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DISPERSAL BEHAVIOR OF MOSQUITOFISH (*GAMBUSIA HOLBROOKI*)

by

SHIREEN ALEMADI

B.A. Minnesota State University Moorhead, 2004

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Arts and Sciences
at the University of Central Florida
Orlando, Florida

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ABSTRACT

Mosquitofish (*Gambusia holbrooki*) are native to the southeastern United States but invasive elsewhere, and are dominant predators in many ecosystems that they inhabit. Information on dispersal behavior will help better understand and predict mosquitofish metapopulation dynamics and invasions. I experimentally tested dispersal behavior of individual mosquitofish under a range of laboratory conditions relevant to field situations. Preliminary experiments showed that gender, lighting conditions, hunger and acclimation time did not significantly affect net dispersal rate. Power analysis based on this preliminary experiment determined that 6 replicate fish were sufficient for each subsequent experiment; I used 24 fish, and each fish was tested one time. Three factors that potentially could affect net swimming rate were tested: habitat of origin (permanent vs. temporary waters), water depth (3-24 mm), and the interaction between water depth and leaf litter type (upland and wetland). Fish from a temporary pond dispersed significantly faster than fish from a permanent pond, and fish dispersed significantly faster in deeper water than in shallower water. However, leaf litter significantly inhibited fish dispersal at all depths tested. Based on these experiments, *G. holbrooki* disperse more readily through relatively open and deeper (several centimeters) pathways between habitats such as roadside ditches, drainage canals and trails in flooded conditions. My results are useful for understanding mosquitofish dispersal behavior based on the abiotic and biotic factors examined in this experiment. I predict that mosquitofish can spread from a point of introduction at about 800 m per day, given an unobstructed path of only ≥ 6 mm depth.

ACKNOWLEDGMENTS

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INTRODUCTION

Dispersal is an important process because it generates metapopulation structure and gene flow (Endler, 1977; Kareiva, 1990; Hanski and Gilpin, 1991; Tilman, 1994) and because motility correlates with an organism's ability to invade new habitats (Ehrlich, 1986; Lodge, 1993b; Sakai et al., 2001). Dispersal can prevent negative effects of inbreeding (Ralls et al., 1979) and permits colonization of new habitats (Amezaga et al., 2002). Organisms with poor dispersal ability risk reduced access to genetically diverse mates, food resources and refugia. Various definitions of dispersal appear in the literature (Howard 1960; Koenig et al. 1992), but I operationally define dispersal as movement of an organism from one place to another, including the phenomena of migration and invasion (Wiens 2001). Dispersal may be limited by absence of habitat connections (e.g. corridors) and organism adaptations, or obstacles between habitats. Inability to successfully traverse obstacles can negatively influence populations by diminishing rates of reproduction and survival, which over time will reduce population growth rates (Dunning et al., 1992; Noss et al., 1996; Vos and Chardon, 1998; Clark et al., 2001), and gene flow between separated populations (Jaeger et al., 2005).

Two major threats to biodiversity in freshwater systems are related to dispersal: biological invasions (Elton, 1958) and habitat modification or destruction (Everett, 2000). Ecological changes caused by invasive organisms such as the zebra mussel (*Dreissena polymorpha*) and salmonids are well documented in lacustrine and riverine systems (Moyle, 1986; Krueger and May, 1991; Lodge, 1993a; Johnson and Carlton, 1996; Kolar and Lodge, 2000). However, few studies of invasions have examined dispersal ability alone (Rehage and

Sih, 2004), which is of particular importance to understanding invasions and better predicting spread of introduced species.

Landscape modification, such as road construction (Diamondback, 1990; Bennett, 1991; Noss and Cooperrider, 1994), can affect aquatic ecosystems by changing the physical environment, altering animal behavior and increasing the spread of exotic species (Trombulak and Frissell, 2000). Roads may unequally affect ecosystems and species because roads alter population sizes, species composition and hydrology, and negatively affect ecosystems that form aquatic landscapes (Trombulak and Frissell, 2000). Ditches often are associated with roads, and permit the spread of introduced species (Taylor et al., 1984; Duryea et al., 1996; Swanson et al., 1996); invasions can go unnoticed for a long time in previously isolated habitats (Mura, 2001) such as wetlands. Some fish can exploit temporary connections due to weather events (hurricanes and flooding) and further spread into naturally fishless wetlands through roadside ditches and other hydrological connections.

Many studies have examined the importance of wetland connectivity to fish assemblages (Kushlan, 1976; Snodgrass et al., 1996; Poizat and Crivelli, 1997; Baber et al., 2002). However, research on linkages among “isolated” wetlands that are naturally fishless is limited (King et al., 1996; Tiner et al., 2002, Eason and Fauth, 2002), including studies on invasions and dispersal. Understanding how fishes invade isolated, ephemeral wetlands is important for understanding how to prevent the invasions in the first place.

Mosquitofish (*Gambusia holbrooki* and *Gambusia affinis*, Poeciliidae) are among the 100 worst invasive species in the world (ISSG, 2000); because they disperse well following introduction to a new region. Mosquitofish can survive in stagnant water, and have been introduced to many wetlands outside their native range for biological control of mosquitoes

(Leyse et al., 2004). Poeciliid fishes, including mosquitofish, have generation times notably shorter than other fish groups and live-bearing females can store sperm from many males; one fertilized female can start a new population with little or no damaging founder effects (Chesser et al., 1984; Zane et al., 1999). Thus, mosquitofish and other poeciliids (e.g., guppies, sailfin molly) can quickly establish large populations after dispersing into a new habitat. For example, *Gambusia* originally was released into disturbed areas of Australia and New Zealand, but has since spread into less-developed areas (Arthington and Lloyd, 1989). After colonizing a new habitat, mosquitofish are major predators that affect entire food webs. *Gambusia holbrooki* caused declines of some endemic North American fishes (Meffe et al., 1983; Meffe 1984) by eating their eggs and newly hatched fry. Mosquitofish also prey on amphibian eggs and tadpoles (Gamradt and Kats, 1996; Goodsell and Kats, 1999), as well as invertebrates (Courtenay and Meffe, 1989). The combination of r-selected life history traits and aggressive predation make mosquitofish an important invader, but information on their dispersal behavior is lacking.

Short-term behavioral tests can determine key information (Milinski and Heller, 1978; Gilliam and Fraser, 1987; Abrahams and Dill, 1989) useful in predicting long-term population-level responses in natural systems (Rehage, 2003), and are needed to study dispersal (Rehage and Sih, 2004). To date, little research has examined the importance of behavior in the success or failure of fish species invasions (Holway and Suarez, 1999; Sol et al., 2002). I experimentally tested the effects of six variables on dispersal behavior of *Gambusia holbrooki*: gender, hunger state, acclimation time, source habitat, water depth, and leaf litter type. The first three variables were examined in preliminary experiments to determine their effect on net dispersal time, which allowed me to conduct more powerful subsequent experiments. The latter three variables were tested because they relate to mosquitofish dispersal behavior in nature. I generated data useful

for predicting mosquitofish dispersal behavior and the limits of that dispersal into otherwise fishless isolated wetlands. My results will be useful for understanding mosquitofish dispersal behavior based on the abiotic and biotic factors examined in this experiment.

My initial predictions were:

- 1) Net dispersal rates of fish in dark conditions will be significantly faster than fish in lighted conditions. I expected fish would disperse faster in the dark to avoid potential nocturnal predators.
- 2) Net dispersal rate of females will be significantly faster than that of males. Females would disperse to look for more food resources and also to avoid predators.
- 3) For different pretrial conditions (hunger state and acclimation time), net dispersal rate of satiated fish having long acclimation periods will be faster than other treatment combinations. I expected fish that are satiated to have more energy, and a longer acclimation time allows fish to better acclimate to new surroundings.
- 4) Fish from a temporary pond will have significantly faster net dispersal rates than fish from a permanent lake. Fish from a temporary pond are in a habitat with high hydrological variation, and when the water rises fish will explore new areas and therefore disperse faster.
- 5) Increasing water depths (3, 6, 12, 24 mm), with (6 mm) being average body height, will cause fish to swim at progressively slower rates. At shallow depths, fish will disperse faster in an attempt to find deeper water.
- 6) Different water depths with different leaf litter types (upland and wetland) will cause differences in net dispersal rates, with fish in either litter type and 12 mm and 24 mm depth conditions dispersing faster than fish in the 3 mm and 6 mm depth conditions with

leaf litter. I predict that leaf litter type alone will not significantly affect net dispersal rate.

At deeper depths with leaf litter fish will disperse because at shallow depths with leaf litter there will not be sufficient space for fish to move.

MATERIALS AND METHODS

Many factors may affect mosquitofish dispersal. I observed the effect of six variables (gender, hunger state, source habitat, water depth, and leaf litter type) on dispersal behavior, recorded as the time required for a fish to travel a set distance and expressed as net dispersal rate. I chose water depth and leaf litter type because they are obstacles mosquitofish should encounter when dispersing into isolated wetlands. I conducted preliminary experiments to gather information on variation in swim rate. While conducting the preliminary experiments I also recorded gender, acclimation time, lighting treatment, and hunger state to determine how they affected net dispersal rate. Second, I tested fish from two different habitats (temporary and permanent) to determine if habitat of origin affected net dispersal rate. Third, I conducted an experiment with four different water depths, and my final experiment included all combinations of the four depths and upland and wetland litter (Figure 1, Table 1). Statistical tests were conducted after each experiment; the logical sequence of experiments allowed greater power of subsequent experiments and reduced the number of possible treatments. Below is an explanation of methods used in all experiments, followed by a description of each unique experiment.

