# THE IMPORTANCE OF DENSITY-DEPENDENT MECHANISMS IN DETERMINING COHORT SURVIVAL IN LARGEMOUTH BASS

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois, at Urbana-Champaign 2011

Urbana, Illinois

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**Abstract:**

Understanding factors important to recruitment in fishes has proven to be a difficult and challenging problem. Largemouth bass *Micropterus salmoides*, a popular recreational sport fish, is an excellent model species to explore mechanisms of recruitment, because both density-dependent and independent processes have been identified as important in regulating populations. Timing of hatching can influence growth and survival of largemouth bass. Individuals hatched relatively early have a period of growth prior to the swim-up of later-hatched cohorts allowing them to switch to piscivory at an earlier date due to release of gape limitations. Otolith and microsatellite data suggest that earlier hatched fish contribute the most to the final population of age-1 bass recruits. Reduced recruitment of the smaller, later cohorts is currently believed to be a density-independent process; however, individual based models have suggested that density-dependent processes may also contribute. Asymmetrical competition can also explain this phenomenon if early cohorts exploit prey resources prior to later cohort swim-up or through interference competition. In a manipulative pond experiment, I reduced the early cohort in 4 of the 8 ponds. Pond in which the early cohort was reduced had greater growth rates in later cohorts and an overall increase in recruitment to the end of the summer, higher *Ephemeroptera* densities, and largemouth bass consumed more energetic diets. Through this experiment, I was able to determine that early cohorts reduce survival of later cohorts through asymmetrical exploitative competition. Although this study is the first to confirm that early arriving individuals have a competitive advantage in largemouth bass, the phenomenon, priority effects, has been observed in many other kinds of organisms. Unlike previous studies, I was able to document asymmetrical exploitative competition as the primary mechanism of survival. Because evolutionary processes favor early spawning and nest angling targets the larger, early spawning

males, further research is needed to identify how increased contribution of later cohorts affects the long-term population dynamics of largemouth bass.

**Acknowledgements:**

I would like to thank Dr. David H. Wahl for serving as my advisor and for his guidance and assistance throughout my research project. I would also like to thank Drs. David Philipp and Corey Suski for serving on my graduate committee and continuously challenging me to increase the quality and scope of my research. Additional thanks are also due to my fellow graduate students, technicians, and undergraduate students that devoted their time to helping me complete my research project.

**Table of Contents:**

**Chapter 1: Introduction**

Understanding the factors important to recruitment in fishes has proven to be a difficult and challenging problem. Generally, recruitment is driven by the rate of growth and mortality in the early life history stages, with the survivors at the end of the first summer representing cohort strength (Hjort 1914, Houde 2008). Because understanding the variation of abundance in fish stocks is necessary to regulate populations, recruitment dynamics have been studied for over a century. In spite of these efforts, much is still unknown about the primary factors influencing variation in fish recruitment (Hart and Reynolds 2002).

Research in recruitment began with the development of several general theoretical models. The first major recruitment hypothesis was the Critical Period Hypothesis, that suggests the period after yolk absorption is associated with high levels of mortality if fry cannot find suitable amounts of planktonic prey (Hjort 1914). Support for this hypothesis is generally lacking (May 1974, Leggett and Deblois 1994, Cowan et al. 2000). The Match-Mismatch hypothesis, or that the timing and/or location of swim-up fry in relation to prey abundance is crucial to recruitment, was an extension of the Critical Period Hypothesis (Cushing 1974, 1990). Although it has had more success (Ellertsten et al. 1989), Cushing's hypothesis is generally restricted to marine fish where larval stages are greater sources of mortality than for freshwater fish (Houde 1994). Ricker (1954) predicted that there was a relationship between fish stock and recruitment, wherein recruitment initially increases with stock abundance, but eventually decreases due to density-dependent processes. Similarly, Beverton and Holt (1957) predicted that competition for a limited resource would initially increase recruitment with increasing stock until the carrying-capacity is reached, after which an asymptotic relationship would be reached. Data supporting negative density-dependence in stock-relationships is rare, oftentimes only over

a short period of time, and most relevant in depleted stocks (Myers 2001, Myers and Barrowman 1996).   A positive relationship between stock and recruits has been found for multiple species (Myers and Barrowman 1996).

The lack of generality of recruitment theories initiated the need for a multidisciplinary approach (Kendall and Duker 1998, Houde 2008).  A number of processes can influence size, growth, and life-stage retention, which then establish year class strength.  Temperature has a strong influence on the reproductive behavior of adults, and later the metabolism and growth of larval fish (Blaxter 1992).  Other physical processes, such as currents and wind, can also influence dispersal of larvae into good or bad nursery habitats (Hjort 1914, Hinckley et al. 2001). Sufficient amounts of prey contribute to better growth and survival of fish larvae (Rilling and Houde 1999, Zenitani et al. 2007).  Because many piscivores are gape-limited, the bigger and faster a larval fish can grow, the more protection from predators it can receive.  Low prey levels may also lead to longer times in a vulnerable size class and poorer swimming ability, thus exacerbating mortality rates due to predation (Laurence 1972, Jonas and Wahl 1998).  Instead of just one process controlling recruitment, the integration of all processes is needed to understand recruitment dynamics (Ludsin and DeVries 1997, Parkos and Wahl 2002).  Small variation in any process may lead to wide fluctuations in year class strength.

Largemouth bass *Micropterus salmoides*, a popular recreational sport fish, is an excellent model species to explore mechanisms of recruitment.  Processes that have been identified as important for largemouth bass recruitment are both density-dependent such as predation and competition (Dong and DeAngelis 1998, Keast and Eadie 1985), and density-independent, such as water level fluctuations and climate (Clark et al. 2008, Shuter et al. 1980).  The first summer of life has a progression of early-life stages that are associated with different sources of

mortality; failure at any stage can lead to a poor year class. Determining the drivers behind recruitment have been difficult, in part, because factors commonly used to predict recruitment, such as temperature and prey abundances, can vary both within and among lakes and across years (Parkos and Wahl 2002).

When temperatures get to approximately 15˚C, adult male largemouth bass build solitary saucer-shaped depressions in the substrate, and then court females to lay eggs into their nests (Kramer and Smith 1962). After fertilization, parental males provide sole care for their brood for up to 5 weeks (Ridgway 1988). Males fan the eggs to keep them oxygenated and silt-free and aggressively guard the nest from predation until fry are independent (Heidinger 1975, Philipp et al 1997). As the brood develops and the male puts more energy into protecting the nest, the parental male exhibits increasingly more aggressive acts in brood defense (Ridgway 1988). Larger males typically have a larger number of eggs in their nest, which is also positively correlated with aggressive behaviour (Suski and Philipp 2004). The increased brood defense reflects the increasing value of the nest relative to future reproduction, because the likelihood of brood survival increases towards the end of parental care (Andersson et al. 1980). If the male is removed during parental care and the nest size is significantly reduced, the nest will likely fail due to nest predation (Philipp et al. 1997, Suski et al. 2003, Steinhart et al. 2005).

Because the presence of parental care strongly influences survival of young, variation in the extent of parental care can have a strong influence on the contribution of young in the year class. Larger, older males tend to spawn earlier in the year than smaller, younger males and provide parental care for a longer duration of time (Ridway et al. 1991). Variation in the duration of parental care can be partially attributed to the development time required for eggs in colder temperatures (Ridway 1992). Because reproduction and parental care is energetically

3

costly, with males drawing on overwinter fat and protein reserves, large males have an energetic advantage over small males (Cargnelli and Gross 1997, Ridway et al. 1991). Small males with low overwinter reserves may postpone spawning until the cost of parental care is sufficiently low or spring food sources provide enough energy (Perrins 1970, Schultz et al. 1991). The increased energetic input from larger males is further emphasized in the context of parental care theory: individuals with less future reproductive opportunities will spend more energy on current reproductive efforts, whereas individuals with high future reproductive opportunities will delay or spend less energy on current reproductive efforts (Williams 1966). Because larger male largemouth bass spawn earlier and provide more parental care than smaller males, the progeny of early spawners contribute more towards fall recruitment than later spawners (Parkos 2008).

During the embryonic stage, both abiotic and biotic variables are influential in determining largemouth bass recruitment. Water temperature affects hatch, survival, and development (Kramer and Smith 1962, Miller and Kramer 1971, von Geldern and Mitchell 1975, Miller and Stork 1984, Ludsin and Devries 1997, Post et al. 1998). Fluctuations in temperature can cause multi-modal nesting distribution due to egg mortality or nest abandonment. High mortality occurs below 10˚ and above ~30˚ (Badenhuizen 1969, Kelley 1968, McCormick and Wegner 1981) and abandonment of nests by parental males has been observed when water temperatures drop less than 16˚C (Summerfelt 1975, Kohler et al. 1992). Large water level fluctuations (0.23-0.32m) are also linked to high embryonic mortality (Raibley et al. 1997 Mitchell 1982, Kohler et al. 1993, Garvey et al. 2000). Weather patterns are also influential in the nesting success of largemouth bass. Storms, characterized by strong winds and heavy rain, can affect largemouth bass nests by causing a drop in water temperature and wave turbulence. Strong winds can physically cause turbulence in spawning habitat and displace eggs, which then

become susceptible to predation and siltation (Steinhart et al. 1995, Kramer and Smith 1962), while heavy rain can cause changes in water level (Garvey et al 2000, Miller and Kramer 1971). Poor nest substrate may facilitate embryonic mortality (Kramer and Smith 1962, Miller and Kramer 1971). Nest predators also decrease survival, especially when the parental male is not guarding the nest (Eckbald and Shealy 1972, Philipp et al. 1997, Kramer and Smith 1962).

Larval fish are susceptible to many of the same variables as in the embryonic stage. Temperatures greater than ~32°C in laboratory conditions have been observed to significantly increase larval mortality, but not in the field (McCormick and Wegner 1981, Storms et al. 1986, Summerfelt and Shirley 1978). Temperatures also influence larval growth rates, with cooler waters slowing growth (Allan and Romero 1975). When prey resources are rare, larval fish may experience high levels of mortality due to either starvation or predation from starvation-induced decreases in swimming ability (May 1974, Laurence 1972, Jonas and Wahl 1998). Predation upon larval fish may not be a significant source of mortality for largemouth bass, partly because parental care is present prior to the time larval fish learn predator avoidance (Brown 1985).

Perhaps the most studied early-life stage, juvenile largemouth bass are limited by habitat availability, predation, and prey abundance. Fluctuating water levels can influence the abundance and growth of largemouth bass (Miranda et al. 1984, Raibley et al. 1997, Sammons et al. 1999), partly caused by changes in available habitat (Aggus and Elliot 1975, Irwin et al. 1997). As young-of-year largemouth bass grow, they undergo ontogenetic niche shifts, eating increasingly higher energetic prey, specifically preying first upon zooplankton, then benthic invertebrates, and finally on larval fish, which has strong consequences for growth (Mittelbach and Persson 1998, Olson 1996, Post 1997). Unlike earlier stages, water temperature is not a strong source of mortality for juvenile largemouth bass, but may delay the switch to piscivory

and reduce prey resources overwinter (Jackson and Noble 2000, Summerfelt and Shirley 1978, Olson 1996, Adams et al. 1982).  For juvenile largemouth bass, the onset of piscivory greatly improves individual condition and growth (Aggus and Elliot 1975, Ludsin and DeVries 1997, Mittelbach and Persson 1998) and is influenced by prey abundance and bass size (Olson 1996, Pasch 1975, Keast and Eadie 1985).  Young-of-year largemouth bass may not survive to the spring due to starvation (Sullivan 1986, Oliver et al. 1979) or predation (Miranda and Hubbard 1994, Garvey et al. 1998), which has been observed to be size-selective (Toneys and Coble 1979, Gutreuter and Anderson 1985, Ludsin and DeVries 1997, Post et al. 1998).  Because largemouth bass forage and grow during the winter independent of size in mid-latitudes (Fullerton et al. 2000, Garvey et al. 2004, Ostrand et al. 2005), predation appears to have more of an effect on mortality than lipid accumulation.  Predation is especially important in small impoundments where cannibalism is more common (Cooper 1935, Post et al. 1998, Pine et al. 2000).

