RESEARCH ARTICLE



Hydrodynamic sensing and behavior by oyster larvae in turbulence and waves

Heidi L. Fuchs^{1,*}, Gregory P. Gerbi², Elias J. Hunter¹, Adam J. Christman¹ and F. Javier Diez¹

ABSTRACT

Hydrodynamic signals from turbulence and waves may provide marine invertebrate larvae with behavioral cues that affect the pathways and energetic costs of larval delivery to adult habitats. Oysters (Crassostrea virginica) live in sheltered estuaries with strong turbulence and small waves, but their larvae can be transported into coastal waters with large waves. These contrasting environments have different ranges of hydrodynamic signals, because turbulence generally produces higher spatial velocity gradients, whereas waves can produce higher temporal velocity gradients. To understand how physical processes affect oyster larval behavior, transport and energetics, we exposed larvae to different combinations of turbulence and waves in flow tanks with (1) wavy turbulence, (2) a seiche and (3) rectilinear accelerations. We quantified behavioral responses of individual larvae to local instantaneous flows using twophase, infrared particle-image velocimetry. Both high dissipation rates and high wave-generated accelerations induced most larvae to swim faster upward. High dissipation rates also induced some rapid, active dives, whereas high accelerations induced only weak active dives. In both turbulence and waves, faster swimming and active diving were achieved through an increase in propulsive force and power output that would carry a high energetic cost. Swimming costs could be offset if larvae reaching surface waters had a higher probability of being transported shoreward by Stokes drift, whereas diving costs could be offset by enhanced settlement or predator avoidance. These complex behaviors suggest that larvae integrate multiple hydrodynamic signals to manage dispersal tradeoffs, spending more energy to raise the probability of successful transport to suitable locations.

KEY WORDS: Acceleration, *Crassostrea virginica*, Dissipation rate, Energetics, Hydrodynamic signals, Larval behavior

INTRODUCTION

Some dispersing invertebrate larvae respond behaviorally to physical cues, and these responses can have multiple influences on larval transport pathways. Coastal mollusk larvae (veligers) react to strong turbulence by descending toward the seabed (e.g. Barile et al., 1994; Fuchs et al., 2004, 2013). Simple models show that this behavior can raise the probability of larval settlement in energetic nearshore habitats (Fuchs et al., 2007; Fuchs and Reidenbach, 2013). Depth-seeking behaviors generally tend to limit transport by fast-moving surface currents and to enhance local retention (North et al., 2008; Shanks, 2009; Kim et al., 2010). Turbulence-induced sinking also contributed to onshore larval migration within the surf

¹Rutgers University, New Brunswick, NJ 08901, USA. ²Skidmore College, Saratoga Springs, NY 12866, USA.

*Author for correspondence (hfuchs@marine.rutgers.edu)

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zone in a recent model that accounted for non-linear transport by surface gravity waves, known as Stokes drift (Fujimura et al., 2014). Outside the surf zone on the continental shelf, Stokes drift is often shoreward at the surface and may be an important mechanism of onshore larval transport (Monismith and Fong, 2004; Feng et al., 2011; Röhrs et al., 2014). It is unknown whether larvae can modify their behavior to exploit waves as a mechanism of delivery to coastal habitats.

Larval responses to waves likely would involve temporal velocity gradients (accelerations) as a sensory cue, whereas responses to turbulence could involve accelerations or spatial velocity gradients. Spatial velocity gradients include shearing (e.g. strain rate) and rotational (e.g. vorticity) motions classified generally as deformations. Under most conditions, turbulence dominates the production of deformations, whereas waves often dominate the production of accelerations (H.L.F. and G.P.G., unpublished data). Turbulence affects many well-studied aspects of larval life cycles, including external fertilization, predation and settlement fluxes (Abelson and Denny, 1997; Kiørboe, 2011; Crimaldi and Zimmer, 2014); in contrast, waves have better-known influences on benthic organisms (Denny, 1988). Accelerations have been explored as a sensory cue only in the context of organism-induced vibrations (Lang, 1980; Heuch and Karlsen, 1997; Kiørboe et al., 1999), and wave motions have only recently been investigated as a habitat characteristic for larvae outside the surf zone (Reidenbach et al., 2009; Koehl et al., 2013). Both deformations and accelerations are largest in the surf zone, but these signals have unique joint distributions in other seascapes: in sheltered inlets and estuaries, large deformations can occur with small accelerations, whereas on the continental shelf and open ocean, small deformations can occur with large accelerations (H.L.F. and G.P.G., unpublished data). This geographic variation in signals may enable larvae to discriminate among coastal and offshore habitats.

We investigated how hydrodynamic signals from turbulence and waves influence behaviors of oyster larvae, Crassostrea virginica Gmelin 1791. Oysters form reefs in intertidal or shallow subtidal zones of sheltered coastal waters and estuaries (Kennedy and Sanford, 1999). These habitats have strong tide-generated turbulence that is enhanced by drag over coarse reef substrates (Whitman and Reidenbach, 2012). In strong turbulence, oyster larvae exhibit rapid dives that would raise larval contact rates with discrete patches of reef (Fuchs et al., 2013; Fuchs and Reidenbach, 2013). Although oyster habitats are relatively sheltered from waves, larvae disperse for weeks before settling and may encounter large waves if they are transported onto the continental shelf. In shelf regions, larval transport is dominated by along-shelf circulation and upwelling or downwelling (Epifanio and Garvine, 2001; Hare et al., 2002; Shanks and Brink, 2005). However, transport is also influenced by waves through Stokes drift, which intensifies near the surface and can produce large transport velocities approaching the magnitude of net current velocities (Phillips, 1966; Monismith

List o	of symbols and abbreviations
Note, v	vertical velocities are positive upwards.
Α	total peak-to-peak displacement
а	wave amplitude
C_{d}	drag coefficient
d, r	larval shell length and radius
F, F'	vertical structure functions
F_{a}	added mass force vector
F₀	Basset history force vector
F_{d}	viscous Stokes drag force vector
$F_{\rm D}$	combined drag force vector
F_{f}	form drag force vector
F _p	pressure gradient force vector
F _v	velar propulsive force vector
$F_{v,N}$	noise floor of propulsive force estimates
$F_{\rm w}$	weight force vector
t →	oscillation frequency (Hz)
ġ	acceleration due to gravity
h	wave/seiche tank water depth
ĸ	radian wavenumber
I ₁ , I ₂	wave/seiche tank length and width
L	distance between centers of buoyancy and gravity
m	larval mass
$P_{\rm o}, P_{\rm i}$	power output and power input
Rep	particle Reynolds number
<i>u</i> , <i>w</i>	horizontal and vertical land velocity
u _b , w _b	horizontal and vertical absented lengel translational velocity
u _o , w _o V	honzontal and ventical observed larval translational velocity
V _b	fluid component of lengel translational velocity vector
V _f V	absorved larvel translational velocity vector
V _O	land terminal sinking velocity
νν _T	fluid acceleration
r r	sea surface displacement
S A	angle of larval propulsion relative to larval axis
2	wavelength
	dynamic viscosity
بر ۶	vorticity
5	density of fluid and larval particles
ρt, Pp φ	angle of larval axial rotation due to vorticity
Ψ ω	radian frequency
v	kinematic viscosity (=0.01 cm ² s ⁻¹)
8	kinetic energy dissipation rate
n	Kolmogorov length scale
n_	swimming efficiency
· 15	

and Fong, 2004; Rosman et al., 2007). Stokes drift could enhance or reduce return transport to estuaries (Johnson, 1995), and these effects would be magnified if larvae altered their behavior in wavy conditions.

