Spawning Habitat Selection of Sympatric Smallmouth Bass (*Micropterus dolomieu*) and Rock Bass (*Ambloplites rupestris*) in North Temperate Lakes: Habitat Separation in Space and Time

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ABSTRACT

Smallmouth bass and rock bass co-occur throughout much of their respective ranges and are believed to be ecologically similar. As a result, they are often placed into the same functional guild in ecological analyses, yet no such formal analysis of their relationship has been conducted. Smallmouth bass and rock bass clearly exhibit similar spawning behavior; both species spawn in shallow water in early spring and timing of spawning, along with similar habitat use could create competition between these two species, particularly when habitat is limiting. This study evaluated spatial and temporal overlap of spawning by sympatric smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) in three north temperate lakes that have distinctly different littoral zone habitat compositions. The objectives of the study were to assess spawning habitat in relation to available habitat for smallmouth bass and rock bass and to assess the degree of spawning separation that occurred both spatially and temporally. Locations of smallmouth bass and rock bass nests in lakes were surveyed every other day during the spawning season using snorkel and SCUBA gear. Initial date of egg deposition was recorded for nests of both smallmouth bass and rock bass and nest site characteristics were then quantified. To assess habitat selection, logistic regression was used to compare sites where nests of each species were found relative to random sites in each lake. Linear discriminant analysis was used to assess degree of habitat overlap between smallmouth bass and rock bass nest use. The quantitative data from this study showed that spawning habitat selection by smallmouth bass and rock bass was similar; coarse substrates (sand and gravel) and wood or rock cover were selected by both species in all three study lakes. Smallmouth bass and rock bass were also found to overlap in the time they occupy nest sites (>50% in all three study lakes). Nest sites can be discriminated by how smallmouth bass and rock bass utilized similar microhabitat such as the placement of nests relative to cover and the amount of gravel substrate found in the nest. These results suggested smallmouth bass and rock bass can be placed in the same spawning guild for use in ecological analyses, yet show differences that allow both species to successfully coexist.

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Big Crooked Lake Smallmouth Bass Research Project

This project is part of a series of individual projects intended to quantify the functional response of fish to habitat, and specifically to elucidate factors limiting smallmouth bass populations in northern Wisconsin. While habitat is an important component in the life history of smallmouth bass (*Micropterus dolomieu*), it clearly is not the only factor regulating populations. Factors that might affect smallmouth bass populations include size of spawning population (i.e., stock size) (Smith 1976), turbidity, water level fluctuation, water temperature (Neves 1975; Serns 1982; Bulkley 2002; Eipper 2003; Smith et. al. 2005), competition, particularly with other centrarchids (Smith 1976; Werner et al. 1983; Dong and DeAngelis 1998), and predation by walleye (*Sander vitreus*) (Frey 2003). This long term study was designed to assess how habitat quality and quantity affect fish populations in general, and smallmouth bass populations specifically.

To understand the spatial and temporal dimensions of the functional relation of fish to habitat, two study designs were envisioned: a ten-year study on a single lake (Big Crooked Lake, Vilas County, Wisconsin) looking at annual variation in spawning habitat use relative to recruitment success, and annual studies in ten different lakes to assess spatial aspects of habitat use. Initial research (first two years) focused on identifying spawning habitat use and selection by smallmouth bass (Short 2001). As a result, habitat models (i.e., resource selection functions) were developed for spawning smallmouth bass that describe habitat selection of spawning sites at the nest, lake-region, and whole-lake scales (Short 2001). These models provided insight into the distribution of nests, demographics of smallmouth bass populations, and habitat requirements of this species including information necessary to protect smallmouth bass spawning habitat and development of quantitative models for assessing the relative probability of use which could be used in instances of habitat enhancement and mitigation.

The first study by Short (2001) assessed habitat quality based on the results of habitat selection analyses alone (i.e., development of resource selection functions). This is the preferred approach now used in habitat selection studies (Manly et al. 1993; Garshelis 2000). However in this study, no assessment of actual production or survival was used in that study to directly test the assumptions of habitat quality, relative to egg to fry survival or production. The second phase of the study by Saunders (2006) (third and fourth years), specifically quantified habitat quality based on egg and fry production and survival. This work compared models predicting habitat quality as a function of habitat selection to the actual production and survival of different nesting habitats. This analysis specifically tested the most basic premise of currently used habitat models, that habitat selection equals habitat quality.

During the third phase of this project by Brown (2003) (fifth and sixth years), research was conducted to better understand how littoral zone habitat features affected habitat use by young-of-year (YOY) smallmouth bass after emergence from nests. In this study, the first known habitat selection models for YOY smallmouth bass were developed which evaluated ontogenetic changes in habitat selection during the first three months post-hatch. Resource selection functions developed for YOY smallmouth bass during the open-water period were based on habitat characteristics including substrate type, substrate embeddedness, percent woody structure, and distance to rock or wood (Brown 2003), and provided insight into important littoral zone features for YOY smallmouth bass. Moreover, the study assessed how general these findings were across three northern Wisconsin lakes.

Concurrent with the third and fourth years of the long-term smallmouth bass spawning habitat project on Big Crooked Lake, research was conducted to assess predation on and diet overlap of YOY smallmouth bass by other piscivorous fish. Frey (2003) found rock bass (*Ambloplites rupestris*), burbot (*Lota lota*), YOY muskellunge (*Esox masquinongy*), and walleye preyed on YOY smallmouth bass in Big Crooked Lake. Consumption models (i.e., bioenergetic models) suggested that YOY walleye may consume nearly all YOY smallmouth bass in years of high YOY walleye abundance. Frey (2003) also found the most important diet for adult smallmouth bass on Big Crooked Lake was crayfish (*Orconectes*), and their diet overlapped significantly with that of rock bass from July to September. During the course of these projects, not only did rock bass diet overlap with that of smallmouth bass (Frey 2003), but rock bass were also observed by Short (2001), Saunders (2006), and Brown (2003) to be spawning in the same areas as smallmouth bass with some overlap in spawning time.

Because the purpose of the long-term study was to assess how habitat may limit smallmouth bass populations, observations on diet and habitat overlap led to speculation that rock bass might compete for spawning habitat, thus limiting the populations of one or both species. Therefore, the objectives of this study (seventh and eighth years) were to:

1. Quantify spawning chronology and habitat use in relation to available habitat for smallmouth bass and rock bass in three northern Wisconsin lakes.
2. Assess the degree of spawning habitat separation occurring between rock bass and smallmouth bass, thus evaluating one premise of guild placement.

Introduction

Habitat overlap by two sympatric species may lead to competition at higher population densities or low habitat availability resulting in the development of different life history strategies. Two species, smallmouth bass (*Micropterus dolomieui*) and rock bass (*Ambloplites rupestris*) co-occur throughout much of their home ranges (Scott and Crossmen 1973; Becker 1983) and appear to be ecologically similar (e.g., utilize similar spawning habitat, have similar distribution, and can forage on similar diet items) (Balon 1975; Pflieger 1975; George and Hadley 1979; Gross and Nowell 1980; Probst et al. 1984; McClendon and Rabeni 1987; Frey 2003) thus they must have developed different life history strategies to co-occur. Quantitatively understanding spawning habitat selection and habitat use by smallmouth bass and rock bass could help identify the degree of overlap and help elucidate the potential negative effects one species on the other.

Smallmouth bass and rock bass either coexist in the same system by 1) partitioning habitat (e.g., spatially or temporally) if these populations are at carrying capacity, or 2)they can share similar habitat if their populations are limited by some other resource (e.g., food), habitat use is not saturated, or both populations are kept in check by a predator. A third scenario is competitive exclusion; one species displaces (i.e., extirpates) the other (Scott and Irvine 2000). Because habitat use and diet are similar between smallmouth bass and rock bass, there is reasonable potential for competitive interactions to negatively affect either or both species.

Another aspect of similar habitat use by different species is that they may be considered part of the same spawning guild in ecological analyses. Because smallmouth bass and rock bass are sympatric and use similar habitats, biologists have placed them into the same functional guild in many ecological analyses such as the index of biotic integrity (IBI) (Karr 1981; Lyons 1992). Balon (1975) considered smallmouth bass and rock bass to be members of the same spawning guild based on spawning habitat use and spawning behavior. He placed them in the "guarders, nest spawners, and lithophils" guild. His classification however is largely based on qualitative data and detailed studies are needed to assess guild placement of fishes based on quantitative data. Landres (1983) suggested a better approach to defining guilds by first identifing the available resources that are important to the organisms and then, from species lists and data pertaining to those resources, classify species into their respective guilds.

Literature Review

Smallmouth bass and rock bass ecology

Smallmouth bass and rock bass are sympatric over much of their home range. The original distribution of smallmouth bass in North America included the Great Lakes and St. Lawrence River drainages, along with the upper Mississippi, Ohio and Tennessee River systems (Hubbs and Bailey 1938). As smallmouth bass gained popularity among anglers in the 1800's, transfers (i.e., stocking) increased the species' distribution (Robbins and MacCrimmon 1974; Coble 1975). Smallmouth bass now occur throughout the majority of the continental United States, southern Canada, and many places in Europe, Russia, and Africa (Scott and Crossmen 1973).

As with smallmouth bass, the distribution of rock bass also extends across most of east-central North America, from the St. Lawrence River, south to Georgia, to the Gulf of Mexico (Scott and Crossmen 1973) and west to the Mississippi River drainage. In Wisconsin, rock bass inhabit many northern lakes and rivers, the Mississippi River, Lake Michigan, and Lake Superior (Becker 1983).

Smallmouth bass and rock bass primarily occur in clearer, cool-to-warm-water streams or lakes, over gravel-to-rocky substrates in association with an abundance of woody structure and limited vegetation (Hubbs and Bailey 1938; Becker 1983); habitat overlap can be particularly acute during spawning. Smallmouth bass prefer nests constructed on gravel or coarse sand and located near physical cover (Becker 1983; Probst et al. 1984; Hoff 1991; Short 2001; Brown 2004). This use of wood or rock for cover may reduce the nest perimeter that requires defending by the male smallmouth bass and therefore increase nesting success (Hoff 1991; Bozek et al. 2002). Although they have been studied in less detail, rock bass similarly prefer nests constructed primarily of gravel to coarse sand and in close proximity to cover (Gross and Nowell 1980).

There also appears to be overlap in the timing of spawning by smallmouth bass and rock bass. As water temperatures warm to 15^{o}C, the male smallmouth bass excavates a nest in 0.5 to 6.0 m of water (Hubbs and Bailey 1938). The fish will fan a saucer-shaped depression from 0.2 to 2.0 m in diameter (Doan 1940; Pflieger 1966; Scott and Crossmen 1973). Smallmouth bass then initiate spawning when water temperatures rise between 16 – 18^{o}C and cease when temperatures reach 23.9^{o}C (Becker 1983). In contrast, male rock bass clear out nests of similar sizes and shapes to that of a comparably sized smallmouth bass when water temperatures increase to approximately 20^{o}C and spawning will commence shortly thereafter. Rock bass spawning ends when temperatures reach 26.0^{o}C (Scott and Crossmen 1973; Becker 1983).

Both smallmouth bass and rock bass males aggressively defend their nests from the time of construction to the time fry swim up from the nest (Doan 1940; Gross and Nowell 1980; Ridgway 1988). Most smallmouth bass exhibit some “extended” parental care (i.e., beyond fry swim-up), exceeded in duration within Centrarchidae only by the largemouth bass (*Micropterus salmoides*) (Hubbs and Bailey 1938). Ridgway (1988) conducted experimental tests of nest defense by smallmouth bass and found that smallmouth bass may continue to defend their nests even after fry disperse from the nest. However, rock bass guard their young only until fry leave the nest (Gross and Nowell 1980). The extended parental care by smallmouth bass results in males inhabiting their spawning sites for longer periods of time and thus could further interfere with selection of spawning sites by rock bass due to their continued presence.

Habitat

The abundance and quality of spawning habitat is one of the most important factors affecting fish populations (Hoff 199; Paragamian 1991; Bozek et. al. 2002; Saunders 2006). For smallmouth bass, Paragamian (1991) found population densities in northern Iowa streams were two times higher in “good” habitat vs. “fair” habitat. In his study, an increase in sediment loads from the upper watershed resulted in reduced suitable spawning habitat and in turn, reduced smallmouth bass populations. Understanding what constitutes high quality spawning habitat and factors that affect habitat selection is important to developing successful protection and management strategies for maintaining smallmouth bass and rock bass populations.

Survivorship of early life stages of smallmouth bass and rock bass have been found to be correlated to a variety of abiotic and biotic factors (Noltie and Keenleyside 1986; Wiegmann et al. 1992; Knotek and Orth 1998; Smith et al. 2005). Wiegmann et al. (1992) found survival of young smallmouth bass in nests composed of “rock” substrate was greater than in nests constructed primarily of any other substrate. Knotek and Orth (1998) found fungus infection of nests and predation were sources of mortality in young smallmouth bass in a Virginia stream. Mortality of individual broods was found to be 94.1% from egg deposition to the juvenile period. In three rivers Virginia, Smith et al. (2005) found stream discharge during and immediately after spawning was critical to smallmouth bass nest success. In lakes, increased sediment loads to littoral zones may likewise increase egg mortality and suppress recruitment of smallmouth bass (Haines 1973).

The use of optimal spawning habitat is important because young bass are vulnerable during their early life stages. Animals usually select high quality (i.e., optimal) habitat over low quality habitat to maximize survival, and recruitment (Manly et. al. 1997). Survival of smallmouth bass from egg deposition to fall young-of-year (YOY) in Nebish Lake, Wisconsin averaged only 0.3% (0.1-0.5%) from 1979 to 1981 (Serns 1984). Year-class strength, set during the first year of life for many species of fish, regulates future adult populations (Haines 1973; Serns 1982; Hoff 1991; Paragamian 1991) and, theoretically, individuals choose habitat in which their reproductive success is optimized (Haering and Fox 1997; Misenhelter and Rotenberry 2000). For instance, Hoff (1991) concluded that increasing habitat cover for smallmouth bass using half logs in two Wisconsin lakes increased nest success by 183% - 443%, while Saunders et. al. (2002) found distance to cover was significantly related to nest success in Pallette Lake, Wisconsin, and Short (2001) found smallmouth bass selected for cover and substrate variables in two northern Wisconsin lakes.

Less is known about the survival of rock bass from hatch to fry as few detailed studies exist. However, Nolte and Keenleyside (1986) found that the majority of rock bass nest failures occurred in mid-June in the Middle Thames River near London, Ontario, suggesting earlier breeding males were more successful. Earlier breeding males were found to be heavier, longer, and older; all potential indicators of superior fitness. Another theory could be attributed to earlier breeding males having the opportunity to utilize optimal habitats than later breeding rock bass, or that they can access optimal resources quicker due to their greater size.

The availability of high quality habitat may limit the number of successful spawners for both smallmouth bass and rock bass. High quality habitat by definition (i.e., high productivity) produces the greatest number of individuals per unit of habitat. Less optimal habitat, if used under high density conditions (i.e., optimal sites are saturated), may result in reduced production of young at those less optimal sites (Fretwell 1972). In lakes having limited amounts of high quality spawning habitat, competition during spawning could occur between species. Thus, overlap in use of spawning habitat in space and/or time could have a significant effect on nest survival of either species if competition by another species forces a large portion of spawners into suboptimal habitats.

Competitive Interactions

Two species compete when they negatively affect each other by utilizing common resources or controlling access to a limited resource thus causing harm to one or another in the process (Birch 1957). A review of competition by Connell (1983) suggested competition may vary between some species and not others, or competition may take place between sympatric species at different times and places but not at others. For the effects of competition to manifest themselves in aquatic systems, a resource must be limited where use overlaps in space, time, or both (Figure 1). Competition does not occur if the resource is divisional (i.e., it is not utilized in the same time, space, or is not limited) (Scott and Irvine 2000). However, competitive exclusion (MacArthur and Levins 1964; Levin 1970; Armstrong and McGehee 1980) can occur, if partitioning is not sufficient to allow one species or the other to sustain recruitment over time.

