Biomimetic robot lobster performs chemo-orientation in turbulence using a pair of spatially separated sensors: Progress and challenges

Frank W. Grasso \(^a\),* Thomas R. Consi \(^b\), David C. Mountain \(^c\), Jelle Atema \(^c\)

\(^a\) Boston University Marine Program, Marine Biological Lab, Woods Hole, MA 02543, USA
\(^b\) Department of Ocean Engineering, MIT, 77 Massachusetts Ave., Cambridge, MA 02139-4307, USA
\(^c\) Department of Biomedical Engineering, Boston University, Boston, MA, USA

Abstract

Lobsters are capable of tracking turbulent plumes to their sources faster than can be accomplished by estimating a spatial gradient from time-averaging the concentration signal. We have used RoboLobster, a biomimetic robot lobster to investigate biologically scaled chemotaxis algorithms using two point concentration sampling to track a statistically characterized turbulent plume. Our results identify the range of effectiveness of these algorithms and, with studies of lobster behavior, suggest effective strategies beyond this range. They suggest that a lobster’s chemo-orientation strategy entails an unidentified means of dealing with the intermittency of the concentration signal. Extensions of these algorithms likely to improve are discussed.

Keywords: Chemo-orientation; Turbulence; Biomimic; Lobster

1. Introduction

Turbulent dispersal processes make the task of locating chemical sources under natural conditions a challenging problem for scientists and engineers. Turbulence acts in fluid media (i.e., air and water) to break the transmission of chemicals from the source to a tracking agent’s sensor within a plume into (spatially and temporally) intermittent patches of odor \([12,13,30,34,35]\). Many animals have evolved strategies for chemo-orientation that cope with the effects of turbulence and operate on time-scales that are an order of magnitude faster than would be possible if they computed a gradient from a time average of concentration \([19]\). We believe that the study of animal chemo-orientation coupled with explicit testing of animal-inspired and constrained hypotheses in biomimetic robots will allow us to identify these fast strategies.

Several groups have used robots to study strategies of chemo-orientation the past decade. Some groups have studied chemotaxis in small wheeled robots that followed a trail of chemicals laid on the ground \([10,38–40]\). Morse \([33]\) used phototaxis in a table-top robot to model chemotaxis in the microscopic nematode \(C.\ elegans\). Neither of these studies dealt with a turbulent chemical dispersal pattern. Ishida \([23–25]\) and Kuwana \([27]\) studied chemo-orientation in airborne turbulent odor plumes with table-top robots intended to model silk moths. To the best of our
knowledge our efforts represent the first study of chemo-orientation in turbulence at the same spatial scale and indeed in the same exact task and conditions as the model animal.

An approach that uses appropriate fluid-dynamic scaling combined with a biomimetic robot allows direct, quantitative comparison of the performance of an algorithm and the model animal. It also offers ways around two important limitations of the research. First, because the robot is in the real world, the stochastic nature of the concentration signal is preserved. Second, the success of animals at the chemo-orientation task provides an existence proof of a solution. The identification of animal strategies in pursuit of proven solutions provides constraints on the search for algorithms and free parameters thereby making the research more tractable. Our understanding of fluid dynamics on the temporal and spatial scales at which animals make their chemo-orientation decisions (simultaneously sub-second and sub-centimeter) is based on the statistics of long-term averages [16]. This means that simulation studies based on fluid dynamics models, including direct numerical simulation (DNS) and analytic models of turbulence, cannot be used to produce well constrained simulation environments for studies of chemo-orientation strategies on the lobster time-scale. Such time average models can be used to develop simulation environments for studies of very slow moving animals like starfish [7,31] or animals which occupy very small spatial scales where viscous forces dominate like nematodes [14,15] and bacteria [6]. Our strategy to circumvent this shortage of data for constraining simulation environments, is to test the simulations in the actual environment. By checking, with quantitative methods, the performance of our robot against that of the chemo-orienting lobster we hope to converge on algorithms, that will be similar, if not identical, to those the lobster has evolved to exploit its marine niche. The results obtained may provide some insights into the fluid dynamics of chemical dispersal at the animal’s spatio-temporal scales of operation. Consequently, the biomimetic approach, constrained to the same physical conditions as the model animal, offers the best avenue for trying to understand efficient chemo-orientation strategies where turbulence contributes to chemical dispersal.

The process described above of sequential exclusion of alternative hypotheses requires that we work on a well constrained system in order to make progress. We have chosen to study the American lobster (*Homarus americanus*) because we possess a great deal of knowledge about its chemo-orientation behavior [3,32] and olfactory neurobiology [1,2,9,17,18,43]. Much of that chemo-orientation behavior was collected in a fluid dynamic environment which has been well characterized [12,13,19,30]. We have applied Occam’s razor in our robotics studies by evaluating the effectiveness of simple (biologically constrained) chemo-orientation strategies first and adding complexity to the algorithms only when required by the failure of the hypotheses they embody to explain some aspect of the lobster’s behavior [36]. We report here on the results obtained in our first generation of alternative hypotheses.