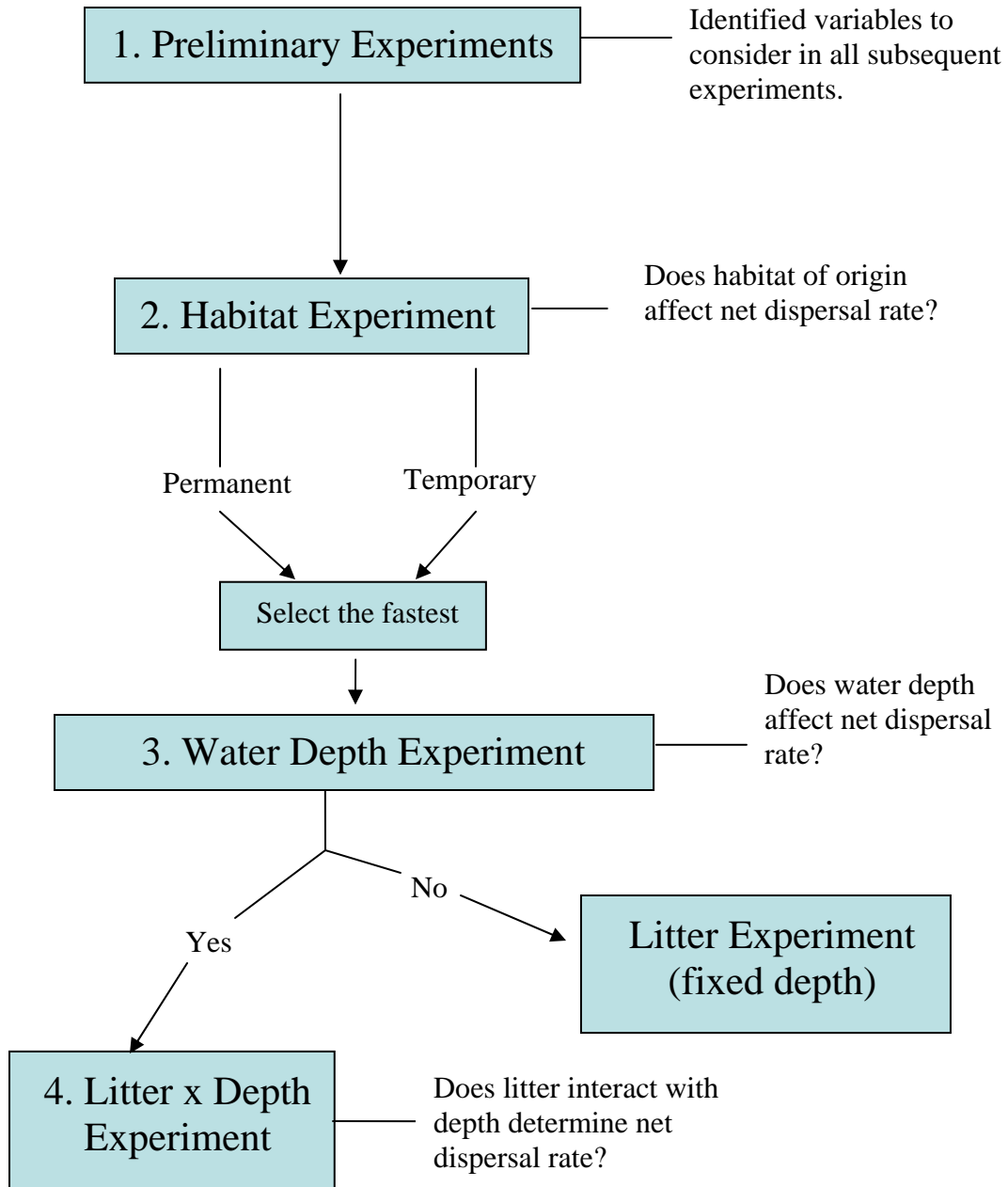


Figure 1: Experiment Flow Chart

Preliminary experiments tested effects of lighting, gender, hunger state and acclimation time on net dispersal rate. Fish from two different habitats (temporary and permanent) were tested for the second experiment. The third experiment tested different water depths, and the fourth and final experiment tested leaf litter in conjunction with water depth.

Table 1: Experimental Designs

Table shows each experiment conducted and the treatments used therein.

Experiment	Lighting	Gender	Hunger State	Acclimation Time (min)	Pond Type	Water Level (mm)	Litter Type
1. Preliminary	Light and Dark	Male, Female	Fed, Not fed	0, 2 and 10	Permanent, Temporary	6	None
2. Habitat	Light	Male, Female	Not fed 24 h	5	Temporary	6	None
3. Water Depth	Light	Male, Female	Not fed 24 h	5	Temporary	3, 6, 12, 24	None
4. Leaf litter x Depth	Light	Male, Female	Not fed 24 h	5	Temporary	3, 6, 12, 24	Upland, wetland litter

Methods and Materials Common to All Experiments

Fish were collected for preliminary experiments from Lake Claire and its neighboring pond ~50 m to the west (hereafter Pond 1) on the University of Central Florida (UCF) Orlando campus (Figure 2). The first experiment compared dispersal rates of fish from Lake Claire and Pond 1. Subsequent experiments used only fish from Pond 1.

I collected fish using minnow traps (Aquatic Eco-Systems, Inc., Apopka, FL) baited with canned tuna or by dipnetting. Fish were transferred in 18.93 L buckets of pond water to the Field Research Building on the UCF campus. Fish were housed in 45.5 L Nanotanks (Transworld Aquatic Enterprises, Inc., Los Angeles, CA) (Figure 3) containing dechlorinated tap water with standard filtration and fed *ad libitum* with Tetramin fish flakes at least 24 h before experiments. This protocol acclimated fish to laboratory conditions and standardized hunger levels.

Experimental trials were conducted in arenas (3 m x 0.08 m x 0.10 m), arrayed in two sets of six (twelve total) within the Field Research Building (Figures 4 and 5). Arenas were filled with dechlorinated tap water. An individual fish was transferred by aquarium net into a holding zone (0.12 m x 0.08 m x 0.10 m), which was partitioned from the rest of the arena by a Plexiglas door. All doors had 10 4-mm drilled flow holes and were attached to a dowel rod that rested across the top of the arena. Doors hinged up and opened simultaneously when I pulled a common, 80-pound test fishing line. To ensure fish did not escape from the holding zone, each door had a transparent, flexible plastic flap attached to its bottom. Each arena was drained through plumbing at the finish-line end after each trial, and arenas were re-filled with dechlorinated tap water to remove residual chemical cues left by previous fish. Arenas were

surrounded by black plastic to ensure human movement around them did not affect fish behavior (Figure 5).

In all trials, fish were timed with a stopwatch to the nearest 1/100s, beginning when doors were opened until fish reached a finish line 2.58 m away from the door (Figure 4). I observed fish crossing the end line using a mirror attached above the arenas, to prevent behavioral responses to my observation. Fish were observed for 30 minutes; if a fish did not cross the finish line within 30 minutes, the time was recorded as 30 minutes for statistical analysis. For each fish, I recorded its arena number, time to finish, site of origin, body height (mm), standard length (mm), and gender (Figure 6).



Figure 2: Aerial Photo of the University of Central Florida (UCF) Campus

Location of Pond 1 and Lake Claire, where fish were collected for experiments. Insert shows the location of the UCF campus and Orange County, Florida.



Figure 3: Fish Housing

Nanotanks contained 45.5 liters of water and housed fish before and after each experiment.

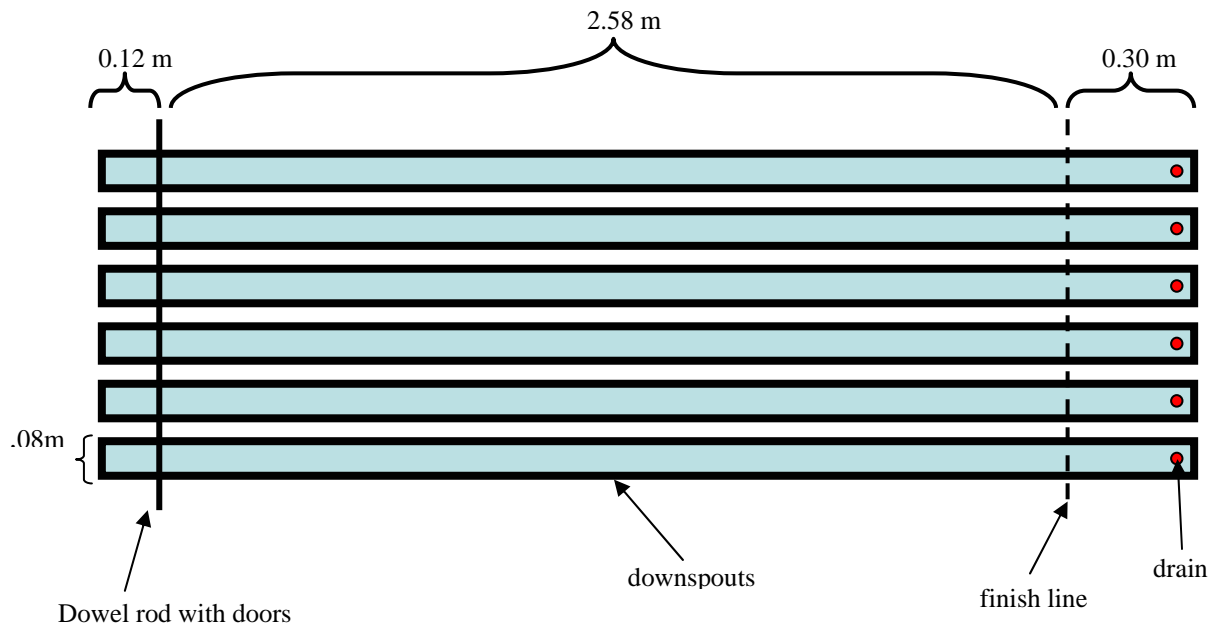


Figure 4: Arena Setup

Testing arenas consisted of six downspouts fitted with plastic end caps. Fish were put into a lane behind Plexiglas doors measuring 96 cm^2 . Total distance between start and finish lines was 2.58 m .



Figure 5: Arenas in the Biology Field Research Center

Top: In this photo, a wide view of both arenas which are screened by black plastic with lighting above. Arenas are screened to prevent interference with fish behavior by activities in the room.
Bottom: A close-up of one set of six arenas inside the opaque screening.

