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SEA LAMPREYS ORIENT TOWARD A SOURCE OF A
SYNTHESIZED PHEROMONE USING ODOR-
CONDITIONED RHEOTAXIS

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Date

SEA LAMPREYS ORIENT TOWARD A SOURCE OF A SYNTHESIZED PHEROMONE USING ODOR-CONDITIONED RHEOTAXIS

By

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ABSTRACT

SEA LAMPREYS ORIENT TOWARD A SOURCE OF A SYNTHESIZED PHEROMONE USING ODOR-CONDITIONED RHEOTAXIS

By

Azizah Wakeelah Muhammad

Engineers envision a world where odor-tracking, mobile robots can locate the source of toxic gas or detect unexploded ordnance, but such tasks cannot be efficiently executed until olfaction is fully understood. Given the poor sense of smell in humans, it is no wonder that what is known about olfaction is gathered from scientists' observations of the odor-mediated behaviors of organisms. However, these observations are often made in a controlled laboratory environment where animal behaviors are easier to analyze than in their natural habitats. Engineers then use these behaviors as inspiration for odor source localization algorithms, but rarely is this done in cooperation with scientists using actual data from behavioral experiments to test their effectiveness. Perhaps more cooperation between the two communities is needed to solve the odor source localization problem.

This thesis is a collaborative effort between the Department of Fisheries and Wildlife and the Department of Mechanical Engineering at Michigan State University to identify how ovulating female sea lampreys track the male sex pheromone (3kPZS) to its source. Three control algorithms are presented herein that each test a different orientation hypothesis. The algorithms are then evaluated in computer simulations of the natural environment. The resulting trajectories are compared with actual observed trajectories using statistics. Based on this comparison, the best-performing algorithm is chosen. Strong evidence suggests that sea lampreys use odor-conditioned rheotaxis to locate the source of synthesized pheromone, as opposed to chemotaxis or strictly rheotaxis.

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Images in this thesis/dissertation are presented in color.

LIST OF SYMBOLS

ENGLISH SYMBOLS

c = 3kPZS concentration, molar (M)

J = performance cost function, no units

N = number of iterations sea lamprey is allowed to keep its current direction, no units

T = sampling time, seconds (s)

v = magnitude of the velocity of the sea lamprey, meters/second (m/s)

v_{flow} = magnitude of the flow velocity, meters/second (m/s)

$w_{(x,\ y,\ or\ \theta)}$ = random variables from the environment that affects movement of sea lamprey, meters (m) for x and y, degrees (^{o}) for θ

w_{s} = chemo-sensor measurement noise, molar (M)

x = horizontal coordinate of sea lamprey position, meters (m)

$\bar{x}_{st}$ = horizontal centerline of stream, meters (m)

X_{O} = variable storing the horizontal coordinates of all observed trajectories, meters (m)

X_{S} = variable storing the horizontal coordinates of all simulated trajectories, meters (m)

y = vertical coordinate of sea lamprey position, meters (m)

$\bar{y}_{st}$ = vertical centerline of stream, meters (m)

Y_{O} = variable storing the vertical coordinates of all observed trajectories, meters (m)

Y_{S} = variable storing the vertical coordinates of all simulated trajectories, meters (m)

z = noisy measurement of 3kPZS concentration, molar (M)

z_0 = the lowest possible concentration of 3kPZS that sea lamprey can detect, molar (M)

$z_{\max}$ = sea lamprey's memory of the last measured maximum concentration, molar (M)

$z_{t\arg et}$ = concentration of 3kPZS that sea lamprey uses to determine if it has located odor source, molar (M)

z_{th} = concentration of 3kPZS that sea lamprey uses to determine if it is within odor plume, molar (M)

GREEK SYMBOLS

α = amount by which sea lamprey rotates to avoid an obstacle or reacquire odor plume, degrees (°)

δ = threshold for sea lamprey to determine it is directed toward increasing concentration of 3kPZS, molar (M)

$\Delta\theta$ = amount by which sea lamprey is allowed to deviate from "flow direction", degrees (°)

λ = forgetting factor used for sea lamprey to discount $z_{\max}$, no units

θ = direction of sea lamprey relative to the horizontal axis, degrees (°)

θ_d = desired direction of sea lamprey relative to the horizontal axis, degrees (°)

θ_{flow} = flow direction (relative to the horizontal axis) + 180°, degrees (°)

$\rho_{\_,\_}$ = Spearman's rank correlation coefficient between any two quantities, no units

$\sigma_{\_}$ = standard deviation of any quantity, same unit as that quantity

ζ = gain for odor-conditioned rheotaxis strategy, no unit

CHAPTER 1

INTRODUCTION

1.1 Problem Statement

This thesis addresses the problem of identifying the underlying mechanisms used by sea lampreys to locate an odor source. The sea lamprey (*Petromyzon marinus*) is a primitive fish that parasitizes other fish when it reaches adulthood. Afterward, it reaches a sexually mature stage in which it stops feeding and focuses solely on upstream migration for the purpose of reproduction [1]. In recent years, scientists have discovered that *3-keto petromyzonol sulfate* (3kPZS) is a pheromone emitted by sexually mature male sea lampreys to attract ovulating female sea lampreys [2]. Of particular interest is an experiment in which scientists used a synthesized component of 3kPZS and observed the behavior of ovulating female sea lampreys in response to the odor [3]. The animals were able to locate the source of the odor over hundreds of meters.

The development of control algorithms that mimic these behaviors in sea lampreys provides mutual benefit to both engineers and scientists. Such algorithms can improve the odor source-seeking capabilities of autonomous mobile robots, lending themselves to be useful in applications such as locating the source of toxic gas and detecting unexploded ordnance. There are many biologically-inspired odor source localization algorithms in literature (see Chapter 2), but most of them are not compared with actual observed movement data to determine their effectiveness. This thesis goes one step further and develops algorithms that are based on sea lamprey behavior specifically.

Concurrently, sea lamprey chemo-orientation mechanisms can be exploited to control their population in the Great Lakes region, where they have caused much concern to scientists due to the stress they place on other fish populations [1], [4]. Current control methods include the use of *3-trifluoromethyl-4-nitrophenol* (TFM), a lampricide that is used to kill sea lampreys in their larval stage [4]. However, TFM is expensive and can be harmful to other fish, thus the Great Lakes Fishery Commission (GLFC) has reduced its use by half [4], [5].

This thesis presents three algorithms that each test three different orientation hypotheses gathered from behavioral ecology: chemotaxis, rheotaxis, and odor-conditioned rheotaxis (see Section 1.2.2). These hypotheses are used so that the algorithms are easily validated, and a scientist who is not familiar with pseudo-codes can still gain understanding from this thesis. These algorithms are evaluated in computer simulations and compared to observations of ovulating female sea lamprey behaviors observed by scientists in a bifurcated stream. Subsequently, the best-performing algorithm is determined by comparing observed and simulated trajectories by statistics. Furthermore, the best-performing algorithm is evaluated in computer simulations and compared to the observed data from a novel environment using time series analysis.

1.2 Background Information

This section contains some useful information that will aid in the discussion and provide a basis for the modeling methods described in Chapter 3.

1.2.1 Brief Overview of Experiments

Scientists in the Department of Fisheries and Wildlife at Michigan State University conducted two experiments in 2007 and 2008 (not yet published). In these experiments, ovulating female sea lampreys were released from cages and their movements were observed. This section will briefly explain both of these experiments.

