

RECRUITMENT DYNAMICS OF
AGE-0 LARGEMOUTH BASS ALONG A LATITUDINAL GRADIENT OF FLORIDA
LAKES

By

MARK WAYNE ROGERS

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2007

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To Kristin and our future together

ACKNOWLEDGMENTS

My research was funded by a grant from the Florida Fish and Wildlife Conservation Commission (FWC) and I was supported by a UF CALS Alumni Fellowship. Other financial support was provided by the AFS Southern Division Reservoir Committee Robert M. Jenkins Scholarship, FL Chapter of AFS Roger Rottman Scholarship, and travel grants through: UF IFAS, the UF Graduate Student Association, FL Chapter of AFS, and AFS Education Section Skinner Award.

I thank my advisor, Dr. Michael Allen, and other graduate committee members, Dr. Debra Murie, Dr. Tom Frazer, Dr. Craig Osenberg, and Dr. Ramon Littell for their service. I especially thank Dr. Allen for his high expectations and efforts to do everything he could do to benefit my student experiences. My research would not have been possible without the assistance of the following FWC cooperators: John Benton, Rich Cailteaux, Jim Estes, Don Fox, Beacham Furse, Steve Gornak, Jay Holder, Bill Johnson, Earl Lundy, Charlie Mesing, Wes Porak, and Andy Strickland. University of Florida students and staff: C. Barrientos, Mo Bennett, G. Binion, T. Bonvechio, P. Cooney, J. Dotson, D. Dutterer, P. Hall, G. Kaufman, V. Maceina, V. Politano, and N. Trippel conducted field sampling, laboratory sample and data processing. I owe tremendous thanks to my academic mentors: Dr. Micheal Allen, Dr. Michael Hansen, and Dr. Richard Noble and greatly appreciate the willingness of Dr. Carl Walters to share his time to assist with my dissertation work. I also thank Dr. Chuck Cichra, Dr. Karl Havens, Mark Hoyer, and Dr. Bill Pine for enhancing my education.

Most importantly I thank Kristin and our family for their love and support during this process. I appreciate Kate Lazar's friendship to my wife and willingness to entertain Kristin on all the weekends and nights that I was working. I also thank Trinity United Methodist Church for helping me keep my life prioritized.

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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Mark Wayne Rogers

December 2007

Chair: Micheal Allen

Major: Fisheries and Aquatic Sciences

Juvenile fish life history varies across large spatial gradients because of latitudinal influences on growing season length and winter severity. I evaluated recruitment processes (e.g., hatching date, growth, and mortality) affecting largemouth bass *Micropterus salmoides* recruitment to age-1 across a latitudinal gradient of Florida lakes and related my findings to results for this species from more northerly latitudes. I sampled the 2003 and 2004 year classes at six Florida lakes that spanned latitudes from N27°0' to N30°5'. My first objective tested whether 1) early-hatching provided a growth and survival advantage relative to later-hatching through their first summer, and 2) whether overwinter size-selective mortality strongly influenced recruitment to age-1 across Florida's latitudinal gradient. My results did not fully conform to common hypotheses because early-hatched sub-cohorts (i.e., fish hatched at dates in the left tail of the overall hatching distribution) did not exhibit a growth and survival advantage at all lakes and I did not detect strong size-selective overwinter mortality.

My second objective evaluated the relative contributions of genetic and environmental effects on spawning periodicity by rearing Florida largemouth bass *M. s. floridanus* from Lake Okeechobee in south Florida and intergrade largemouth bass *M. s. salmoides x floridanus* (or

vice-versa) from Lake Seminole in north Florida in a similar environment in Gainesville, Florida. Results showed that Florida fish began spawning earlier than intergrade fish in all ponds and Florida fish had a longer spawning season than intergrade fish. Similarly, Florida fish at Lake Okeechobee began spawning earlier and had a longer spawning season than intergrade fish at Lake Seminole. Thus, environmental factors influenced spawning periodicity for both genetic stocks, but spawning periodicity in ponds also reflected characteristics of their source populations.

My last objective explored implications of hatching date-dependent growth and mortality observations for age-0 largemouth bass to evaluate relative effects on recruitment to age-1. Modeling results showed that hatching date-dependent mortality could influence the contributions of differing hatching sub-cohorts to year class composition at age-1, but total age-1 and adult biomass was not largely affected. Thus, my models predicted large compensation potential and strong regulation for largemouth bass recruitment.

CHAPTER I GENERAL INTRODUCTION

Fisheries managers and ecologists struggle to understand fish recruitment because it is variable and many factors influence survival of age-0 fishes (Post et al. 1998). Factors influencing age-0 fish survival differ among latitudes owing to environmental influences (e.g., winter water temperatures) and can result in localized adaptations to adult spawning strategies for maximizing offspring survival (Conover 1992). Thus, both genetic and environmental components likely contribute to adult spawning timing, but their relative contributions and implications for offspring survival are largely unknown. Identifying processes and factors that regulate and control age-0 survival facilitates our ecological understanding of juvenile recruitment processes, adult reproductive timing, and fisheries management across broad latitudinal gradients. The recreational importance and broad distribution of largemouth bass have resulted in extensive research and generalized hypotheses that identified important factors (e.g., hatching date and growth rate) that can limit age-0 survival. Studies commonly concluded that age-0 largemouth bass hatching early in the spawning season had early-life advantages (e.g., lower mortality) and were more likely to survive during winter relative to later-hatched members of a year class (Miranda and Hubbard 1994a; Ludsin and DeVries 1997; Garvey et al. 1998), however all of these studies were conducted at latitudes where growing season length and winter water temperatures would likely strongly affect age-0 largemouth bass survival.

Florida winters are mild relative to latitudes where other age-0 largemouth bass recruitments studies have been conducted (i.e., Alabama to Wisconsin). Mild winters could strongly influence the onset and duration of spawning, growth, and the potential for overwinter mortality, thus suggesting that age-0 recruitment processes may differ for Florida populations relative to more northerly populations. I studied the 2003 and 2004 largemouth bass year classes

at six Florida lakes distributed across three regions (south, central, and north). I evaluated hatching seasons, growth, mortality, and size-selective overwinter mortality across a range of Florida latitudes and related my findings to popular largemouth bass recruitment hypotheses. I reported an experiment to evaluate the contributions of genetic and environmental factors to largemouth bass spawning season initiation and duration with implications for evolution of adult spawning strategies across latitudes. I used a trophic-based ecosystem model to simulate how hatching date-dependent survival would influence within year-class interactions and year class strength, and related my findings to theory on the evolution of parental spawning strategies and addressed implications for fisheries management.

CHAPTER 2
EXPLORING THE GENERALITY OF RECRUITMENT HYPOTHESES FOR
LARGEMOUTH BASS ALONG A LATITUDINAL GRADIENT OF FLORIDA LAKES

Aquatic ecologists and fisheries managers struggle to understand fish recruitment because recruitment is inherently variable, and both density dependent and independent factors influence pre-recruitment survival (Post et al. 1998). Environmental (e.g., temperature) and biological (e.g., energetics and predator-prey relationships) factors interact to influence recruitment processes (e.g., hatching dates, growth, and mortality), but the relative strengths of those recruitment processes can vary greatly with latitude (Conover 1992; Garvey et al. 2002a). Establishing latitudinal patterns in hatching, growth, and survival of juvenile fish is a goal of ecologists (Garvey et al. 2002a) and facilitates understanding of species-specific variation in life-history traits across large spatial gradients (Conover 1992).

Early-life survival in teleost fishes has been closely associated with body size (Miller et al. 1988), which is largely influenced by hatching date and somatic growth rate (Conover 1992; Houde 1997). Spawning initiation generally occurs earlier in the year at lower latitudes than at higher latitudes for broadly distributed species due to influences of temperature (Lam 1983; Conover 1992). Spawning strategies often reflect adaptive characteristics, such that spawning season durations are protracted at lower latitudes relative to higher latitudes because of differences in growing season duration and the strength of over-winter size-dependent mortality (Conover 1992). When spawning distributions are protracted, variation in conditions for early- versus late-hatched sub-cohorts (i.e., fish hatched in a specific period within the total hatching distribution) can be large relative to systems that exhibit contracted spawning distributions, potentially magnifying differences in growth and survival among sub-cohorts within a year class (Phillips et al. 1995; Cargnelli and Gross 1996; Narimatsu and Munehara 1999). Thus, temporal

spawning patterns may result in differing strengths of factors regulating recruitment processes among populations.

Early-hatching often leads to large juvenile size by the end of the first growing season and higher survival relative to later-hatched members of a year class (e.g., Trebitz 1991, Cargnelli and Gross 1996), but biotic interactions (e.g., competition) also can influence this relationship (Olson 1996; Post 2003). Early hatching and increased size have been shown to be beneficial by reducing vulnerability to predators (Christensen 1996; Hambright et al. 1991), providing foraging advantages (Ludsin and DeVries 1997; Mittelbach and Persson 1998), and by improving fish condition for overwinter survival (Shuter and Post 1990; Ludsin and DeVries 1997) relative to smaller members of a year class. Post (2003) suggested that early-hatching provides opportunities that can result in earlier age-at-maturity, and thus, increased lifetime fitness. Therefore, early hatching has often been considered advantageous in fish populations structured by size-dependent mortality.

Life-history strategies across species distributions result from responses to both environmental and genetic influences (Stearns 1976). Because temperature, and thus latitude, can influence spawning success, fish populations are expected to exhibit adaptations to local conditions that maximize progeny survival (Stearns 1976; Conover 1990). Without knowledge of the relative strengths of processes influencing survival among populations, broad scale ecological patterns of recruitment are difficult to establish. Broad recruitment hypotheses have been proposed for largemouth bass; however, Parkos and Wahl (2002) reported that most knowledge concerning recruitment processes for this species was largely derived from studies conducted from only a portion of their distribution. For example, Garvey et al. (1998) hypothesized that the strength of overwinter mortality should increase with decreasing latitude

because warmer winter climates facilitate increased predation during winter. Garvey et al. (1998) developed their hypothesis from populations extending from Wisconsin to central Alabama, but information was not available from the southern extent of the largemouth bass's native range. To evaluate the generality of recruitment hypotheses across latitudinal gradients, recruitment processes need to be evaluated outside the areas used to develop the hypotheses.

Florida's climate ranges from subtropical to temperate, thus potentially providing a prolonged breeding season and minimal winter effects relative to other temperate North American latitudes. My objective was to evaluate the generality of recruitment hypotheses, developed at more northerly latitudes, to juvenile largemouth bass survival in Florida. I compared hatching distributions, growth, and survival of age-0 largemouth bass across a latitudinal gradient of Florida lakes (i.e., at the southern extent of their native distribution) to determine if survival patterns conform to current hypotheses regarding pre-recruitment largemouth bass survival. I tested two hypotheses: 1) that early hatching would result in a growth and survival advantage through the summer (e.g., Phillips et al. 1995; Ludsin and DeVries 1997; Pine et al. 2000), and 2) that size-selective overwinter mortality would strongly influence survival to age-1 (e.g., Miranda and Hubbard 1994; Ludsin and DeVries 1997; Garvey et al. 1998).

Methods

I divided Florida into three study regions (i.e., south, central, and north; per Crawford et al. 2002) and selected two lakes from each region for my study. Study lakes in each region included: 1) north region: Seminole and Talquin Reservoirs, 2) central region: Lakes Harris and Monroe, and 3) south region: Lakes Okeechobee and Istokpoga (Table 2-1; Figure 2-1). Due to Lake Okeechobee's large size, my sampling area ($> 25 \text{ km}^2$) was located in the northwest region

of the lake. Seminole Reservoir is not entirely within Florida; thus, I sampled only the west littoral zone along the Chattahoochee Basin from the Alabama state line to Jim Woodruff Lock and Dam (i.e., Florida waters). Sample sites at other lakes were distributed throughout the entire littoral area. In general, lakes had vast, highly vegetated littoral zones composed of submergent (e.g., *Hydrilla verticillata*), emergent (e.g., pickerelweed *Pontederia cordata*) and floating-leaved (e.g., fragrant water lily *Nymphaea odorata*) plants. Vegetation types and abundances were generally similar across lakes, except for Lake Talquin, where vegetation abundance was lower and less diverse compared to the other lakes (M. Rogers, personal observation). I sampled the 2003 and 2004 year classes of largemouth bass from shortly after hatching through the following spring (i.e., about age-1) at each lake.

Early Age and Growth

I used block nets to sample age-0 largemouth bass during spring and summer at each lake. Due to the potential for earlier-hatching in my south region relative to my central and north regions, Lakes Okeechobee and Istokpoga were sampled in early spring (i.e., February or March) and all lakes were sampled during spring (i.e., late April/May) and summer (i.e., late June/July) in each year. A 100-m block net (3.2-mm knotless nylon mesh) was deployed in a 10m x 10m square (total area = 0.01 ha) and liquid rotenone (Prenfish® 5% active ingredient) was applied at 3 mg/L. Twelve block nets were set at each lake during each sampling event. Samples were collected in shallow (< 2m) littoral zones, and sample sites were selected to be representative of available habitat types (e.g., vegetation type). At each net, all fish were collected by 3-4 wading investigators until fish did not continue to surface, and the net was then moved to another location and set again. My strategy underestimated fish density due to incomplete recovery, but allowed for higher samples sizes per habitat type and lake (Timmons et al. 1978).

All collected fish were placed on ice and returned to the laboratory. Age-0 largemouth bass were measured to nearest 1 mm total length (TL) and weighed to the nearest 0.01 g. Age-0 largemouth bass from each sampling event were placed in 1 cm length groups and sagittal otoliths were removed from a subsample of fish so that the length distribution of aged fish closely reflected the length frequency of the entire fish sample collected in that period (Ludsin and DeVries 1997; Pine and Allen 2001). Otolith preparation and age estimation followed the procedures of Miller and Storck (1982) and Ludsin and DeVries (1997). A sample of 30 known-age largemouth bass from the Richloam Fish Hatchery, Florida, was collected during May 2003 and was used to validate age accuracy. All otoliths were read twice by two independent readers. Between-reader ages differing by less than 3.5 d were used to produce an average age (Maccina et al. 1995).

Hatch date for each fish was estimated by subtracting the number of rings counted on the otolith from the day of year when collection took place. Total length at age data were modeled using both a linear model and an exponential model for each lake, and error variance was compared using a variance ratio test (Zar 1999). The linear and exponential models were fit to TL at age using data from fish between 30-75 d old to ensure that the age and subsequent growth comparisons were similar across hatching cohorts and study lakes. Mean daily growth rate (DGR, mm/d) for each fish was estimated as:

$$\text{DGR} = (\text{TL}_c - 6)/\text{age} \quad (2-1)$$

where TL_c is the total length at capture, age is the number of days from swim-up (i.e., the ring count), and 6 mm is subtracted to correct for total length at swimup (Goodgame and Miranda 1993; Ludsin and DeVries 1997). I used swimup dates as an indicator of hatch dates and an index of adult spawning activities.

I compared mean DGR among hatching periods and lakes. Fish were grouped into early, middle, and late hatch periods by partitioning the entire hatching date distribution for each lake and year into 33 percentile groups. Estimated hatch dates from each sample were pooled to construct the entire hatching distribution for each lake and year because I wanted to incorporate early hatch dates that may not have been detectable in later samples due to mortality (see Isely et al. 1987). Hatching periods that delineated sub-cohorts were lake and year specific to evaluate the general prediction that early-hatching, within any given system, would result in a growth and survival advantage relative to later-hatching. Mean DGR was compared among sub-cohorts (i.e., early, middle, late) and lakes using a two-way analysis of variance (ANOVA) for each year with hatching period and lake as factors. If lakes within regions did not exhibit differences in mean DGR among sub-cohorts, I grouped lakes into regions (north, central, south) and used a two-way ANOVA with regions and hatching periods as factors. Least-squares means with Tukey's modification were used to separate DGR means if differences were significant in the ANOVA.

Water temperature was measured at each lake throughout the study. Temperature loggers manufactured by Onset ® were placed at two stations within the sample areas at each lake between 0.5 and 1 m water depth prior to initiating data collection and they recorded data during the entire study period. Temperature loggers were programmed to record water temperature at six-hour intervals, thus allowing us to relate age-0 largemouth bass hatching frequency distributions and growth rates to water temperatures for each lake, region, and year.

Early survival of age-0 largemouth bass was assessed using changes in abundance-at-age from sequential block net sampling events at each lake. Fish were grouped in 7-day cohorts for each lake and sampling event. Survival of each cohort was estimated as:

$$S_i = N_{i, t} / N_{i, t-1} \quad (2-2)$$

where S_i is the survival rate of cohort i , $N_{i,t}$ is the mean density of fish from cohort i at time t , and $N_{i,t-1}$ is the mean density of cohort i in the preceding sampling event. Survival was estimated between the early spring and spring sampling periods at south lakes and the spring to summer sampling periods at all lakes. Only cohorts that were fully recruited (i.e., > 15 mm TL) to the block nets in each sampling event were used for estimating survival. Seven-day cohorts were grouped into early, middle, and late-hatched sub-cohorts based on dates delineated by the total hatching distribution as described above. I tested for differences in mean survival among sub-cohorts for the early-spring to spring periods in the south lakes combined using a one-way ANOVA. Low sample sizes (the number of cohorts per lake) precluded lake-specific survival assessment for spring to summer sampling periods. Thus, I grouped lakes by region and tested whether mean survival differed among sub-cohorts and regions using a two-way ANOVA. Least-squares means was used to separate means if the overall ANOVA had significant effects ($\alpha = 0.05$).

Size-Dependent Over-Winter Survival

Electrofishing was used to sample fish in fall (October) and spring (March; ~age-1) of each year. Twenty-minute electrofishing transects were conducted in the same habitats where block-netting took place using pulsed DC current, and sampling was continued at each lake until at least 100 juvenile largemouth bass were captured. Otoliths were removed from juvenile largemouth bass collected by electrofishing and examined to ensure lack of an annulus. Size structure of age-0 largemouth bass in each sampling event was used to assess relative overwinter size-specific survival in each lake and year. Differences in size structure between sampling periods were determined using Kolmogorov-Smirnov tests (Zar 1999).

Results

Early Age and Growth

Age-0 largemouth bass hatching seasons varied widely by region in Florida, but were generally similar for both lakes in each region. Spawning periodicity (i.e., the distribution of hatching events during the spawning season) was variable within lakes and resulted in differing hatch dates that corresponded to early-, middle-, and late-hatched sub-cohorts between years (Table 2-2). Largemouth bass from south lakes hatched earlier than central and north lakes fish during both years. Hatching initiation began in early December at south lakes (Figures 2-2, 2-3) and not until early March at north lakes (Figures 2-2, 2-3). In central lakes, age-0 largemouth bass initiated hatching in mid to late February, except at Lake Monroe some fish hatched in January 2004 (Figures 2-2, 2-3). I detected different hatching initiation dates for the south region lakes during 2003. During 2003, hatching began in February at Lake Istokpoga, but in early December at Lake Okeechobee (Figures 2-2, 2-3). Hatching distributions were multimodal in many cases, indicating that spawning activity peaked at several times through the spawning seasons.

Total hatching distributions and water temperatures during spawning also varied among regions, with more protracted hatching distributions in the south relative to north lakes. Hatching durations ranged from 61 d at Lake Harris in 2003 to 160 d at Lake Istokpoga in 2004 (Table 2-2). Hatching durations were longest at south lakes, shorter at central and north lakes, and least variable at north lakes relative to the other lakes (Table 2-2). Water temperatures at hatching initiation were as low as 14.7° C at Lake Talquin and as high as 22.0° C at Lake Istokpoga during the study. Hatching occurred at temperatures up to 29.6° C at Lake Istokpoga

during 2004. Water temperatures at median hatching dates ranged from 19.0° C at Lake Istokpoga during 2003 to 25.7° C at Lake Istokpoga during 2004 (Table 2-2).

Linear models described relationships between mean TL and age (days) as well as exponential models (all Variance Ratio Tests with $P > 0.12$), and thus, I used linear models to describe growth rates. Mean DGR of fish varied among lakes and sub-cohorts, but differences were not always consistent for lakes within regions. The lake*hatching period interaction was significant in 2003 (both $P < 0.001$) indicating that mean DGR varied with both factors, but differences were not consistent across lakes or hatching periods. For example, all sub-cohorts from Lake Istokpoga exhibited relatively rapid growth in 2003 (all hatching periods ≥ 0.60 mm/d), whereas Lake Okeechobee growth rates were low for the early-hatched sub-cohort (0.43 mm/d) and were more rapid for mid- and late-hatched sub-cohorts (0.57 and 0.59 mm/d, respectively; Table 2-3). In 2004, early-hatched sub-cohorts at both south lakes grew slowly (mean DGR 0.40-0.43), whereas middle- and late-hatched sub-cohorts grew faster (mean DGR 0.51-0.59; Table 2-3). The 2003 year class exhibited rapid growth at north lakes with mean DGR ≥ 0.68 mm/d for all sub-cohorts. The 2004 year class had moderate to rapid growth at the north lakes (mean DGR range = 0.59 – 0.82; Table 2-3). Central lakes had moderate growth rates (range 0.53-0.73 mm/d) that did not vary among sub-cohorts during either year. Thus, for three of four lake-year combinations at south lakes, I found that early-hatched sub-cohorts had slow growth relative to later-hatched sub-cohorts and other study lakes in Florida.

Similar to growth-rate data, survival of age-0 largemouth bass varied among sub-cohorts and regions and was generally lowest for early-hatched sub-cohorts at south lakes. In 2003, survival of fish between March and May at south lakes was lower for early (mean $S=0.06$) than for middle-hatched (mean $S=0.38$, $P < 0.02$; Table 2-4) sub-cohorts. Late-hatched sub-cohorts

had not recruited to the block net for comparison of survival between March and May. Survival between the May and July sampling periods for the 2003 year class ranged from 0.16 to 0.29 across regions and sub-cohorts, but mean survival did not differ for either variable (both $P \geq 0.2$; Table 2-4). In 2004, both early and middle-hatched sub-cohorts at south lakes had low survival (0.14 early, 0.11 middle) between February and late April, and these values did not differ ($P > 0.90$). Late-hatched sub-cohorts again had not recruited to the gear for this comparison. Survival between April/May and June/July for the 2004 year class differed by region ($P = 0.02$), with the hatching period effect marginally significant ($P = 0.07$) and the interaction effect not significant ($P = 0.8$). Survival from May to July was higher at north than south lakes ($S = 0.32$ in north lakes, 0.12 in south lakes, $P < 0.01$), and central lakes had intermediate values ($S = 0.19$; Table 2-4). The hatching period effect showed that early-hatched sub-cohorts across all regions had marginally lower survival ($S=0.12$) than middle and late hatched sub-cohorts (both least squares mean $S=0.25$, both $P < 0.2$ in least squares means comparisons; Table 2-4). Thus, the severity of mortality varied among regions and hatching periods with early-hatched sub-cohorts having low survival prior to summer (all $S \leq 0.14$) at south lakes in both years.

Water temperatures after hatching influenced age-0 largemouth bass growth. The mean DGR for a given hatching period was positively related to the average water temperature during the 40 d period following the median hatch date for that hatching period across all lakes and years ($r = 0.60$, $P < 0.001$) (Figure 2-4). Early-hatched sub-cohorts at south lakes endured average temperatures of approximately 18°C for the first 40 days after hatching, except for the early-hatched sub-cohort at Lake Istokpoga in 2003. Later-hatched sub-cohorts at south lakes and all sub-cohorts at middle and north lakes experienced average temperatures $\geq 20^\circ\text{C}$ for the

first 40 days after hatching and all mean DGR for these sub-cohorts were greater than 0.53 mm/d.

Size-Dependent Over-Winter Survival

I found little evidence of size-selective over-winter mortality because length frequency distributions from electrofishing in the fall (age-0) and following spring (age-1) were similar for most lakes in both years (Figures 2-5, 2-6). Only the 2003 length frequency distributions from Lakes Harris and Talquin (Figure 2-5) differed between October and March electrofishing samples (both $P = 0.02$). At Lake Harris, the relative number of small fish declined over winter, but the minimum size between fall and spring did not change and the maximum size increased, thus suggesting that growth occurred for the larger fish. At Lake Talquin, an apparent mode of fish at 9-10 cm during fall increased greatly to 10-13 cm the following spring and both the minimum and maximum sizes increased between fall and spring. Small samples sizes at Lake Monroe during March 2005 (2004 year class, ~ age-1) prevented evaluations of length frequencies from fall to spring, which was likely due to hurricane effects that increased mortality and/or greatly decreased sampling catchability because of extremely high water levels. Maximum size increased from fall to winter at all lakes and years, suggesting that growth occurred over-winter, except at Lake Seminole in 2003 where neither minimum size nor maximum size changed over-winter. If over-winter mortality were highly size-selective for Florida lakes, I expected to see significant changes in the shape of the length frequency distributions between fall and spring, which rarely occurred in either year. Although I was unable to assess the overall strength of overwinter mortality in Florida, my results suggested that mortality during this period was not strongly size-dependent.

Discussion

I found evidence that limited the application of the current conceptual framework regarding hatch date and severity of overwinter mortality for age-0 largemouth bass recruitment. Current hypotheses would have predicted highest survival for early-hatched sub-cohorts relative to later hatched sub-cohorts in all lakes and years (Trebitz 1991, Miranda and Hubbard 1994; Ludsin and Devries 1997; Garvey et al. 1998; Pine et al. 2000). I observed very slow growth for three of four early-hatched sub-cohorts at my lowest latitude lakes and never observed survival advantages for early-hatched sub-cohorts through their first summer at any Florida latitude I evaluated relative to later-hatched sub-cohorts. I also found no evidence that size-selective overwinter mortality would restructure largemouth bass year classes for Florida lakes by limiting survival of smaller fish. Garvey et al. (1998) reviewed 15 studies that investigated overwinter survival of age-0 largemouth bass from Wisconsin to Alabama and predicted reduced overwinter survival for small fish in southern systems with warm winter temperatures and active predators. The addition of my results to those reviewed by Garvey et al. (1998) suggested that size-selective overwinter mortality likely exhibits a parabolic pattern in North America, with highest overwinter mortality at intermediate latitudes of the largemouth bass's distribution (i.e., Missouri - Alabama; see Garvey et al. 1998).

