Partial migration, homing, diel activity, and distribution of adult common carp
across a large, model watershed in the North American Midwest

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Abstract

Long-term and sustainable management of invasive fish requires an understanding of annual patterns in distribution and migration. This study hypothesized that the common carp (*Cyprinus carpio*), an invasive temperate cyprinid fish, employs a complex multi-phase life history strategy that incorporates sequential partial migrations within an annual life cycle. This life cycle may explain its success and invasiveness. A large scale, multi-year, year-round tracking study was conducted in a large watershed of 12 interconnected lakes that is representative of much of North America where it is highly invasive. This is the first known large scale multi-year study on the movement of a partially migratory invasive fish. For three winters, over 90% of adult carp were observed to overwinter and form large aggregations in one lake. Once temperatures were between 5-10°C in the spring, most adults (82% in 2014, 98% in 2015, and 98% in 2016), but not all, performed migrations to shallow lakes to spawn. Of these, most (86% in 2014, 96% in 2015, and 100% in 2016) used one stream of four to migrate. Such a precise form of breeding partial migrations has not previously been documented. Most migratory adults (81%) were then observed using the same lakes each year during spawning. After spawning, some adults (46% in 2014 and 80% in 2015), but not all, left their lakes and then spent the majority of the summer, presumably feeding in just one or two lakes out of 12. This would appear to reflect a second partial migration and a tendency to use home summer feeding ranges. In the fall, most adult carp (57% in 2014 and 93% in 2015) then returned to same lake from which migrations began. This would appear to reflect a third partial migration associated with overwintering. This flexible life history strategy can be categorized by six phases: overwintering, breeding partial migration, spawning in home lakes, summer partial migrations, feeding in home lakes, and partial migration to an overwintering (refuge) lake. We also found evidence of homing in how carp selected migratory paths, spawning lakes, feeding lakes, and overwintering lakes. This flexible, but highly directed life history strategy is seemingly new and could explain the success and invasiveness of common carp while providing options for control.

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the Common Carp

1. Introduction to Migration in Fish

1.1 Migration in fish

Dingle and Drake (2007) defined animal migration as a persistent locomotory activity which occurs on a larger scale, has a longer duration than daily activities, and is typically associated with seasonal movements between regions that fluctuate between favorable and unfavorable conditions. Migrations that involve fish are known to often be associated with breeding, feeding, and avoiding extremes (overwintering) (Lucas and Baras 2001c). For example, in temperate regions, many salmonids, cyprinids, and catostomids overwinter in deep pools or lakes and perform migrations in the spring to spawn (Lucas and Baras 2001c). Many gaps in our understanding of migration occur due to logistical challenges of individual fish traveling hundreds to thousands of kilometers in the ocean or in freshwater (Chapman et al. 2012b). Migration is best understood in the Pacific salmonids (Johnsen and Hasler 1980; Dittman and Quinn 1996; Ueda 2012). Migration can be very complex and correspond to life history phases and driven by environmental cues.

Fish exhibit many migratory strategies that usually correlate with specific ecological conditions and environmental cues (Lucas and Baras 2001c). For example, many freshwater arctic fish species typically exhibit distinct migratory patterns which are influenced by a short season for feeding, growth, and reproduction whereas fish in temperate regions have a longer window for migrations associated with more optimal conditions for growth, survival, and reproduction (Lucas and Baras 2001c). While differences in migratory strategy are relatively well understood in birds (Chapman et al.

2012a), our understanding of the temporal (seasonal and diel) and individual strategies used by migratory fish that spend their entire life in freshwater appear largely unknown. However, recent advances in tracking technology have revealed some of the diversity and complexity of migratory strategies and behavior (Chapman et al. 2012b). Intraspecific variation in migratory behavior appears common as fish from different populations often vary in their use of migratory strategy, migratory distance, and migratory destination (Chapman et al. 2012b). For example, resident brown trout (*Salmo trutta*) live in streams at higher altitudes since migration costs and low recruitment has seemingly selected against migration (Bohlin et al. 2001). Homing, a tendency to return to previously used areas (Gerking 1959), is a topic that is relatively unexplored in the migratory strategies of potomodromous fish (those that migrate only in freshwater).

Binder et al. (2011) estimate that 2.5% of all fish species perform some type of migration. Commercially important Pacific salmonids have not surprisingly been extensively studied and have been documented to perform migrations over thousands of kilometers and migrate in large numbers to natal spawning habitats (Lucas and Baras 2001a). Dittman and Quinn (1996) documented a flexible imprinting strategy influenced by two types of migratory learning that allows fish to home, one that learns and retains freshwater landmarks and one that learns in response to novel environmental stimuli. Studies examining migratory patterns and homing in salmonids have overshadowed studies of migration of other freshwater fish that may be less important economically but demonstrate important strategies for life history requirements including reproduction or avoiding predation (overwintering refuge) (Lucas and Baras 2001a). Bajer and Sorensen

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(2010) describe one population of common carp, *Cyprinus carpio*, in which one-third of the individuals conduct movements (<2km) from deep lakes to shallow marshes in the spring, presumably for reproduction, while two-thirds of the population remain resident in the deep lakes. Skov et al. (2008) found that 23% of roach (*Rutilus rutilus*) in one population and 31% of white bream (*Blicca bjoerkna*) in another population move out of lakes and into streams, which serve as overwintering predation refuges. Dionne et al. (2012) found four complex migratory strategies (river residents and three seasonal forms of coastal emigrants- spring, summer, and fall) that shortnose sturgeon (*Acipenser brevirostrum*) employ for spawning, feeding, and skipped breeding purposes. Many migratory strategies are complex with only certain fractions of populations migrating at certain times of the year for specific purposes in an organism's life history.

1.2 Partial migration

Dingle and Drake (2007) define partial migration as a strategy in which a population can have both resident individuals (those that remain in either the breeding or nonbreeding habitat), and migrant individuals (those that migrate away from the breeding or nonbreeding habitat). Chapman et al. (2012b) describes partial migration as arguably the most common form of migration. Ornithological literature has some of the first descriptions of partial migration, particularly in temperate-zone birds that migrate in response to seasonal conditions (Chapman et al. 2011). For example, in Belgium, resident European robins (*Erithacus rubecula*) achieve higher life-time reproductive success if they select high quality habitat that functions as breeding and wintering habitat compared

to migrants which are forced to migrate and find suitable habitat elsewhere (Adriaensen and Dhondt 1990). Partial migration is presumably an adaptive strategy that has evolved in response to variable environmental conditions. Populations may have both obligate migrants, or individuals that migrate every year, and facultative migrants, or individuals that migrate only in some years (Fieberg and Conn 2014, Bronmark et al. 2008). For example, Fieberg and Conn (2014) found some northern white-tailed deer (*Odocoileus virginianus*) migrated in all years (obligate migrants) whereas others only migrated in years with severe winters (facultative migrants). Bronmark et al. (2008) described two alternative migratory strategies used by individual roach in which some migrate from lakes to streams (overwintering predation refuge) while others remain resident in lakes (foraging gains and higher predation), with the optimal strategy depending on a trade-off between predator avoidance and growth. Migratory strategy may vary with seasonal resource availability. Studies of partial migration should consider that variability in environmental conditions may explain annual variability in partial migration strategies. Partial migration may explain the behavior and movement of many organisms with complex life histories (Kerr et al. 2009).

1.2.1 Partial Migration in Fish

Partial migration varies between species, populations, and individuals (Chapman et al. 2011) and may be very common in fish of which there are almost 30,000 described species. The phenomenon of partial migration has been described for anadromous fish (those that migrate from saltwater to freshwater to spawn), catadromous fish (those that

migrate from freshwater to saltwater to spawn), oceanodromous fish (those that migrate

only in saltwater), potamodromous fish (those that migrate only in freshwater), and

amphidromous fish (those that migrate between freshwater and saltwater with no

reproductive impetus) (Chapman et al. 2012b). Until recently, most reviews on partial

migration in fishes have focused on salmonids (Chapman et al. 2012b). However, this

group contains only approximately 200 species and is not representative of all species.

Partial migration in other species is only described in detail for a few species of

Cypriniformes (Bronmark et al. 2008, Skov et al. 2008, Brodersen et al. 2012, Chapman

et al. 2013) and Perciformes (Skov et al. 2008, Kerr et al. 2009, Kerr and Secor 2009,

Kerr and Secor 2012). Partial migration is complex due to its facultative nature and

variable patterns originating from genetics (Biebach 1983), individual personality

(Chapman et al. 2011), effects of nutritional status (Brodersen et al. 2008, 2011), and

possible phenotypic plasticity due to inter-annual variability in environmental conditions

(Kerr and Secor 2012). The field of partial migration is expanding with a growing

number of studies adopting a consistent lexicon which previously slowed synthesis of

studies with evidence of partial migration. Three types of partial migration are currently

commonly recognized: breeding partial migration, non-breeding partial migration, and

skipped breeding partial migration (Chapman et al. 2012b). Each will be described below

with examples of each type identified in Table 1.

1.2.2 Non-breeding Partial Migration

Non-breeding partial migration can be defined as a migratory strategy in which residents and migrants overwinter apart and breed together (Chapman et al. 2011 and Chapman et al. 2012b). Chapman et al. (2011) suggest non-breeding partial migration as the most basic form of partial migration and it is the foundation of most studies of partial migration. Non-breeding partial migration has been described in Anguilliformes, Cypriniformes, Gadiformes, Gasterostiformes, Perciformes, Petromyzontiformes (Chapman et al. 2012b) (Table 1). For example, overwintering partial migration to avoid adverse conditions is a common form of non-breeding partial migration (Chapman et al. 2012b) in roach (*Rutilus rutilus*) and white bream (Table 1.). A population of roach in a Swedish lake, Lake Krankesjon, and its three tributary streams has been studied intensively for over a decade (Brodersen et al. 2008, Brodersen et al. 2011, Chapman et al. 2012a, 2012b). Chapman et al. (2012b) suggest that this population of roach is the best understood example of potamodromous partial migration. Based on body condition, individual roach choose whether to migrate from lakes (higher predation pressure and more foraging opportunities) to refuges in streams (lower predation pressure and low foraging opportunities) to overwinter (Brodersen et al. 2008). Brodersen et al. (2011) found that the proportion of migrants over six years varied depending on temperature during the pre-migration growth period during summer. At an individual level, Brodersen et al. (2012) found migrants studied multiple years exhibited fidelity to over-wintering streams and consistency in their migration timing. While studies on roach, rudd (*Scardinius erythrophthalmus*), and white bream have advanced the field of non-breeding

partial migrations in cyprinids, most of the work was performed in one small lake system in Sweden. To the best of my knowledge, partial migration has only been studied in four species of Cypriniformes (roach, rudd, white bream, and common carp) (Table 1). I suggest future studies should include more species across a broader range of systems to draw more general conclusions in non-breeding partial migration, particularly in a group like Cypriniformes, a group with over 4,000 species. In addition, I suggest studies of partial migration should investigate potential non-breeding partial migrations performed throughout the entire year and examine possible environmental drivers behind these migrations.

Although some populations and species of European cyprinids (roach, rudd, and white bream (Table 1)) have been studied, patterns of non-breeding partial migration in these cyprinids across populations remain unknown. In addition, ecological cues that drive partial non-breeding migrations at both an individual and population level are virtually unknown among other cyprinid species. Bajer et al. (2015) used data from Bajer and Sorensen (2010) and one other location to describe two common carp populations in North America conducting partial migrations from an overwintering lake to shallow marshes to spawn in the spring (Table 1). However, whether common carp perform additional partial migrations for non-breeding purposes such as overwintering or feeding is unknown.

Partial non-breeding migration has been described in several species of non-cyprinid fish. For example, populations of three-spined sticklebacks (*Gasterosteus aculeatus*) in Japan contain anadromous and resident individuals with smaller juveniles

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migrating to the Pacific Ocean and larger juveniles remaining resident in freshwater

ponds (Kitamura et al. 2006, Table 1). For Atlantic and Pacific eels (*Anguilla spp.*), the

majority (80%) of individuals caught in commercial fishing activities exhibit no evidence

of freshwater migration which may indicate eels with an ocean-based life history

(Tsukamoto et al.1998; Table 1), although migrations to estuaries should be considered.

Dadswell (1979) documented sexually maturing shortnose sturgeon females migrating in

the fall from the St. John River Estuary to deep, freshwater overwintering lakes next to

probable spawning sites. This has been described as an example of a two-step migration

which allows individuals late in gonadal development to perform non-breeding migration

in the fall (step one) for overwintering near the spawning site and perform short

migrations to spawn in the following spring (step two) (Bemis and Kynard 1997, Lucas

and Baras 2001d, Dione et al. 2012). Juvenile Atlantic cod (*Gadus* morhua) have also

exhibited non-breeding partial migrations with up to 70% out-migrating from coastal

fjords in the winter to unknown destinations in deeper water (Cote et al. 2004). Chapman

et al. (2012b) notes that the varied lexicon of researchers using different terms to describe

migratory variation has complicated this growing field of partial migration.

Although partial non-breeding migrations appear common, the etiology of this

behavior is not well understood. Chapman et al. (2012a) describes a body size hypothesis

but tests in fish are lacking, although differences in size correlate with partial non-

breeding migration in *G. aculeatus* (Kitamura et al. 2006) and *G. morhua* (Cote et al.

2004). Two-step partial non-breeding migrations such as those described in sturgeon by

Bemis and Kynard (1997) have not been described for non-sturgeon species. Future

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studies should investigate whether partial migrations in multiple steps are common in other long-lived species. Chapman et al. (2012b) mentions that *Pleuronectes platessa* may exhibit a non-breeding partial migration related to feeding with the majority (>70%) of individuals making feeding migrations. A non-breeding partial migration for the purposes of feeding has not been described in the most recent reviews of partial migration literature in fish (Chapman et al. 2012a, 2012b), although future studies should investigate if non-breeding partial migrations for non-overwintering purposes are common and what environmental factors, if any, drive these migrations. Future work has the opportunity to investigate whether other cyprinids, such as common carp, employ multiple forms of non-breeding partial migration when studied throughout the year and whether these migrations are directed. Brodersen et al (2012) investigated site fidelity of roach in one simple lake system with three streams. Patterns of partial non-breeding migrations and homing in larger interconnected systems with numerous options for migration, overwintering, and feeding remain to be described for cyprinids. Since the common carp is one of the world's most invasive species with established populations on all continents, the carp may be an ideal candidate to examine whether multiple non-breeding partial migrations and homing in interconnected systems may contribute to its invasiveness.

1.2.3 Breeding Partial Migration

Partial breeding migration was defined by Chapman et al. (2012b) as a common seasonal partial migration in which all individuals overwinter together and then a

percentage of them migrate to spawn. There appear to be many variations in this strategy including those used by *Clupea harengus* which use common feeding areas but for which certain individuals use distinct spawning areas (Ruzzante et al. 2006). Species exhibiting breeding partial migrations have important implications for fisheries managers working to conserve genetic diversity across populations which could be severely compromised with generalized management of populations that differ genetically (Ruzzante et al. 2006). Breeding partial migration has been described in Ancipenseriformes, Characiformes, Clupeiformes, Esociformes, Gasterostiformes, Perciformes, and Salmoniformes (Chapman et al. 2012b; Table 1).

There are many examples of fishes that use breeding partial migration. Seven freshwater fish undertake spawning migrations from the Baltic Sea to freshwater include pike (*Esox lucius*), perch (*Perca fluviatilis*), whitefish (*Coregonus sp*), bream (*Abramis brama*), ide (*Leuciscus idus*), roach and burbot (*Lota lota*) (Engstedt et al. 2010). Of these, one population of pike overwinters in the Baltic Sea and reproduces in the spring either in brackish bays or streams and rivers, identifying a partially migratory population (Table 1). Otolith chemistry suggested that 46% of the individuals recruited in freshwater with indications of older fish performing repeated migrations to freshwater (Engstedt et al. 2010). In South America, Godinho and Kynard (2006) observed 79% of zulega (*Prochilodus argenteus*) performing migrations from main-stem non spawning areas to specific spawning areas over multiple years during the November – February spawning season (Table 1). Of the migrating zulega, individuals were also observed migrating to the spawning area multiple times which Godinho and Kynard (2006) suggested could be

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related to males spawning multiple times during the spawning season. In north temperate regions of North America, 10-20% of pike and 10-50% of common carp were observed migrating in specific streams from a few sets of deep overwintering lakes in the spring to spawn in shallow marshes each year (Chizinski et al. 2016; Table 1). The timing of migration varied with pike migrating earlier and migration synchronicity was only apparent for common carp (Chizinski et al. 2016).

Breeding partial migration is not well understood among potamodromous fish. Although freshwater spawning habitats in the Baltic Sea appear valuable to pike (Engstedt et al. 2010), whether other freshwater species in the Baltic Sea adopt similar migratory strategies during breeding is unknown. The finding that zulega (Table 1) perform multiple migrations to spawning grounds which may be dependent on the timing of appropriate environmental cues for spawning (Godinho and Kynard 2006) but has not been studied may be an observation of multiple partial migrations within a single year. Future studies should investigate whether environmental and social cues may drive multiple partial migrations. While Chizinski et al. (2016) observed 10-50% of pike and carp using specific streams during breeding partial migrations, their study is limited as it was performed in two small systems of lakes and marshes. I suggest future studies investigate whether breeding partial migrations are common in specific streams and specific reproductive lakes in more complex systems. For long-lived species such as carp, studies at an individual level in relation to breeding partial migration have not been described, although these studies may further our understanding of consistent patterns of

breeding partial migration, particularly in systems that are complex (many migratory options).

1.2.4 Skipped Breeding Partial Migration

Skipped breeding partial migration has been described by Chapman et al. (2012b) as a common seasonal partial migration in which individuals conduct migrations to breed but not every year. This form of partial migration had not been considered to be a form of partial migration until Shaw and Levin (2011) proposed a model that determines what conditions (constant and stochastic) drive some individuals to skip breeding. Under constant conditions partial migration is favored when mortality risk from migration is high or when forgoing a breeding season increases individual fecundity long-term compared to spawning every year (Shaw and Levin 2011). Skipped breeding partial migration has been described in Acipenseriformes, Berciformes, Clupeiformes, Elasmobranchii, and Salmoniformes (Chapman et al. 2012b). Other species such as Atlantic cod (*Gadus morhua*) (Table 1) exhibit evidence of skipped breeding partial migration (Jorgensen et al. 2006).

Partial skipped spawning migrations may be important for long-lived, slowly maturing fish. For shortnose sturgeon, an unknown proportion of individuals migrate from spring to summer up rivers to spawn (May-June) and seaward in the fall (Dadswell 1979). Dionne et al. (2013) found shortnose sturgeon in the Gulf of Maine (Table 1) exhibit complex migratory patterns that include river residents and coastal emigrants (Dionne et al. 2013). A better understanding of individual homing patterns in seasonal

skipped breeding partial migration could assist in identifying important spawning habitat. Jorgensen et al. (2006) suggested that spawning stock biomass recruit models for species like Atlantic cod (Table 1), known for skipped spawning may be inaccurate due to the false assumption that all sexually mature cod contribute equally. In addition, unknown proportions of adult Atlantic cod undertake spawning migrations. More understanding of individual movement, direction, and homing could assist in identifying potential marine protected areas (MPAs) and the success of established MPAs for spawning habitat. Future studies could investigate whether long-lived species in other groups like cyprinids also employ skipped-breeding migration to expand understanding of species with complex life histories.

1.2.5 Combinations of Different Forms of Partial Migration

Although fish biologists have typically categorized migratory species in specific categories including anadromy, catadromy, oceanodromy, potamodromy, and amphidromy, Chapman et al. (2012b) cautions that specific categories of partial migration may not be mutually exclusive. In other words, a species could in theory exhibit a combination of both non-breeding partial migration and breeding partial migration on annual cycles. While Chapman et al. (2012a, 2012b) summarized many types of partial migrations that may reflect novel strategies, it is possible that some of these may contain multiple phases or components. To my knowledge, few if any studies monitor partial migrations of a fish with a complex life history on a year-round basis and describe multiple partial migrations.

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1.3. Homing

Homing, a tendency to return to previously used areas (Gerking 1959), is a topic that is relatively unexplored in the context of partial migration. Natal site and spawning site fidelity has been observed for pike in one lake in Minnesota over four years (Miller et al. 2010). Chizinski et al. (2016) provide evidence of homing with adult pike and common carp which choose specific inlets or outlets during spawning migrations in the spring, although there was no indication that homing was consistent among individuals over multiple years. After overwintering in refuges, European freshwater eels (*Anguilla Anguilla*) migrate back to foraging areas in the summer where they were recaptured over multiple years (Lucas and Baras 2001b). Dadswell (1979) found shortnose sturgeon in the Saint John estuary exhibited both homing and pair bonding when up to 75% of tagged individuals were recaptured one to three years later in the same foraging area. Godinho and Kynard (2006) found that zulega homed to areas for pre-spawning staging, spawning, and non-spawning periods in their life history with evidence of individuals occupying three distinct reaches in the Sao Francisco River in Brazil during the non-spawning period. Few other species within South America have been studied long enough to understand if homing and partial migration patterns are common.

For homing to be maintained over evolutionary time scales, the benefits must outweigh the costs of not homing. For instance, Pacific salmon likely home to natal streams since migrating in unfamiliar streams or reaches may be risky (Lohmann et al. 2008). Migrations of lemon sharks (*Negaprion brevirostris*) indicate that up to 71% of females learn to return to Bimini, most on a two-year cycle, to give birth to their litter

(Feldheim et al. 2004) which provides evidence that many shark species are philopatric or return to particular area to give birth (Guttridge et al. 2009). Homing and reproductive success in natal areas maintains reproduction in specific areas in the future (Lohmann et al. 2008). Studies exploring whether individuals occupy home ranges during multiple annual migrations, particularly in long-lived partially migratory species, are few.

Whether fish use a home range has been important in understanding which individuals might prefer specific areas for daily activities. Hartney (1996) found evidence of homing tendencies and home ranges of kelp-bed fishes, adult blacksmith (*chromis punctipinnis*) and adult senorita (*Oxyjulis californica*), in a translocation study. While visual observations of tagged fish were low for translocated fish (14 of 57 senorita and 2 of 57 blacksmith), 80% of senorita and 100% of tagged blacksmith were re-sighted at their initial capture site. Hartney (1996) suggests the ability to home back to a reef previously occupied after translocation provides evidence of a home reef, possibly for feeding or refuge purposes. Crook et al. (2004) performed a similar translocation study in the Broken River, Australia with common carp and found 80% of non-translocated carp (4 of 5) remained in home ranges near their capture site and 50% of translocated carp (5 of 10) returned to home ranges near their capture location (Crook et al. 2004). Chizinski et al. (2016) also suggest common carp home. In a month-long experiment, Bajer et al. (2010) found 14 adult carp occupied restricted home ranges in the summer and learned the location of an introduced food reward which provides evidence of cognitive abilities of free-ranging wild carp. Data is lacking for whether carp occupy specific home ranges over the entire summer in interconnected systems with many potential streams,

reproductive lakes, feeding lakes, and overwintering lakes. No study to my knowledge

has investigated whether long-lived fish like common carp perform multiple migrations

annually with a directed homing impetus. Examining homing patterns in relation to

distinct partial migration over the entire life history of species, particularly those that live

over 20 years, would advance our understanding of partial migration and home ranges in

species with complex life histories. Recent reviews by Chapman et al. (2011, 2012a,

2012b) may assist future studies that have evidence of partial migration in adopting

consistent use of partial migration terminology as a common migratory strategy.

2.0 The Common Carp

2.1 Origins and life history of common carp

The common carp has a western (Caspian, Aral, and Black Sea basins) and an

eastern (East and South-east Asia) distribution in its native range of Eurasia (Memis and

Kohlmann 2006). It is one of the most commonly cultured freshwater fish (Memis and

Kohlmann 2006) and has been introduced repeatedly around the world for aquaculture

and recreational fishing purposes (Weber et al. 2011). The common carp is one of eight

fish species included among the 100 of the world's worst invasive species

(<www.issg.org/worst100_species.html>). Life history traits of common carp may

explain its propensity to establish populations in many non-native habitats. Although

poorly understood, the life history of common carp includes: early sexual maturation

between ages of 2 and 3 (Weber and Brown 2009), reproductive migrations of up to

200km to shallow wetlands in the spring (Stuart and Jones 2006b), high fecundity with

females carrying up to 3 million eggs (Swee and McCrimmon 1966, Sorensen and Bajer 2011), fast growth rates of juveniles (up to162 mm at age 1) (Jackson et al. 2008; Weber et al. 2010), and longevity up to 64 years (Koch 2014). The life history of common carp is also flexible, which promotes opportunistic exploitation of unstable habitats during spawning as a predator-avoidance/swamping strategy that is typical of highly fecund, invasive fishes with vulnerable eggs and larvae (Bajer et al. 2012).

The deleterious environmental consequences of introduced common carp on shallow freshwater ecosystems has been well documented. As "generalists," common carp have an omnivorous diet (detritus, macroinvertebrates, zooplankton, and plants) and tolerate wide ranges in temperature, dissolved oxygen, pH, turbidity, and conductivity (Weber and Brown 2009). Reductions in water quality and increasing turbidity are a direct result of the benthic foraging tactics employed by common carp which cause reductions in aquatic macrophytes (Pimentel et al. 2000; Bajer et al. 2009). The common carp has been labeled as an ecosystem engineer which modifies non-native ecosystems by their omnivorous diet (Weber and Brown 2009). The biomass of common carp ~100kg/ha has been associated with ~50% reductions in aquatic macrophytes and waterfowl as a clear lake was transformed into a turbid lake (Bajer et al. 2009), a result of a self-reinforcing cycle that promotes additional deterioration in water quality (Sorensen and Bajer 2011). Bajer et al. (2015) suggest that recruitment of carp across large geographic areas in North America appears to be regulated by water clarity and lake productivity at a large scale and further regulated by micropredators such as bluegill at a smaller scale. Understanding these ecological processes and their interactions advances

our understanding of why some areas support a superabundance of carp associated with high recruitment events and others do not (Bajer et al. 2015).

2.2 Invasiveness and management

Common carp exhibit a flexible life history and establish populations in non-native environments with negative ecological consequences. Management strategies for controlling this invasive species have had mixed results. Relatively early detection of invasive common carp allowed complete eradication of carp from Lake Crescent, Australia (Taylor et al. 2012) but this is an exception. The end goal of eradication is often to restore ecosystems and provide natural habitats for native species (Genovesi 2005; Taylor et al. 2012). Eradication programs have been challenged mostly due to high costs and harmful impacts on native species (Simberloff et al. 2005; Taylor et al. 2012). Whole-lake poisoning using rotenone has been a control strategy for invasive benthivorous fish such as carp in attempts to restore turbid lakes to clear water states, although this has been associated with severe mortalities on native species (Schrage and Downing 2004). Other traditional control strategies have used water level draw-downs, piscicides, and commercial removals of adults, the last of which has been recognized as one of most promising control strategies (Weber et al. 2011).

Understanding the seasonal distribution of carp has been identified as a first step for long-term management of carp (Penne and Pierce 2008). Previous management strategies targeted removal of invasive and non-game fish species such as carp using ultrasonic tracking to locate aggregations of carp during the winter in Lake Mendota,

Wisconsin (Johnsen and Hasler 1977). This technique of managing invasive fish has been advanced with improved tracking technologies and utilizing cost-effective advances such as the Judas technique. The Judas technique utilizes a subset of radio-tagged individuals within a population to locate larger groups of the population for control or eradication of invasive species ranging from feral goats in Hawaii (Taylor and Katahira 1988; Simberloff et al. 2005) to common carp in North America (Bajer et al. 2011). Carp have a tendency to form large winter-time aggregations in ice-covered lakes in north temperate regions of North America (Johnsen and Hasler 1977; Penne and Pierce 2008; Bajer et al. 2011). Commercial seining can occasionally be effective at removing large numbers of carp for control purposes during periods of aggregations (Bajer et al. 2011; Weber et al. 2011). Seining in combination with the Judas technique can be more effective. Bajer et al. (2011) used the Judas technique to quantify a removal efficiency up to 94% for populations of carp that formed winter-time aggregations in Minnesota lakes and emphasized the importance of having radio-tagged fish as aggregations moved throughout the winter. Repeated seining efforts on one population over time become less effective as fish likely learn to avoid the nets with increased exposure.

