

RESEARCH ARTICLE

Effects of organism and substrate size on burial mechanics of English sole, *Parophrys vetulus*

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ABSTRACT

Flatfishes use cyclic body undulations to force water into the sediment and fluidize substrate particles, displacing them into the water column. When water velocity decreases, suspended particles settle back onto the fish, hiding it from view. Burial may become more challenging as flatfishes grow because the area to be covered increases exponentially with the second power of length. In addition, particle size is not uniform in naturally occurring substrates, and larger particles require higher water velocities for fluidization. We quantified the effects of organism and particle-size scaling on burial behavior of English sole, *Parophrys vetulus*. We recorded burial events from a size range of individuals (5–32 cm total length, TL), while maintaining constant substrate grain size. Larger fish used lower cycle frequencies and took longer to bury, but overall burial performance was maintained (~100% coverage). To test the effect of particle size on burial performance, individuals of similar lengths (5.7–8.1 cm TL) were presented with different substrate sizes (0.125–0.710 mm). Particle size did not affect cycle frequency or time to burial, but fish did not achieve 100% coverage with the largest particles because they could not fluidize this substrate. Taken together, these results suggest that both body size and substrate grain size can potentially limit the ability of flatfishes to bury: a very large fish (>150 cm) may move too slowly to fluidize all but the smallest substrate particles and some particles are simply too large for smaller individuals to fluidize.

KEY WORDS: Flatfish, Fluidization, Scaling

INTRODUCTION

Many animals bury in substrate to avoid predators, to hide and ambush prey, or to escape unfavorable conditions, and yet moving through a particulate medium is one of the most energetically costly modes of transport (Hunter and Elder, 1989; Trevor, 1978; White, 2001). To burrow or bury, an animal must displace substrate and overcome the substantial drag forces between its body and the surrounding particles. Burrowing invertebrates such as worms can spread these movements out over long periods of time and take advantage of crack propagation to conserve energy (Dorgan et al., 2007, 2008, 2011), but animals that bury rapidly face a large energetic challenge. Locomotion into and through a wet granular

medium is particularly difficult. For example, it takes approximately four times as much force to penetrate a wet particulate medium than a dry particulate medium of the same grain size (Sharpe et al., 2015).

In response to this mechanical challenge, many aquatic organisms fluidize the substrate, including razor clams (Winter et al., 2012), cephalopods (Montana et al., 2015), sandfish (MacDonald, 2015) and flatfishes (McKee et al., 2016). Fluidization is a process by which energy is imparted to a bed of particles, thereby converting a granular medium from a ‘static semisolid’ (or solid-like) state to a ‘dynamic semifluid’ (or fluid-like) state (Goldman, 2014). Fluidizing a substrate decreases its viscosity (Hosoi and Goldman, 2015), which correspondingly decreases frictional drag experienced by the animal moving through the surrounding particles (Jung et al., 2011; Winter, 2010). This permits burial in cases where a static substrate would not allow it (Hosoi and Goldman, 2015; Jung et al., 2011; Winter et al., 2012).

Flatfishes (Pleuronectiformes) are benthic, bilaterally asymmetrical, laterally compressed fishes that spend most of their adult lives resting on the substrate, looking up into the water column. Most flatfish species cover themselves with particles by fluidizing granular substrate (McKee et al., 2016). During this behavior, undulations of the body and fins force water into the substrate. As the fluid rebounds out of the substrate, it carries substrate particles with it into the water column above the fish. As water velocity decreases, particles fall out of suspension, covering the fish. Because of their deep-bodied, laterally flattened shape, flatfishes must produce jets of water that fluidize sufficient quantities of particles to cover the large surface area presented by the lateral aspect of the body. This becomes more challenging as these fishes grow, because surface area increases with the second power of length (e.g. as a fish grows 4 times larger in length, it will have 16 times as much surface area to cover; see Schmidt-Nielsen, 1984). Substrates with larger particle sizes also present a challenge, because the minimum required velocity for fluidization increases linearly with particle diameter and the increased mass of larger particles will cause them to drop out of solution more rapidly, relative to smaller particles, when fluidized (MacDonald, 2015; Richardson et al., 2002).