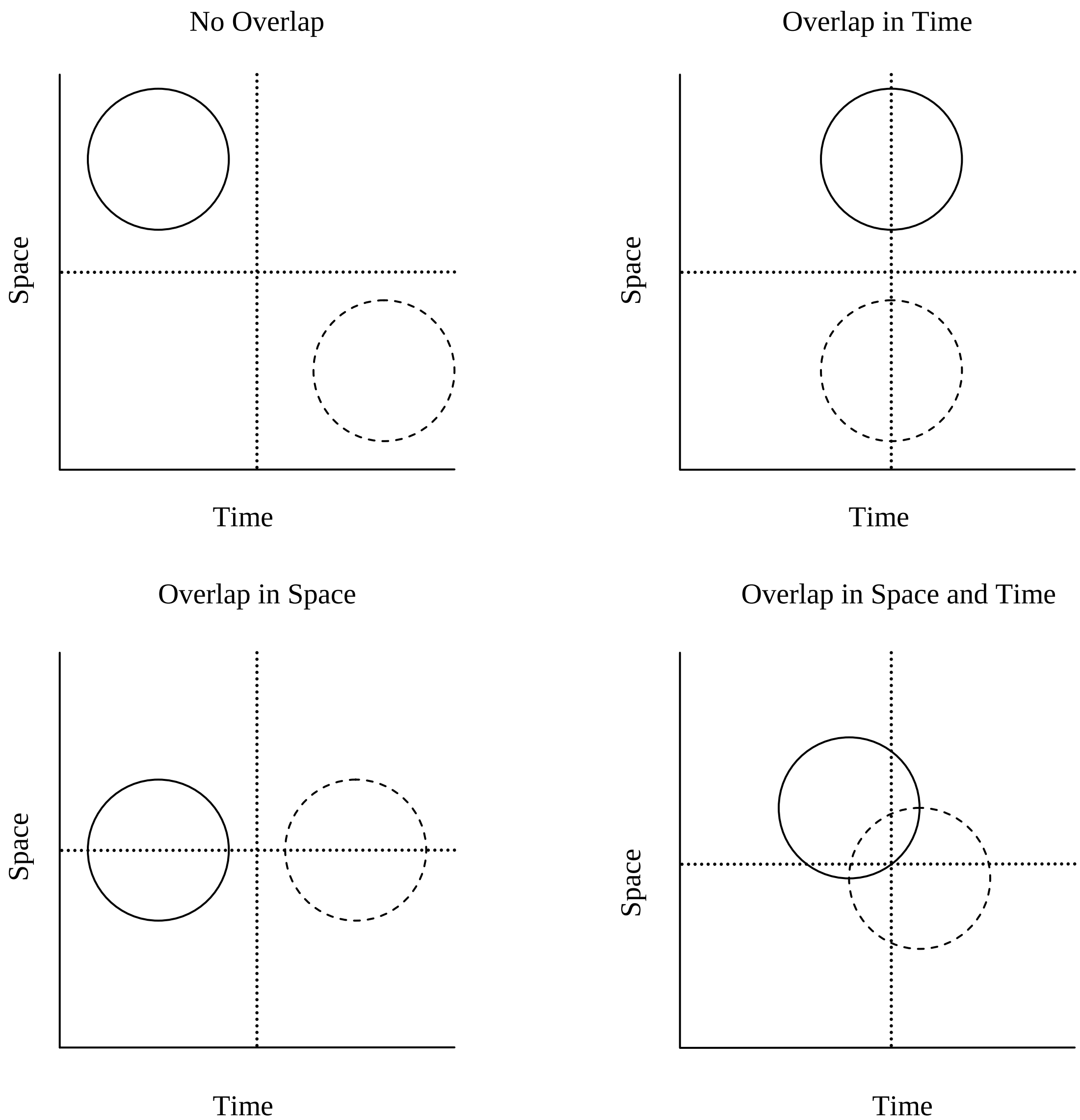

Figure 1. A conceptual diagram of potential spawning habitat overlap in space and time between rock bass and smallmouth bass, represented by complete and dashed circles. Overlap of circles represents potential competition between species during spawning. Space overlap indicates use of the same physical habitat features, while time overlap indicates spawning between species is occurring at the same time. The degree to which both species overlap in space and time determines the degree of competition between species for spawning habitat.

Interspecific and intraspecific competition may affect fish populations by reducing survival, growth, or recruitment (Larkin 1956; Smith 1976; Schoener 1983; Werner 1983; Fisher 2000). The ability for similar species to co-exist under habitat-limiting conditions depends on how effectively limited resources are partitioned. The effects of interspecific competition on habitat selection in fish can be manifested in two ways: competition for habitat (i.e., spawning sites) or competition for food. Through either process, competition between ecologically similar species may lead to altered resource utilization by one or both species (Schoener 1974; Bohn and Amundsen 2001). Larkin (1956) suggested competition for spawning sites tends to occur less frequently than competition for food, however, the effects of competition for spawning sites could be more damaging to a population because habitat does not fluctuate like densities of prey.

Competition has been studied in different fish species although not always conclusively (Smith 1976; Scott and Angermeier 1998; Scott and Irvine 2000). Scott and Irvine (2000) concluded brown trout and rainbow trout in lake tributaries in New Zealand preferred to spawn on gravel. These habitats were found to be limiting and thus increased the mortality of brown trout eggs and in one case, eliminated a brown trout population. Scott and Angermeier (1998) found smallmouth bass in impounded and riverine sections of the New River, Virginia, consistently in areas with steep drop-offs and rocky substrates, while spotted bass were commonly found in areas featuring fine substrate that had woody debris and bank vegetation. Though smallmouth bass and spotted bass separated spatially, diet analyses indicated similar prey was utilized by both species.

Evaluating the spatial and temporal dynamics of smallmouth bass and rock bass spawning habitat is important for ecological and management reasons. Interspecific competition between smallmouth bass and rock bass can potentially cause population changes in either species. Both smallmouth bass and rock bass consume similar diet items (Rabeni 1992; Fry 2003), and utilize similar habitat resources (George and Hadley 1979; Probst et al 1984; Gerber and Haynes 1988), and thus may be competitors. Probst et al. (1984) found both crayfish and fish were the most dominant food item for both smallmouth bass and rock bass in the Current River and the Jacks Fork River in south-central Missouri. In that study, smallmouth bass and rock bass sought similar size and type of prey; because the prey base was not limiting, no ecological separation occurred between the two species. However, George and Hadley (1979) found ecological separation between co-existing young-of-year (YOY) smallmouth bass and rock bass based on both food and habitat used in the upper Niagara River, New York. They concluded that size differences between YOY smallmouth bass and rock bass likely reduced resource overlap as smallmouth bass caught larger prey than rock bass, and smallmouth bass preferred rocky substrates versus rock bass that preferred heavily vegetated substrate. In neither study did resource partitioning occur between adult smallmouth bass and rock bass.

Use as Indicator Species

Fish are useful as bioindicators in aquatic systems (Karr 1981; Lyons 1992; Lyons et al. 1995; Jennings et. al. 1999). Karr (1981) developed the index of biotic integrity (IBI) in order to assess man-induced perturbations of lakes and streams. Due to changes in the environment, he proposed using fish as bioindicators of environmental quality because biological communities reflect watershed conditions. Karr (1981) developed metrics to relate to water quality, such as presence of top carnivores or proportion of individuals that are omnivores. By ranking fish from tolerant to least tolerant and establishing guilds of generalists and specialists he was able to create a rubric to classify stream integrity.

Ecologically, smallmouth bass and rock bass have been used in evaluating water quality and in defining ecosystem structure (Mason et al. 1991; Lyons 1992; Minns et al. 1994; Lyons and Wang 1996; Whittier and Hughes 1998; Jennings et al. 1999; Hatzenbeler et al. 2004). Smallmouth bass are commonly used as an indicator species because they are more intolerant of habitat alteration than other black basses (Robison and Buchanan 1988). For example, Mason et al. (1991) found runoff-related dissolved oxygen (DO) suppression as a possible cause of smallmouth bass fish kills in southwestern Wisconsin streams. The oxygen reduction was attributed to livestock waste washed from barnyards, feeder lots, and manure storage facilities. Rock bass have also been used as an indicator species. Found in 169 lakes of northeastern United States that were sampled for fish, water chemistry, and physical habitat between 1992 and 1994, they were sensitive to water quality changes such as turbidity and total phosphorus, yet, more tolerable to human-related stressors such as human activity in the watershed and around the shoreline then other local fish species (Whittier and Hughes 1998). In Wisconsin, Jennings et al. (1999) began efforts to assess the feasibility of developing an IBI for littoral zone fish assemblages in lakes. They classified smallmouth bass and rock bass as native, intolerant, top predators following Lyons (1992).

Not only are smallmouth bass and rock bass used as indicators of environmental quality but both species often define ecosystem structure because they are commonly found as the top predator in many streams and lakes (Power et al. 1985; Grossman et al. 1995; MacRae and Jackson 2001; Iguchi and Yodo 2004). In turn, they may influence lower trophic level sturcture or change. For instance, Power et al. (1985) found significant differences in the influence that smallmouth bass had on algal biomass due to their predation on small fish that eat algae. Higher algal biomass occurred where reduced densities of prey fish were found in pools stocked with smallmouth bass relative to control pools. In Japan, smallmouth bass are recognized as one of the worst 100 alien species and as such, Iguchi and Yodo (2004) conducted a study to assess the ability of an indigenous egg-eater (*Tribolodon* hakonesis) to eradicate smallmouth bass through biological control. Grossman et. al. (1995) conducted an experimental study to determine if rock bass affected microhabitat use by mottled sculpin in an artificial stream; their study replicated interactions between both co-occurring species in Coweeta Creek, North Carolina. Microhabitat use by most sculpin was not affected by the presence of rock bass. However, in night trials with the absence of rock bass, sculpin did venture farther from cover and over greater amounts of gravel. Because of the strong influence smallmouth bass and rock bass have in different steam and lake ecosystems, further knowledge on the interactions between smallmouth bass and rock bass will help identify their use together in ecological analyses such as the IBI and their future use as members of the same guild.

Guilds

The similarity in both habitat use and levels of tolerance of environmental perturbations by smallmouth bass and rock bass, suggest these species are members of similar functional guilds. Guild, first termed by Root (1967), is defined as a group of species who exploit the same class of environmental resources in a similar way. Root (1967) viewed members of a guild as having characteristics molded by adaptations to the same resources and structured by competition. The use of a guild or guilds focuses on all sympatric species involved in competitive interactions regardless of taxonomic rank, since organisms that are not in the same taxonomic group may have a major effect on community members. Fausch et al. (1990) examined the use of fish communities as indicators of environmental degradation. They determined one of the most common approaches to assessment of environmental degradation by biological means is through the use of indicator taxa or guilds and the use of IBI.

Ecologically similar species are often placed into guilds for management and research purposes (Root 1967; Hairston 1981; Grossman et al. 1982; Angermeier and Karr 1983; Adams 1985; Mac Nally and Doolan 1986; Gorman 1988; Fausch et al. 1990; Minns et al. 1994). A review of the guild concept by Simberloff and Dayan (1991) indicates the most common shared resource used to classify different guilds is forage, but general similarities in species' niches provides alternative strategies for identifying guilds. Mac Nally and Doolan (1986) used multivariate techniques to characterize the typical habitat, and range of habitats occupied by nine species of eastern Australian cicadas (Cicadidae). They defined guild as a set of closely related species that are both sympatric and synchronously active, and that forage on similar items in similar ways. Hairston (1981) tested the validity of accepting a guild as delimited for terrestrial salamanders by using field experiments from 1974-1978. The resource known to be shared among the salamanders is diet; the most common understood definition of guild. In the experiment, Hairston (1981) removed as many individuals as possible of the most abundant species of salamander assuming competition would be revealed by increases in the abundance of any or all of the remaining salamander species resulting in quantitatively assessed guild membership. The results of this study found when the top two abundant species were removed the other species' abundance increased. The data from this study suggested that food is not the resource for which competition occurred between these salamanders. Hairston (1981) suggested that nest sites may be the critical resource limiting abundance of the species based on life histories, but he could not conclude definitively because the study was not designed to assess habitat relationships.

An alternative to forage as a criterion for guild membership is to look at the use of habitat for guild placement (see Balon 1975; Gorman 1988; Leonard and Orth 1988). Balon (1975) used spawning characteristics of fish to identify spawning guilds, basing his findings primarily on form (i.e., preferred spawning areas) and function (i.e., spawning behavior) in early developmental intervals, but while Balon's (1975) guild classification is useful, he did not use any quantitative data to determine guild placement. Habitat separation between guild members might result if some of the guild members are more dominant within the subset of microhabitats used and shared by members of the same guild (Gorman 1988). How guild members overlap in use of habitat could represent a species' habitat selection as modified by interspecific interactions over time and space.

The lack of quantitative data used to determine guild membership is not unusual as most research has not used quantitative methods to define the members of a guild; preferring to define guild placement on taxonomic positions or intuition alone (Jaksic 1981; Simberloff and Dayan 1991). According to Jaksic (1981), guilds need to be recognized quantitatively and not defined *a priori*. Landres (1983) suggested a better approach to defining guilds would be to first identify the available resources important to the organisms, and then, using species lists and data pertaining to those resources, classify species into their respective guilds. In this regard, the potential overlap in smallmouth bass and rock bass spawning habitat use could be indicative of competition for resources needed for spawning.

Quantitative Approaches

Habitat use and selection are two different terms describing areas that animals occupy. Habitat use describes how an animal chooses to utilize habitat characteristics where it is located. Habitat selection describes the use of habitat characteristics in proportion to their abundance (i.e., relative use) (Rosenzweig 1991; Manly et al. 1993; Garshelis 2000). Habitat selection implies an animal is differentially selecting an area for specific reasons relative to random chance. To quantitatively understand the relationships between habitat selection and habitat use, research scientists have used resource selection functions (e.g., logistic regression) and discriminant analysis (Titus and Mosher 1984; Manly et. al. 1993; Mace et. al. 1998).

Manly et al. (1993) described resource selection functions as any function that is proportional to the reletive probability of use by an organism. Resource selection functions have been used to assess habitat selection for a variety of animals including fish, bears, and piscivorous birds. For instance, Mace et al. (1998) used logistic regression (a resource selection function) to model the probabilities of female grizzly bear (*Ursus arctos horribilis*) habitat use from seasonal telemetry data in Rocky Mountain Cordillera of western Montana. For each season, resource selection functions were calculated for used (telemetry) and available (random) resources. They were able to conclude that female grizzly bears selected different habitats in different seasons, although reasons for differential use were not given. In another study, Newbrey et al. (2005) used logistic regression to model effects of lake characteristics and human disturbance on the presence of piscivorous birds in northern Wisconsin. The best models from Newbrey's (2005) study indicated many piscivorous birds were found to be present on large lakes with higher pH values, rather than being affected by human-based disturbances.

Habitat use has also been quantified using linear discriminant analysis. The discriminant function is the linear combination of variables that best accounts for group membership. According to Titus and Mosher (1984), ecologists commonly use discriminant analysis to examine the classification of species by functional or taxonomic group. Misenhelter and Rotenberry (2000) used discriminant analysis to examine the consequences of habitat choice in sage sparrow (*Amphispiza belli*) in southern California. They contrasted occupied territories versus unoccupied territories and successful versus unsuccessful nest sites. Their study concluded birds in southern California preferred to settle in areas in which their nest success rate was lower due to other ecological factors such as predation. Lyons (1991) used discriminant analysis to distinguish habitat variables among sites with and without smallmouth bass from more then 4,500 stations located on approximately 1,700 rivers and streams in the southern and western third of Wisconsin. In his study, five variables were found by stepwise discriminant analysis to significantly distinguish stations with and without smallmouth bass: mean width, amount of rocky substrate, trout classification, lake distance, and amount of boulder substrate.

In the current project, two approaches were used to assess habitat use and overlap between sympatric smallmouth bass and rock bass. First, resource selection functions (RSF's) were developed using logistic regression to assess habitat selection for both species. The best RSF was determined for both smallmouth bass and rock bass by identifying habitat variables that were significant in univariate models and then using these variables in multiple variable models. Second, the degree of separation occurring in habitat use was evaluated using linear discriminant analysis. Both of these analyses have commonly been used to ascertain fish habitat (Titus et al. 1984; Lyons 1991; Haering and Fox 1995; Arthur et al. 1996; Gross and Kapuscinski 1997; Mace et al. 1997; Misenhelter and Rotenberry 2000; Saunders et. al. 2002; Short et al. 2002; Brown 2003; Newbrey et. al. 2005). Additionally, overlap in spawning time was assessed using nesting chronology from egg deposition for both smallmouth bass and rock bass to black fry swim up for smallmouth bass. Percent overlap in spawning time was calculated for individual species and overall.

Objectives

The objectives of this study are to:

1. Quantify spawning habitat use and selection in relation to available habitat for smallmouth bass and rock bass in three northern Wisconsin lakes.
2. Assess the degree of spawning habitat separation occurring between rock bass and smallmouth bass.

Methods

Study Sites

This study was conducted on three north temperate Wisconsin lakes located near Boulder Junction in Vilas County, Wisconsin: Big Crooked Lake (T41N R05E S22 NE1/4 NE1/4), Sparkling Lake (T41N R06E S25 NW1/4 NW1/4), and Katinka Lake (T43N R06E S18 SE1/4 NE1/4). Lake selection criteria used to pick study lakes were: 1) lakes had relatively unexploited fish populations (e.g., closed harvest, high minimum size limits, and limited/low public access) thus minimizing the effects of angling on fish densities, 2) lakes had high water clarity for visual observations, and 3) lakes had no largemouth bass present that might cause additional interspecific competition for habitat with this closely related species.

Big Crooked Lake is located on Dairymen's, Inc. property in north-central Vilas County. Big Crooked is a clear drainage lake with a surface area of 276 ha, 8.1 km of shoreline, and a maximum depth of 11.6 m. Shoreline development of Big Crooked is limited to a lodge and a few cabins along the north shore of the lake. Fishing is restricted to club members with strict adherence to catch and release fishing for smallmouth bass. The riparian area is primarily second-growth, mixed-hardwood forest, and the littoral zone consists primarily of sand (>80%) with areas of gravel (>15%) and cobble (>10%) (Short 2001). Within-lake structure is composed of some boulders with limited (i.e., low) amounts of coarse woody structure (primarily giant boles) and macrophytes. The main fish species located in Big Crooked Lake are walleye, muskellunge, northern pike (*Esox lucius*), smallmouth bass, yellow perch (*Perca flavescens*), rock bass, mimic shiner (*Notropis volucellus*), and white sucker (*Catostomus commersoni*) (Table 1). Rusty crayfish (*Orconectes rusticus*) are also present in the lake.