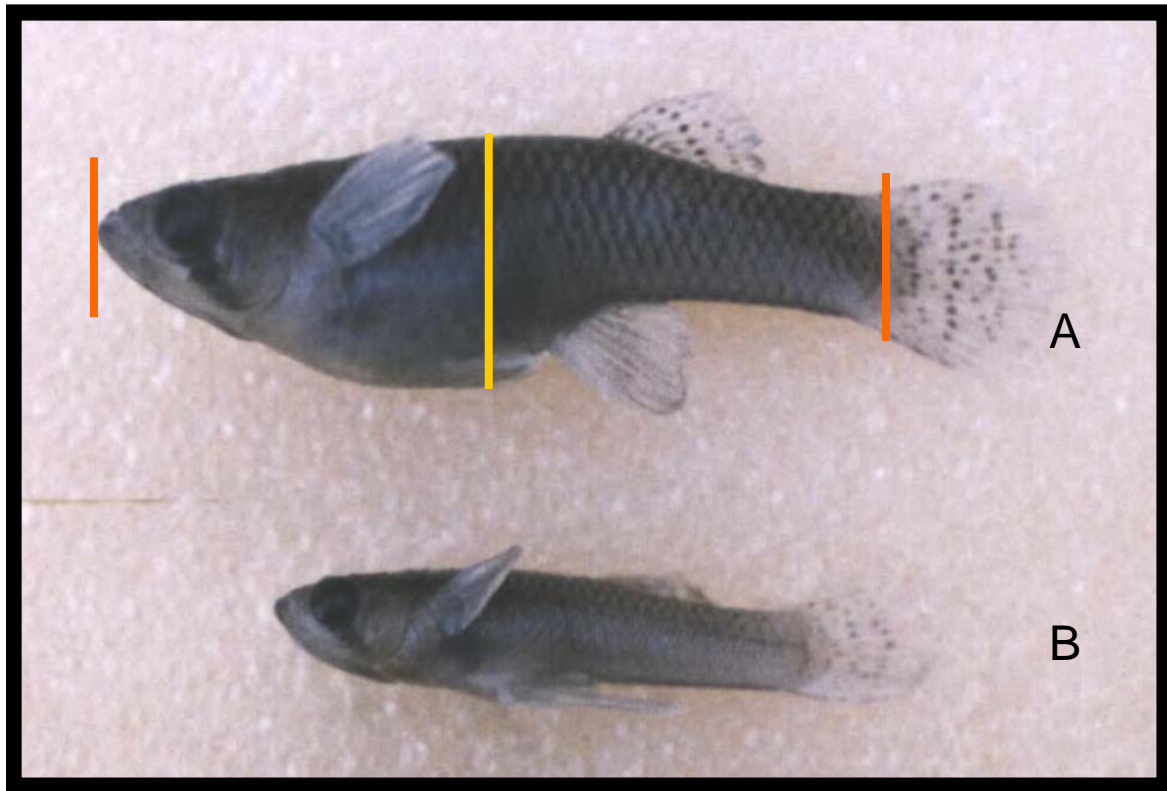


Figure 6: Fish Measurements

Standard length measured from snout to caudal peduncle (distance between orange lines), height measured at the highest point on each fish (yellow line). Fish (A) is a female and fish (B) is a male. Photo courtesy of Richard Moore.

Preliminary Experiments

I examined variation in net dispersal rate among individuals, for the purpose of determining replication levels for later experiments. In preliminary experiments, fish were exposed to different hunger (24 hours pre-trial without food or fed) and acclimation (0, 2, or 10 min) treatments, and I tested for differences in net dispersal time when arenas were lit by Philips Cool White Plus 40 watt, 1.22 meter light bulbs that were 0.76 meters above the arenas or in dim light. I predicted that net dispersal rates would differ significantly among treatments, with satiated female fish in dark conditions and having a long acclimation period dispersing at a faster rate. Water depth in each lane was standardized to 6 cm (10x average body height). Data were analyzed as a completely randomized design with the non-parametric Mann-Whitney and Kruskal-Wallis tests because data could not be transformed to meet the assumptions of normality and homogeneity of variance.

Habitat Experiment

The first main experiment tested for differences in net dispersal rate among fish collected from two habitats: permanent Lake Claire and the nearby Pond 1, a temporary pond. I predicted that fish from different habitats would have significantly different net dispersal rates, with fish from temporary ponds dispersing at a faster rate. Some experimental conditions were determined from preliminary experiments (above). Fish were not fed for 24 hours before the trial to standardize hunger state. All arenas were filled to 6 cm depth and were lit by Philips Cool White Plus 40 watt, 1.22 meter light bulbs that were 0.76 meters above the arenas. For this experiment 24 fish were tested from each of the temporary (Pond 1) and permanent (Lake Claire) habitats. All trials were run on one day to eliminate temporal variation and fish from temporary and permanent ponds were randomly placed in individual testing arenas to account for any possible

spatial variation. Data were analyzed using one-way analysis of variance for a completely randomized design with two treatments. Net dispersal rate data were log-transformed for normality and homogeneity of variance.

Water Depth Experiment

For this experiment fish were only obtained from Pond 1. I predicted that net dispersal rate would differ significantly with water depth, so that fish in shallow water disperse faster. Water depths in the arenas were calculated as ratios of body heights from analyses in preliminary experiments, in which the mean height of the 221 fish was $6 \text{ mm} \pm 1.9 \text{ mm}$ (mean \pm SD), and fish ranged from 4 mm to 12 mm standard height. Individual fish were randomly exposed to one of four depths: 3 mm, 6 mm, 12 mm, or 24 mm. However, all six arenas that comprised one array were interconnected by plumbing, so treatments were randomly assigned to each array instead of each lane. All trials were run on one day to eliminate temporal variation. I analyzed data using two-way ANOVA for a completely randomized design with four levels of one treatment (depth), and two levels of gender. Net dispersal rate was log-transformed for normality and homogeneity of variance. Body dimensions were also recorded for fish in this experiment; I regressed net dispersal rate (m sec^{-1}) against the water depth:body height ratio of individual fish to verify that they were consistent with those of preliminary experiments and to express experimental results relative to the size of each fish.

Litter and Depth Experiment

For the final experiment, fish from Pond 1 were exposed to one of four depths (3 mm, 6 mm, 12 mm or 24 mm) crossed with two litter types: upland or wetland. I predicted that fish in

both litter types and the 12 mm and 24 mm depths would disperse faster than fish in the 3 mm and 6 mm depth conditions.

I calculated the amount of litter to add to each lane from leaf-litter densities in wetland and upland habitats on the UCF campus. Ten 0.1 m² quadrats were tossed behind my back and the litter in each quadrat was collected in plastic grocery bags. I dried litter for 24 h at 105°C in paper bags that had been dried and weighed the day before. After 24 h, mean mass was determined. Mean litter mass (g/m²) averaged 295 g/m² in wetland and 1265 g/m² in upland corresponded to 70 g wetland litter and 303 g upland litter per arena. I also gathered leaf litter from three 9 m² plots in both wetland and upland sites in individual 121 L lawn bags to be dried and used later in the experiments. Wetland litter was composed of pond cypress (*Taxodium distichum*) needles with some maidencane (*Panicum hemitomum*), while upland litter was composed of long leaf pine (*Pinus palustris*) needles, and live oak (*Quercus virginiana*), myrtle oak (*Quercus myrtifolia*) and chapman oak (*Quercus chapmanii*) leaves.

For these experiments, all lanes were first filled with the appropriate depth of water and then litter that had soaked in dechlorinated water for 24 h was carefully added. Each arena aged for 24 h so litter could settle and leach out chemicals, as it would in nature. Only 12 trials could be run per day, so I conducted six trials with upland and six trials with wetland litter each day with the placement of treatments randomized among days (Figure 7). Arenas were drained between trials and a 6.5 hp shopvac (RIDGID, St. Louis, MO) was used to clean out the lanes after each trial. Data for the completely randomized 4x2 factorial design were analyzed with the non-parametric Mann-Whitney test because data could not conform to normality and homogeneity of variance. All data were analyzed data using SPSS V. 11.5 (SPSS Inc., Chicago, IL, USA). Power analysis was conducted with JMP 6.0 (SAS Institute, Cary, NC).

Litter/Depth Experiment

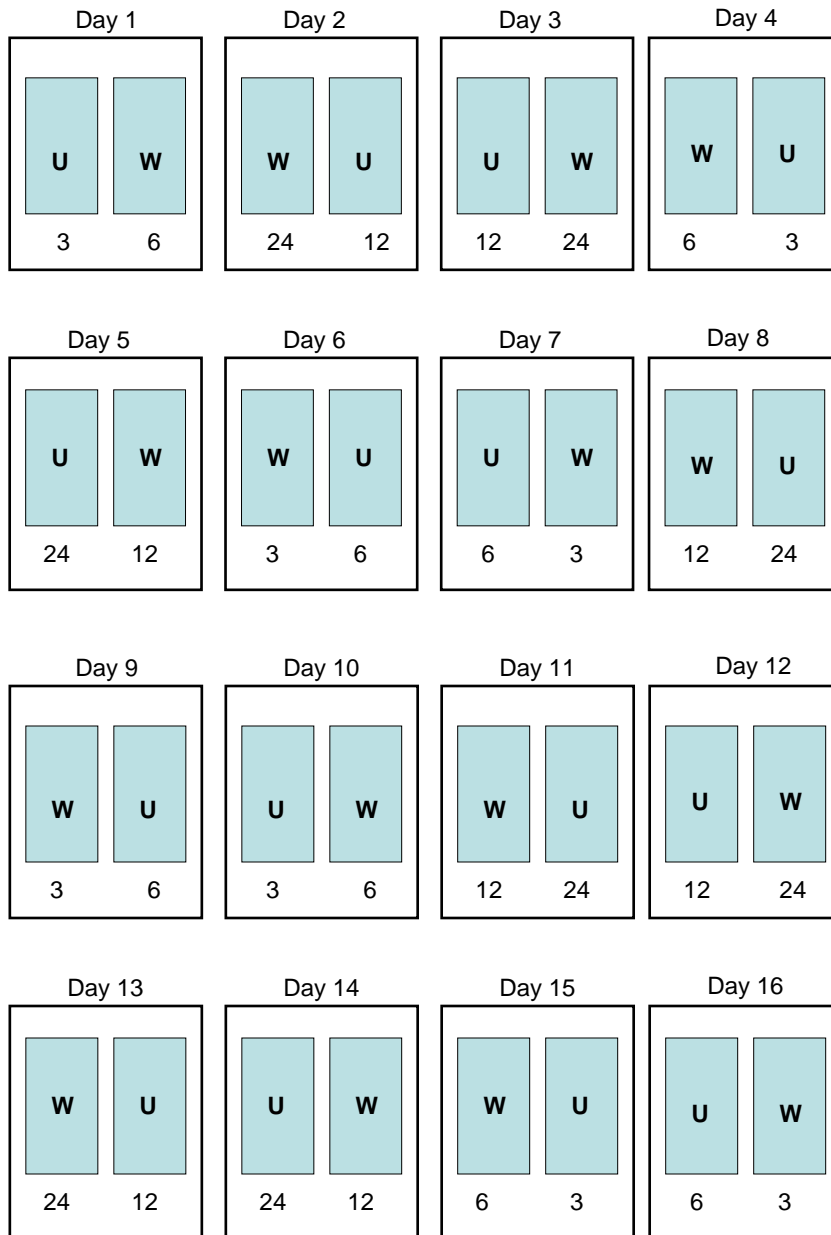


Figure 7: Litter/Depth Experimental Set-up

Sixteen day experimental set up for the Litter/Depth experiment. On each day six trials were with wetland litter and another six trials were with upland litter each with a different depth of water.

