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NATURAL HISTORY, BEHAVIOR AND SPECIES COMPOSITION OF WHIRILIGIG BEETLES (COLEOPTERA: GYRINIDAE) IN FISH AND FISHLESS PONDS

By

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ABSTRACT

NATURAL HISTORY, BEHAVIOR AND SPECIES COMPOSITION OF WHIRLIGIG BEETLES (COLEOPTERA: GYRINIDAE) IN FISH AND FISHLESS PONDS

By

Christine Lewis

Fish are often key predators in many aquatic habitats. In order to obtain an understanding of the influence of fish on gyrinid population distribution and species composition, *Dineutus* and *Gyrinus* adults were observed in natural and experimental fish and fishless environments. Daily gyrinid activity was observed in experimental fish and fishless ponds. Gyrinid population densities in natural fish and fishless ponds of the two genera were estimated. Finally, a transplant experiment was performed which studied dispersal tendencies of gyrinids acclimated to specific fish or fishless habitats. Daily activity of *Dineutus* adults did not differ in fish and fishless ponds or during various times of the day. *Dineutus* adult densities were greatest in natural fishless ponds and *Gyrinus* adult densities were greatest in natural fish ponds. Fishless acclimated *Gyrinus* adults dispersed less from fish enclosures, while no influence of fish presence/absence was found on *Dineutus* adult dispersal. Gyrinid population regulation may be partially controlled by fish predation, inter- and intraspecific competition and predator-prey relationships between gyrinid larvae and other aquatic invertebrates, and also by competition between *Dineutus* and *Gyrinus* adults.

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I. INTRODUCTION AND NATURAL HISTORY

Larval and adult whirligig beetles (Coleoptera: Gyrinidae) are important members in freshwater communities (Heinrich and Vogt 1980). The distribution and abundance of larval and adult gyrinids may be influenced by inter- and intraspecific interactions, through such mechanisms as competition for resources, predation and cannibalism (Istock 1966; Fox 1975b).

Fish may also exert indirect or direct effects on gyrinid distribution and abundance in lakes and ponds. For example, McPeek (1989) found that one group of *Enallagma* sp. (Odonata: Coenagrionidae) were found in lakes containing fish and another distinct group was found in fishless lakes.

The purpose of my study was to compare natural history attributes of *Dineutus* sp. and *Gyrinus* sp., and to compare adult distributions of *Dineutus* sp. and *Gyrinus* sp. in fish and fishless ponds. Natural history attributes that were addressed were egg and brood size, larval growth, larval survival and adult habitat preference. A transplant experiment utilizing fish and fishless acclimated gyrinids was executed in order to determine the influence of fish on gyrinid dispersal. Several possible explanations for the distributions of *Dineutus* sp. and *Gyrinus* sp. in ponds are explained, which could be due to the presence or absence of predatory fish.

Only a limited amount of research has been completed on the family Gyrinidae, and this information is scattered throughout the literature. Therefore, a review of life history attributes for the common gyrinid genera of Michigan is completed. The review not only compiles most of the literature pertaining to gyrinids, but it also provides important background information for the following study.

Adults

Whirligig beetles (Coleoptera: Gyrinidae) inhabit quiet water regions, including ditches, ponds, wetlands, lakes and slow moving sections of streams (Hatch 1925). The north American family Gyrinidae contains three genera, *Gyretes, Dineutus*, and *Gyrinus.* The genus *Gyretes* has not been recorded in Michigan, whereas the genus *Dineutus*, which is comprised of four species (*D. assimilis, D. discolor, D. hornii* and *D. nigrior)*, is common. *Gyrinus* is also widespread and approximately 17 species have been recorded in Michigan (Ferkinhoff and Gundersen 1983). (See Appendix for list) *Dineutus* adult body size ranges from 10 to 13 cm while the smaller *Gyrinus* adult sizes range from three to eight cm (Hilsenhoff 1990).

After diapausing in the pond or stream shore substrate through the winter, adult gyrinids begin to appear on the water's surface between late April and early May (Smith 1926). Solitary individuals often rest motionless or swim slowly over the surface of the water (Hatch 1925). However, more commonly *Dineutus* and *Gyrinus* adults exhibit a unique behavior called rafting. These genera are gregarious in nature and, as a result, are often viewed in large, multi-species aggregates or rafts. Rafts consist from a few individuals up to thousands, though scattered solitary individuals are also commonly observed (Heinrich and Vogt 1980). To aggregate into large groups, adult gyrinids require open water areas, though rafts are usually found along the pond margins.

(Heinrich and Vogt 1980). However, emergent plants may provide a distributional constraint by disrupting the close proximity required by the beetles to form rafts.

Gyrinids are highly adapted members of the neuston, surface-dwelling communities, but are also capable of diving within the water column (Hatch 1925). The surface tension is an important property of water that assists in keeping the adults afloat. Gyrinid adults contain an air store that provides buoyancy, an adaptation that is different from other true neuston taxa. As a result of the air store, adult gyrinids must grasp onto vegetation when underwater in order to maintain their position.

As the beetle rests, its' body is depressed slightly on all sides by water, which lends support (Hatch 1925). Depression of the eyes and a streamlined body form provide a minimal amount of resistance in the water (Hatch 1925). The legs of gyrinids are flat and oar-like, which enables them to be efficient and fast swimmers. *Dineutus* adults are capable of swimming over 16.6 times their body length per second and *Gyrinus* adults 12 times their body length per second (Hatch 1925).

The eyes, located on the head of the insect, and Johnston's organs, located in the antennae, float on the water's surface, aiding adult gyrinids in prey capture, predator avoidance and detecting suitable mates (Kolmes 1983a; Henrikson and Stenson 1993). The Johnston's organs are extremely sensitive to vibrations transmitted on the water's surface, with detection capabilities as small as a few micrometers (Kolmes 1983a). In order to see simultaneously above and below the surface of the water, gyrinids have developed horizontally divided compound eyes. While swimming, the pair of ventral eyes is submerged below the water and the dorsal pair is completely above the water (Bennett 1967). Both sets of eyes contain two groups of visual pigments, one that absorbs light in the UV range, and one that absorbs light in the visible range. However, the ventral eyes are much more sensitive to UV light than the dorsal eyes, possibly enabling gyrinids to see more proficiently underwater (Bennett 1967). The combination of these unusual eyes and Johnston's organs assist adult gyrinids in sensing predators and prey that enter the surface film from above or below.

Communication within individuals of the same species is necessary when detecting predators, prey and potential mates. Several aquatic insects, including water striders, giant water bugs, and possibly whirligig beetles, communicate with each other through perceiving changes in the water's surface, referred to as ripple communication (Wilcox 1995). Gyrinids create circular, capillary waves that are capable of extending up to twelve body lengths in front of them (Tucker 1969). By manipulating the position of their antennae and detecting the reflection of abnormal waves, gyrinids are able to determine the position of solid objects (Tucker 1969). In water striders, these communications convey displays of courtship, copulation, postcopulation, sex discrimination, mate-guarding, enhancement of female foraging, non-territorial individual spacing, and intra- and interspecific territoriality (Wilcox 1995). In giant water bugs, ripple communications may be utilized in male courtship and aggressiveness in oviposition. Gyrinids are also believed to potentially exercise this form of communication, however experiments regarding these forms of communication, have not been conducted (Wilcox 1995).

Another form of communication observed in gyrinids includes touching between two individuals while swimming. While swimming in tight rafts, gyrinids often come into close proximity and bump one another. Three types of contact are most often observed, including head to head touches, middle third of the body touches and posterior third of the body touches (Freilich 1986). *Dineutus* and *Gyrinus* adults exhibit this behavior, however there appears to be species specific variation (Freilich 1986). In fishless ponds during the day, *Dineutus emarginatus* individuals are moderately active and touches are frequent. At night, significantly fewer touches occur, though beetles are more active. Inactive periods occur at sunrise and sunset (Freilich 1989). Touches of *Dineutus assimilis* adults have been observed to be non-random and relate to daily activity patterns, demonstrating that touches may be a form of communication (Freilich 1986). Temperature has also been determined to affect contact rates between gyrinids. In streams, contact rates of *Dineutus* adults increase with elevations in temperature. However, contact rates of adult *Dineutus* living in ponds increase with temperature up to 21° C, after which, rates have been observed to decline (Vulinec and Kolmes 1987).

Live and dead soft-bodied insects trapped in the surface film are the typical prey of adult gyrinids (Heinrich and Vogt 1980; Kolmes 1983a; Romey 1995). Insects found in the surface of the water are either terrestrial, entering the water from nearby shores or the sky, emergent, or are themselves inhabitants of the surface. Abundance and diversity of insects caught in the surface film is greatest between zero and 100 m from shore, thereafter decreasing with distance from the shore (Norlin 1964). In many pond habitats, shrub vegetation is present along the shore. Gyrinids are frequently observed rafting under overhanging shrubs, when emergent plants are not a hindrance. In this microhabitat gyrinids are in a prime location for obtaining the maximum amount of available food, and are protected from aerial predators.

Adult Defensive Mechanisms

Potential predators, such as fish, birds and other vertebrates, commonly co-occur with whirligig beetles in given aquatic habitats. Adult gyrinids display several defensive mechanisms against these threats. Gyrinidal, an aldehyde, is a pheromone produced in a gyrinid's paired pygidial glands (Meinwald *et al.* 1972). This substance is a strong smelling and distasteful substance that is occasionally toxic to fish and other vertebrate predators (Benfield 1972; Henrikson and Stenson 1993). Gyrinids release gyrinidal only under physical attack from a predator, thereby, only utilizing it as a last resort for escape. This pheromone apparently communicates the closeness of predators, due to the evasive behaviors demonstrated by gyrinids when placed in water that is prepared with the defensive secretion (Henrikson and Stenson 1993). Naive predators, such as young of the year fish, often attack adult gyrinids, however, they learn quickly to avoid the beetles (Benfield 1972). The excretion of this distasteful substance is probably the main reason why adult gyrinids are rarely found in the stomachs of fish or birds, where other water beetles are common (Benfield 1972).

The formation of aggregates of many individuals is hypothesized to result from the predation of marginal individuals (Hamilton 1971). When a predator attacks a group of prey from the outside, the individuals along the margin of the group are more likely to be eaten. By moving closer to one's neighbor the risk of predation decreases. Instead of just one individual being the subject of predation, now both of the individuals are equally prone to being consumed. Individuals benefit from moving closer to their neighbors through the dilution effect, resulting from attack rate per individual decreasing with increasing group size. This behavior describes the "selfish herd" hypothesis (Hamilton

1971). Even though attack rate per individual decreases as the group size increases, the overall number of attacks on the entire group is elevated with larger group sizes. Therefore, the individual is not acting unselfishly to ensure the survival of the population or species. Instead, it is selfishly improving its own chance of survival. Similarly, gyrinid rafts may be considered "selfish herds." Watt and Chapman (1998) measured that the number of fish attacks on gyrinid rafts elevates with increasing group size. However, attack rates per individual gyrinid decrease (Watt and Chapman 1998). Rafting behavior therefore increases the individual beetle's fitness.

Gyrinid rafts may also serve as predation deterrents through advertisement of their unpalatability, early detection and predator confusion (fright reaction). By rafting among many individuals, gyrinids advertise their presence through the secretion of gyrinidal and consequently, are easily noticed by experienced predators (Heinrich and Vogt 1980; Henrikson and Stenson 1993). The increased number of eyes in a group and the detection of waves by members of the raft influence early detection (Vulinec and Miller 1989). The smaller the distance among beetles in a raft, the shorter the distance waves must travel to be detected by another beetle. As a result, gyrinids are able to detect predators more quickly when rafting in large groups than when they are solitary.