Timing of hatching can also influences growth and survival of largemouth bass through density-dependent and density-independent processes.  Individuals hatched relatively early have a period of growth prior to the swim-up of later-hatched cohorts.  This initial size advantage allows early cohorts to switch to piscivory at an earlier date than later cohorts due to gape size limitations, because body size is correlated with gape size (Goodgame and Miranda 1993, Post 2003, Phillips et al. 1995, Johnson and Post 1996).  Longer access to piscine prey throughout the summer may allow early cohorts to accumulate a greater amount of lipids and subsequently enhance their survival through winter because of greater energy reserves (Ludsin and DeVries 1997, Miranda and Hubbard 1994 (length dependent winter survival).  The early-hatched cohorts also have a longer growing season than later-hatched cohorts, which facilitates greater sizes at the end of the summer, also increasing overwinter survival from reduced predation potential

(Ludsin and DeVries 1997, Garvey et al. 1998, Miranda and Pugh 1979).  The superior growth and survival of early-hatched cohorts, based otolith and microsatellite data, suggest that bass hatched relatively earlier contribute the most to the final population of age-1 bass recruits (Miller and Stork 1984, Goodgame and Miranda 1993, Parkos 2008).  These studies suggest that the survival bias is density-independent, because the advantages of hatching earlier do not differ with changes in population size.

The decreased recruitment of the smaller, later cohorts in largemouth bass is currently believed to be a density-independent process through differences in growing season and gape-limited access to fish prey.  Individual-based modeling, however, has suggested that density-dependent processes may also contribute to this pattern (Trebitz 1991).  A density-dependent process is one that is influenced by the variation in population size.  An individual-based model based bioenergetics model has been used to examine the influence of spawning date and density-dependent prey intake on young-of-year largemouth bass survival (Trebitz 1991).  An intermediate spacing between the early and later-hatch cohort resulted in the early cohort to become sufficiently larger than the later cohort, allowing the early cohort to exploit the prey resources before the later cohort had access to them.  A larger spacing between cohorts allowed the prey resources to recover prior to when the later cohort was capable of exploitation. Exploitation of prey resources should favor smaller individuals because they can tolerate lower resource levels (Persson 1998); however, larger gapes allow larger individuals to exploit resources unavailable to smaller individuals.  Because gape-limitation is temporally exclusive, early cohorts can exploit smaller prey resources, grow, and then have access to larger, unexploited prey, leaving less appropriately-sized prey for later cohorts.  The ability of large individuals to negatively affect small individuals but small individuals not having an effect on

large individuals is a form of asymmetrical competition, or an unequal sharing of resources among individuals. Asymmetrical competition has also been suggested as a cause of bimodal size distributions in largemouth bass (Huston and DeAngelis 1987), especially in smaller systems where cannibalism is present (Cooper 1936, Garvey et al. 1998). Prolonged asymmetrical competition can eventually remove the lower mode (DeAngelis et al. 1979, Ford 1975). Exploitative competition, or indirect competition among individuals via limited prey resources, may cause asymmetrical competition if the difference in gape-limitation between the two cohorts is substantial enough to cause a niche difference (Wilson 1975). Because larger fish can utilize food sizes unavailable to smaller fish, larger fish have a competitive advantage. If prey sizes available to smaller fish are exploited, smaller fish will be subject to starvation, decreased growth, and therefore increased predation. The competitive advantage of larger individuals will only occur if the minimum resource requirement needed for metabolism is relatively unrelated to body size (Persson et al. 1998), or if the minimum food required for metabolic processes does not exceed the advantage of increased prey availability. Interference competition, or direct competition among individuals via aggression, may also be the underlying mechanism of asymmetrical competition regulating survival in largemouth bass, because it predicts that larger individuals have the competing advantage (Case and Gilpin 1974, Persson 1985). Interference competition from the early cohort can decrease the survival of the later cohort if the early, larger cohort causes shifts into suboptimal habitat, restricting the availability of prey and/or increasing predation risk for the later cohort, or, in its most extreme form, cannibalizes the later cohort. The strength of density-dependent processes in determining largemouth bass recruitment is poorly understood, especially how it relates to differential

survival among cohorts.  The objective of this study is to test the influence of symmetrical and

asymmetrical competition on age-0 largemouth bass abundance at the end of the summer.

**Chapter 2: Research Justification**

Angling has been studied intensely to determine its effects on nest success of largemouth bass.  If a parental male is angled off a nest, his eggs are vulnerable to predation (Philipp et al. 1997, Neves 1975).  If the reproductive benefit of continuing parental care on a depleted nest is less than the perceived benefit of delaying reproduction until the following year, the male will abandon the nest (Williams 1966).  The decision to abandon a nest will depend on multiple variables, such as the amount of time the male was removed from the nest, the size of the remaining nest, and stage of development in young (Hanson et al. 2007, Philipp et al. 1997, Siepker et al. 2009, Suski et al. 2003).  Abandonment rates can be exaggerated with tournament angling as opposed to catch-and-release angling, because guarding males are removed from their nests for several hours (Hanson 2007, Siepker et al. 2009).  If parental bass are angled prior to spawning, produced young will be smaller and weigh less than young of non-angled parents (Ostrand et al. 2004).   Because it is unknown to what extent angling can effect lake-wide recruitment (Siepker et al. 2007), states (N=35) allow fishing during the spawning season (Quinn 2002).  Other states have a range of regulations, from minor restrictions, such as catch-and-release angling and reduced daily creel limits, to major restrictions, such as closed-harvest in the fall/winter or spring and spawning sanctuaries (Suski et al. 2002, Quinn 2002).  Public dissonance and noncompliance with restrictions demands further study into the effect of angling on largemouth bass populations, especially for states that are considering stricter regulations.  Opening angling during the spawning season may also have a greater impact on early spawners.  Early spawners tend to be older, larger individuals with higher levels of aggressiveness than late spawners and therefore an increased risk of angling (Ridgway et al. 1992, Wiegmann and Baylis 1995, Suski and Philipp 2004).  Because of the greater contribution of early-hatched largemouth

bass to recruitment, angling early spawners may have a greater effect on recruitment than

angling later spawners.  My study will help determine how angling early-spawners will influence

recruitment in populations of largemouth bass, a subject that is highly relevant to the

implementation of restricted fishing during the spawning season (Michigan, SALBRC report

2004).  The reduction of fishing access to protect recruitment is controversial for anglers,

especially tournament anglers who provide a substantial amount of economic activity (American

Sportfishing Association 2008), and more research is needed before public opinion will support

any stricter changes in regulations, such as restricted angling seasons or sanctuaries.

**Chapter 3: Priority Effects in an Aquatic Piscivore**

**Abstract**

Priority effects, or the effects of an early arriving individual on later individuals, have been documented in studies of both intra- and interspecific competition. Protracted breeding and bias in survival for the early cohort provides potential that priority effects regulate recruitment success in an aquatic top predator, *Micropterus salmoides*. In 0.4ha experimental ponds, I established 8 populations of *Micropterus salmoides* and removed the first three successful nests, or nests that produced swim-up fry, in 4 of 8 ponds. Removing the early cohort resulted in the later cohort experiencing higher ambient prey densities, higher quality of diet, as well as increased growth and survival. Approximately 5 times as many individuals survived to the end of year compared to unmanipulated ponds. Densities of *Ephemeroptera*, an important prey species for *Micropterus salmoides*, were significantly decreased in the presence of the early cohort. Higher ambient prey densities resulted in all individuals having greater numbers of invertebrates in the diets, regardless of cohort. Higher diet quality resulted in faster growth rates to be greater in individuals from the manipulated ponds, especially in the later cohort. Priority effects via resource preemption by early cohorts negatively affected later cohorts. Priority effects and complex density-dependent dynamics regulate mortality in cohorts in young-of-year *Micropterus salmoides*, strongly effecting recruitment.

**Introduction:**

In stochastic environments, the winners of competitive interactions often depend on the timing of arrival, breeding, or activity of individuals (Lawler and Morin 1993). Such interactions, dubbed priority effects, show that early arriving individuals often have a strong, negative effect on later arriving individuals (Dean and Hurd 1980, Shulman et al. 1983). Studies have shown that later arriving individuals experience lower growth (Wilbur and Alford 1985),

decreased survival (Dayton and Fitzgerald 2005), longer times to maturation (Jones 1987), and longer larval periods (Lawler and Morin 1993). Priority effects have been documented across many taxa, such as anurans (Alford and Wilbur 1985), fish (Geange and Stier 2009), salamanders (Boone 2002), and insects (Blaustein and Margalit 1996), and have been shown to strongly influence community dynamics. The strength of priority effects can depend on both the sequence and timing of individuals through resource preemption, or the driving down of resources before late arriving individuals arrive, and/or varying durations of temporal overlap of early and late arriving individuals (Lawler and Morin 1993, Geange and Stier 2009).

Studies on priority effects have defined many interspecific interactions; however, few studies have demonstrated intraspecific priority effects (*but see* Crowley et al. 1987, Eitam et al. 2005). Species with protracted breeding and multivoltinism have the greatest potential for priority effects to regulate population dynamics. In studies of intracohort priority effects, interference competition and cannibalism has been found to strongly affect survival of later arriving individuals (Crowley et al. 1987, Anholt 1994). Evidence for priority effects through reduction in prey resources has been less supported and primarily identified through modeling efforts (Trebitz 1991, Griffiths 1993, Eitam et al. 2005). The difficulty in exploring mechanisms of intraspecific priority effects is segregating early and late arriving individuals (Eitam et al. 2005). In the current study, I used the extended spawning patterns of largemouth bass, *Micropterus salmoides*, a top predator fish, and daily ages using otolith rings to identify different cohorts and examine intraspecific priority effects.

In highly fecund species, such as fish, insects, and plants, recruits enter systems in large pulses. These large pulses may be strong enough to cause priority effects, even in relatively stable environments. In *Micropterus salmoides*, protracted spawning causes several large pulses

of young-of-year fish to enter a system.  Recent work has shown that early cohorts experience

greater survival than later cohorts of *Micropterus salmoides* (Parkos et al. 2011); however, it is

unclear if this is due to priority effects.  Timing of hatching has previously been shown to have

strong effects on growth of young-of-year *Micropterus salmoides* (Miller and Stork 1984, Parkos

et al. 2011).  Larger, more aggressive males and larger females with large ovaries spawn earlier

(Miranda and Muncy 1987, Ridgway et al. 1991, Wiegmann et al. 1992, Suski and Philipp

2004).  Early, larger parental males also guard the young for a longer period of time, which may

allow early cohorts to develop better predator avoidance capabilities (Brown 1984, Parkos et al.

2011).  Early cohorts have an initial size advantage that facilitates earlier ontogenetic niche shifts

than later cohorts (Goodgame and Miranda 1993, Phillips et al. 1995, Post 2003).   The early

cohorts also have a longer growing season than later cohorts, which facilitates greater sizes at the

end of the summer and increased overwinter survival from reduced predation potential (Miranda

and Pugh 1997, Ludsin and DeVries 1997, Garvey et al. 1998).  Although greater growth and

survival of early cohorts can be explained by density-independent interactions, Trebitz (1991)

found in model simulations that resource preemption influenced survival of later cohorts.