RESULTS

Preliminary Experiments

I determined $N = 24$ was needed in Experiments 1, 2 and 3 for each treatment based on a *post hoc* power analysis conducted on preliminary data. Neither lighting, gender, or pretrial conditions (feeding and acclimation period; Figure 8) significantly affected net dispersal time of mosquitofish. Therefore, all subsequent experiments were conducted with full lighting (for more accurate timing) and a mixture of genders (which were recorded nonetheless for post hoc analysis). Also, fish in subsequent experiments were held for 24 hours pre-trial to standardize hunger, and acclimation periods in holding zones were 5 minutes.

Habitat Experiment

Habitat of origin significantly affected net dispersal rate of mosquitofish (ANOVA: $F_{1,44} = 10.142$, $p = 0.003$); on average, fish from the permanent Lake Claire required 47.5% more time to disperse 2.58 m than fish from the nearby temporary pond (Figure 9). There was no significant difference in net dispersal rate between genders (ANOVA: $F_{1,44} = 0.137$, $p = 0.713$) nor any gender x pond interaction (ANOVA: $F_{1,44} = 0.001$, $p = 0.972$).

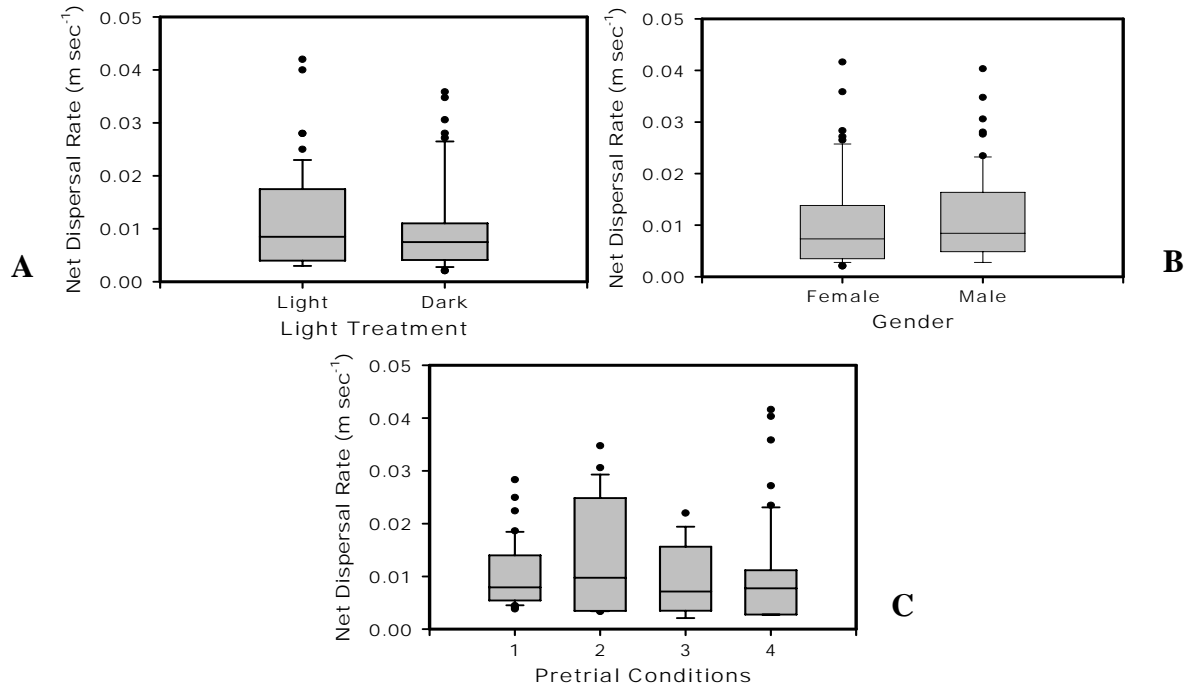


Figure 8: Preliminary Experiments

(A) Net dispersal rate (m sec⁻¹) in relation to lighting treatments, with one outlier visually eliminated. Lower and upper boundaries are the 25th and 75th percentile, with whiskers above and below at the 90th and 10th percentile. The median is depicted by the line within the box. No significant difference existed between treatments (Mann-Whitney, $Z = -1.041$, $p = 0.298$). (B) Net dispersal rate (m sec⁻¹) in relation to gender (female and male), with one outlier visually eliminated. No significant difference existed in net dispersal time (Mann-Whitney, $Z = -0.952$, $p = 0.341$). (C) Net dispersal rate (m sec⁻¹) in relation to four different pretrial conditions, with one outlier visually eliminated: 1) no food for 24 hours, 2 minute acclimation; 2) fed 2 hours before, no acclimation time; 3) fed 2 hours before, 10 minute acclimation; 4) fed 2 hours before, 2 minute acclimation. No significant difference existed (Kruskal-Wallis $p = 0.545$) in net dispersal rate based on pretrial conditions.

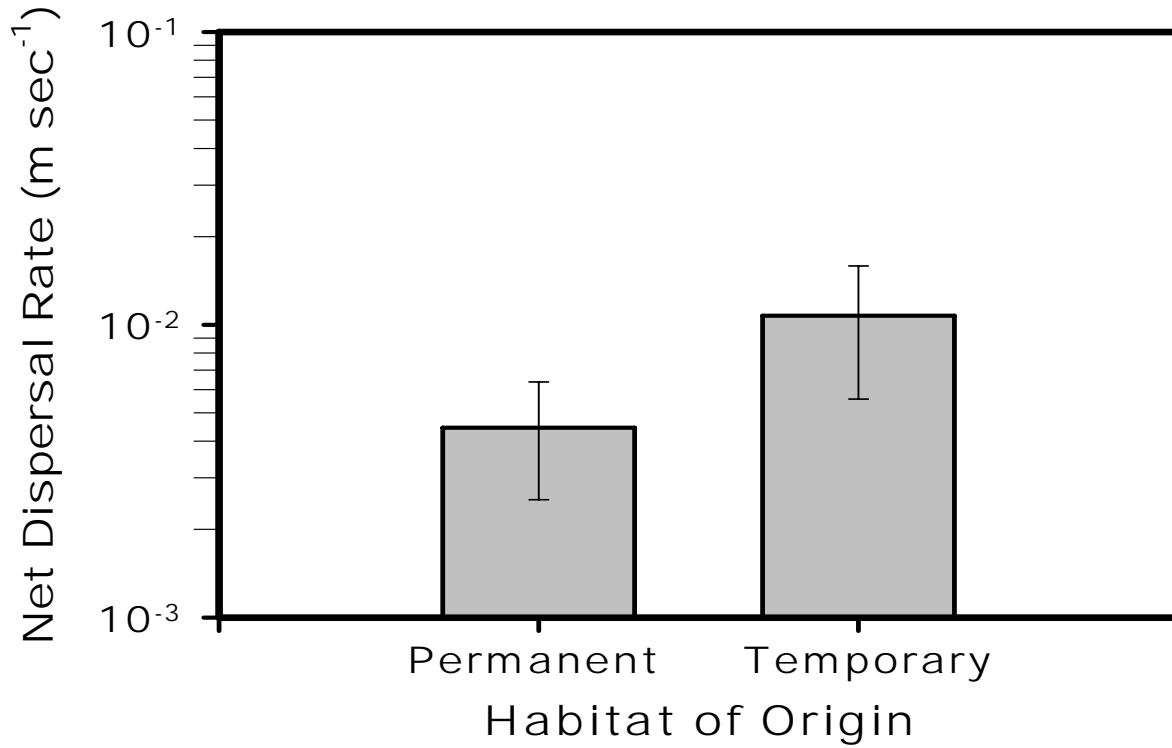


Figure 9: Habitat of Origin

Net dispersal rate (mean and 95% C.I., in m sec⁻¹) of fish in relation to habitat of origin. Note the logarithmic scale of the abscissa. Fish from a temporary ponds dispersed significantly faster (ANOVA: $F_{1,44} = 10.142$, $p = 0.003$) than fish from a temporary pond. Gender (ANOVA: $F_{1,44} = 0.137$, $p = 0.713$) and the gender x pond interaction (ANOVA: $F_{1,44} = 0.001$, $p = 0.972$) did not significantly affect net dispersal time.

Water Depth Experiment

Fish in deeper water dispersed significantly faster (ANOVA: $F_{3,92} = 9.666$, $p < 0.0001$) than fish in shallow water (Figure 10). Mosquitofish dispersed significantly faster in water 12-24 mm deep, than in water 3-6 mm deep. Dispersal rate was intermediate (mean = 0.008 m sec^{-1}) at water depths of 6-12 mm. As observed for absolute depths (experimental treatments), net dispersal rate increased significantly with the ratio of water depth to body height ($p < 0.0001$; Figure 11) though substantial variance existed around this trend ($1-R^2 = 0.774$).

Litter and Depth Experiment

Both total water depth (Mann-Whitney $p = 0.031$, d.f. = 3) and leaf litter type ($Z = -2.172$, Mann-Whitney $p = 0.030$) significantly affected dispersal (Figure 12). However, the depth effect was accentuated by the strong negative effect of leaf litter on net dispersal rate. Leaf litter created a complex 3-dimensional matrix for the fish to navigate and greatly reduced dispersal. Only with 24 mm water levels and wetland litter did fish disperse at a non-zero rate. One individual fish dispersed in each of the 12 mm deep/wetland litter and 24 mm deep/upland litter treatments and six fish dispersed in the 24 mm deep/wetland litter treatment. When statistics were calculated without 24 mm wetland data no significant depth effect existed (Kruskal-Wallis $p = 0.355$), indicating that the 24 mm wetland treatment was solely responsible for significant results. Gender of the fish did not significantly affect net dispersal rate (Kruskal-Wallis $p = 0.816$, d.f. = 1).

In summary, lighting condition, gender and pretrial condition did not significantly affect net dispersal rate; however, habitat of origin, water depth, and leaf litter significantly affected net dispersal rates. On average, mosquitofish from a temporary pond dispersed faster than those from a permanent pond, and fish dispersed faster in deep water and when leaf litter was absent.

