Directed Motion in the Sea: Efficient Swimming by Reef Fish Larvae

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Directed motion of marine organisms is examined with a focus on efficient behaviour, where efficient swimming minimizes either energetic expenditure or transit time. The swimming behaviour of late pelagic stage reef fish larvae is modelled to illustrate relevant concepts. To swim efficiently in the sea, an organism should exploit current-driven movements of the medium. Favourable currents should be ridden and unfavourable currents avoided. Relatively short movements to control advection can have a greater effect than longer swimming bouts used for independent horizontal locomotion. If larvae exploit the vertical structure of the water column, then the extent to which they can influence their dispersal will be substantially increased.

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1. Introduction

Understanding how organisms move is fundamental to understanding their ecology. Many logistical problems must be overcome when studying movement in the sea, but theoretical problems also arise. For example, the definition of distance is ambiguous in the marine environment (or freshwater and aerial environments), because the medium in which organisms are located is dynamic. Is distance the length of the trajectory that can be traversed in the least time, or the length of the one that can be traversed for the least energetic expenditure? Until we answer such questions, we cannot measure the maximum distances that can be travelled or the energetic cost of movements, and therefore, we will struggle to understand how movement can influence population dynamics.

Marine locomotion is well studied over fine spatial scales and particular attention has been given to the efficiencies of different swimming styles (Lighthill, 1975; Barrett *et al.*, 1999; Sfakiotakis *et al.*, 1999). However, population ecologists must understand how large-scale movements of the order of kilometres influence distribution patterns. Studies of marine locomotion over these ecologically important scales are scarce, although Weihs (1977, 1978) provides important examples.

1.1. SPECIFIC APPLICATION

The independent locomotion of tropical reef fish larvae is examined to illustrate relevant concepts. Most reef fishes undergo a pelagic larval stage during which individuals can travel tens or hundreds of kilometres. The numbers and condition of larvae that reach suitable habitats for settlement at the end of this stage could partly determine adult population size (Doherty & Williams, 1988; Doherty & Fowler, 1994; McCormick, 1998; Booth & Hixon, 1999).

Reef fish larvae develop capabilities for both short-duration and prolonged locomotion, and some late pelagic stage larvae can sustain speeds comparable to mean currents for days without

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rest or food (Stobutzki & Bellwood, 1994, 1997). *In situ* observations confirm that larvae utilize their swimming abilities during dispersal (Leis & Carson-Ewart, 1997; Sancho *et al.*, 1997). In order to influence their dispersal through swimming, larvae need some directional sense, and Leis *et al.* (1996) established that larvae orientate with respect to a reef while still over a kilometre away in open water.

Few modelling studies consider the consequences of directed motion by larvae for determining recruitment rates to adult populations. The few that do concentrate on inefficient behaviour; they assume individuals aim straight at their target destination and follow a current-independent course (Werner *et al.*, 1993; Wolanski *et al.*, 1997). This inefficient behaviour limits the number of individuals that reach reefs successfully (Armsworth, 2000) and should be considered a lower bound on larval capabilities. In this paper, I seek to establish what relevant upper bounds would be.

Larvae will not behave perfectly efficiently, but larvae of different species and developmental stages will fall somewhere between the upper and lower bounds on behavioural efficiency. Having a measure of the upper bound is an important step towards placing individuals within this spectrum. If we do not know what constitutes efficient behaviour, and by inference what organisms would want to do were they able to do so, then the process of quantifying their locomotory capabilities is an exercise in extrapolation, where directions for future research are unclear. However, if we know both the upper and lower bounds, then the exercise becomes one of interpolation, and directions for future research should be more apparent.

2. Methods

2.1. EQUATIONS OF MOTION

Only two-dimensional problems are considered for brevity. Individuals swim with velocity $\mathbf{v}$ relative to the surrounding fluid, which itself has velocity $\mathbf{u}$, and their equations of motion are

$$\frac{d\mathbf{x}}{dt} = \mathbf{u} + \mathbf{v}, \tag{1}$$

where $\mathbf{x} = (x, y)$ in Example 1 or (x, z) in Examples 2 and 3.

Two classes of problems are considered. In one class, swimming speed $v = |\mathbf{v}|$ is constant and, in the other, v is a control variable that can vary with time. The direction of swimming, specified by polar angle θ, is a control variable that can vary with time in both.

A variety of simple, characteristic current profiles are examined (Fig. 1). Currents over continental shelf margins are considered here to comprise three main constituents: low-frequency (drift) currents, representing quasi-steady oceanic influences, oscillatory tidal currents and a near-surface component designed to represent the highly sheared wind-driven currents. Currents are reduced by bottom friction in a thin layer above the substrate.

In Example 1, larvae swim towards reefs from a distance of kilometres away. Firstly, the simplest case of a constant drift current is considered,

$$\mathbf{u} = (u_r, 0), \tag{2}$$

where the x-axis defines the "along-shelf" direction, and u_r is the current speed. Then a cross-shelf, monochromatic tidal current is imposed [Fig. 1(a)]

$$\mathbf{u} = (u_r, u_t \sin(\omega t + \alpha)), \tag{3}$$

where u_t represents the amplitude of the tidal current, ω is its angular frequency, and α sets the tidal phase relative to the organism's start time.