Because *Micropterus salmoides* produces large pulses of recruits, the potential exists for priority

effects to drive recruitment success.

   I postulated that differences in growth and survival between early and later cohorts of

*Micropterus salmoides* are caused by priority effects.  Using experimental manipulations, I tested

whether the presence of an early cohort of *Micropterus salmoides* negatively affected growth and

survival of a later cohort.  I predicted that 1) if priority effects were present, the removal of an

early cohort would increase growth and survival of the later cohort of *Micropterus salmoides*,

and 2) if resource preemption causes priority effects, removal of an early cohort would increase

prey availability and influence ontogenetic niche shifts of the later cohort.

**Methods:**

*Study Organism:*

When temperatures get to approximately 15˚C, adult male *Micropterus salmoides* build

solitary saucer-shaped depressions in the substrate, and then court females to lay eggs into their

nests (Kramer and Smith 1962) and spawning distributions may be up to 160 days (Rogers and

Allen 2009). After fertilization, parental males provide sole care for their brood for up to 5

weeks (Ridgway 1988). As young-of-year grow, they undergo ontogenetic niche shifts, eating

increasingly higher energetic prey, specifically preying first upon zooplankton, then benthic

invertebrates, and finally on larval fish, which has strong consequences for growth (Mittelbach

and Persson 1998, Olson 1996, Post 2003).

*Experimental Design:*

Timing of hatching and recruitment to fall was measured in eight experimentally

established populations of wild-caught *Micropterus salmoides*. Each population contained 22

adult largemouth bass (10 males and 12 females), originating from two wild populations in

Illinois (Lake Shelbyville and Forbes Lake) and introduced into eight 0.40-ha ponds at the Sam

Parr Biological Station, Marion County, IL. *Micropterus salmoides* were distributed among

ponds so sizes of adults did not differ among ponds (One-way ANOVA test: males: $F_{7,72} = 0.31$,

$P = 0.94$; females: $F_{7,88} = 0.06$, $P = 0.99$). The ponds also contained juvenile bluegills (3540-

3663/ha) and adult bluegills (75/ha) to provide brood predators and competitors of largemouth

bass (Eipper 1975, Olson et al. 1995). To assess potential sources of variation among ponds,

physical and chemical variables were measured biweekly throughout the summer. Oxygen and

temperature were measured at the surface and at one meter.  To measure chlorophyll-a and phosphorus concentrations, water samples were taken with an integrated tube sampler at 1m depth.  Chlorophyll a was obtained by filtering 100 ml of water onto glass fiber filters (Whatman GF/F), extracting chlorophyll in 90% acetone for 24 h, and then measuring fluorescence (Turner Design, flurometer, model TD700, (Wetzel & Likens 1991).  Total phosphorus concentrations were measured with colorimetric molybdenum blue ascorbic acid method with a persulfate digestion (Wetzel & Likens 1991).  Percent surface area cover of macrophyte densities was estimated in August using 10 transects across each pond.

Daily snorkel surveys were conducted to monitor reproductive activity in each pond during the spring spawning season.  As each new nest was found, the date of initiation was recorded, and external tags were used to identify the nesting site.  Mating success was measured by ranking the size of the nest from one to five based on density and numbers of eggs (Kubacki 1992).  Egg scores were used to estimate fry production in each pond eggs (Kubacki 1992).  Since Parkos et al. (2011) found that the majority of recruits were spawned in the first few days of spawning, the first three nests that produced fry were deemed members of the early cohort and were removed manually in four random ponds.  Removal of young was conducted at the latest stage of nesting so that only young-of-year that would have contributed to recruitment were removed.  Because parental care is energetically costly (Cargnelli and Gross 1997, Ridway et al. 1991), waiting to remove the young until the male is near termination of parental care also discouraged renesting.  Nests in the remaining ponds were left unmanipulated.

*Growth and Survival:*

At least 20 individuals from each pond were collected at monthly intervals through shoreline seining.  Total lengths of all young-of-year were measured to the nearest millimeter

and daily otolith rings were used to determine timing of spawning (Miller and Stork 1982).

Individuals were divided into early and late spawning cohorts for further analysis. Percent of

individuals from early and later cohorts were determined in June and July to assess relative

contribution. Daily growth rates were calculated by dividing the total length of an individual by

the age in days. At the end of summer, each pond was individually drained and the total number

and lengths of surviving juveniles were enumerated. Because errors in reading daily otolith rings

increase with age of young-of-year largemouth bass (Miller and Stork 1982), analysis of cohort

contribution could not be completed at the end of the summer.

*Prey Resources:*

To determine the importance of prey resources, zooplankton and benthic invertebrates

were sampled. Zooplankton were collected at two sites within each pond with a 0.5-m diameter,

64-µm mesh zooplankton net pulled vertically from a depth of 1-m to the surface and preserved

in 4% Lugol's solution (Hoxmeier et al. 2006). Samples were taken monthly, sufficient to test

for changes in zooplankton abundance (Yan 1986, Marmorek and Korman 1993). All

zooplankton were identified to suborder or family and enumerated in subsamples until at least

200 organisms from the two most common taxa were counted (Welker et al. 1994). Benthic

invertebrates were collected at two sites with a modified stove pipe sampler deployed biweekly

to assess relative abundance through time (Cowell and Vodopich 1981, Angermeier 1982) The

benthos was sieved through a 250-µm sieve bucket and preserved in ethanol and Rose Bengal

(McPeek 1990). Benthic invertebrates were identified to order and enumerated. Average length

of each order of invertebrates was determined by measuring total body length (nearest 0.01 mm;

excluding spines, helmets, and caudal rami) of 10 individuals from each sample. A dissecting

microscope (25x magnification) equipped with a drawing tube and electromagnetic digitizing

tablet was used for measurements. Comparisons of densities and average sizes of prey were made between unmanipulated and manipulated ponds.

A sample of at least 20 individual largemouth bass from each pond collected monthly was used to examine the effect of the early cohort on diet of the later cohort. A sample size of 20 was chosen to provide an adequate quantification of diets without significantly affecting survival estimates (Post 1997, 2003). Each prey item was identified to order and enumerated. Average length of each order of invertebrate in the diet was determined by measuring total length to the nearest 0.01mm using a dissecting microscope, a drawing tube, and digitizing tablet. Growth rates were also estimated for early and later cohorts by dividing individual total length by age in days. Comparisons of diet and growth were compared between manipulated and unmanipulated ponds and between early and later cohorts of young-of-year largemouth bass.

*Statistical Analyses:*

Differences in growth and diet analyzed with a Split-Plot ANOVA using the model:

$$y = \mu + T_i + e_1 + C_j + TC_{ij} + e_2$$

wherein $T_i$ = the treatment manipulation and $C_j$ = cohort identity. Percent contribution of early and later cohorts in June and July was analyzed using a One-Way ANOVA (Warton and Hui 2011). Repeated-measures ANOVA with sub-sampling was used to test for the effect of the early cohort on densities of zooplankton and benthic invertebrate throughout the summer. Pearson's correlation was computed to test for correlation between fry production and recruitment success. Differences in physical, chemical, and biological variables between treatments was tested using a One-Way ANOVA. Variables with high Coefficients of Variation were used as covariates in subsequent analyses. Differences in abundance of young-of-year largemouth bass to the end of summer was analyzed using a One-Way ANOVA. Response

variables were compared with Tukey's post-hoc tests when the F-values were statistically

significant.

**Results:**

*Survival:*

Adult largemouth bass were distributed among ponds so that no significant difference in

length was found between treatments for either males ($F_{1,6} = 0.03$, $P > 0.1$) or females ($F_{1,6} =$

0.15, $P > 0.1$). No difference also existed in the number of either age-1 or young-of-year bluegill

between treatments ($F_{1,6} = 0.02$, $P > 0.1$, $F_{1,6} = 1.80$, $P > 0.1$). No differences in physical,

chemical, and biological conditions of ponds were between treatments ($P > 0.05$, Table 3.1).

Coefficients of Variation were similar among variables; however, values of young-of-year

bluegill sunfish, total fry production, and chlorophyll-a concentrations were most variable and

were incorporated as covariates into the survival analysis.

Largemouth bass commenced spawning on April 9th and ceased spawning on May 25th;

however, the first successful nest was spawned on April 18th (Figure 3.1). Nests spawned prior

to April 18th were abandoned and unsuccessful nests spawned after April 18th were the subjects

of the treatment manipulation. Because there was a natural break in spawning, any *Micropterus*

*salmoides* hatched prior to April 28th were considered part of the early cohort and any

*Micropterus salmoides* hatched after April 28th were considered part of the later cohort (Figure

3.1). No initial difference existed between ponds and cohort identity in the number of nests

produced (Figure 3.2; $F_{1,6} = 0.76$, $P > 0.1$). After removing the first three nests that produced

swim-up fry, a significant difference existed between the number of successful nests in the early

cohort in the manipulated ponds compared to the number of nests in the early cohort in

unmanipulated ponds (Figure 3.2; $F_{1,6} = 3.83$, $P = 0.05$). No difference existed between

treatments in pond-wide fry production, but fry production had a moderate positive correlation

with recruitment to the end of the summer ($r(8)= 0.68$, $p = 0.06$).

*Growth and Survival:*

Contribution of different cohorts of young-of-year largemouth bass was assessed in mid-

and July by seining and at the end of the experiment by draining. Recruitment to June was

significantly affected by cohort identity and presence of the early cohort (Figure 3.3; $F_{1,6} =$

29.31, P = 0.001). Early cohorts contributed a greater proportion of recruits in ponds without the

treatment manipulation (44.3% to 9.1%). Recruitment to July was again significantly affected by

cohort identity and presence of the early cohort (Figure 3.3; $F_{1,6} = 32.66$, P = 0.002). Early

cohorts contributed to a greater proportion of recruits in ponds without the treatment

manipulation (20.5% to 3%). Covariate analyses of variation in abundance in young-of-year

largemouth bass at the end of the summer was not explained by macrophyte density ($F_{1,5} = 0.15$,

p > 0.1), age-0 bluegill sunfish ($F_{1,6} = 0.16$, p > 0.1), chlorophyll-a concentrations ($F_{1,5} = 0.11$, p

> 0.1), nor oxygen levels ($F_{1,6} = 0.05$, p > 0.1), but was explained by total fry production ($F_{1,5} =$

9.24, p =0.03). When total fry production was used as a covariate, the presence of the early

cohort had a significant effect on survival to the end of the summer ($F_{1,6} = 19.51$, P = 0.006) and

total biomass of recruits ($F_{1,6} = 9.43$, P = 0.02). Greater numbers of young-of-year largemouth

bass were recovered in manipulated than unmanipulated ponds (Figure 3.4). Back-calculated

hatching dates of largemouth bass collected at the end of the summer had reader errors greater

than 10% because of the high number of compressed rings (Miller and Stork 1982), so estimates

of contribution via otoliths were not possible. The final length-frequency histogram show the

majority of survivors in manipulated ponds were in the smallest size class, between 40mm and

50mm (Figure 3.5). Because length is correlated with age in largemouth bass (Johnson and Post

1996) and only 3% of recruits in July were from the early cohort, the majority of surviving

individuals were likely members of the later cohort.