The growth and survival differences from hatching through the first summer likely influenced the potential for hatching sub-cohorts to contribute to the year class. Early-hatched sub-cohorts of the 2003 and 2004 year classes at south lakes exhibited high mortality, and thus, likely contributed less to the age-1 largemouth bass year classes than later-hatched sub-cohorts. I suspected that adult largemouth bass likely initiated spawning at a similar time at both south lakes in 2003, as seen in 2004, and that a mortality event prevented detection of some early-

hatched fish at Lake Istokpoga in 2003. Evidence includes the truncated hatching distribution at this system in 2003 (Figure 2-2) and an independent radio telemetry study at Lake Istokpoga during the 2003 spawning season that indicated movement of adult largemouth bass into spawning habitats during months when no hatching was detected (i.e., Dec – Jan) (unpublished data, J. Furse, Florida Fish and Wildlife Conservation Commission). Low survival for early-hatched fish also has been reported for other species, including American Shad *Alosa sapidissima* (Crecco and Savoy 1985), bloater *Coregonus hoyi* (Rice et al. 1987), striped bass *Morone saxatilis* (Rutherford and Houde 1995), and Korean sandeel *Hypoptychus dybowskii* (Narimatsu and Munehara 1999), owing to environmental limitations (e.g., storm events, temperature). Reduced growth of early-hatched sub-cohorts at south lakes potentially prolonged the period of vulnerability to gape-limited predators and reduced predator avoidance abilities (e.g., swimming speed), and thus led to increased mortality (Houde 1987; Miller et al. 1988). Bestgen et al. (2006) reported more rapid growth yet higher mortality for early-hatched Colorado pikeminnows relative to later-hatched fish because of temporal patterns in predator abundances in juvenile habitats. Survival and growth disadvantages for early-hatched sub-cohorts at north and central lakes were not as strong as disadvantages detected at south Florida lakes. However, the potential contribution of early-hatched sub-cohorts to year-classes at all lakes in 2004 was likely decreased due to low survival through their first summer relative to later-hatched sub-cohorts.

I was surprised to find that growth rates appeared to be limited by low water temperatures at sub-tropical south Florida lakes. However, adults began spawning in early December in my south region leaving nearly the entire “winter” for cold fronts to influence their progeny. Although early-hatched sub-cohorts at south Florida lakes suffered high mortality, early-hatched

fish that survived to July were larger than fish from the other hatching sub-cohorts. Furthermore, early-hatched fish had more fish prey in diets than smaller, later hatched fish in July (Rogers and Allen 2005). Thus, some of the proposed advantages to early hatching were still evident despite poor survival for early-hatched members of the year class. Similar results were reported for age-0 largemouth bass in Alabama ponds where early-hatched fish exhibited slower growth than later-hatched fish, but they were larger and expressed increased piscivory relative to smaller, later-hatched fish (Ludsin and DeVries 1997). Other early-hatched centrarchids (i.e., bluegill *Lepomis macrochirus* and pumpkinseed *Lepomis gibbosus*) also have exhibited reduced growth rates owing to cool water temperatures after hatching that resulted in low survival relative to later-hatched fish born at warmer water temperatures (Garvey et al. 2002b).

Strong size-selective overwinter mortality has been more commonly reported for southern systems (Boxrucker 1982; Miranda and Hubbard 1994; Ludsin and DeVries 1997, but see Jackson and Noble 2000 and Peer et al. 2006) than at northern and central latitudes (Kohler et al. 1993), however results have varied owing to study system-specific characteristics (e.g., predator presence; Garvey et al. 1998). Starvation and predation are the common mechanisms attributed to size-selective over-winter mortality. Small fish have lower lipid reserves and higher mass-specific metabolism relative to larger fish, thus starvation is typically higher for small juveniles when prey resources and low winter temperatures limit feeding (Oliver et al. 1979; Henderson et al. 1988; Miranda and Hubbard 1994; Ludsin and DeVries 1997, but see Wright et al. 1999). Predation also has been suggested as a major mechanism resulting in overwinter mortality when winter water temperatures reduce activities of juvenile largemouth bass (i.e., $\leq 6^{\circ}\text{C}$; Garvey et al. 1998, Fullerton et al. 2000), but remain warm enough for predators to remain active and preferentially prey on small age-0 fish (Garvey et al. 1998). Although winter water

temperatures were conducive to predation at all Florida study lakes in both years, they also remained above 6° C, and thus, age-0 fish activity was not likely limited. In Florida lakes, size-selective overwinter mortality may not have resulted in a survival bottleneck because most age-0 largemouth bass surpassed 10 cm TL by fall and overwinter growth occurred at almost all lakes, whereas Ludsin and DeVries (1997) reported little overwinter growth in central Alabama ponds and reported significantly higher overwinter mortality for fish < 100 mm than for larger fish. Size-selective predation during winter could have been minimized in my study because lakes generally had highly vegetated littoral zones that potentially provided refuge and localized food resources as suggested by Miranda and Hubbard (1994) and Garvey et al. (1998). Starvation was not apparent in my study because total lipid concentrations did not differ from fall to spring for any size class at my study lakes (Rogers and Allen 2005) and suggested that juvenile largemouth bass in Florida were not reliant on energy reserves for overwinter survival. Similarly, Peer et al. (2006) reported over-winter growth and no evidence of size-selective over-winter mortality for age-0 largemouth bass in southern Alabama (i.e., similar latitudes to my north Florida lakes). Thus, conventional hypotheses that predict strong effects of size-selective over-winter mortality apparently do not apply to systems with available predator refuges and over-winter growth, as suggested by Garvey et al. (1998).

The populations I studied were primarily Florida largemouth bass at south and central regions and naturally introgressed largemouth bass (crosses between Florida largemouth bass and northern largemouth bass *M. s. salmoides*) at my north region (Table 2-1; B. L. Barthel, unpublished data). Genetic differences among my study populations could have influenced my results because these differing genetic strains have been reported to respond differentially to environmental conditions. For example, Cichra et al. (1982) reported lower tolerances to cold

shock for Florida largemouth bass than northern largemouth bass and Isely et al. (1987) reported faster growth for northern and intergrade largemouth bass relative to Florida largemouth bass that were stocked in Illinois ponds. Philipp et al. (1985) hypothesized that Florida and northern largemouth bass spawning seasonality have differentially evolved owing to environmental conditions during spawning seasons, and Rogers et al. (2006) reported that genetic composition contributed to adult largemouth bass spawning times in Florida. Thus, genetic differences among my study populations could have influenced my results. Interestingly, my results indicated that despite a shorter growing season at north lakes relative to other regions, maximum lengths at age-1 were similar across all lakes. These results are suggestive of counter-gradient growth given known genetic differences among these populations; but, growth observations from field studies result from complex ecological interactions (Garvey et al. 2003) and carefully controlled (e.g., without latitudinal mortality influences as in this study) studies would be required to further clarify the potential effects of genetics to my results. Kassler et al. (2002) suggested elevating the *M. s. floridanus* subspecies to the species level (i.e., Florida bass *Micropterus floridanus*) based on meristics and allozyme and mitochondrial DNA analyses, however the populations I studied currently remain recognized as varying genetic strains of the same species. The influence of genetics to my results cannot be discerned from this study, but future research could reveal the importance of genetic variation to latitudinal hypotheses for largemouth bass recruitment as seen for other species (e.g., Conover 1990).

My results suggested that current latitudinal hypotheses for largemouth bass do not always apply to populations at the southern extent of their natural distribution. Hatching distributions appeared to reflect characteristics that would compensate for local environmental conditions when growing season length did not appear to constrain survival. More protracted

distributions at south lakes, relative to north lakes, were likely maintained by effects of annual variability in environmental conditions (e.g., water temperature) following spawning that results in variable hatching-date dependent survival. Winter water temperatures during my study were below the 10-yr average for the period of December to February (unpublished data, South Florida Water Management District, West Palm Beach, Florida). Annual mean water temperature for the December to February time period ranged from 15.6°C to 19.6°C for 1996-2005 with an overall mean of 17.9 °C. The years for this study (2003 and 2004) averaged 16.8 °C and 15.6 °C (the 10-year low), respectively. Thus, the years I sampled had relatively cool water temperatures, and early hatching may provide a survival advantage during years with warmer conditions. At central and north region lakes, water temperatures prevented spawning until later in the year, which limited the duration that juveniles were vulnerable to influences of winter cold fronts relative to south lakes. Garvey et al. (2002*b*) proposed that protracted spawning distributions acted to maximize mean fitness for bluegill and pumpkinseed sunfish at Lake Opinicon, Canada, where spring conditions can result in variable survival for early-hatched fish. Similarly, early spawning of largemouth bass in Florida, relative to other latitudes, likely provides foraging and predator avoidance advantages during favorable years, and protracted spawning should provide some progeny survival during unfavorable years. Largemouth bass life history strategies in Florida's mild climate appeared to differ from mid-temperate latitudes, where growing season length and winter conditions can create size-dependent survival bottlenecks. Recruitment processes vary among latitudes (Garvey et al. 1998), systems at similar latitudes (Garvey et al. 1998), and sites within a system (Peer et al. 2006) because of complex ecological interactions (e.g., among physical, chemical, and biological factors). Thus, our

understanding of recruitment and ability to refine recruitment hypotheses requires evaluations at multiple scales throughout a species' distribution.

Table 2-1. Physical and chemical characteristics of 6 Florida study lakes and genetic characteristics of their largemouth bass populations

Region	Lake	Latitude	Average		Trophic state ^a	TP (mg:L ⁻¹)	TN (mg:L ⁻¹)	Chl-a (mg:L ⁻¹)	SD (m)	MD (m)	SA (m ²)	% FL LMB alleles
			Winter water temperature (°C)	Summer water temperature (°C)								
North	Seminole ^b	30°	12.5	28.5	Eutrophic	35	590	9	1.9	4.5	13,158	59
	Talquin ^b	30°	12.2	28.6	Eutrophic	54	670	29	3.3	3.0	3,560	64
Central	Harris ^c	28°	16.3	30.0	Eutrophic	28	1550	37	0.6	4.0	5,580	99
	Monroe ^d	28°	16.1	29.6	Eutrophic	100	2200	39	0.7	2.3	3,308	100
South	Istokpoga ^c	27°	18.4	29.7	Eutrophic	210	700	10	0.9	1.8	11,207	100
	Okeechobee ^c	27°	18.6	29.8	Eutrophic	92	1480	30	0.5	2.7	173,000	100

winter = Dec - Feb, summer = Jun - Aug, TP = total phosphorus, TN = total nitrogen, Chl-a = chlorophyll a, SD = secchi depth, MD = mean depth, SA = surface area, FL LMB = Florida largemouth bass *Micropterus salmoides floridanus*, a = estimated according to criteria of Forsberg and Ryding (1980). ^bFlorida Lakewatch (2000). ^cBachmann et al. (1996). ^dSeminole County Watershed Atlas (2001). Genetics results are from diagnostic allozyme analyses conducted by the Illinois Natural History Survey (B. Barthel, personal communication).

Table 2-2. Dates corresponding to sub-cohort hatching periods, median hatch dates, and water temperatures (°C) at corresponding median hatch dates for the 2003 and 2004 largemouth bass year classes at 6 Florida study lakes.

Year Class	Region	Lake	Early sub-cohort hatch range	Middle sub-cohort hatch range	Late sub-cohort hatch range	Median hatch date	Water temperature at median hatch
2003	North	Seminole	06 Mar. - 03 Apr.	04 Apr. - 23 Apr.	24 Apr. - 04 Jun.	17 Apr.	22.4
		Talquin	05 Mar. - 14 Apr.	15 Apr. - 24 Apr.	25 Apr. - 02 Jun.	19 Apr.	20.7
	Central	Harris	17 Feb. - 06 Mar.	07 Mar. - 25 Mar.	26 Mar. - 18 Apr.	12 Mar.	24.1
		Monroe	01 Mar. - 22 Mar.	23 Mar. - 17 Apr.	18 Apr. - 06 May	14 Apr.	23.0
	South	Istokpoga	06 Feb. - 03 Mar.	04 Mar. - 05 Apr.	06 Apr. - 05 May	23 Mar.	25.7
		Okeechobee	07 Dec. - 24 Jan.	25 Jan. - 28 Feb.	29 Feb. - 24 Apr.	30 Jan.	19.9
2004	North	Seminole	03 Mar. - 16 Mar.	17 Mar. - 20 Apr.	21 Apr. - 05 Jun.	31 Mar.	20.9
		Talquin	09 Mar. - 23 Mar.	24 Mar. - 20 Apr.	21 Apr. - 25 May	02 Apr.	19.9
	Central	Harris	14 Feb. - 02 Mar.	03 Mar. - 23 Mar.	24 Mar. - 14 May	12 Mar.	19.6
		Monroe	11 Jan. - 02 Mar.	03 Mar. - 23 Mar.	24 Mar. - 06 May	07 Mar.	21.5
	South	Istokpoga	15 Dec. - 10 Feb.	11 Feb. - 06 Apr.	07 Apr. - 23 May	01 Mar.	19.0
		Okeechobee	13 Dec. - 13 Jan.	14 Jan. - 13 Apr.	14 Apr. - 07 May	02 Mar.	19.6

Table 2-3. Mean daily growth rate (mm/d, Mean DGR), and standard deviation (SD) for age-0 largemouth bass collected in block nets during spring and summer of each year.

Year class	Region	Lake	Hatching period	Mean DGR	SD
2003	North	Seminole	Early	0.68	0.11
		Seminole	Middle	0.72	0.14
		Seminole	Late	0.72	0.11
		Talquin	Early	0.76	0.12
		Talquin	Middle	0.78	0.12
		Talquin	Late	0.77	0.15
	Central	Harris	Early	0.57	0.13
		Harris	Middle	0.55	0.11
		Harris	Late	0.61	0.14
		Monroe	Early	0.72	0.11
		Monroe	Middle	0.72	0.10
		Monroe	Late	0.73	0.09
	South	Istokpoga	Early	0.69	0.08
		Istokpoga	Middle	0.60	0.13
		Istokpoga	Late	0.61	0.11
		Okeechobee	Early	0.43	0.07
		Okeechobee	Middle	0.57	0.10
		Okeechobee	Late	0.59	0.10
2004	North	Seminole	Early	0.59	0.13
		Seminole	Middle	0.62	0.17
		Seminole	Late	0.82	0.21
		Talquin	Early	0.73	0.16
		Talquin	Middle	0.64	0.12
		Talquin	Late	0.65	0.13
	Central	Harris	Early	0.53	0.07
		Harris	Middle	0.53	0.09
		Harris	Late	0.56	0.07
		Monroe	Early	0.60	0.10
		Monroe	Middle	0.53	0.11
		Monroe	Late	0.69	0.06
	South	Istokpoga	Early	0.43	0.11
		Istokpoga	Middle	0.52	0.09
		Istokpoga	Late	0.57	0.08
		Okeechobee	Early	0.40	0.09
		Okeechobee	Middle	0.51	0.09
		Okeechobee	Late	0.59	0.10

Table 2-4. Analysis of variance results for survival comparisons among hatching periods and regions of Florida.

Year class	Time period	Comparison	F statistic	P value	Least squares means	
					Hatching sub-cohort	Survival
2003	Mar - May	Hatch period	7.12 _{1,10}	0.02	Early	0.06
					Middle	0.38
	May - Jul	Region	0.45 _{2,45}	0.85	North	0.19
					Central	0.22
		Hatch period	1.66 _{2,45}	0.20	South	0.24
					Early	0.16
2004	Feb - Apr	Hatch period	0.00 _{1,9}	0.96	Middle	0.29
					Late	0.20
	May - Jun/Jul	Region	4.41 _{2,48}	0.02	Early	0.14
					Middle	0.11
		Hatch period	2.81 _{2,48}	0.07	North	0.32
					Central	0.19
				South	0.12	
				Early	0.12	
				Middle	0.25	
				Late	0.25	

Column two defines the period that survival was estimated for, column three gives variables tested in the model for that time period, column four gives the F value and test degrees of freedom, column five reports the significance level for the variable, and columns six and seven give least squares means estimates for the individual groups within each factor. March to May and February to April survival could only be estimated for our south region.

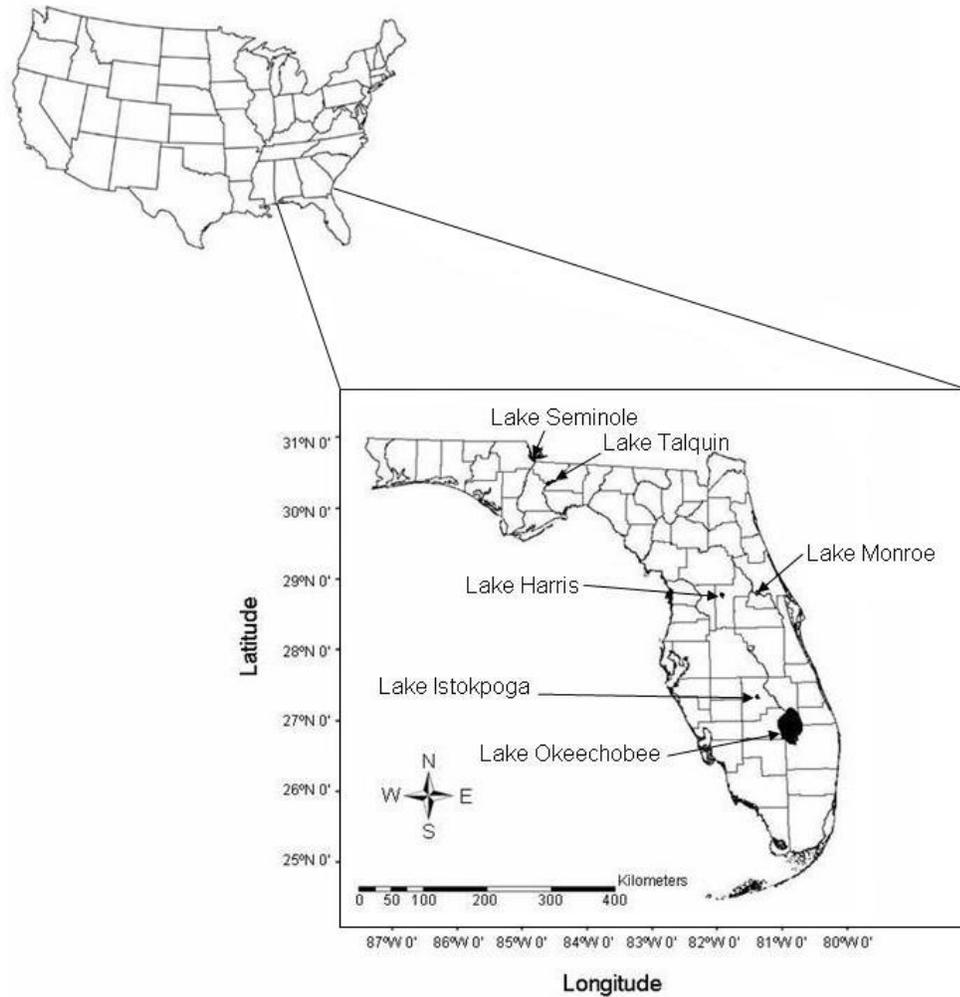


Figure 2-1. Selected north region (Lakes Seminole and Talquin), central region (Lakes Harris and Monroe), and south region (Lakes Istokpoga and Okeechobee) study lakes for comparing hatching distributions, growth, and mortality of age-0 largemouth bass across Florida's latitudinal gradient.

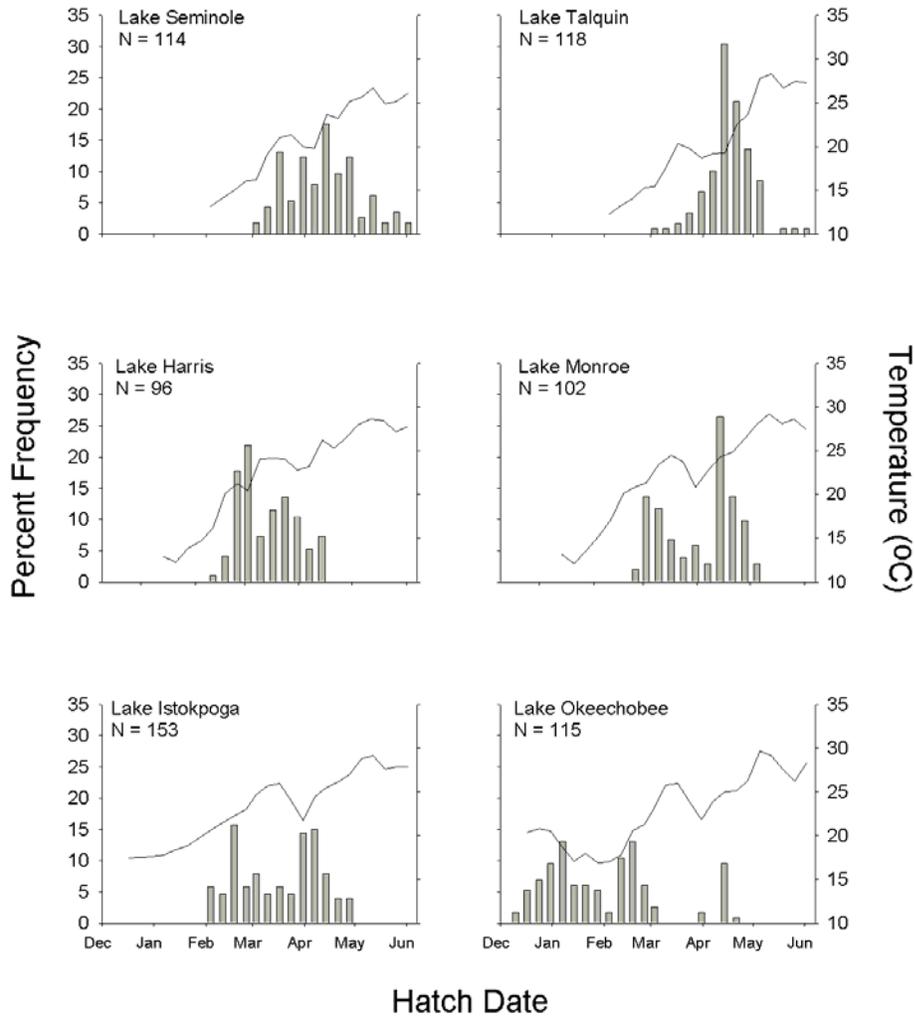


Figure 2-2. Relative frequency distributions (bars, y axes) of age-0 largemouth bass hatching at north lakes (top panels), central lakes (middle panels), and south lakes (bottom panels) in 2003. Hatch dates (x axes) were determined using daily rings on otoliths (N=number of fish aged). Temperature is indicated on the z axis and by the solid line.

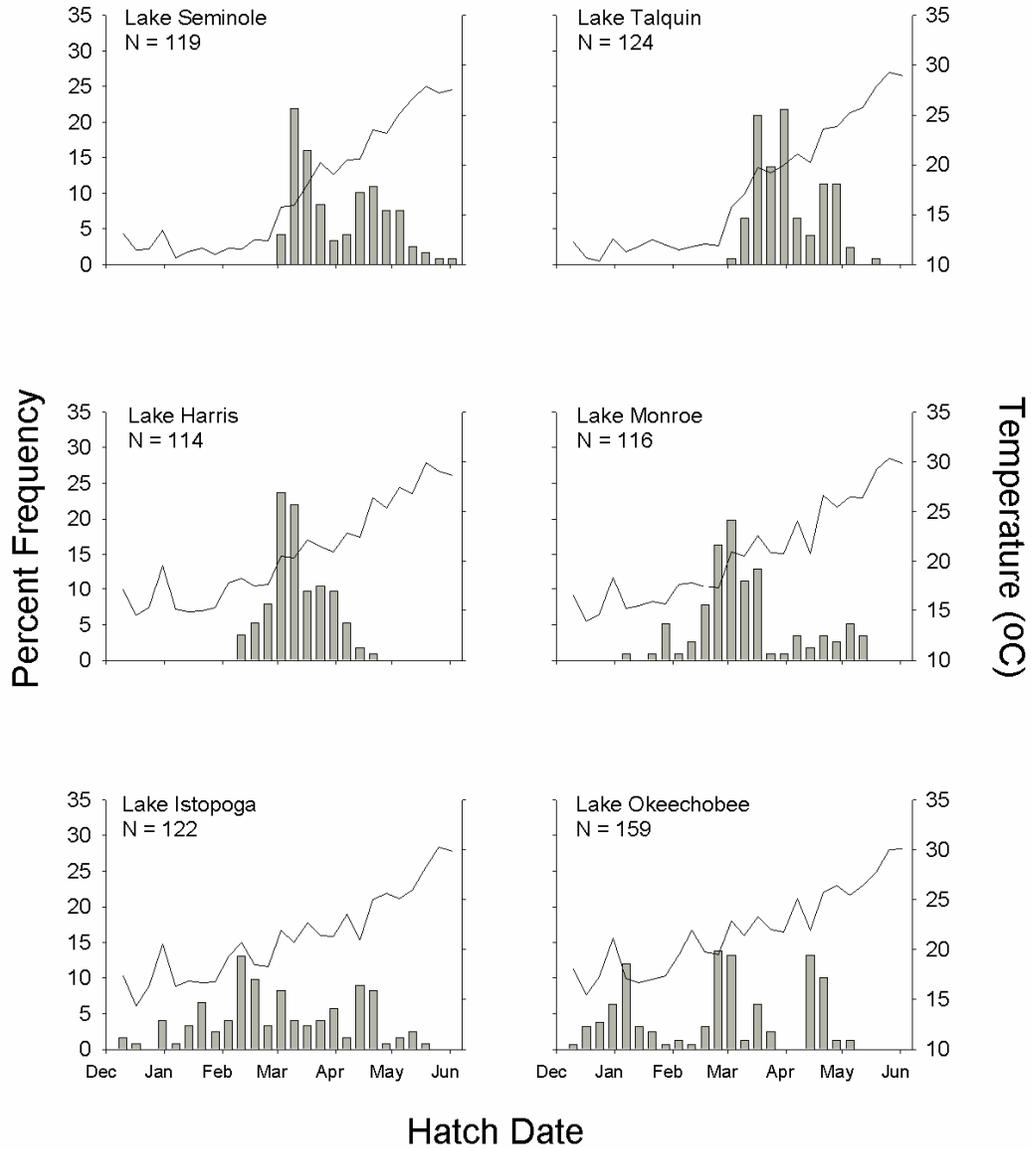


Figure 2-3. Relative frequency distributions (bars, y axes) of age-0 largemouth bass hatching at north lakes (top panels), central lakes (middle panels), and south lakes (bottom panels) in 2004. Hatch dates (x axes) were determined using daily rings on otoliths (N=number of fish aged). Temperature is indicated on the z axis and by the solid line.

