EFFECTS OF SPRING ANGLING, HABITAT FEATURES, AND GUARDING MALE ATTRIBUTES ON LARGEMOUTH BASS (MICROPTERUS SALMOIDES) NEST SURVIVAL AND IMPLICATIONS FOR FALL YOUNG-OF-YEAR ABUNDANCE

By

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## ABSTRACT

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Black bass reproduction and factors affecting individual nest success have been studied extensively, but the effects of these factors at the population level are poorly known. We monitored largemouth bass nests in four southern Michigan lakes with varying fishing pressures during spring 2008 and 2009 and sampled for young-of-year bass abundance and condition during the fall of 2009. We used Program MARK to determine the importance of factors affecting nest survival probabilities and whether a recent change in fishing regulations in Michigan (allowing a May catch-and-immediate release [CIR] season) affected nest survival. Differences in survival among lakes and between stages of offspring development varied between years, but between-year differences may have been due to sample size and method changes. Nest survival was higher during the CIR season than during the subsequent harvest season for both years. Nest survival probability estimates for 5- or 6-day intervals ranged 14-73% among years, lakes, fishing seasons, and stages of development. Differences in nest survival among lakes and between seasons and stages indicated the importance of the timing and development of nests to the observed percent of nests that were successful in each lake. The outcome of the nesting season was strongly linked to fall recruitment during 2009, but the population-level effects of fishing on recruitment appeared complex. We suggest that the CIR season can remain, with continued monitoring of bass populations for long-term effects.

# ACKNOWLEDGEMENTS

# PREFACE

This research was performed collaboratively with input from professionals in the MDNR as well as colleagues at Michigan State University. In the text "we" is used rather than "I" to reflect the contribution of other individuals to the research. However, I have done all statistical analyses, literature reviews, and writing of this thesis.

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**CHAPTER 1**

CAN SPRING ANGLING, HABITAT FEATURES, AND GUARDING MALE ATTRIBUTES
EXPLAIN LARGEMOUTH BASS NEST SURVIVAL?

Introduction:

Black bass (herein referring to largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieu*) are ecologically and economically important fish (Suski and Philipp 2004; Bremigan et al. 2008). These predators are widespread throughout North America and have coevolved throughout their range with native centrarchid prey fish, thereby facilitating healthy prey fish populations (as reviewed in Bremigan et al. 2008). In addition to maintaining healthy fish populations, there is evidence that black bass can positively influence water clarity in lakes through indirect effects of their feeding (Mittelbach et al. 2006). Black bass are also popular sport fish and over $12.8 billion is spent on their fishing in the United States alone (personal communication as cited in Bremigan et al. 2002). The revenue that black bass generate as well as their ecological significance make the reproduction of these species for sustainable populations a special concern.

There is controversy regarding effects of angling during the black bass nesting season on black bass reproductive success. Black bass begin to build nests and spawn when water temperatures reach 15°C (Heidinger 1975; Baylis et al. 1993) and nesting continues into early summer. During nesting, males maintain the nest by continuously fanning the eggs and aggressively defending them from nest predators (Ridgway 1988; Philipp et al. 1997). Male bass continue to guard the nest while eggs develop into larvae (non-mobile embryos) and finally into fry, which swarm the nest area until becoming adequately independent to disperse (Brown 1984; Brown 1985; Ridgway 1988). Fishing during the nesting season is of concern because nests are

left unprotected while guarding male bass are angled. Offspring in nests are very vulnerable to predation by nest predators such as bluegill and pumpkinseed sunfish (*Lepomis* spp.) without the guarding male. Removal of the male for a 24-hour period can result in complete consumption of offspring by nest predators (Ridgway 1988) and on average 35% of the nest's offspring can be consumed if the male is removed for a typical catch-and-release event lasting five minutes (including return time to the nest; Steinhart et al. 2004). Additionally, anglers may "play" the bass during a catch-and-release angling event, increasing the bass's time away from the nest and potentially leading to his exhaustion (Wiegmann et al. 1992; Kieffer et al. 1995; Philipp et al. 1997). Playing the bass decreases his energy reserves substantially, which then inhibits his ability to successfully defend his offspring from nest predators upon his return to the nest and increases the probability that he will abandon the nest, resulting in nest failure (Kieffer et al. 1995; Cooke et al. 2000). Although the potential is well established for angling to negatively affect the reproductive success of individual black bass, especially when nest predators are prevalent, existence of population-level effects of spring angling on bass reproduction is unclear. This uncertainty exists because the compensatory potential of black bass populations in response to factors that negatively affect fry production is not well quantified. Therefore, spring fishing remains controversial and a challenging decision for many agencies seeking to balance the protection of fish populations with the desire to promote angler opportunity and enjoyment.

Quantifying the relative role of angling and sportfishing regulations in determining reproductive success of black bass populations is complex because multiple factors can affect nest survival in addition to fishing activity. For example, features of the nest's surrounding habitat as well as characteristics of the parental male bass can be determinants of nest survival

(Hunt and Annett 2002; Saunders et al. 2002; Wagner et al. 2006). Many of these attributes are interrelated as well and may interact with effects of fishing.

Nest habitat attributes that may affect nest survival include water temperature, and associated nest depth, substrate, wind exposure, cover (coarse woody material and macrophytes), residential development level of the shoreline, and prevalence of nest predators. Spring temperatures are important because offspring develop more quickly in warmer temperatures (so they are vulnerable to predation for less time) and low temperature extremes increase the likelihood of nest abandonment for both largemouth and smallmouth bass (Shuter et al. 1980; Kubacki et al. 2002). Deeper nests not only are more insulated from temperature extremes, but also are typically less susceptible to negative effects of water level drops (Neves 1975) as well as wind-induced wave action, which affects nest success of both largemouth and smallmouth bass by interacting with several other habitat variables. Wave action stirs sediments, which results in egg siltation and suffocation (Wiegmann et al. 1992; Rejwan et al. 1999; Wagner et al. 2006). Accordingly, substrate type can be a significant predictor of fry production in smallmouth bass (Kramer and Smith 1962; Nack et al. 1993; Saunders et al. 2002), presumably because nests on firmer substrates are less likely to fail due to siltation of sediments. Nearby woody cover also provides shelter from wave action and increases the probability of nest success for smallmouth bass, though increased macrophyte cover is associated with lower nest success (Wills et al. 2004). Shoreline development often corresponds to reductions in cover available to littoral fishes, which may explain why nesting largemouth bass preferentially nest in areas with lower levels of development (Christensen et al. 1996; Radomski and Goeman 2001; Hunt and Annett 2002; Jennings et al. 2003; Wagner et al. 2006). Additionally, nest predator abundance in lakes is variable, and areas with higher predator abundance are associated with an increase in the

metabolic rates of parental males in those areas, resulting in depleted energy reserves and a decreased ability to defend nests as time passes (Steinhart et al. 2005a). Correspondingly, nests in areas of high predator abundance have lower rates of nest success, especially if angling is prevalent (Suski et al. 2003).

Characteristics of the parental male are also determinants of nest success and are interconnected with angling and the previously mentioned habitat variables. For example, larger, more aggressive bass are more active in defending their nests from predators, tend to guard more eggs, and are more vulnerable to angling than their smaller, less aggressive counterparts (Suski and Philipp 2004; Cooke et al. 2007). Aggression levels are naturally variable among individual bass, and human-induced evolution of fish behavior (e.g., selection for particular aggression levels) is increasingly of interest. Anglers may harvest or disrupt the nesting of the most aggressive bass disproportionately, resulting in bass that are less aggressive and less active in terms of nest defense having disproportionately higher reproductive success. Because these levels of aggression are heritable, over time less aggressive individuals may become more prevalent in a population that experiences high levels of angling, leading to a greater abundance of unaggressive, inattentive parental males (Garrett 2002; Suski and Philipp 2004; Cooke et al. 2007; Philipp et al. 2009), which may result in lower nest survival and potentially reduced recruitment of the population. In addition, a low aggression level in bass is linked to lower metabolism and lower anaerobic energy expenditure (Redpath et al. 2010). The full extent to which inherited levels of aggression are linked to other physiological characteristics and the potential for selection on aggression to affect wild bass populations is unknown.

There is variation in aggression and nest defense behavior among male bass, but an individual bass also may exhibit different levels of defensive behaviors based on the stage of

development of the offspring in his nest.  Parental care theory predicts that parental investment will increase as the brood ages until the offspring reach a stage when continuing parental care will not significantly increase brood survival, at which point parental care is predicted to decrease (Trivers 1972; Sargent and Gross 1986).  Evidence suggests that bass exhibit stage-specific defense behaviors that peak when nests reach the larval stage (Colgan and Brown 1988; Ridgway 1988; Suski et al. 2003).  Therefore, nest survival probabilities may vary by stage of development, something that has not previously been incorporated into statistical models.

Previous work on nesting bass has focused on smallmouth bass in one lake or parts of large lakes (Raffetto et al. 1990; Wiegmann et al. 1992; Bayliss and Wiegmann 1993; Phillip et al. 1997; Suski et al. 2003; Steinhart at al. 2004) or in some cases multiple lakes (Saunders et al. 2002).  In contrast, our work focuses on whole populations of largemouth bass in multiple, isolated lakes (but see Wagner et al. 2006, also a study of largemouth bass in multiple lakes). We compare three lakes spanning a gradient of low to high fishing pressure across two years of nest data (with an additional lake studied for one year) to determine the relative importance of factors influencing largemouth bass nest survival.

This research is part of a broader, collaborative evaluation of the effects on bass nest survival and population demographics of a 2006 change to sportfishing regulations for bass in Michigan. In Michigan, black bass fishing seasons are set by statute.  Prior to 2006, targeting or harvesting of black bass was not permitted before the traditional late-May Memorial Day weekend harvest season opener.  The Michigan Department of Natural Resources (MDNR) instituted a new fishing regulation in 2006 (to be evaluated after a 5-year period) that opened a catch-and-immediate release (CIR) fishing season from the last Saturday in April until the harvest season opener on Memorial Day weekend in Michigan's Lower Peninsula.  Regulations for the Upper

Peninsula permit a CIR season from May 15 until Memorial Day weekend. The 2006 Michigan fishing regulation change provides an excellent opportunity to study the impact of fishing regulations and other nest attributes on nest survival.

We first explore nest demographics (number of nests observed and their success in producing fry) and the conditions that nests experience within and across lakes in terms of fishing and recreational activity, temperature and habitat features, and male bass behavior to establish the range of conditions captured by this study. Our focus is on the environmental conditions that offspring in nests face, with the intent to explore their relationships with offspring survival. Survival of offspring within and across nests is ultimately of interest, but we recorded our observations at the nest level, such that persistence of any offspring over successive observation events within a given nest was recorded as nest survival. Therefore nest survival does not indicate the number of offspring that persisted within a nest, but rather it tells us that some offspring persisted from that nest. We also specifically test for differences in nest survival by lake, fishing season, and stage of offspring development using Program MARK (White et al. 2006). We expect that nest survival will be highest in low fishing pressure lakes, during the CIR season, and for nests at the larval stage as a result of increased parental care for larvae. Finally, we estimate nest survival probabilities for each lake, fishing season, and stage of development by combining the effects of lake, season, stage, and nest attributes in modeling to determine the biological effect of each variable.

Methods:

*Lake choice:* To structure the 2006 regulation change evaluation, Michigan State University and MDNR personnel collaboratively selected lakes in southern Michigan that were predicted to vary according to fishing pressure but to be as similar as possible in other features (Table 1). In

addition, we constrained the choice of study lakes to those that were sufficiently deep to thermally stratify (like most lakes in Michigan where relatively high angling pressure occurs) and contained no surface water connections to other bass populations to prevent loss or addition of individuals to the study due to migration.

Table 1: Characteristics of each study lake. The percent developed shoreline was the length of shoreline with houses or other structures and maintained lawns, beaches, or retaining walls divided by the total perimeter of the lake. Warner Lake, the low fishing pressure lake, was substantially smaller and less developed than the other lakes, and contained no public boat access. Warner Lake was added to the study for 2009 because our original low fishing pressure lake had extremely few bass nests, precluding analysis of nest survival in that lake.

| Lake | County | Anticipated Angling Pressure | Area (ha) | Maximum Depth (m) | % Developed Shoreline |
|---|---|---|---|---|---|
| Warner | Barry | low | 26 | 16 | 8 |
| North | Washtenaw | medium | 91 | 18 | 62 |
| Chemung | Livingston | high | 126 | 21 | 71 |
| Woodland | Livingston | high | 104 | 11 | 76 |

The levels of angling in each of the study lakes were expected to represent much of the variation in angling that occurs among public lakes in Michigan. Woodland and Chemung lakes were popular, public lakes with relatively large parking lots at the public access sites and located in well-populated areas of southern Michigan. These lakes both tended to be frequented by individual bass anglers as well as bass tournaments and likely were fairly representative of other popular fishing lakes in southern Michigan of their size. North Lake was another public lake, but it had a small, unpaved parking lot and was more secluded in the Pinckney Recreation Area. Thus we viewed North Lake as representative of many lakes throughout southern Michigan, also situated within recreation areas or state game areas, that receive intermediate angling levels. Warner Lake was a small, private lake with no public access and represented Michigan's more secluded, private lakes with low levels of fishing.

*Nest distribution and survival:* We sought to determine if nest survival varied among lakes, between fishing seasons, and by offspring stage of development using data collected in the lakes during 2008 and 2009. Crews monitored bass nests during spring of 2008 and used slightly modified methods during 2009. During both years, we visited each lake approximately every three days and searched their littoral areas in one pass using boats powered by electric trolling motors to find new bass nests and monitor those already located (as per Raffetto et al. 1990; Wagner et al. 2006; Suski and Ridgway 2007). During 2008 crews surveyed the shoreline with two observers on the boat's bow (one observer entered the water after spotting a potential nest site). During 2009, one observer remained on the boat's bow and a snorkeler was harnessed to a tow rope behind the boat at all times to reduce the possibility of missing nests in turbid water. In ideal conditions (clear, sunny days with minimal surface water disturbance) observers in the boat could see into the water at distances of approximately 8 m. Snorkelers could observe bass at shorter distances, approximately 1.5-3 m depending on water clarity. To survey broad, shallow areas, crews steered the boat in a zigzag pattern, alternating between shallow and deep littoral areas. Most of the littoral zone in each lake was not broad and did not require a zigzag search pattern. Once a nest was found, crews recorded its location as a GPS waypoint and anchored a uniquely-numbered marker at the edge of the nest to aid in locating the nest on subsequent visits.

On each sampling date, crews monitored nests to assess the presence or absence of offspring (either eggs, larvae, or fry; Steinhart et al. 2004; Suski and Ridgway 2007). We monitored a nest until it reached the fry stage (a successful nest) or was abandoned and failed (offspring never reached the fry stage; Philipp et al. 1997; Suski and Ridgway 2007). We confirmed each nest failure with two additional visits to ensure that failures were recorded correctly and fry had not been overlooked.

*Nest attributes:* We recorded a variety of data about each nest to be able to consider multiple factors that might affect nest survival. The nest attribute variables that we noted can be categorized as either features of the parental male bass, the nest's habitat nearby, or levels of human activity near the nest site. The following paragraphs describe how we collected data in each category.

We determined several attributes of the guarding male at each nest, for subsequent comparison to the nest's fate. We estimated the bass's total length (2008 and 2009) and characterized his relative aggression level using two metrics (2009 only): a count of total antipredator behaviors (TAB score) and a relative index of nest site tenacity. For each nest, we determined these metrics on the first sampling date that it was discovered. On this first observation date, the snorkeler swam between the boat and the nest several times to record all of the nest attributes. On the snorkeler's first visit to a nest, he/she measured the TAB score in order to disturb the bass as little as possible before observing his behavior. The TAB score is a count of yawning, rushing, and biting behaviors exhibited by the bass in reaction to a life-size bluegill model (102 mm) held by the snorkeler on a 1.5-m pole in the vicinity of the nest for 60 seconds (see Suski and Philipp 2004 for details on the technique). We also recorded a modified TAB score for each bass that included the behavior of "small yawns," much smaller mouth movements, which had not been included by previous researchers who applied the TAB method to typically more aggressive smallmouth bass.

We based our second aggression metric, site tenacity of the parental male, on the male's propensity to remain at the nest site throughout the snorkeler's multiple visits to the nest on the first observation date. A male received a 0 if he was never observed at the nest site, a 1 if he was present during approximately half of the visits the snorkeler made, a 2 if he consistently

remained in the nest area, and a 3 if he remained at the nest site and acted aggressively toward the snorkeler by yawning or striking at him/her or at sampling equipment.

During 2009 we recorded surrogate measures of parental male stress because sources of stress can affect nest survival. Crews recorded any hook wounds on the mouth of the bass as an indicator that the fish had been angled (Philipp et al. 1997; Suski and Philipp 2004). We also recorded observations of Saprolegnian infections (sores) because these occur in largemouth bass with high levels of cortisol, a stress-related hormone, which corresponds to higher levels of nest abandonment than those of bass with low cortisol levels (O'Connor et al. 2009).

We collected data on several nest habitat attributes for use in modeling nest survival. We visually categorized the underlying substrate of each nest as silt, sandy-silt, sand, sandy-gravel, or gravel based on techniques in McMahon et al. (1996). Crews estimated the percent of the immediate area surrounding the nest that had macrophyte cover using a 1 $m^2$ quadrat divided into 16 quadrants as reference. We quantified the presence of coarse woody material (CWM, wood >5cm in diameter, see Christensen et al. 1996) using the quadrat by counting the number of quadrants containing CWM. Crews characterized the development status of the shoreline nearest to each nest as: not developed, developed with a vegetated shoreline, maintained lawn or beach, and developed with a retaining wall or hardened structure (as in Wagner et al. 2006). We measured nest depth using a 2-m long tube with markings every 0.1 m. To determine a nest's relative level of wind exposure (high or low), we compared its GPS location to the predominant direction of wind in each lake, determined from weather reports (as in Wagner et al. 2006).

We quantified estimates of nest predator abundance for each nest using catch data from nest predator traps used throughout the nesting season. Traps were made from 0.5-in hardware cloth and measured 24-in square by 11-in tall with four openings, each 4-in long by 1-in wide (Sherry

2005).  These traps were large enough to capture a range of sunfish sizes (the predominant nest predator in these lakes) without trapping bass swim-up fry or adults (personal observation).  On each sampling date, crews distributed between three and six nest predator traps to haphazard locations distributed throughout the lake with varying substrate and macrophyte cover. Crews removed traps at the end of each day and recorded the number and size of fish caught.   We noted habitat features (depth, shoreline development type, substrate, macrophyte cover, and macrophyte growth form) and GPS location for each trap on each sampling date, for subsequent extrapolation of nest predator counts to individual bass nests using significant stratum determined for each lake (see below).

We monitored water temperature at the lake level, rather than at individual nests, using HOBO temperature loggers recording at hourly intervals.  One HOBO logger was placed in each lake at a depth of 1 m.  Missing data and confounding of temperature with date precluded using temperature data in our modeling.  To determine if storm events or temperature drops should be modeled, we looked for temperature drops of > 2°C (Steinhart et al. 2004).   However, temperatures increased gradually during the nesting period and we found no indication of severe temperature drops or storm events that would be of interest for modeling.

*Angling and recreational activity metrics:* Crews recorded angling and other recreational boat activity that occurred on each lake during the nesting season to test our predictions regarding their effects on nest survival and to aid the MDNR with its evaluation of the 2006 fishing regulation change.   We monitored anglers and recreational activity in two ways: instantaneous counts and continuous observations throughout sample days (methods and metrics described below).   Instantaneous data provided estimates of angler hours and recreational activity hours per lake and season as well as lake-wide angler hours and recreational activity

hours during the lifetime of each nest (referred to as temporal metrics). Continuous observations provided information on the spatial and temporal distribution of angling and recreational activity (referred to as spatial-temporal metrics). Our measure of non-angling recreational activity included both recreational boat traffic, because boats often create waves that may disrupt the substrate in nest areas, and people standing in shallow water, because their movement may also disturb nest sites.

We conducted two instantaneous counts per week (one randomly chosen weekday and one randomly chosen weekend day), during May and June of each lake and year. For 2008, we randomly selected (without replacement) time of day (morning, mid-day, or evening) for each survey. During 2009 we conducted all instantaneous counts in the morning because our 2008 data showed the vast majority of angling occurred during the morning hours in our lakes. (Therefore, any consistent differences between years may have been a result of the method change.) During each instantaneous count, we visually assessed fishing activity, noting the number of anglers in each boat observed fishing, and non-fishing recreational activity (as defined above) on the lake from the vantage of a boat and using binoculars. We followed the methods of Lockwood et al. (1999) to expand each survey count to an estimate of the total number of angler (or recreational activity) hours during that week's period using the equation:

$$\hat{E}_{pdj} = F_p A_{dj}$$

where $\hat{E}$ = estimated angler hours, $F$ = number of fishable morning hours (6-10 am) during the given week's period, $p$ = period (either that week's weekdays or that week's weekend), $A$ = number of boats with anglers (or recreational boats/groups) observed during the instantaneous count, $d$ = day of count, and $j$ = count. We generated a weekend and weekday estimate of $\hat{E}$ for

each week during May and June. We summed the weekend and weekday estimates for each week to generate week-specific estimates of angler (or recreational activity) hours.

We used the week-specific instantaneous estimates of angler hours and recreational activity hours to generate nest-specific temporal metrics (temporal angling and temporal human recreation) that characterized human activity on the lake during the observed lifetime of each nest. We calculated these nest-specific covariates for use in modeling due to concern that lake-wide estimates of angling over an entire fishing season represented too broad a scale (Wagner et al. 2006). Using the weekly estimates generated from the instantaneous counts, we summed these estimates for each nest according to the weeks that the nest was active. Then we took the mean to estimate the average number of angling and recreation hours per week that occurred on each lake during each nest's lifetime controlled for lake size, using the equation:

$$\text{Temporal Metric} = \left( \frac{\sum \text{Weekly Angler or Recreation Hours in Nest Lifetime}}{\text{Weeks of Nest Lifetime}} \right) \times \frac{1}{\text{Lake Area (ha)}}$$

For the continuous observations, we recorded all observed anglers and recreational activity throughout the day as we monitored nests. We recorded the location of each observation on a map, which we charted later in ArcView version 3.2. We created 50-m buffer zones around each nest and selected the angler and recreational observations that were present within those zones during the lifetime of each nest. We chose 50-m zones because anglers could easily come into contact with a nest at that distance through trolling, drifting, and/or casting. With these data we calculated the average amount of daily angling or recreational activity that occurred in the area around each nest during its lifetime (spatial-temporal metrics) using the equation:

$$\text{Spatial - Temporal Metric} = \frac{\sum \text{Obs. of Angling or Recreation w/in 50 m of Nest during Lifetime}}{\text{Days of Nest Lifetime}}$$

*Data Analysis*

*Nest demographics and duration:*  We calculated the total number of nests observed in each lake during each year as well as the number of those nests that we observed to successfully produce fry.  To determine an unbiased estimate of the percent success of nests (percent producing fry), we included only the number of nests that were first observed as eggs or larvae in the denominator, with the numerator being the number of those nests that we subsequently observed at to produce fry.  If nests <u>first</u> observed at the <u>fry</u> stage were included in the calculation, the percent success (number of nests reaching the fry stage divided by the total number of nests) would be biased high because for every nest first observed at the fry stage there may be an unknown number of nests that failed without being observed.

We defined nest duration as the number of days from the first date a nest was observed at the egg stage to the first date that fry were observed at the nest.  We calculated the duration of each stage of development in each lake by counting the number of days a nest existed at a stage before transitioning to another stage (egg to larvae and larvae to fry).  We used only data from successful nests to calculate nest and stage-specific durations.

*Exploring differences in fishing among lakes and fishing seasons:*  To confirm that the study contained lakes from a range of fishing pressures, and to determine the extent to which amount of fishing varied between seasons, we compared values of temporal angling of nests among lakes and seasons.  We used ANOVA to compare lake-season combinations within a year.

*Determining variation in nest attributes:* We first calculated the mean, median, and coefficient of variation (CV) for each continuous nest attribute to represent the overall variation in nesting conditions across all lakes and years of study.  The reason to examine variation in nest attributes was two-fold: first, to understand the observed variation in nest attributes and second,

to identify a subset of nest attributes for further use in modeling nest survival, given that there were too many nest attributes to include all in the modeling. We considered attributes with relatively high CVs and non-zero means and medians to be suitable for further consideration for use in modeling. These criteria indicated a high amount of variation in attribute values (by comparing CVs) as well as a range of values for nests (zero was the lowest possible value of any variable, so we sought variables with non-zero means and medians).

We plotted each categorical nest attribute variable in a histogram to determine the frequency with which each category of each variable was observed in our lakes. We considered a variable to have low levels of variation if it had one category that dominated over the others (at least 75% of the observations were in that category) and did not further investigate it for use in modeling. We explored shoreline development further to compare our observations to those found in Wagner et al. (2006). We used a Chi-square ($\chi^2$) test to determine if bass showed preferences for nesting in front of certain shoreline development types or if they nested in proportion to prevalence of that development type in the lake.

Once we selected the highly-variable nest attributes, we further evaluated their suitability for modeling by considering covariance between variables and hypotheses about which variables were likely to have had the strongest effect on nest survival probabilities. We chose interactions to model based on the variation present in nest attributes and our hypotheses. The variables that we selected based on those criteria were percent plant cover, wind, temporal angling, bass score (2009 only), legal size, and a legal size and season interaction. Full details on the choice of nest attributes are in the Results section under "*Determining variation in nest attributes*". We group-mean centered all of the selected nest attribute variables prior to modeling to remove the

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possibility of nest attributes confounding with the main effects of lake and season using the equation:

$$X'_{ij} = (X_{ij} - \overline{X}_{.j})$$

where $X_{ij}$ is the original covariate value $i$ in group $j$, $\overline{X}_{.j}$ is the mean variable value in group $j$, where each lake-season is a group, and $X'_{ij}$ is the group-mean centered variable value $i$ in group $j$ (Enders and Tofighi 2007).

*Modeling nest survival in Program MARK:* We modeled nest survival using an information-theoretic approach in Program MARK to address our research questions regarding nest survival. We used the multi-state model function with live and dead encounters to enable estimation of survival for each lake, fishing season, and stage of development (main effects) while incorporating survival periods of different length, nests of unknown age, individual covariates, and uncertainty in detecting nests (White et al. 2006). This model type was most appropriate for our data because of the multiple stages of development of offspring and uncertainty in detecting nests on every sampling occasion, which had not been incorporated into previous models of bass nest survival using Program MARK (Steinhart et al. 2005b; Suski and Ridgway 2007). The model function consisted of four estimated parameter types: phi (nest survival probabilities), psi (transition probabilities from one stage of development to another), p (live recapture probabilities, or the likelihood of a nest being found alive, conditional on it being alive) and r (dead recovery probabilities, or the likelihood of a nest failure being recorded by the researcher). Details on how we modeled each parameter are described in the following sections. Additionally, we used simulated annealing, an alternate method of optimization, when modeling because some models were very complex. Simulated annealing was necessary to decrease the likelihood of models converging on local minima for parameter estimates (Goffe et al. 1994).

Occasionally, models were unable to converge on estimates properly despite the use of simulated annealing and had to be deleted from the results.

We performed the modeling in three phases, described in detail in the following sections. We used the Akaike Information Criterion with a correction for sample size (AICc) to rank the performance of models and calculated the deviance of each model for additional understanding of model rankings. A lower deviance indicates a better-fitting model, but the best-fitting model may not be parsimonious and therefore not the best model as ranked using AICc. We also used AICc factor weights to rank the importance of individual effects in comparison to each other (Burnham and Anderson 2002). We calculated the AICc factor weight for a particular effect by summing the weight of every model containing that effect. We interpreted the effect with the highest factor weight as being the most important (Burnham and Anderson 2002). Although recent evidence has suggested that alternative methods may be more appropriate for determining variable importance if variables are correlated or have spurious effects (Murray and Conner 2009), we could not obtain the data necessary from Program MARK to use these alternatives given logistical constraints of the multi-state model function with live and dead encounters. To guard against potential ill effects of our method of calculating factor weights, we did not include highly covarying variables in our models (maximum covariance $< 0.2$). In addition, once all phases of modeling were completed, we summarized the effect of every variable in every model (its AICc factor weight, the consistency of its direction of effect, and whether the $\beta$ confidence interval for that parameter bounded 0 in that model). An inconsistent direction of effect indicated possible confounding and a $\beta$ confidence interval bounding 0 indicated a lack of a discernible effect of that variable in that model (Myers 1990). This information helped us to assure that variables were not confounded and did not have spurious effects.

Calculation of AICc factor weights required that each variable was represented an equal number of times in the *a priori* model list. However, every combination of every main effect with every nest attribute would have been too many models to run. Therefore, we ran main effect and nest attribute models in separate phases and used selection criteria to choose a subset of each for subsequent modeling together in our final phase (see below). This approach allowed us to calculate factor weights within individual phases while also constraining our modeling to a reasonable total number of models

In Phase 1 we modeled all combinations of main effects for ranking with AICc weights (and calculation of AICc factor weights) and selected a subset of important main effects to be used in Phase 3. In Phase 2 we modeled combinations of selected nest attributes for ranking with AICc weights (and calculation of AICc factor weights) and selected a subset of important nest attributes to be used in Phase 3. In Phase 3 we modeled the important main effects from Phase 1 in varying combinations with the important nest attributes from Phase 2 to explore parsimonious variable combinations and to determine the maximum amount of variation that could be explained by main effects and nest attributes in combination.

We used model averaging on models from all phases of the analysis to estimate parameter values (especially nest survival) during each year for every lake, season, and stage combination. Model averaging created parameter estimates (survival [phi], live recapture [p], and dead recovery [r] probabilities) by weighting the parameter estimate produced from each model by the AICc weight of that model. Model averaging was appropriate for this analysis because AICc weights can be distributed across many models and this method addressed the problem of model uncertainty (Buckland et al., 1997, Burnham and Anderson 2004). We did not model average for transition probabilities among stages (explained below).

We compared the relative importance of models and their effects using AICc, but that information did not indicate whether the top model(s) adequately explained variation in our data. Normally, one would estimate the overdispersion factor, ĉ, to determine goodness of fit of the top model(s). However, Program MARK did not have this capability for the model structure we used. The creators of the program suggested plotting residuals of the best model that did not have individual covariates (Program MARK could not create reliable residual plots if individual covariates were in the model) because plots lacking trends and with most values near zero indicate good-fitting models (White and Burnham 1999). We examined the residual plots of the best model from Phase 1 of each year for goodness of fit.

*Phase 1: Modeling nest survival by lake, season, and stage of development:* We modeled combinations of main effects equally in single-variable, additive, and interaction models (Table 2). Each of the main effects on survival was combined with effects on live recapture and dead recovery (p and r, general model structures in Table 3) to create a full *a priori* model list for each year (Appendix A, Tables 23 and 24). Effects on live recapture and dead recovery were modeled because water clarity was very different in Woodland Lake. We hypothesized that detection of nests (and consequently probabilities of live recapture and dead recovery) would be lower for this lake.

We did not hypothesize any effects on transition probabilities (psi; Table 3). The model type required that transitions between stages of development for the same starting stage must sum to 1, e.g. psi(eggs to larvae) + psi(eggs to fry) + psi(eggs to eggs) = 1. Because sampling was temporally inconsistent, the biological interpretation of stage-specific transition rates was less meaningful (more frequent sampling would result in a higher probability of finding a nest at the same stage on the subsequent sampling date), so psi was assumed to not vary among stages of

development. We used one parameter to model all transition probabilities and restricted the probability of all impossible transitions (e.g., from the fry stage back to the egg stage) to zero.

Table 2: Basic model structures comprising Phase 1 models of main effects on survival for 2009. The 2008 model structures were identical except Woodland Lake was modeled as a dummy variable instead of Warner because we had no data for Warner during 2008. Phi represents survival parameters.

| Model Description | Model Structure | MARK Notation |
|---|---|---|
| Single estimate of survival | $\beta_0 + \varepsilon_i$ | phi(.) |
| Lake differences in survival | $\beta_0 + \beta_1 Chemung + \beta_2 North + \beta_3 Woodland + \varepsilon_i$ | phi(Lake) |
| Season differences in survival | $\beta_0 + \beta_1 CIR + \varepsilon_i$ | phi(Season) |
| Stage differences in survival | $\beta_0 + \beta_1 Eggs + \varepsilon_i$ | phi(Stage) |
| Lake plus season | $\beta_0 + \beta_1 Chemung + \beta_2 North + \beta_3 Woodland + \beta_4 CIR + \varepsilon_i$ | phi(Lake+Season) |
| Lake plus stage | $\beta_0 + \beta_1 Chemung + \beta_2 North + \beta_3 Woodland + \beta_4 Eggs + \varepsilon_i$ | phi(Lake+Stage) |
| Season plus stage | $\beta_0 + \beta_1 CIR + \beta_2 Eggs + \varepsilon_i$ | phi(Season+Stage) |
| Lake-season interaction | $\beta_0 + \beta_1 Chemung + \beta_2 North + \beta_3 Woodland + \beta_4 CIR +$ $+ \beta_5 Chemung * CIR + \beta_6 North * CIR + \beta_7 Woodland * CIR + \varepsilon_i$ | phi(Lake*Season) |
| Lake-stage interaction | $\beta_0 + \beta_1 Chemung + \beta_2 North + \beta_3 Woodland + \beta_4 Eggs$ $+ \beta_5 Chemung * Eggs + \beta_6 North * Eggs + \beta_7 Woodland * Eggs + \varepsilon_i$ | phi(Lake*Stage) |
| Season-stage interaction | $\beta_0 + \beta_1 CIR + \beta_2 Eggs + \beta_3 CIR * Eggs + \varepsilon_i$ | phi(Season*Stage) |
| Lake-season-stage interaction | $\beta_0 + \beta_1 Chemung + \beta_2 North + \beta_3 Woodland + \beta_4 CIR + \beta_5 Eggs$ $+ \beta_6 Chemung * CIR + \beta_7 North * CIR + \beta_8 Woodland * CIR$ $+ \beta_9 Chemung * Eggs + \beta_{10} North * Eggs + \beta_{11} Woodland * Eggs$ $+ \beta_{12} CIR * Eggs + \varepsilon_i$ | phi(Lake*Season*Stage) |

Table 3: Basic model structures comprising Phase 1 model effects on live recapture (p) and dead recovery (r) for both 2008 and 2009. Psi (transitions between stages) did not vary in any of the models.

| Model Description | Model Structure | MARK Notation |
|---|---|---|
| Single estimate of recapture | $\beta_0 + \varepsilon_i$ | p(.) |
| Woodland different | $\beta_0 + \beta_1 Woodland + \varepsilon_i$ | p(Woodland) |
| Single estimate of transitions | $\beta_0 + \varepsilon_i$ | psi(.) |
| Single estimate of recovery | $\beta_0 + \varepsilon_i$ | r(.) |
| Woodland different | $\beta_0 + \beta_1 Woodland + \varepsilon_i$ | r(Woodland) |

We used AICc factor weights to determine if the effects of lake, fishing season, and stage of development (or their interactions) were important in estimating nest survival. Any main effect that had an AICc factor weight greater than the weight associated with the unconditional models (no effect) continued to Phase 2 to form the basic structure of models with nest attributes. Due to the hierarchical structure of the data (nests were sampled within lakes and often occurred during different seasons), it was important to include important main effects in models used for nest attribute selection in Phase 2. Additionally, any main effect in a model that garnered at least 5% of the AICc weight in Phase 1 continued to Phase 3 for modeling main effects in combination with nest attributes.

*Phase 2: Modeling effects of nest attributes on nest survival:* We used the same modeling approach as Phase 1 to explore the effects of individual nest attributes (as well as the interaction between legal size and fishing season) that had been retained for modeling due to their relatively high levels of variation among nests. Our *a priori* model list contained every one- and two-way additive combination of these variables (treating the legal size by fishing season interaction as a variable) as well as a full additive model with every selected nest attribute variable and the legal

size by fishing season interaction (Tables 4 and 5). Every Phase 2 model also included the important main effects as well as effects on p and r from Phase 1 to incorporate the hierarchical structure of our data (Appendix A, Tables 25 and 26 for full list of models for 2008 and 2009). We determined the relative importance of selected nest attributes and the hypothesized interaction included in Phase 2 by calculating AICc factor weights from a list of models containing an equal representation of each variable and the legal size and fishing season interaction. Any nest attributes present in Phase 2 models that received at least 5% of the AICc model weight continued to Phase 3 for further modeling.

*Phase 3: Estimating nest survival probabilities by lake, season, and stage:* We interpreted Phase 1 and Phase 2 model output to draw inferences about the relative importance of individual main effects and individual nest attributes, respectively, in explaining variation in nest survival. In Phase 3 we calculated nest survival probabilities, taking into account important main effects and nest attributes. To do so, we combined the main effects from models with at least 5% of the AICc weight from Phase 1 with the nest attributes from models with at least 5% of the AICc weight from Phase 2 in all possible combinations. We then compiled all models from Phase 1, Phase 2, and Phase 3 into one file on which we performed model averaging to estimate nest survival probabilities for each lake, fishing season, and stage of development for each year (Appendix A, Tables 27 and 28 for 2008 and 2009, respectively). We could only model average for survival probability estimates that corresponded to interval lengths that were present in our study. As a result, we generated 6-day and 5-day nest survival probabilities for 2008 and 2009, respectively. We also used model averaging to estimate p and r (live recapture and dead recovery probabilities) to assess our ability to detect live and failed nests across study lakes and between years.

Table 4: Basic model structures comprising Phase 2 effects of nest attributes on survival for 2008. Phi represents survival parameters.

| Model Description | Model Structure | MARK Notation |
|---|---|---|
| Percent plant cover effect on survival | $\beta_0 + \beta_1 Cover + \varepsilon_i$ | phi(Cover) |
| Wind effect on survival | $\beta_0 + \beta_1 Wind + \varepsilon_i$ | phi(Wind) |
| Temporal angling effect on survival | $\beta_0 + \beta_1 TAng + \varepsilon_i$ | phi(TAng) |
| Legal size effect on survival | $\beta_0 + \beta_1 Legal + \varepsilon_i$ | phi(Legal) |
| Legal size by season interaction effect on survival | $\beta_0 + \beta_1 Legal + \beta_2 CIR + \beta_3 Legal*CIR + \varepsilon_i$ | phi(Legal*Season) |
| Percent plant cover and Wind effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Wind + \varepsilon_i$ | phi(Cover+Wind) |
| Percent plant cover and Temporal angling effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 TAng + \varepsilon_i$ | phi(Cover+TAng) |
| Percent plant cover and Legal size effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Legal + \varepsilon_i$ | phi(Cover+Legal) |
| Percent plant cover and Legal size by season interaction effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal*CIR + \varepsilon_i$ | phi(Cover +Legal*Season) |
| Wind and Temporal angling effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 TAng + \varepsilon_i$ | phi(Wind+TAng) |
| Wind and Legal size effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 Legal + \varepsilon_i$ | phi(Wind+Legal) |
| Wind and Legal size by season interaction effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal*CIR + \varepsilon_i$ | phi(Wind +Legal*Season) |
| Temporal angling and Legal size effects on survival | $\beta_0 + \beta_1 TAng + \beta_2 Legal + \varepsilon_i$ | phi(TAng+Legal) |
| Temporal angling and Legal size by season interaction effects on survival | $\beta_0 + \beta_1 TAng + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal*CIR + \varepsilon_i$ | phi(TAng +Legal*Season) |
| Percent plant cover, Wind, Temporal angling, Legal size by season interaction effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Wind + \beta_3 TAng + \beta_4 Legal + \beta_5 CIR + \beta_6 Legal*CIR + \varepsilon_i$ | phi(Cover+Wind +TAng +Legal*Season) |

Table 5: Basic model structures comprising Phase 2 effects of nest attributes on survival for 2009. Phi represents survival parameters.

| Model Description | Model Structure | MARK Notation |
|---|---|---|
| Percent plant cover effect on survival | $\beta_0 + \beta_1 Cover + \varepsilon_i$ | phi(Cover) |
| Wind effect on survival | $\beta_0 + \beta_1 Wind + \varepsilon_i$ | phi(Wind) |
| Temporal angling effect on survival | $\beta_0 + \beta_1 TAng + \varepsilon_i$ | phi(TAng) |
| Bass score effect on survival | $\beta_0 + \beta_1 BScore + \varepsilon_i$ | phi(BScore) |
| Legal size effect on survival | $\beta_0 + \beta_1 Legal + \varepsilon_i$ | phi(Legal) |
| Legal size by season interaction effect on survival | $\beta_0 + \beta_1 Legal + \beta_2 CIR + \beta_3 Legal * CIR + \varepsilon_i$ | phi(Legal*Season) |
| Percent plant cover and Wind effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Wind + \varepsilon_i$ | phi(Cover+Wind) |
| Percent plant cover and Temporal angling effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 TAng + \varepsilon_i$ | phi(Cover+TAng) |
| Percent plant cover and Bass score effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 BScore + \varepsilon_i$ | phi(Cover+BScore) |
| Percent plant cover and Legal size effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Legal + \varepsilon_i$ | phi(Cover+Legal) |
| Percent plant cover and Legal size by season interaction effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal * CIR + \varepsilon_i$ | phi(Cover +Legal*Season) |
| Wind and Temporal angling effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 TAng + \varepsilon_i$ | phi(Wind+TAng) |
| Wind and Bass score effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 BScore + \varepsilon_i$ | phi(Wind+BScore) |
| Wind and Legal size effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 Legal + \varepsilon_i$ | phi(Wind+Legal) |
| Wind and Legal size by season interaction effects on survival | $\beta_0 + \beta_1 Wind + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal * CIR + \varepsilon_i$ | phi(Wind +Legal*Season) |

Table 5 (cont'd)

| | | |
|---|---|---|
| Temporal angling and Bass score effects on survival | $\beta_0 + \beta_1 TAng + \beta_2 BScore + \varepsilon_i$ | phi(TAng+BScore) |
| Temporal angling and Legal size effects on survival | $\beta_0 + \beta_1 TAng + \beta_2 Legal + \varepsilon_i$ | phi(TAng+Legal) |
| Temporal angling and Legal size by season interaction effects on survival | $\beta_0 + \beta_1 TAng + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal * CIR + \varepsilon_i$ | phi(TAng +Legal*Season) |
| Bass score and Legal size effects on survival | $\beta_0 + \beta_1 BScore + \beta_2 Legal + \varepsilon_i$ | phi(BScore+Legal) |
| Bass score and legal size by season interaction effects on survival | $\beta_0 + \beta_1 BScore + \beta_2 Legal + \beta_3 CIR + \beta_4 Legal * CIR + \varepsilon_i$ | phi(BScore+Legal*Season) |
| Percent plant cover, Wind, Temporal angling, Bass score, Legal size by season interaction effects on survival | $\beta_0 + \beta_1 Cover + \beta_2 Wind + \beta_3 TAng + \beta_4 BScore + \beta_5 Legal + \beta_6 CIR + \beta_7 Legal * CIR + \varepsilon_i$ | phi(Cover+Wind +TAng +BScore+Legal*Season) |

Results:

*Nest demographics and duration:* Nesting demographics varied among lakes and between years (Table 6). Though sampling methodology changed slightly between years, we did not expect methodology to affect nest demographic or duration information apart from improved identification of the larval stage. The total number of nests observed per lake declined during 2009 relative to 2008 in North and Woodland, but increased substantially in Chemung. Generally a relatively high number of nests was associated with a relatively high number of successful nests, though this relationship was not observed in Woodland Lake. Although we detected fewer nests overall in Woodland Lake during 2009 (compared to 2008), we observed more successful nests there during 2009 than 2008. Changes in the number of nests observed at the egg or larval stage (prior to fry development) between years followed the same pattern in each lake as did the total number of nests observed. Warner Lake had the highest percent of nests observed to be successful (72% for 2009) while North Lake had consistently low levels of success (31% and 33% for 2008 and 2009, respectively). These lakes were anticipated low and medium fishing pressure lakes, respectively, so this result for North Lake was contrary to expectations. In Chemung and Woodland lakes, the two anticipated high fishing pressure lakes, estimates of percent of nests that were successful were higher during 2009 (47% and 53% for Chemung and Woodland, respectively) than 2008 (28% and 10%, respectively). Maps of the locations of observed successful and failed nests in each lake are in Appendix B.