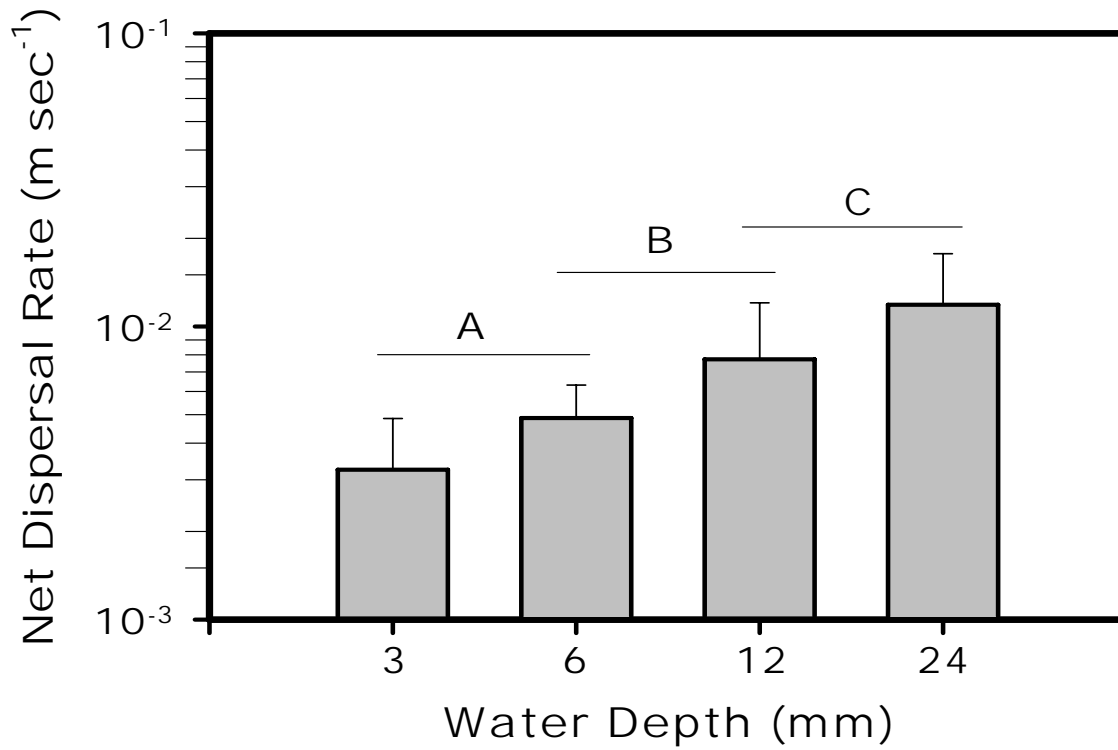


Figure 10: Water Depth

Net dispersal rate (mean and 95% C.I., in m sec^{-1}) in relation to depth (mm). Fish in deeper water dispersed significantly faster than fish in shallow water (ANOVA: $F_{3,92} = 9.666$, $p < 0.0001$). Letters join treatment means that did not differ significantly (Tukey's HSD; $p \geq 0.05$).

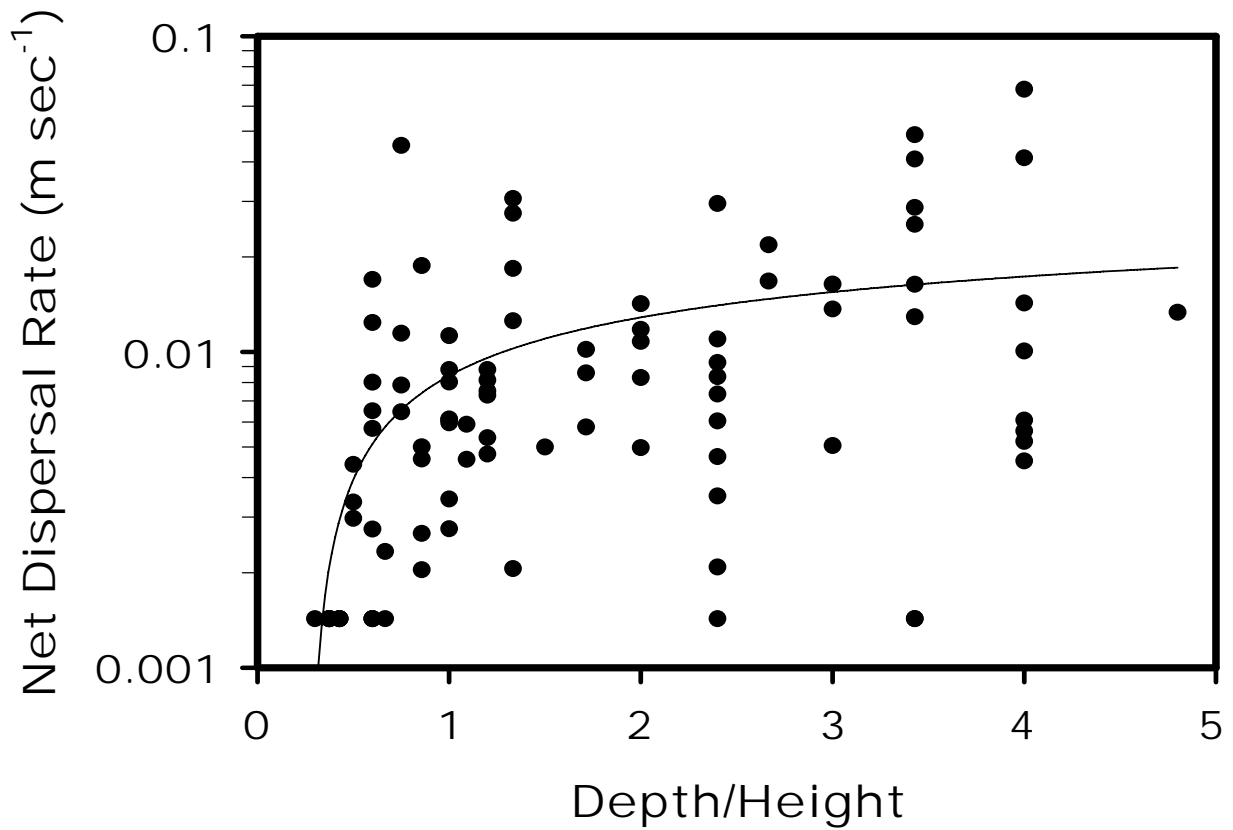


Figure 11: Depth/Height Interaction

The relationship between net dispersal rate (m sec^{-1}) and depth/height for mosquitofish. Most fish dispersed at about the same rate regardless of depth/height, until this ratio was less than one-half or two-thirds of body height. Regression equation: $(\text{rate}(\text{m s}^{-1}) = 0.0064 \log(\text{depth/height}) + 0.0084, 1-R^2=0.774, p<0.0001)$.

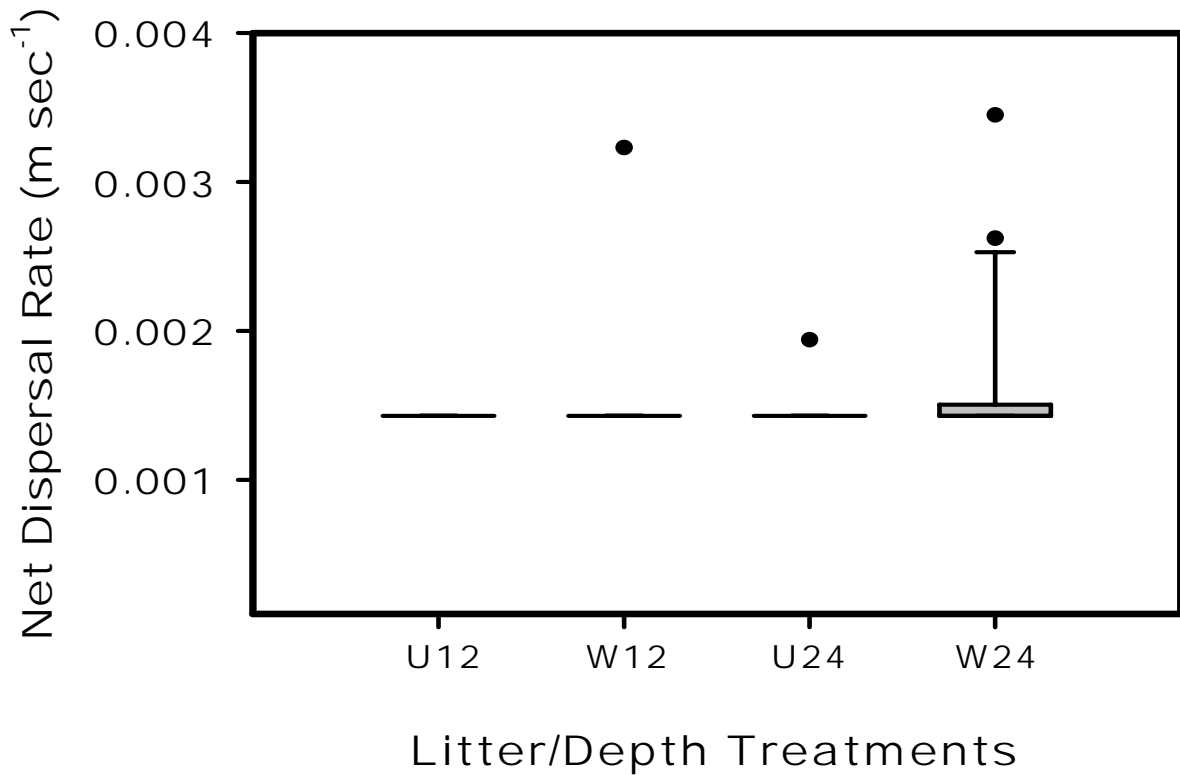


Figure 12: Litter and Depth Experiment

Water depth significantly affected net dispersal time (Mann-Whitney $p=0.031$) when combined with leaf litter in this experiment. Type of leaf litter also significantly affected net dispersal time (Mann-Whitney $p=0.030$) of the fish. Box plots that appear as lines are because fish did not disperse to the finish line within 30 minutes (in fact, most fish did not disperse out of the holding areas).