The interaction between treatment manipulation and cohort identity moderately effected

growth of young-of-year largemouth bass in June and July.   In June, growth rates were

marginally higher ($F_{1,185} = 3.33$, $P = 0.07$) in the later cohort in manipulated ponds and lowest in

the later cohort in unmanipulated ponds (Figure 3.6).  Presence of the early cohort also

moderately effected growth in July recruits ( $F_{1,5} = 3.92$, $P = 0.1$).  Growth rates later in the

summer were greater in manipulated ponds (0.61mm/day) than in unmanipulated ponds

(0.50mm/day, Figure 3.6).  Although growth rates were only moderately different between

treatments, the majority of largemouth bass, regardless of treatment, were in the smallest size

classes at the end of the summer (Figure 3.5).

*Prey Resources:*

Strength of the early cohort did not significantly influence overall densities of

zooplankton ($F_{1,7} = 0.04$, $P > 0.1$; Figure 3.7a), but did moderately influence densities of benthic

invertebrates ($F_{1,6} = 4.54$, $P = 0.07$; Figure 3.7b).  Densities of the order *Ephemeroptera* were

also significantly affected by the treatment manipulation throughout the summer ($F_{1,6} = 6.17$, $P =$

0.04; Figure 3.7c).  Densities of benthic invertebrates and *Ephemeroptera* were greater in ponds

with the early cohort reduced throughout the summer.  No other order of prey species was

significantly affected by the treatment manipulation, nor were any differences in mean size of

prey found between treatments in June ($F_{1,6} = 2.53$, $P > 0.1$) or July ($F_{1,6} = 2.90$, $P > 0.1$).  No

significant interactions between treatment manipulation and cohort identity were observed in the

diets.  The early cohort significantly affected the number of benthic invertebrates ($F_{1,6} = 6.21$, P

$= 0.01$) and macrozooplankton ($F_{1,6} = 10.20$, $P = 0.01$)  found in the diet of June recruits (Table

21

3.2). Greater numbers of benthic invertebrates and macrozooplankton in the diet were observed in manipulated ponds compared to unmanipulated ponds. No effect on diet was observed for July recruits in either benthic invertebrates ($F_{1,5} = 0.35$, $P > 0.1$) or macrozooplankton ($F_{1,5} = 0,19$ $P > 0.1$) from the presence of the early cohort. The average size of invertebrates in the diets were similar among treatment manipulations in June ($F_{1,6} = 0.18$, $P > 0.1$) and July ($F_{1,4} = 1.14$, $P > 0.1$).

**Discussion:**

I examined how priority effects influence differences in growth and survival between the early and later cohorts of *Micropterus salmoides*. Previous research suggests that the later cohort would experience decreased growth and survival in the absence of the early cohort due to a shorter growing season and increased mortality attributed to increased size-selective predation (Johnson and Post 1996, Garvey et al. 1998). Priority effects via resource preemption could also explain outcomes if the early cohort exploits prey prior to feeding by the later cohort. I found that following removal of the early cohort, the later cohort experienced higher ambient prey densities, higher quality of diet, and increased growth that resulted in approximately 5 times as many individuals surviving to the end of year compared to unmanipulated ponds. Results of this study suggest resource preemption by early cohorts can negatively affect later cohorts.

Reducing the number of successful nests resulted in a lower proportion of early cohorts recruited to June and July, but an increase in the overall number of recruits to the end of the summer. Because previous studies have found no evidence of negative density-dependent interactions for survival in *Micropterus salmoides* (Gutreuter and Anderson 1985, Pope, *this study*) and that recruitment was dominated by individuals from the early cohort (Parkos et al. 2011), producing more recruits by removing the early cohort was unexpected; however, my

results are consistent with predictions from other studies of priority effects, or that survival of the later cohort was limited by the presence of the early cohort (Lawler and Morin 1993, Shorrocks and Bingley 1994, Boone et al. 2002, Geange and Stier 2009).  Previous studies similarly concluded that later-arriving individuals experienced decreased growth and survival than early-arriving individuals. However, most of these studies examined interspecific or interference competition rather than intraspecific and exploitative competition that I found to be important.

Total zooplankton was not influenced by the presence of the early cohort; however, benthic invertebrates and *Ephemeroptera*, an important prey item for young-of-year *Micropterus salmoides* (Keast and Eadie 1985, Olson 1996), showed decreased densities in ponds with the early cohort intact.  A strong early cohort was also associated with decreased number of macrozooplankton and benthic invertebrates in the diet and lower growth early in the summer. Young-of-year *Micropterus salmoides* undergo ontogeny from zooplankton to benthic invertebrates shortly after hatching and timing can depend on prey densities (Olson 1996, Galarowicz et al. 2006).  It appears that the early cohort altered the invertebrate community enough to decrease the ability of later cohorts of largemouth bass in unmanipulated ponds to successfully switch to and maintain an invertebrate diet.  Delayed ontogeny in later cohorts may explain the observed pattern of later cohorts generally experiencing equal or reduced growth rates in field populations of young-of-year largemouth bass (Maceina and Isely 1986, Goodgame and Miranda 1993, Phillips et al. 1995, Ludsin and DeVries 1997.  Removing the early cohort produced greater densities of high energy prey in the ponds resulting in compensatory growth. The release from competition from the early cohort increased growth and survival for the later cohort.

Although this study was able to find strong effects from the treatment manipulation, the small scale of the experimental ponds may limit predictive ability for larger systems. Because the experimental ponds are relatively small and lack a pelagic zone, I was unable to represent all ecosystem processes in natural systems. (Shindler 1998, Semlitsch & Boone 2009). Replicating the experiment in natural waterbodies will provide stronger evidence that priority effects influence survival in young-of-year largemouth bass. The study was also conducted in one field season. Previous work has highlighted the importance of large-scale climate and inter-annual variability in weather patterns for successful smallmouth bass reproduction (Suski and Ridgway 2007). Replicating the experiment over multiple years is needed to account for the influence of large-scale drivers in largemouth bass recruitment. Contact rates between predators and prey may have been elevated through coaggregation along the edges of the ponds (Kaiser 1983). These interactions may have strengthened the effect of size-selective predation on the later cohort. The current design does not allow refutation that the effects of removing the first three nests of the early cohort would not be the same as removing three random nests; however, Parkos, *unpublished data*, found a positive relationship between numbers of nests and recruitment under the similar experimental conditions. Based on these data, it is unlikely that removing three random nests would have resulted in a similar outcome. Previous research on largemouth bass recruitment has identified a multitude of factors that can influence survival including primary productivity, bluegill sunfish abundance, and reproductive success. Although this study attempted to account for these factors by measuring a suite of variables, the low sample size of the experiment did not allow for simultaneous testing of alternative hypotheses. Variables with high levels of variance were included as covariates when testing for differences in abundance of young-of-year largemouth bass; however, none significantly explained any

variation in abundance.  Increased replication will be needed in future studies to assess the

relative contribution of each alternative hypothesis in explaining abundance in young-of-year

largemouth bass.  Further research in field populations of largemouth bass is needed to

understand the strength of exploitive priority effects in natural populations.

Early spawning in *Micropterus salmoides* maximized individual growth and survival by

allowing young to exploit resources prior to them becoming limited in this study.  Abundant

resources coupled with an initial size advantage may explain the faster ontogenetic niche shifts

by early cohorts in the field (Post 2003, Galarowicz et al. 2006, Huss et al. 2008).  Late spawners

in this study were disadvantaged by the presence of the early cohort because the environment has

shifted to lower ambient densities of desirable prey, which caused a lower quality diet, reduced

growth rates, and even decreased survival.  The persistence of late spawning is likely caused by

the environmental risks of early spawning, such as reductions in temperatures.  If temperatures

drop below 15°C, abandonment is likely in *Micropterus salmoides* (Summerfelt 1975, Kohler et

al. 1992).  If temperatures fluctuate early in the spring, late spawners would provide the first

larvae to enter the system and would contribute a greater number of recruits to fall (Garvey et al.

2002, Santucci and Wahl 2003).  Higher recruitment to fall is generally correlated to greater

recruitment to age-1 largemouth bass (Fuhr et al. 2002, Parkos and Wahl 2010); however, a year

class comprised entirely of individuals from the later cohort may not follow this pattern as

individuals in the later cohort are generally the smallest individuals in fall.  Because overwinter

mortality is typically size-selective, the later cohort would be susceptible to higher overwinter

mortality and may produce a weak year class (Johnson and Post 1996, Ludsin and DeVries 1997,

Garvey et al. 2004).  Further studies should assess cohort growth and survival through the

following spring.

Priority effects have been previously demonstrated between intercohorts of anurans (Lawler and Morin 1993), salamanders (Boone et al. 2002), *Drosophila* (Shorrocks and Bingley 1994), and other fishes (Geange and Stier 2009). Few studies have examined variation in survival caused by intracohort competition (*but see* Anholt 1994, Chen et al. 2001, Geange and Stier 2009). Empirical evidence of intracohort priority effects via resource preemption is even rarer (*but see* Eitam et al. 2005). I found reductions in important prey resources similar to Eitam et al. 2005; however, exploitation by *Micropterus salmoides* was linked with reductions in quality of diet and daily growth rates. I was able to provide a mechanistic understanding of resource preemption in intracohort priority effects. These findings strengthen the evidence of resource preemption as a mechanism of priority effects (Trebitz 1991, Lawler and Morin 1993, Griffiths 1993, Eitam et al. 2005).

Identifying intracohort competition as a major contributor to mortality in young-of-year *Micropterus salmoides* contributes to the general understanding of recruitment in this species. Previous work on density-dependence via symmetrical competition revealed negative relationships between largemouth bass abundance and prey densities and/or growth rates (Post et al. 1997, Garvey et al. 2000, Gillooly et al. 2000). Although exploitation of resources affected growth rates (Post et al. 1997, Garvey et al. 2000, Gillooly et al. 2000), effects were not strong enough to influence survival (Allen et al. 2011). Incorporating temporal dimensions to examining density-dependent relationships revealed complex dynamics experienced by young-of-year *Micropterus salmoides* that suggest a comprehensive mechanistic approach will be needed to understand competition in other species.

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Table 3.1: Mean levels and Coefficients of Variation of abiotic and biotic variables in ponds with the early cohort present (unmanipulated) oe absent (manipulated) that show potential sources of among-pond variation in response variables. Asterisks denote significant differences between treatments. Data are presented as Mean (SE).

| Treatment Group | Unmanipulated | | Manipulated | | CV | p-value |
|---|---|---|---|---|---|---|
| **Largemouth Bass** | | | | | | |
| Adult Male Length (mm) | 315 | (6) | 313 | (5) | 18 | 0.79 |
| Adult Female Length (mm) | 306 | (1) | 303 | (1) | 13 | 0.13 |
| Age-0 Largemouth Bass Length (mm) | 65 | (4) | 51 | (3) | 16 | 0.03* |
| Age-0 Largemouth Bass Weight (g) | 7 | (1) | 5 | (0) | 23 | 0.00* |
| Total Number of Largemouth Bass Fry | 23221 | (7984) | 34171 | (13762) | 75 | 0.48 |
| Total Number of Largemouth Fry / Nest | 2127 | (608) | 3887 | (2137) | 101 | 0.16 |
| **Bluegill Sunfish** | | | | | | |
| Number of Age-0 Bluegill Sunfish | 5,394 | (2,502) | 1,921 | (665) | 105 | 0.23 |
| Number of Stocked Age-1 Bluegill Sunfish | 1440 | (14) | 1437 | (13) | 2 | 0.88 |
| **Physical Characteristics** | | | | | | |
| Phosphorus (mg/L) | 45 | (8) | 30 | (6) | 35 | 0.29 |
| Chlorophyll-a (µg/L) | 27 | (4) | 20 | (2) | 72 | 0.35 |
| Secchi Depth (m) | 1.4 | (0.1) | 1.4 | (0.1) | 31 | 0.77 |
| Surface $O_2$ (mg/L) | 11 | (0.4) | 11 | (0.3) | 19 | 0.73 |
| $O_2$ at 1m depth (mg/L) | 9 | (1) | 9 | (0) | 37 | 0.59 |
| Surface Temperature ($^0$C) | 25.6 | (0.8) | 25.4 | (0.7) | 17 | 0.92 |
| Temperature at 1m Depth ($^0$C) | 24.3 | (0.6) | 24.4 | (0.6) | 15 | 0.52 |
| Percent Macrophytes Cover | 68 | (15) | 81 | (4) | 30 | 0.42 |

Table 3.2: Mean Number of Items in the diet of age-0 largemouth bass in June and July from ponds with the early cohort present (un-manipulated) or absent (manipulated).