2. Materials and methods

2.1. The robot

RoboLobster is essentially an underwater mobile sensor platform (Figs. 1 and 2). Table 1 summarizes the robot’s major specifications. Technical details of an earlier version of RoboLobster are described by Consi et al. [8].

RoboLobster’s steering and propulsion are effected by a pair of DC-brush motors with 76:1 gearheads (Micro-Mo, Clearwater, FL) attached to rubber wheels. Each gearmotor is mounted in a water-proof Delrin housing and the shaft of the gearmotor exits through an O-ring seal. The motor cable exits the opposite end of the housing through a water-proof plastic ferrule fitting (Upchurch Scientific, Oak Harbor, WA). The pressure hull is a Lexan (3.25 inch ID, 3.5 inch OD) cylinder with a removable polyethylene endcap at the front end, containing two O-ring seals, and a permanently sealed plastic endcap, at the rear end. Six water-proof cable pass-throughs are provided by plastic ferrule fittings mounted on the polyethylene endcap. Interconnections between the various components of the robot (hull, motors, sensors, etc.) are provided by water-proof electrical connectors (Lemo USA, Santa Rosa, CA) attached to each cable. The hull is mounted on a polyethylene base with plastic tie-wraps and the motor housings are inserted into holes on either side of this base. A caster in the center rear of the base provides balance (Fig. 2). A lead
plate is attached to the bottom of the base to make the robot negatively buoyant. A removable plastic rod can be mounted on the rear end of the Lexan hull to pass the tethers (power and communications, see below) up and out of the water to keep them from interfering with the movement of the robot.

The robot is controlled by an MC68332-based on-board computer (Tattletale Model 7, Onset Computer, Pocasset, MA) with 256 K of RAM, 2 M of pseudo-static RAM (PSRAM), 512 K of flash EEPROM and a 20 MB hard disk drive. The sensors are interfaced to the computer via a 4 channel, 12 bit analog to digital converter. The motors are powered by an LM18293 four channel push–pull driver (National Semiconductor, Santa Clara, CA) which is configured to run each motor bi-directionally. The driver receives direction and speed (variable duty-cycle PWM signal) commands for each motor from the on-board computer. There is no feedback from the motors and they are run open-loop. RoboLobster’s primary sensors are a pair of conductivity electrodes, each consisting of a pair of stainless steel wires, 2 cm in length. An alternating current is passed between the wires and that current is converted to a DC voltage which is proportional to the conductance of the medium surrounding the electrode. These sensors are mounted on plastic shafts in a housing mounted to the polyethylene endcap of the robot (Fig. 2). The position of these shafts can be adjusted across the forward aspect of the housing face to produce different inter-sensor separations. The sensors were mounted vertically in this housing so they are at the approximate height off the flume floor that the lobster holds its antennules (chemo-sensory organs). Two light-emitting diodes (LEDs) are mounted on a plastic rod on top of the hull, one centered between the sensors and another to the rear (Fig. 2). These LEDs provide the cues for the position and orientation of the robot used in the frame by frame analysis of the videotaped trajectories. The robot also contains a turning-rate gyroscope (Murata Erie, Smyrna, GA) that was not used in the experiments described in this paper.

Power for autonomous operation is provided by 16-AA alkaline batteries configured in two parallel banks of eight cells in series for +12 V. This power is converted to the appropriate voltage levels required by the on-board electronics by voltage regulators. Power can also be provided from an external source via a tether. We used external power for the experiments described in this paper in order to conserve batteries.
Table 1

<table>
<thead>
<tr>
<th>RoboLobster specifications</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dimensions</strong></td>
</tr>
<tr>
<td>Length</td>
</tr>
<tr>
<td>Width</td>
</tr>
<tr>
<td>Height</td>
</tr>
<tr>
<td>Weight</td>
</tr>
<tr>
<td>Displacement</td>
</tr>
<tr>
<td>Maximum speed</td>
</tr>
<tr>
<td>Turning radius</td>
</tr>
<tr>
<td>Power usage</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Propulsion</td>
</tr>
<tr>
<td>On board computer</td>
</tr>
<tr>
<td>Programming language</td>
</tr>
<tr>
<td>Sensors</td>
</tr>
</tbody>
</table>

Software for the robot is written in C and cross-compiled on a Macintosh computer. The executable code is downloaded to the robot via an RS-232 wire link (the communications tether). Once downloaded the code automatically executes on the robot’s onboard computer. The first stage of execution involves initialization in which the program receives parameters from the user via the communications tether. A time delay is then invoked which allows time to position the robot in the flume. The program then runs the algorithm in real time causing the robot to attempt to track the plume while simultaneously logging its sensor data. At the end of the run the program stores the sensor data onto the hard drive and waits to be re-initialized for another run. After the experiments the data is uploaded to the Macintosh for analysis. The part of the code that performs the plume tracking consists of two nested loops. An inner loop records the sensor data at 25 Hz, performs a moving window average to smooth the readings, and stores the readings in the on-board computer’s PSRAM. We used an averaging window of 10 values so our effective sensor sampling rate was 2.5 Hz. This rate is within the range of the sampling rate of a lobster [17,18] and the averaging removed much of the noise caused by the internal electronics of the robot. The outer loop runs at 5 Hz and contains the algorithm under test which evaluates the sensor data and issues the appropriate motor commands.

