

Host location by larvae of a parasitic barnacle: larval chemotaxis and plume tracking in flow

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*Numerous studies describe stimulation and/or enhancement of larval settlement by distance chemoreception in response to chemical factors emitted by conspecific adults, host and prey species and microbial films. However, active upstream tracking of odor plumes, needed in order to locate specific, spatially limited settlement sites, has thus far received little scientific attention. This study examines host location in flow and still water by larvae of the parasitic barnacle *Heterosaccus dollfusi*, which inhabits the brachyuran crab *Charybdis longicollis*. Experiments included analysis of larval motion patterns under four conditions: still water, in flow, in still water with waterborne host metabolites and in flow with host metabolites. Our results show that *H. dollfusi* larvae are capable of actively and effectively locating their host in still water and in flow, using chemotaxis and rheotaxis and modifying their swimming pattern, direction, velocity, determination and turning rate to accommodate efficient navigation in changing environmental conditions.*

INTRODUCTION

Location of suitable substrates for settlement by larvae of marine invertebrates is a crucial process in all benthic marine habitats, with profound importance for dispersal, recruitment and population dynamics [e.g. (Pawlik, 1992; Walters *et al.*, 1997)]. This is further emphasized for marine invertebrates that live in obligatory symbiotic interactions with hosts, and for which host-location by larvae is critical for survival and successful growth. The most reliable known environmental cues for location of specific settlement sites such as prey (Pechenik *et al.*, 1995) and conspecific adults (Toonen and Pawlik, 1996) are soluble chemical metabolites released from the target organisms. These cues stimulate larvae of many studied marine invertebrates to settle (Morse, 1990; Morse and Morse, 1991). The reaction of larvae to target-cues was found to be mainly vertical [e.g. (Butman, 1986)], commonly consisting of a rapid descent in the water column, sometimes coupled with an increase in the swim turning rate (Tamburri *et al.*, 1996). These behavior patterns are designed to keep the larva as close as possible to the spot where it first encountered the cue, thus enhancing its chances of randomly discovering the target.

Such a behavioral pattern may satisfy the settlement-site location needs of species inhabiting spacious substrates, e.g. algal turfs (Krug and Manzi, 1999) or barnacle beds (Raimondi, 1988). However, this strategy is not likely to prove effective for a larva that seeks a specific and spatially-limited target such as a specific host animal. In order to cope with the problem of locating spatially-limited settlement sites, it is more likely that the larva will have to follow actively the host's chemical plume upstream, against the flow, until it reaches the organism secreting the odor. This orientation method relies on the fact that the target organism releases specific chemical metabolites which are carried downstream with the flow, forming a chemical plume that resembles a trackable 'olfactory highway' (Nevitt *et al.*, 1995).

Upstream tracking of chemical plumes is well known for species of crustaceans [(Grasso and Basil, 2002) and references therein], but only for the large, adult animals; hitherto, plume tracking by invertebrate larvae has received little scientific attention. One of the few examples is the cryptoniscus larvae of the parasitic isopod *Probopyrus pandalicola*, which swim upstream in water containing metabolites of their shrimp host *Palaemonetes pugio*, while remaining stationary or moving downstream

in control solutions (Anderson and Dale, 1989). The aim of the present study was to substantiate the suggestion that specific, spatially-limited settlement sites such as host organisms can be located in flow by diminutive marine larvae, utilizing the combined cues of flow direction (rheotaxis) and host chemicals (chemotaxis). To address our aim, we quantitatively characterized the swimming pattern, direction, velocity, determination and turning rate, as well as host-location ability, of larvae of the parasitic barnacle *Heterosaccus dollfusi* Boschma (Crustacea: Rhizocephala). These factors were analyzed in various combinations of flow and host metabolites, and their effects on the host-location behavior of the larvae were examined.