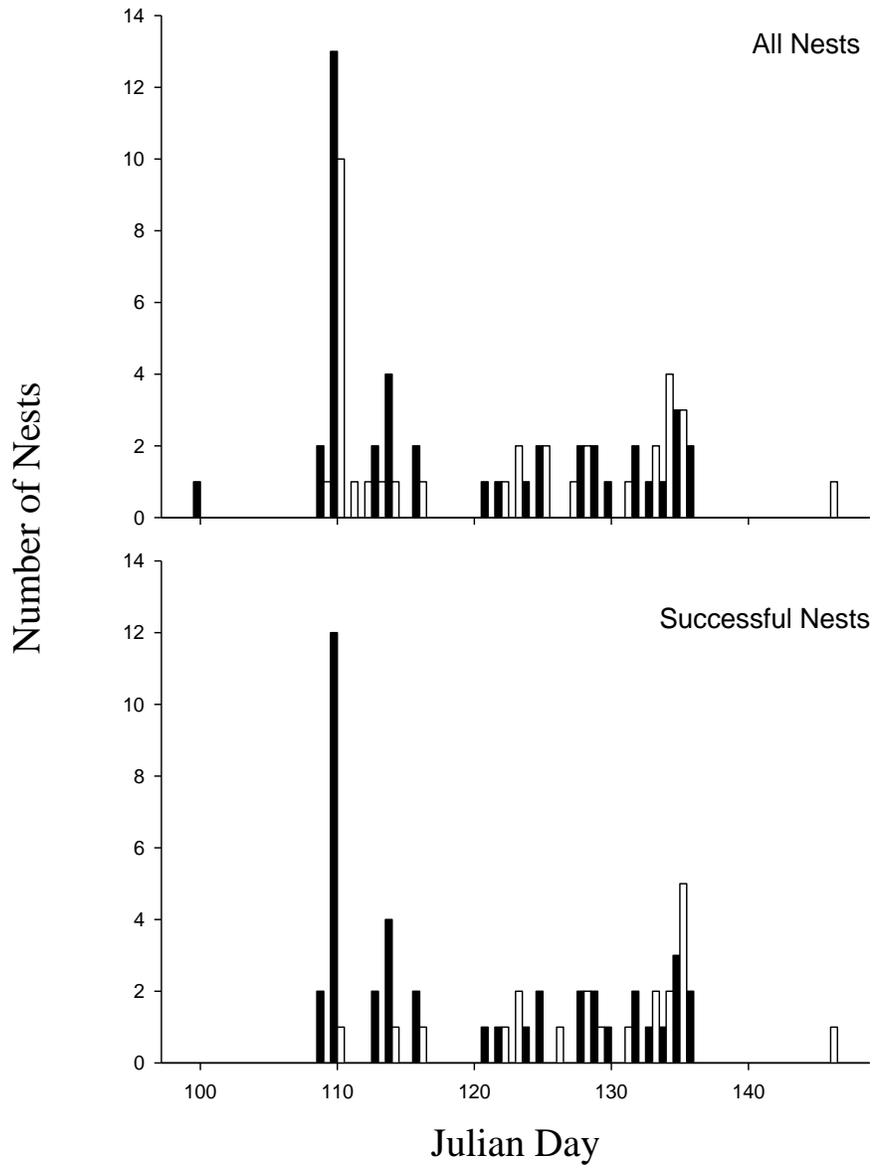| Treatment | Unmanipulated | | Manipulated | | p-value |
|---|---|---|---|---|---|
| **June** | | | | | |
| **Macrozooplankton** | 25.2 | (12.8) | 83.19 | (12.8) | 0.02* |
| **Benthic Invertebrates** | 2.27 | (0.9) | 3.95 | (0.8) | 0.01* |
| **July** | | | | | |
| **Macrozooplankton** | 74.09 | (25.3) | 88.47 | (21.9) | 0.68 |
| **Benthic Invertebrates** | 3.84 | (0.7) | 3.37 | (0.5) | 0.56 |

Figure 3.1: Number of total nests (top panel) and reproductively successful nests (bottom panel) produced in unmanipulated (solid bars) and manipulated (open bars) ponds.
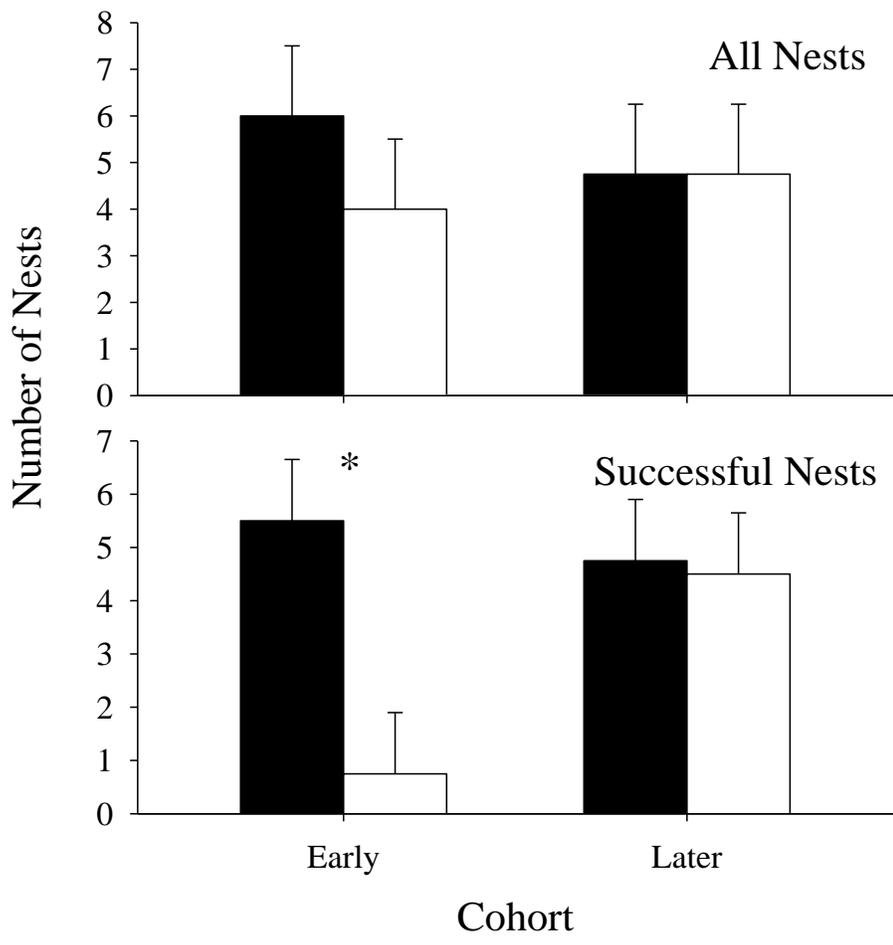
Figure 3.2: Number of total nests (top panel) and reproductively successful nests (bottom panel) produced from early and later spawning adult largemouth bass in unmanipulated (solid bars) and manipulated (open bars) ponds.
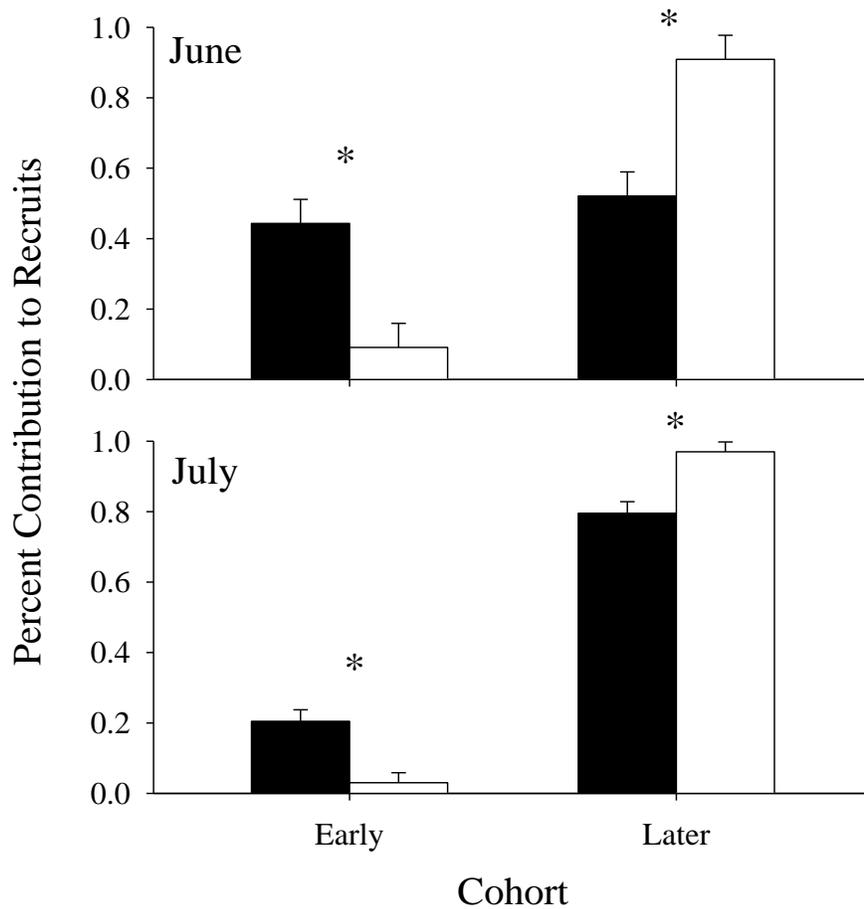
Figure 3.3: Percent contribution of recruits from the early and later cohorts of young-of-year largemouth bass in unmanipulated (solid bars) and manipulated (open bars) ponds to June (top panel) and July (bottom panel).

