

Smallmouth Bass Nest Site Selection and Success in Four Northern Wisconsin Lakes:

Linking Habitat Selection with Habitat Quality

By

Rory Saunders

A thesis submitted in partial fulfillment of the requirements of the degree

Master of Science

College of Natural Resources

University of Wisconsin – Stevens Point

Stevens Point, Wisconsin

August, 2006

Approved by the committee of:

---

Dr. Michael A. Bozek, Chair

---

Dr. Eric M. Anderson

---

Dr. Neal D. Niemuth

## **Abstract**

Habitat models based on nest site selection and spawning success are important in understanding the effects of riparian area and littoral zone alterations on smallmouth bass (*Micropterus dolomieu*) survival and recruitment. A common approach to developing habitat models is the use of resource selection functions that determine the relative probability of use of particular subsets of available habitat. Application of these models presupposes that habitat selection infers habitat quality and study of both are critical to testing this assumption. The objectives of this study were to assess smallmouth bass nest site selection, to evaluate nest site quality, and to assess the relations between habitat selection and habitat quality. Smallmouth bass nest characteristics and egg survival were quantified on four lakes in the summers of 1997 to 2000. Habitat variables were quantified at each nest site and along random transects that were placed perpendicular to the shoreline to a depth of three meters, which corresponds to the maximum depth that nests are found in the study lakes. Eggs and pre swim-up fry were estimated at each nest site to quantify individual nest success. Resource selection functions (i.e., logistic regression) were used to elucidate habitat features used disproportionately as nest sites. Nest site quality was quantitatively evaluated using egg survival and fry production as dependent variables and nest site characteristics as independent variables. Linear regression was used to assess the relations between habitat selection (i.e., probability of selection) and habitat quality (i.e., survival and fitness). Habitat variables that predicted nest site selection as well as those that predicted nest site quality were variable across lakes and across years. The percent gravel in a nest and its proximity to cover (e.g., wood or rock) were the most common variables present in both habitat selection models

and habitat quality models. Our results also show that habitat selection only inferred habitat quality when adult population densities were high ( $> 10$  adults per hectare) and thus high quality habitat was saturated. These results suggest that models based on habitat selection may only reflect habitat quality under specific conditions where habitat is limited.

## **Acknowledgements**

I thank the Wisconsin Cooperative Fishery Research Unit, U.S. Forest Service, Wisconsin Department of Natural Resources, and Dairymen's Inc. for technical and financial support for this study. These contributions gave me the opportunity to obtain a Master of Science degree from the University of Wisconsin – Stevens Point, and for that I am truly grateful.

Much thanks goes to my major advisor, Dr. Michael Bozek. His patience, understanding, and encouragement have made me a better scientist and a better person. He was especially helpful in preparing various presentations that I made along the way. He never let me make a total fool of myself but did allow me the freedom to say things the way that I felt they needed to be said. I thank Dr. Eric Anderson and Dr. Neal Niemuth for helping me understand the math behind the science, especially when I first arrived on campus. Steve Newman and Gary Kubenick were helpful throughout each of my summers in Boulder Junction. I also thank Mr. Fred Kircheis and Dr. Joan Trial for their encouragement and guidance when I began looking into graduate school.

Many of my peers were a tremendous help as well. Pat Short was especially helpful. His assistance allowed me to gather two very solid years' worth of data. He was also a good friend to the new guy in town. Kris Stepenuck, Mike Wilberg, Aaron Frey, Matt Catalano, Benjamin Torrison, and Brian Kray all took time out of their busy schedules to help me out in the field. I am forever indebted to Brian Perzentka. He gave up an entire summer to help me collect data. He never became discouraged even when he found out that we would be sharing a tiny apartment (with no bathroom door) all summer. He was always fun to have around and made the summer fly by.

Finally, I wish to thank my family for love and support over the past two years. I thank my mother, Lynnette Barnes, for her unending encouragement. Though I have not been the best son (she did not hear from me for an entire month my first summer in Wisconsin), she has always been there when I needed news from home or simply to hear that she is proud of me. I also thank my mother-in-law and father-in-law, Rita and Richard Hitchcock, for continuous updates from Maine and for raising a perfect daughter. Which brings me to Alyson. I thank you for putting up with me and for being the best companion I could ever ask for.

## Table of Contents

List of Tables.....	ix
List of Figures.....	xi
Background.....	1
Smallmouth bass biology.....	1
Impetus for the study.....	3
Habitat modelling.....	6
Objective 1.....	7
Objective 2.....	8
Objective 3.....	9

### Chapter I: Habitat features affecting smallmouth bass nesting success in four northern

Wisconsin lakes.....	10
Abstract.....	10
Introduction.....	11
Methods.....	13
Study area.....	13
Data collection.....	13
Analyses.....	19
Results.....	19
Discussion.....	34

Chapter II: Linking habitat selection with habitat quality.....	39
Abstract.....	39
Introduction.....	40
Methods.....	44
Study area.....	44
Available habitat.....	44
Used habitat.....	48
Habitat selection.....	50
Habitat quality.....	51
Assessing relations between habitat selection and habitat quality.....	52
Results.....	53
Available habitat.....	53
Used habitat.....	55
Habitat selection.....	58
Habitat quality.....	63
Relations between habitat selection and habitat quality.....	66
Discussion.....	71
Appendix A.....	76
Appendix B.....	77
Appendix C.....	78
Appendix D.....	79
Appendix E.....	80
References.....	83



## List of Tables

- Table 1. Limnological features of the four study lakes.
- Table 2. Nest site habitat characteristics used in analyses of smallmouth bass nest site quality.
- Table 3. Demographic features of smallmouth bass populations in the study lakes. Population estimates include 95% confidence intervals in parentheses.
- Table 4. Physical characteristics of smallmouth bass nests in the littoral zone of four north temperate lakes. Values represent the mean  $\pm$  1 standard error. Characteristics of nests in Big Crooked Lake were not significantly different across years and thus values were pooled. Statistically different groups (Kruskall-Wallis test) are noted with lower case letters above the values.
- Table 5. Habitat features significantly related to egg survival at the nest scale. Values reported are  $R^2$  values associated with significant relations. Alpha was set at  $P < 0.05$ .
- Table 6. Habitat features significantly related to smallmouth bass egg survival in each study lake; across lake comparisons using best regression models.
- Table 7. Habitat features significantly related to fry production at the nest scale. Values reported are  $R^2$  values associated with significant relations. Alpha was set at  $P < 0.05$ .
- Table 8. Habitat features significantly related to smallmouth bass fry production in each study lake; across lake comparisons using best regression models.
- Table 9. Demographic features of smallmouth bass populations in the study lakes. Population estimates include 95% confidence intervals in parentheses.
- Table 10. Limnological features of the four study lakes.
- Table 11. Physical characteristics of smallmouth bass nests in the littoral zone of four north temperate lakes. Values represent the mean  $\pm$  1 standard error. Characteristics of nests in Big Crooked Lake were not significantly different across years and thus values were pooled. Statistically different groups (Kruskall-Wallis test) are noted with lower case letters above the values.

- Table 12. Summary of the best univariate (u), the best overall multivariable (m), the most parsimonious (p), and the most transferable (t) RSFs predicting smallmouth bass presence/absence in Big Crooked (1998-2000), Sanford (1998), Bear (1999), and Palette Lakes (2000). All variables in multiple logistic regression models are significant at  $P \leq 0.05$ .
- Table 13. Mean survival and fitness ( $\pm 1$  S.E.) of nests in Big Crooked Lake (1998 and 2000) and Bear Lake (1999) relative to the probabilities of selection generated using the best multivariable RSF. Mann-Whitney U-tests ( $\alpha = 0.008$ ) assessed differences in survival and fitness.

## List of Figures

- Figure 1. Substrate particle size distributions from the littoral zones of four lakes. (1) fine organic material, (2) silt, (3) sand, (4) gravel, (5) cobble, (6) rubble, (7) small boulders, (8) large boulders, and (9) bedrock.
- Figure 2. Relation between estimated number of eggs (panel a) and fry (panel b) on the nest using a 30x30 cm and 36x36 cm grid and the actual number counted after full removal from nest. Note different scale on graphs.
- Figure 3. Distribution of total lengths (mm) of parental male smallmouth bass on active nests in four north temperate lakes. Lengths were similar across years (1998-2000) in Big Crooked Lake and were pooled (ANOVA  $F=1.028$ ,  $p=0.361$ ).
- Figure 4. Difference (ranked ANOVA and Scheffe's multiple range test) in mean smallmouth bass survival from egg through black swim-up fry (per nest) ( $\pm 1$  S.E.) among study lakes. Mean ranked survival was significantly different ( $F=13.4$ ,  $P<0.001$ ) among lakes. Lakes are: (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.
- Figure 5. Difference (ranked ANOVA and Scheffe's multiple range test) in smallmouth bass black swim-up fry production (per nest) ( $\pm 1$  S.E.) among study lakes. Mean ranked fry production was significantly different ( $F=43.2$ ,  $P<0.001$ ) among lakes. Lakes are: (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.
- Figure 6. Distribution of total lengths (mm) of parental male smallmouth bass on active nests in four north temperate lakes. Lengths were similar across years (1998-2000) in Big Crooked Lake and were pooled (ANOVA  $F=1.028$ ,  $p=0.361$ ).
- Figure 7. Substrate particle size distributions from the littoral zones of four lakes. (1) fine organic material, (2) silt, (3) sand, (4) gravel, (5) cobble, (6) rubble, (7) small boulders, (8) large boulders, and (9) bedrock.
- Figure 8. Relations between nest construction date and the amount of gravel in the nest in four north temperate lakes. Significant relations are plotted as a solid line.

- Figure 9. Difference (ranked ANOVA and Scheffe's multiple range test) in mean smallmouth bass survival from egg through black swim-up fry (per nest) ( $\pm 1$  S.E.) among study lakes. Mean ranked survival was significantly different ( $F=13.4$ ,  $P<0.001$ ) among lakes. Lakes are: (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.
- Figure 10. Difference (ranked ANOVA and Scheffe's multiple range test) in smallmouth bass black swim-up fry production (per nest) ( $\pm 1$  S.E.) among study lakes. Mean ranked fry production was significantly different ( $F=43.2$ ,  $P<0.001$ ) among lakes. Lakes are: (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.
- Figure 11. Relations between habitat selection and habitat quality. Significant relations are plotted with a solid line.

## **Background**

Smallmouth bass are an important fish species both ecologically and economically. They are an important component of fish communities in many aquatic systems across North America. Because they are the top predators in many of these systems, they can influence the abundance of fish and invertebrates at lower trophic levels (Power et al. 1985). Moreover, smallmouth bass are an ecological indicator species. They are more intolerant to habitat alteration than other black basses (Robison and Buchanan 1988) and are used to denote intolerant fish communities in indices of biotic integrity (Lyons et al. 1996). In the future, smallmouth bass populations may become an important tool in analyzing watershed quality. Smallmouth bass egg and fry development should be especially important as indicators because these life-stages are the most sensitive to environmental changes (Rejwan et al. 1999).

### *Smallmouth Bass Biology*

General information regarding habitat requirements of smallmouth bass are known (Barans and Tubbs 1973, Rejwan et al. 1997). Hubbs and Bailey (1938) suggest the best lake characteristics for smallmouth bass include a surface area greater than 100 acres, maximum depth greater than 30 feet, clear water, little vegetation, and large shoals and shoreline areas of rock and gravel. Quantitative studies have shown that adult smallmouth bass prefer predominantly rocky areas near sharp drop-offs (Munther 1970, Hubert and Lackey 1980).

Spawning habitat requirements of smallmouth bass are quite specific. Females deposit eggs in nests that are constructed and guarded by males. Nests are highly visible,

saucer-shaped depressions dug out of the substrate (Stroud and Clepper 1975). Nests are typically built in water depths between 0.5m and 2.5m on rock, rubble, cobble, sand, and primarily gravel substrates (Wiegert 1966). Often, nests are placed close to a large rock or log for cover. It is thought that the presence of cover makes it easier for the male to guard the nest from predators since the nest is vulnerable from fewer sides (Hubbs and Bailey 1938).

Many aspects of smallmouth bass nesting ecology have already been studied including the general pattern of yearly spawning activity in particular. Smallmouth bass are solitary spawners (Pflieger 1966, Vogele 1981). When water temperatures approach 15° C in the springtime, males begin nest construction. After nest construction, the male courts and spawns with a female. After spawning, the female leaves the area and the male stays at the nest site for up to four weeks to provide care and protection for the developing brood (Ridgway 1988). Parental male nest defense is extremely well developed in this species (Becker 1983). During this period of nest defense, males are extremely aggressive and consequently vulnerable to angling (Kiefer et al. 1995).

Detailed studies of smallmouth bass nesting behavior provide insight into further understanding smallmouth bass recruitment. The largest males in a population exhibit behaviors that make them particularly important to future year classes. Larger males procure larger broods since females prefer to spawn with them (Wiegmann et al. 1992), show the most aggression in defending their nest (Wiegmann and Baylis 1995, Philipp et al. 1997), and consequently produce more fry (Neves 1975). Therefore, the nesting activities of the largest males may be the most valuable to the long-term well-being of any given population. Nest site fidelity is also well developed in this species. Ridgway

et al. (1991) found that 81% of re-nesting males returned to within 200 m of their previous nest site. The remainder nested within 1200 m of their previous nest site. This evidence suggests that habitat selection in smallmouth bass may be a combination of innate as well as learned behaviors.

### *Impetus for the Study*

Increasing concern over anthropogenic factors that may limit smallmouth bass recruitment exists (Ridgway and Shuter 1997), yet detailed studies of the effects of these factors at the population level have yet to be conducted. Anthropogenic factors affecting smallmouth bass populations in lakes include habitat alteration of littoral zones and riparian areas (i.e., shoreline development and nearby land use practices) and increased angling pressure. Poor land-use practices and alterations to riparian and littoral zones can jeopardize smallmouth bass populations (Robison and Buchanan 1988). Shoreline development and other practices that remove riparian vegetation have the potential to increase the fine sediment load in the littoral zone which may increase egg mortality and suppress recruitment (Haines 1973, Stroud and Clepper 1975). Shoreline development activities also reduce the amount of in-lake cover available to nesting males (Christensen et al. 1996) and may result in lower recruitment and consequently lower population levels (Hoff 1991).

Spawning habitat quality for smallmouth bass is believed to be critical to reproductive success and recruitment of smallmouth bass. Several researchers have begun to examine factors that may be affecting smallmouth bass productivity (Webster 1945, Serns 1982, Serns 1984, Raffetto et al. 1990) though most of these studies only

examined temperature at the lake-wide scale. No studies explicitly examine relations between habitat and survival at the nest scale in lakes. Some habitat-survival relations have been examined in streams, but the effects of variable water flow that displace nesting males confounded the results (Lukas and Orth 1995). Only male size and behavior in relation to recruitment has been studied in lakes at the nest scale (Neves 1975, Wiegmann and Baylis 1995). Often, larger and more tenacious males are more reproductively successful (Wiegmann et al. 1992). The possible effects of temperature, water flow, and water level at the population level have been examined using computer-based simulations (Shuter et al. 1980, and Jager et al. 1993). These studies suggest that thermal regimes may structure smallmouth bass populations but these studies had no experimental validation. Because smallmouth bass select specific habitat features for nesting, features such as substrate size, substrate embeddedness, and proximity to structure may be mediating egg survival at the nest scale. However, surprisingly little is known about the relations between these habitat variables and egg survival at the nest scale. These relations may be understudied because gathering the necessary metrics of survival and habitat features requires specialized equipment (i.e., SCUBA gear), is extremely labor intensive, and is therefore a very expensive undertaking.

Another anthropogenic factor that may be limiting smallmouth bass populations is angling. Angling pressure on smallmouth bass has risen substantially since the late 1980's. Bass tournaments have become increasingly common (Schupp 1979, Duttweiler 1985, Schramm et al. 1991). Though the vast majority of tournaments are catch and release only, there is still an average of 6.5% initial mortality and 18.1% delayed mortality on those fish that are caught, retained, and later released (Wilde 1998).



Additionally, removing a male from a nest as he guards his offspring can lead to male abandonment resulting higher levels of nest predation that would otherwise not occur (Philipp et al. 1997). Because parental males are extremely vulnerable to angling while guarding a nest in the spring (Kiefer et al. 1995), many resource management agencies have adopted closed season policies, catch-and-release only policies, various length and harvest limits, and combinations of these strategies to maximize smallmouth bass reproductive success. These policies operate on the assumption that individual reproductive success is positively correlated with lakewide recruitment, yet few studies have begun to address this assumption.

If there is a correlation between individual reproductive success and lakewide survival, then angling could be a severe impediment to smallmouth bass recruitment for a variety of reasons. First, females prefer to spawn with larger males so larger males have larger broods (Neves 1975, Wiegmann et al. 1992). Second, parental investment decision rules dictate that males with the largest broods (large males) defend their broods most aggressively (Philipp et al. 1997). Third, large males are disproportionately targeted by anglers (through a combination of large male bass behavior and angler preference), so large broods are especially vulnerable to higher levels of nest predation and parental abandonment. Consequently, large males that are the most productive and important to the population are those at most risk from angling

Clearly, many smallmouth bass populations are being affected by anthropogenic factors. A mechanistic understanding of the relations between smallmouth bass populations and their habitats is required before we can fully understand, much less predict, the effects of anthropogenic perturbations to lentic systems.

### *Habitat Modelling*

Fishery and wildlife scientists can study habitat and organismal responses to habitat in three general ways. These include studies of habitat use, habitat selection, and habitat quality (Hall et al. 1997). Habitat use is the way an animal uses or consumes a collection of physical and biological components in a habitat. Habitat use does not consider availability of the resource and consequently is the response most often studied because gathering this data is relatively quick and inexpensive. However, habitat use information may not transfer across systems particularly where environments differ substantially (Bozek and Rahel 1992). Habitat selection is a hierarchical process involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment (Hutto 1985). This definition implies choice of one habitat over another with respect to availability. Therefore habitat selection studies should include biologically meaningful measurements of available habitat (Peek 1986). Therefore, habitat selection is more time consuming, difficult, and expensive to study than habitat use due to the additional set of data required. One inherent assumption of habitat selection studies is that habitat selection is correlated to higher reproductive success or survival (Fretwell and Lucas 1970), though this assumption has not been adequately examined (Garshelis 2000). Habitat quality is the ability of the environment to provide conditions appropriate for individual and population persistence (Hall et al. 1997). In studying habitat quality, researchers must include measurements of population performance (i.e., survival). This often makes these studies extremely time consuming and expensive. Gathering accurate nest-specific survival data in aquatic environments presents an even greater challenge to researchers.

In aquatic systems, most habitat modelling has been based largely on habitat use and, more recently, habitat selection. These modelling efforts are meant to infer habitat quality from habitat use or habitat selection because greater use should occur in higher quality habitat (Schamberger and O'Neil 1986). The habitat suitability index (HSI) is the most commonly used index of habitat quality (Bovee 1982, Morantz et al. 1987). However, few studies have validated this technique's ability to predict habitat quality (Guay et al. 2000), and those few validations have been contradictory (Orth and Maughan 1982, Scott and Shirvell 1987, Bourgeois et al. 1996, Bovee et. al 1998). For example, Pajak and Neves (1987) examined the relation between HSI values and standing stocks in two streams in Virginia. In one stream, they found a significant positive relation between HSI values and standing stock though they found no relation between the HSI values and standing stock in the second stream. These results suggest that demographic response studies are the only means of truly evaluating the relative importance of habitats for supporting animal populations (Hobbs and Hanley 1990, Garshelis 2000).