METHOD

Experimental set-up

Larvae were tested under the following five combinations of flow and host metabolites: (i) still water without host odor; (ii) still water with host odor—chemical metabolites produced by the host while caged behind a permeable mesh inside the flume (Figure 1, H); (iii) slow flow ($<1.5 \text{ mm s}^{-1}$) without host odor; (iv) flow (between $0\text{--}5 \text{ mm s}^{-1}$) with host odor—in which larvae were released downstream from the host; and (v) fast flow (between 1.5 and 5 mm s^{-1}) without host odor. It should be noted that in experiments containing flow and host odor, larvae exhibited no significant differences between slow

and fast flow, and these results were therefore pooled. In all experiments containing flow, flow speeds of $>5 \text{ mm s}^{-1}$ caused larvae to drift downstream. Fluorescein dye observations made prior to the actual experiments revealed that after $\sim 1 \text{ h}$ from the insertion of the host into the nylon mesh (pore size $70 \mu\text{m}$) cage, the dye reached the farthest edge of the viewing field (Figure 1, V). Therefore, in all the experiments containing a host (in still water and flow), larvae were gently pipetted into the viewing field 1 h after insertion of the host into the mesh cage. Larval motion was then videotaped for 10 min using high-magnification lenses at 1–3 cm above the flume bottom. Contrary to most larval habitat selection experiments in flow, larvae were not allowed passes over the host, but rather were only filmed in the viewing field downstream of the host, sensing only those host metabolites that have drifted with the flow. After 10 min of videotaping, the flume was emptied, washed and filled with fresh filtered seawater, and the experiment began again using a fresh larval cohort and a new host crab. Each experimental combination was repeated three times, recording 11 individual larvae each time for a total of 33 larval trajectories per combination.

Flume

The experiments were conducted in a transparent, round Plexiglas flume (external diameter 30 cm, channel width 7 cm, height 5 cm; Figure 1) in which $0.45 \mu\text{m}$ filtered seawater was circulated by a paddlewheel to flow velocities of up to 5 mm s^{-1} . Annular flumes have been used in sediment transport studies (Wainright, 1990) and larval motion studies (Hedvall *et al.*, 1998), and are effective, low-cost solutions for flow experiments. We examined the water velocity profile using videofilming of neutrally buoyant passive particles (Pliolite VT; Goodyear Co., USA) in $\sim 2 \text{ cm}$ water depth over the Plexiglas bottom at a velocity of 5 mm s^{-1} in the center part of the flume. Twenty particles were filmed at the horizontal plane, i.e. from above (Figure 1, camera a), and another twenty at the vertical plane, i.e. from the side of the flume (Figure 1, camera b). Motion trajectories for the particles were drawn and their direction of motion was analyzed as explained below. The still water was analyzed using the same methodology. It should be stressed that this study did not attempt either to fully describe the flow, or to simulate natural flow patterns over the seabed, but merely to study the behavior and physical capabilities of the larvae in still and flowing water.

Animals

Host crabs, *Charybdis longicollis* Leene, were trawled off the Mediterranean coast of Israel at depths of 30–45 m, between the months of May and December of 1998 and 1999. Crab sizes ranged between 3 and 10 cm, measured between

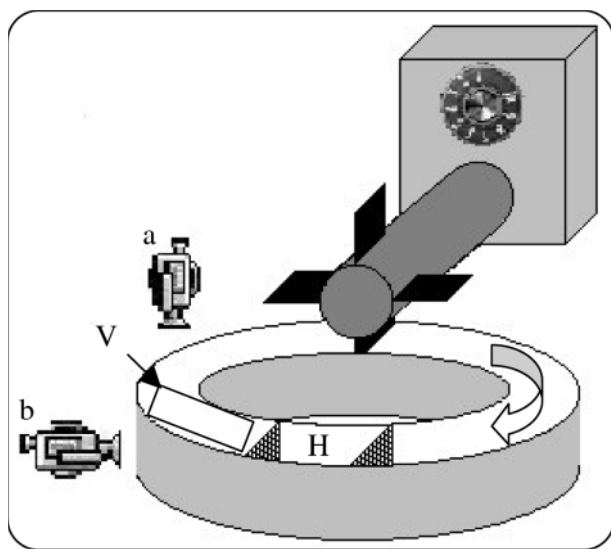


Fig. 1. Flow-tank used to examine swimming patterns of *H. dollfusi* larvae in various test solutions and flow conditions. A paddlewheel was used to generate a laminar flow which passed over the hostcage (H) between two nylon mesh nets, into the camera view field (V) where the larvae were released.

