WALLEYE (SANDER VITREUS) SPAWNING HABITAT SELECTION AND DYNAMICS IN A NORTH-TEMPERATE WISCONSIN LAKE

by

Joshua K. Raabe

A Thesis

submitted in partial fulfillment of the

requirements of the degree of

MASTERS OF SCIENCE

IN

NATURAL RESOURCES (FISHERIES)

College of Natural Resources

UNIVERSITY OF WISCONSIN

Stevens Point, Wisconsin

December 2006

APPROVED BY THE GRADUATE COMMITTEE OF:

Dr. Michael A. Bozek, Co-chair
Unit Leader
Wisconsin Cooperative Fishery Research Unit

Dr. Ronald L. Crunkilton, Co-chair
Professor of Water Resources
College of Natural Resources

Dr. Eric M. Anderson
Professor of Wildlife
College of Natural Resources

THESIS ABSTRACT

Critical to the conservation and management of sustainable populations of walleye, *Sander vitreus,* throughout North America is the need to understand what comprises and compromises high quality spawning habitat. In particular, questions remain regarding the actual selection of spawning habitat by walleye, how physical characteristics and functional dynamics (e.g., thermal conditions, wave energy, water levels) impact habitat quality, and the quantity of spawning habitat necessary to sustain healthy walleye populations. Therefore, the spawning habits and habitat of naturally reproducing walleye in Big Crooked Lake, a north temperate Wisconsin lake, were evaluated in 2004 and 2005, with specific objectives to: 1) describe the physical characteristics of natural walleye spawning reefs in order to develop detailed blueprints of successful natural walleye spawning habitat and to develop walleye spawning habitat resource selection functions, 2) evaluate thermal conditions on walleye spawning reefs and the relative affect they have on reproductive success across two years, and 3) assess the potential impact of wind activity, wave energy, and water level on walleye egg movement and survival. Walleye spawned primarily close to shore (outer boundary $\bar{x}$ distance = 2.72 m), in shallow water (outer boundary $\bar{x}$ depth = 0.29 m) and over gravel substrate ($\bar{x}$ coverage = 64.3%) with low embeddedness ($\bar{x}$ = 1.30) at all sites. Only 39% of available rock shoreline (14% of total shoreline) and no offshore reefs were utilized by walleye. The best resource selection function (overall correct classification = 97.6%) predicted that the relative probability of egg deposition increased with gravel and cobble substrates and decreased with distance from the shoreline, higher substrate embeddedness, and with increasing sand and fine organic material. Evaluating habitat quality (i.e., egg survival), regression models found percent cobble substrate to be the only variable positively related to the percent survival of deposited eggs in egg collection chambers. Two- and three-dimensional spawning reef blueprints were developed to visually depict the successful natural walleye spawning habitat studied. Evaluating thermal conditions, despite gradual and stable rises in water temperature and high densities of eggs in 2004, percent survival was lower than in 2005, potentially due to lower thermal lethal limits (<6°C) exceeded the first six days of the spawning period. In 2005, water temperature fluctuated, prolonging the development and hatching of walleye embryos but had minimal direct impact on egg survival. Significant differences ($p < 0.05$) in mean daily water temperature throughout the spawning period were observed between reefs and sometimes within reefs. Close to shore, shallow water responded more to fluctuations in air temperatures than further, deeper water at all reefs. Wind and wave velocities showed a positive, significant ($p < 0.001$) correlation. Periods of wave energy were sufficient to initiate movement of walleye eggs over 28% of the incubation period and also to move various substrate size classes, potentially impacting egg survival through transportation or exposure, abrasion, and burial. Egg movement was primarily closer towards shore and along shorelines of the littoral zone having sand substrates. Larger substrates and steeper riparian shoreline areas at reefs retained eggs better than flatter sand regions. Water level fluctuations were minimal (±1.20 cm) and most likely did not impact the amount of available habitat or strand and desiccate eggs. This study increases our quantitative understanding of walleye spawning areas and can assist biologists in understanding future processes affecting habitat quality and in developing protection strategies of natural reefs and potentially aid in the design of artificial reefs.

ACKNOWLEDGEMENTS

I would like to thank the University of Wisconsin – Stevens Point and the Wisconsin Cooperative Fishery Research Unit for the opportunity to obtain a Master's degree. I thank Michael Bozek for his guidance, flexibility, passion, and development of my knowledge in habitat, statistics, and life. Ronald Crunkilton was always helpful and influential in attaining and making my teaching assistantship a worthwhile experience and I was fortunate to learn the art of interactive teaching from Eric Anderson. I also thank Brian Sloss for discussing career and life options and his overall influence.

Tremendous assistance was offered throughout my field research. I thank Dairymen's Incorporated for access to the beautiful Big Crooked Lake. Special thanks go to Steven Newman for walleye knowledge and data, Gary Kubiak for helpful tips and equipment and the WNDR - Escanaba crew for delicious cookouts. Anthony Hentz and John Musch were patient field technicians as I felt my way through my first field season. Jacob Lindloff was an extremely efficient technician and a great friend. I thank all of the graduate students that also assisted in portions of the cold, tedious work.

I thank my family, old friends, and all of the new friendships I developed for the support, encouragement and much needed breaks to make it through the years. Ryan Franckowiak and Nick Scribner were especially helpful during my early days and Andrea Musch was truly invaluable for the entire duration. I cherish all of the great memories from my time at UW – Stevens Point and look forward to continuing friendships. My parents have provided unconditional support, love, and at times, necessary motivation and advice. I thank them and all of my friends and family for believing in me and finding an interest in my work. I hope I have had a positive influence on all of you as well.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

LIST OF APPENDICES

CHAPTER 1

LITERATURE REVIEW

Overview

Walleye, *Sander vitreus,* is an economically and ecologically important species of fish found throughout north-central North America. Walleye annually generate billions of dollars in the commercial food, retail, and tourism industries (Eschmeyer 1950, Scott and Crossman 1973). As a sportfish, this species continues to gain popularity throughout its range (Quinn 1992) and is highly sought after in Wisconsin (Becker 1983, Staggs et al. 1990, McClanahan 2003). Angling activities in Wisconsin generate over two billion dollars annually (ASA 2002), and walleye angling accounts for a significant portion of this amount (Staggs et al. 1990). Ecologically, walleye are the terminal predator in many aquatic systems and directly or indirectly influence fish communities and the entire ecosystem (Eschmeyer 1950, Forney 1974, Lyons and Magnuson 1987). For instance, in years when the preferred prey of yellow perch was scarce in Sparkling Lake, Wisconsin, walleye preyed heavily upon adult darters (*Percidae*) and minnows (*Cyprinidae*)(Lyons and Magnuson 1987). This predation reduced the population of darters but did not appear to affect the minnow populations in Sparkling Lake.

Walleye populations often fluctuate naturally due to a number of potential factors, but may exhibit long-term declines or extirpation, especially after heavy exploitation or habitat loss (Koonce et al. 1977, Hansen et al. 1998, Sullivan 2003). An example of this is occurring in Alberta, Canada, where walleye tend to grow and mature slowly and also receive high angling pressure. Passive management prior to the 1990s allowed for a relatively high fishing mortality to occur and did not prevent widespread, major declines in the walleye fisheries (Sullivan 2003).

To assist walleye populations and sustain quality fisheries, fishery biologists may stock young, alter regulations, or conduct habitat projects for restoration or enhancement (Kohler and Hubert 1999). Stocking varies in success, often depending on the natural reproductive status of the lake, and may only be a temporary fix (Kempinger and Churchill 1972, Ellison and Franzin 1992, Li et al. 1996a, 1996b). In Escanaba Lake, Wisconsin, only one out of four supplemental stocking events significantly contributed to the population, and only a 13% increase (Kempinger and Churchill 1972). Li et al. (1996a) conducted a meta-analysis on nearly 2,000 Minnesota lakes and concluded that stocking increased walleye abundance in lakes without natural reproduction, but did not have a significant effect on lakes with natural reproduction; return of stocked fish was between 8 and 10%. Regulations also vary in success and are largely dependent on angler acceptance and abidance (Serns 1978, Brousseau and Armstrong 1987, Beard et al. 2003, Sullivan 2003). In order for regulations to have the intended effect, some lakes may need anglers to harvest fewer fish while other lakes require a certain size class of fish to be protected. However, anglers may respond differently to regulations. For instance, changes in daily bag limits in specific Wisconsin lakes led anglers to target less restrictive lakes (Beard et al. 2003). Minimum length limits are intended to protect smaller fish and increase the mean size of fish, but in Big Crooked Lake, Wisconsin, this type of regulation led to decreased harvest and walleye size; density dependence was suspected as the causal factor for these changes (Serns 1978). Habitat enhancement and rehabilitation projects are often conducted using a limited scientific framework, causing success to vary and focus is rarely put on habitat protection (Neuswanger and Bozek 2004, see Kerr 1993, for examples).

For walleye habitat projects, the construction of artificial spawning reefs as a management tool has gained in popularity (Neuswanger and Bozek 2004). These projects are premised on the principle that insufficient quality spawning habitat limits annual recruitment by reducing the extent of egg deposition or the survival of eggs to fry (Johnson 1961, Nate et al. 2003). However, evaluations have shown that artificial reefs hold little promise in improving walleye recruitment in lakes (McKnight 1975, Wagner 1990, Neuswanger and Bozek 2004). For example, although walleye spawned on an artificial reef in Jennie Webber Lake, Wisconsin, there was no recruitment to adult walleye (McKnight 1975). In another example, Neuswanger and Bozek (2004) evaluated reef projects in 20 northern Wisconsin lakes, and none of the lakes showed a significant increase in walleye recruitment without other management applied.

Before constructing additional artificial reefs, emphasis should be placed on preserving and protecting natural, productive walleye spawning reefs. Yet, current quantitative information is insufficient for even identifying and fully understanding natural reefs and habitat. General observations are that walleye spawn on wave-washed gravel and cobble shorelines in lakes (Eschmeyer 1950, Johnson 1961, Priegel 1970). However, walleye have successfully spawned to varying degrees on other substrates such as flooded vegetation, root masses, and sand (Eschmeyer 1950, Johnson 1961, Priegel 1970), thereby precluding any simple understanding of functional processes influencing the production of young walleye. Functional dynamics including water temperature, wind and wave activity, and water levels within a system or on spawning reefs can potentially change the quantity and quality of spawning habitat annually (Johnson 1961, Priegel 1970, Chevalier 1977). Therefore, quantitative studies of natural spawning reefs are necessary to further understand characteristics and dynamics of successful walleye spawning reefs. With this information, the identification and proper protection of natural spawning reefs, along with an efficient design and placement for artificial reefs to restore or enhance lakes would assist in the management of important walleye populations.

Life cycle

In Wisconsin, a typical walleye life span is around seven years but individuals may live as long as 15 years of age (Niemuth et al. 1959, Serns 1986). Walleye broadcast spawn at ice-out and demonstrate no parental care (Eschmeyer 1950, Priegel 1970, Becker 1983). Immediately upon hatching, walleye fry are limited to vertical movement through tail thrusts and are dependent upon their yolk sac until they begin exogenous feeding (Mathias and Li 1982). While studies are limited, recently hatched fry are believed to live a pelagic life (Eschmeyer 1950, Priegel 1970). After 10 to 12 days, controlled swimming movements are possible due to the development of paired fins (Priegel 1970). Spring and early-summer diets of young-of-year walleye, ranging between 10-50 mm in size, rely heavily on the consumption of invertebrate prey such as copepods and cladocerans, but occasionally consume small fish (Priegel 1970, Mathias and Li 1982, Frey 2003). By mid-summer to early fall, individuals are often large enough, between 51-100 mm in size, to shift to a demersal, piscivorous mode and may continue to prey on invertebrates (Eschmeyer 1950, Priegel 1970, Mathias and Li 1982, Frey 2003). Juvenile and adult walleye often form schools and tend to be crepuscular to nocturnal, remaining in deeper or darker water during daytime hours. They are opportunistic feeders and will consume most fish species and larger invertebrates (Niemuth et al. 1959, Becker 1983, Frey 2003). Often, male walleyes are mature after two to three years of age, while females mature later at three to eight years (Mraz 1968, Colby et al. 1979, Serns 1982a). Mature females are typically 360 to 400 mm, while males tend to be smaller in size (Priegel 1970, Forney 1976, Henderson and Nepzy 1994).