The quantification of burial kinematics and performance in flatfishes offers an opportunity to partition the effects of morphological scaling and scaling of environment–animal interactions by varying these two parameters independently. We used *Parophrys vetulus* Girard (1854), the English sole, as a model flatfish to (1) determine how scaling of body length (fish size) influences burial performance and (2) quantify the effects of scaling of particle size (substrate) on burial performance. In experiment 1, we filmed burying individuals across a 30 cm body size range, with substrate grain size held constant. Because the surface area to be covered increases with the second power of length, we predicted that larger fish must either undulate at a higher cycle frequency or increase the duration of the burial event. In experiment 2, we filmed

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burial of several individuals of approximately the same size and varied the particle size of the substrate. For this experiment, we predicted that as particle size becomes larger, a fish must either undulate at higher cycle frequency or increase the duration of the burial event.

MATERIALS AND METHODS

Experimental conditions

Parophrys vetulus were collected by beach seines at Jackson Beach (48.520°N, 123.010°W) and by otter trawls at East Sound (48.637°N, 122.87°W to 48.621°N, 122.857°W) in the San Juan Islands, WA, USA. The fish were housed in flow-through sea tables with locally collected sandy substrate at Friday Harbor Laboratories (Friday Harbor, WA, USA) and were fed mysid shrimp (family Mysidae) and tails of shrimp (family Pandalidae). Protocols for animal husbandry and experimentation were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC #4238-03).

In experiment 1, we varied the size of the fish while sediment size remained constant (Fig. 1A). Fish of a size range of 5.0 to 31.9 cm total length (TL) were used for this experiment ($n=15$ individuals). Individuals were chosen to evenly cover the total size range available. We recorded five burial events for each fish using a locally collected sandy substrate with an average particle size of 0.516 mm (range: 0.124–0.70 mm). In experiment 2, we used individuals of similar size (5.7–8.1 cm TL, $n=5$ individuals) but varied sediment size ($n=5$ sediment types; Fig. 1B). For substrate, we used aluminium oxide particles with diameters of 0.125, 0.250, 0.355, 0.500 and 0.710 mm. Each fish was recorded burying once on each substrate size, with substrate size presented in random order. Substrate randomness was determined with a custom-written R script randomizing order of five numbers.

Video analysis

For both experiments, fish were recorded from a lateral view using a Fastec SC500ME Sportscam capturing images at 250 frames s^{-1} . Dorsal photos of each fish were taken before and after each burial

event to determine the percentage of the body covered by sediment after burial (percent coverage). Burial event duration and undulation frequency were calculated for each burial event. We quantified burial event duration as time from the beginning of fin motion to the end of fin motion during a burial event, regardless of whether the fish was completely covered. Undulation frequency was calculated as the number of undulations of the body divided by the total duration of the burial event. To determine percent coverage, we measured the amount of surface area left uncovered after burial and compared it with the total surface area of the fish. The ratio of uncovered surface to total surface was then subtracted from 1 to obtain percent coverage. All video and still images were analyzed using Fiji (ImageJ) v2.0.0 (Schindelin et al., 2012; Schneider et al., 2012).

Statistical analysis (general)

We used R v3.1.3 package ‘stats’ (<http://www.R-project.org/>) to conduct statistical analyses. For experiment 1, we calculated the means for each variable (duration, cycle frequency and percent coverage) from 3–5 burial events for each of the 15 individuals. Mean values were then used to compute linear regressions to evaluate relationships between log fish length and log undulation rate, log duration of burial event and log area covered. We also regressed log undulation frequency and log burial event duration versus log percent coverage to identify possible associations between behavioral variables and burial performance, using percent coverage as the metric of burial success. We used a Pearson’s product-moment test for correlation between the number of undulations and time to burial.

For experiment 2, we did not take the mean of burial performance and kinematic values across individuals, but instead used measured values for the five individuals at each of the five grain sizes for our statistical analyses. The relationship between log size of the granular media and log undulation rate, log burial event duration and log area covered was quantified using linear regression.