Recent studies have recommended a more integrative approach to carp control, one that utilizes multiple control efforts throughout various life history stages (Bajer and Sorensen 2010; Weber et al. 2011; Koch 2014). Inability to control all size classes of carp is a major limitation to commercial removal techniques including under ice seining (Weber et al. 2011). There is a need to develop a more complete understanding of population movements in complex, shallow-lake systems to identify both overwintering

and reproductive home ranges in addition to critical migration corridors connecting these habitats.

2.3 Seasonal movement patterns of common carp

Shallow lake complexes of the Midwest are highly productive and are susceptible to common carp invasion (Weber and Brown 2009). Many lake complexes are characterized by having both stable (abundant dissolved oxygen year round) and deeper habitats interconnected with unstable (low dissolved oxygen during certain times of the year) and shallow habitats. Bajer and Sorensen (2010) described seasonal patterns in which 11 – 37% of the adult carp population moving from a pair of overwintering lakes connected to a single shallow putative nursery lake in the spring to spawn in 2006, 2007, and 2008. This nursery lake occasionally experienced hypoxic conditions in winter. Carp were not tracked continuously throughout the year so their activity in the summer and winter is not known, nor is it known how they might behave in larger, more complex (many migratory options) systems that are more typical of this region. However, a related study of adult capture rates from the same pair of overwintering lakes found that 10 – 50% left every spring when water temperatures rose above 10°C, with movement usually associated with rain events (Chizinski et al. 2016). Although carp appear to prefer particular streams and lakes (Chizinski et al. 2016), homing and the specific relationship of migratory behavior to spawning (or post-spawning) has not be addressed. Bajer et al. (2010) tracked 34 adult carp in one lake for three weeks and found evidence of nocturnal activity and summer home ranges, but data are lacking for more complex systems. In the

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Broken River, Australia, Crook et al. (2004) found that out of 15 carp (5 released at capture location, 5 translocated upstream of capture location, and 5 translocated downstream of capture location), four of the non-translocated carp maintained home ranges near their capture location and five of the translocated carp returned to their original capture location and occupied home ranges in that area. This study was performed March – July of one year in one Australian river, but data are lacking in describing intern-annual homing throughout the year.

The seasonal movements of carp are also poorly understood. In particular, no study has continuously tracked individual carp year-around to determine this species' complete life history. Further, while adult common carp have been reported to form large aggregations under the ice (Bajer et al. 2011), no study has documented when and how they form these aggregations or when and how they might break up. While Chizinski et al. (2016) observed pre-spawning aggregations prior to reproductive migrations in the spring, the timing of the transition from a winter aggregation to a pre-spawning aggregation is not studied. Chizinski et al. (2016) also documented adult carp leaving overwintering lakes and migrating in specific streams, although there were no data documenting return to overwintering lakes as carp were removed from the system upon capture. In addition, no data exists on when individual fish enter spawning lakes or which lakes they choose for spawning. While Bajer and Sorensen (2010) documented one-third of the adult carp population moving to a shallow marsh to spawn, data on individual patterns and whether this movement strategy is facultative or obligatory among migrants is unknown. The migratory options were limited as connections between lakes and

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marshes were intermittent or dry during certain times of the year. Data on summer

distribution are also limited in large interconnected systems. Both Bajer et al. (2010) and

Crook et al. (2004) documented feeding home ranges during a short period of time (1-5

months) in one year. Data are lacking for home ranges occupied during the entire summer

for a long-lived fish like carp in systems that are continuously connected to both

overwintering and spawning habitats. The presence of migrations associated with non-

breeding drivers such as feeding or overwintering in larger systems that have continuous

connections between lake habitats is unknown. Whether individual variation is common

or consistent, particularly in complex (more than two choices) and large (>2km) systems,

over multiple years and during multiple migratory periods is unknown.

2.4 Partial migration in common carp

　　　Breeding partial migration of common carp is poorly understood. In particular,

partial migration has only been analyzed during the spring migratory period and primarily

in three relatively small and simple systems, the Riley Creek, Purgatory Creek, and

Phalen Chain of Lakes Watersheds (Bajer et al. 2015; Chizinski et al. 2016). The

behavior of carp in these systems may not necessarily represent their behavior in larger

systems with multiple migratory pathways that are continuously connected to adjacent

lake habitats. While Chizinski et al. (2016) observed synchronous partial migrations by

adult carp in specific streams, this study only documented movements out of the

overwintering lake with no information on spawning location or if individuals showed

consistent partial migration patterns each year. Studies should examine partial migrations

over the entire life history of carp as there may be partial migrations associated not only with reproduction but also overwintering. Partial migrations at other times of the year may be common although they have not been studied or described in large interconnected lake systems that have continuous connections between habitats. When and why carp aggregate in deep lakes is still poorly understood. Bajer and Sorensen (2010) noted that some carp did not return to the deep lake prior to winter which may be evidence of a partial overwintering migration. Whether carp exhibit partial feeding migrations and whether these migrations are directed has not been studied. Future studies of partial migration of adult carp should address these unknowns to determine if partial reproductive migrations documented by Bajer and Sorensen (2010) and Chizinski et al. (2016) are representative of other watersheds and whether partial migrations at other times of the year may also contribute to their invasiveness in certain regions like the North American Midwest.

The causes and consequences of these partial spawning migrations are of increasing importance with broad applications for partially migratory fish and more specifically for invasive carp management. The success of three of the eight fish species in 100 of the world's worst invasive alien species (<www.issg.org/worst100_species.html>), *salmo trutta*, *oncorhynchus mykiss*, and common carp, may be attributed to their partial migration behavior (Bajer et al. 2015). Invasive adult carp experience minimal predation risk once they reach adulthood in the absence of native predators. Patterns in partial reproductive migrations have emerged. Understanding how partial migration has led to the superabundance of carp in the North

American Midwest may assist in understanding how introduced populations in other regions such as the Murray-Darling River Basin (MDRB) in Australia became dominant (Bajer et al. 2015). While Australia is a more moderately temperate environment than north temperate regions in North America, summer hypoxia may create predator-free lateral habitat for carp during spawning (Bajer et al. 2015) similar to winter hypoxia experienced in shallow lake systems in the North American Midwest. In addition, seasonal flooding allow carp to opportunistically access temporarily available habitats that may initially be free of predators and function as carp nurseries (Stuart and Jones 2006b; Bajer and Sorensen 2010). Accessing these unstable habitats in conjunction with partial migration may be a predator-avoidance/swamping strategy that is typical of highly fecund, invasive fishes with vulnerable eggs and larvae (Bajer et al. 2012). Seasonal partial migration patterns, individual patterns, and homing in common carp, a species with a complex life history, form the basis of my thesis.

3.0 Introduction to this thesis

My thesis has two chapters. Following this introductory chapter is chapter 2 which is entitled, "Adult common carp perform a series of seasonal partial migrations to home spawning, feeding and winter lakes in a complex, model North American watershed." The annual distribution and movement patterns of adult common carp (*Cyprinus carpio*), an invasive cyprinid, was documented for 2.5 years in a large system of 12 interconnected lakes to determine partial migrations, seasonal home ranges, and patterns of individual movement. We found that adult carp exhibit a flexible life history

strategy that can be categorized by six components: overwintering, reproductive partial migration, spawning in home lakes, summer partial migrations to feeding in home lakes, feeding, and partial migration to an overwintering (refuge) lake. All three partial migrations were directed to specific locations and most carp used one stream of four with evidence of home spawning, feeding, and overwintering lakes. This is the first study to my knowledge involving any fish species to describe a novel phenomenon documenting a multi-phase partial migration strategy with homing to specific water bodies for each phase of partial migration. This work expands our understanding of partial migration even in well studied orders such as Cypriniformes and more specifically common carp. This chapter is written in the style of Canadian Journal of Fisheries and Aquatic Sciences. When submitted, I will be first author, John Fieberg will be second author, and Peter Sorensen will be the final author. Supportive appendices and a bibliography follow the main chapters.

Table 1. Examples of partial migration types and the proposed ecological mechanism for each partial migration by species.

Order Reference	Species	Migratory Type	Partial Migration Evidence	% Migrant Study Site	Proposed Ecological Mechanism
Acipenseriformes Dionne et al. 2013	Shortnosed sturgeon (*Acipenser brevirostrum*)	Partial skipped breeding migration	Acoustic telemetry	70% Penobscot River, Gulf of Maine	Sexual status, resource availability, density
Anguilliformes Tsukamoto et al.1998	European eel (*Anguilla anguilla*) American eel (*A. rostrate)* Japanese eel (*A. japonica*)	Partial non-breeding migration	Otolith microchemistry (Ca and Sr)	20-39% North Sea East China Sea River Elbe River Tone	Unknown, possibly body condition
Berciformes Bell et al. 1992	Orange roughy (*Hoplostethus atlanticus*)	Partial skipped breeding migration	Gonadosomatic index (GSI), i.e. gonad weight as a percentage of total body weight	Unknown Australia, Pacific Ocean	Fecundity, individual condition
Centrarchiformes Mesing and Wicker 1986	Largemouth bass (*Micropterus salmoides floridanus*)	Partial breeding migration	Radio telemetry	40% - 86% Lake Yale and Lake Eustis, Florida	Reproductive success in protected spawning areas
Characiformes Godinho and Kynard 2006	Zulega (*Prochilodus argenteus*)	Partial breeding migration	Radio telemetry	79% Sao Francisco River, Brazil	Reproduction
Cypriniformes Skov et al. 2008	Roach (*Rutilus rutilus*) Rudd (*Blicca bjoerkna*) White bream (*Scardinius erythrophthalmus*)	Partial non-breeding migration	Passive telemetry	23% 3.7% 31% Lake Kran-kesjo̎n, Sweeden	Predation risk

Order Reference	Species	Migratory Type	Partial Migration Evidence	% Migrant Study Site	Proposed Ecological Mechanism
Cypriniformes Brodersen et al. 2012	Roach (*Rutilus rutilus*)	Partial non-breeding migration	Passive telemetry	15% Lake Kran-kesjo¨n, Sweeden	Predation risk
Bronmark et al. 2008; Chapman et al. 2013	Roach (*Rutilus rutilus*)	Partial non-breeding migration	Passive telemetry	Unk. Lake Kran-kesjo¨n, Sweeden	Predation risk, growth trade off
Chizinski et al. 2016	Common carp (*Cyprinus carpio*)	Partial breeding migration	Stream trapping	10-50% Riley Creek Watershed, MN	Reproduction
Bajer and Sorensen 2010	Common carp (*Cyprinus carpio*)	Partial breeding migration	Radio telemetry	33% Riley Creek Watershed, MN	Reproduction
Esociformes Engstedt et al. 2010	Northern pike (*Esox Lucius*)	Partial breeding migration	otolith microchemistry	46% Baltic Sea	Reproduction
Skov et al. 2008	Pike (*Esox Lucius*)	Possible partial breeding migration	PIT telemetry	<2% Lake Krankesjo¨n in Sweeden	Unknown
Chizinski et al. 2016	Pike (*Esox Lucius*)	Partial breeding migration	Stream trapping	10-20% Lakes Riley and Susan (MN)	Unknown, likely reproductive
Gadiformes Pulliainen and Korhonen 1993	Burbot (*Lota lota*)	Partial skipped breeding	Otolith growth patterns	29-93% Kemi and Kitinen Rivers, Finland	Unknown
Gadiformes Jorgensen et al. 2006	Atlantic cod (*Gadus morhua*)	Partial skipped breeding	Flexible life history model	Unknown Northeast Arctic Ocean	Individual fitness/growth rate, Fecundity
Gasterostiformes Kitamura et al. 2006	Three-spined stickleback (*Gasterosteus Aculeatus*)	Partial non-breeding migration	Dip-net, trap net	Unknown Shiomi River, Japan	Unknown, body size

Order Reference	Species	Migratory Type	Partial Migration Evidence	% Migrant Study Site	Proposed Ecological Mechanism
Perciformes Kerr et al. 2009	White Perch (*Morone Americana*)	Breeding partial migration	Otolith microchemistry, age at dispersal	85% Patuxent River estuary	Individual fitness/growth rate, Fecundity
Kerr and Secor 2009	White Perch (*Morone Americana*)	breeding partial migration	Juvenile migrant and resident collection, lab tests for bioenergetics	Unknown Patuxent River estuary	bioenergetics
Skov et al. 2008	Perch (*Perca fluviatus*)	unknown	PIT telemetry	<0.9% Lake Krankesjö¨n, Sweden	Unknown
Nanami et al. 2014	White-streaked grouper (*Epinephelus ongus*)	Partial breeding migration	Acoustic telemetry	17% East China Sea (Pacific Ocean)	Spawning migration
Salmoniformes Paez et al. 2011	Atlantic salmon (*Salmo salar*)	Partial non-breeding migration	Rotary trap	73% Sainte-Marguerite River, Canada	Larger body size determines smoltification and migrants
McPhee et al. 2007	Rainbow Trout (*Onchorhynchus. mykiss*)	Non-breeding partial migration (Summer run steelhead) and breeding partial migration (winter-run steelhead)	Hook and line, gillnets, microsatellite analysis	56% Kamchatka Peninsula	Fecundity, mortality trade off, growth rate
Ohms et al. 2013	Rainbow Trout (*O. mykiss*)	Partial breeding migration	Rotary screw traps during emigration season	Unknown Western North America	Fecundity, mortality trade off, growth rate, female biased out-migrant ratio

Order Reference	Species	Migratory Type	Partial Migration Evidence	% Migrant Study Site	Proposed Ecological Mechanism
Salmoniformes Robillard et al. 2011	Brook Trout (*Salvelinus fontinalis*)	Non-breeding partial outmigration	Vertebrae and otoliths for length at age Hook and line, stream electrofishing	Unknown Lake Superior and tributary streams	Growth rate
Olsson and Greenberg 2004	Brown Trout (*Salmo trutta*)	Non-breeding partial outmigration, Breeding migration	PIT tag antenna arrays	15-18% Grea°na River, Sweden	Mortality risk, energy expenditure, Growth rate, habitat use
Wysujack et al. 2009	Brown Trout (*Salmo trutta*)	Non-breeding partial outmigration	Phenotype determined by experimental feeding trials	Unknown. River Klara¨lven, Sweden	Prey availability
O'Neal and Stanford 2011	Brown Trout (*Salmo trutta*)	Partial Breeding migration	Floy tag, mark-recapture	98.1 – 98.7% Rio Grande, South America	Growth rate, food supply limited growth of residents forcing anadromy

Chapter 2: Adult common carp perform a novel series of seasonal partial migrations to

home spawning, feeding and winter lakes in a complex, model North American

watershed

Chapter Summary

The annual distribution and movement patterns of adult common carp (*Cyprinus carpio*), an invasive cyprinid, was documented for 2.5 years in a model watershed with a dozen interconnected lakes. For three winters, over 90% of all adult carp were observed to overwinter and form large aggregations in a single deep lake. In the spring, and once temperatures rose to between 5-10°C, most adults (82% in 2014, 98% in 2015, and 98% in 2016), migrated to shallow lakes to spawn with most using a single stream (86% in 2014, 96% in 2015, and 100% in 2016) to enter specific home lakes (81%) each year. Such a precise breeding partial migration has not been previously documented in fish. After spawning, many, but not all, adults (46% in 2014 and 80% in 2015) left their spawning lakes and entered a different set of 1-2 lakes where they presumably fed. This appears to reflect a second partial migration and a tendency to use home summer feeding ranges. In the fall, most adult carp (57% in 2014 and 93% in 2015) then returned to a single common overwintering lake. This appears to reflect a third partial migration associated with overwintering. This life history strategy is characterized by six annual components: an overwintering phase, a breeding partial migration, spawning in home lakes, summer partial migration to feeding home ranges, feeding phase, and partial migration to an overwintering (refuge) lake. This flexible, but highly directed life history strategy has seemingly not been described in fish before and could explain the success and invasiveness of common carp while providing options for control.

Introduction

Migrations are directed, seasonal movements that occur on large scales that exceed those of daily movements and are motivated by organisms' need to find food, select mates, seek shelter and avoid predators and/or environmental extremes (Jonsson and Jonsson 1993; Dingle and Drake 2007; Chapman et al. 2012a). Partial migrations refer to scenarios in which not all individuals within a population move so there are both resident and migratory individuals (Dingle and Drake 2007). Eighteen taxonomic groups of fish have been observed to exhibit partial migration in both marine and freshwater environments (Chapman et al. 2012b). These include three types of seasonal partial migrations: non-breeding, breeding, and skipped-breeding. Non-breeding partial migrations reflect a strategy in which a portion of the population migrates for non-reproductive purposes such as overwintering and is exemplified by the roach (*Rutilus rutilus*) (Skov et al. 2008, Brodersen et al. 2012). Breeding partial migration is a strategy in which a portion of the population migrates for reproductive purposes and is exemplified by the white perch (*Morone americana*) in the Patuxent River and Chesapeake Bay (Kerr and Secor 2009). Skipped breeding migration is a strategy in which a portion of the population skips one or more years or spawning and is exemplified by the shortnosed sturgeon (*Acipenser brevirostrum*) (Dadswell 1979; Dionne et al. 2013). While 2.5% of all fish species possess migratory life histories (Binder et al. 2011) and evidence suggests that most of these are some type of partial migration, the topic is poorly understood and there may be many other forms of partial migration. Year-long studies to document the full complexity of any partial migration strategy, including the

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possibility that species might use a series of novel strategies in different seasons, could advance the expanding field of partial migration.

The common carp, *Cyprinus carpio*, is a good candidate to explore the full complexity of partial migration over the course of a year because is a globally distributed, and long-lived. The common carp typically matures at an age 2 or 3 (Weber and Brown 2009) and exhibits high fecundity (Swee and McCrimmon 1966; Sorensen and Bajer 2011). In its native habitat, the adult common carp is known for spending most of the year, including winters, in large rivers or shallow brackish seas (Balon 1995). In the spring, adults are thought to migrate from rivers into shallow wetlands to spawn (Balon 2004). This species is invasive and globally distributed, and in the non-native habitats of Midwestern North America where carp inhabit systems of lakes and marshes, adult common carp aggregate in deep lakes (which act as overwintering refuges), and migrate into shallow wetlands in the spring to spawn (Sorensen and Bajer 2011) (Bajer et al. 2010). In Australia where the common carp is also invasive in large rivers, adult common carp use rivers as a refuge and migrate to shallow floodplains to spawn, and then move back to rivers after spawning (King et al. 2003). These movements are poorly understood, and rarely studied for more than a few months in any location. Bajer et al. (2015) suggested that partial migration may be linked to invasiveness because migratory individuals often produce larger numbers of offspring than individuals that do not migrate. Invasive fish like common carp present unique opportunities to examine how seasonal partial migration and homing (i.e., a return to a previously occupied area Gerking (1959)) fits into the full life history of partially migratory fish.

Recent studies in North America seem to describe adult common carp performing partial migrations for the purpose of breeding from deep lakes to shallow lakes and marshes in the spring. In a system of two lakes with a centrally-located marsh, Bajer and Sorensen (2010) observed up to 33% of adult carp move from these lakes in the spring to the marsh to spawn with most appearing to move back after spawning. In another system comprised of a single lake connected to a marsh, Bajer et al. (2015) found most (70%) of the adult carp population moved from the lake to the marsh each spring to spawn with 88% of these fish moving back in the summer. Finally, in another set of two simple chains of lakes connected to marshes, Chizinski et al. (2016) found that 10-50% of adult carp moved from the lakes to marshes to spawn but because all carp removed as they moved, return movements were unknown. While Chizinski et al. (2016) conclude that adult carp perform partial migrations that likely involve some type of homing, all studies to date have focused exclusively on springtime reproductive migrations in small, simple systems and did not continue beyond early summer. We expand on this body of work by exploring the behavior of free ranging adult carp in a much larger system of lakes and marshes, not inhibited by barriers, and by following fish for multiple years. By studying carp throughout the year, we were able to further test how these movements tie in to a life history strategy that others suggest may involve discrete well defined feeding ranges (Penne and Pierce 2008; Bajer et al. 2010) and specific overwintering lakes (Johnsen and Hasler 1977; Penne and Pierce 2008; Bajer et al. 2011). The possibility that these fish might home was also addressed.

We hypothesized that the common carp, an invasive cyprinid fish, employs a complex multi-component life history that incorporates sequential partial migrations within its annual life cycle. Associated hypotheses include the possibility that: 1) adult carp use a breeding partial migration that reflects a tendency to home; 2) adult carp use a home range for feeding in the summer; 3) and carp perform an overwintering partial migration that reflects a tendency to home. To address these hypotheses, we conducted a large scale, multi-year, year-round tracking study in a large watershed of 12 interconnected lakes that is representative of much of North America where it is highly invasive. Specifically, we tracked the weekly distribution of adult carp for 2.5 years (17 individuals (8 mortalities, 1 unknown) from November 8, 2013 – October 27, 2014, 53 individuals (8 mortalities, 3 unknown) from October 29, 2014 – December 31, 2015, and 43 individuals (1 mortality, 2 unknown) in 2016) to determine if they perform a multi-phase partial migration and homing in a system with many choices. This is the first large scale multi-year study on the movement of a partially migratory fish to our knowledge.

Materials and Methods

Study Site

This study was conducted in the Rice Creek Watershed, a relatively large urban system of interconnected lakes, and tributary of the Mississippi River in Minnesota, USA (45.0536N, 93.1142W; Fig. 1). This site is typical of many lake systems in the Upper Mississippi River Basin that consist of interconnected systems of lakes and marshes (Bajer et al. 2012). Connections between lakes are maintained year-round, although one

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major dam blocks fish passage to the upper-most reaches of the watershed. The habitat in the middle and lower reaches of the Rice Creek watershed has high connectivity and includes approximately 52 km of streams and 719 ha of lakes (Fig. 1). Long Lake, a deep lake (>2m), is connected to nine shallow lakes (<2m) and two deep lakes (Table 1a) which allowed for the assessment of inter-annual homing to spawning and overwintering sites. Three tributaries and one outlet (Table 1b) to Long Lake provided four potential migratory paths to study the consistencies of inter-annual migratory patterns in complex, interconnected systems (more than two migratory paths, spawning lakes, and overwintering lakes). One chain of shallow lakes (Baldwin, Rice, Marshan, Reshanau, and George Watch lakes) was located upstream of Long Lake. All are well connected by Rice Creek which flows year-round. Rice Creek also flows west to Locke Lake and then to the Mississippi River. Two small tributaries to the south of Long Lake connect two deep lakes (Pike and Johanna Lakes) and three shallow lakes (Interstate Pond, Farrel's (wetland) Complex, and Valentine Lake). These systems are also upstream of Long Lake. The abundance of carp within this watershed was estimated using mark-recapture and winter seining in Long Lake during the winter of 2016 when over 90% of adult carp were documented to overwinter in this lake. The population estimate was 20,686 individuals with a biomass of 773 kg/ha and average weight of 2.6 kg (P. G. Bajer personal communication).

Experimental Design

We monitored the year-around distribution of adult carp in a large watershed to determine partial migrations, seasonal home ranges, and patterns of individual movement. Long Lake was the primary site for radio-tagging in the spring and fall because commercial fish harvests showed it to have many adult carp present in winter (Rice Creek Watershed District 2010), leading us to hypothesize it was serving as a key overwintering refuge lakes (a hypothesis that was eventually borne out). A total of 67 adult common carp (33 Males, 31 Females, and 3 Unknowns) were collected in Long Lake in late fall of 2013, early spring of 2014, and fall of 2014, implanted with radio transmitters as detailed below, and released at their capture site (Table 2). A total of 29 adult common carp (11 Males and 18 Females) were also tagged in two adjacent shallow lakes (Locke and Reshanau) in late fall of 2013 (Table 2). Weekly tracking was performed manually throughout the year to document year-around distribution and migratory patterns. A remote tracking station (stationary receiver and data logger) was assembled to cycle through each individual radio transmitter for automated tracking along a tributary to Long Lake from spring to fall, a period when adult carp were predicted to perform migrations between overwintering and spawning lakes. To provide context for any observed movement patterns during the four seasons (winter, spring, summer, and fall), we set out temperature loggers in Long Lake (overwintering lake), Rice Creek (major tributary to Long Lake), and Rice Lake (shallow lake upstream of Long Lake). Visual observations of spawning activity, characterized by splashing in floating or submerged vegetation, were performed bi-weekly during May and June in

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Long Lake, five shallow upstream lakes (Baldwin, Rice, Reshanau, Marshan, George Watch), and Rice Creek in 2014, 2015, and 2016. The range of water temperature during spawning was recorded.

Data Collection

After capture of adult carp via boat electrofishing, radio-transmitters (F1850, mortality option, Advanced Telemetry Systems Inc., Isanti, MN, USA) were surgically implanted following established procedures (Penne and Pierce 2008; Bajer et al. 2010). Radio-tagged carp were then located weekly from October 2013 to November 2015, bi-weekly from January 2016 to March 2016, and weekly from May 2016 to June 2016. Carp locations were bi-angulated from a small boat or from shore. Some locations were determined by directly approaching the location of fish (~ within 30 m) judged by strong unidirectional signal. Bi-angulation was used between October 2013 to November 2015 and unidirectional signal technique was used from January 2016 to March 2016 and from May 2016 to June 2016. Data from bi-angulation were entered into computer software (LOAS® 4.0; Ecological Software Solutions, CA, USA) to calculate the intersection of bearings for the estimated location and plotted on ArcMap 10.2 (ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute). Tracking efficiency was tested using two dummy tags (i.e. tags not implanted in fish and hidden underwater) and two tags recovered in dead fish (identified by tags that entered mortality mode and did not move for 24 consecutive hours). Observers identified the correct water body for each individual's location, and tracking efficiency reflected a range within 0 –

20m of the estimated bi-angulation location. A stationary receiver (R4500SD, Advanced Telemetry Systems Inc., Isanti, MN, USA) was also installed on Rice Creek upstream of Long Lake and operated from April 2014 – October 2014, March 2015 – November 2015, and March 2016 – June 2016 to monitor movements between overwintering and spawning areas.

Data Analysis

Seasonal Distribution

To test the overarching hypothesis that adult common carp employ sequential partial migrations over an annual cycle, we first analyzed telemetry data across 2.5 years to identify seasonal patterns in carp distribution. Fish locations were plotted weekly and by month. By doing so we aimed to identify phases associated with: breeding, feeding, overwintering, and transitions between major phases. We also calculated Net Squared Displacement (NSD), defined as the square of the distance from a point of reference to subsequent locations in the movement path of an animal (Singh et al. 2012). We used the southernmost point of Long Lake, the main overwintering site, as a reference location (i.e. NSD =0). We calculated NSD for all fish and for every location, and averaged these values across all individuals by study week. Plotting average weekly values of NSD, separately for year, allowed us to estimate distance, timing, and duration of migratory movements (Borger and Fryxell 2012), and helped us to determine trends in distribution patterns during all phases in the annual life cycle of adult common carp. NSD values during each phase (breeding, feeding, and overwintering) were evaluated using a one-

way ANOVA. We also plotted NSD for 20 adult carp (monitored October 2014 –

November 2015) that were representative of three observed distribution patterns: 1) adult

carp that left Long Lake and did not return; 2) adult carp that left Long Lake and

returned; 3) adult carp that were resident in Long Lake. We used individual-level NSD

patterns to identify the number of individuals in each movement category (migrant and

resident). Residents were defined as fish that exhibited no movement out of Long Lake

while migrants were defined as fish that performed out and back movements, originating

from Long Lake. Tags that entered mortality mode were recorded and no longer tracked

if mortality was observed during the following week.

Analysis of reproductive migration and distribution

To test the hypothesis that adult common carp employ a breeding partial

migration with a tendency to occupy distinct seasonal home ranges, we first evaluated

how many carp migrated from their overwintering lake (Long Lake) by documenting the

number of residents and migrants from Long Lake for each of the three years in the

spring. We assigned individuals as migrants if movement out of Long Lake was

observed, indicated by values of NSD > 4. We assigned individuals as residents if no

movement out of Long Lake was observed (i.e., all NSD < 4). Then, we used chi-square

goodness-of-fit test to evaluate whether carp showed a preference for one or more

migratory paths out of Long Lake during the partial breeding migration. The null

hypothesis was that all four movement options from Long Lake (Fig. 1) had equal

probabilities of being selected. For individuals that chose more than one migratory

direction, only the initial migratory direction was analyzed by chi-square. Next, we plotted locations of all fish to evaluate the distribution of carp during the reproductive period (defined by the first and last date of observed spawning), focusing on the six individuals monitored for three consecutive years. We also calculated Bhattacharyya's affinity (BA), an index of similarity, to determine if carp maintained similar reproductive home ranges during the observed spawning period over multiple years. Individuals that use the same set of lakes and same amount of time spent in each lake during two seasons will have a BA = 1, whereas BA indices = 0 indicate non-overlapping distributions during two seasons. We calculated BA for all individuals monitored for two or more consecutive spawning seasons.