Another method to deter predation involves a fright reaction. The fright reaction is initiated when a visual stimulus, such as a diving bird, or a tactual stimulus, such as moving water or contact with a foreign object, disturbs the beetles. Gyrinids respond by dispersing from their rafts and increasing their rate of turning and swimming. The combination of which produces the rapid gyrations associated with the "fright" reaction (Hatch 1925; Brown and Hatch 1929; Newhouse and Aiken 1986). The accelerated movement of the beetles disorients the predator, increasing the beetle's chance of escape. The fright reaction is amplified when beetles raft in large groups, thereby increasing the number of rapidly moving prey. If left undisturbed after the initial stimulus, gyrinids will rejoin their rafts within a few minutes (Newhouse and Aiken 1986).

The behavior of adult *Dineutus* varies depending on the presence or absence of predatory fish in their environment (Fitzgerald 1987). In fishless ponds, beetles tend to raft in the open water in the morning when temperatures are cooler, and reactions to predators are slower. Rafting in the sun increases body temperature and confers a greater degree of safety from predators. In the afternoon, the population becomes more evenly distributed over the water's surface, and individuals from rafts swim towards the margins to defend territories against beetles of the same sex. Gyrinids that are not able to successfully defend a territory are often observed individually in the center of the pond. Upon nightfall, when shady and sunny regions of the water body are the least distinct, gyrinids forage and at this time exhibit a distribution that is the most evenly dispersed (Fitzgerald 1987).

Gyrinid behavior changes considerably in ponds or lakes where predatory fish are prevalent. Adult gyrinids raft continuously throughout the day and disperse to feed at night (Heinrich and Vogt 1980). As dusk approaches, beetles start to slowly move within their rafts. Circumference and beetle activity within each raft increase with the onset of nightfall. Beetles may disperse from the rafts to feed individually in straight lines, or in small groups. As sunrise approaches, beetles begin to follow one another, in a train-like pattern, back to their respective rafts (Heinrich and Vogt 1980). Raft locations are considered to be 'safe' from predators, because most individuals, which are attacked by fish, have dispersed from the rafts (Heinrich and Vogt 1980). The presence or absence of predators can influence the daily behavioral patterns of gyrinids.

Dispersal

An individual's propensity to disperse grows with increasing environmental variability and unpredictability (Svensson 1998). In a continuously changing habitat, such as temporal ponds that dry up for a length of time during the year, insects must disperse to other favorable habitats in order to survive. Gyrinids often inhabit temporal ponds or ditches that frequently disappear during the summer. Several studies have investigated the dispersal of gyrinids under such conditions (Eijk 1983; Svensson 1985; Nurnberger and Harrison 1995; Nurnberger 1996; Svensson 1998). No differences in dispersal rates or distance of individual dispersals have been observed between male and female gyrinids. However, there are disagreements as to the frequency of dispersal among gyrinids and the distance of the average dispersal movement. Eijk (1983) states that dispersal is infrequent, not exceeding five percent. Nurnberger and Harrison (1995) describe that immigration rates are large but highly variable. Svensson (1985) observed that dispersals were mainly between regions and ponds of great distance. The use of mitochondrial DNA (mtDNA) indicates that gene flow is important with *D. assimilis* over a wide geographic range but genetic drift in local populations counteracts this force (Nurnberger and Harrison 1995).

There may be several benefits and costs associated with the dispersal of individual adult gyrinids. Benefits include the ability to disperse when habitat quality diminishes (pond dries up or plant cover decreases the amount of available habitat), and the ability to

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spread ones propagules to several locations, thereby increasing the chance of offspring survival. Costs of gyrinid dispersal include the concept that habitat availability is sparse in comparison with the overall landscape (Nurnberger and Harrison 1995). Immigration into empty sites, where gyrinids are absent, can be potentially dangerous due to possible exclusion of adult gyrinids by predatory fish (Nurnberger 1996).

In temperate areas, dispersal is greatest during May and June and decreases throughout the summer (Eijk 1983; Svensson 1985; Nurnberger 1996). Tenerals, newly emerged adults, are incapable of flying due to their soft elytra and undeveloped flight muscles. Tenerals are absent in May and June, when dispersal is at its highest, but are the dominant component of the adult population in late summer when dispersal is low (Eijk 1983; Svensson 1985). This pattern of dispersal can also be explained based on gyrinid flight most frequently occurring above temperatures of 19° C, which is more likely to occur during the beginning of the summer. In temperatures greater than 30° C, which coincides with later summer temperatures, gyrinids become inactive and seek shelter from the sun (Eijk 1983).

Reproduction

Gyrinids normally exhibit univoltine life histories (Istock 1966; Merritt and Cummins 1996), reproducing during only one period of their lives. However, some gyrinids have been observed to live several years, reproducing during several mating seasons (Svensson 1998). Life-span ranges from one to two years. The adults are not active during the winter months, while they are in diapause. Adult gyrinids, which have successfully over-wintered, will reproduce the following summer, as soon as they appear on the surface of the water (Eijk 1986a). The first generation dies soon after it has reproduced. Roughly one week after oviposition, larval gyrinids hatch. Larvae require four to five weeks to reach maturity, resulting in a mid-summer emergence of adults from the second generation. These adults do not reproduce, but will instead over-winter and reproduce during the next mating season (Eijk 1986a; Hatch 1925).

Whirligig reproduction involves many activities, including precopulatory behavior, copulation/fertilization, and oviposition (Eijk 1986a). Precopulatory behavior in *D. discolor* is initiated by the female behavior of "proleg-up" (Kolmes 1983b). During this act, the female extends the prothoracic leg as high above the surface of the water as possible. This structure is the only sexually dimorphic region on the adult gyrinid, with the exception of the genitalia. This precopulatory communication identifies the female's sexual identity and willingness to copulate (Kolmes 1983b). Male gyrinids also display a precopulatory behavior referred to as mounting. Without extending the male genitalia, females mount males and males mount males. Therefore, this behavior is viewed as a signal and not as unsuccessful attempts to copulate (Kolmes 1883b). Precopulatory behavior is essential in choosing appropriate mates.

Copulation is the next stage of reproduction. *Dineutus* and *Gyrinus* adults copulate on the surface of the water (Hatch 1925). The male initially assumes a position on the back of the female. The tip of the male abdomen contains the genitalia. The abdomen is curved down and makes contact with the tip of the female's abdomen, which contains the female genitalia. Copulation, with the male on top of the female, can take up to a day before completion (Hatch 1925).

Egg production, which follows copulation, proceeds from April until mid-August (Eijk 1986a). While ovipositing, females adhere each egg individually onto submerged vegetation or other suitable underwater substrates. The number of *Gyrinus* eggs laid per oviposit averages approximately 32 in the spring, and approximately 25 eggs in the summer (Eijk 1986a). A single *Dineutus* female lays approximately 20 to 50 eggs per brood (Hatch 1925). Production of eggs and percent of ovipositing females increases with a female's age (Eijk 1986a). Egg production is at its maximum in mid-May and decreases throughout the summer. A decline in egg production as the summer proceeds may be the outcome of increasing food shortages, decreasing frequency of copulations and an average younger age of adult female gyrinids (Eijk 1986a).

Larvae

Larvae that quickly hatch from eggs exhibit a slow seasonal life history cycle, which is characteristic of many aquatic insects (Hynes 1970). Gyrinids exhibit this life history pattern, based on a one to several week incubation period before hatching, and because gyrinids diapause as adults instead of eggs (Eijk 1986a),

Gyrinid larvae have several distinguishing characteristics that separate them from other Coleopteran larvae. Gyrinids possess paired gills on the first eight abdominal segments (one gill on each side of the segment), two pairs of gills on the last abdominal segment (two gills on each side of the segment) and two tarsal claws on each leg. Four apical hooks are located on its' last abdominal segment and assist the gyrinid larvae in crawling out of the water before pupation (Hatch 1925; Merritt and Cummins 1996). Paired gills enable gyrinid larvae to live continuously several meters underwater on submerged vegetation, while other Coleopteran larvae, without gills, must surface to obtain oxygen (Hatch 1925). Larvae feed voraciously on invertebrates and some small vertebrates by sucking out their internal organs (Hatch 1925). When given the opportunity, gyrinid larvae are cannibalistic (Istock 1966).

Population Control

Freshwater insect populations can be specious, and controlled by a variety of mechanisms including cannibalism, competition for resources and predation. Cannibalism is a density-dependent regulating component of some aquatic insect populations (Istock 1966; Fox 1975a, b; Sih 1982; Buskirk 1987 and 1989; Orr *et al.* 1990). Densities of adult dragonfly populations, which emerge from ponds free of fish, are controlled largely by interactions in the larval stage. Larger dragonflies frequently prey upon smaller instars, decreasing their rate of survival. Cannibalism reduces the variation in size distributions among larval dragonfly populations and enables adult dragonflies to synchronously emerge (Burskirk 1989). Due to decreased densities of smaller instars, cannibalism also reduces competition for resources in the population as a whole. Higher proportions of dragonfly adults emerge from habitats where larval densities are low, resulting from reduced competition for resources (Bruskirk 1987).

As a result of decreased food availability, hemipteran notonectids also frequently cannibalize smaller conspecifics. Thus, the population size declines before starvation ensues and the population size-structure is modified. These population modifications determine the number of adults which reach maturity (Fox 1975a). Even when alternative prey are abundant, cannibalism occurs when age-classes coexist on vegetation

(Fox 1975b). When various larval instars occupy the same region, earlier instars actively change their utilization of space, reducing their risk of predation from larger instars and adults (Sih 1982).

Populations of gyrinids are also largely controlled by larval cannibalism (Istock 1966). *D. assimilis, D. hornii,* and *D. nigrior* coexist in the northern Midwest United States. When placed together, the outcome of cannibalism was discovered to be determined by the size of the individuals, food availability and water temperature (Istock 1966). As with notonectids, altered population size-structure and food availability, resulting from decreased competition, determines the number of adult gyrinids that reach maturity.

Competition among conspecifics and other freshwater insects are also contributing mechanisms, which assist in controlling gyrinid populations. Larval gyrinids compete for food, not only amongst themselves (Istock 1966), but also with other aquatic invertebrates. Adult gyrinids prey on soft bodied insects that become trapped in the water's surface, forcing them to compete with conspecifics, fish and other macroinvertebrates that look to the surface for foraging opportunities (Heinrich and Vogt 1980; Kolmes 1983a; Romey 1995). As an example, larger instars of notonectids were found to mainly prey on terrestrial insects that fall onto the surface (Orr *et al.* 1990).

Whirligig populations appear to be partially controlled by predaceous vertebrates. Although, adult gyrinids are infrequently encountered in the stomachs of fish or birds, because of their unpalatability (Benfield 1972), gyrinid larvae are often found in fish stomachs (Forbes 1890). Therefore, the adult population numbers could be largely determined by the overall survival of the larvae.

A minimal amount of research has investigated the influence of fish on species composition of adult gyrinids (Nurnberger 1996). Nurnberger (1996) observed that the presence of bluegill and largemouth bass had a strong negative impact on the occurrence of *Dineutus assimilis*. However, no study has analyzed whether *Dineutus* sp. or *Gyrinus* sp. are preferentially preyed upon by fish. There is also no comparison of the spatial distribution between the two genera in regards to the presence or absence of predatory fish.

II. METHODS

Site Descriptions

Gyrinid beetles were observed at three sites in southern Michigan during the summers of 1997 and 1998. The Kellogg Biological Station (KBS) is located in lower southwestern Michigan on the east shore of Gull Lake. The station lies approximately 19 km northwest of Battle Creek and approximately 24 km northeast of Kalamazoo. A total of 1,645 ha are owned by the Kellogg Biological Station. An experimental pond facility that was built in the 1970's, with 18 replicate ponds, is located in the immediate vicinity of the station. Each pond has a diameter of approximately 29 m, a depth of 2 m, volume of approximately 1007 m^3 and has developed some degree of macrophyte cover. Six ponds were used in this study. Macrophytes present within the experimental ponds include, *Typha* sp., *Potamogeton* sp., *Nuphar* sp. and *Nymphaea* sp.