#### *Objective 1: Evaluating Nest Site Selection*

A quantitative understanding of fish-habitat relations is necessary to accurately assess the consequences of changes in habitat quantity and quality on fish populations. Despite the importance of habitat, few models exist that accurately predict spawning habitat use and selection by fish (Knapp and Preisler 1999) including smallmouth bass (Rejwan et al. 1999). Habitat models have been used to describe general habitat use of smallmouth bass (Todd and Rabeni 1989), predict standing stocks and production of fish (Fausch et al. 1988, Lyons 1991, Sowa and Rabeni 1995), and to mitigate the effects of

alterations to aquatic environments (U.S. Fish and Wildlife Service 1980, Schamberger et al. 1982, Edwards et al. 1983). In streams, these habitat use and selection models have been key components of habitat restoration and protection strategies based on techniques such as the Habitat Evaluation Procedures and the Instream Flow Incremental Methodology (Stalnaker 1979, U.S. Fish and Wildlife Service 1980, Schamberger et al. 1982, Beecher et al. 1993). The deployment of habitat selection models in lakes may provide a useful tool to help manage lake habitats as well.

The habitat selection models in this study are embedded within chapter II. Several of these models were developed by a previous research assistant (Patrick Short) and some were developed for this study. Because much of this information was for another Master's Thesis, this document will not cover habitat selection model development extensively.

*Objective 2: - Chapter I - Evaluating Nest Site Quality*

Understanding how habitat characteristics of smallmouth bass nests affect survival in the nest is prerequisite to not only developing predictive models, but also developing strategies to protect prime spawning areas and techniques to restore degraded smallmouth bass spawning habitat. However, most habitat modelling efforts in aquatic systems have been based only on habitat use and habitat selection without assessing actual habitat quality (Lyons 1991, Todd and Rabeni 1995). Demographic response studies are the only means of truly evaluating the relative importance and suitability of habitats for supporting animal populations and should be further investigated (Kirsch 1996, Garshelis 2000).

*Objective 3: - Chapter II - Evaluating the Linkages Between Nest Site Selection and Nest Site Quality*

Theoretically, habitat selection models broadly reflect habitat quality (i.e. reproductive potential) (Fretwell and Lucas 1970, Boyce and McDonald 1999). Habitat models based on habitat selection rather than habitat use are thought to be preferable because they attempt to account for differences in resource availability (Manly et al. 1993). However, the development of habitat selection models that accurately reflect habitat quality and are transferable has been problematic because of differences in habitat availability across systems (Bozek and Rahel 1991, Arthur et al. 1996). Moreover, habitat selection studies have not attempted to validate relations between habitat selection and habitat quality. This study attempts to quantitatively evaluate how well habitat selection reflects habitat quality.

Chapter I: Habitat Features Affecting Smallmouth Bass Nesting Success in  
Four Northern Wisconsin Lakes

**Abstract**

Evaluating spawning success in relation to habitat characteristics of nests sites provides critical information necessary to assess the effects of riparian and littoral zone habitat alterations on smallmouth bass (*Micropterus dolomieu*) survival and recruitment. The objective of this study was to evaluate smallmouth bass nest site quality in lakes in order to assess the importance habitat features have on nesting success. We evaluated smallmouth bass egg survival and fry production as a function of nest characteristics in four northern Wisconsin lakes from 1998 to 2000 using simple and multiple linear regression analyses. Mean smallmouth bass egg survival and fry production were significantly different (ANOVA) among lakes; nests in Big Crooked and Bear Lakes had higher egg survival and fry production than Palette and Sanford Lakes. Relations were variable among lakes, indicating that no single habitat feature consistently predicted nest success across lakes. Habitat features accounted for up to 27% (distance to cover) of the variation in egg survival and up to 50% (size of nearest cover) of the variation in fry production. Measures of substrate size were the most predominant nest characteristic associated with variation in both egg survival and fry production among lakes but they were not significant in all lakes. Other features related to nest cover, nest position, and morphology explained some variation in egg survival and fry production but they were inconsistent across lakes. This study shows that habitat characteristics affecting smallmouth bass nesting success are extremely variable across lakes and will require further study to elucidate how habitat quality influences nesting success.

## Introduction

Spawning habitat is important to reproductive success and recruitment of smallmouth bass (*Micropterus dolomieu*) (Neves 1975, Serns 1984, Lukas and Orth 1995, Sowa and Rabeni 1995). However, few studies have explicitly examined reproductive success in relation to habitat features at the individual nest scale in lakes (Rejwan et al. 1997) even though linking environmental conditions to demographic features of populations (e.g., reproduction) is critical to understanding population dynamics (Garshelis 2000). Such studies of habitat quality (Hall et al. 1997) are uncommon in aquatic systems.

Previous studies provide general descriptions of nesting habitat use. Smallmouth bass generally use gravel substrates but may use sand, silt, and organic material and are usually associated with rock or woody cover (Scott and Crossman 1973, Winemiller and Taylor 1982, Reynolds and O'Bara 1991). However, the relations between nest habitat features and nesting success are unclear and largely untested in lakes. Moreover, other factors (e.g., behavior, climate) can also influence nesting success which can confound discrete relations between nest characteristics and nesting success. For instance, Lukas and Orth (1995) found that temperature and streamflow masked the effects of nest scale habitat features in a Virginia stream while Wiegmann and Baylis (1995) found that size and behavior of parental males influenced nesting success. At the population level, effects of temperature, water flow, and water level have been modeled with computer-based simulations (Shuter et al. 1980, Jager et al. 1993) but these studies have had no experimental validation.

Smallmouth bass occur in a wide variety of lakes and streams having variable physical characteristics throughout their native range. Stationary locations of nest aggregations (Rejwan et al. 1997) and site-fidelity in adults (Ridgway et al. 1991) suggest that adults select specific habitat features for nesting, such as substrate size and embeddedness, and proximity to cover which may mediate fry production at the nest scale. Moreover, natural selection has likely caused populations to evolve toward conditions where most individuals possess keen habitat selection abilities and thus habitat quality may mediate survival of eggs and fry (Morrison et al. 1992). However, surprisingly little is known about microhabitat features of smallmouth bass nests and the quantitative relationship between these habitat features and egg survival or fry production at the nest scale in lakes. In salmonids, specific substrate matrix compositions clearly affect survival to emergence (Young et al. 1991). This information may be lacking in lacustrine smallmouth bass populations because gathering the necessary measures of relative nest success and habitat features requires specialized equipment (e.g., SCUBA gear), is extremely labor intensive, and costly. But the information is necessary to understanding how changes in habitat may affect smallmouth bass population dynamics. Therefore, the objective of this study was to assess nest scale habitat features affecting smallmouth bass egg survival and fry production in four lakes with varying habitat features.



## **Methods**

### *Study Area*

Big Crooked, Sanford, Bear, and Palette Lakes are glacial lakes located in north central Wisconsin. The study lakes range in size from 31 to 276 hectares (Table 1) and differ in predominant substrate (Figure 1). All four study lakes have limited access and very little development along their shorelines. Big Crooked, Sanford, and Bear Lakes are privately owned. Angling in these lakes is limited to members only and release of all smallmouth bass is required. Palette Lake is located in the Northern Highland Fishery Research Area and access is limited to walk-in only. Here, smallmouth bass fishing is by permit only and harvest is limited to fish in excess of 40.6 cm (16 in.). Smallmouth bass harvest from Palette Lake is documented with a complete creel census. Therefore, nests where parental males were harvested were not included in analyses of nest success.

### *Data Collection*

Smallmouth bass nest site location, habitat characteristics, and nesting success were documented on all lakes during the smallmouth bass spawning seasons from 1998 to 2000. Each lake was surveyed and all nests visited every other day until all smallmouth bass fry emerged from the nests. Smallmouth bass nests were located with several methods. First, nests were located by slowly boating around the entire margin of each lake and visually observing the shallow water (<2 m) for nests using polarized sunglasses. Nests were also located by snorkeling and by towing SCUBA divers around the 2.0 m, 2.5 m, and 3.0 depth contour of each lake. SCUBA gear was necessary to locate deeper nests (2 to 3 m). Previous work has demonstrated that 3.0 m is the

Table 1. Limnological features of the four study lakes.

Lake feature	Big Crooked Lake	Sanford Lake	Bear Lake	Palette Lake
Surface area (ha)	276	36	31	70
Maximum depth (m)	12	16	10	18
Woody cover (pieces/m <sup>2</sup> )	0.05 (174/3380)	0.38 (428/1139)	0.11 136/1171	0.04 141/3460
Shoreline slope	0.046	0.143	0.130	0.049
Color (Pt units)	8.9	30.4	27.8	14.5
pH	7.1	5.9	7.9	6.6
Total alkalinity (mg L <sup>-1</sup> )	14.0	6.0	91.1	9.0

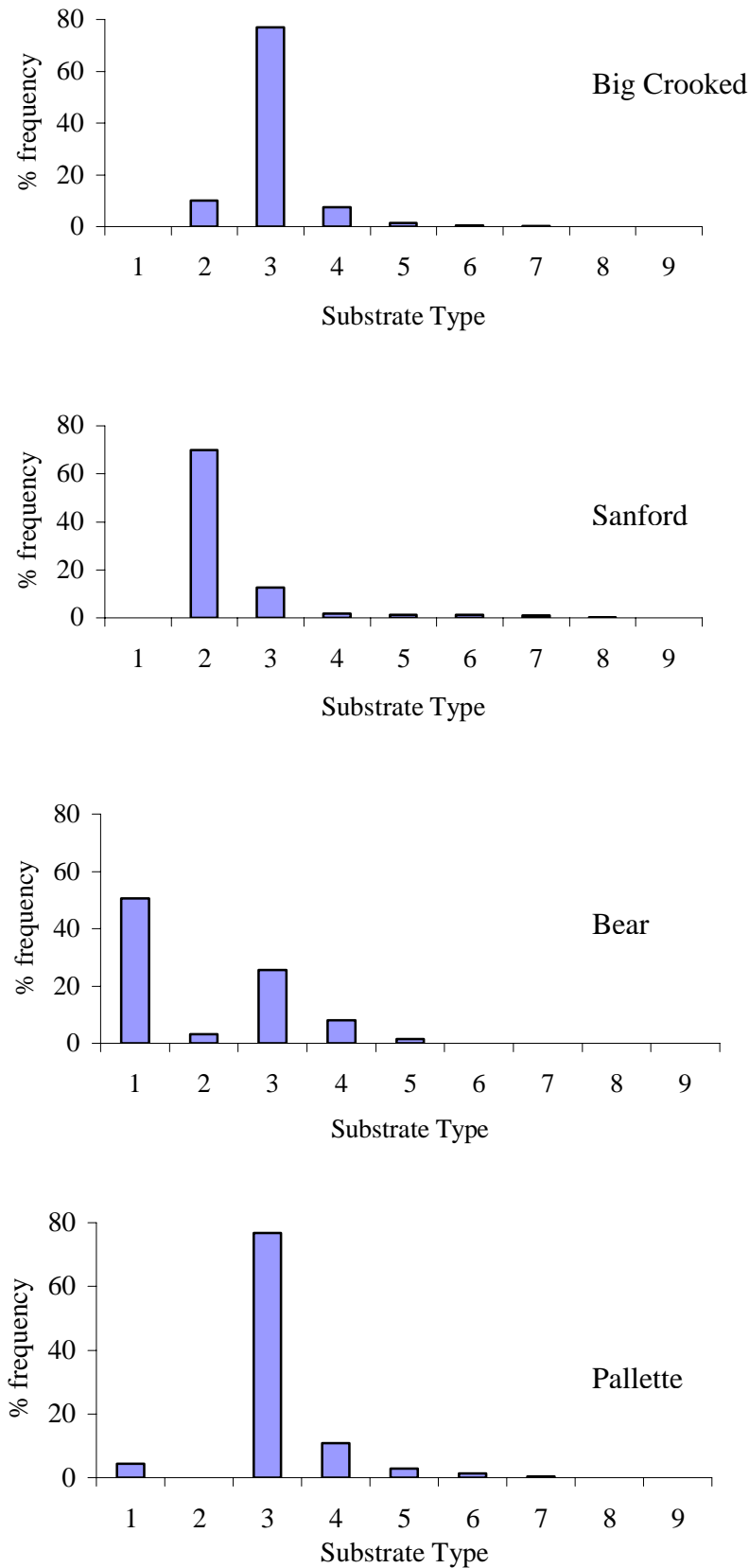


Figure 1. Substrate particle size distributions from the littoral zones of four lakes. (1) fine organic material, (2) silt, (3) sand, (4) gravel, (5) cobble, (6) rubble, (7) small boulders, (8) large boulders, and (9) bedrock.

maximum depth to which nests are located in the study lakes and occasional surveys beyond this depth were conducted to reconfirm this distributional pattern. After locating each nest, a uniquely numbered flag was placed on the lake bottom near the nest. Each nest was also marked on a map of the lake to facilitate relocation for subsequent data collection.

Habitat and biological data at each nest were collected using SCUBA gear. Egg estimates were visually conducted using a 30x30 cm wire grid composed of 25 smaller (6x6 cm) squares. This grid was placed across the top of the aggregation of eggs. The number of eggs in each smaller square was estimated and then summed for an overall nest estimate. Fry estimates were conducted in a similar manner but using a larger (36x36 cm) grid with 36 (6x6 cm) squares. The larger grid was necessary as fry covered a larger area in the nest. Fry estimates were standardized by stage of development (Hubbs and Bailey 1938); fry estimates were conducted only after they had black pigmentation prior to swim-up. At this time, fry briefly orient themselves on top of the substrate in the nest before they begin to disperse to forage.

Egg and fry estimates were validated by comparing the number of eggs or fry estimated using the grid to an actual count conducted on a sub-sample of 12 nests (six for egg estimates, six for fry estimates). For validating estimates, we carefully removed all eggs or fry from each nest using low pressure suction, removed all substrates to insure inclusion of all eggs or fry, and counted all eggs or fry after each estimate. Linear regression was then used to determine the accuracy of the estimate (i.e., coefficient of determination). A slope of 1.0 indicates that on average, the estimate reflects the true number of eggs or fry. For analyses, estimates were corrected by multiplying the egg or

fry estimate by the inverse of the regression slope that relates the actual number of eggs or fry on the nest to the estimated number of eggs or fry on the nest. Eggs and fry were immediately placed back into the nest after the validation, though these nests were not used in subsequent analyses of nest success.

Immediately after fry emergence, habitat characteristics (Table 2) from each nest were quantified and used to predict survival and fry production. Percentages of each substrate size (Wentworth 1922, Platts et al. 1983) were visually estimated. Embeddedness of each substrate category was also visually estimated as the degree to which fine substrate was embedded in the nest matrix. We used a system modified from Platts et al. (1983) whereby highly embedded substrates were coded as 4 and clean substrates were coded as 0 (Appendix A). Nest cover was also quantified at each nest; cover was judged to be used if it was less than 1.5 m from the rim of the nest. Distance to and dimensions of large rocks and logs used for cover were measured. Nest orientation to cover (i.e., under or adjacent) was also recorded. Shoreline slope was measured at two scales. General shoreline slope at the nest site was measured by dividing the depth from the deep rim of the nest by the distance to the shoreline water interface. Nest site slope was measured as the difference between water depth 2 m from the nest towards shore and 2 m from the nest away from shore divided by the linear distance (above water) between those depth measurements.

Table 2. Nest site habitat characteristics used in analyses of smallmouth bass nest site quality.

<u>Independent variables</u>	<u>Dependent Variables</u>
Nest diameter	Survival (egg to swim-up)
Nest depth	Fry production (number of fry emerging)
Distance from shore	
Slope	
Distance to nearest active nest	
Substrate size (in nest)	
Substrate embeddedness (in nest)	
Cover type	
Size of nearest cover	
Proximity to cover	
large rocks	
woody structure	
Position of nest relative to cover	
under	
adjacent	
none	

### *Analyses*

Two sets of analyses were performed on the two dependent variables, each representing a different measure of nest success: egg survival and fry production.

Survival was calculated as:

$$\text{Survival \%} = \text{number of fry} / \text{number of eggs} \times 100$$

Fry production was the corrected count of black fry just prior to emergence.

We used simple and multiple linear regression to assess the importance of each habitat feature in explaining variation in nest success in each lake. Models were significant at  $P \leq 0.05$ . Independent variables were transformed using log, inverse, and square root transformations to normalize residuals, when appropriate (Neter et al. 1996). Arcsine transformations were applied to survival (%) to normalize residuals when appropriate. Log, inverse, and square root transformations were applied to normalize residuals when the dependent variable was fry production (Neter et al. 1996). We used 95% confidence intervals to compare mean egg survival and fry production across lakes. We also used ANOVA to assess differences in parental male lengths across lakes.

### **Results**

Visual estimates of eggs and fry were quite accurate in enumerating actual numbers of eggs and fry on nests (Figure 2). Coefficients of determination ( $R^2$ ) were 0.98 for egg estimates and 0.97 for fry estimates. Slopes of both lines were less than 1.0

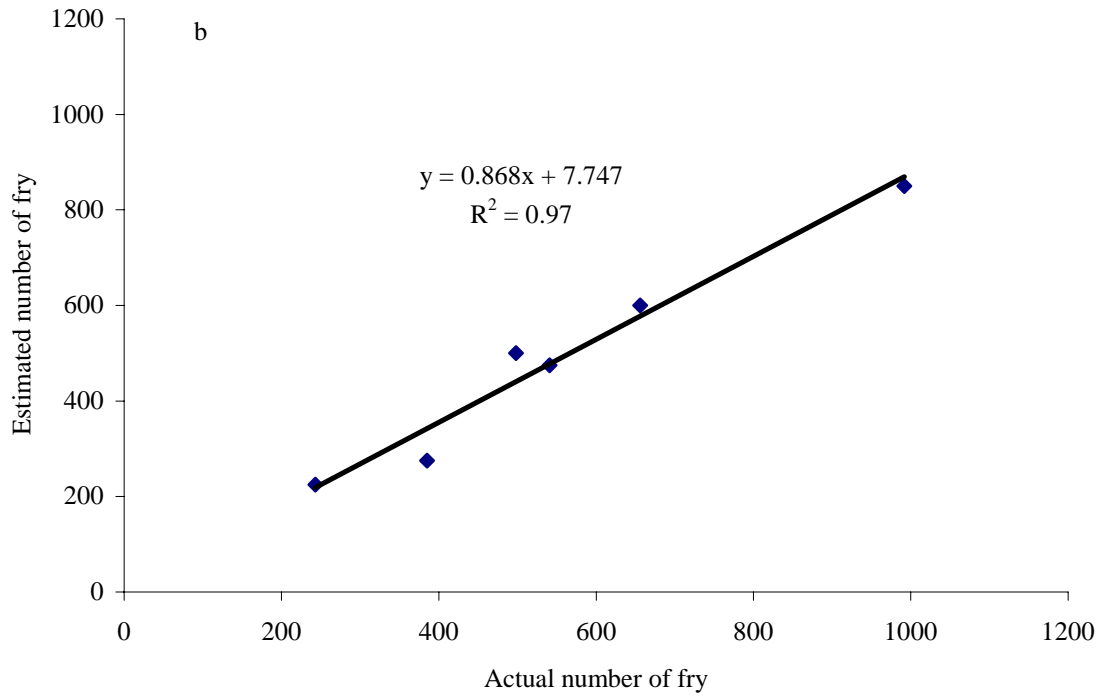
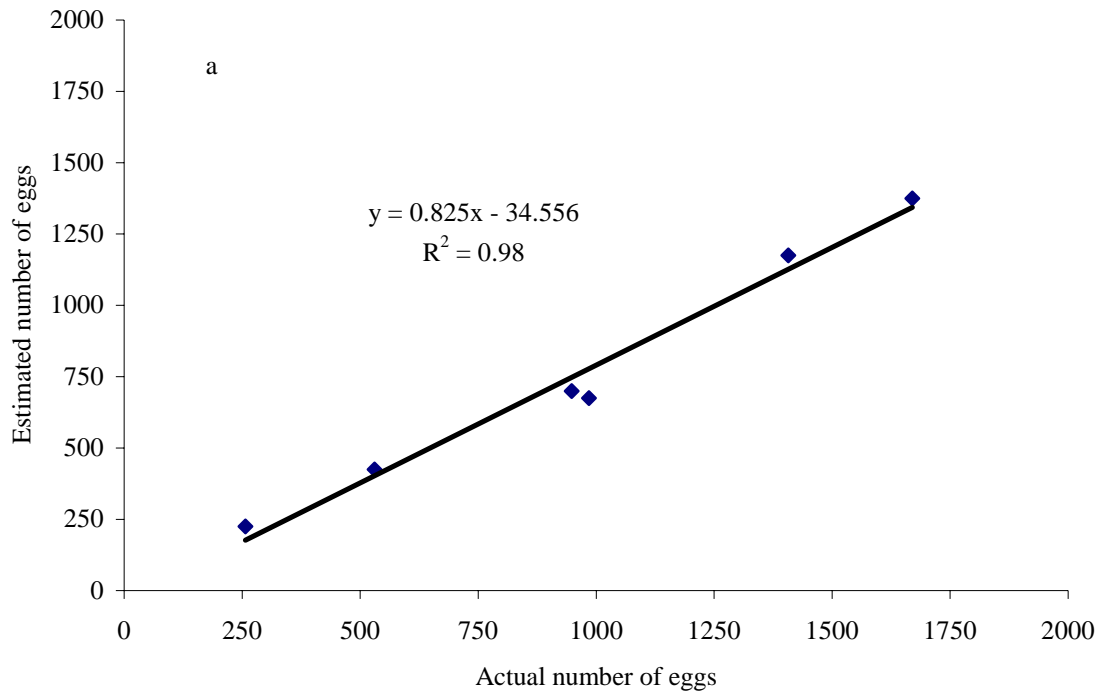


Figure 2. Relation between estimated number of eggs (panel a) and fry (panel b) on the nest using a 30x30 cm and 36x36 cm grid and the actual number counted after full removal from nest. Note different scale on graphs.