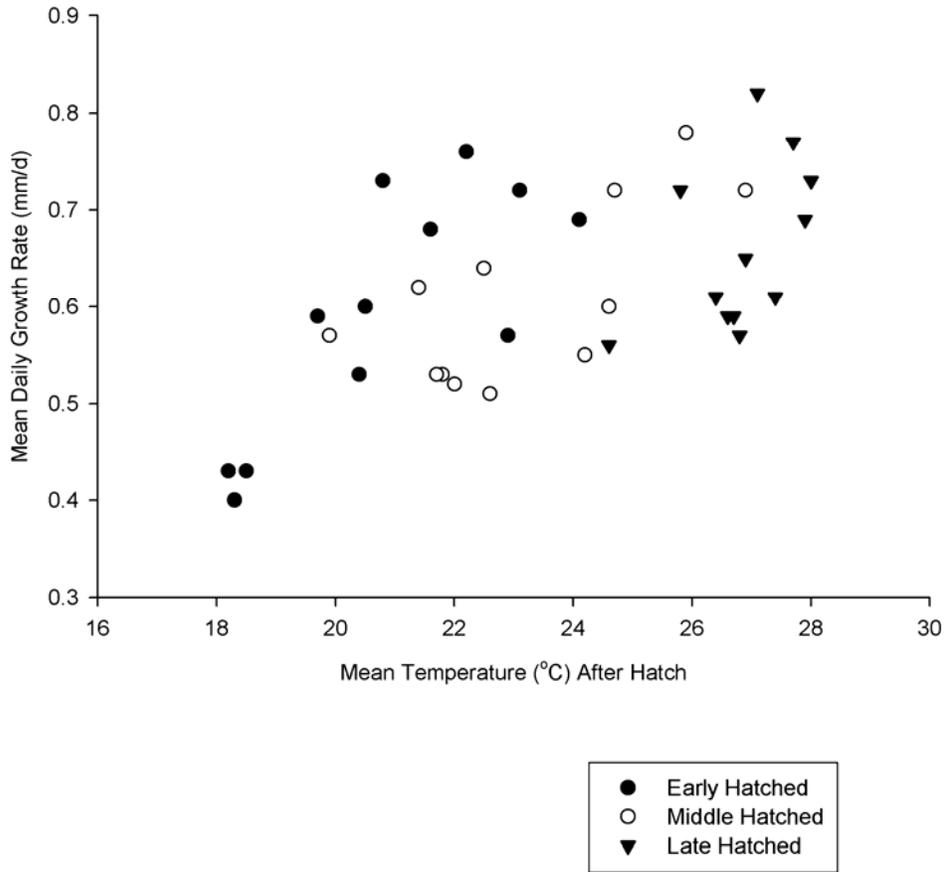


Figure 2-4. Relationship between mean daily growth rates and average temperatures from the 40-day period following the median hatch date for early, middle, and sub-cohorts, from 6 Florida lakes during 2003 and 2004. Data points (n = 3) closest to the origin result from slow-growing early-hatched sub-cohorts at Lake Okeechobee during 2003 and 2004, and at Lake Istokpoga during 2004.

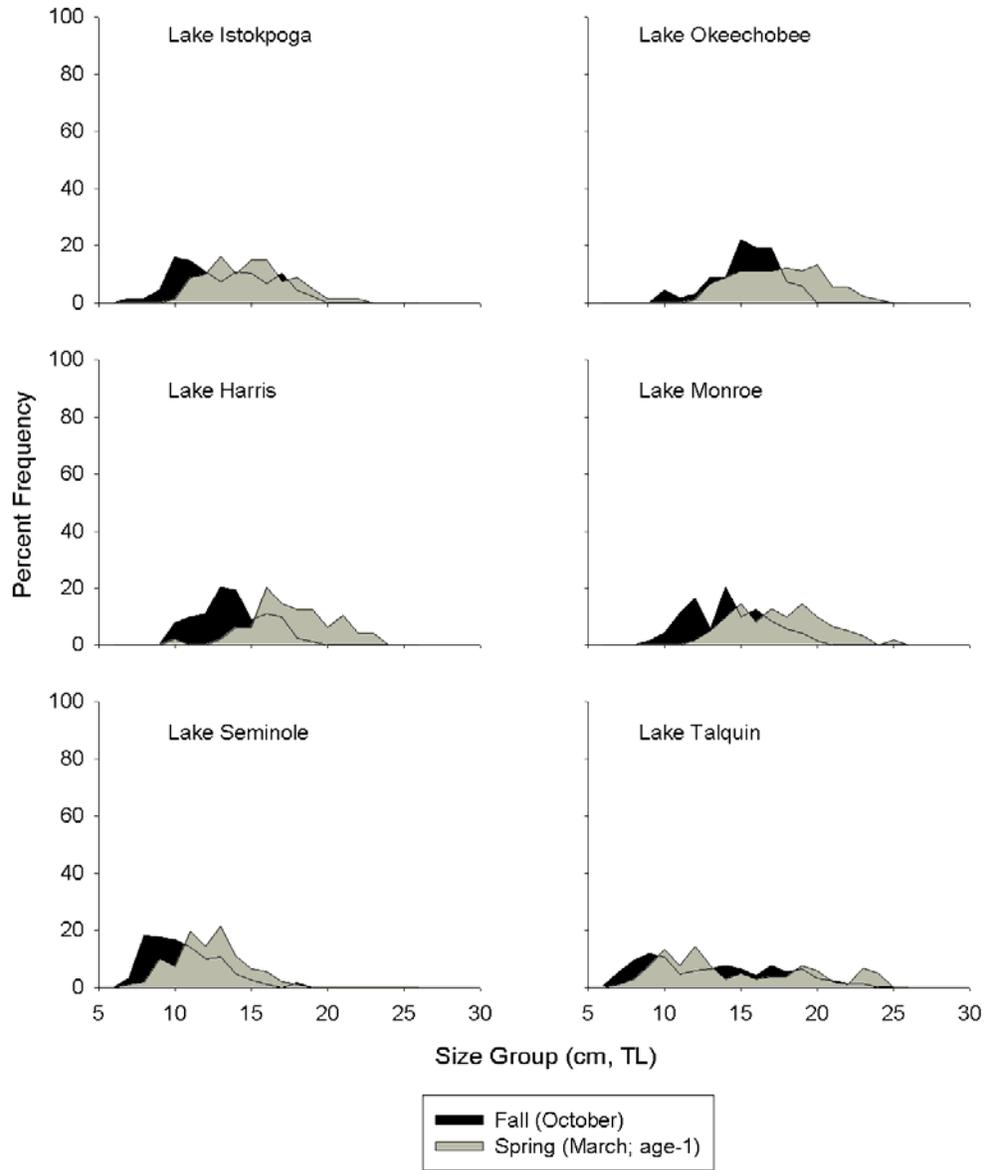


Figure 2-5. Length frequency distributions for 2003 fall and spring (~age-1) samples of age-0 largemouth bass collected by electrofishing at north (Lakes Seminole and Talquin), central (Lakes Harris and Monroe), and south (Lakes Istokpoga and Okeechobee) Florida lakes.

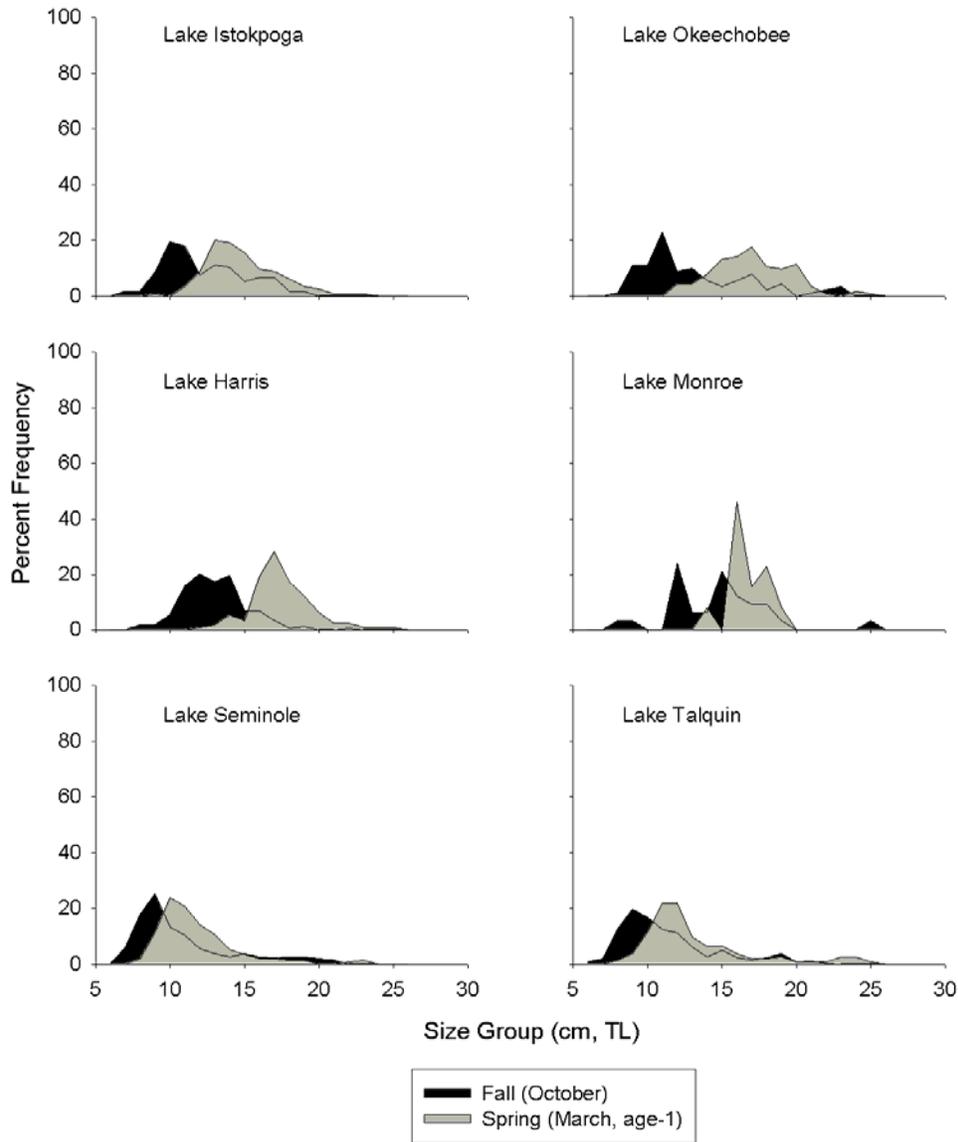


Figure 2-6. Length frequency distributions for 2004 fall and spring (~age-1) samples of age-0 largemouth bass collected by electrofishing at north (Lakes Seminole and Talquin), central (Lakes Harris and Monroe), and south (Lakes Istokpoga and Okeechobee) Florida lakes.

CHAPTER 3
SEPARATING GENETIC AND ENVIRONMENTAL INFLUENCES ON TEMPORAL
SPAWNING DISTRIBUTIONS OF LARGEMOUTH BASS (*Micropterus salmoides*)

Genetic and environmental factors influence fish spawning periodicity (i.e., the distribution of spawning events during the breeding season), but their relative contributions are often difficult to discern. Many studies (e.g., Ludsin and DeVries 1997; Garvey et al. 1998) have illustrated the importance of hatching date to growth and survival of age-0 fishes, but few have evaluated the factors influencing spawning periodicity (i.e., duration and frequency of spawning events through the season). Spawning initiation (i.e., the onset of the breeding season) is regulated by environmental factors such as temperature and photoperiod (Kramer and Smith 1960; Lam 1983), and thus, spawning seasons occur later in the year at high latitudes relative to low latitudes (Conover 1992). Spawning season duration is often inversely related to latitude, in part, because adults cease spawning when offspring no longer have a chance for over-winter survival (Johannes 1978; Munro et al. 1990; Conover 1992). Spawning periodicity has been related to multiple environmental factors such as water temperature (Conover 1992), photoperiod (Heidinger 1975), changes in water levels (Ozen and Noble 2002), and food availability during gonadal development (Koslowski 1992). For example, Baltic cod (*Gadus morhua*) spawning was delayed during years of cooler spring water temperatures (Wieland et al. 2000). Largemouth bass began spawning in a Puerto Rico reservoir, which was thermally stable (24-30 °C) through the year, when photoperiod began to increase during winter (Ozen and Noble 2005). Spawning duration was also related to water level fluctuations in Puerto Rico reservoirs (Ozen and Noble 2002).

Genetic composition of a stock also influences spawning periodicity. Reproductive processes in fish are regulated, in part, by endogenous hormone cues (Patiño 1997; Van Der

Kraak et al. 1998), which are regulated by genes (e.g., Denslow et al. 2001). Genotypic effects have led to synchronous spawning of predators in relation to prey abundance, thus resulting in high availability of food resources for newly hatched larvae, assuming increased foraging opportunities at hatching leads to increased survival for offspring (Hjort 1914; Cushing 1975). Atlantic herring (*Clupea harengus harengus*) exhibit genotypic influences to spawning periodicity across their broad latitudinal range because hatching within specific larval retention areas is related to increased local food availability (i.e., plankton blooms) for larvae in that specific locale (Cushing 1975; Sinclair and Tremblay 1984). Similarly, genetics can influence spawning periodicity because evolution of multiple spawning or a prolonged spawning season duration may prevent loss of an individual's annual reproductive output due to environmental conditions (Conover 1992; Fox and Crivelli 1998). However, the relative contributions of genetic and environmental influences are poorly understood, and variable spawning initiation and periodicity are often attributed to phenotypic plasticity (Baylis et al. 1993; Conover and Schultz 1997). Contributions of genotypic variability to phenotypic patterns have largely been ignored (Conover and Schultz 1997).

Largemouth bass provide an excellent species for evaluating genetic and environmental influences on spawning periodicity because they have a wide native geographic distribution with a natural genetic gradient, as indicated by latitudinal clines in allele frequencies at several loci (Philipp et al. 1983). Ecologically, juvenile largemouth bass suffer from differing mortality factors across latitudes (Garvey et al. 1998), and spawning periodicity strongly influences juvenile largemouth bass survival and recruitment (Ludsin and DeVries 1997; Pine et al. 2000). Thus, differing selection pressures may exist along the latitudinal distribution of largemouth bass that would facilitate localized adaptations for spawning periodicity. Comparisons between

genetically verified fish indicated that NLMB spawned earlier than FLMB and ILMB when stocked together in Illinois ponds and a Texas reservoir (Isely et al. 1987; Maceina et al. 1988), but those studies occurred outside the native range of FLMB. No studies have separated environmental influences on spawning periodicity from genetic influences by comparing populations with known genetic contrasts while monitoring environmental conditions.

Genetic differences across the distribution of largemouth bass have been recognized for decades. Northern and Florida largemouth bass have been recognized as distinct subspecies for more than 50 years (Bailey and Hubbs 1949). Northern largemouth bass are endemic to the northern United States, FLMB naturally occur in south Florida, and intergrades (ILMB) occur in north Florida, several southeastern states (e.g., Georgia, Alabama, Mississippi, South Carolina, North Carolina, Virginia and Maryland), and other areas where introductions have occurred. Kassler et al. (2002) recommended elevating the status of FLMB from a subspecies to species status (i.e., Florida bass, *M. floridanus*) based on discriminate function analysis of meristic characters, allozyme analysis, and mitochondrial DNA (mtDNA) data. Physiological attributes (e.g., temperature tolerances) and relative survival differences have also been reported for translocated fish in several performance evaluations (e.g., Cichra et al. 1982, Philipp and Whitt 1991). However, phenotypic variability in morphometric and life history traits of broadly distributed species is not uncommon (Schultz et al. 1996). At the time of my study, the taxonomic nomenclature accepted by the American Fisheries Society remains at the subspecies level.

I compared temporal hatching distributions between a population of FLMB from Lake Okeechobee in south Florida and an ILMB population from Lake Seminole at the Florida-Georgia border. Lake Okeechobee represents a pure population of FLMB, and Lake Seminole is

an intergrade population (ILMB, Philipp et al. 1983). I used estimated hatch dates, from sagittal otoliths as indices of spawning periodicity assuming that hatching occurred two days after fertilization. Spawning periodicity was compared between brood sources for fish reared in environmentally similar experimental ponds at an intermediate latitude. I also assessed whether the trends found in experimental ponds corresponded to the spawning periodicity for the two natural populations at their source lakes. My study design allowed us to maintain similar environmental conditions during brood fish sexual maturation at the intermediate latitude and evaluate influences of genetic factors to spawning periodicity. If genetic composition affected spawning periodicity, I expected spawning of translocated fish to reflect the periodicity of their source populations. In contrast, I surmised that if environmental factors more strongly influenced spawning periodicity, then translocated fish that spawned in ponds would have similar distributions, and pond distributions would differ from both source lake populations.

Methods

Pond Methods

Brood largemouth bass were captured by electrofishing at Lake Okeechobee, Florida (latitude: 27°N 7') and Lake Seminole, Florida (latitude: 30°N 44 ') during September 2003 (Figure 3-1). Using broodfish from Lakes Okeechobee and Seminole allowed us to nearly encompass the maximum latitudinal distance in Florida, and therefore, nearly the maximum environmental gradient (i.e., temperature and photoperiod) acting as selective pressures on spawning periodicity. Philipp et al. (1983) observed clinal variation in allele frequencies at several loci in largemouth bass that had been collected from Lake Seminole in north Florida down to Lake Okeechobee. Philipp et al. (1983) failed to detect NLMB alleles at Lake Okeechobee and estimated a subspecific NLMB:FLMB genomic presence of 49:51, respectively,

at Lake Seminole based on electrophoresis of two diagnostic enzyme loci. Recent analyses at the same loci also detected no northern alleles at Lake Okeechobee, and indicated that largemouth bass at Lake Seminole were highly introgressed and had likely been introgressed for an extended time period (B.L. Barthel, Illinois Natural History Survey, 1816 South Oak Street, Champaign, Illinois, 61820, unpublished data). Analyses of mtDNA and allozyme data have resulted in Lakes Seminole and Okeechobee being grouped into separate largemouth bass genetic conservation management units within Florida (B.L. Barthel, unpublished data).

Broodstock from source populations were size selected within 300-430 mm total length (TL) so that fish were of a reproductively mature size (Chew 1974) and to avoid influences of brood fish size on spawning periodicity (Miranda and Muncy 1987; Goodgame and Miranda 1993). Adult fish were transported to Gainesville, Florida (latitude: 29°N 43') using an aerated 2x3 meter fish transport tank within 24 h of capture (Figure 3-1).

I stocked six experimental ponds in Gainesville, Florida with brood fish. Ponds approximately measured 25 m x 5 m with an average maximum depth of 1 m, and were parallel to each other with a 3 m levee separating each pond. One week prior to stocking, the ponds were treated with rotenone (5% liquid rotenone; $>3 \text{ mg}\cdot\text{L}^{-1}$), drained to ensure no fish remained, and then refilled. Each pond was randomly assigned 10 - 11 brood stock from a single lake (N = 3 replicates per brood source) assuming a similar sex ratio for each group (Chew 1974). Brood fish were fed 90-110 mm (TL) golden shiners (*Notemogonus chrysoleucas*) at 3.5% of largemouth bass biomass per day (Miranda and Hubbard 1994) until spawning behavior was observed in spring. Aquatic vegetation in ponds was maintained at a minimum using manual removal, but removals were ceased when largemouth bass spawning bed construction was first observed to prevent disturbance of spawning activity. Pond water levels were maintained at

bank-full to avoid influences of water level on timing of bass spawning (Sammons et al. 1999; Ozen and Noble 2002). Water temperature was measured four times daily in each pond, at 1 m depth, using remote temperature recorders (Onset Incorporated). Age-0 fish were collected during April and May using dipnets and electrofishing. Rotenone was also used during the May sample to maximize the likelihood that all sizes and ages of age-0 largemouth bass were collected from each pond. The experiment was terminated in May 2004 to reduce potential effects of cannibalism and high water temperatures effects on age-0 largemouth bass, and to avoid increased maintenance due to rapid evaporation.

Field Methods

Hatching dates at source lakes were estimated using age-0 largemouth bass captured at Lake Okeechobee during February, April, and June, 2004 and at Lake Seminole during May and July, 2004. The earlier trip at Lake Okeechobee was conducted because of the potential for early hatching at low latitudes (Gran 1995). Age-0 largemouth bass were collected using 10 m x 10 m blocknets and applying rotenone at 3 mg•L⁻¹. Twelve block nets were set at each lake during each sampling event and fish were collected using dip nets by wading investigators.

Laboratory Analyses

A subsample of age-0 largemouth bass from experimental ponds and source lakes were size selected for age estimation so that the age sample mirrored the length-frequency of the fish collected at each waterbody (Pine et al. 2000). Selected age-0 largemouth bass were measured (TL; mm) and weighed (wet weight; 0.001 g), and their sagittal otoliths were removed. Sagittal otoliths were prepared using the methods of Miller and Storck (1982). Each otolith was read by two independent readers and ages were averaged when they agreed within three days between readers. If agreement was not met, the otolith was re-read by both readers and discarded if

agreement was not met ($N = 0$ for pond fish). Some early hatched age-0 fish from source populations were too old (>150 days) for reliable age estimation in July, but I assumed their hatch dates were represented in samples collected earlier in the year (i.e., February or April-May). Median hatch date in ponds was compared between stocking sources using a non-parametric median test (Zar 1999). Mean hatch date, mean water temperature at first and median hatch date, and mean hatching duration in ponds were compared between broodstock sources using one-way analysis of variance (ANOVA). Quantitative comparisons between pond and source lake spawning distributions were not performed due to differences in parental size distributions. However, source lake spawning patterns were used to evaluate whether spawning periodicity observed in ponds was similar to source populations in their native environment.

Results

Several largemouth bass nests ($N \geq 3$ per pond), with guarding males, were observed in each pond, and age-0 bass were captured in all six experimental ponds. Female largemouth bass may use multiple nests and deposit multiple egg clutches during a spawning season (Heidenger 1975), thus I assumed that bass progeny in my experimental ponds represented offspring from several families. About twenty age-0 bass were selected for age estimation from each pond during each sample. Age estimates were only made for 30 age-0 bass from pond *a* (Lake Okeechobee broodstock) because of a low sample size ($N \cong 25$) and small total length distribution during April. The low sample size in April was likely due to a high mortality event because all fish collected were less than 25 mm, except one individual was 32 days older and much larger than any other fish in that sample.

In ponds, FLMB had initial hatching dates beginning as early as 26 January and as late as 12 February (Table 3-1; Figure 3-2). In contrast, the range of initial hatch dates was 22 February

to 7 March for ILMB (Table 3-1; Figure 3-2). On average, median hatch date in ponds was 11 days earlier for FLMB than ILMB ($\chi^2 = 31.22$, $df = 1$, $P < 0.001$), and mean hatch date in ponds was five days earlier for FLMB ($F = 5.10$, $P = 0.025$) (Table 3-1). Florida largemouth bass began spawning at cooler water temperatures (12.3 – 15.1 °C) than ILMB (15.7– 20.6 °C) in experimental ponds ($F = 7.82$, $df = 4$, $P = 0.049$), but water temperatures at median hatch date did not differ between brood types ($F = 0.010$, $df = 4$, $P = 0.771$) (Table 3-1). Hatching duration in experimental ponds ranged 24 -72 days for FLMB and 10-12 days for ILMB (Table 3-1). Florida largemouth bass hatching duration was marginally different than ILMB hatching duration ($F = 5.40$, $df = 4$, $P = 0.08$), but low statistical power ($N = 3$ per treatment) reduced my ability to detect a difference (Peterman 1990). Florida largemouth bass hatching occurred as late as 7 April, whereas the last ILMB hatch occurred on 18 March in experimental ponds. Florida largemouth bass began spawning earlier and also had a longer spawning season duration than ILMB in experimental ponds.

My experimental pond results were corroborated by data from Lakes Okeechobee and Seminole. Age-0 bass at Lake Okeechobee began hatching as early as 12 December, whereas the earliest fish collected from Lake Seminole hatched on March 1 (Figure 3-3). The median hatch date at Lake Okeechobee occurred 29 days earlier than the median hatch date at Lake Seminole. Unlike my pond results, water temperatures at first hatch were similar between source lakes (Lake Okeechobee = 17.9 °C and Lake Seminole = 16.3 °C), and water temperatures at median hatch date were similar at Lake Okeechobee and Lake Seminole (19.6 °C and 20.9 °C, respectively), as seen in my pond study. Hatching duration results also supported experimental pond results because Lake Okeechobee hatching duration (146 d) was substantially longer than the Lake Seminole hatching duration (97 d) (Figure3-3). In summary, FLMB had earlier

spawning and longer spawning season duration than ILMB in both research ponds and at their respective source lakes.

My results indicated both environmental and genetic effects on spawning periodicity of largemouth bass. Translocation illustrated environmental effects on hatching periodicity because rearing FLMB in research ponds at a higher latitude led to later hatching than at Lake Okeechobee. Similarly, rearing ILMB in research ponds at a lower latitude led to earlier hatching in ponds than at Lake Seminole (Figure 3-4). Genetic effects on hatching periodicity were also evident because translocated fish reflected characteristics of their brood source populations. For example, FLMB hatched earlier and had longer hatching distributions than ILMB in both the pond experiment and at brood source lakes (Figure 3-4).

Relative differences in spawning times between brood sources in ponds were detected despite the low number of families and adult sizes represented by my pond brood fish relative to source lake populations. Although my intent was to compare relative differences between brood sources in ponds, source lake hatching patterns mirrored my pond results providing further support for a genetic contribution to spawning periodicity. This corroboration occurred even though my brood fish samples were not representative of the entire spawning population from the source lakes (i.e., lower range in brood fish size in ponds compared to lakes).

Discussion

Environmental and genetic factors influenced spawning timing and periodicity of translocated largemouth bass. Environmental and genetic effects to breeding periodicity have rarely been investigated, but have been shown in some cases for terrestrial (e.g., Japanese macaques *Macaca fuscata*; Fooden and Aimi 2003) and aquatic species (e.g., Atlantic salmon, *Salmo salar*; Donaghy and Verspoor 1997). For example, Atlantic salmon exhibited a reversal in

hatching order between two populations when reared in a hatchery versus their native rivers (Donaghy and Verspoor 1997). Donaghy and Verspoor (1997) attributed the reversal in hatching order to a genotype-environmental interaction; although they could not explain the mechanism leading to the reversal they suggested that local genetic adaptations to water temperatures were responsible.

Environmental influences were evident by a temporal shift in the onset of spawning for translocated broodfish. In my research ponds, FLMB began spawning later than their source population did at Lake Okeechobee, which is located much further south. In contrast, ILMB in research ponds began spawning before their source population at Lake Seminole, which is further north. Water temperatures were the most plausible explanation for observed temporal shifts because temperatures at median hatch date were similar between FLMB and ILMB in experimental ponds and field collections, but similar patterns in ponds and source lakes suggested a genetic component to spawning periodicity.

Genetic factors played a role in spawning timing because FLMB from Lake Okeechobee spawned earlier in the research ponds than ILMB from Lake Seminole, even though temperatures, photoperiod, and water levels were similar in all ponds during brood fish sexual maturation and spawning. Adaptations for reproductive strategies that maximize individual fitness via offspring survival and reproductive success should occur within an environment given a heritable component and selection pressure on phenotypic variability (Endler 1986). Einum and Fleming (2000) documented “critical episode of selection” following the emergence of Atlantic salmon fry, which resulted in a phenotypic shift towards earlier emergence. A heritable component to breeding date has been established for some salmonids (Siitonen and Gall 1989; Gharrett and Smoker 1993), thus Einum and Fleming (2000) concluded that local adaptations for

breeding dates are possible and may explain the variability in breeding dates within and among Atlantic salmon populations. The evidence of a genetic component to breeding times in my study and other studies is not surprising given that local populations of fishes, with restricted gene flow, have an underappreciated capacity to adapt to local selection (Conover and Schultz 1997).