Analysis of summer distribution

To test the hypothesis that adult common carp use a different home range for feeding in the summer than used for spawning, we first evaluated their distribution after spawning and until temperatures dropped to below 10°C, a level where carp were unlikely to be feeding (Song bo et al. 2012). Data were more limited during the summer due to mortalities between the summer of 2014 and the summer of 2015 and because we did not collect data during the summer of 2016. Thus, we did not calculate BA indices to evaluate consistency of summer distributions.

Analysis of overwintering migration and distribution

To test the hypothesis that adult common carp employ an overwintering partial migration that reflects a tendency to occupy consistent home ranges in the winter, we evaluated shifts in carp distribution between feeding and overwintering. Feeding was defined by the period after spawning and before temperature dropped below 10°C when carp feeding is minimal (Song Bo et al. 2012). We plotted the distribution of all individuals for three consecutive winters to assess whether adult carp select specific lakes during the overwintering phase. We again calculated BA indices to evaluate if carp used similar areas during the winter phase in different years.

Results

Seasonal Distribution

Evaluating plots of carp distribution, it became clear that adult carp exhibited three seasonal shifts in their distribution each year which began in an overwintering lake (Long Lake), shifted to shallow upstream lakes in the spring and summer, and shifted back to Long Lake prior to winter (Fig. 2). These distributions appear to be punctuated by migrations along mostly one path from Long Lake to the upstream shallow lakes in the spring and from these same shallow lakes to Long Lake in the fall (Fig. 2). Analysis of average NSD of all individuals confirmed that most adult carp used Long Lake as a home overwintering lake (Fig. 3) Using average NSD, we identified six distinct components to their distribution: overwintering, movement away from the overwintering lake, a plateau of movement during spawning, movement back to overwintering lake, movement to feeding areas, and movement back to overwintering lake in 2014 and 2015 (Fig. 3). An

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overwintering phase was characterized by low NSD (near 0.0 +/- 1SD) from January 13 – April 14, 2014. Standard deviation demonstrates variability among individuals in their distance from Long Lake. Individuals moved away from Long Lake from April 14 – May 12, 2014 and most were blocked 2 km upstream due to high water velocity (1.52 – 1.67 m/s). This delay was followed by a rapid increase in NSD (> 0.0 +/- 1SD) with high standard deviation confirming movement upstream from the overwintering lake from May 12 – June 9, 2014 once temperatures rose between 5 - 10°C (Fig. 3). This was followed by a plateau and peak in NSD with high standard deviation from June 9 – June 20, 2014 during which spawning was observed (Table 6) and temperatures were above 20 °C. A gradual decrease in NSD confirmed movement back towards the overwintering lake from June 20 – August 4, 2014 and temperatures remained above 20 °C (Fig. 3). This was followed by a relatively stable period with periodic increases in NSD from August 4 – October 20, 2014 during which temperatures declined from 25 °C to 5 °C. As temperatures declined below 5 °C, a decrease in NSD to near or at 0 with small standard deviation (+/- 3.21 SD) indicated movement back to Long Lake from October 20 – October 27, 2014. As temperatures declined below 5 °C, a low NSD and small average standard deviation (+/- 2.98 SD) confirmed no movement out of the overwintering lake from October 27 – December 29, 2014, and a return to the overwintering phase.

Six phases in the distribution of the carp were also observed in 2015 (Fig. 3b). The overwintering phase was confirmed by low NSD from January 12 – March 30, 2015. A rapid increase in NSD confirmed movement upstream from the overwintering lake from March 30 – May 18, 2015 once temperatures rose between 5 - 10°C. This was

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followed by a plateau and peak in NSD with high standard deviation from May 18 – June 22, 2015 during which spawning was observed (Table 6) and temperatures were above 15 ℃. A rapid decrease in NSD confirmed movement downstream towards the overwintering lake from July 8 – July 29, 2015 and temperatures remained above 20 ℃. This phase overlapped with the end of observed spawning. A rapid increase in NSD followed by a relatively stable period with high standard deviation confirmed movement upstream from the overwintering lake with temperatures above 15 ℃ from July 29 – September 21, 2015. This was followed by a movement downstream to the overwintering lake confirmed by rapid decrease in NSD to near or at 0 as temperatures decreased below 10 ℃ from September 21 – October 12, 2015. As temperatures declined below 5 ℃, a low NSD confirmed no movement out of the over wintering lake from October 12 – November 23, 2015, and a return to the overwintering phase.

Due to an incomplete year of data collection, only two phases were observed in 2016. The overwintering phase was confirmed by low NSD with small standard deviation between January 18 – March 7, 2016 and temperatures were below 5 ℃. A high NSD from May 9 – June 27, 2016 during which spawning was observed (Table 6) confirmed a spawning phase with temperatures above 15 ℃.

Average NSD values during phases of winter, spawning, and feeding were compared across all years using ANOVA (Table 3). In 2014, winter NSD differed significantly from NSD in spawning and feeding, although there was no difference between spawning and feeding NSD (Table 3). In 2015, NSD for all phases were

significantly different (Table 3). In 2016, overwintering and spawning NSD showed significant differences (Table 3).

Individual movement Patterns

Weekly NSD confirmed individual variation in movement patterns and two movement strategies (Fig. 4a, 4b). All individuals overwintered in Long Lake (NSD = 0 from January 12 – March 30, 2015). In the spring, all but one individual (95%) moved out of Long Lake from March 30 – May 18, 2015 and to the shallow upstream lakes prior to spawning. A decline in water temperatures below 20 °C after the initial rise in the spring of 2015 corresponded with some individuals returning to the overwintering lake for a brief period before returning to the shallow lakes for spawning (Fig. 3). From May 18 – June 22, 2015, most individuals (95%) had moved away from the overwintering lake (NSD > 0) during spawning and one individual (5%) remained resident (NSD = 0) the whole year. Of those that moved upstream of Long Lake for spawning, most individuals (85%) returned to Long Lake (NSD = 0). Of these, most (60%) then moved back upstream to the shallow lakes (NSD > 0) at least once during summer. Prior to winter, most of the individuals (95%) that left Long Lake moved back to Long Lake (NSD =0).

Variation was common among fish and five examples are described. One fish (Fig. 4; ID 48.101) left the overwintering lake prior to spawning, remained in the shallow upstream lakes during spawning, and returned to the overwintering lake for the rest of the year after spawning. Another fish (Fig. 4; ID 48.871) remained resident in the overwintering lake for the entire year. One fish (Fig. 4; ID 49.351) performed a total of

six significant movements over the course of a year that included leaving the overwintering lake prior to spawning and returning to the overwintering lake after spawning. Then, this individual left the overwintering lake again, returned to the same location used during spawning, and later returned to the overwintering lake in summer. After one week in the overwintering lake, this individual left the overwintering lake once more, returned to the same location previously used in the upstream shallow lakes, and finally returned to the overwintering lake for the remainder of the year. A different movement pattern was observed for one individual (Fig. 4; ID 48.438) that left the overwintering lake prior to spawning, remained in one location for most of the summer, and did not return to the overwintering lake. Yet another individual (Fig. 4; ID 49.461) left the overwintering lake prior to spawning, remained in one location during spawning and summer, and then returned to the overwintering lake.

For some fish, there is a clear increase and then a return to an NSD value near 0 (migrants), whereas a small number of fish had NSD values near 0 for the whole year (residents) (Fig. 4; Table 4). Migrants were the most prevalent movement category (82-98%) among all individuals in all years. Residents made up 2-18% of all individuals.

Tagged Fish in Locke and Reshanau Lakes

Adult common carp tagged in adjacent shallow lakes in 2014 demonstrated limited to no movement compared to fish tagged in Long Lake. All 15 adult carp tagged in Reshanau Lake in the fall of 2013 remained in Reshanau to overwinter and all were observed in mortality mode in February 2014 (Table 2), likely due to low oxygen

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concentrations (<1mg/L). Of the 14 adult carp tagged in Locke Lake, downstream of Long Lake, no carp moved out of Locke Lake during the breeding migration in 2014 and five carp entered into mortality mode from May 24 – July 3, 2014 (Table 2). One individual moved downstream of Locke Lake and into the Mississippi River during the summer of 2014 and did not return to Locke Lake. Another individual moved out of Locke Lake and upstream to Rice Lake in late summer before returning to overwinter in Long Lake in the fall of 2014. Of the eight carp remaining in 2015 that were originally tagged in Locke Lake, two moved out of Locke Lake to the shallow upstream lakes in 2015 with one returning to Locke Lake after spawning. Five individuals did not move out of Locke Lake, two of which were confirmed mortalities on May 31, 2015 (Table 2). The individual tagged in Locke Lake that overwintered in Long Lake moved out of Long Lake to the shallow upstream lakes in the spring where it was confirmed in mortality mode on June 19, 2015.

Analysis of breeding migration and distribution

Most adult carp (82% in 2014, 98% in 2015, and 98% in 2016) left Long Lake each year (Table 4) when water temperatures were between 5 and 10°C (Fig. 3; Table 7). Of these, most adult carp left Long Lake via one connection all years (Table 5). Movements typically occurred prior to spawning between March 14 and April 15 each year (Fig. 3; Table 6). Movements upstream of Long Lake occurred between April 20 – June 5 in 2014 and April 6 – May 20 in 2015. Tracking was not conducted in the spring of 2016. In 2014, carp appeared blocked by high flows upstream of Long Lake in

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movement path A. Two individuals that initially chose movement path A selected other migratory options (B and C) rather than remaining resident in the overwintering refuge to spawn.

Spawning was observed in Long Lake and the shallow upstream lakes (Table 7) between May 22 – June 20 in 2014, May 18 – June 22 in 2015, and May 9 – June 20 in 2016 when water temperatures ranged between 14 and 27 °C (Table 6). The first confirmed movement away from the overwintering lake occurred prior to spawning in all years. Most spawning observations were observed in shallow lakes and streams upstream of the overwintering refuge (Table 7).

The distribution of adult carp was plotted during spawning each year (Fig. 5a, 5b). Due to mortalities in 2013 and 2014, only six individuals had distributions that could be compared for all three years (Fig. 5a, 5b). All six of these individuals overwintered in Long Lake prior to spawning in all years. Of these six, five migrated at least one year and four migrated all years. Of the four that migrated each year, distributions during the spawning period demonstrated that they were found in the same one or two lakes each year (Fig. 5a, ID: 48.101, 48.201, 48.251; Fig. 5b, ID: 49.004). One individual (Fig. 5b, ID: 48.871) was resident in Long Lake all three years during spawning. Another individual (Fig. 5b, ID: 48.950) was resident in Long Lake in 2014 and 2016 but migrated to one lake in 2015.

For individuals monitored during consecutive spawning seasons, distribution patterns were similar across years. Six individuals were monitored for three consecutive spawning seasons (2014, 2015, and 2016). Of these, five (83%) used the same lake for

spawning at least two of the three years with BA statistics equal to 1 (Fig. 6). Thirty-two individuals were monitored for two consecutive spawning seasons (2015 and 2016). Of these, 26 (75%) showed similar distributions in their choice of lake with BA statistics > 0.75 (Fig. 6). In total, 43 individuals were monitored for at least two consecutive spawning seasons. Of these, 34 (79%) had BA statistics > 0.75 and displayed a similar use in lakes during spawning (Fig. 6).

Analysis of summer migration and distribution

After spawning, 46% and 80% of adult carp left their breeding lakes in 2014 and 2015, respectively, and moved back to the overwintering lake. Then, 8% (1 out of 12) in 2014 and 49% (21 out of 43) in 2015 moved back to the upstream shallow lakes. Individuals returned to slightly different locations than they used during spawning two to three times (i.e. 2-3 round trips) (Fig. 4). Average NSD values during feeding were 103.6 km^2 in 2014 and 122.4 km^2 in 2015 which differed from areas used during aggregation each year (p<0.05) and spawning in 2015 (p<0.05) from ANOVA. Water temperatures were above 15°C during the summer. Six carp were tracked for 3 years and demonstrated a strong tendency to stay in a few lakes in the summer (Fig. 7).

Analysis of overwintering migration and distribution

When temperatures dropped below 5 °C in October 2014 and 10°C in September 2015, most carp (67% in 2014 and 95% in 2015) in the upstream shallow lakes moved downstream to Long Lake. Of the individuals still in the shallow lakes in October 2014

and September 2015, only a small number remained to overwinter there (22% in 2014 and 5% in 2015).

The distribution of adult carp during winter varied little between years, providing evidence for overwintering home ranges during the winters of 2013 – 2014, 2014 – 2015, and 2015 – 2016 (Fig. 8). Average NSD value during overwintering was 1.06 km^2 in 2014, 1.97 km^2 in 2015, and 1.98 km^2 in 2016 which differed from areas used during spawning and feeding (2014 and 2015 only) each year ($p<0.05$) from ANOVA.

Most carp then remained in Long Lake for overwintering in all years (100% in 2013-2014, 96% in 2015-2016, and 95% in 2015-2016). Distribution in this one lake was most dispersed in November. Aggregations started forming in December and became denser in January, February, and March. Aggregations moved between the south and north basins each year and to different areas of the lake. Low dissolved oxygen (< 1mg/L) was measured in the north basin of Long Lake in January and February of 2014 during which no adult carp were located in the north basin. Dissolved oxygen was >2mg/L in both basins in Long Lake in November, December, and March of 2014 and all of 2015. For individuals monitored during consecutive overwintering seasons, distribution patterns showed tendencies of home overwintering ranges, with 40 of 45 individuals having BA indices equal to 1 (Fig. 9).

Discussion

This study demonstrated that a globally invasive cyprinid, the common carp, has a multi-component life cycle that includes three distinct, and directed partial migratory

phases, each of which results in different activity (spawning, feeding, and overwintering). To our knowledge, this is the first study to document a multi-phased partial migration that follows an annual cycle. While breeding partial migrations in common carp have previously been observed (Bajer and Sorensen 2010; Bajer et al. 2015; Chizinski et al. 2016), partial migrations associated with feeding and overwintering have not. This demonstrates that partial migration is not mutually exclusive to a specific season during the annual life cycle of adult carp. We also demonstrate that adult carp employ specific home ranges for spawning, feeding and overwintering, and that these are associated with extremely specific (but flexible) abilities to home. Such a precise, yet complex form of partial migration has not to the best of our knowledge been demonstrated before. By employing a series of annual seasonal migrations, the carp have evolved a flexible life history that presumably is extremely adaptive and might explain carp's success and invasiveness. A multi-phased strategy of partial migrations presumably maximizes individual fitness by affording a greater flexibility in accessing resources in spatially complex, temperate habitats for spawning, feeding, and overwintering. In complex systems with multiple potential paths for migrations, consistent homing to specific areas might increase fitness for this long-lived invasive fish.

This study clearly establishes that the carp uses breeding partial migration. We observed consistent annual breeding migrations of most but not all individuals to lakes where spawning was observed each year. The majority of all radio-tagged carp (all but one in 2015 and 2016) migrated out of Long Lake and upstream to a single chain of shallow upstream lakes each spring prior to spawning. Interestingly, the percentage of

adult carp that migrated in our system was higher than that observed by previous authors (Bajer and Sorensen 2010; Bajer et al. 2015; Chizinski et al. 2016). We speculate this might be because of greater connectivity of overwintering, breeding, and feeding habitats year-round. Migrating to shallow lakes and marshes in the spring which are susceptible to winter hypoxia in severe winters has been linked to high recruitment events in the absence of egg and larval predators following hypoxic events (Bajer et. al 2015).

This study also observed precise homing to specific spawning lakes over consecutive years which may reflect natal lakes. This may be related to Pacific salmon that demonstrate homing to natal streams. For Pacific salmon, the fact that homing to natal streams has been maintained over evolutionary time scales suggests the benefits must outweigh the costs of not homing (Lohmann et al. 2008). However, all anadromous Pacific salmonids die after spawning and homing for individuals across multiple years is not possible with the exception of Steelhead trout (*Oncorhynchus mykiss*) that can perform multiple spawning migrations. Migrations of lemon sharks (*Negaprion brevirostris*) indicate that up to 71% of females return to specific areas, most on a two-year cycle, to give birth to their litter (Feldheim et al. 2004) which provides evidence that many shark species are philopatric (i.e. returning to a particular area to give birth) (Guttridge et al. 2009) and may employ skipped-breeding partial migration. Lohmann et al. (2008) suggest that homing and reproductive success in natal areas requires certain environmental conditions that are limited to specific geographic areas.

Variation in habitat quality, deep lakes connected to shallow and outlying spawning marshes, may explain partial breeding migrations by adult carp. While complex

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systems may provide more high quality spawning habitat, migrants may experience higher mortality rates by migrating and remaining in habitats susceptible to winter hypoxia (Bajer et al. 2015). Despite this risk, we found most (> 90%) individuals were migratory which appears to be unique for a long-lived partially migratory cyprinid. Of the five fish (four tagged in Long and 1 tagged in Locke) that overwintered in shallow upstream lakes, all survived at least one winter which positioned them near the spawning area. This may be advantageous in eliminating the need to perform a costly migration prior to spawning. This finding is an interesting aspect of their flexible life history and may be related to the two-step migrations documented in shortnosed sturgeon, another long-lived but slowly maturing species. However, the fact that some fish moved performed up to three out and back migrations between shallow upstream lakes and Long Lake suggest migrations between these areas may not be as costly compared to other species like shortnose sturgeon that migrate longer distances. Two-step migrations have been observed in shortnose sturgeon late in gonadal development that perform non-breeding migration in the fall (step one) for overwintering near the spawning site and perform short migrations to spawn in the following spring (step two) (Bemis and Kynard 1997; Lucas and Baras 2001d; Dione et al. 2012). Given the fact that common carp are a long-lived species, evidence from our multi-year study suggest individuals may adopt a strategy to be resident or migratory during reproductive partial migrations. With more years of monitoring, however, "residents" may be observed to migrate and thus become classified as facultative migrators (Fieberg et al. 2008). Other long lived slowly maturing species such as shortnosed sturgeon and Atlantic cod (*Gadus morhua*) have been

documented to exhibit skipped breeding partial migration (Dadswell 1977; Jorgensen et al. 2006; Dionne et al. 2013) which may be a strategy to maintain higher reproductive fitness long-term by forgoing breeding every 2-5 years. However, this skipped breeding strategy has not been described for long-lived species such as common carp that mature within 1-2 years.

Our study demonstrated a tendency of adult carp to occupy home feeding ranges in summer within a complex system. Bajer et al. (2010) also observed summer home ranges of adult carp in a small lake. Whether the summer partial migrations observed in this study were associated with feeding was not assessed, although possible since all migrations were performed above 15°C, a temperature that Bajer et al. (2010) noted carp were actively feeding. Although we did not observe spawning after June, it is possible that these partial migrations in the summer may represent an additional spawning event. Multiple spawning times have been observed in Australia, another region where carp are invasive (Forsyth et al. 2013). We suggest that spawning lakes may sometimes serve a dual purpose for both spawning and feeding purposes. Summer partial migrations of common carp are a new finding and whether they also contribute to invasiveness is unknown, although Bajer et al. (2015) suggested breeding partial migrations may be linked to invasiveness. Further investigations on how summer partial migrations coincide with specific life history phases is a future opportunity for investigating strategies of multi-component partial migration.

We also observed consistent patterns in annual overwintering partial migrations with most individuals returning to Long Lake. While no previous study has described

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overwintering partial migrations in common carp, previous studies have documented aggregations of adult carp forming in deep lakes under the ice (Johnsen and Hasler 1977; Penne and Pierce 2008; Bajer et al. 2011), and these aggregations moved throughout the winter (Bajer et al. 2011). As water temperatures consistently declined and decreased below 10°C, migrations from the shallow peripheral lakes to the one overwintering lake were more common and likely associated with the onset of early winter conditions. All but two individuals in 2014 and three in 2015 performed overwintering partial migrations to the primary overwintering refuge lake, Long Lake. This suggests a small portion of available habitat may serve as an overwintering refuge similar to streams that serve as a overwintering predation refuge for roach and white bream (Skov et al. 2008). However, carp in this study are invasive and do not have native predators. Thus, the high proportion of fish found overwintering in Long Lake (residents and migrants) may be associated with instability of shallow lake basins in the region (Bajer and Sorensen 2010, Bajer et al. 2012). Bajer et al. (2015) suggest higher mortality rates among migrants that may overwinter in hypoxic-prone lakes rather than return to refuge lakes. During one week in October 2015, fourteen individuals were observed performing an overwintering partial migration which may suggest synchronous migrations in the fall. Chizinski et al. (2016) observed synchronous breeding partial migrations in the spring in a small system but whether synchronous migrations apply to other times of the year in more complex systems needs further study.

Following overwintering partial migrations, we also observed the transition in distribution from an overwintering partial migration phase to the winter aggregation

phase. This appeared to include a progression from widely distributed individuals in November, loose aggregations forming in December, and aggregations becoming more tightly grouped as winter progressed (January, February, and March) before breaking up in late March. These aggregations have been associated with a type of shoaling behavior as carp transition from foraging to a predator defense strategy which may have been retained from their native range where otters and seals were known to be piscivorous (Bajer et al. 2011). While aggregations moved to different basins of the lake every year, they were most commonly found in the north basin which typically has less disturbances in the winter (e.g. ice fishing is common in south basin). Adult carp have been known to be responsive to disturbances in the winter (Bauer and Schlott 2004). This study is the first to show individual carp using specific overwintering refuges in complex systems and how these aggregations form and break up between partial migration phases.

This study confirmed Chizinski et al.'s (2016) suggestion of homing along specific migratory paths during breeding partial migrations. We observed consistent homing to specific areas over multiple years in complex systems. In all three years, one of four migratory routes was used. During spawning, one chain of five shallow lakes (Baldwin, Rice, Reshanau, Marshan, and George Watch) upstream of Long Lake was the primary spawning area. For overwintering, one lake (Long Lake) was the preferred overwintering refuge and individuals formed aggregations under the ice. Such precise homing and use of home water bodies during migration, spawning, and overwintering advances the field of partially migratory invasive fish and Cypriniformes.

Understanding the homing abilities of carp opens up new possibilities for their control as homing can be exploited. For example, in the spring of 2014, snowpack in winter and rains in spring promoted conditions that created high flows at the outlet of a culvert in Rice Creek, the main connection between the overwintering lake and spawning lakes. A velocity barrier and perhaps a trap could be installed at this location. In our case, two individuals initially migrated upstream in Rice Creek during the breeding partial migration phase in 2014, but after repeated locations in the creek below the culvert (presumably due to the velocity barrier), these individuals selected other migratory paths. This observation suggests that migratory fish blocked for extended periods of time in one direction may choose to migrate in a different direction during specific phases such as reproduction rather than remain resident in the overwintering lake. While carp tend to use specific paths each year for reproductive partial migrations, some years may create conditions that require managers to target other migratory routes that are used less but may be important for recruitment. This is an important management consideration due to the longevity of carp since partial breeding migrations can maintain invasive populations of carp just once every 20 years (Bajer et al. 2015).

This new understanding that adult carp employ a flexible life history strategy may provide other guidance for control of this invasive fish. Stream trapping may prove effective during migrations at other times of the year such as overwintering partial migration, a strategy relatively unexplored in systems that maintain continuous connections year round. The finding that adult carp appear to select specific lakes during spawning can also direct management efforts to particular areas that may serve as

recruitment hotspots that support the entire population in complex watersheds. Preventing access to these areas may prove a viable option for long-term control since distribution during spawning suggests reproduction in the overwintering lake in this system may be low due to the presence of more egg and larval predators. The finding that adult carp also select a specific lake during overwintering also has management implications that can direct control efforts for targeting aggregations to specific lakes in complex systems. This study demonstrated that understanding migratory and homing patterns over all phases in the flexible life history strategy of adult carp can provide guidance for integrated pest management strategies for partially migratory invasive fish. The carp may serve as an important model to guide conservation strategies of other partially migratory fish through a better understanding of multi-phased partial migration strategies and homing patterns.

Tables

Table 1a. Known area, maximum depth, secchi depth, phosphorus concentration, and potential to winterkill (dissolved oxygen <1mg/L) in interconnected lakes in the Rice Creek Watershed.

Lake	Area (ha)	Maximum Depth (m)	Average Summer Secchi depth (m)	Phosphorus Average (ug/L)	Potential to Winterkill (yes/no)
Baldwin	76	1.5			Yes
Rice	150	1.5			Yes
Reshanau	136	4.9	-0.8	94	Yes
Marshan	82	1.5			Yes
George Watch	196	1.5			Yes
Long	69	9.1	-1.0 North basin -1.7 South basin	64 North basin 46 South basin	No
Pike		2.7			Yes
Locke	9.3	1.5	-1.0	69	Yes
Valentine					Yes
Interstate Pond					Yes
Farrel's Complex					Yes
Johanna	84			32	No

Table 1b. Known distance, depth, and discharge of four streams in the Rice Creek Watershed.

Movement Paths	Distance (km)	Maximum Depth (m)	Maximum Discharge 2016 (m^3/s)	Minimum Discharge 2016 (m^3/s)
Path A: Middle Rice Creek	32.6	3	5.66	0.23
Path B: E2 Creek	5.9	<1		
Path C: Unnamed creek	2.0	<1		
Path D: Lower Rice Creek	13.7	2		

Table 2. Individual identification, lake implanted, time monitored, status of tag at last contact, sex, length, and number of contacts of radio-tagged adult common carp (*Cyprinus carpio*) in Long Lake, Locke Lake, and Reshanau Lake, MN, USA.

