

Scaling of Burial Mechanics in *Parophrys vetulus*, the English Sole

Katherine A. Corn^{1,2} and Adam P. Summers^{1,3}

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¹Friday Harbor Laboratories, Friday Harbor, WA, 98250

²Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY, 14850

³Department of Biology, School of Fisheries and Aquatic Sciences, University of Washington, Seattle, WA, 98195

Katherine Corn
Department of Ecology and Evolutionary Biology
Cornell University
Corson-Mudd Hall
215 Tower Road
Ithaca, NY 14850
kac372@cornell.edu

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ABSTRACT

Flatfishes (Pleuronectiformes) rapidly bury themselves under sediments using body undulations and fin movements. During burial, a fish must fluidize a volume of the substrate to displace it into the water column and distribute it over the surface of the body. Thus the burial behavior forces the fish to interact with the fluid environment and a granular medium and is affected by size of the organism and grain size. We used the English Sole, *Parophrys vetulus*, as a model to explore the effects of scaling on burial. We recorded burial events from 15 fish across a size range (5 to 30 cm in total length), keeping sand grain size consistent, using high speed video at 250 fps and determined undulation frequency, time to burial, and percent body coverage. We found larger fishes took longer to bury and moved with a lower undulation frequency, but were able to cover themselves as effectively as smaller fish (91.6%). Undulation frequency decreased with body length to the -0.53 power; time to burial increased to the 0.67 power. We also used 5 individual fish of similar size (5.7 – 8.1 cm) and changed the size of the particle provided as substrate (125 – 710 microns). We found grain size does not affect the undulation frequency or time to burial of small fish, but as particle size increases, the percentage of the body covered decreases. It is possible that fish cannot fluidize particles of larger grain sizes as effectively as they can smaller grain sizes. Taken together, these results reveal that the timing of flatfish burial is a function of fish size and the success of the behavior is affected by the relative grain size of the sediment.

INTRODUCTION

Burial is an essential method for many taxa to avoid predation (Bellwood, 2002; Colgan 1974). From terrestrial lizard “sandfish” to real fish in sand, burial spans clades and morphologies to provide a common method of escape and, accordingly, a variety of burial methods are used (Hosoi & Goldman, 2015; Jung et al., 2010; Crofts & Summers 2011).

Here we focus on burial in a “*big and slow*” substrate fluidizer: an organism that is substantially bigger than the substrate into which it buries and buries in flow with low Reynold’s number (Hosoi & Goldman 2015). Substrate fluidizers alter the properties of the substrate to avoid the high energetic cost that digging requires, by altering a solid medium to a liquid and displacing it to over the body of the organism. In Hosoi and Goldman (2015)’s *big and slow* organism model, the force required to penetrate the granular medium (F_f) scales with velocity of digging (V), the scale length of the burier (a), and = the effective resistance of the substrate (μ), which is subject to the local volume fraction of particles (ϕ), according to the equation $F_f \sim \mu(\phi)Va$. Thus, the effective undulation rate (V) and the length of the burying organism are key in the ability of animals in the *big and slow* regime to fluidize the substrate and bury effectively.

Scaling, the study of how organisms interact with their environment as their size changes, is key. As terrestrial animals increase in size, their locomotor performance takes a penalty due to increased stress on the structures and allometric scaling (Biewener, 1990; Gatesy 1991), and it is reasonable to expect similar changes based on size in fishes’ swimming and burial (Winger et al. 2004; Webb, 2002; Yanase & Arimoto, 2007). Relative performance decreases due to the lower rate of increase in muscular ability, which

increases to the second power, relative to the rate of increase of mass of the organism, which increases to the third power (Schmidt-Nielsen, 1984).

Flatfishes (Order *Pleuronectiformes*) are a clade of bottom-dwelling fishes. With approximately 800 species, they are a highly diverse group, but all are characterized by a laterally compressed body form and the migration of one eye to the other side of the head (Sæle et al., 2006). This bizarre cranial anatomy enables the benthic lifestyle of the fishes, as they bury their bodies in the sand, often leaving only their eyes exposed. Flatfishes also use cryptic color change to camouflage their bodies and match the local substrate (Ellis et al., 1997). The English sole, *Parophrys vetulus*, is a flatfish widely distributed across the Eastern North Pacific, particularly distinguished by the upper eye, set on the midline, visible from the blind side (Eschmeyer & Herald, 1983; Lamb & Edgell 1986). Flatfishes are an exciting study system for burial due to their ability to do so with a counterintuitive morphology that does not appear lend itself to the task.

We used *Parophrys vetulus*, the English sole, as a model to explore the effects of scaling on burial. Our goals were four-fold: 1) to quantify the effect of fish length on undulation frequency and time to burial; 2) determine the relative importance of total length and undulation frequency in determining percent coverage 3) characterize the kinematics of flatfish burial; and 4) quantify individual variation in burial parameters.