We used a Bonferroni correction to determine significance to reduce the likelihood of Type I error, implemented by dividing a

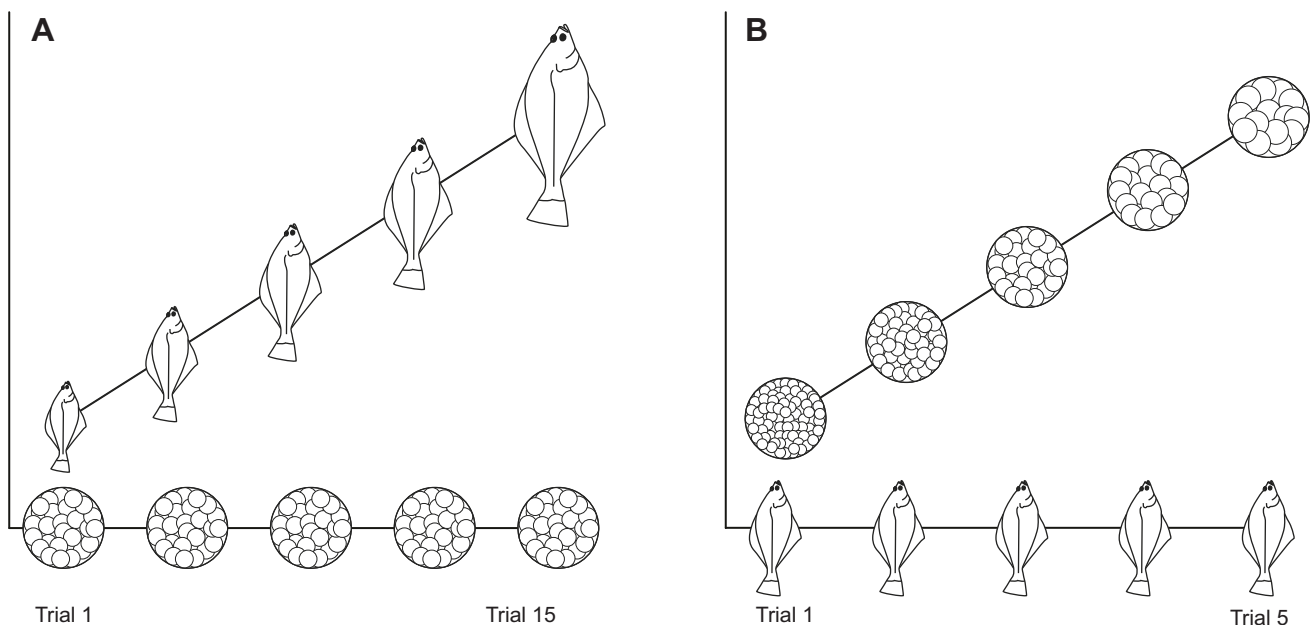


Fig. 1. Experimental design across a two-part experiment separating effects of substrate size and body size. (A) Experiment 1 used fish between 5 and 32 cm on substrate of a single size. (B) Experiment 2 used fish between 5 and 8 cm on substrate between 0.125 and 0.710 mm.

standard P -value cutoff (0.05) by the number of regressions run using the dataset. Bonferroni correction indicates a corrected P -value of 0.01 for experiment 1 and 0.016 for experiment 2 (5 and 3 regressions per dataset, respectively). To account for the possibility of Type 1 error suggested by our Bonferroni correction in experiment 2, we used Bayesian Information Criterion (BIC) (Schwarz, 1978) to select the best model given all possible combinations of predictors. This was implemented with *regsubsets* in the R package *leaps* (<https://CRAN.R-project.org/package=leaps>) and quantified the relationship between variables inherent to the fish (as determined by experiment 1: undulation rate and duration of burial event) or manipulated by us (substrate particle size) and the total percentage of the fish's body covered with sediment after the burial event. All data are publicly available from the Dryad digital repository (Corn et al., 2018).

RESULTS

Characterization of flatfish burial

We observed a distinct set of motions that comprised a single burial event. The burial event began when a posteriorly moving wave of undulation passed down the length of both the dorsal and anal fins. After at least one fin undulation was completed, the body began to rapidly undulate, and the entire body appeared to act as an undulating plate. Undulations of the body continued until a portion or all of the upper body surface was covered by substrate to the fish's satisfaction. The dorsal and anal fins continued to undulate through at least one additional cycle after the end of movement of the body.