Radio Tag ID	Lake Implanted	Date Implanted	Last Contact	Tag Status	Sex	Length (mm)	Contacts
48.081	Long	9/26/2013	4/15/2014	Mortality	M	555	12
48.090	Long	9/26/2013	11/21/2013	Mortality	M	505	2
48.101	Long	9/26/2013	5/30/2016	Mortality	F	582	81
48.111	Long	9/26/2013	6/25/2014	Mortality	F	543	23
48.120	Long	9/26/2013	5/7/2014	Mortality	M	553	16
48.131	Long	9/19/2013	11/8/2013	Mortality	F	670	1
48.151	Long	9/19/2013	11/8/2013	Mortality	M	605	1
48.171	Long	9/19/2013	5/15/2015	Unknown	F	566	49
48.190	Long	9/19/2013	11/8/2013	Mortality	M	600	1
48.201	Long	9/19/2013	6/10/2016	Active	M	546	63
48.211	Long	9/19/2013	8/26/2015	Mortality	F	515	76
48.221	Long	9/19/2013	7/1/2015	Mortality	F	568	67
48.241	Long	9/19/2013	6/8/2015	Mortality	F	562	66
48.251	Long	9/19/2013	6/20/2016	Active	M	522	94
48.261	Long	9/19/2013	9/19/2013	Unknown	M	573	0
48.271	Reshanau	9/24/2013	2/22/2014	Mortality	F	651	9
48.281	Reshanau	9/24/2013	2/22/2014	Mortality	F	694	9
48.290	Reshanau	9/24/2013	2/22/2014	Mortality	F	640	9
48.301	Reshanau	9/24/2013	2/22/2014	Mortality	M	567	9
48.341	Reshanau	9/24/2013	2/22/2014	Mortality	F	571	9
48.351	Reshanau	9/24/2013	2/22/2014	Mortality	F	587	9
48.361	Reshanau	9/24/2013	2/22/2014	Mortality	M	650	9
48.371	Reshanau	9/24/2013	2/22/2014	Mortality	M	582	9
48.411	Reshanau	9/24/2013	2/22/2014	Mortality	M	590	9
48.421	Reshanau	9/24/2013	2/22/2014	Mortality	F	515	9
48.451	Reshanau	9/27/2013	2/22/2014	Mortality	F	729	9
48.470	Reshanau	9/27/2013	2/22/2014	Mortality	F	643	9
48.501	Reshanau	9/27/2013	1/11/2014	Mortality	M	541	6
48.561	Reshanau	9/27/2013	2/22/2014	Mortality	M	562	9
48.610	Reshanau	9/27/2013	2/22/2014	Mortality	M	548	9
48.670	Locke	10/25/2013	7/3/2014	Mortality	M	680	22
48.680	Locke	10/25/2013	6/19/2015	Mortality	F	600	58
48.691	Locke	10/25/2013	6/18/2014	Mortality	F	620	21
48.701	Locke	10/25/2013	6/20/2016	Active	M	650	87
48.711	Locke	10/25/2013	5/31/2015	Mortality	F	740	58
48.730	Locke	10/25/2013	5/31/2015	Mortality	M	830	58
48.741	Locke	10/25/2013	6/9/2014	Mortality	M	581	20
48.751	Locke	10/25/2013	5/24/2014	Mortality	F	575	16

48.771	Locke	10/25/2013	10/16/2014	Unknown	F	545	29
48.791	Locke	10/25/2013	5/18/2016	Active	F	605	81
48.800	Locke	10/25/2013	6/9/2014	Mortality	F	720	20
48.811	Locke	10/25/2013	5/18/2016	Active	F	538	79
48.821	Locke	10/25/2013	5/18/2016	Active	F	752	81
48.841	Locke	10/25/2013	5/18/2016	Active	F	612	80
48.851	Long	4/21/2014	8/27/2014	Mortality	M	564	16
48.871	Long	4/21/2014	6/20/2016	Active	U	559	78
48.881	Long	4/21/2014	6/12/2014	Mortality	F	586	6
48.89	Long	4/21/2014	7/11/2015	Unknown	M	672	39
48.911	Long	4/21/2014	7/24/2014	Mortality	U	533	12
48.931	Long	4/21/2014	9/16/2014	Mortality	F	573	19
48.95	Long	4/21/2014	6/20/2016	Active	F	515	81
48.971	Long	4/21/2014	7/25/2014	Mortality	M	567	13
49.004	Long	4/21/2014	6/20/2016	Active	F	556	78
49.014	Long	4/21/2014	8/30/2015	Mortality	M	567	50
49.034	Long	4/21/2014	5/18/2014	Mortality	U	570	2
49.34	Long	10/7/2014	6/20/2016	Active	M	596	56
49.351	Long	10/7/2014	6/20/2016	Active	F	715	56
49.387	Long	10/10/2014	6/11/2016	Active	M	531	53
49.407	Long	10/7/2014	6/20/2016	Active	F	593	56
49.424	Long	10/7/2014	6/19/2015	Mortality	M	670	27
49.438	Long	10/7/2014	6/20/2016	Active	F	669	44
49.444	Long	10/9/2014	6/20/2016	Active	M	564	51
49.451	Long	10/10/2014	6/11/2016	Active	M	545	46
49.461	Long	10/10/2014	6/20/2016	Active	F	568	58
49.481	Long	10/7/2014	6/20/2016	Active	F	570	57
49.491	Long	10/7/2014	6/20/2016	Active	F	514	57
49.504	Long	10/7/2014	6/20/2016	Active	F	612	48
49.514	Long	10/9/2014	6/20/2016	Active	M	594	51
49.531	Long	10/7/2014	6/20/2016	Active	M	626	55
49.55	Long	10/7/2014	6/20/2016	Active	M	545	55
49.611	Long	10/10/2014	6/20/2016	Active	F	505	57
49.631	Long	10/10/2014	6/20/2016	Active	F	581	58
49.641	Long	10/9/2014	6/10/2016	Mortality	M	532	56
49.651	Long	10/7/2014	6/20/2016	Active	F	543	57
49.661	Long	10/7/2014	6/20/2016	Active	M	540	55
49.671	Long	10/10/2014	6/20/2016	Active	M	631	56
49.691	Long	10/10/2014	6/20/2016	Active	M	577	55
49.71	Long	10/7/2014	6/20/2016	Active	M	616	55
49.721	Long	10/7/2014	5/28/2015	Mortality	M	655	23
49.73	Long	10/7/2014	5/20/2015	Mortality	M	604	23
49.74	Long	10/20/2014	7/2/2015	Unknown	F	623	27
49.751	Long	10/9/2014	6/20/2016	Active	M	605	51

49.76	Long	10/20/2014	10/12/2015	Mortality	F	686	41
49.771	Long	10/20/2014	6/20/2016	Active	F	606	57
49.78	Long	10/20/2014	6/20/2016	Active	F	607	50
49.79	Long	10/9/2014	6/20/2016	Active	M	550	55
49.801	Long	10/20/2014	5/2/2016	Unknown	F	646	51
49.81	Long	10/10/2014	6/20/2016	Active	M	573	56
49.821	Long	10/10/2014	5/2/2016	Unknown	F	523	50
49.851	Long	10/9/2014	6/20/2016	Active	M	567	54
49.861	Long	10/9/2014	6/20/2016	Active	F	553	54
49.871	Long	10/9/2014	6/20/2016	Active	M	542	48
49.901	Long	10/20/2014	6/20/2016	Active	F	612	58
49.91	Long	10/20/2014	6/20/2016	Active	M	582	55
49.921	Long	10/20/2014	6/20/2016	Active	F	651	56
49.931	Long	10/20/2014	6/20/2016	Active	F	620	55

Table 3. Mean net squared displacement differences (+ sd) of adult common carp by phase and year. Different letters indicate significant differences in the displacement away from Long Lake by year (ANOVA, $p < 0.05$).

	Winter NSD (km^2)	Spawning NSD (km^2)	Feeding NSD (km^2)
2014	1.06 (0.2) a	97.3 (118.03) b	103.6 (122.48) b
2015	1.97 (1.15) a	285.9 (125.2) b	122.4 (116.2) c
2016	1.98 (1.52) a	269.5 (30.97) b	

Table 4. Migrant and resident adult common carp (*Cyrpinus carpio*) identified using weekly Net Squared Displacement, the square of the distance from a point of reference (Long Lake).

Movement Strategy	2014	2015	2016
Migrants	82% (n=14)	98% (n=52)	98% (n=47)
Residents	18% (n=3)	2% (n=1)	2% (n=1)
Total	17	53	48

Table 5. Three inlets (A, B, and C) and one outlet (D) to Long Lake, an overwintering lake, represent movement paths for adult common carp (*Cyprinus carpio*) and chi-square tests demonstrated preference for movement path A during the spring in 2014, 2015, and 2016.

	Movement Path (Fig. 1.)					
Year	A	B	C	D	Chi-square Test	Total Individuals
2014	71% (n=12)	12% (n=2)	0% (n=0)	0% (n=0)	$p < .05$	17
2015	96% (n=51)	2% (n=1)	0% (n=0)	0% (n=0)	$p < .05$	53
2016	98% (n=47)	0% (n=0)	0% (n=0)	0% (n=0)	$p < .05$	48

Table 6. Observations of spawning adult common carp (*Cyprinus carpio*), water temperature during spawning, and first confirmed annual movement in a large interconnected and representative lake system in the Upper Mississippi River Basin in 2014, 2015, and 2016.

Year	Spawning Observations	Water Temperature During Spawning	First Confirmed Movement Date
2014	5/22/14 – 6/20/14	15 – 23 °C	4/15/14
2015	5/18/15 – 6/22/15	14 – 27 °C	4/7/15
2016	5/9/16 – 6/20/16	18 – 26 °C	3/14/16*

*Movement date confirmed by autonomous stationary tracking.

Table 7. Spawning observations during weekly tracking of adult common carp (*Cyprinus carpio*) in Long Lake (in bold), five shallow lakes located upstream, and a creek (Rice Creek) that connected them (sampling effort included time required to locate all tags within a water body or one pass throughout the water body if no tags were found).

Year	**Long**	Baldwin	Rice	Reshanau	Marshan	George Watch	Rice Creek
2014	1	0	3	0	2	1	3
2015	0	4	5	0	1	1	3
2016	1	5	5	0	5	5	0

Figures
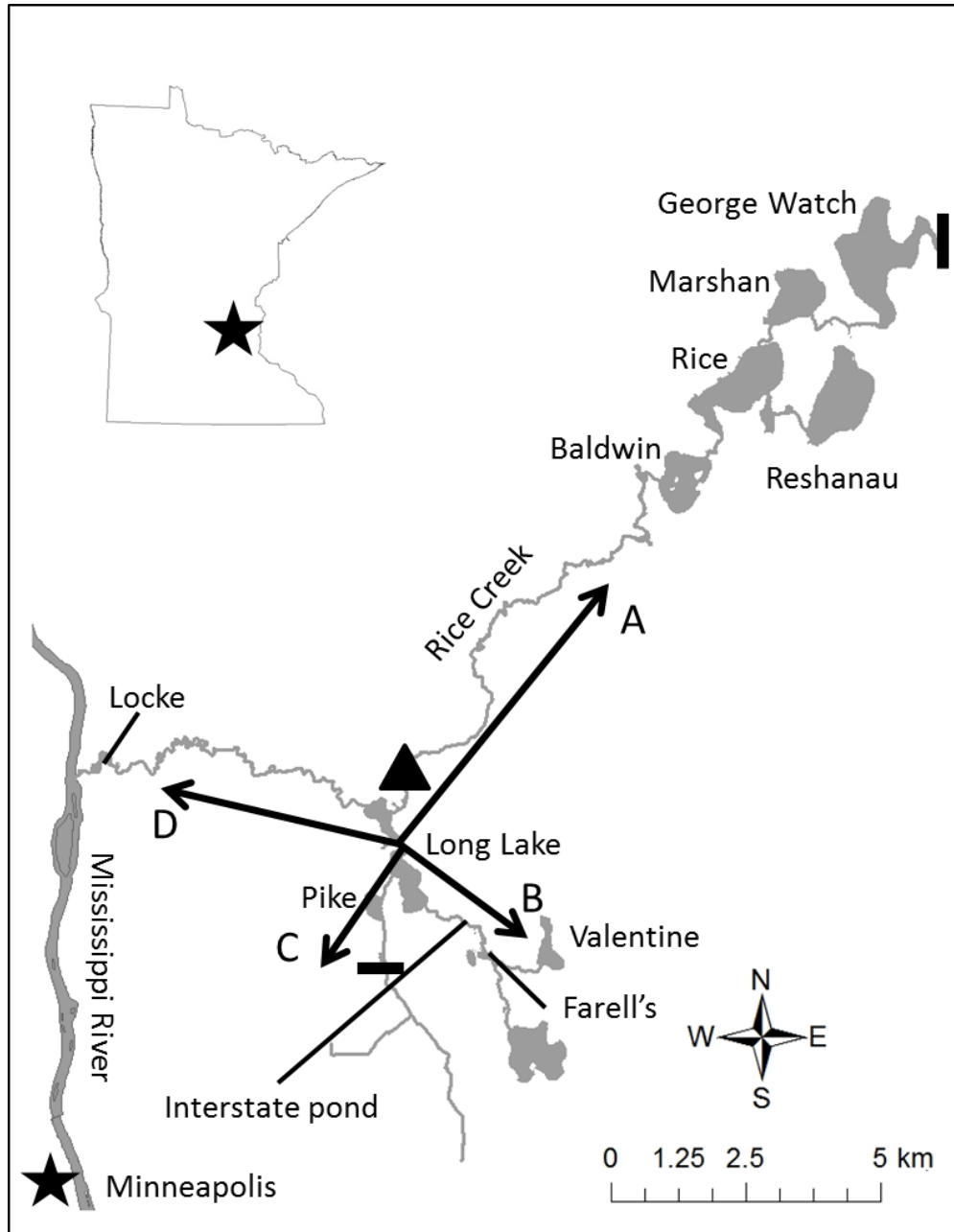
Fig. 1. Study site within the Rice Creek Watershed showing all connections to and from Long Lake, the primary overwintering refuge lake where adult common carp were radio-tagged. Migration routes A, B, and C are tributaries to Long Lake while migration route D is the outlet of Long Lake. The Rice Creek watershed flows into the Mississippi River upstream of Minneapolis, Minnesota. Bars indicate major dams limiting connectivity and fish passage, although downstream passage at all dams was possible. The triangle upstream of Long Lake indicates the location of a stationary tracking station.

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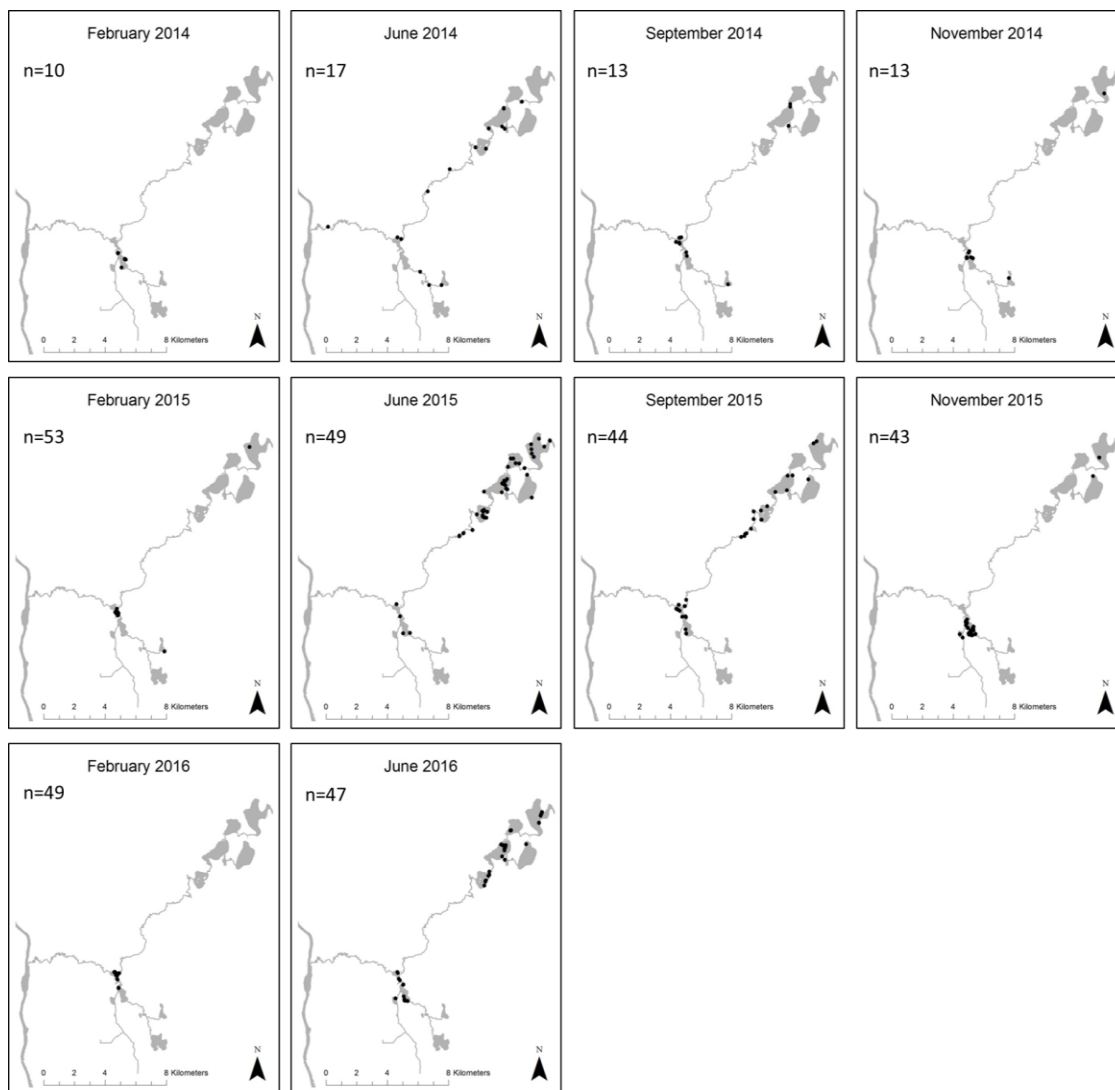
Fig. 2. Seasonal distribution of adult common carp in 2014, 2015, and 2016. Each dot represents an individual radio-tagged common carp. Each month was chosen to represent distribution across different seasonal periods (February – overwintering, June – spawning, September – feeding, and November – pre-winter) using weekly locations of individuals.
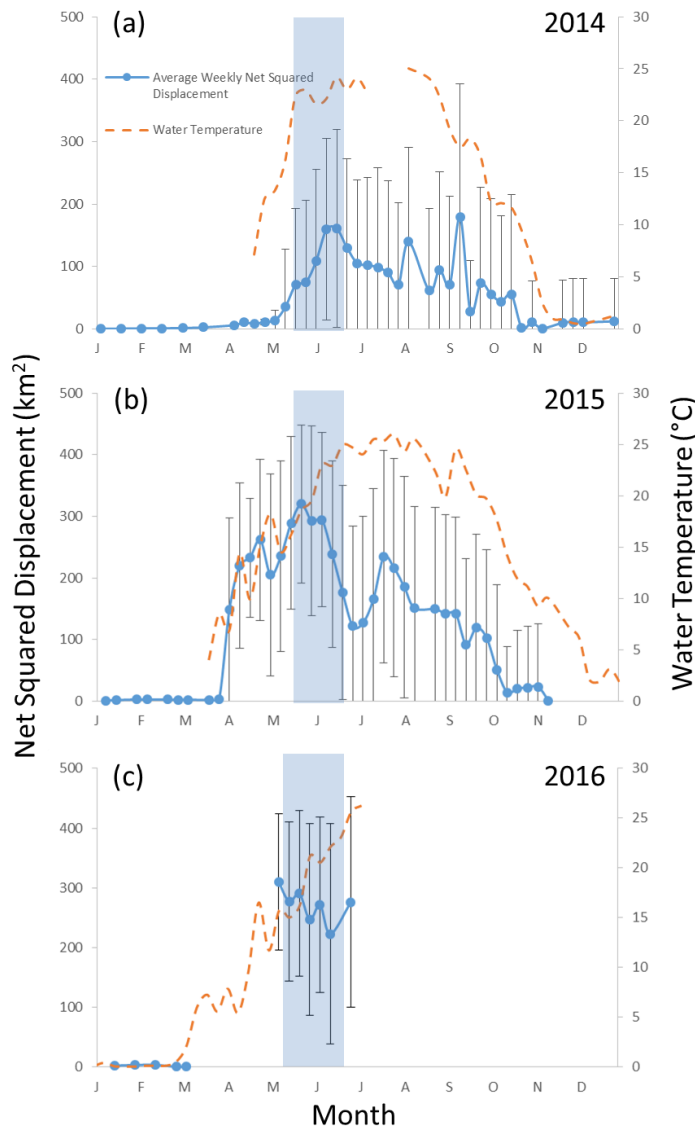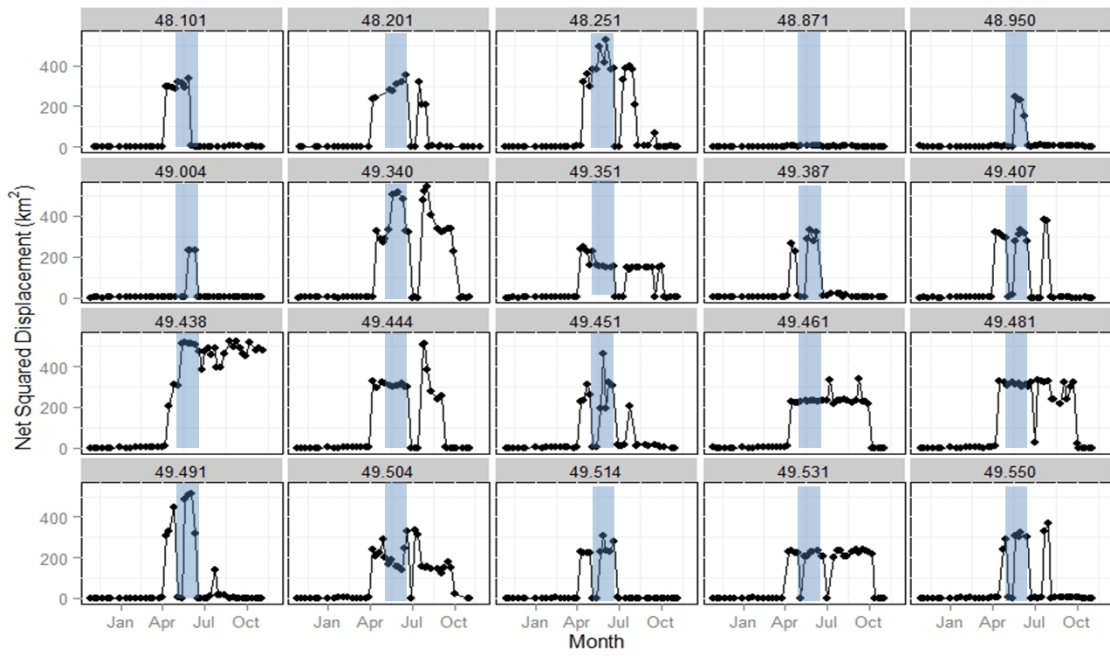
Fig. 3. Net Squared Displacement (NSD), the square of the distance from a point of reference (southern end of Long Lake) to subsequent locations in the movement path of an animal was calculated for individual adult common carp radio-tagged in Long Lake. NSD for each individual was sorted by week. We then calculated average NSD by week across fish (n $\geq$ 8 from January 13 – October 27 and n $\geq$ 40 from October 29 – December 29 in 2014, n $\geq$ 40 in 2015, and n $\geq$ 25 in 2016). Data were collected over 41 weeks in 2014, 41 weeks in 2015, and 12 weeks in 2016. NSD values will be near 0 when all individuals are in Long Lake. Error bars indicate +/- 1 standard deviation. Changes in average NSD over time are indicative of changes in population-level distribution patterns. Average NSD showed movements away from Long Lake from April 14 – October 20 (3a), March 30 – October 12 (3b), and May 9 – June 27, 2016 (3c). Temperature (dashed line) in Rice Creek is included to show different seasonal periods in relation to seasonal variation in average NSD.

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Fig. 4. Net Squared Displacement (NSD), the square of the distance from a point of reference (southern end of Long Lake) to subsequent locations in the movement path of an animal was calculated for individual adult common carp radio-tagged in Long Lake. Weekly NSD for 20 individual adult common carp (*Cyrpinus carpio*) monitored over time from October 2014 – November 2015. NSD values will be near 0 when individuals are in Long Lake. Changes in NSD over time are indicative of changes in individual-level distribution patterns. NSD provides evidence for two movement categories: resident (A) and migrant (B). Migration is indicated by a movement away and return from NSD near 0 and resident by a flat line near NSD = 0. Shading defines observations of spawning in 2015.
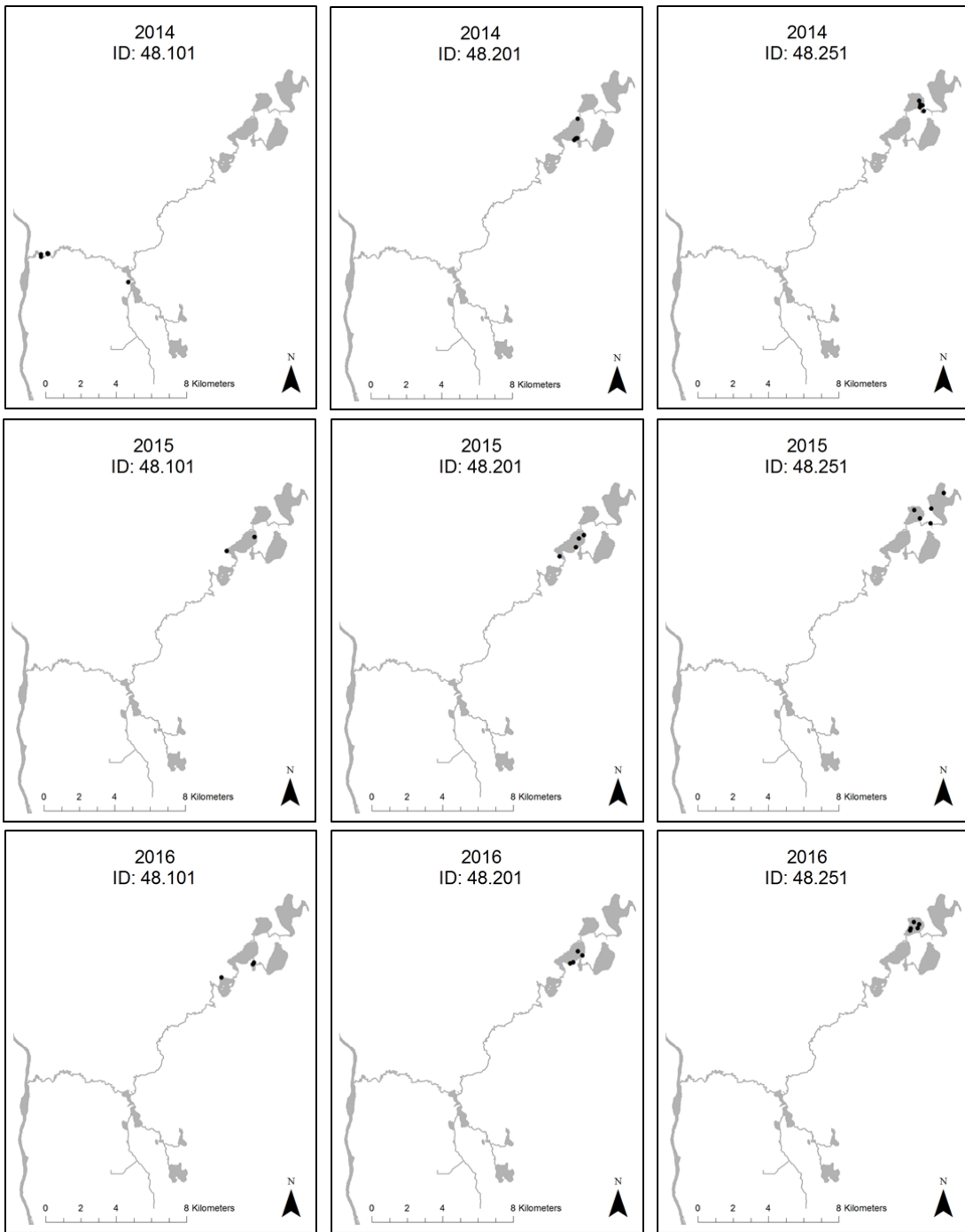
Fig. 5a. Distribution for three radio-tagged adult carp monitored over three consecutive spawning seasons demonstrates selection of specific lakes. High flows in the spring of 2014 limited access to upstream spawning lakes. All individuals were originally radio-tagged in Long Lake, the primary overwintering lake in the Rice Creek Watershed, and left Long Lake during spawning season in all years.