Attention shifts to vertical movements in Example 2, and a structured flow regime is considered with the water column divided into three layers. Within each layer the current profile is assumed not to depend on depth, but by moving between layers an organism samples different water velocities [Fig. 1(b)]. All three current constituents act in the direction of the x-axis,

$$\mathbf{u} = \begin{cases} (u_w + u_r + u_t \sin(\omega t + \alpha), 0) & \text{[upper layer]}, \\ (u_r + u_t \sin(\omega t + \alpha), 0) & \text{[middle layer]} \\ (0, 0) & \text{[benthic boundary layer]}, \end{cases} \tag{4}$$
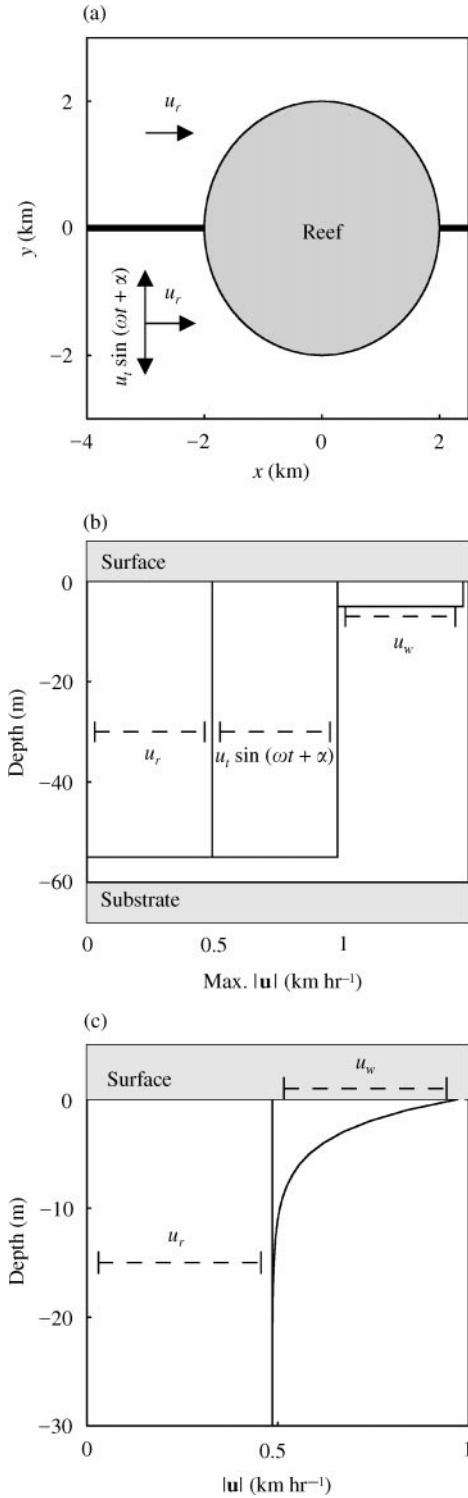
FIG. 1. Characteristic current profiles used in (a) Example 1, (b) Example 2, and (c) Example 3.

where u_w is the strength of the wind-driven currents that are confined to the top few metres of the water column for simplicity.

In Example 3, a smoothed vertical profile is considered, but temporally varying tidal currents are neglected, and

$$\mathbf{u} = (u_r + u_w \exp(\beta(z - h)), 0), \qquad (5)$$

where β is some positive constant and h is the height of the surface above some chosen datum [Fig. 1(c)].

2.2. OBJECTIVES

Two definitions of efficient swimming are considered. In the minimum time problem, efficient swimming minimizes the time taken to travel between two locations at a fixed swimming speed.

In the minimum energy problem, efficient swimming minimizes the energetic expenditure when travelling between two destinations in a specified time interval. Reynolds numbers for swimming late stage larvae are typically in the thousands (Fisher et al., 2000). For such larvae, inertial forces dominate during motion, and the drag force scales approximately with the square of the velocity (Kundu, 1990). The rate of energetic expenditure is assumed to scale with velocity cubed, and the total energetic expenditure is

$$E = \int_0^{t_f} cv(t)^3 \, dt, \qquad (6)$$

where c is a constant and t_f is the terminal time. This may underestimate larval capabilities depending on the efficiency of the swimming style employed by larvae (Weihs, 1977).

2.3. VARIATIONAL CALCULUS

Variational calculus is the appropriate methodology for examining efficient movement in the presence of a current field. Introductions to the method are given by Gregory & Lin (1992), Hartl et al. (1995), and others. For many detailed applications see Bryson & Ho (1969), which is the main reference for this work.

If Hamiltonian functions

$$H = 1 + \lambda^T \cdot (\mathbf{u} + \mathbf{v}) \quad [\text{min. time}],$$

$$H = cv^3 + \lambda^T \cdot (\mathbf{u} + \mathbf{v}) \quad [\text{min. energy}] \qquad (7)$$

are defined where $\lambda^{\mathrm{T}} = (\lambda_x, \lambda_y)$ and (λ_x, λ_z) are adjoint variables, then optimal solutions must simultaneously solve the Euler-Lagrange equations

$$\frac{d\lambda_x}{dt} = -\frac{\partial H}{\partial x}, \frac{d\lambda_y}{dt} = -\frac{\partial H}{\partial y}, \frac{\partial H}{\partial \theta} = 0,$$

[minimum time],

$$\frac{d\lambda_x}{dt} = -\frac{\partial H}{\partial x}, \frac{d\lambda_y}{dt} = -\frac{\partial H}{\partial y}, \frac{\partial H}{\partial \theta} = 0, \frac{\partial H}{\partial v} = 0,$$

[minimum energy]   (8)

and the equations of motion (1), subject to boundary conditions. In addition,

$$H(t_f) = 0 \qquad (9)$$

in the minimum time problem, because t_f is not specified.

3. Example 1: Swimming towards the Reef

Example 1 examines swimming towards reefs by larvae prior to settlement. As a first abstraction the current field is assumed constant (2) and the reef is circular with radius R. A straightforward geometric argument determines the minimum time path (Gandner, 1998).