Organism scaling

All regression statistics from experiments 1 and 2 are summarized in Table 1, where intercept and slope reference a and b , respectively, are used in the scaling equation $y=bx+a$, where slope is considered the scaling coefficient. With increasing fish length (L), body undulations became less frequent (e.g. fewer undulations were produced per unit time) and the time to burial increased (Fig. 2A,B). The scaling coefficients for undulation rate versus length and duration of burial versus length were $L^{-0.52}$ ($P<0.001$) and $L^{0.68}$ ($P<0.001$), respectively (Table 1). Percent coverage was not a significant predictor of either undulation frequency ($P=0.23$) or duration of burial ($P=0.18$); that is, all fish buried themselves to a similar extent, regardless of undulation frequency or total burial time. However, the total number of undulations increased with fish length ($L^{0.15}$, $P<0.05$), while the percentage of the fish covered in sediment following burial remained unchanged as fish became larger ($P>0.05$) (Fig. 2C). Therefore, fish required more cycles of slower movement to bury themselves as they grew larger. We also measured the total number of undulations during burial, but did not conduct statistical analyses on this variable because it is correlated with the total duration of burial ($P<0.001$, estimate=0.778).

Environment scaling

When presented with substrates of different grain sizes, fish did not alter their burial behavior. There was no relationship between body undulation frequency ($P=0.21$) or duration of burial ($P=0.16$) with substrate grain (particle) size (Fig. 3A,B): fish produced approximately the same frequency of movement and took the same amount of time to bury across all substrate sizes. However, percent coverage decreased with increasing grain size ($L^{-1.83}$, $P=0.022$) (Fig. 3C). At the largest grain sizes, small fish were only able to cover a maximum of 35% of their bodies during the burial behavior. Additional regression statistics are shown in Table 1. The *regsubsets* model comparison results indicate that the model

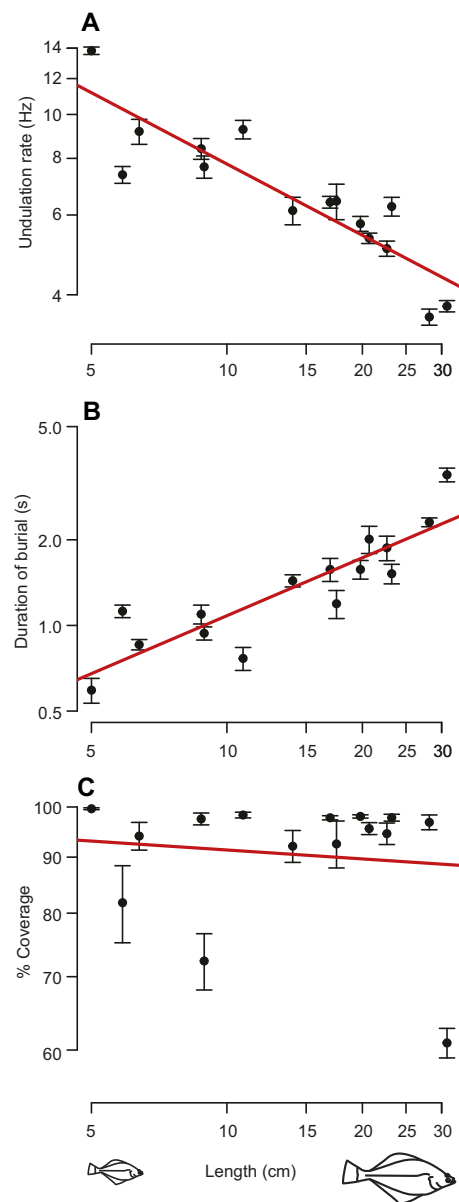


Fig. 2. Fish kinematics change with increasing fish size. Larger fishes moved with a lower undulation frequency and took longer to bury, but were able to bury as effectively as smaller fish (an average of 91.6% of body covered with sediment after the burial behavior). Fish buried in substrate of average size 0.516 mm. Data were \log_{10} transformed. Bars and points indicate mean \pm s.e.m. values per individual of $n=15$ individuals over 3–5 trials. (A) Undulation frequency decreased with increasing body size. (B) Duration of burial event increased with body size. (C) Body size had no effect on burial success (percentage of body covered in substrate after burial event). Additional regression statistics are shown in Table 1.

'percent coverage~duration+grain size of burial', which excludes undulation rate, is the best model.