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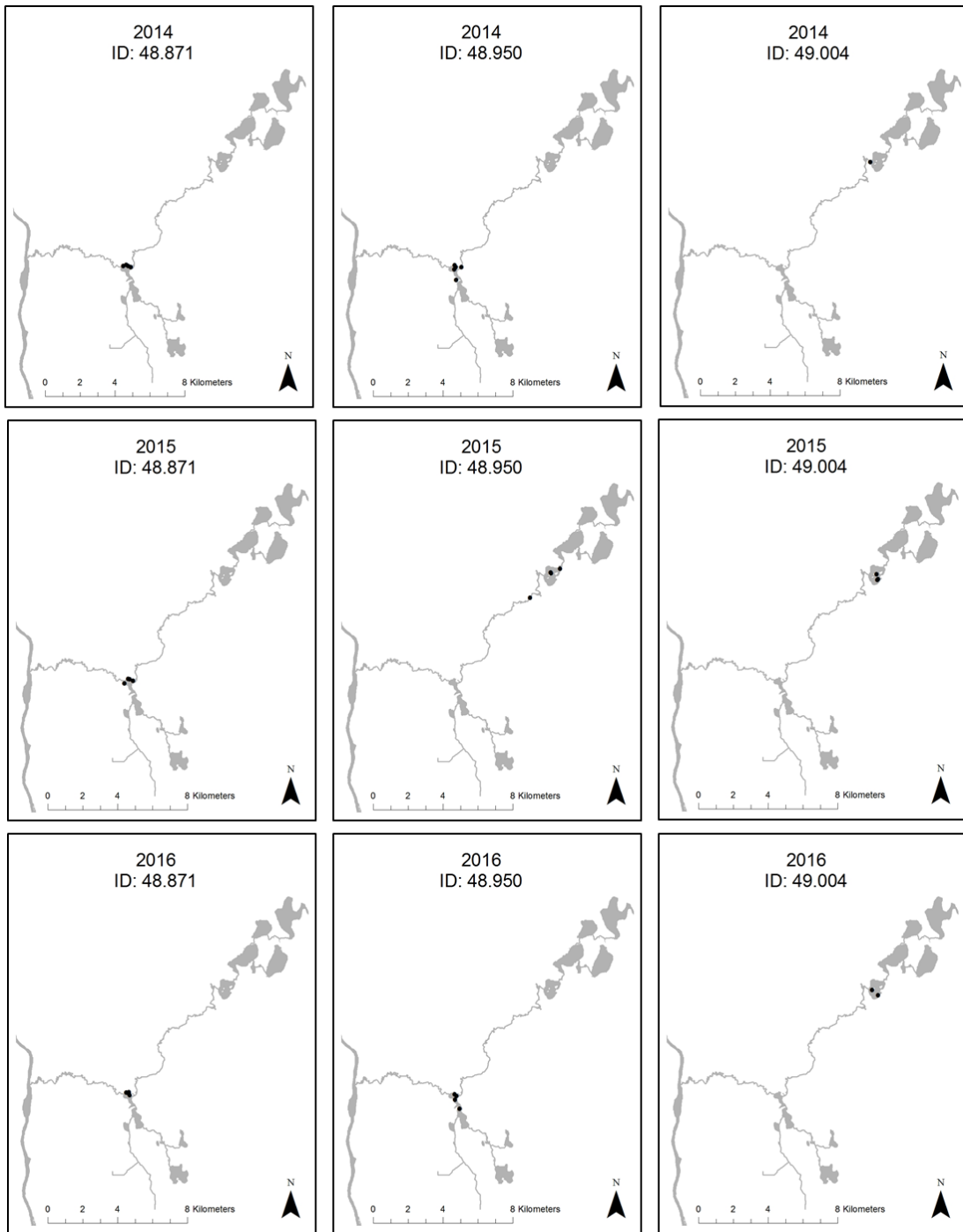
Figure 5b. Distribution for three radio-tagged adult carp monitored over three consecutive spawning seasons demonstrates selection of specific lakes. High flows in the spring of 2014 limited access to upstream spawning lakes. All individuals were originally radio-tagged in Long Lake, the primary overwintering lake in the Rice Creek Watershed, and either remained resident or left Long Lake during spawning season in all years. For fish ID: 48.950, individual variation demonstrates flexibility in choice of being migrant or resident.
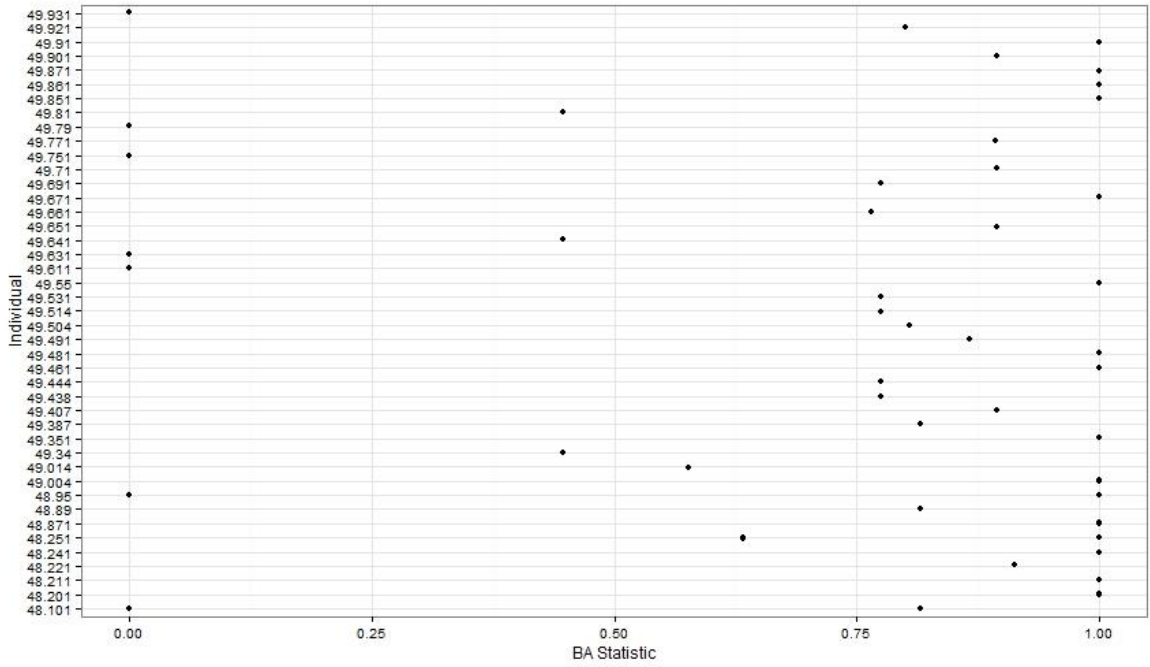
Fig. 6. Bhattacharyya's affinity (BA) index of similarity for all individuals monitored for more than one spawning season (n=43). Individuals that were monitored for three years will have three values (year 1, year 2), (year 2, year 3), and (year 1, year 3). Fish that have identical distributions (same lakes and same amount of time spent in each lake during two spawning seasons) will have a BA = 1, whereas BA indices = 0 indicate non-overlapping distributions in lakes used during two spawning seasons.
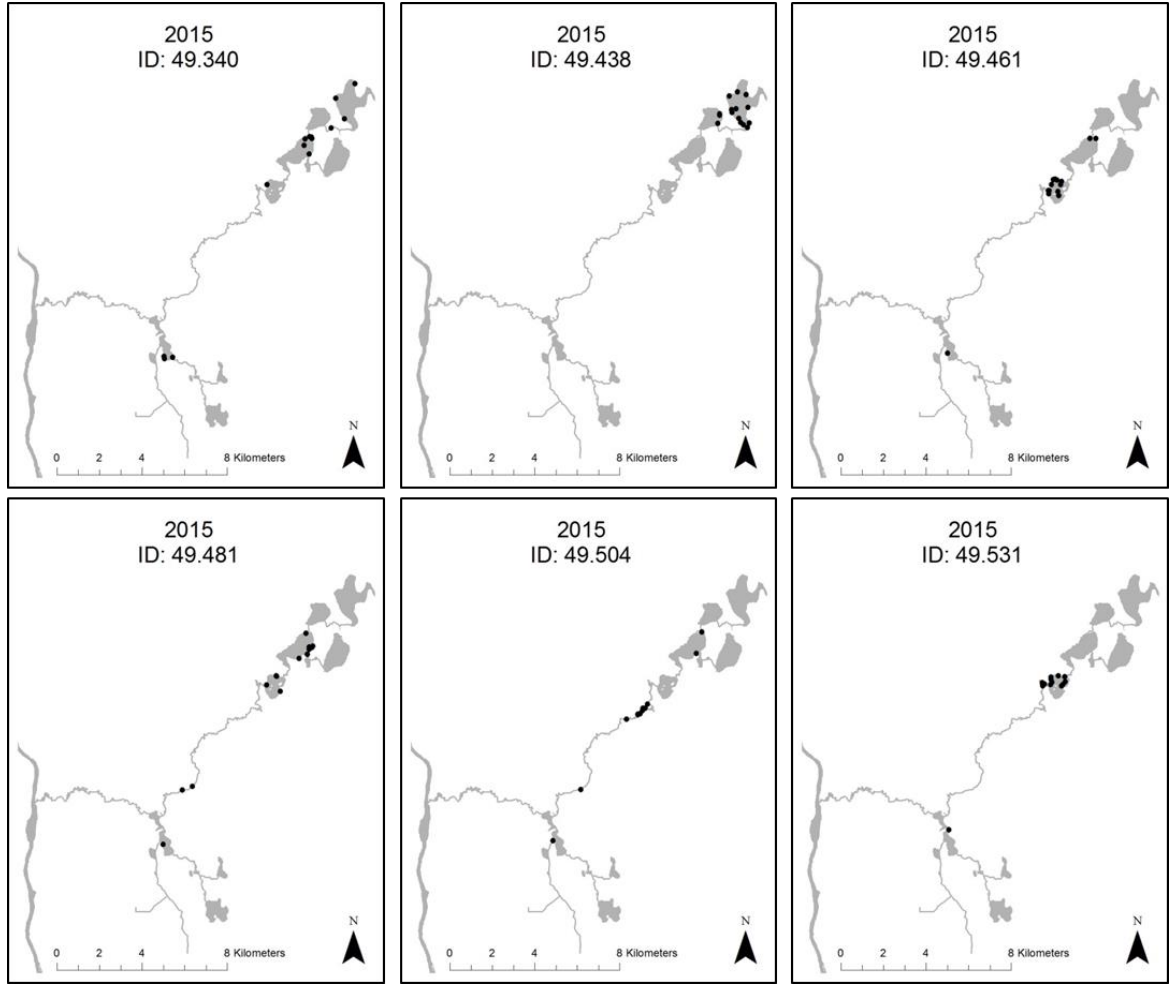
Fig. 7. Locations of adult common carp in the summer of 2015 between June (after spawning) and October (before overwintering) for six representative individuals in Long Lake and the shallow upstream lakes.

Fig. 8. Overwintering distribution of individual adult common carp in 2014, 2015, and 2016 in Long Lake, the overwintering refuge lake where all individuals were radio tagged. Each month was chosen to represent distribution across the entire winter. While two individuals in 2015 and two individuals in 2016 overwintered in lakes >2km away from Long Lake, most individuals overwintered in Long Lake. Only Long Lake and adjacent Pike Lake (west of Long Lake) are shown to illustrate how distributions change throughout the lake over winter. Overwintering distribution showed individuals widely distributed in November and tightly clustered in February and March in all years.
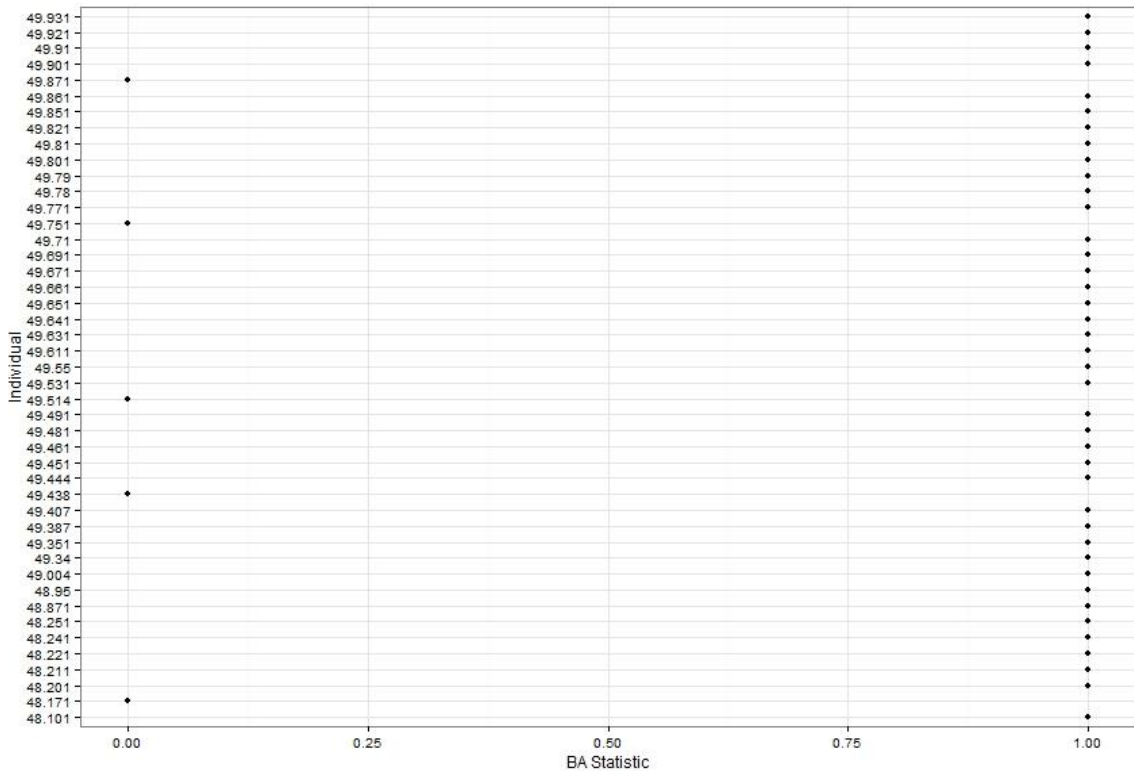
Fig. 9. Bhattacharyya's affinity (BA) index of similarity for all individuals monitored for more than 1 winter (n=45). Fish that have identical distributions (same set of lakes and same amount of time spent in each lake during two overwintering seasons) will have a BA = 1, whereas BA indices = 0 indicate non-overlapping distributions during two overwintering seasons.

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Appendix 1: Diel movement of adult common carp January – October 2015

A1.0 Critical Review of Daily Movement Patterns in Fish

Movement patterns can be monitored at different temporal scales, diel and seasonal. The majority of animals demonstrate diel movement patterns of activity given the daily rhythm of light and dark cycles in addition to seasonal movements given cyclic environmental and climatic changes. Cymborowski (2010) described these diel cycles as daily rhythms of activity that may be nocturnal, diurnal or crepuscular.

A1.1 Diel activity patterns in fish

Helfmann (1981) noted that diel activity patterns in coral reef fishes are more predictable with relatively constant day, night, and crepuscular periods whereas temperate freshwater fish have evolved under more variable light conditions which correspond to more variable diel activity. The crepuscular changeover period, defined as "cover seeking or disappearance of diurnal fishes," is an interesting time to examine diel patterns and temporal organization in freshwater fish communities (Helfmann 1981). Context-dependent behavior and movement has become important in understanding diel movement especially in relation to effort required during migration or predation pressure (Keefer et al. 2013). For five upstream-migrating anadromous fishes in the Columbia River (Chinook salmon, *Oncorhynchus tshawytscha*; sockeye salmon, *O. nerka*; steelhead, *O. mykiss*; Pacific lamprey, *Entosphenus tridentatus*; and American shad, *Alosa sapidissima*), diel activity varied among species depending on the environmental conditions encountered during this freshwater stage of migration. While all species were

active during most of the diel cycle in low-gradient, hydraulically simple reaches with low predator density, lampreys were primarily nocturnal in high-gradient, complex reaches with high predation pressure whereas salmonids and shad were primarily diurnal (Keefer et al. 2013). While seasonal movements demonstrate large-scale habitat shifts between non-breeding and breeding habitats (Meyer et al. 2007a), context-specific diel activity demonstrate small-scale movement variability in response to changing environmental conditions that include photoperiod, water temperature, hydrologic complexity, and predator density which occur over small spatial (kilometers to tens of kilometers) and temporal (hours to days) scales (Keefer et al. 2013). Diel cycles in fish are thus important for identifying flexibility in life history strategies that allow individuals to maximize growth while minimizing costs such as predation and mortality (Jonsson and Jonsson 1993, Alerstam et al. 2003, Chapman et al. 2012, Keefer et al. 2013).

Migration in fish may occur at a range of spatial and temporal scales, from diel migration among habitats to seasonal migrations on a landscape level (Skov et al. 2008). Seasonal movement studies have often been performed in conjunction with diel movement studies, most often with acoustic monitoring (Meyer et al. 2007a, Meyer et al. 2007b, Parsley et al. 2008). Understanding diel cycles has been useful for developing strategies for Marine Protected Area design for commercially important species such as the green jobfish (*Aprion virescens*) and giant trevally (*Caranx ignobilis*) in Pacific coral atolls (Meyer et al. 2007a, Meyer et al. 2007b). Management and restoration of fish populations has served as the impetus for many studies of seasonal and diel movements

(Parsley et al. 2008). Data on diel activity can compliment large-scale movement data when trying to identify habitats and develop appropriate stock sampling programs for species like white sturgeon (*Acipenser transmontanus*) (Parsley et al. 2008). Recreational fisheries for largemouth bass (*Micropterus salmoides floridan*) can also benefit from diel studies as managers can determine the areas and times for the highest catch rates in sport fishing (Mesing and Wicker 1986). Mangers can use diel movement data to recommend changes in fishing gear deployment in an attempt to reduce bycatch for species like ocean sunfish (*Mola mola*). With an understanding that ocean sunfish spend 75% of their time within 20m of the surface at night and gillnets are typically set overnight at a minimum depth of 12m, managers may recommend lowering the minimum depth of gillnets to reduce bycatch of ocean sunfish (29% of total bycatch in drift gillnet fisheries in western United States) (Cartamil and Lowe 2004). Seasonal and diel studies in marine fisheries appear more common. Future studies should explore seasonal and diel patterns of freshwater fish that perform partial migrations. Having a better understanding of activity patterns on both small and large scales can provide important information for management of partially migratory species. Studies of this nature for partially migratory fish in freshwater are understudied.

A1.2 Diel activity in partially migratory fish

The simple diel cycle of the rising and setting sun influences patterns in behavior of when fishes feed, breed, aggregate and rest, in addition to the prey eaten, method of feeding, and predator avoidance (Helfman 1986). Understanding diel activity in the

context of partial migration is important as it is a powerful force shaping the distribution of fishes across space and time, and influences processes at all scales, from individuals to entire ecosystems (Chapman et al. 2012). Diel distribution of three partially migratory cyprinids, roach (*Rutilus rutilus*), white bream (*Blicca bjoerkna*), and rudd (*Scardinius erythrophthalmus*), were evaluated in winter and spring in relation to their piscivorous predators, pike (*Esox lucius*) and perch (*Perca fluviatilis*), between a shallow lake and its streams. Clear diel patterns were found for each cyprinid, showing most fish entered the streams during late afternoon in autumn/winter and during morning in spring. The observed diel movement patterns were suggested to be linked to reduced light intensity around dawn and dusk, although further studies are needed to confirm this hypothesis (Skov et al. 2008). Based on body condition, individual roach choose between the tradeoff to migrate out of lakes to tributary refuge streams with low predation pressure or remain in lakes with higher predation pressure and higher growth rates in the winter (Brodersen et al. 2008). Diel activity of cyprinids varied between species dependent upon an individual's risk of mortality and the cost of migration into the stream (Skov et al. 2008), indicating that diel patterns among other partially migratory species may be common.

Dualism, an ability for fish to exhibit both diurnal and nocturnal patterns, has been described for Atlantic salmon (*salmo salar*), Arctic charr (*Salvelinus alpinus*), rainbow trout (*Onchorhynchus mykiss*), European seabass (*Dicentrachus labrax*), gilthead seabream (*Sparus aurata*), and zebrafish (*Danio rerio*) although the mechanisms that drive dualism are unknown (Lopez-Olmeda and Sanchez-Vazquez 2010). Whether

dualism may be related to patterns in partial migration behavior has not been described. Even though partially migratory species such as roach within Cypriniformes are well studied, patterns and mechanisms of other partially migratory cyprinids are largely unknown. Future studies should elaborate on the specific triggers of migration in order to further our understanding of ecosystem and management implications of seasonal migration in cyprinid fish over large and small temporal scales.

A1.2.1 Diurnal patterns

Diel patterns result from the need to concentrate vital activities to the time of day when the balance between food availability and predation risk is optimal (Helfman 1993). Visual predators like salmonids are considered diurnal, although peaks in activity have been observed during dawn and dusk. However, this activity can be seasonally dependent. For example, Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) hide in streambeds during the day in winter, and increase activity at night (Alanärä and Brännäs 1997). Off the Caribbean coast of Panama, striped parrotfish (*Scarus iserti*) migrate diurnally from shallow-water feeding areas to deeper nocturnal resting areas along specific migratory routes. Individual variation in migratory routes to and from their feeding grounds were dependent on individual characteristics such as size, sex and phase (Ogden and Buckman 1973). In order to complete these observations, fish had to be captured and relocated which could have affected observed movements patterns. Future studies should also examine natural diurnal patterns without influence of experimental manipulation to see if the observed patterns are confirmed.

When food is limited and competition for it is high, individual fish may adopt different diel activity patterns. In a study by Alanärä and Brännäs (1997), food was supplied at low and high rewards to five replicate groups of Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*). Diurnal Arctic char and rainbow trout exhibited higher foraging activity and faster growth which resulted in a higher social position compared to nocturnal fish that exhibited slower growth and lower foraging activity (Alanärä and Brännäs 1997). However, this study was completed in clear water rearing ponds and not in a natural ecosystem. The observed interactions must be studied in greater detail before further conclusions can be made.

A1.2.2 Nocturnal patterns

Hobson (1970) found predominantly nocturnal activity in carnivorous species and diurnal activity in herbivorous species in the Gulf of California with photoperiod influencing activity. In all cases light intensity could be regarded as the releaser. This is in accordance to the strict relationship between the durations of the dark phase and the fish's presence in the pelagic zone. Many plankton feeding fish such as roach (*Rutilus rutilus*), rudd (*Scardinius erythrophtalamus*), bream (*Abramis brama*) and bleak (*Alburnus alburnus*) migrate vertically in a diel pattern following their prey (Bohl 1979) but examples of horizontal movements are known as well (Hobson 1970).

Largemouth bass (*Micropterus salmoides*) in a Mississippi lake were tracked using underwater telemetry from March 1977 to April 1978 to determine environmental factors that affect fish movement. Water temperature had previously been shown as the

only variable to influence activity levels. Diurnal movement was prevalent in the spring and fall while nocturnal movement increased as water temperature approached summer highs. As water temperatures reached 27 °C, nocturnal activity and movement increased (Warden and Lorio 1975). However, the extent of nocturnal tracking was less compared to diurnal tracking, identifying a need to study both periods equally for accurate comparisons.

A nocturnal mobility pattern was observed throughout the study on European catfish (*Silurus glanis*). During daytime, catfish were consistently located in the littoral zone and spent extended periods of the day hidden in concealed habitats. Catfish movements were in a radial pattern with upstream and downstream excursions followed by returns to a previously occupied location. Significant individual variations in movement pattern were observed among the tagged fish and within the 24 h cycle for each fish. Mean instantaneous swimming speed was 0.17 body lengths per second (BL·s^{-1}) at night but 0.09 BL·s^{-1} during the daytime (Carol et al. 2007). Future studies of invasive species like European catfish should examine diel movement patterns both seasonally and spatially in order to understand possible ecological impacts on native species.

A1.2.3 Crepuscular patterns

Crepuscular fishes, those active during dusk and dawn, include Atlantic salmon and rainbow trout which have overlapping activities from diurnal and nocturnal periods during crepuscular periods (Lopez-Olmeda and Sanchez Vazquez 2010). The spatial

distribution of juvenile roach (*Rutilus rutilus*), rudd (*Seardinius erythrophtalamus*),

bream (Abramis brama) and bleak (*Alburnus alburnus*) was documented using echo

sounding in small Bavarian lakes in an analysis of diel vertical migration. Changing light

conditions during twilight hours influenced the speed of migration which was accelerated

in seasons of short dusk and dawn and slowed in times of twilight phases or in cloudy

weather (Bohl 1979). Variations in light intensity also influenced activity levels and

movements of brown trout during each hour during twilight and night than during the day

(Young 1999). The precise ecological mechanisms triggering crepuscular and nocturnal

movements of trout and other species should be investigated further to examine if these

patterns are local or more widespread. In addition, the cyprinid study by Bohl (1979) was

limited in its conclusions of crepuscular movements due to analysis of gut content as the

only evidence of crepuscular movements. There could be several other factors

contributing to crepuscular movements such as additional social and environmental cues

of these and other cyprinids that should be considered in future studies.

A1.3 Circadian rhythms

Circadian rhythms are defined as endogenous rhythms that occur within an

individual and without influence of external environmental forces such as light and dark

(Cymborowski 2010). Ueda (2012) suggested Pacific Salmon have a biological clock for

accurate timing of two parts of their spawning migration: first, from the feeding grounds

to their natal stream and second, from the stream mouth to the spawning grounds. Sex

steroids of Pacific salmon peak prior to spawning in late autumn and decrease after

(Oliveira and Sanchez-Vazquez 2010). At the basic level, a biological clock functions in the following order: environmental receptors, input pathway, biological clock, output pathway, and circadian rhythm. The external inputs (feeding/fasting periods, social cues, or noise) serve as synchronizers (time cues) to a clock (pacemaker) that results in a circadian rhythm, although inputs do not directly influence the endogenous process of a circadian rhythm (Cymborowski 2010). To analyze circadian reproductive rhythms, rainbow trout were kept in constant light (Light:Dark, 6:18), temperature (8.5-9.0°C), and feeding conditions for three consecutive cycles of gonadal maturation and ovulation. Rainbow trout in these conditions maintained a self-sustaining circannual spawning rhythm for three consecutive cycles without inputs such as seasonal environmental changes which suggested an endogenous control of rhythms for at least three reproductive cycles. Similar self-sustaining circannual rhythms have been observed for Indian catfish (*Heteropneustes fossilis*) and European sea bass (Oliveira and Sanchez-Vazquez 2010).

Zeitgebers or recurrent time cues reset an individual's clock in order to be in synchrony with biological rhythms throughout the year (Oliveira and Sanchez-Vazquez 2010). Over 20 species of tropical fish have documented lunar reproductive rhythms including *Siganus guttatus* (Rahman et al. 2000), *Sigansu doliatus* (Park et al. 2006), *Sparus aurata* (Saavedra and Pousao-Ferreira 2006), and *Solea senagalensis* (Oliveira et al. 2009). Lunar cues synchronize biological and physiological processes for tropical fish in latitudes with relatively constant light and temperature conditions (Oliveira and Sanchez-Vazquez 2010). There is evidence of reproductive circadian rhythms of partially

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migratory fish such as common carp, although circadian rhythms in the context of partial migration is rarely described. Melatonin is a hormone that synchronizes with seasonal environmental conditions and gonadal steroids are hormones signaling conspecifics of individual gonadal maturity. Both hormones synchronize together for full gonadal maturation during the spawning season for common carp in the spring (Popek et al. 2010).

A1.4 Diel activity patterns in common carp

While diel movements in fish are important for fisheries management and conservation, most studies have documented marine fishes with little attention given to diel cycles in freshwater fish (Parsley et al. 2008). Few studies have documented diel movement of adult common carp (Crook et al. 2001, Bajer et al. 2010, Daniel et al. 2011, Hennen and Brown 2014, Benito et al. 2015), although diel activity patterns may be very important for management and control (Benito et al. 2015). Diel movement may also be considered a complimentary component to large seasonal movement studies and management for this partially-migratory, invasive fish. Crook et al. (2001) found diurnal associations were linked to habitat variables of depth, current velocity, substrate and cover but these associations were not as pronounced during nocturnal periods (Crook et al. 2001). However, this was only one study in one system for ten days in Australia and may not be representative of diel patterns in other systems or during other times of the year. Daniel et al. (2011) found less conclusive results in koi carp in New Zealand with nearly equal movement during the day and night, although the largest daily movement

distances were during the spawning season (Daniel et al. 2011). Detailed analysis of diel movements was lacking in Daniel et al. (2011) as diel activity was estimated using estimates from acoustic receiver detections which potentially misses undetected diel activity. Benito et al. (2015) conducted the most recent study on diel activity of carp. Carp were observed performing diel vertical migrations in summer which included migrating to the reservoir bottom during the night in hypoxic waters with decreased activity and migrating to the reservoir surface during the day (Benito et al. 2015). Several diel studies with carp have been performed in North America. In South Dakota, no differences were found in diel activity within or between months during open water periods of June, July, August, and October despite movements in Australia being highly variable in open water periods (Hennen and Brown 2014). However, Hennen and Brown's (2014) random selection of four radio tagged fish to be tracked over one 24 hour cycle per month is not representative of diel patterns that can compare consistency among individuals and only conducted during four months of the year. In Minnesota, Bajer et al. (2010) found carp feed predominantly at night and further demonstrated nocturnal feeding with radio-tagged carp learning the location of an introduced food reward, moving to the food reward location at night, and returning to their original home range at sunrise. However, this nocturnal feeding patterns was done only during a one month in one system and may not be representative of diel patterns of carp at other times of the year. Further examining the diel cycles in partially migratory carp over annual cycles will provide valuable information of daily activity patterns during specific behavioral phases that include aggregation, breeding migration, spawning, and feeding.

A1.5 Materials and Methods

A1.5.1 Study Site

This study was conducted in the Rice Creek watershed, a relatively large urban system of interconnected lakes, and tributary of the Mississippi River in Minnesota, USA (45.0536N, 93.1142W; Fig. 1) that was known to contain ~20,000 adult common carp with a biomass of 773 kg/ha and average weight of 2.6 kg (P. G. Bajer personal communication). Interconnected lake and marsh systems are typical in the Upper Mississippi River Basin (Bajer et al. 2012). This study was conducted in the middle and lower reaches of the Rice Creek watershed which contains 52 km of streams and 719 ha of lakes. High connectivity between major water bodies by three tributaries and one outlet to Long Lake allowed for the assessment of diel movement patterns during seasonal phases between two deep lakes (>2m) and ten shallow lakes (<2m), all of which were used by adult carp (Banet 2016).