2.2. The plume and trial environment

We ran our trials in a flow-through flume (360 × 90 × 36 cm³) bearing a stream of fresh water approximately 24 cm deep at the downstream end. The flume was tilted so that the downstream end lay about 3 cm lower than the upstream. The background, or mean, flow was reasonably laminar at a rate of ~1 cm/s.

Into this background flow we injected a jet of saline to create a turbulent plume (Fig. 3). Saline is denser than fresh water and sinks. To produce a neutrally buoyant plume we added ethanol. We found that a 1 M NaCl solution diluted by 23% with 100% ethanol produced a neutrally buoyant salt plume (final solution ~0.76 M NaCl). We added 0.3% (gm/wt) crystal violet dye to allow us to visualize the plume.
We can reliably reproduce this plume and so we have come to call it the “standard plume”. We did not choose this plume arbitrarily. This plume models the hydrodynamic output from a filter-feeding bivalve (clam, mussel, oyster etc.) a natural food item of lobsters [29]. We know that lobsters can perform the task of tracking this plume to its source from number of studies of lobster chemo-orientation behavior have been undertaken under exactly these conditions [3,32]. The results of these behavioral studies form a referent for direct comparison of lobster and robot performance.

The lobster studies were not carried out with salt plumes. Instead a jet of food odor (squid or fish extract) was injected into a salt water background flow. Parallel studies of the physics of the odor distribution were carried out for this exact plume regime (i.e., the standard plume) in both salt water and fresh water background flows. Moore and Atema [30] and Grasso et al. [19] added a tracer compound (dopamine) in the food plume and used an electrovoltamic probe to measure concentration dynamics in the salt water background flow. For the RoboLobster stimulus, a salt water plume in a fresh water background, we employed a conductivity probe to measure concentration dynamics [12,13]. The results of these studies indicate that the concentration distribution statistics of the salt and fresh-water versions of the standard plume are not significantly different over the distances the lobster and robot traversed in these parallel studies [12,13,19]. This is because the major distributing force on this scale is turbulence and not diffusion. Diffusion acts at the molecular level and, in this plume, does not have time to exert an appreciable effect on the centimeter scale chemical distribution.

2.3. Experimental design

Lobsters appear to require both of their lateral antennules (chemo-sensory organs) for normal chemo-taxis [4,11]. The two algorithms tested in these experiments (discussed below) represent what we consider the simplest forms of dual sensor chemo-orientation mechanisms. Our performance measures, have been applied to quantify both lobster and robot behavior. This enables us to achieve two goals, the direct comparison of robot and lobster behavior and the overall evaluation of plume tracking efficacy by the robot.

RoboLobster has six points of “biomimetic” scaling critical to the study of lobster-like plume tracking behavior. The size of the robot (~24 cm in length) is comparable to that of actual lobsters. We choose its operating speed (9 cm/s, note this is not the maximum speed of the animal [32] and turning rate to match that of a chemo-orienting lobster. The sensors are mounted in a position and height (9 cm) off the substrate that matches that of the chemo-orienting lobster. The inter-sensor separation was held constant to the lobster’s approximate 3 cm antennular separation.
in all experiments except the one where we explicitly studied the effect of sensor separation. These sensors penetrate the free stream flow above the robot as the antennules of lobster do over the carapace of a tracking animal. This configuration, though improvable in detail, is reasonable as a first approximation of the robot of the lobster’s hydrodynamic situation. The robot’s sensors sample the ambient salt concentration at a 2.5 Hz rate that agrees well with neurophysiological studies of lobster chemo-reception time constants which suggest a 2–4 Hz resolution of pulses in lateral antennule chemo-receptor cells [18]. The length of one conductivity sensor on the robot matches that of the receptor-bearing region of a single lobster lateral antennule (∼2 cm).

Our overall strategy was to observe the behavior of the robot as we systematically varied the conditions of the trial such as starting location, orientation relative to the mean flow, and inter-sensor separation of the robot. A critical experiment involved reversing the steering rule (rule 1) so that the robot steered to the side of the lower concentration. Contrasting the results obtained with the normal and reversed rules gave us the ability to demonstrate (or fail to demonstrate) the existence of information in the chemical signal that could provide guidance toward the source. This required fewer experimental runs than comparing the normal rule 1’s performance to a “random walk” implemented in the robot.

We used timed trials as a way of rapidly accumulating paths to analyze for indications of information in the concentration signal that would lead to effective chemotaxis. The person digitizing robot’s path did not determine the duration of the analysis; at the end of the allotted time the program terminated and the robot stopped where it was automatically. A direct path from the starting point 100 cm downstream from the source at 9 cm/s should take the robot 11 seconds to travel. We decided to set each trial duration at 30 seconds, about two and a half times the optimal travel time. We thought that this would give the robot ample time to demonstrate the relative strengths and weaknesses of the algorithms tested on this task.