DISCUSSION

Across the flatfish body sizes considered here, animal size did not limit burial performance, but substrate particle size did. This finding has implications for habitat use: flatfishes are likely to be limited in the size of substrate they can use for camouflage. Behavioral preference tests conducted using other flatfish species show that juvenile flatfishes avoid sediments too coarse for them to bury in

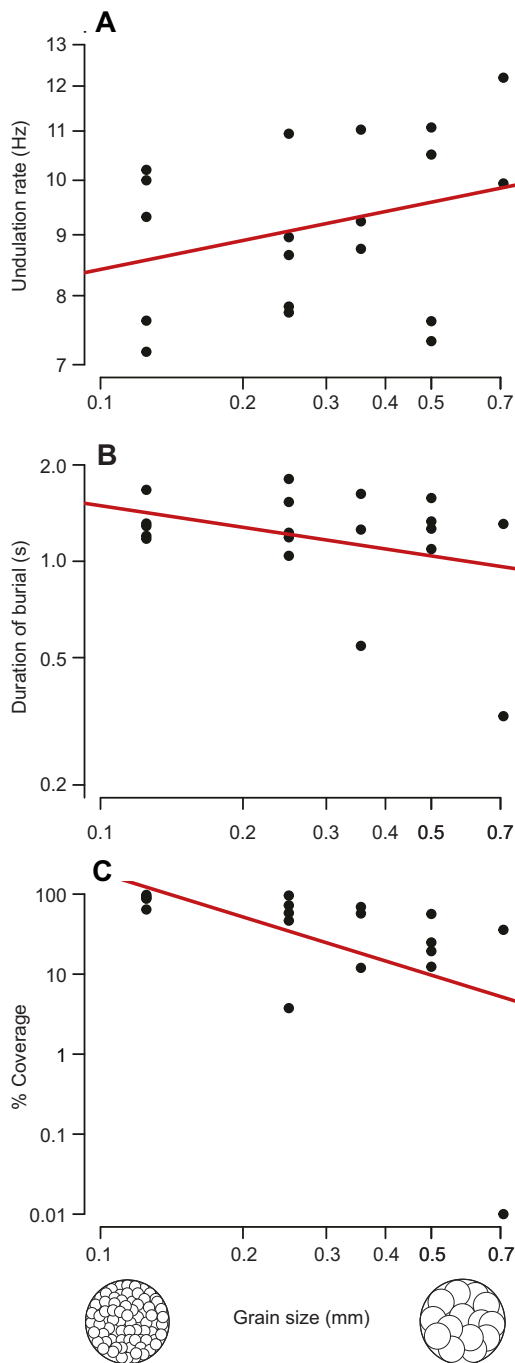


Fig. 3. Burial success decreases with increasing substrate particle size.

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 by particles decreases. Data were \log_{10} transformed. Points indicate individual fish. (A) Undulation frequency did not change with increasing particle size. (B) Duration of burial event did not change with increasing particle size. (C) The data suggest that overall burial success (percent coverage) decreased with increasing particle size. Additional regression statistics are shown in Table 1.

(Moles and Norcross, 1995; Gibson and Robb, 2000). However, it is important to note that sediment composition preferences (McConnaughey and Smith, 2000; Stoner and Ottmar, 2003) are species specific, which suggests that some flatfish species may be capable of fluidizing larger particles, relative to other species. This is consistent with recent laboratory observations that burial

kinematics including time to burial and undulation frequency in flatfishes vary by species (McKee et al., 2016).

Larger fish took more time to bury, which is consistent with our *a priori* prediction that larger fishes would increase the duration of burial effort to cover their larger surface area. However, instead of the predicted increase in burial effort by increasing undulation frequency, larger fish produced fewer undulations per unit time. We suggest that individuals of *P. vetulus* are unable to produce higher frequency undulations at larger body sizes because of physiological limitations. The scaling pattern seen here is similar to consistent limits on tail beat frequency of swimming fishes (e.g. Wardle, 1975; Videler and Wardle, 1991), where smaller fishes have higher tail beat frequencies than larger fishes. This pattern is observed both across species with different adult body sizes and across a size range of a single fish species. Based on isolated muscle experiments, it appears this phenomenon occurs, at least in part, because muscle power output (work over time) declines as cycle duration increases as fish become larger (Altringham and Johnston, 1990; Anderson and Johnston, 1992). If we assume that flatfish length scales with mass (M) to the one-third power ($L \propto M^{1/3}$ and $f \propto L^{-1/2}$, where maximum cycle frequency f scales with mass to the $-1/6$: $f \propto M^{-1/6}$; see Bejan and Marden, 2006), then the intraspecific scaling exponent for cycle frequency observed here is what would be predicted based on the observed relationship between maximum cycle frequency and body mass for a swimming animal. Like swimming fishes, *P. vetulus* do not appear to be able to produce sufficient power to maintain a rapid body undulation frequency as they grow larger.