Table 6: Summary of nest success data by lake and year.  We did not sample Warner Lake during 2008.

| Lake | Year | Total # Nests Observed | Total # Successful Nests Observed | Total # Nests Observed as Eggs or Larvae | % Successful of Nests Observed as Eggs or Larvae |
|---|---|---|---|---|---|
| Warner | 2008 | - | - | - | - |
| | 2009 | 35 | 30 | 18 | 72% |
| North | 2008 | 83 | 41 | 36 | 31% |
| | 2009 | 56 | 22 | 43 | 33% |
| Chemung | 2008 | 81 | 28 | 32 | 28% |
| | 2009 | 138 | 91 | 66 | 47% |
| Woodland | 2008 | 77 | 48 | 20 | 10% |
| | 2009 | 66 | 53 | 15 | 53% |

Stage-specific nest duration varied slightly between years.  These differences may be partly attributable to an improvement of identification of the larval stage during 2009.  Relatively more nests were observed at the larval stage during 2009 than 2008.  Mean duration of a nest from eggs to fry ranged between 11 and 13 days across lakes and years, indicating that a male bass had to defend his offspring for at least 1.5-2 weeks in order to have reproductive success (Table 7).  The length of each stage of development varied slightly among lakes and years, but in no consistent pattern.  We observed fry at a relatively broad range of lengths (most observations ranged 0.5-3 cm in length), contributing to variation in durations involving the fry stage.  Overall, the duration of each stage was longer than the 5- or 6-day survival probabilities that we calculated using Program MARK.

Table 7: Durations of each stage of development in days in each lake and year. Lakes are in order of low to high fishing pressure. We did not collect data during 2008 in Warner Lake.

| Lake | Year | Duration | # of Nests Contributing Data | Min (days) | Max(days) | Mean (days) |
|---|---|---|---|---|---|---|
| Warner | 2009 | E to L | 1 | 5 | 5 | 5.0 |
| | | L to F | 5 | 3 | 5 | 3.4 |
| | | E to F | 4 | 8 | 16 | 11.3 |
| North | 2008 | E to L | 5 | 5 | 13 | 6.6 |
| | | L to F | 3 | 3 | 9 | 7.0 |
| | | E to F | 11 | 5 | 36 | 11.0 |
| North | 2009 | E to L | 14 | 3 | 10 | 6.9 |
| | | L to F | 10 | 3 | 7 | 4.8 |
| | | E to F | 11 | 5 | 15 | 11.3 |
| Chemung | 2008 | E to L | 14 | 4 | 12 | 7.4 |
| | | L to F | 5 | 7 | 11 | 8.6 |
| | | E to F | 10 | 7 | 20 | 12.8 |
| Chemung | 2009 | E to L | 28 | 2 | 10 | 6.5 |
| | | L to F | 13 | 4 | 15 | 7.0 |
| | | E to F | 27 | 5 | 23 | 11.7 |
| Woodland | 2008 | E to L | 6 | 5 | 6 | 5.8 |
| | | L to F | 0 | - | - | - |
| | | E to F | 3 | 6 | 14 | 10.7 |
| Woodland | 2009 | E to L | 2 | 3 | 8 | 5.5 |
| | | L to F | 3 | 5 | 10 | 6.7 |
| | | E to F | 7 | 7 | 15 | 12.3 |

*Exploring differences in fishing among lakes and fishing seasons:* We examined differences in our nest-level angling metrics (temporal angling and spatial-temporal angling) by lake and fishing season to determine if our study design captured human activity gradients as expected. Temporal angling varied as expected, with nests in low and medium fishing pressure lakes (Warner and North) receiving generally lower amounts of fishing than nests in Chemung and Woodland lakes when comparing within a fishing season (Figures 1 and 2). During 2008, temporal angling estimates varied among lakes (Brown-Forsythe $F[5, 38.86] = 61.05$, $p < 0.01$; Welch $F[5, 40.79] = 97.87$, $p < 0.01$). Games-Howell *post hoc* comparisons (significant at the $p < 0.05$ level) revealed that the North CIR season had significantly lower levels of temporal

angling than the Chemung CIR season and both the North and Chemung CIR seasons had significantly lower levels of temporal angling than all other lake-seasons except the Woodland CIR season (Figure 1). The harvest seasons in North and Chemung lakes had similar levels of temporal angling to each other as well as the Woodland CIR season, but had significantly lower estimates than the Woodland harvest season, which had higher levels of temporal angling than all other lake-seasons.

Temporal angling varied among lakes during 2009 as well (Brown-Forsythe $F[6, 39.09] = 27.24$, $p < 0.01$; Welch $F[6, 18.07] = 41.03$, $p < 0.01$). Games-Howell *post hoc* comparisons (significant at the $p < 0.05$ level) revealed that temporal angling during the Warner CIR season was significantly lower than all other seasons and lakes except for the Warner harvest season, which was not different from any lake-season (Figure 2). There was 0 variation in temporal angling in the North harvest season (there were only 3 nests observed during the 2009 North harvest season and all had the same estimate of temporal angling), so it could not be included in the test. The North CIR season had significantly lower temporal angling estimates than Chemung's CIR and harvest seasons; in turn, Woodland's CIR season and the Chemung harvest season had lower estimates than the Woodland harvest season. Temporal angling varied more than expected during Woodland's CIR season for both years and during the Warner harvest season for 2009. Overall, our study design to include lakes that differed substantially in fishing pressure was verified.

Any consistent difference between years in the amounts of temporal angling observed at nests in each lake may have been due to different methods used in each year. During 2008, we chose observation times randomly, which often resulted in afternoon and evening sampling periods. These times were popular with recreational boat traffic, but unpopular with anglers.

During 2009, we performed our instantaneous observations only in the morning in an attempt to better capture the amount of angling that occurred on each lake. Estimates of temporal angling appeared to increase as a result of the change in our methods, which may have differentially influenced the effect size of temporal angling in each year's modeling.

The other fishing variable, spatial-temporal angling, did not vary significantly by lake or by fishing season in either year, in part because most nests had no observations of angling within 50 m of them during their lifetime (median value was 0, Table 8). We created this variable to capture variation in fishing at a spatial scale more relevant to nests and in response to other work that suggested fishing metrics needed to be more specific to nests (Wagner et al. 2006). However, 50 m may have been too small of a distance to use as a cutoff given our data. The scale of the maps used to record locations of anglers may not have been sufficiently fine for crews to record anglers and recreational boats with 50-m precision. Alternatively, the number of observations that we had may have been insufficient for this level of analytical detail. See Appendix C for locations of all anglers observed during 2008 and 2009.
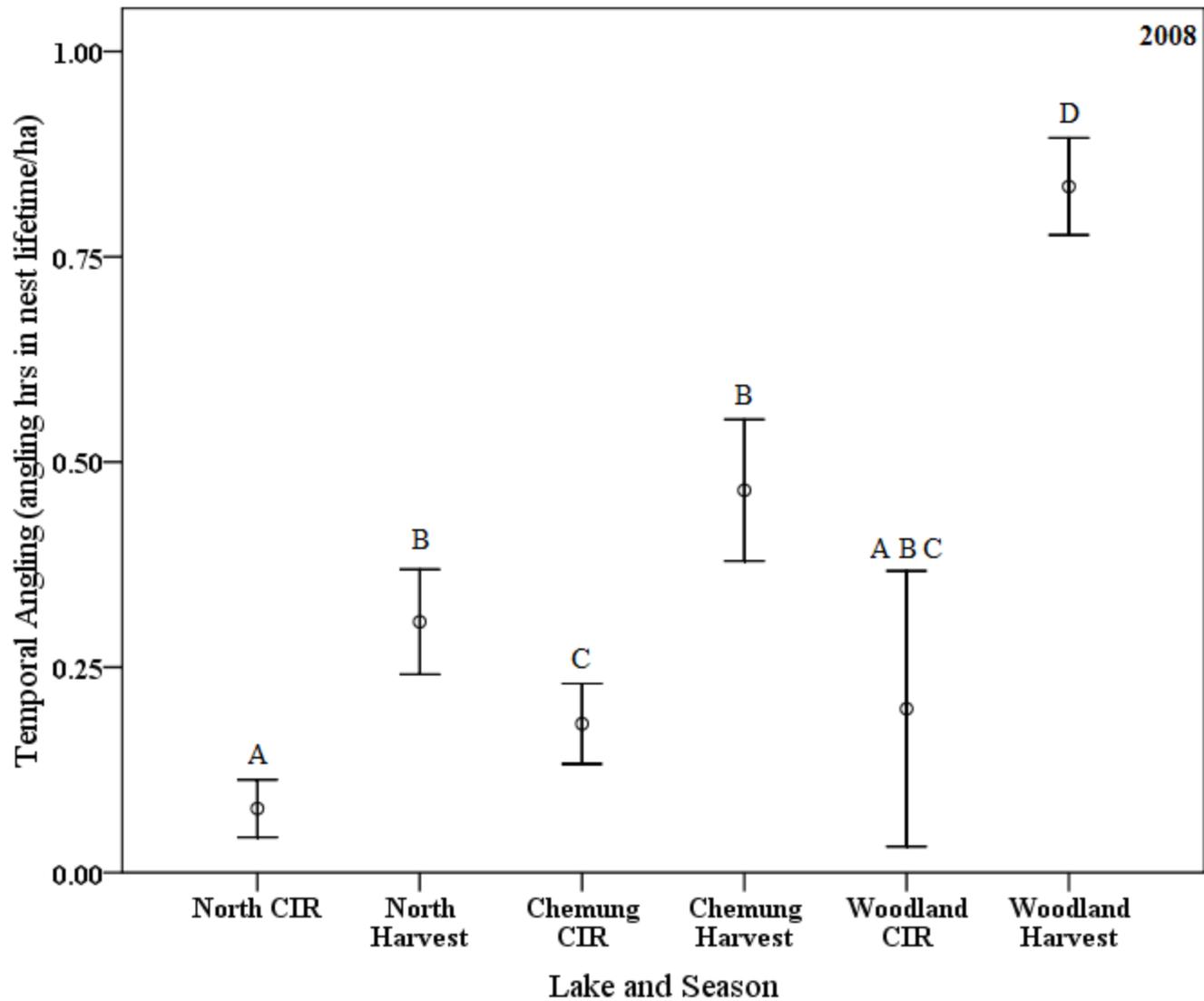
Figure 1: Temporal angling (angling hours in nest lifetime/ha) by lake and season for 2008. Lakes are in order from low to high anticipated fishing pressure. Error bars represent +/- two standard errors and different letters above bars denote statistically significant differences among lake-seasons.
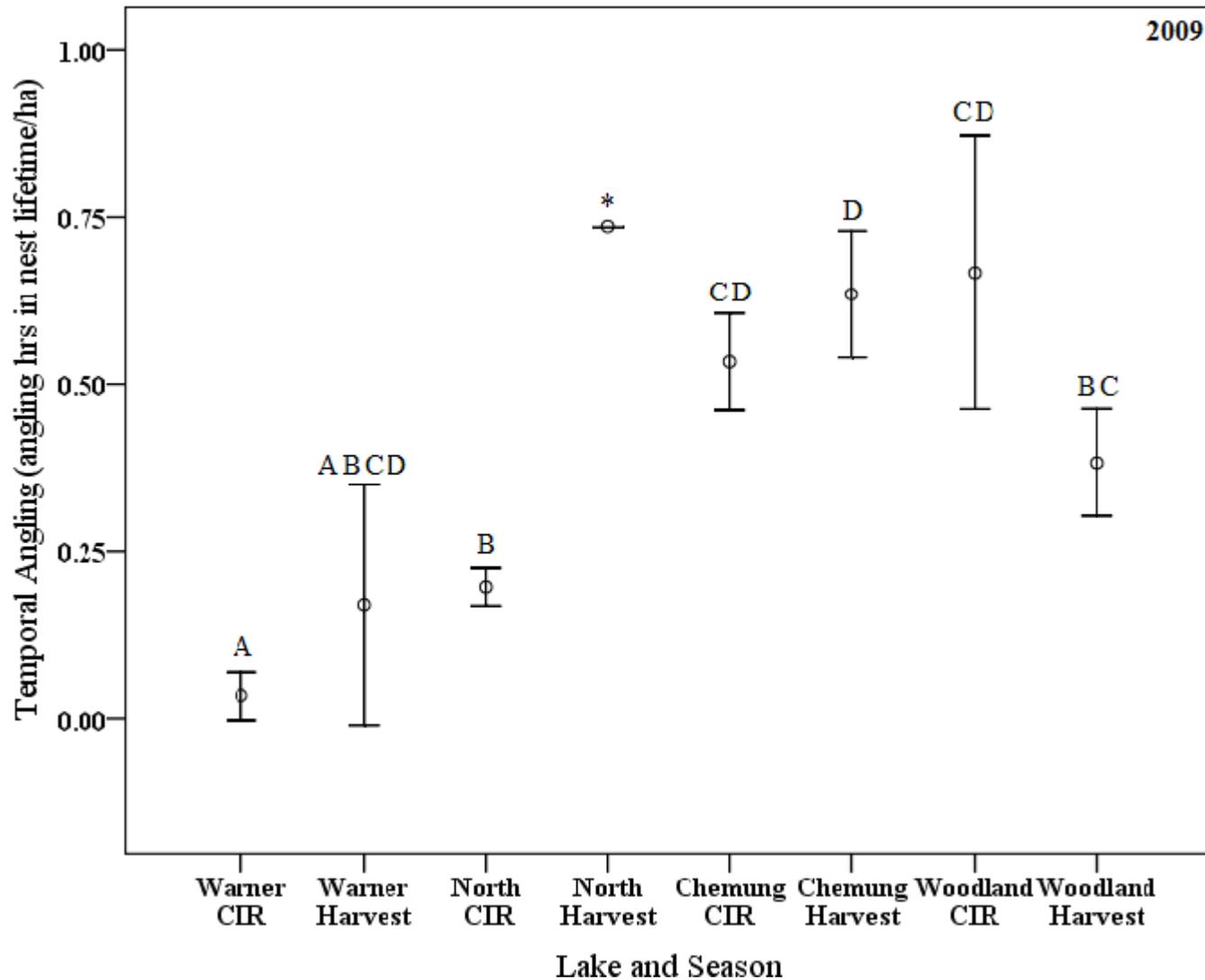
Figure 2: Temporal angling (angling hours in nest lifetime/ha) by lake and season for 2009. Lakes are in order from low to high anticipated fishing pressure. Error bars represent +/- two standard errors and different letters above bars denote statistically significant differences among lake-seasons. The North harvest season is starred because there was no variation in temporal angling among nests observed during that season and therefore it could not be included in statistical testing.

*Determining variation in nest attributes*:  Before variation in each nest attribute could be evaluated, we calculated estimates of nest predator abundance for nests.  Nest predator abundance varied by different habitat and season characteristics in each of the lakes.  Therefore, the approach we used to assign nest predator counts to each nest varied among lakes.  We determined the stratum (habitat feature, spatial area, and/or month [May vs June]) that explained a significant level of variation in nest predator abundance among trap locations for each lake. We then assigned average nest predator abundance (mean of all sites in a stratum) to each nest based on significant strata in each lake and the stratum of each nest's location.  Warner Lake did not have substantial variation in nest predator abundance by habitat feature, location, or month, so we assigned the overall mean of nest predator abundance to each nest in Warner Lake.  In North Lake, nest predator catches varied by month (June > May), macrophyte cover (high > low > none), and substrate (silt > sand).  Therefore we assigned predator abundances to nests that corresponded with each of these 12 strata.  Lake Chemung had two spatial areas with significantly higher nest predator abundances than other areas, but our habitat features could not account for this difference.  Therefore, we assigned the average nest predator count at the high catch sites to nests that occurred in their proximity.  All other nests were assigned the average nest predator count from the remaining traps.  Nest predator trap catches in Woodland Lake resulted in four strata based on macrophyte cover (high > medium/low/none) and substrate (silt > sand).

The variation in many of the habitat, guarding bass, and fishing activity nest attributes that we observed in our study lakes was substantial, though some variables showed much more variation among nests than others (Tables 8 and 9). We compared amounts of variation observed in each nest attribute variable to assess its potential to explain variation in nest survival.  We

would not expect to detect important modeling effects of nest attributes that had identical values for most nests.

Several of the nest habitat attributes showed substantial variation among nests; they were percent plant cover, nest predator abundance, shoreline development, substrate, wind, temporal angling, temporal recreation, legal size, and bass score. Percent plant cover ranged from 0-100% and had a relatively high coefficient of variation (CV) when compared to other variables that had non-zero means and medians (another indicator of variation). Nest predators (sampled during 2009 only) often correlated positively with plant cover in the lakes and showed a relatively high amount of variation among nests, with values ranging from 0 to 28 fish per trap and a CV of 1.09.

Overall we observed nests in all four development categories. Bass appeared to nest along shoreline development types in correspondence to their availability in Woodland (predominantly developed) and Warner (primarily undeveloped) lakes ($\chi^2$, $p > 0.05$), but showed preference for maintained shorelines in Chemung and North (Chemung 2008 $\chi^2$ [2, $N = 81$] = 44.06, $p < 0.01$, Chemung 2009 $\chi^2$ [3, $N = 138$] = 21.91, $p < 0.01$, North 2008 $\chi^2$ [2, $N = 83$] = 66.56, $p < 0.01$, North 2009 $\chi^2$ [3, $N = 56$] = 67.91, $p < 0.01$). Of those lakes, we observed the majority of nests along developed shorelines, with a higher prevalence at developed sites with maintained lawns or beaches (46% and 39% of nests for 2008 and 2009) than at developed sites with retaining structures (33% and 31% of nests for 2008 and 2009).

We observed nests in each of the categories of substrate and wind exposure as well, with sand being the most common substrate for both years (observed at 67% and 53% of the nests

during 2008 and 2009, respectively) and low wind exposure being slightly more prevalent than high wind exposure (51% and 63% of nests during 2008 and 2009, respectively).

A few of the parental male bass variables also showed variation. We recorded bass site tenacity scores in all possible score categories. We also noted fairly substantial levels of variation in the size of nesting male bass, with the estimated total length of individuals ranging from 7.5 to 20 inches. Interestingly, the majority of nesting male bass were shorter than the legal size limit in both years (70% for 2008 and 61% for 2009; see Appendix D for the size distribution in each year). This observation is important to note because any bass less than 14 inches must be released immediately during both the CIR and harvest fishing seasons.

Several of the nest attributes were relatively uninformative; they were CWM, TAB and modified TAB scores, hook wounds, sores, and spatial-temporal angling and recreation. Thought it may appear that some of these variables showed variation due to their CV values, the CV did not indicate how much variation was present among the majority of nests. For example, we observed CWM at relatively few nest sites, with the mean and median values being approximately zero. A few nests contained substantial CWM, which resulted in relatively high coefficient of variation (CV) values. However, the majority of nests (95%) contained no CWM in their vicinity and there was thus relatively little variation among most of the nests observed. Both TAB and modified TAB scores presented a similar result, with both scores having median values of 0 (76% of bass had TAB scores of 0 while 65% of bass had modified TAB scores of 0). Hook wounds, sores, and spatial-temporal angling and recreation displayed relatively little variation among most of the nests as well.

Table 8: Summary information for continuous variables collected at each nest (except temperature, which was recorded by lake). We have no data (-) for TAB and modified TAB scores, and nest predator abundance for 2008 because these were added for 2009. CV is the coefficient of variation of each variable. Temperature data are included for informational purposes only and were not included in the modeling. See the methods section for details on how we calculated temporal and spatial-temporal metrics.

| Environmental Variable | Min 08 | Min 09 | Max 08 | Max 09 | Mean 08 | Mean 09 | Median 08 | Median 09 | CV 08 | CV 09 |
|---|---|---|---|---|---|---|---|---|---|---|
| Bass Length (in) | 7.5 | 8.0 | 17.0 | 20.0 | 12.5 | 12.7 | 13.0 | 12.0 | 0.14 | 0.15 |
| TAB Score | - | 0 | - | 16 | - | 1 | - | 0 | - | 2.82 |
| Modified TAB Score | - | 0 | - | 42 | - | 2 | - | 0 | - | 2.59 |
| Nest Depth (m) | 0.4 | 0.3 | 2.3 | 2.5 | 1.0 | 1.1 | 0.9 | 1.1 | 0.42 | 0.33 |
| Percent Plant Cover | 0 | 0 | 100 | 100 | 56 | 56 | 60 | 60 | 0.54 | 0.53 |
| Nest Predator Abundance | - | 0 | - | 28 | - | 3 | - | 2 | - | 1.09 |
| CWM (# / m$^2$) | 0 | 0 | 6 | 8 | 0.2 | 0.2 | 0 | 0 | 5.08 | 4.81 |
| Temporal Angling (hrs/ha) | 0 | 0 | 0.98 | 1.38 | 0.30 | 0.41 | 0.25 | 0.32 | 0.95 | 0.74 |
| Temporal Recreation (hrs/ha) | 0 | 0 | 3.14 | 0.27 | 0.77 | 0.06 | 0.51 | 0.03 | 1.04 | 1.04 |
| Spatial-Temporal Angling | 0 | 0 | 1 | 3 | 0 | 0.29 | 0 | 0 | 0.26 | 2.02 |
| Spatial-Temporal Recreation | 0 | 0 | 2 | 2 | 0 | 0.13 | 0 | 0 | 5.02 | 2.88 |
| Temperature (°C) | 13.95 | 13.76 | 24.22 | 22.90 | 18.88 | 18.21 | 19.21 | 18.62 | 0.17 | 0.13 |

Table 9: Summary for categorical variables collected at each nest. Data shown are the percent of nests with features in each category, by variable and year. We added first bass score, hook wounds, and sores as a variable for 2009, as well as the category "developed with a vegetated shoreline" (DV). Other categories of shoreline development were: not developed (ND), developed with maintained lawn or beach (ML), and developed with a retaining wall (DR).

| Hook Wounds | | | Sores | | | Substrate | | | Shoreline Devel. | | | Wind | | | 1st Bass Score | | | Legal Size | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2008 | 2009 | | 2008 | 2009 | | 2008 | 2009 | | 2008 | 2009 | | 2008 | 2009 | | 2008 | 2009 | | 2008 | 2009 | |
| NA | 78% | N | NA | 93% | N | 19% | 29% | Silt | 21% | 21% | ND | 51% | 63% | Low | NA | 11% | 0 | 70% | 61% | Sub |
| NA | 22% | Y | NA | 7% | Y | 5% | 9% | Silty-Sand | NA | 9% | DV | 49% | 37% | High | NA | 15% | 1 | 30% | 39% | Legal |
| | | | | | | 67% | 53% | Sand | 46% | 39% | ML | | | | NA | 61% | 2 | | | |
| | | | | | | 7% | 4% | Sandy-Gravel | 33% | 31% | DR | | | | NA | 13% | 3 | | | |
| | | | | | | 2% | 5% | Gravel | | | | | | | | | | | | |

We further assessed the nest attributes of percent plant cover, nest predator abundance, shoreline development, substrate, wind, temporal angling, temporal recreation, legal size, and bass score because we had too many variables available in the habitat- and human-related categories for modeling. We calculated the covariance of the habitat-related nest attributes to help inform our decision. Percent plant cover and substrate negatively covaried (-0.3 and -0.45 for 2008 and 2009, respectively) whereas percent plant cover and nest predator abundance positively covaried (0.26 for 2009), but less so. Wind exposure and substrate covaried somewhat for 2008 (0.26), meaning that sand and gravel were somewhat more prevalent in high wind exposure areas. Similarly, wind and shoreline development covaried slightly for 2009 (0.25), meaning that retained shorelines were somewhat more prevalent in high wind exposure lake areas. Based on this information and our hypotheses, we chose to model percent plant cover and wind exposure. Percent plant cover and wind had relationships with other variables but not with each other, were expected to play roles in nest survival, and were observed during both years of the study. Considering human-related metrics, we chose to model temporal angling instead of temporal recreation because our study was focused on determining the effect of the Michigan fishing seasons on nest survival. Temporal angling and temporal recreation positively covaried for both years, though less so for 2009 (0.62 and 0.19 for 2008 and 2009, respectively). Finally, considering bass-related metrics, we expected both the legal size and first bass score metrics to strongly impact nest survival, so we included both in the modeling.

The following paragraphs describe the modeling results from the three phases of analysis. We discuss the results of Phases 1 and 2 briefly because their main function was to provide a means for selecting subsets of main effects and nest attributes to be combined in Phase 3 and to contribute to model averaging. Results regarding the direction of effect of each variable and the

strength of those effects are discussed with the outcome of the Phase 3 analysis and model averaging results.

*Phase 1: Modeling nest survival by lake, fishing season, and stage of development*: Modeling of the main effects (lake, stage of development, and fishing season) did not result in one model that carried a large proportion of the AICc weight for 2008. The top model carried only 25% of the weight, which indicated high model uncertainty (Table 10). AICc factor weights ranked lake and season as the most important main effects for 2008. The additive and interactive effects of lake and season were also highly ranked (Table 11). Effects of lake and season were expected, though stage was not as important as anticipated, and models with this variable carried an AICc factor weight of only 0.12 for 2008. Models lacking any main effect received only 2% of the AICc factor weight, which indicated that there were differences among lakes and seasons. Models with a different live recapture (p) and dead recovery probability (r) parameters for Woodland Lake received lower AICc factor weights than those without a separate parameter (Table 11), suggesting that Woodland's recovery probability was not substantially different from those of the other lakes during that year. Based on our criterion for a main effect to be used in Phase 2 (main effect AICc factor weight had to be greater than the AICc factor weight associated with unconditional models), the interaction among lake, season, and stage were used in Phase 2, but not any effects of Woodland on live recapture (p) or dead recovery (r). The main effects that continued to Phase 3 were any that were present in models that garnered at least 5% of the AICc weight (Table 10).

Results for 2009 were different from 2008, which was unexpected. The AICc weight was distributed across more models (Table 12) and the top model captured only 17% of the AICc weight. Similar to 2008, season was ranked as a somewhat important effect given that models

with season effects carried an AICc factor weight of 0.34 (AICc factor weight was 0.77 for 2008). Contrary to 2008 results, models with lake effects did not receive high AICc weights, whereas stage was an important effect with an AICc factor weight of 0.60. There were no important interactions among main effects in the 2009 models. Models lacking any main effect received a higher percentage of the weight (25%) than they had for 2008. A different live recapture ($p$) probability for Woodland Lake was important in the modeling for 2009 (AICc factor weight for a Woodland effect was 0.78; Table 13), but there was more evidence for similar dead recovery ($r$) probabilities among lakes, as it was for 2008 (AICc factor weight for lakes having similar dead recovery probabilities was 0.62). Based on our criterion for a main effect to be used in Phase 2 (main effect AICc factor weight had to be greater than the AICc factor weight associated with unconditional models), the effects of season and stage and a Woodland effect on live recapture ($p$) were used in Phase 2, but not any effects of Woodland dead recovery ($r$). The main effects that continued to Phase 3 were any that were present in models that garnered at least 5% of the AICc weight (Table 12).

Deviance residuals plots indicated possibilities for overdispersion and lack of fit in both years' modeling. The residuals plot of the top model for 2008 did not show any positive or negative trends but many of the residuals were large (far from 0) and indicated extra-binomial variation not explained by the model. The deviance plot for 2009 was similar, though the majority of the large residuals were positive. We did not adjust for overdispersion in our models because Program MARK could not estimate ĉ for our model type.

Table 10: Abbreviated table of model results containing main effects models from Phase 1 for 2008 with ΔAICc < 7. The full, 48-model list used to calculate factor weights for each main effect can be found in Table 29 (Appendix E). Tables 2 and 3 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season)p(.)Psi(.)r(.) | 1045.19 | 0.00 | 0.25 | 10 | 1024.26 |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | 1045.99 | 0.80 | 0.17 | 11 | 1022.87 |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | 1046.34 | 1.15 | 0.14 | 11 | 1023.22 |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | 1047.25 | 2.06 | 0.09 | 12 | 1021.92 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(.) | 1047.51 | 2.32 | 0.08 | 14 | 1017.70 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(.) | 1048.49 | 3.30 | 0.05 | 15 | 1016.41 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) | 1049.00 | 3.81 | 0.04 | 15 | 1016.92 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(Woodland) | 1049.90 | 4.71 | 0.02 | 16 | 1015.54 |
| phi(Lake*Stage)p(.)Psi(.)r(.) | 1049.99 | 4.80 | 0.02 | 10 | 1029.05 |
| phi(Lake)p(.)Psi(.)r(.) | 1050.83 | 5.64 | 0.01 | 7 | 1036.36 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | 1050.92 | 5.73 | 0.01 | 11 | 1027.80 |
| phi(Lake)p(Woodland)Psi(.)r(.) | 1051.40 | 6.21 | 0.01 | 8 | 1034.79 |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | 1051.52 | 6.33 | 0.01 | 11 | 1028.40 |
| phi(.)p(.)Psi(.)r(.) | 1051.89 | 6.70 | 0.01 | 5 | 1041.64 |
| phi(Lake)p(.)Psi(.)r(Woodland) | 1051.99 | 6.80 | 0.01 | 8 | 1035.38 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | 1052.07 | 6.88 | 0.01 | 12 | 1026.74 |

Table 11: AICc factor weights of main effects for 2008 from Phase 1. The key indicates which models were included in the calculation of the AICc factor weight of each survival factor. Psi is not represented because we did not model effects on transition probabilities.

| Survival Factor | AICc Weight | Live Recapture Factor | AICc Weight | Dead Recovery Factor | AICc Weight |
|---|---|---|---|---|---|
| No effect[1] | 0.02 | No effect | 0.61 | No effect | 0.65 |
| Lake[2] | 0.96 | Woodland | 0.39 | Woodland | 0.35 |
| Season[2] | 0.86 | | | | |
| Stage[2] | 0.27 | | | | |
| Lake+Season[3] | 0.85 | | | | |
| Lake+Stage[3] | 0.26 | | | | |
| Season+Stage[3] | 0.20 | | | | |
| Lake*Season[4] | 0.83 | | | | |
| Lake*Stage[4] | 0.24 | | | | |
| Season*Stage[4] | 0.19 | | | | |
| Lake+Season+Stage[5] | 0.01 | | | | |
| Lake*Season*Stage[5] | 0.19 | | | | |

Key
1 AICc Weight summed across models lacking main effects on survival
2 AICc Weight summed across single, additive, and interaction models
3 AICc Weight summed across additive and interaction models
4 AICc Weight summed across interaction models
5 AICc Weight summed across models with main effects in the specified combination

Table 12: Abbreviated table of model results containing main effects models from Phase 1 for 2009 with ΔAICc < 7. The full, 44-model list used to calculate factor weights for each main effect can be found in Table 30 (Appendix E). Tables 2 and 3 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Stage)p(Woodland)Psi(.)r(.) | 4243.66 | 0.00 | 0.17 | 7 | 4229.34 |
| phi(.)p(Woodland)Psi(.)r(.) | 4244.18 | 0.53 | 0.13 | 6 | 4231.95 |
| phi(Stage)p(Woodland)Psi(.)r(Woodland) | 4244.84 | 1.18 | 0.09 | 8 | 4228.43 |
| phi(Season+Stage)p(Woodland)Psi(.)r(.) | 4245.26 | 1.60 | 0.07 | 8 | 4228.85 |
| phi(.)p(Woodland)Psi(.)r(Woodland) | 4245.40 | 1.75 | 0.07 | 7 | 4231.08 |
| phi(Season)p(Woodland)Psi(.)r(.) | 4245.90 | 2.24 | 0.05 | 7 | 4231.58 |
| phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) | 4246.47 | 2.82 | 0.04 | 9 | 4227.96 |
| phi(Stage)p(.)Psi(.)r(.) | 4246.51 | 2.85 | 0.04 | 6 | 4234.27 |
| phi(Stage)p(.)Psi(.)r(Woodland) | 4246.79 | 3.13 | 0.03 | 7 | 4232.47 |
| phi(Season*Stage)p(Woodland)Psi(.)r(.) | 4247.05 | 3.39 | 0.03 | 9 | 4228.53 |
| phi(Season)p(Woodland)Psi(.)r(Woodland) | 4247.14 | 3.49 | 0.03 | 8 | 4230.73 |
| phi(.)p(.)Psi(.)r(.)} | 4247.15 | 3.50 | 0.03 | 5 | 4236.98 |
| phi(.)p(.)Psi(.)r(Woodland) | 4247.44 | 3.78 | 0.03 | 6 | 4235.20 |
| phi(Season+Stage)p(.)Psi(.)r(.) | 4248.14 | 4.49 | 0.02 | 7 | 4233.82 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | 4248.16 | 4.50 | 0.02 | 10 | 4227.53 |
| phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) | 4248.27 | 4.62 | 0.02 | 10 | 4227.64 |
| phi(Season+Stage)p(.)Psi(.)r(Woodland) | 4248.45 | 4.80 | 0.02 | 8 | 4232.04 |
| phi(Lake)p(Woodland)Psi(.)r(.) | 4248.56 | 4.90 | 0.01 | 9 | 4230.04 |
| phi(Season)p(.)Psi(.)r(.) | 4248.90 | 5.24 | 0.01 | 6 | 4236.66 |
| phi(Season)p(.)Psi(.)r(Woodland) | 4249.20 | 5.54 | 0.01 | 7 | 4234.88 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) | 4249.36 | 5.70 | 0.01 | 11 | 4226.60 |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | 4249.67 | 6.02 | 0.01 | 10 | 4229.04 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) | 4249.80 | 6.14 | 0.01 | 11 | 4227.04 |
| phi(Season*Stage)p(.)Psi(.)r(.) | 4249.92 | 6.27 | 0.01 | 8 | 4233.51 |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | 4250.17 | 6.51 | 0.01 | 10 | 4229.54 |
| phi(Season*Stage)p(.)Psi(.)r(Woodland) | 4250.21 | 6.55 | 0.01 | 9 | 4231.69 |

Table 13: AICc factor weights of main effects for 2009 from Phase 1. The key indicates which models were included in the calculation of the AICc factor weight of each survival factor. Psi is not represented because we did not model effects on transition probabilities.

| Survival Factor | AICc Weight | Live Recapture Factor | AICc Weight | Dead Recovery Factor | AICc Weight |
|---|---|---|---|---|---|
| No effect[1] | 0.25 | No effect | 0.22 | No effect | 0.62 |
| Lake[2] | 0.10 | Woodland | 0.78 | Woodland | 0.38 |
| Season[2] | 0.34 | | | | |
| Stage[2] | 0.60 | | | | |
| Lake+Season[3] | 0.03 | | | | |
| Lake+Stage[3] | 0.06 | | | | |
| Season+Stage[3] | 0.22 | | | | |
| Lake*Season[4] | 0.00 | | | | |
| Lake*Stage[4] | 0.01 | | | | |
| Season*Stage[4] | 0.06 | | | | |

Key

1 AICc Weight summed across models lacking main effects on survival

2 AICc Weight summed across single, additive, and interaction models

3 AICc Weight summed across additive and interaction models

4 AICc Weight summed across interaction models

*Phase 2: Modeling effects of nest attributes on nest survival*: Modeling the nest attributes alongside the important main effects from Phase 1 did not result in one model that carried a large proportion of the AICc weight for 2008 (Table 14), though it did for 2009 (Table 15). The most influential variables were wind exposure for 2008 and temporal angling and percent plant cover for both years. These variables garnered AICc factor weights of 0.57, 0.44, and 0.27, respectively in the 2008 models and 1 (temporal angling) and 0.99 (percent plant cover) in the 2009 models (Tables 16 and 17 for 2008 and 2009). Though the high-ranking variables were similar, their relative ranks and how much weight they received varied. Interestingly, legal size was actually represented in more models than the other variables but was one of the least important variables for both years, as was the legal size by season interaction. The nest attribute combinations that continued to Phase 3 for 2008 were any that were present in models that garnered at least 5% of the AICc weight (Table 14).

Phase 2 resulted in high model uncertainty for 2008 because the AICc weight was distributed among several of the models. However, results for 2009 were very different and one model, which included temporal angling and percent plant cover in addition to season and stage effects, garnered 99.9% of all AICc model weight. These nest attributes contributed strongly to explaining variation in nest survival during 2009. The nest attribute combinations that continued to Phase 3 for 2009 were temporal angling and plant cover because those were the only nest attributes present in models that garnered at least 5% of the AICc weight (Table 15).

Table 14: Abbreviated table of model results from Phase 2 of 2008 containing lake-season mean centered nest attribute models with ΔAICc < 7. The full, 15-model list used to calculate factor weights for each nest attribute can be found in Table 31 (Appendix E). All models were run with the important main effects from Phase 1 (lake*season*stage). Tables 4 and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season*Stage+Wind)p(.)Psi(.)r(.) | 1046.84 | 0.00 | 0.21 | 15 | 1014.76 |
| phi(Lake*Season*Stage+Wind+TAng)p(.)Psi(.)r(.) | 1047.45 | 0.61 | 0.16 | 16 | 1013.08 |
| phi(Lake*Season*Stage+TAng)p(.)Psi(.)r(.) | 1047.52 | 0.68 | 0.15 | 15 | 1015.44 |
| phi(Lake*Season*Stage+Cover+Wind)p(.)Psi(.)r(.) | 1048.43 | 1.59 | 0.10 | 16 | 1014.06 |
| phi(Lake*Season*Stage+Wind+Legal)p(.)Psi(.)r(.) | 1048.96 | 2.12 | 0.07 | 16 | 1014.60 |
| phi(Lake*Season*Stage+Legal)p(.)Psi(.)r(.) | 1049.39 | 2.55 | 0.06 | 15 | 1017.31 |
| phi(Lake*Season*Stage+Cover+TAng)p(.)Psi(.)r(.) | 1049.40 | 2.56 | 0.06 | 16 | 1015.04 |
| phi(Lake*Season*Stage+Cover)p(.)Psi(.)r(.) | 1049.58 | 2.74 | 0.05 | 15 | 1017.50 |
| phi(Lake*Season*Stage+TAng+Legal)p(.)Psi(.)r(.) | 1050.01 | 3.17 | 0.04 | 16 | 1015.65 |
| phi(Lake*Season*Stage+Wind+Legal*Season)p(.)Psi(.)r(.) | 1051.18 | 4.35 | 0.02 | 17 | 1014.51 |
| phi(Lake*Season*Stage+Cover+Legal)p(.)Psi(.)r(.) | 1051.50 | 4.66 | 0.02 | 16 | 1017.14 |
| phi(Lake*Season*Stage+TAng+Legal*Season)p(.)Psi(.)r(.) | 1051.67 | 4.83 | 0.02 | 17 | 1014.99 |
| phi(Lake*Season*Stage+Legal*Season)p(.)Psi(.)r(.) | 1052.24 | 5.40 | 0.01 | 16 | 1017.87 |
| phi(Lake*Season*Stage+Cover+Wind+TAng+Legal*Season)p(.)Psi(.)r(.) | 1053.72 | 6.88 | 0.01 | 19 | 1012.37 |

Table 15: Abbreviated table of model results from Phase 2 of 2009 containing lake-season mean centered nest attribute models with a ΔAICc < 7. The full, 18-model list used to calculate factor weights for each nest attribute as well as details on which models did not converge can be found in Table 32 (Appendix E). All models were run with the important main effects from Phase 1 (season+stage). Tables 4 and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Season+Stage+ Cover+ TAng)p(Woodland)Psi(.)r(.) | 4155.79 | 0.00 | 0.999 | 10 | 4135.16 |

Table 16:   AICc factor weights of lake-season mean centered nest attributes for 2008.   The † indicates a variable that was not represented in the model list with the same frequency as the other variables due to the presence of the legal size*season interaction (models with legal*season automatically included legal size in the model, which resulted in four additional models with legal size and one fewer model with legal size*season ).

| Survival Covariate | AICc Weight |
| --- | --- |
| Wind Exposure | 0.57 |
| Temporal Angling | 0.44 |
| Legal Size† | 0.27 |
| Percent Plant Cover | 0.24 |
| Legal Size*Season† | 0.07 |

Table 17: AICc factor weights of lake-season mean centered nest attributes for 2009.  The ‡ indicates that one or more models including this variable did not converge on estimates and had to be deleted, which resulted in slightly unequal representation of this variable in the model list.  The † indicates a variable that was not represented in the model list with the same frequency as the other variables due to the presence of the legal size*season interaction (models with legal size*season automatically included legal size in the model, which resulted in five additional models with legal size and one fewer model with legal size*season ).

| Survival Covariate | AICc Weight |
| --- | --- |
| Temporal Angling‡ | 1.000 |
| Percent Plant Cover | 0.999 |
| Legal Size† | 0.001 |
| Legal Size*Season† | 0.001 |
| Bass Score‡ | 0 |
| Wind Exposure‡ | 0 |

*Phase 3: Estimating nest survival probabilities by lake, season, and stage*: Combining the highly ranked main effects models from Phase 1 with the highly ranked nest attribute models from Phase 2 yielded different results for each year. No variable type (main effect versus nest attribute) clearly explained more of the variation in nest survival probabilities for 2008. The majority of models had very similar AICc values (53% of models had ΔAICc < 7, Table 18). However, for 2009, temporal angling appeared in every top model and no other models were within 7 AICc of the top model, which carried 99.9% of AICc weight, (Table 19 for model ranks, Table 20 for β estimates of this model). For these reasons, temporal angling was one of the most influential predictor variables, but percent plant cover, fishing season, and stage of development were also important because they were also in the top model with 99.9% of AICc weight.

Differences in important main effects for each year were reflected in the direction and strength of the βs associated with main effects as well as the model-averaged survival probability estimates. The AICc factor weights strongly supported a lake by season interaction for 2008 (AICc factor weight of 0.83), but the β confidence intervals for parameters associated with the lake by season interaction for 2008 always bounded 0 (Table 21), calling into question the biological significance of this interaction. In general, the CIR season exhibited higher nest survival probabilities (Figure 3). The lake by season interaction likely was driven by unexpected findings for North Lake. The β representing North Lake was often positive and only bounded 0 in the lowest ranked 52% of the models, indicating that North Lake was frequently estimated in the models to have higher nest survival probabilities than Chemung or Woodland for 2008. North Lake had the highest 6-day mean survival probabilities of any of the lakes (the lake with the lowest average temporal angling during 2008), but survival was also unexpectedly higher in

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the harvest season (during which lake-season centered temporal angling was also higher). The temporal angling variable was standardized by lake-season, so apparent differences in survival probabilities among lakes and seasons may be attributable to differences in mean values of temporal angling that were removed from the variable when it was centered. Chemung and Woodland, high fishing pressure lakes, exhibited the expected relationship of lower nest survival during the harvest season than the CIR season during 2008. The β for Lake Chemung had a confidence interval that bounded 0 in 79% of the highest ranked models, suggesting that survival probabilities were not different between Chemung and Woodland lakes. However, this was not one of the *a priori* hypotheses that we tested. Despite the evidence that suggested differences by lake and season during 2008, no lake, season, or stage's survival probability estimate could be distinguished from any other due to error (Figure 4). Some of this variation was due to model uncertainty; model variation contributed up to 40% of the variation in the survival estimates. Additionally, dead recovery probabilities (r) were much lower during 2008 than 2009 (approximately 0.56 as compared to 0.84), which added more uncertainty to survival predictions.