3.1. GEOMETRIC PROOF

Consider the relative motion of the reef and a larva with respect to a passively advected particle released from $\mathbf{x}_0$ at time $t = 0$. The reef has velocity $(-u_r, 0)$ and the larva $(v\cos\theta, v\sin\theta)$. The minimum transfer time occurs at the first intersection of the circles in Fig. 2. Applying Pythagoras,

$$(u_r^2 - v^2)t_f^2 + 2(u_r x_0 - vR)t_f + x_0^2 + y_0^2 - R^2 = 0 \qquad (10)$$

and the minimum time is the smaller positive root.

If larvae swim strongly ($u_r < v$), there is a single positive root, but if larvae are weak swimmers ($u_r > v$), then two conditions must hold for them to reach the reef successfully,

$$\frac{(x_0 v - u_r R)^2}{y_0^2} \geqslant (u_r^2 - v^2) \quad \text{and} \quad \frac{vR}{u_r} > x_0. \quad (11)$$

A weak swimming larva located within an upstream cone, which can sense the reef, can reach it. The boundaries of the cone depend on the ratio of current speed to swimming speed.

The optimal heading satisfies

$$\tan\theta = \frac{y_0}{x_0 + u_r t_f}. \qquad (12)$$

Trajectories are straight line paths (upper half of Fig. 3). To follow a straight line path an organism must anticipate and compensate for the future effect of current advection, so that the net velocity (currents + swimming) remains directed towards the target. In comparison, current-unadjusted trajectories are curved, and tend to over-shoot the target (Armsworth, 2000).

3.2. VARIATIONAL APPROACH

The optimal solution can also be derived with the variational method, which permits several extensions. From the Euler–Lagrange equations, (8), adjoint variables (λ_x, λ_y) are constant.
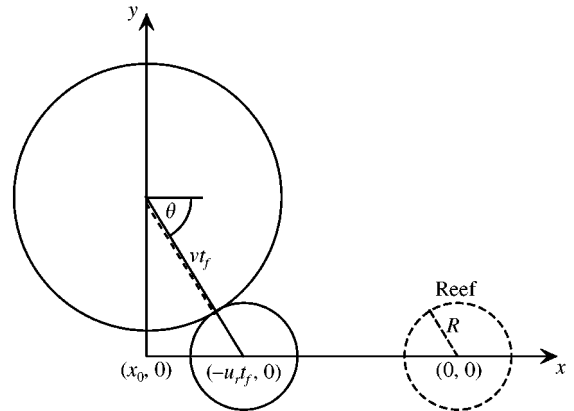

FIG. 2. Simple geometric argument for solving the minimum time problem in Example 1 with a constant drift current (2) (adapted from Gandner, 1998).
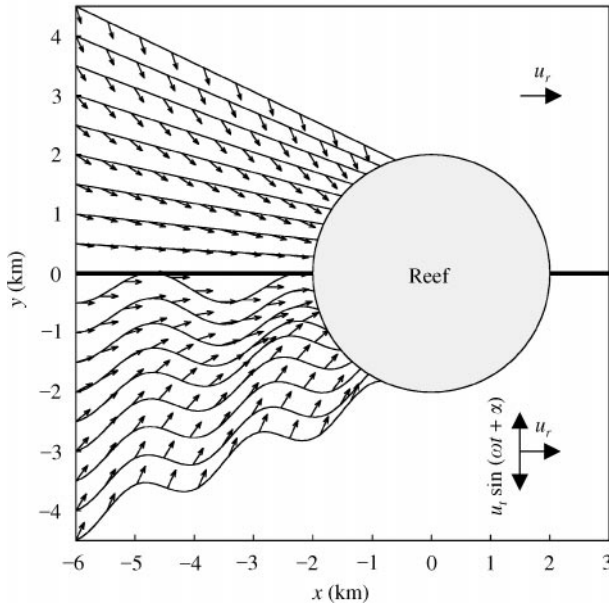
FIG. 3. Optimal trajectories and control choices for the minimum time problem in a constant along-shelf drift current (upper half-plane), and a constant along-shelf drift current with superimposed monochromatic, cross-shelf tidal current (lower half-plane); $v = 8\,\mathrm{cm\,s}^{-1}$ and $u_r = u_t = 13.5\,\mathrm{cm\,s}^{-1}$.

Minimization requires

$$\frac{\partial H}{\partial \theta} = 0 \Rightarrow \frac{\lambda_y}{\lambda_x} = \tan\theta, \qquad (13)$$

so θ is also constant and $\mathbf{x}$ is linear. The earlier optimality condition (12), is recovered by solving the boundary conditions.

When tides are included (3), the optimal θ satisfies

$$\tan\theta = \frac{u_t/\omega(\cos\alpha - \cos(\omega t_f + \alpha)) + y_0}{x_0 + u_r t_f}. \qquad (14)$$

The boundary conditions determine t_f, and were solved numerically. The simple geometric argument continues to characterize trajectories well, although θ follows a periodic variation with tidal phase (lower half of Fig. 3). To behave efficiently this time, larvae must anticipate how currents will change. This allows θ to be adjusted for the net tidal excursion.

In the minimum energy problem, eqn (8) implies θ, v, λ_x and λ_y are constant. Condition (12) is
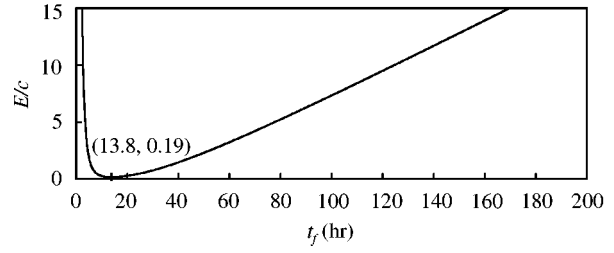

FIG. 4. Dependence of total energetic expenditure in the minimum energy problem on given terminal time t_f for $(x_0, y_0) = (-5, 5)\,\mathrm{km}$ and $u_r = 13.5\,\mathrm{cm\,s}^{-1}$.

recovered and determines θ, because t_f is given. The least energy path for a given t_f does not coincide with the minimum time path in general, but the solutions share a common geometric structure (Fig. 2).