Reproduction

In north temperate lakes, walleye spawning activity commences before or at ice-out from mid-April to early May and is often regulated by water temperature. As water temperatures reach 2 to 7°C, walleye migrate toward spawning areas (Eschmeyer 1950, Ellis and Giles 1965, Priegel 1970). Walleye are believed to have homing behaviors, and may return to a certain river or similar area of a lake to spawn in subsequent years (Crowe 1962, Olson et al. 1978, Jennings et al. 1996). Male walleye often arrive at spawning reefs before females and congregate in groups or schools. As females arrive, slight courtship behaviors occur, such as males circling and physically contacting females (Ellis and Giles 1965, Priegel 1970).

Actual spawning begins when a female advances towards and stops near the shoreline. A group of males, ranging from one to six, follow tightly, surround the female, and align vents. Physical contact and vigorous body shaking occurs, resulting in a broadcast release of eggs and milt (Eschmeyer 1950, Ellis and Giles 1965, Priegel 1970). A female typically spawns out in one night and returns to deeper water. Females are highly fecund, depositing between a few thousand to millions of eggs (Forney 1976, Serns 1982a). Individual eggs range from 1.63 mm to 1.73 mm in diameter (Wolfert 1969, Serns 1982a). Males may spawn over a period of nights and with various females.

Males have been observed at reefs after completion of spawning, but are not believed to guard the eggs (Ellis and Giles 1965, Priegel 1970).

The initiation and duration of the walleye egg deposition period can be influenced by thermal conditions. Walleye have been observed spawning in water temperatures ranging from 2.2 to 15.6°C (Priegel 1970, Hokanson 1977). Peak spawning typically occurs in the range of 5.6 to 10°C (Niemuth et al. 1959, Becker 1983). Fluctuations in water temperature, especially descending temperatures may prolong spawning or result in females retaining eggs as suggested by Derback (1947), although egg retention or resorbtion is unstudied, if true. Since thermal fluctuations differ annually the spawning period may last a few days to weeks (Priegel 1970).

Once deposited, eggs develop through different life stages and may be transported from the original deposition point. Deposited eggs are initially adhesive to other eggs and the substrate. The duration of this adhesive stage is variable; Priegel (1970) suggested eggs are adhesive for one to two hours, but in hatchery experiments, adhesiveness persisted for about five hours when stirred constantly (Waltemyer 1976) and stirred eggs have remained clumped together for four days (Krise et al. 1986). As water hardens the external membrane, the eggs separate and lie upon the substrate, settle into interstitial spaces, or move with wave action (Johnson 1961, Priegel 1970, Scott and Crossman 1973). Fertilized eggs remain clear, or hyaline, and have a fairly firm chorion during early stages of development. Closer to hatching, walleye eggs develop distinct black pigmentation in the eyes and the chorion is more flaccid. Unfertilized eggs or dead embryos develop a white speck, eventually turn opaque and are often covered with fungus as they deteriorate (Eschmeyer 1950, Johnson 1961, Priegel 1970).

Walleye typically have a high degree of egg mortality, potentially due to lack of fertilization, unviable eggs, no parental care, or variation in environmental conditions during incubation. Egg survival estimates through hatching in Lake Gogebic, Michigan, ranged from 25 to 50% (Eschmeyer 1950). Johnson (1961) estimated egg survival from 0.6 to 35.7% in Lake Winnibigoshish, Minnesota. Engel et al. (2000) reported artificially fertilized egg survival rates at 19 to 62% in enclosed chambers in a north temperate Wisconsin lake. In Oneida Lake, New York, it was estimated that 99% mortality occurred before walleye larvae reached 9-10 mm in size and most of this mortality was attributed to the egg stage (Forney 1976). On two offshore reefs in Lake Erie, egg survival rates ranged from 7 to 43% (Roseman et al. 1996). Studies have shown that most mortality occurs within a few days, suggesting a lack of fertilization or unviable eggs are the cause (Fox 1993, Holtze and Hutchinson 1989, Heidinger et al. 1997). For example, in a laboratory study, an estimated 83-90% of egg mortality occurred within six hours of fertilization and 93-96% within 72 hours of fertilization (Heidinger et al. 1997). A white speck, indicating mortality, was visible by 72 hours; however no differentiation was possible between unfertilized versus unviable eggs (Heidinger et al. 1997). Fertilization may be affected by how the eggs and milt are deposited. For instance, eggs piled 4.0 mm deep had an 86% fertilization that was significantly more fertile than 77% at 7.0 mm deep and 65% at 10.0 mm of egg depth in a laboratory study (Moore 2003). Also, three subsequent releases of 3.0 mL of milt every 30 seconds resulted in a slightly higher fertilization than one single 9.0 mL milt addition (Moore 2003).

Studies have shown correlations between year-class strength and spring water temperatures (Johnson 1961, Busch et al. 1975), while others have found weak or no relation (Kempinger and Carline 1977, Serns 1982b, Madenjian et al. 1996). Based on egg survival rates, Johnson (1961) felt that reproductive success in walleye was higher in years with stable, rising water temperatures. In Lake Erie, year-class strength was most related to the rate of water warming (Busch et al. 1975). The authors stated that since warming water accelerates embryo development, this may limit the period that eggs are subjected to environmental stresses or predation, thus increasing hatching success. Madenjian et al. (1996), also working in Lake Erie, was able to explain 21% of the variation in walleye recruitment based on spring water temperatures and the relationship was positive, but weak. In contrast, Kempinger and Carline (1977) did not find a relation between walleye recruitment and spring water temperatures during incubation in Escanaba Lake, Wisconsin. Also in Escanaba Lake, Wisconsin, Serns (1982b) found that year-class strength correlated more with variation in May water temperature than variation in water temperature during the first 30 days after ice-out. The variation in May water temperatures was also included in a model by Hansen et al. (1998), with increased water temperature variation equaling fewer recruits in Escanaba Lake, Wisconsin. However, other temperature variables, such as the mean, standard deviation, and warming rates were less descriptive (Hansen et al. 1998).

The variation in the importance of spring water temperature suggests that it can directly and indirectly impact egg or larval survival. Annual spring water temperature may factor into hatching success as it influences fertilization and determines the rate of embryo development. In the laboratory, optimum fertilization occurred at temperatures between 6 and 12°C, with success decreasing with increasing temperatures (Koenst and Smith 1976). This optimum falls within the temperature range often observed on spawning grounds (Niemuth et al. 1959, Priegel 1970, Hokanson 1977). On average, eggs incubated between 9 and 15°C resulted in the highest hatching percentage (Koenst and Smith 1976); peak hatching occurs around 15°C (Koenst and Smith 1976, Engel et al. 2000). In both the laboratory and the field, egg development accelerated with warmer temperatures, thus decreasing the days to hatch and the overall incubation period (Johnson 1961, Priegel 1970, Koenst and Smith 1976). Incubation to swim-up fry periods have ranged from 10 to 27 days in the wild (Niemuth et al. 1959, Johnson 1961, Priegel 1970, Engel et al. 2000) and from five to 30 days in a laboratory setting (Hurley 1972, Koenst and Smith 1976, McElman and Balon 1979).

Studies have closely followed the development of embryos in the laboratory and equations have been developed to predict hatching dates. McElman and Balon (1979) followed the hourly development of embryos in a laboratory and based the development on temperature or thermal units (TU). In their study, thermal units were the sum of the mean daily water temperature above 0°C for each day post-fertilization. Incubating at a consistent 15°C, the black-eyed stage, or eye pigmentation, was evident in most embryos by 76.2 TU. Obvious movement occurred at 81.2 TU and embryos hatched at 135.0 TU, or nine days (McElman and Balon 1979). In a laboratory study by Hurley where water temperature fluctuated between 7.8 to 11.1°C (1972), eyed eggs were observed at 152.2 TU, initiated hatching at 194.9 TU, and the majority of hatching occurred between 257.7 and 265.5 TU. Using egg incubation data from Smith et al. (1975), a quadratic regression equation was developed by Jones et al. (2003) to describe the relationship between temperature and daily egg development: $Y = 0.0479T^2 - 0.2385T + 2.499$, where Y is the predicted percent, or "units," of development per day towards hatching and T is the mean daily water temperature in degrees Celsius. The development units were successively summed each day during the spawning period. The authors assumed that eggs would hatch after 100 egg development units (Jones et al. 2003).

Walleye eggs are fairly robust to moderate temperature fluctuations, yet stress or mortality can occur with drastic temperature fluctuations. In the laboratory, development to the black-eyed stage was unaffected by fluctuations as great as 21.1°C (Albaugh and Manz 1964). In another laboratory study, eggs subjected to 20.2°C swings over 12 hours had similar survival to the black-eyed egg stage when compared to eggs with minimal or no temperature fluctuations (Schneider et al. 2002). Schneider et al. (2002) found that percent hatching success was not significantly affected by swings up to 13.6°C over 12 hours compared to eggs incubated with minimal or no temperature fluctuations. While eggs can reach the eyed development stage and hatch successfully with large temperature swings, extreme water temperatures may stress developing embryos and increase the percentage of abnormal fry that hatch (Koenst and Smith 1975, Schneider et al. 2002). Koenst and Smith (1975) recorded 1.0% and 3.8% abnormal fry for eggs incubated at 6°C and 15°C, respectively. However, the number of abnormal fry increased to 15% and 18% for eggs incubated at 18°C and 21°C, respectively. Extended or consistent incubation periods below 6°C and above 19-21°C proved lethal to walleye embryos (Koenst and Smith 1975, Schneider et al. 2002). Therefore, although warm water decreases the incubation period, extremely warm water can be detrimental towards egg survival. In addition, Colby et al. (1979) mentioned that warmer water temperatures may increase the growth of fungus on walleye eggs. Overall, annual water temperatures and fluctuations on walleye spawning reefs may not result in direct mortality, but may influence the development rate and stress level of embryos.

The negative correlation of May water temperature to year-class strength in various studies was attributed to influences on not only egg incubation and hatching, but also the early stages of fry survival and development (Serns 1982b). For instance, temperature affects the timing of zooplankton blooms, a primary food source for walleye fry and fingerlings (Priegel 1970, Serns 1982b, Frey 2003). Studies have also shown that water temperatures can directly and indirectly impact fry survival through development rates and stresses such as increased respiration or metabolism (Koenst and Smith 1976, Hokanson 1977, Clapp et al. 1997). Although water temperature clearly affects reproduction and recruitment, its causality is unclear. Water temperature is most likely influential in these models because it may affect the adults during the spawning period, slow embryo development rates, and influence egg or fry mortality rates either directly or indirectly through other factors such as prey abundance, metabolism and growth rates (Chevalier 1973, Hokanson 1977, Koonce et al. 1977).