To begin, there were some procedures common to both experiments that are worth mentioning. First, synthesized 3kPZS was dissolved in methanol and river water before being applied to the stream. Second, rhodamine dye was used to visualize the 3kPZS plume in the stream. The distribution and dilution of the plume were measured at various dye sampling locations and then interpolated. Third, a flow meter was used to measure the velocity[1] of the stream at each dye sampling location. The velocity was interpolated. Fourth, the plume structure and flow velocity were mapped[2]. Finally, scientists visually observed sea lamprey movements which were recorded and plotted to the plume and flow velocity maps. Since movements were observed at discrete locations, this data was interpolated as well. The behaviors of the individual females were assumed to be independent [2], [3].

Experiments Conducted in Bifurcated Stream (2007)

Synthesized 3kPZS was applied to each channel of a bifurcated stream as in Fig. 4. One-hundred and forty-four ovulating female sea lampreys were released from cages that were 250 m downstream from the sources of 3kPZS. The scientists began movement

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[1] Although the word "velocity" is used, it refers to a scalar quantity (magnitude with no direction).

[2] These maps contain only spatial data, and it is assumed that the plume and flow velocity are relatively constant over time.

observations 110 m downstream from the sources of 3kPZS, and only 44 sea lampreys entered this segment. The scientists observed the full movement trajectories of 33 ovulating female sea lampreys that entered either the left or right channel. The number that entered each channel and the number that reached each 3kPZS source were recorded.

Experiments Conducted in Novel Environment (2008)

This experiment was conducted in the minor channel of a bifurcated stream as in Figs. 5 and 6. The channel was 25 m long. The flow of the stream was controlled by a sandbag wing-dam to create flow and no-flow conditions. To create the flow condition, the wing-dam was positioned to reroute flow from the major channel into the minor channel to increase water velocity. To create the no-flow condition, the wing-dam was used to prevent water from entering the minor channel. However, in the no-flow case, flow velocity was not completely negligible due to some leakage of the wing-dam and subsurface water flow. The scientists alternated between applying 3kPZS and no 3kPZS (or control solvent) to the channel. In summary, there were four conditions: flow with 3kPZS application, flow with control solvent application, no flow with 3kPZS application, and no flow with control solvent application. The control solvent consisted of methanol and river water only. The number of sea lampreys to move upstream was recorded.

1.2.2 Orientation Hypotheses

Taxis (synonymous to orientation with regard to animal behavior) is "an organism's maintaining its body position, changing its body position, or both, with regard to stimulus direction." There are many types of taxis, most of which are defined in terms of the kind of stimulus and stimulus reception [6]. For instance, bacteria use *chemotaxis* (taxis in which a chemical is the stimulus) to locate glucose, serine, and other sources that provide them energy [7].

It is easy to hypothesize that sea lampreys use chemotaxis, since the objective of this thesis is to determine the ovulating female's response to pheromone. *Rheotaxis* (taxis in which the water current is the stimulus) is another assumption to make, because sea lampreys dwell in water. However, in a natural environment, a single sense can become unreliable as stimuli become unavailable [8]. Sea lampreys may be able to locate an odor source if the chemical is always present. But if the chemical is unavailable, will they stop their search or continue using another sense? The former could very well be their demise, and so they will have to rely on other senses for survival.

Many organisms exhibit chemoreception combined with some other sensory cue. For instance, foraging blue crabs use *chemotropotaxis* (a type of chemotaxis in which multiple sensors are used simultaneously to detect chemicals) and rheotaxis to locate the odor emitted by their food source [9]. Since chemical molecules are primarily transported by advection [10], rheotaxis is just as important as chemotropotaxis for the blue crab to locate its food source. Just as blue crabs rely on mechanoreception for odor source localization, so do male cockroaches. They modulate their orientation to the wind in response to the female sex pheromone. This movement pattern is called *odor-modulated anemotaxis* (taxis in which the wind is the stimulus) [11].

Due to this evidence, this thesis will consider *odor-conditioned rheotaxis* [12] as a strong hypothesis for sea lamprey behavior. Odor-conditioned rheotaxis can be described as rheotactic or upstream[3] behavior that is initiated or enhanced by an odor, usually at some threshold. If the perceived odor does not meet the threshold requirement, movement patterns will be exploratory.

In summary, this thesis will consider the following three hypotheses: chemotaxis, rheotaxis, and odor-conditioned rheotaxis.

1.3 Purpose and Content of Thesis

The purpose of this study is to explain the underlying mechanisms used by sea lampreys to locate an odor source. This paper seeks to combine behavioral ecology and control theory to accomplish this while providing mutual benefit to members of the scientific and engineering communities.

Orientation hypotheses will be used as the foundation for sea lamprey control algorithms. Each algorithm will be evaluated in computer simulations. These simulated results will be compared with the observed behaviors from the bifurcated stream experiment using statistics. It is the hope of the author that the simulated behaviors resemble the observed behaviors within reasonable error.

Based on how well each algorithm performs, one will be chosen to explain the odor source localization mechanisms of the sea lamprey. This approach will be applied to the novel environment and evaluated in computer simulations. If the best-performing algorithm effectively models sea lamprey chemo-orientation, then when applied to a novel environment, it should still mimic the movements of real sea lamprey.

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[3] Taxes can be either positive (toward the stimulus, i.e. upstream rheotaxis) or negative (away from the stimulus, i.e. downstream rheotaxis). Since this thesis studies the ovulating female sea lamprey's orientation toward the male sex pheromone, all taxes hypothesized here is considered to be positive.

The remainder of this thesis is organized as follows. Chapter 2 discusses the various biologically-inspired odor source localization methods in literature. Chapter 3 describes the theory and logic that leads up to the development of the three control algorithms. Also in this chapter is the protocol used to determine the best-performing algorithm. Chapter 4 shows the simulated results and compares them with the observed data. Chapter 5 derives conclusions from the results presented in Chapter 4 and provides recommendations for future work.

CHAPTER 2

RELATED WORK

This chapter reviews the current biologically-inspired algorithms and techniques for odor source localization. It is important to note that there aren't any algorithms inspired by the sea lamprey or any other vertebrates yet. This is because invertebrates have proven themselves to be a worthier model for olfactory research than vertebrates [8]. Hence not much is known about the underlying chemo-orientation mechanisms of vertebrates. On the other hand, the odor-mediated behaviors of invertebrates and the simplest of organisms are relatively well-documented. With that in mind, the approaches discussed in this chapter may or may not be sufficient to identifying sea lamprey chemo-orientation mechanisms. This chapter begins with the most-studied of all invertebrates: the moth.

2.1 The Moth Approach

The female moth releases a sex pheromone to attract the male. Upon reception of the pheromone, the male turns into the wind by an optomotor reaction to the perceived movement patterns of the ground (optomotor anemotaxis[4]) [13]. When the male losses the scent of the pheromone, he switches to a "casting" behavior in which he flies about perpendicular to the mean wind direction with left-right reversals.

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[4] An optomotor reaction or reflex is "an individual's attempting to maintain its entire body, or part of its body, in a constant position with regard to a moving environment" [6]. Optomotor anemotaxis can only be defined as an individual's attempt to maneuver upwind with regard to an environment that only appears to be moving because the individual is in motion. This mechanism requires the use of visual cues.

In [14], an unmanned aerial vehicle called the AMOTH (artificial moth) was used to locate a source of ethanol in a wind tunnel (3 × 4 × 0.54 m (width × length × height)) using moth optomotor anemotaxis. The absence and presence of ethanol caused the AMOTH to switch between two behaviors, casting and surge, respectively. The left-right reversals of the casting behavior resulted in a "zigzag" trajectory. The surge behavior consisted of the AMOTH aligning itself with the wind and traveling against it. Meanwhile, the AMOTH was constantly checking its path for obstacles using visual cues. The detection of an obstacle overrode the search strategy and collision was avoided.