Larval responses to hydrodynamic signals may also impact fitness by altering the energetic costs of dispersal. Strong turbulence induces oyster larvae to propel themselves with greater force, swimming faster upward or rapidly diving (Fuchs et al., 2013). The combined increase in propulsive force and speed raises the useful work done to the environment (power output P_0), which is related to the metabolic cost of swimming (power input P_i) by swimming efficiency η_s :

$$\eta_{\rm s} = P_{\rm o}/P_{\rm i} \tag{1}$$

(Tucker, 1975). Thus, faster swimming requires either greater efficiency or a higher active metabolic rate. At higher swimming speeds, active metabolism consumes a larger fraction of total metabolism (Crawford, 1992) and can use up energy reserves, reducing the viable larval duration and leading to poor post-

metamorphic condition (Wendt, 1998; Bennett and Marshall, 2005). Swimming in any direction requires more energy than passive sinking, and active diving by oyster larvae suggests a fitness tradeoff between the need to conserve energy and the need to descend rapidly to achieve high settlement rates in turbulent environments (Eckman, 1990; Crimaldi et al., 2002; Fuchs et al., 2007). Propulsive force and power are rarely estimated for larvae but are needed to illuminate how flow-induced behaviors affect the energetic costs of dispersing through turbulent, wavy environments.

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Although oyster larvae respond behaviorally to hydrodynamic cues, the signaling mechanism remains unknown. Previous experiments in grid-stirred turbulence (Fuchs et al., 2013) were unable to resolve whether larvae respond to fluid deformation, rotation or acceleration, because in turbulence all velocity gradients are correlated with the dissipation rate (Tennekes and Lumley, 1972). Grid-generated turbulence also lacks the large accelerations generated by waves. Oyster larvae are potentially capable of sensing both deformations and accelerations using cilia or statocysts (Mackie et al., 1976; Budelmann, 1988). Additional experiments are needed to identify larval reactions and sensing mechanisms in the turbulent and wavy conditions that larvae encounter during dispersal.

We investigated oyster larval responses to turbulence- and wave-generated signals representative of both coastal and offshore regions. Here, turbulence and waves are characterized using the dissipation rate ε of turbulent kinetic energy and the magnitude of fluid acceleration α . The dissipation rate is highly correlated with deformations and is the best descriptor of turbulence dynamics at small scales (Tennekes and Lumley, 1972; Jumars et al., 2009). Dissipation rate is also correlated with accelerations in turbulence, but these signals become de-correlated in the presence of waves (H.L.F. and G.P.G., unpublished data). We varied accelerations independently from dissipation rate to test whether larvae respond to waves. It was infeasible to use a wave flume. because these flumes have large volumes that preclude using a high larval concentration. Instead we observed larvae in small tanks that produced wavy turbulence, a seiche and sinusoidal, rectilinear accelerations (Fig. 1). These flows lack some natural wave characteristics but produce hydrodynamic signals representative of most oceanic conditions. We quantified the larval propulsive force, the flow-induced change in larval orientation (Fig. 2) and the resulting swimming motion and power output in unsteady flows. This holistic picture of behavior suggests that larval responses to flow are energetically costly but may improve fitness by aiding larval delivery to adult habitats.

RESULTS

Generated flow conditions

Of the flows used here, only wavy turbulence produced mainly turbulent rather than oscillatory fluid motions (Fig. 3). Although there were velocity peaks associated with the frequency of plate oscillation, that motion was asymmetric and accompanied by vibrations that produced small, non-linear waves and turbulence. Unlike infinite oscillating boundaries studied in geophysical flows (e.g. Shome, 2013), this finite plate oscillated below the surface and generated turbulence at its edges and mounting bars. The subsurface horizontal plate was an unconventional method of generating either turbulence or waves, used here to introduce stronger accelerations into a turbulent flow, and there was no suitable theory for predicting velocity statistics. The seiche was more successful in producing linear waves whose velocities closely matched theoretical predictions for a given amplitude. The seiche motions were



Fig. 1. Schematic diagrams of flow tanks. Oscillating flow tank in (A) wavy turbulence and (B) seiche configurations and (C) shaker flask with vertical and horizontal orientations.

sensitive to small variations in the motor's oscillation frequency, and the three lowest amplitude seiche treatments produced similar flow conditions (Table 1). The shaker flask generated highly reproducible, regular oscillations with velocities that were well predicted by theory.

The three flow conditions exposed larvae to many combinations of hydrodynamic signals and provided good resolution of conditions found in natural seascapes (Table 1, Fig. 4). Compared with the grid-stirred turbulence used by Fuchs et al. (2013), wavy turbulence was less isotropic (Table 1) and had lower maximum dissipation rates ($\varepsilon_{max}=9$ versus 37 cm² s⁻³). The shaker flask produced a wide range of accelerations at relatively low dissipation rates, whereas the seiche produced narrower ranges of low to intermediate dissipation rates and accelerations. The combined data



resolved three common flow conditions. The calmest conditions ($\varepsilon \le 10^{-3}$ cm² s⁻³, $\alpha \le 1$ cm s⁻²) would be representative of deep water or slack tides in estuaries. Strong turbulence with small waves ($\varepsilon \ge 10^{-1}$ cm² s⁻³, $\alpha \le 10$ cm s⁻²) would be representative of turbulent bottom boundary layers and sheltered tidal inlets and estuaries. Weak turbulence with large waves ($\varepsilon \le 10^{-3}$ cm² s⁻³, $\alpha \ge 10$ cm s⁻²) would be representative of model conditions on the continental shelf and open ocean. Neither tank produced the combined high dissipation rates and high accelerations that are typical in the surf zone (Elgar et al., 1988; Gaylord, 1999; Trowbridge and Elgar, 2001; Gaylord et al., 2013). This data gap was unavoidable given the need to use small tanks to attain a high larval concentration.

Larval measurements

Measurements of *C. virginica* larvae were consistent across experiments and replicates (Table 2). Still-water observations were made during the seiche experiment and produced behaviors comparable to those in previous still-water observations (vertical behavioral velocity w_b =-0.02 cm s⁻¹, velar propulsive force magnitude $|\vec{F}_v| = 2.4 \times 10^{-8}$ N; Fuchs et al., 2013), except that previously ~2% of larvae dived in still water, whereas here no larvae dived in still water. Larval behavior in still water was generally similar to behavior in the calmest flow treatments in each tank, where all larvae had nearly identical propulsive forces and swimming velocities within w_b =±0.03 cm s⁻¹.



Fig. 2. Larval orientation diagram. Axial rotation angle ϕ is measured relative to the Cartesian axis (black), and propulsion angle θ_v is measured relative to the larval axis (white) defined by the passively stable, velum-up larval orientation. Larvae are classified as swimming if propulsive force \vec{F}_v is directed upward relative to the larval axis (light gray shaded region) and as sinking or diving if propulsive force is directed downward relative to the larval axis (dark gray shaded region).

Fig. 3. Sample velocity time series from most energetic flows. (A) Wavy turbulence, (B) seiche, (C) shaker with horizontal oscillation and (D) shaker with vertical oscillation. Solid lines are horizontal (red, u) and vertical (blue, w) velocities averaged over PIV image. Dashed black lines indicate theoretical velocity amplitudes given by Eqns A8–A9 for seiche and Eqn A12 for shaker.