Additional factors, such as wind and wave activity, that may be collinear to storm fronts and changes in water temperature, may also be important to reproduction and recruitment. The occurrence and severity of storms each year, that track changes in air temperature due to thermal fronts, and the resulting wave activity may factor into hatching success. Live walleye eggs have been observed on shorelines, apparently washed up by heavy wave activity, that ultimately would lead to mortality through desiccation or predation (Eschmeyer 1950, Johnson 1961, Priegel 1970). For instance, in Lake Gogebic, Michigan, adhesive eggs were found on rocks above the water level

(Eschmeyer 1950), and dead eggs were also observed washed onto shorelines and appeared more susceptible to wave energy (Eschmeyer 1950, Johnson 1961). In Lake Winnibigoshish, Minnesota, Johnson (1961) observed dead eggs washed onto shore after three days of 6.7-11.1 m/s ("moderate") easterly winds (Johnson 1961). In other situations, heavy wave activity has resulted in egg mortality by carrying eggs to deeper, less suitable spawning habitat such as silt and detritus (Johnson 1961, Busch et al. 1975, Roseman et al. 1996, 2001). Johnson (1961) recorded a mean decrease of egg abundance from 93 to 46 eggs per 0.09 m^2 after "very strong winds during the night." Busch et al. (1975) believed that any storm and wind activity resulting in turbulence and daily water temperature reversals of greater than or equal to 0.5°C would be detrimental to walleye eggs. The wind velocity capable of creating this effect in western Lake Erie ranged from 4.0 to 5.7 m/s, depending on wind direction. Yet, the authors did not find a correlation between wind activity and year-class strength. Roseman et al. (1996, 2001) found that larvae production was higher in years of low storm activity in Lake Erie than in years of reoccurring or severe storms (Roseman et al. 1996, 2001). For instance, a severe storm in Lake Erie, with winds in excess of 22.2 m/s and waves in excess of 4 m, resulted in an 80% decrease of eggs on a spawning reef, apparently transported due to wave energy (Roseman et al. 2001). However, Serns (1982b) did not find any direct correlation between wind activity and walleye year-class strength in Escanaba Lake, Wisconsin. The severity of wind and resulting waves may be dissipated by the short fetch (maximum 1.7 km) and a heavily forested riparian area found there (Serns 1982b).

Water level fluctuation during spawning and incubation periods is another physical factor that may affect reproductive success of walleye as receding water levels may limit the amount of available spawning habitat, force walleye to utilize lower quality spawning habitat, or strand eggs (Johnson 1961, Priegel 1970, Chevalier 1977). Over a four-year study (1956-1959) on Lake Winnibigoshish, Minnesota, the water level in 1958 was more than 0.60 m lower than other years (Johnson 1961). Therefore, areas previously utilized as walleye spawning habitat were unavailable and walleye instead spawned in areas that received limited use in other years. The resulting year-class appeared less abundant in summer seine and trawl catches (Johnson 1961). In the Lake Winnebago system (Wisconsin), walleye are unable to use traditional marsh habitat due to extremely low water levels in certain years and no hatches occurred in these areas that were previously successful spawning habitat (Priegel 1970). In 1963, water levels were sufficient for spawning but then receded rapidly, resulting in complete mortality of deposited eggs. Priegel (1970) also felt that water level fluctuations affected egg mortality on rock shoals in the lake, but did not provide details. Other studies have also suggested that receding water levels may desiccate eggs deposited in shallow water (Johnson 1961, Priegel 1970, Chevalier 1977). Spring water levels correlated with variation in the commercial catch-per-effort of walleye five years (age-5 recruits) later in Rainy Lake, Minnesota (Chevalier 1977).

Although more annually stable than the above physical factors, reproductive success can also be influenced by the water quality of a system. While severe wave action may cause mortality, mild wave energy is important in oxygenating eggs and preventing suffocation caused by sedimentation (Daykin 1965). Oseid and Smith, Jr. (1976) showed that dissolved oxygen concentrations above 5 to 6 ppm are optimal for walleye egg incubation. Auer and Auer (1990) suggested that low dissolved oxygen, along with elevated concentrations of ammonia-nitrogen and hydrogen sulfide at the sediment-water interface in a reach of the Fox River, Wisconsin, limited success of walleye reproduction. Other studies have shown that pollutants or contaminants, such has heavy metals, may decrease reproductive and hatching success (Waltemyer 1975). For example, tannin which is a metal ion chelator, was used to decrease initial egg adhesiveness for walleye hatcheries. Laboratory studies determined that tannin can significantly reduce spermatozoa motility and fertilizing capacity (Waltemyer 1975). The ideal pH for reproduction and incubating eggs is in the range of 6.0-9.0 (Hulsman et al. 1983, Holtze and Hutchinson 1989, Bergerhouse 1992). In the outlet waters of George Lake, Ontario, walleye eggs were artificially fertilized and incubated in water with either a pH of 5.4 or 6.0 (Hulsman et al. 1983). While a relatively low mortality, 22.5-33.5%, was observed at the 6.0 pH site, at the 5.4 pH site mortality between fertilization and the eyed-egg stage was quite high at 90.5% (Hulsman et al. 1983).

In inland lakes, predation of walleye eggs occurs but is not believed to be a prevalent cause of mortality (Johnson 1961, Priegel 1970). White sucker, *Catostomus commersoni*, spawn shortly after walleye in littoral areas and have been observed in walleye spawning areas during egg incubation, but do not appear to actively prey on walleye eggs or compete for spawning habitat (Priegel 1970, Wolfert et al. 1975, Corbett and Powles 1986). In Jennie Weber Lake, Wisconsin, walleye eggs developed to the black-eyed egg stage but no fry were captured (McKnight 1975). For possible explanations, the author speculated that eggs were preyed upon by crayfish but did collect any data to substantiate speculations. In an Ontario stream, Corbett and Powles (1986) found that yellow perch and spottail shiners, *Notropis hudsonius*, preyed extensively on walleye eggs but the affect on reproductive success was not determined. Seven of eleven adult yellow perch had eggs in their stomachs, with a mean of 44 eggs per stomach. Four of ten spottail shiners contained a mean of 13 eggs per stomach (Corbett and Powles 1986). In the Great Lakes, predation of walleye eggs appears to be more prevalent. Wolfert et al. (1975) observed predation of walleye eggs by yellow perch, spottail shiner, stonecat, *Noturus flavus*, and white sucker in Lake Michigan. Female yellow perch had a daily mean range of 36 to 734 eggs while males consumed a mean of four to 237 eggs per day over the three-year study. The other three species did not prey nearly as extensively on walleye eggs (Wolfert et al. 1975). In Lake Erie, 86% of captured white perch, *Morone americana*, contained a mean of 349 walleye eggs in their stomachs (Roseman et al. 1996). While predation did occur, neither study could determine the overall effect on reproductive success. In addition, both articles suggested that predation on walleye eggs would be a key factor only in years of slow water warming rates where prolonged incubation periods cause walleye and perch reproduction to overlap, resulting in higher degrees of walleye egg predation by spent adult perch (Wolfert et al. 1975, Roseman et al. 1996).

Recruitment

Additional factors influence the recruitment of year-classes in walleye. The stock size, or number of reproducing adults, may be the most important factor affecting the recruitment of a year-class (Chevalier 1977, Madenjian et al. 1996, Hansen et al. 1998). For instance, Chevalier (1977) determined a positive correlation with stock size and recruitment. In theory, a higher number of adult females produce more deposited eggs that may result in more fry and an overall increase in recruitment (Chevalier 1977).

However, Busch et al. (1975) found this correlation to be weak, while others have determined that maximum recruitment occurred in years with a lower number of spawning adults, showing that recruitment may be density-dependent (Madenjian et al. 1996, Hansen et al. 1998, Beard et al. 2003). Stock size alone explained 20% of the variation in walleye recruitment in western Lake Erie and it predicted that a lower number of spawners (13 compared to 28-42 million) would produce more recruits (Madenjian et al. 1996). The abundance of age-5 and older walleyes in Escanaba Lake, Wisconsin, explained 32% of recruitment variation and the greatest number of recruits was produced by fewer than 1,000 spawning individuals (Hansen et al. 1998). Inversely, 3,000 spawning individuals, which was the highest number in the study, produced the fewest recruits (Hansen et al. 1998). Last, in a meta-analysis of Wisconsin lakes, it was determined that recruitment was density-dependent and that stock size could explain 10% of annual variation in age-0 walleye recruitment (Beard et al. 2003).

The amount of available prey may influence survival and growth of young walleye. It has been suggested that growth rate is dependent on available prey and is important for general survival, reducing predation risk, and increasing overwinter survival in developing walleye (Chevalier 1973, Forney 1974, 1976). During the first few weeks after hatching, walleye larvae are heavily dependent on zooplankton as forage, so the timing and extent of phytoplankton/zooplankton "blooms" are important in this early stage (Priegel 1970, Hokanson 1977, Serns 1982b). The abundance of prey fish also may be important when young walleye switch to piscivory in the first growing season (Eschmeyer 1950, Forney 1976, Frey 2003). In Oneida Lake, New York, larger young-of-year walleye appeared to have higher overwintering success, possibly because the smaller walleye were selected for first by predators (Chevalier 1973). Also in Oneida Lake, predation on small walleye was lower with higher abundance of yellow perch, which was an alternate food source for developing walleye (Forney 1973). In a later study in Oneida Lake, Forney (1976) determined that predation on walleye 170 mm and larger was probably quite low, especially compared to young walleye that reached the 127-146 mm range in their first growing season.

The amount of available prey can also influence maturation and reproduction of juvenile and adult walleye. For instance, it can influence the maturation rate of gonads and gamete numbers for developing juveniles and adults (Forney 1976, 1977). Walleye fecundity, which is related to body size (Serns 1982a, Henderson and Nepszy 1994), decreases with a decrease of prey availability. This reduced abundance of prey may also determine whether individual females spawn every year (Henderson and Nepszy 1994). In Lake Erie, the preferred prey by walleye is gizzard shad (*Dorosoma cepedianum),* and its abundance determines the lipid reserves of female walleye during the winter. Females lacking adequate lipid reserves did not spawn the following spring (Henderson and Nepszy 1994). In turn, the strength of walleye year-classes correlated with the annual abundance of gizzard shad (Henderson and Nepszy 1994, Madenjian et al. 1996).

Intraspecific and interspecific competition between walleye increases with decreasing prey abundance and may lead to cannibalism, thus further affecting year-class strength. Adult and other young walleye may prey on small walleye if other prey is scarce, as observed in Oneida Lake, New York (Chevalier 1973, Forney 1976). In Oneida Lake, walleye fry and fingerlings growing at faster rates preyed on smaller walleye (Chevalier 1973, Forney 1976). Interestingly, an abundance of preferred prey may also negatively effect recruitment. This situation was seen in Escanaba Lake, Wisconsin, as high yellow perch numbers correlated with low walleye recruitment, most likely due to predation by or interspecific competition with yellow perch (Hansen et al. 1998). Interspecific competition and predation also occurs with other top predatory fish such as northern pike, *Esox lucius*, lake trout, *Salvelinus namaycush*, and smallmouth bass, *Micropterus dolomieui* (Forney 1976, Johnson et al. 1977, Nate et al. 2003).

Lake characteristics influence the composition of the fish community that may in turn influence recruitment of walleye. In larger lakes, walleye can coexist as top predators with northern pike, lake trout, and smallmouth bass (Johnson et al. 1977). Larger lakes may have both adequate habitat and food resources for top predators to coexist or fill different ecological niches. However, in smaller lakes, walleye and northern pike often do not to coexist at high densities, either due to competition or spawning habitat differences (Johnson et al. 1977, Nate et al. 2003). Nate et al. (2003) found a similar inverse relation with walleye and black basses in small lakes and Potter (1995) saw differences in angler catch-per-effort for walleye and smallmouth bass in Wisconsin.

Various lake characteristics are common in naturally recruiting walleye lakes and may be important to their life history. Walleye are found in lakes having a wide range of productivity, but attain optimal growth and reproductive rates in mesotrophic lakes (Niemuth et al. 1959, Leach et al. 1977, Schupp and Macins 1977). Large lakes typically have adequate oxygen and optimal temperature levels for growth rates and maturation of walleye (Hokanson 1977, Nate et al. 2001). Considering that walleye are native to and appear best adapted to riverine systems, large, but relatively shallow lakes have extensive littoral and sub-littoral habitat similar to riverine habitat (Kitchell et al. 1977). Walleye have thrived in lakes with these characteristics, such as Lake St. Clair, western Lake Erie, and Lake Oneida, New York (Kitchell et a. 1977). Large lakes also often provide diverse habitat for all walleye life stages (Johnson et al. 1977). In addition, the fetch and shape of a lake influence wind and wave action, that may influence dissolved oxygen, egg transport or damage and ultimately affect walleye reproduction and recruitment (Daykin 1965, Johnson et al. 1977, Nate et al. 2003).