A1.5.2 Experimental Design

This study of adult common carp monitored diel movements in a large watershed to determine differences in diel activity by phase (aggregation, migration, spawning, and feeding), diurnal and nocturnal periods, sex, and individual. Long Lake was selected for radio-tagging in the spring and fall because commercial fish harvests showed it to have many adult carp present in winter (Rice Creek Watershed District 2010) and it was connected to many streams and shallow lakes. Adult common carp were collected in Long Lake in late fall of 2013, early spring of 2014, and fall of 2014, inserted with radio

transmitters, and released at their capture site. Banet (2016) confirmed Long Lake was the primary overwintering lake after tagging in other shallow lakes resulted in mortalities overwinter. From January – October 2015, diel movement patterns were monitored consistently for 15 individuals and twice per month at four hour intervals beginning at 06:00 and concluding at 10:00. During the same time, diel movement patterns were monitored once per month for five individuals selected at random. Diel movements were analyzed in four well-defined phases: overwintering, breeding partial migration, spawning, and feeding. Visual observations for spawning activity, noted by splashing in floating or submerged vegetation, were performed bi-weekly during May and June in both Long Lake and Lino Lakes in 2015.

A1.5.3 Data Collection

After capture of adult carp via boat electrofishing, radio-transmitter (F1850, mortality mode, Advanced Telemetry Systems Inc., Isanti, MN, USA) were surgically implanted following established procedures (Penne and Pierce 2008; Table 1). Weekly tracking performed by Banet (2016) identified locations of individuals prior to diel tracking. Locations were mapped over two 24-h cycles for the 15 fish monitored consistently every month between January 2015 – October 2015 and over one 24-h cycle for the five random fish selected each month between January 2015 – October 2015. For each 24-h cycle, carp locations were bi-angulated every 4-h (starting at 06:00) from a small boat, kayak, or from shore using a loop antenna. Each 24-h cycle concluded by 10:00 the following day. Data from bi-angulation were evaluated using computer

software (LOAS® 4.0; Ecological Software Solutions, CA, USA) and plotted on ArcMap 10.2 (ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute). Tracking efficiency was tested using two dummy tags (i.e. tags not implanted in fish and hidden underwater) and two tags recovered in dead fish (identified by tags that entered mortality mode and did not move for 24 consecutive hours). Observers identified the correct water body for each individual's location, and tracking efficiency reflected a range within 0 – 20m of the estimated bi-angulation location.

A1.5.4 Data Analysis

For all tests of hypotheses and analyses, we sought to identify diel patterns in distance moved in relation to four explanatory variables: phase, time of day, sex, and lake habitat. These analyses were restricted to the 12 adult carp monitored for the entire diel monitoring period. In the multi-phase life cycle of adult carp, phases in this study were defined by overwintering, reproductive partial migration, spawning, and feeding (Banet 2016). Phases were defined within the windows of data collection. The overwintering phase was from January 2, 2015– March 13, 2015. The breeding partial migration phase was from April 15, 2015 – April 30, 2015. The spawning phase was from May 21, 2015 – June 22, 2015. The feeding phase was from August 3, 2015 – October 2, 2015. The gap from June 22, 2015 – August 3, 2015 was not analyzed since it appears to be a transitional summer partial migration phase that is poorly understood (Banet 2016). Time of day was defined by diurnal and nocturnal periods by phase according to average sunrise and sunset time within each phase. Of the 12 carp, three were male and nine were female. Lake habitat was defined as either Long Lake or Lino Lakes. Exploratory

analysis found 2 – 6 individuals were very active or very inactive depending on the diel period tracked in a particular phase. We performed diagnostic plotting to check the normality assumption by diagnostic plotting. When we found the data was skewed, we used the Box-Cox method and it suggested a log transformation. A least squares transformation under log base 2 was calculated for distance traveled for each individual during each 4-h period. The least squares transformation was used for all analyses.

Data were plotted during exploratory analysis to determine possible patterns between distance traveled during diel tracking and the variables: phase, time of day, sex, lake habitat, and individual. Telemetry data were first analyzed by calculating distance traveled for each individual in each 4-h period between consecutive 4-h tracking intervals and used to estimate a distance per hour. An average distance for each individual per phase was then calculated and assigned to each 4-h interval. Data were also sorted by sex, lake habitat, and individual. After exploratory analysis, we determined a linear mixed-effects model was appropriate for our longitudinal data set to test our hypotheses: 1) adult common carp employ differences in activity by phase; 2) adult common carp employ patterns in diel activity based on time of day and phase; 3) adult common carp employ patterns in diel activity by sex and by phase; 4) adult common carp employ patterns in diel activity by lake habitat and phase. Individual variation can be modeled using random effects.

A1.5.5 Linear Mixed-effects Model

Distance traveled was the response variable during diel intervals and four factors were determined to influence the response: sex, phase, time of day, and lake habitat. Log2Distance was used as the response in the model. From the explanatory plot of lake habitat, we find the data is not complete for all combinations of phase and lake, hence we cannot distinguish the effects of phase and lake. For this reason, we create a new variable, phaselake, which is the combination of phase and lake habitat. Fixed effects were selected for sex, phase, time of day (day or night) and phaselake which were assumed to have consistent impacts on the response distance. Random effects were selected for day (date data were collected) and individual. From the individual plots, certain individuals are very active on particular days and inactive on other days. For this reason, individual could not be separated from day. A crossed random effects model was selected as the most appropriate for our data structure as different individuals can be measured on the same day. We considered individual and day as independent random effects and the interaction of individual and day for our final model. After performing a likelihood ratio test on these candidate models, we found the interaction of individual and day to be the most appropriate. We only considered two-way interactions for ease of interpretation.

A fixed-effect model matrix found individual variation from the 12 fish monitored throughout diel tracking explains little of the total variation each month. For this reason, data for the model included the 12 individuals monitored throughout diel tracking and the five individuals selected at random each month. An ANOVA was run to which factors (sex, time of day, and phaselake) and interactions of significance (sex:phaselake, time of

day:phaselake, sex:time of day) were significant at the significance level 0.05. An underline diagram was drawn to identify significant differences between the different phases. Significant interactions between the factors were plotted against the response distance for average distance moved.

A1.6 Results

Average Distance per Period by Phase

The dashed line shows the average distance per 4-hour period.
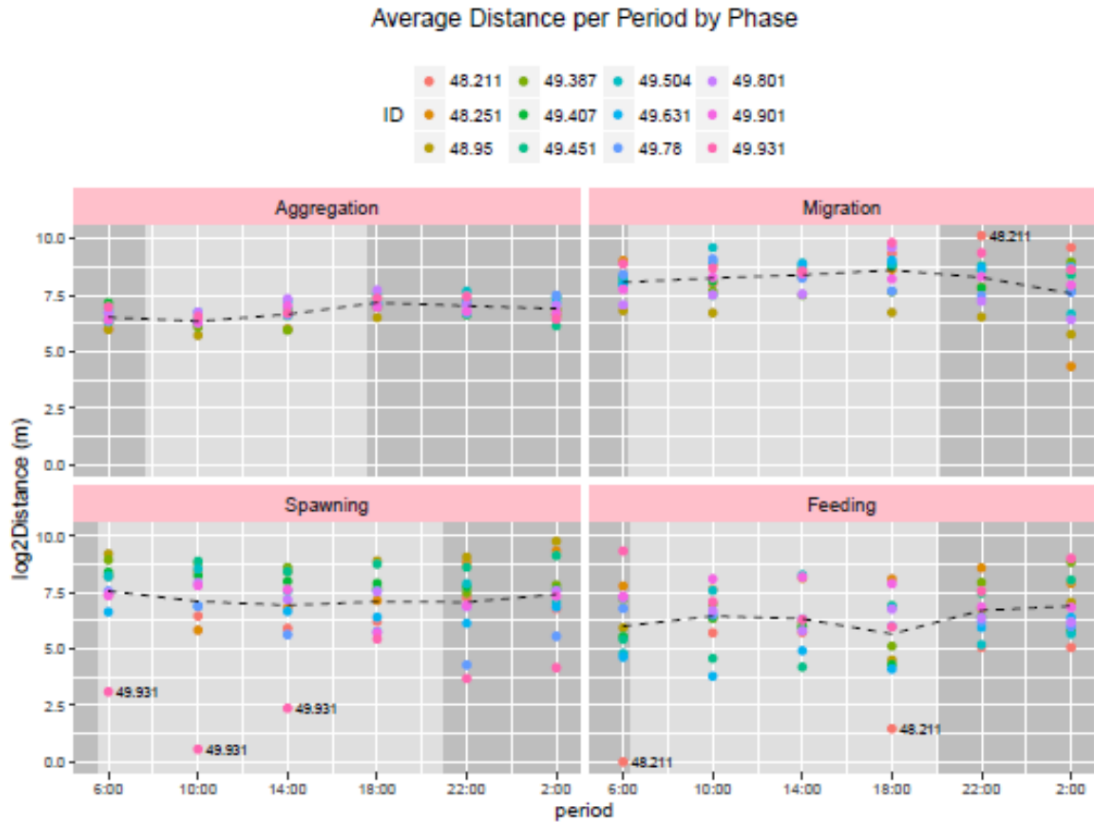
Figure A1.1: The 12 carp monitored consistently from January – October 2015 are the most active during migration phase. They are the least active during aggregation and feeding phases. The plot can also be used to assess the day and night difference shown by shade. Each phase has a different range with more clustering of points in the aggregation phase compared to other three phases. This suggested we may need to treat each phase respectively.

Sex Difference during 24 Hours in Different Phases
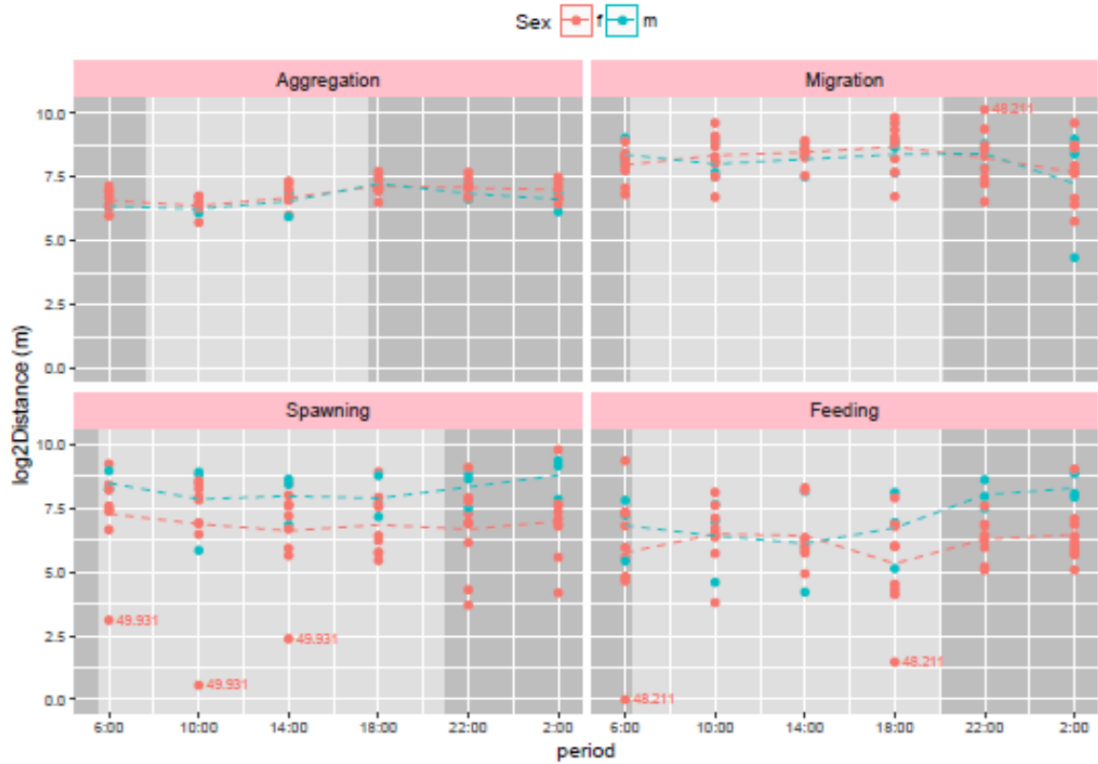
The dashed lines represent the average distance per period by phase for male and female carp.

Figure A1.2: The three males (green points) were more active than the 9 females (red points) in the spawning and feeding phases of the 12 adult carp monitored consistently from January – October 2015. Males and females followed similar patterns in the agrregation and migration phases. Average log2Distance (m) for males and females during 4-h intervals is represented by dashed green and red lines respectively.
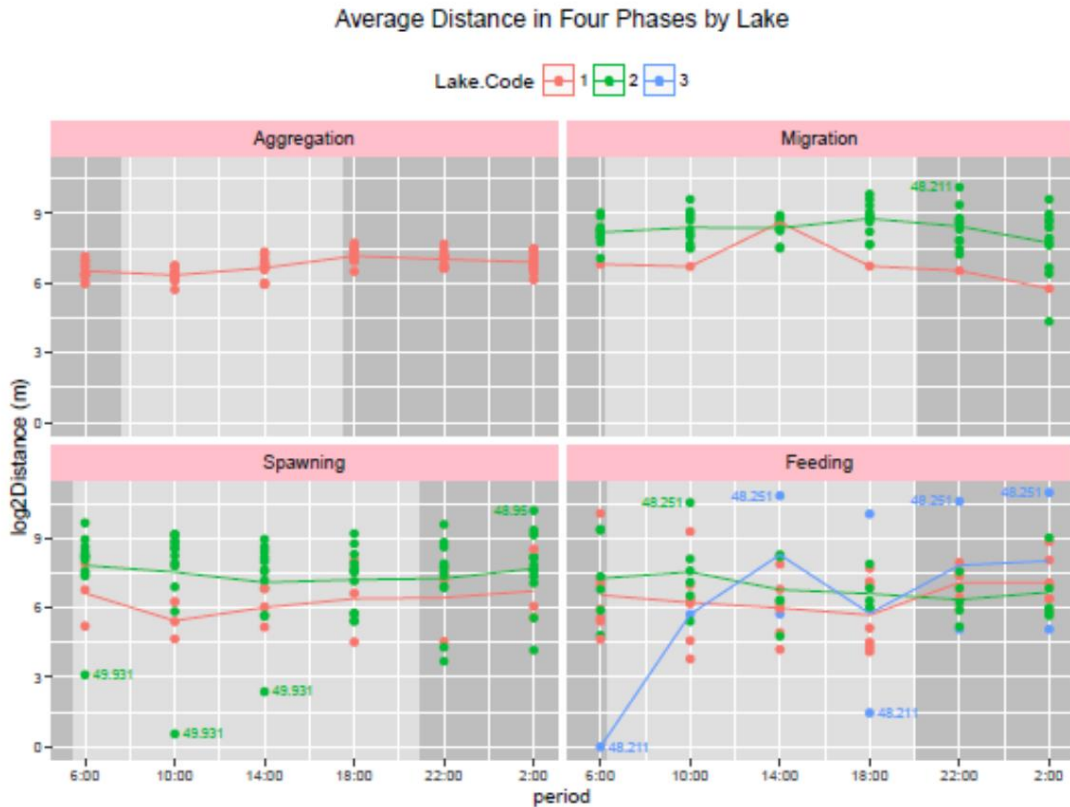
Figure A1.3: Of the 12 adult carp monitored from January – October 2015, lake habitats (Long Lake – 1, shallow upstream lakes – 2, and Rice Creek – 3) and the diel movements within each lake habitat were assigned to each individual. Adult carp in lake zone 2 have more activity than those in zone 1. Carp were active in zone 3 during feeding phase, although this was the only phase carp were found in this habitat during the diel monitoring period. There are only a few observations in the long lake (zone 1) during migration and spawning phases.
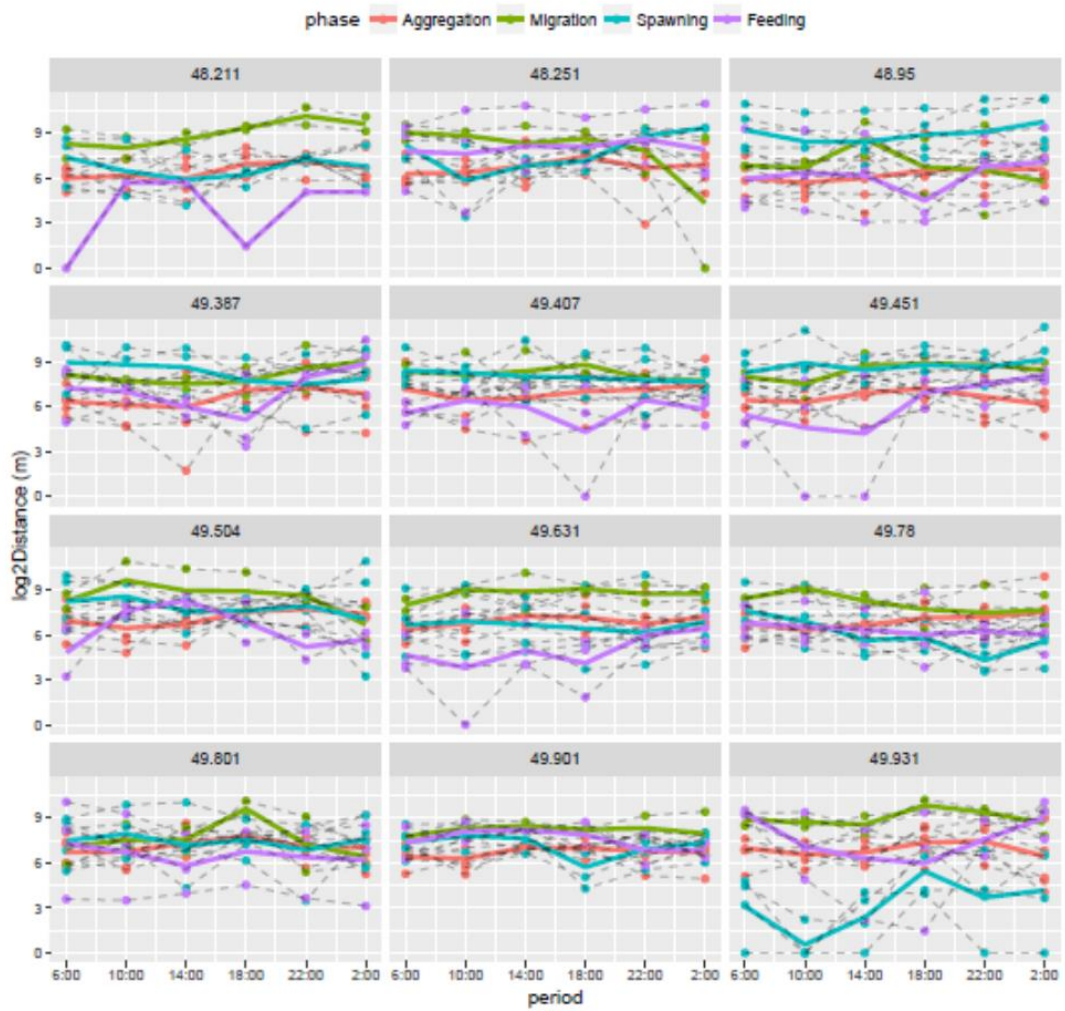
Figure A1.4: All diel tracking periods during each phase are plotted for each individual. Points identify distance moved during each phase (red – aggregation, green – migration, teal – spawning, and purple – feeding) and the dashed lines connect points measured on the same day. The average distance moved during each phase for each indivdual is shown by solid lines.

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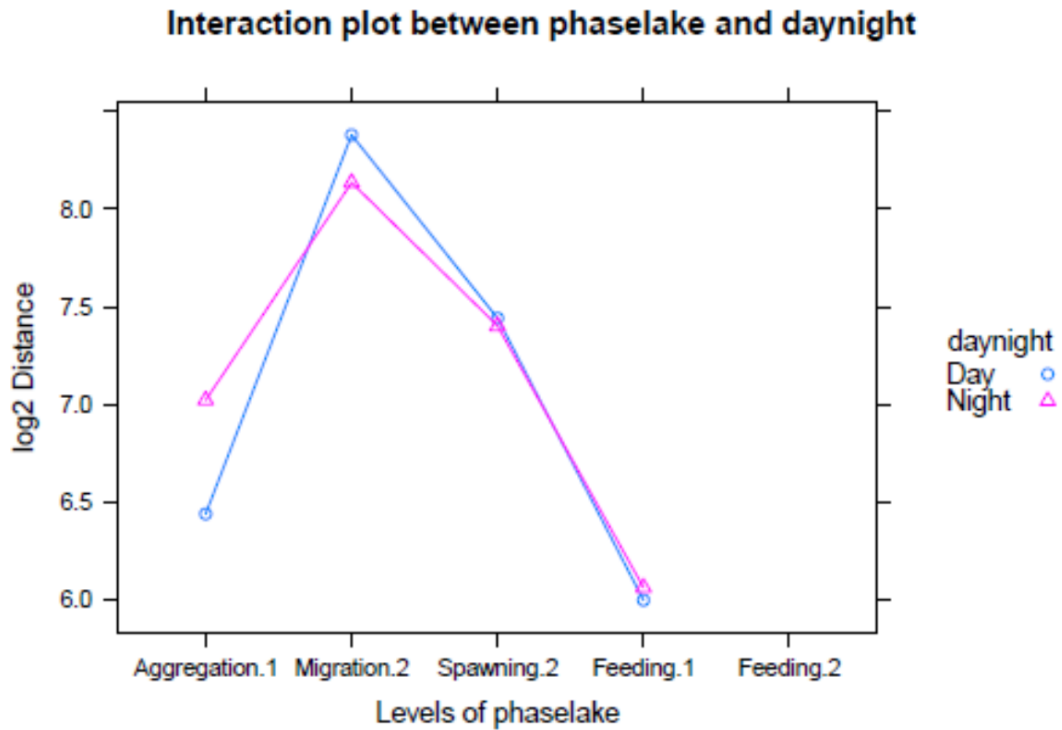
Figure A1.5: The 12 individuals monitored consistently and 5 individuals chosen randomly each month from January – October 2015 were plotted in a linear mixed-effects model to demonstrate interactions between phaselake:DayNight in response to distance moved. Significant differences (p < 0.0001) between day (pink triangles and line) and night (blue circles and line) were apparent during the aggregation phase and lake habitat 1 (Long Lake). Non parallel lines are apparent during other phases, although not statistically significant.

Interaction plot between phaselake and Sex
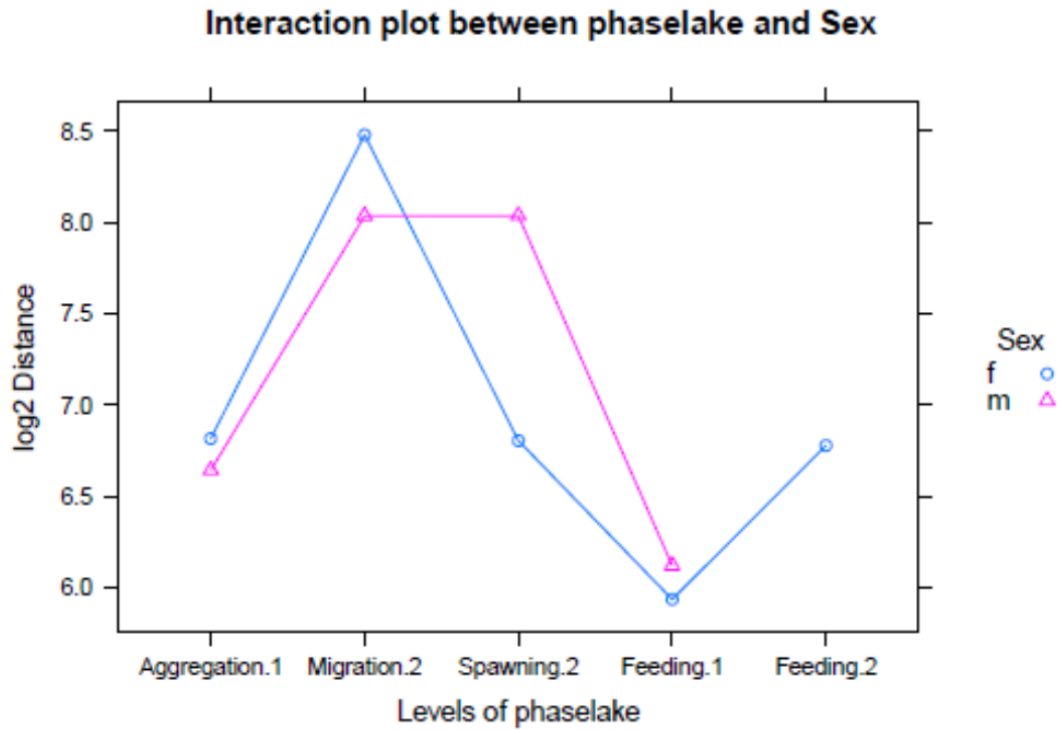
Figure A1.6: The 12 individuals monitored consistently and 5 individuals chosen randomly each month from January – October 2015 were plotted in a linear mixed-effects model to demonstrate interactions between phaselake:sex in response to distance moved. Significant differences ($p = 0.0021$) between male (pink triangles and line) and female (blue circles and line) adult carp were apparent during the spawning phase in lake habitat 2 (shallow upstream lakes). Non parallel lines are apparent during other phases, although not statistically significant. No male carp were tracked in lake habitat 2 (shallow upstream lakes) during the feeding phase.