Table 1. Mean experiment parameters

Flow	f (s ⁻¹)	A (cm)	\bar{u}_{max} (cm s ⁻¹)	\overline{w} (cm s ⁻¹)	$\overline{\langle w_{\rm rms}/u_{\rm rms} \rangle}$	$\bar{\alpha}_{max}$ (cm s ⁻²)	$ar{\sigma}_{lpha}$ (cm s ⁻²)	$\overline{\epsilon}$ (cm ² s ⁻³)	η̄ (cm)	Δx (cm)	FPS (pairs s ⁻¹)	N _T	No
Wavy turb.	0.03	115	0.64	0.09	0.81	0.76	0.08	4.0×10^{-4}	0.22	0.2	10	1209	20,441
	0.06	115	1.36	0.11	0.82	2.46	0.24	4.7×10 ⁻³	0.12	0.1	10	2746	29,085
	0.09	115	2.70	0.28	0.87	4.59	0.57	1.9×10 ⁻²	0.08	0.1	14	4457	37,351
	0.12	115	4.69	0.11	0.71	10.2	1.46	1.1×10 ⁻¹	0.06	0.05	14	4141	26,901
	0.15	115	4.37	0.02	0.77	11.5	1.66	1.7×10 ⁻¹	0.05	0.05	14	2350	11,173
Seiche	0.51	1.79	3.18	-0.003	0.39	12.5	3.26	2.8×10 ⁻⁴	0.24	0.2	14	754	4484
	0.51	2.00	3.47	0.002	0.39	13.3	3.43	2.9×10^{-4}	0.24	0.2	14	1086	6009
	0.51	2.25	3.74	-0.014	0.39	14.8	3.90	3.0×10^{-4}	0.24	0.2	14	731	4402
	0.51	3.02	5.21	-0.007	0.39	20.4	5.16	1.2×10 ⁻³	0.17	0.2	14	344	1703
	0.51	6.04	10.6	0.056	0.39	42.6	10.7	1.8×10 ⁻³	0.15	0.2	25	269	1287
Shaker	0.07	2	0.55	0.01	0.04	0.77	0.15	1.5×10 ⁻⁵	0.51	0.16	7.4	1685	8725
	0.22	2	1.44	0.02	0.02	3.34	0.59	2.3×10 ⁻⁵	0.45	0.16	7.4	1442	6397
	0.71	2	4.68	0.01	0.01	28.5	6.27	1.2×10 ⁻⁴	0.30	0.16	14	1594	8065
	2.24	2	15.4	0.02	0.01	282	62.6	2.2×10 ⁻³	0.15	0.16	25	494	1433
	3.70	2	25.0	0.04	0.02	621	148	5.2×10 ⁻³	0.12	0.16	25	46	111

f, oscillation frequency; *A*, the total peak-to-peak oscillation distance (=2*a* in wavy turbulence and shaker flask and =4*a* in the seiche); \bar{u}_{max} , measured velocity amplitude; \bar{w} , vertical velocity; $\langle w_{rms}/u_{rms} \rangle$, isotropy ratio, where rms indicates root mean square; $\bar{\alpha}_{max}$, measured acceleration amplitude; $\bar{\sigma}_{\alpha}$, acceleration s.d.; $\bar{\epsilon}$, dissipation rate; $\bar{\eta}$, Kolmogorov length scale; Δx , vector spatial resolution; FPS, image capture rate, as number of frame pairs per second; N_{T} , total number of larval trajectories; N_{O} , number of instantaneous observations in each treatment for combined replicates. Over-bars indicate averages over replicates.

Larval behavior in flow

In wavy turbulence, results were similar to those in previous turbulence experiments (Fuchs et al., 2013) except that diving larvae were observed less frequently (Fig. 5). Under the calmest conditions, all larvae propelled themselves upward and had positive vertical swimming velocities. For swimming larvae, defined as those with propulsive forces directed upward, propulsive force increased by 14% or 27% and swimming speed increased nearly 10 times over the observed ranges of acceleration or dissipation rate, respectively. These increases were significant; see regression statistics in Table 3. Passive sinking was observed infrequently over all conditions, whereas active diving was observed more consistently in energetic conditions ($\alpha > 10^{-0.5}$ cm s⁻² and $\varepsilon > 10^{-2} \text{ cm}^2 \text{ s}^{-3}$). Propulsive forces of divers spanned over an order of magnitude and reached $|\vec{F}_v| \approx 10^{-7}$ N, corresponding to descent velocities of about three times the terminal fall velocity. Observed dives were sparse and scattered; although trends were nonsignificant, active dives were generally more forceful and faster in stronger turbulence.

In the seiche, sinking and diving were rarely observed (Fig. 6). Under the calmest conditions, all larvae propelled themselves upward but had negative vertical swimming velocities. For swimming larvae, both propulsive force and swimming velocity decreased with acceleration but increased with dissipation rate. These trends were significant but weak (Table 3). Only one observed descent was associated with an active dive. Of all flows used, the seiche motions produced the weakest swimming response and the fewest descents.

In the shaker flask, vertical rather than horizontal accelerations induced the strongest upward swimming and the most frequent descents (Figs 7, 8). In both oscillation directions, the propulsive force and vertical swimming velocity increased significantly with acceleration, and swimming velocities switched from negative to positive at $\alpha \approx 10 \text{ cm s}^{-2}$. In horizontal oscillations, sinking and diving were observed infrequently and only at low accelerations ($\alpha \leq 2 \text{ cm s}^{-2}$), but in vertical oscillations larvae dived frequently at high accelerations ($\alpha > 10^2 \text{ cm s}^{-2}$). At intermediate accelerations, divers used a large propulsive force and descended at about double the terminal fall velocity. At higher accelerations, dives became significantly weaker; larvae used less propulsive force and

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descended slowly. Compared with wavy turbulence, the shaker flask motions induced a similarly strong, upward swimming response and more frequent, but weaker, active dives.



Fig. 4. Distribution of instantaneous hydrodynamic conditions experienced by larvae in all experiments. (A) Ranges of data from each tank; (B) ranges of frequently occurring hydrodynamic conditions in marine seascapes. Background colors indicate the total number of instantaneous larval observations grouped in bins of fluid acceleration α and dissipation rate ϵ at larval locations. The colored lines in A indicate ranges of observations in wavy turbulence (blue), seiche (red) and shaker flask (purple). In B, the thick black line indicates the relationship between acceleration s.d. and mean dissipation rate in isotropic turbulence (IT), and thin black lines enclose ranges of frequently occurring acceleration s.d. and mean dissipation rate in conditions typical of the surf zone (SZ), inlets and estuaries (IE), continental shelf (CS) and open ocean (OO) (values from H.L.F. and G.P.G., unpublished data).



turbulence. (A,B) Percentage of larvae sinking or diving, (C,D) propulsive force magnitude $|\vec{F}_{v}|$, (E,F) vertical behavioral velocity w_b for larvae swimming (light filled circles) and (G,H) vertical behavioral velocity w_b for larvae passively sinking (dark open circles) and actively diving (dark filled circles). Symbols are averages of 300 instantaneous observations binned by fluid acceleration magnitude α (A,C,E,G) or by dissipation rate ε (B,D,F,H), and error bars are ±1 s.d. Some error bars are smaller than symbols for swimming larvae or absent for sinking or diving larvae in bins containing only one non-swimming larva. Dashed lines in C and D indicate the noise floor $|\vec{F}_{v,N}|$ estimated for the propulsive force magnitude of larvae sinking passively. Black lines in E-H indicate neutral buoyancy ($w_{\rm b}$ =0, solid) and larval terminal fall velocity ($w_b = w_T$, dashed). Blue lines are linear regressions (log10 scale except for $w_{\rm b}$) with significance P<0.05; non-significant regressions are omitted.