Sparkling Lake is a smaller, oligotrophic lake located on Highway 51 in Vilas County. Sparkling Lake is a seepage lake with a surface area of 64.0 ha, a shoreline of 4.3 km, and a maximum depth of 20 m. Shoreline development is limited to a few houses (<10) on the north shore along with an unimproved boat launch and small wayside on the west side of the lake. There is a restrictive 18 inch (45 cm) minimum size limit on smallmouth bass. The riparian area is primarily second-growth, mixed-hardwood forest and the littoral zone consists of mostly sand (>35%) and fine organic debris (>75%) with some gravel (>25%). Within-lake habitat structure consists of coarse woody structure and a few macrophyte beds that are increasing in area and plant density with manual control of rusty crayfish (Hein et. al. 2004). Some of the common fish species in Sparkling Lake include northern pike, bluntnose minnow (*Pimephales notatus*), common shiner (*Notropis cornutus*), horneyhead chub (*Nocomis biguttatus*), smallmouth bass, rock bass, bluegill, yellow perch, walleye, and rainbow smelt (*Osmerus mordax*), a recently introduced exotic species (Table 1).

Katinka Lake, located near Presque Isle, Wisconsin, is a 69 ha drainage lake and has a maximum depth of 18 m. Shoreline development consists of (<40) year-round homes and cottages and access is restricted to lake property owners only. The riparian area is primarily forested and the littoral zone consists mostly of sand (>20%) and large and small organic debris (>80%). Within-lake structure consists of abundant coarse woody structure and a few rock reefs containing small (150.0 – 303.9 mm) to medium (304.0 – 500.0 mm) boulders.

Table 1. Fish species composition for Big Crooked Lake, Sparkling Lake and Katinka Lake, Wisconsin.

Common Name	Scientific Name	Big Crooked	Sparkling	Katinka
Black crappie	*Pomoxis nigromaculatus*		•	
Blacknose shiner	*Notropis heterolepis*		•	
Bluegill	*Lepomis macrochirus*	•	•	•
Bluntnose minnow	*Pimephales notatus*	•	•	
Brook stickleback	*Culaea inconstans*		•	
Burbot	*Lota lota*	•	•	•
Cisco	*Coregonus artedii*		•	
Common shiner	*Notropis cornutus*	•	•	
Golden shiner	*Notemigonus chrysoleucas*		•	
Grass pickerel	*Esox americanus vermiculatus*		•	
Hornyhead chub	*Nocomis biguttatus*	•	•	•
Iowa darter	*Etheostoma exile*		•	
Johnny darter	*Etheostoma nigrum*		•	
Largemouth bass	*Micropterus salmoides*	•	•	•
Log perch	*Percina caprodes*		•	
Mimic shiner	*Notropis volucellus*	•	•	
Mottled sculpin	*Cottus bairdi*		•	
Mud minnow	*Umbra limi*	•	•	
Muskellunge	*Esox masquinongy*	•	•	•
Ninespine stickleback	*Pungitius pungitius*		•	
Northern pike	*Esox lucius*	•	•	
Pumpkinseed	*Lepomis gibbosus*	•	•	•
Rainbow smelt	*Osmerus mordax*		•	
Rainbow trout	*Oncorhynchus mykiss*	•		
Rock bass	*Ambloplites rupestris*	•	•	•
Rosyface shiner	*Notropis rubellus*		•	
Smallmouth bass	*Micropterus dolomieui*	•	•	•
Walleye	*Sander vitreus*	•	•	•
White sucker	*Catostomus commersoni*	•	•	•
Yellow perch	*Perca flavescens*	•	•	•

Katinka also includes seven undeveloped islands. Some of the common fish species found in Katinka Lake include muskellunge, hornyhead chub, white sucker, burbot, smallmouth bass, rock bass, bluegill, pumpkinseed, yellow perch, and walleye (Table 1).

Smallmouth Bass and Rock Bass Population Estimates

Population estimates for smallmouth bass and rock bass adults were completed in May whereas YOY estimates for smallmouth bass were completed in late summer/early fall (August/September); no estimates were made for YOY rock bass. In spring, adult bass were captured using fyke nets set shortly after ice-out and monitored until approximately one week prior to nesting. Fyke nets had 1.3 cm stretch-bar mesh with 1.2 m hoops. Five to eight nets were placed randomly around the littoral zone of each lake and were checked daily. Captured adult smallmouth bass and rock bass were marked using a top caudal hole-punch. Only a temporary mark for population estimates was needed because recapture runs were conducted within two weeks of marking runs. Recapture runs were conducted at night by electrofishing the entire shoreline of each lake until approximately 10% of marked fish were recaptured. Adults caught during recapture runs were marked with a lower caudal hole-punch, weighed (g), and measured (total length mm). In Big Crooked Lake, individually numbered floy-tags were also placed in fish over 250 mm as part of the long-term obligations to the overall study. In fall, YOY smallmouth bass were first captured using a bag seine, then marked with a top caudal fin clip, measured (TL mm), and weighed (g). During recapture runs using electrofishing, fall YOY were marked with a lower caudal fin clip, measured, and weighed. No YOY rock bass were seined or electrofished in the fall, therefore no YOY population estimate was made for this species.

Adult smallmouth bass and rock bass populations were estimated using the adjusted Peterson estimator (Ricker 1975):

$$N = \frac{(M+1)(C+1)}{R+1}$$

Where: N = the number of fish estimated to be in the population

M = the number of marked fish in the population

C = the number of fish recaptured using a second method

R = the number of marked fish recaptured

Due to the abundant woody structure along the shoreline and difficulty in seining for YOY smallmouth bass in Sparkling and Katinka Lakes, alternative gear types were not used. YOY were captured during repeated electrofishing runs and populations were estimated using the Schnabel estimator:

$$N = \frac{\sum(C_t M_t)}{\sum R_t} = \frac{\sum(C_t M_t)}{R}$$

Where: C_t = total sample taken on day t

M_t = total marked fish at large at the start of the t^{th} day

R_t = number of recaptures in the sample C_t

$R = \sum R_t$, total recaptures during the experiment

The Schnabel estimator allows for the use of one gear type while the Peterson method requires two; electrofishing was the only gear used in capturing YOY smallmouth bass in both Sparkling and Katinka Lakes.

Nesting Habitat

Surveys locating nests of both species were conducted every other day (i.e., alternating between two lakes each year starting in 2003) starting prior to the first smallmouth bass spawning in May until spawning by rock bass terminated in July. Nests were located combining three different visual methods. First, shallow (<1.5 m) nests were located by placing an observer on the bow of a survey boat using polarized sunglasses and slowly traveling (i.e., idle speed) around each lake shoreline. Second, an observer using SCUBA or snorkel gear was towed at the 2 m and 3 m (depth) contour interval looking for deeper nests. The littoral zone below 3 m was assessed using SCUBA; no smallmouth bass or rock bass nests were found beyond 3 m deep. Third, SCUBA and snorkel gear were used to dive the littoral zone looking for nests in hard to observe areas with the boat such as areas with high amounts of woody structure. Previous work on Big Crooked Lake and other study lakes had shown that nearly all smallmouth bass nests were located in water less then 3 m deep (Short 2001; Saunders 2002; Brown 2003).

Each smallmouth bass and rock bass nest observed was marked and the date when eggs were initially found was recorded. Smallmouth nests were marked with individually numbered flags and rock bass nests were marked with numbered washers and flagging. All nest locations in Big Crooked and Katinka were recorded on a GPS unit. Nests were observed every other day until fry swim-up or complete nest failure (i.e., eggs were 100% dead or missing) occurred; dates were recorded for each for smallmouth bass.

Once all fry swam off the nest, habitat characteristics of each nest (Table 2) were quantified using SCUBA gear. Characterization of smallmouth bass and rock bass nests follows Saunders and Bozek (2002). Nest diameter was determined by placing a tape measure at two locations from nest rim to nest rim at 90^{o} angles; the final nest diameter was the average of the two measurements. Nest concavity was determined by measuring the water depth of the nest at the rim and at the nest center, then subtracting these two measurements. Distance to shore was measured from the rim of the nest closest to shore to the closest (perpendicular distance) dry land (< 30 m). Nest slope was determined by making two depth measurements: the first taken 2 m closer to shore and the second 2 m further from shore relative to the respective nest rim locations. Slope was then calculated by using the formula:

$$\text{Slope} = \frac{\text{Depth}_1 - \text{Depth}_2}{4}$$

Cover (large wood or rock) within a 10 m radius of each nest was quantified: rocks with at least one length greater than 303 mm, and coarse woody structure with a diameter greater than 50.9 mm was considered cover. The distance from the nest rim to the closest cover structure was measured. For each piece of coarse woody structure (CWS), the length and diameter was recorded. Rocks were measured in three dimensions were measured: first (x) the width from the rock side parallel to the nest rim, second (y) the height from the substrate to the top of the rock nearest the water surface, and third (z) the width of the rock

Table 2. Habitat measurements collected at nest sites and along numbered transects representing available habitat at sampling sites.

	Location measured	
Habitat Variable	**Nest**	**Random Site**
Water depth (m)	•	•
Slope (%)	•	•
Substrate percentage	•	•
Substrate type (size)	•	•
Substrate embeddedness	•	•
Proximity to cover (m)	•	•
Cover type (wood or rock)	•	•
Dimensions of cover (mm) (length, width, height)	•	•
Distance to shore (m)	•	•
Nest diameter (m)	•	
Macrophyte type	•	•
Percent macrophyte coverage	•	•
Submergent macrophyte height (mm)	•	•
Buried substrate		•
Distance to nearest nest (m)	•	
Substrate types within 1 m of nest	•	
Substrate percentage within 1 m of nest	•	
Substrate embeddedness within 1 m of nest	•	

Perpendicular to the nest rim. Substrate size categories (Table 3), composition (%), and embeddedness were visually estimated inside the nest and encompassing 1 m directly surrounding the nest rim. Substrate size and percent coverage were rounded to the nearest 5% with up to four substrate size classes estimated in descending order of spatial area covered. Substrate particle size was classified using a modified Wentworth scale (Wentworth 1922) (Table 3). Embeddedness of each substrate type (i.e., the degree to which fine particles surround coarse substrate) was also estimated (see Figure 2). Substrate sizes consisting of gravel and larger were assigned an embeddedness code of 0 to 4. An embeddedness of 0 indicated the top two layers of substrate was clean of fine material (sand or silt), whereas an embeddedness of 4 indicated highly embedded substrates. For analysis purposes, sand substrates were assigned an embeddedness value of 4. Percent vegetation (percent area covered), height, and type (i.e., floating, emergent, or submergent) were also recorded.

Available Habitat

To develop resource selection functions, available habitat was assessed in all three lakes using 100 randomly selected transects placed perpendicular to the shoreline perimeter. Transect locations were determined by using the length of time (in seconds) it took to travel around the lake at just above idle speed using a john boat and using elapsed time from the boat landing to assign random points. One hundred randomly selected numbers that referred to the seconds it took to travel around the lake were used to select the transect locations. Once transects were selected, the lake was traveled again at idle speed and buoys were placed

Table 3. Substrate particle size classification used for nest sites and available sites. Particle sizes are modified from Wentworth (1922).

Material	**Code Number**	**Size**
Bottom Substrate		
Fine organic matter	1	Fine particulate organic matter is discernible
Silt	2	<0.2 mm
Sand	3	0.2 – 6.3 mm
Gravel	4	6.4 – 76.0 mm
Cobble	5	76.1 – 149.9 mm
Rubble	6	150.0 – 303.9 mm
Small Boulder	7	304.0 – 609.9 mm
Large Boulder	8	≥610.0 mm
Bedrock	9	Consolidated parent material
Coarse organic matter	10	Coarse particulate organic matter is discernible
Wood		
Fine Woody Structure	W1	<20.5 mm in diameter
Medium Woody Structure	W2	20.6 – 50.8 mm in diameter
Coarse Woody Structure	W3	≥50.9 mm in diameter

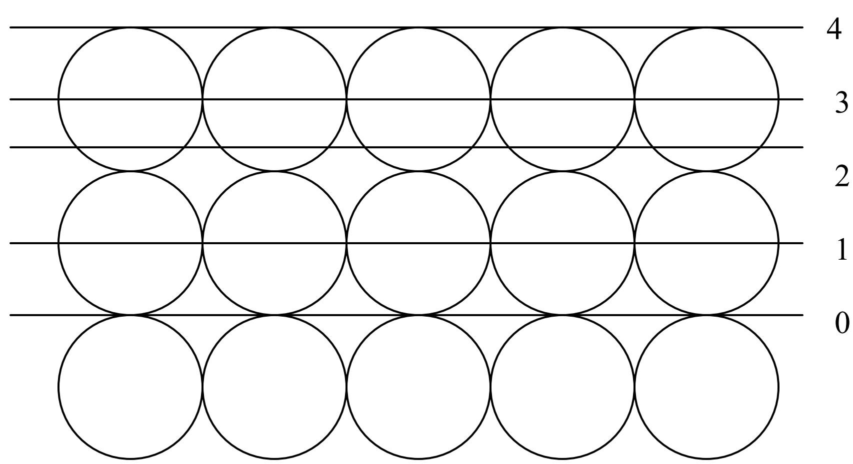

Figure 2. Schematic of the embeddedness of substrate. Horizontal lines indicate the level to which fine particles (e.g., sand or silt) fill the space between areas of larger substrate (e.g., gravel, cobble, and rubble).

at transect locations; GPS coordinates were recorded at each transect location for Big Crooked and Katinka Lakes.

At each transect, a measuring tape was placed perpendicular to shore out to a depth of 3 m. Habitat variables were quantified within a 1 m^2 quadrat every other meter starting from shore to 3 m deep. Variables quantified at the nest site were also quantified along the available habitat transect including water depth, coarse woody structure, rock cover, and vegetation (Table 2). Coarse woody structure was classified as wood "3" (≥50.9 mm in diameter), wood "2" (20.6 – 50.8 mm in diameter), or wood "1" (<20.5 mm in diameter) (Table 3). Diameter and length were recorded for each piece of wood "2" and wood "3" encountered. Because fish sometimes nest in larger substrates that are buried under finer substrates which they excavate, "buried" substrate was also quantified in four corners of each available quadrat; each corner was excavated and the first substrate encountered within 12 cm of the surface substrate was recorded. This depth corresponded to the depth that smallmouth bass nests were generally found to be excavated.

Temporal Overlap

To assess temporal overlap of nesting between smallmouth bass and rock bass, nest chronology was recorded. The date nests for smallmouth bass and rock bass were located and eggs deposited was recorded. Smallmouth bass nests were monitored every other day until the black fry positioned themselves on top of substrate indicating they were ready to leave the nest. At this time the date was recorded and labeled as fry date. Individual percent spawning overlap was calculated for smallmouth bass and rock bass by dividing the number of active (i.e., a smallmouth bass or rock bass nest that contained eggs or fry) nests for each species by the total number of nests being monitored by that species. To determine overall spawning overlap the total number of nests active for both species was divided by the total number of nests found.

Data Analysis

Spawning overlap of smallmouth bass and rock bass was first analyzed by using histograms of occurrence to determine patterns of habitat use versus its availability. Resource selection functions were then used to quantify which habitat variables were selected by spawning smallmouth bass and rock bass. Finally linear discriminant function analysis was used to determine the amount of habitat separation occurring based on habitat use for smallmouth bass and rock bass.

Logistic regression was used to develop resource selection functions for habitat characteristics selected during nesting (Manly et al. 1993). Resource selection functions are models that yield values proportional to the probability of use relative to a resource unit's availability (Manly et al. 1993). In this study, the relative probability of presence of a nest was determined based on habitat features used by smallmouth bass and rock bass, relative to the availability of the features in each lake (Manly et al. 1993). Logistic regression was used because the independent variable (smallmouth bass and rock bass nest presence/absence) is binary (Cox and Snell 1989). Logistic regression uses the function:

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

Where: π = the probability of nest presence

e = the inverse natural logarithm of 1

$u = k + m_1 x_1 + m_2 x_2 + \ldots + m_i x_j$

Where:

k = constant

m_i = regression coefficients

x_j = the values of independent variables

The -2 log likelihood statistic was used to assess the significance of each model. This statistic assesses whether models deviate from random null models. If the sample size is constant, lower values indicate improved model fit (Manly et al.1993). The significance of -2 log likelihood ($p \leq 0.05$) indicates at least one of the regression coefficients is significantly different from zero. The Wald Chi-square value was examined to determine the significance of each individual variable within the model ($p \leq 0.05$). Numerous model iterations were performed using habitat variables found significant in univariate logistic regressions until final models were derived. Once all regression coefficients were significant, the resource selection function was considered significant. Parallel to this traditional approach, model fit was also assessed using Akaike's Information Criterion (AIC) (Burnham and Anderson 1998). Akaike's general approach allows the best model in the set to be identified, but also allows the rest of the models to be easily ranked (Burnham and Anderson 2001). Models with a change in AIC of < 2 units relative to the best model were considered alternate models (Burnham and Anderson 1998).

To assess separation in microhabitat use, linear discriminant function analysis (DFA) was used to discriminate smallmouth bass nests from rock bass nests based upon habitat characteristics used by each species. Linear DFA is used to ascertain the degree of separation of groups (e.g., smallmouth bass vs. rock bass) and to identify how each nest habitat feature (using structure coefficients) contributes to the ability to separate groups (Rice et al. 1983). In DFA, structure coefficients were assessed to determine which habitat variables provided the most separation between smallmouth bass and rock bass. The closer the structure coefficients were to -1 or 1, the greater the variable was correlated to the discriminant axis thus providing separation. The overall correct classification rate was also evaluated to assess model fit. A high correct classification rate indicated distinct nest characteristics were used between species (i.e., habitat use was different). All statistical analyses were conducted using NCSS 97 (Number Cruncher Statistical Software, Kaysville, UT, USA) and SAS (SAS Institute, Cary, NC, USA).