This system was able to navigate the wind tunnel with the obstacles and effectively locate the source of ethanol. It was able to detect the ethanol at almost 4 m from the source (first detection coincides with first switch to surge mode), about the maximal length of the wind tunnel. From this observation, the authors of [14] drew the conclusion that the model can exploit the full dynamic range of the odor plume. However, at such a short distance to the odor source, and with the wind direction in the tunnel being uniform, it is not for certain how effective the model truly is. Even in these limited conditions, the AMOTH's trajectory was determined to be suboptimal and inconsistent with the documented behaviors of real moths. Although the authors did not compare the trajectories with actual moth trajectories, so it is not known in exactly what way the AMOTH was suboptimal and inconsistent.

Perhaps it has something to do with the manner in which real moths anemotax as opposed to the direct upwind surges described in [14]. According to [15], real moths make regular turns across the direction of wind flow whether they are in contact with the odor plume or not. This differs from the "surge" technique described in [14] and most other algorithms. In [15], the performance of two different algorithms was compared using Digiduca [16], a virtual wind tunnel. The first algorithm consisted of a simple surge-cast switching strategy. The second algorithm was a modified version of the first that included counterturning across the direction of wind flow while making upwind progress when the odor was detected.

Model parameters for both algorithms were constrained to values obtained from moth experiments. For the first algorithm, less than 5% of the individuals flown into the wind tunnel located the odor source in the time allowed. The second (modified) algorithm had a success rate of about 30%. Success rates for real moths solving the same problem were at least 50% and often 90%. The improved success rates when using the modified algorithm suggests that including a counterturning mechanism at all times (as opposed to surging when odor is present) could improve the optimality and consistency with real moth behaviors. However, the modified approach still fell short of the performance of real moths. The authors attributed this to the selection of model parameters and used a genetic algorithm (GA) to determine the best combination of parameters. These optimal parameter values yielded similar success rates but different behaviors in comparison to real moths. Therefore, [15] shows that there was a trade-off between performance (i.e. success rates) and behaviors.

In [17], the silkworm moth's wing-fanning technique is applied to a robotic platform. The male silkworm moth, who walks when tracking pheromone rather than fly like other moths, uses wing vibrations to draw the pheromone to him and determine the direction of the pheromone source [18]-[20]. A comparison was made between moths with wings removed and moths with wings intact. Odor source localization took longer and was much more difficult for the moths with removed wings. Hence, the robotic platform developed in [17] has a directional probe that consists of a small fan and a semiconductor gas sensor, mimicking the moth's wings and antennae respectively. This replaced the need for plural gas sensors to measure the concentration gradient and anemometric sensors used in other systems [21], [22].This localization system was able to successfully locate the source of ethanol in wind tunnel but in much longer time than it took real moths to locate the source of pheromone. An improvement to the directional probe made the system feasible in a clean room with multiple wind sources that created a non-uniform wind profile.

2.2 The Bacterium Approach

Bacteria such as E. coli use chemotaxis to locate food sources. They are able to progress up an odor concentration gradient in a series of run and tumble behaviors. Run is when a bacterium swims in one direction, and tumble is when it randomly chooses a new direction. The frequency at which it switches between these two behaviors is modulated with respect to the odor concentration gradient. In other words, it tumbles less frequently when the odor concentration gradient is found to be positive. When there is no concentration gradient, the bacterium executes a random walk [23].

Ref. [24] describes how bacterial chemotaxis – termed "biased random walk" – can be used for the location of gradient sources, whether odor, light, or heat. Simulations of the biased random walk were conducted in a two-dimensional grid model of the real world. Robots traveled with a mean free path (MFP) of 10 units of distance before tumbling whenever the concentration gradient was absent (run and tumble as described and was much more difficult for the moths with removed wings. Hence, the robotic platform developed in [17] has a directional probe that consists of a small fan and a semiconductor gas sensor, mimicking the moth's wings and antennae respectively. This replaced the need for plural gas sensors to measure the concentration gradient and anemometric sensors used in other systems [21], [22].This localization system was able to successfully locate the source of ethanol in wind tunnel but in much longer time than it took real moths to locate the source of pheromone. An improvement to the directional probe made the system feasible in a clean room with multiple wind sources that created a non-uniform wind profile.

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2.3 The Aquatic Organism Approach

When it comes to aquatic organisms, invertebrates (i.e. crustaceans) are still more studied by scientists than vertebrates (i.e. fish). Unlike fish that swim freely in an ocean, lake, or river, the aforementioned crustaceans each dwell at the lowest level of water at the interface of the ocean floor and fluid [26], [27]. As such, an odor signal takes longer to reach their antennules and they have to flick them, similar to wing fanning in silkworm moths, to enhance the perception of odors and determine the direction of the source [26].

The authors in [28], believe that comparing the known behavior of a robot to the unknown behavior of an animal will provide information about that animal's chemo-orientation mechanisms. They used a biomimetic robot, Robolobster, to test (and discard) chemo-orientation hypotheses. It is about the size of a real lobster with comparable turning ability and speed, but it is not intended to match the lobster in appendages or mode of locomotion. Rather it is programmed with two simple algorithms to understand Robolobster's interaction with the turbulent plume. The first algorithm has two rules: the robot will steer toward the side of the chemo-sensor receiving the higher concentration signal; otherwise the robot moves forward with a constant speed. The second algorithm is the same as the first with the addition of a third rule: if both chemo-sensors do not receive any concentration signal, the robot will back up at half speed. This third step improved Robolobster's accuracy but diminished its speed.

Ref. [29] is a continuation of this study. The Robolobster is made to track a plume of salt to its source in the same conditions as real lobsters that were observed orienting to a source of food extract. The Robolobster used the second algorithm in [28]. The authors compared Robolobster's behavior to that of real lobster and were able to determine that lobsters steer toward the antennules receiving the highest concentration signal. Although the algorithm was not able to fully characterize lobster chemo-orientation, the authors gained much insight into lobster behavior and can make improvements to the algorithm.

An underwater robot was developed in [30] mimicking the odor-mediated behavior of the crayfish. It consists of an array of electrochemical sensors and a pair of fanning devices mimicking the antennule flicking of the crayfish. The robot was placed in an aquarium with stagnant flow and its ability to locate the source of a chemical was monitored. The robot was able to locate the chemical source successfully, although this conclusion was not drawn in direct comparison to crayfish behavior.

CHAPTER 3

METHODS

3.1 Control Algorithms

All three algorithms are a discrete-time kinematic model, which can be considered as an averaged or sampled kinematic model, of the sea lamprey behavior. They each test the three orientation hypotheses below.

1. Chemotaxis: The sea lamprey swims in the direction of increasing 3kPZS concentration. Otherwise it randomly explores a new direction. Movements are made independent from θ_{flow}.
2. Rheotaxis: The sea lamprey swims upstream when it is able to perceive flow. Movements are made independent from the level of 3kPZS concentration.
3. Odor-conditioned rheotaxis: The sea lamprey swims in an upstream direction (rheotaxis) when it detects 3kPZS at or above a concentration threshold (i.e. when it is within the odor plume). Otherwise it executes a counterturning maneuver and is allowed to swim downstream if necessary to reacquire the odor plume. Movements are always made with respect to θ_{flow}.

The three control algorithms regulate θ while keeping v constant to direct the sea lamprey toward the odor source. The decision for θ depends on one of three parameters: z (chemotaxis and odor-conditioned rheotaxis), θ_{flow} (rheotaxis and odor-conditioned rheotaxis), and obstacles (all control algorithms).