DISCUSSION

Mosquitofish are a dominant predator in most habitats they enter and are responsible for the decline in indigenous fish, invertebrates and amphibians and change community structure (Courtenay and Meffe 1989) so it is important to eliminate mosquitofish dispersal corridors (Rupp 1996). My experiments showed that mosquitofish dispersed well through relatively low complexity habitat and in water deep enough to maintain gill immersion regardless of gender, hunger, and lighting conditions. Understanding mosquitofish dispersal is important because they prey on local fauna (Meffe et al., 1983; Meffe, 1985) and are an important invasive species in many parts of the world (ISSG, 2000). Mosquitofish also use natural (Snodgrass et al., 1996; Taylor, 1997) or man-made wetland connections (Taylor et al., 1984; Duryea et al., 1996; Swanson et al., 1996); the ability of mosquitofish to gain access to these waterways is enhanced by deliberate introductions for mosquito control (Leyse et al., 2004).

Negative effects of mosquitofish on wetland communities extend beyond those for mosquito control. Initially it was thought that mosquitofish eliminated mosquitoes by eating larvae (Krumholz, 1948) but a debate continues on whether they effectively control mosquitoes (Courtenay and Meffe, 1989). Mosquitofish introduction has negative consequences for everything but the mosquitofish because they are very destructive to the community structure of the habitats they invade (Lloyd et al., 1986; Courtenay and Meffe, 1989; Belk and Lydeard, 1994; Gamradt and Kats, 1996; Webb and Joss, 1997; Goodsell and Kats, 1999; Baber and Babbitt, 2003).

Considered together, mosquitofish from temporary ponds with ~ 1 cm of water depth and a relatively clear path are likely to quickly disperse into hydrologically connected habitats.

Mosquitofish have few limitations to spreading into new habitats, which may be related to their status as one of the 100 worst invasive species (ISSG, 2000). The ability of mosquitofish to colonize new habitats and re-colonize after extinction events make them a model organism for the study of metapopulation dynamics (Gilpin and Hanski, 1997; Bascompte and Sole, 1998; Dieckmann et al., 2000; Doebeli and Killingback, 2003).

My results showed a difference in dispersal behavior phenotype between the temporary and permanent populations I tested, but whether that difference is genetically-based is unknown. Individuals that disperse into temporary ponds may take advantage of increased food availability and reduced predation by larger fish, and continue to reproduce. Many temporary ponds persist less than a year, depending upon interannual climate variation. If fish in temporary habitats disperse again (before a pond dries down) then the disperser genotype will persist (or even increase) in a population. Also, the depths of hydrological connections are critical for this dispersal, given the observed effect of depth on dispersal rates.

Gender-specific dispersal in animals has been observed in many studies (Escorza-Trevino and Dizon 2000; Julliard, 2000; Proctor et al., 2004). However, gender was repeatedly tested in my study and did not affect the net dispersal rate of mosquitofish. Based on my results, mosquitofish dispersal ability is not gender-specific. Mosquitofish have a one-to-one sex ratio at birth, but as they mature the sex ratio becomes female-biased (Snelson, 1989). As adults, females are typically larger than males and one gravid female can found a new population (Meffe and Snelson, 1989). However, it appears unlikely that populations would be founded by a single gravid female, unless by a stochastic process, given no gender difference in dispersal and the fact that smaller males disperse faster in shallower water than larger females. Therefore, it is unlikely

that mosquitofish populations should exhibit strong founder effects. Instead, it is more likely that populations are founded by multiple individuals of both sexes.

To determine if hunger state affected dispersal behavior I subjected mosquitofish to two different hunger treatments: not fed for 24 hours or fed 2 hours prior to trials. Like gender, hunger had no significant effect on dispersal. I had predicted that satiated mosquitofish would disperse more quickly because the food would provide energy. I did not provide food at the end of the arena because I wanted to measure dispersal without the influence of prey searching behavior. Other studies have also examined the effects of hunger on dispersal behavior of animals (Levin, 1994; Osmundson, 1998). Outcomes depended on the organism tested, the question asked, and the experimental design. It is possible that longer periods without food would yield different results for mosquitofish.

Lighting can affect animal behavior in many habitats (Petrell and Ang, 2001). The same was not true for mosquitofish: dispersal rate did not differ significantly between light and dark conditions. My results indicate that mosquitofish will disperse as long as there is a sufficient hydrological connection, whether it is day or night.

Mosquitofish dispersed in depths as shallow as 3 mm, although dispersal at this depth was restricted. In the absence of leaf litter, net dispersal rate increased progressively as water depth increased from 3-24 mm. Combined with results from the gender, light and hunger trials, the water depth experiment shows that mosquitofish can disperse under diverse conditions (Rehage and Sih, 2004) provided hydrological connections are unimpeded. At any body height, diminishing water depth increasingly inhibited dispersal, but these small fish still dispersed in water depths as shallow as 3 mm. If mosquitofish are introduced in a region, they likely will

invade temporary ponds and other aquatic habitats using ephemeral connections as shallow as 1 cm depth and relatively free of obstacles such as leaf litter.

The ability of an invasive species to spread depends on factors such as distance among habitats and rate of dispersal (Parker and Reichard, 1998). Variation in dispersal distances and rates is well documented for many invasive taxa (Swingland, 1983; Bradford and Taylor, 1997). I found that most mosquitofish dispersed at rates of $\sim 0.01\text{m/s}$ with only 12-24 mm of water and an unimpaired pathway. Based on a 24-h dispersal behavior and observed rates, mosquitofish disperse at a rate of $\sim 864\text{ m/day}$ or 25,791 body lengths per day (33.5 mm mean body length). Extrapolated to natural conditions, it is little wonder that mosquitofish spread rapidly into a region upon introduction.

Some small fish preferentially inhabit shallow areas as a means to avoid large piscivorous fish (Bain et al., 1988). Mosquitofish may practice this avoidance behavior (Garcia-Berthoun, 1999), and if so, are likely to disperse through shallow connections between habitats. Mosquitofish can disperse into “isolated” wetland habitats and any others that are hydrologically connected to their present habitat.

A landscape feature that increases potential mosquitofish spread to new areas is the construction of roads and drainage ditches (Trombulak and Frissell, 2000) that form more direct corridors between aquatic habitats. Ditches create connections where previously there were none, and create dispersal corridors for mosquitofish (Courtenay and Meffe, 1989). Changes caused by widespread road construction and drainage structures have changed landscape hydrology and probably promoted spread of mosquitofish within their native range (SE USA) and in regions where they are exotic. Mosquitofish can survive and reproduce under diverse conditions

(Courtenay and Meffe, 1989), including low oxygen levels (McKinsey and Chapman, 1998) which gives them an advantage compared to many other fish.

The addition of leaf litter to the testing arenas increased the complexity of the experimental conditions, and greatly reduced dispersal rates of mosquitofish. Many studies have examined the effect of habitat heterogeneity on dispersal (Turner, 1987; Kolasa and Pickett, 1991; Hansson et al., 1995; Gardner et al., 1989; Johnson et al., 1992). In my experiment mosquitofish did not disperse in shallow water in the presence of either leaf litter type, possibly because pathways for dispersal were limited. Based on my results, mosquitofish are unlikely to disperse through upland litter unless water depths exceed 24 mm. It is much more likely that mosquitofish disperse between wetlands via shallow natural (deer paths) or anthropogenic (trails, ditches, etc.) corridors that lack leaf litter. A clear management application that emerges from this study is to re-fill unused ditches, such as plow lines used to contain wildfires. Harvesting and burning of leaf litter also eliminate potential obstacles to mosquitofish dispersal and may be selectively managed to mitigate mosquitofish spread. Mosquitofish entry into isolated wetlands could be managed by maintaining paths and corridors with upland litter that would permit natural drainage yet block mosquitofish access. Alternatively, shallow mosquitofish dispersal corridors (e.g., trails in wetland vegetation) could be blocked by shallow earthen berms, or unneeded ditches and fire breaks could be plowed under to eliminate the corridors.

This series of short-term laboratory experiments is relevant to future studies of mosquitofish metapopulation dynamics (Hanski and Gilpin, 1991) and invasiveness. With this foundation researchers can undertake studies determining how mosquitofish populations are spatially structured and how their dispersal affects community structure. Understanding more about dispersal behavior will help manage mosquitofish invasions around the world. Future

experiments could be conducted on: 1) genetics of mosquitofish from different habitats that have different dispersal rates, 2) dispersal through more types of litter with varying percentages of total biomass found in nature, 3) dispersal through non-linear corridors, 4) mosquitofish in natural habitats, 5) whether or not the presence of upland litter will prevent dispersal of mosquitofish into new habitats (a field experiment).

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APPENDIX A: Preliminary Data

L-D	min	sec	1/100th	tottime	sex	length	height	pretrial
Dark	1	55	20	115.2	F	35	5	1
Dark	2	54	16	174.16	F	32	6	1
Dark	6	10	4	370.04	F	34	5	1
Dark	11	13	37	673.37	F	24	4	1
Dark	4	11	24	251.24	F	27	6	1
Dark	5	3	14	303.14	F	32	7	1
Dark	5	31	25	331.25	F	38	9	1
Dark	6	59	36	419.36	F	34	7	1
Dark	8	17	15	497.15	F	35	8	1
Dark	10	18	36	618.36	F	21	3	1
Dark	12	45	14	765.14	F	30	8	2
Dark	12	20	35	740.35	F	43	8	2
Dark	12	18	37	738.37	F	44	9	2
Dark	12	26	17	746.17	F	36	6	2
Dark	1	37	39	97.39	F	43	8	2
Dark	12	48	13	768.13	F	40	8	2
Dark	6	16	51	376.51	F	31	7	3
Dark	3	26	88	206.88	F	32	6	3
Dark	15.5	0	0	930	F	46	9	3
Dark	15.5	0	0	930	F	45	10	3
Dark	4	17	0	257	M	30	5	4
Dark	4	34	0	274	M	22	4	4
Dark	5	44	0	344	F	32	5	4
Dark	6	15	0	375	M	38	7	4
Dark	9	23	0	563	F	31	6	4
Dark	7	45	0	465	M	20	3	4
Dark	1	35	0	95	F	38	6	4
Dark	2	17	0	137	M	25	3	4
Dark	4	35	0	275	M	38	8	4
Dark	2	45	0	165	F	42	8	4
Dark	4	1	0	241	M	40	8	4
Dark	5	3	0	303	F	41	8	4
Dark	3	21	0	201	F	38	9	4
Dark	5	36	0	336	M	30	6	4
Dark	15.5	0	0	930	F	35	7	4
Dark	2	31	0	151	M	31	6	4
Dark	4	7	0	247	F	34	6	4
Dark	5	2	0	302	F	32	5	4
Dark	5	6	0	306	M	18	3	4
Dark	15.5	0	0	930	F	38	7	4
Dark	5	30	0	330	F	32	6	4
Dark	1	12	0	72	F	22	3	4
Dark	15.5	0	0	930	F	35	6	4
Dark	15.5	0	0	930	M	32	6	4
Dark	15.5	0	0	930	M	17	2	4
Dark	0	17	0	17	F	35	7	4
Dark	4	35	0	275	M	26	4	4
Dark	3	56	0	236	F	32	5	4
Dark	15.5	0	0	930	M	26	5	4