Figure 3.4: The number of young-of-year *Micropterus salmoides* recruits produced in unmanipulated with the early cohort present (closed bars) and manipulated with the early cohort absent (open bars) ponds as determined by draining at the end of summer.
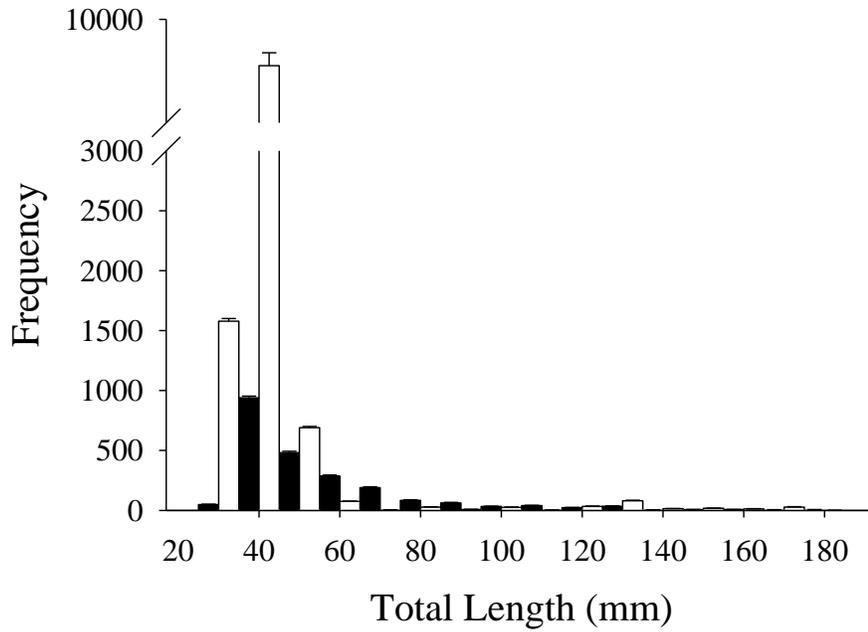
Figure 3.5: Length frequency histogram of young-of-year largemouth bass from unmanipulated (solid bars) and manipulated (open bars) ponds at the end of the summer.

Figure 3.6: Growth rates of early and later cohorts of young-of-year largemouth bass in unmanipulated (solid bars) and manipulated (open bars) ponds in June (top panel) and July (bottom panel).
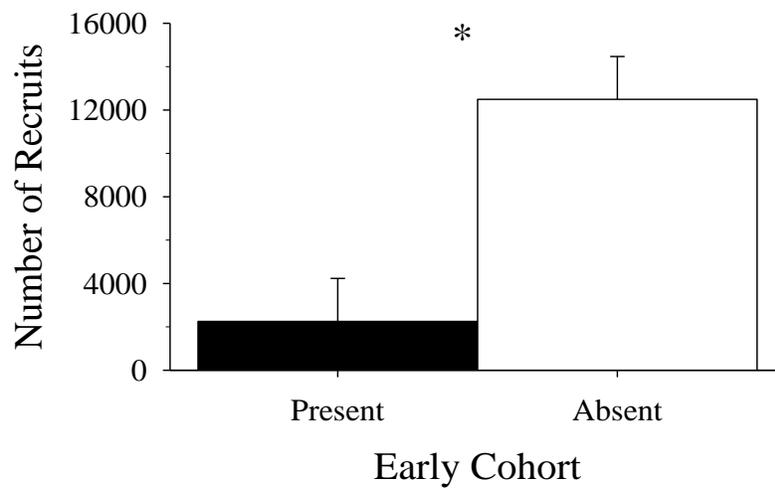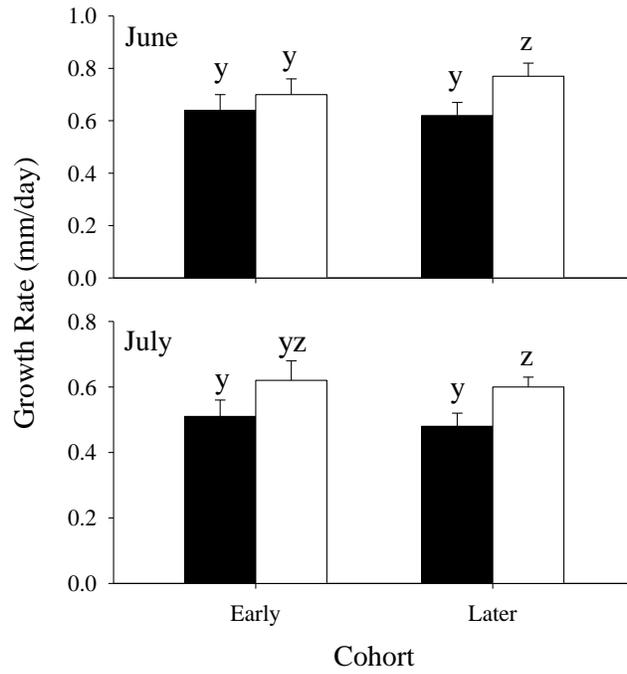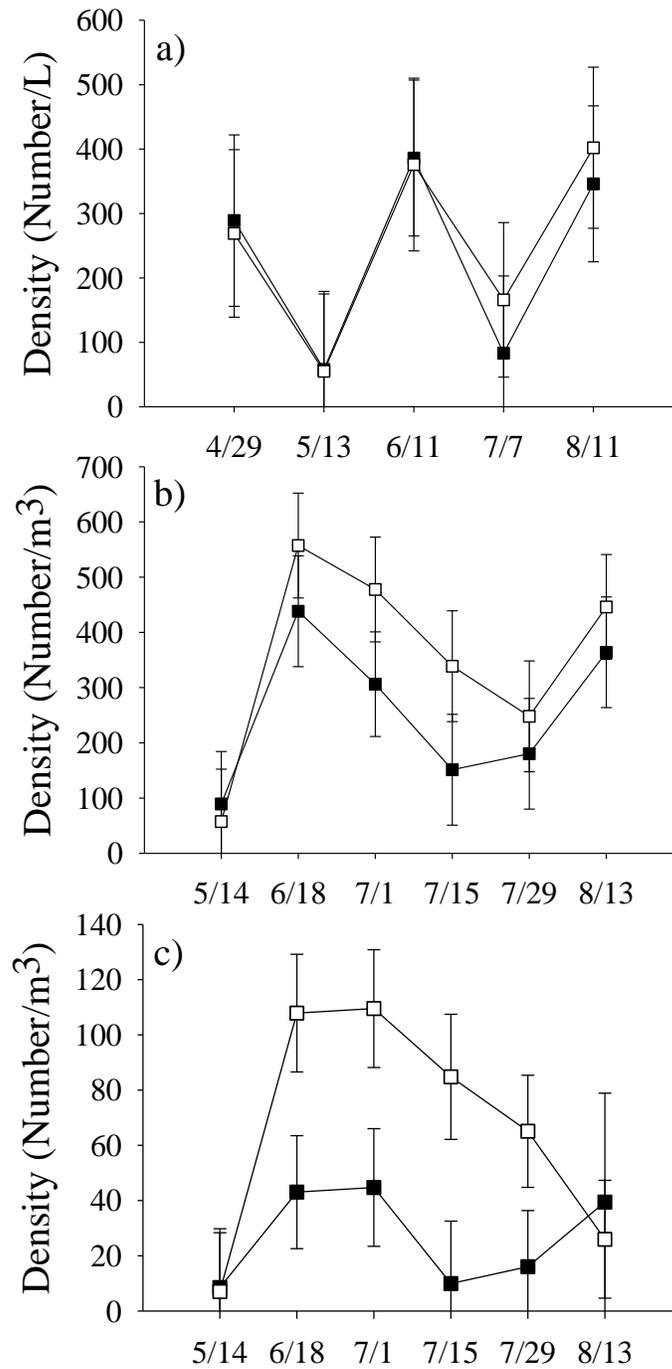
Figure 3.7: Densities of a) zooplankton, b) benthic invertebrates and c) *Ephemeroptera* in unmanipulated (solid squares) and manipulated (open squares) ponds throughout the summer.

**Chapter 4: Summary and Conclusion**

Understanding the complex interactions of abiotic and biotic factors that determine recruitment is the "holy grail" of fisheries. Largemouth bass makes an excellent model species to explore recruitment mechanisms because both density-dependent and density-independent processes have been defined (Shuter et al. 1980, Dong and DeAngelis 1998, Keast and Eadie 1985, Clark et al. 2008). Timing of hatching has also been found to be important, with early hatched individuals experiencing better growth and survival than their later arriving counterparts. Previous research has attributed this advantage to a period of growth prior to the swim-up of later hatched individuals. Early cohorts switch to piscivory at an earlier date than later cohorts due to release from gape limitations and as a result have longer growing seasons. Early cohorts are also typically larger and less susceptible to size-selective predation (Johnson and Post 1996, Garvey et al. 1998). Although differences in growth and survival can be explained through density-independent process, individual based models suggest that density-dependent processes may also contribute to this pattern. Priority effects via resource preemption could also explain this phenomenon if the early cohort exploits prey prior to feeding by the later cohort. In a manipulative pond experiment, I removed the early cohort and found a strong increase in the number of recruits to the end of the summer. The manipulated ponds also responded with greater benthic invertebrates and *Ephemeroptera* densities, higher energetic diets and greater growth rates in later cohorts. My results demonstrate that exploitation from early cohorts can drastically reduce survival of later cohorts. Although this study was the first to confirm that early arriving individuals have a competitive advantage in largemouth bass, the phenomenon has been observed in many other kinds of organisms; however, my study was one of the first to document exploitative competition as a primary mechanism of survival.

I was able to contribute to the understanding of the ecological mechanisms limiting survival of later cohorts of young-of-year largemouth bass. Through the reduction of the early cohort, the later cohort experienced higher ambient prey densities, higher quality of diet, and increased growth that resulted in approximately 5 times as many individuals surviving to the end of year compared to unmanipulated ponds. Although there was some suggestion that this might happen from individual-based models, no previous experimental studies on largemouth bass recruitment linked mortality of the later cohort to the presence of the early cohort. The literature suggests that the later cohort, regardless of the presence of the early cohort, would experience smaller or similar growth rates as the early cohort, a lower quality diet than the early cohort, and significant lower survival than the early cohort (Maceina and Isely 1986, Miller and Stork 1984, Phillips et al. 1995). Finding contradictory results in this study argues that although an extensive body of literature exists on largemouth bass recruitment, more information is needed to be able to accurately predict recruitment success.

The first year of life in largemouth bass is characterized by several critical life stages: nesting success/timing of hatching, the switch to piscivory, and overwinter survival (Ludsin and DeVries 1997). I found that the interaction of nesting success and timing of hatching was responsible for the majority of mortality in the experimental ponds. Although the treatment was applied in the nesting stage, the mortality difference did not manifest until the early juvenile stage. These results emphasizes a point raised by Ludsin and DeVries (1997): scientists need to understand multiple life stages in order to develop an accurate understanding of recruitment success.

Northern populations of largemouth bass are known to have higher survival of early cohorts, whereas these effects are absent for southern populations. Modeling efforts of southern

41

populations found no influence of early cohorts on survival of later cohorts (Rogers and Allen 2009, 2010). Latitudinal variation in the survival of early cohorts of largemouth bass suggests that environmental conditions can regulate the existence of priority effects. I examined individuals from a northern population of largemouth bass. Northern populations also experience a more constricted spawning season compared to southern populations. Because prey exploitation was found to be a mechanism limiting survival, the increased difference in timing of arrival of cohorts from southern populations may allow prey resources to recover prior to the arrival of the later cohort (Trebitz 1991, Lawler and Morin 1993). Differences in latitudinal variation may also be attributed to variation in genotype between Florida and Northern largemouth bass (Rogers et al. 2006, Barthel et al. 2010).

Evolutionary pressure will bias survival towards the early cohort; however, recent work has highlighted the ability of humans to significantly affect survival of early cohorts through angling pressure. Angling nesting adult largemouth bass causes the nest to be unprotected and susceptible to predation (Philipp et al. 1997, Neves 1975). If predation or time off the nest is great enough, depending on the developmental stage of the young, the nesting adult will abandon the young in the nest (Hanson et al. 2007, Philipp et al. 1997, Siepker et al. 2009, Suski et al. 2003). Angling may have a greater impact on early spawners than later spawners and early spawners tend to be older and larger males of a bass population (Ridgway et al. 1992, Wiegmann and Baylis 1995). Because size of adult male bass is also correlated with levels of aggressiveness, large adults are more susceptible to angling than small males (Suski et al. 2003). As a result, humans may be artificially selecting for increased survival of later cohorts of young-of-year largemouth bass.