(0.825 for eggs and 0.868 for fry) indicating that estimates slightly underestimated the actual number of individuals on the nest.

Demographic features of smallmouth bass in each lake were variable (Table 3). These features were constant across years for Big Crooked Lake but were different across other lakes. Adult smallmouth bass population densities were lowest in Big Crooked Lake (0.6 to 0.8 adults per hectare) and highest in Palette Lake (10.3 adults per hectare). Parental male size structure also varied across lakes with the largest males found in Big Crooked Lake (ANOVA  $F=12.956$ ,  $P<0.001$ ) (Figure 3).

Littoral zone habitat differed substantially across lakes. In Big Crooked and Palette Lakes, littoral zone substrates were dominated by sand. In Sanford and Bear Lakes, finer substrates such as silt and organic matter were common in the littoral zone and coarser substrates were almost completely absent. Cover in littoral zones also differed among lakes. Big Crooked and Palette Lakes had few boulders or pieces of coarse woody structure whereas the littoral zones of Sanford and Bear Lakes had abundant coarse woody structure and few boulders.

Habitat characteristics of smallmouth bass nests varied across lakes (Table 4). Nests in Big Crooked Lake were composed almost entirely of gravel and cobble whereas nests in the other study lakes were composed mostly of gravel and sand. In fact, 19% of nests in Palette Lake had  $\geq 50\%$  sand with four nests being composed entirely of sand. The mean percentage of sand in nests was similar in Sanford, Bear and Palette Lakes (24% to 31%). In contrast, mean percentage of sand in nests in Big Crooked Lake was 5% and rarely exceeded 20% even though sand is the dominant substrate in the littoral zone. Substrates directly outside of the actual nests reflected the general spawning area

Table 3. Demographic features of smallmouth bass populations in the study lakes. Population estimates include 95% confidence intervals in parentheses.

Lake	Big Crooked 1998	Big Crooked 1999	Big Crooked 2000	Sanford 1998	Bear 1999	Palette 2000
Adult population estimate	168 (93-336)	233 (114-837)	207 (82-518)	165 (108-264)	79 (43-198)	722 (492-1243)
Adults per hectare	0.6	0.8	0.8	4.6	2.5	10.3
Number of nests	38	49	48	51	28	107
Nests per shoreline km	3.5	4.5	4.4	9.6	6.1	26.6
Mean ( $\pm$ S.E.) distance from nest to nest (m)	44.3 $\pm$ 5.3	46.2 $\pm$ 9.1	40.0 $\pm$ 5.0	46.0 $\pm$ 5.6	23.9 $\pm$ 7.0	18.6 $\pm$ 1.5

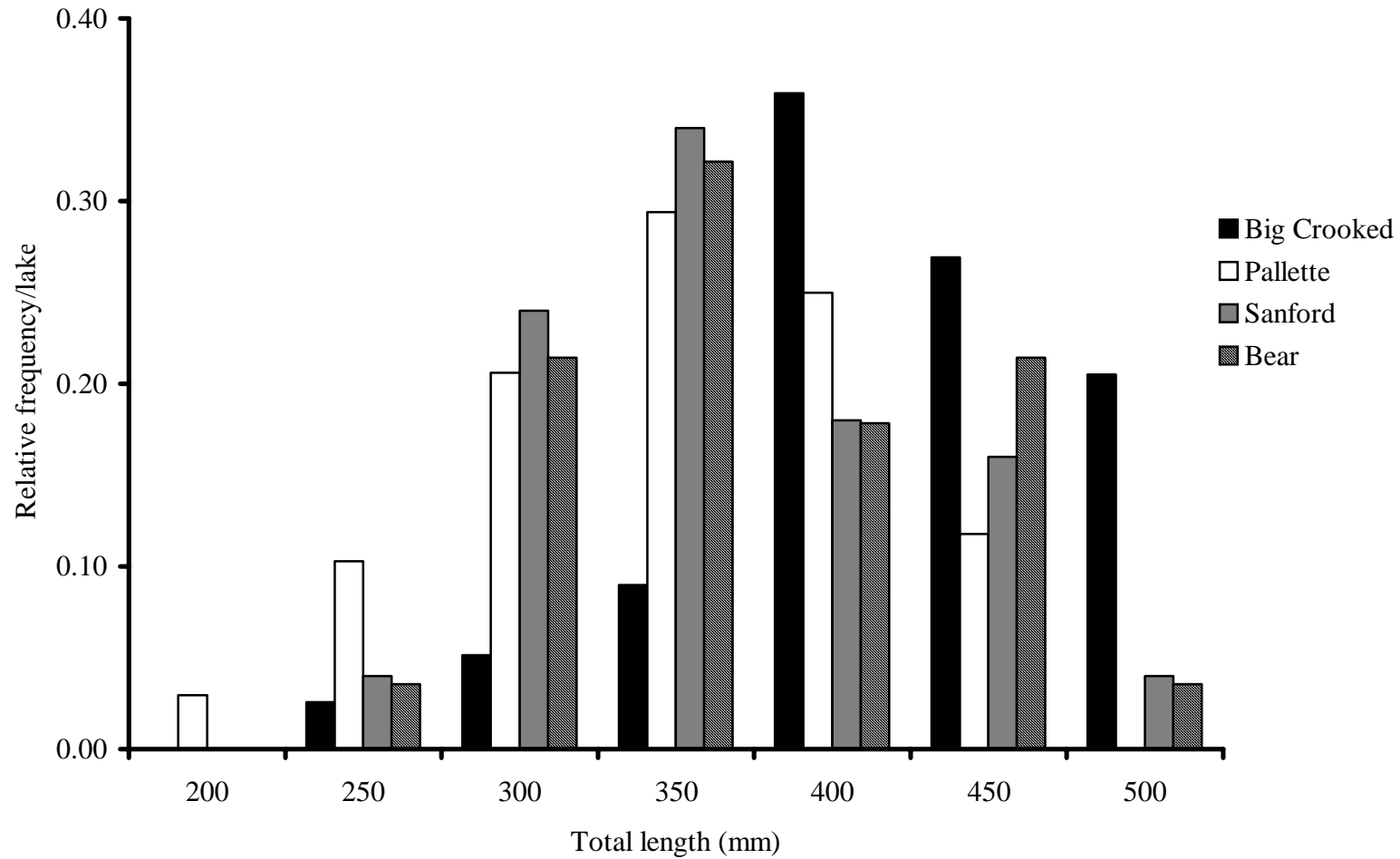


Figure 3. Distribution of total lengths (mm) of parental male smallmouth bass on active nests in four north temperate lakes. Lengths were similar across years (1998-2000) in Big Crooked Lake and were pooled (ANOVA  $F=1.028$ ,  $p=0.361$ ).

Table 4. Physical characteristics of smallmouth bass nests in the littoral zone of four north temperate lakes. Values represent the mean  $\pm$  1 standard error. Characteristics of nests in Big Crooked Lake were not significantly different across years and thus values were pooled. Statistically different groups (Kruskall-Wallis test) are noted with lower case letters above the values.

Nest characteristic	Big Crooked Lake	Sanford Lake	Bear Lake	Palette Lake	K	P
	a	b	b	b		
Nest diameter (m)	0.93 $\pm$ 0.03	0.68 $\pm$ 0.02	0.56 $\pm$ 0.03	0.52 $\pm$ 0.03	103.8	<0.001
	a	b	b	b		
Sand (%)	5 $\pm$ 0.9	31 $\pm$ 3.9	24 $\pm$ 3.5	26 $\pm$ 2.8	66.2	<0.001
	a	b	ab	b		
Gravel (%)	75 $\pm$ 1.9	63 $\pm$ 4.1	70 $\pm$ 4.1	62 $\pm$ 2.8	17.4	0.001
	a	b	b	b		
Cobble (%)	19 $\pm$ 1.8	5 $\pm$ 1.0	6 $\pm$ 1.3	6 $\pm$ 1.1	39.9	<0.001
	a	b	b	b		
Substrate embeddedness	1.2 $\pm$ 0.1	2.6 $\pm$ 0.1	3.0 $\pm$ 0.1	2.4 $\pm$ 0.1	94.6	<0.001
Percent nests near rocky cover	74	10	0	32		
Percent nests near woody cover	11	78	100	36		
Percent nests near both rocky and woody cover	14	6	0	21		
Percent nests with no cover	0	6	0	11		

characteristics. Coarse substrates were located outside nests in Big Crooked Lake whereas finer substrates occurred outside nests in the other lakes. Similarly, embeddedness of nests reflected substrate composition. Big Crooked Lake had the least embedded nests whereas Palette, Sanford, and Bear Lakes had higher mean embeddedness. Although limited in supply, large rocks and small boulders were consistently used as cover (74% of nests) for nesting males in Big Crooked Lake. In contrast, only two (1998) to four (2000) nests in Big Crooked Lake were placed near woody structure each year. The opposite was true in Sanford and Bear Lakes where 86% and 100% of nests respectively, were placed next to woody structure. In Palette Lake, 36% of nests were placed near woody structure, 32% of nests were placed near a rock, 21% of nests were placed near woody structure and a rock, and 11% of nests were not close to any cover at all.

### *Nesting Success*

Both survival and fry production were variable across lakes, and in Big Crooked Lake, also across years (Figures 4,5). Overall, nests in Big Crooked and Bear Lakes had higher mean egg survival than nests in Palette and Sanford Lakes. Survival did not vary across years in Big Crooked Lake.

Habitat features that affected egg survival were variable across lakes and, in Big Crooked Lake, also across years (Table 5). No single variable was a significant predictor of egg survival across lakes. In fact, few variables were significant in more than one lake. Our best models predicting egg survival were univariate relations

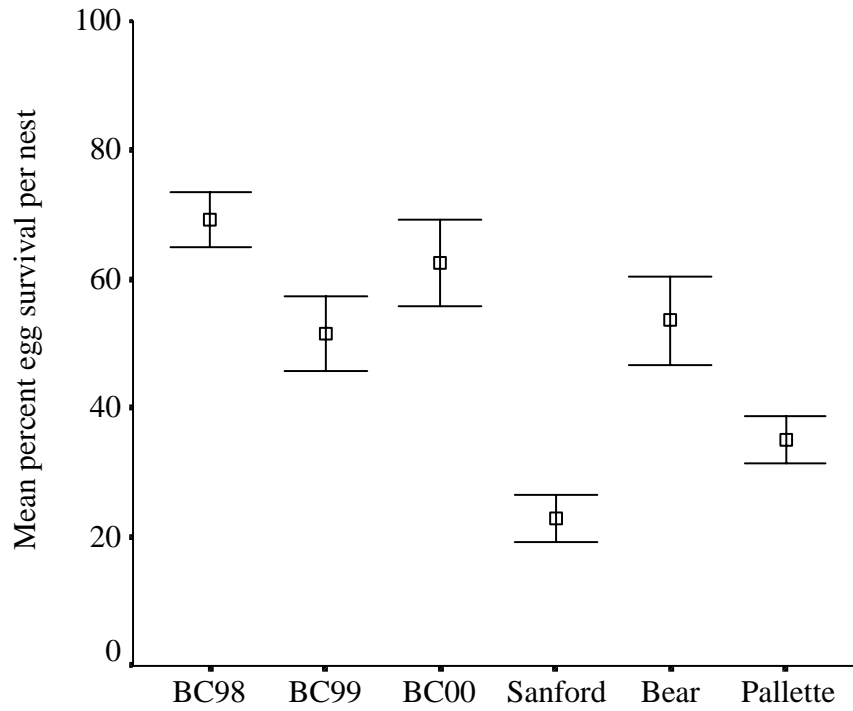


Figure 4. Mean survival ( $\pm 1$  S.E.) of smallmouth bass from egg through black swim-up fry in each study lake. (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.

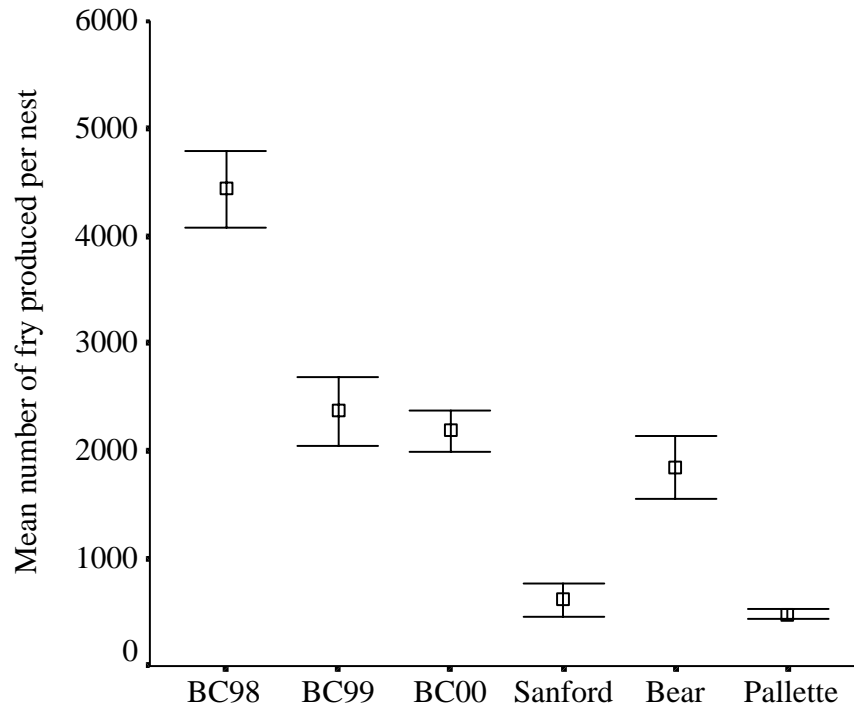


Figure 5. Mean fry production ( $\pm 1$  S.E.) per nest in four north temperate lakes. (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.

Table 5. Habitat features significantly related to egg survival at the nest scale. Values reported are  $R^2$  values associated with significant relations. Alpha was set at  $P < 0.05$ .

	<u>Lake</u>					
	BC 98	BC 99	BC 00	Sanford	Bear	Palette
<b><i>Substrate</i></b>						
Percent Sand in the Nest	--	--	--	0.19	--	0.08
Percent Gravel in the Nest	--	--	--	--	--	--
Percent Cobble in the Nest	--	0.14	0.24	0.25	--	--
Average Embeddedness	--	--	--	--	--	-
<b><i>Cover</i></b>						
Nearest Cover Size	--	--	--	--	--	--
Distance to Cover	--	--	--	--	--	0.27
Percent of Nest Located Under a Log	--	--	--	--	--	--
<b><i>Other Prominent Features</i></b>						
Distance to Shore	--	--	--	--	--	--
Nest Concavity	--	--	--	--	--	--
Slope	--	--	--	--	--	--
Nest Diameter	--	--	--	--	--	--
Nest Depth	--	--	--	--	--	--
Distance to Nearest Nest	0.16	--	--	--	--	--



accounting for between 14% and 27% of the variation in egg survival based on habitat features (Table 6). Nest substrate size (e.g., cobble) was the most consistent predictor of egg survival in Big Crooked and Sanford Lakes but not in Palette and Bear Lakes.

Only one measure of cover was significantly related to egg survival. Distance to cover in Palette Lake accounted for 27% of the variation in survival. The only other prominent habitat feature affecting egg survival was distance to nearest active nest in Big Crooked Lake 1998. No multiple regression models were significantly related to egg survival in any lake.

As with egg survival, fry production also varied across lakes, and in Big Crooked Lake, across years. Nests in Big Crooked Lake in 1998 had higher mean levels of fry production than in other lakes or other years in Big Crooked Lake. Big Crooked (1999 and 2000) and Bear Lakes had intermediate levels of fry production. Nests in Sanford and Palette Lakes had the lowest mean fry production.

Habitat features affecting fry production were variable across lakes and, in Big Crooked Lake, also across years (Table 7). In general, substrate was a better predictor of fry production in Sanford and Palette Lakes than in Big Crooked or Bear Lakes. All four metrics of nest substrate (e.g., sand, gravel, cobble, and embeddness) were significantly related to fry production in Sanford and Palette Lakes whereas only the percent sand in nests was significantly related to fry production in Bear Lake. Substrate was significantly related to fry production in Big Crooked Lake in 1998 and 2000.

Cover was significantly related to fry production only in Palette Lake and Bear Lake. In Palette Lake, only the percentage of the nest that was under a log was

Table 6. Habitat features significantly related to smallmouth bass egg survival in each study lake; across lake comparisons using best regression models.

Lake	Year	Equation	R <sup>2</sup>	Model p-value
Big Crooked	1998	$\arcsin(\text{survival}) = 1.17 - 5.67 * \log(\text{distance to nearest nest})$	0.16	0.028
Big Crooked	1999	$\text{survival} = 0.41 + 0.05 * \sqrt{\text{percent cobble}}$	0.14	0.049
Big Crooked	2000	$\arcsin(\text{survival}) = 1.42 - 0.60 * \log(\text{percent cobble})$	0.24	0.048
Sanford	1998	$\arcsin(\text{survival}) = 0.14 + 0.02 * (\text{percent cobble})$	0.25	<0.001
Bear	1999	--	--	--
Palette	2000	$\arcsin(\text{survival}) = 0.27 + 0.43 * (\text{nearest distance to cover})$	0.27	0.003

Table 7. Habitat features significantly related to fry production at the nest scale. Values reported are  $R^2$  values associated with significant relations. Alpha was set at  $P < 0.05$ .