Within each experiment we collected 15 repetitions of each trial condition. Both the state of the plume and the robot could drift with time. Changes in water temperature from day to day could produce subtle shifts in plume shape. To minimize the contribution of these effects to the results obtained we randomized the order of trial conditions tested in each experiment.

2.4. General procedures for running a trial

Because the plume represents a stochastic rather than deterministic input signal we took care to minimize other sources of noise that would have confused the interpretation of the robot’s performance. We paid special attention to the calibration of the sensors and the motors.

2.4.1. The sensors

The robot sensed the plume’s salt concentration by measuring conductivity via its left and right electrodes. Conductivity was found to vary linearly with salt concentration over the range of concentrations used in these experiments. The threshold values for turns (rule 1) and back-ups (rule 2) were determined from the variability and noise of the sensor signals. They represent two standard deviations above the mean signal level for the sensors in 10−5 M NaCl solutions (our estimate of the lowest detectable signal in the plume) and in flume background water respectively.

Prior to each experimental session the sensors were calibrated. The responses of each sensor to a series of salt solutions in half log steps were used to compute the regression of conductivity on salt concentration. The gain of each sensor circuit could be adjusted as needed to keep the sensors operating in the linear range under plume conditions. As it turned out this adjustment was only required once in the course of the experiments. The regression lines of each sensor were used to calibrate the sensors inputs to the control algorithm.

Daily calibration was required because variations in water temperature between trial days, metal oxidation or small deformations of the sensors metal rods could lead to differences in the sensitivity of the electrodes. We were careful to measure the regression of each sensor at the end of each session to verify the equality of sensor input during that day’s experiments. On a number of occasions we re-measured the regression lines when we observed trials in which the robot evidenced unexpected behavior. Though we were prepared to exclude from analysis trials where the sensor calibration had drifted we never observed any appreciable drift.
in calibration within a trial session and day-to-day we observed only modest drifts in sensor calibration.

2.4.2. Motor calibration

Since we ran the motors in an open-loop configuration it was necessary to calibrate the motors prior to each session. This calibration was constrained to find values which produce a ground speed of 9 cm/s (a normal walking rate for a chemo-orienting American lobster). Given this requirement we identified pairs of motor commands (percent of maximum power, resolution 1.0%) for the left and right motors that produced straight paths over a distance of 2 meters. We identified a separate pair of values for the robot when it backed up. These values were called in the control algorithm whenever forward motion or backward motion were required in the course of a trial.

Turns were produced by reducing the power on the side of the desired turn to zero: locking that wheel in place. The power on the opposite side was adjusted to determine command values that produced equal left and right turning rates based on the average of three complete rotations about the “off” wheel. The target rotation speed for this was 40 degrees per second which would maintain the 9 cm/s velocity. In actual practice however these speeds were not always reliably obtainable and higher speeds were often required to keep the robot moving through a complete 360° rotation. We therefore settled for a balanced left–right speed in the vicinity of 40–50 degrees per second within an experimental session.

If we noticed unexpected behavior by RoboLobster we would check the validity of these motor commands by re-running the calibration trials. If motor performance was found to have significantly drifted since the determination of the motor commands a correction for the problem was sought and a second series of calibrations were run. The trials suspect trials were removed from the pool of analyzable data and replacement trials were run with new motor command values to fill out the experimental slate. At the end of a session we also checked the validity of the motor commands by re-running the calibration trials and comparing the performance against the last time that the values had been set. Of the 327 trials run in the experiments reported here 15 (~4.5%) had to be excluded due to this type of “motoric drift”.

2.4.3. Starting conditions

The robot began each trial in the center of the flume. This also placed it directly downstream from the source in the middle of our axisymmetric plume (Fig. 3). We were careful to avoid transients in plume structure which might result from the development of the plume or the introduction of the robot into the flow. A trial was only begun after the plume was well established around the settled robot and there were no asymmetries of structure visible in the dyed plume. Depending on the experimental protocol the robot was started either 60 or 100 cm downstream from the source. Except in experiments that explicitly studied the effects of starting orientation the robot always began a trial pointed directly upstream toward the source.

2.5. Evaluation and analysis of robot performance

A simple measure of performance is to count the number of times the robot “hits” the source. We defined a hit as having occurred when the point between robot’s sensors passed within 5 cm of the source. The hit rate is a difficult measure to interpret in lobsters because lobsters have multiple demands to satisfy and the motivation to locate an odor source is not guaranteed.

Quantitative analyses of paths produced by RoboLobster provide more sensitive measures of performance that also allow us to make direct comparisons with lobster behavior. A second reason for performing path analysis lay in our choice of timed trial durations. We choose to use timed trials in order to ensure that the performance measures across experimental conditions would be comparable. The trial duration, 30 seconds, was chosen a priori as a reasonable time for the robot to reach the source given its speed and the distance it had to travel. In actuality, it led to lower hit rates than might be encountered if the robot had been allowed more time. The algorithms we studied proved to produce far more circuitous paths in RoboLobster than are typically observed in lobsters. Consequently, analyses of the robot’s path geometry provided us with a more refined means of analyzing performance.