Fig. 5. Larval behavior in wavy

Force balance

The forces on individual larvae were dominated by the weight force \vec{F}_{w} and the propulsive force \vec{F}_{v} , which had similar magnitudes, except in the highest accelerations or dissipation rates (Fig. 9). All forces except \vec{F}_{w} grew larger in more energetic turbulence or wave motions; the drag forces and added mass force grew larger because larvae swam or dived at a higher speed or acceleration, whereas the pressure gradient force grew larger with the fluid acceleration (see Appendix). Under calm conditions, the largest force (after \vec{F}_{w} and \vec{F}_{v}) was viscous drag \vec{F}_{d} , followed by the Basset history force \vec{F}_{b} , form drag \vec{F}_{f} , added mass \vec{F}_{a} and the pressure gradient force \vec{F}_{v} . In the seiche, larvae had behavioral velocities and accelerations near zero, and all other forces were negligible compared with \vec{F}_{w} and \vec{F}_{v} . In wavy turbulence, the viscous drag \vec{F}_{d} and Basset history force \vec{F}_{b} always remained larger than \vec{F}_{f} , \vec{F}_{a} and \vec{F}_{p} , and the viscous drag

Table 2. Larval measurements

approached the magnitude of the weight force in strong turbulence. In the shaker flask, the drag forces and weight force were exceeded by the pressure gradient force \vec{F}_p at high accelerations. Thus, although larval propulsive force increased in more energetic conditions, this excess force was used partly to offset drag in strong turbulence and to offset pressure gradient forces in large wave motions.

Aggregated behavior observations

The combined data suggested that oyster larvae would react both to strong turbulence in nearshore regions and to large waves in the open ocean (Fig. 10). Most larvae propelled themselves upward and were classified as swimming, but some diving was observed in strong turbulence (ϵ >10⁻¹ cm² s⁻³) or in large waves (α >10 cm s⁻²) (Fig. 10A,B). The larval rotation angle increased

Tank	Replicate no.	<i>d</i> (μm)	$w_{\rm T} ({\rm cm \ s}^{-1})$	$ ho_{p}$ (g cm ⁻³)	$w_{\rm b} ({\rm cm \ s}^{-1})$	\vec{F}_{v} (×10 ⁻⁷ N)	P _o (×10 ⁻¹² W)
Wavy turbulence	1	311±10	-0.66±0.06	1.17			
	2	311±18	-0.69±0.09	1.18			
Seiche	1	310±11	-0.71±0.13	1.17	-0.03±0.05	0.24±0.02	7.2
	2	312±12	-0.74±0.14	1.18	-0.02±0.09	0.26±0.03	5.2
	3	309±10	-0.70±0.10	1.18	-0.03±0.10	0.23±0.03	6.9
Shaker	H1	306±10	-0.76±0.07	1.19			
	H3	321±9	-0.74±0.04	1.17			
	V1	312±9	-0.62±0.07	1.14			
	V2	313±10	-0.73±0.03	1.17			
	V3	321±10	-0.71±0.07	1.16			

Data are means±1 s.d.

d, shell length; w_{T} , terminal sinking velocity; ρ_{p} , estimated larval density; w_{b} , vertical behavioral velocity; \vec{F}_{v} , propulsive force; P_{o} , estimated power output in still water. w_{b} and \vec{F}_{v} were only measured during the seiche experiment.

Larval densities were single estimates calculated from mean shell length and terminal velocity. For shaker flask measurements, V and H indicate vertical and horizontal replicate number (H2 sample was lost).



Fig. 6. Larval behavior in the seiche. Lines and symbols as in Fig. 5, except that symbols are averages over bins of 100 instantaneous observations.

steadily with the dissipation rate, which is highly correlated with vorticity (Fig. 10C,D), but was otherwise unaffected by wavegenerated accelerations because there is no vorticity under linear waves. Swimming larvae used more propulsive force in both turbulence and waves (Fig. 10E,G). In strong turbulence the vorticity-induced rotations limited the ability of larvae to swim upward, whereas in energetic waves the lack of vorticity-induced rotation enabled larvae to convert their excess propulsive force into faster upward swimming. Descending larvae behaved differently in strong turbulence, which elicited stronger active dives, and in energetic wave motions, which mainly elicited passive descents or weak dives (Fig. 10F,H). Swimming larvae had 100 times higher power outputs in both turbulence and waves than in still water, whereas diving larvae had ~10 times higher power outputs in strong turbulence than in large waves (Fig. 10I,J, Table 2).

Table 3. Regression	statistics for (A)	larval vertical behavioral	velocity and (B)) propulsive force
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	Behavior	Versus a				Versus ε			
Flow		b ₀	b ₁	R^2	Р	b ₀	b ₁	R^2	Р
A. Larval vertical veloci	ty								
Wavy turbulence	Swim	0.02	0.07	0.37	<10 ⁻³	0.01	0.09	0.48	<10 ⁻³
	Dive	-0.25	-1.0	0.10	0.20	-0.18	-1.3	0.16	0.18
Seiche	Swim	-0.01	-0.02	0.09	<10 ⁻³	0.01	0.02	0.31	<10 ⁻³
Shaker									
Horizontal	Swim	0.01	-0.01	0.29	<10 ⁻³	0.02	0.06	0.56	<10 ⁻⁴
	Dive	-0.37	-1.0	0.11	0.63	-0.48	-3.1	0.09	0.14
Vertical	Swim	0.02	-0.01	0.22	<10 ⁻²	0.03	0.12	0.43	<10 ⁻³
	Dive	0.34	-1.2	0.79	0.03	0.56	1.4	0.66	0.04
B. Propulsive force									
Wavy turbulence	Swim	0.02	-7.6	0.58	<10 ⁻⁴	0.01	-7.6	0.58	<10 ⁻⁴
-	Dive	0.33	-7.6	0.27	0.10	0.18	-7.3	0.26	0.10
Seiche	Swim	-0.01	-7.6	0.08	<10 ⁻⁴	0.01	-7.6	0.32	<10 ⁻⁴
Shaker									
Horizontal	Swim	0.01	-7.6	0.40	<10 ⁻⁴	0.02	-7.5	0.43	<10 ⁻³
	Dive	0.42	-7.4	0.72	<10 ⁻²	-0.23	-8.4	0.38	0.02
Vertical	Swim	0.02	-7.6	0.11	<10 ⁻²	0.05	-7.4	0.32	<10 ⁻²
	Dive	-0.10	-7.5	0.25	0.03	-0.02	-7.82	0.01	0.02

Slope b_0 , intercept b_1 , coefficient of determination R^2 and P-value for linear regression of larval vertical behavioral velocity w_b or propulsive-force magnitude $|\vec{F}_v|$ against fluid acceleration α or dissipation rate ϵ . All regression variables except w_b were on a log₁₀ scale. Seiche experiments produced only one observation of larval diving. *P*-values in bold are significant at α =0.05.



Fig. 7. Larval behavior in the shaker flask with horizontal oscillations. Lines and symbols as in Fig. 5, except that symbols are averages over bins of 100 instantaneous observations.

DISCUSSION

Both turbulence and waves induced eyed *C. virginica* larvae to swim faster upward or to dive actively, and these responses suggest tradeoffs between reducing energy expenditure and optimizing

larval transport in different environments. Different seascape types can be defined in part by their distributions of hydrodynamic signals (H.L.F. and G.P.G., unpublished data), represented here by the dissipation rate and fluid acceleration. Within this parameter space,



Fig. 8. Larval behavior in the shaker flask with vertical oscillations. Lines and symbols as in Fig. 5, except that symbols are averages over bins of 100 instantaneous observations.

Regression line (swim) Regression line (dive)



Fig. 9. Magnitude of forces on larvae (Eqn 4) versus fluid acceleration magnitude α and dissipation rate ε . Force magnitude versus α (A–D) and ε (E–H) is shown in wavy turbulence (A,E), seiche (B,F), shaker flask with horizontal oscillation (C,G) and shaker flask with vertical oscillation (D,H). Symbols are averages of instantaneous observations (*N*=100 except in wavy turbulence *N*=300) binned by acceleration magnitude or dissipation rate. Forces are added mass force \vec{F}_a , Basset history force \vec{F}_b , form drag force \vec{F}_f , pressure gradient force \vec{F}_p , viscous drag force \vec{F}_d , weight force \vec{F}_w and propulsive force \vec{F}_v .

our experiments revealed different behaviors associated with three flow conditions: (1) calm water, representing deep water or slack tides, (2) strong turbulence with weak waves, representing bottom boundary layers, inlets and estuaries, and (3) weak turbulence with energetic waves, representing the continental shelf or open ocean. In calm water, larvae used just enough propulsive force to maintain a vertical velocity near zero; this hovering behavior would promote efficient feeding (Gallager, 1993; Fenchel and Ockelmann, 2002) and would distribute larvae evenly through the water column (McNair et al., 1997; Visser, 1997). In the absence of strong physical signals or other cues (e.g. chemicals; Tamburri et al., 1992; Turner et al., 1994), larvae likely focus on food uptake and are transported passively.