The minimum energy path depends on the prescribed terminal time. In Fig. 4, t_f is an independent variable and minimum energetic expenditures are graphed. The speed required to reach the reef and the energy expended in doing so increase asymptotically as $t_f \to 0$. For large t_f, the swimming direction for larvae is almost directly upstream, and most energy is expended, not in reaching the reef, but in maintaining position; $v \to u_r$ as $t_f \to \infty$, and $E \approx c u_r^3 t_f$. Between these extremes, the optimal energetic expenditure achieves a minimum as a function of t_f. This is a minimum across all controls *and* all possible terminal times. The optimal trajectory for the optimal t_f involves larvae swimming so they are located upstream of the reef and riding the longshore current.

4. Example 2: Structured Vertical Shear

When considering current fields that depend on position, one pertinent question for reef fish concerns the importance of vertical movements by larvae. Again, we start with a simplified abstraction [4, Fig. 1(b)].

4.1. MINIMUM TIME

The origin is chosen to lie at the half-way depth of the mid-layer and the distance to the other layers is h. Firstly, the problem of minimizing transfer time from $(0,0)$ to $(a,0)$ is examined, where a, u_r, u_w and u_t are positive.

The current field is discontinuous at $z = \pm h$. Following Bryson & Ho (1969, p. 104), we define Hamiltonians on either side of the discontinuities in the usual manner and treat the discontinuities as interior point constraints that the solution must satisfy. The Euler–Lagrange equations imply λ_x, λ_z, and θ are constant in each region with $\lambda_z/\lambda_x = \tan \theta$. Minimization requires

$$\lambda(t_1^-) = \lambda(t_1^+) + \gamma \nabla(z - h) \quad \text{and}$$

$$H_1(t_1^-) = H_2(t_1^+) - \gamma \frac{\partial(z - h)}{\partial t}, \qquad (15)$$

where γ is a Lagrangian multiplier, t_1 is the time at which the upper discontinuity is reached, and $t_1^+ = t_1 + \varepsilon$ and $t_1^- = t_1 - \varepsilon$ for some $\varepsilon > 0$ (Bryson & Ho, 1969, p. 101). Similar relationships hold at $z = -h$.

If individuals remain in the mid-water column, $\mathbf{x}$ is linear, the optimal path is a straight line, and t_f is the time taken for an organism with net velocity $(u_r + v)$ to travel distance a adjusted for the net tidal excursion.

However, any solution satisfying (8) need only be a local stationary solution, i.e. these conditions are necessary but not sufficient for identifying a minimum. Another likely choice would be a trajectory that entered the upper water column. Let subscripts 1, 2, and 3 denote solution segments located in the mid-water column for the first time, the upper water, and the mid-water column for the second time. Let t_1 denote the entry time into the upper layer, and t_2 the exit time.

For segment 1,

$$x_1 = (u_r + v \cos \theta_1)t + \frac{u_t}{\omega}(\cos \alpha - \cos(\omega t + \alpha)),$$

$$z_1 = vt \sin \theta_1 \quad \text{for } t \in [0, t_1] \quad \text{and} \quad t_1 = \frac{h}{v \sin \theta_1}$$

$$(16)$$

and similarly for the other segments.

At t_1 and t_2, eqn (15) holds, and therefore, $\cos \theta_1 = \cos \theta_3 = v/(u_w + v)$. The following implicit equation for the transfer time can be obtained:

$$a = u_r t_f + u_w \left(t_f - \frac{2h}{v \sin \theta} \right) + v \left(t_f - \frac{2h(1 - \cos \theta)}{v \sin \theta} \right)$$

$$+ \frac{u_t}{\omega}(\cos \alpha - \cos(\omega t_f + \alpha)), \qquad (17)$$

where $\theta = \theta_1 = -\theta_3$, and this gives a second candidate solution that satisfies the necessary conditions for a minimum.

Other candidate solutions can be constructed by piecing together segments on different layers. For example, there is a stationary solution that enters the lower boundary layer once, and some that enter both boundaries. When considering positive a and favourable currents, the solution that enters the upper layer once is the global minimum for large regions of parameter space. Exceptions occur when horizontal distance a is short relative to h, or where tidal currents are strong relative to drift currents and a is large enough to necessitate a transfer time spanning several tidal cycles. The profile that never leaves the mid-layer proves optimal in the former case, and in the latter the optimal solution can switch between the mid-layer and the benthic boundary layer to exploit the flood and ebb tides (see also Weihs, 1978).

Two stationary solutions are shown in Fig. 5. Individuals were required to travel a horizontal distance of 12 km and were released at a depth of 30 m. The trajectory that enters the top layer is optimal. Points are plotted at 20 min intervals on the horizontal segments and every minute on the vertical segments. Vertical movements to and from the upper layer take less than 6 min out of 8.8 hr swimming time. Vertical distances involved are orders of magnitude less than horizontal distances. Even if exploiting vertical velocity gradients only confers a minor advantage, efficient swimmers would do so, because the costs involved are small.