Paths were recorded at 30 Hz by an overhead monochrome video camera (Hitachi KP 110 CCD, 6 mm f1.2 lens) with a field of view that encompassed
Table 2
Performance parameters

<table>
<thead>
<tr>
<th>Name</th>
<th>Unit</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closest approach</td>
<td>(cm)</td>
<td>The shortest observed distance between the robot and the source in a trial.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>This distance was measured with reference to the point between the sensors.</td>
</tr>
<tr>
<td>Time to closest approach</td>
<td>(s)</td>
<td>The time from the start of the trial of the closest approach</td>
</tr>
<tr>
<td>Distance traveled</td>
<td>(cm)</td>
<td>The total length of the robot’s path in the 30 s trial</td>
</tr>
<tr>
<td>Speed</td>
<td>(cm/s)</td>
<td>The speed averaged over the entire path</td>
</tr>
<tr>
<td>Path tortuosity</td>
<td>(cm²/s)</td>
<td>The angular variance of turns measured between video samples over the entire path</td>
</tr>
</tbody>
</table>

the region within the flume where the robot operated. In the course of video analysis we found this region was covered with minimal distortion and did not need to effect lens corrections. The paths were digitized at 3 Hz on a Macintosh computer IIvx with Quick Capture Frame Grabber (Data Translation). Frame-by-frame analysis was performed using the public domain NIH image program version 1.55 (written by Wayne Rasband at the US National Institute of Health and available on the Internet by anonymous FTP from zippy.nimh.nih.gov or on floppy disk from NTIS, 5285 Port Royal Rd., Springfield, VA 22161, part number PB93-504868) with the Color Image Supplement written by Joe Ayers. From these digitized paths we were able to extract five parameters from each path. These are listed in Table 2. For each experiment an analysis of variance, ANOVA [41] was performed on each of these measures to determine the effect of the experimental variables: algorithm, starting location, starting orientation, algorithm polarity or sensor separation. We set our default significance level at  \( p < 0.05 \). In the following section all five path parameters were analyzed for each experiment. We report only significant differences discovered unless we see the absence of a significant effect or a marginal effect as worthy of comment.

2.6. The algorithms

Our strategy with the robot has been to work from simple, to more sophisticated, algorithms: modifying the control algorithms as necessary to improve performance and to test hypotheses of lobster chemo-orientation. In these studies we worked with the two simplest algorithms we could imagine which used two sensors positioned as those of the lobster. Our first goal was to determine how effective pure chemotaxis (i.e., guidance from chemical cues alone) could be in tracking turbulent odor plumes to their source. In these studies, we programmed RoboLobster to respond to neutrally buoyant salt plumes (explained below, and see [13]) in a laminar fresh-water background flow. In the studies we report here we explored two rules:

1. RoboLobster either turns toward the side of the higher salt concentration signal or moves forward if the inter-sensor difference drops below 9 µ Siemens.
2. RoboLobster moves backward if both sensors detect background concentrations (fresh water); both sensors register < 7 µ Siemens.

From these two rules we constructed two algorithms. Algorithm 1 used rule 1 alone. Algorithm 2 added rule 2 to supersede rule 1 when its condition, no concentration signal above background, was encountered by the robot. As we will later show, the addition of this simple second rule kept RoboLobster in the plume long enough to study both the plume and concentration based orientation strategies. Without it, guided solely by left–right concentration differences, RoboLobster was prone to drift out of the plume, unable to return.

3. Results

3.1. Effects of algorithm polarity and starting distance on Algorithm 1 performance

The robot never scored a hit of the source while running algorithm 1 regardless of whether it began
3.2. Effects of algorithm polarity and starting distance on Algorithm 2 performance

Algorithm 2 never hit the source with reversed sensors. It did however score 1 hit (~7%) at the 100 cm starting distance and 4 (~27%) at the 50 cm starting distance with sensors in the forward connectivity configuration. This overall improved performance, compared to algorithm one, is due to the fact that the back-up instruction keeps the robot inside the plume. Algorithm 1, upon exiting the plume, continues on a straight path from its point of exit and could never, given the plume’s geometry, re-enter the plume. In contrast with Algorithm 1 in the previous experiment it often appeared that the robot, having started at 50 cm downstream from the source, would eventually have hit the source given more time. Those trials in which the robot succeeded we distinguished from those that did not by an initial turn away from the midline of the plume which consumed trial time as the robot oscillated in and out of the plume edge (Fig. 6).