Lux Arbor Reserve is located approximately 10 km northwest of the KBS in southern Barry County. A total of 535 ha are distributed into approximately 249 ha of agricultural land, 92 ha of deciduous wood-lot and 194 ha of ponds, wetlands and open land (KBS'er 1991). There are approximately 29 natural ponds of various sizes and vegetative cover, of which 10 were used in this study (Table 2.1).

Barry State Game Area lies within Yankee Springs, Thornapple, Rutland, Orangeville and Hope townships in Barry County. The area is comprised of approximately 6,597 ha with an additional 1,012 ha located adjacent to the Yankee Springs Recreation Area (Bishop, *pers. comm.*). The land consists of approximately

60% forested, 17% permanent openings, 15% upland brush and 8% wetlands areas (Bishop 1998, *pers.comm.*). A total of seven ponds were used in this study (Table 2.1)

Table 2.1 Surface acreage, dominant macrophyte and the presence or absence of predatory fish in ponds used in this study.

	Pond	**Surface Area (m^2)**	**Dominant Macrophytes**	**Fish/ Fishless**
Lux Arbor Reserve	1	843	Poaceae	Fishless
	5	32106	*Nuphar* sp., *Nymphaea* sp.	Fish
	7	33526	*Nuphar* sp., *Nymphaea* sp.	Fish
	8	1005	Poaceae, *Potamogeton* sp.	Fishless
	9	3266	*Potamogeton* sp., *Nymphaea* sp.	Fishless
	11	714	*Lemna* sp.	Fishless
	13	1395	*Potamogeton* sp.	Fishless
	16	780	*Nymphaea* sp., *Potamogeton* sp., Poaceae	Fishless
	23	20109	*Nuphar* sp., *Nymphaea* sp.	Fish
	26	36891	*Nuphar* sp., *Nymphaea* sp.	Fish
Barry State Game Area	Johns 9	16096	*Nuphar* sp., *Nymphaea* sp.	Fishless
	Johns 11	7030	*Nuphar* sp., *Nymphaea* sp.	Fishless
	Orch 1	158	Poaceae, *Potamogeton* sp.	Fishless
	Orch 2	264	Poaceae, *Potamogeton* sp.	Fishless
	Shaw 1	2534	*Nuphar* sp., *Nymphaea* sp.	Fishless
	Shaw 2	4208	*Nuphar* sp., *Nymphaea* sp.	Fishless
	Upton 6	4337	*Nuphar* sp., *Nymphaea* sp.	Fishless

Gyrinid Quadrat Observations in Fish and Fishless Ponds

The purpose of this observation was to investigate whether adult *Dineutus* beetles' activity varied in fish and fishless ponds at sunrise, midday and sunset. At the KBS experimental pond facility, two ponds, each containing approximately 400 fish (Mittelbach *pers. comm.*) (one pond with pumpkinseed (*Lepomis gibbosus*) and one pond with redear (*Lepomis microlophus*) sunfish), and two ponds without fish were chosen to observe the behavior of adult *Dineutus*.

One m^2 quadrats were used to observe gyrinid activity. This quadrat size was easily viewed by the observer. In each pond, one quadrat was randomly positioned on the water's surface in the center of the pond. Four small floats were tied to four bricks with string which delineated the corners of the quadrat. The sides of the quadrat were left open, enabling the beetles to swim in and out of it.

From June 15 through August 15, 1997, each quadrat was observed five separate times, each for a period of five minutes. The first two observations were performed approximately 10 minutes before and after sunrise. Next, an observation was performed at midday, anytime from 12 p.m. to 2 p.m. Finally, two observations were performed approximately 10 minutes before and after sunset. Activity observations were performed by several people and were made only if air temperature was above 10°C, wind speed was below 3.5 m/s and there was no rain, as monitored by a weather station at the experimental pond lab facility (within 0.25 miles). Even though air temperature dropped as low as 11°C, surface water temperature remained above 20°C. Water and air temperature were monitored because beetle activity decreases with colder temperatures (Vulinec and Kolmes 1987). Wind speed and rain were concerns because ripples in the water made it difficult to observe the beetles and could have possibly altered their normal behavior. Observations were made from a rowboat, which was always at least one m from the quadrat. After the boat was in place, the observer waited five minutes to allow the beetles to regain their normal behavior. During the observations, the number of beetles that swam in and out of the quadrat were counted. Observations were recorded on a tape-recorder and transcribed later. Weighted averages of the number of gyrinids observed in the quadrat per second during each of the five minute observations were calculated using equation one.

$$(1)\ \frac{\text{average \# of beetles}}{\text{second}} = \frac{(\#\text{ seconds})(0\text{ gyrinids})+(\#\text{ seconds})(1\text{ gyrinid})\ldots+(\#\text{ seconds})(n\text{ gyrinids})}{300\text{ seconds}}$$

At the end of the observational period, adult beetles were photographed and counted in one fish and one fishless pond, in order to estimate differences in adult densities.

Non-parametric statistics, Kruskal-Wallis one-way ANOVA, and sequential Bonferroni adjustments (Rice 1989), were performed on the weighted observation means from each time of day using Systat, in order to distinguish differences in daily activity.

Gyrinid Density Estimations in Natural Ponds

Adult gyrinids densities were observed in order to investigate the relative abundance of *Dineutus* and *Gyrinus* in fish and fishless ponds. During the middle of August in 1997, a total of 17 ponds were selected from within the Lux Arbor Reserve and Barry State Game Area. Six fishless and four fish ponds were in the Lux Arbor Reserve, and seven fishless ponds were in the Barry State Game Area (Table 2.1). Fishless ponds were considered to be truly fishless or contained only small mudminnows and/or fathead minnows (Turner 1994; Chase 1998), which are considered non-predators of gyrinids. Fish ponds contained bluegill (*Lepomis macrochirus)* and pumpkinseed (*Lepomis gibbosus*) sunfish, largemouth bass (*Micropterus salmoides)* etc. (Turner 1994; Chase 1998). Density estimations were repeated in late May, late June and late July in 1998.

Gyrinid rafts were observed from a one-person kayak. While paddling in the ponds each raft was either photographed, if the raft was large, or individuals in the raft were counted, if the raft was small. The closeness of the individuals to each other in the raft were qualitatively estimated by eye, and the raft's location was drawn on a map of the pond, relative to the location of other rafts. Later, photos and slides were either scanned into a computer and adult gyrinids were counted using Adobe Photoshop or a slide projector.

Surface areas of the ponds at Lux Arbor Reserve were calculated using a polar-planimeter and a scaled map (Lind 1985). Surface areas of the ponds at Barry State Game Area were measured by J. Chase and A. Downing by obtaining the length and several width measurements of each pond.

The amount of surface area covered by aquatic macrophytes was estimated by eye in the ponds during each of the four observation dates in order to calculate the amount of surface water that was habitable by gyrinids. The percent of open surface water for each pond was then multiplied by the surface area of the pond to estimate the area of water that was habitable by gyrinids. This estimated area was used to calculate the densities of *Dineutus* and *Gyrinus* adults.

Mean adult gyrinid densities per pond, from the four observation dates, were compared using non-parametric statistics, Mann-Whitney U-test, with sequential Bonferroni adjustments (Rice 1989), which were performed on Systat. Non-parametric statistics were used because no assumption of normality is required and non-parametric statistics are more conservative than parametric statistics (Sokal and Rohlf 1995). Sequential Bonferroni adjustments were used because multiple tests were made on the same data set. This conservative approach decreases the possibility making type I errors

(Sokal and Rohlf 1995). Observations from 1997, made in pond 26 at the Lux Arbor Reserve were not used in the analysis because density estimates were not made of the entire very large pond. Using a Pearson's correlation and a linear regression, total mean number of gyrinids observed per pond from the middle of August 1997, were compared to the amount of pond surface area covered by macrophytes (n=17 ponds used).

In 1998, four of the ponds located in the Barry State Game Area were completely covered with *Nuphar sp.*, *Nymphaea sp.* and *Potamogeton sp.* and gyrinids were absent. Since the intent of these observations was to analyze influences of fish on gyrinid densities, ponds absent of gyrinids or heavily covered with macrophytes were discarded from the 1998 observations (n=4 ponds discarded).

Fish Collection and Stomach Analyses

In July 1998, fish were collected from pond 23 in the Lux Arbor Reserve using 1.0 m^2 and 1.0 m x 0.5 m (length by height) hoop-nets, in order to determine the presence or absence of genera specific predation by fish. This pond was chosen because it contained a large abundance of both *Dineutus* and *Gyrinus* adults, and the density ratio between the two genera was the closest to one. Therefore, gyrinid larvae and adults would be more readily available as fish prey. Pumpkinseed sunfish (*Lepomis gibbosus*) were collected and measured (mean body length = 48.02 ± 15.83 (Std Dev) mm; n = 194). Forty of these fish were euthanized immediately after capture, using MS-222, and preserved in 70% ethanol for later stomach content analysis (mean body length = 72.23 ± 7.48 (Std Dev) mm). Larger fish were used in the stomach content analysis because they would be more likely to have eaten larger macroinvertebrates, such as gyrinid larvae. The remainder of the fish were released back into the pond. In the laboratory, stomachs and intestines were extracted from the fish and their contents were identified via a microscope and then recorded.

Adult *Dineutus* and *Gyrinus* Species Body Measurements and Identification

In order to investigate differences in body length and species composition of adult gyrinids among ponds, five to 15 *Dineutus* and *Gyrinus* adults were collected from 11 ponds at the Lux Arbor Reserve and Barry Game Reserve, which were among the ponds in the 1997 observations. Gyrinids were not collected or identified from six ponds that contained minimal densities of the adults, or where only female adults were captured. The sex of an individual is determined by distinguishing characteristics in the anterior tarsi (Ferkinhoff and Gundersen 1983). However, this was not determined until the beetle was identified in the laboratory. The adults were preserved in 75% ethanol and measured later. A total of 72 adult male body lengths were measured with an millimeter ruler from the tip of the head to the end of the last abdominal segment. Adult female gyrinid lengths were not measured due to the similarity of female genitalia that makes species specific identification difficult. Adult male gyrinids were identified to species by examining their genitalia following the keys by Ferkinhoff and Gundersen (1983) and Hilsenhoff (1990). Questionable identifications were verified by Dr. Hilsenhoff at the University of Wisconsin.

***Dineutus* and *Gyrinus* Larval Rearing and Growth**

In order to investigate preferential foraging of fish on two genera of gyrinid larvae, *Dineutus* and *Gyrinus* adults were captured from pond 8 and pond 23 at the Lux Arbor Reserve in an attempt to rear the larvae. Individuals of each genus were segregated into separate plastic wading pools with a diameter of 1.2 m and a depth of 0.2 m. The beetles were fed 10 large pinches of fish food (dried chironomids) daily. *Potamogeton sp.*, collected from the Lux Arbor Reserve were placed in a dish of sand. The plants were placed around the inside edges of both plastic wading pools to simulate a natural pond and to give female gyrinids a place to oviposit. In case the macrophytes died, plastic plants were also used. They were attached to bricks at the bottom of the pools and allowed to float to the surface, simulating real macrophytes. Wading pools were covered with window screen to prevent gyrinids from escaping.

Both real and plastic macrophytes in the pools were examined several times a week for eggs. If eggs were found, the section of the macrophyte (leaf or stem) in which the eggs were adhered was removed and placed into an eight ounce plastic cup filled with tap water. Eggs from each genus were separated into different cups and brood sizes were recorded. When larvae hatched, each individual was placed into its own marked eight ounce cup to prevent cannibalism. Larvae were fed an ample number of small crustacean amphipods, so that there were always extra amphipods in the cup. Water was changed twice a week using a turkey baster. Eggs were left in their cups for two weeks in order to minimize the disturbance to the eggs and to ensure that all possible viable larvae had hatched. Remaining egg lengths were measured. *Gyrinus* eggs were not measured because they had decayed.