During respiration, the sea lamprey samples a plume of odor by moving water into and out of the olfactory epithelium[5] [31]. For each sniff, it takes a noisy measurement of c

$$z(k) = c(k) + w_s(k)$$

where $w_s \sim N(0, \sigma_s^2)$ is the measurement noise modeled as Gaussian white noise[6]. The control algorithms (except rheotaxis) are applied to spatial 3kPZS plume structure maps and image processing is used to convert the colors to raw values of 3kPZS concentration in molar at each location on the maps.

The flow direction θ_{flow} is important because moving upstream will get the sea lamprey closer to the source [3]. Image processing is used on the flow velocity maps (except chemotaxis) to convert the colors to raw values of v_{flow} each location on the maps. The "flow direction"[7] θ_{flow} is assumed to be parallel to the banks of the stream.

Finally, each control algorithm incorporates an obstacle avoidance strategy[8], because real sea lampreys are not physically able to go through them. Without such a strategy, a simulated sea lamprey is able to disobey this rule and a robotic sea lamprey will get stuck at an obstacle. Given that obstacles constrain where the sea lamprey can

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[5] The olfactory epithelium is a thin protective layer of tissue in the nasal cavity that is used to detect odors.

[6] Low-level Gaussian noise effectively models noises due to central and peripheral functions of olfactory neural systems [32].

[7] The "flow direction" θ_{flow} is analogous to the actual stream flow direction: θ_{flow} = stream flow direction +180°. See appendices for more detail.

[8] Given the fact that sea lampreys do not use vision during upstream migration [1], their obstacle avoidance strategy will have to differ from that of animals who avoid colliding with obstacles by relying on optomotor reflexes (i.e. silkworm moths). A sea lamprey may not be able to actually avoid an obstacle but can push away from it or follow its contour).

move and affect the flow, this strategy overrides the main orientation strategy of the control algorithms [33].

All algorithms begin with an "INITIALIZE" process in which the initial values for (x, y), θ, and other parameters are set. The remaining processes for the algorithms are presented below with flowcharts that show the sequence of their execution. Each process contains steps that are presented in the appendices.

Each control algorithm is developed with "what ifs" in mind: "what if" there is no flow velocity or "what if" there is no odor present. It is assumed that a sea lamprey would know what to do in these situations, no matter what strategy it is acting by, because it is able to swim hundreds of meters to locate a source of 3kPZS. Therefore, the control algorithms are designed so that when the stimulus or stimuli that each relies on is absent, the sea lamprey will not just remain at one location and wait. Rather it will seek it out.

Within each algorithm there are parameters whose values affect the movement trajectories generated in the simulations (see appendices). The utmost care must be given to the calibration of these parameters, and so J is defined to be used with parameter optimization [34].

$$\begin{aligned} J = {} & \frac{\left|\sigma_{X_O} - \sigma_{X_S}\right|}{\bar{x}_{st}} + \frac{\left|\sigma_{Y_O} - \sigma_{Y_S}\right|}{\bar{y}_{st}} \\ & + \frac{\left|\bar{X}_O - \bar{X}_S\right|}{\bar{x}_{st}} + \frac{\left|\bar{Y}_O - \bar{Y}_S\right|}{\bar{y}_{st}} \\ & + (1 - \rho_{X_O, X_S}) + (1 - \rho_{X_O, X_S}) \end{aligned}$$

By statistical theory [35], if two trajectories are the same then they have equivalent standard deviations and equivalent means. Likewise, ρ with a magnitude of 1 indicates that two trajectories are perfectly monotonically related. Therefore, the parameters that result in simulated trajectories that best resembles the observed trajectories are those that will minimize J.

3.1.1 Control Algorithm 1: Chemotaxis

1. DETECT ODOR: This process will begin if the sea lamprey does not detect the odor at the onset of the simulation (i.e. $z(1) < z_0$[9]). First, the sea lamprey picks a random direction to explore. It continues in that same direction for N_0 iterations or until an obstacle is detected. When either of these events happens, it will orient itself in a new random direction. It repeats this sequence until the odor is detected.
2. FIND ODOR SOURCE: At the first sign of odor, this process will begin. The sea lamprey uses chemotaxis to swim in the direction of increasing 3kPZS concentration. It determines that the concentration is increasing by comparing it with a stored maximum concentration. If the 3kPZS concentration does not increase for N_1 iterations, it will explore a new direction at random. This sequence was inspired by the "run" and "tumble" observed in bacterial chemotaxis [23]. This process ends when the odor source is found (i.e. $z(k) > z_{t\arg et}$).

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[9] This value is $z_0 = 10^{-14}$ M, the lowest concentration at which it was observed by scientists that 3kPZS elicited a response from ovulating female sea lampreys.

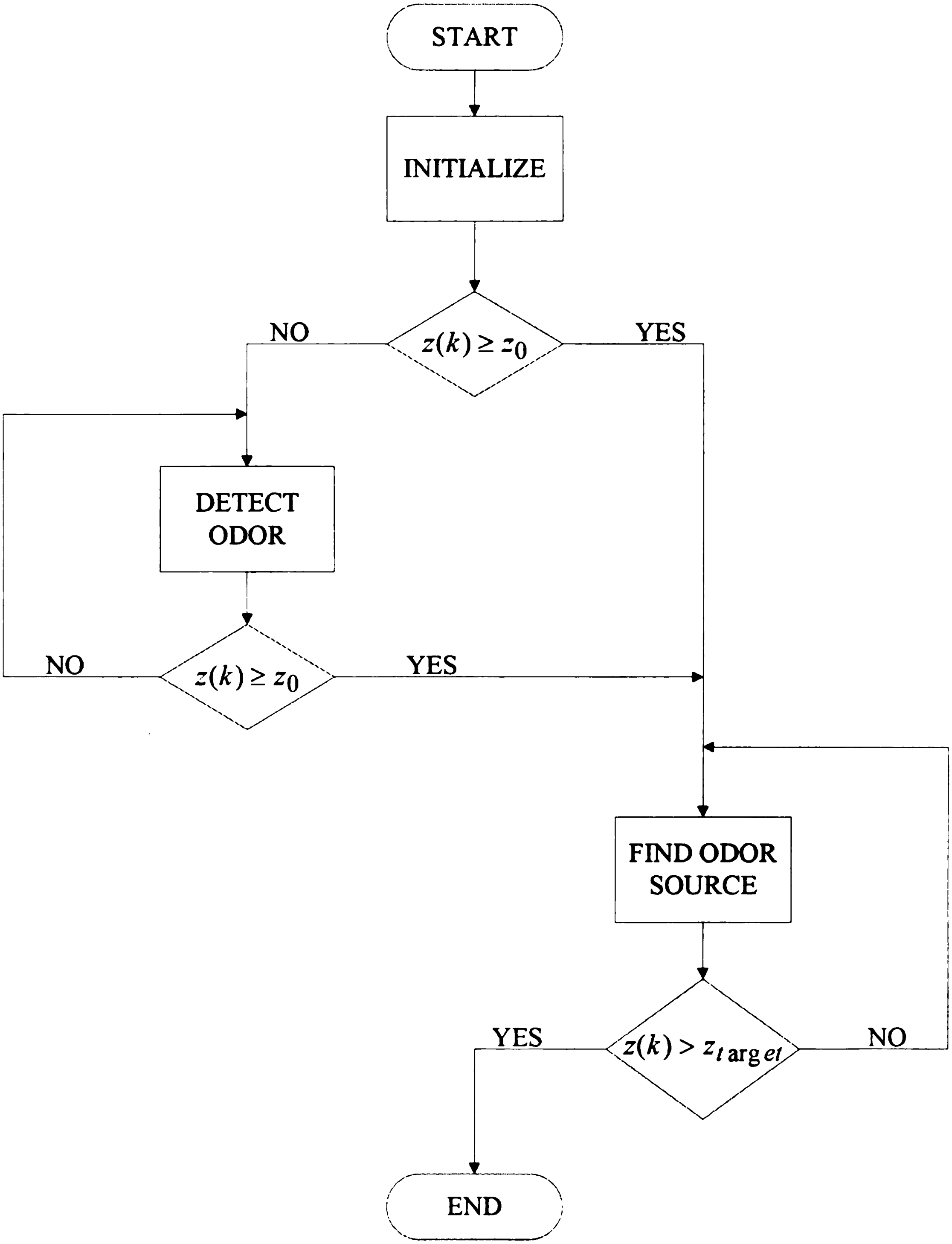

Figure 1: Flowchart for control algorithm 1 (chemotaxis)