Results

Available Habitat

General lake basin characteristics differed among lakes. Big Crooked Lake is relatively round and has an extensive, wide, flat littoral zone compared to that of Sparkling Lake which is oval and has relatively steep slopes and a basin morphology similar to that of a bowl. Katinka Lake has an irregular shoreline and complex littoral zone containing some steep sloped shore lines, flat relatively shallow bays, and rock bars. Big Crooked Lake contains two islands and two offshore reefs ($\leq$3 m in depth), Katinka Lake contains seven islands and five rock reefs extending from shore and there are no islands present in Sparkling Lake. There was little to no vegetation present in Big Crooked Lake, while 12% and 29% of transects in Sparkling Lake and Katinka Lake, respectively, contained submergent vegetation during the summer months. Very little aquatic vegetation was present when smallmouth bass and rock bass spawned in all three lakes.

Specific littoral zone habitat characteristics differed substantially among all three study lakes. In Big Crooked Lake, sand occurred in over 90% of the littoral zone plots; whereas fine organic debris also occurred at 73.2% (Figure 3). Lesser amounts of gravel, cobble, silt, rubble, small boulders, large boulders, and coarse organic debris occurred throughout the littoral zone as well. In Sparkling Lake, fine organic debris occurred in 77.6% of the plots, followed by sand (34.6%) and gravel (28.6%). The littoral zone was

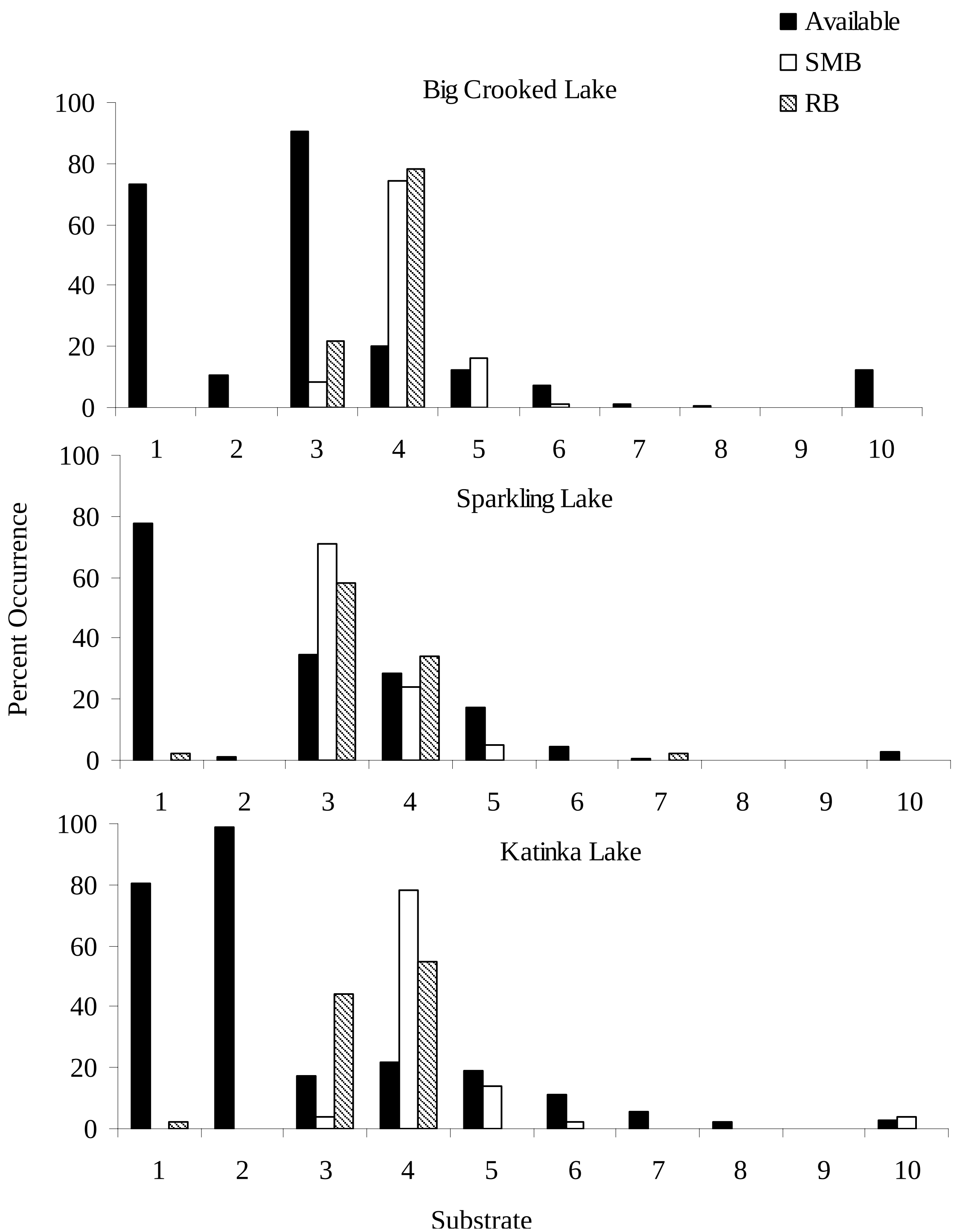

Figure 3. Occurrence of available substrate within each lake and dominant substrate use by spawning smallmouth bass and rock bass. Substrate size classes are 1) fine organic debris, 2) silt, 3) sand, 4) gravel, 5) cobble, 6) rubble, 7) small boulder, 8) large boulder, 9) bedrock, and 10) coarse organic debris. Because multiple substrates can occur in each quadrat, summed values exeed 100% for available substrate.

also covered by smaller amounts of cobble, rubble, silt, and small boulders. In contrast, the littoral zone of Katinka Lake was predominately covered by silt (99.0% plot occurrence) and fine organic debris (80.4% plot occurrence). The rest of the littoral zone was composed of sand (17.2%), gravel (22.0%), and cobble (19.2%).

The quantity and distribution of cover (e.g., wood and rock) differed among study lakes as well. Large wood (≥50.9 mm in diameter) occurred within 10 m of 34.4% of available quadrats in Big Crooked Lake, while large boulders (304 mm or larger) only occurred within 10 m of 17.6% of quadrats. In Sparkling Lake, 81.6% of available quadrats were within 10 m of wood, and 3.9% of quadrats were within 10 m of a rock. While, Katinka Lake had an abundant amount of wood <5 m from shore then either Sparkling Lake or Big Crooked Lake, 58.0% of available quadrats were found within 10 m of wood, and 16.8% were within 10 m of rock (Figure 4).

Spawning Habitat

In Big Crooked Lake, smallmouth bass nests and rock bass nests were segregated by habitat from each other. Smallmouth bass nests were found at an average depth of 1.7 m ± 0.057 m, composed mainly of gravel, with an average embeddedness of 1.2 ± 0.1, and located within 1.9 m ± 0.438 m of cover (Table 4) (Figure 3). In contrast, Big Crooked Lake rock bass nests were generally found deeper than smallmouth bass nests. Rock bass nest depth averaged 2.5 m ± 0.119 m of water, with the nest composed mainly of gravel; the average embeddedness for rock bass nests in Big Crooked Lake is 1.4 ± 0.2, and the average distance

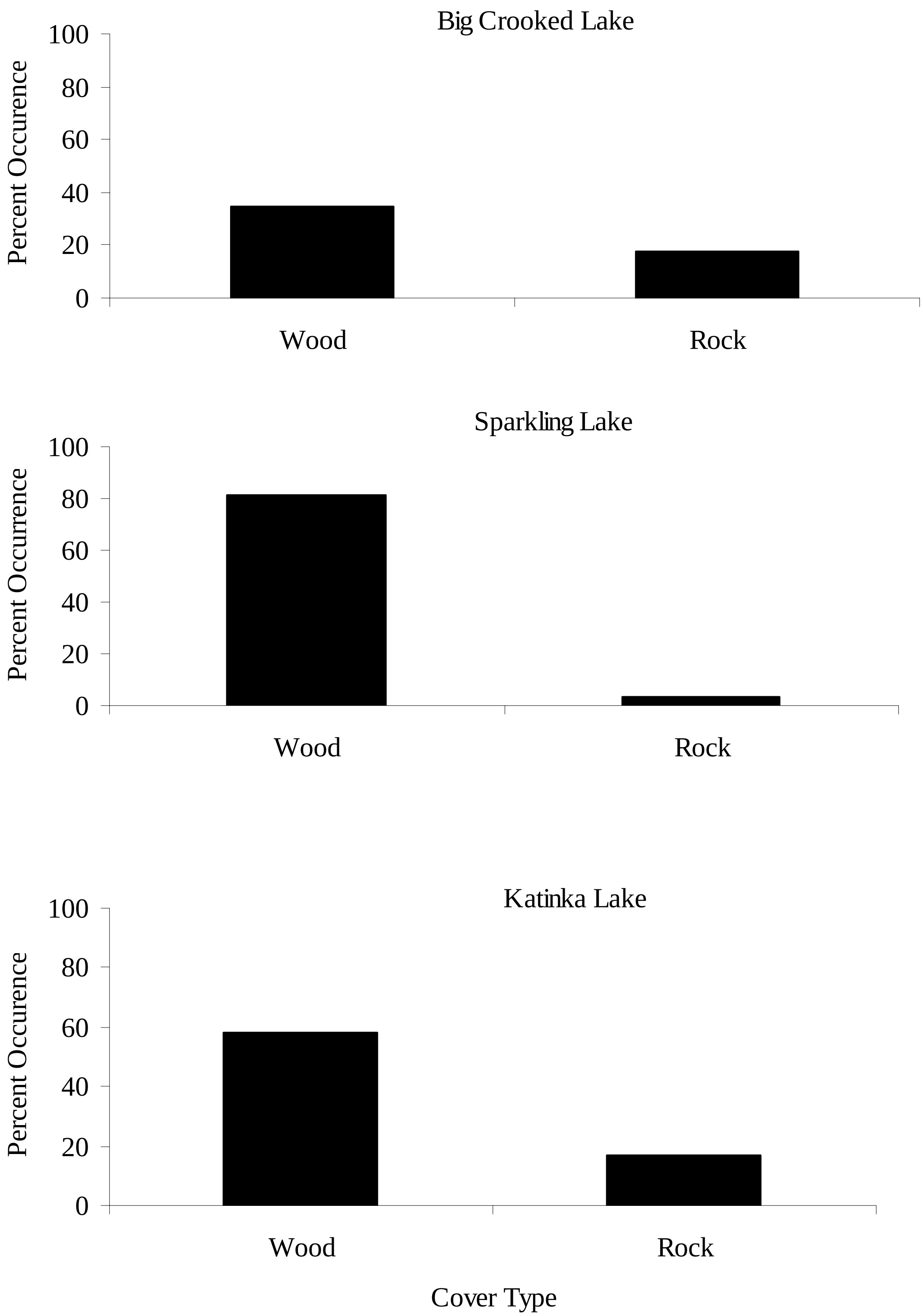

Figure 4. Available wood and rock cover for all three study lakes based on 500 random data points. Values indicate the percent of available quadrats containing wood or rock cover.

Table 4. General nest site habitat characteristics and lake demographics for smallmouth bass and rock bass from three north temperate Wisconsin Lakes.

	Big Crooked Lake					
Nest Characteristic	Smallmouth Bass			Rock Bass		
Lake size (ha)	276			276		
Adult population estimate	229.8			362.4		
Adult number per hectare	0.83			1.31		
Number of nests	75			38		
Water depth (m)	1.72	±	0.057	2.49	±	0.119
Dominant nest substrate	4.0	±	0.1	4.0	±	0.1
Dominant nest embeddedness	1.2	±	0.1	1.4	±	0.2
Distance to cover (m)	1.88	±	0.438	0.31	±	0.263
Nest diameter (m)	0.84	±	0.029	0.35	±	0.009
Slope	0.062	±	0.0085	0.134	±	0.0188
	Sparkling Lake					
Nest Characteristic	Smallmouth Bass			Rock Bass		
Lake size (ha)	64			64		
Adult population estimate (95% CI)	280.5			1632.3		
Adult number per hectare	4.3			25.5		
Number of nests	75			50		
Water depth (m)	1.21	±	0.038	1.28	±	0.092
Dominant nest substrate	3.0	±	0.1	3.0	±	0.1
Dominant nest embeddedness	3.1	±	0.02	3	±	0.2
Distance to cover (m)	0.39	±	0.069	0.04	±	2.15
Nest diameter (m)	0.73	±	0.020	0.35	±	0.016
Slope	0.101	±	0.0055	0.132	±	0.0085
	Katinka Lake					
Nest Characteristic	Smallmouth Bass			Rock Bass		
Lake size (ha)	69			69		
Adult population estimate	964.9			3880.4		
Adult number per hectare	13.9			56.2		
Number of nests	49			55		
Water depth (m)	2.29	±	1.204	0.75	±	0.048
Dominant nest substrate	4.0	±	0.2	4.0	±	0.1
Dominant nest embeddedness	1.5	±	0.1	2.7	±	0.2
Distance to cover (m)	0.43	±	0.285	0.25	±	0.183
Nest diameter (m)	0.69	±	0.030	0.36	±	0.013
Slope	0.198	±	0.0151	0.149	±	0.0137

to cover was 0.3 m ± 0.263 m. In fact, 62% of rock bass nests were located under cover while only 21% of smallmouth bass nests were located under cover.

In Sparkling Lake, smallmouth bass and rock bass nests were less segregated by habitat characteristics used relative to the fish in Big Crooked Lake. The average nesting depth for smallmouth bass was 1.2 m ± 0.038 m versus 1.3 m for rock bass; both species' nests were predominately found on sand having an average embeddedness of 3.1 ± 0.02 for smallmouth bass and 3.0 ± 0.2 for rock bass. While smallmouth bass nest placement relative to cover averaged 0.39 m ± 0.069 m, rock bass tended to nest much closer to cover at 0.04 m ± 2.15 m; 56% of rock bass nests were actually under cover (0 distance to cover).

In Katinka Lake, smallmouth bass and rock bass were again segregated by habitat. Smallmouth bass nests were found at an average depth of 2.3 m ± 1.204 m, while rock bass nests were found shallower at an average depth of 0.7 m ± 0.048 m. The dominant substrate used for both species was gravel, with an average embeddedness of 1.5 ± 0.1 for smallmouth bass and 2.7 ± 0.2 for rock bass. Smallmouth bass and rock bass utilized cover with an average distance of 0.43 m ± 0.285 m and 0.25 m ± 0.183 m, respectively.

Discriminant analysis indicated substantial separation in spawning habitat used by smallmouth bass and rock bass in Big Crooked Lake. The percent correct classification rates for discriminating nest types was high for both species: 96.0% of smallmouth bass nests were correctly classified as a smallmouth bass nest based on habitat features, while 84.0% of rock bass nests were correctly classified as a rock bass nest (overall correct classification rate

90%; Wilks' Lambda =0.289 p <0.001) (Table 5). Loadings on structure coefficients indicated that the two nesting features best discriminating smallmouth bass nests from rock bass nests in Big Crooked Lake were percent of nest under cover (-0.710) followed by water depth (-0.398) (Table 6). Rock bass were found to place their nests directly under cover compared to smallmouth bass that generally place their nests next to cover, and rock bass nests were generally found deeper than smallmouth bass nests. To remove the effect of nest position (i.e., how fish used habitat) on physical structure differences used between nests a discriminant analysis was conducted removing the variable percent nest under cover variable. Removing this variable had the greatest effect in Big Crooked Lake. Correct classification of nests dropped 8% for both species indicating percent nest under cover helped identify conditions that separate smallmouth bass nests from rock bass nests in Big Crooked Lake.

As in Big Crooked Lake, discriminant analysis in Sparkling Lake also indicated substantial separation of habitat characteristics used by smallmouth bass and rock bass. The percent correct classification rates were high for both species; 89.0% of smallmouth bass nests were correctly classified, while 72.0% of rock bass nests were correctly classified (overall correct classification rate 81%; Wilks' Lambda =0.587 p <0.001) (Table 5). Loadings of structure coefficients indicated that the top three nesting features discriminating smallmouth bass nests from rock bass nests in Sparkling Lake were percent of nest under cover, followed by distance to cover, and nest site slope (Table 6).

Discriminant Analysis Correct Classification

Analysis using percent nest under cover					Analysis excluding percent nest under cover			
	Predicted			Big Crooked Lake		Predicted		
Actual	SMB	RB	Total		Actual	SMB	RB	Total
SMB	96 (72)	4 (3)	75		SMB	88 (66)	12 (9)	75
RB	16 (6)	84 (32)	38		RB	23 (9)	76 (29)	38
Total	78	35	90 (113)		Total	75	38	82 (113)
	Predicted			Sparkling Lake		Predicted		
Actual	SMB	RB	Total		Actual	SMB	RB	Total
SMB	89 (66)	11 (8)	74		SMB	75 (56)	24 (18)	74
RB	28 (14)	72 (36)	50		RB	16 (8)	84 (42)	50
Total	80	44	81 (124)		Total	64	60	79 (124)
	Predicted			Katinka Lake		Predicted		
Actual	SMB	RB	Total		Actual	SMB	RB	Total
SMB	84 (41)	16 (8)	49		SMB	81 (40)	18 (9)	49
RB	25 (14)	75 (41)	55		RB	25 (14)	75 (41)	55
Total	55	49	79 (104)		Total	54	50	78 (104)

Table 5. Correct classification rates for linear discriminant analysis of smallmouth bass and rock bass nests using habitat characteristics from all three study lakes. Actual number of observations are in parentheses. Numbers along the diagonal indicate the correct classification rate. Analysis on right eliminated the variable "percent nest under cover" because it can be considered a behavioral response trait, rather then just habitat.