Beyond remaining in the plume, we observed a profound difference in the behavior of the robot in these trials compared to Algorithm 1 (Fig. 5). When the robot started at 60 cm from the source, the robot more frequently backed up to avoid the source, causing it to exit the plume and oscillate. This behavior suggests that the robot is more sensitive to the concentration gradient and is able to maintain a closer approach to the source when it is able to maintain its position within the plume.
robot, running Algorithm 2, started 100 cm from the source its path was marked by numerous abrupt turns and invocations of the back-up command. When it started 50 cm from the source the path was typically, smooth and showed a series of smooth alternating left and right turns within the cone of the plume. On this basis we came to recognize two phenomenological regions of the plume which we termed the proximal jet (PJ) near the source and the distal patch field (DPF) further downstream. We conclude that the irregular paths in the DPF result from the intermittency of the plume concentration distribution. This intermittency is largely absent in the PJ because momentum of the jet gives the plume spatial continuity at the robot’s sampling rate; as the plume moves downstream the plume spreads out into numerous patches across the plume and loses its spatial continuity.

The path analysis showed significant primary effects of both polarity ($F(1,1.56) = 62.3, p < 0.001$) and starting distance ($F(1,1.56) = 141.3, p < 0.0001$) on closest approach to the source, without a significant interaction. The normal sensor configuration led to paths that on average brought the robot closer to the source while starting closer to the source also led to significantly closer approaches to the source. There was also a significant effect of polarity on distance traveled by the robot: the robot tended to have much shorter total paths in the DPF than in the PJ. This is probably due to the frequent turns and stops the robot made in the DPF. An interpretation supported by a marginally significant ($p < 0.07$) increase in path tortuosity in the DPF compared to the PJ.

### 3.3. Effect of starting orientation

The tendency for Algorithm 2 to make progress towards the source in the last experiment might be at-
Fig. 6. Algorithm 2 paths starting distance 50, 100 cm and normal and reversed sensors. The layout is the same as in Fig. 5. Note that compared to Fig. 5 the robot remains in the plume, that the sum of the plume paths delineate the plume’s extent. In the upper left panel (60 cm start, normal sensors) the many invocations of the back-up command in the DPF make for markedly different path segments compared with the smooth path segments in the PJ.

tributable to the fact that the robot began each trial pointed at the source. The one hit scored when the robot started in the DPF might be explained in this way. Though the circuitous paths the DPF induced make this explanation unlikely we wanted to determine if there were any directional information available to these dual sensor algorithms in the DPF so we conducted an explicit test of the effects of starting orientation on chemotaxis in the robot.

Initially, we set out to test a range of starting orientations varying from 0°, 45° and 90° with respect to the long axis of the flume. We found however that a 90° start, given the robot speed and the width of the flume tended to lead to trials in which the robot struck the flume wall. This was not the case with 0° and 45° starts, so we restricted our study to 0° and 45° conditions at 50 and 100 cm downstream from the source.

In the 30 trials where the robot started 100 cm downstream from the source the robot scored no hits. The robot hit the source three times (20%) from 0° and five (33%) at 45° starting 50 cm downstream from the source. As with the previous experiment it often appeared that the robot would have arrived at the source given more time.

The path analysis found no significant effects of starting orientation on any of the analyzed path parameters. Consistent with the last experiment however there was a significant effect ($F(1,1,56) = 152.7, p < 0.0001$) of starting distance on closest approach to the source. There was also a marginal interaction ($p < 0.08$) of starting distance with initial orientation on path length. This shortening of total distance traveled by the robot in the DPF compared to the PJ probably reflects an increased proportion of time lost in
backing up in the DPF with a 45° start. An initial bias toward the PJ, resulting from starting orientation, results in less trial time expended backing up (Fig. 6).

3.4. Effect of inter-sensor separation

Taken together the above results suggest that there is no concentration gradient information available to either algorithm in the DPF. One interpretation is that the inter-sensor spacing and sampling time combined are too small to detect a concentration gradient if it existed. We choose to explicitly study the effect of inter-sensor separation as a means of determining whether such a gradient existed among the intermittent patches of salt in the DPF. In this experiment we systematically varied the inter-sensor separation to bracket that employed by the American lobster (3 cm) when it tracks odor plumes. We ran RoboLobster in the standard plume in trials with inter-sensor separations of 1, 3, 5 and 7 cm at the usual starting distances of 50 and 100 cm downstream from the source.

Regardless of sensor separation the robot scored no hits running algorithm two when it started 100 cm downstream from the source. Starting 50 cm downstream from the source the robots hit rate increased as a function of sensor separation (Fig. 7).

We found a significant primary effect of inter-sensor separation on path tortuosity ($F(3,1,87) = 8.73, \ p < 0.001$) that was reflected a trend of highly convoluted paths at low sensor separations and relatively smooth paths at higher sensor separations (Fig. 8). Consistent with the results of the previous experiments we found significant primary effects of starting distance on closest approach ($F(3,1,87) = 11.80, \ p < 0.001$) and distance traveled ($F(3,1,87) = 9.01, \ p < 0.001$). We conclude that a gradient exists in the PJ that allows effective chemotaxis on the spatio–temporal sampling scale of the lobster. That gradient is the high concentration difference at the spatially well defined plume edge in that region. In the DPF no such high contrast boundary exists so we conclude an absence of directional information accessible by these algorithms regardless of sensor separation.