the tips of the two prominent anterolateral carapace spines. Infected crabs showing parasitic externae were kept in aerated plastic containers and fed twice a week with fish. *Heterosaccus dollfusii* nauplii were collected as described by Walker (Walker, 1985), reared to the cyprid stage (animal length $\sim 270 \mu\text{m}$), and taken for experiments 48 h after metamorphosis to the cyprid stage. Cyprid gender was determined by antennular characteristics (Walker, 1985), and only batches that contained $>50\%$ male cyprids were used. Concurrently, only crabs bearing parasitic virgin female externae were used as hosts. This was done in order to enable maximal potential attraction, since male kentrogonid rhizocephalan cyprids are most probably attracted by chemicals emanating from the virgin externa (Walker, 1995; Werner, 2001). It should be noted that it is unknown whether the exact origin of the attractant(s) is the externa or the host, so we simply refer to it in this study as ‘host odor’. Host crabs were also checked carefully under a stereo-microscope to ensure that their body bore no encrusting organisms of any kind which may release chemical substances into the water.

Trajectory analysis

Larval paths were observed only by camera a, for as long as they remained within the camera viewing field (see Table I for path durations and lengths). Trajectories were manually drawn on acetate sheets at a sampling rate of one point per frame (25 points s^{-1}), and were subsequently digitized at a 1 point/pixel resolution using ImageJ 1.29, public-domain image-processing software (<http://rsb.info.nih.gov/ij>). Digitized trajectories were analyzed using MATLAB 6.5 (The MathWorks, Inc.) to discover their direction of motion at each point in time. These data were then pooled for all the trajectories in the same experimental combination and presented as polar-axis histograms (see Figure 3). Also shown in Figure 3 are the combined percentages of motion direction when the horizontal space is divided into the four ‘compass directions’, namely north (90°), south (270°), east (0°) and

west (180°), when the host (if present) is located to the east and flow (if present) runs from east to west. MATLAB was also used to calculate the following values for each trajectory: (i) swimming velocity; (ii) determination: the net displacement of the path, i.e. the distance between the first and last points, divided by the total path length and multiplied by 100; and (iii) RCDi: rate of change of direction, i.e. the total amount of degrees that the larva has turned, divided by the path duration. For each of these three values, one-way ANOVA tests ($\alpha = 0.05$) were used to determine possible differences between the five experimental combinations, and subsequent *post hoc* Scheffe tests (at 95% confidence interval) were used to determine the sources of these differences.

Host-location ability (HLA)

In all experimental combinations, 20 larvae were randomly chosen and watched until they disappeared from the viewing field or reached the nylon mesh. HLA was calculated as the percentage of larvae to reach the mesh, and this was repeated five times for a total of 100 larvae/combination.

RESULTS

Direction analysis results of the passive particles from the vertical and horizontal planes did not vary significantly (Kruskal–Wallis test, $P = 0.32$) and were therefore pooled. The particles exhibited a downstream motion which was almost totally straight (Figures 2f and 3f), meaning that the flow was essentially laminar in both planes. In still water, in the vertical plane, of the 20 passive particles, four remained in the water column, nine sank to the bottom and seven rose to the surface, indicating some degree of motion in the water; however, this degree was judged to be small since, in the horizontal plane, no significant motion of the particles could be detected.