Discriminant Analysis Structure Coefficients

	Big Crooked		**Sparkling**		**Katinka**	
Variable	With percent nest under cover	Without percent nest under cover	With percent nest under cover	Without percent nest under cover	With percent nest under cover	Without percent nest under cover
Water depth	-0.398	0.672	0.081	0.102	0.150	-0.163
Slope	-0.242	0.408	0.334	0.417	0.269	-0.292
Dominant substrate type	0.194	-0.327	0.043	0.053	0.485	-0.525
Dominant substrate embeddedness	-0.048	0.080	-0.044	-0.054	-0.566	0.614
Sub-dominant substrate type	0.263	-0.444	-0.151	-0.188	-0.195	0.211
Sub-dominant substrate embeddedness	0.242	-0.407	0.223	0.279	-0.376	0.408
Clearance	-0.092	0.154	0.114	0.143	0.208	-0.225
Percent nest under cover	-0.710	-	0.641	-	-0.293	-
Distance to cover	0.148	-0.250	-0.434	-0.542	0.059	-0.064
Cover size	-0.186	0.314	0.114	0.143	0.132	-0.143
Percent vegetation	-	-	-0.260	-0.325	-0.050	0.055
Wilks' Lambda	0.289	0.536	0.587	0.690	0.555	0.595
Alpha	< 0.001	< 0.0001	< 0.001	< 0.0001	< 0.001	< 0.0001

Table 6. Discriminant analysis structure coefficients for each study lake used to discriminate smallmouth bass nests from rock bass nests. Analyses were conducted both with and without the variable "percent nest under cover". Big Crooked Lake smallmouth bass and rock bass nests contained no vegetation.

Discriminant analysis on Katinka Lake also indicated substantial separation of spawning sites between smallmouth bass and rock bass. The percent correct classification rates were high for both species; 84.0% of smallmouth bass nests were correctly classified, while 75.0% of rock bass nests were correctly classified (overall correct classification rate 79%; Wilks' Lambda 0.555 $p < 0.001$) (Table 5). Loadings of structure coefficients indicated that the top three nesting features discriminating smallmouth bass nests from rock bass nests in Katinka Lake were dominant substrate embeddedness followed by dominant substrate type, and sub-dominant substrate embeddedness (Table 6). Notably, percent nest under cover did not load as heavily in Katinka Lake as it had in Big Crooked Lake or Sparkling Lake. This could be due to the abundant availability of cover in Katinka Lake, allowing smallmouth bass and rock bass to utilize all cover. Katinka Lake rock bass were found to nest in shallower water and on gravel with a higher embeddedness than smallmouth bass.

Habitat Selection

Smallmouth bass and rock bass clearly selected distinct habitat features for spawning, but there were differences between species and among lakes. Univariate logistic regression analysis for Big Crooked Lake smallmouth bass indicated dominant substrate type (+) was the single best variable for predicting nest site selection (see Appendix D for all univariate models) by correctly classifying 92.0% (69 of 75) of smallmouth bass nests, whereas the best univariate model for rock bass was distance to rock cover (-), correctly classifying 86.84% (33 of 38) rock bass nests (Table 7). The best overall resource

		Regression		Wald		Correct Classification (%)		
Species	**Variable**	**Coefficient**	**Intercept**	**Chi-Square**	**P**	**Overall**	**Presence**	**Absence**
Big Crooked Lake								
Smallmouth Bass	Dominant substrate type	3.55	-14.11	108.00	< 0.001	92.7	92.0	92.8
Rock Bass	Distance to rock	-0.64	0.03	36.30	< 0.001	97.2	86.8	98.0
Sparkling Lake								
Smallmouth Bass	Percent sand substrate	0.04	-3.36	98.99	< 0.001	88.0	45.3	94.4
Rock Bass	Percent under cover	0.07	-2.97	47.27	< 0.001	94.4	40.0	99.8
Katinka Lake								
Smallmouth Bass	Percent gravel substrate	0.06	-4.18	93.90	< 0.001	92.2	46.9	96.6
Rock Bass	Percent gravel substrate	0.04	-3.21	79.11	< 0.001	91.4	32.7	97.8

Table 7. Best univariate resource selection functions for each species in all three study lakes. Correct classification: overall, presence, and absence, are percentages.

selection function for smallmouth bass in Big Crooked Lake contained four variables: dominant substrate embeddedness (-), water depth (+), distance to shore (-), and dominant substrate type (+) correctly predicting 81% of nests (Table 8). Akaike's Information Criteria suggested that one alternate model was also found for Big Crooked Lake smallmouth bass; it contained the variables dominant substrate embeddedness (-), water depth (+), and distance to cover (-), and correctly classified 80% of smallmouth bass nest presence. The single best resource selection function found for rock bass in Big Crooked Lake contained the variables water depth (+), percent sand (+), percent gravel (+), and distance to rock (-) with an overall correct classification for rock bass nest >84%. No alternate models were found for rock bass.

In contrast to Big Crooked Lake, the best univariate logistic regression analysis for predicting smallmouth bass nest presence in Sparkling Lake was percent sand (+) with a correct classification of 45.3% (34 of 75) of smallmouth bass nests (Table 7). Percent nest under cover (+) was the single best predictor of rock bass nest presence in Sparkling Lake with a correct classification of 40.0% (20 of 50) of rock bass nests. The best resource selection function for Sparkling Lake smallmouth bass contained five variables including percent sand (+), percent gravel (+), cover clearance (+), distance to cover (-), and the interaction term percent sand*percent vegetation (+) (Table 9). The correct classification of smallmouth bass nest presence was greater then 86%. The best resource selection function for rock bass contained six variables: distance to shore (-) percent sand (+), percent gravel (+), percent nest under cover (+), distance to cover (-), and the interaction of percent vegetation*distance to cover (+). The correct classification of

Table 8. Best resource selection functions for predicting nest presence in Big Crooked Lake in 2004.

Variables	Coefficient	Chi Square	P	-2 Log	AIC	Correct Classification (%) Overall	Presence	Absence
Smallmouth Bass								
Best Model		296.92	< 0.001	148.38	158.38	94.1	81.3	96.0
Intercept	-1.508	0.78	0.378					
Dominant substrate embeddedness	-1.548	44.59	< 0.001					
Water depth	1.292	16.46	< 0.001					
Distance to shore	-0.02	4.65	0.031					
Dominant substrate type	0.754	4.66	0.031					
Alternate Model		296.56	< 0.001	148.73	156.73	93.9	80.0	96.0
Intercept	2.452	22.51	< 0.001					
Dominant substrate embeddedness	-1.827	94.79	< 0.001					
Water depth	0.828	11.48	0.001					
Distance to cover	-0.158	7.94	0.005					
Rock Bass								
Best Model		238.49	< 0.001	36.19	46.19	98.3	84.2	99.4
Intercept	-23.223	15.43	< 0.001					
Water depth	2.051	13.19	< 0.001					
Percent sand	0.189	12.44	< 0.001					
Percent gravel	0.281	15.27	< 0.001					
Distance to rock	-0.767	13.90	< 0.001					

Table 9. Best resource selection functions for predicting nest presence in Sparkling Lake in 2003.

Variables	Coefficient	Chi Square	P	-2 Log	AIC	Correct Classification (%)		
						Overall	Presence	Absence
Smallmouth Bass								
Best Model		354.62	< 0.001	90.68	102.68	97.0	86.7	98.6
Intercept	-7.155	24.21	< 0.001					
Percent sand	0.060	16.20	< 0.001					
Percent gravel	0.092	23.45	< 0.001					
Cover clearance	12.766	19.78	< 0.001					
Distance to cover	-1.230	8.67	0.003					
Percent sand*percent vegetation	0.002	8.20	0.004					
Rock Bass								
Best Model		276.16	< 0.001	58.94	72.93	98.4	96.0	98.6
Intercept	-4.296	4.51	0.034					
Distance to shore	-0.214	9.98	0.002					
Percent sand	0.073	12.76	< 0.001					
Percent gravel	0.077	9.26	0.002					
Percent under cover	0.036	4.85	0.028					
Distance to cover	-7.26	9.82	0.002					
Percent vegetation*distance to cover	0.081	10.98	0.001					
Alternate Model		268.01	< 0.001	98.6		98.2	94.0	98.6
Intercept	-4.391	4.96	0.026					
Distance to shore	-0.182	10.14	0.001					
Percent sand	0.077	14.19	< 0.001					
Percent gravel	0.089	12.34	< 0.001					
Distance to cover	-8.627	12.88	< 0.001					
Percent vegetation*distance to cover	0.093	13.72	< 0.001					

rock bass nest presence in Sparkling Lake was 98.4%. An alternate model for Sparkling Lake rock bass consisted of the variables distance to shore (-), percent sand (+), percent gravel (+), distance to cover (-), and percent vegetation*distance to cover (+).

In Katinka Lake, univariate logistic regression indicated gravel substrate (+) was the single best predictor of both smallmouth bass and rock bass nest presence (Table 7). Smallmouth bass had a correct classification rate of 47% (23 of 49), and rock bass had a correct classification of 33% (18 of 55). The best resource selection function for Katinka Lake smallmouth bass contained six variables: percent sand (+), percent gravel (+), percent cobble (+), cover clearance (+), distance to cover (-), and cover size (-) (Table 10). This resource selection function correctly classified over 89% of smallmouth bass nests present in Katinka Lake. The best resource selection function for rock bass in Katinka Lake contained five variables including percent sand (+), percent gravel (+), distance to coarse woody structure (-), distance to rock (-), and cover size (-) and correctly classified over 90% of rock bass nests present in Katinka Lake. An alternate model for Katinka Lake rock bass included the four variables percent gravel (+), distance to coarse woody structure (-), distance to rock (-), and cover size (-). This model also correctly classified over 90% of rock bass nests.

Table 10. Best resource selection functions for predicting nest presence in Katinka Lake in 2004.

						Correct Classification (%)		
Variables	Coefficient	Chi Square	P	-2 Log	AIC	Overall	Presence	Absence
Smallmouth Bass								
Best Model		286.09	< 0.001	44.20	58.20	98.4	89.8	99.2
Intercept	-8.599	8.29	0.004					
Percent sand	0.078	5.90	0.015					
Percent gravel	0.111	11.64	0.001					
Percent cobble	0.131	7.08	0.008					
Cover clearance	20.419	10.59	0.001					
Distance to cover	-0.272	6.02	0.014					
Cover size	-4.494	10.44	0.001					
Rock Bass								
Best Model		325.30	< 0.001	33.344	45.344	98.6	90.9	99.4
Intercept	11.183	5.40	0.020					
Percent sand	0.036	4.02	0.045					
Percent gravel	0.050	6.85	0.009					
Distance to coarse woody structure	-1.146	12.63	0.000					
Distance to rock	-0.621	8.56	0.003					
Cover size	-13.283	6.89	0.009					
Alternate Model		320.94	< 0.001	37.702	47.702	98.9	90.9	99.8
Intercept	19.016	10.72	0.001					
Percent gravel	0.035	5.58	0.018					
Distance to coarse woody structure	-1.485	14.37	0.000					
Distance to rock	-0.930	13.25	0.000					
Cover size	-20.832	9.75	0.002					

Temporal Overlap in Spawning Times

In all three lakes, smallmouth bass started spawning earlier than rock bass. However rock bass began spawning in all three study lakes while a portion of smallmouth bass still inhabited their nesting sites (Table 11). In 2004, smallmouth bass spawning in Big Crooked Lake commenced on May 29th at a temperature of 12.8°C and ceased on July 8th at a temperature of 18.1°C. Rock bass spawning began on June 10th at a temperature of 16.7°C and ended on July 20th at a temperature 22.9°C. The overall percentage of overlap (i.e., the number of nests active for both species during the time when both species had at least one active nest) for Big Crooked Lake smallmouth bass and rock bass was 82%. The individual percentage of overlap (i.e., the percent of smallmouth bass or rock bass nests active while at least one nest of the opposite species was active) is 74% for smallmouth bass and 95% for rock bass in Big Crooked Lake.

In 2003, Sparkling Lake smallmouth bass spawning began on May 26th at a temperature of 15.0°C and concluded on June 23rd at a temperature of 21.6°C. Spawning for rock bass commenced on June 9th and ceased on July 1st at temperatures of 16.9 and 21.3°C, respectively. The overall spawning overlap between smallmouth bass and rock bass in Sparkling Lake was 63%. The individual percent overlap was 41% and 100% for smallmouth bass and rock bass, respectively.

Table 11. Temporal overlap in spawning between smallmouth bass and rock bass from Big Crooked Lake 2004, Sparkling Lake 2003, and Katinka Lake 2004. Number of nests indicates the total number of nests observed for spawning fish, date of first nest indicates the date first nest was found with eggs, date of last nest indicates for smallmouth bass the last date a nest was found with black fry and for rock bass the date the last nest was found with eggs. Start and end temperature refer to the water temperature on the first and last date of nesting for both species. Individual percent overlap represents the portion of active nests for each species while there are active spawners of the other species. Overall percent overlap represents the portion of spawners in each lake that have active nests while there is at least one active nest for both species.

Nesting Feature	**Big Crooked**		**Sparkling**		**Katinka**	
	SMB	*RB*	*SMB*	*RB*	*SMB*	*RB*
Number of nests	75	38	74	50	49	55
Date of first nest	29-May	10-June	26-May	9-June	23-May	9-June
Date of last nest	8-July	20-July	23-June	1-July	19-June	3-July
Start temperature (^oC)	12.8	16.7	15.0	17.0	13.2	19.9
End temperature (^oC)	18.1	22.9	21.6	21.3	19.7	21.9
Individual percent overlap	74	95	41	100	86	93
Overall percent overlap	82		63		89	

Katinka Lake smallmouth bass began spawning on May 23rd at a temperature of 13.2°C and ceased on June 19th at a temperature of 19.7°C. Rock bass started spawning on June 9th and ceased on July 3rd at temperatures of 19.9 and 21.9°C, respectively. The overall spawning overlap between smallmouth bass and rock bass in Katinka Lake was 89%. The individual percent spawning overlap in Katinka lake for smallmouth bass was 86% and 93% for rock bass.

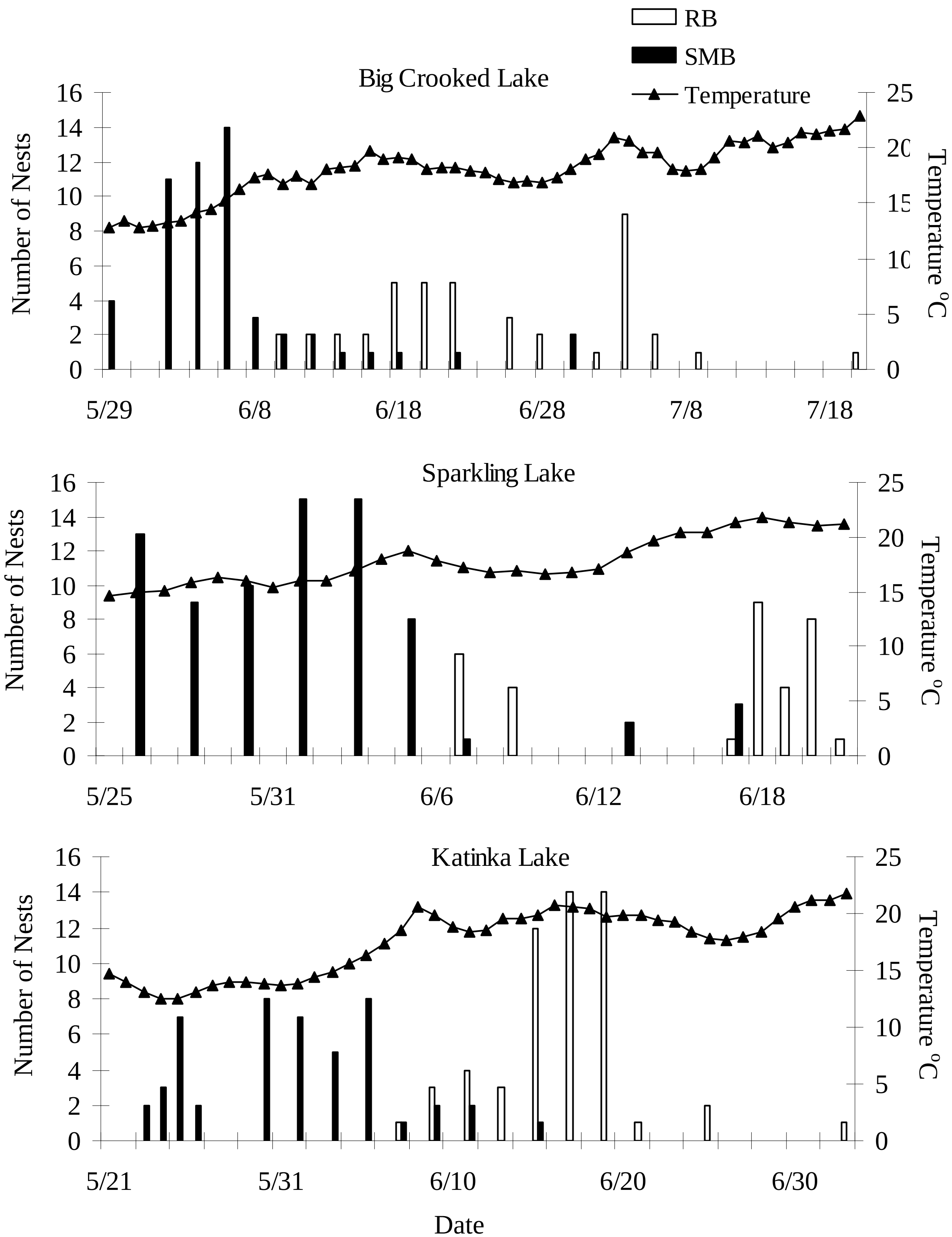

Figure 5. Temporal overlap in initial nesting dates for smallmouth bass and rock bass in Big Cooked Lake, Sparkling Lake, and Katinka Lake. Notice start date and end date are not the same in all three study lakes.