	<u>Lake</u>					
	BC 98	BC 99	BC 00	Sanford	Bear	Palette
<b><i>Substrate</i></b>						
Percent Sand in the Nest	--	--	--	0.20	0.26	0.20
Percent Gravel in the Nest	--	--	--	0.13	--	0.08
Percent Cobble in the Nest	--	--	--	0.35	--	0.06
Average Embeddedness	--	--	--	0.23	--	0.12
<b><i>Cover</i></b>						
Nearest Cover Size	--	--	--	--	0.50	--
Distance to Cover	--	--	--	--	--	--
Percent of Nest Located Under a Log	--	--	--	--	--	0.14
<b><i>Other Prominent Features</i></b>						
Distance to Shore	--	0.19	--	--	0.24	--
Nest Concavity	--	0.17	--	--	--	--
Slope	--	--	--	--	--	--
Nest Diameter	--	--	--	--	--	0.13
Nest Depth	--	--	--	--	0.39	--
Distance to Nearest Nest	--	--	--	--	--	--

significantly related to nest fry production. In Bear Lake, the diameter of the nearest log accounted for 50% of the variation in fry production. This was the strongest relation between any habitat feature and fry production that we found across all lakes and all variables.

Other prominent habitat features affecting fry production were also variable. Distance to shore and nest concavity were significantly related to fry production in Big Crooked Lake in 1999, but these relations were not consistent across years. The only other significant relations were nest diameter in Palette Lake and distance to shore and nest depth in Bear Lake.

Unlike models for egg survival, our best models predicting fry production were either univariate or bivariate models (Table 8). We could account for between 0% and 50% of the variation in fry production based on habitat with our best models. However, no single habitat feature was significant more than once across lakes. We could account for more of the variation in fry production in Sanford and Bear Lakes than in Big Crooked and Palette Lakes. In Sanford and Bear Lakes, models accounted for between 43% and 50% of the variation in fry production, whereas in Big Crooked and Palette Lakes, models only accounted for between 0% and 25% of the variation in fry production.

Table 8. Habitat features significantly related to smallmouth bass fry production in each study lake; across lake comparisons using best regression models.

Lake	Year	Equation	R <sup>2</sup>	Model p-value
Big Crooked	1998	--	--	--
Big Crooked	1999	fry = 1238.943 + 20.094*(distance to shore)	0.19	0.017
Big Crooked	2000	--	--	--
Sanford	1998	log(fry) = 1.81 + 0.04*(percent cobble) + 1.03*(nest diameter)	0.44	<0.001
Bear	1999	log(fry) = 2.64 + 1.91*(nearest log diameter)	0.50	0.001
Palette	2000	log (fry) = 2.79 – 0.01*(percent sand)	0.18	<0.001

## Discussion

Previous studies have identified ecological processes and general lake features influencing survival and recruitment of smallmouth bass. Early descriptive studies (Hubbs and Bailey 1938, Pflieger 1966) noted that spawning habitat of smallmouth bass was likely mediating recruitment although quantitative analyses were lacking. These early observations identified habitat features such as nesting substrate and cover as important in sustaining a healthy smallmouth bass fishery. Lukas and Orth (1995) quantitatively examined differences between successful and unsuccessful nests in a Virginia stream and found that physical habitat features did not differ between successful and unsuccessful nests. However, these findings are not transferable to lentic systems because stream flow was the primary cause of nest failure. Rejwan et al. (1999) found that habitat features significantly affect nest site distribution in lakes but did not examine relations between habitat and nesting success. In addition to these habitat features, demographic and behavioral characteristics are also thought to affect smallmouth bass nesting success. Several researchers have examined the relation between parental male size and nesting success. Neves (1975) and Ridgway and Friesen (1992) found that larger males are associated with larger broods. This is not surprising since larger males procure more eggs (Wiegmann et al. 1992). Behavioral attributes of parental males have also been associated with increased brood size. Ridgway (1988) found that the tenacity of parental male guarding behaviors increased with brood development while Wiegmann and Baylis (1995) found the opposite to be true.

In our study, smallmouth bass nest site characteristics and the factors affecting nest success were extremely variable across lakes and across years in Big Crooked Lake.

Habitat features in the littoral zone of the study lakes were quite different. This indicates that smallmouth bass can use a wide range of habitat features though some features are clearly more conducive to successful nesting than others as evidenced by the wide range in survival among lakes. Littoral zone substrates in Big Crooked Lake are dominated by sand yet sand was rarely found to be a major nest component in this lake. In contrast, sand is also quite common in the littoral zones of Palette, Sanford, and Bear Lakes. In these lakes, sand was quite abundant in smallmouth bass nests because there were few rocky areas. Surprisingly, the highest densities of smallmouth bass were not found in Big Crooked Lake, but rather in lakes having more fine substrates. Other factors clearly affect survival and recruitment. Differential mortality beyond very young stages that we measured may be due to both interspecific and intraspecific competition and predation (Hall and Werner 1977, Werner et al. 1983a) that may ultimately lead to lower adult population densities.

Nesting cover was also quite different across lakes but unlike substrate, cover use did seem to reflect relative availability in each lake. Most nests in Big Crooked Lake were near small boulders, nests in Palette Lake were near small boulders and woody structure, and nests in Sanford and Bear Lakes were near woody structure almost exclusively which reflected cover availability. Despite the inconsistency in models across lakes, these features are clearly important to nesting smallmouth bass because nesting males will apparently use whatever cover is available to them.

Survival and fry production were variable across lakes and across years in Big Crooked Lake. The range of survival among nests in all study lakes was 0%-100% (nest failures quantified in this study were the result of fungus infestation with a guarding male

still present and not abandonment). At present, no other published literature exhibits this degree of variability in egg survival in smallmouth bass nests. Most likely, this is because very few studies have examined egg survival at the nest scale and those that have examined egg survival have extremely small sample sizes. The ranges of fry production in Big Crooked Lake (0-9570) and Sanford Lake (0-6330) were similar to those reported by Neves (1975) (451-7856) and Ridgway and Friesen (1992) (400-7000). While the ranges of fry production in Palette Lake (0-1900) and Bear Lake (0-4296) were similar to other studies by Surber (1942) (1525-3148), Pflieger (1966) (1651-3952), Clady (1975) (175-2608), and Lukas and Orth (1995) (98-1802).

Habitat features related to survival and fry production were variable across lakes and across years in Big Crooked Lake. No single habitat feature consistently predicted survival across lakes. Significant associations between habitat features and survival accounted for between 14% and 27% of the variation in survival. Significant associations between habitat features and fry production accounted for between 6% and 50% of the variation in fry production. In Big Crooked Lake (1998 and 2000), there were no habitat features significantly associated with fry production. In Sanford Lake, multiple regression models accounted for a greater portion of the variation in fry production than the best univariate model in that lake.

Fry production was more predictable in Sanford and Bear Lakes than in Big Crooked and Palette Lakes. Multiple regression models accounted for between 44% and 50% of the variation in fry production based on habitat alone in Sanford and Bear Lakes. However, habitat features only accounted for between 0% and 19% of the variation in fry production in Big Crooked and Palette Lakes. In Big Crooked Lake, low adult



population density may result in parental males using only “high” quality nest sites resulting in low variation of independent variables used to model nesting success. Consequently, few of the models are significant and those that are significant predict little of the variation in fry production. Higher population densities, negative relations between sand and fry production, and the sheer abundance of sand and finer substrates in Palette, Sanford, and Bear Lakes all suggest competition for high quality nest sites. These results suggest that nesting smallmouth bass habitat use could be characterized as ideal-free (Fretwell and Lucas 1970) in Big Crooked Lake because individual nesting success appears to be unaffected by density. Conversely, nesting smallmouth bass habitat use in Palette Lake more closely resembles ideal-despotic distribution (Fretwell 1972). Whereas nesting smallmouth bass habitat use in Bear and Sanford Lakes is not easily characterized with either distribution theory. Density dependent habitat use has been documented in riverine communities (Bohlin 1977, Bohlin 1978, Hughes 1992, Bult et al. 1999) but not in lacustrine nesting smallmouth bass populations.

Habitat features associated with survival were different than those features associated with fry production. Only five of 11 habitat features were consistent predictors of either survival or fry production. This result could be from a variety of factors. First, there is the effect of parental male size and behavior. Larger males often have larger broods (Neves 1975), larger males have the ability to procure more eggs from females (Wiegmann et al. 1992), and larger males may also defend their broods more aggressively than smaller males (Philipp et al. 1997). Random chance alone suggests that more eggs will translate to more fry so it should not be surprising that the factors affecting survival are not necessarily identical to those factors affecting fry production.

This study provided insight into habitat features affecting smallmouth bass survival and fry production, yet additional work needs to be done. There is increasing concern over how anthropogenic factors may affect smallmouth bass recruitment (Ridgway and Shuter 1997). Direct and indirect alterations to habitat (i.e. shoreline development and riparian/upland land-use practices) (Jennings et al. 1999), eutrophication (Haines 1973), decreasing amounts of woody structure (Christensen et al. 1996), and increased angling pressure (Philipp et al. 1997) threaten current and future smallmouth bass populations. Understanding how habitat affects survival in the nest is prerequisite to not only developing predictive models, but also to developing strategies to protect prime spawning areas and techniques to restore degraded smallmouth bass spawning habitat. Our results show that different processes appear to be regulating survival and fry production at the nest scale. Likely, this indicates that there are also different processes regulating smallmouth bass recruitment in each of these lakes as well. We believe that a good understanding of limnological, habitat, and biological features of each and every lake is essential before we can begin to thoroughly understand how habitat quality affects smallmouth bass recruitment dynamics much less how changes to littoral zones may affect smallmouth bass populations.

## Chapter II:

### Linking habitat selection with habitat quality

#### **Abstract**

Habitat selection by animals is viewed as evidence of the importance of a particular habitat component for a given species. One inherent assumption of habitat selection studies is that habitat selection infers habitat quality, which in turn infers fitness. The objective of this study is to evaluate the linkages between habitat selection and habitat quality. We chose nesting smallmouth bass populations in four lakes in Vilas County, Wisconsin to evaluate these relations. General littoral zone habitat characteristics, smallmouth bass nest characteristics, nest-specific egg survival, and nest-specific fitness were quantified on four lakes in the summers of 1997, 1998, 1999, and 2000. Habitat variables were collected at each nest site and along random transects that were placed perpendicular to the shoreline to a depth of three meters, the maximum depth that nests are found in the study lakes, in order to assess nest site selection. Resource selection functions (i.e., logistic regression) were used to elucidate habitat features used disproportionately as nest sites and from which we could calculate the probability of each nest site being used. Egg and fry estimates were conducted at each nest site to quantify individual nest site quality. We then used linear regression to assess the relations between habitat selection and habitat quality. Our results show that habitat selection only infers habitat quality when adult population densities are high (> 10 adults per hectare) and habitat becomes limited. This suggests that studies of habitat selection only reflect habitat quality under specific conditions.

## **Introduction**

Quantifying habitat selection and habitat quality in fish and wildlife populations is critical to understanding processes limiting population sizes and species distributions (Hobbs and Hanley 1990, Manly et al. 1993). Habitat selection, the use of a specific habitat characteristic in greater proportion to its availability (Johnson 1980), is viewed as evidence of the relative importance of a particular habitat component (Alldredge et al. 1998) and differential habitat selection is one of the principal ecological tenets that allows species to coexist (Schoener 1974, Rosenzweig 1981). Habitat quality (Hall et al. 1997) is especially important in all queries of habitat use by animals because studies of habitat selection are only an indirect approach toward measuring habitat-specific survival and fitness (Garshelis 2000). Therefore, relations between habitat selection and habitat quality need to be thoroughly defined in order to clearly understand how habitat can be useful in managing fish and wildlife populations.

Habitat selection has been studied extensively in terrestrial and aquatic communities alike (Witzel and MacCrimmon 1983, Livingston et al. 1990, Prescott and Collister 1993, Knapp and Preisler 1999). Habitat selection studies were initially derived from forage ratios (Scott 1920, Savage 1931, Williams and Marshall 1938) and electivity indices for diet (Ivlev 1961, Murdoch 1969, Rapport and Turner 1970). These techniques are limited because they provide a ratio of use to availability but do not use a statistical test to assess significant responses (Alldredge and Ratti 1986). Therefore, the interpretation of selectivity indices is problematic because values can represent differences in availability as well as actual differences in preference (Strauss 1979). Hypothesis testing later became a widely used tool among researchers assessing habitat

selection. Numerous statistical tests including Chi-square goodness of fit (Neu et al. 1974), Wilcoxon's signed rank (Talent et al. 1982), and multiple response permutation procedures (Alldredge et al. 1991) have all been used to evaluate habitat selection. While these methods provide a structured way to determine selection and compare the strength of selectivity, they do not make use of the multivariate nature of selectivity data nor are researchers able to control the type I error rate (Thomas and Taylor 1990, Manly et al. 1993). Manly et al. (1993) noted these shortcomings of selectivity indices and hypothesis tests and proposed that a unified statistical theory was needed for habitat selection studies.

Resource selection functions (RSFs) provide a unifying theoretical framework for selection studies and have come into widespread use in studies of habitat selection for a variety of reasons (Alldredge et al. 1998). First, they provide an unbiased estimate of the probability (or a value proportional to the probability) that a habitat will be selected (Manly et al. 1993). For example, Mladenoff et al. (1995) clearly demonstrated the importance of how human perturbations affected eastern timber wolf (*Canis lupus lycaon*) population recovery dynamics by demonstrating higher probabilities of selection in roadless areas. Second, the interpretability of RSFs also makes them a popular tool. For example, Berkelman et al. (1999) used RSFs to predict lake selection by nesting Madagascar Fish-Eagles (*Haliaeetus vociferoides*). From the RSFs they developed, they predicted that anthropogenic impacts such as forest degradation, siltation of lakes and rivers, and conversion of wetlands to rice paddies would likely be detrimental to current and future Fish-Eagle populations.

Despite the increasing use and acceptance of RSFs in studying habitat selection, many problems still remain. A fundamental, yet often overlooked assumption of RSFs (and habitat selection studies in general) is that habitat selection infers habitat quality, which in turn infers fitness (Fretwell and Lucas 1970, Peek 1986). These linkages are tenuous at best, and largely untested (Garshelis 2000). Hobbs and Hanley (1990) illustrated that intraspecific competition can alter use:availability ratios such that they may not reflect the true quality of a habitat in terms of its ability to sustain population growth. They also noted that use:availability ratios can only reflect habitat quality when: 1) animals are distributed in an ideal-free manner (*sensu* Fretwell and Lucas 1970), 2) environmental conditions permit long term stable equilibria between animal populations and limiting resources, and 3) use:availability data are obtained after equilibria are achieved. They felt that these assumptions would rarely be met in open ecological systems. Garshelis (2000) presents a comprehensive discussion of these and other issues of habitat selection studies.

In light of the numerous problems with habitat selection models, several authors have suggested a shift in research focus away from habitat selection toward direct measurements of habitat quality (Hobbs and Hanley 1990, Kellner et al. 1992, Kirsch 1996). Rather than relying on ratios of use and availability or relative habitat saturation, direct measurements of habitat-specific survival and fitness provide causal evidence of relative habitat quality (Garshelis 2000). Other researchers recognize the aforementioned advantages of RSFs, and advocate future investigations of habitat selection (Mladenoff et al. 1995, Arthur et al. 1996, Boyce and McDonald 1999). As

biologists continue to study the role that habitat plays in regulating animal populations, the linkages between habitat selection and habitat quality must be understood.

In order to test the fundamental relations between habitat selection and habitat quality, we evaluated habitat selection (using RSFs) and habitat quality of smallmouth bass (*Micropterus dolomieu*) spawning sites in four lakes. Additionally, we evaluated habitat selection and habitat quality in one lake for three years to assess temporal variability in the relation between habitat selection and habitat quality. We chose nesting smallmouth bass to evaluate the relations between habitat selection and habitat quality for several reasons. The general patterns of smallmouth bass reproduction have been well studied (Hubbs and Bailey 1938, Shuter et al. 1980, Ridgway 1988, Lukas and Orth 1995). Smallmouth bass reproduce in the littoral zone of lakes that are typically heterogeneous environments both physically and biologically. Male smallmouth bass construct nests which are saucer-shaped depressions excavated in the substrate which contain offspring after spawning and fertilization. Before nest construction, smallmouth bass appear to select specific habitats for nest sites because habitat requirements for successful reproduction are not satisfied throughout all regions of the littoral zone of lakes (Rejwan et al. 1999), though few quantitative relations between general habitat features and nest locations exist (Rejwan et al. 1997). Smallmouth bass nests also show high variation in fitness among nests and across years (Surber 1942, Neves 1975, Ridgway and Friesen 1992).

## **Methods**

### *Study Area*

This study was conducted in four lakes in Vilas County, Wisconsin. Surveys were conducted during three consecutive years in Big Crooked Lake (1998-2000), and in Sanford Lake in 1998, Bear Lake in 1999, and Palette Lake in 2000. Smallmouth bass harvest is restricted in each lake. No smallmouth bass harvest is allowed in Big Crooked, Sanford, or Bear Lake while Palette Lake has a 40.6 cm (16 inch) minimum length limit, effectively eliminating most harvest of fish. Smallmouth bass harvest from Palette Lake is low as documented by a complete, mandatory creel census; therefore harvest can be accounted for in analyses of nest success. Species richness of each lake is low (8-12 species) (Appendix B), yet similar to other lakes in the Northern Lakes and Forests Ecoregion (Omernick and Gallant 1988). Demographic characteristics of smallmouth bass populations were variable across lakes but similar across years for Big Crooked Lake (Table 9). Adult smallmouth bass populations were highest in Palette Lake and lowest in Bear Lake while population densities were highest in Palette Lake and lowest in Big Crooked Lake. Parental male size structure varied across lakes with the largest males found in Big Crooked Lake (Figure 6).

### *Available Habitat*

Habitat characteristics of each lake's littoral zone, to a depth of 3.0 m, were quantified using 100 transects randomly placed along the perimeter of each lake's shoreline. A maximum depth of 3.0 m was used because smallmouth bass did not construct nests in depths greater than 3.0 m in any of the study lakes. Specific transect



Table 9. Demographic features of smallmouth bass populations in the study lakes. Population estimates include 95% confidence intervals in parentheses.