The body lengths of individuals from one *Dineutus* larval species were measured from the day that they hatched until the day they all had died. Species identification was not possible because of inadequate keys. A total of 25 larvae, which hatched on the same day, were randomly chosen and measured. Every five or seven days after the larvae had hatched, another 25 larvae were randomly chosen and measured. When fewer than 25 larvae remained alive, all larval body lengths were measured. This continued until all larvae had died, approximately 40 days. Later in the trial, individuals from a different species of *Dineutus* hatched. These larvae were considered to be a second species of *Dineutus*, due to their distinctly different morphological characteristics. One individual of the second species of *Dineutus* was measured in order to compare growth rates of the two different species of larvae. Two larvae of each species were preserved in 70% ethanol.

Dispersal Experiment

In order to observe influences of fish on adult *Dineutus* and *Gyrinus* dispersal, an experiment was conducted at the Kellogg Biological Station experimental pond facility. Corrals, circular structures, were used to confine the gyrinids and fish to one area of the pond and to deter resident gyrinids and fish from invading the water inside of the corral (Figure 2.1). Each corral was constructed using four Styrofoam cylindrical structures combined together with short pieces of PVC pipe, creating a 1.8 m diameter circle. Clear plastic sheeting (1.2 m in length) was attached, using cable ties, around the outside of the circle, which was formed by the Styrofoam, and the edges were sealed with an iron. At the bottom of the corral, wire was sealed into half of the plastic perimeter in order to hold the shape of the corral. Weighted rope was attached evenly around the bottom of the plastic to hold it vertically in the water column. Finally, window screen (mesh size approximately 1.0 mm^2) was stapled to the bottom of the plastic, closing the bottom of each corral. The window screen served two purposes; (1) to prevent the gyrinids from swimming out and under the corral, and (2) to allow small food for the fish to swim up through the screen and into the corral.

The dispersal experiment was a 2x2 factorial design (Figure 2.2). It was conducted in a total of four ponds, two with fish and two without, and each treatment had three replicate corrals. The two fish ponds, one with resident redear sunfish (*Lepomis microlophus*) and one with resident pumpkinseed sunfish (*Lepomis gibbosus*), at the KBS experimental pond facility, were chosen because they were the only ponds with near natural densities of fish, (300-400 fish per pond; 0.3-0.4fish/m^3). The two fishless ponds were chosen because surface waters were only minimally covered with macrophytes, allowing maximum habitat availability for adult gyrinids. The experiment was unbalanced because each pond contained two corrals of one treatment and one corral of another treatment. More ponds could not have been used due to the lack of adequate fish ponds. Only three replicate corrals for each treatment were constructed because of an insufficient amount of time and supplies.

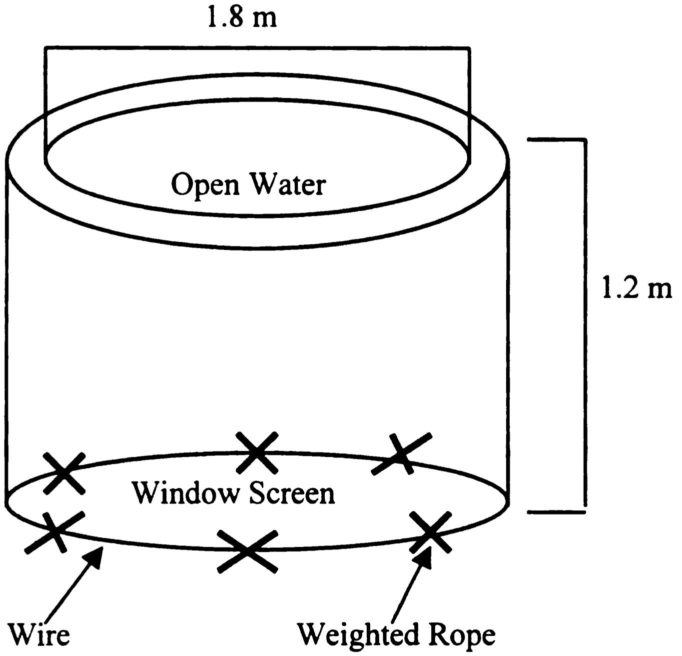

Figure 2.1 Dispersal corral. (Not to scale).

Two treatments consisted of 60 adult *Dineutus* and 60 adult *Gyrinus* that were captured from fishless ponds at the Lux Arbor Reserve. Ten adults from both genera were randomly placed together into three fish and three fishless corrals located in two experimental ponds. The other two treatments included 60 adult *Dineutus* and 60 adult *Gyrinus* captured from fish ponds at the Lux Arbor Reserve, which were randomly placed into three fish and three fishless corrals located in the other two experimental ponds (Figure 2.2). All gyrinids were observed immediately after their placement into the corrals to ensure that all beetles had survived the transplant. The experiment lasted for one week, beginning on Aug. 14, 1998 and ending on Aug. 21, 1998.

Each corral was observed daily from the first day of the experiment, recording the number of remaining beetles from each genus in each treatment. The counts from each treatment were compared to each other to test for any differences in remaining gyrinid adults in the fish and fishless ponds. A repeated measures ANOVA test was performed on SAS to detect any significant difference in dispersal of the beetles among the different treatments. This statistical analysis accounts for the lack of independence of measurements obtained on consecutive days (Gurevitch and Chester 1986).

Three weeks after the initiation of the experiment, the total number of adult *Gyrinus,* present in the four ponds where the corrals were located, was estimated in order to obtain density estimates of adult *Gyrinus* after the beetles would have acclimated to their new environment. This observation was possible because there were no prior resident *Gyrinus* adults present in the ponds. Therefore, it was assumed that the only remaining *Gyrinus* adults in the ponds were transplanted from the Lux Arbor Reserve. Density estimates were not calculated for *Dineutus* because, prior to the experiment, resident *Dineutus* inhabited the ponds. Therefore, it was not possible to distinguish between resident *Dineutus* and the *Dineutus* transplanted from the experiment.

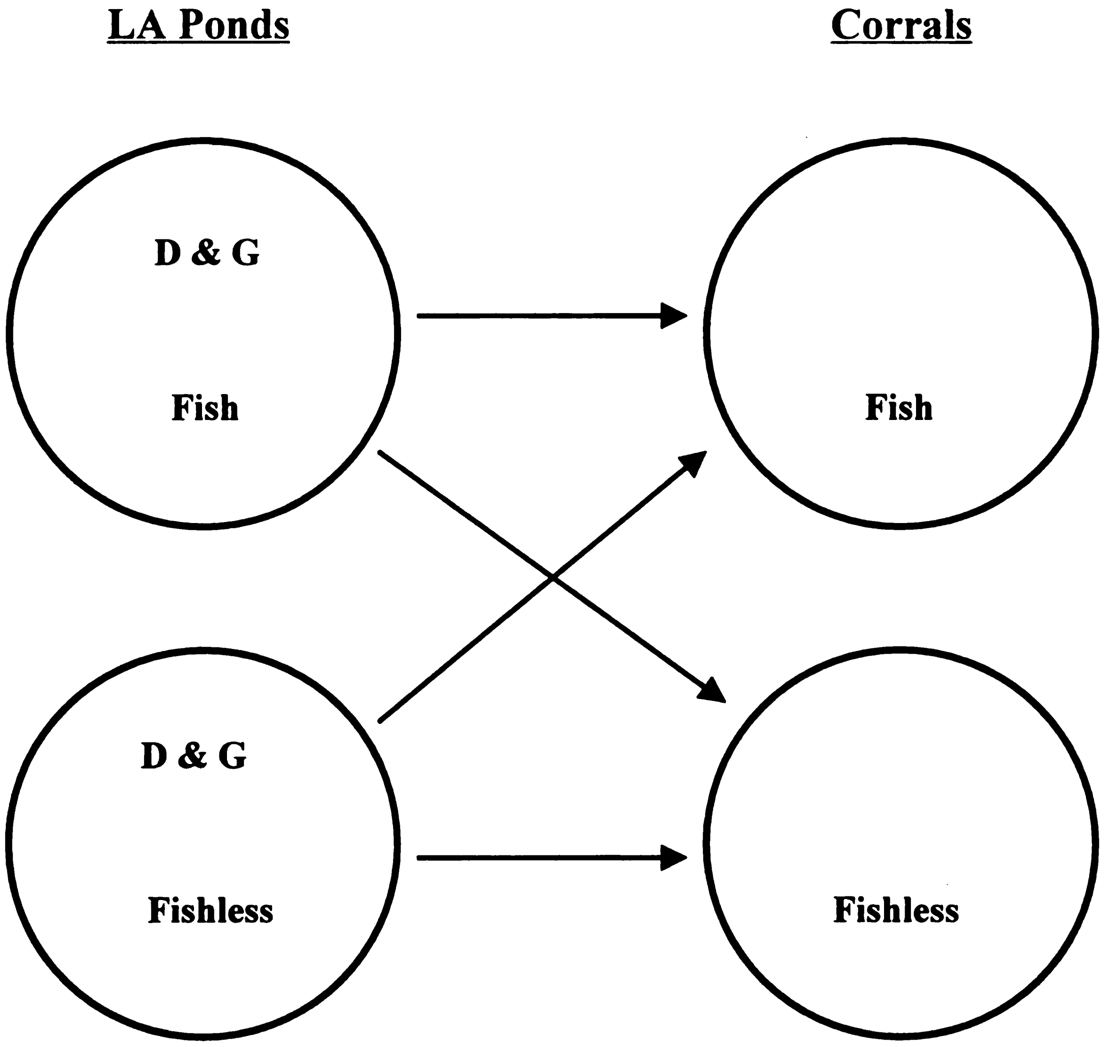

Figure 2.2 Dispersal experiment (2x2) factorial design. Fish and fishless acclimated gyrinids were taken from two LA ponds and transplanted into the fish and fishless dispersal corrals. Each treatment had three replicates. (D = *Dineutus*; G = *Gyrinus*)

III. RESULTS

Adult *Dineutus* Activity

Dineutus adults were observed in the open-water habitat of fish and fishless ponds at the KBS pond facility during sunrise (10 minutes before and after sunrise), mid-day (12:00 - 2:00 p.m.) and sunset (10 minutes before and after sunset) in the summer of 1997. The average number of *Dineutus* adults per second that were observed before and after sunrise and sunset in the fish and fishless open-water quadrats were not significantly different from each other after using the sequential Bonferroni correction technique (Fish: p= 0.044, 0.624; Fishless: p= 0.132, 0.108, respectively). Therefore, the before and after measurements were averaged together in order to obtain a single mean sunrise and sunset value.

Adult *Dineutus* activity in the open-water quadrats did not significantly differ from sunrise to mid-day to sunset in either fish (p= 0.909) or fishless (p= 0.263) ponds (Figure 3.1). Although, no significant differences in activity were found among the three observation periods, mean adult *Dineutus* activity observed in fishless ponds increased from sunrise to sunset (Figure 3.1).

At one time during the activity observations, a total of 183 *Dineutus* adults and 713 *Dineutus* adults were counted in one fish and fishless pond. Mean beetle activity estimations in fish ponds (0.44 ± 0.21 (standard deviation (Std Dev)) beetles s^{-1}) were smaller than mean activity estimations in fishless ponds (2.37 ± 0.69 (Std Dev) beetles s^{-1}) (Figure 3.1).