Lake and the lake by season interaction were not important for 2009 (AICc factor weight of 0.104 and 0.001, respectively) and the confidence interval for βs associated with those parameters bounded 0 in 84-100% of models (Table 22). However, the season effect did not bound 0 in 2009's top model, which garnered 99.9% of AICc weight and therefore contributed very highly to model-averaged survival estimates (model averaging may not have been necessary for 2009, but we performed it on both years for consistency and to account for all model uncertainty, however little). The CIR season had higher survival probability estimates than the harvest season in that top model, which was reflected in the model-averaged survival estimate results (Figure 4).

The model-averaged estimates of nest survival did not vary by stage of development for 2008 (Figure 3). Egg and larval survival probabilities were nearly identical (within lakes and fishing seasons), which corresponded with their low AICc factor weight and the fact that 100% of 2008's models had β confidence intervals for the stage parameter bounding 0. However, the model-averaged estimates of nest survival varied by offspring stage of development for 2009 (Figure 4). The stage effect was present in all of the highest ranking models for that year, including the one that received 99.9% of the weight. Larvae had higher survival probabilities than eggs (reflected in the negative β for the egg stage in every model). The confidence interval of the β for eggs did not bound 0 in the top models. No interactions between stage and other main effects were important for either year.

Differences in live recapture (p) probability estimates between Woodland and the other lakes were not important for 2008 (probability estimates of live recapture were 0.38 (95% CI 0.24-0.54) for Woodland Lake and 0.33 (95% CI 0.28-0.40) for all other lakes during 2008.), but a separate live recapture probability for Woodland was highly weighted for 2009 (AICc factor weight of 0.78). The β associated with Woodland's live recapture probability was present in the top model, which carried 99.9% of the weight, and it bounded 0 in only 22% of the models (Table 22). The direction of the Woodland effect on live recapture was negative for 2009, indicating that we had a lower probability of seeing a nest alive in Woodland, given that it was there and alive. Probability estimates of live recapture (p) were 0.21 (95% CI 0.13-0.32) for Woodland Lake and 0.35 (95% CI 0.31-0.40) for all other lakes during 2009. We did not see a strong Woodland effect on dead recovery (r) in any year and 100% of the models had β confidence intervals that bounded 0. However, overall estimates of dead recovery probabilities for all lakes increased for 2009. Probability estimates of dead recovery were 0.54 (95% CI 0.43-

0.72) for Woodland Lake and 0.58 (95% CI 0.44-0.64) for all other lakes during 2008, but they were 0.84 (95% CI 0.74-0.90) for all lakes during 2009.

Though not a main effect, interval length was present in every model to account for the number of days between sampling dates at each lake. Interestingly, whenever the β for the interval length parameter did not bound 0, the direction of the effect was negative (the β never bounded 0 for 2009 and did so only in the lowest-ranked 11% of 2008's models). The negative effect indicated that the longer the period of time between observations, the less likely the nest was to survive. Alternatively, this could also have indicated that the longer the period of time between visits to a lake, the less likely we were to observe offspring at a nest even if they had survived the interval. We revisited nests multiple times to confirm that offspring were not present and to help reduce uncertainty around dead recoveries (r, which improved for 2009 when snorkeling efforts increased), but there may have been some cases in which a nest developed from larvae into fry and dispersed before we revisited the nest. However, we often observed fry from the same nest on multiple consecutive visits, so we do not expect the likelihood of our crews missing a successful nest to be very high. Therefore, we believe the negative effect of interval length is largely attributable to lower survival during longer intervals and not to an inability to locate living offspring.

Some of the lake-season mean centered nest attributes also had strong effects on nest survival probabilities. Percent plant cover negatively affected nest survival in both years. However, 100% of 2008's models had β confidence intervals for percent plant cover that bounded 0, which indicated a lack of a meaningful effect on nest survival probabilities (Table 21). For 2009, the β confidence interval for percent plant cover did not bound 0 in the top model, which carried almost all of the AICc weight (Table 22). The effect of percent plant cover in that model was

negative (higher percent plant cover in a 1-m area around the nest was associated with lower nest survival probabilities).

Temporal angling had a positive effect in every model in which it was included for both years. For 2008, the β confidence intervals of temporal angling bounded 0 in 78% of models, indicating that it infrequently had a meaningful effect on nest survival probabilities (Table 21). The models for 2009, however, showed that temporal angling had a very strong effect. Temporal angling was in every one of 2009's top models (including the one that had 99.9% of the AICc weight, Table 34 in Appendix E) and none of the β confidence intervals for temporal angling bounded 0 (Table 22). The direction of its effect was consistently positive, which was unexpected and may have been due to temporal trends in survival within fishing seasons (see the Discussion section for further details).

Legal size and the legal size by season interaction were not important in either year, receiving low AICc factor weights (legal size had a weight of 0.27 for 2008, but otherwise these variables had weights of 0.07 or less; Tables 21 and 22). Legal size had a positive effect in most models for 2008 (indicating that a nest with a guarding male of legal size had higher survival probabilities), but a negative effect for 2009 (legal size guarding males were associated with lower survival probabilities). The legal size by season interaction in both years indicated that survival was lower for legal size bass in the CIR season than in the harvest season. However, the β confidence intervals of these parameters bounded 0 in 80-100% of models, so neither variable had a strong effect on nest survival probabilities.

Wind exposure did not have a strong effect in either years' models, and trends in the effect of wind exposure differed between years. For 2008, wind was the highest ranked nest attribute from Phase 2 (AICc factor weight of 0.57; Table 21). However, 100% of models that included

wind had a β confidence interval for wind that bounded 0. Therefore, though the direction of effect of wind was consistently negative for 2008 (indicating a trend toward lower survival in high wind areas), it had no discernible effect on nest survival probabilities during 2008. The β value for wind was consistently positive for 2009, but again the β confidence interval bounded 0 in every model (Table 22).

Table 18: Abbreviated table of models with ΔAICc < 7 resulting from Phases 1, 2, and 3 together that were used for model averaging for 2008. The full, 95-model list used to model average for parameter estimates can be found in Table 33 (Appendix E). Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season+TAng)p(.)Psi(.)r(.) | 1043.76 | 0.00 | 0.08 | 11 | 1020.64 |
| phi(Lake*Season+Wind)p(.)Psi(.)r(.) | 1044.22 | 0.47 | 0.06 | 11 | 1021.10 |
| phi(Lake*Season+Wind+TAng)p(.)Psi(.)r(.) | 1044.48 | 0.73 | 0.05 | 12 | 1019.15 |
| phi(Lake*Season+TAng)p(Woodland)Psi(.)r(.) | 1044.57 | 0.81 | 0.05 | 12 | 1019.24 |
| phi(Lake*Season+TAng)p(.)Psi(.)r(Woodland) | 1044.94 | 1.18 | 0.04 | 12 | 1019.60 |
| phi(Lake*Season+Cover+TAng)p(.)Psi(.)r(.) | 1044.97 | 1.21 | 0.04 | 12 | 1019.63 |
| phi(Lake*Season+Wind)p(Woodland)Psi(.)r(.) | 1045.04 | 1.28 | 0.04 | 12 | 1019.71 |
| phi(Lake*Season)p(.)Psi(.)r(.) | 1045.19 | 1.43 | 0.04 | 10 | 1024.26 |
| phi(Lake*Season+Wind+TAng)p(Woodland)Psi(.)r(.) | 1045.31 | 1.56 | 0.03 | 13 | 1017.75 |
| phi(Lake*Season+Wind)p(.)Psi(.)r(Woodland) | 1045.40 | 1.64 | 0.03 | 12 | 1020.07 |
| phi(Lake*Season+Wind+TAng)p(.)Psi(.)r(Woodland) | 1045.68 | 1.92 | 0.03 | 13 | 1018.12 |
| phi(Lake*Season+Cover+TAng)p(Woodland)Psi(.)r(.) | 1045.75 | 1.99 | 0.03 | 13 | 1018.19 |
| phi(Lake*Season+Cover+Wind)p(.)Psi(.)r(.) | 1045.85 | 2.09 | 0.03 | 12 | 1020.52 |
| phi(Lake*Season+TAng)p(Woodland)Psi(.)r(Woodland) | 1045.85 | 2.10 | 0.03 | 13 | 1018.29 |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | 1045.99 | 2.24 | 0.02 | 11 | 1022.87 |
| phi(Lake*Season+Cover+TAng)p(.)Psi(.)r(Woodland) | 1046.18 | 2.42 | 0.02 | 13 | 1018.62 |
| phi(Lake*Season+Wind+Legal)p(.)Psi(.)r(.) | 1046.33 | 2.57 | 0.02 | 12 | 1020.99 |
| phi(Lake*Season+Wind)p(Woodland)Psi(.)r(Woodland) | 1046.33 | 2.57 | 0.02 | 13 | 1018.77 |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | 1046.34 | 2.59 | 0.02 | 11 | 1023.22 |
| phi(Lake*Season+Wind+TAng)p(Woodland)Psi(.)r(Woodland) | 1046.62 | 2.86 | 0.02 | 14 | 1016.81 |
| phi(Lake*Season+Cover+Wind)p(Woodland)Psi(.)r(.) | 1046.64 | 2.88 | 0.02 | 13 | 1019.08 |
| phi(Lake*Season*Stage+Wind)p(.)Psi(.)r(.) | 1046.84 | 3.08 | 0.02 | 15 | 1014.76 |
| phi(Lake*Season+Cover+Wind)p(.)Psi(.)r(Woodland) | 1047.06 | 3.30 | 0.01 | 13 | 1019.49 |
| phi(Lake*Season+Cover)p(.)Psi(.)r(.) | 1047.06 | 3.31 | 0.01 | 11 | 1023.94 |
| phi(Lake*Season+Cover+TAng)p(Woodland)Psi(.)r(Woodland) | 1047.07 | 3.31 | 0.01 | 14 | 1017.26 |

Table 18 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(Lake*Season+Wind+Legal)p(Woodland)Psi(.)r(.) | 1047.16 | 3.40 | 0.01 | 13 | 1019.60 |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | 1047.25 | 3.49 | 0.01 | 12 | 1021.92 |
| phi(Lake*Season+Legal)p(.)Psi(.)r(.) | 1047.38 | 3.62 | 0.01 | 11 | 1024.25 |
| phi(Lake*Season*Stage+Wind+TAng)p(.)Psi(.)r(.) | 1047.45 | 3.69 | 0.01 | 16 | 1013.08 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(.) | 1047.51 | 3.75 | 0.01 | 14 | 1017.70 |
| phi(Lake*Season*Stage+TAng)p(.)Psi(.)r(.) | 1047.52 | 3.76 | 0.01 | 15 | 1015.44 |
| phi(Lake*Season+Wind+Legal)p(.)Psi(.)r(Woodland) | 1047.52 | 3.76 | 0.01 | 13 | 1019.96 |
| phi(Lake*Season+Cover)p(Woodland)Psi(.)r(.) | 1047.87 | 4.11 | 0.01 | 12 | 1022.53 |
| phi(Lake*Season+Cover+Wind)p(Woodland)Psi(.)r(Woodland) | 1047.96 | 4.20 | 0.01 | 14 | 1018.15 |
| phi(Lake*Season+Legal)p(Woodland)Psi(.)r(.) | 1048.20 | 4.44 | 0.01 | 12 | 1022.87 |
| phi(Lake*Season+Cover)p(.)Psi(.)r(Woodland) | 1048.24 | 4.48 | 0.01 | 12 | 1022.91 |
| phi(Lake*Season*Stage+Cover+Wind)p(.)Psi(.)r(.) | 1048.43 | 4.67 | 0.01 | 16 | 1014.06 |
| phi(Lake*Season+Wind+Legal)p(Woodland)Psi(.)r(Woodland) | 1048.47 | 4.71 | 0.01 | 14 | 1018.66 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(.) | 1048.49 | 4.73 | 0.01 | 15 | 1016.41 |
| phi(Lake*Season+Legal)p(.)Psi(.)r(Woodland) | 1048.55 | 4.79 | 0.01 | 12 | 1023.22 |
| phi(Lake*Season*Stage+Wind+Legal)p(.)Psi(.)r(.) | 1048.96 | 5.20 | 0.01 | 16 | 1014.60 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) | 1049.00 | 5.24 | 0.01 | 15 | 1016.92 |
| phi(Lake*Season+Cover)p(Woodland)Psi(.)r(Woodland) | 1049.15 | 5.39 | 0.01 | 13 | 1021.58 |
| phi(Lake*Season*Stage+Legal)p(.)Psi(.)r(.) | 1049.39 | 5.63 | 0.00 | 15 | 1017.31 |
| phi(Lake*Season*Stage+Cover+TAng)p(.)Psi(.)r(.) | 1049.40 | 5.64 | 0.00 | 16 | 1015.04 |
| phi(Lake*Season+Legal)p(Woodland)Psi(.)r(Woodland) | 1049.48 | 5.72 | 0.00 | 13 | 1021.92 |
| phi(Lake*Season*Stage+Cover)p(.)Psi(.)r(.) | 1049.58 | 5.82 | 0.00 | 15 | 1017.50 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(Woodland) | 1049.90 | 6.14 | 0.00 | 16 | 1015.54 |
| phi(Lake*Stage)p(.)Psi(.)r(.) | 1049.99 | 6.23 | 0.00 | 10 | 1029.05 |
| phi(Lake*Season*Stage+TAng+Legal)p(.)Psi(.)r(.) | 1050.01 | 6.25 | 0.00 | 16 | 1015.65 |

Table 19: Abbreviated table of models with ΔAICc < 7 resulting from Phases 1, 2, and 3 together that were used for model averaging for 2009. The full, 95-model list used to model average for parameter estimates can be found in Table 34 (Appendix E). Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Season+Stage+Cover+TAng)p(Woodland)Psi(.)r(.) | 4155.79 | 0.00 | 0.999 | 10 | 4135.16 |

Table 20: Parameter estimates for βs in the 2009 top model that garnered 99.9% of AICc weight. Parameters with a dash under notation were present in every model to accommodate model structure (intercepts) or the effect of variation in sampling dates on survival probabilities. They had no special notation for model naming.

| Parameter Estimates of 2009 Top Model | | | | | |
|---|---|---|---|---|---|
| phi(Season+Stage+Cover+TAng)p(Woodland)Psi(.)r(.) | | | | | |
| Parameter | Notation | Beta | SE | Lower CI | Upper CI |
| Survival Probability | – | | | | |
| Intercept | | 1.34 | 0.24 | 0.86 | 1.81 |
| CIR | phi(Season) | 0.64 | 0.12 | 0.40 | 0.88 |
| Eggs | phi(Stage) | -0.84 | 0.15 | -1.13 | -0.55 |
| Cover | phi(Cover) | -0.77 | 0.21 | -1.18 | -0.35 |
| TAng | phi(TAng) | 2.75 | 0.44 | 1.89 | 3.62 |
| Interval Length | – | -0.49 | 0.08 | -0.63 | -0.34 |
| | | | | | |
| Live Recapture All | | | | | |
| Lakes but Woodland | p(.) | -0.62 | 0.09 | -0.80 | -0.43 |
| Live Recapture | | | | | |
| Woodland Only | p(Woodland) | -0.72 | 0.31 | -1.33 | -0.12 |
| Transition | – | | | | |
| Probability Intercept | | -0.71 | 0.09 | -0.88 | -0.54 |
| Dead Recovery All | | | | | |
| Lakes | r(.) | 1.62 | 0.29 | 1.05 | 2.19 |

Table 21: Evaluation of directions of effects and β confidence intervals of main effect and nest attribute parameters for 2008. AICc factor weights are from Phase 1 for main effects and Phase 2 for nest attributes. Data on the direction of effect and confidence intervals of each β were summarized across models of all phases to examine how each variable contributed to model averaging for survival estimates (phi) and live recapture (p) and dead recovery (r). Interval length was present in every model to accommodate the effect of variation in sampling dates on survival probabilities and had no special notation for model naming.

| Parameter | Notation | AICc Factor Weight | % of Models with CI Bounding 0 | % of Models with Positive β |
|---|---|---|---|---|
| Chemung | phi(Lake) | 0.958 | 79% | 100% |
| North | | | 52% | 100% |
| CIR | phi(Season) | 0.862 | 100% | 71% |
| Eggs | phi(Stage) | 0.273 | 100% | 72% |
| Chemung CIR | phi(Lake*Season) | 0.828 | 100% | 100% |
| North CIR | | | 100% | 0% |
| Chemung Eggs | phi(Lake*Stage) | 0.241 | 100% | 0% |
| North Eggs | | | 100% | 0% |
| CIR Eggs | phi(Season*Stage) | 0.189 | 100% | 22% |
| Cover | phi(Cover) | 0.243 | 100% | 0% |
| Wind | phi(Wind) | 0.572 | 100% | 0% |
| TAng | phi(TAng) | 0.438 | 78% | 100% |
| Legal Size | phi(Legal) | 0.268 | 100% | 59% |
| Legal*Season | phi(Legal*Season) | 0.070 | 100% | 0% |
| Interval Length | – | 1.000 | 79% | 17% |
| Live Recapture All Lakes | p(.) | 0.606 | 0% | 0% |
| Live Recapture Woodland Lake | p(Woodland) | 0.394 | 100% | 100% |
| Dead Recovery All Lakes | r(.) | 0.651 | 100% | 100% |
| Dead Recovery Woodland Lake | r(Woodland) | 0.349 | 100% | 100% |

Table 22: Evaluation of directions of effects and β confidence intervals of main effect and nest attribute parameters for 2009. AICc factor weights are from Phase 1 for main effects and Phase 2 for nest attributes. Data on the direction of effect and confidence intervals of each β were summarized across models of all phases to examine how each variable contributed to model averaging for survival estimates (phi) and live recapture (p) and dead recovery (r). Interval length was present in every model to accommodate the effect of variation in sampling dates on survival probabilities and had no special notation for model naming.

| Parameter | Notation | AICc Factor Weight | % of Models with CI Bounding 0 | % of Models with Positive β |
|---|---|---|---|---|
| Chemung | | | 84% | 0% |
| North | phi(Lake) | 0.104 | 84% | 0% |
| Woodland | | | 100% | 0% |
| CIR | phi(Season) | 0.343 | 89% | 89% |
| Eggs | phi(Stage) | 0.600 | 87% | 0% |
| Chemung CIR | | | 100% | 100% |
| North CIR | phi(Lake*Season) | 0.001 | 100% | 100% |
| Woodland CIR | | | 100% | 20% |
| Chemung Eggs | | | 100% | 100% |
| North Eggs | phi(Lake*Stage) | 0.009 | 100% | 100% |
| Woodland Eggs | | | 100% | 40% |
| CIR Eggs | phi(Season*Stage) | 0.060 | 100% | 100% |
| Cover | phi(Cover) | 0.997 | 91% | 18% |
| Wind | phi(Wind) | 0.000 | 100% | 100% |
| TAng | phi(TAng) | 1.000 | 0% | 100% |
| BScore | phi(BScore) | 0.000 | 100% | 100% |
| Legal Size | phi(Legal) | 0.003 | 90% | 0% |
| Legal*Season | phi(Legal*Season) | 0.002 | 80% | 20% |
| Interval Length | – | 1.000 | 0% | 0% |
| Live Recapture All Lakes | p(.) | 0.221 | 0% | 0% |
| Live Recapture Woodland Lake | p(Woodland) | 0.779 | 22% | 0% |
| Dead Recovery All Lakes | r(.) | 0.622 | 0% | 100% |
| Dead Recovery Woodland Lake | r(Woodland) | 0.378 | 100% | 0% |
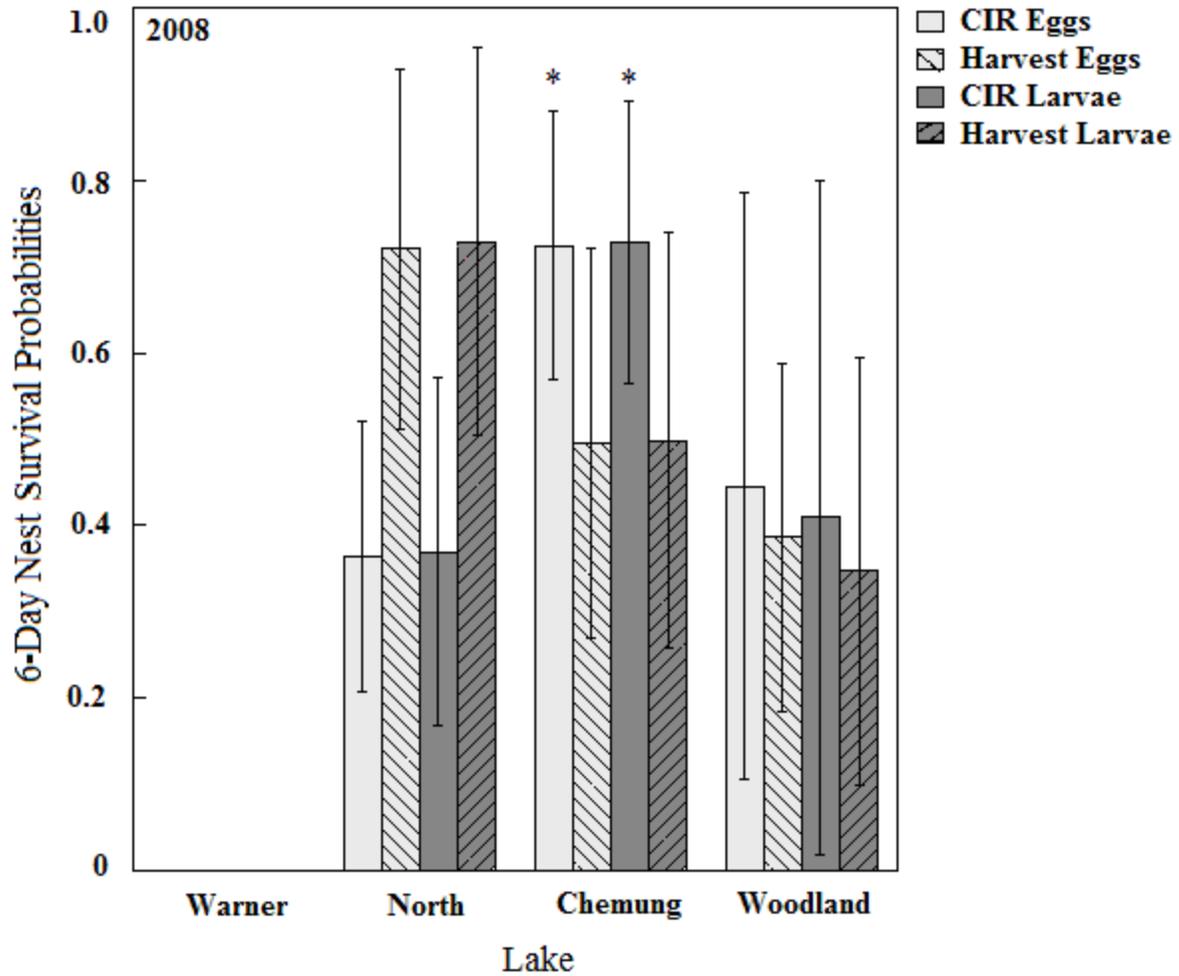
Figure 3: Six-day nest survival probabilities by lake, season, and stage of development for 2008. Lakes are in order of low to high fishing pressure. Error bars represent +/- two standard errors. There were no 6-day survival periods in Chemung during the CIR season for 2008. The starred bars are based on 5-day survival periods and are slightly higher than a 6-day survival estimate would be. We had no data for Warner Lake for 2008.
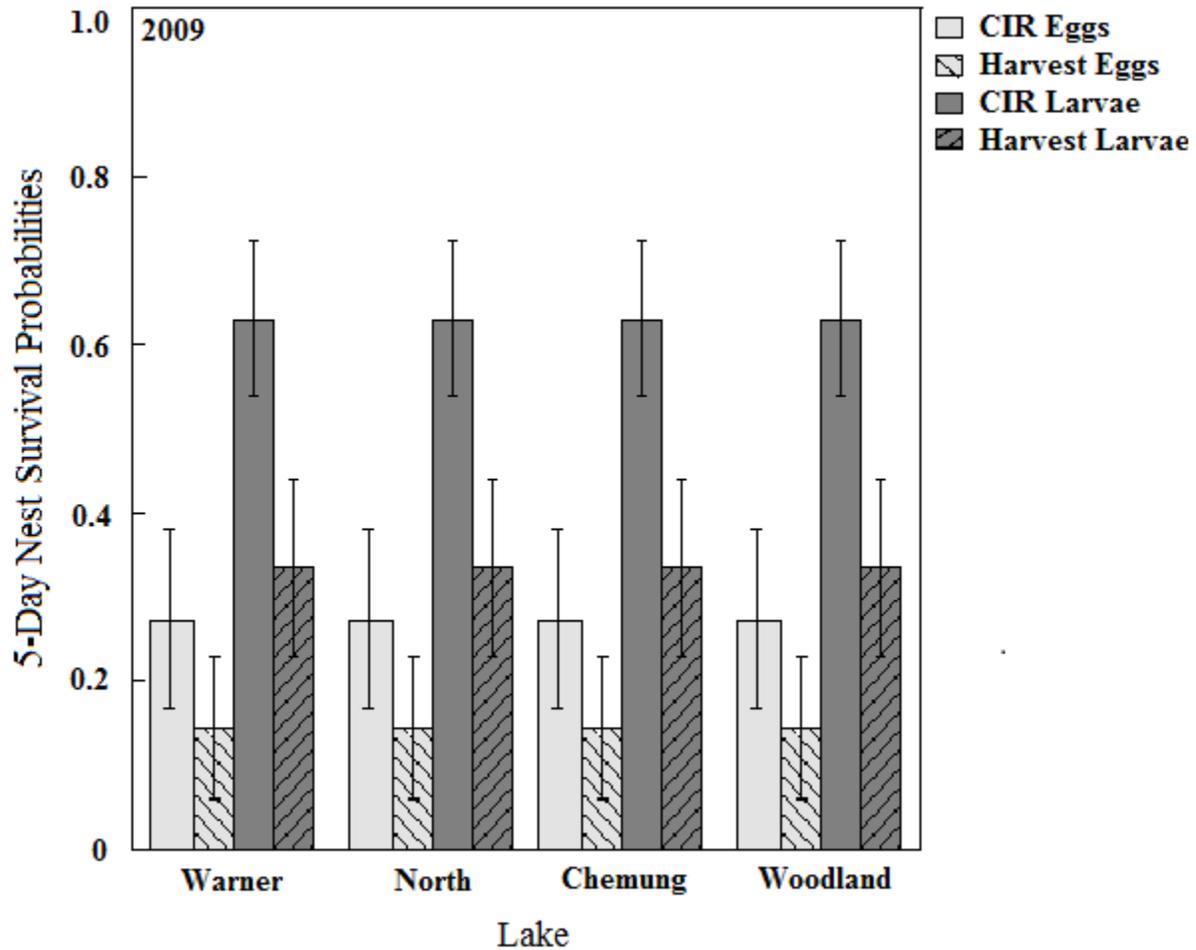
Figure 4: Five-day nest survival probabilities by lake, season, and stage of development for 2009. Lakes are in order of low to high fishing pressure. Error bars represent +/- two standard errors.

Discussion:

Our modeling revealed some similarities and some differences regarding bass nest survival probabilities, and the factors influencing them, during 2008 and 2009. Most notably, both years had higher survival in the CIR fishing season than in the subsequent harvest season and temporal angling (centered within each lake and season) had a positive relationship with nest survival probabilities. However, only 2009 analyses (for which the data are more reliable, see below) showed strong effects of those variables. Surprisingly, no attributes of the guarding male explained substantial amounts of variation in nest survival probability in either year. However,

vegetative cover at the nest site and temporal angling were strongly related (negatively and positively, respectively) to nest survival in 2009's dominant model. Indeed, the model results for 2009 included one model that garnered 99.9% of the AICc weight for that year and clearly indicated effects of fishing season, stage of development, and lake-season centered temporal angling and percent plant cover on nest survival probability. In contrast, very few main effects or nest attributes showed strong effects on survival for 2008.

We believe that high model uncertainty for 2008 coupled with relatively low dead recovery (r) probabilities that year increased the error surrounding survival probability estimates and resulted in the lack of strong effects. These characteristics of our 2008 modeling (as compared to 2009) likely resulted from aspects of data collection during 2008. First, during 2009 all nests were observed by a snorkeler, whereas during 2008 some nests were observed from the boat and some by a snorkeler. Difficulties in identifying failed nests from the boat during 2008 as well as unforeseen time periods during which some nests were not monitored due to inclement weather during 2008 likely introduced substantial uncertainty into determination of nest fate that year. In addition, it was more difficult for crews to distinguish eggs from larvae when viewing nests from the boat during 2008. This may have affected how often the different stages were interchanged erroneously, thereby affecting the survival probability estimates of each stage for 2008. Evidence of the improvement in identification of the larval stage during 2009 was present in the data, given that only 22% of pre-fry observations were of larvae during 2008, while this number increased to 35% during 2009. Overall, error was much reduced for 2009, likely due to an increase of snorkeling efforts and crew experience that enabled more consistent identification of stages and of failed nests. The increased dead recapture probability for 2009 (0.84) relative to 2008 (ranging 0.54-0.58 among lakes) further demonstrated enhanced data reliability during

2009 relative to 2008 (something that could not have been quantified without our approach to Program MARK analysis; see implications below).

In addition to procedural differences between years, there were also more nests during 2009 (particularly in Lake Chemung), which increased the sample size overall and may have contributed to a reduction of the error associated with survival estimates for 2009 as well. Because we used model averaging to estimate survival probabilities, the amount of uncertainty associated with each model also affected nest survival probabilities and their confidence intervals. Due to the wide confidence intervals of 2008's nest survival probability estimates as well as the lack of strong effects (as evidenced by parameter estimates for 2008 top models having confidence intervals bounding 0), we focus below on the results of 2009's modeling. We discuss 2008 model results only when any contrast from 2009's analysis cannot be clearly explained by the procedural concerns discussed above.

In the interest of being thorough, here we first note one statistically-discernible difference between the years and illustrate how it was likely influenced by differences in data collection between 2008 and 2009. Nest survival probabilities for 2008 were estimated to be higher than those of 2009 (confidence intervals did not overlap between the years) for: (a) nests at the egg stage during both seasons in Lake Chemung, and (b) nests at either the egg or larval stage during the harvest season in North Lake. A higher estimate of egg survival for 2008 may have been due to low proficiency by the crew to distinguish eggs from larvae during 2008, which may have resulted in inflated egg survival estimates if, as in 2009's models, larvae had higher survival probabilities. Therefore, overall nest survival probabilities may have been more similar between years than our modeling indicated.

Below, we first consider lake, season, and stage effects on nest survival probabilities and then consider nest attribute effects. We follow our discussion of factors explaining variation in nest survival probabilities with consideration of the biological relevance of actual survival probability estimates that we determined using model averaging. In so doing, we present a *post hoc* model for 2009 and consider additional insights that it suggests about among lake differences in nest survival probabilities. Finally, we consider the implications of our approach and findings to black bass biology and management.

*Modeling survival by lake, fishing season, and stage of development:* In terms of lake effects, we had predicted that nest survival probabilities would be lower in Chemung and Woodland, our high fishing pressure lakes, but our top models did not support this hypothesis for 2009 (or 2008). There was no effect of lake in 2009's highly ranked models, though the sample size may not have been large enough to estimate the number of parameters required to model differences among lakes, given our use of dummy variables to represent lakes. Richards (2005) has noted that AICc model rankings can change based on the number of samples available to estimate parameters.

Consistent with our predictions, fishing season was an important predictor of nest survival probability for both years. For 2009, the harvest season had lower survival probabilities than the CIR season for all lakes and stages of development (harvest survival probabilities were 13% lower for eggs and 30% lower for larvae). Fishing season was more highly ranked for 2008 than 2009 (AICc factor weights of 0.86 and 0.34 for 2008 and 2009, respectively), which corresponded to generally greater differences in mean temporal angling between seasons during 2008 than during 2009 (Figures 1 and 2). The generally higher levels of temporal angling during the harvest season (except for Woodland during 2009) indicated that the CIR season was utilized

less by anglers than the harvest season and may have driven differences in nest survival by season. Differences in mean amounts of angling between seasons may have been due to many reasons, including cold spring weather during the CIR season (deterring anglers) or an increase in angling opportunities (including competitive tournaments) during the harvest season (when both harvest and catch-and-delayed release was legal, in addition to CIR). Higher survival during the earlier part of the nesting season was an interesting result, given that we expected nest survival to increase later in the season as temperatures increased. Lower survival estimates in the harvest season seemed to indicate a negative effect of mean levels of fishing during that season on nest survival rates that outweighed any positive effect of warming water temperatures.

For 2009, we saw no indication of a significant lake by season interaction, possibly due to a lack of power to detect such an effect. Woodland, North, and Warner lakes had very few nests present during the harvest season to contribute to nest survival probability estimates. In contrast to 2009, the lake by season interaction received a high AICc factor weight for 2008, although the β confidence intervals for some of the parameters involved in that interaction frequently bounded 0, calling into question its overall relevance. The lake by season interaction for 2008 appears to have been driven by dynamics in North Lake which differed from the other lakes. Our modeling approach allowed us to determine if survival probabilities differed by lake, but we did not include all possible combinations of lake differences in our models. In other words, we used dummy variables to code for the lakes, but we did not explicitly model all possible combinations of 3 lakes being similar and 1 lake being different, 2 pairs of lakes being similar, etc. Our interpretation that the lake by season interaction was driven by North Lake reflects that the β confidence interval for North Lake did not bound 0 in the top models of 2008. Whereas parameter estimates for Chemung and Woodland lakes indicated higher nest survival

probabilities in these lakes during the CIR than during the harvest season, the opposite was the case for North (Table 21). The lake by season interaction suggested that there may have been other factors affecting nest survival other than angling given that angling was higher during the harvest than during the CIR season in all three lakes during 2008.

Stage of development was an important factor for 2009 (but not for 2008). For 2009, larvae had higher survival probabilities than eggs during both of the fishing seasons, with the difference being substantially greater during the early CIR season (larval survival probabilities were 35% higher than that of eggs during the CIR season and 19% higher during the harvest season). We expected that larval survival would be higher than eggs, but did not anticipate a differential effect in each season. Larval survival may have been higher than egg survival during the CIR season because of the combined effects of longer nest durations in the early season and increased parental care of older offspring. Parental care theory predicts that a bass will be less likely to prematurely abandon offspring in which he has already invested much time and energy (Trivers 1972; Sargent and Gross 1986). Because nest duration was longer during the CIR season when temperatures were lower, parental protection would be that much more important during that time. Alternatively, if bass defend larvae more aggressively than eggs, their defense behaviors would increase their vulnerability to angling, which was more prevalent in the harvest season. Angling may then have had a stronger negative effect on nest survival of larvae during the harvest season than during the CIR season because of the interaction between bass aggression and angling levels. Another hypothesis is that larvae may be inherently more durable than eggs, though there is some evidence to the contrary in that eggs have been observed to be more resilient under extreme temperature changes than larvae (Landsman et al. 2011).

*Variation in Nest Attributes and Modeling Implications:* Many of the nest attributes did not show sufficient variation to be modeled or had no impact on the models. Many of the guarding male attributes fell into this category; most nests were guarded by male bass with similarly low values for TAB, modified TAB, hook wounds, and sores and who were of sublegal size. Suski and Philipp (2004) reported TAB scores of at least 1 for most of the 90 largemouth bass in their study in southeastern Ontario, whereas most of the largemouth bass in our Michigan study lakes showed no aggressive responses to the model nest predator (76.5% had a TAB score of 0). Only 18% of bass in our study had TAB scores ranging from 1-3, whereas average responses ranged from 1-2.5 as reported by Suski and Philipp (2004). The difference may be related to different fishing regulations, given that legal bass angling began on the last Saturday in June in the Ontario lakes and therefore bass likely would not have been subject to the same fishing pressure during the nesting season as they would have been in our study lakes (i.e., selection against aggressive nest defense behaviors may not have been as strong in Ontario). Alternatively, the simulated bluegill or subtleties of the technique we used when testing for TAB scores may have differed from those used by Suski and Philipp (2004).

The relatively low number of nests with bass of legal size (30% for 2008 and 39% for 2009) in our study may have dampened the effect of fishing season in modeling because anglers had to release undersize bass immediately in both seasons. We chose to model a legal size categorical variable in lieu of bass length to address the differential effect of the fishing season on bass above 14 inches, the legal size limit of largemouth bass in Michigan. We expected the harvest season to have a more detrimental effect on nest survival because a bass could have been permanently (or for an extended period of time, in the case of catch-and-delayed release) removed from the nest, at which point nest predators could have consumed eggs. For example,

Ridgway (1988) documented complete loss of eggs at nests from which the bass was removed for 24 hours. The legal size variable was not very highly ranked in the modeling as compared to other variables, which indicated that the bass's size and corresponding differences in treatment received while angling did not have much of an effect on nest survival probabilities. Though fishing season did have an effect on nest survival probabilities (as discussed later), the effect did not stem from a differential effect on legal size bass.

Few of the nest attributes for which substantial variation occurred and which we included in our modeling analysis had discernible effects on nest survival. For 2008, the confidence intervals of every β associated with a nest attribute bounded 0, which indicated a lack of a relationship with nest survival probabilities. However, two nest attributes stood out as predictors of nest survival for 2009; they were temporal angling and percent plant cover.

Temporal angling was one of the most important predictors of all nest attributes and main effects in 2009's modeling. It was present in the highest nine ranking models, more than any other variable, and the highest ranked model without temporal angling had a ΔAICc of 86.05 from the top model. Additionally, none of 2009's models had β confidence intervals for temporal angling that bounded 0 and the direction of its effect was consistent. The only other variable with similar importance was the live recapture (p) parameter for Woodland.

Though temporal angling was a very important variable, its effect may have been due to a spurious correlation rather than to an actual effect of fishing. Temporal angling had a very strong positive effect on nest survival probability, which is contrary to previous studies (Ridgway 1988; Kieffer et al. 1995; Cooke et al. 2000; Steinhart et al. 2004) and our expectations. The positive effect in our models may have been related to a temporal trend within seasons because temporal angling increased throughout the CIR season and then decreased

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during the harvest season. We controlled for differences in angling between seasons as well as among lakes by group-mean centering by lake-season, which aided our interpretation of main effects versus nest level attributes. Though we centered by lake-season, trends in temporal angling within a lake-season remained in our analysis of it as a nest attribute. Temporal angling peaked at the middle of the nesting season in most lakes, around Memorial Day weekend. To gain insight into factors underlying the positive effect of temporal angling on nest survival, we explored the relationship between temporal angling and the start date of nests in each lake and season. The correlations between temporal angling and nest start date were not significant in all cases, but there were significant correlations for both of Chemung's fishing seasons, with temporal angling increasing with nest start date during the CIR season ($r[57] = 0.540$, $p < 0.001$) and decreasing with nest start date during the harvest season ($r[21] = -0.877$, $p < 0.001$; Figure 5). Chemung had the highest number of nests contributing to the dataset of any of the lakes, so a significant trend for the nests in that lake may have been the driving force behind the importance of the temporal angling variable. More specifically, we hypothesize that the trend in temporal angling in Lake Chemung may have combined with low nest survival at the beginning and end of the nesting season and high survival mid-season to result in a spurious correlation between lake-season mean centered temporal angling and nest survival.

We did not have sufficient data to model survival at a finer temporal scale than at the season level, so this hypothesis could not be confirmed. However, plotting temporal angling and nest success by nest start date lent some support to that explanation (Figure 5). There appeared to be a greater proportion of failed nests that started near the beginning or end of the nesting season. Nest successes and failures were both common mid-nesting season (near Memorial Day weekend), though successful nests appeared slightly more prevalent during that time. We

hypothesize that if this peak time period for nest survival occurred, it may have corresponded to a balance between warming temperatures during May through June increasing nest development rates (leading to shorter stage durations and higher survival) and higher levels both of angling and nest predator abundance in the harvest season (leading to lower nest survival probabilities for that season). However, nest predator abundance in our 2009 traps was greater in the harvest than CIR seasons only in North Lake ($t[13] = -2.87$, $p = 0.013$).
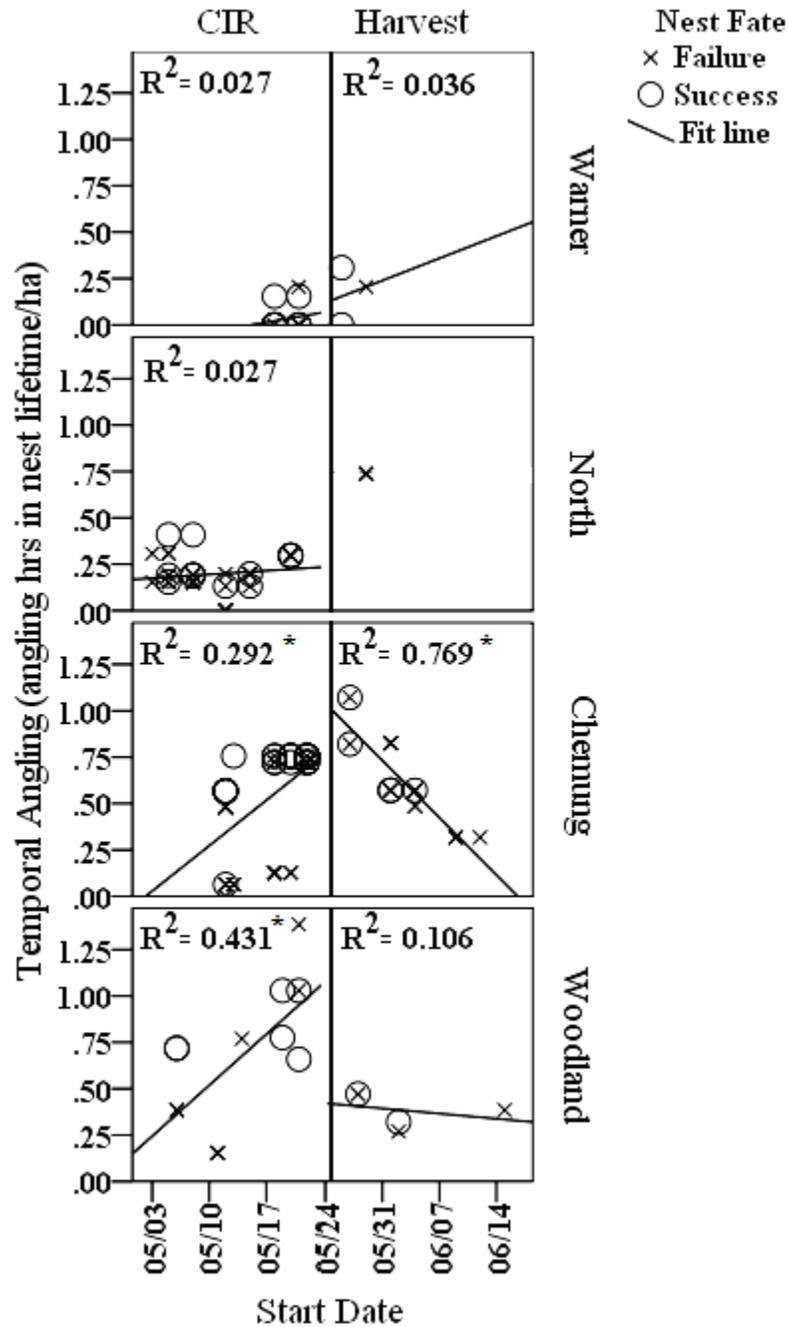
Figure 5: Correlations between temporal angling and nest start date for 2009. Individual data points represent nests and whether those nests ultimately succeeded (produced fry) or failed is indicated by an X or an open circle. The vertical line at May 25th shows when the CIR season ended and the harvest season began. The $R^2$ for each correlation is in the upper left corner of each box and significant correlations are marked with an asterisk. A correlation could not be calculated for North Lake's harvest season because values of temporal angling were constant and all nests began on the same date in that season.