Lake	Big Crooked 1998	Big Crooked 1999	Big Crooked 2000	Sanford 1998	Bear 1999	Palette 2000
Adult population estimate	168 (93-336)	233 (114-837)	207 (82-518)	165 (108-264)	79 (43-198)	722 (492-1243)
Adults per hectare	0.6	0.8	0.8	4.6	2.5	10.3
Number of nests	38	49	48	51	28	107
Nests per shoreline km	3.5	4.5	4.4	9.6	6.1	26.6
Mean ( $\pm$ S.E.) distance from nest to nest (m)	44.3 $\pm$ 5.3	46.2 $\pm$ 9.1	40.0 $\pm$ 5.0	46.0 $\pm$ 5.6	23.9 $\pm$ 7.0	18.6 $\pm$ 1.5



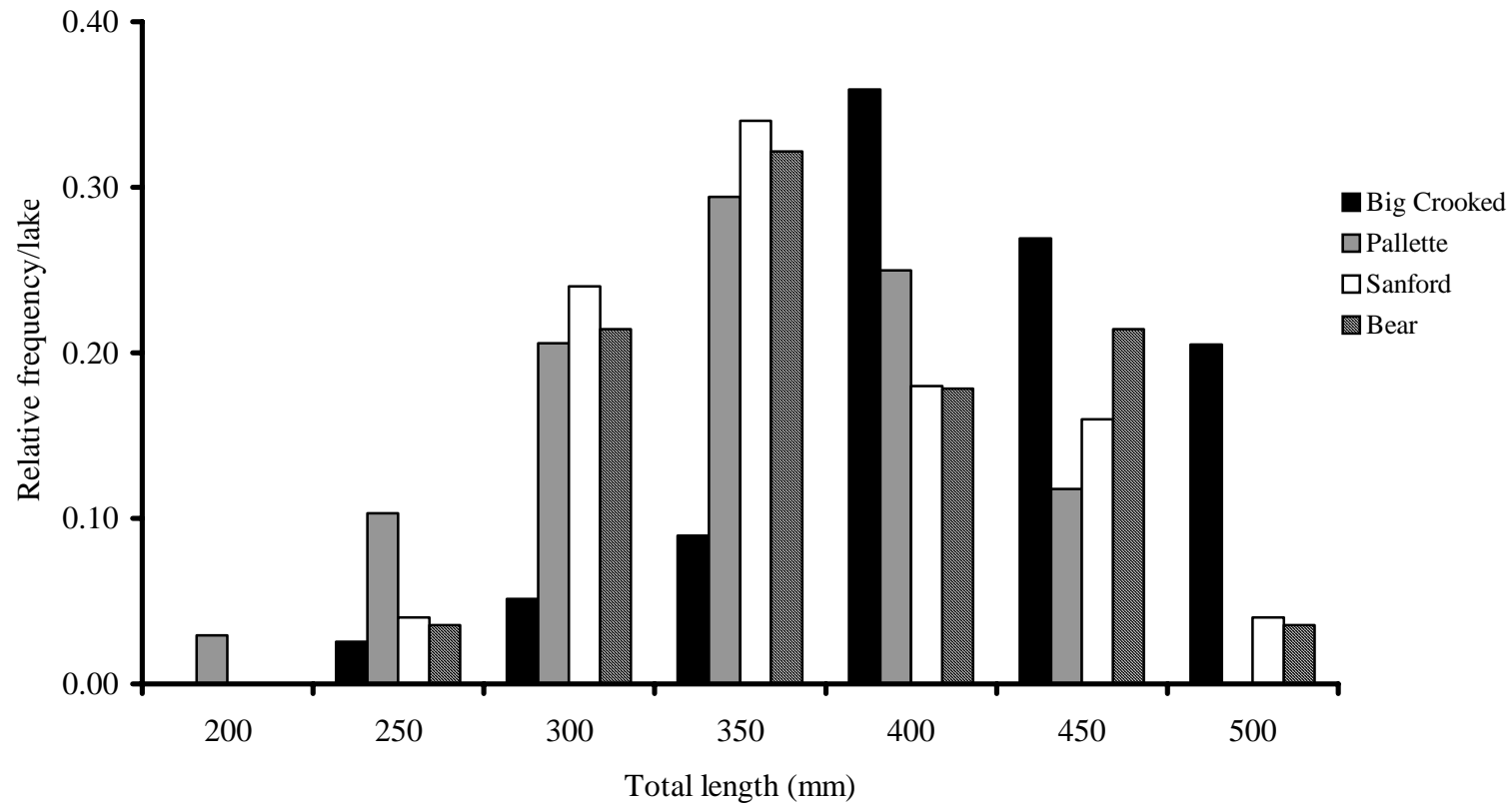


Figure 6. Distribution of total lengths (mm) of parental male smallmouth bass on active nests in four north temperate lakes. Lengths were similar across years (1998-2000) in Big Crooked Lake and were pooled (ANOVA  $F=1.028$ ,  $p=0.361$ ).

locations were selected based on elapsed time traveled from an arbitrary start location on the shore of each lake. A mean elapsed time to idle the survey boat around the entire lake along the 2-m contour was calculated and then individual transects were placed at the locations corresponding to the 100 randomly drawn times. Habitat variables were collected along each transect using a one m<sup>2</sup> quadrat at points located every two meters from shore until a depth of 3.0 m. Slope was calculated as the difference in depths (rise) collected at the two transect points immediately before and after the sample point, divided by that distance (run). The same variables and techniques used to quantify nest habitat (i.e., used habitat) were also used to quantify habitat at each transect point.

#### *Used Habitat*

Nest location procedures and habitat assessments were consistent across lakes and years. The entire littoral zone of each lake was surveyed every other day during the spawning season to locate nests as they were being constructed. Nest sites were located by visual observations while motoring along the 1.0 m and 2.0 m depth contours of each lake and by snorkeling and SCUBA diving in deeper water. SCUBA divers were towed around the 2.0 m, 2.5 m, and 3.0 m depth contours to ensure that deeper nests were located. Surveys in deeper water revealed no nests occurred deeper than 2.79 m. Eggs and fry were enumerated throughout the spawning season while nest habitat was quantified after fry had emerged from the nest and were no longer in close proximity to the parental male. Habitat variables measured at each nest included distance from shore; water depth; nest concavity; nest diameter; substrate size; substrate embeddedness; orientation, type, distance to, and size of cover; and bottom slope. Distance to shore,

water depth, and distance to cover (e.g., woody structure or rocks that provide potential refuge from predatory attacks or competitive interactions) were measured to the nearest 0.1 m with a tape measure to the edge of the nest. Nest concavity quantified the depth to which substrate was excavated in nest construction and was measured with a tape measure from the center of a plastic rod laid across the nest, rim to rim, to the bottom of the nest. Nest diameter was the mean of two perpendicular transects measured by stretching a tape measure from nest edge to nest edge. Percentages of each substrate particle size (Wentworth 1922, Platts et al. 1983) were visually estimated in 5% increments using a 36x36 cm enumeration grid composed of 36 (6x6 cm) grid squares. Substrate embeddedness was visually estimated and rated as the degree to which the smaller substrate particles surrounded or covered larger particles. We used a system modified from Platts et al. (1983) whereby highly embedded substrates were coded as 4 and clean substrates were coded as 0 (Appendix A). Woody structure (>0.1 m in diameter and > 1.0 m in length) and large rocks (>0.1 m in diameter) were measured as cover when they were less than 1.5 m away from the rim of the nest. Nest orientation to cover was recorded as either near cover (within 1.5 m), no cover, or under cover (at least 5% of nest was below a cover item). If a nest was under cover (e.g., a tree bole), the percentage of the nest under the cover item was visually estimated to the nearest 5% increment. Nest site slope was calculated by dividing the difference between two depth measurements (rise) by the nest diameter (run); the two depths were measured where two points of a transect tape, laid perpendicular to shore across the nest, intersected the nest rim.

### *Habitat Selection*

Resource selection functions (RSFs) defining the relative probability of use of a site by smallmouth bass for nesting were developed for each lake and for each year in Big Crooked Lake. Logistic regression was used to develop the RSFs because it is the preferred analysis for differentiating between two classes of response variables (e.g., presence/absence) (Press and Wilson 1978, Prager and Fabrizio 1990, Manly et al. 1993).

Logistic regression uses the function:

$$\pi = e^u / (1 + e^u)$$

where:  $\pi$  = the probability of nest presence

$e$  = the inverse natural logarithm of 1

$$u = k + m_1x_1 + m_2x_2 + \dots + m_ix_j$$

$k$  = constant

$m_i$  = the regression coefficients

$x_j$  = the values of independent variables

The G-statistic was used to test the significance of each RSF. This statistic measures the deviation of the observed values from predicted values in the RSF and is analogous to the residual sum-of-squares in linear regression (Hosmer and Lemeshow 1989). Chi-square analyses were used to test the significance of individual regression coefficients in each function with Alpha set at  $P < 0.05$ . All habitat variables and interactive terms were used in univariate RSFs to determine best model fit in describing the probability of nest site selection. All variables were considered for entry into the multiple logistic regression analyses if  $P \leq 0.20$  in univariate analyses, Pearson correlation matrix coefficients were less than 0.65, and the variables were biologically

relevant when added to the model. All other variables were removed from consideration to help ensure that residual explanatory power was not masked by colinearity (Hosmer and Lemeshow 1989). We then evaluated the correct classification rates and the McFadden  $Rho^2$  statistic for each significant model. As each new variable was added to each model, the model was sequentially compared to the previous model using the G-score assessing the increase in model fit (Linhart and Zucchini 1986, Hosmer and Lemeshow 1989). The best univariate, best multivariable, most parsimonious, and the most transferable RSFs were developed for each lake and for each year in Big Crooked Lake. We selected the best univariate and multivariable models according to correct classification rates and McFadden  $Rho^2$  statistics. We selected the most parsimonious model based on the Akaike Information Criterion (AIC) value (Anderson et al. 2000); the model with the lowest AIC was considered the most parsimonious. We selected the most transferable RSF based on predictive capabilities (correct classification and McFadden  $Rho^2$ ) and statistical significance (G-scores) across lakes.

### *Habitat Quality*

The number of eggs and fry were quantified at each nest. Egg estimates were conducted on each nest within two days of spawning to control for potential differences among nests caused by predation over time. Egg abundance was visually estimated using a 30x30 cm grid composed of 25 smaller (6x6 cm) squares. This grid was placed across the top of the aggregation of eggs. The number of eggs in each smaller square was individually estimated and then later summed for an overall nest estimate. Fry estimates were conducted in a similar manner but using a larger (36x36 cm) grid with 36 smaller

(6x6 cm) squares. The larger grid was necessary because fry covered a larger area in each nest. Fry estimates were standardized by stage of development (Hubbs and Bailey 1938) and conducted only after they had black pigmentation prior to swim-up. At this time, fry briefly orient themselves on top of the substrate in the nest just before they begin to disperse to forage (i.e., swim-up).

Egg and fry estimates were validated by comparing the number of eggs or fry estimated using the grid to an actual count conducted on a sub-sample of 12 nests (six for egg estimates, six for fry estimates). For validating estimates, we carefully removed all eggs or fry from each nest using low pressure suction, removed all substrates to insure inclusion of all eggs or fry, and counted all eggs or fry after each estimate. Linear regression was then used to determine the accuracy of the estimate (i.e., coefficient of determination). A slope of 1.0 indicates that on average, the estimate reflects the true number of eggs or fry. For analyses, estimates were corrected by multiplying the egg or fry estimate by the inverse of the regression slope that relates the actual number of eggs or fry on the nest to the estimated number of eggs or fry on the nest. Eggs and fry were immediately placed back into the nest after the validation, though these nests were not used in subsequent analyses of nest success.

#### *Assessing Relations Between Habitat Selection and Habitat Quality*

We used linear and non-linear regression to test the fundamental assumption that habitat selection was related to habitat quality (i.e., nests with higher probabilities of selection should have higher egg survival and fitness relative to nests with low probabilities of selection). In each lake, we generated the probability of selection for



each nest using four RSFs developed in each lake: the best univariate RSF, the best overall RSF, the most parsimonious RSF, and the most transferable RSF. We regressed probabilities of selection against the two metrics of habitat quality (e.g., survival and fitness). In each test, we used egg survival (number of fry/ number of eggs \* 100) as the dependent variable because habitat selection studies are an indirect approach of measuring habitat-specific survival (Garshelis 2000). We also used fitness, defined herein as the number of fry/ lake-specific maximum number of fry, as the dependent variable relating habitat selection to habitat quality because fitness is of ultimate importance to habitat selection and habitat quality studies alike (Fretwell and Lucas 1970). We used linear regression to examine the relation between the probability of selection and nest success, with a positive significant relation confirming the assumption of habitat selection reflecting habitat quality. We also used Mann-Whitney U-tests with Bonferroni type I error corrections when linear regression was not appropriate because of extreme non-normal distributions of the independent variable (i.e., binomial distributions). In this case, the assumption of habitat selection reflecting habitat quality would be confirmed if nests with high probabilities of selection ( $\geq 0.50$ ) had significantly higher survival or fitness than nests with low probabilities of selection ( $< 0.50$ ).

## **Results**

### *Available Habitat*

In general, littoral zone habitat differed substantially among lakes. Sand was the most abundant substrate size in Big Crooked and Palette Lakes. While sand was also widespread in Sanford and Bear Lakes (Figure 7), finer substrates such as silt and organic

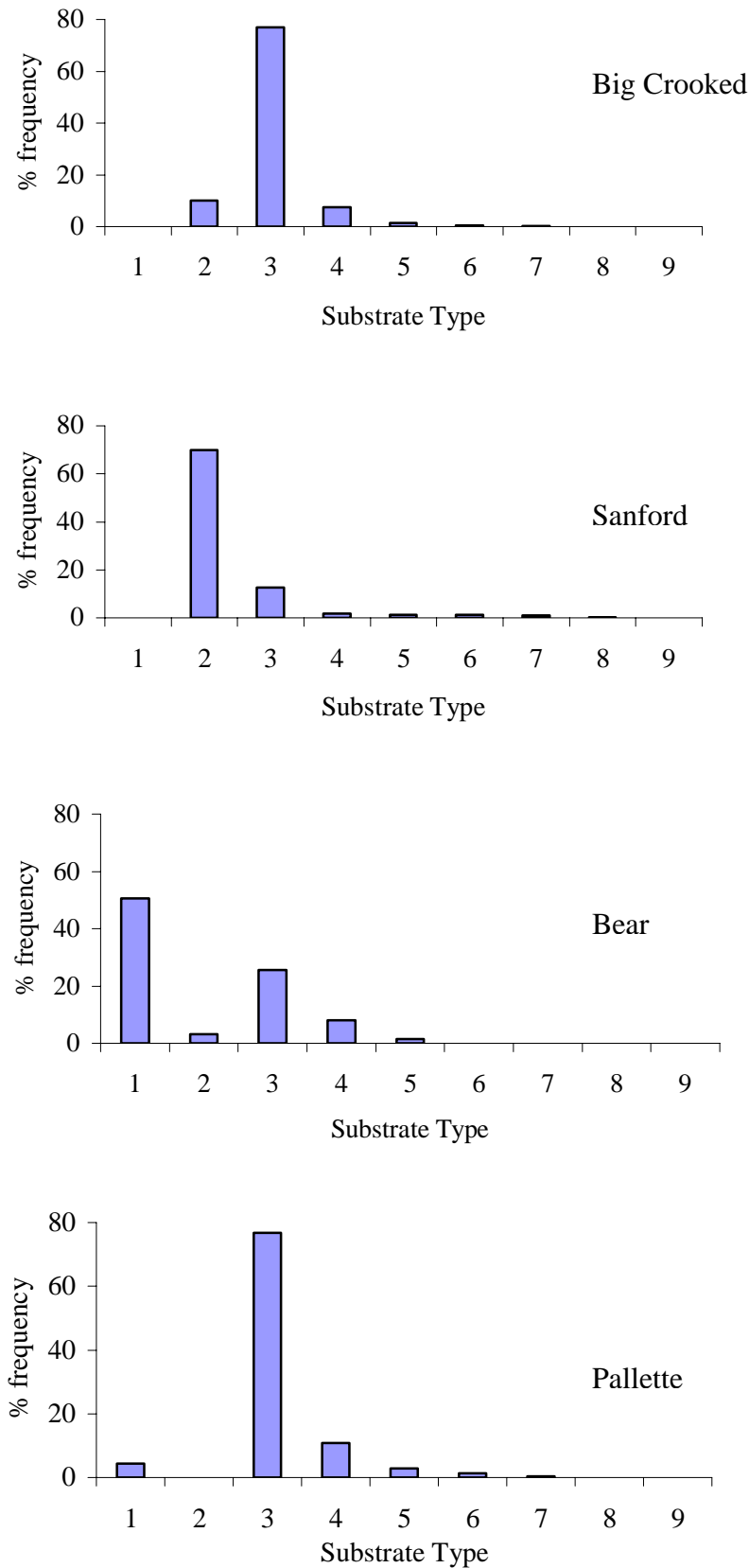


Figure 7. Substrate particle size distributions from the littoral zones of four lakes. (1) fine organic material, (2) silt, (3) sand, (4) gravel, (5) cobble, (6) rubble, (7) small boulders, (8) large boulders, and (9) bedrock.

matter that were rare in Big Crooked and Palette Lakes, were common in the littoral zones of Sanford and Bear Lakes. Fine substrates were less common in Big Crooked and Palette Lakes. Big Crooked and Palette Lakes also had substantial areas of gravel (>5% occurrence) while Sanford and Bear Lakes had few areas of this type. Cover in littoral zones also differed among lakes (Table 10). Big Crooked and Palette Lakes had few boulders or pieces of coarse woody structure whereas the littoral zones of Sanford and Bear Lakes had abundant coarse woody structure and few boulders. Differences in slope were also apparent among lakes with Sanford and Bear Lakes having steeper slopes than Big Crooked and Palette Lakes.

#### *Used Habitat*

Habitat characteristics associated with smallmouth bass nests varied across lakes (Table 11). Nests in Big Crooked Lake were composed almost entirely of gravel and cobble whereas nests in the other study lakes were composed mostly of gravel and sand. In fact, 19% of nests in Palette Lake were composed of  $\geq 50\%$  sand substrate and four of these nests were composed entirely of sand. The mean percent sand in the nests was similar (24% to 31%) in Sanford, Bear and Palette Lakes. In contrast, percentages of sand in Big Crooked Lake nests rarely exceeded 20% even though sand is the dominant substrate in the littoral zone. Substrates directly outside of the actual nests reflected the general spawning area characteristics. Coarse substrates were located outside nests in Big Crooked Lake whereas finer substrates occurred outside nests in the other lakes. Similarly, embeddedness of nests reflected substrate composition. Big Crooked Lake had the least embedded nests whereas Palette, Sanford, and Bear Lakes had higher mean

Table 10. Limnological features of the four study lakes.

Lake feature	Big Crooked Lake	Sanford Lake	Bear Lake	Palette Lake
Surface area (ha)	276	36	31	70
Maximum depth (m)	12	16	10	18
Woody cover (pieces/m <sup>2</sup> )	0.05 (174/3380)	0.38 (428/1139)	0.11 (136/1171)	0.04 (141/3460)
Shoreline slope	0.046	0.143	0.130	0.049
Color (Pt units)	8.9	30.4	27.8	14.5
PH	7.1	5.9	7.9	6.6
Total alkalinity (mg L <sup>-1</sup> )	14.0	6.0	91.1	9.0

Table 11. Physical characteristics of smallmouth bass nests in the littoral zone of four north temperate lakes. Values represent the mean  $\pm$  1 standard error. Characteristics of nests in Big Crooked Lake were not significantly different across years and thus values were pooled. Statistically different groups (Kruskall-Wallis test) are noted with lower case letters above the values.

Nest characteristic	Big Crooked Lake	Sanford Lake	Bear Lake	Palette Lake	K	P
	a	b	b	b		
Nest diameter (m)	0.93 $\pm$ 0.03	0.68 $\pm$ 0.02	0.56 $\pm$ 0.03	0.52 $\pm$ 0.03	103.8	<0.001
	a	b	b	b		
Sand (%)	5 $\pm$ 0.9	31 $\pm$ 3.9	24 $\pm$ 3.5	26 $\pm$ 2.8	66.2	<0.001
	a	b	ab	b		
Gravel (%)	75 $\pm$ 1.9	63 $\pm$ 4.1	70 $\pm$ 4.1	62 $\pm$ 2.8	17.4	0.001
	a	b	b	b		
Cobble (%)	19 $\pm$ 1.8	5 $\pm$ 1.0	6 $\pm$ 1.3	6 $\pm$ 1.1	39.9	<0.001
	a	b	b	b		
Substrate embeddedness	1.2 $\pm$ 0.1	2.6 $\pm$ 0.1	3.0 $\pm$ 0.1	2.4 $\pm$ 0.1	94.6	<0.001
Percent nests near rocky cover	74	10	0	32		
Percent nests near woody cover	11	78	100	36		
Percent nests near both rocky and woody cover	14	6	0	21		
Percent nests with no cover	0	6	0	11		

embeddedness values. There was a significant negative relation between the day of the spawning season and percent gravel per nest only in Palette Lake (Figure 8).

Use of cover differed among lakes. Although limited in supply, large rocks and small boulders were consistently used as cover (74% of nests) for nesting males in Big Crooked Lake. Whereas, only two (1998) to four (2000) nests were placed near woody structure in Big Crooked Lake each year. The opposite was true in Sanford and Bear Lakes where 86% and 100% of nests respectively, were placed next to woody structure. In Palette Lake, 36% of nests are placed near woody structure, 32% of nests are placed near a rock, 21% of nests are placed near woody structure and a rock, and 11% of nests were not close to any cover at all.