In my study, FLMB exhibited protracted spawning periods in both ponds and lakes relative to ILMB. Protracted spawning distributions increase the likelihood that individuals with differing hatching dates will experience differing environmental conditions (Narimatsu and Munehara 1999). Mild winter water temperatures that typically occur in peninsular Florida likely prevent exposure of early-hatched fish (e.g., hatch in December) to very cold temperatures (<12 °C) that would limit survival as per Philipp et al. (1985). Atypical winter cold fronts can reduce growth or survival of early-hatched largemouth bass at Lake Okeechobee, thus reproductive success may vary among years for early versus late hatched fish. Garvey et al. (2002) found a similar pattern for bluegill at Lake Opinicon, Ontario, and hypothesized that protracted spawning distributions maximized lifetime fitness in variable environments where temperature regulates juvenile survival. Conversely, early spawning (e.g., December) of largemouth bass at Lake Seminole would likely result in very limited offspring survival. Lake Seminole fish began spawning at suitable temperatures in March, and spawned over a relatively shorter period compared to Lake Okeechobee fish. A contracted spawning distribution at Lake Seminole maximizes the growing season for most age-0 bass (e.g., Conover 1992) at the more northern latitude. Contracted spawning seasons for ILMB at Lake Seminole could be the result of stabilizing selection, where progeny from both early and late hatching times are at a survival disadvantage, which ultimately led to individuals adapted to spawning within a shorter time

period (Schultz 1993). Protracted spawning distributions of Lake Okeechobee fish and contracted spawning distributions of Lake Seminole fish appear better suited for the environments found at each source lake and inherent environmental influences on juvenile survival.

Philipp et al. (1985) found a lower α -threshold temperature (i.e., the theoretical lower limit to embryonic development) for FLMB than ILMB. Philipp et al. (1985) hypothesized that NLMB evolved strategies that delay spawning to prevent exposure of embryos to lethally cold temperatures, whereas FLMB evolved to allow spawning at lower and higher temperatures relative to NLMB. My results support this hypothesis, and I concluded that largemouth bass spawning seasons are locally adapted to environmental conditions.

Natural selection may also lead to spawning periodicity that is synchronized with prey species abundance to maximize food availability for progeny (Sinclair and Tremblay 1984). The relationship between reproductive timing and food supply has been described by the “match/mismatch hypothesis,” which asserts that temperate fishes spawn at a fixed time corresponding to peaks in plankton production, and offspring success or survival depends on how well their production matches with food production (Cushing 1975, 1990). At Lake Okeechobee, prey fish likely spawn earlier than at Lake Seminole because of earlier spring warming. Earlier hatching of fish at Lake Okeechobee, relative to hatching times at more northern latitudes, may lead to increased survival due to a size advantage relative to prey fish, which is a prerequisite for piscivory (Mittelbach and Persson 1998). Potential prey fish at low latitudes commonly have extended spawning seasons (Conover 1992) (e.g., mummichog, *Fundulus heteroclitus*; Conover 1990) relative to spawning seasons at more northern latitudes.

Thus, differences in spawning periodicity I observed may have resulted from selection for optimal environmental conditions, food availability, or a combination of these factors.

Previous studies comparing spawning timing of largemouth bass indicated that northern and ILMB hatched earlier and at cooler water temperatures than FLMB (Isely et al. 1987; Maceina et al. 1988), which is contrary to my findings. These previous comparisons were conducted in Illinois and Texas, respectively, which are outside the native range of FLMB and have much cooler winter water temperatures than FLMB experience in their native range. My pond study was conducted in a transition zone where both pure FLMB and ILMB populations naturally occur (Philipp et al. 1983), so brood fish were reared in temperatures that did not vary as widely from local conditions compared to Isely et al. (1987) and Maceina et al. (1988). Isely et al. (1987) and Maceina et al. (1988) also used sympatric populations of NLMB and FLMB potentially allowing for confounding effects of hormonal cues and/or reproductive behaviors, which may have influenced spawning times. I used separate ponds for each genetic source to prevent interbreeding and behavioral influences among brood source types. Broodstock lengths may have also contributed to differing results among studies because larger largemouth bass have been shown to spawn earlier than smaller individuals (Goodgame and Miranda 1993), and a large range in length distribution of spawning bass likely leads to extended spawning activities (Miranda and Muncy 1987). In my study, I used similar-sized brood stock from both sources to minimize potential size effects on spawning in ponds. Adult size distributions in ponds did not reflect adult size distributions at source lakes, thus I focused my comparisons of spawning distributions between ponds and used lake spawning periodicities to evaluate the relative differences. Adult size structures did not drastically differ between source lakes (M.W. Rogers, unpublished data), thus fish size effects on spawning periodicity were probably similar for both

source populations. I standardized brood fish size in ponds and spawning periodicity trends were similar to lake populations for each source, providing further evidence of a genetic component to spawning periodicity.

Comparisons of spawning periodicity using otoliths only reveal data for survivors and not the true distribution if age or size-selective mortality occurs (Miller and Storck 1984; Isely et al. 1987). My analyses only allowed for comparisons of surviving offspring among brood sources, which is the main concern for management and conservation purposes, but fish that hatched and incurred high short-term mortality had lower detection probability in my study. Sampling timing is important to my results because differing mortality among ponds could have biased spawning periodicity results, especially if sensitivities to mortality factors differed by source. For example, FLMB are less tolerant of cold temperatures than ILMB (Williamson and Carmichael 1990; Philipp and Whitt 1991). I found only one individual in one of the Lake Okeechobee broodstock experimental ponds that was hatched in January, suggesting a high mortality event. My median hatch date results for Lake Okeechobee experimental fish would not have differed without capturing the early-hatched individual, but the spawning duration for that pond would have been shorter. My age-0 fish from both ponds and lakes were in the range of 13-73 days and 18-136 days, respectively, which provided a valid assessment of relative spawning times between sources. Interpretation of my results should consider potential biases of sampling timing on combined spawning distributions. Fish hatched prior to April collections were potentially available for collection during both samples, which would shift median estimates to earlier in the year. In contrast, early-hatched fish also endured mortality factors for a longer time period relative to later hatched fish, which could potentially shift my estimated spawning distributions towards later in the year. Lastly, termination of my experiment in mid-May could

have led to an under-representation of fish that would have hatched later, however I detected no hatching during the 30-day period prior to ending the experiment suggesting that my data represent the entire spawning distributions. In summary, comparisons of my results with future studies should consider the time of collection for age-0 fish and potential influences on the apparent spawning distributions.

Environmental experiences of brood fish prior to relocation may persist and confound apparent genetic effects in common environment studies (Conover and Schultz 1997). Earlier spawning of FLMB could be partially due to environmental influences prior to relocation if FLMB were further in their annual reproduction cycle and gamete development was more advanced than ILMB when they were translocated. I stocked broodfish into experimental ponds in mid-September when such effects should have been minimized. Gross et al. (2002) reported that plasma sex steroid concentrations were low for male and female FLMB in September for fish reared at Gainesville, Florida in their study. Increased gonadosomatic index (GSI) of FLMB reared in Gainesville, Florida began in November and peaked in February-March, which was strongly correlated with gonadal maturation (Gross et al. 2002). I translocated brood fish at least three months before spawning occurred at either lake. A future study utilizing progeny of translocated fish would further reveal genetic influences on spawning periodicity. Transplanting studies are useful for evaluating the genetic basis of phenotypic variation in spawning periodicity, but the genetic component I identified suggests further need to test and develop hypotheses to determine natural selection processes responsible for observed differences (Conover and Schultz 1997).

An important consideration when interpreting my study results is that my fish were only from two lakes, thus I did not have a random sample of FLMB or ILMB genotypes. Recent

genetic studies concluded that my source populations were from differing genetic conservation management units (B.L. Barthel, unpublished data), however I did not include brood fish from a range of lakes for each genetic conservation unit.

My study has implications to management decisions regarding fish stocking programs. Outbreeding depression effects (e.g., lower recruitment, adult abundance, and fish size structure) of stocking FLMB with native LMB populations have not been reported throughout a widely distributed range of public water bodies stocked in the United States. However, Gharett et al. (1999) reported outbreeding depression in the F2 generation of pink salmon (*Oncorhynchus gorbuscha*) that were hybrids of stocks with distinctly different breeding seasons, and warned that deleterious effects of outbreeding depression may take decades to detect. In a series of common garden experiments, Philipp et al. (2002) concluded that hybridization of largemouth bass from widely separate geographic locations (e.g., Florida, Illinois, Texas, and Wisconsin) with native Illinois fish led to a more than a 50 percent reduction in reproductive fitness relative to the original, local stock. My study did not address individual or population level effects of mixing ILMB and FLMB, but genetic factors played a role in spawning timing and periodicity of translocated largemouth bass. Observed spawning periodicity appeared to be better suited for, and a local adaptation to, the environments found at each source lake. Genetic variation among local populations is likely prevalent (Conover and Schultz 1997), therefore I recommended that agencies take a conservative approach in stocking programs to avoid potential outbreeding depression. I also recommended that agencies develop long term studies that evaluate effects of mixing stocks with phenotypic differences in life history strategies.

Table 3-1. Earliest, median, and latest hatch dates of Florida (Lake Okeechobee fish) and intergrade (Lake Seminole fish) largemouth bass (*Micropterus salmoides*) translocated to experimental ponds at Gainesville, Florida in 2004 and corresponding water temperatures

Pond	Source	N	Earliest	Median	Latest	Hatch range (d)	Water temperature (°C)		
							Earliest hatch	Median hatch	Latest hatch
pond a	Okeechobee	30	26 Jan	02 Apr	07 Apr	72	12.4	18.2	18.6
pond b	Okeechobee	40	01 Feb	29 Feb	09 Mar	37	12.3	12.3	18.4
pond c	Okeechobee	41	12 Feb	21 Feb	07 Mar	24	15.1	15.4	22.6
pond d	Seminole	40	07 Mar	12 Mar	18 Mar	11	17.7	14.2	17.7
pond e	Seminole	40	22 Feb	27 Feb	05 Mar	12	15.7	14.0	19.6
pond f	Seminole	40	06 Mar	11 Mar	16 Mar	10	20.6	16.0	19.4

(N = number aged, Earliest = earliest estimated hatch date, Median = median estimated hatch date, Latest = last estimated hatch date, Earliest hatch water temperature = mean water temperature for earliest hatch date, Median hatch water temperature = mean water temperature for median hatch date, Latest hatch water temperature = mean water temperature for latest hatch date).

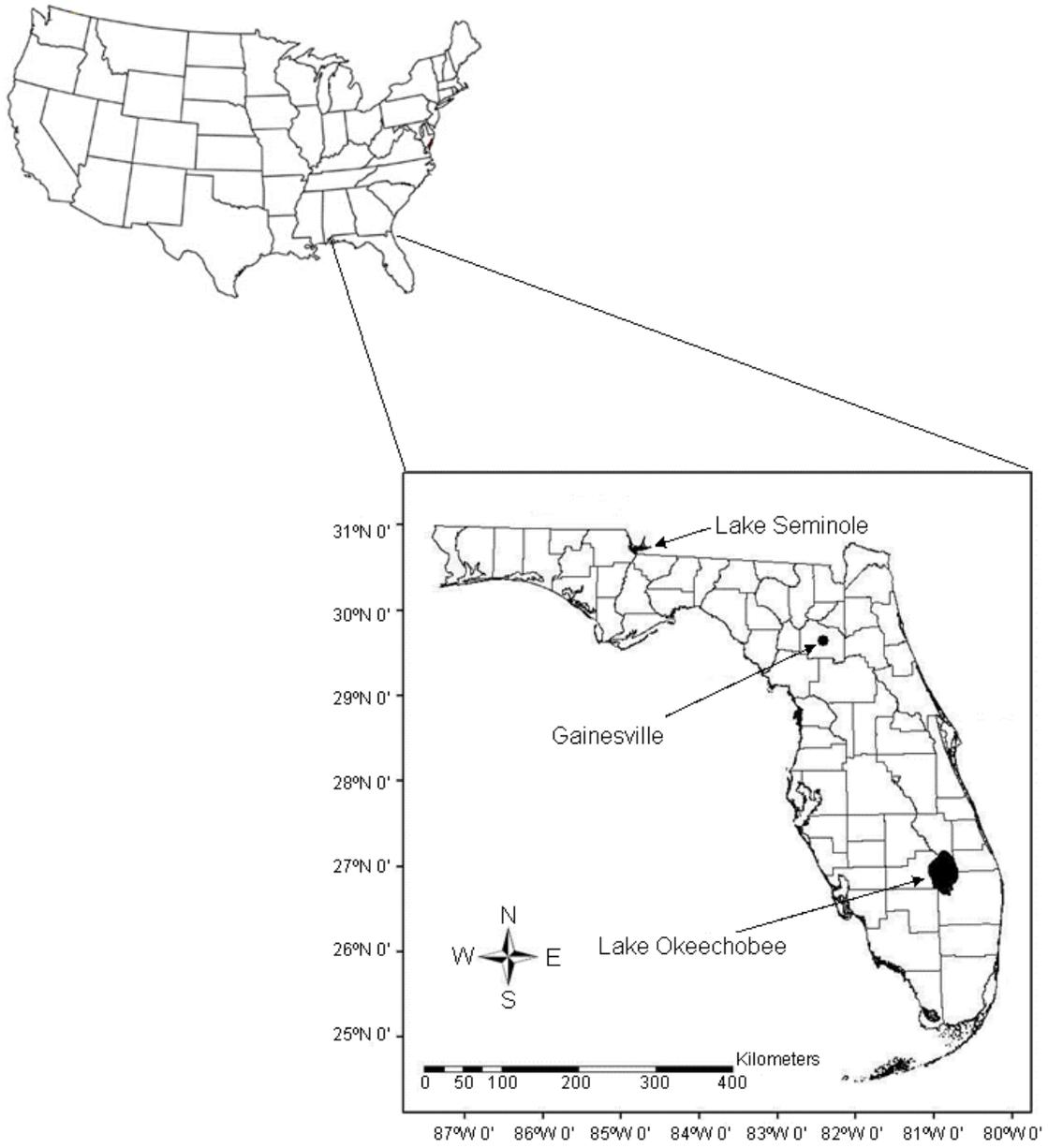


Figure 3-1. Locations and latitudes for Lake Seminole, Lake Okeechobee and Gainesville, Florida, USA.

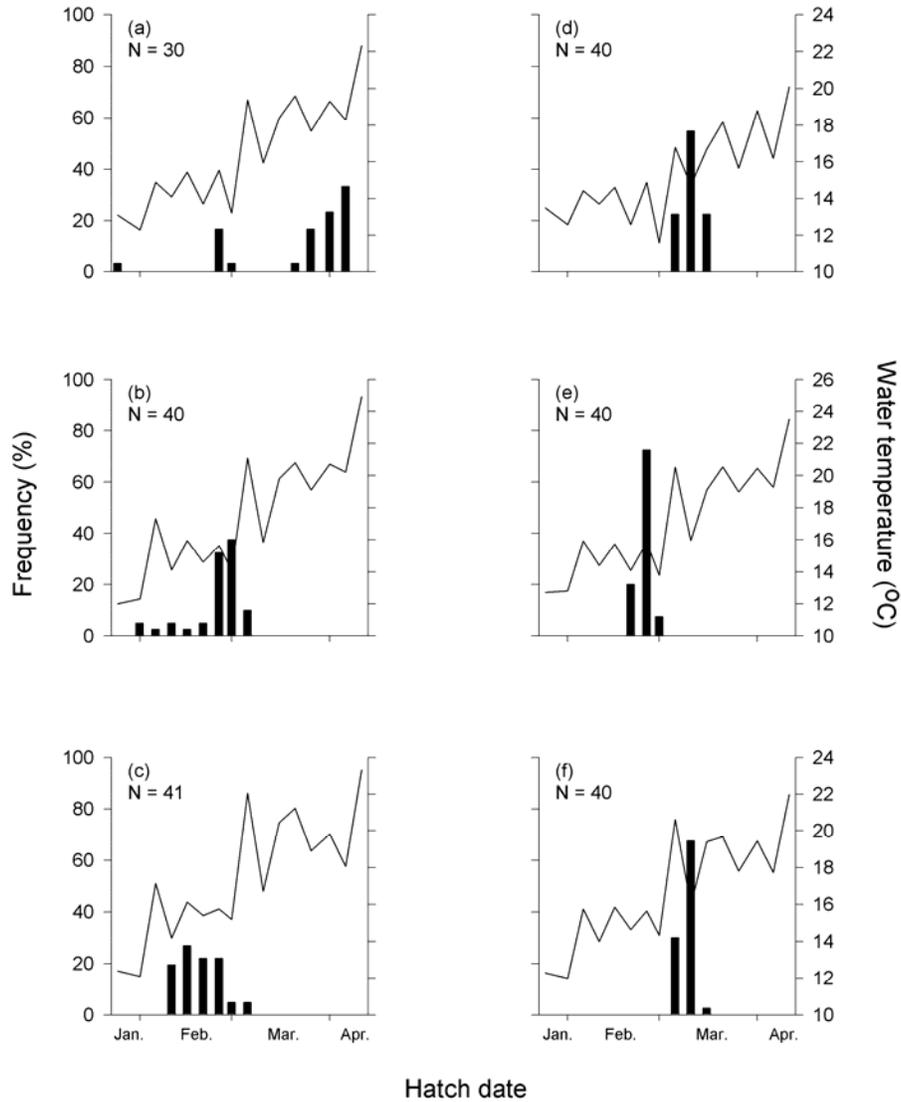


Figure 3-2. Five-day cohort percent hatching distribution (y-axis) for age-0 largemouth bass hatched in research ponds at Gainesville, Florida across dates (x-axis) and corresponding mean water temperatures (z-axis). Sampling occurred on 15 April and 10 May, 2004. Left column (a – c) brood source was Lake Okeechobee and right column (d – f) brood source was Lake Seminole.

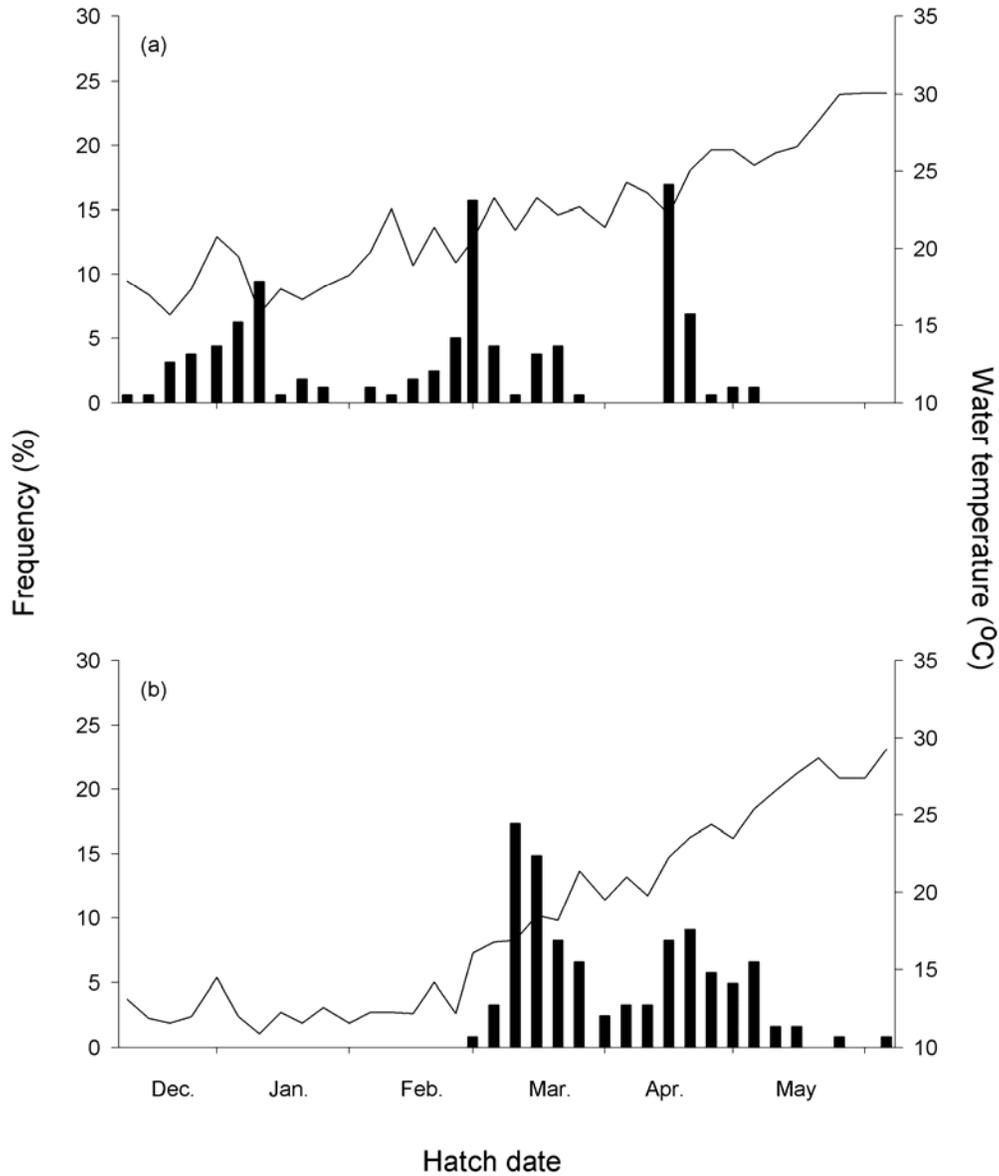


Figure 3-3. Five-day cohort percent hatching distribution (y-axis) for age-0 largemouth bass collected at (a) Lakes Okeechobee (N = 159) and (b) Seminole (N = 121) across dates (x-axis) and corresponding mean water temperatures (z-axis). Sampling occurred at Lake Okeechobee on 15 – 16 February, 22 April, and 21 – 22 June, 2004. Sampling occurred at Lake Seminole on 12 – 13 May, and 13 – 14 July, 2004.

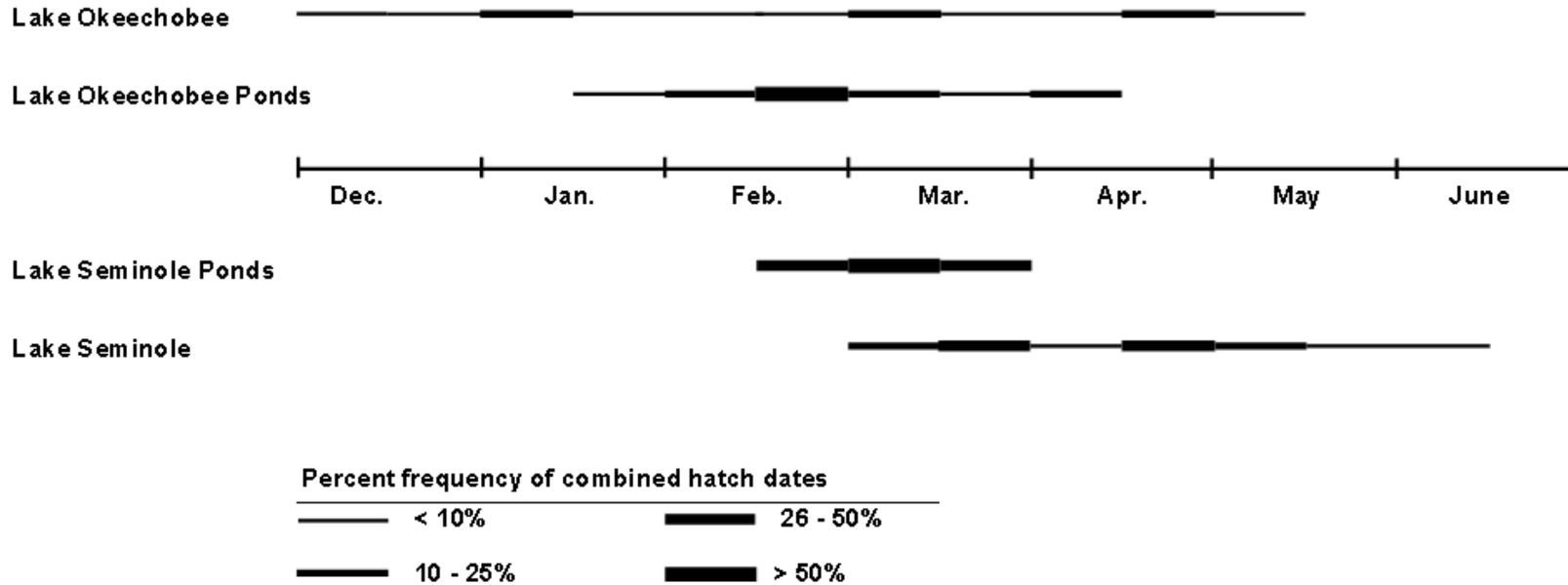


Figure 3-4. Semi-monthly hatching distributions for age-0 largemouth bass reared in research ponds in Gainesville, Florida and in source populations at Lake Seminole and Lake Okeechobee in 2004. Figure lines are weighted to represent percent frequency.

CHAPTER 4
SIMULATED INFLUENCES OF HATCH-DATE SPECIFIC SURVIVAL ON
RECRUITMENT OF LARGEMOUTH BASS

Density-dependent processes can dampen or magnify juvenile mortality, but the resulting pattern is relatively stable average recruit abundances across a broad range of spawner abundances for many fish stocks (Walters and Korman 1999). Density-dependent mortality is believed to result in compensatory juvenile survival at low egg production and regulation of juvenile survival at high egg production, thus causing the observed stability in stock-recruitment relationships for many species (Walters and Martell 2004). Regulation can be influenced by multiple biotic (e.g., predation and starvation) and abiotic (e.g., temperature and water clarity) factors, which have greatest effects during early life stages (i.e., “crucial period,” Shepherd and Cushing 1990) and interact to affect survival. Although density-dependent mortality in juvenile fishes has received much attention, few cases exist where mechanisms leading to regulatory processes have been identified (Shepherd and Cushing 1990) or how those mechanisms may act within year classes to influence recruitment.

The relative effect of mechanisms influencing survival, and thus, resulting in compensation and regulation, have been shown to vary with hatching dates such that members of a year class born at different times may suffer from differing mortality forces. For example, Bestgen et al. (2007) reported that early hatched Colorado pikeminnow *Ptychocheilus lucius* have higher mortality during early life than later hatched members of a year class due to temporal habitat overlap with their predators. In contrast, early hatching may result in increased survival by enhanced foraging or reduced predation mortality to gape-limited predators (e.g., Ludsin and DeVries 1997). Hatch-date dependent survival has often been identified for both marine and freshwater fishes, but effects of hatching-date dependent survival on total year class

abundance and composition (i.e., contributions of differing hatching sub-cohorts) are difficult to investigate.