Although I study found much greater numbers of recruits were produced when the early cohort was removed, the majority of recruits were in the smallest size class. If recruits were able to survive size-selective overwinter morality, the year class would be inundated with small young-of-year largemouth bass. If overwinter survival is an important source of mortality, the majority of recruits would perish in their first winter, reducing year classes of largemouth. If overwinter morality did not significantly affect young-of-year largemouth bass, individuals in the late cohort may experience delayed maturation, as has been reported in smallmouth bass, mosquitofish, and fathead minnows (Wiegmann et al. 1997, Reznick el al. 2006, Divino and Tonn 2007). Previous work has found that late cohorts delayed maturation to attain larger sizes before reaching sexual maturity. Delaying maturation allows an individual to have greater reproductive success the following year, but risks the chance of mortality prior to reproduction (Reznick el al. 2006, Roff 1984). Individuals with lower numbers of reproductive bouts potentially reduces recruitment (Wright and Trippel 2009) if annual mortality of individuals between age-1 and age at first reproduction is high.

Altered population size structure could also have pronounced effects on largemouth bass populations by disrupting alternating cycles of age at first reproduction. Previous work found that late cohorts delayed maturation to attain larger sizes before reaching sexual maturity (Wiegmann et al. 1997, Divino and Tonn 2007). Late cohorts that delayed maturation will become early spawners the following year, while early cohorts will become late spawners in the current year (Weigmann el al. 1997). In this case, progeny would alternate age at first reproduction between early and late spawning. If the majority of individuals in a year class are comprised of later cohorts, most will delay maturation to the following year and become early spawners. In this scenario a large portion of the population would then be highly susceptible to

43

angling and produce lower numbers of late spawning individuals. If alternating age at first reproduction exists in largemouth bass populations, bias for late spawning individuals would disrupt reproductive strategies and result in fewer progeny each year. Further work is needed to identify the long-term effects of increasing the contribution of later cohorts of young-of-year largemouth bass in a population.

If angling affects the early spawning adult largemouth bass and causes a deleterious effect on largemouth bass populations, restrictions could be used to ameliorate the effects. Although angling restrictions are controversial among the public, reducing access of anglers to early spawning adults may improve the long-term sustainability of largemouth bass fisheries. The difficulty of restricting angling on early spawners is that the initiation of spawning is rarely known and varies annually. In order to appropriately protect early spawners, angling would legally need to be prohibited for the entire spawning period (Garvey et al. 2002). Increasing minimum length limit regulations may also help sustain populations by reducing mortality of individuals delaying maturation (Latta 1975, Wiegmann et al. 1997). If no long-term deleterious effects occur from increasing the contribution of later cohorts, restrictions protecting early spawners from anglers may not be needed. In the future, it will be important for managers to balance quality and quantity of recruits in developing sustainable fisheries.

Asymmetric competition has been shown to be an important mechanism in many other fish species, functioning primarily through dominance hierarchies. Winners of dominance hierarchies, wherein individuals at the top of the hierarchy receive a greater amount of resources than individuals at the bottom, will be the larger individuals in a population (Case and Gilpin 1974, Persson 1985). These general patterns may be influenced by prior residency, winner/loser effects, and potentially physiological state (Johnsson et al. 1999, Webster and Hixon 2000,

Sloman and Armstrong 2002, Chase et al. 2002). Dominant individuals may also obtain a

territory, or a particular resource-rich area under defense from other conspecifics, dependent on

competitor density, resource abundance, clumping of resources, and predictability of resources

(Grant and Guha 1993, Grant 1997, Webster and Hixon 2000). Although dominance hierarchies

are a common form of asymmetrical competition, exploitation has also been found to be an

important aspect of population dynamics (Hamrin and Persson 1986, Persson et al. 1998).

Winners of exploitative competition are typically smaller individuals, since they have lower

metabolic demands, and can often cause population oscillations (Hamrin and Persson 1986).

Evidence of larger individuals winning exploitive competitions is rare, because the foraging

advantage of larger individuals is thought only to hold true if metabolism does not scale with

body size (Persson et al. 1998). Incorporating temporal dimensions in competition studies such

as mine reveals new dynamic interactions between individuals, and creates the possibility of

large individuals being the superior competitors through resource preemption.

Understanding density-dependence in recruitment is fundamental to sustainably manage

fish populations, because populations with strong compensation are robust to loss of spawning

adults; however, general models of density-dependence, such as the Ricker curve, have little

support, and as a result, identifying the magnitude of compensation necessary to sustain a

population is difficult (Houde 2008, Myers et al. 1994). Life-history theory provides a better

framework to understand compensation, because it integrates multiple processes that may

influence mortality (Rose el al. 2001). I used a life-history approach to identify that releases

from exploitative asymmetrical competition in the juvenile stage allows strong compensation to

occur in later cohorts of largemouth bass. Knowledge of priority effects as the cause of

compensation in young-of-year largemouth bass will stimulate further investigations to identify

the effects of high early cohort mortality at the population-level and will ultimately allow managers to develop appropriate regulations in order to maintain the integrity of largemouth bass populations.

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# Chapter 6: Appendix

The influence of early cohorts on later cohort growth and survival in young-of-year largemouth bass was examined in a manipulative pond experiment. Members of the early cohort were removed in the manipulated ponds.

Table 6.1: Resulting abundance and biomass of produced and final lengths and weights of age-0 largemouth bass in the ponds at the end of summer with final lengths and weights are reported. Data on age-0 largemouth bass are reported as Mean (Range, *where applicable*). Lengths of stocked adult male and largemouth bass are reported as Mean (Range). The total number of nests, total egg score (measure of reproductive output), and average size of the nest (Egg Score/Nest) are reported as Mean (Range, *where applicable*). The draining date (conclusion of the experiment) of each pond is also provided. The number of age-1 bluegill sunfish stocked and the number of age-0 bluegill sunfish produced at the end of the summer in each pond are reported. Potential sources of variation in physical characteristics among ponds are reported. Levels of phosphorus concentrations, chlorophyll-a concentrations, secchi depth, oxygen concentrations at the surface and 1 meter depth, and temperature at the surface and 1 meter depth are reported as Summer Mean (Range). Physical characteristics were collected biweekly; phosphorus concentrations were collected monthly. Concentrations of phosphorus were too low to be detected during certain sampling dates during the experiment; immeasurable minimum values are denoted as N/A. Percent surface area cover of peak macrophyte densities are reported. One-Way ANOVAs were conducted to test for differences between treatments. Resulting p-values are reported; asterisks denote significant p-values less than 0.05.

Table 6.2: Measured values of physical characteristics in the ponds. Levels of phosphorus concentrations, chlorophyll-a concentrations, secchi depth, oxygen concentrations at the surface and 1 meter depth, and temperature at the surface and 1 meter depth are reported for each sample date.

Table 6.3: Total Length of the parental male and Egg Scores of the nests that were removed as a result of the treatment manipulation.

Figure 3.1: Total length frequencies of young-of-year largemouth bass at the end of summer. The early cohort in ponds 1, 4, 6 & 7 (left) was removed, while the early cohort in ponds 2, 3, 5, & 8 (right) was left intact.

Table 6.1: Mean levels of abiotic and biotic variables in ponds

| Treatment Group | Pond # | Unmanipulated | | | | Manipulated | | | | p-value |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 5 | 8 | 1 | 4 | 6 | 7 | |
| Largemouth Bass | Number of Age-0 Largemouth Bass | 1,266 | 2,577 | 3,903 | 1,265 | 12,262 | 11,672 | 6,365 | 19,649 | 0.01* |
| | Total Biomass of Age-0 Largemouth Bass | 9,693 | 22,464 | 28,142 | 7,904 | 66,727 | 56,585 | 31,074 | 100,566 | 0.02* |
| | Age-0 Largemouth Bass Length (mm) | 74 (41-149) | 54 (30-181) | 66 (34-148) | 65 (38-186) | 50 (37-153) | 46 (32-158) | 49 (36-188) | 59 (30-183) | 0.03* |
| | Age-0 Largemouth Bass Weight (g) | 8 (2-30.4) | 9 (0.2-67.9) | 7 (0.6-33.3) | 6 (0.8-79.0) | 5 (0.7-46.4) | 5 (0.5-50.1) | 5 (0.3-83.4) | 5 (0.8-67.1) | 0.004* |
| | Adult Male Length (mm) | 309 (257-394) | 316 (260-453) | 305 (257-381) | 331 (257-446) | 302 (252-352) | 319 (255-518) | 325 (253-480) | 306 (257-404) | 0.79 |
| | Adult Female Length (mm) | 309 (259-388) | 303 (257-389) | 308 (255-377) | 305 (247-362) | 306 (255-391) | 303 (246-370) | 301 (244-409) | 302 (212-390) | 0.13 |
| | Total Number of Nests | 10 | 10 | 12 | 9 | 7 | 5 | 4 | 5 | 0.001* |
| | Total Number of Largemouth Bass Fry | 32447 | 10194 | 37370 | 10194 | 13031 | 63717 | 8550 | 51385 | 0.48 |
| | Total Number of Largemouth Bass Fry / Nest | 3245 | 1019 | 3114 | 1133 | 1862 | 12743 | 2138 | 10277 | 0.16 |
| | Draining Date | 8/17 | 8/24 | 8/19 | 8/25 | 8/21 | 8/20 | 26-Aug | 8/18 | |
| Bluegill Sunfish | Number of Age-0 Bluegill Sunfish | 12,554 | 2,777 | 4,954 | 1,292 | 1,362 | 3,743 | 1,949 | 629 | 0.23 |
| | Number of Stocked Age-1 Bluegill Sunfish | 1,465 | 1,465 | 1,415 | 1,415 | 1,465 | 1,453 | 1,415 | 1,415 | 0.88 |
| Physical Characteristics | Phosphorus (mg/L) | 23 (N/A-65) | 51 (N/A-122.9) | 28 (N/A-86) | 71 (12-111) | 25 (N/A-90) | 26 (N/A-86) | 37 (N/A-110.6) | 33 (N/A-115) | 0.29 |
| | Chlorophyll-a (ug/L) | 13 (4-19) | 42 (3-111) | 22 (9-29) | 30 (12-49) | 14 (5-24) | 18 (3-29) | 18 (6-31) | 29 (19-43) | 0.35 |
| | Secchi Depth (m) | 1.4 (0.7-1.9) | 1.5 (0.5-2.3) | 1.5 (0.8-1.9) | 1.1 (0.8-1.3) | 1.4 (0.9-1.9) | 1.5 (0.8-1.9) | 1.6 (1.4-1.7) | 1.2 (0.9-1.6) | 0.77 |
| | Surface $O_2$ (mg/L) | 9 (4-14) | 11 (10-14) | 10 (10-13) | 11 (9-16) | 12 (11-14) | 11 (9-14) | 10 (7-12) | 10 (8-13) | 0.729 |
| | $O_2$ at 1m depth (mg/L) | 8 (2-13) | 11 (9-13) | 10 (8-14) | 9 (5-11) | 12 (10-13) | 10 (8-13) | 9 (7-12) | 10 (6-14) | 0.59 |
| | Surface Temperature (°C) | 25.8 (16.3-31.2) | 24.9 (14.7-30.2) | 25.1 (16.8-28.9) | 26.5 (16.9-35.5) | 25.4 (16.5-29.8) | 24.9 (18.0-31.8) | 25.3 (13.2-32.4) | 26.5 (16.9-29.9) | 0.92 |
| | Temperature at 1m Depth (°C) | 24.6 (15.6-28.5) | 24.1 (14.2-28.1) | 24.5 (16.4-27.9) | 24.1 (17.9-28.8) | 24.5 (15.7-27.6) | 24.7 (17.6-28.4) | 24.1 (12.8-28.1) | 24.5 (16.3-27.9) | 0.52 |
| | Percent Macrophytes Cover | 25 | 65 | 85 | 95 | 85 | 80 | 90 | 70 | 0.42 |