### *Habitat Selection*

In all study lakes, smallmouth bass generally selected areas having coarser substrates and cover proximal to the nest relative to its availability in the lakes. However, specific habitat features selected as nest sites varied across lakes and varied across years in Big Crooked Lake (Table 12), though consistent patterns were apparent. The variables gravel and nest rock cover were the most consistent predictors of nest site location among lakes and across years in Big Crooked Lake.

The RSFs developed for each lake predicted nest absence extremely well (96%-99%) but were variable in their ability to predict nest presence (19%-92%). The best univariate RSF in each lake correctly classified nest presence with 28% to 73% accuracy with McFadden  $Rho^2$  values ranging from 0.391 to 0.775. The best overall RSFs

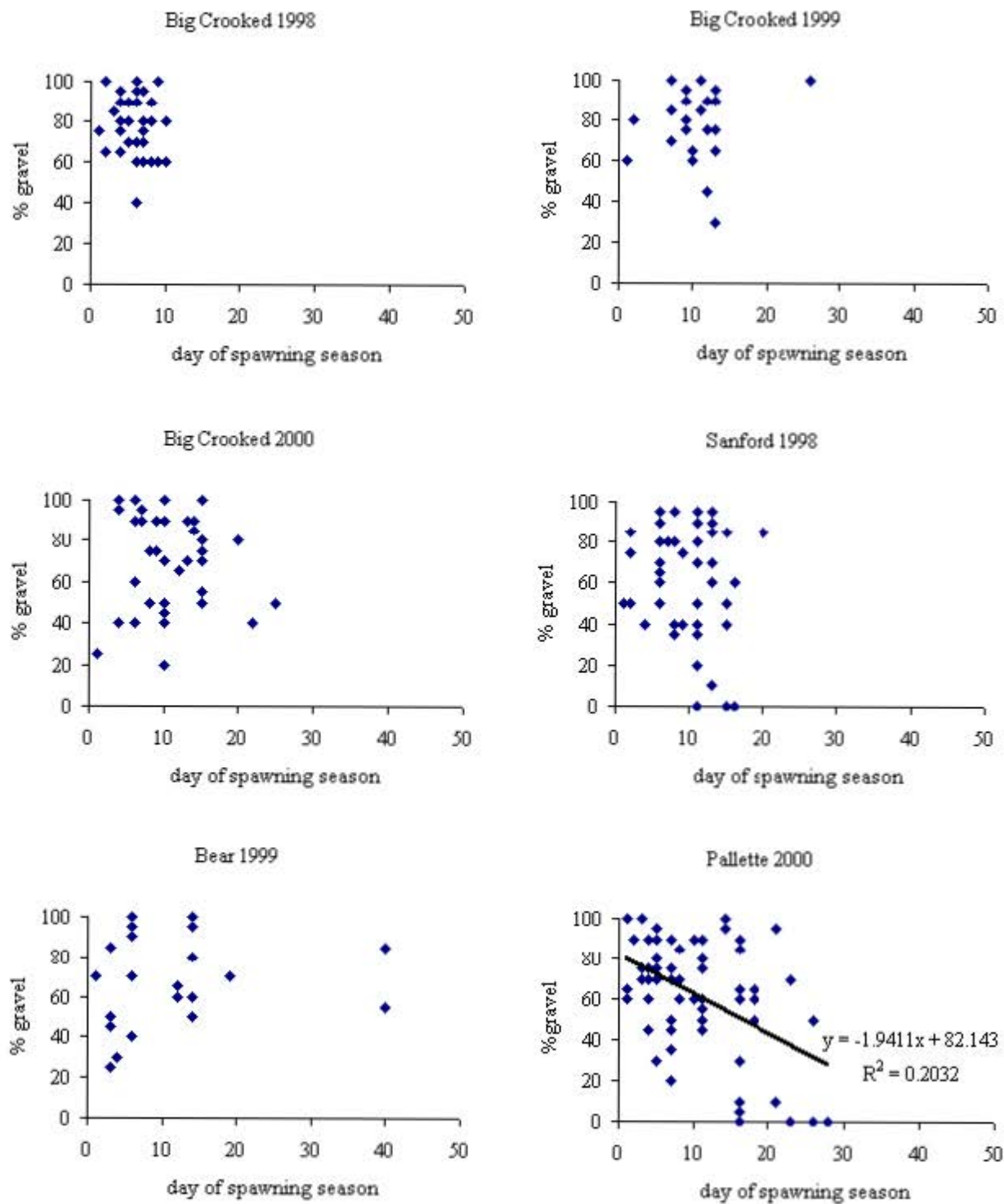


Figure 8. Relations between nest construction date and the amount of gravel in the nest in four north temperate lakes. Significant relations are plotted as a solid line.

Table 12. Summary of the best univariate (u), the best overall multivariable (m), the most parsimonious (p), and the most transferable (t) RSFs predicting smallmouth bass presence/absence in Big Crooked (1998-2000), Sanford (1998), Bear (1999), and Palette Lakes (2000). All variables in multiple logistic regression models are significant at  $P \leq 0.05$ .

Model type	Variables in model	Regression coefficient	Constant	-2 Log Likelihood	McFadden $Rho^2$	P	Classification rates	
							Presence	Absence
<b>Big Crooked 1998</b>								
u, p	Nest Rock Cover	1.468	-11.259	210.86	0.494	<0.001	30	98
m	Sand	0.529	-71.634	63.044	0.882	<0.001	77	99
	Gravel	0.543						
	Cobble	0.511						
	Nest Rock Cover	3.823						
	Embeddedness	-2.007						
t	Nest Rock Cover	0.088	-18.048	134.174	0.687	<0.001	51	99
	Gravel	1.662						
<b>Big Crooked 1999</b>								
u	Gravel*Nest Rock Cover	0.018	-9.762	119.766	0.641	<0.001	46	99
m, p	Gravel*Nest Rock Cover	0.038	-19.506	64.058	0.808	<0.001	72	99
	Cobble	0.179						
	Sand	0.215						
	Embeddedness <sup>2</sup>	-0.787						
	Total Wood	0.503						
t	Nest Rock Cover	1.524	-17.537	120.172	0.640	<0.001	44	99
	Gravel	0.089						



Table 12 (con't). Summary of the best univariate (u), the best overall multivariable (m), the most parsimonious (p), and the most transferable (t) RSFs predicting smallmouth bass presence/absence in Big Crooked (1998-2000), Sanford (1998), Bear (1999), and Palette Lakes (2000). All variables in multiple logistic regression models are significant at  $P \leq 0.05$ .

Model type	Variables in model	Regression coefficient	Constant	-2 Log Likelihood	McFadden Rho <sup>2</sup>	P	Classification rates	
							Presence	Absence
<b>Big Crooked 2000</b>								
u	Nest Rock Cover	1.583	-11.745	224.720	0.530	<0.001	33	99
m, p	Gravel	0.225	-44.502	72.230	0.849	<0.001	78	99
	Cobble	0.238						
	Nest Rock Cover	3.729						
	Gravel*Total wood	0.060						
	Sand	0.215						
	Depth*Embeddedness	-1.236						
	Depth	1.755						
t	Nest Rock Cover	1.471	-13.817	183.03	0.617	<0.001	41	99
	Gravel	0.049						
<b>Sanford 1998</b>								
u	Gravel	0.120	-5.416	122.002	0.710	<0.001	73	99
m, p	Sand	0.058	10.034	43.692	0.896	<0.001	92	99
	Gravel	0.141						
	Embeddedness	-3.906						
	Nest Rock Cover	-1.342						
t	Gravel	0.143	-3.082	78.184	0.814	<0.001	85	99
	Nest Rock Cover	-1.148						

Table 12 (con't). Summary of the best univariate (u), the best overall multivariable (m), the most parsimonious (p), and the most transferable (t) RSFs predicting smallmouth bass presence/absence in Big Crooked (1998-2000), Sanford (1998), Bear (1999), and Palette Lakes (2000). All variables in multiple logistic regression models are significant at  $P \leq 0.05$ .

Model type	Variables in model	Regression coefficient	Constant	-2 Log Likelihood	McFadden Rho <sup>2</sup>	P	Classification rates	
							Presence	Absence
<b>Bear 1999</b>								
u	Gravel*Total wood	0.081	-6.503	49.326	0.775	<0.001	72	99
m, p	Gravel	3.608	-363.490	12.396	0.943	<0.001	90	99
	Cobble	3.601						
	Total wood	6.975						
	Sand	3.528						
t	Gravel	0.086	-18.949	67.886	0.590	<0.001	38	98
	Nest Rock Cover	2.739						
<b>Palette 2000</b>								
u	Embeddedness <sup>2</sup>	-0.401	1.329	568.130	0.391	<0.001	28	98
m, p	Cobble	-0.036	1.237	375.024	0.591	<0.001	49	99
	Embeddedness	-1.782						
	Depth*Gravel	0.031						
	Wood1	0.180						
	Total wood	0.985						
	Gravel*Wood1	0.010						
t	Gravel	0.044	-7.851	627.996	0.327	<0.001	19	96
	Nest Rock Cover	0.627						

correctly classified nests with 49% to 92% accuracy (McFadden  $Rho^2$  from 0.591 to 0.943). The bivariate model that most consistently predicted nest presence across lakes included the variables gravel and nest rock cover. Therefore, we chose this model as the most transferable. These bivariate models correctly classified nests with 19% to 85% accuracy (McFadden  $Rho^2$  from 0.327 to 0.814). The most parsimonious models in each lake were the best overall multivariable models.

### *Habitat Quality*

Visual estimates of smallmouth bass eggs and fry visual were quite accurate in enumerating actual numbers of eggs and fry on nests. Coefficients of determination were 0.98 for egg estimates ( $y = 0.825*x - 34.556$ ) and 0.97 for fry estimates ( $y = 0.868*x + 7.747$ ). Slopes of both lines were less than 1.0 indicating that estimates slightly underestimated the actual number of individuals on each nest.

Both survival and fry production were variable across lakes (Figures 13, 14). Overall, nests in Big Crooked and Bear Lakes had higher mean egg survival than nests in Palette and Sanford Lakes. Survival did not vary across years in Big Crooked Lake. As with egg survival fry production also varied across lakes, and in Big Crooked Lake, across years. Nests in Big Crooked Lake in 1998 had higher mean levels of fry production than nests in other lakes or other years in Big Crooked Lake. Big Crooked (1999 and 2000) and Bear Lakes had intermediate levels of fry production. Nests in Sanford and Palette Lakes had the lowest mean fry production.

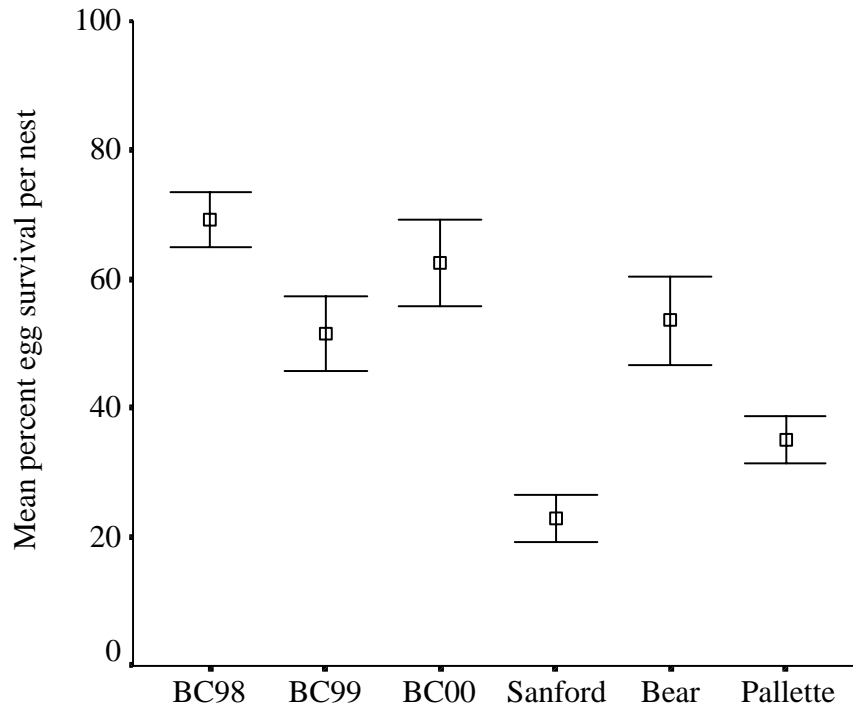


Figure 13. Mean survival ( $\pm 1$  S.E.) of smallmouth bass from egg through black swim-up fry in each study lake. (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.

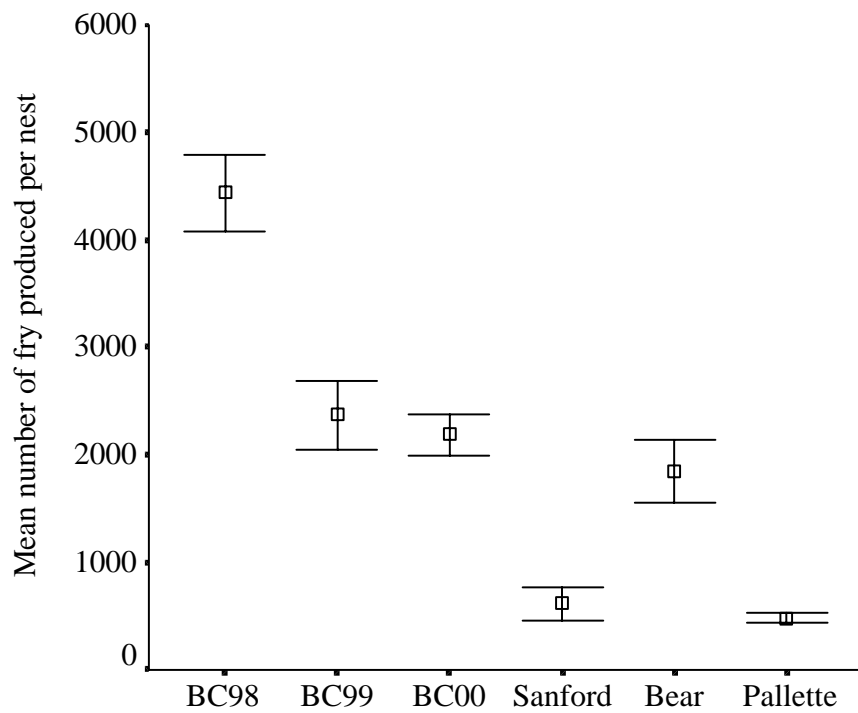


Figure 14. Mean fry production ( $\pm 1$  S.E.) per nest in four north temperate lakes. (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000

*Relations Between Habitat Selection and Habitat Quality*

Relations between habitat selection and habitat quality were rarely statistically significant. Habitat selection was only significantly related to habitat quality in Palette Lake. Here, the probability of selection from each RSF tested was significantly related to fitness but not survival. Neither survival nor fitness was significantly related to the probability of selection in other lakes.

The distributions of probabilities of selection generated from each RSF were often non-normal and made regression analyses problematic (Figure 15). The best univariate RSF in Big Crooked Lake 1998 and Big Crooked Lake 2000 indicated that nests had fewer than six distinct probabilities of selection. The best multivariable RSFs in Big Crooked Lake 1998, Big Crooked Lake 2000, and Bear Lake 1999 generated probabilities of selection for each nest that were skewed toward high values with little variation in between. The probabilities of selection generated from RSFs from other lakes were more evenly distributed and therefore regression analyses were appropriate. For lakes where regression analyses were not appropriate, Mann-Whitney U-tests indicated that survival and fitness of nests that were likely to be selected (probability of selection  $>0.50$ ) did not differ from those nests that were not likely to be selected (probability of selection  $<0.50$ ) (Table 13).

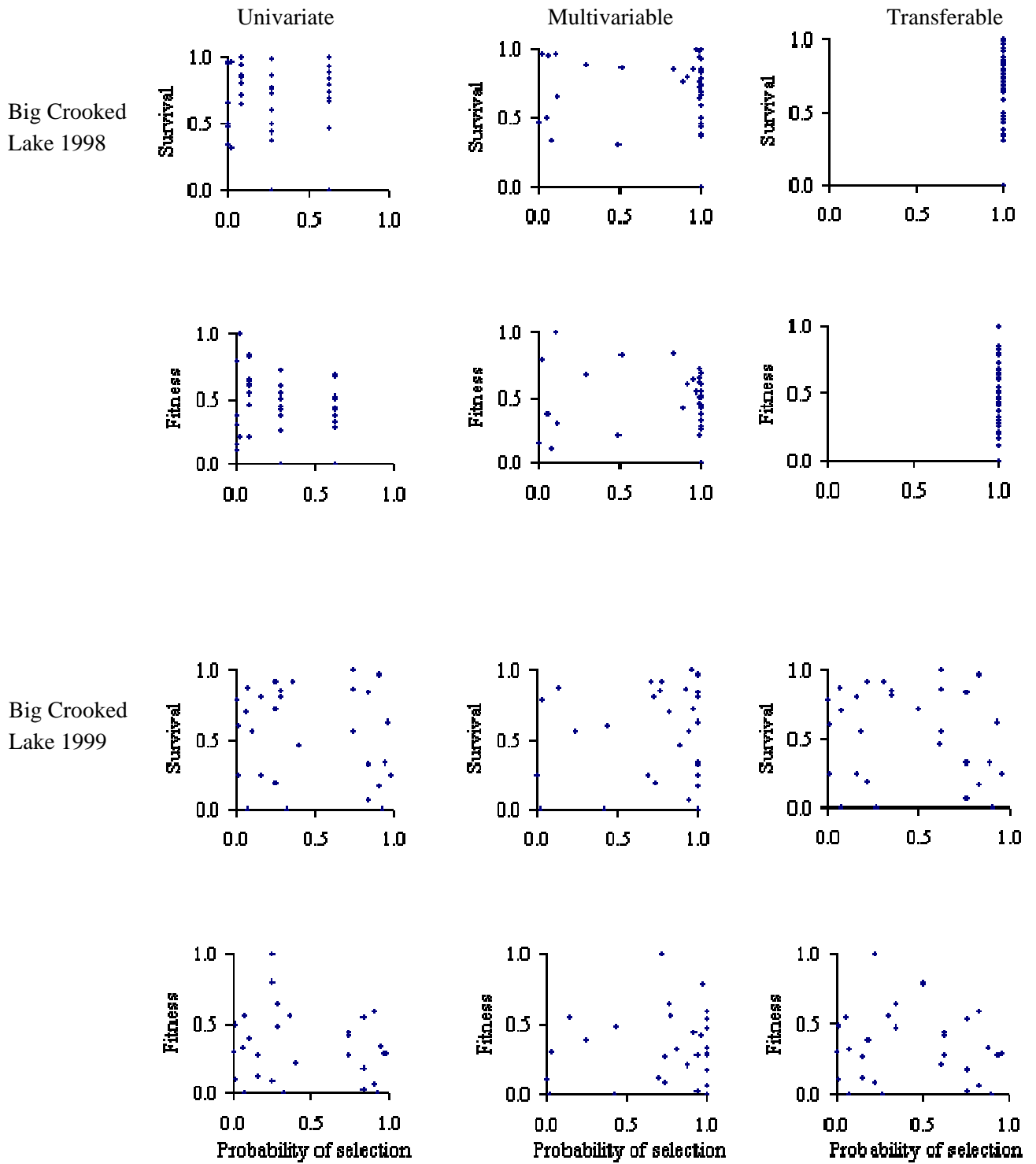


Figure 15. Relations between habitat selection and habitat quality. Significant relations are plotted with a solid line.