In still water in the absence of odor, larvae exhibited a swimming pattern comprising helical, cyclic and straight motion (Figure 2a). Swimming was uniformly directed

Table I: Summary of trajectory statistics in the different experimental conditions

Condition	<i>n</i>	Observation	Length	Velocity	Determination	RCDi	
		time (s)	(mm)	(mm s^{-1})	(%)	(deg s^{-1})	
Flow	Odor						
–	–	33	23.6 \pm 15.6	36.2 \pm 23.0	1.7 \pm 0.6	39.7 \pm 25.6	441.1 \pm 208.2
Slow	–	33	12.3 \pm 4.5	23.4 \pm 8.6	1.9 \pm 0.5	71.8 \pm 28.2	343.5 \pm 61.9
Fast	–	33	16.2 \pm 8.5	41.5 \pm 20.9	2.9 \pm 0.8	68.6 \pm 15.9	275.0 \pm 87.7
–	+	33	153.3 \pm 75.7	86.7 \pm 30.6	0.6 \pm 0.2	17.6 \pm 3.9	37.3 \pm 11.1
+	+	33	38.7 \pm 6.1	23.4 \pm 3.0	0.6 \pm 0.1	98.1 \pm 1.1	39.8 \pm 10.4

Values are mean \pm 1 SD.

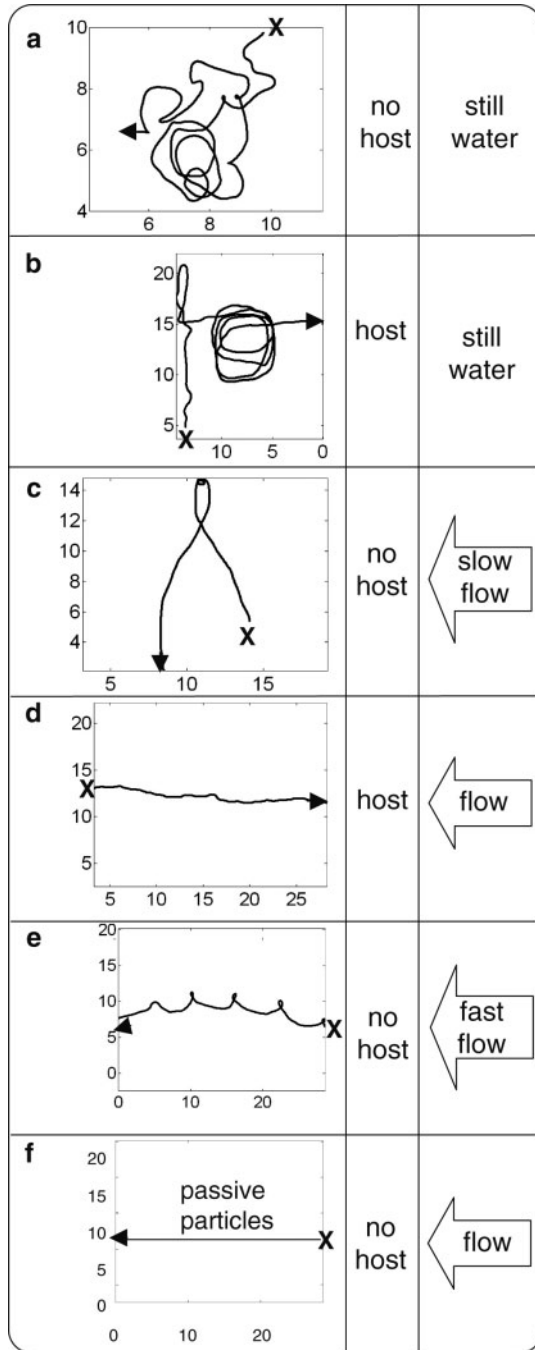


Fig. 2. Typical examples of larval motion patterns. Typical motion patterns comprised at least 50% of motion patterns. The right column indicates flow condition and direction; the middle column indicates presence or absence of a host through which water passes en route to the larvae. The left column indicates typical observed larval motion, where motion trajectories begin at the × sign and end with a small arrow. Horizontal and vertical axes are in mm.