Spawning Habitat

Historically, walleye are known to spawn over clean, windswept gravel, cobble, and rubble substrate shorelines (Eschmeyer 1950, Johnson 1961, Priegel 1970). Large substrates are often considered ideal for walleye, as the interstitial spaces provide protection for eggs and larvae from waves or predation (Daykin 1965, Johnson 1961). Small patches of firm, rock substrate including fine gravel, in otherwise sand-dominated areas, have been selected for by walleye (Eschmeyer 1950, Johnson 1961). However, walleye have been observed spawning on numerous other types of substrate such as sand, silt, muck-detritus, vegetation, and root masses, thus calling into question generalizing spawning habitat (Eschmeyer 1950, Niemuth et al. 1959, Johnson 1961, Priegel 1970). In fact, in the Lake Winnebago system (Wisconsin), walleye select for vegetation (e.g., sedges, *Carex* spp., rice cut-grass, *Leersia oryzoides*, and reed canary grass, *Phalaris arundinacea*) in flooded marshes along the Wolf River (tributary river) over shoreline rock substrate (Priegel 1970).

Generalization of walleye spawning habitat is further confounded by habitat not used; walleye may select one spawning area but avoid another area that appears similar.

In Lake Gogebic, Michigan, walleye primarily utilized the eastern shoreline for spawning (Eschmeyer 1950). The spawning grounds extended for over 16 km, with a continuous substrate mixture of gravel, rubble, and boulders. It was also noted that the entire shoreline was heavily forested and areas with overhanging trees were occupied by spawning walleyes. Similar rock substrate and depth were present on the western shoreline but was rejected by spawning walleye. Eschmeyer (1950) hypothesized that this area may not be utilized due to less wind and wave action, more organic matter, softer substrates, steeper slopes, or less nearshore habitat. He felt that the prevailing northwest winds made the eastern shoreline ideal for walleye spawning habitat. However, walleye spawning is not restricted to eastern shoreline habitat, as walleye did utilize northern spawning reefs in Lake Gogebic and moreover, entire shorelines (i.e., lake perimeters) in other Michigan lakes were used by walleyes for spawning (Eschmeyer 1950). Walleye spawned on northern and western rock shorelines, a southwestern sand shoreline, and a western, wave-washed muck-detritus shoreline in the Lake Winnibigoshish system (Minnesota)(Johnson 1961).

Based on observation of spawning activity and physical egg collections, walleye tend to spawn close to shore and in shallow water in inland lakes (Eschmeyer 1950, Johnson 1961, Priegel 1970). In Lake Gogebic, Michigan, nearly all spawning activity occurred close to shore and in water less than 61.0 cm, with a few eggs collected in 122.0 cm of water (Eschmeyer 1950). Johnson (1961) noted that walleye typically spawned in water between 30.5 and 76.0 cm in depth, but eggs were found as shallow as 5.0 cm and the deepest eggs were estimated at 122.0 cm in Lake Winnibigoshish, Minnesota. Walleye spawned as far as the water extended into the flooded marshes of the Lake

Winnebago system (Wisconsin), when water levels were high, but only spawned in deeper channels entering the marshes when water levels were low (Priegel 1970). In the Great Lakes, walleye tend to spawn in deeper water and utilize offshore reefs. For instance, in Lake Erie, walleye utilize reefs that reach within 0.6 to 1.2 m from the surface and eggs were rarely collected deeper than 3.6 m (Busch et al. 1975), amazingly shallow for such a larger waterbody. Roseman et al. (1996) found that egg densities were typically higher on Lake Erie sites that were less than 5.0 m in depth.

The survival rate of eggs on different substrates may be an important selection factor for walleye. Johnson (1961) studied walleye egg survival based on substrate type in the Lake Winnibigoshish system (Minnesota). Eggs incubating in soft muck-detritus substrate, including undecomposed aquatic plants, had the poorest survival rates, ranging from 0.6 to 4.5%. This is similar to other studies that have observed or suggested high egg mortality when eggs are deposited or carried onto muck-detritus substrate (Eschmeyer 1950, Priegel 1970, Busch et al. 1975). In Johnson's (1961) study, survival rates were intermediate (2.7 to 13.2%) for eggs incubating on firm, fine sand. However, eggs were easily removed by wave activity from the sand areas, which was also observed by Priegel (1970). A gravel and rubble area had egg survival rates of 17.5 and 17.9%, in 1956 and 1957, respectively. The highest egg survival (34.3%) occurred on a different gravel and rubble spawning reef, while a 60% gravel, 40% sand spawning area had a survival rate of 17.4% (Johnson 1961).

It has been suggested that naturally reproducing walleye populations may be limited by the quantity or quality of spawning habitat, such as rock and rubble substrate. For instance, Auer and Auer (1990) suggested that walleye reproduction does not occur in a reach of the Fox River, Wisconsin due to a lack of gravel-cobble substrate, and an abundance of muck-sand substrate. Nate et al. (2003) used substrate as a variable in modeling walleye presence in lakes, and found that both percentage of sand and muck substrate where inversely related to adult walleye abundance. In years of low water levels, the amount of primary spawning habitat may decrease, forcing walleye to utilize secondary spawning areas or less favorable substrate. Water level was considered a factor in weak year-classes in several lakes (Johnson 1961, Chevalier 1977), while recruitment in others lakes were not effected by decreased water levels (Priegel 1970, Busch et al. 1975). This suggests that walleye spawning habitat may be a limiting factor in certain lakes, while other lakes have sufficient habitat even when primary spawning habitat is altered.

Many questions remain regarding walleye spawning habitat, in part due to the lack of quantitative information. Johnson (1961) completed quantitative work on egg survival based on various substrates. However, he did not quantify the substrate composition as no substrate particle size scale was provided; most areas were described generally (e.g., sand, gravel-rubble), and the most detailed description was 60% gravel, 40% sand. Other studies describe the spawning substrate in a similar general method (Eschmeyer 1950, Priegel 1970).

Structural characteristics of spawning areas have also not been quantified. Johnson (1961) provided mean depths and the overall area of each reef he studied (either 93 or 139 m^2), while Eschmeyer (1950) verbally described physical characteristics of reefs. However, neither quantified other aspects of utilized reefs such as total length, distance extended from the shoreline, or slope. While these studies provided a foundation for understanding walleye spawning habitat, they do not provide adequate information to identify and fully understand successful spawning habitat characteristics.

Quantitative analyses are also lacking for understanding how often dynamic processes in spawning areas affect reproductive success. Temperature has been shown to influence development rates and potentially hatching success (Johnson 1961, Priegel 1970, Koenst and Smith 1975). However, thermal differences within or among reefs in lakes is unknown and may influence spawning location, egg deposition, or egg survival. Eggs have been observed washed onto shore or into unfavorable habitat due to wind and wave activity (Eschmeyer 1950, Johnson 1961, Roseman et al. 2001), however, quantitative work has been restricted to the Great Lakes (Busch et al. 1975, Roseman et al. 2001). For Escanaba Lake, Wisconsin, wind activity did not correlate with year-class strength (Serns 1982b), but the dynamics of actual wave activity and resulting egg movement has not been quantified.

Overall, general observations of walleye spawning habitat are prevalent, but detailed quantitative work regarding spawning substrate, physical structure, and dynamics of spawning reefs, along with selection by spawning walleye are lacking. Therefore, additional work is necessary to fully understand and to protect successful, high quality walleye spawning reefs.

Artificial Spawning Habitat

Artificial spawning reefs have been constructed to enhance or restore walleye spawning habitat, an important factor in walleye reproduction and recruitment. These projects are premised on the principle that insufficient quality spawning habitat limits annual recruitment by reducing the extent of egg deposition or the survival of eggs to fry (see Johnson 1961, Nate et al. 2003). The construction of artificial reefs is often based on the general previous knowledge of individual biologists relative to their perceptions of natural walleye spawning reefs. Therefore, projects vary in design, composition, or placement due to differing ideas among biologists of what comprises successful spawning habitat. Although different types of reefs have been constructed in various types of waterways, only one studied project has been considered successful. In order to evaluate his findings that gravel-rubble substrates produced the highest egg survival, Johnson (1961) enhanced a sandy area in Lake Winnibigoshish, Minnesota, that was utilized by spawning walleye in previous years. Gravel and rubble (2.5 to 40.6 cm diameter) were placed on top of firm, fine sand substrate. The enhanced area covered 92.9 m^2 with a gravel-rubble thickness of 2.5 cm. Walleye used this artificial site more extensively as egg abundance was more than 10 times greater than observed on the former sandy bottom. In addition, egg survival on the enhanced area was estimated to improve by more than 100 times when compared to data from egg survival on the former sandy bottom. However, the lake-wide impact on walleye recruitment is unclear.

From this study, improved walleye spawning sites appeared promising, but success has been minimal since this original study (Weber and Imler 1974, McKnight 1975, Newburg 1975, Wagner 1990, Neuswanger and Bozek 2004). Limited unbiased peer-reviewed evaluations have been conducted and focused on evaluating artificial spawning reefs; along with agency reports, they have determined marginal to no success in reef projects. Weber and Imler (1974) evaluated the success of artificial reefs in a Colorado reservoir and determined that no significant change in the adult walleye population occurred. Artificial reefs placed in Jennie Weber Lake, Wisconsin were utilized by spawning walleyes, eggs developed to the black-eyed stage, but fry or fingerling were never discovered (McKnight 1975). Increased usage of improved spawning areas was observed by Newburg (1975) in Lake Oasis, Minnesota, but again this did not lead to a significant increase in fry production. He provided criteria for design and placement of walleye reefs, but no studies have evaluated these suggestions. Wagner (1990) estimated deposition and success of artificial reefs in Six Mile Lake, Michigan, and also did not find a significant change in walleye populations. Neuswanger and Bozek (2004) evaluated 20 case studies of artificial walleye spawning reef projects throughout northern Wisconsin. While many of these case studies lacked rigorous scientific evaluation (i.e., adequate pre- and post-evaluation) or were confounded by stocking or other management projects, the expected subsequent increase in recruitment or adult walleye populations was universally absent unless other management actions were also undertaken.

It is possible that constructed artificial reefs may either have low hatching success or that spawning habitat was not previously limiting in these lakes prior to reef construction. Other physical or biological factors may also affect or limit the recruitment of walleye such as the fish community (e.g., other top predators, available prey), water quality (e.g., summer water temperature, trophic level), or lake morphology (e.g., fetch, shape). Additional studies should be conducted to determine the success of artificial reefs as they continue to be constructed with high costs, have shown limited success, and altering habitat may have potentially negative effects on aquatic communities.

Quantitative research on both natural and artificial reef studies would compliment the present knowledge of factors influencing recruitment. Quantitative data could be used to construct detailed blueprints of spawning reefs and the development of models that predict walleye selection of spawning reefs. Additional information and tools such as blueprints and models would aid managers in decision making processes, including identifying and protecting walleye spawning habitat and the design and placement of artificial reefs.

OJBECTIVES

The overall goal of this study was to quantitatively increase the understanding of physical characteristics and functional dynamics that impact the quantity, quality, and physical selection of natural walleye spawning habitat.

The specific objectives of this study were to:

1) describe the physical characteristics of natural walleye spawning reefs in order to develop detailed blueprints of successful natural walleye spawning habitat and to develop walleye spawning habitat resource selection functions,
2) evaluate thermal conditions on walleye spawning reefs and the relative affect they have on reproductive success across two years, and
3) assess the potential impact of wind activity, wave energy, and water level on walleye egg movement and survival.

