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Undulation frequency affects burial performance in living and model flatfishes

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ABSTRACT

Flatfishes bury themselves under a thin layer of sand to hide from predators or to ambush prey. We investigated the role of undulation frequency of the body in burial in five species of flatfishes (*Isopsetta isolepis, Lepidopsetta bilineata, Hippoglossoides elassodon, Parophrys vetulus*, and *Psettichthys melanostictus*). High-speed videos show that undulations begin cranially and pass caudally while burying, as in forward swimming in many other fishes. The flatfishes also flick the posterior edge of their dorsal and anal fins during burial, which may increase the total surface area covered by substrate. We built a simple physical model – a flexible, oval silicone plate with a motorized, variable-speed actuator – to isolate the effect of undulation frequency on burial. In both the model and actuated dead flatfish, increased undulation frequency resulted in an increase in the area of sand coverage. Complete coverage required an undulation frequency of no more than 10 Hz for our models, and that was also sufficient for live flatfishes. The model shows that undulation is sufficient to bury the animal, but live flatfishes showed a superior ability to bury, which we attribute to the action of the median fins.

1. Introduction

Many animals bury themselves, or are buried by circumstance, including both vertebrates and invertebrates. Burial occurs when an organism is covered by substrate and remains submerged without moving beneath the surface. Many species, including some crabs and squid (Bellwood, 2002; Rodrigues et al., 2010) bury themselves to avoid predation or to ambush prey. Some lizards use different burial kinematics when burying in wet or dry sand and generally use undulation to “swim” through the sand (Sharpe et al., 2013, 2015). Burial is common in ray-finned fishes (Actinopterygii), where body form among buriers is diverse. Examples include the sand lance (*Ammodytes* spp.), midshipman (*Porichthys notatus*), sandfish (*Trichodon trichodon*), and staghorn sculpin (*Leptocottus armatus*) (Arora, 1948; Eschmeyer et al., 1983; Pinto et al., 1984; Morioka, 2005; Gidmark et al., 2010). Thin, elongate fishes such as sand lances dive headfirst into the sand to bury themselves (Gidmark et al., 2010). More deep-bodied fishes, such as midshipman, Pacific sandfish, and sculpin, combine movements of their bodies and their fins to scoop sand out from beneath them (Arora, 1948; Eschmeyer et al., 1983; Morioka, 2005). Stingrays (Droge and Leonard, 1983) and flatfishes bury themselves with rapid undulations that cause a cloud of substrate to fall onto the body (Kruuk, 1963).

The 678 species of flatfishes in the order Pleuronectiformes (Nelson, 2006) are laterally compressed, asymmetrical fishes that bury themselves in the substrate, typically with only their eyes showing. The diversity of their body shapes ranges from narrow ovals (e.g., *Microstomus pacificus*) to nearly perfectly circular fishes (e.g., *Pleuronichthys coenosus*), with rhomboidal deviations from the circular-oval continuum (e.g., *Platichthys stellatus*). The substrates on which the fishes are found include mud, silt, fine to coarse sand, and fine to medium gravel. Some species spend substantial time foraging in the water column (e.g., *Hippoglossus stenolepis*), but most either forage in the substrate or ambush prey from hiding. This diversity in body shape, substrate and habit makes flatfishes useful models for understanding the mechanics, tradeoffs and constraints of burial. Burial in flatfishes is a complex behavior that includes coordinated movements of the body and fins, generation of powerful flow patterns, and sensory feedback about substrate and burial stage. Flatfishes perform this behavior for a variety of purposes, including to avoid predation (Kruuk, 1963; Ellis et al., 1997), to

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ambush prey (Stoner and Ottmar, 2003), and to conserve energy by reducing an individual's activity levels (Gibson and Robb, 2000). A burial event resembles the undulation seen in normal locomotion, but rather than proceeding forward the fish remains in place while fluidizing substrate from underneath it and around the edges of its body. When the fish stops undulating, the agitated substrate falls through the water column to conceal the fish.

Burial requires moving substrate from beneath and around an animal to above it, ideally leaving an even distribution of particles that completely conceals. Several factors may affect burial time and coverage, as well as the energy needed to bury. Strong currents of water must be generated by body movements, and these currents are shaped and accelerated by both the fins and the body of the fish. Therefore, we expect that both the kinematics of body movement and the shape of the body have significant effects on burial. Also, in flatfishes, the dorsal and anal fins form a perimeter around the body. The amplitude and frequency of the undulatory wave of the body is likely the most important determinant of flow, but we expect small movements of the fins to have substantial effects on flow direction. The substrate must be fluidized by the flow, so in addition to velocity, the particle size distribution and density will also determine burial parameters.

We used a combination of high-speed videography and physical models to determine the effects of body shape and kinematics on burial performance. Based on observations of the body movements of live fishes, we developed a physical model to determine if undulation frequency could have a significant role in burial. The goals of the present study were four-fold: (1) to quantify time to burial, percent coverage and frequency of undulation in five species of flatfishes; (2) to look for patterns in burial performance that can be explained by morphology or kinematic variation; (3) to undulate dead flatfishes to isolate the role of frequency on burial performance; and (4) to actuate canonical models of flatfishes to determine whether the patterns seen in the live fishes (see goal 2) were reflected in generalized flapping foils.