4.2. MINIMUM ENERGY

Suppose a is some upstream distance in the minimum energy problem. On each layer, λ, θ and v are constant. Once again there is a candidate solution that does not leave the mid-layer.
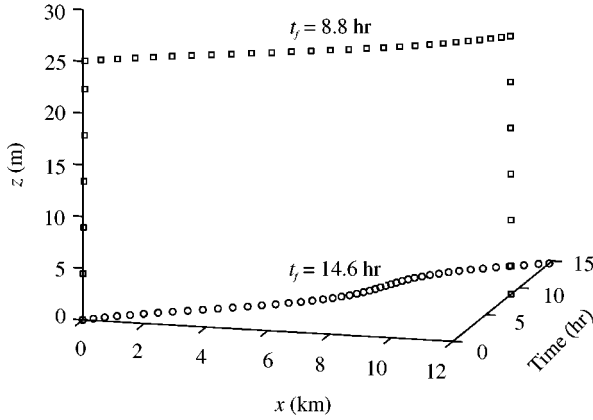
FIG. 5. Minimum time paths for a horizontal distance of 12 km with $v = 8\,\mathrm{cm\,s^{-1}}$ and $u_r = u_t = u_w = 13.5\,\mathrm{cm\,s^{-1}}$ in the presence of vertically structured flow (4). The mid-water column solution is shown with circles plotted every 20 min. The global minimum solution, which enters the upper layer once, is shown with squares plotted every minute in the mid-water column and every 20 min in the upper layer.

Trajectories that enter the benthic boundary layer are also likely candidates for a minimum. By entering the boundary layer, individuals avoid tidal currents for one segment of the trajectory, and the optimal control choices are no longer symmetric: $\theta_1 \neq -\theta_3$ and $v_1 \neq v_3$. A system of simultaneous equations, which were solved numerically, determines this stationary solution.

A comparison of trajectories and associated energetic costs is given in Fig. 6 for the problem of position maintenance ($a = 0$) over a 12 hr tidal cycle. The most efficient trajectory enters the benthic boundary layer. It involves swimming almost vertically downwards, until the boundary layer is reached. During vertical movement, the individual is washed downstream. Once in the boundary layer the organism swims slowly upstream passing by the target destination. Then, it exits the boundary once the required time has almost elapsed, and moves nearly vertically through the water column. Currents carry the organism downstream once more, so that it arrives at its target destination. Efficient individuals do not attempt to resist currents. The most efficient strategy that does not enter the benthic boundary layer is the optimal mid-water strategy, which incurs more than 2000 times the energetic cost of the benthic strategy. Larvae that enter
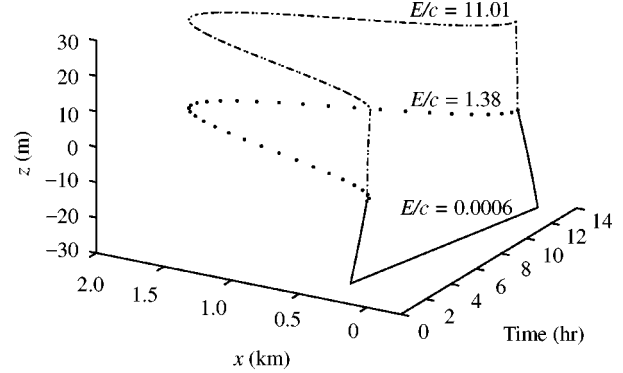

FIG. 6. Minimum energy paths for position maintenance in vertically structured flow (4) for 12 hr with $u_r = u_t = u_w = 13.5\,\mathrm{cm\,s^{-1}}$. Upper layer (dot–dash), mid-water column (dotted) and global minimum benthic boundary layer (solid) solutions shown.

the boundary layer remain within the vicinity of the release site for the whole time and require little swimming. Larvae that follow other strategies undergo a significant tidal excursion, and must swim to resist advection.

5. Example 3: Smooth Vertical Shear

The assumption of structured flow is now relaxed and effects of smooth gradients in the vertical profile are examined. An analytical solution for a steady-state minimum time problem is presented, one in which there are no tidal currents, or in which tides act in the neglected y-direction. The origin lies in the mid-water column, with the surface at height h. Therefore, $z \leqslant h$, and the set of allowable controls corresponds to state variables that do not violate this constraint.

5.1. UNCONSTRAINED SOLUTION

Optimal paths from $(0, 0)$ to $(a, 0)$ in eqn (5) are derived where $a > 0$ and $u_r, u_w > 0$. Let $\hat{u}_w = u_w \exp(-\beta h)$.

As before λ_x is constant, and $\lambda_z / \lambda_x = \tan \theta$. Now, however,

$$\frac{\mathrm{d}\lambda_z}{\mathrm{d}t} = -\lambda_x \frac{\partial u}{\partial z} \Rightarrow \frac{\mathrm{d}\theta}{\mathrm{d}t} \sec^2 \theta = -\frac{\partial u}{\partial z}. \quad (18)$$

The total time derivative of the Hamiltonian is zero, $\mathrm{d}H/\mathrm{d}t = 0$, and eqn (9) implies $H \equiv 0$.

Therefore,

$$\lambda_x = \frac{-\cos\theta}{v + u(z)\cos\theta} = \frac{-\cos\theta_f}{v + (u_r + \hat{u}_w)\cos\theta_f}, \quad (19)$$

where $\theta_f = \theta(t_f)$,

$$u(z) = u_r + \hat{u}_w + v\sec\theta_f - v\sec\theta \Rightarrow$$

$$z = \frac{1}{\beta}\log\left(\frac{v}{\hat{u}_w}(\sec\theta_f - \sec\theta) + 1\right), \quad (20)$$

and $\theta_0 = -\theta_f$.