Though temporal angling did not have the effect that we anticipated, percent plant cover had the expected negative effect on nest survival probabilities. Percent plant cover was not consistently important in every model (its β confidence interval almost always bounded 0), but it had a strong negative effect in the top model of 2009, which had 99.9% of the AICc weight. The negative effect of percent plant cover was consistent with another study that showed a negative effect of plant cover on the percent of smallmouth bass nests observed to be successful (Wills et al. 2004). Plant cover may have negatively impacted nests by serving as a refuge for nest predators and allowing them to predate on bass offspring more easily. Indeed, in 2009, percent plant cover and nest predator abundance covaried positively (0.26). Additionally, given the negative covariation between percent cover and substrate, low nest survival probabilities at high percent cover may correspond to poorer conditions for offspring associated with silty substrate.

*Post hoc modeling to explore lake differences and fishing effects during 2009:* Overall, the effects of season and stage on nest survival probabilities that our Program MARK analysis revealed made biological sense. In addition, the effect of fishing season in our analysis was consistent with the hypothesis that spring angling can influence nest survival, given that nest survival probabilities were lower during the harvest than the CIR season. Because water temperatures gradually warmed as fishing seasons changed, the effects of these two variables were potentially confounded. However, we would have expected nest survival probabilities to increase with warming temperatures because offspring development times would be inversely correlated with temperature. Therefore, lower nest survival probabilities during the warmer harvest season argues against development time as the driving mechanism. Warmer temperatures during the harvest season likely also corresponded to higher activity levels of and consumption rates by nest predators. Although we cannot completely distinguish the effects of

angling from the effects of nest predators on nest survival probabilities, we noted that nest predator abundances did not differ between seasons in three of our lakes. Only in North Lake were nest predators more prevalent in our traps during the harvest season of 2009. This implicates spring fishing as having a negative effect on nest survival probabilities, given higher observed angling pressure during the harvest than CIR season. However, seasonal estimates of angling varied more among lakes than between seasons, begging the question, 'If spring fishing is an important driver of nest survival probabilities, then why did we not detect lake differences in our 2009 modeling?'.

To address this question, we performed a *post hoc* analysis by constructing a model that included the lake-season means of temporal angling as a variable additional to the other parameters of our top-ranked model for 2009. This *post hoc* model was a substantial improvement over our previous top model ($\Delta$AICc of 24.13). Though this *post hoc* model ranked much higher than our previous top model, results of the two models were consistent. Specifically, survival probabilities for both larvae and the CIR season within a lake were consistently higher than those for eggs and the harvest season (Figure 6). Yet in contrast to our previous results for 2009, differences in survival among lakes (as expressed by their relationship to lake-season angling mean values) also appeared in the *post hoc* model. We hypothesize that the difference between our *a priori* top model and the *post hoc* model results stems from the difference in our approach to modeling lake differences between the two models. Modeling lake-season means of temporal angling in our *post hoc* model used only one parameter to express lake differences whereas dummy variable coding in our original modeling exercise used three parameters. Therefore, we believe that there were likely differences in survival probability

among lakes during both years that we could not detect previously and that these differences can be explained, at least in part, by lake-season mean differences in temporal angling.

Our *post hoc* model suggests that lake-season means of temporal angling are an important predictor of nest survival probabilities in our study. Surprisingly however, survival probabilities for both eggs and larvae in the CIR season increased from our lowest fishing pressure lake to our highest fishing pressure lake based on the *post hoc* model (Figure 6), whereas all lakes had similarly low survival probabilities during the harvest season (confidence intervals overlapped). We suggest that these *post hoc* findings present an interesting hypothesis to be tested by subsequent research. We hypothesize that among-lake differences in nest survival probabilities during the CIR season are reflective, in large part, of inherent differences among lakes in the productive capacity of their bass populations. A positive relationship between nest survival probabilities during the CIR season and general fishing pressure levels could reflect that bass anglers spend more time fishing in lakes with more productive bass populations. The seasonal difference in nest survival probabilities within lakes (higher survival during the CIR season) could reflect negative effects of intensified fishing hours and/or practices during the harvest season (see Chapter 2 for linkages between spring reproduction and recruitment, and implications of these results).

To more fully explore the relationship between our angling metric and nest survival probabilities, we plotted 5-day survival probabilities against the temporal angling lake-season means for each lake, season, and stage of development (Figure 7). Nest survival probabilities for the CIR season increased in lakes in order from low to high fishing pressure, consistent with the hypothesis that anglers invest more time in lakes with more productive bass populations. However, Woodland and North lakes exchanged ranks during the harvest season because angling

increased more than expected during that season in North Lake, but decreased in Woodland. Despite a decrease in angling during the 2009 Woodland harvest season, survival probabilities decreased for that season. This suggested that there were additional factors affecting seasonal variation in nest survival apart from lake-season mean levels of temporal angling. Evidence to support this claim was present in the *post hoc* model because, although lake-season means of temporal angling explained much of the seasonal variation, the $\beta$ representing the CIR season did not bound 0 in that model; rather, the CIR $\beta$ explained remaining variation in survival probabilities between seasons for which differences in temporal angling could not account.
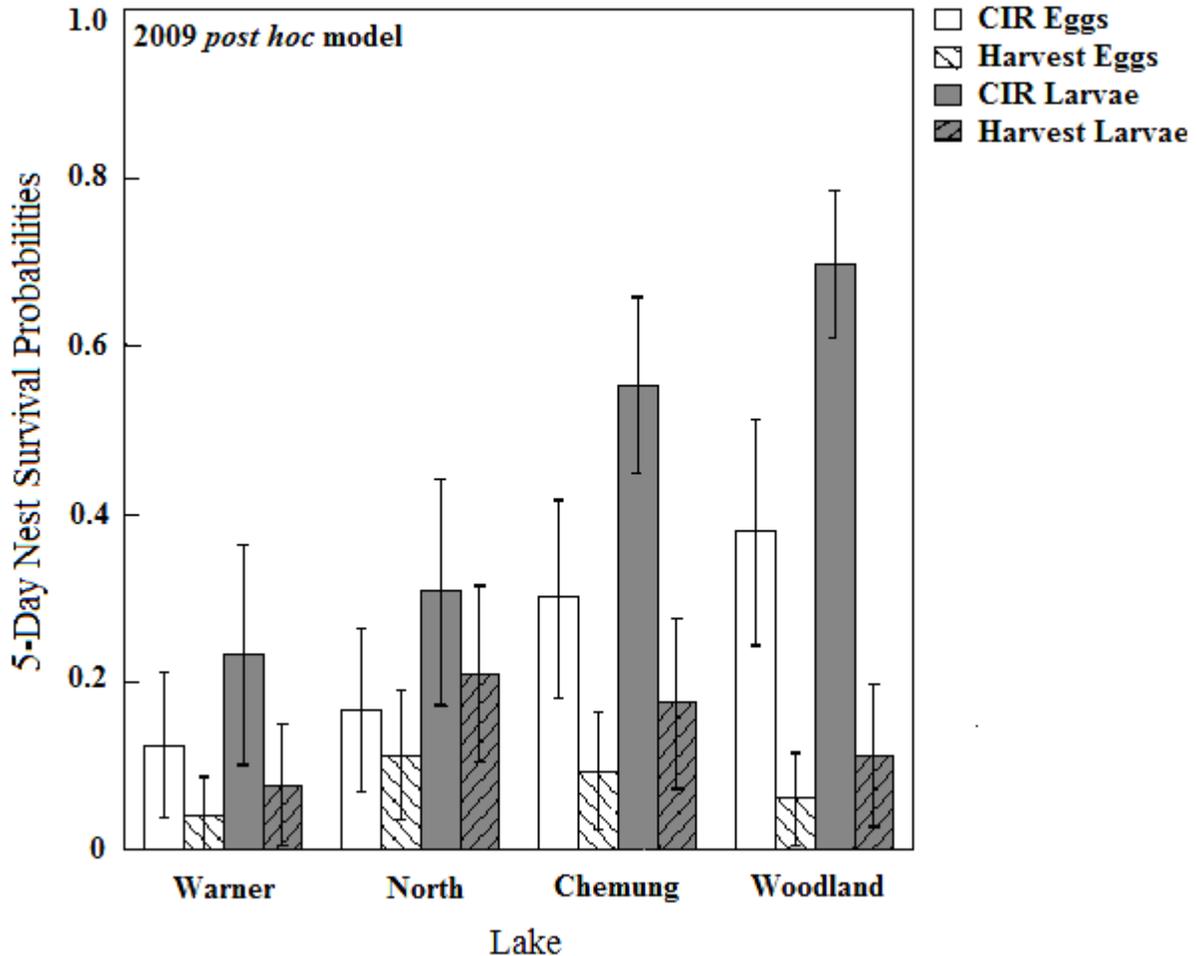


Figure 6: Five-day nest survival probabilities by lake, season, and stage of development for 2009's *post hoc* model. Lakes are in order of low to high fishing pressure. Error bars represent +/- two standard errors.
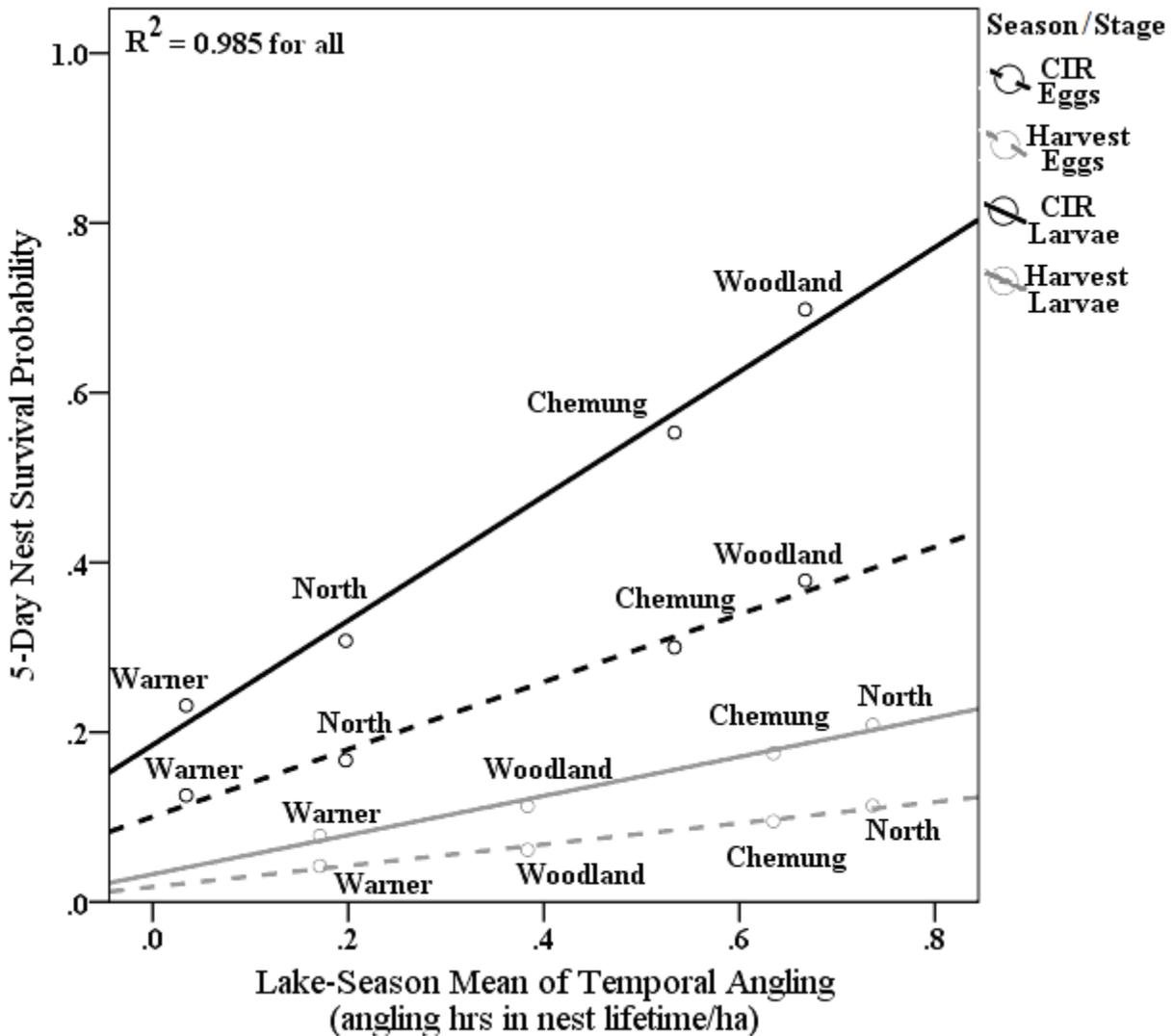
Figure 7: Correlations between 5-day nest survival probabilities from the *post hoc* model and lake-season means of temporal angling. This figure demonstrates that much of the variation in nest survival probabilities for 2009 could be explained by lake-season means of temporal angling. The $R^2$ for each correlation was the same. The CIR season is represented by black coloration and the egg stage is represented by dashes.

*Comparing our survival probabilities by to other systems:* Upon completion of all *a priori* phases of modeling for 2009, one model was clearly the best at predicting nest survival because it had 99.9% of the AICc weight. This model included season, stage, temporal angling, percent plant cover, and a separate live recapture (p) probability for Woodland and had discernible differences among survival parameter estimates due to reduced model uncertainty and β values with confidence intervals that did not bound 0. The *post hoc* model included all of the variables

from the top *a priori* model in addition to the temporal angling lake-season mean estimates. When the *post hoc* model was compared to all previous models, it garnered 99.9% of the AICc weight, had β values with confidence intervals that did not bound 0, and had discernible (and biologically relevant) differences in survival parameter estimates among lakes, seasons, and stages. Probabilities of surviving five days in our study lakes during 2009 that resulted from these models varied among seasons and stages (and lakes, for the *post hoc* model) and were relatively low, when compared to the literature. From the top models (*a priori* top model results are first and *post hoc* results, which differ among lakes, are in parentheses), the probability of eggs surviving five days was estimated to be 27% (13%-38% across lakes) in the CIR season and 14% (6-11%) in the harvest season. The probability of larvae surviving the same length of time was higher, though only significantly so during the CIR season for the *a priori* top model. Survival probabilities were estimated to be 62% (23-70%) for CIR larvae and 33% (8-21%) for harvest larvae.

These estimates of survival were much lower than those observed in other studies that have used Program MARK to estimate nest survival (but without distinguishing egg and larval stages). For example, the 5-day survival probability estimates reported by Steinhart et al. (2005b) for nests in Lake Erie were 49.8-62% and those reported by Suski and Ridgway (2007) in Lake Opeongo in Ontario, Canada were higher yet, at 81.5%. Only our estimates of CIR larval survival were roughly similar to those other studies. However, both of those studies focused on smallmouth bass and neither study separated survival by stage of development or used model averaging. In comparison to their estimates, the survival probabilities of largemouth bass nests in Michigan's inland lakes seemed much lower, suggesting that nests in these lakes may have been subjected to additional factors that decreased their survival probability. One such factor

could have been fishing.  Angling occurred during all of the nesting season in Lake Erie and in the latter half of the nesting season in Lake Opeongo, but sufficient data were not provided to compare existing amounts of fishing between those studies and ours and their relationship to nest survival probabilities.  Comparing these metrics is a promising area of future research to examine reproductive dynamics across a broad range of environmental and angling conditions.

*Links between nest survival and nest success:* Although a few researchers have used Program MARK to estimate nest survival probabilities (Steinhart et al. 2005b; Suski and Ridgway 2007), most studies of black bass nesting report the percent of nests observed to produce fry, though the method of calculating this metric may vary among studies (hereafter referred to as nest success; see Steinhart et al. 2005b for summary table).  While we would generally expect nest survival probabilities and nest success measures to be positively correlated, few studies (except Steinhart et al. 2005b and Suski and Ridgway 2007, each in part of one large lake) have used both analytical methods.  Therefore, our study provides a unique opportunity to compare these two metrics of bass population reproductive success.  Surprisingly, we found many inconsistencies between our Program MARK nest survival probabilities and our observed nest success rates. First, low estimates of nest success during 2008 did not correspond to low estimates of nest survival probabilities for that year.  Additionally, differences in nest success among lakes for 2009 did not consistently correspond to relative differences among lakes in nest survival probabilities.  For example, there were no among-lake differences in *a priori* model results and differences resulting from *post hoc* model results did not correspond perfectly to differences in success rate.  Specifically, Warner Lake had our highest estimate of successful nests at 72%, but relatively low survival probabilities.  There was also a large increase in percent success for Woodland Lake for 2009 as compared to 2008, but Program MARK survival probabilities for

Woodland were not substantially higher during 2009 than for 2008 except for CIR larvae. Additionally, the increase in percent success in Lake Chemung between years does not correspond to an increase in nest survival during 2009 because survival was actually higher for Chemung's eggs during each fishing season of 2008. Finally, survival in the harvest season was approximately 40-58% higher (the difference was even more pronounced using *post hoc* model results) for North Lake during 2008 than 2009, but the years were quite consistent in terms of observed percent success. These findings indicate that the relationship between nest survival and nest success is more complex than anticipated and that caution should be exercised when combining findings from the two approaches. Nest success rates as they are traditionally measured ignore the substantive differences in nest dynamics related to offspring stage and season. Also, nest success is not calculated with any measure of uncertainty and these factors may limit its use.

One factor underlying the observed discrepancies between approaches may be the timing of nests relative to modeled periods of high or low probabilities of survival. For example, the timing of nesting and offspring development varied in each lake relative to fishing season (see Appendix F for the number of nests observed at each stage by date). The number of nests that occurred in each season as well as the timing of the transition from the egg to the larval stage relative to fishing seasons may have affected percent success given that survival probabilities varied by season and stage during 2009. Nest success rate should be a function of nest survival probabilities, weighted by the number of nests to which survival probabilities for a given lake, season, and stage apply. For example, if most nests with eggs occurred in the harvest season, the majority of nests would have experienced higher levels of fishing and had lower survival probabilities, which may be of concern. However, this was not the predominant pattern in our

data. For most lakes and years, nesting peaked prior to the harvest season (though during 2008, North's nesting was fairly distributed over time and most nests occurred in the harvest season in Woodland). Therefore, nests often occurred when survival probabilities were highest, likely resulting in higher levels of nest success than would have been observed had nesting been more evenly distributed over time.

*Implications*

*Future work:* In addition to fisheries management concerns (discussed below), this research has implications for those who study bass reproduction. Modeling results clearly showed that stage of development can affect nest survival probabilities because it was a strong effect for 2009, when the ability to observe larvae improved. Previous studies that have used Program MARK to estimate survival of bass nests (Steinhart et al. 2005b; Suski and Ridgway 2007) have not estimated survival separately for each stage of development, despite evidence from previous studies suggesting eggs and larvae may not be equally likely to survive due to stage-specific guarding behaviors by bass or resilience to environmental fluctuations (Colgan and Brown 1988; Ridgway 1988; Suski et al. 2003; Landsman et al. 2011). Differences between egg and larval five-day survival probabilities were 35% in the CIR season and 19% in the harvest season. That is a substantial difference in survival probabilities between stages, especially given that the egg and larval stages often lasted longer than five days and survival probability decreased when a longer period of time was involved. Future research should incorporate differences in nest survival by stage of development in modeling to improve survival probability estimation.

Previous work of this nature also has not incorporated estimation of detection probabilities into models. An assumption of the nest survival model function in Program MARK is that detecting nests is a certainty, i.e., that live recapture (p) and dead recovery (r) are equal to 1. Our

data showed that probabilities of p and r did not equal 1 in our study. Probabilities of live recapture ranged from 0.21 to 0.38 for both years, while dead recapture probabilities were approximately 0.54-0.58 during 2008 and 0.84 during 2009, depending on the lake. The fact that probabilities varied among years and even among lakes within a year suggests that nest detection is not always certain and that other studies should consider this when estimating nest survival probabilities.

Another suggestion that we can make for those who model bass nest survival is to incorporate model uncertainty. Neither Steinhart et al. (2005b) nor Suski and Ridgway (2007) used model averaging, though their top models only received 62% and 57% of AICc weight, respectively. Model averaging corrects for model uncertainty by weighting parameter estimates by the AICc weight of each model and widening the confidence intervals of parameter estimates to take the uncertainty into account. Model averaging should be used when multiple models have similar AICc values and model uncertainty is present (Burnham and Anderson 2002).

*Fisheries management:* Because nest survival probabilities relate, but are not equivalent, to nest success and these numbers as well as overall numbers of nests vary among lakes and seasons, we questioned whether the number of nests in a lake, the percent success of those nests, or both affect the total number of successful nests in a lake (which is strongly related to fry production, see Chapter 2). To roughly estimate the interaction between density of nests in a lake and the percent success of nests, we used the maximum and minimum number of each metric observed (0.62 and 1.35 nests/ha and 10% and 72% success), multiplied them together in combination, and compared the relative contribution of each metric to the predicted density of successful nests. Because there was high variation in the density of nests observed in our lakes as well as the percent success of nests, both metrics were important determinants in the total

number of successful nests in a lake (0.97 successful nests/ha resulted from high nest density and a high success rate, as opposed to a range of 0.06-0.44 nests/ha when at least one metric was at its minimum value). This information may be important if one of the goals of management is to increase spring fry production, which was highly related to fall YOY bass abundance in these lakes during 2009 and possibly recruitment (Chapter 2). Managers may want to explore options that both increase the density of nests in a lake (perhaps by creating more spawning habitat) and increase nest survival probabilities (discussed below), if recruitment is known to be limiting in a system.

Modeling results indicated that the effect of the fishing season on nest survival was important, and that survival was generally higher during the CIR season, particularly for larvae. There are no other studies on largemouth bass nest survival with which we can compare our specific survival probability estimates, but we can say that the observed percent success values of nests in this study were comparable to those in other studies in other systems (which ranged from 21-96%), except for Woodland during 2008, which was quite low at 10% (summary in Steinhart et al. 2005b). We cannot say if opening the CIR season for angling resulted in a higher proportion of failed nests than occurred prior to 2006, when bass fishing was closed prior to the possession season, because we do not have data from previous years. There may have been significant bass fishing in the spring before 2006 despite the closed season given that Schneider et al. (1991) reported that 69% of bass anglers on southeastern Michigan lakes self-reported illegally targeting bass in the spring prior to their legal fishing season. It is difficult to evaluate the regulation change without pre-data, but we believe we can make some recommendations from our analysis of seven lake-years of data.

We suggest that the early CIR season can remain because observed percent nest success values in our study lakes were comparable to other studies and the CIR season had higher levels of nest survival than the harvest season. However, managers should remain cautious. Timing of nesting may vary by year and the majority of nests may not occur prior to the harvest season in all cases (e.g., it did not in North and Woodland Lakes during 2008). Additionally, survival probabilities were at times very low (estimates from the 2009 top models were as low as 14% and 4% for eggs during the harvest season from *a priori* and *post hoc* models, respectively). Other studies have presented strong evidence against spring fishing due to increased stress to the parental male bass, reduced energy stores for parental care, and brood loss through predation (Ridgway 1988; Kieffer et al. 1995; Steinhart et al. 2004; Thompson et al. 2008; Cooke et al. 2000) and suggest minimizing fishing while bass are nesting (Ridgway and Shuter 1997; Kubacki et al. 2002; Suski et al. 2003).

A prolonged CIR season, which was associated with demonstrably higher levels of survival, may be a compromise between allowing angling and bass nest vulnerability if angler turnout was lower due to the type of fishing season. The CIR season was different from the harvest season in terms of both the amount of fishing that occurred and the options for treatment of bass once they were caught. However, we did not find evidence that the type of fishing (immediate release versus delayed release or harvest) that occurred during each season had an impact on nest survival because there were not differential effects on nest survival due to legal size. Our data suggest that the amount of fishing that occurred may be a very important predictor of bass nest survival. We do not know exactly why levels of angling were lower in the CIR season (lower temperatures, illegality of bass harvesting, or another reason), so this may be an opportunity to survey anglers to determine the answer. We also did not find evidence to suggest that lakes that

consistently draw the attention of anglers may soon have poor bass populations. The *post hoc* analysis from 2009 suggested that popular fishing lakes may fare better than those that have traditionally had lower amounts of angling. However, there may be a negative impact on bass in lakes should angling increase substantially during the CIR season or during years in which bass spawn at later dates. We recommend that monitoring of bass populations continue both in popular fishing lakes and those that are less commonly considered for fishing to determine the long-term effect of the CIR season.

**APPENDICES**

# APPENDIX A

## COMPLETE LISTS OF CANDIDATE MODELS USED IN PROGRAM MARK

Table 23: Complete list of the 48 Phase 1 candidate models used to model main effects of lake, fishing season, and stage of development in Program MARK for 2008. Tables 2 and 3 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| 2008 Main Effects Model List | |
|---|---|
| phi(.)p(.)Psi(.)r(.) | phi(Lake+Season+Stage)p(.)Psi(.)r(.) |
| phi(.)p(.)Psi(.)r(Woodland) | phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) |
| phi(.)p(Woodland)Psi(.)r(.) | phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) |
| phi(.)p(Woodland)Psi(.)r(Woodland) | phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake)p(.)Psi(.)r(.) | phi(Lake*Season*Stage)p(.)Psi(.)r(.) |
| phi(Lake)p(.)Psi(.)r(Woodland) | phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake)p(Woodland)Psi(.)r(.) | phi(Lake*Season*Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | phi(Lake*Season*Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season)p(.)Psi(.)r(.) | phi(Season)p(.)Psi(.)r(.) |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | phi(Season)p(.)Psi(.)r(Woodland) |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | phi(Season)p(Woodland)Psi(.)r(.) |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | phi(Season)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Stage)p(.)Psi(.)r(.) | phi(Stage)p(.)Psi(.)r(.) |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | phi(Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | phi(Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | phi(Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Season)p(.)Psi(.)r(.) | phi(Season*Stage)p(.)Psi(.)r(.) |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) | phi(Season*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | phi(Season*Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) | phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Stage)p(.)Psi(.)r(.) | phi(Season+Stage)p(.)Psi(.)r(.) |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) | phi(Season+Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | phi(Season+Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) | phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) |

Table 24: Complete list of the 45 Phase 1 candidate models used to model main effects of lake, fishing season, and stage of development in Program MARK for 2009. Tables 2 and 3 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery). Three fewer models were run for 2009 because only one variation of the lake*stage*season interaction models could numerically converge on survival probability estimates.

| 2009 Main Effects Model List | |
| --- | --- |
| phi(.)p(.)Psi(.)r(.) | phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(.)p(.)Psi(.)r(Woodland) | phi(Lake+Season+Stage)p(.)Psi(.)r(.) |
| phi(.)p(Woodland)Psi(.)r(.) | phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) |
| phi(.)p(Woodland)Psi(.)r(Woodland) | phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake)p(.)Psi(.)r(.) | phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake)p(.)Psi(.)r(Woodland) | phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake)p(Woodland)Psi(.)r(.) | phi(Season)p(.)Psi(.)r(.) |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | phi(Season)p(.)Psi(.)r(Woodland) |
| phi(Lake*Season)p(.)Psi(.)r(.) | phi(Season)p(Woodland)Psi(.)r(.) |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | phi(Season)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | phi(Stage)p(.)Psi(.)r(.) |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | phi(Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake*Stage)p(.)Psi(.)r(.) | phi(Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | phi(Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | phi(Season*Stage)p(.)Psi(.)r(.) |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | phi(Season*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake+Season)p(.)Psi(.)r(.) | phi(Season*Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) | phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | phi(Season+Stage)p(.)Psi(.)r(.) |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) | phi(Season+Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake+Stage)p(.)Psi(.)r(.) | phi(Season+Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) | phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | |

Table 25: Complete list of the 15 Phase 2 models used to model nest attributes with important main effects from Phase 1 in Program MARK for 2008. Tables 4 and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| 2008 Nest Attribute Model List |
|---|
| phi(Lake*Season+Stage+Cover)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Cover+Legal)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Cover+Legal*Season)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Cover+TAng)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Cover+Wind)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Legal)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Legal*Season)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+TAng)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+TAng+Legal)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+TAng+Legal*Season)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+TAng+Wind)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Wind)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Wind+Legal)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Wind+Legal*Season)p(Woodland)psi(.)r(Woodland) |
| phi(Lake*Season+Stage+Cover+Wind+TAng+Legal*Season)p(Woodland)psi(.)r(Woodland) |

Table 26: Complete list of the 18 Phase 2 models used to model nest attributes with important main effects from Phase 1 in Program MARK for 2009. Tables 4 and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery). The models including phi(Season+Stage+TAng+BScore), phi(Season+Stage+Wind+TAng), and phi(Season+Stage+Cover+Wind+TAng+BScore+Legal*Season) are not listed because they could not converge on parameter estimates and had to be deleted from the results.

| 2009 Nest Attribute Model List |
| --- |
| phi(Season+Stage+BScore)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+BScore+Legal)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+BScore+Legal*Season)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Cover)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Cover+BScore)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Cover+Legal)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Cover+Legal*Season)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Cover+TAng)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Cover+Wind)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Legal)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Legal*Season)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+TAng)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+TAng+Legal)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+TAng+Legal*Season)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Wind)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Wind+BScore)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Wind+Legal)p(Woodland)psi(.)r(.) |
| phi(Season+Stage+Wind+Legal*Season)p(Woodland)psi(.)r(.) |

Table 27: Complete list of the 99 models used to model important nest attributes (from Phase 2) with important main effects (Phase 1) to create a full model list for Phase 3 in Program MARK for 2008. This model list was used for model averaging. Tables 2, 3, 4, and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| 2008 Full Model List for Model Averaging |
| --- |
| phi(.)p(.)Psi(.)r(.) |
| phi(.)p(.)Psi(.)r(Woodland) |
| phi(.)p(Woodland)Psi(.)r(.) |
| phi(.)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake)p(.)Psi(.)r(.) |
| phi(Lake)p(.)Psi(.)r(Woodland) |
| phi(Lake)p(Woodland)Psi(.)r(.) |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season*Stage)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season*Stage+Cover)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Cover+Legal)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Cover+Legal*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Cover+TAng)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Cover+Wind)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Cover+Wind+TAng+Legal*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Legal)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Legal*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+TAng)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+TAng+Legal)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+TAng+Legal*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Wind)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Wind+Legal)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Wind+Legal*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season*Stage+Wind+TAng)p(.)Psi(.)r(.) |
| phi(Lake*Season+Cover)p(.)Psi(.)r(.) |
| phi(Lake*Season+Cover)p(.)Psi(.)r(Woodland) |
| phi(Lake*Season+Cover)p(Woodland)Psi(.)r(.) |
| phi(Lake*Season+Cover)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season+Cover+TAng)p(.)Psi(.)r(.) |

Table 27 (cont'd)

phi(Lake*Season+Cover+TAng)p(.)Psi(.)r(Woodland)
phi(Lake*Season+Cover+TAng)p(Woodland)Psi(.)r(.)
phi(Lake*Season+Cover+TAng)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Season+Cover+Wind)p(.)Psi(.)r(.)
phi(Lake*Season+Cover+Wind)p(.)Psi(.)r(Woodland)
phi(Lake*Season+Cover+Wind)p(Woodland)Psi(.)r(.)
phi(Lake*Season+Cover+Wind)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Season+Legal)p(.)Psi(.)r(.)
phi(Lake*Season+Legal)p(.)Psi(.)r(Woodland)
phi(Lake*Season+Legal)p(Woodland)Psi(.)r(.)
phi(Lake*Season+Legal)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Season+TAng)p(.)Psi(.)r(.)
phi(Lake*Season+TAng)p(.)Psi(.)r(Woodland)
phi(Lake*Season+TAng)p(Woodland)Psi(.)r(.)
phi(Lake*Season+TAng)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Season+Wind)p(.)Psi(.)r(.)
phi(Lake*Season+Wind)p(.)Psi(.)r(Woodland)
phi(Lake*Season+Wind)p(Woodland)Psi(.)r(.)
phi(Lake*Season+Wind)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Season+Wind+Legal)p(.)Psi(.)r(.)
phi(Lake*Season+Wind+Legal)p(.)Psi(.)r(Woodland)
phi(Lake*Season+Wind+Legal)p(Woodland)Psi(.)r(.)
phi(Lake*Season+Wind+Legal)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Season+Wind+TAng)p(.)Psi(.)r(.)
phi(Lake*Season+Wind+TAng)p(.)Psi(.)r(Woodland)
phi(Lake*Season+Wind+TAng)p(Woodland)Psi(.)r(.)
phi(Lake*Season+Wind+TAng)p(Woodland)Psi(.)r(Woodland)
phi(Lake*Stage)p(.)Psi(.)r(.)
phi(Lake*Stage)p(.)Psi(.)r(Woodland)
phi(Lake*Stage)p(Woodland)Psi(.)r(.)
phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland)
phi(Lake+Season)p(.)Psi(.)r(.)
phi(Lake+Season)p(.)Psi(.)r(Woodland)
phi(Lake+Season)p(Woodland)Psi(.)r(.)
phi(Lake+Season)p(Woodland)Psi(.)r(Woodland)
phi(Lake+Season+Stage)p(.)Psi(.)r(.)
phi(Lake+Season+Stage)p(.)psi(.)r(.)
phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland)
phi(Lake+Season+Stage)p(.)psi(.)r(Woodland)
phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.)
phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland)

Table 27 (cont'd)

     phi(Lake+Stage)p(.)Psi(.)r(.)
     phi(Lake+Stage)p(.)Psi(.)r(Woodland)
     phi(Lake+Stage)p(Woodland)Psi(.)r(.)
     phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland)
     phi(Season)p(.)Psi(.)r(.
     phi(Season)p(.)Psi(.)r(Woodland)
     phi(Season)p(Woodland)Psi(.)r(.
     phi(Season)p(Woodland)Psi(.)r(Woodland)
     phi(Season*Stage)p(.)Psi(.)r(.)
     phi(Season*Stage)p(.)psi(.)r(.)
     phi(Season*Stage)p(.)Psi(.)r(Woodland)
     phi(Season*Stage)p(.)psi(.)r(Woodland)
     phi(Season*Stage)p(Woodland)Psi(.)r(.)
     phi(Season*Stage)p(Woodland)Psi(.)r(Woodland)
     phi(Season+Stage)p(.)Psi(.)r(.)
     phi(Season+Stage)p(.)Psi(.)r(Woodland)
     phi(Season+Stage)p(Woodland)Psi(.)r(.)
     phi(Season+Stage)p(Woodland)Psi(.)r(Woodland)
     phi(Stage)p(.)Psi(.)r(.)
     phi(Stage)p(.)Psi(.)r(Woodland)
     phi(Stage)p(Woodland)Psi(.)r(.)
     phi(Stage)p(Woodland)Psi(.)r(Woodland)

Table 28: Complete list of the 68 models used to model important nest attributes (from Phase 2) with important main effects (Phase 1) to create a full model list for Phase 3 in Program MARK for 2009. This model list was used for model averaging. Tables 2, 3, 4, and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| 2009 Full Model List for Model Averaging |
|---|
| phi(.)p(.)Psi(.)r(.) |
| phi(.)p(.)Psi(.)r(Woodland) |
| phi(.)p(Woodland)Psi(.)r(.) |
| phi(.)p(Woodland)Psi(.)r(Woodland) |
| phi(Cover+TAng)p(Woodland)Psi(.)r(.) |
| phi(Cover+TAng)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake)p(.)Psi(.)r(.) |
| phi(Lake)p(.)Psi(.)r(Woodland) |
| phi(Lake)p(Woodland)Psi(.)r(.) |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season)p(.)Psi(.)r(.) |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake*Stage)p(.)Psi(.)r(.) |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Season)p(.)Psi(.)r(.) |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Season+Stage)p(.)Psi(.)r(.) |
| phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Lake+Stage)p(.)Psi(.)r(.) |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) |
| phi(Season)p(.)Psi(.)r(.) |
| phi(Season)p(.)Psi(.)r(Woodland) |
| phi(Season)p(Woodland)Psi(.)r(.) |
| phi(Season)p(Woodland)Psi(.)r(Woodland) |
| phi(Season*Stage)p(.)Psi(.)r(.) |

Table 28 (cont'd)

phi(Season*Stage)p(.)Psi(.)r(Woodland)
phi(Season*Stage)p(Woodland)Psi(.)r(.)
phi(Season*Stage)p(Woodland)Psi(.)r(Woodland)
phi(Season+Cover+TAng)p(Woodland)Psi(.)r(.)
phi(Season+Stage)p(.)Psi(.)r(.)
phi(Season+Stage)p(.)Psi(.)r(Woodland)
phi(Season+Stage)p(Woodland)Psi(.)r(.)
phi(Season+Stage)p(Woodland)Psi(.)r(Woodland)
phi(Season+Stage+BScore)p(Woodland)Psi(.)r(.)
phi(Season+Stage+BScore+Legal)p(Woodland)Psi(.)r(.)
phi(Season+Stage+BScore+Legal*Season)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Cover)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Cover+BScore)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Cover+Legal)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Cover+Legal*Season)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Cover+TAng)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Cover+Wind)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Legal)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Legal*Season)p(Woodland)Psi(.)r(.)
phi(Season+Stage+TAng)p(Woodland)Psi(.)r(.)
phi(Season+Stage+TAng+Legal)p(Woodland)Psi(.)r(.)
phi(Season+Stage+TAng+Legal*Season)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Wind)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Wind+BScore)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Wind+Legal)p(Woodland)Psi(.)r(.)
phi(Season+Stage+Wind+Legal*Season)p(Woodland)Psi(.)r(.)
phi(Stage)p(.)Psi(.)r(.)
phi(Stage)p(.)Psi(.)r(Woodland)
phi(Stage)p(Woodland)Psi(.)r(.)
phi(Stage)p(Woodland)Psi(.)r(Woodland)
phi(Stage+Cover+TAng)p(Woodland)Psi(.)r(.)
phi(Stage+Cover+TAng)p(Woodland)Psi(.)r(Woodland)