The observed swimming responses to turbulence and waves have different potential benefits in coastal and offshore regions. In coastal waters with strong turbulence, swimming larvae must use more propulsive force to offset vorticity-induced rotation and to maintain vertical motion (McDonald, 2012; Fuchs et al., 2013). No excess propulsive force is needed to maintain vertical swimming in linear waves lacking vorticity. Upward swimming in waves may be justified when larvae are offshore and unlikely to return to estuarine environments through passive drifting. Ascending in waves would enable larvae to approach the surface where Stokes drift can induce shoreward transport (Phillips, 1966; Johnson, 1995; Monismith and Fong, 2004). Near-surface Stokes drift is often shoreward over the continental shelf (Monismith and Fong, 2004) but not necessarily in the open ocean, where wave directions are less uniform (Kubota, 1994). The observed maximum swimming speeds were small (millimeters per second) but would enable larvae to reach waveaffected surface waters from most mixed-layer depths within a day. Wave-induced upward swimming may be a desperate strategy for shoreward transport, used by larvae that will otherwise be lost in waters far from natal habitats.

The fitness benefits of upward swimming would come at a considerable energetic cost. Swimming larvae had ~100 times higher power outputs in strong turbulence or waves than in still water. If swimming efficiency remains constant, this result implies a ~ 100 times increase in the active metabolic rate. Thus, even if active metabolism consumes only 1% of the total metabolism in still water (Crawford, 1992), it likely dominates the total metabolism in turbulent or wavy conditions. Larvae may also gain less energy from feeding when they swim faster in turbulence or waves, as feeding is optimized by hovering (Gallager, 1993; Fenchel and Ockelmann, 2002). In turbulence, the reduced feeding efficiency by faster swimmers could be offset by higher contact rates with prey (Kiørboe and Saiz, 1995). Compared with calmwater behavior, however, flow-induced upward swimming appears poorly adapted to enhance feeding but well adapted to enable control over directed transport.

Active diving also has different potential benefits in turbulent coastal waters and in wavy offshore waters. In the strong turbulence found over oyster reefs, high-speed dives would be an effective means of delivering larvae to adult habitats. Compared with hovering or passive sinking, active diving confers both higher



Fig. 10. Characteristics of larval swimming (left) and sinking or diving (right) behavior as a function of instantaneous fluid acceleration magnitude α and dissipation rate ε for all tanks combined. (A,B) Percentage of larvae performing each behavior, (C,D) axial rotation angle ϕ , (E,F) propulsive force magnitude $|\vec{F}_{v}|$, (G,H) behavioral vertical velocity $w_{\rm b}$ and (I,J) power output P_{o} (excludes passive sinkers). Instantaneous observations are averaged over small bins of acceleration and dissipation rate. and colors indicate the magnitude of the effect. The number of observations is shown in Fig. 4; bins containing only one observation or <1% sinking or diving (B,D,F,H,J) are omitted for clarity. Gray lines outline typical ranges of acceleration s.d. and mean dissipation rate in different seascapes as in Fig. 4. Black dashed lines (B,D,F,H,J) indicate the dissipation rate and acceleration associated with increased diving in isotropic turbulence (Fuchs et al., 2013). Color-bar scales differ on left and right.

settlement probabilities and higher settler densities on oyster reef patches; the former would reduce larval wastage, while the latter would promote upward reef growth (Fuchs and Reidenbach, 2013). There is no settlement advantage to diving in large waves, which are most common in the surf zone or offshore. The weaker dives that we observed at high accelerations ($\alpha \ge 10^2 \text{ cm s}^{-2}$) may enable larvae to avoid predation by suction-feeding fish, which generate accelerations of the order of 10^2 to 10^3 cm s^{-2} (Higham et al., 2006; Holzman et al., 2008). Weak dives produced higher speeds at lower energetic costs than upward swimming (Fig. 10G–J) and would be a better escape mechanism than steady swimming. Thus, turbulence-induced dives would enhance settlement, whereas acceleration-induced dives could reduce predation mortality.

Unlike swimming larvae, diving larvae expended ~10 times more power in strong turbulence than in large waves. These differences in power output imply that the fitness benefits of successful settlement outweigh those of escaping predation. This idea is consistent with observations that some crab larvae accomplish rapid estuarine transport using behaviors that expose larvae to added predation risks (Morgan and Anastasia, 2008). Active diving is also more energetically demanding than passive gravitational sinking, which has no metabolic cost, and these two behaviors likely serve different purposes. Veligers occasionally stop the cilia or retract the velum to sink passively (Cragg, 1980; Jonsson et al., 1991; Gallager, 1993; Fuchs et al., 2013), possibly as a resting behavior. Passive sinking produces initial downward accelerations and high terminal velocities that may have been misclassified as diving in previous studies (Finelli and Wethey, 2003; Wheeler et al., 2013). The force balance used here distinguishes between passive descents, which conserve energy, and active dives, which are energetically costly but have potential fitness payoffs in predator avoidance or enhanced settlement.

The estimated power outputs for oyster larvae are reasonable based on limited data for ciliary swimmers. Power output is often calculated from swimming efficiency η_s and active metabolic rates P_i inferred from respiration measurements (Eqn 1). Large ciliates have power inputs of $P_i \approx 10^{-12}$ to 10^{-9} W, giving a maximum power output of $P_o \approx 10^{-12}$ W at an efficiency of $\eta_s \le 0.1\%$ (Crawford, 1992; Katsu-Kimura et al., 2009). This estimate is ~10³ times lower than the maximum power output for oyster larvae (Fig. 10I,J), but the difference is reasonable given that oyster larvae are negatively buoyant and must use more propulsive force to counteract gravitational sinking. For example, a swimming speed of 0.1 cm s⁻¹ requires ≥ 100 times more propulsive force in oyster larvae than in *Paramecia* (Sleigh and Blake, 1977; Guevorkian and Valles, 2006; Fig. 10). Oyster larvae may also achieve an efficiency closer to $\eta_s=1\%$ by swimming with compound cilia (Sleigh and Blake, 1977). Active metabolism has rarely been measured for larvae, but swimming bryozoan larvae have $P_i\approx 3.6\times 10^{-7}$ W (Wendt, 2000). Assuming an efficiency of $\eta_s=0.1\%$ to 1%, the power output of $P_o\approx 10^{-10}$ to 10^{-9} W for bryozoan larvae is comparable to our estimates for the strongest swimming and diving oyster larvae.

Larvae in wavy turbulence dived infrequently compared with previous observations in turbulence (Fuchs et al., 2013). In the previous study, double stirring grids produced higher maximum dissipation rates and an upward mean circulation $(0.02 \le w \le 1.9 \text{ cm s}^{-1})$ that may have raised the probability of observing larval dives. Here, the vertical circulation was weak (Table 1) and may have limited our ability to observe the strongest swimmers or divers. Different larval batches may also have been unequally competent to metamorphose, as morphological characteristics such as eyespots are imperfect indicators of competency (Coon et al., 1990; Baker, 1994; Finelli and Wethey, 2003). It is unknown whether competency is required for flow sensing or whether turbulence hastens the onset of competency (Gaylord et al., 2013). Sensitivity to turbulence would vary with both competency and size if larvae sensed flow using the statocysts, which form at the eyed larval stage (Ellis and Kempf, 2011). Larvae could become more sensitive to flow-induced rotation over time as the statoliths grow larger and more able to deform the sensory hair cells lining the statocyst. Size effects on sensitivity could explain why other researchers observed few turbulence-induced dives by oyster larvae that were $\sim 30\%$ smaller than those used here (Wheeler et al., 2013).