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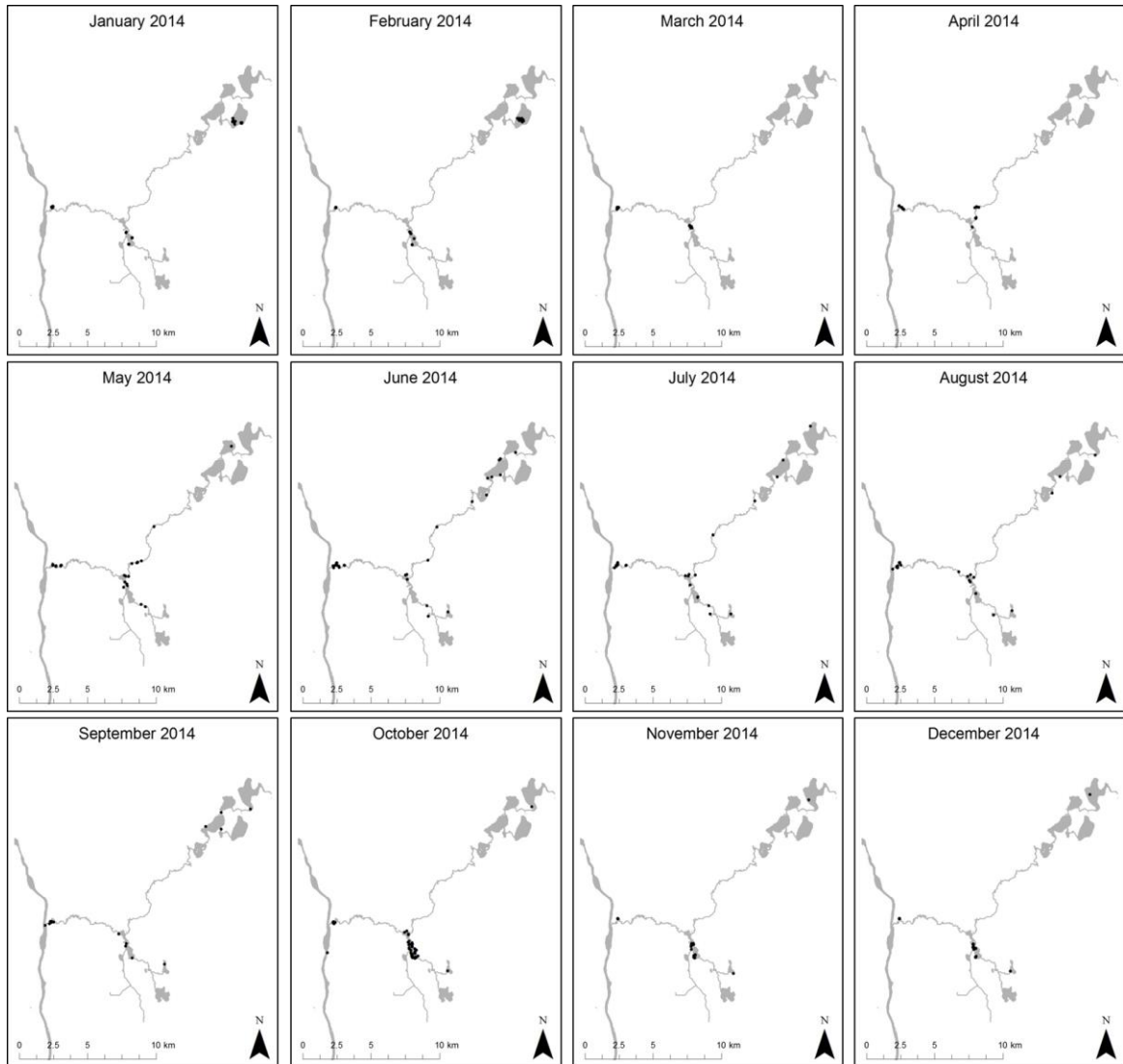
Figure A2.1. Seasonal distribution of adult common carp in 2014. Each dot represents an individual radio-tagged common carp. In the fall of 2013, tags were released in three lakes shown in January and February 2014. In February 2014, tags in the northern lake were confirmed in mortality mode and not tracked further. One week during each month was chosen to represent distribution across different seasonal phases.
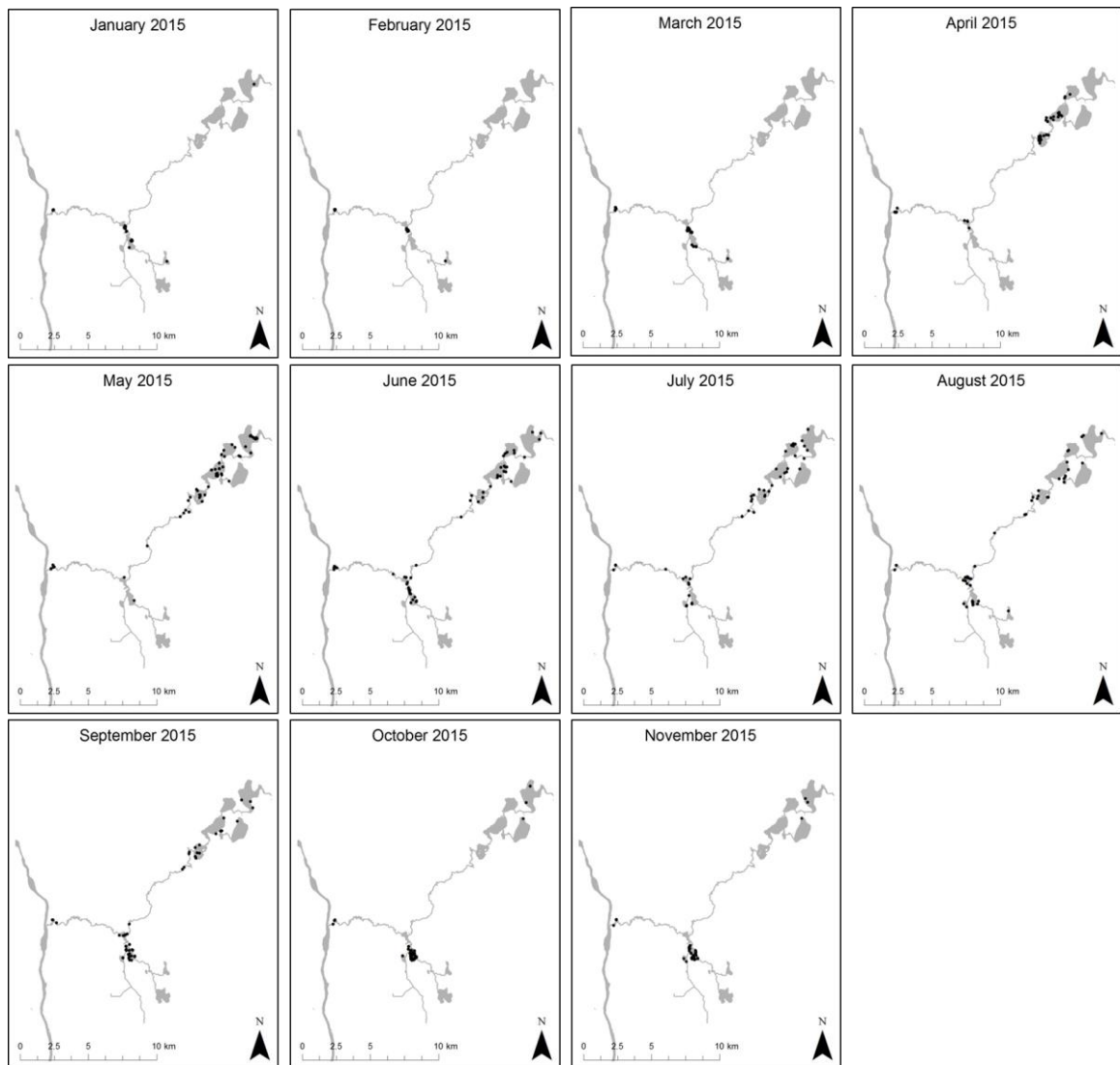
Figure A2.2. Seasonal distribution of adult common carp in 2015. Tracking in 2015 concluded in November. Each dot represents an individual radio-tagged common carp. One week during each month was chosen to represent distribution across different seasonal phases.
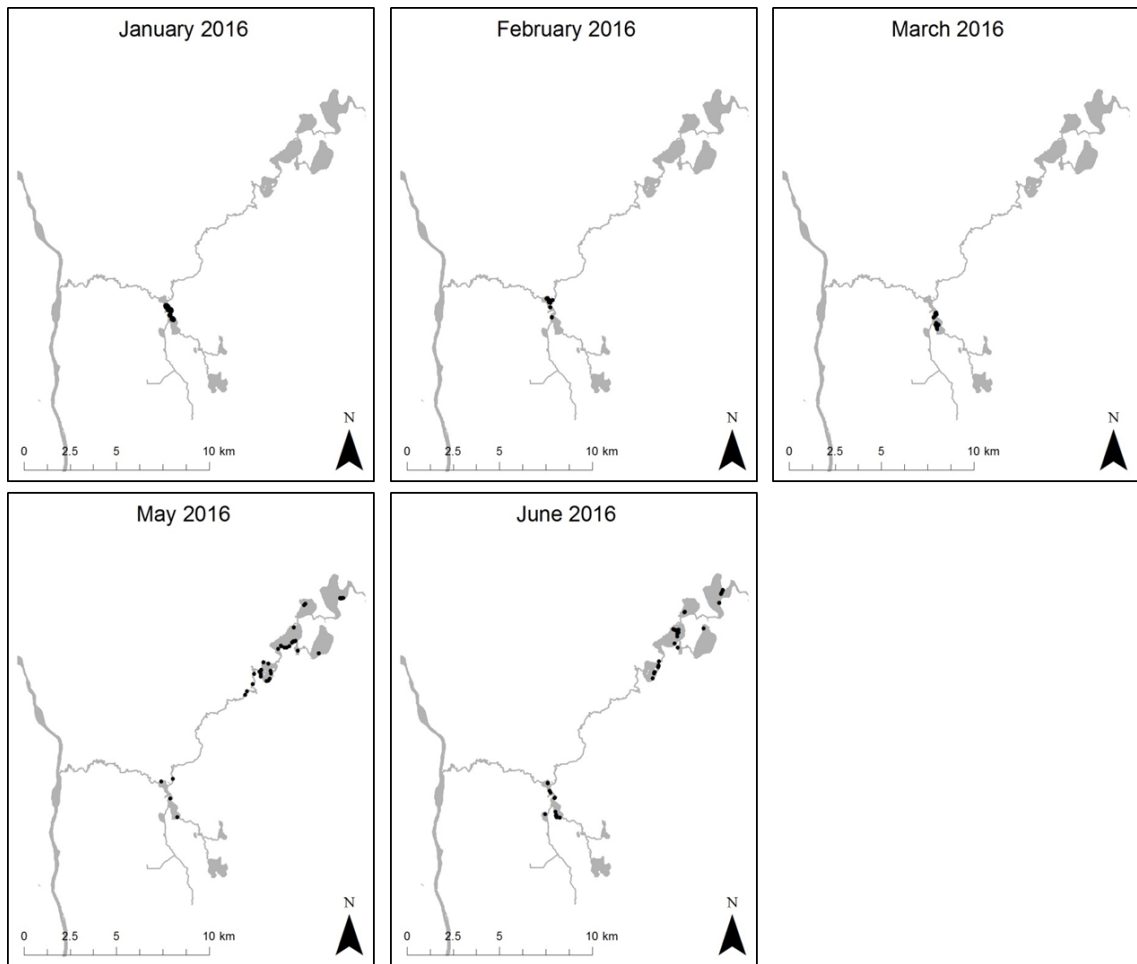
Figure A2.3. Seasonal distribution of adult common carp in 2016. Tracking was conducted in 2016 only in January, February, March, May, and June. Each dot represents an individual radio-tagged common carp. One week during each month was chosen to represent distribution across different seasonal phases.

Table A2.1. Weekly tracking of adult carp was performed weekly, and for Figures A2.1-3, each month is represented by a specific week.

Month Tracked	Week(s) Tracked 2014	Week(s) Tracked 2015	Week(s) Tracked 2016
January	1/20/14 – 2/2/14	1/12/15 – 1/18/15	1/11/16 – 1/17/16
February	2/17/14 – 3/2/14	2/23/15 – 3/1/15	2/8/16 – 2/14/16
March	3/17/14 – 3/30/14	3/23/15 – 3/29/15	2/29/16 – 3/6/16
April	4/14/14 – 4/20/14	4/20/15 – 4/26/15	
May	5/19/14 – 5/25/14	5/25/15 – 5/31/15	5/9/16 – 5/15/16
June	6/23/14 – 6/29/14	6/22/15 – 6/28/15	6/6/16 – 6/12/16
July	7/21/14 – 7/27/14	7/20/15 – 7/26/15	
August	8/11/14 – 8/17/14	8/24/15 – 8/30/15	
September	9/15/14 – 9/21/14	9/21/15 – 9/27/15	
October	10/13/14 – 10/19/14	10/19/15 – 10/25/15	
November	11/24/14 – 11/30/14	11/2/15 – 11/8/15	
December	12/8/14 – 12/14/14		

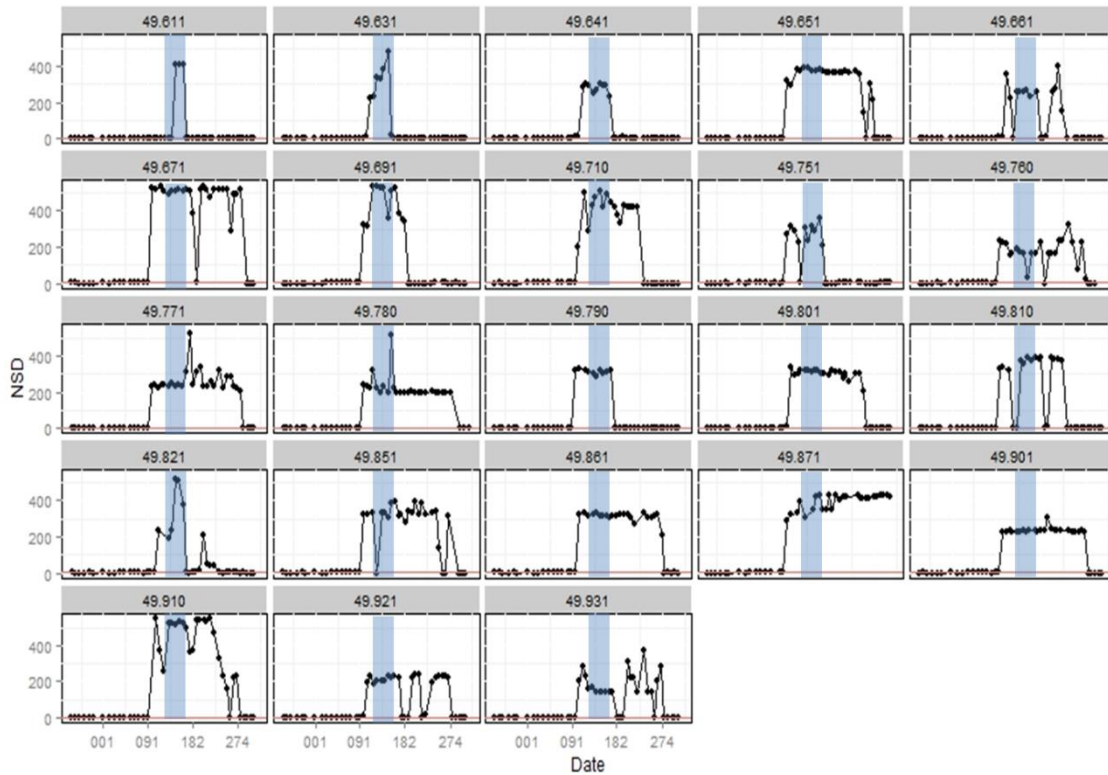**Appendix 3: Net squared displacement**
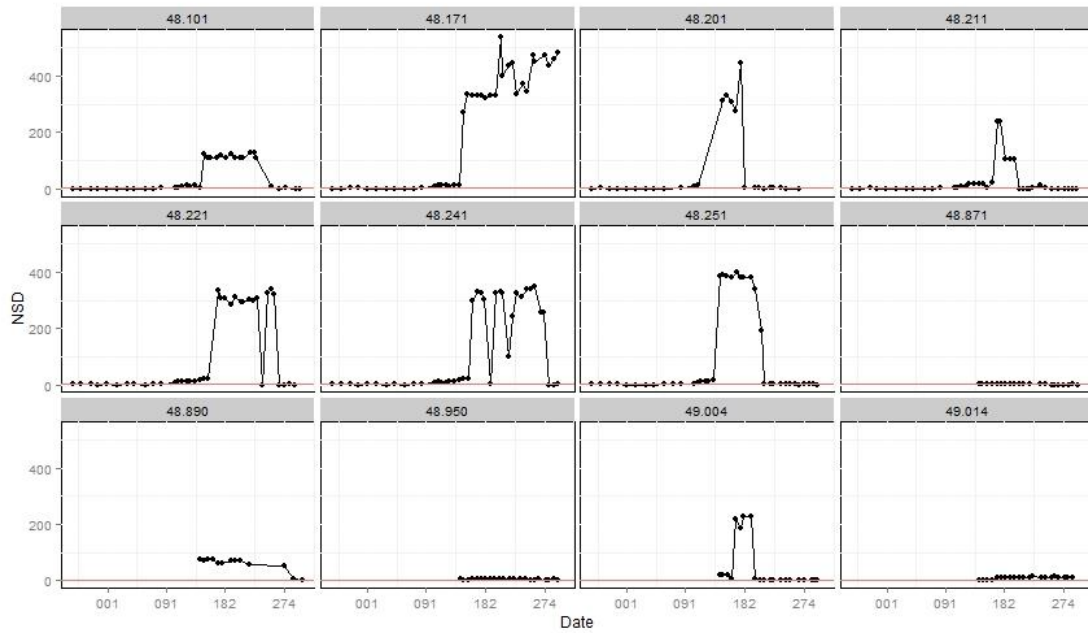
Figure A3.1. Net Squared Displacement (NSD), the square of the distance from a point of reference (Long Lake) to subsequent locations in the movement path of an animal was calculated for individual adult common carp radio-tagged in Long Lake. Weekly NSD for 12 individual adult common carp (*Cyrpinus carpio*) monitored for an entire year from October 2013 – December 2014 that did not have mortality. NSD values will be near 0 when individuals are in Long Lake. Changes in NSD over time are indicative of changes in individual-level distribution patterns. Migration is indicated by a movement away and return from NSD near 0 and resident by a flat line near NSD = 0.

Figure A3.2. Net Squared Displacement (NSD), the square of the distance from a point of reference (Long Lake) to subsequent locations in the movement path of an animal was calculated for individual adult common carp radio-tagged in Long Lake. Weekly NSD for 23 individual adult common carp (*Cyrpinus carpio*) monitored over time from October 2014 – November 2015 (For 20 other individuals in 2015, see ch. 2, Fig. 4). NSD values will be near 0 when individuals are in Long Lake. Changes in NSD over time are indicative of changes in individual-level distribution patterns. Migration is indicated by a movement away and return from NSD near 0 and resident by a flat line near NSD = 0. Shading defines observations of spawning in 2015 (Table 6 –spawning dates).

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Net Squared Displacement of Adult Movement Strategy
Net squared displacement analysis determined movement strategies for migrants (Figure A3.3), dispersers (Figure A3.4), and residents (Figure A3.5). Timing of migrants or residents that entered mortality mode were also analyzed (Figure A3.6).
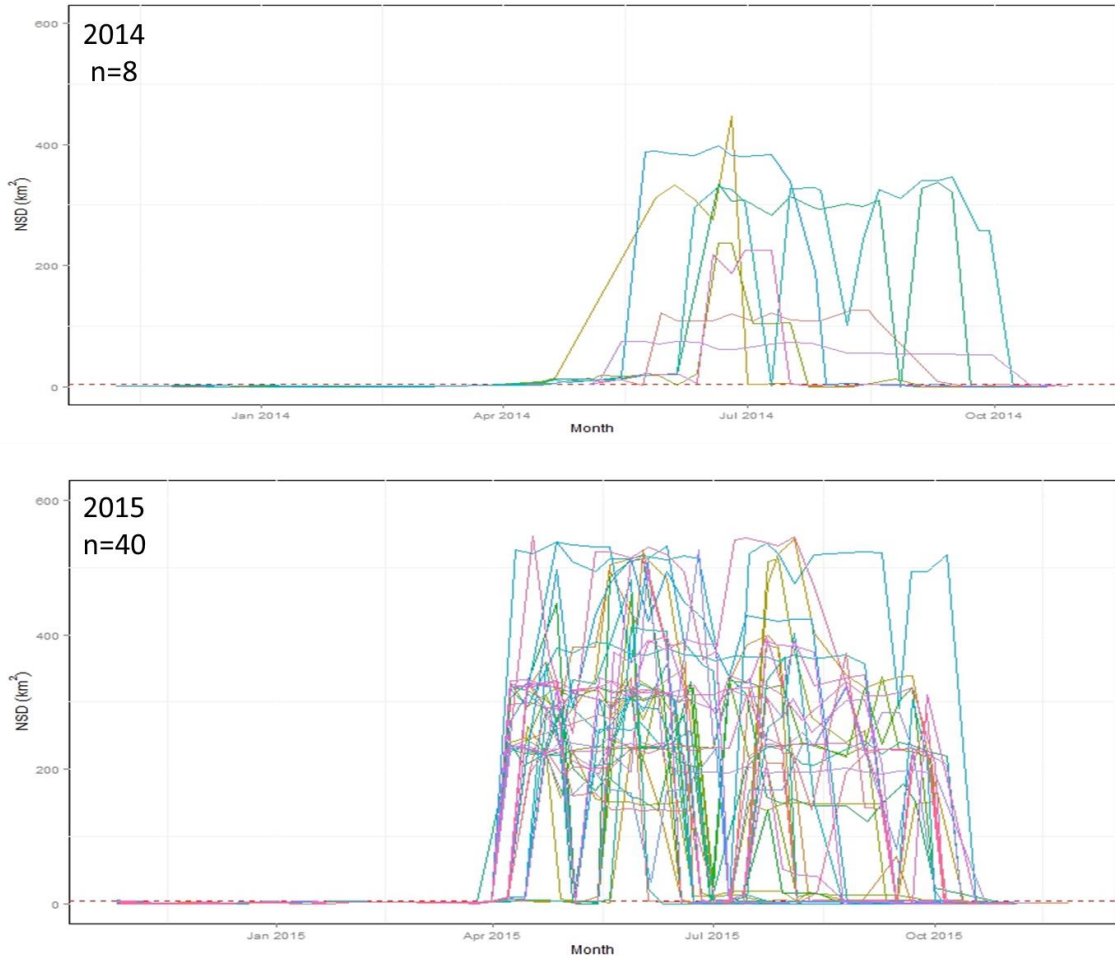
Figure A3.3. Individual adult carp classified as migrants in 2014 (n=8) and 2015 (n=40)
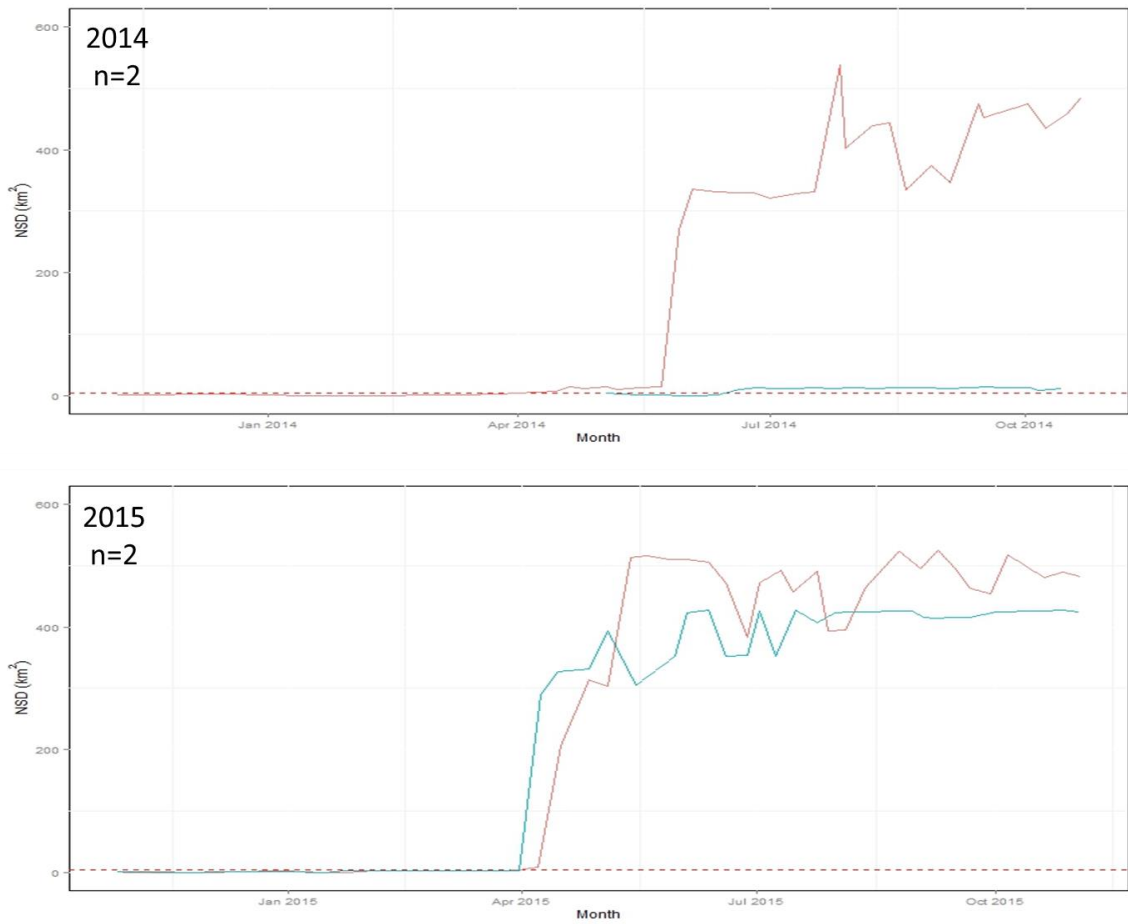
Figure A3.4. Individual adult carp classified as dispersers in 2014 (n=2) and 2015 (n=2). Dispersers in 2014 chose two different directions compared to only one direction in 2015.
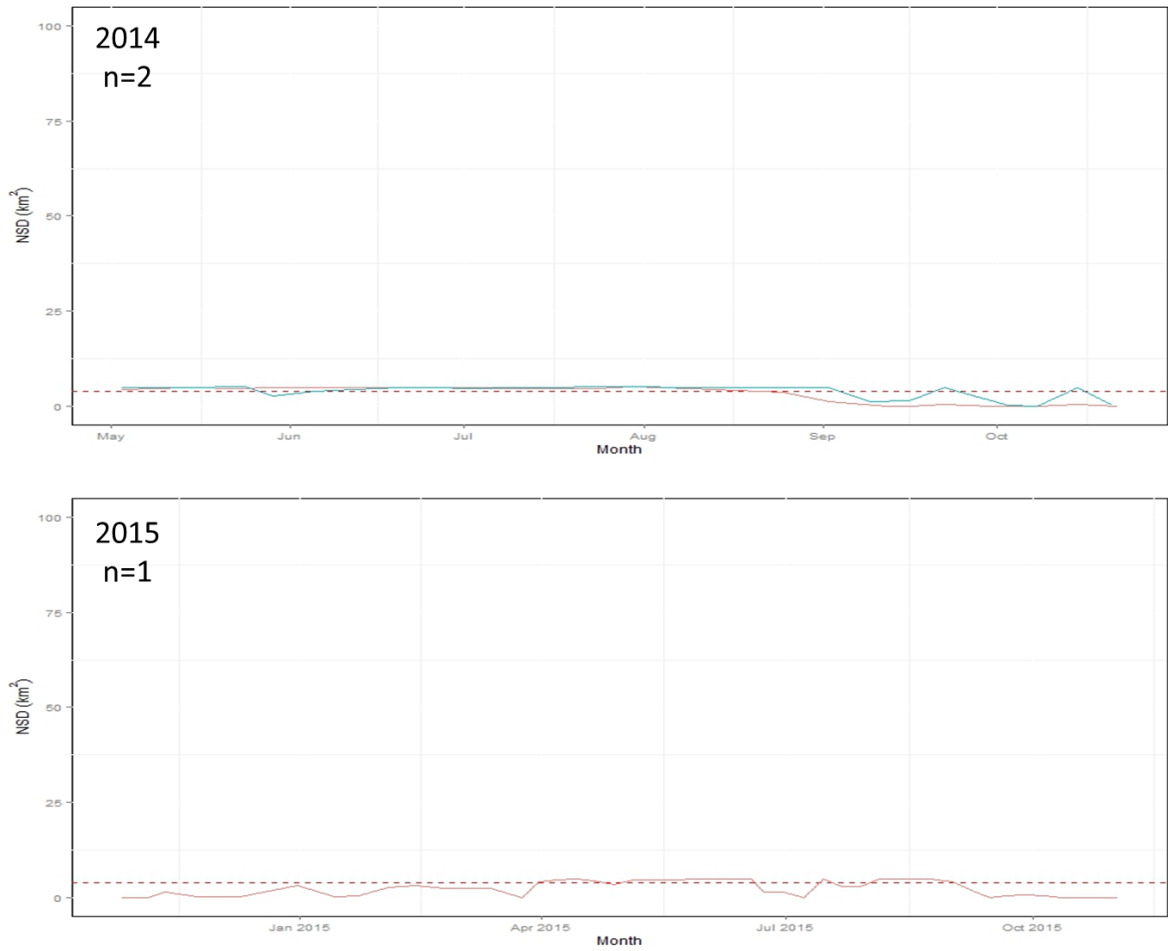
Figure A3.5. Individual adult carp classified as residents in 2014 (n=2) and 2015 (n=1).
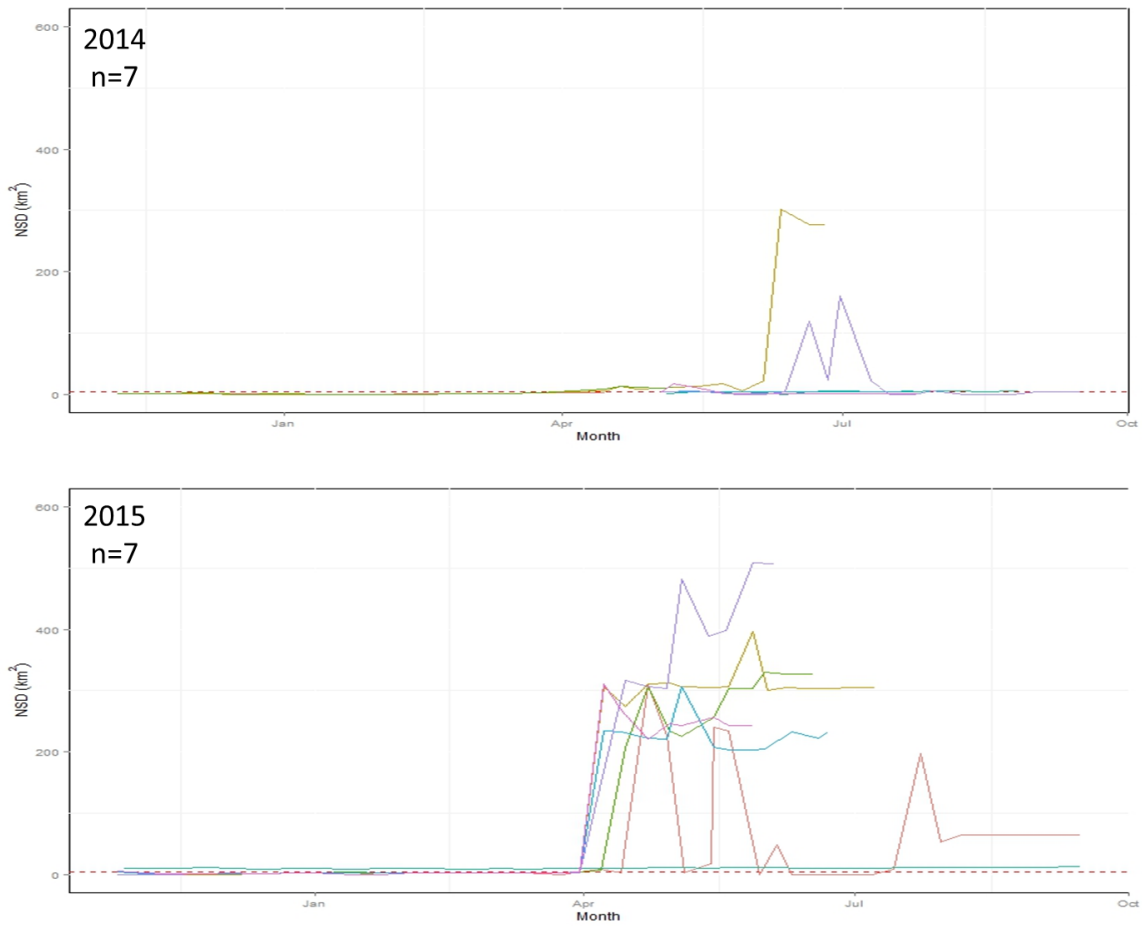
Figure A3.6. Individual adult that endured mortality or expelled transmitters in 2014 (n=7) and 2015 (n=7). Only individuals that survived more than two months after radio tag implantation were included in mortality analysis as mortalities within two months were likely associated with surgery complications or infection. Most mortalities in 2015 occurred during spawning (May 18 – June 20) or soon after spawning. Two tags in 2015 were lost and not included in mortality analysis since final fate was unknown.