My field study (Chapter 2) showed that survival and growth of age-0 largemouth bass were hatch date specific. Here, I explored the long term implications of observed sub-cohort-specific growth and mortality on total recruitment to age-1 and adult biomass. I also assessed how those metrics would change if mortality observations had persistently differed for a given sub-cohort or among sub-cohorts. Thus, I evaluated the potential for compensation and regulation at varying levels of sub-cohort specific mortality relative to my field observations. I used trophic-based ecosystem models to evaluate relationships between sub-cohort mortality and recruitment to the adult population. Models were evaluated for largemouth bass and represented a south Florida population and a north Florida population to incorporate among system variation in juvenile largemouth bass population characteristics and community composition.

Methods

I used Ecopath with Ecosim (EWE; www.ecopath.org) ecological modeling software to evaluate influences of hatching sub-cohort-specific survival on year class structure and biomass. Two EWE models were developed to explore how results may vary among populations (i.e., between a north Florida system and south Florida system). Models differed via observed differences in hatching distributions due to latitudinal (e.g., temperature) and source population (e.g., differing genetic composition) influences and community composition (e.g., prey fish abundance). A mass-balance food web model was developed (Ecopath process) for each population and simulations were performed to predict effects of differential sub-cohort survival on age-1 biomass, adult biomass, and year class composition at equilibrium (Ecosim process).

Ecopath Models

An Ecopath model is a static mass-balance representation of production and losses among living components (i.e., functional groups) of an ecosystem. Balance occurs when production is equal to predation mortality, non-predation mortality, and fishing harvests (i.e., in the absence of immigration or emigration) (Pauly et al. 2000) for each prey functional group (i) and predator functional group ($j=1$ to n predator groups) according to the Ecopath master equations:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i = \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i \quad (4-1)$$

and

$$Q_i = P_i + R_i + U_i \quad (4-2)$$

where:

where B_i and B_j are biomasses of i and j , $(P/B)_i$ is the production/biomass ratio for i and should be entered as the total instantaneous mortality rate (Z_i) for vertebrate groups or turnover rate for invertebrates and primary producers, EE_i is the fraction of $(P/B)_i$ specified in the model, $(Q/B)_j$ is the total food consumption per unit biomass of j , DC_{ij} is the proportion of prey group i to predator group j 's total diet, Y_i is harvest of group i , R_i is respiration of group i , and U_i is the unassimilated portion of group i 's consumption according to the equations (Christensen et al. 2005):

$$\text{ecotrophic efficiency} = EE_i = \frac{M_{2(i)} + Y_i}{P_i} \quad (4-3)$$

$$\text{total predation mortality} = M_{2(i)} = \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} \text{ for } j = 1 \text{ to } n \text{ predators} \quad (4-4)$$

$$\text{other mortality} = M_{0(i)} = P_i(1 - EE), \text{ where } P_i = Y_i + B_i \cdot M_{2(i)} + P_i(1 - EE_i) \quad (4-5)$$

$$\text{harvest} = Y_i = \sum_{w=1}^n F_w \cdot B_i \text{ for } w = 1 \text{ to } n \text{ fisheries, } F_w \text{ is fleet specific mortality on } i \quad (4-6)$$

(Figure 4-1). Input rates (e.g., P/B) are entered using annual estimates. Components of my ecosystems consisted of functional groups with similar foraging life histories (Table 4-1). Linkages among functional groups were input by a diet composition matrix for each model that described the percent weight of each prey functional group to each predator functional group's diet (i.e., DC_{ij}).

Each of my models (i.e., one for north Florida and one for south Florida lakes) was comprised of over 20 functional groups, but at least 12 of these represented multiple (i.e., four to five) age stanzas for early, middle, and late-hatched largemouth bass hatching sub-cohorts (Tables 4-2, 4-3; see Chapter 2 for hatching dates corresponding to sub-cohorts). The age stanzas for each sub-cohort were used to track fish through their ontogeny, so that different information (e.g., P/B , diet composition, etc.) could be specified for each life stage and sub-cohort. The stanza structure also allowed specification of sub-cohort-specific age at a given time period due to differences in hatching dates among sub-cohorts. For example, the “summer to fall” age stanza would have relatively older fish for the early hatched sub-cohort compared to the late hatched sub-cohort in each model. Ecopath required several inputs for each functional group that allowed the model to balance population additions and losses. For each functional group, the model required three of the four following inputs: B (kg/ha), P/B (year^{-1}), Q/B (year^{-1}), and EE . Ecopath creates a series of linear models (Equation 4-1) (i.e., one for each functional group) and simultaneously solves the equations for the parameter not input by the user (i.e., either B , P/B , Q/B , or EE) (Christensen et al. 2005). Individual fisheries and functional-group specific exploitation rates were also model inputs as described below.

Input data for my Ecopath models were obtained from my field data and published literature (see Tables 4-2 and 4-3 for specific sources). Field data were collected at two south

Florida lakes (i.e., Lakes Istokpoga and Okeechobee) and two north Florida lakes (i.e., Lakes Seminole and Talquin) during 2003 and 2004. Biomass for each functional group was estimated from average summer (i.e., June/July) block-net catches for each region (see Chapter 2 for block-netting methods). Production/biomass for juvenile largemouth bass stanzas were estimated from hatching sub-cohort specific survival rates in consecutive block-netting samples. Other functional group P/B and all Q/B estimates were derived from www.fishbase.org and published literature (Tables 4-2 and 4-3). A weighted average (weighted by species abundance) was used for each non-largemouth bass fish functional group's B , P/B , and Q/B inputs. Juvenile largemouth bass diet matrices were obtained from field data (see Chapter 2), whereas other functional group diet matrices were derived from www.fishbase.org and published literature (see Appendices 1 and 2). Diet contents were specified for each sub-cohort through their first summer. I could not estimate ages (i.e., specify sub-cohorts) for age-0 largemouth bass after summer, and thus, I assumed that all sub-cohort diet matrices and survival were the same for a given age following their first summer through their adult stages (see Appendices 1 and 2).

For fishes exhibiting negative exponential mortality through time and length at age following the von Bertalanffy growth function, P/B ratios are equivalent to total instantaneous mortality (Z) (Allen 1971) such that:

$$P/B = Z = F + M_2 + M_0 \quad (4-7)$$

(Christensen et al. 2005). Four fisheries were established in each of my Ecopath models. A recreational fishery exploited each adult largemouth bass functional group at 20%, assuming that fishing mortality in these ecosystems was similar to fishing rates from other Florida and southeast black bass fisheries (Renfro et al. 1999; O'Bara et al. 2001; Allen et al. In Press). An individual fishery was created to target each largemouth bass hatching sub-cohort soon after

hatching, which allowed me to vary mortality in simulations. Thus, I used the fishing mortality function to modify total mortality of each juvenile largemouth bass hatching sub-cohort in Ecosim (see below).

Ecosim Simulations

Ecosim provides temporally dynamic simulations of functional group biomass changes via system perturbations relative to Ecopath's baseline (balanced) conditions. Ecosim is flexible in how system perturbations can be modeled, but most common applications involve simulations by varying fishing mortality rates relative to baseline conditions. Ecosim estimates biomass changes for functional groups using differential equations similar to those in Ecopath.

Abundance changes for age-specified multi-stanzas are modeled using Deriso-Schnute delay-difference models (Deriso 1980; Schnute 1987; Walters et al. 2000). Following a simulated system perturbation in Ecosim, functional group consumption rates and predation rates on those functional groups are moderated by prey behaviors that limit predation exposure (Walters et al. 1997; Christensen et al. 2005). Ecosim models have been described as “hungry predator models” (Plaganyi and Butterworth 2004) where predators compete for vulnerable prey and predator-prey interactions are estimated with foraging arena assumptions (Walters et al. 2000).

Vulnerable (V_{ij}) and non-vulnerable ($B_i - V_{ij}$) prey biomasses are modeled with differential equations as:

$$\frac{dV_{ij}}{dt} = v_{ij}(B_i - V_{ij}) - v'_{ij}V_{ij} - a_{ij}V_{ij}B_j \quad (4-8)$$

$$\frac{d(B_i - V_{ij})}{dt} = -v_{ij}(B_i - V_{ij}) + v'_{ij}V_{ij} \quad (4-9)$$

where v_{ij} is a flow rate for prey i from invulnerable to vulnerable, v'_{ij} is a flow rate for prey i from vulnerable to invulnerable, $a_{ij}V_{ij}B_j$ is total consumption rate Q_{ij} of prey i by predator j , B_j is

abundance of predator functional group j , and a_{ij} is an effective search rate for prey i by predator j (Figure 4-2). Solving the vulnerability equations (Equations 4-8 and 4-9) when changes to v_{ij} are zero (i.e., assuming that the distribution of prey i between vulnerable and invulnerable states reaches equilibrium faster than changes in total biomass; Walters and Martell 2004) and substitution results in the equation used by Ecosim to describe trophic flows of prey group i to predator j :

$$Q_{ij} = a_{ij}v_{ij}B_iB_j / (v_{ij} + v'_{ij} + a_{ij}B_j) \quad (4-10)$$

(Christensen et al. 2005). Equation 4-10 results in ratio dependent predation (Walters and Martell 2004) and has been extended in recent EWE software to incorporate other components of predator foraging such as: prey and predator feeding times, handling times, mediation forcing effects, and long-term or seasonal forcing effects (see Christensen et al. 2005). Thus, consumption of predator j on prey i is a function of search and predator and prey biomasses, but is constrained by vulnerabilities following foraging arena theory (Walters and Martell 2004). Modeling functional groups without foraging time adjustments or switching power results in changes to predator diets according to foraging arena theory relative to encounter rates (see Walters and Martell 2004). Thus, predator diet compositions change proportionally with changes in prey functional group abundances following the assumption that a reduction in a prey biomass reduces intraspecific competition among remaining prey and reduces prey risk to predator functional groups (i.e., lowering encounter rates), but this relationship is mediated by vulnerabilities.

Vulnerabilities are required inputs of Ecosim and represent the maximum predation mortality a predator can exert on a prey functional group relative to baseline (i.e., Ecopath) predation mortality due to mediation via vulnerability flow rates. Low vulnerabilities (e.g., one)

for a prey functional group represent slow flows from the invulnerable to the vulnerable state and make prey availability to predators largely independent of predator biomasses. High vulnerabilities (e.g., 100) represent fast flows from the invulnerable to vulnerable state and result in large changes to predation mortality for a prey functional group following predator biomass increases (Christensen et al. 2005). Vulnerabilities for the earliest age-stanzas of all largemouth bass sub-cohorts were low (i.e., close to one) to emulate factors resulting in very low vulnerability to predators shortly after hatching (e.g., a spatial refuge, schooling, or parental nest guarding) and were allowed to exhibit risk-sensitive foraging behaviors (i.e., allowed to vary foraging times), thus resulting in Beverton-Holt shaped stock-recruitment relationships (Christensen et al. 2005). For the other age stanzas, I allowed Ecosim to estimate the vulnerability for the most abundant LMB hatching sub-cohort from each age stanza (i.e., time period) and used a scaling factor to estimate vulnerabilities for other LMB hatching sub-cohorts within that age/time stanza. Sub-cohort vulnerabilities for each stanza were scaled such that the vulnerability value for a sub-cohort times their base biomass was equal across all sub-cohorts, thus resulting in increased vulnerabilities for sub-cohorts with lower biomass (as suggested by Carl Walters, personal communication). Scaling vulnerabilities relative to baseline biomasses allowed for increased predator consumption as biomasses increased for initially less abundant largemouth bass sub-cohorts. In general, all functional group vulnerabilities were entered such that $1 < v < 6$. Estimated subchort vulnerabilities were higher for older age stanzas than at their initial life stages. These groups were not allowed to change foraging times relative to baseline conditions. The result of these specifications was compensatory growth with biomass changes as predicted by foraging arena theory (Walters and Martell 2004).

Simulations increased and decreased hatching sub-cohort specific mortality by $\pm 50\%$ relative to baseline conditions. Simulated mortality changes were incorporated by changing sub-cohort specific fishing mortality (F in Equation 4-7), which resulted in changes to Z for a sub-cohort. Mortality was applied until the system re-equilibrated. Changes to mortality were applied to the first age stanza for each sub-cohort to represent an early-life mortality source, where that early mortality could have represented multiple factors commonly reported to result in early juvenile mortality (e.g., predation, Bestgen et al. 2006; or environmental factors, Steinhart et al. 2005). Importantly, the simulated changes in mortality were applied to juvenile biomasses estimated from block-net samples (all > 15 mm total length, TL), and thus, the 50% mortality was additional to mortality acting on these hatching sub-cohorts from their hatching date to 15 mm TL. I used hatching sub-cohort specific biomass estimates at age-1 and adult stages as evaluation metrics for the relative effects of hatching-date dependent mortality on year class abundance and composition.

Results

Ecopath Results

Ecopath models did not initially balance because EE estimates exceeded one for some functional groups, thus indicating that losses were greater for those groups than production using my initial inputs. Model balances were achieved following suggestions by Christensen et al. (2005) and Gu nette et al. (2001), rather than using the automated mass-balance routine (Kavanaugh et al. 2004). In general, I modified input values (i.e., B , P/B , Q/B , or DC_{ij}) for fish functional groups using diagnostics (e.g. P/Q and M_2) recommended by Christensen et al. (2005), C. Walters (personal communication), and personal knowledge of field data. I used Ecopath's sensitivity analyses routine to evaluate how changes to my input parameter values for

the balanced models would affect basic parameters estimated by Ecopath. Ecopath's sensitivity routine varies each input parameter from -50% to +50%, in 10% steps, and reports a percent change in estimated parameters relative to estimates using the original parameter value (Christensen et al. 2005). In general, biomass and production inputs had greater effects than consumption inputs on estimates of *EE*, such that a $\pm 30\%$ change in input values could result in up to a 43% change in *EE* estimates for that functional group (see Appendices 3 and 4). Underestimating *B* and *P/B* input values resulted in stronger effects on Ecopath estimates for that functional group than overestimating those values within the range of variation I evaluated. Varying *Q/B* values only had strong effects (i.e., 20-30% change) for *EE* estimates of other predators, sunfish, and insect prey functional groups. Sensitivity of Ecopath estimates to other fish functional group inputs including adult largemouth bass, when varied $\pm 30\%$, were less than 10%. Sensitivity analyses suggested that inputs for my lowest trophic levels could have large effects on Ecopath's estimates for those trophic levels, but those inputs had very little effect on estimates of upper trophic level biomasses (generally less than 0.02 kg/ha) with large changes in lower trophic level inputs (i.e., $\pm 100\%$). Thus, input values of a functional group had more effect on Ecopath's estimates for that functional group than estimates for other functional groups, and input values for top predators had more influence on Ecopath estimates than input values for lower trophic levels.

Ecopath uses a modification of Pianka's (1973) niche overlap index to describe similarities in prey use between predator functional groups (Christensen et al. 2005) via the diet matrix input from field data. Ecopath estimates of prey niche overlap indicated high similarities in prey types among LMB hatching sub-cohorts in spring and summer, but niche overlap values were not always intuitive based on hatching sequence. For example, prey niche overlap

estimates for the north lakes model indicated that the early hatched sub-cohort had lower prey niche overlap with the middle hatched sub-cohort in July (estimate = 0.57) than with the late hatched sub-cohort (estimate = 0.84, Table 4-4). At south lakes, early and middle hatched sub-cohorts had high prey niche overlap in May (estimate = 0.82, Table 4-4). There were no estimates for the late-hatched sub-cohort's diet overlap with other hatching sub-cohorts in May because these fish were just beginning to enter the population at this time. In July, the early hatched sub-cohort had similar diet overlap with both late and middle-hatched sub-cohorts (estimates = 0.78 and 0.79, respectively) and middle and late-hatched sub-cohorts had very high prey niche overlap (estimate = 0.97, Table 4-4). Thus, prey niche overlap was not always consistent with my expectations of finding highest diet similarities between closest age sub-cohorts.

Ecosim Results

Hatching-date specific mortality influenced contributions of hatching sub-cohorts to the year class, but the strength of influence varied among simulations. At north lakes, increased survival of the early-hatched sub-cohort resulted in similar biomass changes in age-1 abundance of both middle and late-hatched sub-cohorts (< 1% difference between them). However, decreased survival of the early-hatched sub-cohort resulted in stronger age-1 biomass changes for the middle-hatched than the late-hatched sub-cohort relative to baseline conditions (25% increase versus 17% increase, respectively) (Figure 4-3). Variable survival of the middle-hatched sub-cohort, which had the highest baseline biomass at age-1, had similar influences on age-1 biomass of early and late hatched sub-cohorts ($\leq 3\%$ difference between early and late-hatched sub-cohorts) (Figure 4-3). Similarly, variable survival of the late-hatched sub-cohort had similar influences on early and middle-hatched sub-cohort biomasses at age-1 ($\leq 3\%$

difference between early and middle-hatched sub-cohorts) (Figure 4-3). Patterns between hatching date-specific sub-cohort survival and biomass were similar for age-1 and adult abundance at north lakes (left versus right panels on Figure 4-3), except increased early-hatched sub-cohort survival had similar effects on middle and late-hatched sub-cohort adult biomass. At south lakes, variable mortality applied to individual hatching sub-cohorts resulted in < 15% changes in age-1 biomass for other sub-cohorts (Figure 4-4). The late-hatched sub-cohorts revealed the most sensitivity to mortality of other hatching sub-cohorts, because their age-1 biomass changed the most (up to 14 %) as result of changes in the early-hatched sub-cohort's survival, whereas the middle-hatched and early hatched sub-cohorts age-1 biomasses never changed more than 11% (Figure 4-4). Effects of hatch date specific sub-cohort mortality at south lakes were more pronounced for adult biomasses than for age-1 biomasses (Figure 4-4). Thus, hatching date specific sub-cohort mortality influenced contributions of other sub-cohorts to the year class, and those influences varied in magnitude among simulations.

Among-lake differences appeared to influence effects of variable sub-cohort specific mortality simulations. In almost all cases, effects of simulated mortality of a given hatching sub-cohort had greater influences on other hatching sub-cohorts for the north Florida model compared to the south Florida model, and these results applied to biomass estimates at both age-1 and adult stages. Exceptions occurred when the early-hatched sub-cohort mortality was reduced which resulted in similar changes in age-1 biomass (14 %) for late-hatched sub-cohorts in both regions and slightly higher late-hatched sub-cohort adult biomass for the south Florida model (21% versus 17% change; Figures 4-3, 4-4). Thus, models predicted that hatching sub-cohort specific survival influenced year class biomass and composition, but patterns should be expected to vary among systems.

Discussion

Ecosystem models predicted that persistent changes in mortality of hatching sub-cohorts could affect equilibrium year class composition and revealed high compensation in juvenile survival under differing mortality treatments. The models also showed strong regulation effects on total age-1 biomass with changes in sub-cohort mortality, via predation and cannibalism. Model predictions indicated that effects of sub-cohort survival will likely vary among systems due to differences in population and community characteristics. Results of my models were somewhat expected based on ecological theory, but suggested that these types of models can be useful for exploring population dynamics and recruitment questions within a large ecosystem context.

Processes that regulate juvenile fish survival have received much attention, and it is now recognized that survival to age-1 results from a series of interdependent events during larval and juvenile stages (Ludsin and Devries 1997). The severity of mortality along this series of life-stages can vary among hatching sub-cohorts and result in disproportionate contributions of specific hatching sub-cohorts to the year class relative to their proportion of total fry production (Cargnelli and Gross 1996). Given the identification of hatching date specific mortality, remarkably little work has addressed how hatching date-dependent mortality may influence dynamics within cohorts. My simulations showed weak effects of sub-cohort mortality on overall biomass at age 1 and adult biomass, because 50% changes in survival of a specific sub-cohort did not lead to large overall changes in other sub-cohort biomasses. However, biomasses of other sub-cohorts did exhibit compensation where total age-1 and adult biomass did not decline substantially as a result of higher mortality of a specific sub-cohort. My simulations suggested weaker linkages among sub-cohorts than expected based on hatching-date sequence.

For example, early and middle-hatched sub-cohorts responded similarly to simulated changes in late-hatched sub-cohort survival, whereas I expected sub-cohorts hatched consecutively to interact more strongly.

The level of diet niche overlap among predators does not provide a reliable index of competition (e.g., Olson et al. 1995), however it does provide information on use of resource types among consumers (Abrams 1980). Ecopath estimated high prey niche overlap for all juvenile largemouth bass sub-cohorts in spring and summer except for middle versus early-hatched sub-cohorts from the north region. Prey resource use for gape-limited juvenile fishes is often limited by body size, because larger offspring that were hatched earlier and/or had faster growth can use a larger range of prey species than smaller offspring that were later-hatched and/or slower growing (Mittelbach and Persson 1998). In my models, the large overlap in prey resource use was potentially due to the high similarity in TL among sub-cohorts and large TL ranges for each sub-cohort. For example, the early-hatched sub-cohort at north lakes in July were 46-128mm TL (median TL = 92 mm), whereas the late-hatched sub-cohort were 28-100 mm TL (median TL = 58 mm). Thus, high prey overlap would be expected based on gape limitation considerations, but length similarity did not explain the lower diet overlap estimated for middle and early-hatched sub-cohorts at north lakes in July. Differences in growth rates among hatching sub-cohorts (see Chapter 2) likely led to similar length ranges and high diet overlap among hatching sub-cohorts. Although individual variability in the timing of ontogenetic diet shifts of similar sized/age fish influences the relationship between largemouth bass size/age and prey use (Post 2003; Olson 1996), within functional group diet variability was incorporated into the diet matrices of my Ecopath models based on observed sub-cohort specific diet compositions. My inability to assign age-specific diet components for sub-cohorts in fall

and spring precluded diet overlap estimates for these stanzas, but the similarities in TL among the sub-cohorts during this period suggested that all sub-cohorts could have potentially used similar prey resources (i.e., similar gape limitations across all sub-cohorts). Diet overlap estimates indicated that largemouth bass hatching sub-cohorts used many of the same prey resources through summer, suggesting that variable survival of individual hatching sub-cohorts could have strong effects on recruitment if prey abundances limited survival during early life. However, high diet overlap did not strongly influence predicted biomass at age-1 and adult populations in my Ecosim simulations, indicating that prey densities from my field data did not infer strong prey limitations.

Complex interactions among predators and juvenile largemouth bass functional groups largely regulated proportional contributions of hatching sub-cohorts to the year class. Predicted increases in sub-cohort biomasses via lower mortality resulted in increased numbers of adult bass acting as predators in the system, and thus, biomass reductions for other hatching sub-cohorts. Importantly, functional groups were modeled such that foraging times did not vary with prey or predator abundances, except for the youngest largemouth bass age stanzas which were assumed to restrict feeding times rather than maximize growth when food was abundant as has been shown for Atlantic salmon *Salmo salar* (Orpwood et al. 2006). Increased mortality for individual hatching sub-cohorts decreased biomasses at all life stages for that sub-cohort, increased prey fish functional group biomasses, and therefore increased biomasses of other hatching sub-cohorts. Following induced mortality for a given sub-cohort, biomass increases for other hatching sub-cohorts were regulated by predators and suggested a “competitive juvenile bottleneck” (Werner and Hall 1979; Byström et al. 1998) between “other predators” and largemouth bass functional groups. Decreased survival of a given hatching sub-cohort resulted

in decreased predation on “other predators” because there were fewer largemouth bass adults acting as predators at equilibrium, and thus, increased biomass for “other predators” and increased predation on other LMB hatching sub-cohorts. In contrast, the opposite phenomenon occurred under simulated increased survival of juvenile largemouth bass hatching sub-cohorts. Thus, the model suggested cultivation of largemouth bass juveniles through adult influences on “other predators”, however the model did not exhibit depensation because largemouth bass hatching sub-cohort biomasses always rebounded to baseline levels if induced mortality was returned to base Ecopath levels. Depensation may not have been evident in my models because enough predators always existed in the systems to maintain restricted habitat use/foraging activities of competitors (see Walters and Kitchell 2001). Evaluation of the hypothesized “competitive juvenile bottleneck” between juvenile largemouth bass functional groups and “other predators” would require further data that allowed more complex stage-structuring in the model, however this type of relationship has commonly been found in freshwater ecosystems (e.g., between bluegill and largemouth bass; Olson 1996, Aday et al. 2005).

My simulation results are dependent on Ecopath and Ecosim assumptions (e.g., foraging arena theory), model constraints, and data from regions with differing largemouth bass genetics (see Chapter 3). Ecopath and Ecosim have many years (> 20 and > 10, respectively) of modification, improvement, and review; however model estimates, their errors, and their application require scrutiny (see Plagányi and Butterworth 2004). Essington (2007) used simulations to show that the precision of Ecopath estimates for B and EE were equivalent to the precision of the input data and he concluded that “bad data led to bad predictions.” I collected all the fish functional group biomass data for my models and attempted to obtain other inputs from the same or similar systems, but inputs derived from other models and published literature

certainly contributed to Ecopath estimates in ways that may not mirror the populations I simulated. Essington (2007) also reported that Ecopath inputs were more sensitive to B and P/B inputs than to diet composition data. Uncertainties regarding EWE parameter inputs and estimates are similar to those reported for other commonly used ecosystem and bioenergetics-based models (e.g., Ney 1990, Plagányi 2007). Model estimates were also dependent on specified stock-recruitment relationships that were assumed to be the same for all largemouth bass sub-cohorts. Identifying stock and recruitment relationships is one of the most difficult problems in biological assessment (Hilborn and Walters 1992), thus there is undetermined uncertainty in these in my models despite the tremendous body of largemouth bass literature. However, my stock-recruitment relationships did conform to Beverton-Holt functions, which are common across a wide range of fish species and populations (Walters and Martell 2004). Furthermore, I could not account for parental effects on juveniles (e.g., parental size and juvenile performance; Miranda and Muncy 1987; Baylis et al. 1993; Wright and Gibb 2005; and Jorgensen et al. 2005). Thus, outcomes of these types of models should be treated as hypotheses that direct future research and data collection.

One of the most fundamental bases for Ecosim involves assumptions for how prey fishes compete and adjust their behaviors with changes in opportunities (i.e., prey supply) and risks (i.e., predation). The vulnerabilities schedule for functional groups as predators on their prey is one of the most important parameters in Ecosim and one of the hardest to know with reliability (Plagányi 2004). In my models, increasing vulnerability values changed the magnitude of biomass responses, however the overall trends of my results remained the same. Default vulnerability values in Ecosim (i.e., $v = 2$) represent mixed bottom-up and top-down trophic flows, however using this default value can cause misleading results (Shannon et al. 2000).