Table 6.2: Measured values of physical characteristics in ponds.

| Date | Treatment Group | Pond # | 4/20 | 5/6 | 5/20 | 6/2 | 6/15 | 7/1 | 7/13 | 7/28 |
|---|---|---|---|---|---|---|---|---|---|---|
| **Phosphorus (mg/L)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 69 | N/A | 70 | N/A | 55 | N/A | N/A | 49 |
| | | 3 | 55 | N/A | 111 | N/A | 14 | N/A | N/A | 49 |
| | | 5 | 43 | N/A | 15 | N/A | 14 | N/A | 41 | N/A |
| | | 8 | 61 | N/A | 72 | N/A | 78 | N/A | 6 | 104 |
| | Manipulated | | | | | | | | | |
| | | 1 | 23 | N/A | 35 | N/A | 27 | N/A | N/A | N/A |
| | | 4 | 83 | N/A | 0 | N/A | 31 | N/A | 16 | N/A |
| | | 6 | 31 | N/A | 55 | N/A | 35 | N/A | 45 | N/A |
| | | 7 | 62 | N/A | 8 | N/A | 29 | N/A | N/A | 14 |
| **Chlorophyll-a (µg/L)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 7 | 6 | 4 | 12 | 16 | 19 | 12 | 14 |
| | | 3 | 7 | 3 | 10 | 10 | 68 | 21 | 16 | 112 |
| | | 5 | 29 | 17 | 12 | 24 | 23 | 28 | 23 | 9 |
| | | 8 | 13 | 12 | 36 | 26 | 32 | 14 | 49 | 32 |
| | Manipulated | | | | | | | | | |
| | | 1 | 13 | 9 | 5 | 14 | 16 | 13 | 13 | 24 |
| | | 4 | 10 | 7 | 3 | 6 | 21 | 15 | 26 | 29 |
| | | 6 | 10 | 6 | 13 | 27 | 18 | 23 | 31 | 24 |
| | | 7 | 43 | 30 | 27 | 30 | 27 | 32 | 29 | 19 |
| **Secchi Depth (m)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 1.9 | 1.5 | 1.3 | 1.3 | 1.6 | 0.7 | 1.5 | 1.7 |
| | | 3 | 1.3 | 2.2 | 2.3 | 1.2 | 0.5 | 2.1 | 1.5 | 1.6 |
| | | 5 | 1.8 | 1.6 | 1.3 | 0.8 | 1.9 | 1.4 | 1.6 | 1.7 |
| | | 8 | 0.8 | 1.2 | 1.0 | 1.3 | 1.2 | 1.6 | 1.3 | 1.1 |
| | Manipulated | | | | | | | | | |
| | | 1 | 1.7 | 1.7 | 1.7 | 0.9 | 1.1 | 1.3 | 1.4 | 1.9 |
| | | 4 | 1.8 | 1.9 | 1.7 | 1.2 | 1.6 | 0.8 | 1.3 | 1.9 |
| | | 6 | 1.7 | 1.6 | 1.7 | 1.4 | 1.6 | 1.6 | 1.6 | 1.6 |
| | | 7 | 1.2 | 0.9 | 0.9 | 1.6 | 0.9 | 1.3 | 1.1 | 1.6 |
| **Surface $O_2$ (mg/L)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 11 | 10 | 7 | 4 | 9 | 7 | 14 | 13 |
| | | 3 | 10 | 11 | 11 | 10 | 12 | 11 | 14 | 10 |
| | | 5 | 9 | 10 | 10 | 10 | 10 | 10 | 13 | 11 |
| | | 8 | 10 | 9 | 10 | 9 | 17 | 9 | 10 | 12 |
| | Manipulated | | | | | | | | | |
| | | 1 | 14 | 13 | 12 | 11 | 11 | 11 | 13 | 12 |
| | | 4 | 10 | 9 | 9 | 11 | 10 | 10 | 14 | 12 |
| | | 6 | 10 | 11 | 10 | 9 | 8 | 7 | 12 | 12 |
| | | 7 | 9 | 8 | 9 | 8 | 9 | 11 | 13 | 12 |
| **$O_2$ at 1m depth (mg/L)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 11 | 8 | 6 | 2 | 5 | 7 | 13 | 12 |
| | | 3 | 11 | 11 | 11 | 9 | 11 | 10 | 13 | 10 |
| | | 5 | 10 | 8 | 10 | 9 | 10 | 10 | 14 | 11 |
| | | 8 | 8 | 5 | 10 | 8 | 10 | 9 | 11 | 11 |
| | Manipulated | | 13 | 12 | 12 | 11 | 10 | 11 | 13 | 12 |
| | | 1 | | | | | | | | |
| | | 4 | 9 | 9 | 10 | 8 | 9 | 9 | 13 | 10 |
| | | 6 | 10 | 9 | 10 | 7 | 7 | 8 | 12 | 10 |
| | | 7 | 8 | 7 | 9 | 7 | 7 | 11 | 14 | 12 |
| **Surface Temperature (ºC)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 16 | 25 | 28 | 23 | 27 | 24 | 30 | 31 |
| | | 3 | 15 | 19 | 25 | 28 | 25 | 29 | 25 | 30 |
| | | 5 | 17 | 21 | 26 | 28 | 25 | 25 | 29 | 29 |
| | | 8 | 18 | 23 | 25 | 27 | 23 | 24 | 32 | 36 |
| | Manipulated | | | | | | | | | |
| | | 1 | 17 | 22 | 26 | 29 | 25 | 28 | 24 | 30 |
| | | 4 | 18 | 23 | 24 | 24 | 32 | 25 | 27 | 31 |
| | | 6 | 13 | 23 | 26 | 28 | 25 | 24 | 30 | 32 |
| | | 7 | 17 | 25 | 25 | 24 | 24 | 28 | 30 | 29 |
| **Temperature at 1m depth (ºC)** | | | | | | | | | | |
| | Unmanipulated | | | | | | | | | |
| | | 2 | 16 | 24 | 24 | 24 | 28 | 25 | 28 | 29 |
| | | 3 | 14 | 18 | 24 | 28 | 25 | 27 | 25 | 28 |
| | | 5 | 16 | 20 | 24 | 28 | 26 | 25 | 27 | 28 |
| | | 8 | 18 | 22 | 22 | 26 | 24 | 24 | 25 | 29 |
| | Manipulated | | | | | | | | | |
| | | 1 | 16 | 21 | 25 | 27 | 25 | 27 | 24 | 28 |
| | | 4 | 18 | 21 | 23 | 25 | 27 | 25 | 27 | 28 |
| | | 6 | 13 | 22 | 25 | 27 | 25 | 25 | 28 | 28 |
| | | 7 | 16 | 23 | 24 | 24 | 25 | 28 | 28 | 28 |

Table 6.3: Data are listed as Adult Male Total Length and Egg Score of their devalued nest, *respectively*.

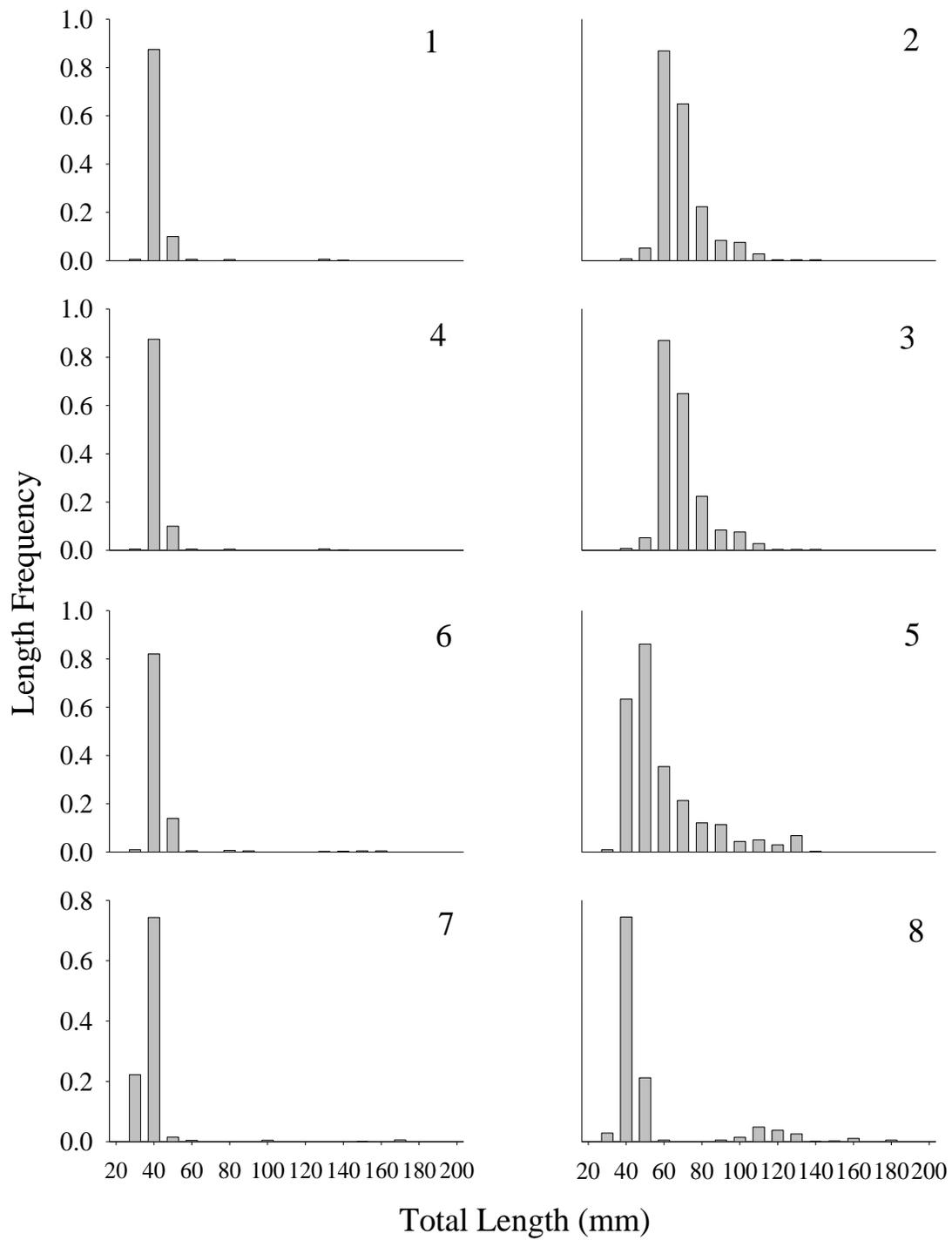| Pond # | Adult Male Total Length (mm) | Egg Scores |
|--------|------------------------------|------------|
| 1 | (279, 356, 264) | (2, 1, 1) |
| 4 | (265, 279, 259) | (1, 2, 2) |
| 6 | (269, 262, 306) | (3, 1, 3) |
| 7 | (229, 254, 305) | (1, 4, 3) |

Figure 6.1: Total length frequencies of young-of-year largemouth bass at the end of summer.