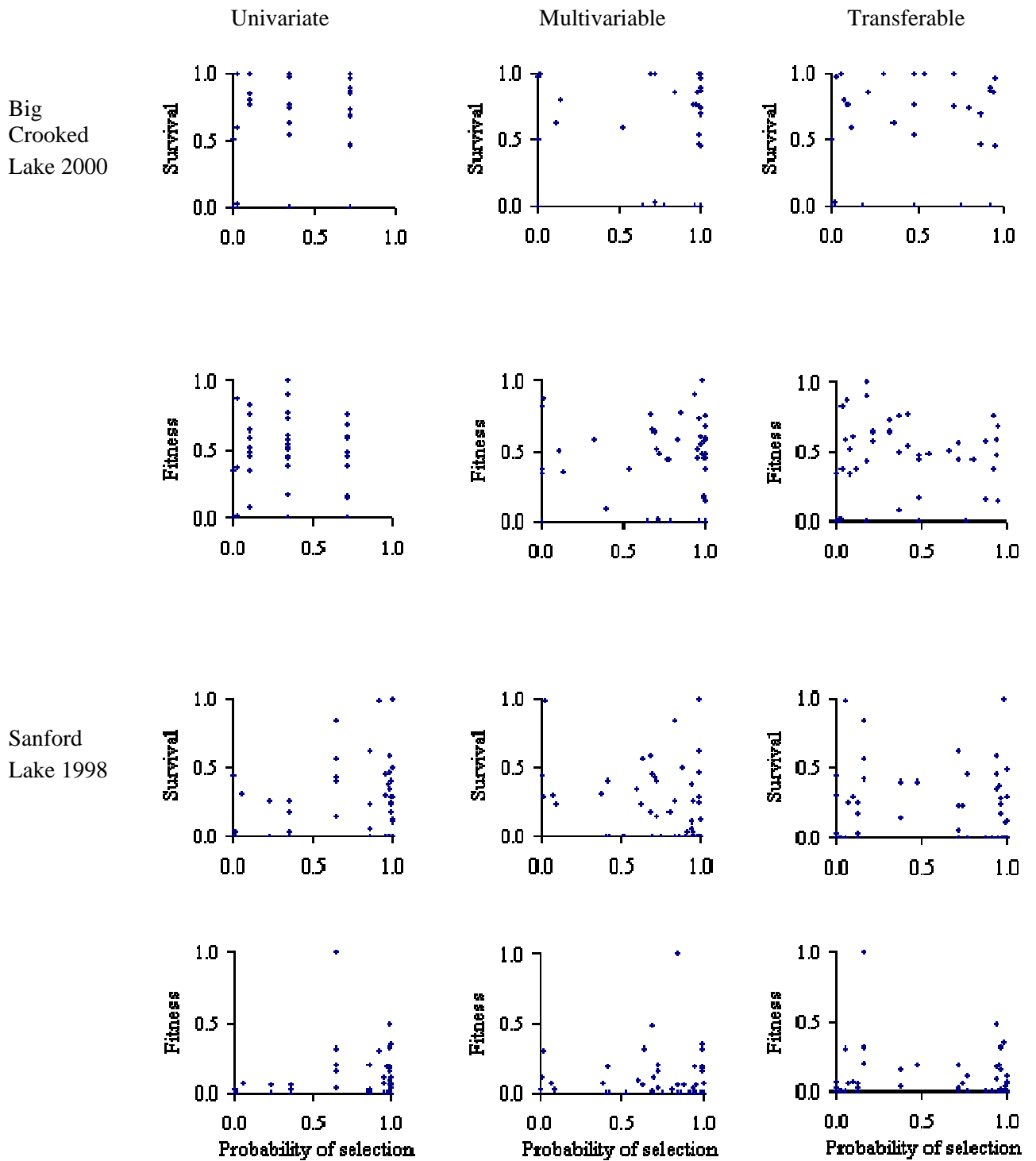


Figure 15 (con't). Relations between habitat selection and habitat quality. Significant relations are plotted with a solid line.



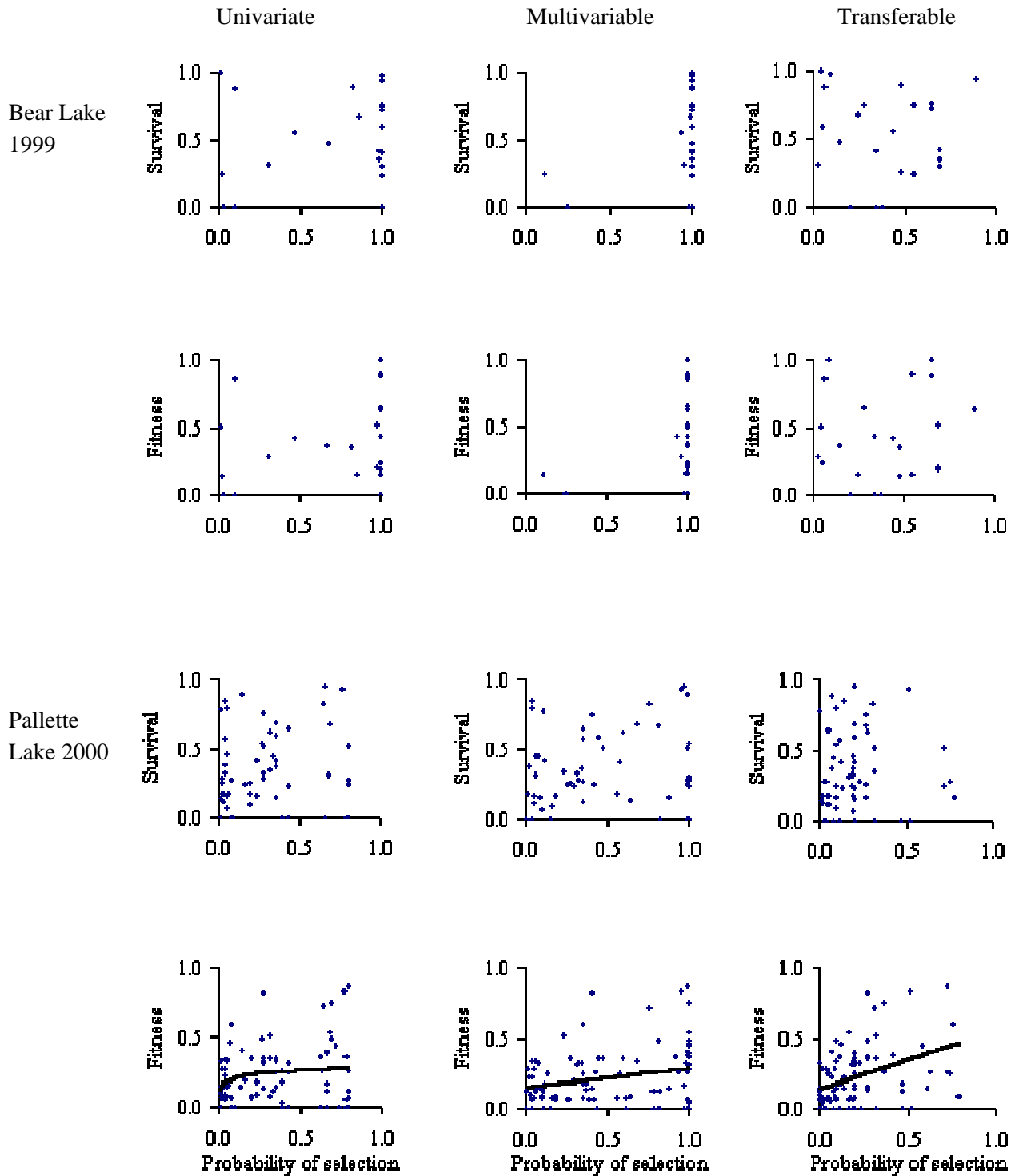


Figure 15 (con't). Relations between habitat selection and habitat quality. Significant relations are plotted with a solid line.

Table 13. Mean survival and fitness ( $\pm 1$  S.E.) of nests in Big Crooked Lake (1998 and 2000) and Bear Lake (1999) relative to the probabilities of selection generated using the best multivariable RSF. Mann-Whitney U-tests ( $\alpha = 0.008$ ) assessed differences in survival and fitness.

	Big Crooked Lake 1998	Big Crooked Lake 2000	Bear Lake 1999
	<u>Survival</u>		
Probability of selection $< 0.5$	$0.67 \pm 0.09$	$0.65 \pm 0.15$	$0.13 \pm 0.13$
Probability of selection $\geq 0.5$	$0.70 \pm 0.04$	$0.59 \pm 0.08$	$0.57 \pm 0.07$
U	125.5	77.5	4.0
P	0.864	0.774	0.063
	<u>Fitness</u>		
Probability of selection $< 0.5$	$0.44 \pm 0.10$	$0.44 \pm 0.10$	$0.07 \pm 0.07$
Probability of selection $\geq 0.5$	$0.47 \pm 0.05$	$0.47 \pm 0.05$	$0.46 \pm 0.07$
U	109.5	137.0	3.0
P	0.470	0.229	0.049

## Discussion

Our current understanding of smallmouth bass habitat requirements comes mostly from models based on habitat use (e.g., Lyons 1991, Lukas and Orth 1995).

Unfortunately, these types of models are not transferable across systems because of substantial differences in available habitat nor do they allow us to make meaningful predictions regarding anthropogenic changes to riparian and littoral zones (Bozek and Rahel 1991, Jennings et al. 1999). Habitat selection models are thought to be preferable to those based on use because they incorporate measurements of habitat availability. However, ratios of use to availability may or may not reflect true habitat quality in terms of the habitat's ability to support population growth and persistence over time (Manly et al. 1993). Demographic response studies are the only means of truly evaluating the relative importance of habitats for supporting animal populations (Garshelis 2000).

Few studies have examined smallmouth bass nest-site selection (Rejwan et al. 1997). As Manly et al. (1993) noted, habitat selection studies are a useful starting point. If we learn that there is selection or avoidance of a particular habitat component, then this is a starting point for further study (Petrides 1975).

In all study lakes, smallmouth bass generally selected areas having coarser substrates and cover proximal to the nest relative to its availability in the lakes. However, specific habitat features selected as nest sites varied across lakes and varied across years in Big Crooked Lake, though consistent patterns were apparent there. For example, the variables gravel and nest rock cover were consistent predictors of nest site location each year in Big Crooked Lake. In fact, these two variables were significant predictors of nest site location in each lake. Therefore, the bivariate resource selection

function (RSF) with these two variables was the most transferable model across lakes. From this information, future investigators could develop methods to quickly identify areas in lakes that are most likely to be used as nest sites.

Habitat selection, the use of a specific habitat characteristic in greater proportion to its availability (Johnson 1980), is viewed as evidence of the relative importance of a particular habitat component (Alldredge et al. 1998) and has been studied extensively in terrestrial and aquatic communities alike (Witzel and MacCrimmon 1983, Livingston et al. 1990, Prescott and Collister 1993, Knapp and Preisler 1999). A fundamental, yet often overlooked, assumption of habitat selection studies is that habitat selection infers habitat quality, which in turn infers fitness (Fretwell and Lucas 1970, Peek 1986). These linkages are tenuous at best, and largely untested (Garshelis 2000).

In our study, the relations between habitat selection and habitat quality were only significant in Palette Lake where the probability of selection from each RSF was significantly related to fitness but not survival. These significant positive relations confirm the assumption that RSFs reflect habitat quality only in Palette Lake which had the highest adult smallmouth bass density. Neither survival nor fitness was significantly related to the probability of selection in other lakes.

These results suggest that the assumption that habitat selection infers habitat quality is largely invalid and might be a density dependent response. Palette Lake differs from the other lakes as it has the highest adult smallmouth bass population density as well as the most nests per shoreline kilometer of any of our study lakes. Fretwell (1972) suggests that under ideal despotic conditions, organisms saturate habitat and start to use sub-optimal sites. It appears that smallmouth bass may be using progressively

poorer areas as preferred habitats are saturated. As population density increases in the most preferred habitats, resources become less available to each individual, forcing them to use less suitable spawning sites (Werner et al. 1983b, Ridgway and Shuter 1994). As a result, it appears that there is enough variation in probabilities of selection only in Palette Lake to detect a significant relation between habitat selection and habitat quality. In Palette Lake, the distribution of probabilities of selection was evenly distributed while this distribution in other lakes was often highly skewed toward high probabilities of selection. Smallmouth bass populations in the other lakes may not have saturated the high quality habitat enough to detect the relation between habitat selection and habitat quality.

Further evidence of habitat saturation in Palette Lake exists. First, there was a significant negative relation between the day of spawning and the amount percent of gravel in each nest only in Palette Lake. In all lakes, smallmouth bass selected spawning sites that were composed primarily of gravel substrates. Early in the season, smallmouth bass selected areas with suitable amounts of gravel substrate. Later in the season, they progressively selected nest sites with lower amounts of gravel. Second, smallmouth bass in each of our study lakes strongly selected sites that were near cover. In Palette Lake, 11% of nests had no cover whereas 94% to 100% of nests in the other study lakes were near cover, suggesting limitation of available cover in Palette Lake in addition to substrate limitation. Finally, nests in Palette Lake had the lowest mean egg survival and fry production of any study lake suggesting density dependent nest success possibly due to habitat limitation. These lines of evidence suggest habitat saturation in Palette Lake

and habitat saturation may be necessary to detect a significant relation between habitat selection and habitat quality (sensu Fretwell 1972).

Our results underlie the importance of considering population density and habitat availability in inquiries of animal-habitat relationships. One implicit assumption in habitat modelling is that habitat selection does not change with density (Bult et al.1999). However in territorial animals, the ideal-despotic theory predicts that habitat use should change with density (Fretwell 1972). Habitat selection, and the models that predict habitat selection, should therefore change as well. In contrast, the ideal-free distribution theory predicts that the relative density of non-territorial animals will not vary with population density (Fretwell and Lucas 1970, Parker 1974). Therefore, the assumption of habitat selection not changing with respect to density may hold true with non-territorial animals. But regardless of territoriality, preferred habitats should be settled first in expanding populations (Fretwell and Lucas 1970). If habitat selection is measured during a period of population expansion, then the assumption of habitat selection being static with respect to density may be unrealistic.

Our results suggest that the predictive abilities of RSFs may be compromised at high population densities or low habitat availability. Correct classification rates and McFadden  $Rho^2$  statistics were lowest in Palette Lake which had the highest population density. These results are likely due to selection of marginal sites that reflected the majority of the available habitat which was mostly sand.


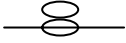

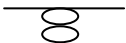
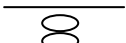
Finally, our results suggest that the assumption of RSFs reflecting habitat quality is often unrealistic. As Manly et al. (1993) noted, “researchers should proceed cautiously when using the results of selection studies to determine the relative importance of

resources". Given the aforementioned constraints of selection studies, we recommend close consideration of these limitations to future investigators of habitat selection.

## **Appendices**



Appendix A. Description of embeddedness code. The schematic of the substrate is a cross-section of two uppermost diameters (ovals) and the level of fine sediments (line) in the substrate matrix.

Embeddedness code	Description of substrate	Schematic of substrate
0	Two particle diameters void of fine sediments	
1	Upper particle diameter is void of fine sediments but the layer beneath is partially covered (no more than 50%)	
2	Upper particle diameter is partially covered (no more than 50%) with fine sediments and the particle beneath is completely covered	
3	Two particle diameters covered and interstices filled with fine sediments	
4	Substrate completely covered with a layer of fine sediments	

## Appendix B. Fish species assemblage in each study lake.

<u>Fish species</u>	<u>Big Crooked Lake</u>	<u>Sanford Lake</u>	<u>Bear Lake</u>	<u>Palette Lake</u>
<u>Centrarchidae</u>				
Smallmouth bass	X	X	X	X
Largemouth bass	X			
Rock bass	X	X	X	X
Pumpkinseed		X	X	
Bluegill		X		
<u>Percidae</u>				
Walleye	X	X	X	
Yellow perch	X	X	X	X
Log perch	X	X		X
<u>Esocidae</u>				
Muskellunge	X	X	X	X
Northern pike	X			
<u>Catostomidae</u>				
White sucker	X	X	X	X
<u>Cyprinidae</u>				
Mimic shiner	X			X
Golden shiner		X		
Bluntnose minnow	X	X	X	X
<u>Salmonidae</u>				
Lake trout				X
<u>Gadidae</u>				
Burbot	X			
<u>Ictaluridae</u>				
Yellow bullhead				X
Brown bullhead	X			



Appendix D. Data sheet used to collect used (i.e., nest site) habitat data in the field.

Nest #							
Transect #							
Nest Dia.							
Dist. to nest							
Dist. to shore							
Water depth							
Nest depth							
Slope							
Sub / % / emb							
Sub / % / emb							
Sub / % / emb							
Sub / % / emb							
Dist. to wood							
Wood dia.							
Wood length							
% underlog							
Pos. on tree							
Dist. to rock							
x							
y							
z							

Appendix E. Descriptions of variables used in Excel and Systat databases for analyses of nest site selection and success.

Number – each observation was numbered sequentially to keep data in sequential order so the data could be reconstructed during a catastrophic event, like a miss sort

Year – defines the year data was collected (e.g., 1999).

Lake – defines the lakes the data was collected on. Big Crooked = 1, Sanford = 2, Bear = 3, Palette = 4.

Date – day of the spawning season that the nest received eggs. Day one begins when the first nest receives eggs.

Transect – used to collect habitat variables in littoral areas of lakes. Numbered from 1 to N for each lake

Offshore – defines data as collected on a reef or from shore (1 or 0, respectively)

Nest – defines a nest site as present or absent on transects (1 or 0, respectively) 1 = to a nest site and 0 = a quadrat on a random transect

Meter – defines the distance (m) from shore to a quadrat on a transect (1, 3, 5. . .)

Depth – defines the depth (m) for a specific quadrat on a transect. Depth readings were collected every other meter until a depth  $\geq 3.0$  meters was reached.

COD – Course organic debris that consists of leaves, pine needles, small pieces of bark and twigs

Wood1 – the percentage of the small wood found in the quadrat

Wood2 – the percentage of the medium-sized wood found in the quadrat

Dia2 – the diameter (m) of the medium-sized piece of wood

Lgth2 – the length (m) of the medium-sized piece of wood

CrossT2 – identifies if the medium-sized piece of wood crosses the transect or runs parallel to the transect (yes or no)

Wood3 – the percentage of large wood found in the quadrat

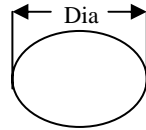
Dia3 – the diameter (m) of the large piece of wood found in the quadrat

Lgth3 – the length (m) of the large piece of wood

Appendix E con't. Descriptions of variables used in Excel and Systat databases for analyses of nest site selection and success.

CrossT3– identifies if the large piece of wood crosses the transect or runs parallel to the transect (yes or no)

Ndia – the diameter in meters of the smallmouth bass nest taken from edge to edge (e.g., 0.75, 0.85)



D\_N\_N – the distance (m) from the nest sampled to the next closest nest, if applicable

N\_D\_Sho – the distance (m) from the nest site to shore, unless nest site was located on a reef

O\_N\_Wdth – the water depth (m) directly outside the nest to the surface of the water

I\_N\_Wdth - the water depth (m) from center of the bottom of the nest to the surface of the water

Dugout – nest concavity, calculated as  $O\_N\_Wdth - I\_N\_Wdth$

Slope – the slope directly outside of the nest

N\_Sub1 - the dominant substrate found in the nest (e.g., 1, 2, 3, ... 9).

N\_%\_1 – the percentage of the dominant substrate found in the nest (e.g., 10, 20, 100).

N\_Emb\_1 – the embeddedness of the dominant substrate (e.g., 1, 2)

N\_Sub2 - the next dominant substrate found in the nest (E.g., 1, 2, 3, ... 9).