(Figure 3a) and pooling of the motion directions into the four ‘compass directions’ revealed that the larvae did not swim significantly in one direction over the others

(Figure 3a; d.f. = 3, $F = 0.23$, $P = 0.87$). In still water with host metabolites, larvae exhibited a swimming pattern consisting of alternating cyclic and straight segments (Figure 2b). Direction of motion was not uniform but concentrated on the 0, 90, 180 and 270° (Figure 3b). Pooled motion directions revealed that overall the larvae swam more towards the host, but not significantly so (Figure 3b; d.f. = 3, $F = 3.53$, $P = 0.07$). Nevertheless, HLA was $52 \pm 9\%$ (Figure 4), and larvae were capable of locating the target from a range of 3 cm (the maximal distance in our experimental set-up). In flow without host metabolites, larval behavior depended upon the speed of the flow. At flow speeds $<1.5 \text{ mm s}^{-1}$, motion consisted mainly of straight swim segments (Figure 2c) directed perpendicular to the flow (Figure 3c), significantly southward (d.f. = 3, $F = 11.15$, $P < 0.01$). At speeds of $>1.5 \text{ mm s}^{-1}$, larvae drifted with the flow while performing a helical motion (Figure 2e); motion was significantly directed downstream (Figure 3e; d.f. = 3, $F = 58.89$, $P < 0.01$). In flow ($0\text{--}5 \text{ mm s}^{-1}$, results did not vary in different flow speeds) with host metabolites, larval motion was straight (Figure 2d) and directed exclusively upstream (Figure 3d; d.f. = 3, $F = 12700$, $P < 0.01$). Larval success in locating the host was $58 \pm 17\%$, significantly different from both no-host controls but not significantly different from a host in still water (Figure 4, one-way ANOVA test, d.f. = 3, $F = 39.09$, $P < 0.01$, with subsequent Scheffe *post hoc* tests).

The swimming velocity of the larvae seemed to be influenced mainly by the presence or absence of host odor (Figure 4; Table I). In its absence, whether in flow or in still water, swimming velocity was $\sim 1.8 \text{ mm s}^{-1}$; in its presence, velocity decreased dramatically to a third of that figure, 0.6 mm s^{-1} , again irrespectively of whether larvae were in flow or in still water. This significant difference (d.f. = 3, $F = 41.79$, $P < 0.01$) does not take into account the larval ‘drifting velocity’ when in fast flow without odor, since that is determined by the speed of the flow. The swimming speeds we refer to in this study are the net speeds seen through the camera, and do not take into account the speeds needed in order to oppose the water flow; as a result, the actual swimming speeds may be faster.

Rate of change of direction (RCDi) values were significantly different between the various experimental conditions (Figure 4; Table I; d.f. = 4, $F = 23.44$, $P < 0.01$). Subsequent Scheffe *post hoc* tests revealed that RCDi is also influenced mainly by the presence or absence of host odor. In its absence, whether in fast flow, slow flow or still water, values were high—over 300° s^{-1} , while in its presence, they decreased dramatically to a sixth of that figure, under 50° s^{-1} , again irrespectively of whether larvae were in flow or in still water.