The physiological limit on cycle frequency suggests that the duration of burial behavior must increase to allow the fish to cover an increasingly large body surface area as they grow longer. Over the range of body sizes considered here, *P. vetulus* maintained burial performance by adding cycles to the behavior (thereby increasing the duration of burial), which allowed them to achieve $\sim 100\%$ coverage. However, very large flatfishes are unlikely to be able to bury effectively, unless the substrate is composed of very small grain sizes that can be fluidized by lower water velocities. Pacific halibut, *Hippoglossus stenolepis*, for example, can reach 250 cm TL (see Moiseev, 1955; cited in Orlov et al., 2011). Assuming that Pacific halibut follow a similar scaling relationship to that of English sole (Table 1), we would expect that a 250 cm Pacific halibut would undulate at $0.0126 \text{ cycles s}^{-1}$ and one complete cycle of burial would take more than a minute. Thus, for very large flatfishes, body undulations may not produce effective burial in sediment with particles of the size used in our organism-scaling experiment. Correspondingly, limitations on body undulation rate may ultimately determine what substrates can be used by larger flatfishes. This inference is supported by surveys of Pacific halibut that reveal that large ($>100 \text{ cm}$) halibut prefer fine sediments, whereas smaller halibut prefer coarser sediments (Carlson et al., 2005).

Although fish in our study maintained performance across a range of body sizes at a fixed particle size, they could not maintain performance as particle size increased. The best model of the data indicated that a combination of grain size and duration of burial predicted percent coverage. We hypothesize that this is due to an inability of flatfish to fluidize larger grain sizes. This scaling phenomenon has been seen in other animals that fluidize substrate, such as the octopus *Octopus kaurana*, which showed decreased sub-surface burrowing performance with increased sediment size (Montana et al., 2015), the Pacific sandfish, *Trichodon trichodon*, which cannot produce an adequate flow of water out of the gill

Table 1. Regression statistics

Regression model	Intercept	Slope	d.f.	P-value	Adjusted r^2
Undulation rate~length	1.41	-0.52	13	<0.001	0.77
Duration~length	-0.64	0.68	13	<0.001	0.75
% Coverage~length	1.99	-0.027	13	0.68	0
% Coverage~undulation rate	1.85	0.13	13	0.23	0.04
% Coverage~duration	-0.11	-0.11	13	0.18	0.064
% Coverage~duration+grain size	0.57	-1.24	16	<0.01	0.43
Undulation rate~grain size	1.01	0.081	17	0.21	0.39
Duration~grain size	-0.051	-0.22	17	0.16	0.63
% Coverage~grain size	0.44	-1.83	17	0.022	0.23

Results of linear model regressions of experiments 1 and 2. Data were \log_{10} transformed and averaged prior to performing statistical analyses in experiment 1, where we tested a 27 cm size range of fish on constant substrate size, and \log_{10} transformed prior to performing statistical analyses in experiment 2, where we tested fish of constant size across a 0.6 mm range of substrate grain size.

openings to fluidize larger substrate particles (MacDonald, 2015), and juvenile European plaice, *Pleuronectes platessa*, which show a negative asymptotic relationship between substrate particle size and burial success (Gibson and Robb, 1992). The likely mechanism underlying this pattern is that particles of larger size require greater fluid velocity to fluidize (MacDonald, 2015; Richardson et al., 2002). In the case of *P. vetulus*, individuals did not adjust burial kinematics to compensate for increased particle size and were unable to overcome this constraint (Fig. 3A,B). We compared the performance of our fish with a published model of burial in juvenile *P. platessa* (Gibson and Robb, 1992), and found that our small fish underperformed at larger grain sizes when compared with predictions of juvenile plaice of the same size (predicted: 91–98% coverage at 0.710 mm grain substrate; actual coverage: 0–35%). We attribute this discrepancy to interspecific differences in burial behavior and kinematics.