3.1.2 Control Algorithm 2: Rheotaxis

FIND ODOR SOURCE: If there is no flow at the onset of the simulation (i.e. $v_{flow}(1) = 0$), the sea lamprey will explore a random direction. It will keep that direction until an obstacle is encountered or it detects flow. Once it detects flow, it will swim against it. If the flow becomes absent for whatever reason, the sea lamprey will continue swimming in the same direction until flow is detected again when it will swim against as before. Since a sea lamprey acting on this control algorithm is not informed of the odor source location by chemical information, the steps in this algorithm will be executed in an infinite loop as shown in Figure 2.

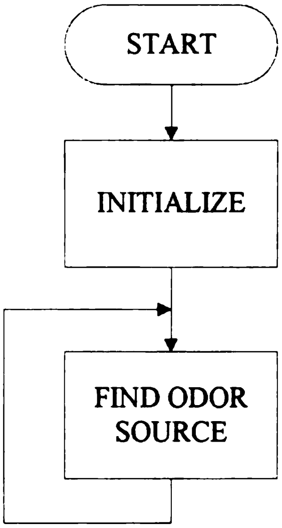

Figure 2: Flowchart for control algorithm 2 (rheotaxis)

3.1.3 Control Algorithm 3: Odor-conditioned rheotaxis

1. FIND PLUME: If at the onset of the simulation the sea lamprey is not within the odor plume (i.e. $z(1) < z_{th}$ [10]), this process will be executed. The sea lamprey begins in an upstream direction or a random direction if no flow is detected as in control algorithm 2. It continues in this direction until an obstacle is encountered. Once the sea lamprey determines it is within the odor plume, it will proceed to the next step.
2. TRACK PLUME: The sea lamprey is within the odor plume at the onset of this process and will try to track the plume to the odor source using rheotaxis. If the sea lamprey leaves the plume, it will execute the next process. This process ends when the sea lamprey locates the odor source.
3. REACQUIRE PLUME: The sea lamprey will counterturn with respect to θ_{flow} so that it re-enters the odor plume[11]. This process ends when the sea lamprey reacquires the odor plume.

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[10] On the plume structure maps, the "plume" of 3kPZS is depicted by the yellow region. The lowest concentration of this region is z_{th}.

[11] This uses the assumption that if θ is greater (less) than θ_{flow}, decreasing (increasing) θ will result in the sea lamprey re-entering the plume.

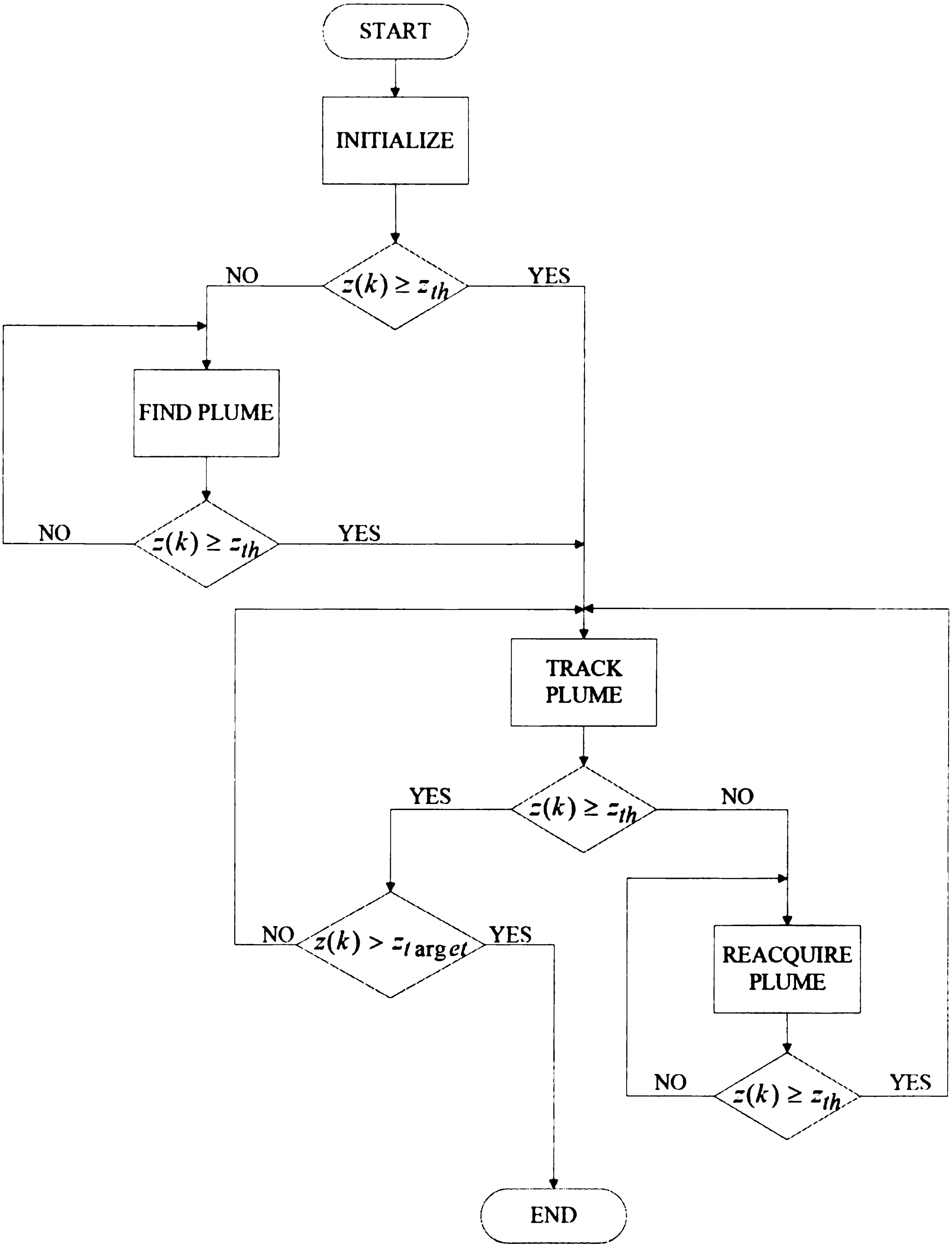

Figure 3: Flowchart for control algorithm 3 (odor-conditioned rheotaxis)

3.2 Determination and Validation of Best-Performing Control Algorithm

The simulated trajectories by control algorithms 1, 2, and 3 are compared to the observed movements in the bifurcated stream experiments (2007). The comparison is restricted to the 110 m segment of the bifurcated stream where the scientists monitored for sea lamprey movements. The initial positions recorded by the scientists for the 33 different observed trajectories are chosen as starting points for the 33 simulated runs of each algorithm. The observed trajectories were recorded at non-uniform sampling times. For a fair comparison, the trajectory points of the observed data are interpolated to make their sampling time uniform and equivalent to the sampling time of the simulated movements.