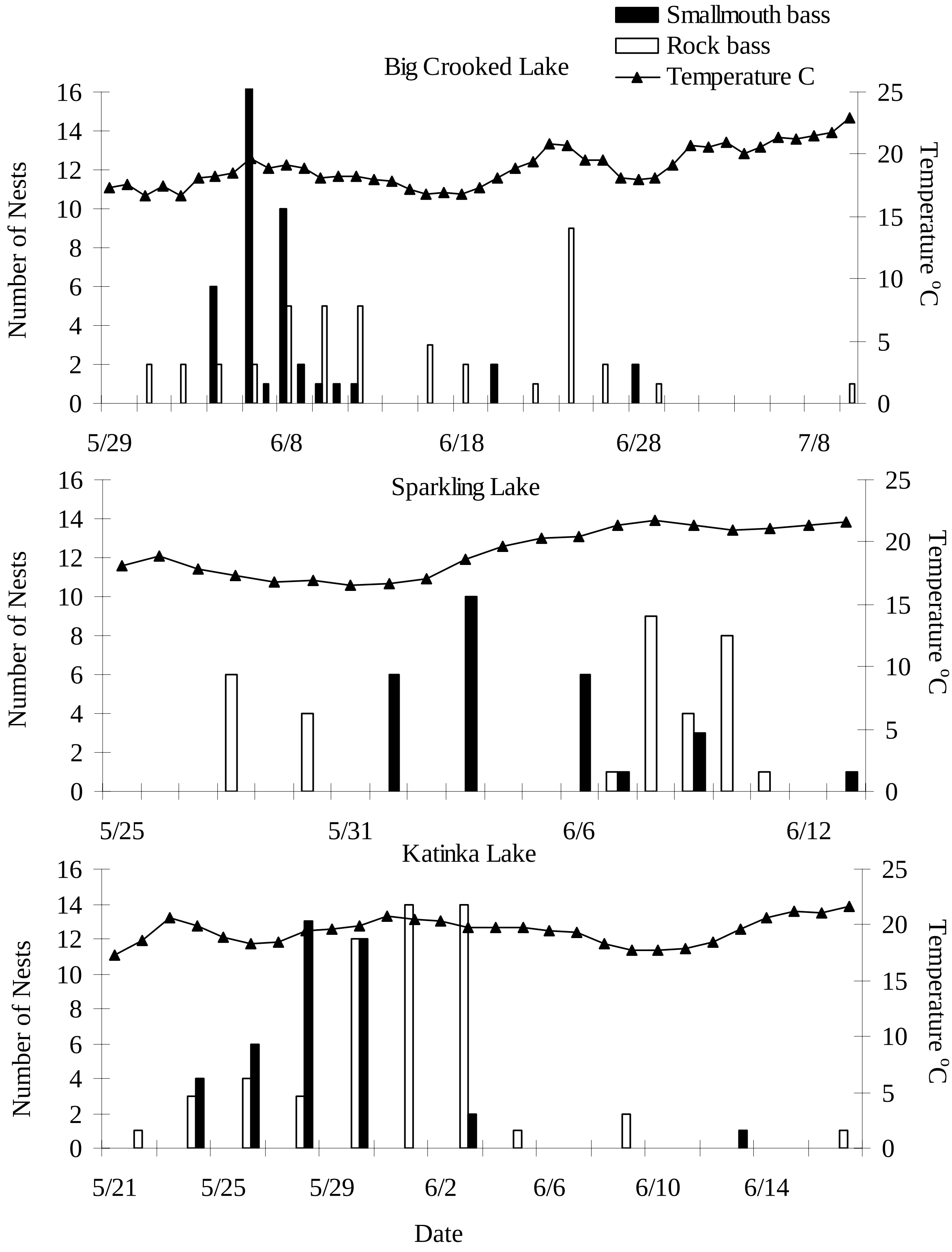

Figure 6. Temporal overlap in initial egg placement for rock bass nests and black fry date for smallmouth bass nests in Big Crooked Lake, Sparkling Lake, and Katinka Lake. Notice the start date and end date are different in all three graphs.

Discussion

Habitat selection by smallmouth bass in Big Crooked, Sparkling, and Katinka Lakes was generally similar to smallmouth bass habitat selection found in other studies (Short 2002; Brown 2004; Saunders 2006), but was not necessarily consistent among study lakes. While smallmouth bass selected for gravel substrate in all three study lakes, they also selected for cover features and sand substrate in Sparkling Lake and Katinka Lake. And in Big Crooked Lake, smallmouth bass selected for nest closer to shore and in shallower water depth.

The difference in habitat selection among the current study lakes was likely attributed to differences in habitat availability and population densities of smallmouth bass rather than ecological or behavioral differences. For instance, Big Crooked Lake is a 276 ha lake that has an excessively large littoral zone with less wood and rock cover available than occurs in Sparkling Lake and Katinka Lake. Along with being the largest study lake, Big Crooked Lake also had the smallest number of smallmouth bass per hectare than the other two study lakes (0.83 for Big Crooked Lake vs. 4.3 for Sparkling Lake and 13.9 for Katinka Lake). Because Sparkling Lake and Katinka Lake have higher fish densities and less littoral zone, spawning habitat saturation could be occurring causing smallmouth bass in these lakes to select the most abundant habitat available (e.g., sand and wood or cover), while Big Crooked Lake smallmouth bass could select for less available habitat such as gravel (McLoughlin et. al. 2006). Similar to the current study, both Saunders et al. (2002) and Short et al. (2002) found smallmouth bass in Big Crooked Lake and surrounding lakes to selected for spawning habitat variables associated with coarser substrates and cover relative to its availability within lakes. Specifically, Saunders, et al. (2002) found spawning habitat selection of smallmouth bass in three lakes with distinctly different littoral zone habitat features, Sanford, Bear, and Pallette Lakes, used higher amounts of sand and wood cover while using lesser amounts of gravel and cobble compared to the smallmouth bass in Big Crooked Lake.

Rock bass were more consistent in spawning habitat selection than smallmouth bass among study lakes. In all three study lakes, rock bass selected for habitat variables associated with sand and gravel substrates and distance to cover. In addition, Big Crooked Lake rock bass selected for deeper water, while Sparkling Lake rock bass selected for nests closer to shore. In contrast, Katinka Lake rock bass also selected for smaller cover. A similar study conducted by Noltie and Keenleyside (1986) on stream and lake dwelling rock bass of the Middle Thames River near London, Ontario, found rock bass also selected for depth, and utilized gravel substrate more often then other substrates. Contrary to the current study, a study conducted by Gross and Nowell (1980) suggested rock bass showed no tendency to nest near physical objects. Their study, which focused on the reproductive behavior of rock bass in Lake Opinicon, Ontario, found rock bass nested on coarse sand and light gravel. Few nests were near physical objects despite the presence of rock cover and woody debris available within areas of suitable substrate and water depth for nesting rock bass in Lake Opinicon. The differences in spawning habitat selection between the study conducted by Gross and Nowell (1980) and the current study could be attributed to interactions with other species such as the smallmouth bass or the population density of rock bass within the study lakes. For instance, in Big Crooked Lake, Sparkling Lake, and Katinka Lake, rock bass began spawning after smallmouth bass, but since most smallmouth bass still inhabited their nesting sites, when rock bass began to spawn, rock bass had less available spawning area to choose from. Along with smallmouth bass nest inhabitance, another difference between rock bass using cover in this study versus the Gross and Nowell (1980) study could have been rock bass population density. Possible higher densities in the current study lakes versus Lake Opinicon, could have contributed to potential spawning habitat saturation causing rock bass to choose similar spawning habitat (i.e., gravel substrate and cover) while not selecting for cover in the study conducted by Gross and Nowell (1980).

In this study, resource selection functions for smallmouth bass and rock bass, while not identical, were similar in the selection of substrate and cover features in all study lakes. Similar habitat selection has been noted in rivers as well as lakes and thus might be universally generalizable. Similar to the current study of lacustrine smallmouth bass, a study conducted by McClendon and Rabeni (1987) found cover (e.g., logjams, root wads, and boulders) to be important to both species in rivers. Their results suggested that when minimum environmental requirements such as depth and stream-flow are met, cover variables then assume importance in predicting biomass and density of smallmouth bass and rock bass in the Jack Forks River, Missouri. Studies conducted by Lyons (1991), Walters and Wilson (1996), and Rankin (1986) also found smallmouth bass to select for similar habitat features in streams and rivers. Rankin (1986) found smallmouth bass habitat selection was influenced by substrate type (gravel to boulder size), depth, and current velocity. Walters and Wilson (1996) also found smallmouth bass to consistently select for cobble, undercut banks, depth, and light in pools of the Buffalo River, Arkansas.

With the use of resource selection functions we were able to identify that habitat variables smallmouth bass and rock bass selected for among lakes were generally similar (i.e., cover and coarse substrates). However habitat use analyses suggested smallmouth bass and rock bass utilized selected resources differently. Discriminant analysis found smallmouth bass in Big Crooked Lake tended to nest in shallower water and adjacent to some form of cover (e.g. wood or rock), while rock bass tended to utilize cover by placing their nests directly underneath it. Both smallmouth bass and rock bass predominately spawned on gravel; however, more smallmouth bass nests contained cobble as the sub-dominant substrate whereas the majority of rock bass nests contained sand as the sub-dominant substrate. The differences in microhabitat (i.e., nest placement relative to cover and sand vs. cobble as subdominant substrate) use between smallmouth bass and rock bass in Big Crooked Lake could be a function of fish body size. Smallmouth bass are generally larger than rock bass and therefore can excavate a cleaner nest causing larger substrates to be exposed. Conversely, the smaller body size of rock bass could provide more opportunities for placing their nests under a greater range of cover.

As in Big Crooked Lake, the variables contributing to the highest separation between smallmouth bass and rock bass in Sparkling Lake also included distance to cover and percent nest under cover. Rock bass in Sparkling Lake utilized cover more often than smallmouth bass and they commonly placed their nests directly underneath it. Interestingly, this habitat partitioning, while distinct in detail, still showed similar habitat features (e.g., cover) were used in general. The general findings of habitat use from this study concurred with the study conducted by Probst et al. (1984) where the mean distance from cover was found to be less for rock bass than for smallmouth bass and most rock bass using cover were positioned inside the interstitial spaces of structure while smallmouth bass were generally found next to cover. However, the study conducted by Probst et al. (1984) looked at general resource use by stream dwelling smallmouth bass and rock bass, not specifically spawning habitat use.

Some of the separation in discriminant analyses was due to subtle differences in how these two species use habitat rather than what they used. For instance, smallmouth bass and rock bass nests both were often close to woody structure when available; however rock bass nests were located under cover versus smallmouth bass nests that were often adjacent to cover. Because use of cover played such an important role in the separation of nests in Big Crooked and Sparkling Lakes, a second discriminant analysis was conducted removing the variable percent nest under cover because this variable could be considered behavioral (larger smallmouth bass place their nests adjacent to cover while smaller rock bass place their nests under cover). Discrimination of Big Crooked Lake smallmouth bass and rock bass nests, after eliminating nest position, only reduced the correct classification by 8% (90% to 82% overall), and Sparkling Lake and Katinka Lake correct classifications did not change after removal of the variable. The minimal drop in correct classification of Big Crooked Lake nests could be attributed to the lower amount of cover available to spawning fish and greater amounts of sand and gravel available thus, cover (thought to be more limiting) affecting separation more than substrates in Big Crooked Lake. However, the overall correct classification of nests was still high indicating nest position was not driving the separation between smallmouth bass nests and rock bass nests in all three study lakes, but it was still very important in their separation. A similar function of body size is presented in a study conducted by Witzel and MacCrimmon (1983) on redd-site selection by brook trout and brown trout in a southwestern Ontario stream. They found that in sympatric populations of these two species an overlap in spawning time occurred for up to three weeks with a similar selection in water depth for redd placement. However, due to the larger body size of mature brown trout, they were able to utilize faster water velocities than the brook trout and as such, were found over coarser gravels. Whereas the smaller body size of rock bass could allow them to use a wider range of cover then smallmouth bass. Discriminant analysis performed on separating smallmouth bass nests from rock bass nests in Katinka Lake used dominant substrate type, dominant substrate embeddedness, and sub-dominant substrate embeddedness. This was in contrast to analyses in Big Crooked and Sparkling Lakes which separated based primarily on cover features. In Katinka Lake, smallmouth bass and rock bass both spawned on gravel; however a greater percentage of rock bass also chose to spawn on sand, and to a lesser extent, smallmouth bass chose to spawn on cobble and rubble. The separation of smallmouth bass nests from rock bass nests in Katinka Lake by substrate (as opposed to cover) might be attributed to the large amount of available cover close to shore which reduces competition for this cover type.

In all three study lakes, smallmouth bass began spawning earlier than rock bass, but there was considerable temporal overlap, which affects habitat partitioning. Overlap was significant because rock bass started to spawn before some YOY smallmouth bass had left their nests. Because smallmouth bass are the second longest nest defender next to largemouth bass in the family Centrarchidae (Ridgway 1987), this behavior likely contributed to a higher overlap. Overlap in Big Crooked Lake was 82%, in Katinka Lake

89%, and in Sparkling Lake 63%. A study conducted by Farrel et al. (1996) found similar patterns of separation between sympatric spawning northern pike and muskellunge. They determined in the Thousand Islands section of the St. Lawrence River, New York, a large overlap in the use of spawning areas occurred; there was a two week overlap in spawning times. Apparently, to help compensate for the overlap in spawning time, northern pike spawned over a wider range of water depths than muskellunge do, indicating other mechanisms regulate the ability for these species to coexist. Similarly, the larger separation in spawning time between smallmouth bass and rock bass in Sparkling Lake could be attributed to the smaller littoral zone (i.e., spawning area) and, greater population density of both species compared to that of Big Crooked Lake and Katinka Lake. These factors along with the ability for rock bass to utilize a wider variety of cover than smallmouth bass, could have provided the means for both species in Sparkling Lake to separate based on temporal aspects along with habitat features within the lake.

Similarities in specific spawning habitat features selected suggest smallmouth bass and rock bass could be placed in the same spawning guild based on the definition and functional use of the term guild. Balon (1975) placed smallmouth bass and rock bass in the same spawning guild, and classified them as guarders, nest spawners, and lithophils. However, his classification was largely based on general qualitative data. The quantitative data from this study clearly shows spawning habitat selection and use by smallmouth bass and rock bass was similar; selection of coarse substrates and wood or rock cover. Also, they overlap in the time they occupy nest sites, yet nest sites can be discriminated by how smallmouth bass and rock bass utilize similar microhabitat variables selected for, such as the placement of nests relative to cover and amounts of gravel substrate found in the nest. With this information the placement of smallmouth bass and rock bass into a spawning guild is a reasonable assertion.

It is interesting that smallmouth bass and rock bass use such similar habitat to be considered from the same guild, yet coexist in aquatic systems. They would need to partition resources effectively while in sympatry or face competitive interactions that could reduce one or both populations, maintain lower population sizes, or lead to extirpation. For instance, a study conducted by Smith (1976) documented interspecific competition for space by spawning largemouth bass with sunfish (Lempomis sp.). The observations from that study concluded that reduced or complete inhibition of spawning by largemouth bass occurred in Florida ponds where dense populations of sunfish existed therefore reducing the largemouth bass population. In the current study, smallmouth bass and rock bass were found to effectively partition spawning habitat based on subtle differences in nest site characteristics (i.e., use of gravel and placement relative to cover), however they also had a significant overlap in spawning time and similar habitat selection (i.e., cover and gravel) indicating there could be a conflict in spawning habitat if an important resources such as cover, became limiting or and increase in population size of one or both species occurred.

Smallmouth bass and rock bass not only select for similar microhabitat spawning features and overlap temporally in nest inhabitance, they also utilize similar forage (Frey 2003). So how have they been able to coexist? The presence of predators to control populations of either or both species, or the ability to utilize spawning habitat features differently (using more or less cover, nest placement relative to cover) are two possibilities of resource partitioning. The second theory has been shown in the current study by differences of spawning habitat use between species in all study lakes but more work is needed in the form of experimental studies, which need to be conducted to understand how limiting spawning habitat could affect recruitment over time. For instance, in the absence of cover would spawning habitat selection differ between smallmouth bass and rock bass than what we have seen in the current study, or would they partition more in timing of spawning? In the current study smallmouth bass and rock bass inhabited all three lakes; comparison of spawning habitat use in the absence of the other species would be beneficial to help answer how these species coexist and to better understand niche breath. As well as habitat analysis, density-dependent factors affecting survival of YOY for both smallmouth and rock bass need to be estimated to determine if recruitment for either species is affected by the other. Bult et al. (1999) conducted an experimental study assessing the density dependant habitat selection by juvenile Atlantic salmon. They concluded that habitat selection was temperature and density dependent, implying that habitat models will need to vary with temperature and population density. Fukushima and Smoker (1998) also found density dependant factors played a role in the habitat segregation between sockeye and pink salmon in Lake Creek, southeast Alaska. They found as the spawning density increased in Lake Creek, the degree of habitat segregation declined.