Biomechanical and physiological constraints of burial are key predictors of sediment preference (Bizzarro et al., 2016) that can inform spatial planning efforts and habitat management for the conservation of commercially and ecologically important marine species, including flatfishes. Some juvenile flatfishes have demonstrated a preference for seafloor habitats consisting of small grain sizes (Abookire and Norcross, 1998; Moles and Norcross, 1995; Stoner and Ottmar, 2003; Tanda, 1990). Alternatively, because relatively smaller flatfishes can produce very high frequency movements, perhaps they can displace disproportionately larger particles and use the same habitat as larger members of the same species. We provide a biomechanical context for substrate size limitation in habitat preference in flatfishes that has the potential to inform decisions regarding essential fish habitat for these economically and ecologically important species.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.C.F., A.P.S., A.C.G.; Methodology: K.A.C., S.C.F., A.P.S., A.C.G.; Formal analysis: K.A.C.; Investigation: K.A.C., S.C.F., A.C.G.;

Writing - original draft: K.A.C., S.C.F.; Writing - review & editing: K.A.C., S.C.F., A.P.S., A.C.G.; Supervision: S.C.F., A.P.S., A.C.G.; Project administration: A.P.S.; Funding acquisition: A.P.S. We also thank two anonymous reviewers for their helpful comments on the manuscript.

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Data availability

All data are publicly available from the Dryad digital repository (Corn et al., 2018): <https://doi.org/10.5061/dryad.45b5g>

References

- Abookire, A. A. and Norcross, B. L. (1998). Depth and substrate as determinants of distribution of juvenile flathead sole (*Hippoglossoides elassodon*) and rock sole (*Pleuronectes bilineatus*), in Kachemak Bay, Alaska. *J. Sea Res.* **39**, 113–123.
- Altringham, J. D. and Johnston, I. A. (1990). Scaling effects on muscle function: power output of isolated fish muscle fibres performing oscillatory work. *J. Exp. Biol.* **467**, 453–467.
- Anderson, M. E. and Johnston, I. A. (1992). Scaling of power output in fast muscle-fibers of the atlantic cod during cyclical contractions. *J. Exp. Biol.* **170**, 143–154.
- Bejan, A. and Marden, J. H. (2006). Unifying constructal theory for scale effects in running, swimming and flying. *J. Exp. Biol.* **209**, 238–248.
- Bizzarro, J. J., Peterson, A. N., Blaine, J. M., Balaban, J. P., Greene, H. G. and Summers, A. P. (2016). Burrowing behavior, habitat, and functional morphology of the Pacific sand lance (*Ammodytes personatus*). *Fish. B-NOAA* **114**, 445–460.
- Carlson, P. R., Hooge, P. N. and Cochrane, G. R. (2005). Discovery of 100–160-year-old iceberg gouges and their relation to halibut habitat in glacier bay, Alaska. *Am. Fish. S. S.* **41**, 235–243.
- Corn, K. A., Farina, S. C., Summers, A. P. and Gibb, A. C. (2018). Data from: Effects of organism and substrate size on burial mechanics of English sole, *Parophrys vetulus*. Dryad Digital Repository. <https://doi.org/10.5061/dryad.45b5g>
- Dorgan, K. M., Arwade, S. R. and Jumars, P. A. (2007). Burrowing in marine muds by crack propagation: kinematics and forces. *J. Exp. Biol.* **210**, 4198–4212.
- Dorgan, K. M., Arwade, S. R. and Jumars, P. A. (2008). Worms as wedges: effects of sediment mechanics on burrowing behavior. *J. Mar. Res.* **66**, 219–254.
- Dorgan, K. M., Lefebvre, S., Stillman, J. H. and Koehl, M. A. R. (2011). Energetics of burrowing by the cirratulid polychaete *Cirriiformia moorei*. *J. Exp. Biol.* **214**, 2202–2214.
- Gibson, R. N. and Robb, L. (1992). The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. *J. Fish Biol.* **40**, 771–778.
- Gibson, R. N. and Robb, L. (2000). Sediment selection in juvenile plaice and its behavioural basis. *J. Fish Biol.* **56**, 1258–1275.
- Girard, C. (1854). Descriptions of new fishes collected by AL Heermann, naturalist attached to the survey of the Pacific Railroad route under Lieut. RS Williamson. *Proc. Acad. Nat. Sci. Phila.* **7**, 129–140.
- Goldman, D. I. (2014). Colloquium: biophysical principles of undulatory self-propulsion in granular media. *Rev. Mod. Phys.* **86**, 943.
- Hosoi, A. E. and Goldman, D. I. (2015). Beneath our feet: strategies for locomotion in granular media. *Annu. Rev. Fluid Mech.* **47**, 431–453.
- Hunter, R. D. and Elder, H. Y. (1989). Burrowing dynamics and energy cost of transport in the soft-bodied marine invertebrates *Polyphysia crassa* and *Priapulus caudatus*. *J. Zool.* **218**, 209–222.
- Jung, S., Winter, A. G. and Hosoi, A. E. (2011). Dynamics of digging in wet soil. *Int. J. Non-Linear Mech.* **46**, 602–606.