CHAPTER 1: Structural components and selection of natural walleye spawning reefs in a north temperate lake

ABSTRACT

Spawning habitat is the cornerstone of self-sustaining, naturally reproducing walleye (*Sander vitreus*) population, but limited quantitative research has been conducted on structure and function of natural walleye spawning reefs. Therefore, the spawning habits and habitat of naturally reproducing walleye in Big Crooked Lake, a north temperate Wisconsin lake, were evaluated in 2004 and 2005. Walleye utilized similar spawning habitat in both years, including three major geomorphic spawning sites: a linear shoreline, a point bar, and an island. Walleye spawned primarily close to the shore (outer boundary $\bar{x}$ distance = 2.72 m), in shallow water (outer boundary $\bar{x}$ depth = 0.29 m) and over gravel substrate ($\bar{x}$ coverage = 64.3%) with low embeddedness ($\bar{x}$ = 1.30) at all sites. Walleye utilized only 14% of the total shoreline and 39% of the available rock shoreline. The best resource selection function had an overall correct classification of 97.6% and predicted the relative probability of egg deposition increased with gravel and cobble substrates and decreased with distance from shore, higher substrate embeddedness, and with increasing sand and fine organic material. Evaluating habitat quality (i.e., egg survival), regression models found cobble substrate to be the only variable positively related to the percent survival of deposited eggs in egg collection chambers. Based on survey data, two- and three-dimensional spawning reef blueprints were developed to visually depict successful natural walleye spawning habitat. The quantified spawning habitat information, predictive models and blueprints will assist biologists in understanding walleye habitat selection, developing walleye spawning reef protection strategies and potentially aid in designing artificial spawning reefs.

INTRODUCTION

Natural walleye (*Sander vitreus)* spawning habitat, a cornerstone of self-sustaining populations, is an aspect of their management not often quantitatively evaluated. Historically, walleye are known to spawn over clean, windswept gravel, cobble, and rubble substrate shorelines (Eschmeyer 1950, Johnson 1961, Priegel 1970). Large substrates have been considered ideal for walleye as interstitial spaces presumably provide protection for eggs from wave scouring (Johnson 1961) or provide higher dissolved oxygen flow (Daykin 1965). However, small patches of firm, rock substrate including fine gravel, in otherwise sand-dominated areas, have been selected for by walleye (Eschmeyer 1950, Johnson 1961). In addition, walleye have been observed spawning on numerous other substrate types such as sand, silt, muck-detritus, vegetation, and root masses, thus calling into question generalizing spawning habitat convention (Niemuth et al. 1959, Johnson 1961, Priegel 1970). Conversely, generalization of walleye spawning habitat is further confounded as walleye may select one spawning area but avoid a different area that visually appears similar (Eschmeyer 1950, Johnson 1961).

Based on general observation of spawning activity and egg collection in inland lakes, walleye tend to broadcast spawn near shore and in relatively shallow water (Eschmeyer 1950, Johnson 1961, Ellis and Giles 1965, Priegel 1970). Depth of egg deposition in previous studies has typically ranged from 30.5 to 76.0 cm, and rarely deeper than 122.0 cm (Eschmeyer 1950, Johnson 1961, Priegel 1970). In fact for inland lakes, no known study has clearly recorded walleye spawning in water over 1.5 m or on offshore reefs. However, while most of these studies provided information on water depth, they do not present distance to shore. Despite a lack of scientific observation, the placement of artificial spawning reefs away from shore and in deep water commonly occurs (Neuswanger and Bozek 2004), suggesting an assumption among biologists that walleye routinely use deep, offshore reefs.

While walleye appear to spawn over a variety of substrates, the survival of deposited eggs clearly appears to differ with substrate type. Johnson (1961) determined that eggs incubating in soft muck-detritus substrate, including undecomposed aquatic plants, had the poorest survival rates in the Lake Winnibigoshish system (Minnesota). This finding is similar to other studies that have observed or suggested high egg mortality when eggs are deposited or carried onto silt or muck-detritus substrate (see Eschmeyer 1950, Priegel 1970, Busch et al. 1975). In contrast, in Johnson's (1961) study, egg survival rates were intermediate for eggs incubating on firm, fine sand and highest on gravel and rubble spawning areas. However, one problem with Johnson's (1961) research was that he did not provide a substrate scale nor directly quantify the overall substrate composition. This, and other studies have described the spawning areas only in general terms, such as sand or gravel/rubble (Eschmeyer 1950, Johnson 1961, Priegel 1970), a common problem in fisheries. And other structural components (e.g., overall reef length, distance extended from shoreline, slope) of spawning reefs have not been quantified in these studies.

Along with the quality of spawning habitat, the quantity of high quality spawning habitat in a lake may limit natural reproduction in walleye populations. Nate et al. (2003) developed models for predicting the probability of walleye presence in lakes and found that both the percentage of sand and muck substrate were inversely related to adult walleye abundance. Receding or low waters levels, that may decrease available spawning habitat, were considered a factor in weak year-classes in several lakes (Johnson 1961, Chevalier 1977), while recruitment in others lakes were not effected by decreased water levels (Priegel 1970, Busch et al. 1975). These contrasting results suggest that walleye spawning habitat may be a limiting factor in certain lakes, while other lakes may have sufficient habitat even when primary spawning habitat is altered. However, the relative total amount of spawning habitat needed to sufficiently sustain walleye populations has not been studied.

Overall, general observations in past studies have provided a foundation for understanding walleye spawning habitat, but some information on certain structural components remains incomplete. Questions remain regarding the quantity and quality (e.g., spawning substrate, structural components) of spawning habitat, along with the actual selection and generalization of habitat by spawning walleye. These areas need to be addressed to better understand, identify and protect successful walleye natural spawning reefs if they are to be managed towards maintaining self-sustaining populations. Therefore, the objectives of this project were to:

1) determine the locations and quantity of utilized spawning habitat,
2) evaluate habitat features related to the selection of spawning habitat,
3) evaluate the quality of selected spawning habitat, and
4) provide detailed descriptions and visual blueprints of successful natural walleye spawning reefs.

METHODS

Study Site

This study was conducted in Big Crooked Lake, Vilas County, Wisconsin, in 2004 and 2005. Big Crooked Lake is entirely surrounded by land owned by Dairymen's Incorporated, a private resort near Boulder Junction. The riparian area is forested, with development along the 8.1 km of shoreline limited to a lodge and several cabins on a stretch of the north shore. The lake is oligotrophic, 276 ha in size, and has a maximum depth of 11.6 m. The fish community consists of walleye, smallmouth bass (*Micropterus dolomieu*), muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), white sucker (*Catostomus commersoni*) and various minnows (*Cyprinida*e) and darters (*Percidae*). Currently, the lake is one of four lakes in the ceded territory of northern Wisconsin utilized by the Wisconsin Department of Natural Resources (WDNR) for walleye exploitation rate research. Big Crooked Lake has a naturally reproducing, self-sustaining walleye population and no stocking occurs. Walleye may have initially been introduced to the lake (S.P. Newman, WDNR, personal communication), but reliable historical records of introduction are absent.

Big Crooked Lake contains three classical walleye spawning habitat types: rock shorelines, point bars, and islands and each geomorphic type was evaluated during the study. Specifically, the three study reefs were: a relatively linear rock shoreline in the northwest corner of the lake ("shoreline"), a point rockbar in the south-central portion of the lake ("point"), and an island located in the southeastern bay ("island")(Figure 1-1).

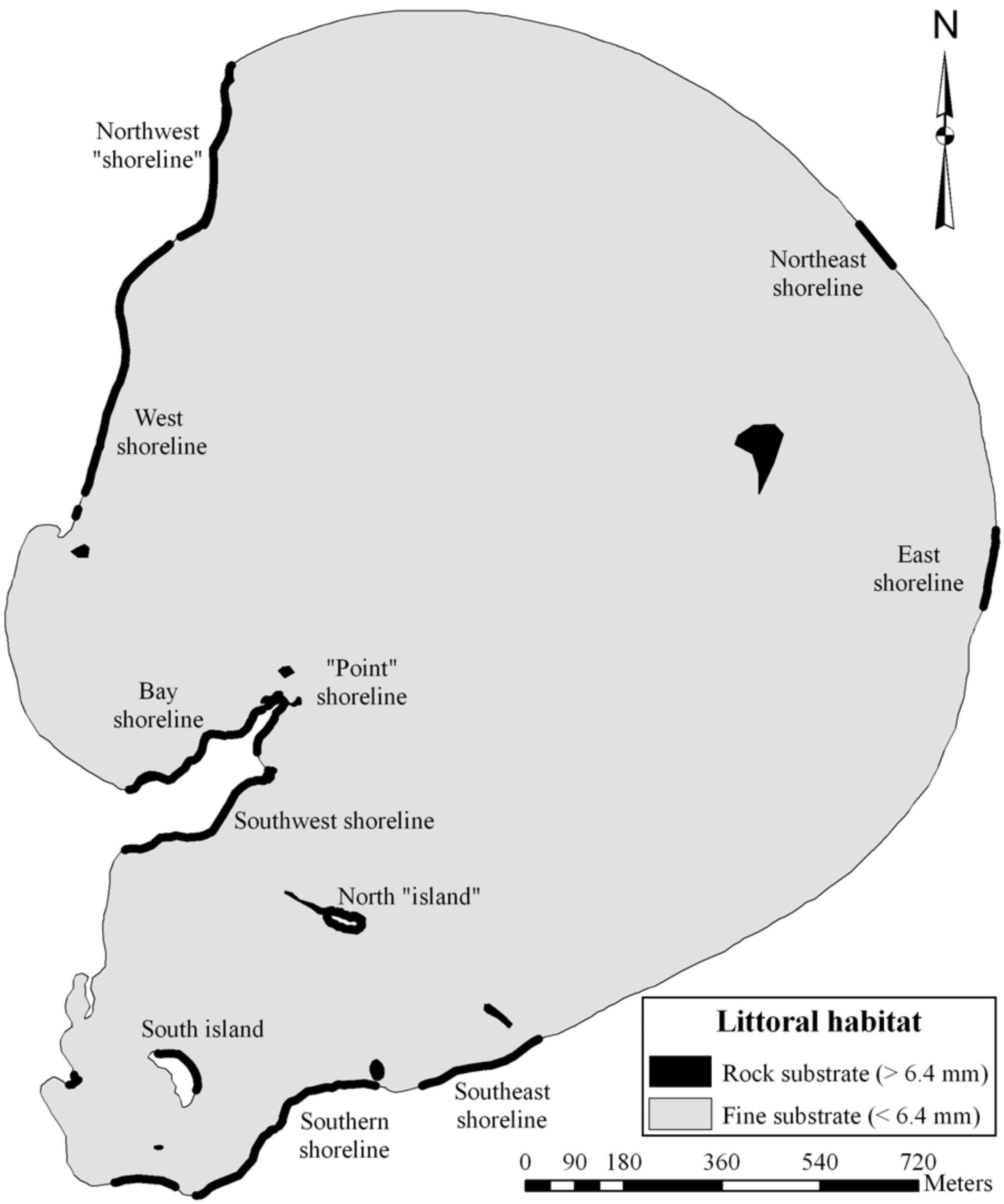


Figure 1-1. Locations of rock substrates (gravel, cobble, rubble, etc.)(any material ≥ 6.4 mm) compared to fine substrates in the Big Crooked Lake littoral zone (<3.0 m of water depth). Sand substrate dominated the littoral habitat, while rock substrate was primarily nearshore and in the western half of the lake. The three study reefs are identified in quotations marks.

Spawning Chronology

The spawning chronology of adult walleye and embryo development was followed throughout the 2004 and 2005 spawning seasons in Big Crooked Lake. In order to follow spawning adult walleye, six standardized WDNR fyke-nets were installed perpendicular to shore immediately upon lake-wide ice-out. These nets were checked daily and each sampled walleye was fin clipped until an adequate number of fish were marked (approximately 10% of the population). Individual walleye were recaptured using a standardized AC, WDNR boom electrofishing boat. The point at which 85% of adults spawned and the peak of spawning were estimated by nightly catch numbers and reproductive status. Population estimates were also conducted in the spring using the Peterson method (Ricker 1975) in order to estimate the walleye stock size:

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

Where: N = size of population at time of marking

M = number of walleye marked

C = sample taken for census (catch)

R = number of recaptured walleye in sample

In addition to spawning activity, 30 live eggs were collected daily from spawning areas to track embryo development and larval emergence (see McElman and Balon 1979). In particular, the initial development of black-eye pigment and later physical movement of individual embryos within the chorion were considered two late, separate stages of development. For these evaluations, eggs were collected at the point study reef in 2004 and the shoreline study reef in 2005. To collect eggs, the bottom substrate was agitated by foot and a mesh collector was brought through the turbulent water to collect suspended eggs. Using forceps, viable eggs were removed from the collector and placed into a labeled vial containing 10% formalin. Field observations of embryo development were recorded along with laboratory observations using a dissecting microscope. The commencement of fry hatching was determined by visual observations of hatching in samples and through collections of walleye fry during night boat tow-net surveys.