Although it is imperative to increase vulnerability values for functional groups that were likely sampled at levels much lower than B_{\max} (e.g., highly exploited marine stocks; Pauly 1995), there is no reason to suspect that these values should have been largely changed for functional groups in my models. Recent trends indicated relatively low fishing mortality rates for largemouth bass (Quinn 1996; Allen et al. In Press), and thus, the low vulnerabilities in my models infer that large increases in largemouth bass abundance are not expected. Vulnerabilities I used resulted in similar fish functional group biomasses to those reported for southeastern reservoirs (e.g., Jenkins 1975).

Implications

Much research has indicated that juvenile fish survival is strongly density-dependent as a result of regulating processes such as predation, starvation, and cannibalism (Shepherd and Cushing 1990). Several authors have shown that the importance of the processes resulting in strong density dependence is rarely specified (Walters and Juanes 1993 and references therein), and Shepherd and Cushing (1990) suggested that a weak regulatory process could result in regulation at high stock sizes and when fishing mortality is low (as is likely for largemouth bass). My simulations suggested that hatching specific sub-cohort mortality could have large influences on relative contributions of individual hatching sub-cohorts to a year class, however total age-1 biomass was relatively stable across all simulations. Simulations that induced and reduced mortality of individual largemouth bass hatching sub-cohorts had small effects on age-1 total biomass (maximum biomass increase = 5.5% and maximum biomass decrease = 7.0%) relative to Ecopath baseline estimates, thus suggesting high compensation following increased sub-cohort mortality and strong regulation following decreased sub-cohort mortality. Predation was the most important regulating process acting on recruitment. Although responses to variable

hatching sub-cohort mortality were stronger for the north Florida population than for the south Florida population, predation still regulated total recruitment to age-1 for both spawning strategies. Walters and Juanes (1993) proposed that mortality should result in selection for a balance between growth and survival of juvenile fishes due to shorter foraging times and smaller foraging volumes in the presence of high predator abundance, and thus, increased competition and exaggerated density-dependent effects on growth rates. Sub-cohort-specific survival could largely influence predation risks and feeding activities to result in strong competition, which has implications for energy allocations that could affect life-history metrics such as age at maturity, overwinter condition, and lifetime fitness.

My results also have implications for fisheries management. Other authors have proposed that fishing regulations should consider the influence of removing spawning adults during periods of assumed high juvenile survival (e.g., Trebitz 1991) or when progeny from any spawning period may have survival advantages depending on inter-annual environmental variability (e.g., Garvey et al. 2002). Similarly, previous studies have suggested the potential for reduced progeny survival following the removal of nest guarding adults for black bass *Micropterus spp.* (e.g., Philipp et al. 1997, Suski et al. 2003). My results suggested that indirect effects of fishing on juvenile survival would not likely have overwhelming effects on year-class strength because ecological interactions were predicted to regulate total biomass and that survival of other sub-cohorts would be expected to compensate if fishing greatly reduced survival of one portion of a year class. My results also indicated only small increases in total largemouth bass biomasses with large increases in hatching sub-cohort survival, which may extend to stocking practices assuming that stocking induces similar dynamics as increased sub-cohort survival in my simulations. Walters and Juanes (1993) presented similar reasoning for

failures in northwest Pacific salmonid stockings. Potential trade-offs between parental spawning times and inter-sub-cohort interactions affecting juvenile survival necessitate further investigation for understanding recruitment regulation, population level characteristics, and fisheries management.

Table 4-1. Species composition of non-largemouth bass fish groups.

Functional Group Name	Species common name	Species taxonomic name	south model	north model
other predators	Atlantic needlefish	<i>Strongylura marina</i>	x	x
	Black acara	<i>Cichlasoma bimaculatum</i>	x	
	Black crappie (> 200 mm TL)	<i>Pomoxis nigromaculatus</i>	x	x
	Bowfin	<i>Amia calva</i>	x	x
	Chain pickerel	<i>Esox niger</i>	x	x
	Florida gar	<i>Lepisosteus platyrhincus</i>	x	x
	Longnose gar	<i>Lepisosteus osseus</i>	x	
	White catfish (> 250 mm TL)	<i>Ameiurus catus</i>	x	x
killifish-topminnows	Yellow bullhead (>250 mm TL)	<i>Ameiurus natalis</i>		x
	Bluefin killifish	<i>Lucania goodei</i>	x	x
	Eastern starhead topminnow	<i>Fundulus escambiae</i>		x
	Golden topminnow	<i>Fundulus chrysotus</i>	x	x
	Least killifish	<i>Heterandria formosa</i>	x	x
	Lined topminnow	<i>Fundulus lineolatus</i>		x
	Mosquitofish	<i>Gambusia holbrooki</i>	x	x
	Sailfin molly	<i>Poecilia latipinna</i>	x	
sunfish	Seminole killifish	<i>Fundulus seminolis</i>	x	x
	Banded pygmy sunfish	<i>Elassoma zonatum</i>		x
	Black crappie	<i>Pomoxis nigromaculatus</i>	x	x
	Bluegill	<i>Lepomis macrochirus</i>	x	x
	Bluespotted sunfish	<i>Enneacanthus gloriosus</i>	x	x
	Dollar sunfish	<i>Lepomis marginatus</i>	x	x
	Everglades pygmy sunfish	<i>Elassoma evergladei</i>	x	
	Okfenokee pygmy sunfish	<i>Elassoma okfenokee</i>		x
generalists/minnows	Redbreast sunfish	<i>Lepomis auritus</i>		x
	Redear sunfish	<i>Lepomis microlophus</i>	x	x
	Spotted sunfish	<i>Lepomis punctatus</i>	x	x
	Warmouth	<i>Lepomis gulosus</i>	x	x
	Brook silverside	<i>Labidesthes sicculus</i>	x	x
	Coastal shiner	<i>Notropis petersoni</i>		x
	Flagfish	<i>Jordanella floridae</i>	x	
	Golden shiner	<i>Notemigonus crysoleucas</i>	x	x
benthic fish	Inland silverside	<i>Menidia beryllina</i>	x	x
	Pugnose minnow	<i>Opsopoeodus emiliae</i>	x	x
	Taillight shiner	<i>Notropis maculatus</i>	x	x
	Blue tilapia	<i>Tilapia aurea</i>	x	
	Brown bullhead	<i>Ameiurus nebulosus</i>	x	x
	Channel catfish	<i>Ictalurus punctatus</i>	x	x
	Clown goby	<i>Microgobius gulosus</i>	x	
	Gizzard shad	<i>Dorosoma cepedianum</i>	x	x
	Lake chubsucker	<i>Erimyzon sucetta</i>	x	x
	Pirate perch	<i>Aphredoderus sayanus</i>		x
	Plated catfish	<i>Hoplosternum littorale</i>	x	
	Suckermouth catfish	<i>Hypostomus plecostomus</i>	x	
	Swamp darter	<i>Etheostoma fusiforme</i>	x	x
	Tadpole madtom	<i>Noturus gyrinus</i>	x	x
	Threadfin shad	<i>Dorosoma petenense</i>	x	x
	White catfish	<i>Ameiurus catus</i>	x	x
	Yellow bullhead	<i>Ameiurus natalis</i>		x

mm TL = total length in millimeters, x indicates that species was collected in that region and is represented in the model

Table 4-2. Ecopath inputs for a north Florida eutrophic lake based on data from Lakes Seminole and Talquin collected in 2003 and 2004.

Group number	Functional group (age)	Biomass (kg/ha)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE
1	Other predators	2.56 ^a	0.40 ^c	3.20 ^c	
2	LMB late-hatched (to summer)	0.19 ^b	8.51 ^a	41.04 ^b	
3	LMB late-hatched (to fall)	1.46 ^a	4.16 ^a	13.70 ^b	
4	LMB late-hatched (age-1)	1.78 ^b	2.00 ^j	6.51 ^b	
5	LMB late-hatched (adult)	5.29 ^b	0.71 ^e	3.34 ^c	
6	LMB middle-hatched (to summer)	0.19 ^b	8.77 ^a	41.26 ^b	
7	LMB middle-hatched (to fall)	1.37 ^a	4.16 ^d	13.70 ^b	
8	LMB middle-hatched (age-1)	1.67 ^b	2.00 ^j	6.51 ^b	
9	LMB middle-hatched (adult)	4.96 ^b	0.71 ^e	3.34 ^c	
10	LMB early-hatched (to summer)	0.15 ^b	7.48 ^a	40.18 ^b	
11	LMB early-hatched (to fall)	1.29 ^a	4.16 ^d	13.70 ^b	
12	LMB early-hatched (age-1)	1.58 ^b	2.00 ^j	6.51 ^b	
13	LMB early-hatched (adult)	4.67 ^b	0.71 ^e	3.34 ^c	
14	killifish / topminnows	3.49 ^a	2.82 ^c	44.00 ^c	
15	sunfish	53.50 ^a	1.30 ^c	19.38 ^c	
16	generalists/minnows	9.25 ^a	1.60 ^c	27.80 ^c	
17	benthic fish	37.00 ^a	1.39 ^c	18.68 ^c	
18	crustaceans	26.00 ^{b*}	13.90 ^{b*}	22.00 ⁱ	
19	insects		30.20 ^f	38.00 ^h	0.70 ^h
20	zooplankton		15.00 ⁱ	35.00 ⁱ	0.80 ⁱ
21	macrophytes	61824.00 ^a	2.60 ^g	-	
22	phytoplankton		35.00 ⁱ	-	0.75 ⁱ
23	detritus	100.00 ⁱ	-	-	-

P = production, B = biomass, Q = consumption, EE = ecotrophic efficiency. ^ameasured in this study. ^bestimated by Ecopath. ^{b*}estimated by Ecopath based on inputs from Schramm et al. (1983) and Bull et al. (1991). ^cderived from www.fishbase.org. ^dderived from Wicker and Johnson (1987). ^eAllen et al. (2002). ^fLobinske et al. (2002). ^gwithin range reported in Westlake (1982). ^hPoepperl (2003). ⁱwithin range reported from published Ecopath models. ^jDeAngelis et al. (1993)

Table 4-3. Ecopath inputs for a north Florida eutrophic lake based on data from Lakes Istokpoga and Okeechobee collected in 2003 and 2004.

Group number	Functional group (age)	Biomass (kg/ha)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE
1	Other predators	8.27 ^a	0.22 ^c	3.50 ^c	
2	LMB late-hatched (to spring)	0.03 ^b	0.00 ^a	48.99 ^b	
3	LMB late-hatched (to summer)	0.45 ^b	6.31 ^a	20.73 ^b	
4	LMB late-hatched (to fall)	0.54 ^a	4.16 ^d	11.00 ^b	
5	LMB late-hatched (age-1)	0.98 ^b	2.00 ^j	6.35 ^b	
6	LMB late-hatched (adult)	2.90 ^b	0.71 ^e	3.26 ^c	
7	LMB middle (to spring)	0.11 ^b	5.82 ^a	50.07 ^b	
8	LMB middle-hatched (to summer)	0.75 ^b	5.94 ^a	22.01 ^b	
9	LMB middle-hatched (to fall)	2.12 ^a	4.16 ^d	11.00 ^b	
10	LMB middle-hatched (age-1)	2.17 ^b	2.00 ^j	5.99 ^b	
11	LMB middle-hatched (adult)	7.04 ^b	0.71 ^e	3.17 ^c	
12	LMB early-hatched (to spring)	.16 ^b	12.72 ^a	52.35 ^b	
13	LMB early-hatched (to summer)	0.48 ^b	6.72 ^a	21.48 ^b	
14	LMB early-hatched (to fall)	1.06 ^a	4.16 ^d	11.00 ^b	
15	LMB early-hatched (age-1)	1.61 ^b	2.00 ^j	5.96 ^b	
16	LMB early-hatched (adult)	4.77 ^b	0.71 ^e	3.06 ^c	
17	killifish / topminnows	10.40 ^a	2.32 ^c	44.00 ^c	
18	sunfish	73.15 ^a	0.85 ^c	17.17 ^c	
19	generalists/minnows	11.30 ^a	2.00 ^c	39.00 ^c	
20	benthic fish	12.00 ^a	1.15 ^c	22.30 ^c	
21	crustaceans	31.00 ^{b*}	11.00 ^{b*}	22.00 ⁱ	
22	insects		30.20 ^f	38.00 ^h	0.70 ^h
23	zooplankton		15.00 ⁱ	35.00 ⁱ	0.80 ⁱ
24	macrophytes	91232.00 ^a	2.60 ^g	-	
25	phytoplankton		35.00 ⁱ	-	0.75 ⁱ
26	detritus	100.00 ⁱ	-	-	-

P = production, B = biomass, Q = consumption, EE = ecotrophic efficiency. ^ameasured in this study. ^bestimated by Ecopath. ^{b*}estimated by Ecopath based on inputs from Schramm et al. (1983) and Bull et al. (1991). ^cderived from www.fishbase.org. ^dderived from Wicker and Johnson (1987). ^eAllen et al. (2002). ^fLobinske et al. (2002). ^gwithin range reported in Westlake (1982). ^hPoepperl (2003). ⁱwithin range reported from published Ecopath models. ^jDeAngelis et al. (1993)

Table 4-4. Ecopath estimates of diet niche overlap among age-0 largemouth bass hatching sub-cohorts

Model	Age		Late	Middle
North	In July	Late	1.000	
		Middle	0.734	1.000
		Early	0.838	0.574
South	In May	Late	1.000	
		Middle	-	1.000
		Early	-	0.823
	In July	Late	1.000	
		Middle	0.965	1.000
		Early	0.783	0.793

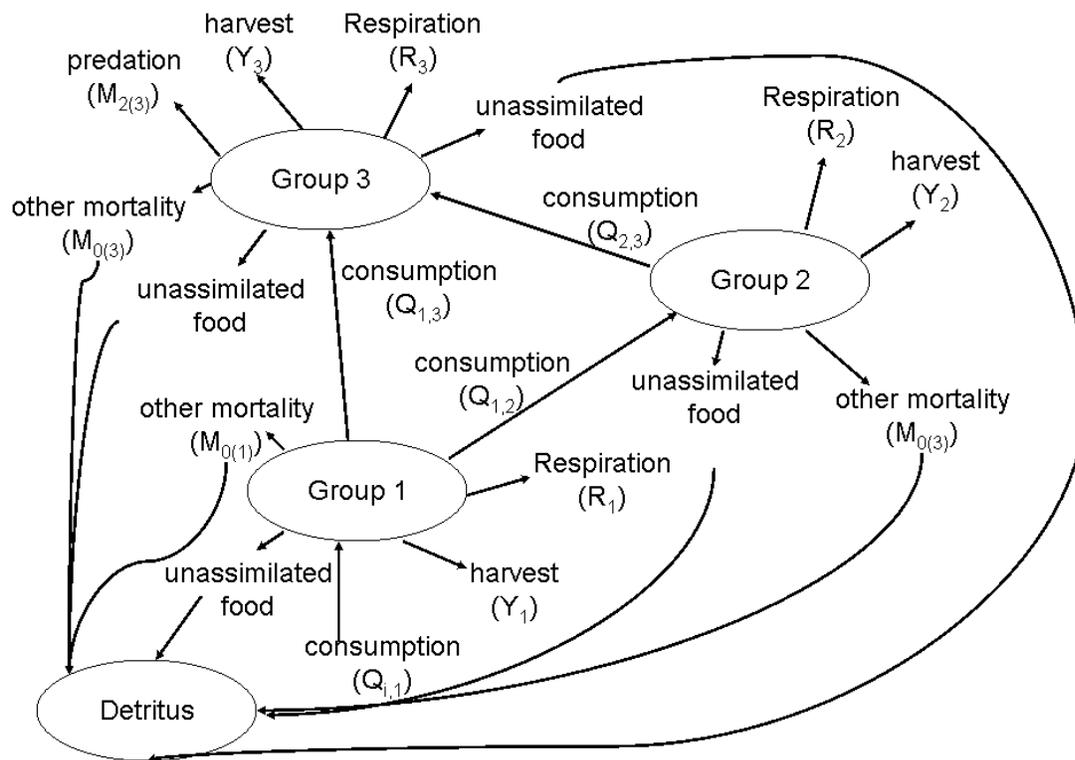


Figure 4-1. Representation of ecosystem flows for components of an Ecopath model consisting of three consumer groups and a detritus group such that predation on a group results in production for their predators

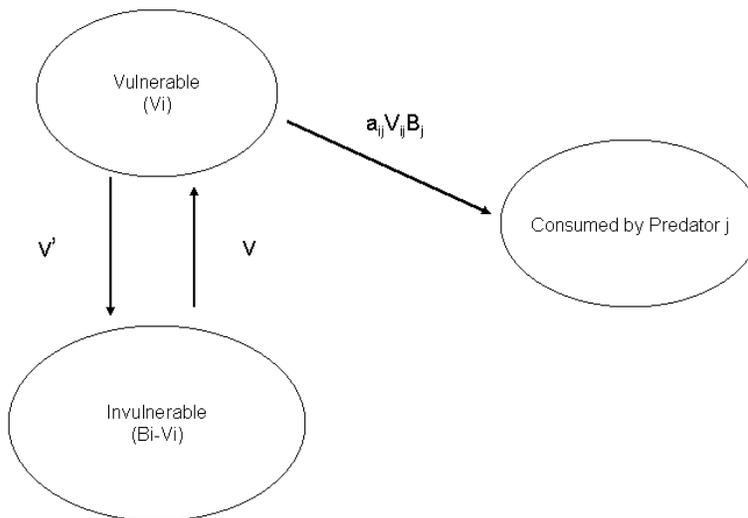


Figure 4.2. Representation of vulnerable and invulnerable states of prey functional group biomass and predator consumption.

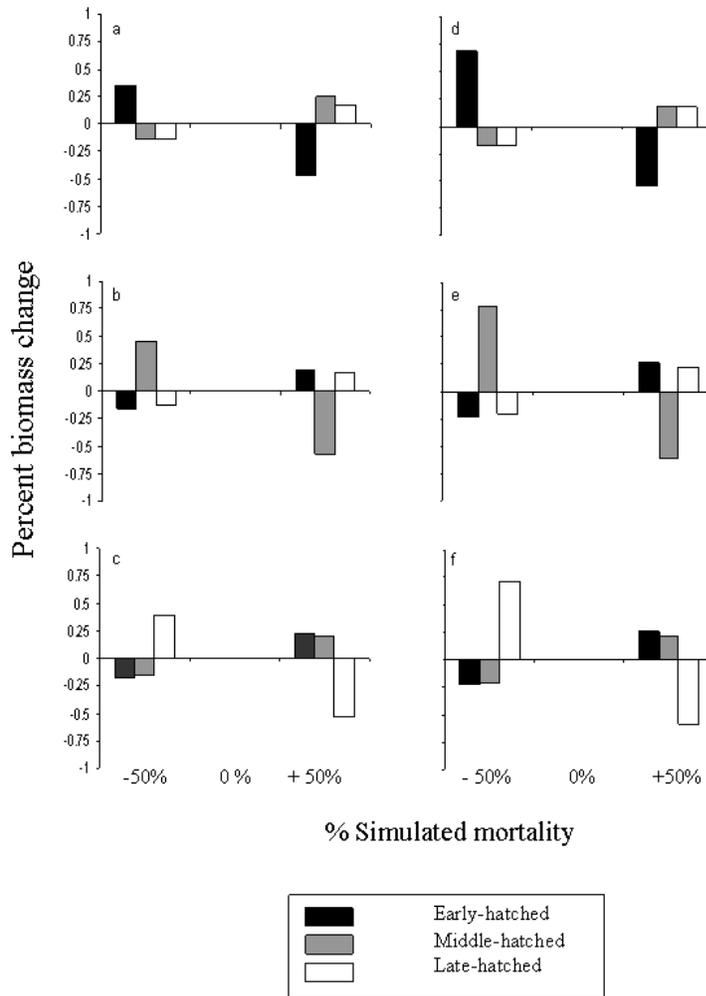


Figure 4-3. Percent biomass change at equilibrium relative to baseline Ecopath values for simulations of variable hatch-date specific mortality for a north Florida lake. Left column panels (a-c) represent changes in total biomass at age-1 for varying mortality for early-hatched (a), middle-hatched (panel b), and late-hatched (panel c) largemouth bass. Right column panels (d-f) represent estimated changes in total adult biomass for varying mortality for early hatched (d), middle-hatched (panel e), and late-hatched (panel f) largemouth bass.

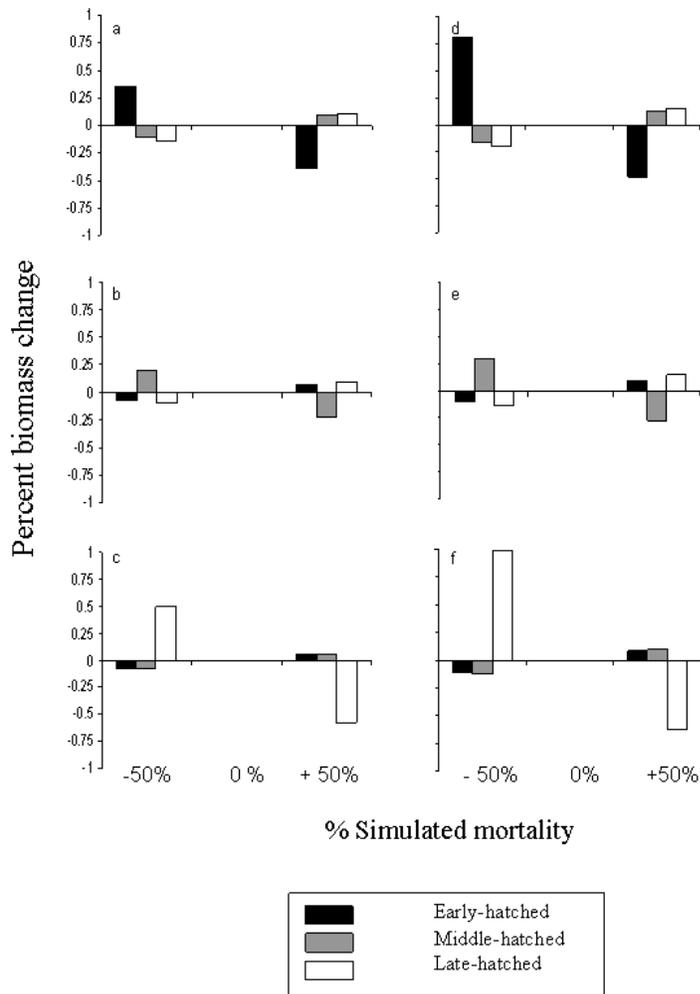


Figure 4-4. Percent biomass change at equilibrium relative to baseline Ecopath values for simulations of variable hatch-date specific mortality for a south Florida lake. Left column panels (a-c) represent changes in total biomass at age-1 for varying mortality for early-hatched (a), middle-hatched (panel b), and late-hatched (panel c) largemouth bass. Right column panels (d-f) represent estimated changes in total adult biomass for varying mortality for early hatched (d), middle-hatched (panel e), and late-hatched (panel f) largemouth bass.

CHAPTER 5 SYNTHESIS AND FUTURE RESEARCH

Age-0 Largemouth Bass Recruitment

The results presented in this study suggested that hatching date-specific sub-cohort characteristics had large implications to the composition of recruits to age-1 for juvenile largemouth bass in Florida lakes. Hatching date was important to growth and survival of age-0 largemouth bass, but the strength of importance differed among latitudes. I identified slower growth for the early-hatched largemouth bass sub-cohorts at south Florida lakes relative to early-hatched sub-cohorts at north Florida lakes. I also found no evidence of survival advantages for early-hatched sub-cohorts relative to later-hatched sub-cohorts through the end of summer. These findings contrasted a popular recruitment hypothesis for largemouth bass (i.e., that early-hatching is always advantageous), but suggested support for Garvey et al.'s (2002) hypothesis that protracted spawning may be advantageous to adult fitness where environments may be quite variable over the spawning season. My findings also contrasted the hypothesis that size-selective overwinter mortality would largely affect survival to age-1 at southern latitudes. A lack of strong size-selective overwinter mortality was likely due to winter water temperatures that did not limit age-0 largemouth bass activities, and thus, facilitated foraging and predator avoidance relative to winter water temperatures at more northerly latitudes. My research was conducted at a lower latitude than other largemouth bass recruitment work that has contributed to recruitment hypotheses for this species and provided evidence that limited the application of those hypotheses at the extreme southern range of largemouth bass distributions.

My results also provided insight and potential hypotheses regarding the evolution of parental spawning strategies across Florida's latitudinal gradient. Experimental results presented in this dissertation showed that both environmental and genetic factors contributed to parental

spawning times. Environmental conditions were conducive to spawning from December to May at south Florida lakes, whereas spawning at north Florida lakes was restrained to beginning in March due to water temperatures. Spawning distributions differed between adult fish from north and south Florida when they were translocated and spawned in similar environments, however translocated spawning distributions exhibited temporal shifts relative to in-situ populations. Thus, I concluded that both genetic and environmental factors contributed to population spawning periodicity. Having found little evidence for size-selective overwinter mortality in Florida, I sought other explanations for this observation. Simulation modeling in this dissertation suggested that parental spawning strategies could affect interactions among hatching sub-cohorts such that variable mortality of hatching sub-cohorts could differentially influence other hatching sub-cohorts and that strength of interactions depended on hatching distributions. Thus, simulations provided hypotheses regarding mechanisms that regulate juvenile survival and may impose selection for adult spawning times across Florida's latitudinal gradient.

Fisheries Management

Fisheries managers are most interested in age-0 survivors and management activities that may increase the number of juveniles surviving to enter a fishery. My study identified differences in hatch-date specific survival among Florida latitudes during the period from hatching through the first summer. These results appeared to be due to environmental influences, and thus, suggested that annual conditions during spring may provide insight to fisheries managers relative to the strength of the year class. My results also had implications for stocking strategies in Florida lakes. I identified largemouth bass spawning seasons and size-distributions across Florida's latitudes, and this information can be used by state resource managers to identify preferable timing and sizes at stocking. Fish stocking strategies such as

“matching the hatch” (i.e., stocking fish at similar sizes to naturally spawned fish) or stocking fish at lengths corresponding to the right tail of the length-frequency of natural fish, which has been successful at Lake Talquin, Florida (C. Mesing, FWC, personal communication), both require expected spawning dates for hatchery planning. Experimental results provided further evidence that genetic stocks should not be translocated throughout Florida because of the contribution of genetics to parental spawning times. Lastly, my simulations suggested that variable mortality among individual hatching sub-cohorts should not have strong effects on total age-1 biomass, however year class structure (i.e., percent contributions of individual hatching sub-cohorts) could be strongly affected by variable hatching sub-cohort-specific mortality.