Our results provide strong evidence that statocysts are involved in flow sensing. The sensory abilities of both statocysts and cilia are undescribed for C. virginica larvae, but these organs sense motion in other species. Cilia are the most likely means of sensing spatial velocity gradients as stretching, bending or straining motions (Mackie et al., 1976; Echevarria et al., 2014). Statocysts can function as accelerometers or as gravity detectors and could sense linear accelerations or vorticity-induced rotation (Chia et al., 1981; Budelmann, 1988). Here, high accelerations induced stronger swimming or weak diving even in the absence of high deformations, suggesting that waves were sensed by statocysts acting as accelerometers. We were unable to resolve the role of cilia, however, because turbulence-induced dives could be a response either to straining motions or to vorticity-induced rotations. These signals are linked in turbulence but would be sensed with different receptors. To identify the cue for turbulence-induced diving, and hence the role of cilia, we are currently investigating larval responses to flows where the straining and rotational motions are decoupled (Kiørboe et al., 1999).

This study also highlights a gap in our understanding of ciliary swimming energetics at intermediate Reynolds numbers and in realistic flows. Ciliates such as *Paramecia* have particle Reynolds numbers $Re_p<1$ and can be modeled as densely ciliated spheres that experience only viscous drag (Crawford, 1992; Michelin and Lauga, 2010; Osterman and Vilfan, 2011). Ciliary swimmers with $Re_p>1$, including many invertebrate larvae, have more complex shapes and experience form drag, making them less conducive to theoretical treatments. In unsteady flow, organisms also experience pressure gradient forces and Basset history forces (see Appendix) that can be large relative to drag (Fig. 9) and may reduce the swimming efficiency. For larvae, both reduced efficiency and flow-induced behavioral changes could substantially raise the energetic cost of passing through turbulent or wavy environments (Fig. 10). Swimming energetics determine whether larvae can successfully disperse to suitable habitats before exhausting their energy reserves (Wilkin and Jeffs, 2011) and require further study.

MATERIALS AND METHODS Flow tanks

To test whether larval responses to turbulence vary in the presence of waves, we used two configurations of an oscillating flow tank with length l_1 =160 cm, width l_2 =30 cm and water depth h=30 cm. In the first tank configuration ('wavy turbulence'; Fig. 1A), a horizontal plate (50.2×27.3 cm) oscillated below the surface. The plate moved parallel to the long axis of the tank with a constant amplitude and five oscillation frequencies (Table 1). The plate and its mounting bars generated turbulence and oscillatory motions.

To create more linear waves with weaker turbulence and larger accelerations, we used the same tank in a second configuration ('seiche'; Fig. 1B) that produced standing waves. In this configuration, a bottomhinged, vertical plate was oscillated at five different amplitudes to generate seiche motions at the natural frequency of the tank (Table 1). The seiche is formed by two progressive waves that travel in opposite directions and reflect off the ends of the tank. The fluid velocities and accelerations can be characterized using wave equations detailed in the Appendix.

To determine whether larval behavior depended on the acceleration direction, we also observed larvae in unidirectional sinusoidal accelerations ('shaker flask'; Fig. 1C). The machine consisted of a 250 ml tissue culture flask mounted on a motor-driven, linear slide and was modeled after the oscillating chamber used by Kiørboe et al. (1999). The flask was oscillated at a constant amplitude and five frequencies (Table 1) and was used in both horizontal and vertical orientations. The linear motion produced oscillating velocities and accelerations as detailed in the Appendix.

Experiments

Eyed oyster larvae (*C. virginica*) were shipped overnight from Horn Point Laboratory (MD, USA) and used within 2 days. Different batches of larvae were used in each flow condition: experiments were done in wavy turbulence on 31 May to 1 June 2012, in the seiche on 7–8 August 2013, and in the shaker flask on 21–23 August 2012. Larvae were kept in 101 buckets of filtered seawater, aerated and fed *Isochrysis galbana* (T-Iso, 10^5 cells ml⁻¹) at 20°C. Experiments were done at room temperature: 20–25°C for the wave/seiche tank and 20.5°C for the shaker flask. Salinities of cultures and experiments were adjusted to match those at which larvae were reared (10–14 S_P).

All experiments used nearly identical designs and observational approaches. Larvae and algae were added at concentrations of 0.3–0.6 larvae ml⁻¹ and ~10⁵ cells ml⁻¹, respectively, and gently mixed. After ~30 min in still water, larvae were observed in five flow treatments in random order with 10 min recovery times between treatments. Each treatment included a 10 min acclimation period followed by 7–10 min of observations. Experiments were replicated twice in wavy turbulence, three times in the seiche and three times in the shaker flask, with one replicate per day in each orientation. In the seiche experiments, larvae were also observed in still water after the initial 30 min acclimation period to provide baseline behavior estimates.

Larval behavior and flow were observed simultaneously using nearinfrared particle-image velocimetry (IR PIV). The PIV system consisted of a 4 megapixel CCD camera (FlowSense, Dantec Dynamics) with a 100 mm lens (Tokina) and a pulsed diode laser (NanoPower 7 W, 808 nm) with a \sim 2 mm beam width. The infrared laser and natural algal seeding particles (concentrated \sim 18 µm diatoms, *Thalassiosira weissflogii*, Reed Mariculture) were used to avoid larval behavioral artifacts (Fuchs et al., 2013). Image planes were vertical and parallel to the long axis of each container. In the wave/seiche tank, the image plane was 6.6 cm wide and centered 35 cm from the end wall and 15 cm above the bottom (Fig. 1A,B). In the shaker flask, the image plane was 5.1 cm wide and centered in the rectangular section of the flask (Fig. 1C). The rate of image capture was varied (Table 1) to ensure that larvae could be easily tracked between image pairs.

After each replicate, larvae were ethanol-killed for measurement of shell length and terminal sinking velocity. Shell length d (N=30-50 per replicate) was measured digitally on larvae photographed under a stereomicroscope using cellSens software (Olympus). Terminal velocity w_T (N=44-2711 per replicate) was measured from videos of larvae sinking through a 2 l settling column at room temperature. Larval density ρ_p was estimated from mean size and terminal velocity measurements using Rubey's modification of Stokes' law, which accurately predicts settling speeds of particles in the larval size range (Rubey, 1933; Fuchs et al., 2013).

Image processing and analysis

Larvae and fluid often moved in different directions, so their velocities were analyzed separately from PIV video using techniques for two-phase flow (e.g. Kiger and Pan, 2000; Khalitov and Longmire, 2002; Cheng et al., 2010). Fluid velocities were estimated from pre-processed images of the seeding particles with larvae masked out. In pre-processing, the time-averaged intensity was subtracted from each image to remove spatial variation in laser illumination. To mask the larvae, we first removed seeding particle images and enhanced the larval images by applying a median filter (Kiger and Pan, 2000). The images were then binarized to identify particles with area >100 pixels as larvae, and these larval images were subtracted from the original images to leave only the seeding particles.

We processed the paired images of seeding particles using adaptive correlation algorithms in Dynamic Studio (Dantec) with variable interrogation areas and a 50% overlap to give vector resolutions Δx near the Kolmogorov length scale η (Table 1). A resolution of $\Delta x \approx \eta$ is preferred for limiting errors in dissipation rate estimates (e.g. Antonia et al., 1994; Saarenrinne and Piirto, 2000). In the shaker flask, the vectors generally resolved scales smaller than the average η except during flow reversals, when $\Delta x \approx \eta$. When $\Delta x < \eta$ in turbulence, a correction is needed to offset added measurement noise (Tanaka and Eaton, 2007); here, no correction was used because the fluid generally moved as a solid body. The analysis of seeding particle images produced fluid velocity vectors *u* and *w* in the horizontal *x* and vertical *z* directions (positive upwards), respectively.