2. Materials and methods

2.1. Animal collection and care

Flatfishes were collected at Friday Harbor Laboratories (FHL) from June 17 to July 2, 2014 via beach seines (Jackson Beach 48°31′13.0″N 123°00′35.1″W) and trawls (San Juan Channel 48°35′10.9″N 123°02′18.7″W; Orcas Eastsound 48°38′26.9″N 122°52′14.0″W; Lopez Upright Head 48°34′45.4″N 122°53′03.2″W). We used five species of flatfishes that vary in shape and ecology (*Isopsetta isolepsis* (n = 6), *Lepidopsetta bilineata* (n = 6), *Hippoglossoides elassodon* (n = 3), *Parophrys vetulus* (n = 4), and *Psettichthys melanostictus* (n = 3); see Table 1). Fishes were kept in flow-through seawater tanks (11–13 °C) without substrate with similarly collected fishes of other species and fed mysid shrimp every 2–3 days.

The animals were maintained according to animal care practices outlined in University of Washington IACUC protocol 4208-03 and were released at the conclusion of the study. Two *L. bilineata* individuals died in captivity prior to video data collection and were frozen for later use.

2.2. High-speed videography

We recorded each individual using a high-speed camera (Troubleshooter LE500MS; Fastec GmbH, Paderborn, Germany) positioned over a tank with approximately 5–7 cm of fine-grain sand (collected at Eagle Cove, San Juan Island, WA, USA) on the bottom. Individuals were transferred to the filming tank and an acrylic divider was added to restrict the movement of the fish to within the frame of the camera. One burial event was recorded for each fish using high-speed videography (250 frames per second, shutter speed of 1/2500 s, 640 × 480 resolution, gamma of 1.5). Before and after burial, photographs were taken with a scale bar in the frame. All fishes were videotaped within five weeks of collection.

2.3. Video analysis

Duration of behavior(s) was measured between the start of the first undulation and the end of all motion. Time to burial was defined as the amount of time from the start of the first undulation to when the body was completely covered. Undulation frequency (Hz) was the ratio of the number of observable undulations (before the animal was obscured by sand) and the time taken to perform those undulations. We used ImageJ (Rasband, 1997–2014) to measure the percent of surface area that was buried during each trial by analyzing photographs using the pictures taken before and after the burial. Because flatfishes are known to have sand particle preferences that may affect their burial behavior (Moles and Norcross, 1995; Phelan et al., 2000; Stoner and Ottmar, 2003), all trials were run on the same sand, rinsed between uses. An estimate of the shape of the flatfish was found by taking the fineness ratio (ratio of a fish's length to its maximum diameter) of each fish. Two fineness ratios were determined, one which included the width of the fins, and one which included the width of the body without the fins.

2.4. Modeling

To test the effect of shape and undulation frequency on burial performance, a 100 mm x 170 mm x 8 mm oval flatfish model was molded using silicone rubber (EcoFlex 0050; shore 5A hardness: 00-50, tear strength: 8756 N m^{-1}, density: 1069 kg m^{-3}, elongation at break: 980%; Smooth-On, East Texas, PA, USA). The model was actuated by a variable speed orbital jigsaw (DW 318; DeWalt Industrial Tool Co., Baltimore, MD, USA) set to vertical motion only and modified with a 5 mm diameter metal rod in place of a blade (Fig. 1). The saw was clamped on either side of a wooden plank that rested over a tank of water and was held in place by two cinderblocks. The model was undulated by the jigsaw at various frequencies (3.7–31.9 Hz) over sand in the water to simulate flatfish burial. The model was undulated with an amplitude of 2.54 cm.

Experiments were recorded using the same high-speed camera and settings as above, except with a shutter speed of 1/1250 s instead of 1/2500 s. We analyzed the video to determine the fre-

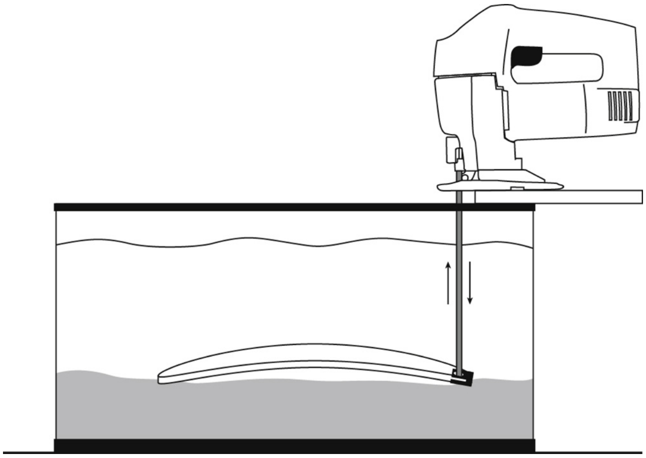

Fig. 1. Model setup. A DW318 variable speed orbital jigsaw was attached to a metal pole, where the blade would normally have gone, which acted as an actuator, moving a silicone fish model with fixed frequencies.