The number of simulated sea lampreys that entered the left and right channels and successfully located the 3kPZS source in each channel according to control algorithms 1, 2, and 3 are compared to the observed data. Furthermore, Eq. (1) is used to quantify the similarities (or lack thereof) between the simulated and observed trajectories. The best-performing control algorithm is chosen to be that with the lowest value of J.

Once the best-performing control algorithm is determined, it is evaluated in a computer simulation of the novel environment (2008). The algorithm parameters calibrated in the bifurcated stream are used. The simulated trajectories are compared with the observed trajectories using Eq. (1) to validate the best-performing control algorithms applicability to any environment. Next the results are presented.

CHAPTER 4

RESULTS

4.1 Bifurcated Stream Results

Without the use of flow data, the sea lampreys simulated by control algorithm 1 (chemotaxis) were unable to progress upstream to either source of 3kPZS in the bifurcated stream[12]. A reason for this is that in a turbulent environment, the odor plume becomes intermittent and the concentration gradient has many local maxima and minima [8], [36]. Even in the absence of turbulence, odor plumes tend to meander large distances from the source [37]. Taking into account that 3 out of 33 (Table 1) of the sea lampreys simulated by control algorithm 1 were able to progress into one of the two channels suggests a possibility that it could work if the sea lampreys are in proximity to the odor source, but not over hundreds of meters.

The absence of olfaction in control algorithm 2 (rheotaxis) caused the sea lampreys to swim past both sources of 3kPZS. However, they were able to progress upstream into either of the channels. A lesser number of sea lampreys simulated by control algorithm 2 entered the right channel than the real sea lampreys (12 out of 33 compared to 20 out of 33 respectively; Table 1).

Control algorithm 3 simulated sea lampreys whose movements into the left and right channel were not different than real sea lampreys. With the combination of chemo- and mechano-reception, the simulated sea lampreys located the sources of 3kPZS with a

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[12] The computer simulations timed out if the sea lampreys did not locate the source of 3kPZS in 10,000 iterations, which corresponds to 5,000 seconds. Running the simulations for longer lengths of time requires more memory than is available on a computer.

success rate comparable to that of real sea lampreys. Tables 1 and 2 both show significant evidence that control algorithm 3 is the best strategy in the bifurcated stream. This is also true by a qualitative comparison as shown in Fig. 4.

Table 1: Localization comparison of movement patterns of ovulated female sea lampreys in bifurcated stream. The number of ovulated female sea lampreys and simulated females according to control algorithms 1 (chemotaxis), 2 (rheotaxis), and 3 (odor-conditioned rheotaxis) that entered the left channel ("Left") and right channel ("Right"). Percent success left and right is the percent of the sea lampreys that entered the left or right channel that also entered within 0.5 m^2 of the left 3kPZS source or right 3kPZS source respectively.

Data Source	Observed	Left	Right	% Success Left	% Success Right
Exp.	33	13	20	92%	95%
Alg. 1	33	1	2	0%	0%
Alg. 2	33	21	12	<5%	0%
Alg. 3	33	12	21	83%	57%

Table 2: Statistical comparison of movement patterns of ovulated female sea lampreys in bifurcated stream. Means and standard deviations of J generated twenty times for simulated sea lampreys according to control algorithms 1 (chemotaxis), 2 (rheotaxis), and 3(odor-conditioned rheotaxis).

	Alg. 1	Alg. 2	Alg. 3
$\bar{J}$	6.2240	3.2684	2.3970
σ_J	2.0583	0.9841	1.5411

Figure 4: Sea lamprey movement trajectories in bifurcated stream. Observed movement trajectories of ovulating female sea lampreys (a) and simulated trajectories by control algorithms 1 (b), 2(c), and 3 (d). Magenta trajectories are the females that entered the left channel and cyan trajectories are females that entered the right channel. Color-coding indicates the estimated concentration of synthesized 3kPZS (M) through the stream.

(a) Observed movements

(b) Control algorithm 1

Fig. 4 cont.

(c) Control algorithm 2

(d) Control algorithm 3

4.2 Novel Environment Results

Based on the performance results in Tables 1 and 2, control algorithm 3 was applied to four environmental data sets described in Section 1.2.1 to validate it in different physical habitats that were not used for calibrating it (bifurcated stream). Simulated movements of sea lampreys by control algorithm 3 in the novel environment match well with observed movements. This strongly supports odor-conditioned rheotaxis, and more specifically control algorithm 3, as an underlying mechanism for chemo-orientation in sea lampreys. It is interesting that the simulated trajectories by control algorithm 1 in the bifurcated stream (Fig. 4 (b)) resemble more closely the observed movements in the no-flow and 3kPZS case (Fig. 5 (c)) than control algorithm 3 (Fig. 6 (c)). This could be due to any of the following reasons:

1. The sea lamprey switches strategies when there is no flow but a presence of 3kPZS, so it progresses upstream in a purely chemotactic manner.
2. Control algorithm 3 is able to use the most minuscule value of v_{flow} to determine θ_{flow} as long as it is not zero, although real sea lampreys do not seem to be able to detect such low quantities of v_{flow}. Control algorithm 3 needs to take into account a threshold value for v_{flow}, i.e. the minimum flow velocity at which the sea lamprey is able to discern θ_{flow}.
3. Rather than have the sea lamprey use the previous measurement of θ_{flow} when $v_{flow} = 0$, θ_{flow} needs to be a random direction.

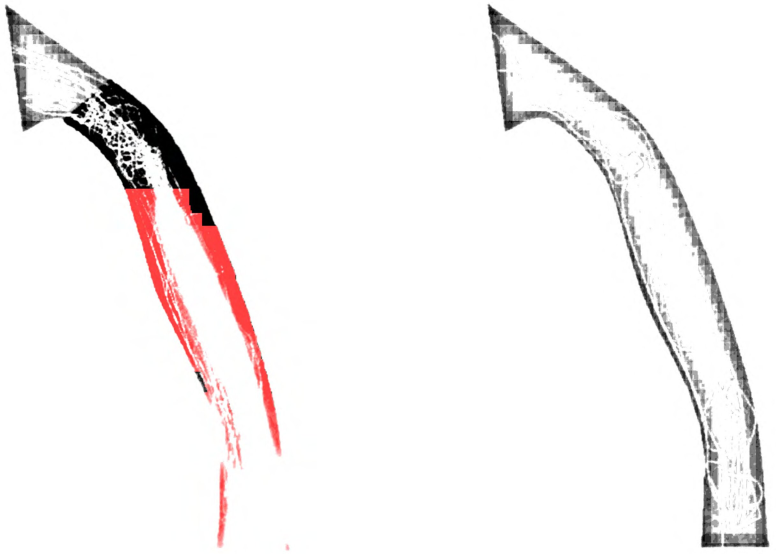
These possibilities lead to the conclusions of this thesis and recommendations for future work.

Table 3: Statistical comparison of movement patterns of ovulated female sea lampreys by control algorithm 3 in novel environment. Means and standard deviations of J generated twenty times for simulated sea lampreys according to control algorithm 3.