The net observed larval translational velocities u_0 and w_0 were estimated from the images of larvae identified in the pre-processed images (shaker flask) or original PIV images (wave/seiche tank). Images 1 and 2 of each PIV frame pair were treated as separate image sequences, and larval trajectories in each sequence were constructed by particle tracking in Matlab. Trajectories from the paired sequences were matched and rejected if they were of unequal lengths. Translational velocities u_0 and w_0 were estimated from motion of larvae from one image pair to the next, while fluid velocities u and w were estimated from motion of particles between paired frames. To synchronize the larval and fluid velocities, we interpolated u and w to larval observation times using 3-dimensional (3D) linear interpolation for wavy turbulence and spline interpolation for the harmonic flows (seiche and shaker flask). Fluid velocities were then interpolated to individual larval locations using 2-dimensional (2D) linear interpolation, assuming that velocity gradients are linear at Kolmogorov-scale resolution (e.g. Lazier and Mann, 1989).

We quantified larval behaviors by analyzing the 2D velocities of individual larvae as approximations of their 3D motion. Instantaneous larval behavioral velocities were estimated as $u_b = u_o - u$ and $w_b = w_o - w$, where *u* and *w* are instantaneous values at larval locations and observation times, assuming that particle and fluid velocities are independent and additive (e.g. Reeks, 1977). Accelerations were estimated from the difference between paired image sequences of velocity vectors \vec{V}_f , \vec{V}_o and \vec{V}_b corresponding to fluid velocities at larval locations, larval translational velocities and larval behavioral velocities, respectively, where over-arrows denote vectors. For example, larval behavioral accelerations were estimated as $d\vec{V}_b/dt = (\vec{V}_{b2} - \vec{V}_{b1})/\delta t$, where δt is the time step between paired frames, and the subscripts 1 and 2 indicate the image sequence number. Sequence 2 was used only for calculating accelerations, and hereafter subscripts are omitted.

Velocity gradients were estimated from the fluid velocities interpolated to larval observation times and used to estimate 2D turbulence statistics. Dissipation rates were calculated as:

$$\varepsilon = 3\nu \left[\overline{\left(\frac{\partial u}{\partial x}\right)^2} + \overline{\left(\frac{\partial w}{\partial z}\right)^2} + \overline{\left(\frac{\partial u}{\partial z}\right)^2} + \overline{\left(\frac{\partial u}{\partial z}\right)^2} + 2\overline{\left(\frac{\partial u}{\partial x}\right)^2} + 2\overline{\left(\frac{\partial u}{\partial z}\frac{\partial w}{\partial x}\right)} + \frac{2}{3}\overline{\left(\frac{\partial u}{\partial x}\frac{\partial w}{\partial z}\right)} \right],$$
(2)

where v is kinematic viscosity, assuming that the out-of-plane gradients were of the same order as the average in-plane gradients (Doron et al., 2001). Fluid acceleration was calculated as:

$$\alpha = \left[\left(\frac{\partial u}{\partial t} \right)^2 + \left(\frac{\partial w}{\partial t} \right)^2 \right]^{0.5}.$$
 (3)

Dissipation rates and accelerations were interpolated to larval locations as described above to characterize the instantaneous flow environments around individual larvae.

We estimated the magnitude and direction of larval propulsive force using an equation of motion for spherical particles (e.g. Maxey and Riley, 1983; Mei et al., 1991; Mei, 1996) with additional terms for inertia and propulsion (Fuchs et al., 2013):

$$m\frac{d\vec{V}_{\rm o}}{dt} = \vec{F}_{\rm a} + \vec{F}_{\rm p} + \vec{F}_{\rm w} + \vec{F}_{\rm d} + \vec{F}_{\rm f} + \vec{F}_{\rm b} + \vec{F}_{\rm v}, \tag{4}$$

where *m* is the larval mass, \vec{F}_a is the added mass or acceleration reaction force, \vec{F}_p is the force on the larva due to acceleration-induced pressure gradients, \vec{F}_w is the net gravitational force due to a larva's weight, \vec{F}_d is the viscous Stokes drag force, \vec{F}_f is the inertial form drag force, \vec{F}_b is the Basset history force and \vec{F}_v is the velar propulsive force. Details are provided in the Appendix. All terms in Eqn 4 except \vec{F}_v were measured or estimated, enabling us to compute the magnitude and direction of forces that individual larvae used to propel themselves and to characterize how different flows affected the forces on larvae. To relate propulsion to energetic costs of swimming, we calculated the power output as:

$$P_{\rm o} = |\vec{V}_{\rm b}| \, |\vec{F}_{\rm v}| \tag{5}$$

(e.g. O'Dor, 1988), where vertical brackets indicate vector magnitude.

The force balance (Eqn 4) gives the direction of propulsion relative to Cartesian coordinates, so we also estimated the direction of propulsion relative to the larva's body axis as defined by a passively stable orientation (Fig. 2; Fuchs et al., 2013). This stable orientation is maintained by a gravitational torque created by an asymmetric density distribution, but larvae can also be rotated by vorticity-induced viscous torque (e.g. Kessler, 1986). At equilibrium, the angle of axial rotation is:

$$in \phi = \frac{3\mu\xi}{L\rho_{\rm p}g},$$
(6)

where μ is the dynamic viscosity, $\xi=\partial w/\partial x - \partial u/\partial z$ is the vorticity, *L* is the distance between the centers of buoyancy and gravity, ρ_p is the larval density and \vec{g} is the acceleration due to gravity (Kessler, 1986; Jonsson et al., 1991). Although Eqn 6 gives the rotation angle at equilibrium, there is no straightforward equivalent for time-varying vorticity. We assumed that larval orientation responded rapidly to changes in the flow and used Eqn 6 to represent the instantaneous rotation angle. We used $L\approx 3 \,\mu\text{m}$, or ~1% of the larval length, and used ϕ to correct the Cartesian direction of larval propulsion to θ_v , the direction of propulsion relative to the larval axis (Fig. 2; Fuchs et al., 2013).

Propulsive force and larval vertical velocity can have different signs and require specific terminology. For example, if a larva propels itself upward with insufficient force to overcome the opposing forces of drag and gravity, the larva will have a positive propulsive force and a negative vertical velocity. Fuchs et al. (2013) classified positive and negative vertical velocities as ascents and descents and classified larvae with propulsive force directed upward and downward, relative to the larval axis, as swimming and diving. Here, we further divided larvae with downward-directed propulsive

force into active divers and passive sinkers. If larvae stop propelling themselves, either by stopping the cilia or by retracting the velum, they sink passively and reach a terminal velocity w_T at which there is no behavioral acceleration. For passive sinkers, our analysis (Eqn 4) still produces a non-zero estimate of propulsive force \vec{F}_v that must be at or below a noise floor. We estimated the noise floor $|\vec{F}_{v,N}|$ as the \log_{10} scale mean propulsive force magnitude $|\vec{F}_v|$ associated with larval descent velocities within ±1 s.d. of the mean terminal velocity w_T estimated for dead larvae in each experiment. The noise floor estimates were used to subdivide larvae previously classified as divers into active divers $(|\vec{F}_v| > |\vec{F}_{v,N}|)$ and passive sinkers $(|\vec{F}_v| \leq |\vec{F}_{v,N}|)$.