# APPENDIX B


# LAKE MAPS OF NEST LOCATIONS AND FATES
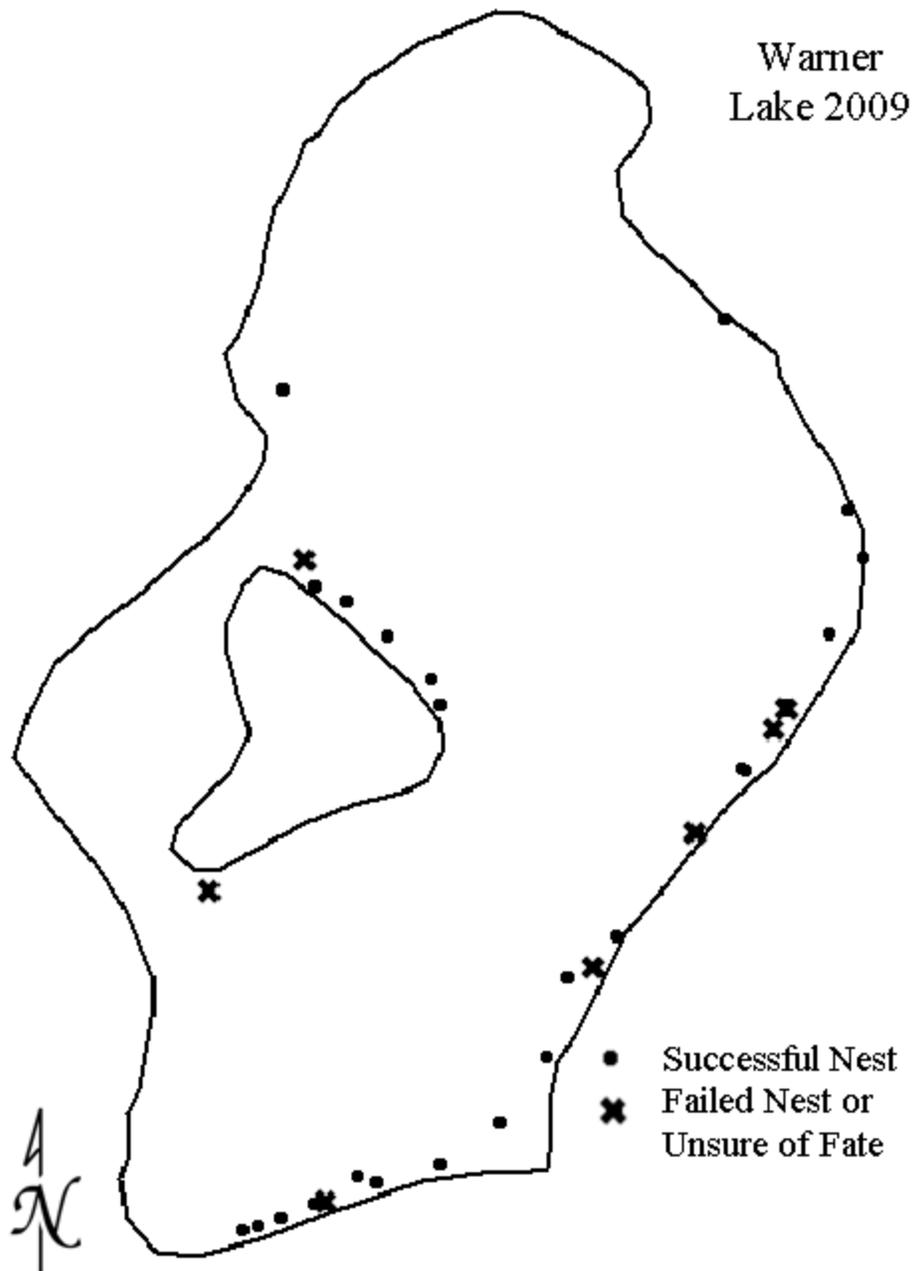
Figure 8: Distribution and fate of nests in Warner Lake, a low fishing pressure lake, for 2009. Failed nests are represented by an X while successful nests are denoted by a closed circle. Warner Lake was not monitored during 2008.
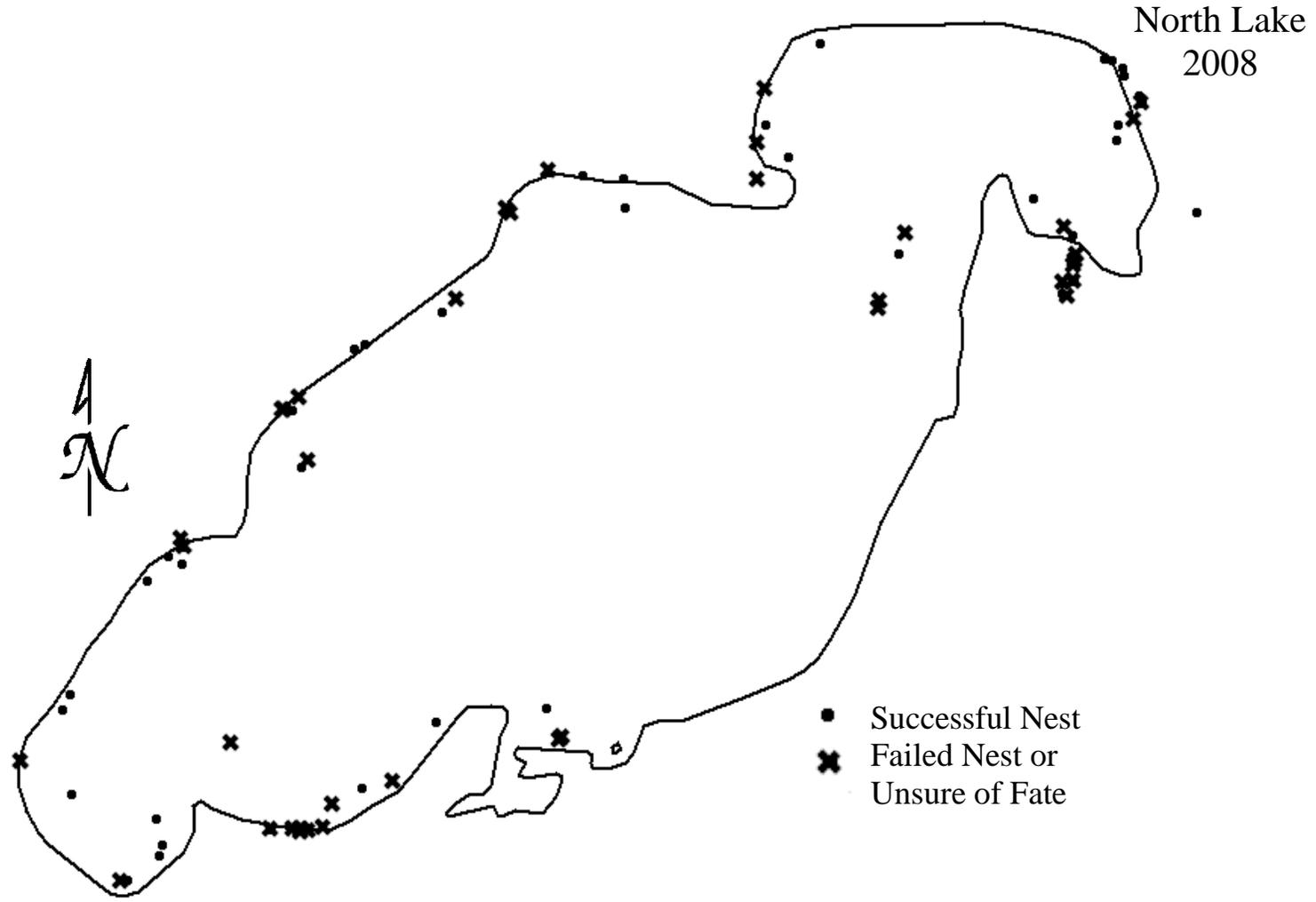
Figure 9: Distribution and fate of nests in North Lake, an intermediate fishing pressure lake, for 2008. Failed nests are represented by an X while successful nests are denoted by a closed circle. A small channel that contained nests (see northeastern section of lake) and a few other locations were not part of the lake polygon in GIS.
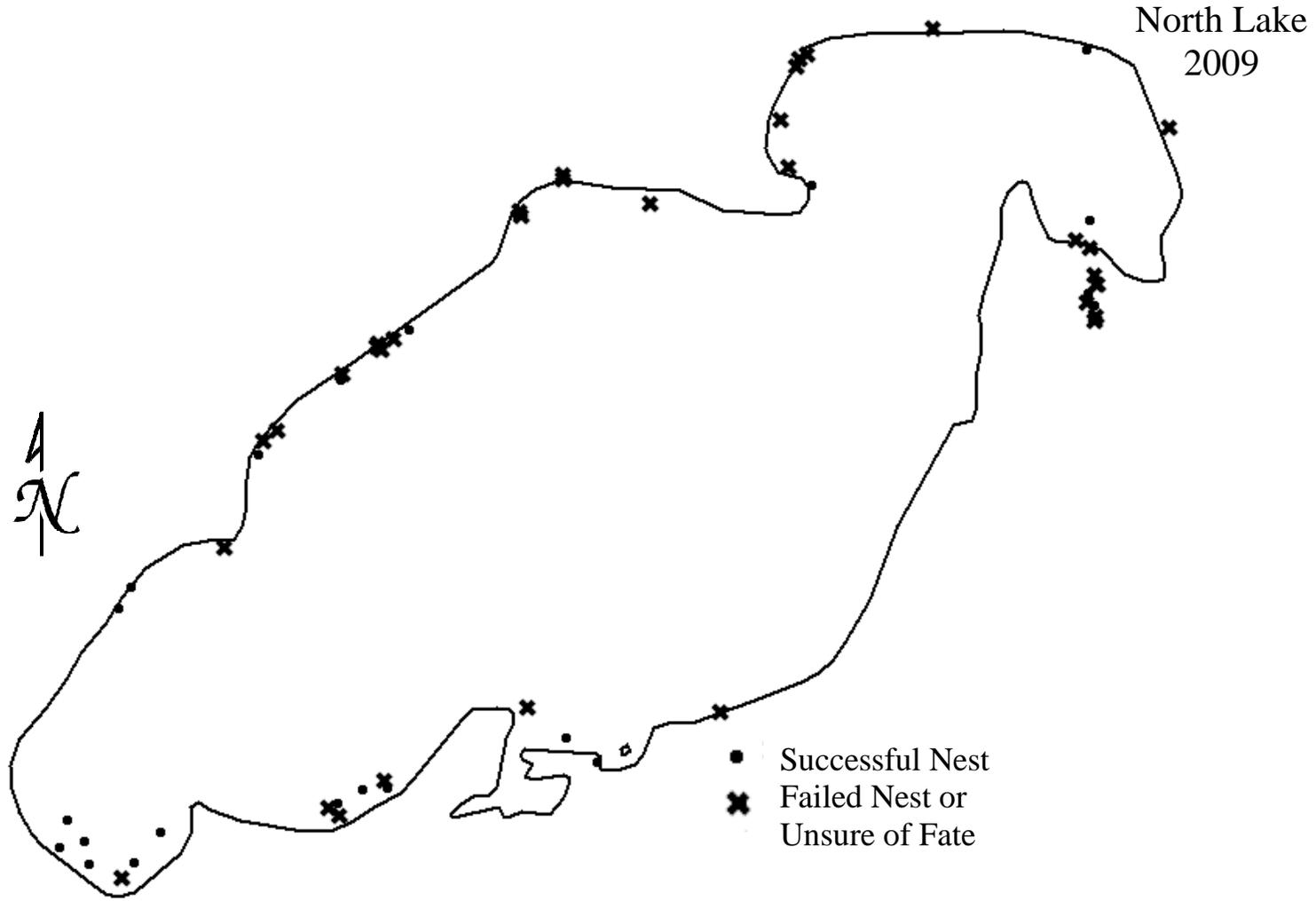
Figure 10: Distribution and fate of nests in North Lake, an intermediate fishing pressure lake, for 2009. Failed nests are represented by an X while successful nests are denoted by a closed circle. A small channel that contained nests (see northeastern section of lake) and a few other locations were not part of the lake polygon in GIS.
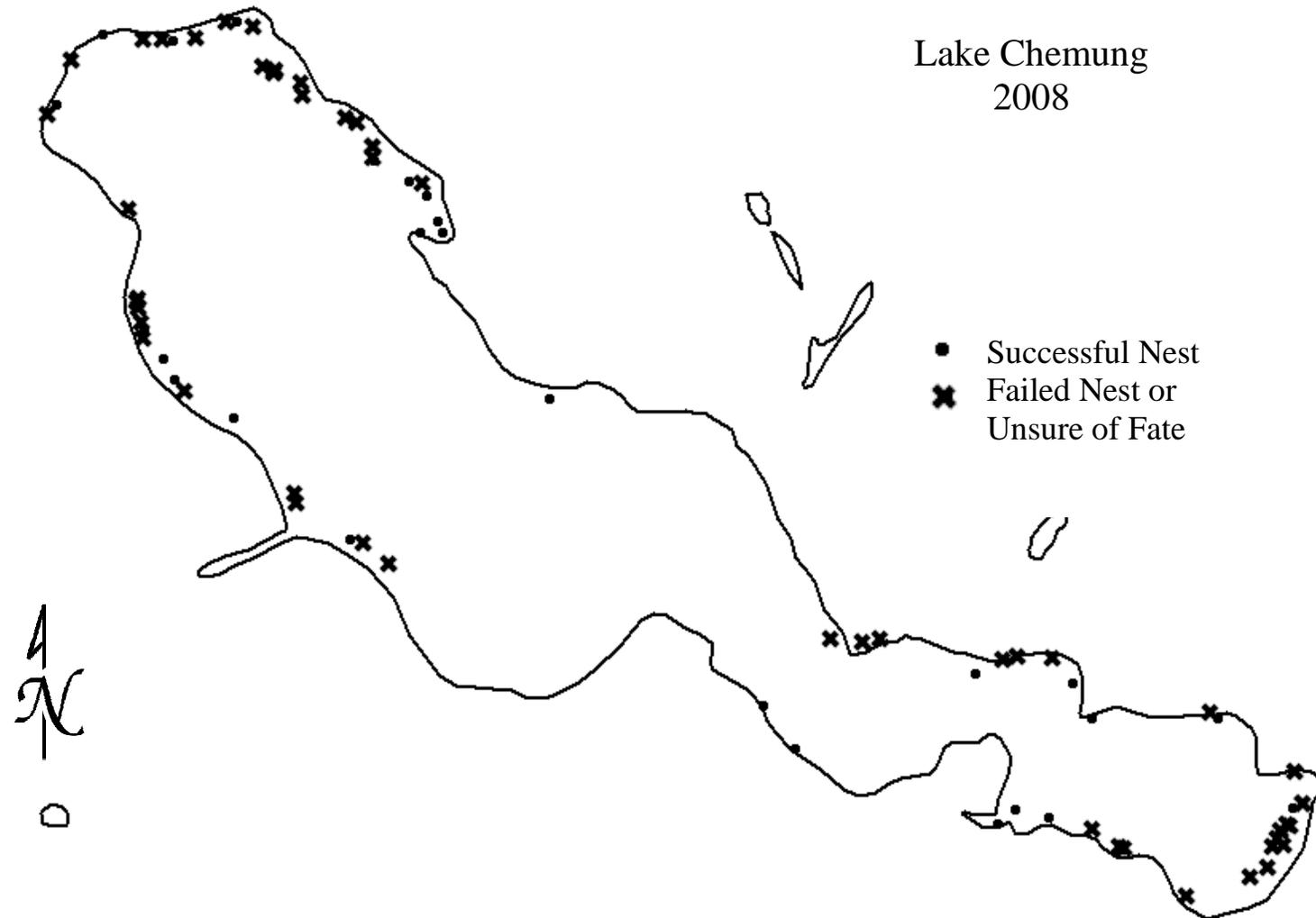
Figure 11: Distribution and fate of nests in Lake Chemung, a high fishing pressure lake, for 2008. Failed nests are represented by an X while successful nests are denoted by a closed circle.

Lake Chemung
2009

• Successful Nest
✖ Failed Nest or
Unsure of Fate
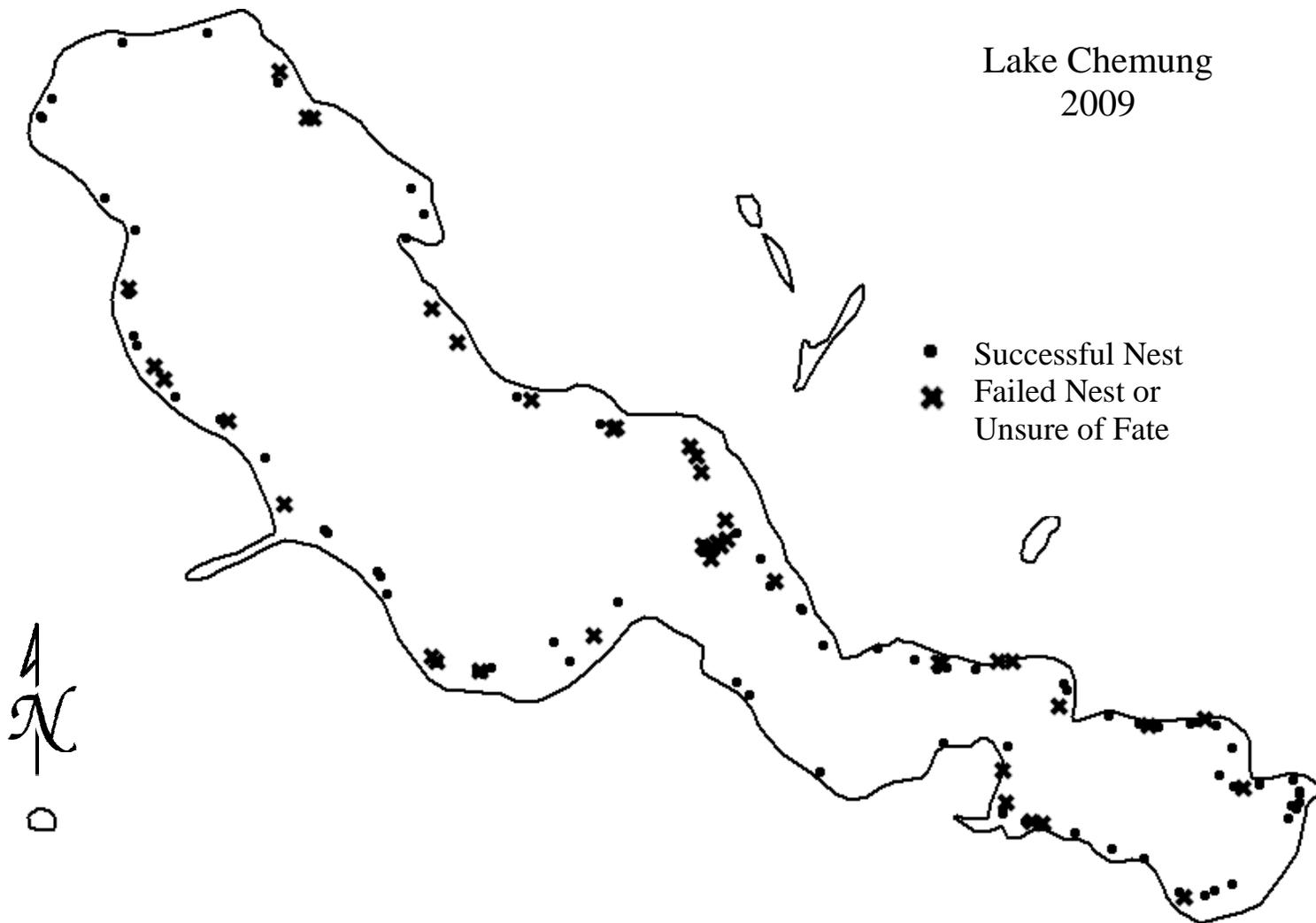
Figure 12: Distribution and fate of nests in Lake Chemung, a high fishing pressure lake, for 2009. Failed nests are represented by an X while successful nests are denoted by a closed circle.
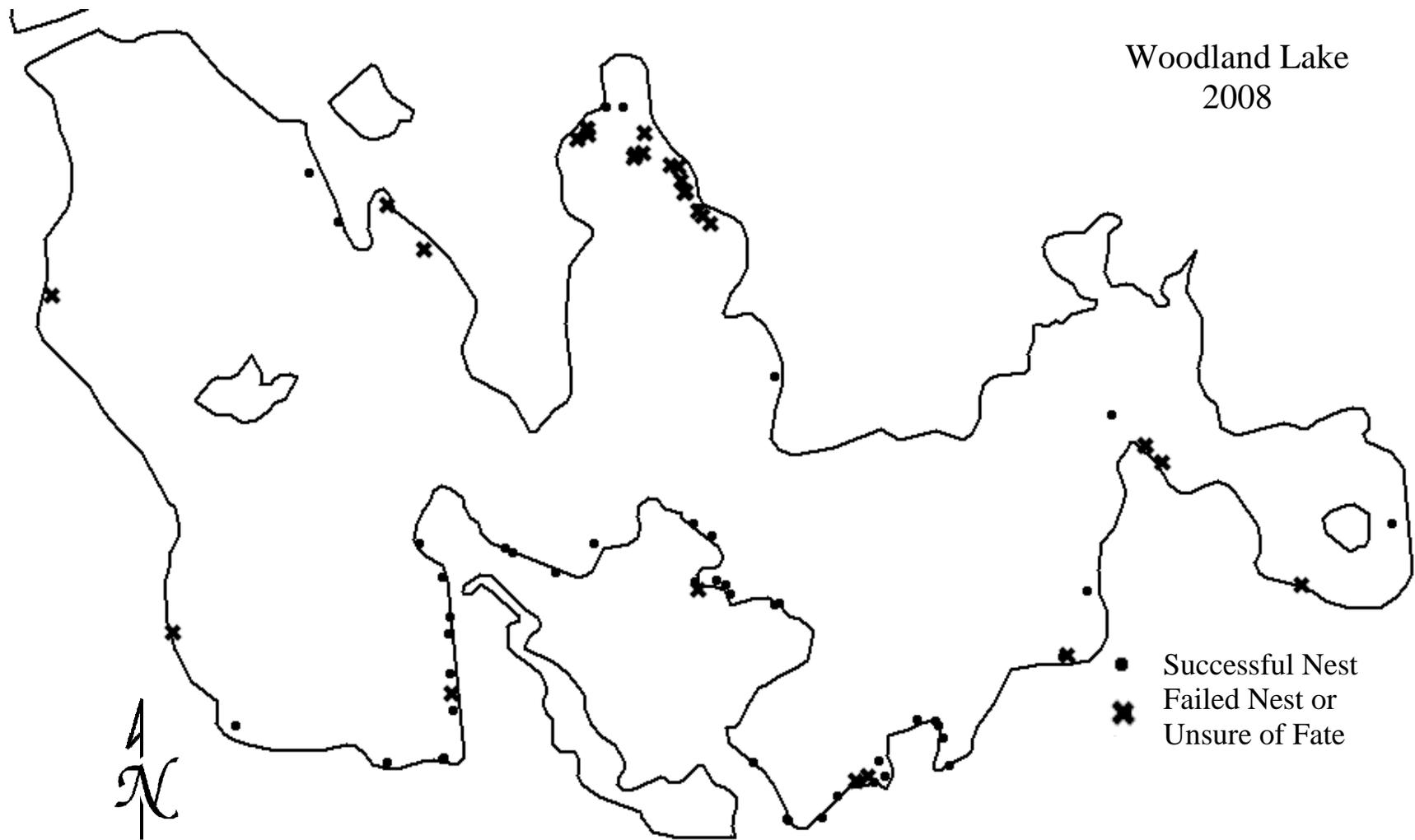
Figure 13: Nest distribution and fate in Woodland Lake, a high fishing pressure lake, for 2008. Failed nests are represented by an X while successful nests are denoted by a closed circle.
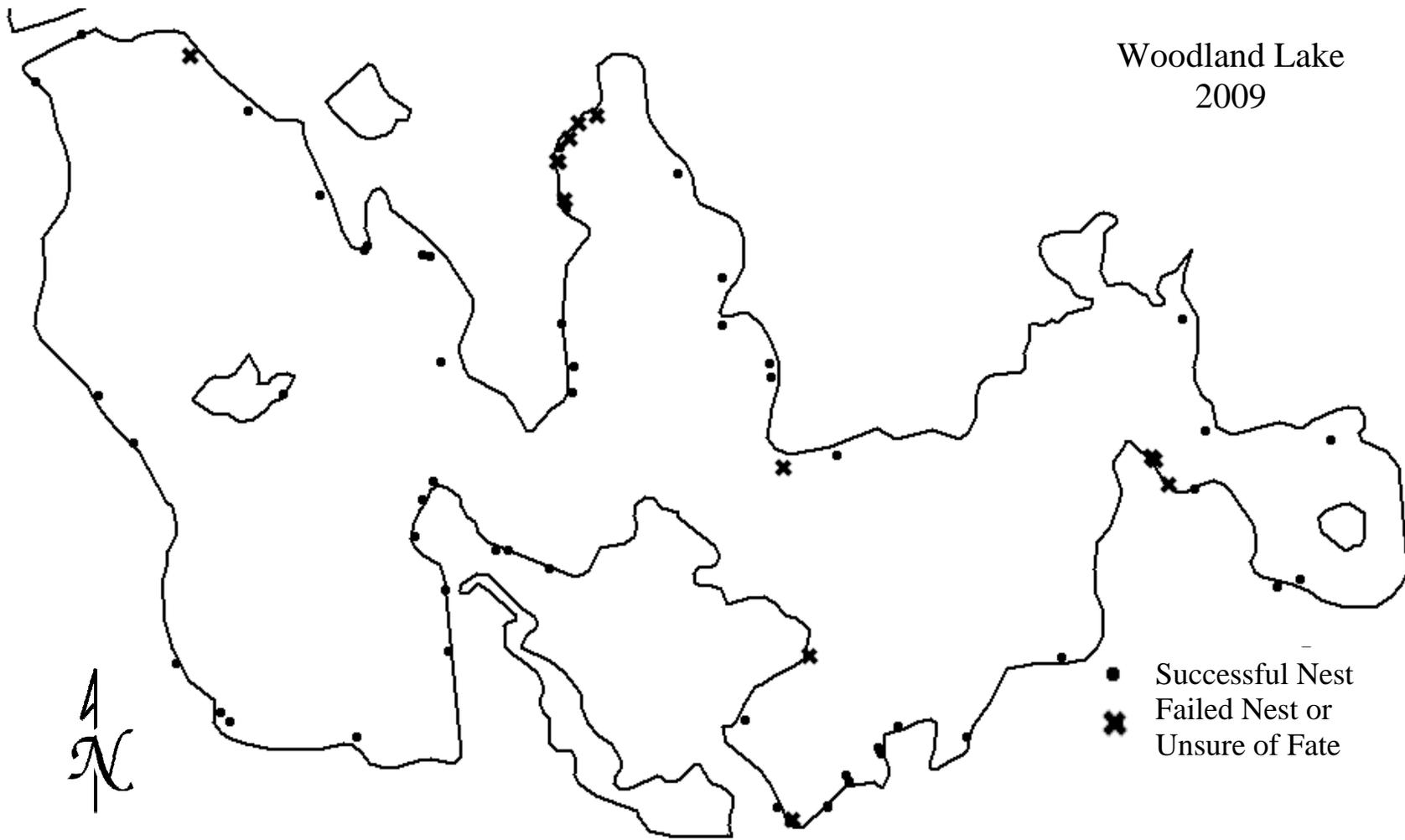
Figure 14: Nest distribution and fate in Woodland Lake, a high fishing pressure lake, for 2009. Failed nests are represented by an X while successful nests are denoted by a closed circle.

# APPENDIX C

# SPATIAL DISTRIBUTION OF ANGLERS IN LAKES
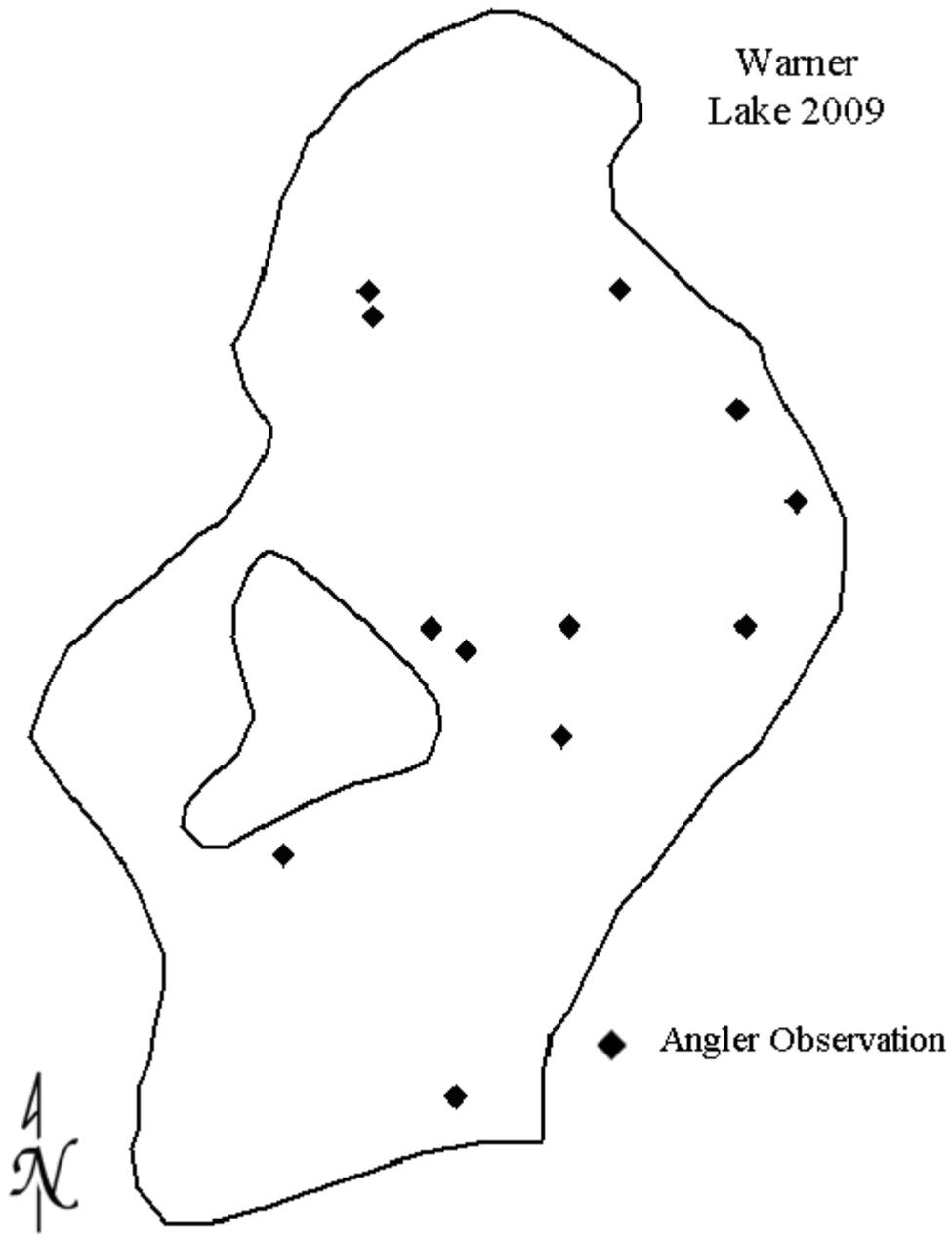
Figure 15: Locations of observations of anglers in Warner Lake, a low fishing pressure lake, during 2009. This map includes observations from both temporal and spatial-temporal data.
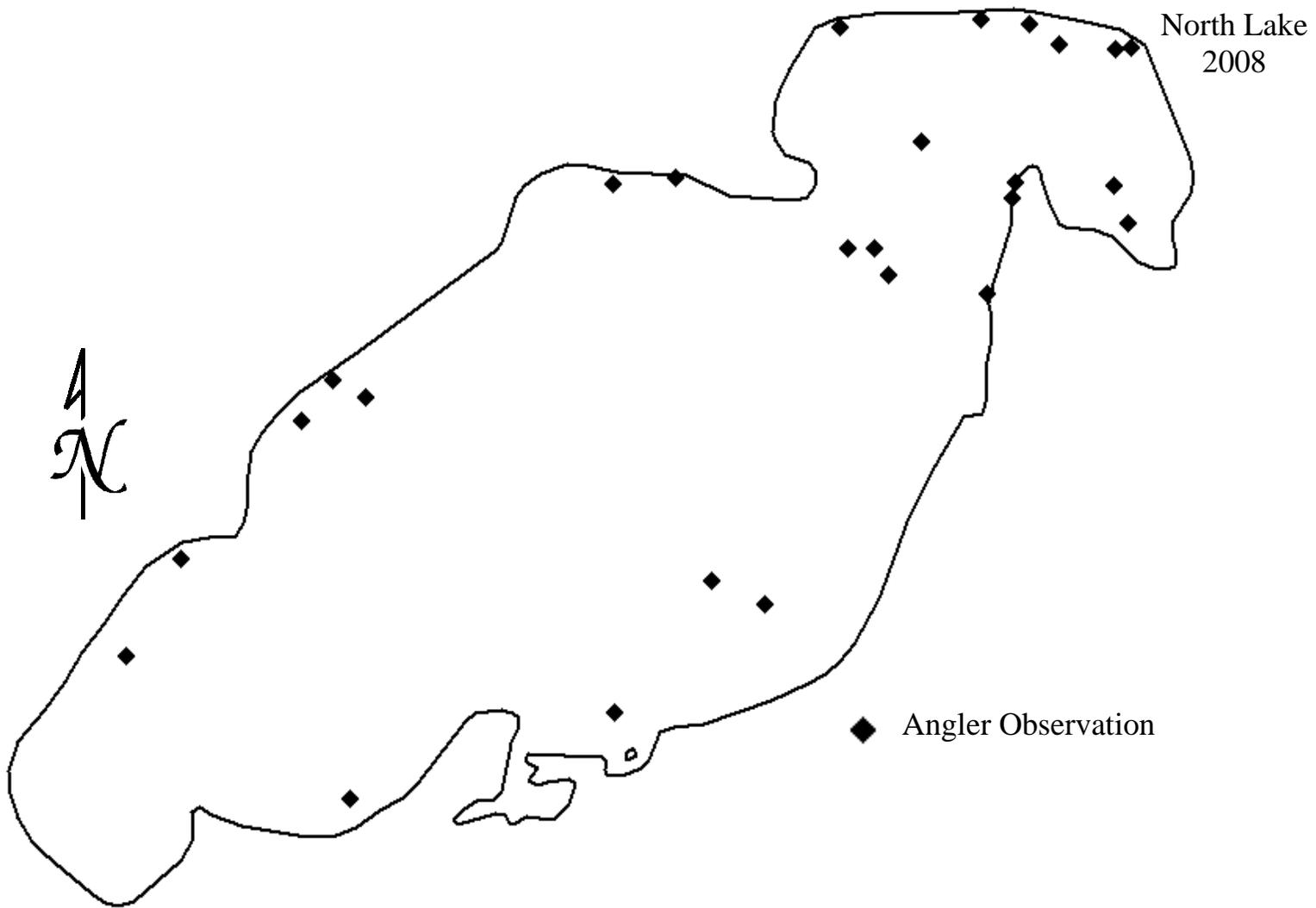
Figure 16: Locations of observations of anglers in North Lake, an intermediate fishing pressure lake, during 2008. This map includes observations from both temporal and spatial-temporal data.
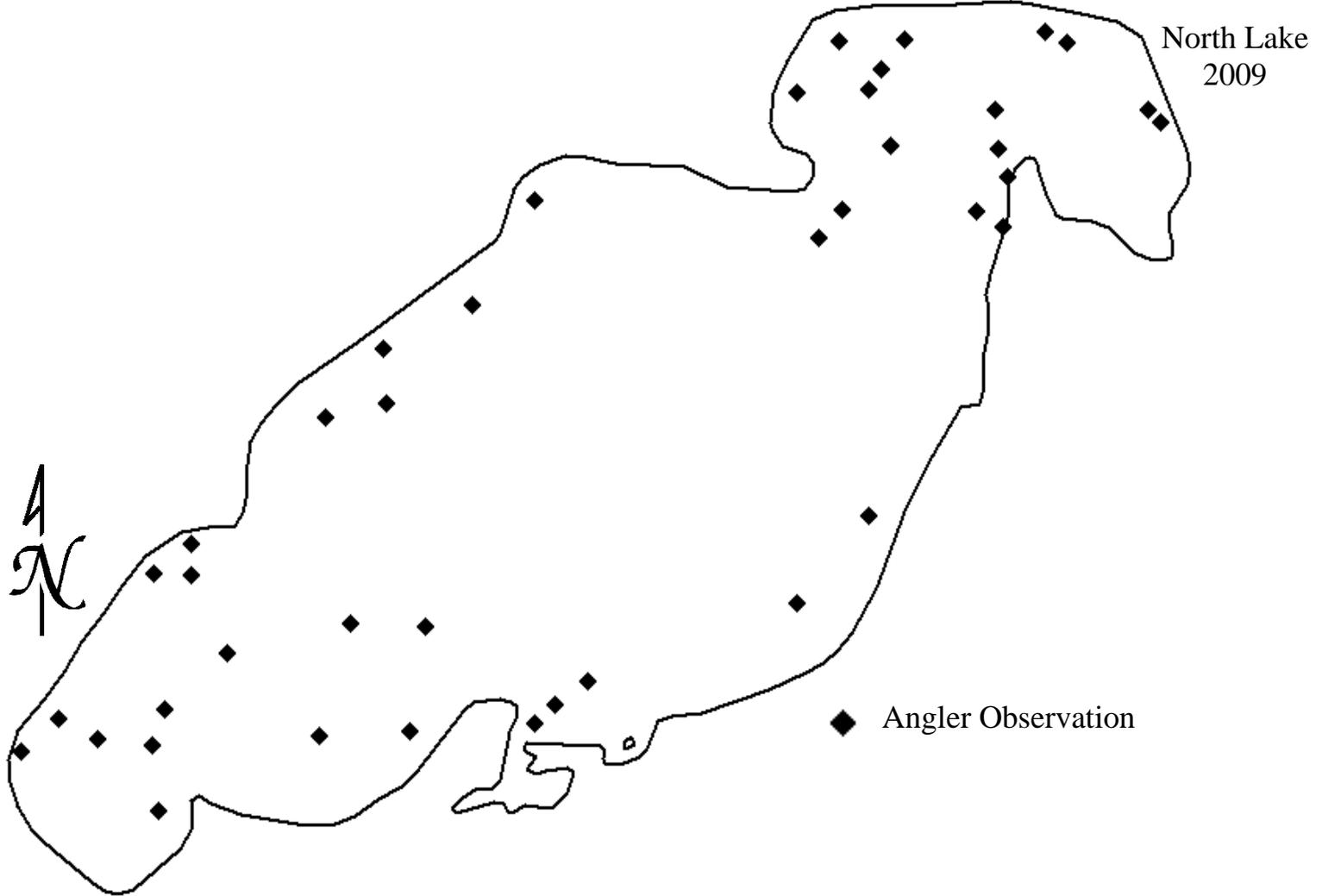
Figure 17: Locations of observations of anglers in North Lake, an intermediate fishing pressure lake, during 2009. This map includes observations from both temporal and spatial-temporal data.
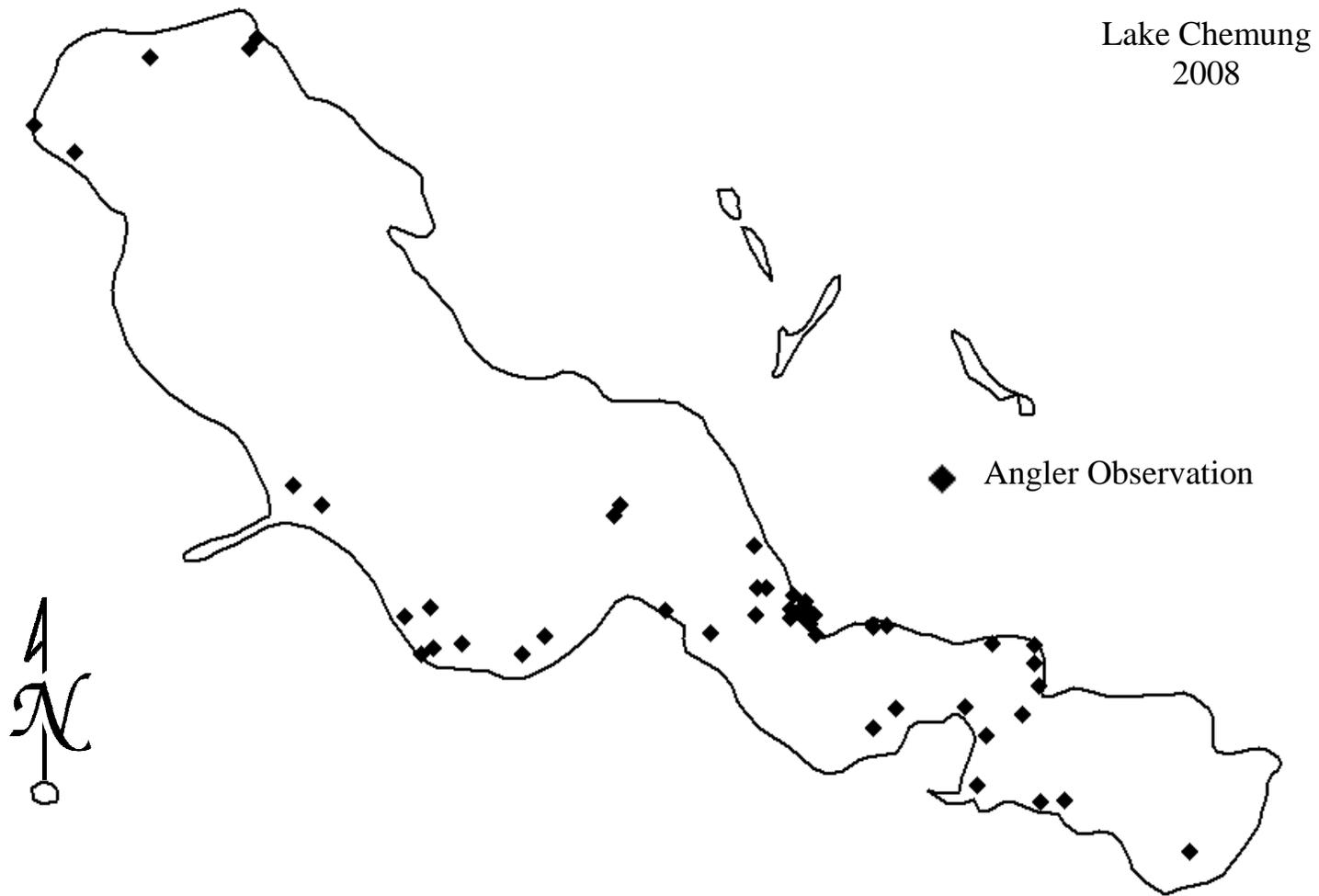
Figure 18: Locations of observations of anglers in Lake Chemung, a high fishing pressure lake, during 2008. This map includes observations from both temporal and spatial-temporal data.
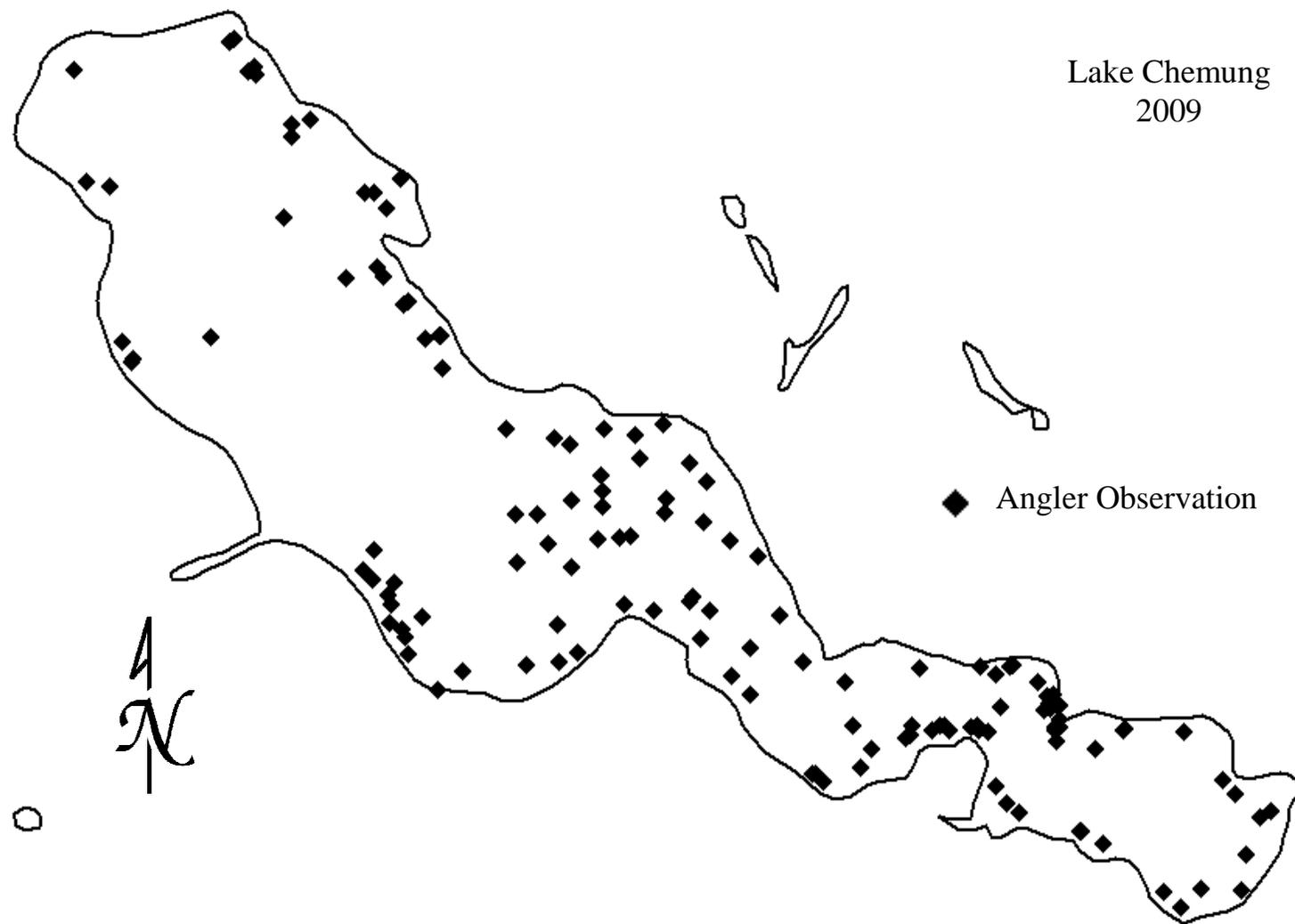
Figure 19: Locations of observations of anglers in Lake Chemung, a high fishing pressure lake, during 2009. This map includes observations from both temporal and spatial-temporal data.
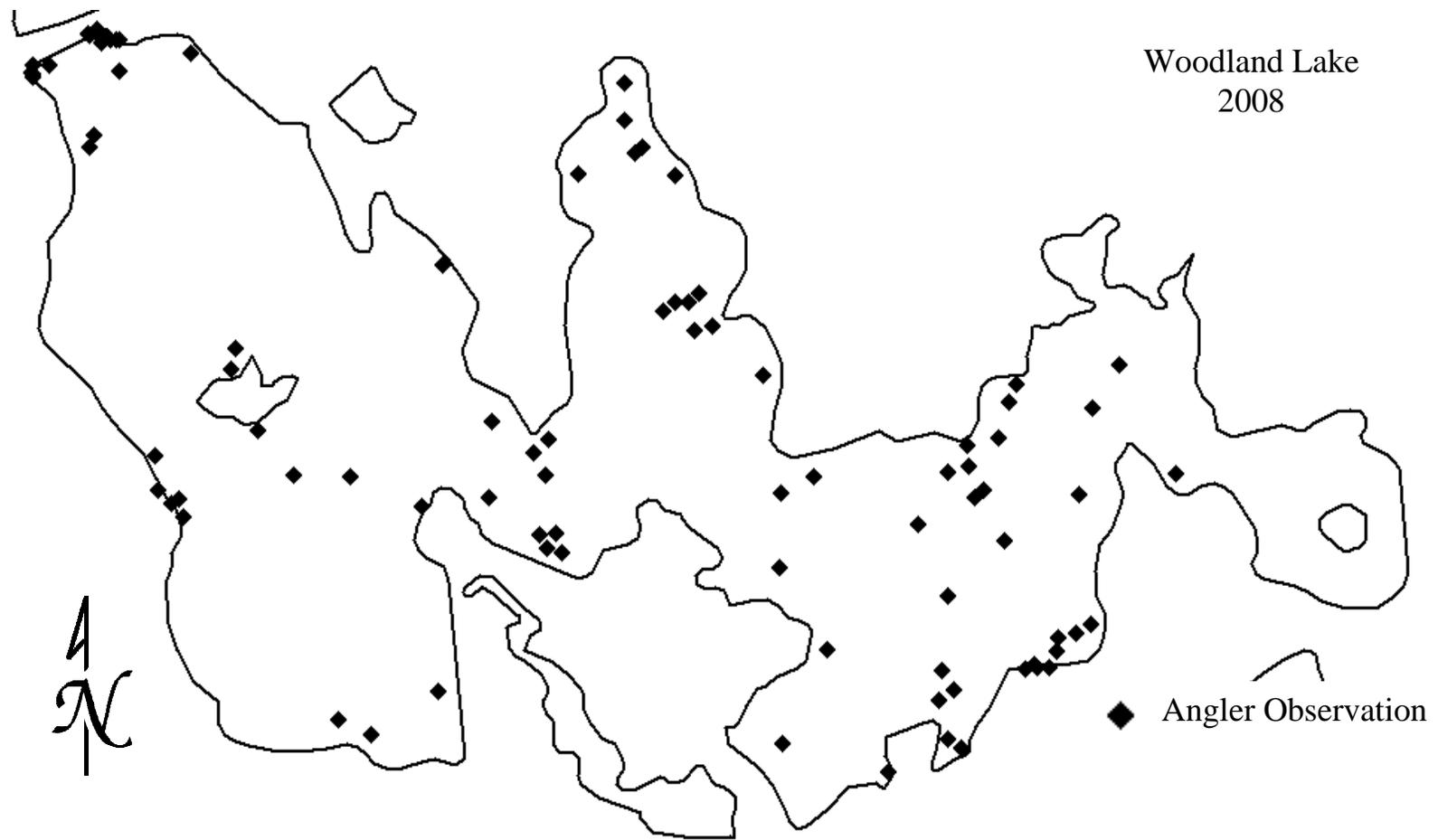
Figure 20: Locations of observations of anglers in Woodland Lake, a high fishing pressure lake, during 2008. This map includes observations from both temporal and spatial-temporal data.