Equation (18) yields optimal control θ,

$$\frac{d\theta}{dt} = -(u(z) - u_r)\beta\cos^2\theta$$

$$\Rightarrow v\beta(t_f - t) = \log\left(\frac{|\sec\theta_f + \tan\theta_f|}{|\sec\theta + \tan\theta|}\right)$$

$$+ b(\Gamma(\theta_f) - \Gamma(\theta)), \quad (21)$$

where $b = \hat{u}_w/v + \sec\theta_f$ and

$$\Gamma(\theta) = \frac{2}{(b^2-1)^{1/2}}\operatorname{atanh}\left(\frac{(b+1)(\cos\theta-1)}{(b^2-1)^{1/2}\sin\theta}\right). \quad (22)$$

Solving

$$\frac{dx}{d\theta} = \frac{v\cos\theta + u_r + \hat{u}_w + v\sec\theta_f - v\sec\theta}{\beta(v - (\hat{u}_w + v\sec\theta_f)\cos\theta)\cos\theta} \quad (23)$$

gives

$$\beta(x - a) = \frac{u_r}{v}\log\left(\frac{|\sec\theta + \tan\theta|}{|\sec\theta_f + \tan\theta_f|}\right)$$

$$+ \tan\theta_f - \tan\theta$$

$$+ (1 + bu_r/v)(\Gamma(\theta) - \Gamma(\theta_f)). \quad (24)$$

Substituting in the initial conditions determines θ_f and t_f, and yields the minimum time path in the unconstrained problem (dashed lines in Fig. 7).

The unconstrained trajectory rises rapidly from release, and violates the upper boundary constraint for most reasonable parameter sets (Fig. 7). The unconstrained solution is the minimum time path for those unusual circumstances in which the surface constraint is never active; for example, this occurs when a is small (of the order of tens of metres).

5.2. CONSTRAINED SOLUTION

The optimal constrained solution is comprised of unconstrained (regions 1 and 3) and constrained (region 2) arcs (Fig. 7). On the constrained arc, $z = h$ and $\theta = 0$. The unconstrained problem is solved in region 1 using the constraint conditions as terminal conditions and in region 3 using these as initial conditions. These unconstrained solutions are then matched with the constrained segment.

Subscripts are used to denote the three regions that feature in the solutions as in Section 4.1. On the unconstrained segments, eqns (20) and (24) hold. If t_1 is the time of entry into the boundary, then $\theta_1(t_1) = 0$ and

$$t_1 = \frac{1}{v\beta}\left(\log\frac{1}{|\sec\theta_0 + \tan\theta_0|} - b_1\Gamma(\theta_0)\right), \quad (25)$$

where $b_1 = \hat{u}_w/v + \sec\theta_0$. A similar expression determines $(t_f - t_2)$.

On the boundary itself,

$$z = h \quad \text{and}$$

$$x_2 = (v + u_r + \hat{u}_w e^{\beta h})(t - t_1) + x_1(t_1). \quad (26)$$

Demanding continuity, so that $x_2(t_2) = x_3(t_2)$, gives a single equation in the last remaining unknown $(t_2 - t_1)$, which was solved numerically (solid curves in Fig. 7).

The optimal constrained solution leaves the release point in the mid-water column, and rises rapidly $(\theta_0 \approx \pi/2)$. During this time there is a small amount of downstream advection. The trajectory enters the boundary tangentially [Fig. 7(b)]. Most horizontal distance is covered during the constrained segment with the individual exploiting the maximum downstream velocity in the wind-driven layer. Just prior to
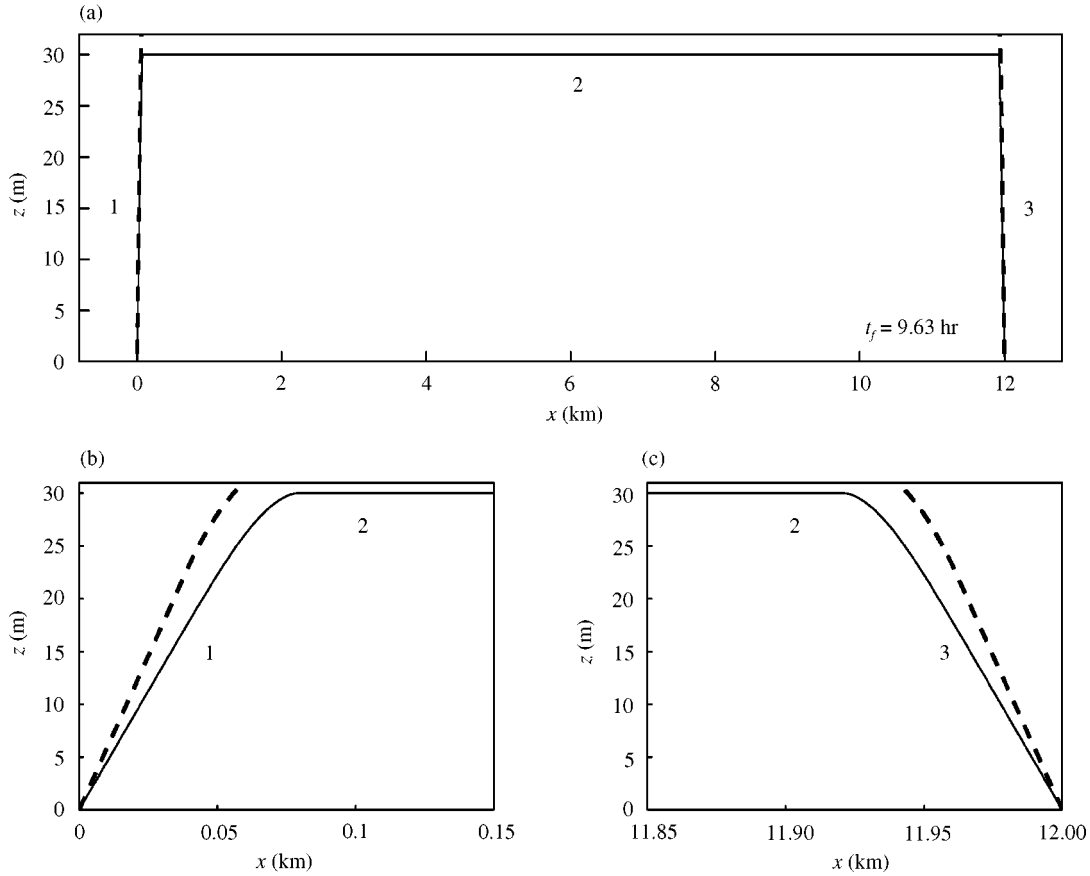
FIG. 7. Minimum time path for a horizontal distance of 12 km with $v = 8\,\mathrm{cm\,s^{-1}}$ and $u_r = u_w = 13.5\,\mathrm{cm\,s^{-1}}$ in the presence of smooth shear flow (5). The unconstrained solution is dashed. The corresponding optimal constrained solution is solid. Graphs (b) and (c) show the unconstrained segments (1 and 3) in more detail.