Quantity of Available Spawning Habitat

In order to determine where and to what extent walleye spawned throughout Big Crooked Lake, two different qualitative surveys were conducted to locate spawning areas. Walleye eyes reflect light and a spotlight was utilized to locate and observe spawning activity by boat after sunset. The entire shoreline was surveyed a minimum of three nights between ice-out and the completion of egg deposition; areas where walleye were observed and any spawning activity were recorded. In combination with boat surveys, SCUBA/snorkel visual surveys were conducted along the shoreline and offshore rock reefs to locate egg deposition areas. Once an estimated 85% of female walleye spawned, surveyors snorkeled and SCUBA dove the entire shoreline and deeper water to locate deposited eggs. The starting and end point of areas of deposition were marked with GPS points (Wisconsin Transverse Mercator coordinate system) using a handheld GPS unit (Garmin GPSmap 765) and also with marking tape on the shoreline. The length of utilized areas was measured with a tape measure and delineated onto a lake map in ArcGIS Version 9.1 (ArcGIS)(ESRI 2004).

The locations of general egg deposition zones were delineated in 2004 and 2005 at each of the three study reefs and at any additional areas where eggs were observed during qualitative surveys. Once an estimated 85% of females spawned, general egg deposition zones were delineated with the "continuous" placement of metal washers along the boundaries of egg deposition. The snorkeler began at the start of observed eggs and moved perpendicular from the shoreline and then progressed in a 90° zig-zag motion. Egg deposition boundaries were established by placing washers at the deepest, furthest point from shoreline that eggs were observed; points had to have a minimum of ten live eggs in approximately a 0.5 x 0.5 m area to be considered. The surveyor also searched deeper water and past the transition from rock to sand substrate to assure eggs were not present in those locations. At times, eggs were visible on top of the substrate, and other times the substrate was slightly moved or agitated to temporarily suspend eggs. This method continued across the reefs, with washers being placed approximately every five m along the egg perimeter. After the eggs hatched, the distance from shore, total water depth, and reef location (total distance in m from first observed eggs) were recorded for each placed washer.

Surveys of physical reef dimensions and structural characteristics to quantify habitat used by walleye for spawning began once all larvae emerged and dispersed. To achieve a concrete representation of the utilized habitat, a minimum of 200 sample points were taken within each reef egg deposition zone. Of particular interest was the location and characteristics (i.e., substrate) of the egg deposition compared to the overall reef and to the entire littoral zone. The number of transects (*T*) and the distance between transects (*D*) was determined by:

$$T = \frac{200}{\left[1 + \left(\overline{X} / 0.5\right)\right]} \text{ then } D = \frac{L}{T}$$

Where: T = number of transects

$\bar{x}$ = mean distance (m) of eggs from shoreline

D = distance (m) between transects

L = total reef length (m)

The mean distance of eggs ($\bar{x}$) from shoreline was determined based on tape measurements of the washers placed during the spawning delineation. The total reef length (L) was measured from the starting point to ending point of egg deposition along the shoreline. In order to ensure 200 sample points, the number for $\bar{x}$ was rounded down to the nearest 0.5, and uneven numbers for T and D were also rounded down.

To quantify habitat at each transect, a tape measure was extended at a 90° angle from the shoreline. At the first sample point, the front of a 0.3 x 0.3 m quadrat was placed at the shoreline-water interface and then every 0.5 m from the shoreline within the egg deposition zone. A sample point was taken at the "transition point;" the location where the eggs were furthest from the shoreline based on the placed washers. The next sample point was 1.0 m from the transition point and every 1.0 m until fine substrate (i.e., sand) was reached to assess characteristics of the adjacent habitat. Transition from rock (reef) to fine substrate was often distinct, but in certain locations was more gradual. Once sand or silt (i.e., fines) was reached, an additional three sample points were taken, each 1.0 m apart to provide quantitative data showing the change in reef characteristics. At each 0.3 x 0.3 m sample point, habitat features such as distance to shoreline, water depth, percent substrate composition and substrate embeddedness were estimated or recorded. The distance from the shoreline was recorded at the front of the quadrat facing the shoreline. The depth was measured at the center of the sample point with a meter stick, or in deeper areas, a tape measure attached to a float. Slope was determined for each sample point by the difference between the depths at the previous and current sample point divided by the distance between the two sample points. The percent substrate composition was estimated according to substrate size classes (Table 1-1). The top four substrates (based on area covered) were estimated to the nearest 5% for a total of 100%. The substrate embeddedness, or degree that fine material (sand and finer substrate) surrounds rock substrate (gravel and coarser substrate), was also estimated on a scale of 0 to 4 (Figure 1-2). In order to know where the sample point was located relative to the rock reef (e.g., within egg deposition zone, rock reef, or off-reef in fine substrate) five different classifications were developed and recorded for each sample point (Table 1-2)(Appendix A).

To assess available littoral zone habitat, habitat data was collected at 100 random transects throughout the lake during 2004. Transects were established by determining the length of time (in seconds) to motor a boat just above idle speed around the entire shoreline. Then 100 random numbers were assigned with each number representing a time in seconds. Proceeding in a boat at the same speed and direction, buoys were then dropped at the 100 random seconds to establish transect locations. The transect locations were marked on the shoreline with numbered marking tape and recorded with a handheld GPS unit.

Along each transect, a tape measure was stretched at a 90° angle and sample points were recorded in a 1.0 x 1.0 m quadrat. Data was collected every 1.0 m until a water depth of 3.0 m; the first sample point was at the shoreline-water interface. A depth of 3.0 m was used as the final collection depth since walleye have not been observed

Table 1-1. Habitat substrate size classes and organic materials used in composition estimations (modified from Wentworth 1922)

Habitat variable	Diameter (mm) or description
Substrates	
Silt	<0.2
Sand	0.2-6.3
Gravel	6.4-76.0
Cobble	76.1-149.9
Rubble	150.0-303.9
Small boulder	304.0-609.9
Large boulder	≥610.0
Bedrock	Consolidated parent material
Organic Materials	
Fine	Fine particulate organic matter is discernible
Coarse	Coarse particulate organic matter is discernible

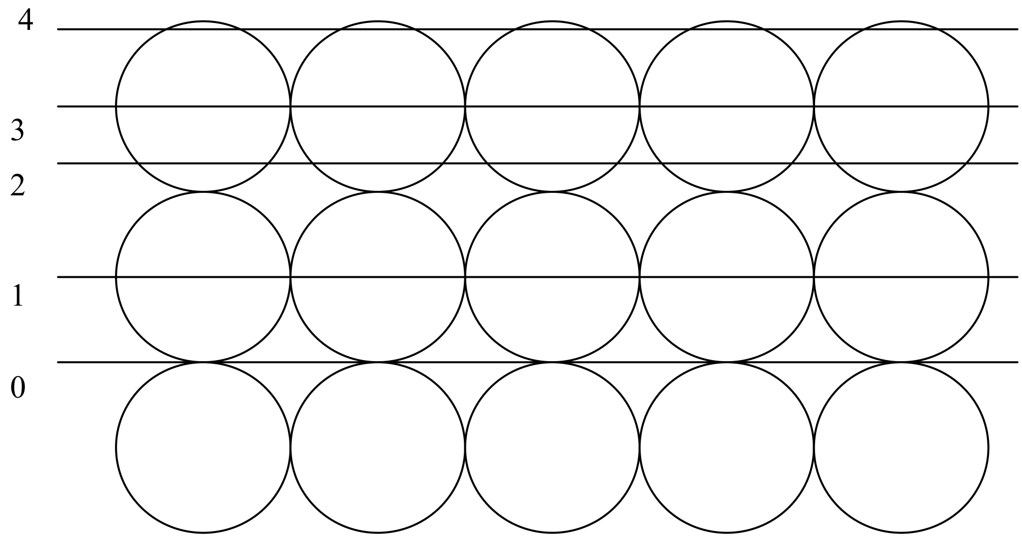


Figure 1-2. Diagram of substrate embeddedness. Horizontal lines indicate the level that sand (≤6.3 mm) and other fine particles fill the interstitial spaces between areas of gravel (≥6.4 mm) and coarser substrate. Numbers 0-4 represent assigned embeddedness value.

Table 1-2. Classification of sample points relative to the egg deposition zone and substrate features at spawning reefs as determined along snorkeling transects.

Sample point location
- Within egg deposition zone
- Transition point from egg deposition zone to area where no eggs present
- Outside of egg deposition zone, but on contínguous rock reef substrate
- Sand/silt substrate, outside of egg deposition zone and rock reef substrate
- Laterally adjacent to spawning reef - eggs never present along any portion of transect

spawning at this depth or deeper in Big Crooked Lake, or according to previous studies, in inland lakes, thus assuring all spawning habitat is covered in the assessment of available littoral habitat. This depth also insured adequate sampling to determine the importance of depth at spawning sites while avoiding inflation of its importance. Distance to shore, water depth, percent substrate composition, substrate embeddedness, and slope were recorded as described above.

Both raw field survey data and geographic information systems (GIS) were utilized to determine the overall quantity of spawning habitat utilized by walleye in Big Crooked Lake. Utilized spawning and available habitat was reconstructed in ArcGIS by inputting GPS points and adding additional points based on field data. Shoreline lengths were determined by either field data or measuring the shoreline in the GIS program. Areas (km^2) of littoral rock substrate and utilized spawning habitat were obtained from calculations in ArcGIS. Map layouts were also constructed in the GIS program.

Selection of Spawning Habitat

In order to gain an understanding of how wave dynamics affect the development of habitat selection models (i.e., actual spawning sites versus wave-transported egg incubation sites), the shoreline study reef was selected to locate recently deposited, adhesive eggs. Adhesive eggs denote the actual sites selected by spawning female walleye. To delineate these polygons, a snorkeler moved along the entire reef in search of adhesive eggs immediately upon ice-out in 2005 and each morning thereafter. In laboratory studies, eggs have remained adhesive for five hours under constant stirring (Waltemeyer 1976) and clumped together up to four days (Krise et al. 1986). In this study, eggs were adhesive for approximately 15 to 24 hours. Polygons of adhesive eggs were delineated by placing colored, daily numbered (e.g., “1” for first day of the spawning season, “2” for the second day of the spawning season, etc.) metal washers around the entire perimeter of the area to establish individual polygons. Surveys were continued daily until egg deposition ceased. Once eggs hatched, the depth, distance from shoreline, and reef location was recorded from the center of the washer polygon. The reef location was recorded as the shoreline distance relative to the start of the egg deposition zone on the southern end of the reef. In addition, the length and width of each adhesive egg polygon were measured. Percent substrate composition and substrate embeddedness were quantified within a 0.3 x 0.3 m quadrat placed in the center of each polygon as previously described.

Location of each adhesive egg polygon was superimposed on two-dimensional spawning reef blueprints to depict the selection of spawning habitat (e.g., adhesive egg polygons) relative to the available rock substrate portion of the shoreline reef. Descriptive statistics of the utilized substrates, substrate embeddedness, distance to shore, and depth were computed in Microsoft Excel (Microsoft Corporation 2001). In addition, the densities of adhesive polygons relative to reef location and spawning date were also evaluated. Raw field survey data and GPS points were used to reconstruct physical reef characteristics data (e.g., distance from shoreline, reef length, rock-sand transition) and the location of adhesive egg polygons in ArcGIS and exported as two-dimensional blueprint images.