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Migration distance

Differences between male and female individuals for maximum NSD and average NSD were compared between 2014 and 2015 (Table A3.1). This analysis was for individuals performing out and back migrations from Long Lake and did not include migrating individuals that resulted in mortalities or becoming lost. In April 2014, additional tags were added to Long Lake due to mortalities from initial tagging in 2013. To compare the migratory individuals for the new and old tags in 2014, NSD values from May 3, 2014 to October 21, 2014 were analyzed. For 2015, NSD values from October 27, 2014 to November 2, 2015 were analyzed. In 2014, no differences were observed when comparing male and female maximum NSD (pvalue=0.493) or average NSD from Long Lake (pvalue=0.6984). In 2015, no differences were observed when comparing male and female maximum NSD (pvalue=0.1003) or average NSD from Long Lake (pvalue=0.258).

Environmental conditions resulting in high water levels and discharge through a restricted culvert prevented individuals in the spring of 2014 from migrating significant distances above Long Lake before April 20, 2014. Thus, the smaller window of analysis in 2014 compared to 2015 did not affect NSD comparisons between years.

Table A3.1. Maximum average NSD and average NSD for males and females in 2014 and 2015 performing out and back migration from Long Lake. For NSD values in 2014, values on and after May 3, 2014 were compared due to additional tags being added to the sample size in April 2014. Four females (49740, 28211, 48221, 48241) and four males (48890, 49424, 49721, 49730) were not included in NSD due to mortalities or being lost.

Table A3.1. Maximum Average NSD and Average NSD for 2014 and 2015 separted by males and females.

	Male	Female
Maximum NSD Average (SD) 2014	306.28 km^2 (164.70), n =3	238.90 km^2 (81.82), n=6
Average NSD (SD) 2014	107.03 km^2 (40.10), n=3	97.01 km^2 (69.48), n=6
Maximum NSD Average (SD) 2015	418.88 km^2 (96.05), n=19	367.30 km^2 (92.59), n=21
Average NSD (SD) 2015	113.38 km^2 (59.24), n =19	93.92 km^2 (44.76), n=21

Maximum NSD averages for males and females were less in 2014 than in 2015, confirmed by field observations. This may be explained by both males and females in 2014 utilizing less of the total available spawning habitat compared to 2015.

Time away from refuge lake (Long Lake)

For migrants, time spent away from the refuge lake and number of out and back migrations was analyzed for males in females in 2014 and 2015 (Table A3.6). No difference was observed for migration duration between males and females in 2014 (pvalue=0.6553) and 2015 (pvalue = 0.6021). No difference was observed for number of out and back trips from the refuge and back between males and females in 2014 (pvalue = 0.5165) and 2015 (pvalue = 0.05186).

Table A3.2. Average total days of migrants spent away from refuge lake and average number of out and back trips from refuge lake.

Sex and Year	Average Days Away from Refuge Lake	Average Number of Out and Back Trips from Refuge Lake
Male 2014 (SD)	82 (23.62), n=3	1 (0), n=3
Female 2014 (SD)	68.83 (39.79), n=6	1.2 (0.37), n=6
Male 2015 (SD)	120 (39.16), n=19	2.2 (0.84), n=19
Female 2015 (SD)	128 (59.98), n=21	1.7 (0.83), n=21

Appendix 4: Reproductive site fidelity and BA analysis
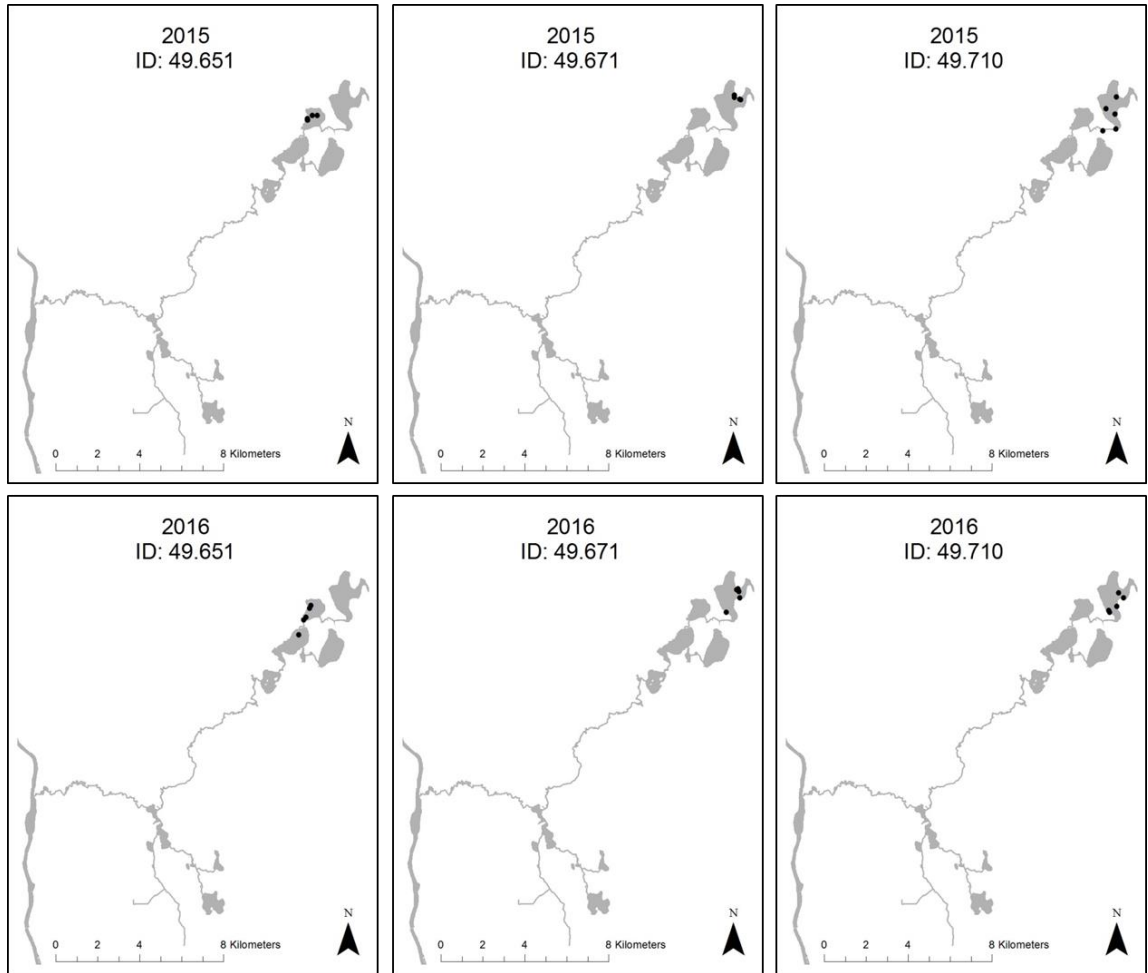
Figure A4.1. Carp maintained defined ranges during the reproductive period in 2015 using three individuals (49.651, 49.671, and 49.710) in Figure A3.2.
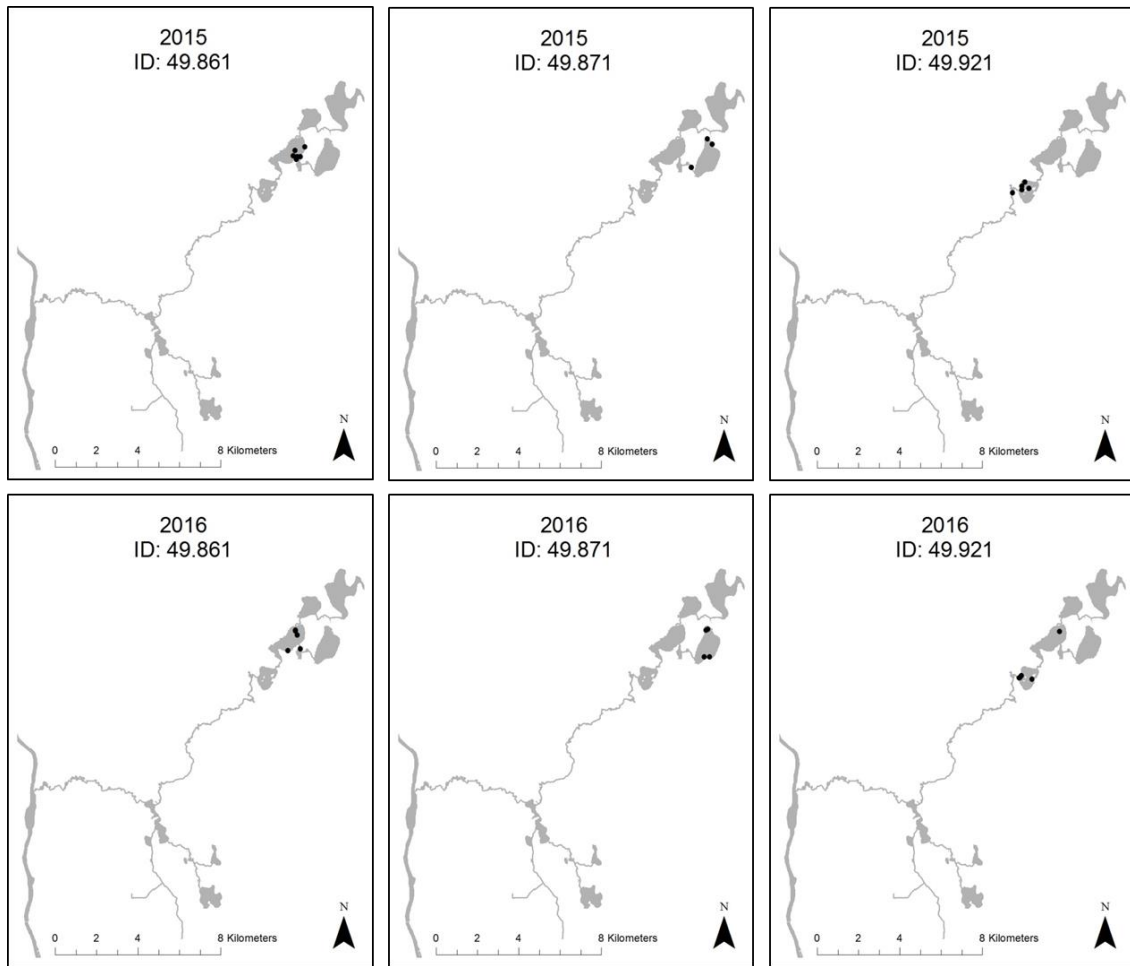
Figure A4.2. Carp maintained defined ranges during the reproductive period in 2015 (Table 6) using three individuals (49.861, 49.871 and 49.921) in Figure A3.2.
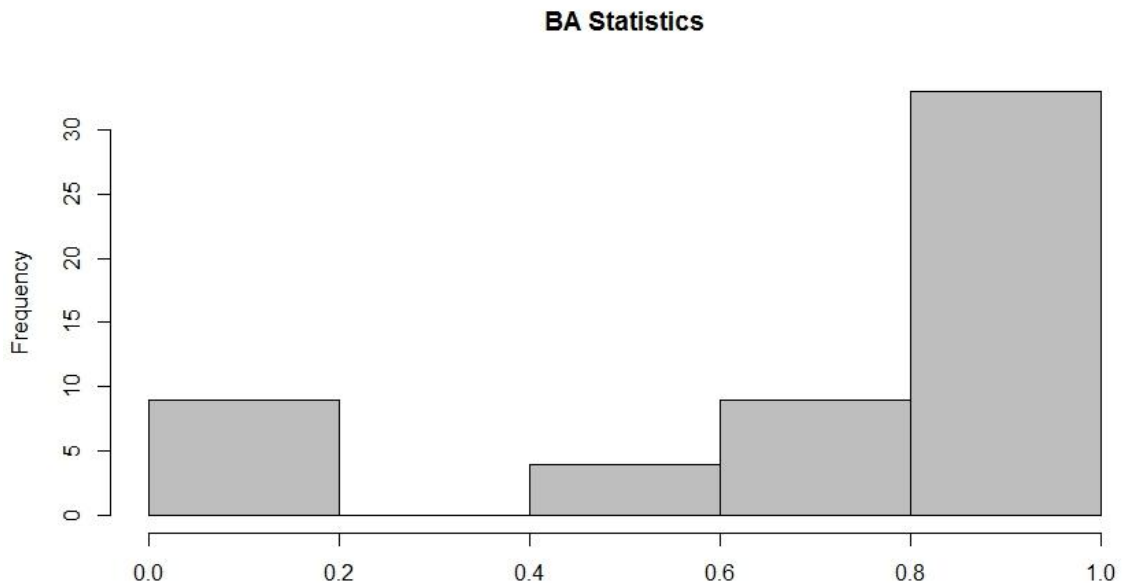
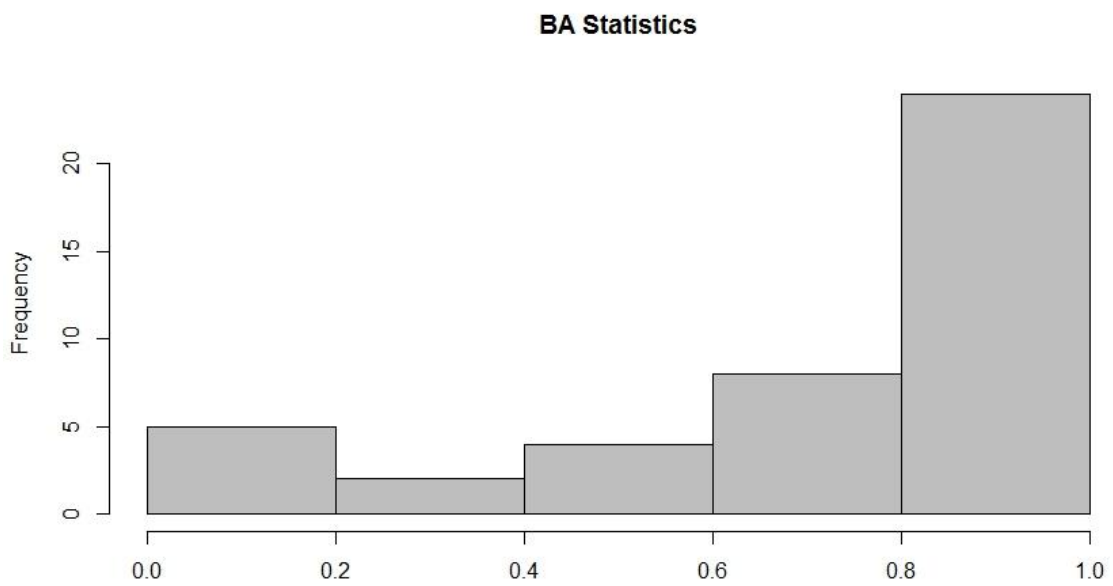Figure A4.3. BA statistics for all individuals and comparison between reproductive seasons of 2014, 2015, and 2016.

Figure A4.4. BA statistics averaging among all individuals for reproductive seasons in 2014, 2015, and 2016.
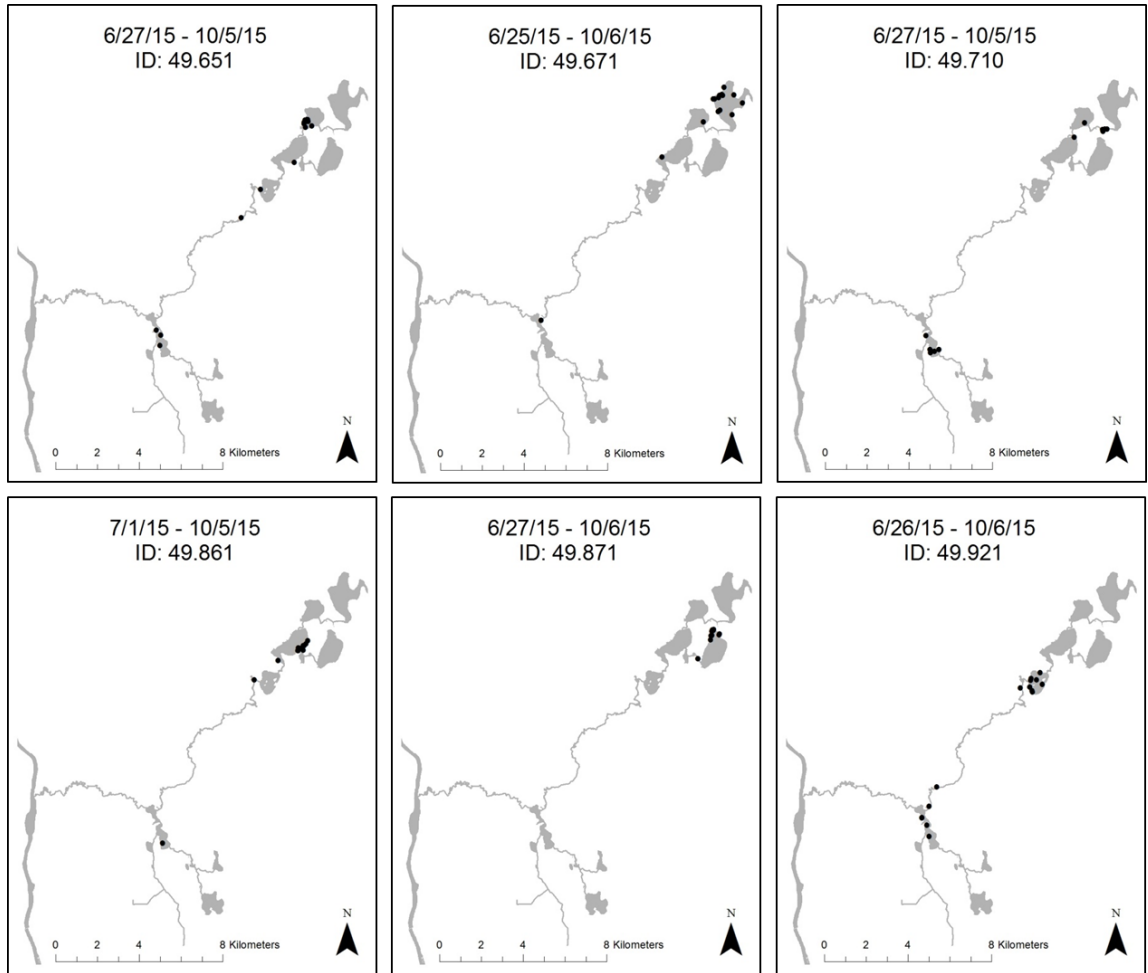
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Appendix 5: Summer home range of adult carp 2015

Figure A5.1. Locations of summer distribution in 2015 between June (after spawning) and October (before overwintering) for six representative individuals in Long Lake and the shallow upstream lakes.

Appendix 6: Winter distribution of adult carp and dissolved oxygen in Reshanau
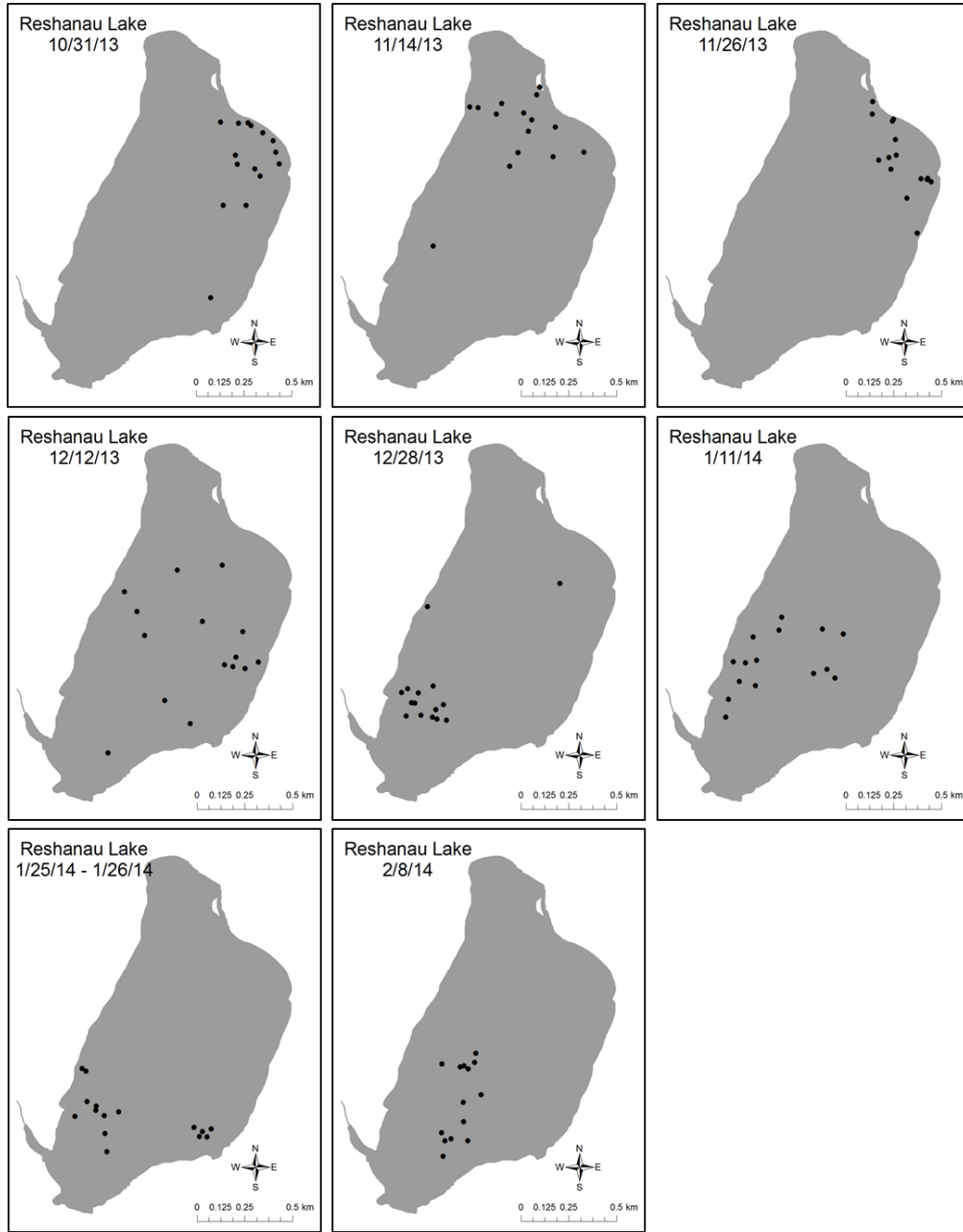
Lake

Figure A6.1. Distribution of individual adult carp (n=15) in Reshanau Lake from October 2013 – February 2014 with loose and tight aggregations shifting locations over winter. All tags were confirmed in mortality mode on February 8, 2014, an event likely correlated with low oxygen conditions.
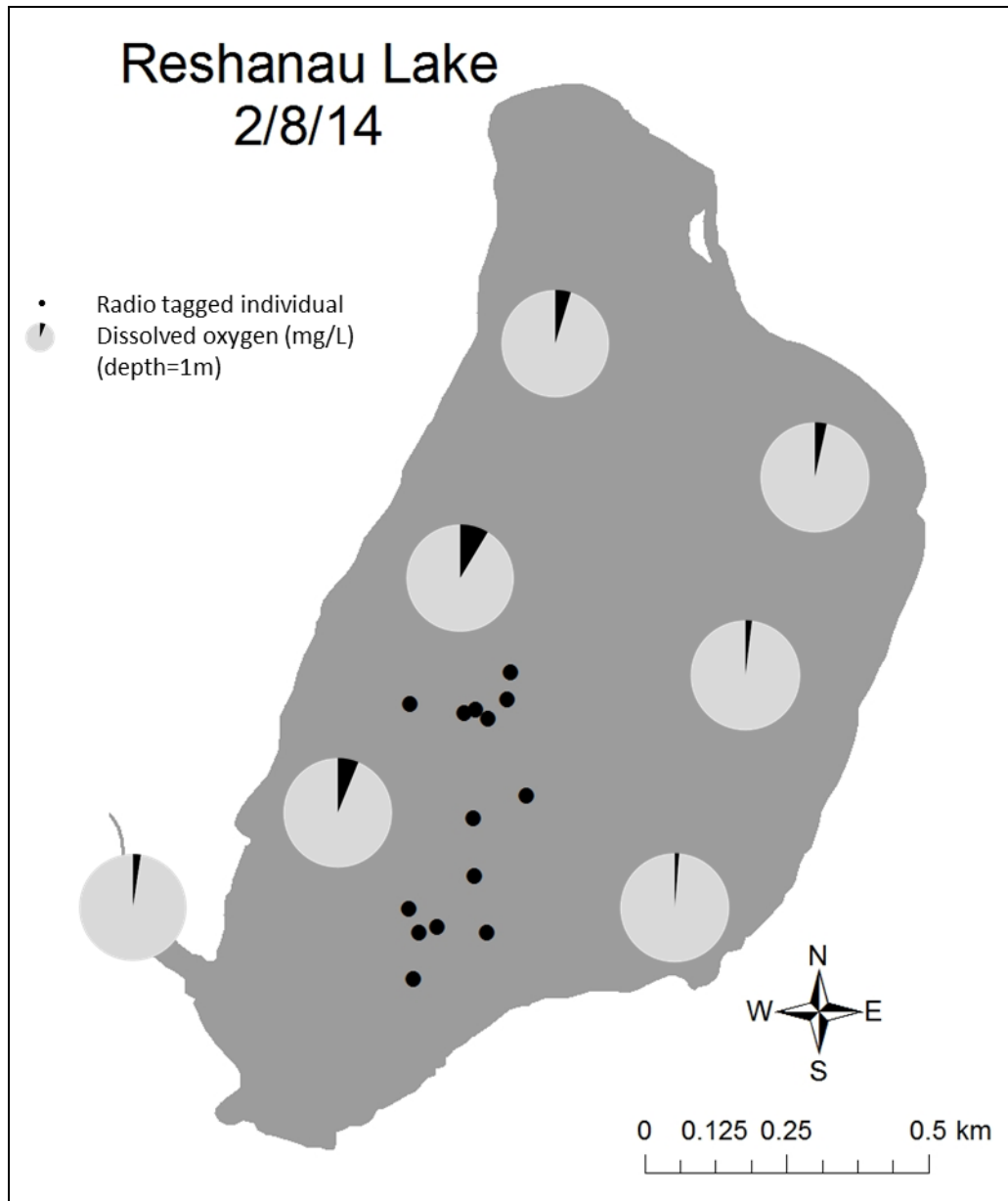
Figure A6.2. Distribution of 15 adult carp in Reshanau Lake when all 15 individual tags were first confirmed in mortality mode during February 2014. Dissolved oxygen (mg/L) is shown in black shading in the pie charts at seven locations throughout the lake and displays concentrations at 1m below the ice surface.