Figure 21: Locations of observations of anglers in Woodland Lake, a high fishing pressure lake, during 2009. This map includes observations from both temporal and spatial-temporal data.

# APPENDIX D

## SIZE DISTRIBUTION OF NESTING MALE BASS BY YEAR
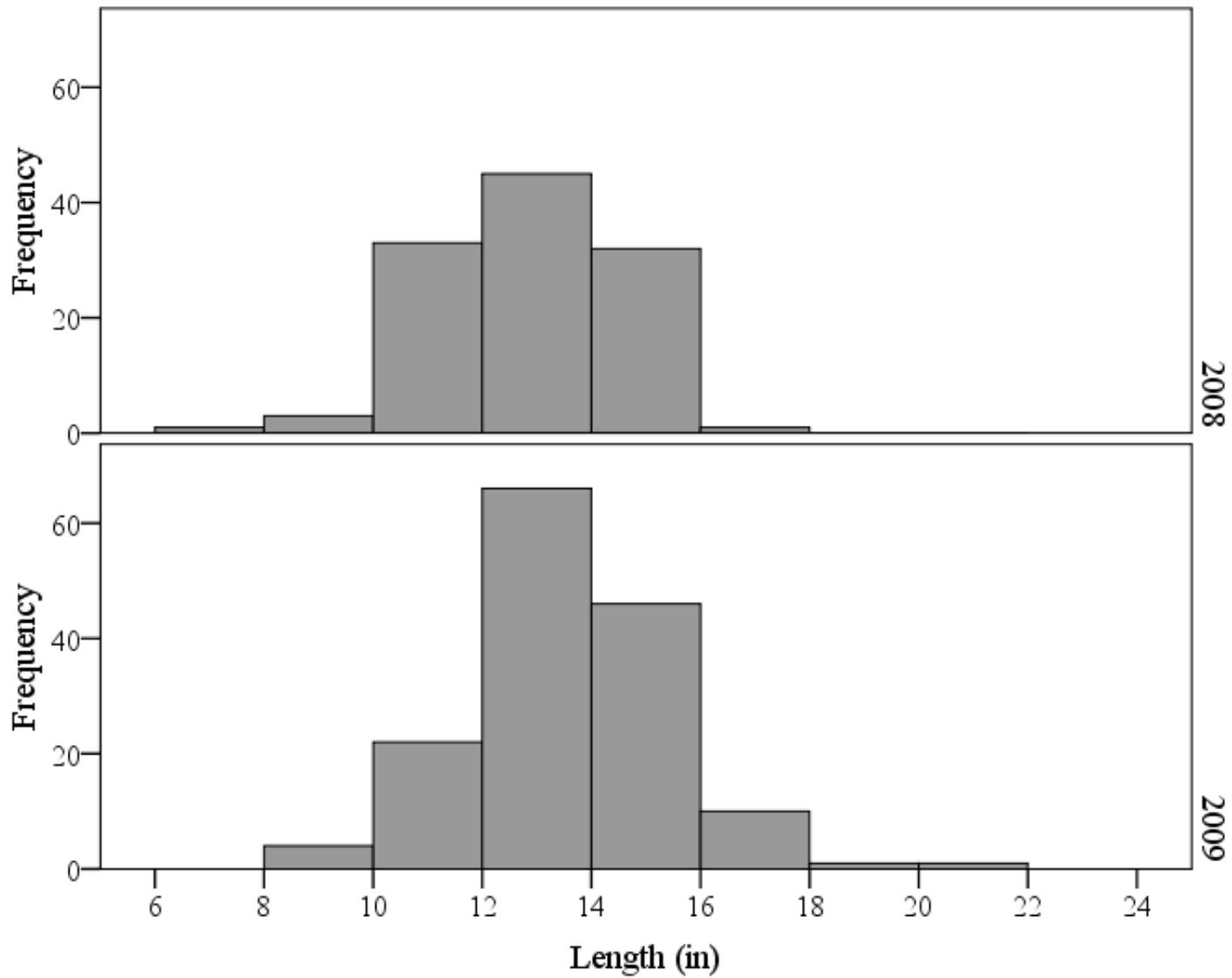
Figure 22: Size distributions of nesting male bass lengths for 2008 and 2009. The legal limit for largemouth bass is 14 in.

# APPENDIX E

# COMPLETE TABLES OF PROGRAM MARK MODEL RESULTS

Table 29: Complete table of model results containing main effects models from Phase 1 for 2008. Tables 2 and 3 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season)p(.)Psi(.)r(.) | 1045.19 | 0.00 | 0.25 | 10 | 1024.26 |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | 1045.99 | 0.80 | 0.17 | 11 | 1022.87 |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | 1046.34 | 1.15 | 0.14 | 11 | 1023.22 |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | 1047.25 | 2.06 | 0.09 | 12 | 1021.92 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(.) | 1047.51 | 2.32 | 0.08 | 14 | 1017.70 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(.) | 1048.49 | 3.30 | 0.05 | 15 | 1016.41 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) | 1049.00 | 3.81 | 0.04 | 15 | 1016.92 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(Woodland) | 1049.90 | 4.71 | 0.02 | 16 | 1015.54 |
| phi(Lake*Stage)p(.)Psi(.)r(.) | 1049.99 | 4.80 | 0.02 | 10 | 1029.05 |
| phi(Lake)p(.)Psi(.)r(.) | 1050.83 | 5.64 | 0.01 | 7 | 1036.36 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | 1050.92 | 5.73 | 0.01 | 11 | 1027.80 |
| phi(Lake)p(Woodland)Psi(.)r(.) | 1051.40 | 6.21 | 0.01 | 8 | 1034.79 |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | 1051.52 | 6.33 | 0.01 | 11 | 1028.40 |
| phi(.)p(.)Psi(.)r(.) | 1051.89 | 6.70 | 0.01 | 5 | 1041.64 |
| phi(Lake)p(.)Psi(.)r(Woodland) | 1051.99 | 6.80 | 0.01 | 8 | 1035.38 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | 1052.07 | 6.88 | 0.01 | 12 | 1026.74 |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | 1052.67 | 7.48 | 0.01 | 9 | 1033.91 |
| phi(Lake+Season)p(.)Psi(.)r(.) | 1052.70 | 7.51 | 0.01 | 8 | 1036.09 |
| phi(.)p(.)Psi(.)r(Woodland) | 1052.85 | 7.66 | 0.01 | 6 | 1040.50 |
| phi(Lake+Stage)p(.)Psi(.)r(.) | 1052.97 | 7.78 | 0.01 | 8 | 1036.36 |
| phi(.)p(Woodland)Psi(.)r(.) | 1053.15 | 7.96 | 0.00 | 6 | 1040.80 |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | 1053.26 | 8.07 | 0.00 | 9 | 1034.50 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | 1053.55 | 8.36 | 0.00 | 9 | 1034.79 |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) | 1053.89 | 8.70 | 0.00 | 9 | 1035.13 |
| phi(Season)p(.)Psi(.)r(. | 1053.93 | 8.75 | 0.00 | 6 | 1041.58 |
| phi(Stage)p(.)Psi(.)r(.) | 1053.99 | 8.80 | 0.00 | 6 | 1041.64 |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) | 1054.14 | 8.95 | 0.00 | 9 | 1035.38 |

Table 29 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(.)p(Woodland)Psi(.)r(Woodland) | 1054.26 | 9.07 | 0.00 | 7 | 1039.79 |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) | 1054.57 | 9.38 | 0.00 | 10 | 1033.63 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) | 1054.84 | 9.65 | 0.00 | 10 | 1033.91 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(.) | 1054.85 | 9.66 | 0.00 | 9 | 1036.09 |
| phi(Season)p(.)Psi(.)r(Woodland) | 1054.92 | 9.73 | 0.00 | 7 | 1040.45 |
| phi(Stage)p(.)Psi(.)r(Woodland) | 1054.97 | 9.78 | 0.00 | 7 | 1040.50 |
| phi(Season)p(Woodland)Psi(.)r(. | 1055.19 | 10.00 | 0.00 | 7 | 1040.72 |
| phi(Stage)p(Woodland)Psi(.)r(.) | 1055.27 | 10.08 | 0.00 | 7 | 1040.80 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) | 1055.43 | 10.24 | 0.00 | 10 | 1034.50 |
| phi(Season*Stage)p(.)Psi(.)r(.) | 1055.61 | 10.43 | 0.00 | 8 | 1039.01 |
| phi(Season+Stage)p(.)Psi(.)r(.) | 1056.05 | 10.86 | 0.00 | 7 | 1041.58 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) | 1056.06 | 10.87 | 0.00 | 10 | 1035.13 |
| phi(Season)p(Woodland)Psi(.)r(Woodland) | 1056.31 | 11.12 | 0.00 | 8 | 1039.71 |
| phi(Stage)p(Woodland)Psi(.)r(Woodland) | 1056.40 | 11.21 | 0.00 | 8 | 1039.79 |
| phi(Season*Stage)p(.)Psi(.)r(Woodland) | 1056.68 | 11.49 | 0.00 | 9 | 1037.92 |
| phi(Season*Stage)p(Woodland)Psi(.)r(.) | 1056.75 | 11.56 | 0.00 | 9 | 1037.99 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) | 1056.76 | 11.57 | 0.00 | 11 | 1033.63 |
| phi(Season+Stage)p(.)Psi(.)r(Woodland) | 1057.05 | 11.86 | 0.00 | 8 | 1040.44 |
| phi(Season+Stage)p(Woodland)Psi(.)r(.) | 1057.32 | 12.13 | 0.00 | 8 | 1040.71 |
| phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) | 1057.96 | 12.77 | 0.00 | 10 | 1037.02 |
| phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) | 1058.46 | 13.27 | 0.00 | 9 | 1039.70 |

Table 30: Complete table of model results containing main effects models from Phase 1 for 2009. Tables 2 and 3 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Stage)p(Woodland)Psi(.)r(.) | 4243.66 | 0.00 | 0.17 | 7 | 4229.34 |
| phi(.)p(Woodland)Psi(.)r(.) | 4244.18 | 0.53 | 0.13 | 6 | 4231.95 |
| phi(Stage)p(Woodland)Psi(.)r(Woodland) | 4244.84 | 1.18 | 0.09 | 8 | 4228.43 |
| phi(Season+Stage)p(Woodland)Psi(.)r(.) | 4245.26 | 1.60 | 0.07 | 8 | 4228.85 |
| phi(.)p(Woodland)Psi(.)r(Woodland) | 4245.40 | 1.75 | 0.07 | 7 | 4231.08 |
| phi(Season)p(Woodland)Psi(.)r(.) | 4245.90 | 2.24 | 0.05 | 7 | 4231.58 |
| phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) | 4246.47 | 2.82 | 0.04 | 9 | 4227.96 |
| phi(Stage)p(.)Psi(.)r(.) | 4246.51 | 2.85 | 0.04 | 6 | 4234.27 |
| phi(Stage)p(.)Psi(.)r(Woodland) | 4246.79 | 3.13 | 0.03 | 7 | 4232.47 |
| phi(Season*Stage)p(Woodland)Psi(.)r(.) | 4247.05 | 3.39 | 0.03 | 9 | 4228.53 |
| phi(Season)p(Woodland)Psi(.)r(Woodland) | 4247.14 | 3.49 | 0.03 | 8 | 4230.73 |
| phi(.)p(.)Psi(.)r(.)} | 4247.15 | 3.50 | 0.03 | 5 | 4236.98 |
| phi(.)p(.)Psi(.)r(Woodland) | 4247.44 | 3.78 | 0.03 | 6 | 4235.20 |
| phi(Season+Stage)p(.)Psi(.)r(.) | 4248.14 | 4.49 | 0.02 | 7 | 4233.82 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | 4248.16 | 4.50 | 0.02 | 10 | 4227.53 |
| phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) | 4248.27 | 4.62 | 0.02 | 10 | 4227.64 |
| phi(Season+Stage)p(.)Psi(.)r(Woodland) | 4248.45 | 4.80 | 0.02 | 8 | 4232.04 |
| phi(Lake)p(Woodland)Psi(.)r(.) | 4248.56 | 4.90 | 0.01 | 9 | 4230.04 |
| phi(Season)p(.)Psi(.)r(.) | 4248.90 | 5.24 | 0.01 | 6 | 4236.66 |
| phi(Season)p(.)Psi(.)r(Woodland) | 4249.20 | 5.54 | 0.01 | 7 | 4234.88 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) | 4249.36 | 5.70 | 0.01 | 11 | 4226.60 |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | 4249.67 | 6.02 | 0.01 | 10 | 4229.04 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) | 4249.80 | 6.14 | 0.01 | 11 | 4227.04 |
| phi(Season*Stage)p(.)Psi(.)r(.) | 4249.92 | 6.27 | 0.01 | 8 | 4233.51 |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | 4250.17 | 6.51 | 0.01 | 10 | 4229.54 |
| phi(Season*Stage)p(.)Psi(.)r(Woodland) | 4250.21 | 6.55 | 0.01 | 9 | 4231.69 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | 4250.67 | 7.01 | 0.00 | 13 | 4223.61 |

Table 30 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(Lake+Stage)p(.)Psi(.)r(.) | 4250.92 | 7.26 | 0.00 | 9 | 4232.40 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) | 4251.04 | 7.39 | 0.00 | 12 | 4226.14 |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) | 4251.18 | 7.52 | 0.00 | 10 | 4230.55 |
| phi(Lake)p(.)Psi(.)r(.) | 4251.28 | 7.63 | 0.00 | 8 | 4234.87 |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) | 4251.33 | 7.67 | 0.00 | 11 | 4228.56 |
| phi(Lake)p(.)Psi(.)r(Woodland) | 4251.46 | 7.81 | 0.00 | 9 | 4232.95 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | 4252.19 | 8.53 | 0.00 | 14 | 4222.97 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(.) | 4252.61 | 8.95 | 0.00 | 10 | 4231.98 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) | 4252.90 | 9.25 | 0.00 | 11 | 4230.14 |
| phi(Lake+Season)p(.)Psi(.)r(.) | 4252.94 | 9.28 | 0.00 | 9 | 4234.42 |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) | 4253.15 | 9.49 | 0.00 | 10 | 4232.51 |
| phi(Lake*Stage)p(.)Psi(.)r(.) | 4253.47 | 9.82 | 0.00 | 12 | 4228.57 |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | 4254.09 | 10.44 | 0.00 | 13 | 4227.04 |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | 4254.95 | 11.29 | 0.00 | 13 | 4227.89 |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | 4256.17 | 12.51 | 0.00 | 14 | 4226.95 |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | 4257.93 | 14.27 | 0.00 | 13 | 4230.87 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) | 4261.00 | 17.34 | 0.00 | 18 | 4222.98 |
| phi(Lake*Season)p(.)Psi(.)r(.) | 4298.73 | 55.07 | 0.00 | 12 | 4273.83 |

Table 31: Complete table of model results containing group-mean centered nest attribute models from Phase 2 of 2008. All models were run with the important main effects from Phase 1 (lake*season*stage). Tables 4 and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season*Stage+Wind)p(.)Psi(.)r(.) | 1046.84 | 0.00 | 0.21 | 15 | 1014.76 |
| phi(Lake*Season*Stage+Wind+TAng)p(.)Psi(.)r(.) | 1047.45 | 0.61 | 0.16 | 16 | 1013.08 |
| phi(Lake*Season*Stage+TAng)p(.)Psi(.)r(.) | 1047.52 | 0.68 | 0.15 | 15 | 1015.44 |
| phi(Lake*Season*Stage+Cover+Wind)p(.)Psi(.)r(.) | 1048.43 | 1.59 | 0.10 | 16 | 1014.06 |
| phi(Lake*Season*Stage+Wind+Legal)p(.)Psi(.)r(.) | 1048.96 | 2.12 | 0.07 | 16 | 1014.60 |
| phi(Lake*Season*Stage+Legal)p(.)Psi(.)r(.) | 1049.39 | 2.55 | 0.06 | 15 | 1017.31 |
| phi(Lake*Season*Stage+Cover+TAng)p(.)Psi(.)r(.) | 1049.40 | 2.56 | 0.06 | 16 | 1015.04 |
| phi(Lake*Season*Stage+Cover)p(.)Psi(.)r(.) | 1049.58 | 2.74 | 0.05 | 15 | 1017.50 |
| phi(Lake*Season*Stage+TAng+Legal)p(.)Psi(.)r(.) | 1050.01 | 3.17 | 0.04 | 16 | 1015.65 |
| phi(Lake*Season*Stage+Wind+Legal*Season)p(.)Psi(.)r(.) | 1051.18 | 4.35 | 0.02 | 17 | 1014.51 |
| phi(Lake*Season*Stage+Cover+Legal)p(.)Psi(.)r(.) | 1051.50 | 4.66 | 0.02 | 16 | 1017.14 |
| phi(Lake*Season*Stage+TAng+Legal*Season)p(.)Psi(.)r(.) | 1051.67 | 4.83 | 0.02 | 17 | 1014.99 |
| phi(Lake*Season*Stage+Legal*Season)p(.)Psi(.)r(.) | 1052.24 | 5.40 | 0.01 | 16 | 1017.87 |
| phi(Lake*Season*Stage+Cover+Wind+TAng+Legal*Season)p(.)Psi(.)r(.) | 1053.72 | 6.88 | 0.01 | 19 | 1012.37 |
| phi(Lake*Season*Stage+Cover+Legal*Season)p(.)Psi(.)r(.) | 1054.01 | 7.18 | 0.01 | 17 | 1017.34 |

Table 32: Complete table of model results from Phase 2 of 2009 showing effects of group-mean centered nest attributes on nest survival probability. All models were run with the important main effects from Phase 1 (season+stage). Tables 4 and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery). The models including phi(Season+Stage+TAng+BScore), phi(Season+Stage+Wind+TAng), and phi(Season+Stage+Cover+Wind+TAng+ BScore+Legal*Season) are not listed because they could not converge on parameter estimates and had to be deleted from the results.

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Season+Stage+ Cover+ TAng)p(Woodland)Psi(.)r(.) | 4155.79 | 0.00 | 0.999 | 10 | 4135.16 |
| phi(Season+Stage+ TAng+ Legal*Season)p(Woodland)Psi(.)r(.) | 4170.07 | 14.27 | 0.001 | 11 | 4147.31 |
| phi(Season+Stage+ TAng+ Legal)p(Woodland)Psi(.)r(.) | 4171.79 | 16.00 | 0.000 | 10 | 4151.16 |
| phi(Season+Stage+ TAng)p(Woodland)Psi(.)r(.) | 4172.33 | 16.54 | 0.000 | 9 | 4153.81 |
| phi(Season+Stage+ Legal)p(Woodland)Psi(.)r(.) | 4245.71 | 89.91 | 0.000 | 9 | 4227.19 |
| phi(Season+Stage+ BScore)p(Woodland)Psi(.)r(.) | 4246.90 | 91.11 | 0.000 | 9 | 4228.38 |
| phi(Season+Stage+ Cover)p(Woodland)Psi(.)r(.) | 4247.21 | 91.41 | 0.000 | 9 | 4228.69 |
| phi(Season+Stage+ Wind)p(Woodland)Psi(.)r(.) | 4247.27 | 91.48 | 0.000 | 9 | 4228.76 |
| phi(Season+Stage+ BScore+ Legal)p(Woodland)Psi(.)r(.) | 4247.40 | 91.61 | 0.000 | 10 | 4226.77 |
| phi(Season+Stage+ Cover+ Legal)p(Woodland)Psi(.)r(.) | 4247.79 | 92.00 | 0.000 | 10 | 4227.16 |
| phi(Season+Stage+ Legal*Season)p(Woodland)Psi(.)r(.) | 4247.79 | 92.00 | 0.000 | 10 | 4227.16 |
| phi(Season+Stage+ Wind+ Legal)p(Woodland)Psi(.)r(.) | 4247.82 | 92.03 | 0.000 | 10 | 4227.19 |
| phi(Season+Stage+ Cover+ BScore)p(Woodland)Psi(.)r(.) | 4248.85 | 93.05 | 0.000 | 10 | 4228.21 |
| phi(Season+Stage+ Wind+ BScore)p(Woodland)Psi(.)r(.) | 4248.94 | 93.14 | 0.000 | 10 | 4228.30 |
| phi(Season+Stage+ Cover+ Wind)p(Woodland)Psi(.)r(.) | 4249.31 | 93.52 | 0.000 | 10 | 4228.68 |
| phi(Season+Stage+ BScore+ Legal*Season)p(Woodland)Psi(.)r(.) | 4249.52 | 93.73 | 0.000 | 11 | 4226.76 |
| phi(Season+Stage+ Cover+ Legal*Season)p(Woodland)Psi(.)r(.) | 4249.88 | 94.09 | 0.000 | 11 | 4227.12 |
| phi(Season+Stage+ Wind+ Legal*Season)p(Woodland)Psi(.)r(.) | 4249.92 | 94.13 | 0.000 | 11 | 4227.16 |

Table 33: Complete table of models resulting from Phases 1, 2, and 3 together that were used for model averaging for 2008. Tables 2, 3, 4, and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season+TAng)p(.)Psi(.)r(.) | 1043.76 | 0.00 | 0.08 | 11 | 1020.64 |
| phi(Lake*Season+Wind)p(.)Psi(.)r(.) | 1044.22 | 0.47 | 0.06 | 11 | 1021.10 |
| phi(Lake*Season+Wind+TAng)p(.)Psi(.)r(.) | 1044.48 | 0.73 | 0.05 | 12 | 1019.15 |
| phi(Lake*Season+TAng)p(Woodland)Psi(.)r(.) | 1044.57 | 0.81 | 0.05 | 12 | 1019.24 |
| phi(Lake*Season+TAng)p(.)Psi(.)r(Woodland) | 1044.94 | 1.18 | 0.04 | 12 | 1019.60 |
| phi(Lake*Season+Cover+TAng)p(.)Psi(.)r(.) | 1044.97 | 1.21 | 0.04 | 12 | 1019.63 |
| phi(Lake*Season+Wind)p(Woodland)Psi(.)r(.) | 1045.04 | 1.28 | 0.04 | 12 | 1019.71 |
| phi(Lake*Season)p(.)Psi(.)r(.) | 1045.19 | 1.43 | 0.04 | 10 | 1024.26 |
| phi(Lake*Season+Wind+TAng)p(Woodland)Psi(.)r(.) | 1045.31 | 1.56 | 0.03 | 13 | 1017.75 |
| phi(Lake*Season+Wind)p(.)Psi(.)r(Woodland) | 1045.40 | 1.64 | 0.03 | 12 | 1020.07 |
| phi(Lake*Season+Wind+TAng)p(.)Psi(.)r(Woodland) | 1045.68 | 1.92 | 0.03 | 13 | 1018.12 |
| phi(Lake*Season+Cover+TAng)p(Woodland)Psi(.)r(.) | 1045.75 | 1.99 | 0.03 | 13 | 1018.19 |
| phi(Lake*Season+Cover+Wind)p(.)Psi(.)r(.) | 1045.85 | 2.09 | 0.03 | 12 | 1020.52 |
| phi(Lake*Season+TAng)p(Woodland)Psi(.)r(Woodland) | 1045.85 | 2.10 | 0.03 | 13 | 1018.29 |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | 1045.99 | 2.24 | 0.02 | 11 | 1022.87 |
| phi(Lake*Season+Cover+TAng)p(.)Psi(.)r(Woodland) | 1046.18 | 2.42 | 0.02 | 13 | 1018.62 |
| phi(Lake*Season+Wind+Legal)p(.)Psi(.)r(.) | 1046.33 | 2.57 | 0.02 | 12 | 1020.99 |
| phi(Lake*Season+Wind)p(Woodland)Psi(.)r(Woodland) | 1046.33 | 2.57 | 0.02 | 13 | 1018.77 |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | 1046.34 | 2.59 | 0.02 | 11 | 1023.22 |
| phi(Lake*Season+Wind+TAng)p(Woodland)Psi(.)r(Woodland) | 1046.62 | 2.86 | 0.02 | 14 | 1016.81 |
| phi(Lake*Season+Cover+Wind)p(Woodland)Psi(.)r(.) | 1046.64 | 2.88 | 0.02 | 13 | 1019.08 |
| phi(Lake*Season*Stage+Wind)p(.)Psi(.)r(.) | 1046.84 | 3.08 | 0.02 | 15 | 1014.76 |
| phi(Lake*Season+Cover+Wind)p(.)Psi(.)r(Woodland) | 1047.06 | 3.30 | 0.01 | 13 | 1019.49 |
| phi(Lake*Season+Cover)p(.)Psi(.)r(.) | 1047.06 | 3.31 | 0.01 | 11 | 1023.94 |
| phi(Lake*Season+Cover+TAng)p(Woodland)Psi(.)r(Woodland) | 1047.07 | 3.31 | 0.01 | 14 | 1017.26 |
| phi(Lake*Season+Wind+Legal)p(Woodland)Psi(.)r(.) | 1047.16 | 3.40 | 0.01 | 13 | 1019.60 |

Table 33 (cont'd)

| Model | AICc | Delta AICc | w | K | Deviance |
|---|---|---|---|---|---|
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | 1047.25 | 3.49 | 0.01 | 12 | 1021.92 |
| phi(Lake*Season+Legal)p(.)Psi(.)r(.) | 1047.38 | 3.62 | 0.01 | 11 | 1024.25 |
| phi(Lake*Season*Stage+Wind+TAng)p(.)Psi(.)r(.) | 1047.45 | 3.69 | 0.01 | 16 | 1013.08 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(.) | 1047.51 | 3.75 | 0.01 | 14 | 1017.70 |
| phi(Lake*Season*Stage+TAng)p(.)Psi(.)r(.) | 1047.52 | 3.76 | 0.01 | 15 | 1015.44 |
| phi(Lake*Season+Wind+Legal)p(.)Psi(.)r(Woodland) | 1047.52 | 3.76 | 0.01 | 13 | 1019.96 |
| phi(Lake*Season+Cover)p(Woodland)Psi(.)r(.) | 1047.87 | 4.11 | 0.01 | 12 | 1022.53 |
| phi(Lake*Season+Cover+Wind)p(Woodland)Psi(.)r(Woodland) | 1047.96 | 4.20 | 0.01 | 14 | 1018.15 |
| phi(Lake*Season+Legal)p(Woodland)Psi(.)r(.) | 1048.20 | 4.44 | 0.01 | 12 | 1022.87 |
| phi(Lake*Season+Cover)p(.)Psi(.)r(Woodland) | 1048.24 | 4.48 | 0.01 | 12 | 1022.91 |
| phi(Lake*Season*Stage+Cover+Wind)p(.)Psi(.)r(.) | 1048.43 | 4.67 | 0.01 | 16 | 1014.06 |
| phi(Lake*Season+Wind+Legal)p(Woodland)Psi(.)r(Woodland) | 1048.47 | 4.71 | 0.01 | 14 | 1018.66 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(.) | 1048.49 | 4.73 | 0.01 | 15 | 1016.41 |
| phi(Lake*Season+Legal)p(.)Psi(.)r(Woodland) | 1048.55 | 4.79 | 0.01 | 12 | 1023.22 |
| phi(Lake*Season*Stage+Wind+Legal)p(.)Psi(.)r(.) | 1048.96 | 5.20 | 0.01 | 16 | 1014.60 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) | 1049.00 | 5.24 | 0.01 | 15 | 1016.92 |
| phi(Lake*Season+Cover)p(Woodland)Psi(.)r(Woodland) | 1049.15 | 5.39 | 0.01 | 13 | 1021.58 |
| phi(Lake*Season*Stage+Legal)p(.)Psi(.)r(.) | 1049.39 | 5.63 | 0.00 | 15 | 1017.31 |
| phi(Lake*Season*Stage+Cover+TAng)p(.)Psi(.)r(.) | 1049.40 | 5.64 | 0.00 | 16 | 1015.04 |
| phi(Lake*Season+Legal)p(Woodland)Psi(.)r(Woodland) | 1049.48 | 5.72 | 0.00 | 13 | 1021.92 |
| phi(Lake*Season*Stage+Cover)p(.)Psi(.)r(.) | 1049.58 | 5.82 | 0.00 | 15 | 1017.50 |
| phi(Lake*Season*Stage)p(Woodland)Psi(.)r(Woodland) | 1049.90 | 6.14 | 0.00 | 16 | 1015.54 |
| phi(Lake*Stage)p(.)Psi(.)r(.) | 1049.99 | 6.23 | 0.00 | 10 | 1029.05 |
| phi(Lake*Season*Stage+TAng+Legal)p(.)Psi(.)r(.) | 1050.01 | 6.25 | 0.00 | 16 | 1015.65 |
| phi(Lake)p(.)Psi(.)r(.) | 1050.83 | 7.07 | 0.00 | 7 | 1036.36 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | 1050.92 | 7.16 | 0.00 | 11 | 1027.80 |
| phi(Lake*Season*Stage+Wind+Legal*Season)p(.)Psi(.)r(.) | 1051.18 | 7.42 | 0.00 | 17 | 1014.51 |
| phi(Lake)p(Woodland)Psi(.)r(.) | 1051.40 | 7.64 | 0.00 | 8 | 1034.79 |
| phi(Lake*Season*Stage+Cover+Legal)p(.)Psi(.)r(.) | 1051.50 | 7.74 | 0.00 | 16 | 1017.14 |

Table 33 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | 1051.52 | 7.76 | 0.00 | 11 | 1028.40 |
| phi(Lake*Season*Stage+TAng+Legal*Season)p(.)Psi(.)r(.) | 1051.67 | 7.91 | 0.00 | 17 | 1014.99 |
| phi(.)p(.)Psi(.)r(.) | 1051.89 | 8.13 | 0.00 | 5 | 1041.64 |
| phi(Lake)p(.)Psi(.)r(Woodland) | 1051.99 | 8.23 | 0.00 | 8 | 1035.38 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | 1052.07 | 8.31 | 0.00 | 12 | 1026.74 |
| phi(Lake*Season*Stage+Legal*Season)p(.)Psi(.)r(.) | 1052.24 | 8.48 | 0.00 | 16 | 1017.87 |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | 1052.67 | 8.91 | 0.00 | 9 | 1033.91 |
| phi(Lake+Season)p(.)Psi(.)r(.) | 1052.70 | 8.94 | 0.00 | 8 | 1036.09 |
| phi(.)p(.)Psi(.)r(Woodland) | 1052.85 | 9.09 | 0.00 | 6 | 1040.50 |
| phi(Lake+Stage)p(.)Psi(.)r(.) | 1052.97 | 9.21 | 0.00 | 8 | 1036.36 |
| phi(.)p(Woodland)Psi(.)r(.) | 1053.15 | 9.39 | 0.00 | 6 | 1040.80 |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | 1053.26 | 9.50 | 0.00 | 9 | 1034.50 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | 1053.55 | 9.79 | 0.00 | 9 | 1034.79 |
| phi(Lake*Season*Stage+Cover+Wind+TAng+Legal*Season)p(.)Psi(.)r(.) | 1053.72 | 9.96 | 0.00 | 19 | 1012.37 |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) | 1053.89 | 10.13 | 0.00 | 9 | 1035.13 |
| phi(Season)p(.)Psi(.)r(. | 1053.93 | 10.18 | 0.00 | 6 | 1041.58 |
| phi(Stage)p(.)Psi(.)r(.) | 1053.99 | 10.24 | 0.00 | 6 | 1041.64 |
| phi(Lake*Season*Stage+Cover+Legal*Season)p(.)Psi(.)r(.) | 1054.01 | 10.25 | 0.00 | 17 | 1017.34 |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) | 1054.14 | 10.39 | 0.00 | 9 | 1035.38 |
| phi(.)p(Woodland)Psi(.)r(Woodland) | 1054.26 | 10.50 | 0.00 | 7 | 1039.79 |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) | 1054.57 | 10.81 | 0.00 | 10 | 1033.63 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) | 1054.84 | 11.08 | 0.00 | 10 | 1033.91 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(.) | 1054.85 | 11.09 | 0.00 | 9 | 1036.09 |
| phi(Season)p(.)Psi(.)r(Woodland) | 1054.92 | 11.16 | 0.00 | 7 | 1040.45 |
| phi(Stage)p(.)Psi(.)r(Woodland) | 1054.97 | 11.21 | 0.00 | 7 | 1040.50 |
| phi(Season)p(Woodland)Psi(.)r(. | 1055.19 | 11.43 | 0.00 | 7 | 1040.72 |
| phi(Stage)p(Woodland)Psi(.)r(.) | 1055.27 | 11.51 | 0.00 | 7 | 1040.80 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) | 1055.43 | 11.67 | 0.00 | 10 | 1034.50 |
| phi(Season*Stage)p(.)Psi(.)r(.) | 1055.61 | 11.86 | 0.00 | 8 | 1039.01 |

Table 33 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(Season+Stage)p(.)Psi(.)r(.) | 1056.05 | 12.29 | 0.00 | 7 | 1041.58 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) | 1056.06 | 12.30 | 0.00 | 10 | 1035.13 |
| phi(Season)p(Woodland)Psi(.)r(Woodland) | 1056.31 | 12.56 | 0.00 | 8 | 1039.71 |
| phi(Stage)p(Woodland)Psi(.)r(Woodland) | 1056.40 | 12.64 | 0.00 | 8 | 1039.79 |
| phi(Season*Stage)p(.)Psi(.)r(Woodland) | 1056.68 | 12.92 | 0.00 | 9 | 1037.92 |
| phi(Season*Stage)p(Woodland)Psi(.)r(.) | 1056.75 | 12.99 | 0.00 | 9 | 1037.99 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) | 1056.76 | 13.00 | 0.00 | 11 | 1033.63 |
| phi(Season+Stage)p(.)Psi(.)r(Woodland) | 1057.05 | 13.29 | 0.00 | 8 | 1040.44 |
| phi(Season+Stage)p(Woodland)Psi(.)r(.) | 1057.32 | 13.56 | 0.00 | 8 | 1040.71 |
| phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) | 1057.96 | 14.20 | 0.00 | 10 | 1037.02 |
| phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) | 1058.46 | 14.70 | 0.00 | 9 | 1039.70 |
| phi(Season*Stage)p(.)psi(.)r(Woodland) | 956.82 | 11.25 | 0.00 | 9 | 937.95 |
| phi(Season*Stage)p(.)psi(.)r(.) | 957.02 | 11.45 | 0.00 | 8 | 940.33 |
| phi(Lake+Season+Stage)p(.)psi(.)r(Woodland) | 957.09 | 11.52 | 0.00 | 10 | 936.03 |
| phi(Lake+Season+Stage)p(.)psi(.)r(.) | 957.11 | 11.54 | 0.00 | 9 | 938.24 |

Table 34: Complete table of models resulting from Phases 1, 2, and 3 together that were used for model averaging for 2009. Tables 2, 3, 4, and 5 provide a guide to model notation. Parameters are phi (survival), p (live recapture), psi (transition), and r (dead recovery).

| Model | AICc | Delta AICc | AICc Weights | # Parameters | Deviance |
|---|---|---|---|---|---|
| phi(Season+Stage+Cover+TAng)p(Woodland)Psi(.)r(.) | 4155.79 | 0.00 | 0.999 | 10 | 4135.16 |
| phi(Season+Stage+TAng+Legal*Season)p(Woodland)Psi(.)r(.) | 4170.07 | 14.27 | 0.001 | 11 | 4147.31 |
| phi(Season+Stage+TAng+Legal)p(Woodland)Psi(.)r(.) | 4171.79 | 16.00 | 0.000 | 10 | 4151.16 |
| phi(Season+Stage+TAng)p(Woodland)Psi(.)r(.) | 4172.33 | 16.54 | 0.000 | 9 | 4153.81 |
| phi(Season+Cover+TAng)p(Woodland)Psi(.)r(.) | 4199.80 | 44.00 | 0.000 | 9 | 4181.28 |
| phi(Stage+Cover+TAng)p(Woodland)Psi(.)r(.) | 4203.35 | 47.56 | 0.000 | 9 | 4184.83 |
| phi(Stage+Cover+TAng)p(Woodland)Psi(.)r(Woodland) | 4204.78 | 48.99 | 0.000 | 10 | 4184.15 |
| phi(Cover+TAng)p(Woodland)Psi(.)r(.) | 4210.20 | 54.41 | 0.000 | 8 | 4193.79 |
| phi(Cover+TAng)p(Woodland)Psi(.)r(Woodland) | 4211.81 | 56.02 | 0.000 | 9 | 4193.30 |
| phi(Stage)p(Woodland)Psi(.)r(.) | 4243.66 | 87.86 | 0.000 | 7 | 4229.34 |
| phi(.)p(Woodland)Psi(.)r(.) | 4244.18 | 88.39 | 0.000 | 6 | 4231.95 |
| phi(Stage)p(Woodland)Psi(.)r(Woodland) | 4244.84 | 89.04 | 0.000 | 8 | 4228.43 |
| phi(Season+Stage)p(Woodland)Psi(.)r(.) | 4245.26 | 89.47 | 0.000 | 8 | 4228.85 |
| phi(.)p(Woodland)Psi(.)r(Woodland) | 4245.40 | 89.61 | 0.000 | 7 | 4231.08 |
| phi(Season+Stage+Legal)p(Woodland)Psi(.)r(.) | 4245.71 | 89.91 | 0.000 | 9 | 4227.19 |
| phi(Season)p(Woodland)Psi(.)r(.) | 4245.90 | 90.11 | 0.000 | 7 | 4231.58 |
| phi(Season+Stage)p(Woodland)Psi(.)r(Woodland) | 4246.47 | 90.68 | 0.000 | 9 | 4227.96 |
| phi(Stage)p(.)Psi(.)r(.) | 4246.51 | 90.71 | 0.000 | 6 | 4234.27 |
| phi(Stage)p(.)Psi(.)r(Woodland) | 4246.79 | 90.99 | 0.000 | 7 | 4232.47 |
| phi(Season+Stage+BScore)p(Woodland)Psi(.)r(.) | 4246.90 | 91.11 | 0.000 | 9 | 4228.38 |
| phi(Season*Stage)p(Woodland)Psi(.)r(.) | 4247.05 | 91.26 | 0.000 | 9 | 4228.53 |
| phi(Season)p(Woodland)Psi(.)r(Woodland) | 4247.14 | 91.35 | 0.000 | 8 | 4230.73 |
| phi(.)p(.)Psi(.)r(.)} | 4247.15 | 91.36 | 0.000 | 5 | 4236.98 |
| phi(Season+Stage+Cover)p(Woodland)Psi(.)r(.) | 4247.21 | 91.41 | 0.000 | 9 | 4228.69 |
| phi(Season+Stage+Wind)p(Woodland)Psi(.)r(.) | 4247.27 | 91.48 | 0.000 | 9 | 4228.76 |
| phi(Season+Stage+BScore+Legal)p(Woodland)Psi(.)r(.) | 4247.40 | 91.61 | 0.000 | 10 | 4226.77 |
| phi(.)p(.)Psi(.)r(Woodland) | 4247.44 | 91.65 | 0.000 | 6 | 4235.20 |