arrival at the downstream location the trajectory leaves the boundary and descends near vertically ($\theta_f \approx -\pi/2$). Advection carries the organism downstream during the descent, allowing it to intersect with its destination [Fig. 7(c)]. Due to the rapid ascents and descents the optimal trajectory bears a strong resemblance to the abstraction in Example 2, although this time the organism rises to the level of maximum down-stream advection at the surface itself. With the smooth vertical profile, there is no longer the possibility of multiple stationary solutions, and instead there is a single candidate for the global minimum time path.

6. Discussion

The concept of the distance between two points along a straight line path is no longer appropriate when locomotion occurs in the presence of a current field. Two alternatives can replace this fundamental measure in studies of marine locomotion: namely, the minimum time path and the minimum energy path. When the imperative to reach the target is pressing, then the former is more appropriate. This would most likely be the case over smaller scales than those considered here, e.g. for short burst-swimming motions used to dart for cover when a predator is sensed. The latter is appropriate when the time of arrival is less pressing, and when the condition of the individual has fitness ramifications.

Efficiently swimming organisms move into and out of regions that experience different flow regimes. Favourable currents should be harnessed and ridden, and swimming directly upstream should be avoided whenever currents are un-favourable. Efficient behaviour often exploits

boundary shear flows, because it is here that differences between current regimes are greatest.

If organisms are well adapted to their environment, then some degree of efficiency in their behaviour should be expected. When considering nektonic organisms, some species should be expected to manipulate currents, because strong selective pressure is likely to act on any trait that favours efficient movement.

An understanding of what constitutes efficient behaviour provides a benchmark that allows one to evaluate the relative efficiency of other suboptimal, but probably more realistic, strategies. Individuals will not be perfectly efficient, but nor will they be completely inefficient. By understanding what constitutes the most and least efficient movement strategies, we can hope that by introducing constraining assumptions on the former, and relaxing such assumptions on the latter, we can converge on an understanding of how organisms actually behave.

6.1. SPECIFIC APPLICATION

The examples are chosen to describe a particular ecological context, that of late pelagic stage larval reef fish using their independent locomotory capabilities to influence their likelihood of successful recruitment. Example 1 examines locomotion towards reefs by larvae from upstream. If larvae swim directly at reefs and do not compensate for currents, then trajectories tend to overshoot the target (Armsworth, 2000). In contrast, efficient swimming involves aiming upstream of the destination so that the net velocity vector points towards it.

Larval locomotory capabilities are sufficient to allow them to exercise some control over their dispersal through horizontal movements (Stobutzki & Bellwood, 1997; Armsworth et al., 2001). Examples 2 and 3 demonstrate that if larvae could position themselves in favourable currents by vertical movement, then their scope for influencing their dispersal would be greatly increased. The spatial scales involved are such that vertical movements are of the order of tens of metres but horizontal movements are of the order of kilometres. These distances mean that working with the full solution in Example 3 may often be unnecessary, and the step-like profile

used in Example 2 could provide sufficient information. It requires a matter of minutes and little energetic expenditure for a larva to traverse the entire water column. If vertical movement through buoyancy control were allowed, the energetic costs could be even less.

Sufficient data are not available to assess how efficiently larvae swim. However, Sancho et al. (1997) document upstream swimming by acanthurids utilising the bottom few centimetres of the water column. Also, various other species have epibenthic larvae, which manipulate flow around fine-scale topographic features to prevent advection (Powles & Burgess, 1978; Breitburg et al., 1995).

6.2. WHAT IS REQUIRED FOR EFFICIENT BEHAVIOUR?

An organism requires certain sensory capabilities to swim efficiently, and the examples illustrate how these requirements operate. It is worth reiterating that one cannot consider directed motion unless one is considering an organism that is capable of independent locomotion and of orientating towards some target destination.

Example 1 explores anticipation. Wehner (1997) reviews evidence on flying insects, which indicates that individuals plot and follow interception courses when pursuing moving targets. Moving through a current field towards a fixed target is equivalent to pursuing a moving target in a fixed frame of reference. If an organism can locate its target, then it can sense the present influence of currents by not swimming and monitoring the relative motion of the object. The optimal course then involves moving to a location which the target will come to occupy at some future instant. When tidal currents are present, the organism would need to anticipate tidal oscillations through prior knowledge. Williams et al. (1984) raise the possibility of reef fish larvae using this as a mechanism for influencing their crossshelf position during dispersal.

Example 2 illustrates how some knowledge of the structure of the water column would allow more efficient behaviour when the current field varies in space. Features such as the retardation of currents in the benthic boundary layer will be consistent through time, and an organism which has experienced these conditions previously may

learn where in the volume of water it wishes to be located. However, prior knowledge alone would be of limited use when currents fluctuate unpredictably over time-scales shorter than those of the motion.