Dark	3	47	0	227	M	38	7	4
Dark	3	16	40	196.4	M	36	7	1
Dark	5	10	30	310.3	M	40	8	1
Dark	8	19	47	499.47	M	27	4	1
Dark	8	23	31	503.31	M	33	6	1
Dark	10	1	43	601.43	M	30	4	1
Dark	8	6	0	486	M	21	4	1
Dark	9	38	58	578.58	M	25	4	1
Dark	8	2	27	482.27	M	29	6	1
Dark	1	24	37	84.37	M	35	7	2
Dark	1	14	25	74.25	M	24	6	2
Dark	12	34	17	754.17	M	40	8	2
Dark	12	20	40	740.4	M	26	4	2
Dark	1	32	8	92.08	M	24	4	2
Dark	6	2	43	362.43	M	21	4	3
Dark	7	5	17	425.17	M	27	5	3
Light	1	43	44	103.44	F	34	6	1
Light	2	38	13	158.13	F	27	5	1
Light	4	39	36	279.36	F	26	5	1
Light	5	34	51	334.51	F	42	9	1
Light	1	31	15	91.15	F	35	7	1
Light	4	0	41	240.41	F	30	6	1
Light	7	2	50	422.5	F	40	9	1
Light	7	47	31	467.31	F	34	6	1
Light	2	38	18	158.18	F	44	9	1
Light	6	0	0	360	F	33	8	4
Light	5	15	0	315	F	31	5	4
Light	15.5	0	0	930	F	39	8	4
Light	15.5	0	0	930	F	32	5	4
Light	15.5	0	0	930	F	35	6	4
Light	6	35	0	395	F	45	10	4
Light	15.5	0	0	930	F	30	5	4
Light	11	19	0	679	F	28	5	4
Light	1	2	0	62	F	35	5	4
Light	2	12	0	132	F	32	5	4
Light	12	18	13	738.13	F	30	5	2
Light	12	22	13	742.13	F	36	8	2
Light	2	14	13	134.13	F	42	9	2
Light	2	34	26	154.26	F	39	9	2
Light	12	14	23	734.23	F	44	8	3
Light	12	16	22	736.22	F	38	5	3
Light	3	56	25	236.25	M	25	4	1
Light	5	59	13	359.13	M	36	9	1
Light	3	36	18	216.18	M	23	4	1
Light	5	21	27	321.27	M	25	4	1
Light	7	19	8	439.08	M	35	6	1
Light	2	39	42	159.42	M	30	4	1
Light	6	0	16	360.16	M	32	5	1
Light	2	18	58	138.58	M	41	8	1
Light	2	32	42	152.42	M	29	5	1

Light	4	5	0	245	M	22	5	4
Light	6	15	0	375	M	27	4	4
Light	8	37	0	517	M	41	7	4
Light	15.5	0	0	930	M	48	8	4
Light	15.5	0	0	930	M	35	7	4
Light	9	44	0	584	M	32	7	4
Light	2	21	0	141	M	35	7	4
Light	12	47	0	767	M	30	5	4
Light	15.5	0	0	930	M	28	5	4
Light	1	50	0	110	M	31	6	4
Light	4	13	0	253	M	39	8	4
Light	15.5	0	0	930	M	31	5	4
Light	1	4	0	64	M	29	5	4
Light	15.5	0	0	930	M	32	8	4
Light	2	54	0	174	M	35	5	4
Light	15.5	0	0	930	M	34	7	4
Light	2	15	35	135.35	M	34	6	2
Light	2	41	28	161.28	M	22	4	2
Light	12	37	36	757.36	M	35	7	2
Light	1	33	36	93.36	M	26	4	2
Light	1	51	16	111.16	M	34	5	2
Light	2	57	32	177.32	M	22	3	3
Light	2	56	42	176.42	M	22	3	3
Light	1	57	32	117.32	M	24	3	3
Light	2	17	37	137.37	M	37	7	3
Light	2	18	41	138.41	M	25	4	3

APPENDIX B: Habitat Data

Pond type	min	sec	1/100th	totaltime	sex	length	height
P	30	5	0	1805	m	21	3
P	2	42	16	162.16	f	29	8
P	3	18	2	198.02	m	30	7
P	6	57	71	417.71	m	27	4
P	4	33	81	273.81	f	33	6
P	5	49	23	349.23	f	31	6
P	30	5	0	1805	m	20	3
P	5	41	12	341.12	m	32	4
P	30	5	0	1805	f	24	5
P	9	20	16	560.16	m	29	6
P	16	2	37	962.37	m	29	6
P	10	23	1	623.01	f	38	7
P	15	41	82	941.82	f	42	9
P	3	51	71	231.71	m	19	3
P	9	2	37	542.37	m	27	5
P	15	9	52	909.52	m	35	7
P	2	45	61	165.61	m	27	5
P	30	5	0	1805	f	41	8
P	13	17	42	797.42	m	21	4
P	30	5	0	1805	f	25	6
P	30	5	0	1805	f	27	6
P	11	31	43	691.43	m	32	7
P	1	27	32	87.32	f	34	7
P	8	4	65	484.65	m	31	5
T	9	30	41	570.41	f	41	10
T	0	42	33	42.33	m	29	5
T	30	5	0	1805	f	38	8
T	3	57	5	237.05	m	41	12
T	6	29	86	389.86	f	39	10
T	4	16	11	256.11	m	26	5
T	4	50	81	290.81	m	29	7
T	2	19	30	139.3	f	36	8
T	1	3	55	63.55	f	29	7
T	3	8	67	188.67	m	25	6
T	4	23	48	263.48	f	43	10
T	11	28	8	688.08	f	41	10
T	4	11	9	251.09	f	38	9
T	5	28	63	328.63	f	28	8
T	9	15	56	555.56	m	33	9
T	1	49	30	109.3	f	37	9
T	3	4	19	184.19	m	31	6
T	2	29	54	149.54	f	29	7
T	0	48	23	48.23	f	34	7
T	3	11	57	191.57	f	30	6
T	6	51	3	411.03	f	32	8
T	30	5	0	1805	m	36	8
T	4	29	81	269.81	f	26	5
T	1	0	69	60.69	m	25	6

APPENDIX C: Water Depth Data

Pond type	min	sec	1/100th	totaltime	depth	sex	length	height
T	6	36	66	396.66	1/2x	f	27	5
T	9	46	14	586.14	1/2x	m	29	6
T	12	51	10	771.1	1/2x	m	32	6
T	14	28	48	868.48	1/2x	m	30	6
T	30	5	0	1805	1/2x	m	25	5
T	30	5	0	1805	1/2x	f	37	8
T	3	45	23	225.23	1/2x	m	24	4
T	7	30	79	450.79	1/2x	f	30	5
T	15	40	34	940.34	1/2x	m	27	5
T	30	5	0	1805	1/2x	f	34	8
T	30	5	0	1805	1/2x	f	37	8
T	30	5	0	1805	1/2x	m	35	7
T	0	57	20	57.2	1/2x	m	30	4
T	2	32	6	152.06	1/2x	f	29	5
T	30	5	0	1805	1/2x	f	35	8
T	30	5	0	1805	1/2x	f	35	7
T	30	5	0	1805	1/2x	m	39	10
T	30	5	0	1805	1/2x	f	38	8
T	3	28	37	208.37	1/2x	f	24	5
T	5	21	86	321.86	1/2x	f	25	5
T	6	39	41	399.41	1/2x	m	22	4
T	30	5	0	1805	1/2x	f	35	8
T	30	5	0	1805	1/2x	f	37	7
T	30	5	0	1805	1/2x	m	38	7
T	5	21	78	321.78	x	m	32	6
T	5	54	16	354.16	x	m	27	5
T	9	23	5	563.05	x	f	33	7
T	15	37	0	937	x	f	35	6
T	16	10	2	970.02	x	f	38	7
T	30	5	0	1805	x	f	40	10
T	2	17	42	137.42	x	f	36	7
T	3	49	48	229.48	x	m	35	6
T	5	16	93	316.93	x	m	29	5
T	5	28	89	328.89	x	f	39	8
T	12	34	67	754.67	x	f	33	6
T	30	5	0	1805	x	f	42	10
T	4	53	60	293.6	x	f	28	6
T	4	53	68	293.68	x	f	24	5
T	7	3	89	423.89	x	m	29	6
T	8	36	13	516.13	x	f	38	7
T	9	3	85	543.85	x	m	26	5
T	18	26	55	1106.55	x	f	34	9
T	5	43	12	343.12	x	f	31	5
T	7	1	9	421.09	x	f	27	6
T	7	13	13	433.13	x	f	30	6
T	8	2	61	482.61	x	m	28	5
T	21	3	72	1263.72	x	m	35	7
T	30	5	0	1805	x	f	37	9