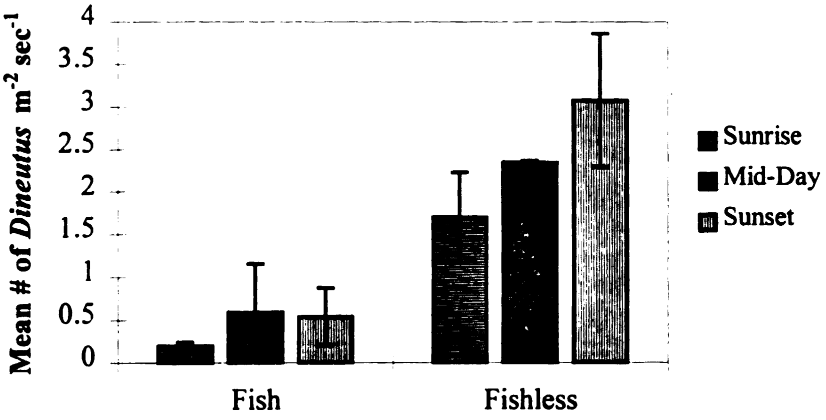

Figure 3.1 Activity of *Dineutus* adults observed at sunrise, mid-day and sunset in fish and fishless ponds. No significant differences in daily activity were found among *Dineutus* adults in fish or fishless ponds (sunrise and sunset, n = 10; midday, n = 5; Error bars are ± standard errors)

Adult Gyrinid Density Estimations and Species Composition in Natural Ponds

Gyrinus and *Dineutus* adults were observed in a total of 17 ponds in the middle of August 1997, and in a total of 13 ponds during the summer of 1998. Pond size ranged from 63.8 to 14,904.0 ha, and dominant macrophyte cover consisted of Poaceae, *Lemna* sp., *Nuphar* sp., *Nymphaea* sp., and *Potamogeton* sp. (Table 2.1).

In August 1997, there were significantly more *Dineutus* than *Gyrinus* adults observed in fishless ponds (p= 0.006) (Table 3.1). No other significant differences in densities between *Dineutus* and *Gyrinus* adults in fish and fishless ponds were detected during the middle of August 1997. However, on average *Dineutus* adults appeared to be more abundant in fishless ponds, while *Gyrinus* adults appeared to be more abundant in fish ponds (Figure 3.2).

Table 3.1 Statistical analyses performed on *Dineutus* and *Gyrinus* adult densities in fish and fishless ponds during the middle of August, 1997 (F= Fish Pond; NF= Fishless Pond; df = 3 and alpha = 0.05 for each Mann-Whitney U-Test)

Variables	**P-Value**
Dineutus in F & *Dineutus* in NF 1997	0.102
Gyrinus in F & *Gyrinus* in NF 1997	0.087
Dineutus in NF & *Gyrinus* in NF 1997	0.006 *
Dineutus in F & *Gyrinus* in F 1997	0.268

* Significant p-values after using sequential Bonferroni corrections.

During the late May 1998 observations, adult gyrinids appeared to be more evenly dispersed across the water's surface as compared to the later part of the summer (personal observation). During this period of the summer distinct rafts had not yet been formed by the beetles, allowing beetles to have been possibly counted more than once. Therefore, late May density estimations were not used in the analyses. Late June gyrinid densities (pooled mean = 0.543 ± 0.44 (Std Dev) beetles m^{-2}) were lower than densities observed in late July (pooled mean = 1.18 ± 1.01 (Std Dev) beetles m^{-2}). Individuals observed during this period were also relatively loosely aggregated, making accurate density estimates difficult. Therefore, late June observations were only used in the pond generic composition analysis where obtaining accurate density estimations was not an issue.

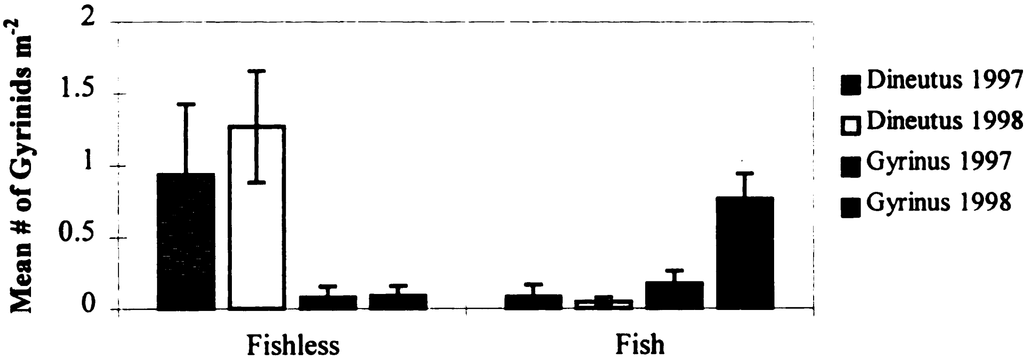

Figure 3.2 Average number of adult *Dineutus* and *Gyrinus* observed in fish and fishless ponds during the middle of August, 1997 and late July, 1998. Refer to Table 3.1 and 3.2 for significance and p-values. (Error bars are ± standard errors)

The same density relationship between *Dineutus* and *Gyrinus* adults, which was observed in the middle of August 1997, was also apparent in late July, 1998. *Dineutus* adults were significantly more abundant in fishless ponds than they were in fish ponds (Figure 3.2; Table 3.2). Adult *Gyrinus* were significantly more abundant in fish ponds than they were in fishless ponds (Figure 3.2; Table 3.2). Adult *Dineutus* densities were significantly more abundant than adult *Gyrinus* in fishless ponds, however, adult *Gyrinus* densities were significantly greater than adult *Dineutus* densities in fish ponds (Figure 3.2; Table 3.2). Observations from pond 13 at the Lux Arbor Reserve were not included in the analyses due to heavy macrophyte cover and either death or dispersal of resident gyrinids.

Mean macrophyte cover of pond surfaces observed in the Lux Arbor Reserve and Barry State Game Area was 60.2 ±32.9 (Std Dev) % (n=17) in the middle of August 1997 (Figure 3.4). In 1998, mean macrophyte cover of the surface increased as the summer progressed from the late May to late July observations (45.4 ± 33.1 (Std Dev) %, 47.9 ± 32.6 (Std Dev) %, and 55.8 ± 40.3 (Std Dev) %, respectively; n=13 for each observation date). Gyrinid densities were found to decrease as macrophyte cover increased, $r = -0.496$ ($p < 0.001$; $y = -0.01 + 0.8765$) (Figure 3.4).

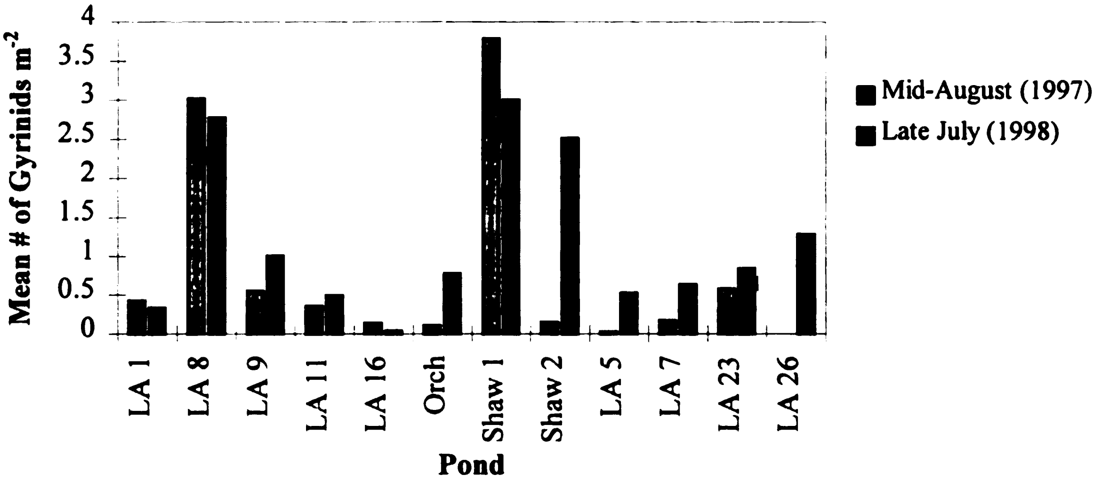

Figure 3.3 Average number of gyrinids per square meter observed in Lux Arbor Reserve and Barry Game Reserve ponds. Refer to Table 2.1 for pond surface areas and fish presence. Density estimations of gyrinids in pond 13 at the Lux Arbor Reserve were only made in late May and late June, 1998 and were therefore not included in the above figure. (LA = Lux Arbor ponds; all others were ponds at the Barry State Game Area)

Adult gyrinid generic composition varied from pond to pond in the Lux Arbor Reserve and Barry State Game Area (Table 3.3). Sole residency of *Dineutus* adults, being the only gyrinid genus present in a pond, was only observed in fishless ponds, while sole residency of *Gyrinus* adults was only observed in fish ponds. *Gyrinus* adults had either all died or dispersed from one of the fishless ponds from the late June to the late July, 1998 observations (Table 3.3).

Table 3.2 Statistical analyses performed on *Dineutus* and *Gyrinus* adult densities in fish and fishless ponds during late July, 1998 (F= Fish Pond; NF= Fishless Pond; df = 3 and alpha = 0.05 for each Mann-Whitney U-Test)

Variables	**P-Value**
Dineutus in F & Dineutus in NF 1998	0.017 *
Gyrinus in F & Gyrinus in NF 1998	0.01 *
Dineutus in NF & Gyrinus in NF 1998	0.006 *
Dineutus in F & Gyrinus in F 1998	0.01 *

* Significant p-values after using sequential Bonferroni corrections.

Male gyrinid *Dineutus* sp. and *Gyrinus* sp., identified from ponds at the Lux Arbor Reserve and Barry State Game Area, included the following species: *D. hornii, D. assimilis, D. nigrior, G. dichrous, G. ventralis, G. affinus* and *G. frosti* (Table 3.4). Beetles from all three *Dineutus* species were found in fish and fishless ponds. *Gyrinus dichrous* and *G. ventralis* adults were only found in fish ponds and *G. affinus* and *G. frosti* adults were only found in fishless ponds. *Dineutus* or *Gyrinus* mean adult body lengths did not differ among species or between residents in fish and fishless ponds (Table 3.4). It was not possible to visually quantify the abundance of gyrinid species.

Gyrinid rafts were observed in all ponds that were monitored during this investigation. Rafts were almost always composed of a single genus. Rafts, containing both *Dineutus* and *Gyrinus* adults were observed in only four out of 79 rafts recorded in the middle of August 1997, in 14 out of 198 rafts recorded in late June 1998, and in seven out of 251 rafts recorded in late July of 1998.

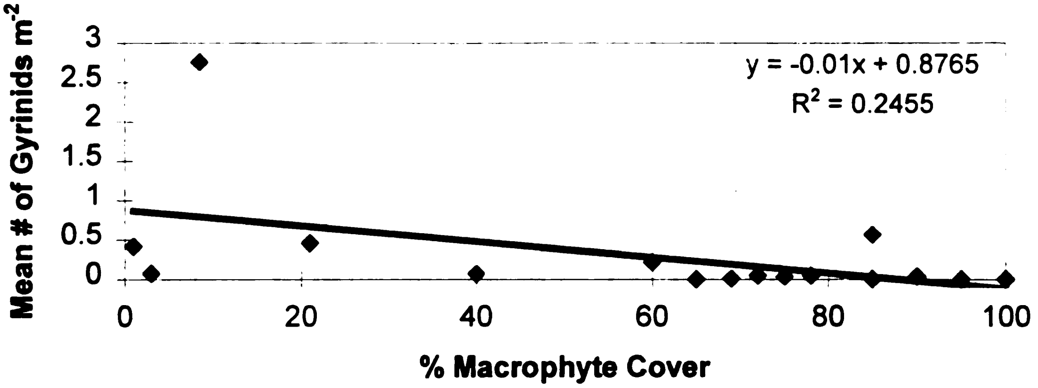

Figure 3.4 The mean number of adult gyrinids observed in ponds at the Lux Arbor Reserve and Barry State Game Area during the middle of August, 1997, as related to the percent of the pond surface that was covered by macrophytes. ($n=17$; $r = -0.496$; $p < 0.001$)

The surface spacing of gyrinids changed over the course of the summer in 1998. Observations made in late May 1998, indicated that gyrinids were evenly dispersed upon the water's surface. As the summer progressed, gyrinids began to assemble into loosely aggregated rafts (late June 1998 observations) and finally tightly aggregated rafts (middle of August 1997, and late July 1998 observations) were observed.