N\_%\_2 – the percent of the next dominant substrate found in the nest (Ex: 10, 20, 30, ... 100).

N\_Emb\_2 – the embeddedness of the next dominant substrate (e.g., 1, 2, 3, 4).

N\_Sub3 - the next dominant substrate found in the nest (e.g., 1, 2, 3, ... 9)

N\_%\_3 – the percent of the next dominant substrate found in the nest (e.g., 10, 20, 30, ... 100)

Appendix E con't. Descriptions of variables used in Excel and Systat databases for analyses of nest site selection and success.

N\_Emb\_3 – the embeddedness of the next dominant substrate (e.g., 2, 3, 4).

N\_Sub4 - the next dominant substrate found in the nest (e.g., 1, 2, 3, ... 9).

N\_%\_4 – the percent of the next dominant substrate found in the nest (e.g., 10, 20, 30, . . .100).

N\_Emb\_4 – the embeddedness of the next dominant substrate (e.g., 1, 2, 3, 4).

Avgemb – average embeddedness of the nest.

N\_Dis\_wd – the distance from the nest to wood. The number 0.001 represents wood was on the edge or directly over the nest. All other distances are in meters (e.g., 0.5)

N\_Wd\_Dia – the diameter of the wood in meters

N\_Wd\_Lth – the length of the wood used as nesting cover in meters (e.g., 2.5)

N\_Dst\_Rk – the distance from the nest to rock. The number 0.01 represents rock edge of the nest. All other distances are in meters (e.g., 0.5)

N\_Rk\_Cov – the cover that was found at a site that could have been used as nesting cover. At available and at nest sites

N\_Rk\_Dia – the diameter of the rock in meters

SMBLth – the estimated length of the male smallmouth bass on the nest.

Eggs – the estimated number or eggs in the nest

Correggs – the corrected number of eggs in the nest

Fry – the estimated number of blackened fry just before they are about to swim off the nest

Corrfry – the corrected number of blackened fry just before they are about to swim off the nest

Survival – the percentage of eggs that produced viable fry which swam off the nest

Corrsurv – the corrected percentage of eggs that produced viable fry which swam off the nest (corrfry/correggs).

## References

- Allredge, A.W., R.D. Deblinger, and J. Peterson. 1991. Birth and bedsite selection by pronghorns in a sagebrush steppe community. *Journal of Wildlife Management* **55**:222-227.
- Allredge, J.R. and J.T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **50**:157-165.
- Allredge, J.R., D.L. Thomas, and L.L. McDonald. 1998. Survey and comparison for study of resource selection. *Journal of Agricultural, Biological, and Environmental Statistics* **3**:237-253.
- Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**:912-923.
- Arthur, S.M., B.F.J. Manly, L.L. McDonald, and G.W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* **77**:215-227.
- Barans, C.A., and R.A. Tubbs. 1973. Temperature selected seasonally by four fishes from western Lake Erie. *Journal of the Fisheries Research Board of Canada* **30**:1697-1703.
- Becker, G.C. 1983. *Fishes of Wisconsin*. The University of Wisconsin Press, Madison, Wisconsin, USA.
- Beecher, H.A., T.H. Johnson, and J.P. Carleton. 1993. Predicting microdistributions of steelhead (*Oncorhynchus mykiss*) parr from depth and velocity preference criteria: test of an assumption of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2380-2387.



- Berkelman, J., J.D. Fraser, and R.T. Watson. 1999. Lake selection by Madagascar Fish-Eagles. *The Auk* **116**:976-983.
- Bohlin, T. 1977. Habitat selection and intercohort competition of juvenile sea-trout *Salmo trutta*. *Oikos* **29**:112-117.
- Bohlin, T. 1978. Temporal changes in the spatial distribution of juvenile sea trout *Salmo trutta* in a small stream. *Oikos* **30**:114-120.
- Bourgeois, G., R.A. Cunjak, and D. Caissie. 1996. A spatial and temporal evaluation of PHABSIM in relation to measured density of juvenile Atlantic salmon in a small stream. *North American Journal of Fisheries Management* **16**:154-166.
- Bovee, K.D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper **12**. U.S. Fish and Wildlife Service. FWS/OBS/-82/26.
- Bovee, K.D., B.L. Lamb, J.M. Bartholow, C.B. Stalnaker, J. Taylor, and J. Henriksen. 1998. Stream habitat analysis using the instream flow incremental methodology. U.S. Geological Survey, Biological Resources Division Technical Report USGS/BRD-1998-0004.
- Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* **14**:268-272.
- Bozek, M.A. and F.J. Rahel. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:552-564.

- Bult, T.P., S.C. Riley, R.L. Haedrich, R.J. Gibson, and J. Heggenes. 1999. Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1298-1306.
- Christensen, D.L., B.R. Herwig, D.E. Schindler, and S.R. Carpenter. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications* **6**:1143-1149.
- Clady, M.D. 1975. Early survival and recruitment of smallmouth bass in Northern Michigan. *Journal of Wildlife Management* **39**:194-200.
- Duttweiler, M.W. 1985. Status of competitive fishing in the United States: trends and state fisheries policies. *Fisheries* **10**:5-7.
- Edwards, E.A., G. Gebhart, and O.E. Maughan. 1983. Habitat suitability information: smallmouth bass. FWS/OBS-82/10.36. U.S. Department of the Interior, U.S. Fish and Wildlife Service.
- Fausch, K.D., C.L. Hawkes, and M.G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-1985. PNW-GTR-213. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Fretwell, S.D. and H.L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* **19**:16-36.
- Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, New Jersey, USA.

- Garshelis, D.L. 2000. Delusions in habitat evaluation: measuring use, availability, selection, and importance. Pages 111-164 in L. Boitani and T.K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.
- Guay, J.C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **57**: 2065-2075.
- Haines, T. A. 1973. Effects of nutrient enrichment and a rough fish population (carp) on a game fish population (smallmouth bass). Transactions of the American Fisheries Society **102**:346-354.
- Hall, D.J. and E.E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. Transactions of the American Fisheries Society **106**:545-555.
- Hall, L.S., P.R. Krausman, and M.L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin **25**:173-182.
- Hobbs, N.T. and T.A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management **54**:515-522.
- Hoff, M.H. 1991. Effects of increased nesting cover on nesting and reproduction of smallmouth bass in northern Wisconsin lakes. Pages 96-103 in D.D. Jackson, editor, First International Smallmouth Bass Symposium. Southern Division of the American Fisheries Society. Bethesda, Maryland, USA.

- Hosmer, D.W., Jr. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons. New York, New York, USA.
- Hubbs, C.L. and R.M. Bailey. 1938. The smallmouthed bass. Cranbrook Institute of Science Bulletin **10**. Bloomfield Hills, Michigan, USA.
- Hubert, W.A. and R.T. Lackey. 1980. Habitat of adult smallmouth bass in a Tennessee river reservoir. Transactions of the American Fisheries Society **109**:364-370.
- Hughes, N.F. 1992. Selection of positions by drift feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences **49**:1999-2008.
- Hutto, R.L. 1985. Habitat selection by non-breeding migratory land birds. in M.L. Cody, editor. Habitat selection in birds. Academic Press, Orlando, Florida, USA.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.
- Jager, H.J., D.L. DeAngelis, M.J. Sale, W.V. Winkle, D.D. Schmoyer, M.J. Sabo, D.J. Orth, and J.A. Lukas. 1993. An individual-based model for smallmouth bass reproduction and young-of year dynamics in streams. Rivers **4**:91-113.
- Jennings, M.J., M.A. Bozek, G.R. Hatzenbeler, E.E. Emmons, and M.D. Staggs. 1999. Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. North American Journal of Fisheries Management **19**:18-27.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

- Kellner, C.J., J.D. Brawn, and J.R. Karr. 1992. What is habitat suitability and how should it be measured? Pages 476-488 in D.R. McCullough and R.H. Barrett, editors. *Wildlife 2001: populations*. Elsevier, London, UK.
- Kieffer, J.D., M.R. Kubacki, F.J.S. Phelan, D.P. Philipp, and B.L. Tufts. 1995. Effects of catch-and-release angling on nesting male smallmouth bass. *Transactions of the American Fisheries Society* **124**:70-76.
- Kirsch, E.M. 1996. Habitat selection and productivity of least terns on the lower Platte River, Nebraska. *Wildlife Monographs* **132**.
- Knapp, R.A. and H.K. Preisler. 1999. Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1576-1584.
- Linhart, H. and W. Zucchini. 1986. *Model development*. John Wiley and Sons. New York, New York, USA.
- Livingston, S.A., C.S. Todd, W.B. Krohn, and R.B. Owen. 1990. Habitat models for nesting bald eagles in Maine. *Journal of Wildlife Management* **54**:644-653.
- Lukas, J.A. and D.J. Orth. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. *Transactions of the American Fisheries Society* **124**:726-735.
- Lyons, J. 1991. Predicting smallmouth bass presence/absence and abundance in Wisconsin streams using physical habitat characteristics. Pages 96-103 in D.D. Jackson, editor. *First International Smallmouth Bass Symposium*. Southern Division of the American Fisheries Society. Bethesda, Maryland, USA

- Lyons, J., L. Wang, and T.D. Simonson. 1996. Development and validation of an Index of Biotic Integrity for coldwater streams in Wisconsin. *North American Journal of Fisheries Management* **16**:241-256.
- Manly, B.F., L.L. McDonald, and D.L. Thomas. 1993. *Resource selection by animals*. Chapman and Hall, London, U.K.
- Mladenoff, D.J., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lakes Region. *Conservation Biology* **9**:279-294.
- Morantz, D.L., R.K. Sweeney, C.S. Shirvell, and D.A. Longard. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**:120-129.
- Morrison, M.L., B.G. Marcot, and R.W. Mannan. 1992. Habitat from an ecological and evolutionary perspective. Pages 16-40 *in* *Wildlife habitat relationships*. University of Wisconsin Press. Madison, Wisconsin, USA.
- Munther, G.L. 1970. Movement and distribution of smallmouth bass in the middle Snake River. *Transactions of the American Fisheries Society* **99**:44-53.
- Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**:335-354.
- Neter, J., M.J. Kutner, C.J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*. 4th edition. McGraw-Hill. Chicago, Illinois
- Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* **38**:541-545.

- Neves, R.J. 1975. Factors affecting fry production of smallmouth bass (*Micropterus dolomieu*) in South Branch Lake, Maine. Transactions of the American Fisheries Society **104**:83-87.
- Omernick J.M. and A.L. Gallant. 1988. Ecoregions of the Upper Midwest States. EPA/600/3-88/037. United States Environmental Protection Agency. Environmental Research Laboratory. Corvallis, Oregon, USA.
- Orth, D.J. and E. Maughan. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. Transactions of the American Fisheries Society **111**:413-445.
- Parker, G.A. 1974. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera:Scatophagidae). IX. Spatial distribution of fertilization rates and evolution of male search strategy within the reproductive area. Evolution **28**:93-108.
- Peek, J.M. 1986. Habitat relationships. *in* A review of wildlife management. Prentiss Hall, Englewood Cliffs, New Jersey, USA.
- Petrides, G.A. 1975. Principle foods versus preferred foods and their relations to stocking rate and range condition. Biological Conservation **7**:161-169.
- Pflieger, W.L. 1966. Reproduction of the smallmouth bass (*Micropterus dolomieu*) in a small Ozark stream. American Midland Naturalist **76**:410-418.
- Philipp, D.P., C.A. Toline, M.F. Kubacki, D.B.F. Philipp, and F.J.S. Phelan. 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. North American Journal of Fisheries Management **17**:557-567.

- Platts, W.S., W.F. Megahan, and G.W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. Technical Report INT-138. Intermountain Forest and Range Experiment Station. United States Forest Service. Ogden, Utah, USA
- Power, M.E., W.J. Matthews, and A.J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* **66**:1448-1456.
- Prager, M.H. and M.C. Fabrizio. 1990. Comparison of logistic regression and discriminant analysis for stock identification of anadromous fish, with applications to striped bass (*Morone saxatilis*) and American shad (*Alosa sapidissima*). *Canadian Journal of Fisheries and Aquatic Sciences* **47**:1570-1577.
- Prescott, D.R.C. and D.M. Collister. 1993. Characteristics of occupied and unoccupied loggerhead shrike territories in southeastern Alberta. *Journal of Wildlife Management* **57**:346-352.
- Press, S.J. and S. Wilson. 1978. Choosing between logistic regression and discriminant analysis. *Journal of the American Statistical Association* **73**:699-705.
- Raffetto, N.S., J.R. Baylis, and S.L. Serns. 1990. Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieu*). *Ecology* **71**:1523-1535.
- Rapport, D.J. and J.E. Turner. 1970. Determination of predator food preferences. *Journal of Theoretical Biology* **26**:365-372.
- Rejwan, C., B.J. Shuter, M.S. Ridgway, and N.C. Collins. 1997. Spatial and temporal distributions of smallmouth bass (*Micropterus dolomieu*) nests in Lake Opeongo, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2007-2013.



- Rejwan, C., N.C. Collins, L.J. Brunner, B.J. Shuter, and M.S. Ridgway. 1999. Tree regression analysis on the nesting habitat of smallmouth bass. *Ecology* **80**:341-348.
- Reynolds, C.R. and C.J. O'Bara. 1991. Reproductive ecology and spawning habitat of smallmouth bass in two small streams of the Tennessee River system. Pages 61-65 in D.C. Jackson, editor. First International Smallmouth Bass Symposium. American Fisheries Society, Bethesda, Maryland.
- Ridgway, M.S. 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieu*). *Canadian Journal of Zoology* **66**:1722-1728.
- Ridgway, M.S., J.A. MacLean, and J.C. MacLeod. 1991. Nest-site fidelity in a centrarchid fish, the smallmouth bass (*Micropterus dolomieu*). *Canadian Journal of Zoology* **69**:3103-3105.
- Ridgway, M.S. and T.G. Friesen. 1992. Annual variation in parental care in smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes* **35**:243-255.
- Ridgway, M.S. and B.J. Shuter. 1994. The effects of supplemental food on reproduction in parental male smallmouth bass. *Environmental Biology of Fishes* **39**:201-207.
- Ridgway, M.S. and B.J. Shuter. 1997. Predicting the effects of angling for nesting male smallmouth bass on production of age 0<sup>+</sup> fish with an individual-based model. *North American Journal of Fisheries Management* **17**:568-580.
- Robison, H.W., and T.M. Buchanan. 1988. *Fishes of Arkansas*. The University of Arkansas Press, Fayetteville, Arkansas, USA. 536 pp.
- Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology* **62**:327-335.

- Savage, R.E. 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fisheries Investigations of the Ministry of Agriculture, Fisheries, and Food **12**:1-88.
- Schamberger, M.A., A.H. Farmer, and J.W. Terrell. 1982. Habitat suitability index models: Introduction. FWS/OBS-82/10. U.S. Department of the Interior, U.S. Fish and Wildlife Service.
- Schamberger, M.L. and L.J. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pages 5-10 *in* J. Verner, M.L. Morrison, and C.J. Ralph, editors. Wildlife 2000: modeling wildlife-habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison Wisconsin, USA.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.
- Schramm, H.L., M.L. Armstrong, N.A. Funicelli, D.M. Green, D.P. Lee, R.E. Manns, B.D. Taubert, and S.J. Waters. 1991. The status of competitive fishing in North America. Fisheries **16**:4-12.
- Schupp, B.D. 1979. 1978 status of bass fishing tournaments in the United States. Fisheries **4**:11-19.
- Scott, A. 1920. Food of Port Erin mackerel in 1919. Proceedings and transactions of the Liverpool Biological Society **34**:107-111.
- Scott, D. and C.S. Shirvell. 1987. A critique of IFIM and observations of flow determination in New Zealand. Pages 27-43 *in* J.F. Craig and J.B. Kemper. Regulated streams: advanced in ecology. Plenum Publishers. New York, New York, USA.

- Scott, W.B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin **184**.
- Serns, S.L. 1982. Relation of temperature and population density to first-year recruitment and growth of smallmouth bass in a Wisconsin lake. Transactions of the American Fisheries Society **111**:570-574.
- Serns, S.L. 1984. First-summer survival, eggs to juveniles, of smallmouth bass in Nebish Lake, Wisconsin. Transactions of the American Fisheries Society **113**:304-307.
- Shuter, B.J., J.A. MacLean, F.E.J. Fry, and H.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society **109**:1-34.
- Sowa, S.P. and C.F. Rabeni. 1995. Regional evaluation of the relation of habitat to distribution and abundance of smallmouth bass and largemouth bass in Missouri Streams. Transactions of the American Fisheries Society **124**:240-251.
- Stalnaker, C.B. 1979. The use of habitat structure preferenda for establishing flow regimes necessary for maintenance of fish habitat. Pages 321-337 in J.V. Ward and J.A. Stanford, editors. The Ecology of Regulated Streams. Plenum Press. New York, New York, USA.
- Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society **108**:344-352.
- Stroud, R.H. and H.E. Clepper, editors. 1975. Black bass biology and management. Sport Fishing Institute, Washington DC USA.

- Surber, E.W. 1942. Observations on the natural and artificial propagation of the smallmouth black bass, *Micropterus dolomieu*. Transactions of the American Fisheries Society **72**:233-245.
- Talent, L.G., G.L. Krapu, and R.L. Jarvis. 1982. Habitat use by mallard broods in south central North Dakota. Journal of Wildlife Management **46**:629-635.
- Thomas, D.L. and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management **54**:322-330.
- Todd, B.L. and C.F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. Transactions of the American Fisheries Society **118**:229-242.
- U.S. Fish and Wildlife Service. 1980. Habitat evaluation procedures (HEP). ESM102. U.S. Department of Interior. U.S. Fish and Wildlife Service. Washington D.C., USA.
- Vogele, L.E. 1981. Reproduction of smallmouth bass (*Micropterus dolomieu*) in Bull Shoals Lake, Arkansas. U.S. Fish and Wildlife Service Technical Paper **106**.
- Webster, D.A. 1945. Relation of temperature to survival and incubation of the eggs of smallmouth bass (*Micropterus dolomieu*). Transactions of the American Fisheries Society **75**:43-47.
- Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. Journal of Geology **30**:377-392.
- Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittlebach. 1983a. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540-1548.
- Werner, E.E., G.G. Mittlebach, D.J. Hall, and J.F. Gilliam. 1983b. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology **64**:1540-1548.

- Wiegert, L.W. 1966. A four-year study of the smallmouth bass in the outlying waters of Door County, Wisconsin. Wisconsin Conservation Department Division of Fish Management Report **11**.
- Wiegmann, D.D., J.R. Baylis, and M.H. Hoff. 1992. Sexual selection and fitness variation in a population of smallmouth bass (*Micropterus dolomieu*). *Evolution* **46**:1740-1753.
- Wiegmann, D.D. and J.R. Baylis. 1995. Male body size and paternal behaviour in smallmouth bass, *Micropterus dolomieu*, (Pisces: Centrarchidae). *Animal Behaviour* **50**:1543-1555.
- Wilde, G.R. 1998. Tournament associated mortality in black bass. *Fisheries* **23**:12-23.
- Williams, C.S. and W.H. Marshall. 1938. Duck nesting studies, Bear River Migratory Bird Refuge Utah, 1937. *Journal of Wildlife Management* **2**:29-48.
- Winemiller, K.O. and D.H. Taylor. 1982. Smallmouth bass nesting behavior and nest site selection in a small Ohio stream. *Ohio Journal of Science* **82**: 266-273.
- Witzel, L.D. and H.R. MacCrimmon. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. *Transactions of the American Fisheries Society* **112**:760-771.
- Young, M.K., W.A. Hubert, and T.A. Wesche. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. *North American Journal of Fisheries Management* **11**:339-346.