Example 3 examines the effects of an ability to detect shear. An organism that could detect velocity gradients would be able to adjust its course in response to shifts in the flow regime. Such an ability would most likely be associated with the development of the lateral line sensory system in reef fishes. The feasibility of detecting velocity gradients would depend on whether they were obscured by fine-scale turbulent motions.

The theoretical results here provide a basis for an experimental program to determine just how efficiently larvae and other nektonic organisms swim. This, in turn, will dictate how important a determinant of recruitment rates and population dynamics swimming behaviour can be.

REFERENCES

ARMSWORTH, P. R. (2000). Modelling the swimming response of late stage larval reef fish to different stimuli. *Mar. Ecol. Prog. Ser.* **195**, 231–247.

ARMSWORTH, P. R., JAMES, M. K. & BODE, L. (2001). When to press on or turn back: dispersal strategies for reef fish larvae. *Am. Nat.*, **157**, 434–450.

BARRETT, D. S., TRIANTAFYLLOU, M. S., YUE, D. K. P., GROSENBAUGH, M. A. & WOLFGANG, M. J. (1999). Drag reduction in fish-like locomotion. *J. Fluid Mech.* **392**, 183–212.

BOOTH, D. J. & HIXON, M. A. (1999). Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus. Oecologia* **121**, 364–368.

BREITBURG, D. L., PALMER, M. A. & LOHER, T. (1995). Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. *Mar. Ecol. Prog. Ser.* **125**, 45–60.

BRYSON, A. E. & HO, Y. C. (1969). *Applied Optimal Control*. Waltham, MA: Ginn and Company.

DOHERTY, P. J. & FOWLER, T. (1994). An empirical test of recruitment limitation in a coral reef fish. *Science* **263**, 935–939.

DOHERTY, P. J. & WILLIAMS, D. McB. (1988). The replenishment of coral reef fish populations. *Ocean. Mar. Biol. Ann. Rev.* **26**, 487–551.

FISHER, R., BELLWOOD, D. R. & JOB, S. D. (2000). The development of swimming abilities in reef fish larvae. *Mar. Ecol. Prog. Ser.*, **202**, 163–173.

GANDNER, M. J. (1998). Note on the optimal intercept time of vessels to a nonzero range. *SIAM Rev.* **40**, 673.

GREGORY, J. & LIN, C. (1992). *Constrained Optimisation in the Calculus of Variations and Optimal Control Theory*. New York: Van Nostrand Reinhold.

HARTL, R. F., SETHI, S. P. & VICKSON, R. G. (1995). A survey of maximum principles for optimal control problems with state constraints. *SIAM Rev.* **37**, 181–218.

KUNDU, P. K. (1990). *Fluid Mechanics*. San Diego: Academic Press.

LEIS, J. M. & CARSON-EWART, B. (1997). In situ swimming speeds of the late pelagic larvae of some Indo-Pacific coral-reef fishes. *Mar. Ecol. Prog. Ser.* **159**, 165–174.

LEIS, J. M., SWEATMAN, H. P. A. & READER, S. E. (1996). What the pelagic stages of coral reef fishes are doing out in blue water: daytime field observations of larval behavioural capabilities. *Mar. Freshwater Res.* **47**, 401–411.

LIGHTHILL, J. (1975). *Mathematical Biofluiddynamics*. Philadelphia: SIAM.

McCORMICK, M. I. (1998). Condition and growth of reef fish at settlement: is it important? *Aust. J. Ecol.* **23**, 258–264.

POWLES, H. & BURGESS, W. E. (1978). Observations on benthic larvae of *Pareques* (Pisces: Sciaenidae) from Florida and Columbia. *Copeia* 1978, 169–172.

SANCHO, G., MA, D. & LOBEL, P. S. (1997). Behavioural observations of an upcurrent reef colonization event by larval surgeonfish *Ctenochaetus strigosus* (Acanthuridae). *Mar. Ecol. Prog. Ser.* **153**, 311–315.

SFAKIOTAKIS, M., LANE, D. M. & DAVIES, J. B. C. (1999). Review of fish swimming modes for aquatic locomotion. *IEEE J. Ocean. Eng.* **24**, 237–252.

STOBUTZKI, I. C. & BELLWOOD, D. R. (1994). An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. *J. Exp. Mar. Biol. Ecol.* **175**, 275–286.

STOBUTZKI, I. C. & BELLWOOD, D. R. (1997). Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* **149**, 35–41.

WEHNER, R. (1997). Sensory systems and behaviour. In: *Behavioural Ecology: an Evolutionary Approach* (KREBS, J. R. & DAVIES, N. B., eds), 4th edn., pp. 19–41. Oxford: Blackwell Science.

WEIHS, D. (1977). Effects of size on sustained swimming speeds of aquatic organisms. In: *Scale Effects in Animal Locomotion* (Pedley, T. J., ed.), pp. 333–338. London: Academic Press.

WEIHS, D. (1978). Tidal stream transport as an efficient method for migration. *J. Cons. Int. Explor. Mer.* **38**, 92–99.

WERNER, F. E., PAYE, F. H., LYNCH, D. R., LOUGH, R. G., PERRY, R. I., GREENBERG, D. A. & SINCLAIR, M. M. (1993). Influences of mean advection and simple behaviour on the distribution of cod and haddock early life stages on Georges Bank. *Fish. Ocean.* **2**, 43–64.

WILLIAMS, D. McB., WOLANSKI, E. & ANDREWS, J. C. (1984). Transport mechanisms and the potential movement of planktonic larvae in the Central Region of the Great Barrier Reef. *Coral Reefs* **3**, 229–236.

WOLANSKI, E., DOHERTY, P. & CARLETON, J. (1997). Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissen.* **84**, 262–268.