Treatment	$\bar{J}$	σ_J
Flow-3kPZS	3.5448	1.0529
Flow-Control	3.6524	1.1987
No-flow-3kPZS	4.1973	1.1235
No-flow-Control	4.2375	1.2783

Figure 5: Observed sea lamprey movement trajectories in novel environment. (a) Flow – 3kPZS application. (b) Flow – control solvent application. (c) No-flow – 3kPZS application. (d) No-flow – control solvent application. Color-coding indicates the estimated concentration of synthesized 3kPZS (M) through the stream.

(a) Flow – 3kPZS (b) Flow – control solvent



(c) No-flow – 3kPZS (d) No-flow – control solvent

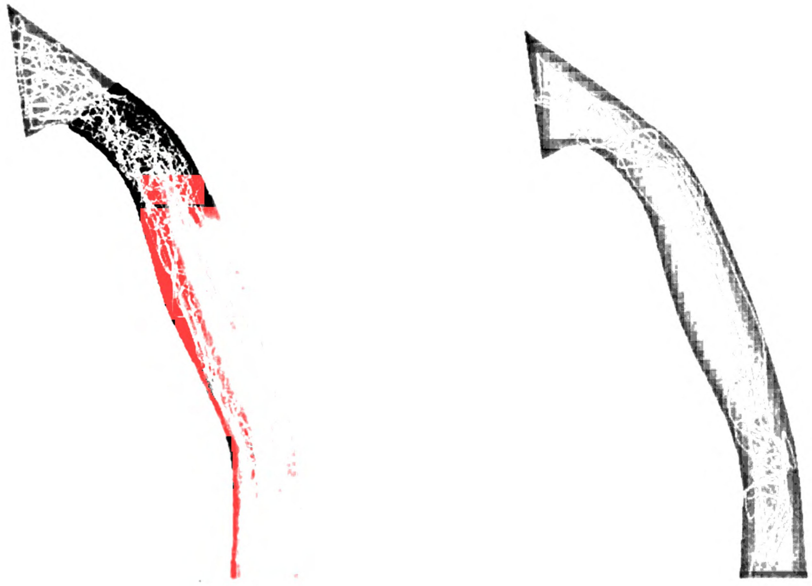
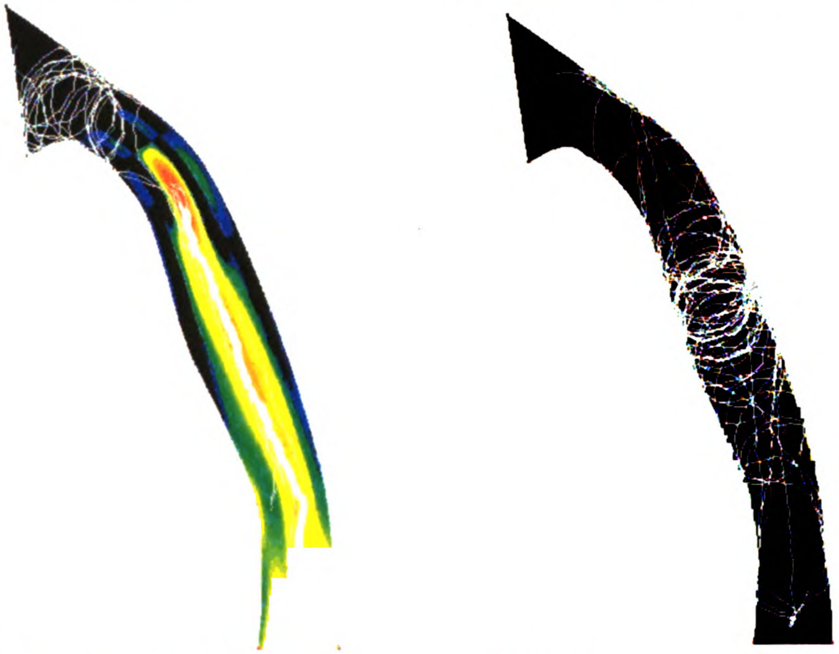
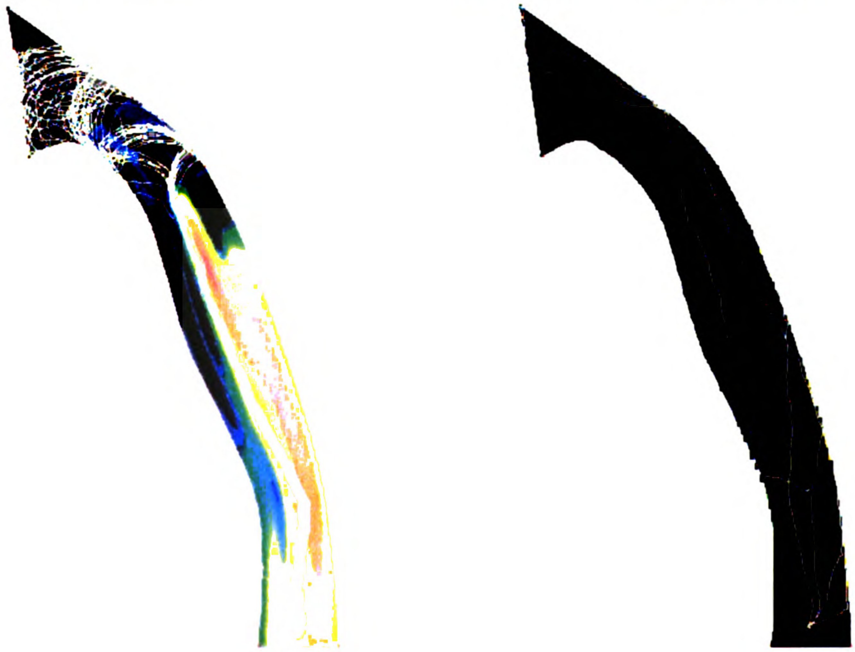


Figure 6: Simulated sea lamprey movement trajectories by control algorithm 3 in novel environment. (a) Flow – 3kPZS application. (b) Flow – control solvent application. (c) No-flow – 3kPZS application. (d) No-flow – control solvent application. Color-coding indicates the estimated concentration of synthesized 3kPZS (M) through the stream.



(a) Flow – 3kPZS

(b) Flow – control solvent



(c) No-flow – 3kPZS

(d) No-flow – control solvent

CHAPTER 5

CONCLUSIONS AND FUTURE WORK

In this thesis, three control algorithms founded on behavioral ecology and control theory are presented. Control algorithm 1 is similar to bacterial chemotaxis [7], [23] and uses only the concentration of 3kPZS to locate the odor source. Control algorithm 2 uses only flow information for the sea lamprey to try to locate the odor source. Control algorithm 3 uses both concentration and flow information. The three algorithms were evaluated in computer simulations and based on the results presented in Chapter 4, control algorithm 3 was highly successful, and thus, odor-conditioned rheotaxis is a sufficient explanation for sea lamprey chemo-orientation. Testing control algorithm 3 in a novel environment validates its robustness. The author believes this thesis to be a helpful contribution to the study of olfaction for both scientists and engineers, particularly in vertebrates which are understudied compared to invertebrates. Although there may be some additional chemo-orientation mechanisms that remain unrevealed, an investigation into the following may provide more insight: determine if sea lampreys switch between odor-conditioned rheotaxis and chemotaxis; take into account a minimum threshold flow velocity at which the sea lamprey can measure the "flow direction"; randomize "flow direction" when flow velocity is zero. The aforementioned investigation will provide improvements (if any) to control algorithm 3, after which the algorithm can be implemented on an autonomous underwater vehicle (AUV) equipped with chemo- and mechano-sensors to locate an odor source.