Table 34 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(Season+Stage+Cover+Legal)p(Woodland)Psi(.)r(.) | 4247.79 | 92.00 | 0.000 | 10 | 4227.16 |
| phi(Season+Stage+Legal*Season)p(Woodland)Psi(.)r(.) | 4247.79 | 92.00 | 0.000 | 10 | 4227.16 |
| phi(Season+Stage+Wind+Legal)p(Woodland)Psi(.)r(.) | 4247.82 | 92.03 | 0.000 | 10 | 4227.19 |
| phi(Season+Stage)p(.)Psi(.)r(.) | 4248.14 | 92.35 | 0.000 | 7 | 4233.82 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(.) | 4248.16 | 92.37 | 0.000 | 10 | 4227.53 |
| phi(Season*Stage)p(Woodland)Psi(.)r(Woodland) | 4248.27 | 92.48 | 0.000 | 10 | 4227.64 |
| phi(Season+Stage)p(.)Psi(.)r(Woodland) | 4248.45 | 92.66 | 0.000 | 8 | 4232.04 |
| phi(Lake)p(Woodland)Psi(.)r(.) | 4248.56 | 92.76 | 0.000 | 9 | 4230.04 |
| phi(Season+Stage+Cover+BScore)p(Woodland)Psi(.)r(.) | 4248.85 | 93.05 | 0.000 | 10 | 4228.21 |
| phi(Season)p(.)Psi(.)r(.) | 4248.90 | 93.10 | 0.000 | 6 | 4236.66 |
| phi(Season+Stage+Wind+BScore)p(Woodland)Psi(.)r(.) | 4248.94 | 93.14 | 0.000 | 10 | 4228.30 |
| phi(Season)p(.)Psi(.)r(Woodland) | 4249.20 | 93.41 | 0.000 | 7 | 4234.88 |
| phi(Season+Stage+Cover+Wind)p(Woodland)Psi(.)r(.) | 4249.31 | 93.52 | 0.000 | 10 | 4228.68 |
| phi(Lake+Stage)p(Woodland)Psi(.)r(Woodland) | 4249.36 | 93.56 | 0.000 | 11 | 4226.60 |
| phi(Season+Stage+BScore+Legal*Season)p(Woodland)Psi(.)r(.) | 4249.52 | 93.73 | 0.000 | 11 | 4226.76 |
| phi(Lake)p(Woodland)Psi(.)r(Woodland) | 4249.67 | 93.88 | 0.000 | 10 | 4229.04 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(.) | 4249.80 | 94.01 | 0.000 | 11 | 4227.04 |
| phi(Season+Stage+Cover+Legal*Season)p(Woodland)Psi(.)r(.) | 4249.88 | 94.09 | 0.000 | 11 | 4227.12 |
| phi(Season+Stage+Wind+Legal*Season)p(Woodland)Psi(.)r(.) | 4249.92 | 94.13 | 0.000 | 11 | 4227.16 |
| phi(Season*Stage)p(.)Psi(.)r(.) | 4249.92 | 94.13 | 0.000 | 8 | 4233.51 |
| phi(Lake+Season)p(Woodland)Psi(.)r(.) | 4250.17 | 94.38 | 0.000 | 10 | 4229.54 |
| phi(Season*Stage)p(.)Psi(.)r(Woodland) | 4250.21 | 94.42 | 0.000 | 9 | 4231.69 |
| phi(Lake*Stage)p(Woodland)Psi(.)r(.) | 4250.67 | 94.87 | 0.000 | 13 | 4223.61 |
| phi(Lake+Stage)p(.)Psi(.)r(.) | 4250.92 | 95.12 | 0.000 | 9 | 4232.40 |
| phi(Lake+Season+Stage)p(Woodland)Psi(.)r(Woodland) | 4251.04 | 95.25 | 0.000 | 12 | 4226.14 |
| phi(Lake+Stage)p(.)Psi(.)r(Woodland) | 4251.18 | 95.39 | 0.000 | 10 | 4230.55 |
| phi(Lake)p(.)Psi(.)r(.) | 4251.28 | 95.49 | 0.000 | 8 | 4234.87 |
| phi(Lake+Season)p(Woodland)Psi(.)r(Woodland) | 4251.33 | 95.53 | 0.000 | 11 | 4228.56 |
| phi(Lake)p(.)Psi(.)r(Woodland) | 4251.46 | 95.67 | 0.000 | 9 | 4232.95 |

Table 34 (cont'd)

| | | | | | |
|---|---|---|---|---|---|
| phi(Lake*Stage)p(Woodland)Psi(.)r(Woodland) | 4252.19 | 96.40 | 0.000 | 14 | 4222.97 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(.) | 4252.61 | 96.82 | 0.000 | 10 | 4231.98 |
| phi(Lake+Season+Stage)p(.)Psi(.)r(Woodland) | 4252.90 | 97.11 | 0.000 | 11 | 4230.14 |
| phi(Lake+Season)p(.)Psi(.)r(.) | 4252.94 | 97.15 | 0.000 | 9 | 4234.42 |
| phi(Lake+Season)p(.)Psi(.)r(Woodland) | 4253.15 | 97.35 | 0.000 | 10 | 4232.51 |
| phi(Lake*Stage)p(.)Psi(.)r(.) | 4253.47 | 97.68 | 0.000 | 12 | 4228.57 |
| phi(Lake*Stage)p(.)Psi(.)r(Woodland) | 4254.09 | 98.30 | 0.000 | 13 | 4227.04 |
| phi(Lake*Season)p(Woodland)Psi(.)r(.) | 4254.95 | 99.16 | 0.000 | 13 | 4227.89 |
| phi(Lake*Season)p(Woodland)Psi(.)r(Woodland) | 4256.17 | 100.38 | 0.000 | 14 | 4226.95 |
| phi(Lake*Season)p(.)Psi(.)r(.) | 4257.62 | 101.83 | 0.000 | 12 | 4232.72 |
| phi(Lake*Season)p(.)Psi(.)r(Woodland) | 4257.93 | 102.14 | 0.000 | 13 | 4230.87 |
| phi(Lake*Season*Stage)p(.)Psi(.)r(Woodland) | 4261.00 | 105.20 | 0.000 | 18 | 4222.98 |

# APPENDIX F

# TIMING OF NESTS BY STAGE RELATIVE TO FISHING SEASON
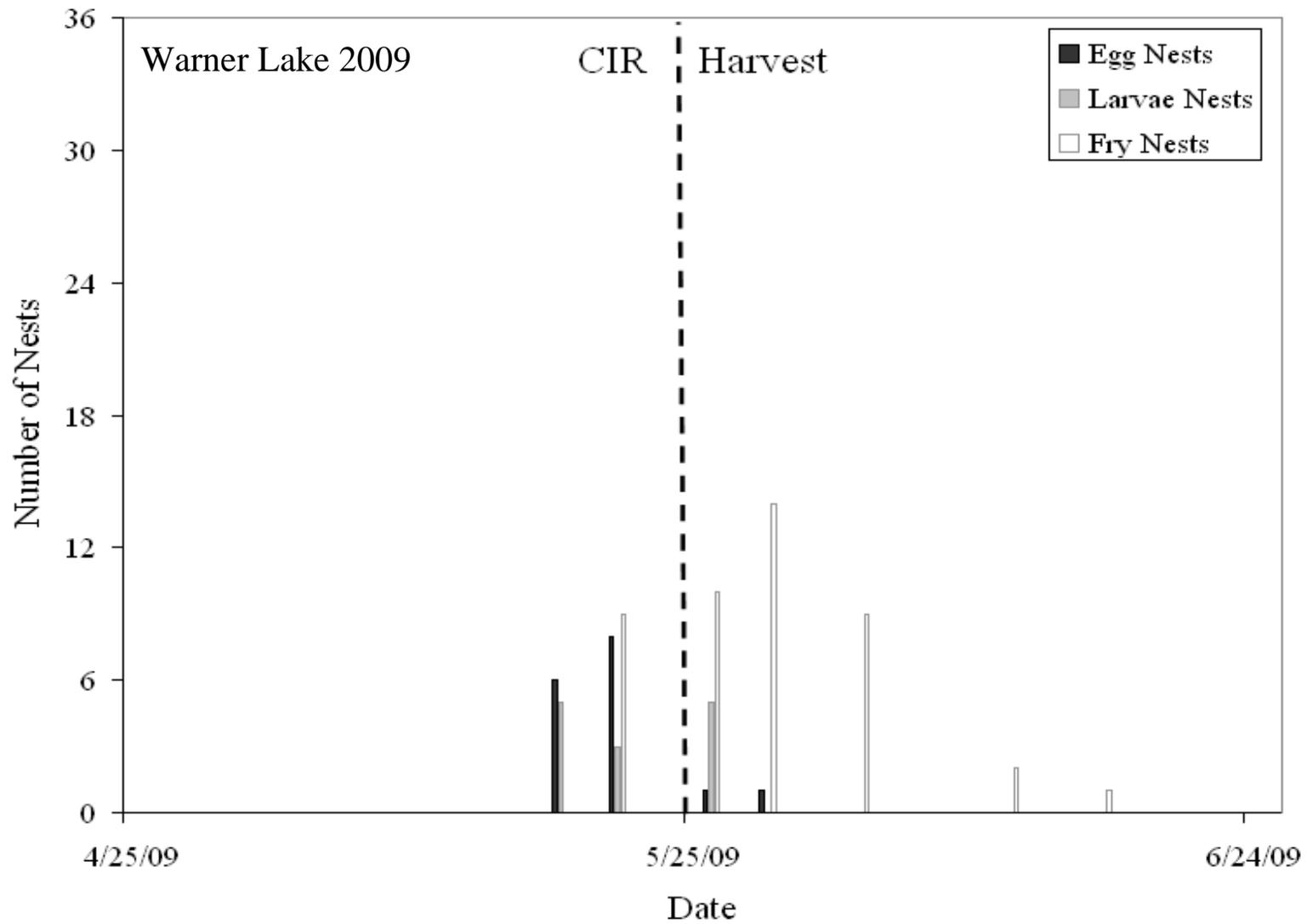
Figure 23: Timing of nests in Warner Lake during 2009. The harvest season began on May 25, 2009. Monitoring of nests in Warner Lake began on May 18, so we do not have records of nests prior to that date.
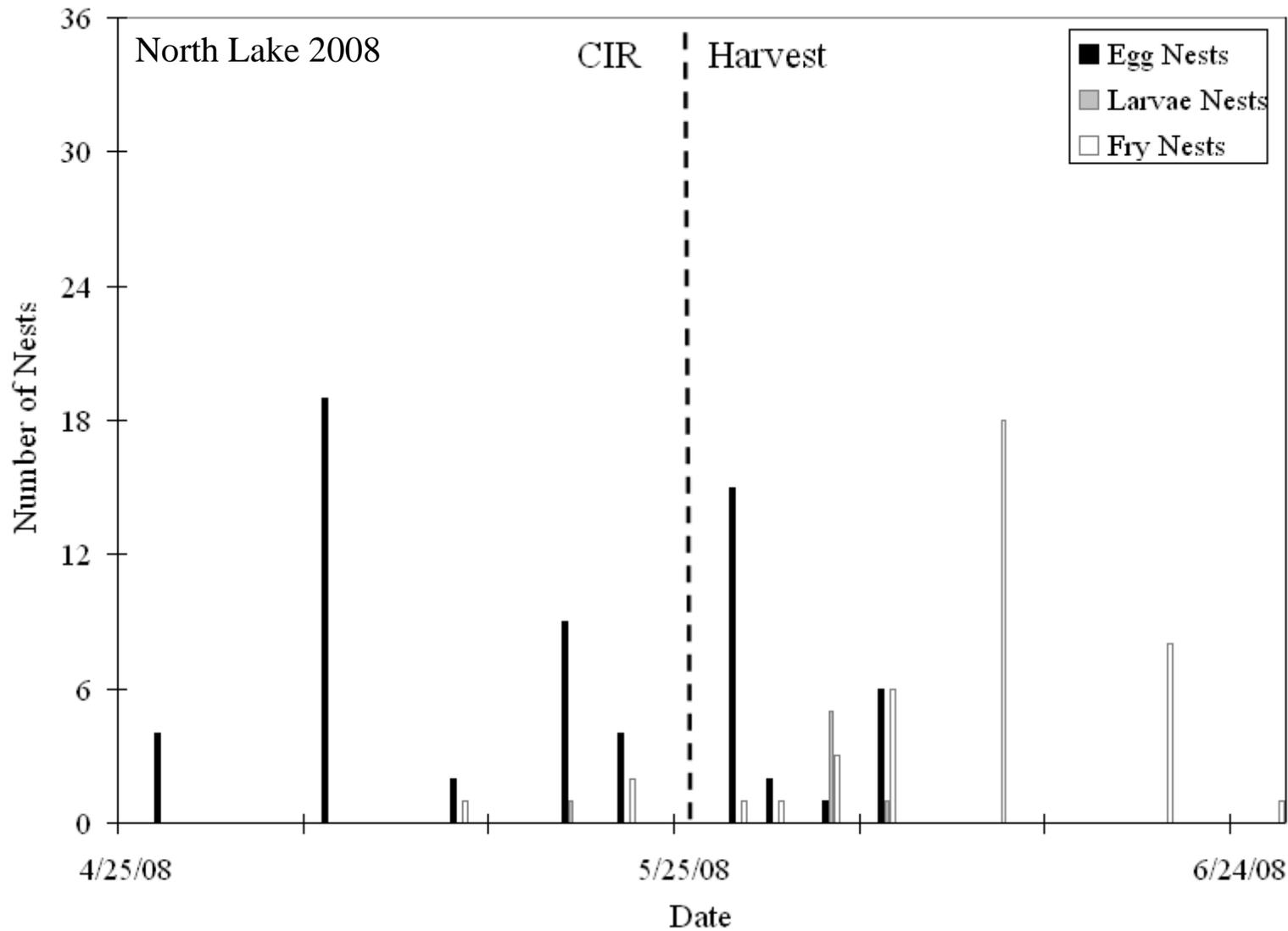
Figure 24: Timing of nests in North Lake during 2008. The harvest season began on May 26, 2008. No nests occurred prior to the CIR season, which began on April 26, 2008.
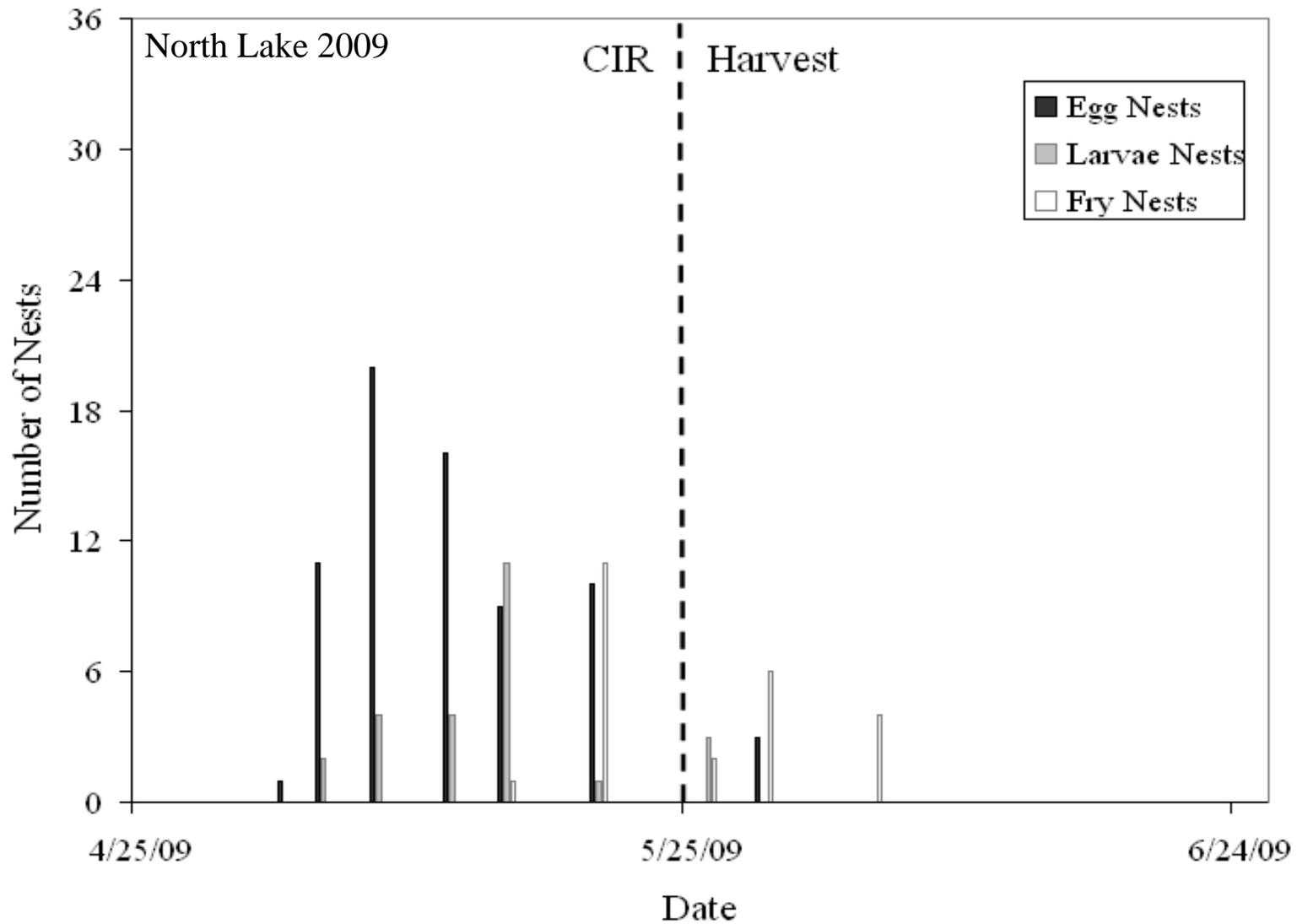
Figure 25: Timing of nests in North Lake during 2009. The harvest season began on May 25, 2009. No nests occurred prior to the CIR season, which began on April 25, 2009.
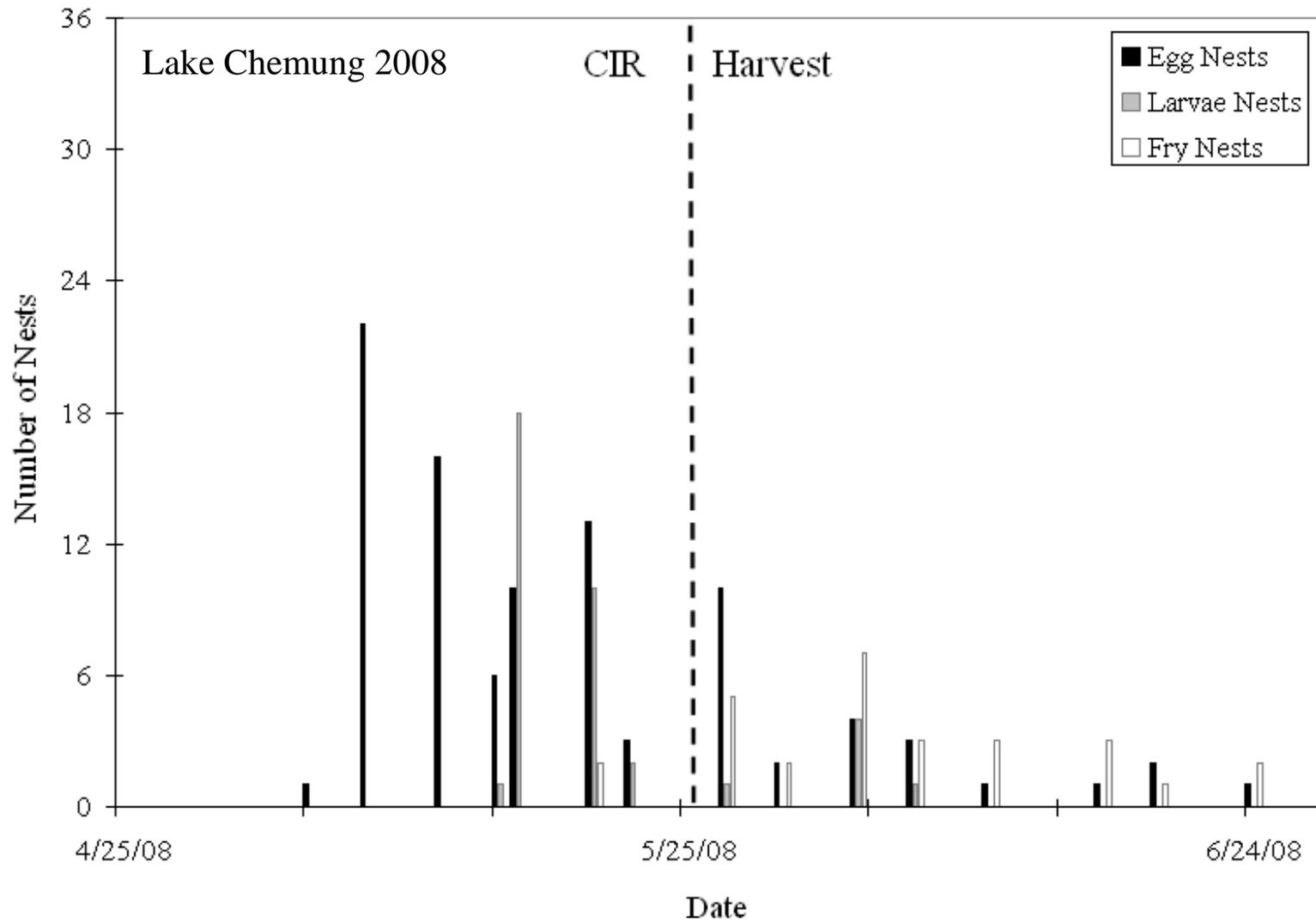
Figure 26: Timing of nests in Lake Chemung during 2008. The harvest season began on May 26, 2008. No nests occurred prior to the CIR season, which began on April 26, 2008.
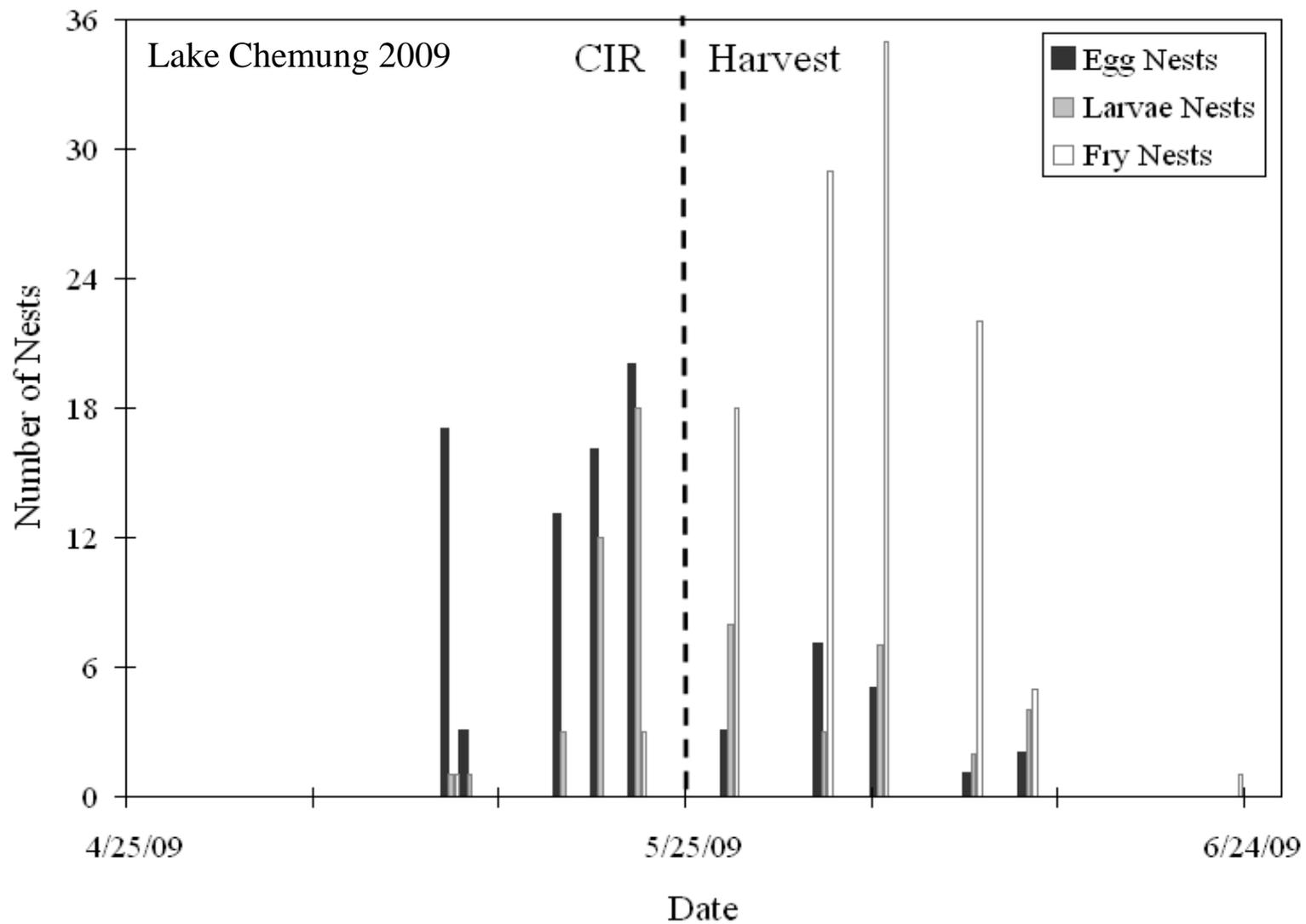
Figure 27: Timing of nests in Lake Chemung during 2009. The harvest season began on May 25, 2009. No nests occurred prior to the CIR season, which began on April 25, 2009.
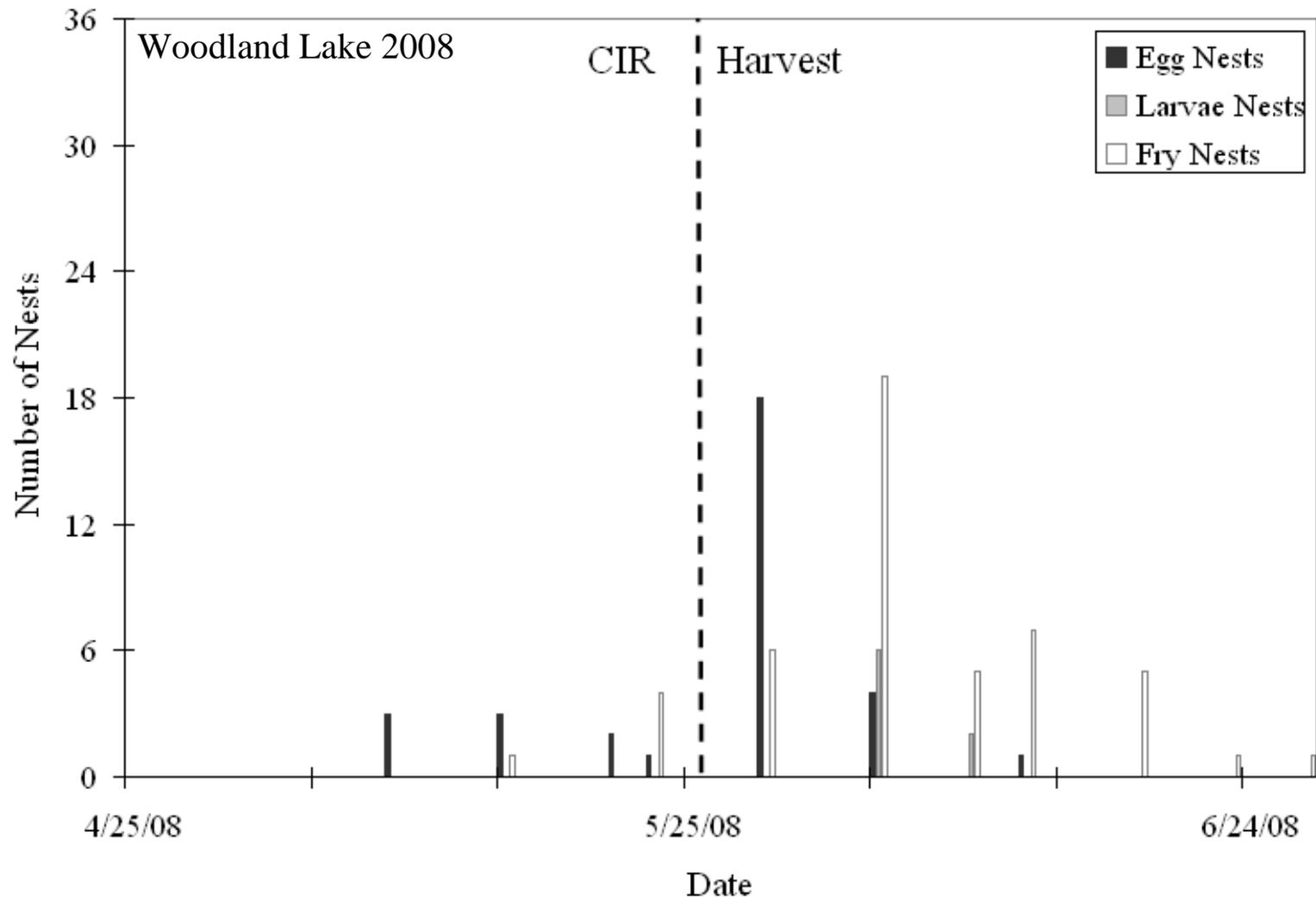
Figure 28: Timing of nests in Woodland Lake during 2008. The harvest season began on May 26, 2008. No nests occurred prior to the CIR season, which began on April 26, 2008.
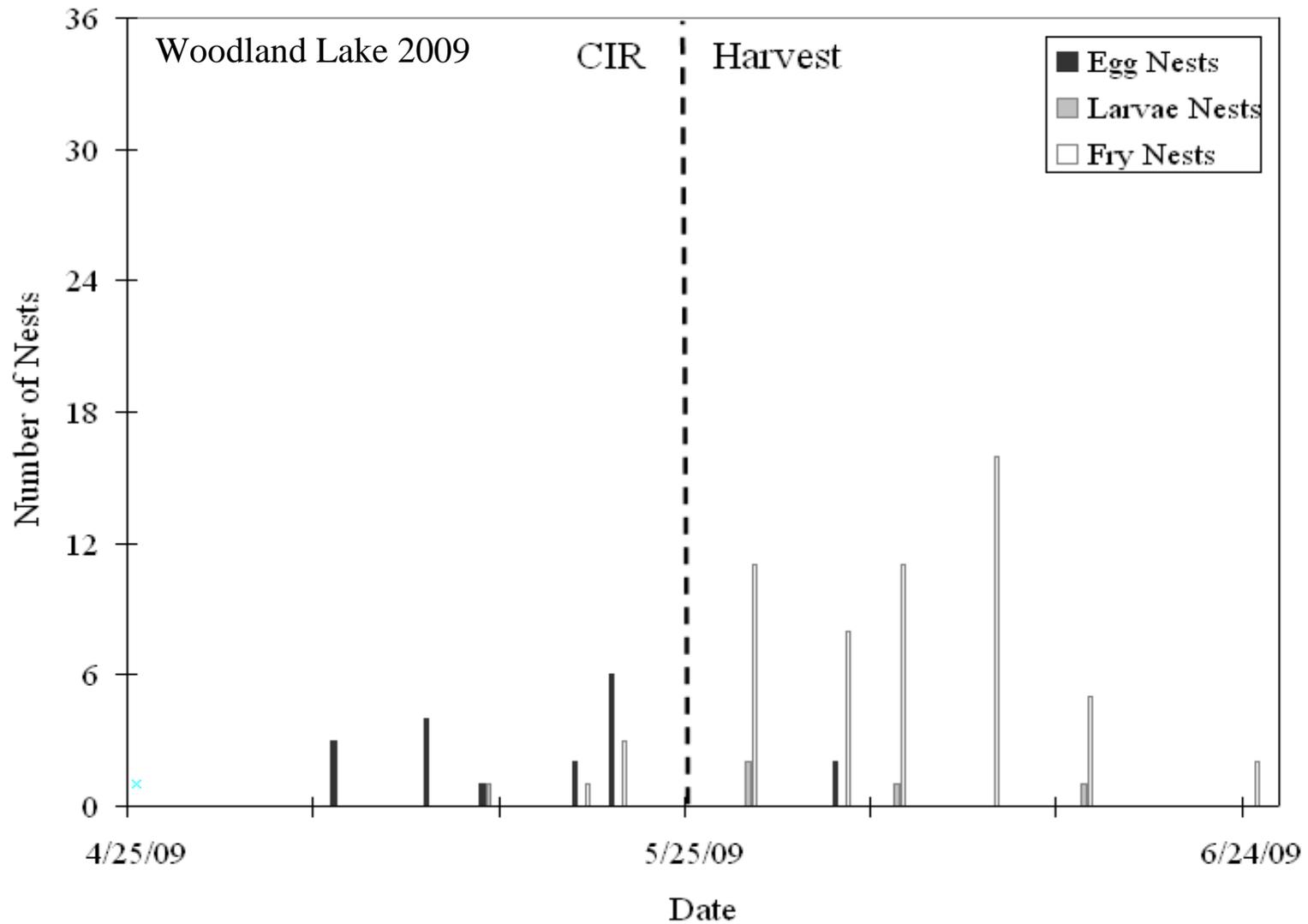
Figure 29: Timing of nests in Woodland Lake during 2009. The harvest season began on May 25, 2009. No nests occurred prior to the CIR season, which began on April 25, 2009.

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**CHAPTER 1**

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# CHAPTER 2

## THE RELATIONSHIPS AMONG SPRING FRY PRODUCTION AND FALL YOY ABUNDANCE AND CONDITION: LINKING NEST SURVIVAL TO RECRUITMENT

<u>Introduction:</u>

Though largemouth bass are popular study organisms, much is still uncertain with regard to factors affecting their recruitment to the population. In particular, the link between spring nest success (production of fry) and recruitment requires further examination because studies generally focus on either reproductive dynamics during the spring nesting season or predator-prey interactions involving young-of-year (YOY) bass during summer and recruitment to the fall or following spring (but see Ridgway and Shuter 1997; Einhouse et al. 2002; Parkos and Wahl 2010). Substantial variation in dynamics throughout the first year of life, both among systems and among years, contributes to uncertainty surrounding spring nest success and its implications for recruitment to the population (Parkos and Wahl 2010). We seek to determine if nest success and production of fry at the end of the nesting period can predict the abundance, size, and condition (a ratio of weight to length) of YOY bass in the fall.

Uncertainty regarding the role of fry production in determining recruitment stems in part from the many factors and life stages that affect recruitment (Post et al. 1998; Kubacki et al. 2002; Parkos and Wahl 2002) and the tendency for many studies to include only a subset of those factors or stages. In particular, few studies calculate estimates of fry production based on observations of nest dynamics as well as estimates of fall YOY abundance. Therefore, the relative importance of fry production and summer survival to recruitment to the fall is infrequently determined.

Ludsin and DeVries (1997) proposed a conceptual model whereby recruitment is affected by four events in largemouth bass early life history: date of hatching, onset of piscivory, fall lipid accumulation, and first winter survival.  They recognized that variation in hatching date alone does not adequately characterize the complexity of offspring survival during nesting.  Indeed, nest survival and resulting fry production are highly variable and are dependent on many biotic and abiotic factors apart from hatching (Ludsin and Devries 1997; Post et al. 1998), such as angling experienced by the nesting male, nesting male bass aggression, nest substrate, and water temperature (see summary in Chapter 1).

Many of these factors can have interrelated effects, with dynamics during one stage potentially affecting those in a subsequent stage.  For example, the timing of hatching affects ontogenetic shifts of YOY largemouth bass to piscivory, with an increased likelihood of earlier-hatching individuals shifting to piscivory before winter, thereby demonstrating the possibility for interconnections among life stages.  Spring YOY bass that hatch later in the season may not be able to shift to a piscivorous diet in the first year, which can result in significant differences in size between early- and late-piscivorous YOY (Post 2003).  Piscivory is linked to fall YOY bass abundance and growth because the abundance of age-0 bluegill during the summer (the predominant food source for piscivorous YOY bass) positively affects the abundance and growth of YOY bass in the fall (Garvey et al. 1998a; Parkos and Wahl 2002).  Because an increase in this food source increases fall YOY bass abundance and growth and because hatch time affects the ability of YOY bass to utilize this food source, the timing of nesting and subsequent hatch date appear important for fall YOY abundance and growth and subsequent recruitment. Complicating this issue, the abundance of YOY bluegill (*Lepomis* spp.) may positively affect fall YOY bass abundance through an alternate mechanism.  Abundant YOY bluegill may yield lower

predation pressure on YOY bass by providing an alternative food source for larger predators (Parkos and Wahl 2010), though there are few studies on the effect of predation on bass offspring through the summer (Parkos and Wahl 2002).

There is conflicting evidence as to whether fall lipid accumulation and first winter survival drive bass recruitment or if fall YOY abundance is the main driver (Ludsin and Devries 1997; Fuhr et al. 2002; Parkos and Wahl 2002; Parkos and Wahl 2010). Fall lipid accumulation is positively related to early onset of piscivory (Ludsin and Devries 1997) and negatively related to density-dependent competition for food during summer (Ridgway et al. 2002). Different results among studies may be due to the use of a variety of study systems; some research is performed in ponds while other work is done in lakes and reservoirs of many sizes and at many different latitudes (latitude and associated severity of winter can strongly affect survival of YOY bass; Fullerton et al. 2000). Modeling and experiments also suggest that fall length and energy stores of YOY bass may or may not be important to winter survival, depending on the type of system (pond, reservoir, etc.), presence of predators, abundance of food for YOY bass, prey forage base, and winter weather conditions (Garvey et al. 1998b; Garvey et al. 2004). It may be true that winter survival is an important bottleneck in recruitment in small systems while recruitment to age-1 is set by survival to the fall in larger systems (Parkos and Wahl 2010).

This study aims to assess the effect of spring fishing on fry production in lakes across a gradient of fishing pressures and to explore the resulting effect on fall YOY largemouth bass abundance and condition. The effects of angling on individual nesting male bass and their brood have been studied extensively (see summary in Chapter 1), but the ways in which angling may affect bass populations require much more investigation. A model of smallmouth bass population dynamics created by Ridgway and Shuter (1997) predicts that an increased likelihood

of catching a nesting male in the spring would have a negative effect on fall YOY abundance because offspring are particularly vulnerable to predators prior to leaving the nest. Increased removal of the bass would result in a decrease in nest success; therefore, increases in spring angling, targeting of nesting male bass, and male bass nest defense behavior in a population (increasing the likelihood of a nesting male bass being angled) are predicted to decrease fall YOY abundance. The simulations predict a dramatic decrease in fall YOY abundance as simulated fishing season start dates move earlier in the nesting season (start dates ranging from extensive to no protection of nesting male bass; Ridgway and Shuter 1997). However, the model's predictions have not been tested in real systems, and there is actually evidence to the contrary. For example, the New York waters of Lake Erie were opened to recreational fishing during the nesting season in 1994, resulting in an increase in angling effort. However, recruitment was more closely related to mean summer water temperatures than to angler effort (the relationship between summer temperature and year-class strength was also documented by Casselman et al. 2002), possibly because nests were too deep for anglers to see (Einhouse et al. 2002). One explanation is that though angler effort increased, it was a relatively small effort compared to the size of Lake Erie. The likelihood of catching a nesting male remained low, so age-0 abundance (and therefore recruitment) may not have been negatively affected by angling.

Survival and growth of YOY bass are often density-dependent, with lower density leading to higher survival and growth (Parkos and Wahl 2002; Ridgway et al. 2002). If survival and growth are density-dependent in our study lakes, then fishing may increase fall YOY condition if it reduces nest success to the point that the density of offspring is reduced and there are more per capita prey items available. However, fishing may also differentially reduce the fitness of nesting bass that are more vulnerable to angling (typically larger and faster-growing individuals)

than others (Biro and Post 2008; Philipp et al. 2009) and may result in populations dominated by smaller, slower-growing bass. To our knowledge, no study has previously explored the link between fishing pressure and spring and fall YOY bass density and condition in lakes.

We examined the link between spring fry production and fall YOY abundance in lakes spanning a range of fishing pressures to explore whether some of Ridgway and Shuter's model predictions (1997) apply to largemouth bass in southern Michigan lakes. Previously, no study has monitored nesting in lakes to obtain a total number of nests in the population, calculated the number of fry produced at each nest, and then sampled the abundance and condition of fall YOY in multiple lakes across a gradient of fishing pressure. Therefore, we sought to determine:

1. Were there positive relationships among the adult stock abundance, the number of nests, the number of successful nests, the number of fry produced in the spring, and the abundance and condition (a ratio of weight to length) of YOY bass in the fall?

2. Was there evidence of density-dependent effects of fry density on fall YOY condition and size?

We expected positive relationships among the number of successful nests, spring fry production, and fall YOY abundance. Because prey abundance is important for survival to the fall, we expected that there would be density-dependent effects of YOY bass density on their fall condition, such that YOY with lower condition would be in lakes with a higher density of spring fry, which we anticipated to be the low fishing pressure lakes.

Methods:

In spring of 2009, crews monitored bass nests in four lakes in southern Michigan that were sufficiently deep to thermally stratify and that contained no surface water connections to other bass populations (Table 1, Chapter 1). Crews monitored nests by visiting each lake

approximately every three days and searching the littoral areas using boats with electric trolling motors to find new bass nests and monitor those nests previously located (as per Raffetto et al. 1990; Wagner et al. 2006; Suski and Ridgway 2007). One observer searched for bass nests from the boat's bow while a snorkeler was harnessed to a tow rope behind the boat at all times to reduce the possibility of missing nests in turbid water. Once a nest was found, crews recorded a GPS waypoint and placed a uniquely-numbered weighted marker at the edge of the nest to aid in locating the nest on subsequent visits.

On sampling dates, crews monitored nests to assess the presence or absence of offspring (either eggs, larvae, or fry) until nests reached the fry stage or were abandoned and failed (Philipp et al. 1997; Steinhart et al. 2004; Suski and Ridgway 2007). Each nest failure was confirmed with two additional visits to ensure that failures were recorded correctly and to reduce the likelihood of misclassification. Crews categorized the fry from each successful nest by size of the school and length of individual fry. Crews categorized school size as small (bowling ball sized, diameter 22 cm), medium (beach ball sized, diameter 51 cm), or large (yoga ball sized, diameter 76 cm), and fry length as small (1-3.49 cm total length) or large (3.5-6 cm).

To estimate the number of fry in a school in each school size/fry length category, crews captured and enumerated fry schools in Patterson Lake (also in southern Michigan), thereby not disturbing nesting bass in our study lakes. Collecting entire schools of fry in one of our study lakes might have caused the guarding males to abandon during sampling or caused harm to the offspring that could have compromised our subsequent analysis of abundance and condition of YOY bass in the fall. In Patterson Lake, when crews located a school of bass fry, they lowered a large corral (approximately 1.5 m x 1.5 m x 1.2 m) from the boat to surround the school of fry. Crews netted any observed fry not captured into the corral using a long-handled dip net. After

this initial capture, we used dip nets to transfer fry from the corral into a container of water in the boat. Crews recorded the total weight of the collected fry and then transferred the fry into a container with slots to subdivide the group into six approximately equal subsamples by volume. Crews randomly selected three of those subsamples, measured the weight of each, and preserved them for abundance and length measurements in the lab. Crews attempted to sample three schools of fry for each school size (bowling ball, beach ball, yoga ball) and fry length (small, large) category, totaling 18 schools sampled. However, sampling constraints resulted in fewer samples than desired and we had no data for some school and fry length categories by the end of the nesting season (see details below). Matt Horsley orchestrated the field sampling and initial analyses of the abundance of fry in each category of school size and fry length as an undergraduate, independent study project.

In each study lake, crews monitored spring angling effort to assess predictions of fishing pressure (see Chapter 1 for an explanation of the method). Woodland and Chemung lakes had relatively higher observed fishing pressure and North and Warner lakes had medium and low observed fishing pressure, respectively. This gradient enabled us to test our predictions that relatively low amounts of fishing would result in more fry production, and higher YOY abundance and lower YOY condition in the fall.