Three sets of logistic regression analyses were performed to develop resource selection functions that evaluated walleye spawning habitat selection. Logistic regression was used to create each resource selection function that predicted the relative probability of the presence or absence of egg deposition based on utilized habitat features relative to their lake-wide availability (Manly et al. 1993). Since the littoral zone of Big Crooked Lake was extensive, two sets of lake-wide resource selections were created. The first set of models compared used habitat to all lake-wide littoral available habitat (to a depth of 3.0 m); the second set of logistic regression analyses compared used habitat to only nearshore (<13.0 m) available littoral habitat to provide a clearer evaluation of spawning habitat selection. These two sets of resource selection functions were developed for each year, but in 2004 only the three study reefs were quantified, while in 2005 all areas where eggs were observed were quantified. Available habitat assessment was quantified in 2004 and used in both years for resource selection functions. A third set of resource selection functions was conducted to evaluate habitat selection within a spawning area using the data from the adhesive eggs areas (used) compared to the available rock habitat at the shoreline study reef in 2005.

For the logistic regression analyses, the independent variable was binary (used/available) for egg deposition (Cox and Snell 1989). Logistic regression has been determined as a preferred method over discriminate function analysis when the response variable is binary and discrete (Press and Wilson 1978). Regression coefficients were estimated using the maximum-likelihood method (Hosmer and Lemeshow 1989). Logistic regression uses the following function:

$$\prod = e^u / \left(1 + e^u\right)$$

Where: $\prod$ = the probability of egg deposition

e = the inverse natural logarithm of 1

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

Where: k = constant

m_i = regression coefficients

x_j = values of independent variables

The significance of each model was tested using the -2 log likelihood statistic, that measures the deviation of observed values from the model (Hosmer and Lemeshow 1989). Improved model fit is indicated by lower values of the statistic. Multiple logistic regression incorporated several significant habitat variables to develop models of spawning habitat selection by adult walleye. Akaike's Information Criterion (AIC) was also used to determine the best model and assess and rank the alternative models. AIC weights were calculated for each model, that indicate the relative likelihood that a specific model is the best of all of the models (Burnham and Anderson 1998). Models were compared based on ΔAIC, or the difference between the lowest AIC value and AIC from all other models (Burnham and Anderson 1998). All models that have a ΔAIC value less than 2.0 relative to the best model were considered alternative models. Logistic regression analyses were conducted in Number Cruncher Statistical Systems (NCSS)(Hintz 2004) while AIC values were obtained in SAS Version 8.2 (SAS Institute, Incorporated 2001).

Quality of Spawning Habitat

To quantify spatial variation in egg deposition rates and survival-to-emergence, egg collection chambers were installed on each of three spawning reefs immediately at ice-out. The collection chambers were round, plastic containers with a diameter of 0.25 m and a depth of 0.15 m. In 2004, five transects were randomly placed in spawning areas, while in 2005 five transects were systematically placed equidistantly across each study reef. Each transect had six chambers with the first chamber placed at the shoreline-water interface (with the entire chamber in the water). The second chamber was located 1.0 m from the shoreline, and the third at 2.0 m from the shoreline. The remaining three were placed equidistantly across the remainder of the reef, differing according to each study reef dimensions. At each location, lake substrate was excavated so that the collection chamber was flush with the surrounding substrate. The excavated substrate was placed in each chamber. Water depth, distance from shoreline, percent substrate composition and substrate embeddedness were estimated for each collection chamber.

Upon completion (100%) of spawning activity and egg deposition, half (15) of the collectors were carefully removed from the substrate to quantify eggs in order to assess distribution of eggs across the reef. Deposited eggs within the chambers were removed, sorted as live or dead, and tallied (< 100 eggs) or measured volumetrically (> 100 eggs). The 15 chambers still in place were fitted with a nylon (6.7 threads/cm) mesh cover in 2004 and Nitex (10.9 threads/cm) mesh cover in 2005 and remained to estimate survival to swim-up fry. Once hatching was complete, these chambers were carefully removed from the substrate and all fry collected in the egg collection chambers were sorted as live or dead, and tallied or measured volumetrically. The developmental stage of live eggs (i.e., eyed or non-eyed) also was recorded.

The total number of eggs deposited and fry produced (i.e., black-eyed eggs) was estimated for each study reef according to egg deposition estimates from the first 15 chambers removed and linear regression equations. To estimate total eggs on each reef, each study reef was divided into 0.25 m (chamber diameter) cells along transects. For each transect, the number of cells out to the egg deposition transition point (i.e., location where eggs were no longer found) was determined. For example, if the deposited eggs extended out to 3.50 m from the shore there would be a total of 14 cells; one cell for every 0.25 m between 0.00 to 3.25 m. The regression equation described the total number of deposited eggs in each cell along each transect. In order to estimate egg densities in the areas between transects, the estimated number of eggs for each cell was multiplied by the distance between transects. For instance, if the transects were 5.0 m apart, each cell was multiplied by 5.0. The estimated number of eggs for all cells was summed to determine an estimated total egg deposition at each reef for both years.

Percent survival and total number of fry were estimated for each study reef. Percent survival was determined by dividing the total number of live eggs by the total number of deposited eggs within collection chambers and then multiplying by 100. The estimated total number of fry was equal to the number of live eggs. The second round of collection chambers (mesh covers) were installed to determine the percent survival to emergence, but very few live fry were recorded. Therefore, the first round of collection chambers was utilized to estimate the total number of fry and was considered an adequate representation of survival. Studies have shown that egg mortality or lack of fertilization is observable by within a few days (i.e., 72 hours)(Holtze and Hutchinson 1989, Heidinger et al. 1997) and the first round of collection chambers were removed after all egg deposition occurred.

Egg density provides insight into habitat quality, but the survival rates of deposited eggs are probably a better indicator of habitat quality. The density of eggs deposited and survival were analyzed as dependent variables relative to specific habitat features of individual egg collection chambers (independent variables). Physical characteristics: depth, distance to shoreline, and substrate size classes were evaluated:

$$y = mx + b$$

Where: y = dependent variable (survival)

x = independent variable

m = coefficient

b = intercept

Forward regression was used to evaluate multiple regression models; only one multiple regression model was significant in these analyses.

Quantitative Description of Spawning Habitat

Because quantitative descriptions of walleye spawning habitat is limited in the literature, individual spawning reefs were quantitatively described to help create two- and three-dimensional spawning reef blueprints. Descriptions of the spawning reefs were developed using observations of walleye spawning activity and subsequent habitat surveys. Descriptive statistics of spawning habitat features were analyzed in Microsoft Excel (Microsoft Corporation 2001). Two-dimensional blueprints were constructed in ArcGIS to depict the available rock substrate and the utilized egg deposition zone at each reef. Physical characteristics data (e.g., depth, distance from shoreline, rock-sand transition) and survey points collected during habitat quantification were reconstructed in ArcGIS, along with the location of eggs and the reef transition from rock to sand substrate. Data points from ArcGIS were transformed into usable datasets and imported into Surfer Version 8 (Golden Software, Incorporated 2002) for three-dimensional capabilities. A three-dimensional blueprint of the shoreline walleye spawning reef in Big

Crooked Lake contained the same characteristics as the two-dimensional blueprint but included water depth (and thus slope) to provide a quantified, visual representation of successful natural spawning habitat.

RESULTS

Spawning Chronology

Walleye spawning chronology differed between 2004 and 2005 in Big Crooked Lake. In 2004, deposited walleye eggs were observed on April 22, the first day of complete ice-out (Figure 1-3). By April 29, 85% of egg deposition had occurred. There was an estimated adult population of 1,992 ± 425 (95% C.I.) individuals, although of few juvenile males may have been included. Incubating eggs began to develop black eyes around May 8, 17 days after the first eggs were deposited (Figure 1-3). Embryo movement was observed within the chorion five days later on May 13, and hatching began two days later on May 15. No live eggs or young-of-year walleye were observed on the spawning reefs after May 23. Therefore, hatching lasted approximately eight days, and the total spawning period lasted 32 days (Figure 1-3).

The spawning period was longer in 2005, lasting a total of 38 days. Deposited eggs were first observed on April 16, one day after lake-wide ice-out (Figure 1-3). Peak spawning was estimated to occur on April 20 and by April 23 an estimated 85% of adults had spawned. Egg deposition appeared to be completed by April 26 as adhesive eggs were not found after this date, except on one occasion; on May 5 a patch of adhesive eggs was observed, however all eggs died, most likely due to a lack of fertilization. The adult walleye population was estimated at 1,174 ± 291 (95% C.I.) individuals, again, a few juvenile males may have been included. The black-eyed embryo stage was first observed

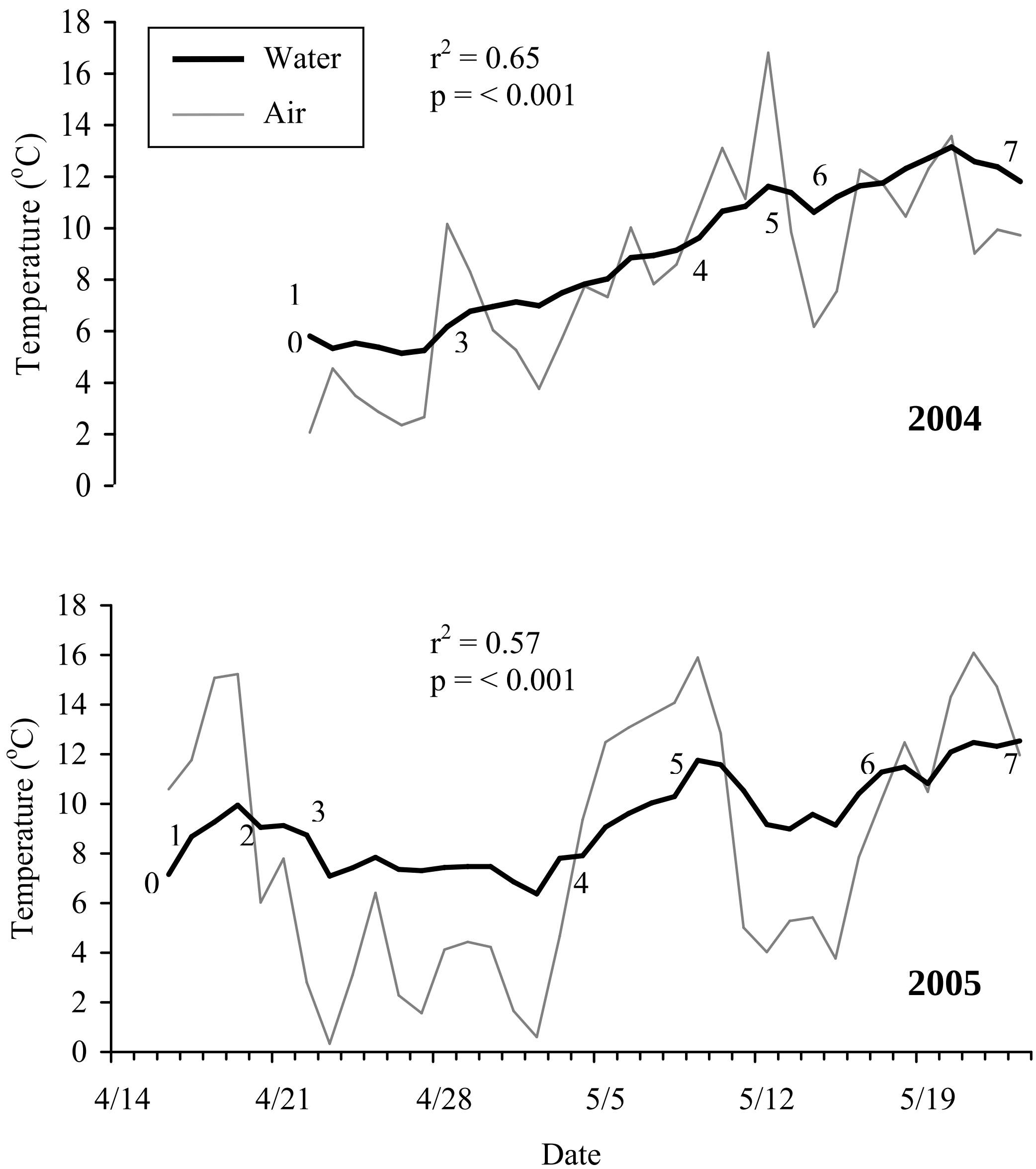


Figure 1-3. Mean daily water and air temperatures during the 2004 and 2005 walleye spawning seasons in Big Crooked Lake. Spawning chronology stages were: 0 = lake-wide ice-out, 1 = egg deposition commencement, 2 = peak spawning, 3 = 85% female spawned, 4 = black-eyed egg stage, 5 = embryo movement stage, 6 = hatching commencement, 7 = hatching completion. Coefficients of determination tested the extent that air and water temperatures are synchronous (2004: $T_{water} = -1.83 + 1.11T_{air}$, $p = <0.001$, $r^2 = 0.65$; 2005: $T_{water} = 7.07 + 0.27T_{air}$, $p = <0.001$, $r^2 = 0.57$).

on May 4, 19 days after the first deposited eggs (Figure 1-3). Embryo movement was observed five days later on May 9, but hatching was not observed for eight more days on May 17. Hatching lasted for approximately six days, as no live eggs were found on the spawning reefs after May 23, for a total spawning period of 38 days (Figure 1-3).