APPENDIX

Wave motions

The seiche is formed by two superimposed progressive waves moving in opposite directions at the natural frequency of the tank. The natural radian frequency ω of the tank is:

$$\omega = \sqrt{(\vec{g}k \tanh(kh))},\tag{A1}$$

where \vec{g} is the acceleration due to gravity, $k=2\pi/\lambda$ is the radian wavenumber, *h* is the tank water depth and $\lambda=2l_1$ is the wavelength. A single progressive wave is described by:

$$\zeta(x,t) = a\cos(kx - \omega t), \tag{A2}$$

$$u(x,z,t) = a\omega F(kz)\cos(kx - \omega t), \qquad (A3)$$

$$w(x, z, t) = a\omega F'(kz)\sin(kx - \omega t), \qquad (A4)$$

where x=0 at the left end of the tank, z=0 at the surface (positive upwards), ζ is the surface displacement, a is the amplitude, defined as half the maximum peak to trough distance at the surface, and F and F' are structure functions that describe the vertical decay of wave orbital velocities:

$$F(kz) = \frac{\cosh[k(z+h)]}{\sinh(kh)},\tag{A5}$$

$$F'(kz) = \frac{\sinh[k(z+h)]}{\sinh(kh)}.$$
 (A6)

The seiche is a sum of two waves with frequencies of opposite sign, described by:

$$\zeta(x,t) = a \cos(kx - \omega t) + a \cos(kx + \omega t), \qquad (A7)$$

$$u(x, z, t) = a\omega F(kz)[\cos(kx - \omega t) - \cos(kx + \omega t)], \qquad (A8)$$

$$w(x, z, t) = a\omega F'(kz) \left[\sin(kx - \omega t) - \sin(kx + \omega t) \right], \qquad (A9)$$

where the combined waves have an amplitude of 2a. The vertical and horizontal accelerations are:

$$\frac{\partial u}{\partial t} = a\omega^2 F(kz) \left[\sin(kx - \omega t) - \sin(kx + \omega t) \right], \tag{A10}$$

$$\frac{\partial w}{\partial t} = -a\omega^2 F'(kz) \left[\cos(kx - \omega t) - \cos(kx + \omega t)\right].$$
(A11)

At the surface, the amplitudes of horizontal velocity and acceleration are $u_{\text{max}}=2a\omega/\tanh(kh)$ and $\alpha_{\text{max}}=2a\vec{g}k$, respectively.

The shaker flask produces simpler linear motion with oscillating velocities and accelerations described by:

$$u(t) = a\omega \,\sin(\omega t),\tag{A12}$$

$$\frac{\mathrm{d}u}{\mathrm{d}t} = a\omega^2 \cos(\omega t),\tag{A13}$$

where *a* is the amplitude, defined as half the peak-to-peak distance, $\omega = 2\pi f$ is the radian frequency and *f* is the oscillation frequency in Hz. The amplitudes of velocity and acceleration are $u_{\text{max}} = a\omega$ and $\alpha_{\text{max}} = a\omega^2$, respectively.

Equation of particle motion

To estimate larval propulsive forces, we assumed that larvae can be treated as spherical particles and solved the equation of particle motion:

$$m\frac{d\vec{V}_{\rm o}}{dt} = \vec{F}_{\rm a} + \vec{F}_{\rm p} + \vec{F}_{\rm w} + \vec{F}_{\rm d} + \vec{F}_{\rm f} + \vec{F}_{\rm b} + \vec{F}_{\rm v}, \qquad (A14)$$

for propulsive force \vec{F}_{v} . The left-hand side of this equation is the product of larval mass *m* and the larval translational acceleration. On the right-hand side, the first term is the added mass force needed for a larva to displace the water that it moves through:

$$\vec{F}_{\rm a} = -\frac{2}{3}\pi r^3 \rho_{\rm f} \frac{\mathrm{d}\vec{V}_{\rm b}}{\mathrm{d}t},\tag{A15}$$

where *r* is the larval radius, ρ_f is the fluid density and \vec{V}_b is the behavioral component of the larval translational velocity vector. The second term is the force due to pressure gradients created by accelerating flow:

$$\vec{F}_{\rm p} = \frac{4}{3}\pi r^3 \rho_{\rm f} \frac{\mathrm{d}\vec{V}_{\rm f}}{\mathrm{d}t},\tag{A16}$$

where \vec{V}_{f} is the fluid component of the larval translational velocity vector. The third term is the net weight force resulting from gravity and buoyancy:

$$\vec{F}_{\rm w} = \frac{4}{3}\pi r^3 (\rho_{\rm p} - \rho_{\rm f})\vec{g},$$
 (A17)

where $\vec{g} = 980 \text{ cm s}^{-2}$ is the downward acceleration due to gravity and ρ_p is the larval density. The fourth term is the viscous drag force given by Stokes' law for spheres:

$$\vec{F}_{\rm d} = -6\pi\mu r \vec{V}_{\rm b} \tag{A18}$$

(Rubey, 1933; Vogel, 1994), where μ is dynamic viscosity. The fifth term is the Basset history force produced by time-varying effects of drag on the boundary layer around a particle (Mei et al., 1991):

$$\vec{F}_{\rm b} = -6r^2 (\pi \rho_{\rm f} \mu)^{0.5} \int_0^t \frac{{\rm d}\vec{V}_{\rm b}}{{\rm d}t'} \frac{1}{\left(t-t'\right)^{0.5}} {\rm d}t'. \tag{A19}$$

The accuracy of \vec{F}_b is limited by the duration of larval tracks, which ranged from 0.16 to 13.7 s but was <2 s on average. The sixth term is the form drag force that accounts for pressure drag on inertial particles:

$$\vec{F}_{\rm f} = -\pi \rho_{\rm f} r^2 \vec{V}_{\rm h}^2 \tag{A20}$$

(Rubey, 1933). All time derivatives were calculated following larval trajectories. The propulsive force \vec{F}_v is unknown and was estimated indirectly from Eqns A14–A20.

This model differs from commonly used force balance equations (Maxey and Riley, 1983; Mei, 1996) by the addition of \vec{F}_v and the form of \vec{F}_f , which we selected to be most accurate for particles with Reynolds numbers in the range of oyster larvae. For larvae, the particle Reynolds number is $Re_p = d |\vec{V}_b|/v$, where *d* is shell length and v is kinematic viscosity, and ranges from $Re_p \approx 0.2$ to 10 (Fuchs et al., 2013). Total drag is sometimes expressed as $\vec{F}_D = 0.5\rho_f A C_d \vec{V}_b^2$, where *A* is projected area and C_d is a coefficient that encompasses contributions from both viscous and inertial drag. At low particle Reynolds numbers ($Re_p < 1$), the inertial drag is negligible, $C_d = 24/Re_p$, and the particle can be treated as spherical, leading to Stokes' drag formula (Eqn A18; e.g. Clift et al., 1978). At higher particle Reynolds

numbers, the inertial drag becomes non-negligible and is usually described with empirical formulas. Theory of inertial drag has advanced little since the work of Oseen, who developed a correction to Stokes' law that separates the drag into viscous and inertial components $\vec{F}_{\rm D} = \vec{F}_{\rm d} + \vec{F}_{\rm f}$ by setting the drag coefficient $C_{\rm d} = 24/Re_{\rm p}+9/2$ (Kundu, 1990). Oseen's correction accurately predicts drag only at $Re_{\rm p}<5$. We used Rubey's form of the inertial drag component (Eqn A20), which differs from the Oseen correction by a leading coefficient on $\vec{F}_{\rm f}$ and performs better at higher particle Reynolds numbers (Rubey, 1933; Guo, 2011).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

H.L.F., G.P.G., and F.J.D. conceived and designed the research, G.P.G. and E.J.H. designed the seiche, A.J.C. and H.L.F. performed the experiments, E.J.H. did the two-phase image processing, H.L.F. analyzed the data, and H.L.F. wrote the paper with contributions from G.P.G. and E.J.H.

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