4. Discussion

Biomimetics occupies a niche between science and engineering. The engineer seeks a create a solution to a problem (such as chemotaxis) from the set of existing solutions in related domains. The scientist aims to identify mechanisms by a progression of experiments which exclude alternative explanations for a given phenomenon. Biomimetics operates on the premise that animal behavior serves as an existence proof of a solution. The scientist-engineer seeking mechanisms to explain the behavior of a biological system may draw on the engineer’s set of well-understood candidate solutions as hypotheses to be ruled in or out as reasonable explanations. By combining these methodologies the biomimetic approach holds the promise of both biological explanation and solutions to hard practical problems. We believe that in the work presented here we have achieved a small measure of both in the field of chemotaxis.

We used great care in controlling the conditions of the experiments so that we could observe directly the interaction of the algorithm with the plume. Our systematic monitoring of sensor and motor calibration allow us a measure of certainty that these sources of variability in our model system do not dominate the results. Our use of random trial sequences and the standard plume represent a parallel effort to minimize the contribution of environmental variability while re-
Fig. 8. Paths of RoboLobster at different inter-sensor separations at the 60 cm starting distance (the 100 cm starting distance paths are not distinguishable from Fig. 6 paths. Note the pronounced alternate turns at the 7 cm inter-sensor separation.

Our experience in these studies has made clear a number of the intricacies of the problem of tracking plumes to their source in turbulence that were not clear at the outset. We have identified the limits of one algorithm that can track odors to their source in a highly variable stochastic environment. Given sufficient time algorithm two can reliably locate our jet odor sources at distances of up to 50 cm. It seems reasonable to propose that this mechanism will work for a variety of jets: as long as the high contrast edge exists along the plume border, that border will (eventually) funnel the robot to the source. Beyond this 50 cm range algorithm two does not work and we must seek other solutions. The behavior of the robot with its numerous turns and invocations of the back-up commands in the DPF points to the intermittency of the plume as the next major problem to be solved.

In one sense the plume, rather than the algorithms or the American lobster, is the entity under the closest scrutiny in these experiments. Our desire to understand how the lobster accomplishes chemo-orientation in turbulence led us to interrogate the plume with RoboLobster, asking the question: what information is available for guidance to the source. The approach of pure chemo-taxis (using just chemical concentration information for steering information) lead us to conclude that there is no directional information in the DPF at the spatial and temporal scale that the robot (mimicking the lobster) sampled. The fact that the robot (running Algorithm 2) moved forward and made turns, rather than constantly backing up, in the
DPF demonstrates that the available signals were well above the sensors detection threshold.

There is another interpretation of the inability of Algorithms 1 and 2 to make upstream progress when they began a trial in the DPF. It is possible that an initial downstream turn upset the plume sufficiently to prevent rapid upstream progress within our timed trials. The lobster faces this problem as well but might posses a more hydrodynamically designed that would disturb the plume less than RoboLobster does. The lobster might also avoid this problem by using its sense of mean flow to make steady upstream progress that would always bring it into undisturbed (except by other animals and moving objects) regions of the plume. In response to this possibility we make two observations. First the sensors were mounted vertically so that they protruded 4–5 cm above the robot’s hull. And second, that we observed many trials which began with an initial downstream turn ended with net upstream progress. In fact, as we observed in the results section, this delay was often the reason that the robot, which had proceeded from the DPF to the PJ appeared about to score a hit when time in the trial ran out. Overall we are inclined to interpret such events as chance paths through the DPF that happened to lead to the PJ. Though we cannot exclude the possibility of hydrodynamic “shadowing” of plume structure by the robot’s own wake, we tentatively retain the conclusion that there is in information in the concentration signal of the DPF on the lobster’s spatial and temporal sampling scale.

Having excluded the most obvious concentration gradient hypothesis with these experiments the natural question is: what cues are these animals using? One obvious cue that is available to the lobster is the sense of mean flow [42,44]. By means of this cue the lobster or robot could cut possible directions to the source from any location in the plume at least in half. The value of this cue for the robot is made clear by the fact that occasionally we observed trials where the robot headed straight downstream. On these occasions the robot, running algorithm two, happened to be turned downstream by the series of signals it received early in the trial. Pointed downstream the robot’s 9 cm/s speed would cause it to overshoot a salt patch which was moving downstream at ~1 cm/s (mean flow dominates dispersal at distances greater than 100 cm in the standard plume). Once it had overshot the patch and moved into fresh water the back-up command would be invoked until it returned to the patch. This led to a cycle of patch entrances and exits that cause the robot to track the patch’s downstream progress. This anecdote provides a convincing demonstration of the absence of directional information in the concentration signals of the DPF. It could also be completely avoided by the addition of a sensible use of mean flow by algorithm two.

The paths RoboLobster produced were not very lobster-like. Actual lobster paths collected under identical physical conditions [3,32] are much straighter and do not show the alternating turns in the PJ that RoboLobster reliably produced. Typical average lobster path tortuosity is <1.0 cm²/s compared to ~7 cm²/s for Algorithm 1 and ~10 cm²/s for Algorithm 2. Thus, while the use of left–right sensor differences are likely components of the lobster’s plume tracking behavior [4,19,22] we can exclude them as complete explanations of this lobster behavior.