APPENDICES

A. Control algorithm 1: chemotaxis

```
INITIALIZE
    I1. Let the initial position and heading angle be $(x(1), y(1))$ and $\theta(1)$ respectively.
    I2. Measure $z(1)$.
    I3. Let $z_{\max}(1) = 0$, $\alpha(0) = 0$ and $\theta_d(0)$ is random direction.
    I4. Let $k = 1$.
DETECT ODOR
    O1. while the sea lamprey does not detect any odor ($z(k) < z_0$) do:
    O2. if obstacle is encountered then: $\theta_d(k)$ is chosen such that the obstacle is
        avoided end if
    O3. if $\theta_d$ has been the same direction for the last $N_0$ iterations then:
        $\theta_d(k)$ is random direction and $\alpha(k) = 0$
        else: $\theta_d(k) = \theta_d(k-1)$ and $\alpha(k) = 0$ end if
    O4. (State update) $x(k+1) = x(k) + Tv\cos\theta(k) + w_x(k)$
                       $y(k+1) = y(k) + Tv\sin\theta(k) + w_y(k)$
                       $\theta(k+1) = \theta_d(k) + w_\theta(k)$
    O5. $z_{\max}(k+1) = \max\{z(k), z_{\max}(k)\}$
    O6. Measure $z(k+1)$.
    O7. Increment $k$ by 1 end while
```

FIND ODOR SOURCE

```
S1. while sea lamprey has not located the odor source ($z(k) < z_{target}$) do:
S2. if obstacle is encountered then: $\theta_d(k)$ is chosen such that the obstacle is avoided
    end if
    else: go to step S2 end if
S3. if 3kPZS concentration is not increasing ($z(k) \le z_{\max}(k) + \delta$) then:
        if sea lamprey does not detect odor ($z(k) < z_0$) then:
            if $\theta_d$ has been the same direction for the last $N_0$ iterations then:
            $\theta_d(k)$ is random direction and $\alpha(k) = 0$
            else: $\theta_d(k) = \theta_d(k-1)$ and $\alpha(k) = 0$ end if
        else:
            if $\theta_d$ has been the same direction for the last $N_1$ iterations then:
            $\theta_d(k)$ is random direction and $\alpha(k) = 0$
            else: $\theta_d(k) = \theta_d(k-1)$ and $\alpha(k) = 0$ end if
        end if
    else: $\theta_d(k) = \theta(k-1)$ and $\alpha(k) = 0$ end if
S4. Perform steps O3-O5.
S5. if $z(k) \le z_{\max} + \delta$ then: $z_{\max}(k+1) = \lambda z_{\max}(k)$
    else: $z_{\max}(k+1) = z(k)$ end if
S6. Measure $z(k+1)$.
S7. Increment $k$ by 1 end while
```

B. Control algorithm 2: rheotaxis

```
INITIALIZE
    I1. Let the initial position and heading angle be $(x(1), y(1))$ and $\theta(1)$ respectively.
    I2. Measure $v_{mag}(1)$.
    I3. if $v_{mag}(1) = 0$ then: lamprey selects a random direction for $\theta_{flow}(1)$
        else: $\theta_{flow}(1)$ is measured at $(x(1), y(1))$ end if
    I4. Let $\alpha(0) = 0$ and $\theta_d(0) = \theta_{flow}(1)$.
    I5. Let $k = 1$.
FIND ODOR SOURCE
    S1. if obstacle is encountered then: $\theta_d(k)$ is chosen such that the obstacle is avoided
        end if
    S2. (State update) $x(k+1) = x(k) + Tv\cos\theta(k) + w_x(k)$
                       $y(k+1) = y(k) + Tv\sin\theta(k) + w_y(k)$
                       $\theta(k+1) = \theta_d(k) + w_\theta(k)$
    S3. Measure $v_{mag}(k+1)$.
    S4. if $v_{flow}(k+1) = 0$ then: $\theta_{flow}(k+1) = \theta_{flow}(k)$
        else: $\theta_{flow}(k+1)$ is measured at $(x(k+1), y(k+1))$ end if
    S5. Increment $k$ by 1
    S6. Perform steps S1-S5.
```

C. Control algorithm 3: odor-conditioned rheotaxis

```
INITIALIZE
    I1. Let the initial position and heading angle be $(x(1), y(1))$ and $\theta(1)$ respectively.
    I2. Measure $z(1)$ and $v_{mag}(1)$.
    I3. if $v_{mag}(1) = 0$ then: $\theta_{flow}(1)$ is random direction
        else: $\theta_{flow}(1)$ is measured at $(x(1), y(1))$ end if
    I4. Let $\alpha(0) = 0$.
    I5. if $z(1) < z_{th}$ then: $\theta_d(0)$ is random direction in
        $[\theta_{flow}(1) - \Delta\theta_1, \theta_{flow}(1) + \Delta\theta_1]$
        else: $\theta_d(0)$ is random direction in $[\theta_{flow}(1) - \Delta\theta_2, \theta_{flow}(1) + \Delta\theta_2]$
    I6. Let $k = 1$.
FIND ODOR PLUME
    P1. while sea lamprey is not in the odor plume ( $z(k) < z_{th}$ ) do:
    P2. if obstacle is encountered then: $\theta_d(k)$ is chosen such that the obstacle is avoided
        end if
    P3. if $\theta(k) < \theta_{flow}(k) - \Delta\theta_1$ AND $\theta(k) > \theta_{flow}(k) + \Delta\theta_1$ then:
        $\theta_d(k) = \theta_{flow}(k)$ end if
    P4. (State update) $x(k+1) = x(k) + Tv\cos\theta(k) + w_x(k)$
                       $y(k+1) = y(k) + Tv\sin\theta(k) + w_y(k)$
                       $\theta(k+1) = \theta_d(k) + w_\theta(k)$
```

```
    P5. Measure $z(k+1)$ and $v_{mag}(k+1)$.
    P6. if $v_{mag}(k+1) = 0$ then: $\theta_{flow}(k+1) = \theta_{flow}(k)$
        else: $\theta_{flow}(k+1)$ is measured at $(x(k+1), y(k+1))$ end if
    P7. Increment $k$ by 1 end while
TRACK PLUME
    T1. while sea lamprey has not located the odor source ($z(k) < z_{target}$) do:
    T2. if sea lamprey exits odor plume ($z(k) < z_{th}$) then: go to step R1
        else: go to step S3 end if
    T3. if obstacle is encountered then: $\theta_d(k)$ is chosen such that the obstacle is avoided
        else: $\theta_d(k) = \theta_d(k-1)$ and $\alpha(k) = 0$ end if
    T4. if $\theta_d(k) < \theta_{flow}(k) - \Delta\theta_2$ OR $\theta_d(k) > \theta_{flow}(k) + \Delta\theta_2$ then:
        $\theta_d(k) = \theta_{flow}(k)$ end if
    T5. Perform steps P4-P6.
    T6. Increment $k$ by 1 end while
REACQUIRE PLUME
    R1. while sea lamprey is not in odor plume ($z(k) < z_{th}$) do:
    R2. if obstacle is encountered then: $\theta_d(k)$ is chosen such that the obstacle is
        avoided
        else: go to step R3 end if
    R3. if sea lamprey exited odor plume on right side then:
```

```
    $\theta_d(k) = \theta_d(k-1) + \alpha(k-1)$ and $\alpha(k) = \zeta \times 10^{13} |z(k) - z_{th}|$
    else: $\theta_d(k) = \theta_d(k-1) - \alpha(k-1)$ and $\alpha(k) = \zeta \times 10^{13} |z(k) - z_{th}|$
    end if
R4. Perform steps P4-P6.
R5. Increment $k$ by 1 end while
```

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