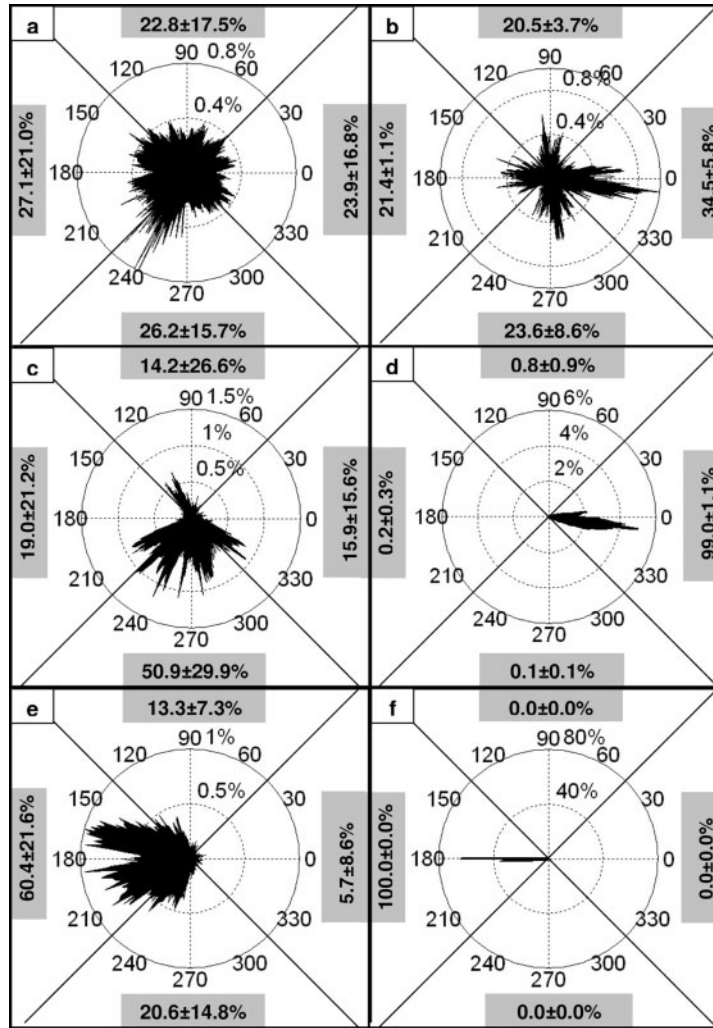


Fig. 3. Directions of motion under the different experimental conditions: 0°, east; 180°, west; 90°, north; 270°, south. The y-axis shows percentage of total motion. The numbers against a gray background are pooled percentages for each ‘compass direction’ (see text for further explanation). (a) Still water without odor, (b) still water with odor, (c) slow flow without odor, (d) flow with odor, (e) fast flow without odor, (f) passive particles in flow.

Determination levels were found to be significantly different between the various experimental conditions (Figure 4; Table I; d.f. = 4, $F = 24.94$, $P < 0.01$). Subsequent Scheffe *post hoc* tests discovered three significantly different levels of determination: low level (~0–50%), which occurred in the still-water treatments; medium level (~50–90%), which occurred in the flow treatments that lacked host odor; and high level (~90–100%), which occurred in the presence of both flow and host odor.

DISCUSSION

The results of this study indicate that male cyprid larvae of *H. dollfusii*, as is suggested for other rhizocephalan male cyprids [(Werner, 2001) and references therein],

do not rely on random chance for encountering their host, but rather actively search and locate it, utilizing environmental cues such as flow direction (by rheoreception) and the odor emanated from the host (by distance chemoreception). The attracting effect of host effluents is evident from the HLA results in Figure 4, where larvae reached the nylon mesh only when there was a host behind it and almost never in the control experiments. This active search was highly efficient, as in all experiments containing host odor, HLA levels exceeded 50%.

According to the motion parameters that were studied, we may classify the larval motion into two distinct classes: ‘search motion’ and ‘guided motion’. In ‘search motion’, which occurs when larvae are in water without odor (regardless of flow conditions), swimming velocity is

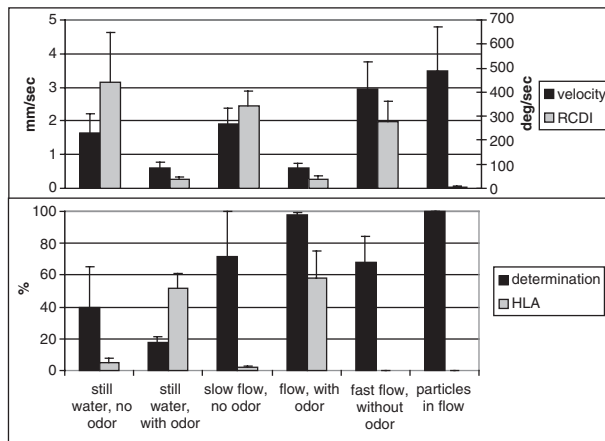


Fig. 4. Larval swimming velocity, rate of change of direction (RCDi), determination and host-location ability (HLA) in the different experimental conditions. Values are mean \pm 1 SD.