Future Research

Genetic Contributions

Largemouth bass populations used for this study encompassed a natural gradient of genetic stocks. North Florida lake populations were intergrade largemouth, whereas central and south Florida lake populations were dominantly Florida largemouth bass (Brandon Barthel, personal communication). Thus, genetic differences may have influenced the growth and survival results I found. Experimental work could discern the contribution of genetics to growth and survival, which would help further identify factors that contribute to age-0 largemouth bass recruitment processes across Florida’s latitudinal gradient. Further research could also potentially identify physiological differences among genotypes that would facilitate energetic analyses for these populations and life history theory.

Evolution of Spawning Strategies

Hatching-date dependent survival and influences on adult fitness have largely depended on short-term studies that typically have only followed one or two year classes. Technological

advances in genetics techniques provide opportunities for long-term research evaluating relationships between parental spawning, offspring survival, and fitness. For example, microsatellite analyses could allow researchers to relate offspring characteristics and survival to parental characteristics (e.g., parent's age or size, and parental spawning time) and parental fitness. DeWoody et al. (1998) used microsatellites to identify paternity and maternity of redbreast sunfish *Lepomis auritus* progeny and found differing levels of progeny success for males with differing reproductive strategies. Genetic markers could also allow the evaluation of offspring production by first-time versus repeat spawners for iteroparous species. Information that could arise from genetics research may have important implications for evolutionary theory and fisheries management (e.g., fishing regulations and stock assessments for commercially fished species).

Latitudinal Patterns in Life History

Conducting work at the geographic extent of the largemouth bass's range suggested that conclusions regarding recruitment processes from more northerly latitudes were not always applicable. Thus, there appears to be a need for further research of populations at the extremes of their species range for understanding latitudinal patterns in factors affecting juvenile life histories and evolution of adult spawning strategies. Evidence that late-hatched progeny likely come from smaller adults (Miranda and Muncy 1988; Baylis et al. 1993) in black bass populations has resulted in hypotheses that propose fitness costs to small parents that spawn late at latitudes with severe size-selective overwinter mortality. However, the apparent lack of size-selective overwinter mortality in Florida lakes suggests that fitness trade-offs associated with spawning at small sizes may not be as large in Florida relative to more northerly latitudes. However, high fitness costs could still be associated with spawning at small sizes in Florida if

progeny survival was low due to increased predation or intra-year class cannibalism relative to survival for earlier-hatched fish. Future research in Florida, and at other latitudes, that can investigate mechanisms regulating juvenile survival from specific parents across several generations would greatly facilitate our understanding of latitudinal patterns in juvenile life history and the evolution of parental spawning strategies.

APPENDIX A
DIET COMPOSITION MATRICES FOR ECOPATH MODELS

Table A-1. Diet composition inputs for north region Ecopath model

Group number	Group name	1 ^b	2 ^a	3 ^a	4 ^a	5 ^c	6 ^a	7 ^a	8 ^a	9 ^c	10 ^a	11 ^a
1	Other predators					0.02				0.02		
2	LMB late-hatched (to summer)	< 0.01										
3	LMB late-hatched (to fall)	0.05				< 0.01				< 0.01		
4	LMB late-hatched (age-1)	0.02										
5	LMB late-hatched (adult)											
6	LMB middle-hatched (to summer)	< 0.01										
7	LMB middle-hatched (to fall)	0.05				< 0.01						
8	LMB middle-hatched (age-1)	0.02								< .01		
9	LMB middle-hatched (adult)											
10	LMB early-hatched (to summer)	< 0.01										
11	LMB early-hatched (to fall)	0.04				< 0.01				< 0.01		
12	LMB early-hatched (age-1)	0.02										
13	LMB early-hatched (adult)											
14	killifish / topminnows	0.09	0.10	< 0.01	0.06	0.01	0.20	< 0.01	0.06	0.01	0.19	< 0.01
15	sunfish	0.26	0.20	0.37	0.10	0.68	0.46	0.37	0.10	0.68	0.19	0.37
16	generalists/minnows	0.08	0.05	0.12	0.06	0.06		0.13	0.06	0.06	0.04	0.13
17	benthic fish	0.04	0.20	0.27	0.64	0.03		0.27	0.64	0.03	0.38	0.27
18	crustaceans	0.13	0.21	0.21	0.07	0.18	0.23	0.21	0.07	0.18	0.10	0.21
19	insects	0.14	0.20	0.01	0.05	< 0.01	0.11	0.01	0.05	< 0.01	0.10	0.01
20	zooplankton	0.05	0.05	< 0.01	0.01		< 0.01	< 0.01	0.01		< 0.01	< 0.01
21	macrophytes											
22	phytoplankton											
23	detritus		< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01			< 0.01
24	import											

^athis study. ^bderived from data at www.fishbase.org. ^cSammons and Maceina (2006). ^dDurant et al. (1979). ^ederived from literature

Table A-1. Continued

Group number	Group name	12 ^a	13 ^c	14 ^d	15 ^b	16 ^b	17 ^b	18 ^e	19 ^e	20 ^e
1	Other predators		0.02							
2	LMB late-hatched (to summer)									
3	LMB late-hatched (to fall)		< 0.01							
4	LMB late-hatched (age-1)									
5	LMB late-hatched (adult)									
6	LMB middle-hatched (to summer)									
7	LMB middle-hatched (to fall)									
8	LMB middle-hatched (age-1)		< 0.01							
9	LMB middle-hatched (adult)									
10	LMB early-hatched (to summer)									
11	LMB early-hatched (to fall)		< 0.01							
12	LMB early-hatched (age-1)									
13	LMB early-hatched (adult)									
14	killifish / topminnows	0.06	0.01							
15	sunfish	0.10	0.68							
16	generalists/minnows	0.06	0.06							
17	benthic fish	0.64	0.03							
18	crustaceans	0.07	0.18	0.05	0.20					
19	insects	0.05	< 0.01	0.70	0.60	0.30	0.60		0.20	
20	zooplankton	0.01		0.25	0.20	0.60	0.20	0.20	0.30	0.10
21	macrophytes								0.40	0.90
22	phytoplankton							0.10	0.10	
23	detritus	< 0.01				0.10	0.20	0.70		
24	import									

^athis study. ^bderived from data at www.fishbase.org. ^cSammons and Maceina (2006). ^dDurant et al. (1979). ^ederived from literature

Table A-2. Diet composition inputs for south region Ecopath model

Group number	Group name	1 ^b	2 ^a	3 ^a	4 ^a	5 ^a	6 ^c	7 ^a	8 ^a	9 ^a	10 ^a	11 ^c
1	Other predators						0.02					0.02
2	LMB late-hatched (to spring)											
3	LMB late-hatched (to summer)	0.02										
4	LMB late-hatched (to fall)	0.02					< 0.01					< 0.01
5	LMB late-hatched (age-1)	0.01										
6	LMB late-hatched (adult)											
7	LMB middle (to spring)	0.01										
8	LMB middle-hatched (to summer)	0.02										
9	LMB middle-hatched (to fall)	0.02					< 0.01					
10	LMB middle-hatched (age-1)	0.01										< 0.01
11	LMB middle-hatched (adult)											
12	LMB early-hatched (to spring)	0.01										
13	LMB early-hatched (to summer)	0.02										
14	LMB early-hatched (to fall)	0.02					< 0.01					< 0.01
15	LMB early-hatched (age-1)	0.01										
16	LMB early-hatched (adult)											
17	killifish / topminnows	0.10		0.10	0.10	0.15	0.01	0.02	0.10	0.17	0.15	0.01
18	sunfish	0.20			0.20	0.40	0.68			0.19	0.40	0.68
19	generalists	0.15				0.15	0.06		0.03	0.09	0.15	0.06
20	benthic fish	0.09				0.20	0.03	0.03		0.05	0.20	0.03
21	crustaceans	0.16		0.20	0.30	0.10	0.18	0.43	0.30	0.24	0.10	0.18
22	insects	0.10		0.50	0.40		< 0.01	0.52	0.40	0.19		< 0.01
23	zooplankton	0.05		0.20					0.17	0.07		
24	macrophytes											
25	phytoplankton											
26	detritus											
27	import		1.00									

^athis study. ^bderived from data at www.fishbase.org. ^cSammons and Maceina (2006). ^dDurant et al. (1979). ^ederived from literature

Table A-2. Continued

Group number	Group name	12 ^a	13 ^a	14 ^a	15 ^a	16 ^c	17 ^d	18 ^b	19 ^b	20 ^b	21 ^e	22 ^e	23 ^e
1	Other predators					0.02							
2	LMB late-hatched (to spring)												
3	LMB late-hatched (to summer)												
4	LMB late-hatched (to fall)					< 0.01							
5	LMB late-hatched (age-1)												
6	LMB late-hatched (adult)												
7	LMB middle (to spring)												
8	LMB middle-hatched (to summer)												
9	LMB middle-hatched (to fall)												
10	LMB middle-hatched (age-1)					< 0.01							
11	LMB middle-hatched (adult)												
12	LMB early-hatched (to spring)												
13	LMB early-hatched (to summer)												
14	LMB early-hatched (to fall)					< 0.01							
15	LMB early-hatched (age-1)												
16	LMB early-hatched (adult)												
17	killifish / topminnows	0.05	0.20	0.30	0.15	0.01							
18	sunfish		0.20	0.25	0.40	0.68							
19	generalists	0.02	0.10	0.10	0.15	0.06							
20	benthic fish			0.05	0.20	0.03							
21	crustaceans	0.03	0.15	0.15	0.10	0.18	0.05	0.20					
22	insects	0.70	0.35	0.10		< 0.01	0.70	0.60	0.30	0.60		0.20	
23	zooplankton	0.20		0.06			0.25	0.2	0.60	0.20	0.20	0.30	0.10
24	macrophytes											0.40	0.90
25	phytoplankton										0.10	0.10	
26	detritus								0.1	0.2	0.70		
27	import												

^athis study. ^bderived from data at www.fishbase.org. ^cSammons and Maceina (2006). ^dDurant et al. (1979). ^ederived from literature

APPENDIX B
SENSITIVITY ANALYSIS RESULTS FOR ECOPATH MODELS

Table B-1. Sensitivity analysis for north region Ecopath model

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
1	Biom	1	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
1	Biom	3	EE	-0.30	-0.24	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.24	0.30
1	Biom	4	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	7	EE	-0.30	-0.24	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.24	0.30
1	Biom	8	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	11	EE	-0.29	-0.23	-0.17	-0.11	-0.06	0.00	0.06	0.11	0.17	0.23	0.29
1	Biom	12	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
1	Prod/biom	1	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
1	Cons/biom	3	EE	-0.30	-0.24	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.24	0.30
1	Cons/biom	4	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	7	EE	-0.30	-0.24	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.24	0.30
1	Cons/biom	8	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	11	EE	-0.29	-0.23	-0.17	-0.11	-0.06	0.00	0.06	0.11	0.17	0.23	0.29
1	Cons/biom	12	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
2	Biom	2	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
2	Biom	14	EE	-0.06	-0.05	-0.04	-0.02	-0.01	0.00	0.01	0.02	0.04	0.05	0.06
2	Prod/biom	2	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
2	Cons/biom	14	EE	-0.06	-0.05	-0.04	-0.02	-0.01	0.00	0.01	0.02	0.04	0.05	0.06
3	Biom	3	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
3	Biom	15	EE	-0.06	-0.05	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.05	0.06
3	Biom	16	EE	-0.09	-0.07	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.07	0.09
3	Biom	17	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
3	Prod/biom	3	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
3	Cons/biom	15	EE	-0.06	-0.05	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.05	0.06
3	Cons/biom	16	EE	-0.09	-0.07	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.07	0.09
3	Cons/biom	17	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
4	Biom	4	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
4	Biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
4	Biom	17	EE	-0.09	-0.07	-0.05	-0.04	-0.02	0.00	0.02	0.04	0.05	0.07	0.09
4	Prod/biom	4	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
4	Cons/biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
4	Cons/biom	17	EE	-0.09	-0.07	-0.05	-0.04	-0.02	0.00	0.02	0.04	0.05	0.07	0.09
5	Biom	1	EE	-0.18	-0.14	-0.11	-0.07	-0.04	0.00	0.04	0.07	0.11	0.14	0.18
5	Biom	3	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
5	Biom	5	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	Biom	7	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
5	Biom	11	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
5	Biom	15	EE	-0.09	-0.07	-0.05	-0.04	-0.02	0.00	0.02	0.04	0.05	0.07	0.09
5	Biom	16	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04

Table B-1. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
5	Prod/biom	5	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	Cons/biom	1	EE	-0.18	-0.14	-0.11	-0.07	-0.04	0.00	0.04	0.07	0.11	0.14	0.18
5	Cons/biom	3	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
5	Cons/biom	7	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
5	Cons/biom	11	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
5	Cons/biom	15	EE	-0.09	-0.07	-0.05	-0.04	-0.02	0.00	0.02	0.04	0.05	0.07	0.09
5	Cons/biom	16	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
6	Biom	6	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
6	Biom	14	EE	-0.12	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.12
6	Prod/biom	6	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
6	Cons/biom	14	EE	-0.12	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.12
7	Biom	7	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
7	Biom	15	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
7	Biom	16	EE	-0.09	-0.07	-0.05	-0.04	-0.02	0.00	0.02	0.04	0.05	0.07	0.09
7	Biom	17	EE	-0.06	-0.05	-0.04	-0.02	-0.01	0.00	0.01	0.02	0.04	0.05	0.06
7	Prod/biom	7	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
7	Cons/biom	15	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
7	Cons/biom	16	EE	-0.09	-0.07	-0.05	-0.04	-0.02	0.00	0.02	0.04	0.05	0.07	0.09
7	Cons/biom	17	EE	-0.06	-0.05	-0.04	-0.02	-0.01	0.00	0.01	0.02	0.04	0.05	0.06
8	Biom	8	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	Biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
8	Biom	17	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
8	Prod/biom	8	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	Cons/biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
8	Cons/biom	17	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
9	Biom	1	EE	-0.17	-0.13	-0.10	-0.07	-0.03	0.00	0.03	0.07	0.10	0.13	0.17
9	Biom	3	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
9	Biom	7	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
9	Biom	9	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
9	Biom	11	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
9	Biom	15	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
9	Biom	16	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
9	Prod/biom	9	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
9	Cons/biom	1	EE	-0.17	-0.13	-0.10	-0.07	-0.03	0.00	0.03	0.07	0.10	0.13	0.17
9	Cons/biom	3	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
9	Cons/biom	7	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
9	Cons/biom	11	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
9	Cons/biom	15	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
9	Cons/biom	16	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
10	Biom	10	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
10	Biom	14	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
10	Prod/biom	10	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
10	Cons/biom	14	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08

Table B-1. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
11	Biom	11	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
11	Biom	15	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
11	Biom	16	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
11	Biom	17	EE	-0.06	-0.05	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.05	0.06
11	Prod/biom	11	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
11	Cons/biom	15	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
11	Cons/biom	16	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
11	Cons/biom	17	EE	-0.06	-0.05	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.05	0.06
12	Biom	12	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
12	Biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
12	Biom	17	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
12	Prod/biom	12	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
12	Cons/biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
12	Cons/biom	17	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
13	Biom	1	EE	-0.16	-0.13	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.13	0.16
13	Biom	3	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
13	Biom	7	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
13	Biom	11	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
13	Biom	13	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
13	Biom	15	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
13	Biom	16	EE	-0.04	-0.03	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.02	0.03	0.04
13	Prod/biom	13	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
13	Cons/biom	1	EE	-0.16	-0.13	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.13	0.16
13	Cons/biom	3	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
13	Cons/biom	7	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
13	Cons/biom	11	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
13	Cons/biom	15	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
13	Cons/biom	16	EE	-0.04	-0.03	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.02	0.03	0.04
14	Biom	14	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
14	Biom	19	Biom	-0.04	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.04
14	Biom	20	Biom	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
14	Biom	21	Cons/biom	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
14	Prod/biom	14	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
14	Cons/biom	19	Biom	-0.04	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.04
14	Cons/biom	20	Biom	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
14	Cons/biom	21	Cons/biom	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
15	Biom	15	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	Biom	18	EE	-0.43	-0.34	-0.26	-0.17	-0.09	0.00	0.09	0.17	0.26	0.34	0.43
15	Biom	19	Biom	-0.25	-0.20	-0.15	-0.10	-0.05	0.00	0.05	0.10	0.15	0.20	0.25
15	Biom	20	Biom	-0.22	-0.18	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.18	0.22
15	Biom	21	Cons/biom	-0.22	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.22
15	Prod/biom	15	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	Cons/biom	18	EE	-0.43	-0.34	-0.26	-0.17	-0.09	0.00	0.09	0.17	0.26	0.34	0.43

Table B-1. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
15	Cons/biom	19	Biom	-0.25	-0.20	-0.15	-0.10	-0.05	0.00	0.05	0.10	0.15	0.20	0.25
15	Cons/biom	20	Biom	-0.22	-0.18	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.18	0.22
15	Cons/biom	21	Cons/biom	-0.22	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.22
16	Biom	16	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
16	Biom	20	Biom	-0.09	-0.07	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.07	0.09
16	Prod/biom	16	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
16	Cons/biom	20	Biom	-0.09	-0.07	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.07	0.09
17	Biom	17	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
17	Biom	19	Biom	-0.17	-0.14	-0.10	-0.07	-0.03	0.00	0.03	0.07	0.10	0.14	0.17
17	Biom	20	Biom	-0.15	-0.12	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.12	0.15
17	Biom	21	Cons/biom	-0.14	-0.12	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.12	0.14
17	Prod/biom	17	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
17	Cons/biom	19	Biom	-0.17	-0.14	-0.10	-0.07	-0.03	0.00	0.03	0.07	0.10	0.14	0.17
17	Cons/biom	20	Biom	-0.15	-0.12	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.12	0.15
17	Cons/biom	21	Cons/biom	-0.14	-0.12	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.12	0.14
18	Biom	18	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
18	Biom	21	Cons/biom	-0.07	-0.06	-0.04	-0.03	-0.02	0.00	0.02	0.03	0.04	0.06	0.07
18	Prod/biom	18	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
18	Cons/biom	21	Cons/biom	-0.07	-0.06	-0.04	-0.03	-0.02	0.00	0.02	0.03	0.04	0.06	0.07
19	Prod/biom	19	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
19	Prod/biom	20	Biom	0.45	0.30	0.19	0.11	0.05	0.00	-0.04	-0.08	-0.10	-0.13	-0.15
19	Prod/biom	21	Cons/biom	0.85	0.57	0.37	0.21	0.10	0.00	-0.08	-0.14	-0.20	-0.24	-0.28
19	Cons/biom	20	Biom	-0.23	-0.18	-0.14	-0.09	-0.05	0.00	0.05	0.09	0.14	0.18	0.23
19	Cons/biom	21	Cons/biom	-0.43	-0.34	-0.26	-0.17	-0.09	0.00	0.09	0.17	0.26	0.34	0.43
19	EE	19	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
19	EE	20	Biom	0.45	0.30	0.19	0.11	0.05	0.00	-0.04	-0.08	-0.10	-0.13	-0.15
19	EE	21	Cons/biom	0.85	0.57	0.37	0.21	0.10	0.00	-0.08	-0.14	-0.20	-0.24	-0.28
20	Prod/biom	20	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
20	EE	20	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
21	Biom	21	Cons/biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
21	Prod/biom	21	Cons/biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33

Table B-2. Sensitivity analysis for south region Ecopath model

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
1	Biom	3	EE	-0.09	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.09
1	Biom	4	EE	-0.36	-0.28	-0.21	-0.14	-0.07	0.00	0.07	0.14	0.21	0.28	0.36
1	Biom	5	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	7	EE	-0.24	-0.19	-0.14	-0.10	-0.05	0.00	0.05	0.10	0.14	0.19	0.24
1	Biom	8	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	9	EE	-0.36	-0.28	-0.21	-0.14	-0.07	0.00	0.07	0.14	0.21	0.28	0.36
1	Biom	10	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	12	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
1	Biom	13	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	14	EE	-0.36	-0.28	-0.21	-0.14	-0.07	0.00	0.07	0.14	0.21	0.28	0.36
1	Biom	15	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Biom	17	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
1	Biom	18	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
1	Biom	19	EE	-0.13	-0.11	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.11	0.13
1	Biom	20	EE	-0.11	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.11
1	Prod/biom	1	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
1	Cons/biom	3	EE	-0.09	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.09
1	Cons/biom	4	EE	-0.36	-0.28	-0.21	-0.14	-0.07	0.00	0.07	0.14	0.21	0.28	0.36
1	Cons/biom	5	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	7	EE	-0.24	-0.19	-0.14	-0.10	-0.05	0.00	0.05	0.10	0.14	0.19	0.24
1	Cons/biom	8	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	9	EE	-0.36	-0.28	-0.21	-0.14	-0.07	0.00	0.07	0.14	0.21	0.28	0.36
1	Cons/biom	10	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	12	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
1	Cons/biom	13	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	14	EE	-0.36	-0.28	-0.21	-0.14	-0.07	0.00	0.07	0.14	0.21	0.28	0.36
1	Cons/biom	15	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
1	Cons/biom	17	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
1	Cons/biom	18	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
1	Cons/biom	19	EE	-0.13	-0.11	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.11	0.13
1	Cons/biom	20	EE	-0.11	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.11
3	Biom	3	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
3	Prod/biom	3	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
4	Biom	4	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
4	Prod/biom	4	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	Biom	5	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	Biom	20	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
5	Prod/biom	5	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	Cons/biom	20	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05

Table B-2. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
6	Biom	18	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
6	Prod/biom	6	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
6	Cons/biom	1	EE	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
6	Cons/biom	18	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
7	Biom	7	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
7	Prod/biom	7	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	Biom	8	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	Biom	17	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
8	Prod/biom	8	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	Cons/biom	17	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
9	Biom	9	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
9	Biom	17	EE	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
9	Biom	18	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
9	Biom	19	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
9	Biom	20	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
9	Prod/biom	9	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
9	Cons/biom	17	EE	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
9	Cons/biom	18	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
9	Cons/biom	19	EE	-0.07	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.07
9	Cons/biom	20	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
10	Biom	10	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
10	Biom	17	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
10	Biom	18	EE	-0.04	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.04
10	Biom	19	EE	-0.06	-0.05	-0.04	-0.02	-0.01	0.00	0.01	0.02	0.04	0.05	0.06
10	Biom	20	EE	-0.11	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.11
10	Prod/biom	10	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
10	Cons/biom	17	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
10	Cons/biom	18	EE	-0.04	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.04
10	Cons/biom	19	EE	-0.06	-0.05	-0.04	-0.02	-0.01	0.00	0.01	0.02	0.04	0.05	0.06
10	Cons/biom	20	EE	-0.11	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.11
11	Biom	1	EE	-0.24	-0.19	-0.14	-0.10	-0.05	0.00	0.05	0.10	0.14	0.19	0.24
11	Biom	4	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07

Table B-2. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
11	Biom	14	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
11	Biom	18	EE	-0.13	-0.10	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.10	0.13
11	Biom	19	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
11	Prod/biom	11	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
11	Cons/biom	1	EE	-0.24	-0.19	-0.14	-0.10	-0.05	0.00	0.05	0.10	0.14	0.19	0.24
11	Cons/biom	4	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
11	Cons/biom	9	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
11	Cons/biom	14	EE	-0.07	-0.06	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.06	0.07
11	Cons/biom	18	EE	-0.13	-0.10	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.10	0.13
11	Cons/biom	19	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
12	Biom	12	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
12	Prod/biom	12	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
13	Biom	13	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
13	Biom	17	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
13	Prod/biom	13	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
13	Cons/biom	17	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
14	Biom	14	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
14	Biom	17	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
14	Biom	19	EE	-0.04	-0.03	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.02	0.03	0.04
14	Prod/biom	14	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
14	Cons/biom	17	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
14	Cons/biom	19	EE	-0.04	-0.03	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.02	0.03	0.04
15	Biom	15	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	Biom	17	EE	-0.03	-0.03	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.02	0.03	0.03
15	Biom	19	EE	-0.04	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.04
15	Biom	20	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
15	Prod/biom	15	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	Cons/biom	17	EE	-0.03	-0.03	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.02	0.03	0.03
15	Cons/biom	19	EE	-0.04	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.04
15	Cons/biom	20	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
16	Biom	1	EE	-0.16	-0.13	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.13	0.16
16	Biom	4	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
16	Biom	9	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
16	Biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
16	Biom	16	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
16	Biom	18	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08
16	Prod/biom	16	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
16	Cons/biom	1	EE	-0.16	-0.13	-0.09	-0.06	-0.03	0.00	0.03	0.06	0.09	0.13	0.16
16	Cons/biom	4	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
16	Cons/biom	9	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
16	Cons/biom	14	EE	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
16	Cons/biom	18	EE	-0.08	-0.07	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.07	0.08

Table B-2. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
17	Biom	22	Biom	-0.11	-0.09	-0.07	-0.05	-0.02	0.00	0.02	0.05	0.07	0.09	0.11
17	Biom	23	Biom	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
17	Biom	24	Cons/biom	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
17	Prod/biom	17	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
17	Cons/biom	23	Biom	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
17	Cons/biom	24	Cons/biom	-0.10	-0.08	-0.06	-0.04	-0.02	0.00	0.02	0.04	0.06	0.08	0.10
18	Biom	18	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
18	Biom	21	EE	-0.41	-0.33	-0.25	-0.16	-0.08	0.00	0.08	0.16	0.25	0.33	0.41
18	Biom	22	Biom	-0.27	-0.22	-0.16	-0.11	-0.05	0.00	0.05	0.11	0.16	0.22	0.27
18	Biom	23	Biom	-0.22	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.22
18	Biom	24	Cons/biom	-0.23	-0.18	-0.14	-0.09	-0.05	0.00	0.05	0.09	0.14	0.18	0.23
18	Prod/biom	18	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
18	Cons/biom	21	EE	-0.41	-0.33	-0.25	-0.16	-0.08	0.00	0.08	0.16	0.25	0.33	0.41
18	Cons/biom	22	Biom	-0.27	-0.22	-0.16	-0.11	-0.05	0.00	0.05	0.11	0.16	0.22	0.27
18	Cons/biom	23	Biom	-0.22	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.22
18	Cons/biom	24	Cons/biom	-0.23	-0.18	-0.14	-0.09	-0.05	0.00	0.05	0.09	0.14	0.18	0.23
19	Biom	19	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
19	Biom	22	Biom	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
19	Biom	23	Biom	-0.13	-0.10	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.10	0.13
19	Biom	24	Cons/biom	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
19	Prod/biom	19	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
19	Cons/biom	22	Biom	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
19	Cons/biom	23	Biom	-0.13	-0.10	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.10	0.13
19	Cons/biom	24	Cons/biom	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
20	Biom	20	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
20	Biom	22	Biom	-0.06	-0.05	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.05	0.06
20	Biom	23	Biom	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
20	Biom	24	Cons/biom	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
20	Prod/biom	20	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
20	Cons/biom	22	Biom	-0.06	-0.05	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.05	0.06
20	Cons/biom	23	Biom	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
20	Cons/biom	24	Cons/biom	-0.05	-0.04	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.04	0.05
21	Biom	21	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
21	Biom	24	Cons/biom	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
21	Prod/biom	21	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
21	Cons/biom	24	Cons/biom	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08

Table B-2. Continued

Group	Input parameter	Group affected	Estimated parameter	Input parameter variation										
				-50	-40	-30	-20	-10	0	10	20	30	40	50
22	Prod/biom	22	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
22	Prod/biom	23	Biom	0.42	0.28	0.18	0.11	0.05	0.00	-0.04	-0.07	-0.10	-0.12	-0.14
22	Prod/biom	24	Cons/biom	0.85	0.57	0.36	0.21	0.09	0.00	-0.08	-0.14	-0.20	-0.24	-0.28
22	Cons/biom	23	Biom	-0.21	-0.17	-0.13	-0.08	-0.04	0.00	0.04	0.08	0.13	0.17	0.21
22	Cons/biom	24	Cons/biom	-0.42	-0.34	-0.25	-0.17	-0.09	0.00	0.09	0.17	0.25	0.34	0.42
22	EE	22	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
22	EE	23	Biom	0.42	0.28	0.18	0.11	0.05	0.00	-0.04	-0.07	-0.10	-0.12	-0.14
22	EE	24	Cons/biom	0.85	0.57	0.36	0.21	0.09	0.00	-0.08	-0.14	-0.20	-0.24	-0.28
23	Prod/biom	23	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
23	EE	23	Biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
24	Biom	24	Cons/biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
24	Prod/biom	24	Cons/biom	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33

REFERENCE LIST

- Abrams, P. 1980. Some comments on measuring niche overlap. *Ecology* 6:44-49.
- Aday, D. D., D. E. Shoup, J. A. Neviackas, J. L. Kline, and D. H. Wahl. 2005. Prey community responses to bluegill and gizzard shad foraging: implications for growth of juvenile largemouth bass. *Transactions of the American Fisheries Society* 134:1091-1102.
- Allen, M. S., C. J. Walters, and R. Myers. In Press. Temporal trends in largemouth bass mortality with fishery implications. *North American Journal of Fisheries Management*.
- Allen, M. S., W. Sheaffer, W. F. Porak, and S. Crawford. 2002. Growth and mortality of largemouth bass in Florida waters: implications for use of length limits. Pages 559-566 *in* D. P. Philipp and M. S. Ridgeway editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Allen, R. R. 1971. Relation between production and biomass. *Journal of Fisheries Research Board of Canada* 28:1573-1581.
- Bachman, R. W., B. L. Jones, D. D. Fox, M. Hoyer, L. A. Bull, and D. E. Canfield, Jr. 1996. Relations between trophic stat indicators and fish in Florida (U.S.A.) lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:842-855.
- Bailey, R.M., and C. L. Hubbs. 1949. The black basses (*Micropterus*) of Florida, with description of a new species. *University of Michigan Museum of Zoology Occasional Papers* 516:1-40.
- Baylis, J. R., D. D. Wiegmann, and M. H. Hoff. 1993. Alternating life histories of smallmouth bass. *Transactions of the American Fisheries Society* 122:500-510.
- Bestgen, K. R., D. W. Beyers, J. A. Rice, and G. B. Haines. 2006. Factors affecting recruitment of young Colorado pikeminnow: synthesis of predation experiments, field experiments, field studies, and individual-based modeling. 2006. *Transactions of the American Fisheries Society* 135:1722-1742
- Boxrucker, J. 1982. First year growth and survival of stocked largemouth bass in a small Oklahoma impoundment. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 36:369-376.
- Bull, L. A., L. J. Davis, J. B. Furse, G. L. Warren, and M. J. Vogel. 1991. Lake Okeechobee-Kissimmee River-Everglades Resource Evaluation. Final Report, submitted to Florida Game and Fresh Water Fish Commission, Tallahassee, FL.
- Byström, P., L. Persson, and E. Wahlstrom. 1998. Competing predators and prey: juvenile bottlenecks in whole-lake experiments. *Ecology* 79:2153-2167.

