotion (Walker and Westneat, 1997; Walker, 2004; Lauder and Madden, 2008) and an analysis by Tytell (2007) who estimated COM velocity in two swimming fish species by digitizing the position of the tip of the snout. Other than these investigations, we are not aware of any measurements of COM motion in steadily swimming fishes.

The overall goal of the present paper is to analyze in three dimensions the COM motion of several fish species (eel, bluegill sunfish, and clown knifefish) swimming with four locomotor modes at three speeds. We used high-speed video and an image cross-correlation technique to enable untethered and unrestrained locomotion, so that COM motion is not influenced by attachment of transducers or any drag forces that might result from transducer wires. Specifically, we quantified COM velocities in three dimensions (x : surge; y : sway, and z : heave) and then calculated COM displacement and acceleration from the velocity data. We tested for differences among species swimming with different locomotor modes, and also wanted to see how changes in swimming speed alter COM motion during undulatory swimming. Hypotheses examined include the following: (i) anguilliform locomotion will show reduced surge COM oscillations compared to carangiform swimming; (ii) labriform locomotion will show reduced sway COM oscillations but increased surge oscillations compared to other undulatory modes; (iii) the gymnotiform combination of simultaneous body and fin motion will permit reduced COM oscillations in both the surge and sway directions; and (iv) surge COM oscillations will occur at either two or four times the tail beat frequency based on the data presented in Tytell (2007).

2. Materials and methods

2.1. Study animals

Four clown knifefish (*Notopterus chitala*, Hamilton, 1822) measuring 19.1 ± 0.5 cm (mean \pm standard error) in total length with masses of 44.9 ± 1.5 g and body surface area of 69.8 ± 1.6 cm² were acquired from a local pet store and kept in 40 l tanks at 25 °C. Three bluegill sunfish (*Lepomis macrochirus*, Rafinesque, 1819) measuring 20.4 ± 0.3 cm with masses of 149.9 ± 10.9 g and body surface area of 104.3 ± 9.8 cm² were collected locally under our scientific collection permit (Massachusetts, USA) and kept in individual 40 l tanks at 18 °C. Three American eels (*Anguilla rostrata*, Lesueur, 1817) measuring 31.0 ± 1.8 cm with masses of 35.6 ± 5.7 g and surface area of 48.7 ± 5.1 cm² were also collected locally and kept in individual 30 l tanks at 18 °C.

These three species were chosen a priori to reflect different locomotor styles and to represent a diversity of modes of swimming in fishes. Bluegill sunfish have a deep and narrow-width body, and use a labriform locomotor mode where thrust forces are generated exclusively by the pectoral fins at swimming speeds of less than about 1.0 body lengths (BL)/s (Gibb et al., 1994; Drucker and Lauder, 1999). At higher speeds bluegill use a carangiform or “subcarangiform” swimming mode in which thrust is generated primarily by body oscillations. This species is thus a good experimental subject for this study as it undergoes a prominent gait transition between the lowest and the two highest swimming speeds tested here. Eels exemplify the anguilliform swimming mode with smaller wavelength body waves that increase in amplitude down the body. Only at speeds higher than those tested here do body waves begin to generate larger lateral oscillations of the anterior half of the fish. The narrow and elongate eel shape contrasts with the deep body of bluegill sunfish. Knifefish display the gymnotiform locomotor

mode in which body undulations combined with undulation of the elongated ventral anal fin are used to power swimming. The elongated anal fin is actuated by fin muscles that are independent of the myotomal body muscles that produce body waves during locomotion, and anal fin and body waveforms are thus somewhat decoupled from each other in swimming clown knifefish.

2.2. Anatomical COM measurement

The anatomical COM of bluegill sunfish (*L. macrochirus*) has been measured in previous studies (Drucker and Lauder, 1999, 2001; Tytell and Lauder, 2008). For *A. rostrata* and *N. chitala*, two specimens each from the Museum of Comparative Zoology (Cambridge, MA, USA) of similar body size to the live specimens studied here were used to calculate COM position. The fish were stiff and straight from preservation and were hung from three points on the body with strings and allowed to come to a rest before being photographed. The photographs were overlaid and the intersection of the strings was taken as the COM.

The anatomical COM position of *L. macrochirus* lies at 40% of total body length (including the caudal fin) from the tip of the nose and 50% of the body width, excluding the dorsal fin (Drucker and Lauder, 2001; Tytell and Lauder, 2008). The mean COM position of *A. rostrata* lies at 46% of the body length from the tip of the nose. Mean COM position of *N. chitala* was at 25% of the body length from the tip of the nose, and just over halfway up the height of the fish.

Since the center of mass marks the midpoint of body mass in three-dimensional (3D) space, the COM moves over the course of a tail beat cycle as the body bends: if the fish body is strongly bent, the COM can be positioned outside the body. For the locomotor modes studied here, the extent of unidirectional body bending is small, the portions of the body that are bending contain little mass relative to the anterior region of the body and head, and wave-like body bending results in only a small change in lateral mass distribution since wave-like motion deflects body mass to both sides of the COM. A previous study (Tytell and Lauder, 2008) tracking the true COM position during a C-start escape response showed only very small variation in COM position even when the tail was bent at almost 90° to the body, due to the low mass of the tail relative to the head region. We estimated that wave-like bending of the body from side to side during steady undulatory swimming moves the COM in the sway (y , or side-to-side) direction approximately 5% of the COM excursion amplitude measured in this paper, and has effectively no influence on the COM position in the surge (x) or heave (z) dimensions. However, as described in more detail below, we quantified the movement of a box-like region surrounding the anatomical COM and this box always contained the actual COM regardless of body posture during swimming.

2.3. Image cross-correlation to measure COM oscillation

We anticipated that COM oscillations during undulatory locomotion would be small and our goal was to interfere with unrestrained fish swimming as little as possible. Therefore, we chose to use image cross-correlation in order to quantify COM motion without attaching transducers with wires to swimming fish and hence possibly altering body motion patterns. One approach would have been to simply digitize the position of a single point near the COM on swimming fishes, but this method is subject to a large error since the COM is not marked, and is time consuming for the number of sequences needed for robust statistical analysis. Instead we used image cross-correlation derived from the technique of particle image velocimetry (PIV) as used in previous research on swimming hydrodynamics (Drucker and Lauder, 1999, 2001; Tytell, 2007; Tytell and Lauder, 2008). We used high-speed video with careful lighting of the swimming fishes to

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