MATERIALS & METHODS

Parophrys vetulus were collected via beach seines at Jackson Beach (48°31'12.6"N 123°00'37.6"W) and otter trawls at East Sound (48°38'14.5"N 122°52'19.5"W to

48°37'14.7"N 122°51'25.7"W). The fish were housed in flow-through sea tables with sandy substrate at Friday Harbor Laboratories (Friday Harbor, WA), with other flatfishes and sculpins. Fish were fed *ad libitum* mysid shrimp and shrimp tails.

A size range of 5.0-31.9 cm fish were used for experiment I. Fish were allowed to bury in sand of average size 516 microns. Fifteen individuals were allowed to bury on camera a minimum of five times; one was allowed to bury ten times; and one was allowed to bury fifteen. For the second study, five fish of similar size (5.7 – 8.1 cm) were selected. We used aluminum oxide particles as a substrate and changed the size of the particle provided as substrate between 125, 250, 355, 500, and 710 microns. Each fish was recorded burying once on each substrate size, in random order. Fish were selected for use nonrandomly to fill in the desired size range and by willingness to bury.

For both experiments, Fish were filmed laterally with a Fastec SC500ME Sportscam at 250 frames per second and a dorsal video for each fish with a CASIO Exilim EX-FH20. Photos were taken after each burial event and of the whole fish to determine percent coverage, standard length, and total fish area, respectively. Undulation frequency and time to bury were calculated for each burial event.

Videos were analyzed using Fiji (ImageJ) v2.0.0 (Rasband 1997-2014). Statistics were completed in R v3.1.3 (R Core Team, 2015). Statistics were performed on an averaged value from up to five burial events for each fish. Log/log graphs were plotted and linear regressions run of logged and unlogged undulation rate and time to burial to identify

scaling coefficients and significance. We used a multivariate regression to test the relationship between length, undulation rate, and time to burial and chose this test because we had two dependent variables and one independent variable. The multivariate regression was visualized with a MANOVA.

RESULTS

We observed a distinct series of actions over the course a single burial event. First, the fins undulate from the anterior to the posterior. This occurs at least once before the body begins to undulate. The fins can accommodate at least one undulation at a time, and as oscillations of the body commence, fins are generally in phase with the body. The movement of the head resembles a bobbing motion around a central node midway along the body. The full body resembles an oscillating plate with two sections that are in phase: the head, and a posterior portion of the body, significantly prior to the tail. Oscillations of the body continue until the surface is covered to the fish's apparent satisfaction. The fins perform at least one full undulation after the end of movement of the plate.

	p-value against length	r ² (adjusted) against length	Scaling coefficient	Scales with
Frequency	7.137e-05	0.6932	-0.52886	-1/Surface Area
Time to Burial	1.66e-05	0.7537	0.67140	Surface Area/Mass

Table 1: Scaling coefficients and relationship with characters.

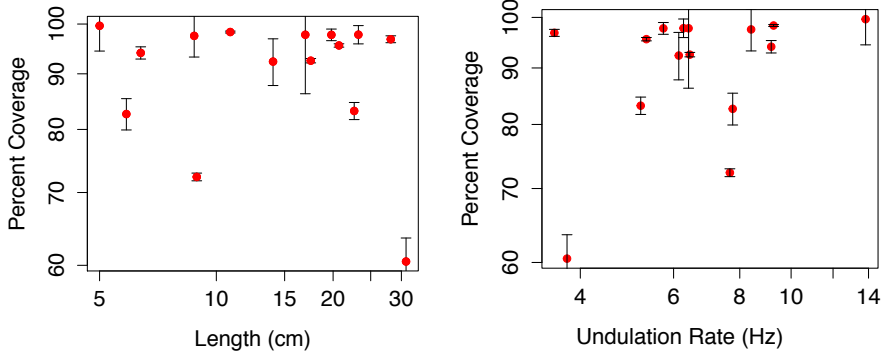


Figure 1:
Neither undulation frequency nor time to burial had a significant relationship with percent coverage.

We found significant effects of length on undulation rate and time to burial with strong r^2 -values (Table 1, Figure 1). We found scaling coefficients of average undulation rate and average time to burial to be -0.53 and 0.67, respectively. The MANOVA returned significant results. Neither undulation frequency nor length had a significant effect on percent coverage (Figure 2).

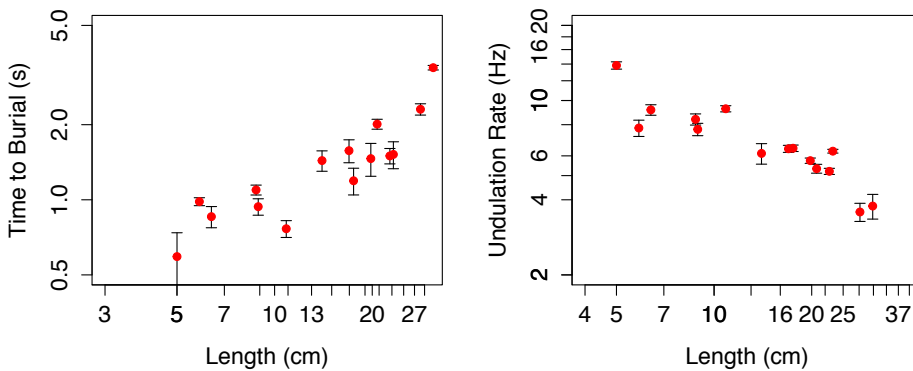


Figure 2:
Larger fishes bury with slower motions and take longer to do so. Log graphs of undulation rate and time to burial against length.