The proximity of rafting gyrinids to one another in the middle of August 1997 and late July 1998, whether they were *Gyrinus* or *Dineutus* adults, did not appear to differ from raft to raft. Individuals rafting in fish and fishless ponds appeared to aggregate with approximately the same proximity to one another, however, no measurements were completed.

Table 3.3 Adult gyrinid generic composition observed in fish (F) and fishless (NF) ponds at the Lux Arbor Reserve and Barry State Game Area. Numerical values indicate the number of ponds in which the respective genera are present.

	Sole Resident of Pond		**Dual Resident of Pond**
Observational Period	***Dineutus***	***Gyrinus***	***Dineutus & Gyrinus***
Middle of August 1997	6 (NF)	2 (F)	4 (NF); 1(F)
Late June 1998	4 (NF)	0	4 (NF); 3 (F)
Late July 1998	4 (NF)	1 (F)	4 (NF); 3 (F)
Sum	**14 (NF)**	**3 (F)**	**12 (NF); 7 (F)**

Table 3.4 *Dineutus* and *Gyrinus* species presence/ absence, mean body lengths in fish and fishless ponds at the Lux Arbor Reserve and Barry State Game Reserve. Parentheses denote the number of gyrinids measured for each species.

	Fish Ponds Length (mm)	**Fishless Ponds** Length (mm)
D. assimilis	10.0 (1)	11.3 ± 0.3 (3)
D. hornii	11.3 ± 0.7 (5)	11.6 ± 0.5 (7)
D. nigrior	12.5 ± 0.7 (2)	11.7 ± 1.1 (19)
G. affinus	-	6.9 ± 0.3 (4)
G. dichrous	4.7 ± 0.3 (26)	-
G. frosti	-	6.8 ± 0.3 (3)
G. ventralis	6.4 ± 0.2 (2)	-

In the middle of August 1997 and late July 1998, locations of gyrinid rafts within a pond differed depending on the species composition of the residents. When *Dineutus* and *Gyrinus* adults inhabited the same pond, *Dineutus* rafts were generally found along the perimeter of the pond under vegetation, while *Gyrinus* rafts were positioned in the center of the pond. When *Dineutus* was the sole gyrinid resident in a pond, rafts were usually located along the perimeter of the pond under vegetation. However, if *Gyrinus* was the sole gyrinid inhabitant in a pond, its rafts were located both along the margin of the pond under vegetation and in the center of the pond.

1997 vs. 1998 Adult Density Estimations

Observations were made in late July instead of the middle of August, as in 1997, because of the increased temperatures during the summer of 1998 (mean air temperatures from May 15- August 15: 17.7°C (1997) and 20.4°C (1998) (Kellogg Biological Station WWW- Page)). A total of 898.5 degree days had accumulated by August 15, 1997, and 910. 5 degree days had accumulated by July 25, 1998. Due to the minimal difference of total degree days, a paired T-Test was used to compare densities in each pond from 1997 to densities of its counterpart in 1998. No significant difference between years was found ($p = 0.196$) (Figure 3.3).

Fish Stomach Content Analyses

Pumpkinseed sunfish (*Lepomis gibbosus*) were collected from pond 23 in the Lux Arbor Reserve. Remnants of invertebrate larvae and adults were found. However, there were no distinguishing characteristics that could be used in identifying individual prey items and no conclusions were made.

Larval Gyrinids

Both *Dineutus* and *Gyrinus* adults were successfully reared in the plastic wading pools. Eggs from females of both genera were oviposited on plastic and real macrophytes, with no preference for one or the other. *Dineutus* eggs were found a couple of times a week during the breeding season (May - July), while *Gyrinus* eggs were only discovered on one occasion. Average *Dineutus* egg length was 1.84 ± 0.15 (Std Dev) mm (n = 74) and average brood size was 25.3 ± 11.5 (Std Dev) eggs per brood (n = 24). Average brood size for *Gyrinus* females was 5.33 ± 4.8 (Std Dev) eggs per brood (n = 6).

Only larvae from *Dineutus* eggs successfully hatched. Two notably different species of *Dineutus* larvae hatched. Larvae from the first species hatched at the end of May, while most individuals from the second species hatched during the first week of June. Individuals from both species exhibited linear growth. The initial number of larvae measured from the first species was 25, but decreased to two larvae by the last measurement. Initial body length of the first species was 4.6 mm and grew approximately 0.22 mm d^{-1}, and initial body length of the second species was 4.9 mm and grew approximately 0.27 mm d^{-1} (Figure 3.5).

Of the 150 *Dineutus* larvae that hatched, every larvae had died by the end of the first week in July (six weeks). Therefore, no foraging trials with fish were conducted. Two percent of the larvae survived the length of the observation period (36 days), however, 77% had died by the 9th day of the observation (Figure 3.6). After 18 days, survival rates equilibrated (Figure 3.6). Death of newly hatched larvae was often caused by individuals becoming trapped in the surface film of the water-filled plastic cups. Mid-way through the observational period, pieces of grass were placed into the plastic cups along with the larvae. This enabled them to grasp onto something, keeping the larvae submerged in the water and away from the surface.

When given the opportunity, larvae showed cannibalistic behavior. Two *Dineutus* larvae, placed in a cup together with other abundant food, would cannibalize each other.

Several larvae were placed into a 25 gallon aquarium, with an abundance of food, and still displayed cannibalistic behaviors. When larvae were not foraging, they either crawled along the bottom of the aquarium, hid under rocks or perched on submerged macrophytes.

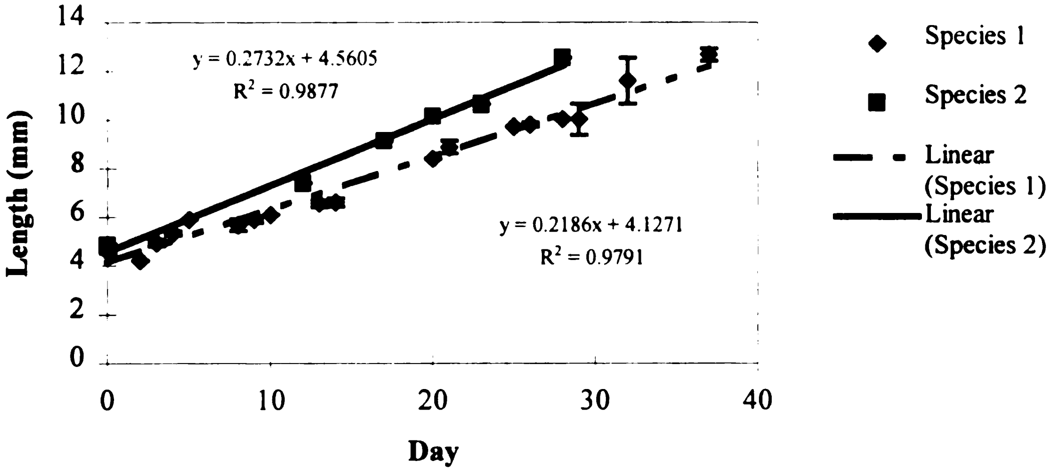

Figure 3.5 Growth of *Dineutus* species one and species two. (Species 1: Initial n = 25; Species 2: Initial n = 1; Error bars are ±standard errors)

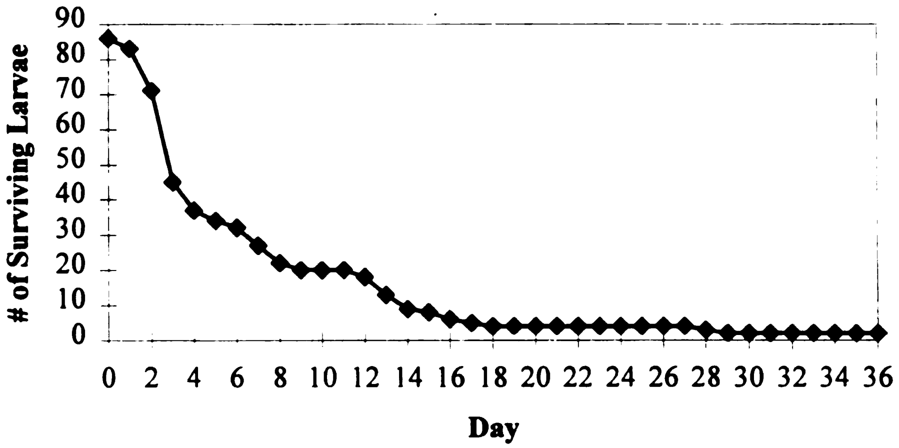

Figure 3.6 Survivorship curve of *Dineutus* species one over the 36 day observational period.

Influence of Fish on Adult Gyrinid Dispersal

Dispersal of adult *Dineutus* and *Gyrinus* from fish and fishless habitats was studied by transplanting fish and fishless acclimated gyrinids into opposing environments (i.e. fish acclimated gyrinids were transplanted into fishless environments and vice versa). Densities of *Dineutus* and *Gyrinus* adults collected from fish ponds and transplanted into fish and fishless corrals decreased as the experiment proceeded (Figure 3.7) as did the densities of fishless acclimated *Dineutus* and *Gyrinus* adults transplanted into fish and fishless corrals (Figure 3.8). Although, most adult gyrinids had left the corrals by the last day of the experiment, on average more *Gyrinus* than *Dineutus* beetles remained (1.1 ± 0.7 (Std Dev) *Gyrinus* corral^{-1}, and 0.3 ± 0.4 (Std Dev) *Dineutus* corral^{-1}).

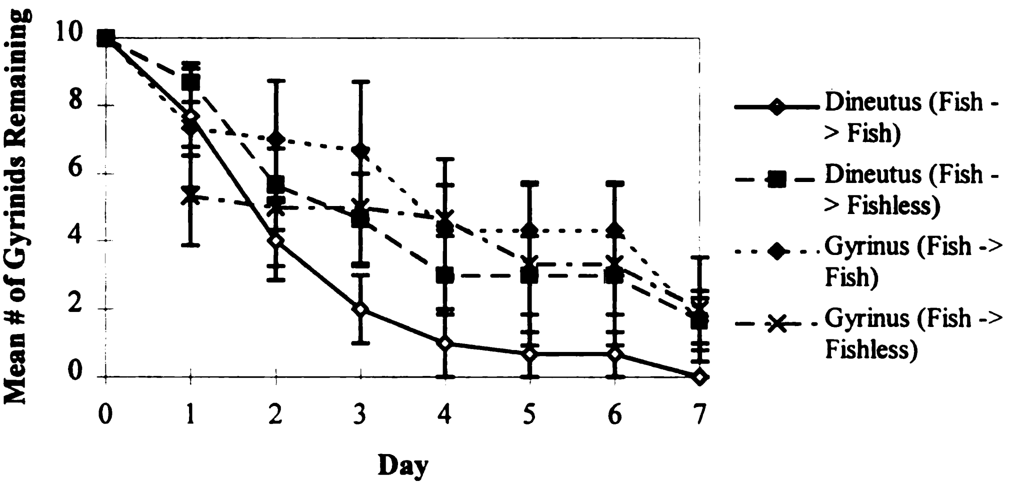

Figure 3.7 Dispersal of fish acclimated gyrinids from fish and fishless corrals. (n = 3 for each treatment; Error bars are ±standard errors)

Once introduced into the corrals, gyrinids began rafting with others from their same genus. As observed at Lux Arbor Reserve and Barry State Game Area, gyrinids rafted whether they were placed into a fish or fishless environment.

A repeated measures ANOVA test that accounted for the lack of independence between measurements obtained on consecutive days was used in the following analyses. *Dineutus* adults did not prefer either the fish or fishless corrals, as beetles in this genus left each type of treatment corral to the same degree ($p = 0.5532$) (Table 3.5; Figure 3.7 and 3.8). *Gyrinus* adults did not disperse more from fish or fishless corrals ($p = 0.0667$) (Table 3.6; Figure 3.7 and 3.8). When *Gyrinus* adults were separated into fish and fishless acclimated, significantly more fishless acclimated *Gyrinus* adults remained in fish corrals than fishless corrals ($p = 0.0358$) (Table 3.6; Figure 3.9). However, no significant difference was found between the number of fish acclimated *Gyrinus* adults remaining in fish and fishless corrals ($p = 0.6687$) (Table 3.6; Figure 3.10). Despite this lack of a significant preference by fish acclimated *Gyrinus*, it appeared that on average more *Gyrinus* beetles remained in fish than fishless corrals (Figure 3.10). These result supports the original hypothesis that *Gyrinus* adults favor habitats with fish. There were no control corrals in the ponds where *Dineutus* and *Gyrinus* adults were captured. Therefore, it is possible that a majority of the dispersal observed in this experiment was due to a corral effect regardless of the treatment.