The information from the current study has started to link the relationship between spawning smallmouth bass and rock bass in northern Wisconsin lakes. Both species selected for course gravel substrate and cover, but smallmouth bass and rock bass nests were easily separated based on specific microhabitat features such as placement of nest relative to cover. And due to continued anthropogenic disturbances of littoral zone habitat through the reduction or elimination of trees for cover, and the reduction of gravel substrate will reduce the amount of available spawning sites for both species. Because, there was similar habitat selection, and temporal overlap in spawning time by smallmouth bass and rock bass in all three study lakes, more work will need to be conducted to understand the effects competition could have on populations of smallmouth bass and rock bass as resources become limiting.

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Appendices

Appendix A. Resource selection models were developed to determine habitat selection within each study lake for both smallmouth bass and rock bass. Due to the large number of available data points, 3970 for Big Crooked, 1366 for sparkling, and 1410 for Katinka; a series of logistic regression analyses were run on Big Crooked Lake smallmouth bass nests in order to maximize percent of nests correctly classified. Dominant substrate type was used in logistic regression analyses for Big Crooked Lake smallmouth bass nests. Regressions containing 333 data points were run on all three lakes. Analyses were run using 100, 200, 300, 500, and 1000 available data points. The combined analysis consisted of combining substrates 1 (fine organic debris) and 2 (silt) together, and also eliminating substrate 10 (coarse organic debris). It was concluded using 500 available data points from the combined data set produced the maximum correct classification of nest presence.

# of Available Points	Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept	Classification Rate	Absence 0	Presence 1
333	Dom. Substrate Type	2.167243	0.2633459	67.73	0.0	0.142966	-8.861116	83.58	98.5	17.33
333	Dom. Substrate Type	1.454736	0.217533	44.72	0.0	0.099222	-6.384573	83.09	97.9	17.33
333	Dom. Substrate Type	0.7445515	0.1643263	20.53	0.0	0.047137	-4.040128	80.1	98.33	17.33
100	Dom. Substrate Type	2.830399	0.3936039	51.71	0.0	0.23012	-10.25574	90.86	90	92
200	Dom. Substrate Type	1.679611	0.2573306	42.6	0.0	0.134988	-6.696843	94.18	95	92
300	Dom. Substrate Type	2.122604	0.2650651	64.13	0.0	0.146699	-8.610604	82.13	98.33	17.33
500	Dom. Substrate Type	0.724656	0.1478812	24.01	0.0	0.040221	-4.324507	85.39	98	1.33
1000	Dom. Substrate Type	0.4001461	6.41E-02	38.98	0.0	0.035059	-3.964956	91.16	98	0
Combined 333	Dom. Substrate Type	4.256839	0.4287805	98.56	0.0	0.19534	-16.28366	92.89	93.09	92
Combined 333	Dom. Substrate Type	4.350303	0.4356685	99.71	0.0	0.199133	-16.53102	93.55	93.9	92
Combined 333	Dom. Substrate Type	4.765701	0.4560703	109.19	0.0	0.208305	-17.86007	95.2	95.91	92
Combined 100	Dom. Substrate Type	4.126211	0.5188723	63.24	0.0	0.267689	-14.80895	91.43	91	92
Combined 200	Dom. Substrate Type	5.207745	0.5555819	87.86	0.0	0.243479	-18.78482	95.64	97	92
Combined 300	Dom. Substrate Type	4.270932	0.4357077	96.08	0.0	0.204835	-16.21274	93.07	93.33	92
Combined 500	Dom. Substrate Type	4.643693	0.4173307	123.81	0.0	0.177685	-17.77126	95.48	96	92
Combined 1000	Dom. Substrate Type	3.420033	0.3007461	129.32	0.0	0.107558	-14.22867	93.67	99.4	17.33
Combined Full	Dom. Substrate Type	2.452621	0.1816748	182.25	0.0	0.043175	-12.11645	97.82	99.34	17.33

Appendix B. Discriminant analysis of all nesting habitat variables for Big Crooked Lake 2004.

Correct Classification Table for Big Crooked Lake

	Predicted		
Actual	SMB	RB	Total
SMB	97	3	75
RB	0	100	38
Total	73	40	99

Structure Coefficients

Variable	Big Crooked Lake
Average Nest Diameter	-0.489
Distance to Next Nest	-0.309
Distance to Shore	0.080
Water Depth	0.279
Nest Depth	0.253
Substrate Removed	-0.117
Slope	0.169
Dominant Substrate Type	-0.136
Dominant Substrate Percent	0.239
Dominant Substrate Embeddedness	0.033
Sub-Dominant Substrate Type	-0.184
Sub-Dominant Substrate Percent	-0.155
Sub-Dominant Substrate Embeddedness	-0.169
Wood Diameter	-0.123
Clearance	0.064
Percent Under Cover	0.497
Distance to Cover	-0.104
Rock Length	0.142
Percent Nest Vegetation	-

Appendix C. Discriminant analysis of all nesting habitat variables for Sparkling Lake.

Correct Classification Table for Sparkling Lake

	Predicted		
Actual	SMB	RB	Total
SMB	95	5	74
RB	2	98	50
Total	71	53	96

Structure Coefficients

Variable	Sparkling Lake
Average Nest Diameter	0.696
Distance to Next Nest	0.139
Distance to Shore	0.218
Water Depth	-0.039
Nest Depth	-0.023
Substrate Removed	-
Slope	-0.161
Dominant Substrate Type	-0.021
Dominant Substrate Percent	0.023
Dominant Substrate Embeddedness	0.021
Sub-Dominant Substrate Type	0.073
Sub-Dominant Substrate Percent	-0.092
Sub-Dominant Substrate Embeddedness	-0.108
Wood Diameter	-0.055
Clearance	-0.055
Percent Under Cover	-0.310
Distance to Cover	0.210
Rock Length	-
Percent Nest Vegetation	0.126

Appendix D. Discriminant analysis of all nesting habitat variables for Katinka Lake 2004.

Correct Classification Table for Katinka Lake

	Predicted		
Actual	SMB	RB	Total
SMB	94	4	49
RB	7	93	55
Total	51	53	93

Structure Coefficients

Variable	Katinka Lake
Average Nest Diameter	-0.733
Distance to Next Nest	-0.043
Distance to Shore	-0.122
Water Depth	-0.095
Nest Depth	-0.097
Substrate Removed	-0.108
Slope	-0.170
Dominant Substrate Type	-0.306
Dominant Substrate Percent	0.126
Dominant Substrate Embeddedness	0.358
Sub-Dominant Substrate Type	0.123
Sub-Dominant Substrate Percent	0.122
Sub-Dominant Substrate Embeddedness	0.238
Wood Diameter	-0.043
Clearance	-0.131
Percent Under Cover	0.185
Distance to Cover	-0.037
Rock Length	-0.072
Percent Nest Vegetation	-

Appendix E. Stepwise discriminant analysis of all nesting habitat variables for Big Crooked Lake 2004.

Classification Big Crooked Lake

	Predicted		
Actual	SMB	RB	Total
SMB	97	3	75
RB	0	100	38
Total	73	40	99

Structure Coefficients

Variable	Big Crooked Lake
Average Nest Diameter	-0.512
Distance to Next Nest	-0.324
Distance to Shore	-
Water Depth	0.292
Nest Depth	-
Substrate Removed	-
Slope	0.177
Dominant Substrate Type	-
Dominant Substrate Percent	-
Dominant Substrate Embeddedness	-
Sub-Dominant Substrate Type	-
Sub-Dominant Substrate Percent	-
Sub-Dominant Substrate Embeddedness	-
Wood Diameter	-0.128
Clearance	0.067
Percent Under Cover	0.521
Distance to Cover	-0.109
Rock Length	0.149
Percent Nest Vegetation	-

Appendix F. Stepwise discriminant analysis of all nesting habitat variables for Sparkling Lake 2003.

Classification Sparkling Lake

	Predicted		
Actual	SMB	RB	Total
SMB	96	4	74
RB	2	98	50
Total	72	52	97

Structure Coefficients

Variable	Sparkling Lake
Average Nest Diameter	-0.712
Distance to Next Nest	-0.142
Distance to Shore	-0.223
Water Depth	0.040
Nest Depth	-
Substrate Removed	-
Slope	-
Dominant Substrate Type	0.021
Dominant Substrate Percent	-
Dominant Substrate Embeddedness	-
Sub-Dominant Substrate Type	-0.074
Sub-Dominant Substrate Percent	-
Sub-Dominant Substrate Embeddedness	0.110
Wood Diameter	-
Clearance	-
Percent Under Cover	0.317
Distance to Cover	-0.214
Rock Length	-
Percent Nest Vegetation	-

Appendix G. Stepwise discriminant analysis of all nesting habitat variables for Katinka Lake 2004.

Classification Katinka Lake

	Predicted		
Actual	SMB	RB	Total
SMB	92	8	49
RB	9	91	55
Total	50	54	91

Structure Coefficients

Variable	Katinka Lake
Average Nest Diameter	-0.779
Distance to Next Nest	-
Distance to Shore	-
Water Depth	-
Nest Depth	-
Substrate Removed	-0.114
Slope	-
Dominant Substrate Type	-
Dominant Substrate Percent	-
Dominant Substrate Embeddedness	0.380
Sub-Dominant Substrate Type	-
Sub-Dominant Substrate Percent	0.130
Sub-Dominant Substrate Embeddedness	-
Wood Diameter	-
Clearance	-
Percent Under Cover	0.197
Distance to Cover	-
Rock Length	-
Percent Nest Vegetation	-

Appendix H. Individual smallmouth bass logistic regression analyses using 500 randomly selected data points for Big Crooked Lake 2004.

Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept Coefficient	Correct Classification	Percent Absence	Percent Presence
Small boulder	-2.40	145.31	0.00	0.99	0.00	-1.89	86.96	100.00	0.00
Rubble	0.06	0.03	4.92	0.03	0.01	-1.96	87.13	100.00	1.33
Cobble	0.15	0.02	92.53	0.00	0.14	-3.04	89.91	98.00	36.00
Gravel	0.08	0.01	119.94	0.00	0.17	-4.02	92	97.40	56.00
Sand	-0.05	0.00	93.34	0.00	0.14	0.18	83.48	90.80	34.67
Sub-dominant substrate type	0.85	0.10	79.23	0.00	0.13	-4.20	87.31	95.01	40.00
Dominant substrate type	3.55	0.34	108.00	0.00	0.16	-14.11	92.7	92.80	92.00
Sub-dominant substrate percent	0.05	0.01	28.04	0.00	0.05	-2.85	86.78	99.80	0.00
Dominant substrate percent	-0.04	0.01	39.84	0.00	0.07	1.33	86.61	99.60	0.00
Distance to rock	-0.23	0.03	57.79	0.00	0.09	-0.27	86.96	100.00	0.00
Rock diameter z	4.28	0.72	35.14	0.00	0.06	-2.28	87.48	99.00	10.67
Embeddedness 6	-0.08	0.38	0.05	0.82	0.00	-1.05	77.55	100.00	0.00
Embeddedness 5	-1.45	0.32	20.68	0.00	0.14	2.38	72.09	81.43	61.02
Embeddedness 4	-1.58	0.24	45.04	0.00	0.18	2.18	77.07	80.15	71.62
Sub-dominant substrate embeddedness	-1.17	0.12	91.03	0.00	0.15	1.75	89.47	96.98	38.24
Dominant substrate embeddedness	-1.85	0.16	134.03	0.00	0.19	3.20	94.26	97.00	76.00
Distance to shore	-0.02	0.00	13.73	0.00	0.02	-1.25	86.96	100.00	0.00
Distance to cover	-0.37	0.05	65.11	0.00	0.10	-0.39	86.96	100.00	0.00
Depth	0.54	0.15	13.05	0.00	0.02	-2.71	86.78	99.80	0.00
CWS length	0.07	0.04	3.03	0.08	0.01	-2.00	86.96	100.00	0.00
CWS distance	-0.10	0.03	9.77	0.00	0.02	-1.13	86.96	100.00	0.00
CWS diameter	0.48	0.76	0.41	0.52	0.00	-1.92	86.96	100.00	0.00
Cover size	0.15	0.12	1.51	0.22	0.00	-1.95	86.96	100.00	0.00
Clearance	6.85	1.65	17.32	0.00	0.03	-2.08	87.83	99.60	9.33
Percent nest under cover	0.22	0.11	4.16	0.04	0.01	-1.97	87.13	99.80	2.67

Appendix I. Individual rock bass logistic regression analyses using 500 randomly selected data points for Big Crooked Lake 2004.

Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept Coefficient	Correct Classification	Percent Absence	Percent Presence
Small boulder	-2.26	146.29	0.00	0.99	0.00	-2.57	92.94	100.00	0.00
Rubble	-5.68	361.31	0.00	0.99	0.00	-2.49	92.94	100.00	0.00
Cobble	0.07	0.02	17.64	0.00	0.03	-2.86	93.11	99.60	5.41
Gravel	0.07	0.01	80.61	0.00	0.13	-4.98	96.47	98.40	71.05
Sand	-0.04	0.01	52.16	0.00	0.09	-0.71	92.94	100.00	0.00
Sub-dominant substrate type	1.15	0.20	34.14	0.00	0.07	-6.83	94.58	98.48	0.00
Dominant substrate type	2.58	0.36	52.08	0.00	0.09	-11.06	92.19	99.20	0.00
Sub-dominant substrate percent	0.05	0.02	10.74	0.00	0.02	-4.32	96.34	100.00	0.00
Dominant substrate percent	0.02	0.01	3.65	0.06	0.01	-4.53	92.94	100.00	0.00
Rock distance	-0.64	0.11	36.30	0.00	0.06	0.03	97.21	98.00	86.84
Rock diameter y	3.51	0.46	59.01	0.00	0.10	-3.52	92.57	98.00	21.05
Embeddedness 5	-2.31	0.67	12.01	0.00	0.13	2.03	84.52	100.00	7.14
Embeddedness 4	-2.04	0.38	28.78	0.00	0.15	1.86	82.53	98.47	22.86
Sub-dominant substrate embeddedness	-1.47	0.22	43.64	0.00	0.08	1.04	96.07	99.78	5.26
Dominant substrate embeddedness	-1.53	0.16	90.80	0.00	0.14	1.87	95.54	97.00	76.32
Distance to shore	-0.01	0.00	3.14	0.08	0.01	-2.19	92.94	100.00	0.00
Distance to cover	-1.42	0.28	24.94	0.00	0.04	-0.15	92.94	100.00	0.00
Depth	1.47	0.24	37.76	0.00	0.07	-5.35	93.49	99.80	10.53
CWS length	-0.33	0.17	3.66	0.06	0.01	-2.37	92.94	100.00	0.00
CWS distance	0.25	0.10	5.83	0.02	0.01	-4.78	92.94	100.00	0.00
CWS diameter	-12.80	5.53	5.36	0.02	0.01	-2.31	92.94	100.00	0.00
Cover size	0.33	0.12	7.03	0.01	0.01	-2.72	92.75	99.80	0.00
Clearance	22.23	2.57	75.01	0.00	0.12	-3.90	95.54	98.80	52.63
Percent nest under cover	0.23	0.06	13.84	0.00	0.03	-4.03	98.14	99.80	76.32

Appendix J. Individual smallmouth bass logistic regression analyses using 500 randomly selected data points for Sparkling Lake 2004.

Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept Coefficient	Correct Classification	Percent Absence	Percent Presence
Submergent vegetation height	-6.55	2.43	7.24	0.01	0.01	-1.63	86.96	100.00	0.00
Submergent vegetation percent	0.02	0.00	14.94	0.00	0.03	-2.19	86.96	100.00	0.00
Small boulder	-1.23	121.37	0.00	0.99	0.00	-1.90	86.96	100.00	0.00
Rubble	-0.04	0.04	0.92	0.34	0.00	-1.87	86.96	100.00	0.00
Cobble	0.00	0.01	0.77	0.38	0.00	-1.92	86.96	100.00	0.00
Gravel	0.03	0.01	31.28	0.00	0.05	-2.29	86.78	98.80	6.67
Sand	0.04	0.00	98.99	0.00	0.15	-3.36	88.00	94.40	45.33
Subdominant substrate type	0.51	0.06	62.53	0.00	0.10	-3.55	90.26	100.00	25.33
Dominant substrate type	0.94	0.11	69.22	0.00	0.11	-4.34	83.65	95.40	5.33
Subdominant substrate percent	0.02	0.01	4.84	0.03	0.01	-2.10	86.96	100.00	0.00
Dominant substrate percent	-0.02	0.01	7.55	0.01	0.01	-0.53	86.96	100.00	0.00
Rock distance	6.36	708.28	0.00	0.99	0.00	-65.44	86.96	100.00	0.00
Percent nest under cover	0.03	0.01	5.41	0.02	0.01	-1.97	87.30	100.00	2.67
Embeddedness 6	-15.13	393.83	0.00	0.97	0.00	0.69	96.15	95.83	100.00
Embeddedness 5	-1.80	0.44	16.73	0.00	0.13	0.74	86.55	96.94	38.10
Embeddedness 4	-2.12	0.34	38.85	0.00	0.15	2.29	88.79	90.71	80.00
Subdominant embeddedness	-0.65	0.10	41.44	0.00	0.11	0.43	84.87	99.62	33.33
Dominant embeddedness	-0.55	0.10	27.58	0.00	0.05	0.03	87.13	99.40	5.33
Distance to shore	-0.05	0.02	10.62	0.00	0.02	-1.25	86.96	100.00	0.00
Distance to cover	-1.12	0.19	34.01	0.00	0.06	-0.61	86.96	100.00	0.00
Depth	-0.43	0.16	6.88	0.01	0.01	-1.32	86.96	100.00	0.00
Coarse woody structure length	0.06	0.03	4.00	0.05	0.01	-2.11	86.96	100.00	0.00
Distance to coarse woody structure	-1.12	0.19	34.01	0.00	0.06	-0.58	86.96	100.00	0.00
Coarse woody structure diameter	3.70	1.14	10.47	0.00	0.02	-2.38	87.11	99.80	1.35
Cover size	0.51	0.70	0.54	0.46	0.00	-1.97	86.96	100.00	0.00
Clearance	11.17	1.56	51.13	0.00	0.08	-2.50	89.22	99.00	24.00

Appendix K. Individual rock bass logistic regression analyses using 500 randomly selected data points for Sparkling Lake 2004.

Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept Coefficient	Correct Classification	Percent Absence	Percent Presence
Submergent Vegetation Percent	0.00	0.01	0.01	0.94	0.00	-2.30	90.91	100.00	0.00
Small boulder	-1.19	121.37	0.00	0.99	0.00	-2.30	90.91	100.00	0.00
Rubble	-2.51	232.68	0.00	0.99	0.00	-2.26	90.91	100.00	0.00
Cobble	-0.02	0.02	0.93	0.34	0.00	-2.25	90.91	100.00	0.00
Gravel	0.04	0.01	49.08	0.00	0.08	-2.99	90.55	98.80	8.00
Sand	0.03	0.00	62.68	0.00	0.10	-3.47	90.91	100.00	0.00
Sub-dominant substrate type	0.04	0.07	0.28	0.60	0.00	-2.38	90.91	100.00	0.00
Dominant substrate type	0.87	0.12	51.59	0.00	0.09	-4.58	90.00	98.80	2.00
Sub-dominant substrate percent	0.02	0.01	8.47	0.00	0.02	-2.62	90.91	100.00	0.00
Dominant substrate percent	-0.02	0.01	8.63	0.00	0.02	-0.58	90.91	100.00	0.00
Rock distance	6.16	709.36	0.00	0.99	0.00	-63.87	90.91	100.00	0.00
Rock diameter	-33.97	1266.20	0.00	0.98	0.00	-2.27	90.91	100.00	0.00
Percent nest under cover	0.07	0.01	47.27	0.00	0.08	-2.97	94.36	99.80	40.00
Embeddedness 5	-1.86	0.62	8.96	0.00	0.08	-0.02	91.59	100.00	0.00
Embeddedness 4	-2.29	0.42	30.34	0.00	0.13	2.48	87.26	90.71	65.52
Sub-dominant embeddedness	-0.16	0.17	0.91	0.34	0.00	-1.67	89.73	100.00	0.00
Dominant substrate embeddedness	-0.65	0.12	28.50	0.00	0.05	-0.04	90.91	100.00	0.00
Distance to cover	-4.35	1.05	17.11	0.00	0.03	-0.58	90.91	100.00	0.00
Distance to shore	-0.12	0.02	22.67	0.00	0.04	-1.05	90.91	100.00	0.00
Depth	-0.28	0.18	2.41	0.12	0.00	-1.91	90.91	100.00	0.00
Coarse woody structure length	0.10	0.03	10.99	0.00	0.02	-2.71	90.91	100.00	0.00
Coarse woody structure distance	-4.27	1.04	16.95	0.00	0.03	-0.56	90.91	100.00	0.00
Coarse woody structure diameter	6.13	1.40	19.06	0.00	0.03	-3.14	90.73	99.80	0.00
Cover size	1.14	0.72	2.49	0.11	0.00	-2.48	90.91	100.00	0.00
Clearance	14.06	1.95	51.83	0.00	0.09	-3.05	90.91	99.00	10.00

Appendix L. Individual smallmouth bass logistic regression analyses using 500 randomly selected data points for Katinka Lake 2004.

Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept Coefficient	Correct Classification	Percent Absence	Percent Presence
Submergent vegetation	-0.04	0.01	11.44	0.00	0.02	-1.80	91.07	100.00	0
Large boulder	-9.85	433.53	0.00	0.98	0.00	-2.30	91.07	100.00	0.00
Small boulder	-2.54	178.03	0.00	0.99	0.00	-2.27	91.07	100.00	0.00
Rubble	0.00	0.02	0.04	0.84	0.00	-2.33	91.07	100.00	0.00
Cobble	0.09	0.01	56.34	0.00	0.09	-3.13	91.80	99.00	18.37
Gravel	0.06	0.01	93.90	0.00	0.15	-4.18	92.17	96.60	46.94
Sand	0.01	0.01	1.84	0.17	0.00	-2.40	91.07	100.00	0.00
Subdominant substrate type	0.39	0.06	37.22	0.00	0.07	-3.29	90.86	100.00	0.00
Dominant substrate type	0.97	0.12	66.13	0.00	0.11	-5.14	89.25	97.40	6.12
Rock distance	0.03	0.05	0.36	0.55	0.00	-2.57	91.07	100.00	0.00
Rock diameter	0.07	0.75	0.01	0.93	0.00	-2.33	91.07	100.00	0.00
Percent nest under cover	0.05	0.01	15.46	0.00	0.03	-2.54	91.07	99.80	2.04
Embeddedness 6	0.14	0.46	0.09	0.76	0.00	-2.40	90.16	100.00	0.00
Embeddedness 5	-0.50	0.23	4.67	0.03	0.03	-0.23	72.18	100.00	0.00
Embeddedness 4	-0.55	0.19	8.57	0.00	0.05	0.11	68.55	95.45	8.16
Subdominant substrate embeddedness	-0.35	0.12	7.84	0.01	0.04	-0.45	77.00	100.00	0.00
Dominant substrate embeddedness	-1.13	0.12	85.87	0.00	0.14	0.73	90.16	98.00	10.20
Distance to cover	-0.46	0.14	11.02	0.00	0.02	-1.73	91.07	100.00	0.00
Distance to shore	-0.10	0.02	17.55	0.00	0.03	-1.07	91.07	100.00	0.00
Depth	0.04	0.03	1.49	0.22	0.00	-2.40	91.24	100.00	2.04
Coarse woody structure length	0.07	0.03	7.41	0.01	0.01	-2.61	91.07	100.00	0.00
Coarse woody structure distance	-0.22	0.05	19.14	0.00	0.03	-1.68	91.07	100.00	0.00
Coarse woody structure diameter	2.70	0.99	7.38	0.01	0.01	-2.62	90.89	99.80	0.00
Cover size	-1.53	0.38	16.46	0.00	0.03	-1.29	91.07	100.00	0.00
Clearance	0.90	0.39	5.33	0.02	0.01	-2.42	90.71	99.60	0.00

Appendix M. Individual rock bass logistic regression analyses using 500 randomly selected data points for Katinka Lake 2004.

Variable	Regression Coefficient	Standard Error	Wald Chi-Square	Prob Level	Last R-Squared	Intercept Coefficient	Correct Classification	Percent Absence	Percent Presence
Submergent vegetation	-0.04	0.01	13.13	0.00	0.02	-1.71	90.09	100.00	0.00
Large boulder	-9.96	433.03	0.00	0.98	0.00	-2.18	90.09	100.00	0.00
Small boulder	-2.56	177.72	0.00	0.99	0.00	-2.15	90.09	100.00	0.00
Rubble	-0.02	0.03	0.55	0.46	0.00	-2.18	90.09	100.00	0.00
Cobble	0.04	0.01	12.25	0.00	0.02	-2.42	89.91	99.80	0.00
Gravel	0.04	0.00	79.11	0.00	0.13	-3.21	91.35	97.80	32.73
Sand	0.03	0.00	57.57	0.00	0.09	-2.88	88.11	96.80	9.09
Subdominant substrate type	0.44	0.06	54.49	0.00	0.09	-3.42	90.41	99.18	12.73
Dominant substrate type	0.75	0.10	52.22	0.00	0.09	-4.16	87.75	97.40	0.00
Subdominant substrate percent	0.08	0.01	65.16	0.00	0.11	-3.45	90.45	98.80	14.55
Dominant substrate percent	-0.03	0.01	21.46	0.00	0.04	0.18	89.91	99.80	0.00
Rock distance	0.05	0.05	0.95	0.33	0.00	-2.61	90.09	100.00	0.00
Rock diameter	-1.50	1.02	2.15	0.14	0.00	-2.12	90.09	100.00	0.00
Percent under cover	0.07	0.01	41.14	0.00	0.07	-2.71	91.35	98.80	23.64
Embeddedness 6	1.22	0.57	4.60	0.03	0.08	-5.19	94.83	100.00	0.00
Embeddedness 5	0.27	0.23	1.42	0.23	0.01	-2.06	82.76	100.00	0.00
Embeddedness 4	-0.15	0.17	0.77	0.38	0.00	-0.61	70.97	100.00	0.00
Subdominant substrate embeddedness	0.17	0.12	1.91	0.17	0.01	-1.53	74.89	100.00	0.00
Dominant substrate embeddedness	-0.60	0.10	35.72	0.00	0.06	-0.26	90.09	100.00	0.00
Distance to shore	-0.18	0.03	29.13	0.00	0.05	-0.48	90.09	100.00	0.00
Distance to cover	-0.75	0.23	10.88	0.00	0.02	-1.51	90.09	100.00	0.00
Depth	-1.61	0.24	43.68	0.00	0.07	-0.31	90.07	100.00	0.00
Coarse woody structure length	0.05	0.03	4.17	0.04	0.01	-2.41	90.09	100.00	0.00
Coarse woody structure distance	-0.26	0.05	22.68	0.00	0.04	-1.52	90.09	100.00	0.00
Coarse woody structure diameter	2.28	0.97	5.48	0.02	0.01	-2.45	89.91	99.80	0.00
Cover size	-1.87	0.44	17.88	0.00	0.03	-1.11	90.09	100.00	0.00
Clearance	0.61	0.40	2.27	0.13	0.00	-2.27	90.09	100.00	0.00

Appendix N. Variable description list.

Distance to shore:	For available habitat distance to shore identified where on a transect the data point fell (m). Measured from the shallow side of quadrat to shore. If the tape read 52.4 m at a depth of 3.0 m, available habitat data was collected starting at 51 m (on the tape) and repeated every other meter (i.e., 51, 49, 47…1). The variable METER from this example would look like 51, 49, 47…1. Distance to shore was measured from the center of the nest up to 30 m away.
Water depth:	The water depth at the site where the habitat measurement was taken (m). This was measured by allowing a float attached to a measuring tape to float to the surface. The tape was placed on the lake bottom and the distance from lake bottom to surface was measured. Water depth was measured from the center of each nest and quadrat.
Substrate %:	Percent of each substrate found in the sample area (i.e., nest or quadrat). See table three for description of substrate categories.
Embeddedness:	Embeddedness value (0-4) assigned to each substrate from gravel (3) through bedrock (9). Embeddedness was also recorded for the top five substrates found in each nest and quadrat.
Dominant substrate type:	Type of the most dominant substrate. Dominant substrate type was collected for the top 5 substrates. See table three for description of substrate size categories.
Dominant substrate %:	Percent recorded for the top five dominant substrate types.
Buried substrate:	Four substrate types reviled when four corners of the quadrat were probed to 12 cm.
% Small woody structure:	Percent of the site that is under a piece of small woody structure (<20.5 mm in diameter, <1.0 m in length).

% Medium woody structure:	The percent of the site that is under medium woody structure (20.5 to 50.8mm in diameter, <1.0 m in length).
Medium woody structure count:	The number of pieces of medium woody structure (20.5 to 50.8mm in diameter, <1.0 m in length) counted within the site.
Medium woody structure length:	The length (m) of the largest piece of medium woody structure (20.5 to 50.8mm in diameter, <1.0 m in length) within the study site.
Medium woody structure diameter:	The diameter of the largest piece of medium woody structure (20.5 to 50.8mm in diameter, <1.0 m in length) within the study site.
% Coarse woody structure:	The percent of the site that is under a piece of course woody structure (≥50.8 mm in diameter, ≥ 1.0 m in length).
Coarse woody structure position:	Categorical variable describing the position of a piece of course woody structure (≥50.8 mm in diameter, ≥ 1.0 m in length). q=within the site, r= within 10m of the site, and t=along transect. (No Unit)
Coarse woody structure distance:	The distance (m) to the nearest piece of course woody structure (≥50.8 mm in diameter, ≥ 1.0 m in length). Distance was measured at both nest and transect (available) sites. The closest log within 10m of nest rim or study site was measured.
Coarse woody structure length:	The length (m) of the nearest piece of course woody structure (≥50.8 mm in diameter, ≥ 1.0 m in length). Length was measured at both nest and transect (available) sites. The closest log within 10m of nest rim or study site was measured.
Coarse woody structure diameter:	The diameter in cm of the nearest piece of course woody structure (≥50.8 mm in diameter, ≥ 1.0 m in length). Diameter was measured at both nest and transect (available) sites. The closest log within 10m of nest rim or study site was measured.

Coarse woody structure clearance:	Average distance (m) from the bowl to the substrate for the closest piece of course woody structure (≥50.8 mm in diameter, ≥ 1.0 m in length) within 10m.
% Emergent vegetation:	The area of a site that is emergent vegetation.
% Floating vegetation:	The area of a site that is floating vegetation.
% Submergent vegetation:	The area of a site that is submergent vegetation.
Submergent vegetation height:	The average height (m) of the submergent vegetation within the study site.
Distance to rock:	The distance (m) to the nearest rock that is a small boulder or larger (≥304.00mm). Distance to rock was measured at both nest and transect (available) sites. The closest rock within 10 m of nest rim or study site was measured.
Rock diameter x:	The width of the rock (cm) taken parallel to the nest rim or edge of study site.
Rock diameter y:	The distance (m) from the embedding substrate to the top (point nearest to the water surface) of the rock.
Rock diameter z:	The width of the rock in cm taken perpendicular to the nest rim or study site.
Egg date:	Date eggs were first observed on the smallmouth bass and rock bass nest.
Fry date:	Date fry estimate was made for smallmouth bass.
Estimated length:	Estimated length in centimeters of the male guarding the nest.
Position:	Categorical variable that describes the position of a nest relative to a piece of course woody structure (1=immediately next to cover, 2=under cover, 3=other).
Nest diameter 1:	The diameter of the nest taken from nest rim to nest rim. (Meter)

Nest diameter 2:	The diameter of the nest taken from nest rim to nest rim at 90˚ to the first measurement (m) using a tape measure stretched across the nest. (Meter)
Mean diameter:	The average of the two diameter measurements.
Water depth:	Distance from the rim of the nest to the water surface in meters. (Meter)
Nest concavity:	The difference between nest depth and water depth. (Meter)
Slope 1:	The distance in m from the substrate to the water surface at a point 2m closer to shore. (Meter)
Slope 2:	The distance in m from the substrate to the water surface at a point 2m further from shore. (Meter)
Slope:	The difference in the two depth measurements (SLOPE1 and SLOPE2) divided by the difference in distance of the two measurements, 4m. (Meter)
Distance to nearest nest:	The distance in meters from the center of a nest to the center of the nearest smallmouth bass nest and rock bass nest. (Meter)
Outside nest substrate %:	The percent of each substrate found outside of the nest rim.
Outside embeddedness:	Embeddedness (0-4) of substrate found outside of the nest rim.
Outside dominant substrate type:	Type of the most dominant substrate. Dominant substrate type was collected for the top 5 substrates. See table three for description of substrate size categories.
Outside dominant substrate %:	The percent of the top five substrates found outside of the nest rim.
Outside dominant embeddedness:	The embeddedness of the top five substrates found outside of the nest rim.

Appendix O. Forms used for field data collection.

Mark or Recap		Lake			Date		Page of	
Collectors		Location			Time Set		Time Tended	
		Gear Type:			Specifics:			Water Temp:
Species	Length	Weight	Sex	Tag applied	Tag read	Mark Present	Mark Applied	Comments

Appendix O cont.

Lake **Date** **Male length is in cm.**

Nest Number | Male length | Aggression

EGG FRY

Nest Number | Male length | Aggression

EGG FRY

Appendix O cont.

Lake ______________________ **Date** _____________ **Species** ___________

	Nest Number									
	Nest diameter									
	Dist. to next smb nest									
	Active Y or N									
	Dist. to next rb nest									
	Acitve Y or N									
	Dist. to shore									
	Water depth									
	Nest depth									
	Slope									
In nest	**Substrate % emb**									
	Substrate % emb									
	Substrate % emb									
	Substrate % emb									
1 m away from nest rim	**Substrate % emb**									
	Substrate % emb									
	Substrate % emb									
	Substrate % emb									
	Dist to wood									
	Wood dia									
	Wood length									
	Clearance									
	% under log or rock									
	Nest Number									
	Position 0,1,2,3									
	Dist. To rock									
	X (length)									
	Y (width)									
	Z (height)									
	Veg. E,F,S %									
	Comments									

Appendix O cont.

Transect ______		**Substrate** (Sub / % / Emb)				Buried Sub	**Wood %**					**Type 3 Wood**			Dist to Type 3	Clear-ance	Dis. To Rock	**Rock Size**			**Vegetation**			Height
Meter	Depth	1	2	3	4		1	2	2 Len	2 Dia	3	Pos	Length	Dia				X	Y	Z	E	F	S	