- MacDonald, I.** (2015). *Burial Mechanics of the Pacific Sandfish: the Role of the Ventilatory Pump & Physical Constraints on the Behavior*. MSc Thesis, Northern Arizona University, Flagstaff, AZ.
- McConnaughey, R. A. and Smith, K. R.** (2000). Associations between flatfish abundance and surficial sediments in the eastern Bering Sea. *Can. J. Fish Aquat. Sci.* **57**, 2410-2419.
- McKee, A., MacDonald, I., Farina, S. C. and Summers, A. P.** (2016). Undulation frequency affects burial performance in living and model flatfishes. *Zoology* **119**, 75-80.
- Moiseev, P. A.** (1955). New data on the distribution of pacific halibut. *Dokl. Akad. Nauk SSSR* **105**, 374-375.
- Moles, A. and Norcross, B. L.** (1995). Sediment preference in juvenile pacific flatfishes. *Neth. J. Sea Res.* **34**, 177-182.
- Montana, J., Norman, M. D. and Finn, J. K.** (2015). Liquid sand burrowing and mucus utilisation as novel adaptations to a structurally-simple environment in *Octopus kaurma* Stranks, 1990. *Behaviour* **152**, 1871-1881.
- Orlov, A. M., Kuznetsova, E. N. and Mukhametov, I. N.** (2011). Age and growth of the Pacific halibut *Hippoglossus stenolepis* and the size-age composition of its catches in the North-Western part of the Pacific Ocean. *J. Ichthyol.* **51**, 306-323.
- Richardson, J. F., Harker, J. H. and Backhurst, J. R.** (2002). *Coulson and Richardson's Chemical Engineering: Particle Technology and Separation Processes*, Vol. 2, 5th edn. Oxford, UK: Butterworth-Heinemann.
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B. et al.** (2012). Fiji: an open-source platform for biological-image analysis. *Nat. Methods* **9**, 676-682.
- Schmidt-Nielsen, K.** (1984). *Scaling: Why is Animal Size so Important?* Cambridge, UK: Cambridge University Press.
- Schneider, C. A., Rasband, W. S. and Eliceiri, K. W.** (2012). NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671-675.
- Schwarz, G.** (1978). Estimating the dimension of a model. *Ann. Stat.* **6**, 461-464.
- Sharpe, S. S., Kuckuk, R. and Goldman, D. I.** (2015). Controlled preparation of wet granular media reveals limits to lizard burial ability. *Phys. Biol.* **12**, 46009.
- Stoner, A. W. and Ottmar, M. L.** (2003). Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. *J. Exp. Mar. Biol. Ecol.* **282**, 85-101.
- Tanda, M.** (1990). Studies on burying and ability japanese in sand and selection sole to the grain size for hatchery-reared marbled flounder. *Nippon Suisan Gakk.* **56**, 1543-1548.
- Trevor, J. H.** (1978). The dynamics and mechanical energy expenditure of the polychaetes *Nephtys cirrosa*, *Nereis diversicolor* and *Arenicola marina* during burrowing. *Estuar. Coast. Mar. Sci.* **6**, 605-619.
- Videler, J. J. and Wardle, C. S.** (1991). Fish swimming stride by stride: speed limits and endurance. *Rev. Fish Biol. Fisher.* **1**, 23-40.
- Wardle, C. S.** (1975). Limit of fish swimming speed. *Nature* **255**, 725-727.
- White, C. R.** (2001). The energetics of burrow excavation by the inland robust scorpion, *Urodacus yaschenkoi* (Birula, 1903). *Aust. J. Zool.* **49**, 663-674.
- Winter, A. G.** (2010). *Biologically Inspired Mechanisms for Burrowing in Undersea Substrates*. PhD Thesis. Massachusetts Institute of Technology, Cambridge, MA.
- Winter, A. G., Deits, R. L. H. and Hosoi, A. E.** (2012). Localized fluidization burrowing mechanics of *Ensis directus*. *J. Exp. Biol.* **215**, 2072-2080.