relatively high and the rate of change of direction is also high, both parameters elevated in order to facilitate more efficient searching, i.e. the covering of more area in less time. The distribution of step-lengths between changes of direction resembles efficient strategies such as Lévy flights (Viswanathan *et al.*, 1999), as shown in another study (Pasternak, Abelson and Blasius, in preparation). Flow conditions, however, affect the pattern and direction of swimming: in still water, the odor cue needs to be searched for everywhere, so the larvae swim uniformly in all directions, with low determination values. In slow flow, conversely, swimming up- or downstream will only waste energy without covering more area: if the larva stays in the same place, it will receive the same odor information it would have received had it swam upstream, and if it swims downstream, it would encounter the same odor information more than once. The most efficient option in this scenario is to use rheoreception to move mainly perpendicularly to the flow, and this the larvae do with high determination, a phenomenon which may resemble the casting motion of moths [e.g. (David *et al.*, 1983)] and blue crabs (Weissburg and Zimmer-Faust, 1994). When the flow is faster, larvae may not be physically able to perform efficient casting, either because of insufficient swimming ability or because the fast flow interferes with sensing or processing of odor cues. So larvae do not waste energy resisting the flow, instead allowing themselves to drift downstream while maintaining a high RCDi by performing helices, presumably until they detect an odor cue or the flow slows again.

In ‘guided motion’, which occurs when larvae are in water containing host odor (regardless of flow conditions), swimming velocity is slow, perhaps in order better

to facilitate receiving or processing of the odor cue. The rate of change of direction is also low, since the objective of the animal is not to search as large an area as possible, but rather to follow the plume and reach the odor source as quickly as possible. Flow conditions, again, affect the pattern and direction of swimming: in still water, larvae swim towards the host in straight segments interspersed with series of large circles, which account for the low levels of determination exhibited here. The purpose of this cyclic swimming pattern may be to re-find an odor cue that was lost or to compare the intensity levels of the cue from all directions, thus mapping the odor gradient and pin-pointing the direction from which it arrives [a method known as temporal chemotaxis, see (Lackey, 1986)]. In flow, on the other hand, the nature of the plume dictates that odor levels increase when nearing the odor source. Thus, larvae may not need to map the gradient fully in order to use chemotaxis effectively: swimming straight against the flow, with high determination, is enough to detect changes in the odor gradient and thus find the host. Alternatively, larvae may not even need to sense the level of the chemical attractant, but only its absence or presence: if the larva senses the chemical, it deduces that it is inside the plume and surges upstream against the mean flow (Figure 2d), since the source of the odor will always be upstream; if it does not sense it, the larva casts perpendicularly to the mean flow (Figure 2c), a motion that might lead it to rediscover the plume.

We suggest that *H. dollfusi* larvae may use a combined plume-tracking mechanism when in flow: chemoreception to initiate the motion and rheoreception to determine its direction. Such a mechanism would resemble the ‘odor-gated rheotaxis’ (Grasso and Atema, 2002) displayed by insects (Murlis *et al.*, 1992) and blue crabs (Weissburg and Zimmer-Faust, 1994). Since odor-gated rheotaxis enables plume tracking with only one spatial chemical sensor (Grasso and Basil, 2002), it seems a feasible navigation tactic to be exploited by very small organisms such as invertebrate larvae. A morphological examination of the rhizocephalan cyprid larva reveals that it is armed with multiple chemosensors such as olfactory hairs, lattice organs and antennular aesthetascs (Walker, 1999), but the flow-sensing apparatus has yet to be discovered.

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