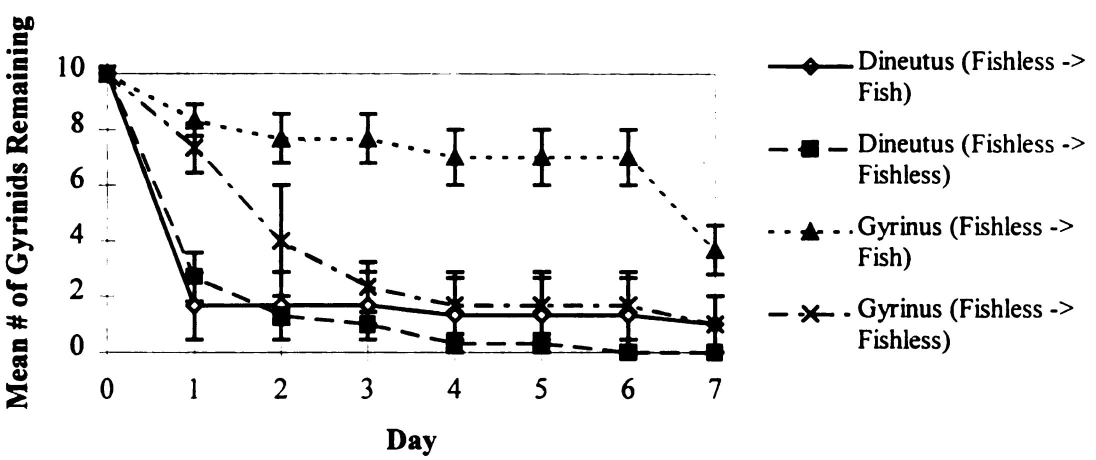

Figure 3.8 Dispersal of fishless acclimated gyrinids from fish and fishless ponds. (n = 3 for each treatment; Error bars are ± standard errors)

Table 3.5 Comparison of the dispersal of *Dineutus* adults from fish and fishless corrals using a repeated measures ANOVA.

Source of Variation	**df**	**F-Value**	**P-Value**
Treatment	1	0.38	0.5532
Day	7	59.29	0.0001*
Day * Treatment	7	0.17	0.8336*

* Greenhouse-Geisser corrected

Three weeks after the experiment had begun, when the gyrinids transplanted into the experimental ponds would have been acclimated to their new environment, remaining *Gyrinus* adults were counted. Forty-eight percent of the originally transplanted *Gyrinus* adults remained in the fish ponds, while only 5.3% of the *Gyrinus* adults remained in the fishless ponds.

Table 3.6 Comparison of the dispersal of *Gyrinus* adults from fish and fishless corrals using a repeated measures ANOVA. (F = Fish; NF = Fishless)

***Gyrinus* Dispersal in F & NF Corrals**

Source of Variation	df	F-Value	P-Value
Treatment	1	4.23	0.0667
Day	7	32.19	0.0001*
Day * Treatment	7	2.12	0.1164*

NF Acclimated *Gyrinus* Dispersal in F & NF Corrals

Source of Variation	df	F-Value	P-Value
Treatment	1	9.68	0.0358
Day	7	28.08	0.0003*
Day * Treatment	7	5.7	0.0296*

F Acclimated *Gyrinus* Dispersal in F & NF Corrals

Source of Variation	df	F-Value	P-Value
Treatment	1	0.21	0.6687
Day	7	12.95	0.0021*
Day * Treatment	7	0.54	0.6137*

* Greenhouse-Geisser corrected

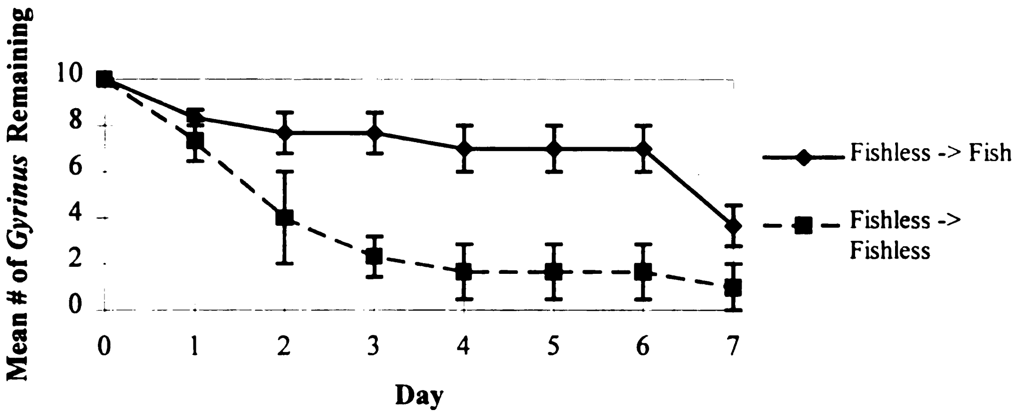

Figure 3.9 Dispersal of fishless acclimated *Gyrinus* from fish and fishless corrals. (n = 3 for each treatment; p = 0.0358; Error bars are ± standard errors)

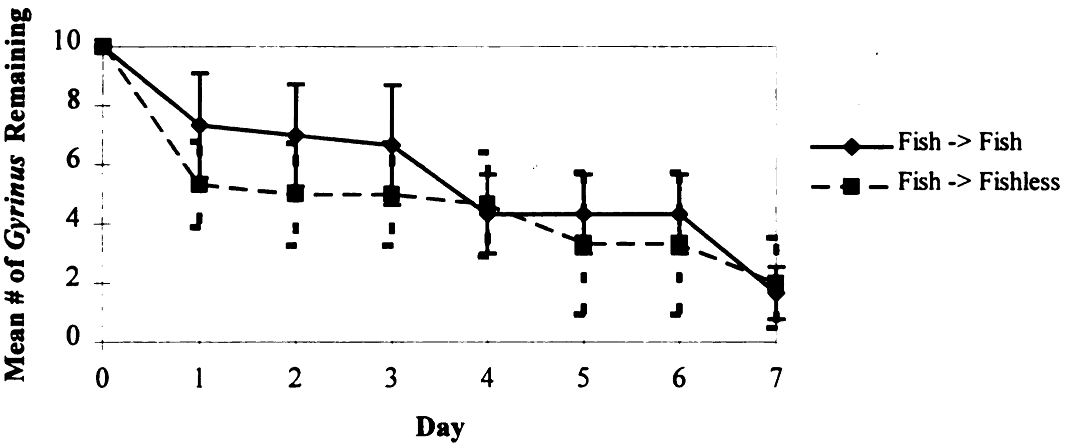

Figure 3.10 Dispersal of fish acclimated *Gyrinus* from fish and fishless corrals. (n = 3 for each treatment; p = 0.6687; Error bars are ± standard errors)

V. DISCUSSION

Adult *Dineutus* Activity

In ponds containing predatory fish, gyrinids have been shown to raft continuously throughout the day, dispersing only at night to forage (Heinrich and Vogt 1980). In my study, no significant differences in gyrinid activity between sunrise, midday or sunset in fish or fishless ponds, were observed. However, a marginal trend in fishless ponds showed adult *Dineutus* becoming more active as the day progressed. Fitzgerald (1987) observed a similar phenomenon in fishless ponds, where gyrinids rafted and were less active in the cooler morning, dispersing from rafts later in the day to defend territories.

The lack of differences in gyrinid daily activity could have been a result of little to no influence by fish on adult *Dineutus* behavior. Gyrinids are known to excrete a substance that makes them unpalatable to predators (Benfield 1972; Henrikson and Stenson 1993), thereby lowering the risk of fish predation. This interpretation could be further evaluated by experimentation using naive fish.

It is also possible that a daily activity pattern was not recognized as a result of the employed censusing methods. Rafting gyrinids were often observed directly beside the quadrat, therefore, the beetles could not be counted. The observations were also made by several people, which could have added error due to observer bias. To overcome these complications, a larger area in each ponds could have been observed in order to capture the activity of a greater number of gyrinids.

Gyrinid behavior changed over the extent of the two month observational period. Similar to the observations made in ponds at the Lux Arbor Reserve and Barry State Game Area, adult gyrinids in the KBS experimental ponds were most evenly dispersed over pond surfaces during the beginning of summer, gradually assembling into tight rafts by the end of the observational period. This behavior could have had a greater influence on structuring a gyrinid's daily activity than the effect of fish predation.

A considerable amount of variation was observed in gyrinid activity. One component of variation may have been observational variation. When beetles were active it was difficult for the observer to notice the movements of every gyrinid swimming in and out of the quadrat. This difficulty was a major factor when observing gyrinids in fishless ponds, which contained densities three times greater than those observed in fish ponds. Greater densities of *Dineutus* adults observed in fishless ponds than in fish ponds were also detected in ponds at the Lux Arbor Reserve and the Barry State Game Reserve.

Adult Gyrinid Density Estimations and Species Composition in Natural Ponds

Similar to the *Dineutus* density results found in the KBS experimental ponds, abundance of *Dineutus* adults in fishless ponds, at the Lux Arbor Reserve and Barry State Game Reserve during late July 1998, were significantly greater than densities in fish ponds. However, the opposite was true of *Gyrinus* densities in fish ponds. Adult *Gyrinus* were more abundant than adult *Dineutus* in fish ponds and adult *Dineutus* were more abundant than adult *Gyrinus* in fishless ponds. A similar observation was made by Bennett and Streams (1986) who found that the dominant notonectid species in fish ponds were also observed in fishless ponds, yet in reduced numbers. The opposite was true for the dominant notonectid species in fishless ponds. Nurnberger (1996) also described that fish were able to exclude *Dineutus assimilis* from inhabiting certain ponds.

Dineutus and *Gyrinus* adults forage on the same prey, live and dead soft-bodied organisms trapped in the surface film (Heinrich and Vogt 1980; Kolmes 1983a; Romey 1995). Although no direct evidence was found, competition for food between *Dineutus* and *Gyrinus* adults may influence the spatial distributions of the two genera in fish and fishless ponds.

When *Dineutus* and *Gyrinus* adults inhabited the same pond, *Dineutus* rafts were located along the perimeter of the pond next to shore, and *Gyrinus* rafts were located in the center of the pond. Abundance and diversity of insects trapped in the surface film, prey of gyrinids, is greatest close to shore and decreases as distance from shore increases (Norlin 1964). Terrestrial vegetation covers a considerable amount of water close to shore around the margin of the ponds, creating potential cover from aerial predation. Therefore, the areas near shore are probably optimal rafting locations because of a high abundance of food and protection from aerial predators. The center of the pond would contain less food and offer little or no cover from aerial predators. When *Dineutus* adults were the sole gyrinid resident, their rafts were almost always located along the margins of the pond. When *Gyrinus* adults were the sole gyrinid resident, their rafts were located not only in the center of the pond, but also along the shore of the pond. Therefore, competition between individuals of the two genera may influence the locations of rafts on the surface of the water.

The presence or absence of fish may directly influence adult gyrinid species composition by predation on larval gyrinids (Nurnberger 1996). The relationship between adult *Dineutus* and *Gyrinus* densities observed in fish and fishless ponds within the Lux Arbor Reserve and Barry State Game Area may be influenced by fish preying the larval stage.