- Cargnelli, L. M., and M. R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:360-367.
- Chew, R. L. 1974. Early life history of the Florida largemouth bass. *Fishery Bulletin* No. 7. Florida Game and Fresh Water Fish Commission, Dingell-Johnson Project F-24-R.
- Christensen, V., C. J. Walters, and D. Pauly. *Ecopath with Ecosim: a user's guide*. November 2005. available at: www.ecopath.org
- Christenssen, B. 1996. Predator foraging capabilities and prey anti-predator behaviours: pre-versus postcapture constraints on size-dependent predator-prey interactions. *Oikos* 76:368-380.
- Cichra, C. E., W. H. Neill, and R. L. Noble. 1982. Differential resistance of northern and Florida largemouth bass to cold shock. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 34(1980):19-24.
- Conover, D. O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. *Transactions of the American Fisheries Society* 119:416-430.
- Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology* 41(supplement b):161-178.
- Conover, D.O., and E. T. Schultz. 1997. Natural selection and the evolution of growth rate in the early life history: what are the tradeoffs? Pages 305-332 in R. C. Chambers and E. A. Trippel, editors. *Early life history and recruitment in fish populations*. Chapman and Hall, New York.
- Crawford, S., W. F. Porak, D. J. Renfro, and R. L. Cailteux. 2002. Characteristics of trophy largemouth bass populations in Florida. Pages 567-581 in D. P. Philipp and M. S. Ridgway, editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Crecco, V. A., and T. F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1640-1648.
- Cushing, D. H. 1975. *Marine Ecology and Fisheries*. Cambridge University Press, London, UK.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish population: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26:250-293.

- DeAngelis, D. L., K. A. Rose, L. B. Crowder, E. A. Marschall, and D. Lika. 1993. Fish cohort dynamics: application of complementary modeling approaches. *The American Naturalist* 142:604-622.
- Denslow, N.D., H. S. Lee, C. J. Bowman, M. J. Hemmer, and L. C. Folmar. 2001. Multiple responses in gene expression in fish treated with estrogen. *Comparative Biochemistry and Physiology B* 129:277-282.
- Deriso, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Canadian Journal of Fisheries and Aquatic Sciences* 37:268-282.
- DeWoody, J. A., D. E. Fletcher, S. D. Wilkins, W. S. Nelson, and J. C. Avise. 1998. Molecular genetic dissection of spawning, parentage, and reproductive tactics in a population of redbreast sunfish, *Lepomis auritus*. *Evolution* 52:1802-1810.
- Donaghy, M. J., and E. Verspoor. 1997. Egg survival and timing of hatch in two Scottish Atlantic salmon stocks. *Journal of Fish Biology* 51:211-214.
- Durant, D. F., J. V. Shireman, and R. D. Gasaway. 1979. Reproduction, growth, and food habits of Seminole Killifish, *Fundulus seminolis*, from two central Florida lakes. *American Midland Naturalist* 102:127-133.
- Einum, S., and I. A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* 54: 628-639.
- Endler, J.A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, N.J.
- Essington, T. E. 2007. Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. *Canadian Journal of Fisheries and Aquatic Sciences* 64:638-637.
- Florida LAKEWATCH. 2000. Florida LAKEWATCH Data 1999. Department of Fisheries and Aquatic Sciences, University of Florida/Institute of Food and Agricultural Sciences. Library, University of Florida. Gainesville, Florida.
- Fooden, J., and M. Aimi. 2003. Birth-season variation in Japanese macaques, *Macaca fuscata*. *Primates* 44:109-117.
- Forsberg, C., and S. Ryding. 1980. Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. *Achiv für Hydrobiologie* 89:189-207.
- Fox, M. G., and A. J. Crivelli. 1998. Body size and reproductive allocation in a multiple spawning centrarchid. *Canadian Journal of Fisheries and Aquatic Sciences* 55:737-748.
- Fullerton, A. H., J. E. Garvey, R. A. Wright, and R. A. Stein. 2000. Overwinter growth and survival of largemouth bass: interactions among size, food, origin, and winter severity. *Transactions of the American Fisheries Society* 129:1-12.

- Garvey, J. E., R. A. Wright, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2414-2424.
- Garvey, J. E., D. R. DeVries, R. A. Wright, and J. G. Miner. 2003. Energetic adaptations along a broad latitudinal gradient: implications for widely distributed assemblages. *Bioscience* 53:141-150.
- Garvey, J. E., R. A. Stein, R. A. Wright, and M. T. Bremigan. 2002a. Exploring ecological mechanisms underlying largemouth bass recruitment along environmental gradients. *In* Black bass: ecology, conservation, and management. Pages 7-23 *in* D. P. Philipp and M. S. Ridgway, editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Garvey, J. E., T. P. Herra, and W. C. Leggett. 2002b. Protracted reproduction in sunfish: the temporal dimension in fish recruitment revisited. *Ecological Applications* 12:194-205.
- Gharrett, A. J., and W. W. Smoker. 1993. Genetic components in life history traits contribute to population structure. Pages 197-202 *in* J. G. Cloud and G. H. Thorgaard, editors. *Genetic Conservation of Salmonid Fishes*. Plenum Press, New York, N.Y.
- Gharrett, A.J., W. W. Smoker, R. R. Reisenbichler, and S. G. Taylor. 1999. Outbreeding depression in hybrids between odd- and even-broodyear pink salmon. *Aquaculture* 173:117-129.
- Goodgame, L. S., and L. E. Miranda. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. *Transactions of the American Fisheries Society* 122:131-138.
- Gran, J. E. 1995. Gonad development and spawning of largemouth bass in a tropical reservoir. M. Sc. Thesis, North Carolina State University, Raleigh, N.C.
- Gross, T.S., C. M. Wieser, M. S. Sepulveda, J. J. Wiebe, T. R. Schoeb, and N. D. Denslow. 2002. Characterization of annual reproductive cycles for pond-reared Florida largemouth bass *Micropterus salmoides floridanus*. Pages 205-212 *in* D. P. Phillip and M. S. Ridgway, editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Guénette, S., V. Christensen, and D. Pauly. 2001. Fisheries impacts on north Atlantic ecosystems: models and analyses. *Fisheries Centre Research Reports* 9(4), Fisheries Centre, University of British Columbia, Canada.
- Hambright, K. D., 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500-508.

- Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11-20 in R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Henderson, P. A., H. A. Holmes, and R. N. Bamber. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *Journal of Fish Biology* 33:221-233.
- Hilborn, R. and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment Choice, Dynamics and Uncertainty. Kluwer Academic Publishers, Massachusetts.
- Hjort, J. 1914. Fluctuations in the great fisheries of the northern Europe viewed in the light of biological research. *Journal du Conseil pour l'Exploration de la Mer* 20:1-228.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17-29 in R. D. Hoyt, editor. Proceedings of the 10th Annual Larval Fish Conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Houde, E. D. 1997. Patterns and consequences of selective processes in Teleost early life histories. Pages 169-193 in R. C. Chambers and E. A. Trippel, editors. Early life history and recruitment in fish populations. Chapman and Hall, New York.
- Isely, J. J., R. L. Noble, J. B. Koppelman, and D. P. Philipp. 1987. Spawning period and first-year growth of northern, Florida, and intergrade stocks of largemouth bass. *Transactions of the American Fisheries Society* 116:757-762.
- Jackson, J. R., and R. L. Noble. 2000. Relationships between annual variations in reservoir conditions and age-0 largemouth bass year class strength. *Transactions of the American Fisheries Society* 129:699-715.
- Jenkins, R. M. 1975. Black bass crops and species associations in reservoirs. Pages 114-124 in R. H. Stroud and H. Clepper, editors. Black Bass Biology and Management. Sport Fishing Institute, Washington, D.C.
- Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* 3:65-84.
- Jørgensen, C., B. Ernande, O. Fiksen, and U. Dieckmann. 2005. The logic of skipped spawning in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 63:200-211.
- Kassler, T. W., and eight coauthors. 2002. Molecular and morphological analyses of the black basses: implications for taxonomy and conservation. Pages 291-322 in D. P. Philipp and M. S. Ridgway, editors. Black Bass: Ecology, Conservation, and Management. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.

- Kavanagh, P., N. Newlands, V. Christensen, and D. Pauly. 2004. Automated parameter optimization for Ecopath ecosystem models. *Ecological Modeling* 172:141-149.
- Kohler, C. C., R. J. Sheehan, and J. J. Sweatman. 1993. Largemouth bass hatching success and first-winter survival in two Illinois reservoirs. *North American Journal of Fisheries Management* 13:125-133.
- Koslowski, J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution* 7:15-19.
- Kramer, R. H., and L. L. Smith, Jr. 1960. First-year growth of the largemouth bass, *Micropterus salmoides*, and some related ecological factors. *Transactions of the American Fisheries Society* 89:222-233.
- Lam, T. J. 1983. Environmental influences on gonadal activity in fish. Pages 65-116 in W. S. Hoar, D. J. Randall, and E. M. Donaldson, eds. *Fish physiology*. Volume IX, Part B, Acad. Press, New York.
- Lobinske, R. J., A. Ali, and J. Frouz. 2002. Ecological studies of spatial and temporal distributions of larval Chironomidae (Diptera) with emphasis on *Glyptotendipes paripes* (Diptera: Chironomidae) in three central Florida lakes. *Environmental Entomology* 31:637-647.
- Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecological Applications* 7:1024-1038.
- Maceina, M. J., B. R. Murphy, and J. J. Isely. 1988. Factors regulating Florida largemouth bass stocking success and hybridization with northern largemouth bass in Aquilla Lake, Texas. *Transactions of the American Fisheries Society* 117:221-231.
- Maceina, M. J., S. J. Rider, and S. T. Szedlmayer. 1995. Density, temporal spawning patterns, and growth of age-0 and age-1 largemouth bass *Micropterus salmoides* in vegetated and unvegetated areas of Lake Guntersville, Alabama. Pages 497-511 in D. C. Secor, J. M. Dean, and S. E. Campana, editors. *Recent Developments in Fish Otolith Research*. University of South Carolina Press, Columbia, South Carolina.
- Miller, S. J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-year largemouth bass. *Transactions of the American Fisheries Society* 111:527-530.
- Miller, S. J., and T. Storck. 1984. Temporal spawning distribution of largemouth bass and young-of-year growth, determined from daily otolith rings. *Transactions of the American Fisheries Society* 113:571-578.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fish: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1657-1670.

- Miranda, L. E., and W. D. Hubbard. 1994. Winter survival of age-0 largemouth bass relative to size, predators, and shelter. *North American Journal of Fisheries Management* 14:790-796.
- Miranda, L.E., and R. J. Muncy. 1987. Recruitment of young-of-year largemouth bass in relation to size structure of parental stock. *North American Journal of Fisheries Management* 7:131-137.
- Miranda, L.E., and R. J. Muncy. 1988. Spawning sequence of largemouth bass, bluegill, and gizzard shad. *Proceedings of the Annual Conference of Southeastern Fisheries and Wildlife Agencies* 41(1987):197-204.
- Mittelbach, G.G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1454-1465.
- Munro, A.D., A. Scott, and T. J. Lam. 1990. Reproductive seasonality in teleosts: environmental influences. CRC Press, Boca Raton, F.L.
- Narimatsu, Y., and H. Munehara. 1999. Spawn date dependent survival and growth in the early life stage of *Hypoptychus dybowskii* (Gasterieformes). *Canadian Journal of Fisheries and Aquatic Sciences* 56:1849-1855.
- Ney, J. J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews of Aquatic Sciences* 2:55-81.
- O'Bara, C. J., C. E. McCracken, and D. C. Peterson. 2001. Angler exploitation and angling mortality of largemouth bass and spotted bass at Norris Reservoir, Tennessee. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 53(1999):150-161.
- Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* 108:130-136.
- Olson, M. H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. *Ecology* 77:179-190.
- Olson, M. H., G. G. Mittelbach, and C. W. Osenberg. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. *Ecology* 76:1758-1771.
- Orpwood, J. E., S. W. Griffiths, and J. D. Armstrong. 2006. Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology* 75:677-685.

- Ozen, O., and R. L. Noble. 2002. Relationship between water level fluctuations and largemouth bass spawning in a Puerto Rico reservoir. Pages 213-220 in D. P. Philipp and M. S. Ridgway, editors. Black Bass: Ecology, Conservation, and Management. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Ozen, O., and R. L. Noble. 2005. Assessing age-0 year class strength of fast growing largemouth bass in a tropical reservoir. North American Journal of Fisheries Management 25:163-170.
- Parkos, J. J., III, and D. H. Wahl. 2002. Towards an understanding of recruitment mechanisms in largemouth bass. Pages 25-45 in D. P. Philipp and M. S. Ridgeway editors. Black Bass: Ecology, Conservation, and Management. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Patiño, R. 1997. Manipulations of the reproductive system of fishes by means of exogenous chemicals. Progressive Fish Culturist 59:118-128.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Tree 10:430.
- Pauly, D., V. Christensen, and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science 57:697-706.
- Peer, A.C., D. R. DeVries, and R. A. Wright. 2006. First-year growth and recruitment of coastal largemouth bass (*Micropterus salmoides*): spatial patterns unresolved by critical periods along a salinity gradient. Canadian Journal of Fisheries and Aquatic Sciences 63:1911-1924.
- Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and management. Canadian Journal of Fisheries and Aquatic Sciences 47:2-15.
- Philipp, D.P., and G. S. Whitt. 1991. Survival and growth of northern, Florida, and reciprocal F₁ hybrid largemouth bass in central Illinois. Transactions of the American Fisheries Society 120:58-64.
- Philipp, D. P., C. Kaminski, and G. S. Whitt. 1985. A comparison of the embryonic development of northern, Florida, and reciprocal F₁ hybrid largemouth bass in different thermal environments. Illinois Natural History Survey Bulletin 33:261-273.
- Philipp, D.P., W. F. Childers, and G. S. Whitt. 1983. A biochemical genetic evaluation of the northern and Florida subspecies of largemouth bass. Transactions of the American Fisheries Society 112:1-20.

- Philipp, D. P., J. E. Claussen, T. W. Kassler, and J. M. Epifanio. 2002. Mixing stocks of largemouth bass reduces fitness through outbreeding depression. Pages 349-363 in D. P. Philipp and M. S. Ridgeway editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society Symposium 31, American Fisheries Society, Bethesda, Maryland.
- Philipp, D. P., C. A. Toline, M. F. Kubacki, D. B. F. Philipp, and F. J. S. Phelan. 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. *North American Journal of Fisheries Management* 17:557-567.
- Phillips, J., J. R. Jackson, and R. L. Noble. 1995. Hatching date influence on age-specific diet and growth of age-0 largemouth bass. *Transactions of the American Fisheries Society* 124:370-379.
- Pianka, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53-74.
- Pine, W. E., III., and M. S. Allen. 2001. Differential growth and survival of weekly age-0 black crappie cohorts in a Florida lake. *Transactions of the American Fisheries Society* 130:80-91.
- Pine, W. E., III, S. A. Ludsin, and D. R. DeVries. 2000. First-summer survival of largemouth bass cohorts: is early spawning really best? *Transactions of the American Fisheries Society* 129:504-513.
- Plagányi, E. E. 2007. Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper* 477, Rome, Italy.
- Plagányi, E. E., and D. S. Butterworth. 2004. A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. *Ecosystem Approaches to Fisheries in the Southern Benguela*. *African Journal of Marine Science* 26:261-287.
- Poepperl, R. 2003. A quantitative food web model for the macroinvertebrate community of a northern German lowland stream. *International Review of Hydrobiology* 88:433-452.
- Post, D. M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology* 84:1298-1310.
- Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2588-2600.

- Quinn, S. 1996. Trends in regulatory and voluntary catch-and-release fishing. Pages 152-162 in S. Miranda and D. DeVries editors. *Multidimensional Approaches to Reservoir Fisheries Management*. American Fisheries Society Symposium 16, American Fisheries Society, Bethesda, Maryland.
- Renfro, D. J., W. F. Porak, and S. Crawford. 1999. Angler exploitation of largemouth bass determined using variable-reward tags in two central Florida lakes. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 51(1997):175-183.
- Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. *Transactions of the American Fisheries Society* 116:703-718.
- Rogers, M. W., and M. S. Allen. 2005. Hatching duration, growth and survival of age-0 largemouth bass along a latitudinal gradient of Florida lakes. Final Report, submitted to the Florida Fish and Wildlife Conservation Commission, Tallahassee, FL.
- Rogers, M. W., M. S. Allen, and W. F. Porak. 2006. Separating genetic and environmental effects on temporal spawning distributions of largemouth bass. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2391-2399.
- Rutherford, E. S., and E. D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *Fishery Bulletin* 97:315-332.
- Sammons, S. M., L. G. Dorsey, P. W. Bettoli, and F. C. Fiss. 1999. Effects of reservoir hydrology on reproduction by largemouth bass and spotted bass in Normandy Reservoir, Tennessee. *North American Journal of Fisheries Management* 19:78-88.
- Sammons, S. M., and M. J. Maceina. 2006. Changes in diet and food consumption of largemouth bass following large-scale hydrilla reduction in Lake Seminole, Georgia. *Hydrobiologia* 560:109-120.
- Schnute, J. 1987. A general fishery model for a size-structured fish population. *Canadian Journal of Fisheries and Aquatic Sciences* 44:924-940.
- Schramm, H. L., Jr., M. V. Hoyer, and K. J. Jirka. 1983. Relative ecological value of common aquatic plants. Final Report, submitted to the Bureau of Aquatic Plant Research and Control, Florida Department of Natural Resources, Tallahassee, FL.
- Schultz, E.T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). *Evolution* 47(2):520-539.

- Schultz, E.T., K. E. Reynolds, and D. O. Conover. 1996. Countergradient variation in growth among newly hatched *Fundulus heterclitus*: geographic differences revealed by common-environment experiments. *Functional Ecology* 10(3):366-374.
- Seminole County Watershed Atlas. 2001. Florida center for communication for design and research. School of architecture and communication design. University of South Florida, Tampa, FL.
- Shannon, L. J., P. M. Cury, and A. Jarre. 2000. Modeling effects of fishing in the southern Benguela ecosystem. *ICES Journal of Marine Science* 57:720-722.
- Shepherd, J. G., and D. H. Cushing. 1990. Regulation in fish populations: myth or mirage? *Philosophical Transactions of the Royal Society of London, Series B* 330:151-164.
- Shuter, B. J., and J. R. Post. 1990. Climate, population, viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119: 314-336.
- Siitonen, L., and G. A. E. Gall. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri*. *Aquaculture* 78:153-162.
- Sinclair, M., and M. J. Tremblay. 1984. Timing of spawning of Atlantic Herring (*Clupea harengus harengus*) populations and the match-mismatch theory. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1055-1065.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3-47.
- Steinhart, G. B., N. J. Leonard, R. A. Stein, and E. A. Marschall. 2005. Effects of storms, angling, and nest predation during angling on smallmouth bass (*Micropterus dolomieu*) nest success. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2649-2660.
- Suski, C. D., J. H. Svec, J. B. Ludden, F. J. S. Phelan, and D. P. Philipp. 2003. The effect of catch-and-release angling on the parental care behavior of male smallmouth bass. *Transactions of the American Fisheries Society* 2003:210-218.
- Timmons, T. J., W. L. Shelton, and W. D. Davies. 1978. Sampling of reservoir fish populations in littoral areas with rotenone. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 32:474-485.
- Trebitz, A. S. 1991. Timing of spawning in largemouth bass: implications of an individual-based model. *Ecological Modelling* 59:203-227.
- Van Der Kraak, G., J. P. Chang, and D. M. Janz. 1998. Reproduction. Pages 465-488 in E. M. Hallerman, editor. *Population Genetics: principles and applications for fisheries scientists*. American Fisheries Society, Bethesda, M.D.

- Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058-2070.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 58:39-50.
- Walters, C., and J. Korman. 1999. Linking recruitment to trophic factors: revisiting the Beverton-Holt recruitment model from a life history and multispecies perspective. *Reviews in Fish Biology and Fisheries* 9:187-202.
- Walters, C. J., and S. J. D. Martell. 2004. *Fisheries Ecology and Management*. Princeton University Press, Princeton, N.J.
- Walters, C., V. Christensen, and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 7:139-172.
- Walters, C., D. Pauly, V. Christensen, and J. F. Kitchell. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: Ecosim II. *Ecosystems* 3:70-83.
- Werner, E. E., and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecology* 60:256-264.
- Westlake, D. F. 1982. The primary productivity of water plants. Pages 165-180 in J. J. Symoens, S. S. Hooper, and P. Compere editors. *Studies on aquatic vascular plants*. Royal Botanical Society of Belgium, Brussels.
- Wicker, A. M., and W. E. Johnson. 1987. Relationships among fat content, condition factor, and first year survival of Florida largemouth bass. *Transactions of the American Fisheries Society* 116:264-271.
- Wieland, K., A. Jarre-Teichmann, and K. Horbowa. 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES Journal Marine Science*. 57:452-464.
- Williamson, J. H., and G. J. Carmichael. 1990. An aquacultural evaluation of Florida, northern, and hybrid largemouth bass, *Micropterus salmoides*. *Aquaculture* 85:247-257.
- Wright, P. J., and F. M. Gibb. 2005. Selection for birth date in North Sea haddock and its relation to maternal age. *Journal of Animal Ecology* 74:303-312.

Wright, R. A., J. E. Garvey, A. H. Fullerton, and R. A. Stein. 1999. Predicting how winter affects energetics of age-0 largemouth bass: how do current models fare? Transactions of the American Fisheries Society 128:603-612.

Zar, J. H. 1999, Biostatistical analysis 4th Ed. Prentice-Hall, Upper Saddle River, N.J.

BIOGRAPHICAL SKETCH

Mark Rogers was born to Wayne and Judy Rogers in fall, 1975, near Atlanta, GA. He moved around the eastern US quite a bit while growing up, but finally settled in the piedmont of North Carolina where he attended high school. This was an important move because it resulted in Mark spending lots of time fishing on High Rock Lake and is likely the reason he is working in fisheries. He decided to attend N.C. State University in fall, 1993, and majored in fisheries and wildlife science. His advisor, Dr. Richard Noble, hired him as a technician and Mark was sent me to Puerto Rico for a summer to work on tropical reservoirs. After college, he worked at Virginia Tech on the king of the darters *Percina rex* under the supervision of Drs. Paul Angermeier, Bill Ensign, and Brett Albanese. Thereafter, he taught high school science for two years before deciding to attend a Master's program. Mark received his Master's from the University of Wisconsin-Stevens Point with Dr. Michael Hansen as his advisor. After graduating in May, 2002, Mark moved to Gainesville, FL to work as a biological scientist for Dr. Micheal Allen. He began his Ph.D. work in fall, 2003 and defended in fall, 2007. Mark feels most fortunate to have lucked into the best three advisors he could have asked for during his academic training (Drs. Noble, Hansen, and Allen). While working on his Ph.D., Mark married Kristin (Henry) Rogers and they look forward to their future endeavors together.