To estimate fall YOY largemouth bass relative abundance, crews used seines and fykenets in haphazardly selected locations throughout the littoral zone of each lake where the habitat was suitable for each gear type (sampling dates ranged from August 19-27 and August 28-September 16, 2009 for seines and fykenets respectively). We preserved each YOY in 100% ethanol to take measurements of length and weight in the lab. Amount of sampling effort varied among lakes because of widely divergent catch rates among lakes (see Table 37 in Results).

Crews also captured bass in the fall using pulsed DC boomshocker boats along the entire shoreline of each lake to estimate adult (> 228.6 mm) stock abundance.  Crews conducted the surveys on four consecutive nights (September 27-October 1, 2009) to estimate bass population abundances and size distributions for each lake using Schumacher-Eschmeyer mark-recapture methods (Schneider 1998).  Our method used the multiple census approach to obtain population estimates (see below for details).

*Analysis*

First, we calculated the number of fry in each of the schools captured in Patterson Lake (representing a category of school size and fry size) by using the equation:

$$\text{Number of Fry in School} = \frac{\dfrac{A_1 \times S}{W_1} + \dfrac{A_2 \times S}{W_2} + \dfrac{A_3 \times S}{W_3}}{3}$$

where $A_i$ is the abundance of fry in a subsample $i$, $W_i$ is the weight of the subsample $i$, and $S$ is the weight of the fry school.  Our estimated number of fry in a school represented an average across the three subsamples and was based on the assumption that the ratio of the weight of fry in a subsample ($W_i$) to number of fry in the subsample ($A_i$) was equal to the ratio of the total number of fry in the school to the total weight of the school ($S$).  We generated extrapolated estimates of total fry abundance for fry school categories that we did not observe in Patterson Lake from categories for which we had data by using a multiplier based on the relative volume of each reference ball size (Table 35).  Finally, we used the extrapolated estimates of fry abundance per category to assign values of estimated number of fry produced from each successful nest in our study lakes, based on each nest's observed school size/fry length category. We summed the values across nests within a lake to generate a lake-wide estimate of total

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number of fry produced and divided this sum by lake area to generate an estimated spring fry density (fry/ha) for each lake.

Table 35: Estimates of number of fry in each school size/fry length category.  Italics indicate that fry abundance estimates for that category were extrapolated from data in another category, using the volume of each reference ball size.

| School Size | Diameter (cm) | Volume (cubic cm) | Fry Length | |
|---|---|---|---|---|
| | | | Small | Large |
| Bowling | 22 | 5269 | 77 | *16* |
| Beach | 51 | 68642 | 1009 | 204 |
| Yoga | 76 | 231667 | *3404* | 551 |

In each study lake, we determined the total number of nests observed and the total number of successful nests (those producing free-swimming fry) based on our spring observations. We calculated the average catch-per-effort (CPE) of largemouth bass YOY caught during late summer/early fall in the seines and fykenets by gear type for each lake.  We used CPE to represent the relative abundance of fall YOY in each lake.  We recorded the total length and preserved weight of each YOY and calculated Fulton's condition for each fish (Ney 1999), which assumed isometric growth, using the equation:

$$K = \frac{W \times X}{L^3}$$

where the condition of an individual fish ($K$) is a function of its preserved weight ($W$), total length ($L$) and a scaling constant ($X$).  $X$ equals 100,000 for metric units, which we used in this study.

We used Schumacher-Eschmeyer mark-recapture formulas to calculate adult stock abundance (bass greater than 228.6 mm) for regression against spring nesting data (Ricker 1975 as cited in Schneider 1998).  We calculated adult stock abundance using the formula:

$$N = \frac{\sum\limits_{d=1}^{n} C_d M_d^2}{\sum\limits_{d=1}^{n} R_d M_d}$$

where $N$ is the population estimate in number of adult fish, $C_d = U_d + R_d$ , the total number of

fish caught during day $d$, $U_d$ is the number of unmarked fish caught during day $d$, $R_d$ is the

number of recaptures during day $d$, and $M_d$ is the number of marked fish available for recapture

at the start of day $d$.

To calculate the 95% confidence interval of $N$ we first determined the sample variance and

from that the variance and standard error of N using the equations:

$$s^2 = \frac{\sum\limits_{d=1}^{n}\left(\frac{R_d^2}{C_d}\right) - \left[\frac{\left(\sum\limits_{d=1}^{n} R_d M_d\right)^2}{\sum\limits_{d=1}^{n} C_d M_d^2}\right]}{m-1}$$

where $s^2$ is the variance of samples and $m$ is the number of days in which fish were actually

caught and

$$\text{Variance of N} = N^2\left(\frac{Ns^2}{\sum\limits_{d=1}^{n} R_d M_d}\right),$$

$$\text{Standard error of N} = \sqrt{\text{Variance of N}},$$

$$\text{95\% confidence limits of N} = N \pm t(\text{Standard error})$$

where Student's $t$ is based on $m$-1 degrees of freedom.

We performed a regression analysis for each relationship of interest (adult stock abundance and the number of nests, number of successful nests and the number of fry produced, number of fry produced and fall YOY abundance, spring fry density and fall YOY total length, preserved weight, and condition factor). The number of fry produced was not necessarily expected to increase with the total number of successful nests in a lake. The number of fry produced was expected to be dependent upon the number of successful nests as well as the percentage of nests that produced fry in each school size (a lake may have many nests with mainly bowling ball-sized schools of fry, but still have fewer fry produced than a lake with fewer nests with mainly yoga ball-sized fry schools). Because there were only four data points contributing to our lake-level regressions, we intended our analysis as an exploration of relationships among variables. Future lake-years of data would greatly contribute to assessing the consistency of the relationships we documented.

Results:

The adult stock abundance estimates from three of the lakes (Chemung, North, and Warner) were very similar, which was surprising because Warner Lake was much smaller than the other lakes. Woodland Lake had approximately three times as many adult fish as any of the other lakes (Table 36).

Table 36: Estimates of adult stock abundance in each lake with 95% confidence intervals. Lakes are in order of low to high fishing pressure. Cut off length for determination of the stock abundance of sexually mature fish was 228.6 mm.

| Lake | Area (ha) | Adult Stock Abundance Estimate | 95% Confidence Interval |
|---|---|---|---|
| Warner | 26 | 912 | 537-1287 |
| North | 91 | 1093 | 591-1594 |
| Chemung | 126 | 1180 | 893-1466 |
| Woodland | 104 | 3382 | 3117-3646 |

Lakes substantially varied in the number of nests and the number of successful nests in each

lake as well as the estimated number and density of fry produced (Table 37). Variables

associated with fall fyke netting and seining of YOY bass (catch per effort, length, weight, and

condition) also varied considerably among lakes. Catch rate of YOY bass was much lower in

North and Warner lakes than in the high fishing pressure lakes, Chemung and Woodland.

Therefore, we conducted more fyke netting in Warner and North lakes in efforts to increase their

sample size contributing to YOY CPE, length, and condition estimates.

Table 37: Summary of data used in regression analysis. Lakes are in order of low to high fishing pressure. Cut off length for determination of the stock abundance of sexually mature fish was 228.6 mm.

|  | Warner | North | Chemung | Woodland |
| --- | --- | --- | --- | --- |
| Adult Stock Abundance >228.6 mm | 912 | 1093 | 1180 | 3382 |
| Number of Observed Nests | 35 | 56 | 138 | 66 |
| Number of Successful Nests | 30 | 22 | 91 | 53 |
| Total Fry Produced | 14464 | 12852 | 54692 | 27088 |
| Total Fry Produced/ha | 556 | 141 | 434 | 260 |
| Total Seine Catch of YOY | 1 | 4 | 65 | 19 |
| # Seine Hauls | 3 | 5 | 5 | 5 |
| Total Fykenet Catch of YOY | 1 | 5 | 139 | 61 |
| # Fykenets Set | 12 | 12 | 6 | 6 |
| Mean YOY CPE in Seines | 0.012 | 0.020 | 0.585 | 0.135 |
| Mean YOY CPE in Fykenets | 0.005 | 0.022 | 1.278 | 0.416 |
| Mean YOY Length in Seines (mm) | 47 | 68 | 56 | 61 |
| Mean YOY Length in Fykenets (mm) | 53 | 63 | 64 | 66 |
| Mean YOY Weight in Seines (g) | 0.87 | 2.60 | 1.55 | 2.07 |
| MeanYOY Weight in Fykenets (g) | 1.34 | 2.17 | 2.36 | 2.66 |
| Mean YOY Seine Condition | 0.84 | 0.78 | 0.85 | 0.87 |
| Mean YOY Fyke Condition | 0.90 | 0.94 | 0.87 | 0.89 |

We detected no positive relationship between adult abundance and the number of nests in

each lake (Figure 30). Assuming a 50:50 sex ratio of adults, this suggests that lakes range from

~4% to ~23% of adult males guarding observed nests (i.e., 66 observed nests in Woodland

represents ~4% of adult stock abundance (3382) divided by 2). The relationship between the

adult stock abundance and the number of successful nests (those that produced fry) also lacked a significant relationship ($p > 0.05$, $R^2 = 0.023$). In both cases, Lake Chemung, one of our high fishing pressure lakes, typically had more than double the number of nests (and successful nests) than the other three lakes, even though Chemung's adult stock abundance was the same as North and Warner's and less than Woodland's abundances.
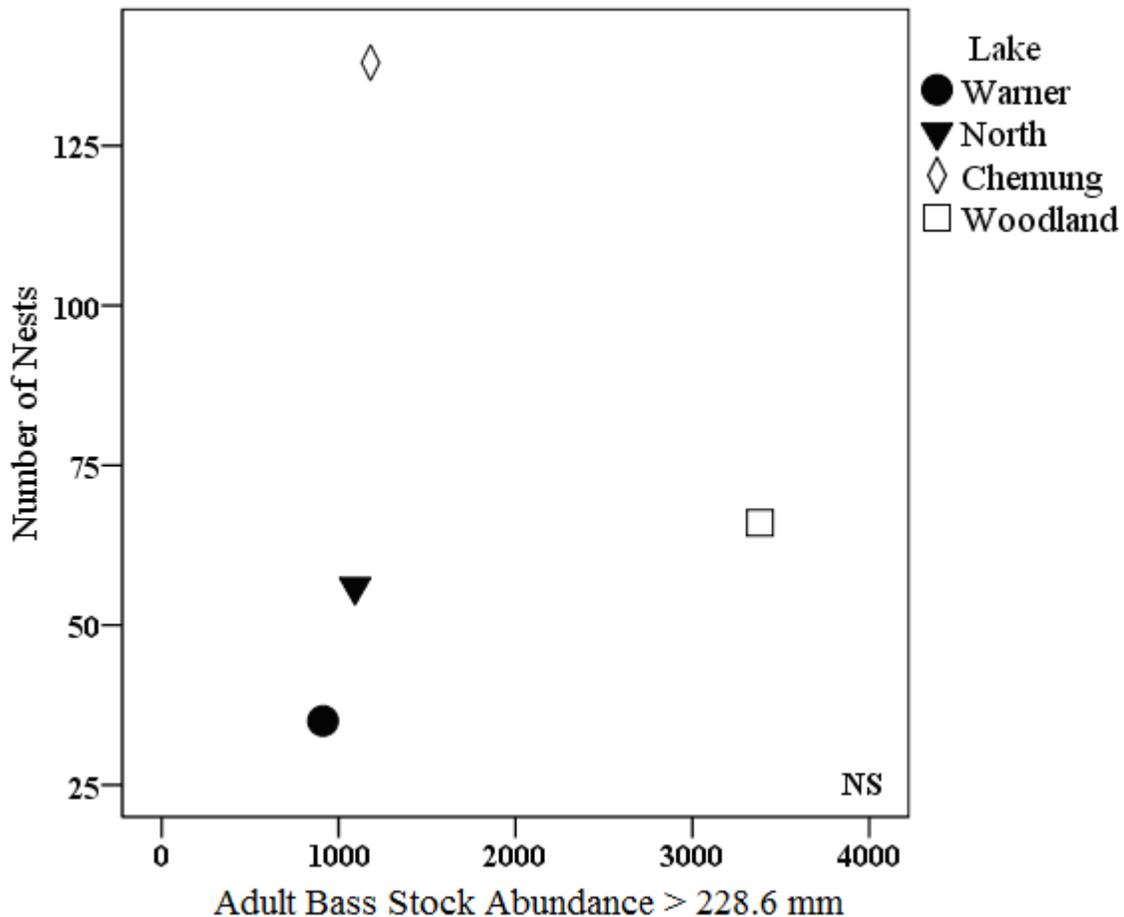


Figure 30: Relationship between the number of nests in a lake and the abundance of adult bass (> 228.6 mm). High fishing pressure lakes are denoted by open symbols while low to medium fishing pressure lakes are represented by closed symbols. The regression was not significant.

We found fairly consistent representation of each school size/fry length category in all lakes (Table 38). The most common fry school category observed in all lakes was a yoga ball-sized school containing large fry. Therefore, we expected a strong positive relationship between the number of successful nests and the number of fry produced (there may have been no relationship

if the numbers of fry schools in each category varied among lakes). Regression analysis

supported this expectation (Figure 31). Interestingly, the lakes with high fishing pressure had a

higher number of successful nests and more fry produced. Warner Lake was much smaller than

the other lakes, so a relatively low number of nests was expected. However, North Lake also had

a low number of nests and a low number of successful nests, which we had not anticipated.

Overall, a similar regression using estimated total abundance of fry per ha (fry density) also

revealed a significant, positive relationship between density of successful nests and fry density,

although the order of lakes in terms of fry density, as compared to fry abundance, was different.

Table 38: The percent of each category of fry school observed in study lakes, which are in order of low to high fishing pressure. In the fry category column, fry school size is listed first (reference ball size) and then length of individual fry (small, <3.5 cm or large, ≥3.5 cm).

| Fry Category | Warner | North | Chemung | Woodland |
|---|---|---|---|---|
| Bowling, Small | 13% | 4% | 4% | 17% |
| Bowling, Large | 5% | 17% | 7% | 4% |
| Beach, Small | 18% | 4% | 5% | 2% |
| Beach, Large | 5% | 21% | 29% | 17% |
| Yoga, Small | 0% | 8% | 4% | 4% |
| Yoga, Large | 59% | 46% | 52% | 56% |
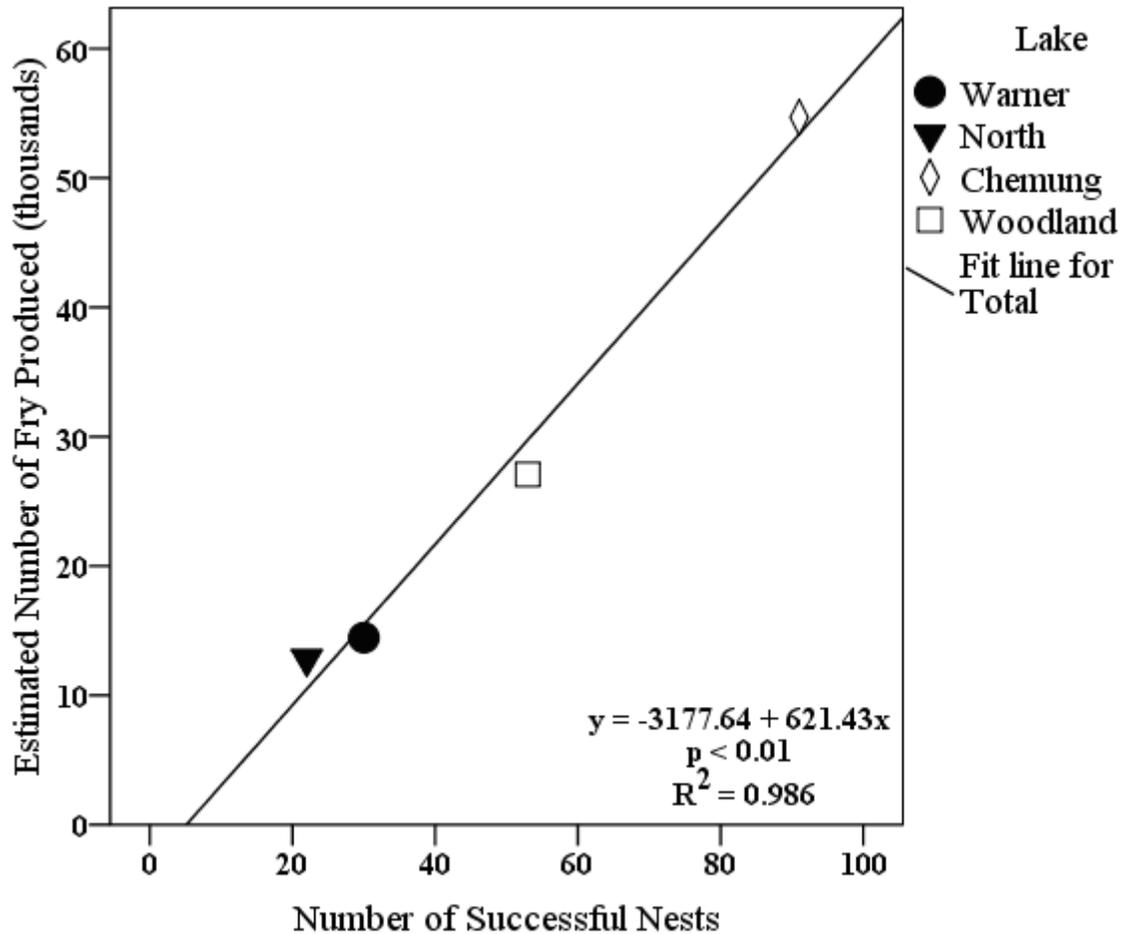
Figure 31: The relationship between the estimated total number of fry produced in thousands and the number of successful nests observed in each lake. High fishing pressure lakes are denoted by open symbols while low to medium fishing pressure lakes are represented by closed symbols.

As anticipated, the number of fry produced in the spring had a strong positive relationship with the relative abundance of YOY bass in the fall (Figure 32). As a result, the lakes with high fishing pressure had the largest abundances of fall YOY. This finding was consistent with the positive correlation between numbers of successful nests and fry production (high fishing pressure lakes had higher overall numbers of successful nests). Considering the relationship between YOY CPE and fry density, a positive relationship remained among North, Chemung, and Woodland lakes, but Warner Lake, with its high fry density but low YOY CPE did not correspond to this relationship.
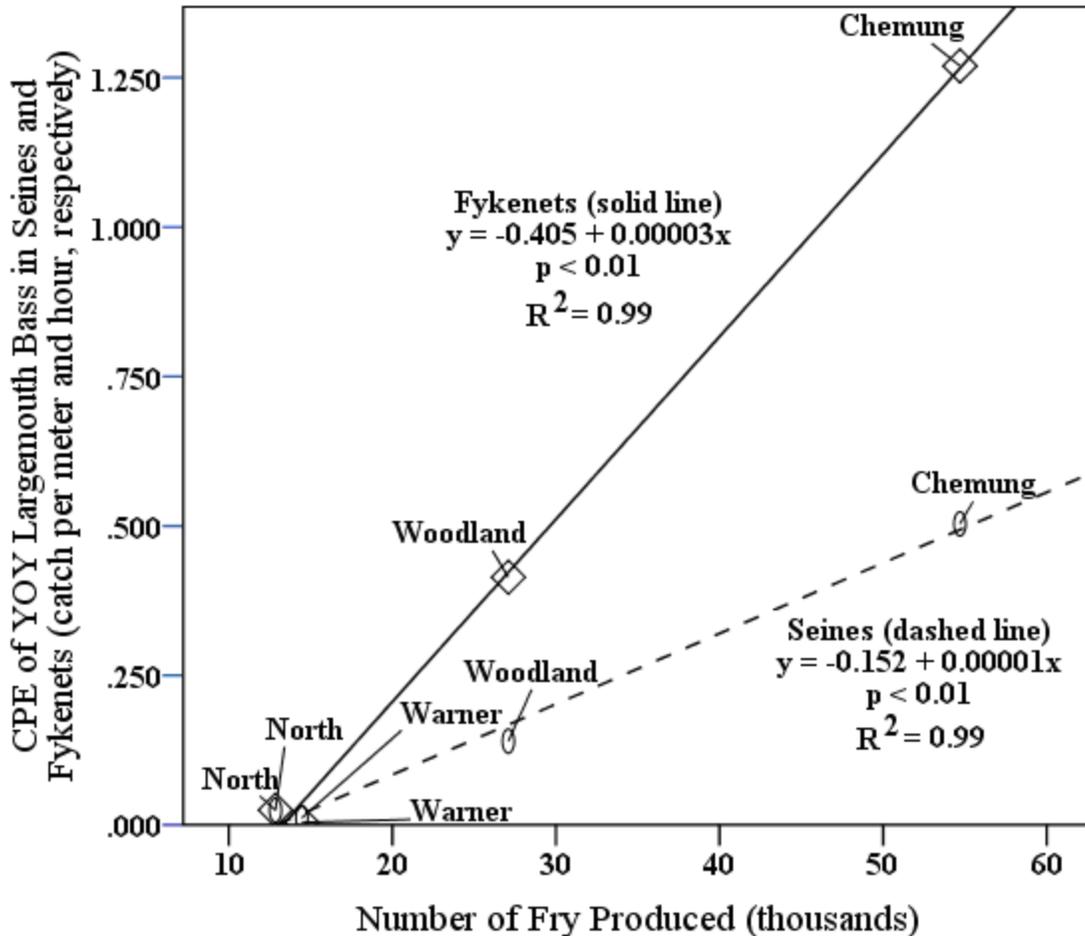
Figure 32: The relationship between the number of fry produced in thousands and the CPE of YOY largemouth bass in the fall by lake. Data from seine hauls are represented by ovals and a dashed line while fykenet data are represented by diamonds and a solid line. North and Warner lakes are the low to medium fishing pressure lakes, but are not shaded due to overlapping symbols.

To assess if density-dependent processes appeared to be affecting YOY bass condition, we regressed mean condition (Fulton's K) of YOY bass in each lake as a function of bass fry density. Counter to our expectations, there was no apparent relationship between these variables (Figure 33). Interestingly, the condition of YOY bass caught in fykenets tended to be higher than the condition of YOY caught in seines, on average.
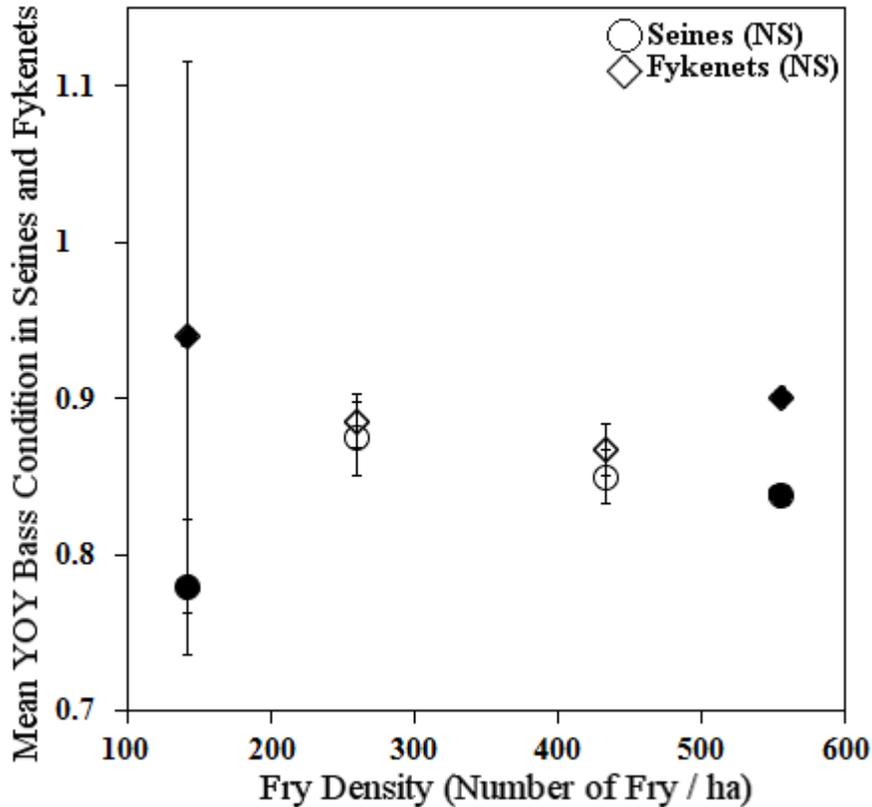
Figure 33: Regression analysis between mean YOY bass condition and fry density by lake. Data from seine hauls are represented by ovals while fykenet data are represented by diamonds. High fishing pressure lakes are denoted by open symbols while low to medium fishing pressure lakes are represented by closed symbols. Error bars represent +/- two standard errors.

The apparent lack of an effect of fry density on fall YOY condition was unexpected, so we performed a regression analysis to explore the impact of spring fry density on fall YOY lengths and weights rather than condition. We expected a negative effect of density on YOY length and weight. The results of the analysis were mixed, with a significant relationship showing smaller YOY (in terms of both length and weight) in lakes with high density fry for data obtained from seines, not no significant relationship for fykenet data (Figure 34). Absolute size may or may not have differed among the lakes. It appeared that YOY bass with the lowest mean total length (TL) were in Warner, in which fry density was highest, and the highest mean TL estimate of YOY bass was in North Lake where fry density was lowest (Figure 34). A lack of data precludes further inference about this relationship (only 2 YOY bass were caught in Warner Lake, 1 in

each gear type). Although the range of YOY bass lengths collected in each lake differed somewhat in accordance with the trends in mean length, the relationship between YOY TL and YOY preserved weight did not appear to differ among lakes (Figures 35 and 36), consistent with our analysis that condition factor did not vary substantively among lakes.
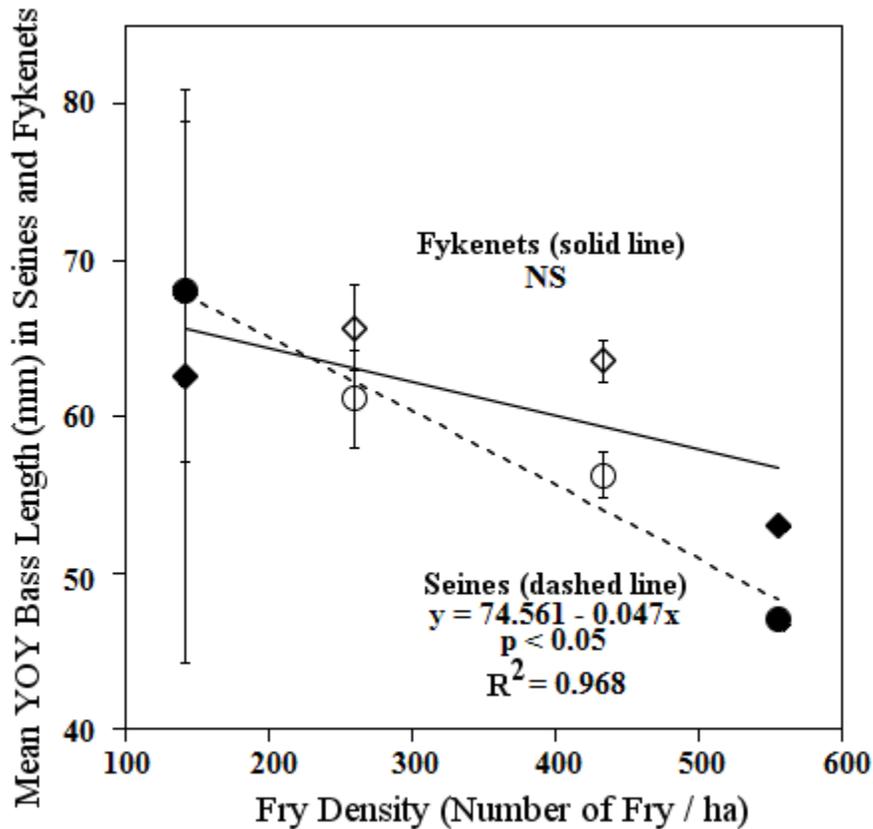


Figure 34: Regression analysis between average YOY length and fry density by lake. Data from seine hauls are represented by circles while fykenet data are represented by diamonds. High fishing pressure lakes are denoted by open symbols while low to medium fishing pressure lakes are represented by closed symbols. Error bars represent +/- two standard error. The relationship was significant for data obtained from seine hauls, but not for those from fykenets. Results for the relationship between average weight of YOY caught in seines and fykenets and fry density were similar ($R^2$ of 0.986 and 0.410 [NS], respectively).
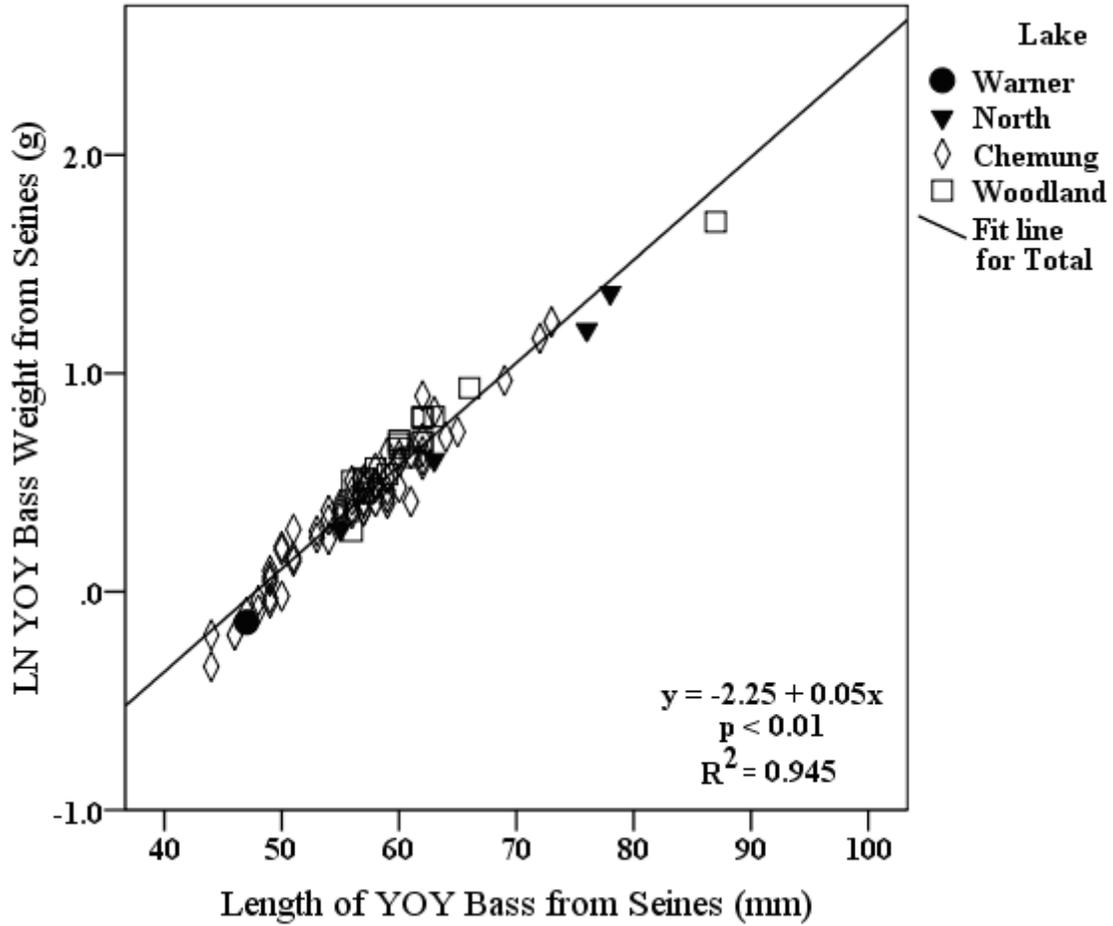
Figure 35: Relationship between fall YOY bass length and bass weight by lake from seine data. High fishing pressure lakes are denoted by open symbols while low to medium fishing pressure lakes are represented by closed symbols.
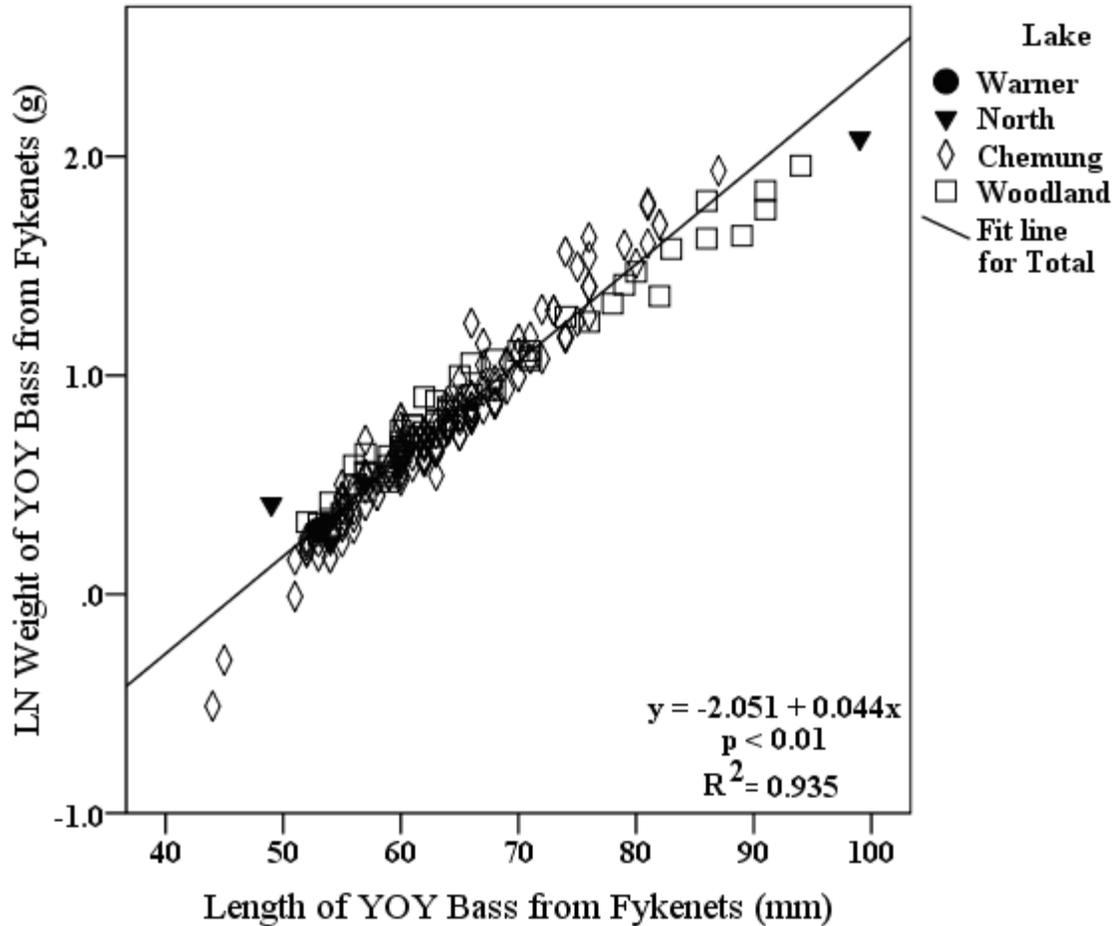
Figure 36: Relationship between fall YOY bass length and bass weight by lake from fykenet data. High fishing pressure lakes are denoted by open symbols while low to medium fishing pressure lakes are represented by closed symbols.

## Discussion:

Our data clearly showed positive relationships among nest abundance and success, fry production, and abundance of fall YOY largemouth bass. Though it is unclear from the literature if recruitment strength is set pre- or post-winter, a high abundance of fall YOY is desirable for strong recruitment if there is no negative effect of density on fish condition. Evidence for fall YOY abundance as an important determinant of recruitment is strong (Parkos and Wahl 2002; Parkos and Wahl 2010), and our data positively linked fall YOY abundance to the number of successful nests and spring fry production. One caveat exists in our data apart from sample size; our smallest lake (Warner) had the second lowest estimate of total number of fry produced, but

the highest value of estimated fry density. Therefore, high fry density in Warner Lake corresponded to low YOY CPE, indicating that summer survival of YOY bass may have been substantially lower in this lake than in the other lakes, complicating our understanding of the relationship between fry production and YOY abundance. Overall, our analysis indicated that spring nest success can be an important factor in determining recruitment strength, which is supported by Ludsin and DeVries's conceptual model (1997). As a result, factors that affect nest success are of importance to fisheries managers interested in managing bass recruitment.

Our comparison across lakes generally supported a positive relationship between success during the nesting stage and recruitment. However, the relative ordering of our lakes was quite different from what we expected, considering how levels of spring angling varied among them. Spring angling has often been cited as a factor that can strongly affect success of individual nests and possibly population recruitment (Kieffer et al. 1995; Philipp et al. 1997; Ridgway and Shuter 1997; Cooke et al. 2000; Suski et al. 2003). Therefore, we expected lower CPE of YOY bass in our high fishing pressure lakes. To the contrary, our high fishing pressure lakes (Chemung and Woodland) had the highest numbers of successful nests, fry production, and fall YOY abundance. This finding was not due to differences in surface area among lakes, because North Lake was similar in size to both of the high fishing pressure lakes and had low fry production and fall YOY abundance. However, high numbers of successful nests in our high fishing pressure lakes may have been due to the positive relationship between number of nests observed and the number of successful nests (Chemung and Woodland lakes had higher numbers of nests than North or Warner, Figure 30). Further evidence that high angling pressure alone does not lead to relatively low recruitment is that Warner Lake, which had the lowest fishing pressure, had very high fry density but a very low CPE of fall YOY bass. Therefore, even if angling had a

negative effect on bass recruitment in our high fishing pressure lakes, other factors overrode that negative effect, resulting in higher recruitment in these popular fishing lakes than in our less angled ones (see below for additional consideration of this topic).

As another unexpected finding from our analysis, fall YOY condition and spring fry density were unrelated, indicating that YOY bass in our high fishing pressure lakes with high fry production did not have relatively low fall YOY bass condition as a result, which would have called into question the likelihood of their overwinter survival. Though the condition of YOY bass in our high fishing pressure lakes may have been relatively high in comparison to our low and medium fishing pressure lakes, the condition of YOY bass in our lakes may have been poor overall, given that no bass's condition was greater than 1. A study of smallmouth bass in Maine reported values of fall YOY condition near 1.4 (Willis 2006), which are higher than any values that we observed (average fall YOY bass condition ranged 0.78-0.94 across lakes). If all of the bass that we sampled were in relatively poor condition in comparison to other systems, then there may have been a minimum condition level that YOY bass needed to survive to the fall that affected our analyses. We may not have observed YOY bass with those low condition values if they died prior to sampling. Missing those data would have affected our ability to detect a relationship between spring fry density and fall YOY condition. Another complicating factor was the fact that fykenets were set over a longer period of time in Warner and North lakes (effort was increased due to low initial catches). YOY bass caught in these later fykenets tended to be larger and have higher condition than those caught in seines in the same lake because they had had more time to grow.

Availability of prey items is an important determinant of survival to the fall (Parkos and Wahl 2010) and fish condition may be an important factor in overwinter survival (Ludsin and

DeVries 1997), so we expected competition to occur among YOY bass in lakes with high densities of fry. Unfortunately, we did not have data on food availability in these lakes, so we could not directly include prey availability in our analysis. Though there was no evidence of intraspecific competition resulting in poor condition in our data, YOY bass in Warner Lake, which had high spring fry density, generally were shorter and less heavy than YOY bass in the other three lakes. Because so few YOY bass were captured in North and Warner lakes (9 and 2 fish, respectively), we hesitate to place strong emphasis on this relationship. However, the smaller size of the relatively few YOY bass captured in Warner Lake suggests that growth rates of age-0 bass may have been lower in this lake or hatch dates of survivors may have been later in this lake, resulting in a shorter growing season for survivors. We did not measure the amount of cannibalism that occurred, but it has been observed in other bass populations (Swenson 2002) and may have also complicated the relationship between spring fry density and fall YOY abundance and condition.

Overall, studies of the effect of pre-winter size structure on overwinter mortality and recruitment have had mixed results. Studies supporting a relationship between size structure and winter mortality include Ludsin and DeVries (1997), Post et al. (1998), and Curry et al. (2005). In contrast, Garvey et al. (2004) suggested a relationship only under certain conditions, and Parkos and Wahl (2010) observed no relationship.

Our data allow an opportunity to assess the relationship between adult bass abundance and nest abundance, which has implications for our understanding of stock-recruitment relationships in bass populations. Adult bass abundances were similar in all of our lakes except Woodland Lake (which had a higher abundance), and we did not observe any obvious linear relationship between adult largemouth bass stock abundance and the number of nests. Adult bass abundance

was unlikely to be correlated strongly with nest abundance because a relatively small percentage of sexually mature adults nest in a particular year (Raffetto et al. 1990). In our study, estimates of percent of adult males that were observed nesting ranged 4-23%. Because it is unlikely that our crews observed all nests, our values may underestimate the actual percent of adults that guard nests in any individual year. Overall, our findings lend support to the statement that the conventional wisdom that bass lack a strong stock - recruitment relationship is not evidence that events during the nesting stage are not important to recruitment, rather that many factors influence nesting and recruitment in complex ways.

Studies have previously shown that nest success varies among lakes and is negatively related to fishing (Philipp et al. 1997; Saunders et al. 2002; as summarized in Steinhart et al. 2005). However, we found no statistically discernible differences in nest survival probabilities by lake from *a priori* modeling in Chapter 1. We observed differences in survival between seasons and *post hoc* modeling suggested that lakes with high fishing pressure had higher levels of nest survival than low to medium fishing lakes. We hypothesized that high fishing pressure lakes may contain more productive bass populations even when experiencing the levels of angling observed in our study, but that within a lake, high levels of fishing have a negative effect (which is why we observed lower nest survival in the harvest season, particularly in our high fishing pressure lakes; see Chapter 1's *post hoc* model). We also demonstrated that nest survival probabilities were related to the success rate of nests when timing of nesting was considered as a mitigating factor.

In this chapter, we observed that the high fishing pressure lakes had the highest number of successful nests and produced the most fry, which lends some support to our hypothesis that high fishing pressure lakes may contain more productive bass populations. Survival probabilities,

nest success, fry production, fall YOY abundance, and population recruitment are all interrelated. Further exploration into these relationships is needed before any conclusive statements can be made because we had only four lakes, one year of data, and small catches of YOY bass in some lakes. As such, our study design takes a 'space for time' approach, inferring that differences documented among lakes, in relation to their levels of fishing pressure, represent the dynamics that would occur within a lake, if fishing pressure were to change. Additional studies are needed that follow the temporal dynamics of individual lakes (and fishing pressure) over time and that experimentally modify fishing pressure within lakes. Despite the limitations on interpretation of our small dataset (in terms of number of lakes and years), our data strongly suggest that timing of high levels of spring fishing is an important factor affecting spring nest survival and success (Chapter 1) and that a higher abundance of successful nests yields more fall YOY (Chapter 2). However, differences among lakes (due to other, unidentified factors) also drive variation among lakes in terms of nest survival and bass population demographics. Management agencies may want to explore actions that would increase nest survival, which may strongly influence fall YOY abundance for bass populations with poor recruitment.

**LITERATURE CITED**

**CHAPTER 2**

# LITERATURE CITED

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