The presence or absence of fish may also indirectly influence adult gyrinid species composition by competition and predation of other macroinvertebrates on gyrinid larvae. Invertebrates, present in fishless ponds, are generally larger than those found in fish ponds, because predatory fish often exhibit optimal foraging behavior, thereby consuming larger prey (Hall *et al.* 1979; Werner *et al.* 1983; Li *et al.* 1985; Persson and Greenberg 1990). Therefore, *Gyrinus* larvae, being relatively small, may be eaten or competitively excluded from fishless habitats. In fish ponds, large invertebrates are generally in small densities (Li *et al.* 1985). As a result, *Gyrinus* larvae may be better competitors in fish habitats. Thus, the distributions of adult gyrinids may be influenced during the larval stage via intra- and interspecific competition, predation and cannibalism.

Generic composition varied from pond to pond. During two of the three observational periods in this study, both genera were present in the majority of the ponds. However, several ponds contained only resident *Dineutus* or *Gyrinus*. Particular ponds may have not been ideal habitats for one or the other genera, resulting from increased intra- and interspecific competition and/or predation.

Adults from all three *Dineutus* sp. were found in fish and fishless ponds, while adults from *G. affinus, G. frosti* were only found in fishless ponds and adults from *G. ventralis* and *G. dichrous* were only found in fish ponds. Distribution of adult gyrinids based on size was unclear, because all sizes of *Dineutus* and *Gyrinus* adults occurred in fish and fishless ponds. A clear distinction of species composition of larvae from *Enallagma* sp. has also been reported in fish and fishless lakes (McPeek 1989).

Increased surface cover by macrophytes may decrease the amount of suitable habitat available to gyrinids and deter large rafts (Heinrich and Vogt 1980). A marginal trend was found, and implied that densities of gyrinids decreased as the surface area of ponds became more covered by macrophytes. However, only 25 percent of the variation in adult gyrinid densities was explained by total percent macrophyte cover of the surface. Therefore, other variables require further investigation. Another important factor may include the degree of fragmentation of the open water. Size and depth of a pond may also influence adult gyrinid density and distribution. The average amount of macrophyte cover of surface water in fishless ponds was greater than that in fish ponds. Fish ponds used in this study were on average larger and deeper than the fishless ponds. Depth of the fish ponds may have prevented optimal macrophyte growth.

Gyrinid Rafts

Adult gyrinid rafts were observed in both fish and fishless ponds. As described before, rafts are hypothesized to be a defensive mechanism against fish predation (Heinrich and Vogt 1980 and Vulinec and Miller 1989). Since gyrinid rafts were noted in both fish and fishless ponds, this hypothesis appears to be unsupported. However, gyrinids also fall prey to birds (Henrikson and Stenson 1993). The influence of bird predation could likely explain the presence of rafts in both fish and fishless ponds. Red-winged black birds were often observed diving at gyrinid rafts in the KBS experimental ponds (personal observation).

The closeness of adult gyrinids to one another increased as the summer progressed, whether the adults were observed in fish or fishless ponds. Adult gyrinids were most evenly dispersed during the spring, assembling into loose rafts by late June and tight rafts by late July. Spring and the beginning of the summer is the main gyrinid mating season (Eijk 1986a), which could have caused the uniform dispersion of gyrinids over the surface of the ponds. Rafts are often comprised of individuals from several species (Heinrich and Vogt 1980), which would not be advantageous when searching for mates. Gyrinid proximity to one another could have increased because they fed more in the spring than in the late summer. Gyrinids, which fast while they over-winter, need to build up their energy stores for the rest of the summer and reproduction (Eijk 1986b). It may have been more profitable to feed and mate while others were not close by, during the early summer, resulting in decreased competition for resources and mates. By the end of the summer, when individuals in a raft were the closest to one another, the main mating season was over and the majority of the food stores were built up. During late summer, predation from aerial predators may have been more influential than competition for mates and food.

Gyrinid raft composition almost always consisted of single genus rafts. Since *Dineutus* adults were almost twice the size of *Gyrinus* adults, it was probably easier for *Gyrinus* adults to compete for resources with individuals of similar size.

1997 vs. 1998 Adult Density Observations

Adult gyrinid densities did not differ from observations made in the middle of August 1997, and late July 1998, probably resulting from the similar number of degree days had passed before each observation period, suggesting that temperature dependent biological processes, such as birth, growth, survival and aging, were concurrent. Although there were no differences in gyrinid densities from the middle of August 1997, and late July 1998, gyrinid densities did increase from late June to late July 1998. This low density of adults may be attributed to the death of spring generation, which had just reproduced, and the absence of the new generation, which was primarily larval (Eijk 1986b). The relationship of adult gyrinid density distributions in fish and fishless ponds was observed to a lesser degree in ponds at the Lux Arbor Reserve and Barry State Game Area during the middle of August 1997.

Fish Stomach Content Analyses

Fish, captured and analyzed for stomach contents, did not exhibit any notable evidence of predation on larval gyrinids. Contents of the stomachs and intestines were nearly fully digested, and no larvae with identifiable gyrinid characteristics were found. The pumpkinseed fish used in this analysis were stunted due to the huge abundance of them in the pond that was sampled. Since fish density was so great, competition for resources was probably heightened. Competition among fish could have resulted in a relatively low rate of consumption and a decreased amount of food in the stomach. A gut content analysis of a much larger insectivorous fish stomachs, over an extended period of sampling, would provide more appropriate evidence for possible predation on larval gyrinids.

Larval Gyrinids

Two species of *Dineutus* were successfully reared in the trial. However, 76 percent of the larvae were dead after only nine days, and only 2.3 percent of the larvae survived to the end of the observation period (36 days). Increased mortality in the lab may indicate a high natural mortality rate. Although, lab techniques and conditions may have induced increased mortality. To improve laboratory conditions, larger containers should have been used to contain the larvae. Amphipods may have not been natural prey, even though they were readily eaten by all larvae. The plastic cups, used to hold the larvae, were filled with well water, which could have lacked or had an over abundance of important minerals and nutrients required for larval growth and survival. If pond water would have been used natural levels of nutrients and minerals would have been present. Even though, water in the cups was changed twice a week, waste could have built up, decreasing growth and survivorship. Temperature and aeration of the water inside the cup may have been greater/less than that of water in natural ponds. Young larvae were often found dead, trapped in the surface film of the water. Lack of vegetation or substrate available for perching, enabling larvae to maintain their position in the water column and away from the surface, may have caused and increase in the younger larval mortality. Pieces of grass were placed into cups alongside larvae that were not involved in the survival observations. These larvae appeared to survive better and were often seen attached to the grass, under the water's surface. Macrophytes should have been placed with the larvae as soon as they had hatched, in order to improve their survival and make their conditions more similar to their natural environment.

Influences of Fish on Adult Gyrinid Dispersal

At the end of the experiment, significantly more fishless acclimated *Gyrinus* were present in fish corrals than in fishless corrals. This result supports the original hypothesis that *Gyrinus* adults prefer to live in fish ponds rather than fishless ponds. Likewise, although not significant, fish acclimated *Gyrinus* appeared to favor fish corrals over fishless corrals. Predators have been found to influence adult gyrinid dispersal by excluding them from certain ponds (Nurnberger 1996). However, this study indicates that fish may positively influence *Gyrinus* adults, resulting in their greater densities found in fish ponds.

Gyrinus adults appeared to favor fish corrals, even though *Dineutus* adults, possible competitors, were nearly absent. Therefore, another mechanism, besides competitive exclusion (described earlier), must be regulating their abundance. Although no direct evidence was found, fish may indirectly influence *Gyrinus* adults by modifying the behavior of other aquatic invertebrates, possibly creating more foraging opportunities for the beetles. Perhaps, *Gyrinus* adults perceive fish ponds as better habitats due to increased survival potential for themselves and their larvae. *Gyrinus* adults may recognize the presence of fish by sight or by identification of a chemical cue, often excreted by fish (Kats *et al.* 1988).

Almost half of the transplanted *Gyrinus* adults remained in the fish ponds, outside of the corrals, up to three weeks after the commencement of the experiment. However, only five percent of the *Gyrinus* adults remained in fishless ponds. By this time, *Gyrinus* adults would have become more acclimated to their environment, and in most instances would have dispersed if they were not comfortable with their surroundings. Therefore, the propensity for *Gyrinus* adults to remain in the fish ponds strengthens the conclusion of fish presence or absence influencing gyrinid species composition. Densities of adult *Gyrinus*, from the enclosure experiment, supported the density observations made at the Lux Arbor Reserve and Barry State Game Area, indicating again that *Gyrinus* adult densities are greater in fish ponds.

There were no control corrals in the ponds where *Dineutus* and *Gyrinus* adults were captured. Therefore, it is possible that a majority of the dispersal observed in this experiment was due to a corral effect regardless of the treatment.

General decreases in density of both *Dineutus* and *Gyrinus* adults over time could be due to the restricted environment of the treatment corral. Although adult gyrinids raft in very close proximity to each other, at night they have been observed dispersing over the surface of ponds to forage (Fitzgerald 1987). The high degree of dispersal, exhibited by *Dineutus* and *Gyrinus* adults, does not support the low dispersal rates of five percent that have been found in previous experiments (Eijk 1983). Therefore, *Dineutus* and *Gyrinus* adults may have dispersed because of their restricted environment, instead of due to the presence or absence of fish. A control corral, placed in the ponds where *Dineutus* and *Gyrinus* adults were obtained for the experiment, could have indicated whether the gyrinid dispersal observed from the experimental corrals was due to a treatment or handling effect.

To obtain a better understanding of the influence of fish on gyrinid dispersal, a greater amount of available open water may be required for each treatment (i.e. entire ponds). This alternative was not possible in this study because of the large densities of resident gyrinids present in the KBS experimental ponds. In order to obtain accurate density estimations, all resident gyrinids would need to be removed, before transplanting the experimental gyrinids.

Many experiments have studied *Dineutus* and *Gyrinus* individuals separately (Eijk 1986; Freilich 1989; Heinrich and Vogt 1980; Istock 1966; Kolmes 1983). However, no experiments have compared the two genera, which is essential in understanding the relationship among *Dineutus* and *Gyrinus* individuals and fish. Since fish are top predators in many freshwater systems, they often exert large influences, direct and indirect, on inter- and intraspecific competition and predator-prey relationships (Bennet and Streams 1986; Rader and McArthur 1995). This study has indicated that fish may be directly and/or indirectly influencing species composition of gyrinid communities. However, to obtain a clear understanding of the factors structuring gyrinid assemblages, more experiments investigating competition between *Dineutus* and *Gyrinus* adults and larvae as well as interactions with other invertebrates are necessary.

CONCLUSIONS

1. *Gyrinus* adults were more abundant in fish ponds, while *Dineutus* adults were more abundant in fishless ponds, possibly resulting from intra- and interspecific competition and predation between *Gyrinus* and *Dineutus* individuals and from other aquatic invertebrates.
2. Adult gyrinid rafts were observed in fish and fishless ponds, implicating possible contributions of both fish and aerial predators on rafting behavior.
3. Adult *Dineutus* species composition did not differ between fish and fishless ponds, yet *G. dichrous* and *G. ventralis* were only found in fish ponds and *G. affinus* and *G. frosti* were only found in fishless ponds.
4. Larval *Dineutus* growth was linear, averaging an increase of 0.22 mm d^{-1}. The survival rate of *Dineutus* larvae by the end of the observation period was only 2.3 percent, due to a combination of experimental methods and a potentially high natural mortality rate. Larval *Dineutus* showed cannibalistic behavior, even when in the presence of abundant food.
5. When transplanted, fish and fishless acclimated adult *Gyrinus* preferred habitats that included fish, which supports field observations in natural ponds.

APPENDIX

***Gyrinus* species recorded in Michigan** (Ferkinhoff and Gundersen 1983)

G. minutus
G. dichrous
G. latilimbus
G. aeneolus
G. hatchi
G. ventralis
G. confinis
G. lecontei
G. aquiris
G. piceolus
G. maculiventris
G. affinis
G. impressicollis
G. pugionis
G. lugens
G. analis
G. frosti

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