We found no effect of repeated burial on undulation rate or percent coverage for two fish who were allowed to bury over 10 and 15 burial events. We found a significant effect of repeated burial on time to bury for a fish that was recorded over 15 burial events (Fig. 4), but none for the fish allowed to bury 10 times.

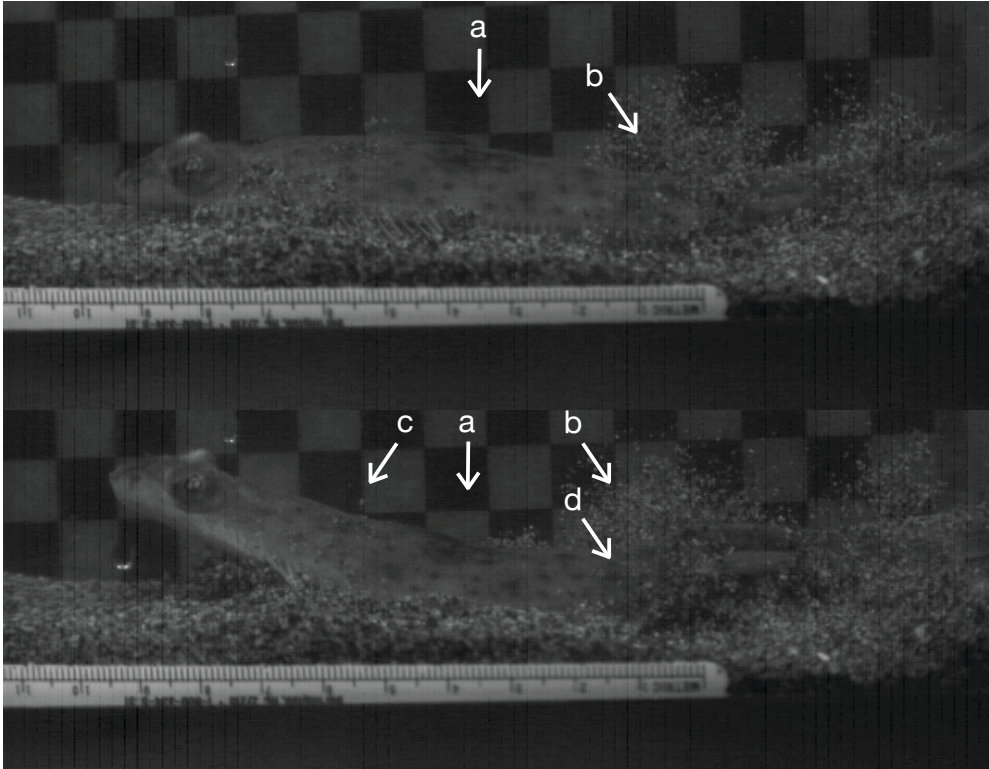


Figure 4.
a: Nodal point around which the body bends.
b: Posterior bending region.
c: Anterior bending region.
d: Bolus of sand moved by water from beneath the fish.

DISCUSSION

Results

A relationship of undulation rate and time to burial with length is consistent with our prediction of the ability of the fish to bury via the Hosoi & Goldman (2015) model of fluidization and its importance of length of the burying animal. The decrease in undulation frequency with increased size is consistent with properties of scaling that predict performance penalties in large animals. We found that grain size does not affect the undulation frequency or time to burial of small fish, but as particle size increases, the percentage of the body covered decreases.

By keeping their undulation frequency low and time to burial high, relatively large flatfishes are able to keep their Reynolds number low and continue to fluidize sand

effectively. It is important to note that with increasing fish body size and greater surface area, the task of the fins to disperse fluidized particulate over the body area becomes greater. However, we found that body size did not affect the ability of the fish to cover themselves with the substrate. Undulation frequency, responsible for dispersal of sand over the body, scales with length to the -0.53 power, which is close to $-1/Surface\ Area$. This indicates a potential relationship between changing surface area with length and changing behavior of the fish to effectively cover itself.

Because the fish lost performance success with increased grain size, we hypothesize that fish cannot fluidize particles of larger relative grain sizes as effectively as they can smaller grain sizes. Differential coverage performance of flatfish across a grain size range could be dependent on the size of the fish relative to the substrate particle size, rather than performance differences of the fish's body.

Repeated Burial

Our results indicate that recording multiple consecutive burial events likely does not alter its performance until many events are recorded. Because the time to burial was significantly different over 15 burial events, we are not concerned about the effect of repeated burial on our dataset, where most fishes were only recorded 5-6 times.

Concluding Remarks

Scaling is affects multiple factors of fish burial performance. Our study indicates that the kinematics of burial are determined by fish size (physiology), and the relative success is influenced by sediment grain size (environment).

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