T	5	0	67	300.67	2x	f	37	7
T	5	11	16	311.16	2x	f	33	6
T	7	17	61	437.61	2x	f	40	11
T	8	30	97	510.97	2x	m	26	4
T	20	38	74	1238.74	2x	m	27	5
T	20	53	12	1253.12	2x	f	37	9
T	1	27	44	87.44	2x	f	26	5
T	3	1	55	181.55	2x	f	31	6
T	3	25	70	205.7	2x	f	38	9
T	3	59	20	239.2	2x	m	32	6
T	9	24	89	564.89	2x	f	40	11
T	30	5	0	1805	2x	m	24	5
T	1	24	38	84.38	2x	f	40	9
T	1	33	90	93.9	2x	f	37	9
T	3	54	89	234.89	2x	m	25	5
T	4	13	43	253.43	2x	f	29	7
T	8	38	71	518.71	2x	m	31	6
T	9	13	90	553.9	2x	m	32	5
T	2	20	46	140.46	2x	f	38	9
T	3	39	16	219.16	2x	m	34	6
T	5	50	77	350.77	2x	m	36	5
T	7	6	58	426.58	2x	f	32	5
T	7	26	56	446.56	2x	f	36	7
T	8	36	28	516.28	2x	m	37	8
T	1	58	13	118.13	4x	f	39	9
T	2	37	42	157.42	4x	f	32	8
T	3	0	83	180.83	4x	m	29	6
T	3	8	65	188.65	4x	f	31	8
T	3	19	81	199.81	4x	f	35	7
T	4	16	49	256.49	4x	m	30	6
T	0	52	94	52.94	4x	m	34	7
T	1	3	28	63.28	4x	m	38	7
T	2	34	1	154.01	4x	f	37	9
T	2	37	58	157.58	4x	f	32	7
T	3	13	35	193.35	4x	m	22	5
T	7	39	37	459.37	4x	f	30	6
T	0	38	2	38.02	4x	m	29	6
T	1	29	97	89.97	4x	f	32	7
T	4	39	9	279.09	4x	f	41	10
T	7	4	69	424.69	4x	m	29	6
T	8	15	99	495.99	4x	f	31	6
T	30	5	0	1805	4x	f	34	7
T	1	2	70	62.7	4x	m	36	6
T	1	41	80	101.8	4x	f	34	7
T	5	9	34	309.34	4x	f	39	10
T	9	31	45	571.45	4x	m	32	6
T	12	18	3	738.03	4x	f	42	10
T	30	5	0	1805	4x	f	33	7

APPENDIX D: Litter/Depth Data

Pond type	min	sec	1/100th	totime	litter type	Depth(mm)	sex	length	height
T	30	5		1805	u	3	f	37	8
T	30	5		1805	u	3	f	23	6
T	30	5		1805	u	3	m	20	4
T	30	5		1805	u	3	f	29	7
T	30	5		1805	u	3	m	31	5
T	30	5		1805	u	3	f	34	6
T	30	5		1805	u	3	m	29	6
T	30	5		1805	u	3	f	35	7
T	30	5		1805	u	3	f	40	9
T	30	5		1805	u	3	f	28	7
T	30	5		1805	u	3	m	34	7
T	30	5		1805	u	3	f	30	6
T	30	5		1805	w	3	f	37	8
T	30	5		1805	w	3	f	41	10
T	30	5		1805	w	3	m	30	5
T	30	5		1805	w	3	f	32	6
T	30	5		1805	w	3	m	37	6
T	30	5		1805	w	3	f	35	6
T	30	5		1805	w	3	f	36	8
T	30	5		1805	w	3	m	33	6
T	30	5		1805	w	3	f	40	9
T	30	5		1805	w	3	m	30	6
T	30	5		1805	w	3	f	35	7
T	30	5		1805	w	3	f	36	7
T	30	5		1805	w	3	f	39	8
T	30	5		1805	w	3	f	44	9
T	30	5		1805	w	3	f	43	9
T	30	5		1805	w	3	f	37	6
T	30	5		1805	w	3	m	34	6
T	30	5		1805	w	3	f	41	10
T	30	5		1805	u	3	f	39	7
T	30	5		1805	u	3	f	42	9
T	30	5		1805	u	3	f	41	9
T	30	5		1805	u	3	m	33	6
T	30	5		1805	u	3	f	39	7
T	30	5		1805	u	3	m	30	5
T	30	5		1805	u	3	f	35	7
T	30	5		1805	u	3	f	40	10
T	30	5		1805	u	3	m	37	7
T	30	5		1805	u	3	f	32	6
T	30	5		1805	u	3	f	45	9
T	30	5		1805	u	3	m	34	6
T	30	5		1805	w	3	m	34	5
T	30	5		1805	w	3	f	38	8
T	30	5		1805	w	3	f	33	6
T	30	5		1805	w	3	f	37	8
T	30	5		1805	w	3	f	40	9
T	30	5		1805	w	3	m	32	5

T	30	5	1805	w	6	f	35	6
T	30	5	1805	w	6	m	32	5
T	30	5	1805	w	6	f	38	9
T	30	5	1805	w	6	m	34	5
T	30	5	1805	w	6	m	36	5
T	30	5	1805	w	6	f	39	9
T	30	5	1805	w	6	f	28	6
T	30	5	1805	w	6	f	34	7
T	30	5	1805	w	6	m	27	5
T	30	5	1805	w	6	f	31	6
T	30	5	1805	w	6	f	36	8
T	30	5	1805	w	6	m	30	6
T	30	5	1805	u	6	f	39	8
T	30	5	1805	u	6	f	28	6
T	30	5	1805	u	6	f	40	10
T	30	5	1805	u	6	m	36	6
T	30	5	1805	u	6	m	34	6
T	30	5	1805	u	6	f	37	8
T	30	5	1805	u	6	f	36	8
T	30	5	1805	u	6	m	24	6
T	30	5	1805	u	6	m	26	6
T	30	5	1805	u	6	f	35	8
T	30	5	1805	u	6	f	29	7
T	30	5	1805	u	6	f	38	7
T	30	5	1805	u	6	m	29	6
T	30	5	1805	u	6	f	42	10
T	30	5	1805	u	6	m	36	7
T	30	5	1805	u	6	f	40	9
T	30	5	1805	u	6	m	31	6
T	30	5	1805	u	6	f	45	10
T	30	5	1805	w	6	f	44	10
T	30	5	1805	w	6	m	35	6
T	30	5	1805	w	6	f	39	8
T	30	5	1805	w	6	f	38	7
T	30	5	1805	w	6	f	38	8
T	30	5	1805	w	6	m	32	6
T	30	5	1805	w	6	f	38	7
T	30	5	1805	w	6	m	31	5
T	30	5	1805	w	6	m	34	6
T	30	5	1805	w	6	f	42	9
T	30	5	1805	w	6	f	40	9
T	30	5	1805	w	6	f	35	7
T	30	5	1805	u	6	f	36	7
T	30	5	1805	u	6	m	27	5
T	30	5	1805	u	6	m	23	4
T	30	5	1805	u	6	f	39	8
T	30	5	1805	u	6	f	28	5
T	30	5	1805	u	6	f	30	7
T	30	5	1805	u	12	f	30	6
T	30	5	1805	u	12	f	34	6

T	30	5		1805	u	12	f	40	10
T	30	5		1805	u	12	f	37	8
T	30	5		1805	u	12	f	29	6
T	30	5		1805	u	12	m	26	5
T	30	5		1805	u	12	m	37	7
T	30	5		1805	u	12	f	39	8
T	30	5		1805	u	12	m	25	6
T	30	5		1805	u	12	m	26	6
T	30	5		1805	u	12	f	40	9
T	30	5		1805	u	12	f	39	9
T	13	18	73	798.73	w	12	m	27	6
T	30	5		1805	w	12	f	40	9
T	30	5		1805	w	12	f	32	7
T	30	5		1805	w	12	f	37	8
T	30	5		1805	w	12	f	35	7
T	30	5		1805	w	12	f	35	7
T	30	5		1805	w	12	f	43	9
T	30	5		1805	w	12	f	36	7
T	30	5		1805	w	12	f	33	6
T	30	5		1805	w	12	f	46	10
T	30	5		1805	w	12	m	27	4
T	30	5		1805	w	12	f	41	8
T	30	5		1805	w	12	f	33	6
T	30	5		1805	w	12	m	32	6
T	30	5		1805	w	12	m	43	8
T	30	5		1805	w	12	m	15	5
T	30	5		1805	w	12	m	26	4
T	30	5		1805	w	12	f	50	10
T	30	5		1805	u	12	m	35	6
T	30	5		1805	u	12	f	44	9
T	30	5		1805	u	12	f	37	6
T	30	5		1805	u	12	f	42	8
T	30	5		1805	u	12	f	41	8
T	30	5		1805	u	12	m	32	6
T	30	5		1805	u	12	m	40	8
T	30	5		1805	u	12	f	37	8
T	30	5		1805	u	12	f	39	8
T	30	5		1805	u	12	f	43	10
T	30	5		1805	u	12	f	39	8
T	30	5		1805	u	12	m	34	6
T	30	5		1805	w	12	f	36	7
T	30	5		1805	w	12	m	29	6
T	30	5		1805	w	12	m	24	5
T	30	5		1805	w	12	f	33	6
T	30	5		1805	w	12	f	39	8
T	30	5		1805	w	12	f	37	6
T	12	27	84	747.84	w	24	m	24	6
T	16	23	81	983.81	w	24	f	31	8
T	30	5		1805	w	24	m	27	6
T	30	5		1805	w	24	f	34	7

T	30	5		1805	w	24	f	38	9
T	30	5		1805	w	24	f	29	7
T	17	4	31	1024.31	w	24	f	33	6
T	27	14	15	1634.15	w	24	f	38	7
T	30	5		1805	w	24	m	30	6
T	30	5		1805	w	24	f	34	8
T	30	5		1805	w	24	f	39	10
T	30	5		1805	w	24	m	35	6
T	22	9	54	1329.54	u	24	f	41	10
T	30	5		1805	u	24	m	27	5
T	30	5		1805	u	24	m	31	6
T	30	5		1805	u	24	f	39	8
T	30	5		1805	u	24	f	38	8
T	30	5		1805	u	24	f	33	6
T	18	44	15	1124.15	w	24	m	35	6
T	23	5	61	1385.61	w	24	f	35	7
T	30	5		1805	u	24	m	30	5
T	30	5		1805	u	24	f	36	8
T	30	5		1805	u	24	m	29	5
T	30	5		1805	u	24	f	34	7
T	30	5		1805	u	24	f	40	9
T	30	5		1805	u	24	f	38	9
T	30	5		1805	u	24	f	40	8
T	30	5		1805	u	24	f	41	8
T	30	5		1805	u	24	f	41	7
T	30	5		1805	u	24	f	38	6
T	30	5		1805	u	24	m	39	5
T	30	5		1805	u	24	m	36	7
T	30	5		1805	w	24	f	45	10
T	30	5		1805	w	24	m	36	7
T	30	5		1805	w	24	m	30	5
T	30	5		1805	w	24	f	43	9
T	30	5		1805	w	24	f	38	7
T	30	5		1805	w	24	f	40	9
T	30	5		1805	w	24	m	38	7
T	30	5		1805	w	24	f	35	6
T	30	5		1805	w	24	m	30	5
T	30	5		1805	w	24	f	45	9
T	30	5		1805	u	24	f	37	8
T	30	5		1805	u	24	f	38	8
T	30	5		1805	u	24	f	35	6
T	30	5		1805	u	24	m	35	6
T	30	5		1805	u	24	f	40	8
T	30	5		1805	u	24	m	27	5