Nevertheless, this work raises a number of interesting biological questions that reflect back on the biology of lobsters, and indeed many benthic chemo-orienting animals. Why, for example, are the American lobster’s antennules as short as they are? The observation that lobsters require both antennules for normal chemo-orientation [4,11,37] suggest that some spatial separation is required. Our results indicate that a greater sensor separation is effective in the PJ, indeed the longer the better. Despite the fact that the lobster can move its antennules, and that it is almost capable of a 7 cm span (if it held its antennules perpendicular to its body axis), the lobster is not observed to maximize its span when chemo-orienting. This short span is apparently sufficient for tracking odor plumes in the DPF. Perhaps longer spans cause some disadvantage that offsets any plume tracking advantage in the proximal jet. Given that in lobsters olfaction is the major sense (it dominates their sensory and social behavior [1] and 40–50% of their brain volume is devoted to processing olfactory information (Deforest Mellon, personal communication), it is tempting to speculate that some evolutionary pressure has selected this length as an effective for this type of task.
Although these results indicate there is not enough information to be had from the concentration signals alone: concentration is not useless in the DPF. There are many examples in the insect literature of animals which use (on/off rather than concentration) odor detection in the tracking of patchily distributed odor plumes [5, 26, 28, 34]. Though these tracking methods require only a single sensor, where the lobster requires two, they provide an indication of useful information content in the airborne equivalent of the DPF. Another possibility is that lobsters are extracting some features of the plume from the concentration dynamics. There is some evidence for information of this type in the fine structure of these plumes [12, 13, 30].

In this work we have narrowed the field of possible explanations for lobster chemotaxis, excluding the most obvious and parsimonious candidate hypothesis. We hold the conviction that the continued pursuit of the solution(s) proven by biological evolution is a productive way to proceed. Through the combined use of the scientist’s analytical method and the engineer’s tool kit for synthetic approaches to problem solving we hope to converge in future studies on a algorithm or set of algorithms that capture and explain the lobsters’ competence in tracking odor plumes through turbulence.

Acknowledgements

This work was supported by NSF Award BES-9315791 to JA with a subcontract to TRC and Professor C. Chryssotomidis at MIT Sea Grant. Portions of these data were previously reported in extended abstract form (Grasso et al [20, 21]). We thank Paul DiNunno, Jonathan Dale, Kevin Dittmer and Christina Manbeck for valuable technical assistance at various stages of these studies. Thanks to Clifford A. Goudey of MIT Sea Grant for the design and fabrication of RoboLobster’s mechanical components and to Jamie Cho, MIT, for software development. We thank Joe Ayers (Northeastern University) for providing us with a free copy of his Color Image Software supplement to NIH Image with which we made our path digitizations and two anonymous reviewers for thoughtful comments on the first draft of this manuscript.

References


Frank W. Grasso grew up in suburban Boston, MA, in the United States. In 1984 he received a B.Sc. in Biology and BioTechnology from Worcester Polytechnic Institute. Following a stint at the University of Vermont Medical School in the Department of Physiology and Biophysics where he studied human neuroanatomy, he entered the Ph.D. program in Neuroscience and Behavior at the University of Massachusetts at Amherst. His Ph.D. awarded in 1994, concerned the representation of natural scenes in the mammalian visual cortex by natural and artificial neural networks. He went on to Post Doctoral work at the Marine Biological Laboratory at Woods Hole, MA, and Boston University studying the representation of
chemical stimuli in the olfactory systems of lobsters. In 1997 he was promoted to Senior Research Associate at the Boston University Marine Program. His research focuses on the application of biomimetic robotics to understanding the relationships between animals’ behavior, their central nervous systems and their physical environments.

**Thomas R. Consi** is a Research Engineer and Lecturer in the Ocean Engineering Department at the Massachusetts Institute of Technology. He holds a Ph.D. in Biology from Columbia University and was a Post-Doc in the Department of Brain and Cognitive Sciences at MIT. He was an early member of the MIT Sea Grant Autonomous Underwater Vehicles Laboratory where he worked on a number of marine robots including RoboLobster. His current research focuses on the biomechanics of marine animals.

**Jelle Atema** is a Professor of Biology at Boston University and the Director of the Boston University Marine Program in Woods Hole, Massachusetts. His research interests are in the sensory biology of aquatic animals. Current research deals with the physics of odor dispersal, the sensor filter properties of chemo- and mechanoreceptors that appear to be involved in the detection of “flavored eddies” and the plume tracking behavior of lobsters as models for underwater navigation by odor signals. He collaborates with Frank Grasso, David Mountain and Tom Consi in the development of an underwater robot with plume tracking capabilities; the robot is inspired by lobsters and designed for mine detection. Other research deals with chemical communication in lobster social behavior and the signals involved in individual recognition, dominance, and gender.