Quantity of Available Spawning Habitat

In Big Crooked Lake, the available littoral habitat was dominated by sand substrate that encompassed the entire northern and eastern portion of the lake, while the majority of rock substrate was located in the nearshore, western portion of the lake (Figure 1-1, Table 1-3). Sand regions were shallow with gradual slopes ($\bar{x}$ = 0.04), extending up to 312.0 m from the shoreline before a depth of 3.0 m was reached. The southwest portion of the southern bay and often deeper littoral habitat (> 2.0 m) was dominated by fine organic material or silt. Coarse organic matter and wood were not very common and decreased with distance to shoreline and depth. Rock substrates (i.e., gravel, cobble, etc.) comprised only 7.5% of the littoral zone, or approximately 22.77 km^2, with gravel being the most common at 5.0% of all littoral substrate (Figure 1-1, Table 1-3). The total length for segments of rock substrate nearshore was 2.96 km. Rock was more common (20.1%) when considering only nearshore littoral habitat (0.0 m to 13.0 m from the shore), with 15.1% consisting of gravel substrate.

Across both years of the study, spawning walleye utilized the three study reefs and also a southeast rock shoreline, a west-central rock shoreline and rock shorelines west and east of the point study reef (Figure 1-4). Eggs were found in these areas during a complete lake-wide survey in 2005 for a total utilized shoreline length of 1.15 km, or 14% of the total shoreline. Almost three km of rock shoreline was available in Big

Table 1-3. Descriptive statistics of the available littoral habitat and the used spawning habitat in 2004, 2005, and the two years combined. For used habitat, the distance to shore and water depth are for the outer boundary of observed eggs along transects. In each substrate size class, the percent coverage of all substrates (mean and maximum values) indicate weighted values (i.e., % area) while percent dominant only incorporates most abundant substrate for each quadrat (Note: Available N = 3,978 for all, N = 663 for 0-13 m; spawning habitat N = 725 in 2004, N = 1,284 in 2005, and N = 2,009 combined).

	Distance	Depth	Slope	FOM	Silt	Sand	Gravel	Cobble	Rubble	Sm. Bld	La. Bld	COM
Available (0-3 m depth)												
Mean	55.75	1.34	0.04	11.1	9.6	69.4	5.0	1.6	0.6	0.2	0.1	2.4
Maximum	312.00	3.51	0.90	100.0	100.0	100.0	95.0	65.0	85.0	25.0	70.0	100.0
Dominant	N/A	N/A	N/A	1.7	9.7	81.5	5.1	0.6	0.1	<0.1	0.1	1.2
Available (0-13 m distance)												
Mean	5.97	0.39	0.05	3.9	3.4	69.1	15.1	4.0	0.9	<0.1	<0.1	3.5
Maximum	12.00	2.61	0.90	50.0	100.0	100.0	85.0	65.0	30.0	15.0	20.0	50.0
Dominant	N/A	N/A	N/A	0.20	3.80	76.90	17.30	1.70	0.00	0.00	0.00	0.0
2004 Used												
Mean	3.79	0.42	0.07	0.7	0.0	13.4	62.4	12.9	3.8	0.9	2.0	3.8
Maximum	11.95	1.04	1.00	25.0	0.0	100.0	100.0	85.0	75.0	80.0	100.0	90.0
Dominant	N/A	N/A	N/A	0.0	0.0	6.8	79.7	5.4	2.5	0.8	2.2	2.6
2005 Used												
Mean	2.34	0.25	0.08	0.1	0.0	12.4	65.2	15.0	3.7	0.3	0.9	2.6
Maximum	9.99	0.95	0.60	10.0	0.0	100.0	100.0	90.0	80.0	55.0	95.0	90.0
Dominant	N/A	N/A	N/A	0.0	0.0	7.1	81.9	6.5	2.6	0.2	1.0	0.6
2004 and 2005 Used												
Mean	2.72	0.29	0.07	0.3	0.0	12.8	64.3	14.2	3.7	0.5	1.3	3.0
Maximum	11.95	1.04	1.00	25.0	0.0	100.0	100.0	90.0	80.0	80.0	100.0	90.0
Dominant	N/A	N/A	N/A	0.0	0.0	6.9	80.1	6.0	2.5	0.4	1.4	1.3

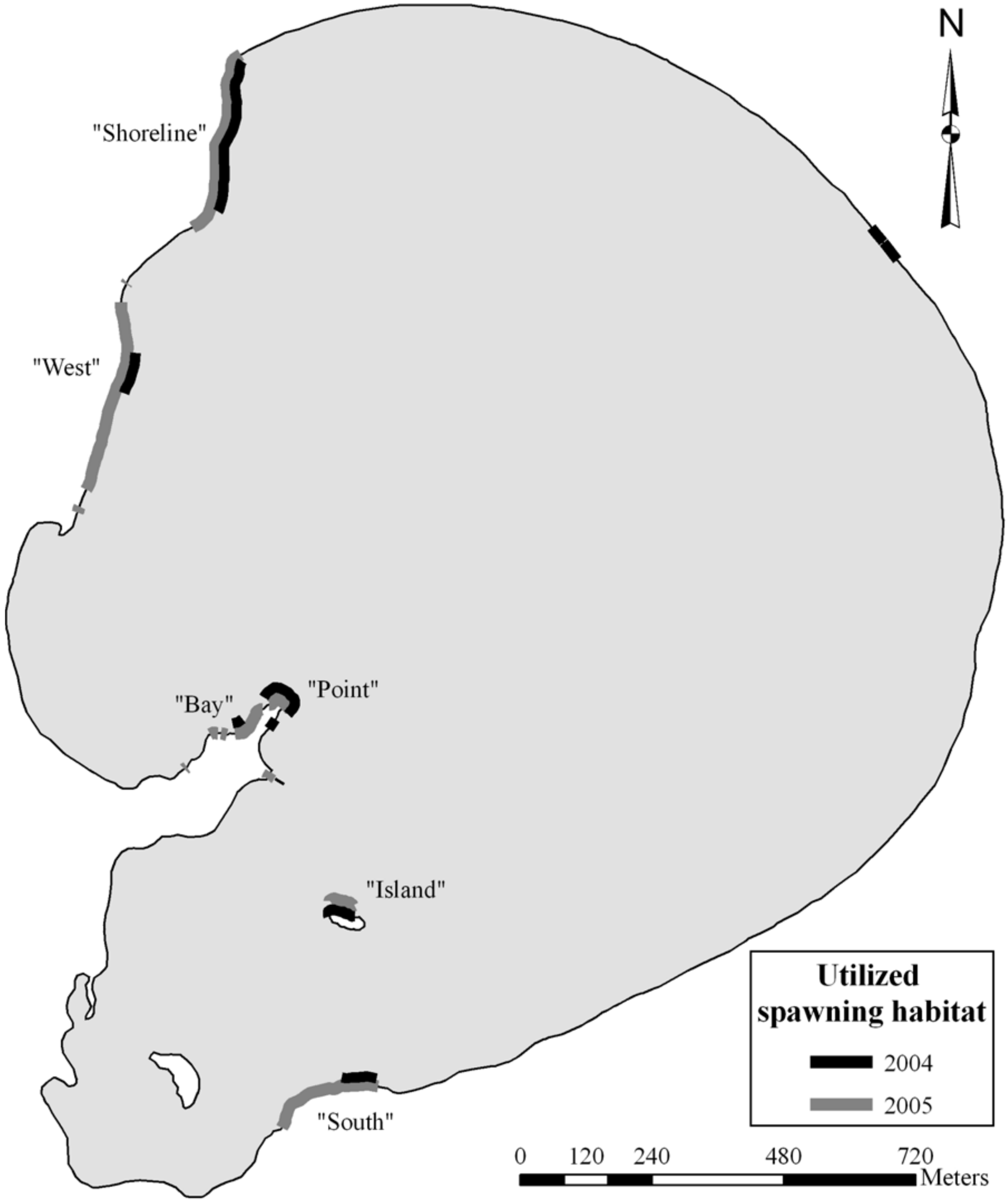


Figure 1-4. Locations of utilized walleye spawning habitat in Big Crooked Lake for the 2004 and 2005 spawning periods. A complete lake-wide survey was completed in 2005, while the 2004 lake-wide survey was intermittent.

Crooked Lake, but walleye only used 38.9% of these areas. When considering the area of available rock substrates in the littoral zone, walleye only utilized 2.39 km^2, or 10.5%. In 2004, eggs were found in similar locations and in portions of the sandbar region, but the specific extent of egg deposition and total shoreline utilized was only determined at the three study reefs (Figure 1-4). Therefore, specific comparisons between the total quantities of habitat used between the two years could not be completed.

Selection of Spawning Habitat

The best representation of actual selection of habitat by spawning walleye was depicted by adhesive eggs polygons at the shoreline study reef in 2005. A total of 121 adhesive egg areas were marked and quantified at the shoreline spawning reef in 2005 (Figures 1-5, 1-6). From the center of each adhesive egg polygon, the mean distance to shore was 1.74 m, while the closest and furthest from shore areas were 0.35 and 7.20 m, respectively. The shallowest adhesive egg polygon was 0.08 m and the deepest 0.79 m, with a mean water depth of 0.21 m for all adhesive sites (Table 1-4). On average, the adhesive egg polygons were 0.81 m long by 1.09 m wide (Table 1-4). Gravel was the most common substrate at all adhesive areas, but only a comprised a mean of 45.0% of the utilized substrates. Sand was prevalent in the selected areas at 30.0% along with cobble at 20.8% of the mean spawning habitat (Table 1-4). Gravel was the dominant substrate at 74 sites or 61% of 121 sites, with sand (27%) and cobble (12%) the only other dominant substrates. Gravel and cobble were often mixed with other substrates, as there were only five sites where gravel and one site for cobble that comprised 80% or higher of the site. Interestingly, there were six sites where sand composed 80% or more of the spawning habitat; including three sites in the northern section of the reef where it

Table 1-4. Descriptive statistics of 121 walleye adhesive egg sites at the shoreline study reef in Big Crooked Lake in 2005. The means are presented for the measurements of individual adhesive areas and the percent composition and as dominant substrate for each substrate size class present within adhesive areas.

	Mean	95% C.I.	Standard Error	Minimum	Maximum	Dominant Substrate
Distance (m)	1.74	0.16	0.08	0.35	7.20	N/A
Depth (m)	0.20	0.01	0.01	0.08	0.8	N/A
Length of Egg Polygon (m)	0.81	0.06	0.03	0.29	2.20	N/A
Width of Egg Polygon (m)	1.09	0.12	0.06	0.30	3.48	N/A
Sand (%)	30.0	4.4	2.2	0.0	100	27
Gravel (%)	45.0	3.8	1.9	0.0	90.0	61
Cobble (%)	20.8	3.2	1.6	0.0	80.0	12
Rubble (%)	2.0	0.9	0.5	0.0	30.0	0
Small Boulder (%)	0.2	0.3	0.2	0.0	20.0	0
Coarse Org. Mat. (%)	1.9	0.9	0.5	0.0	35.0	0

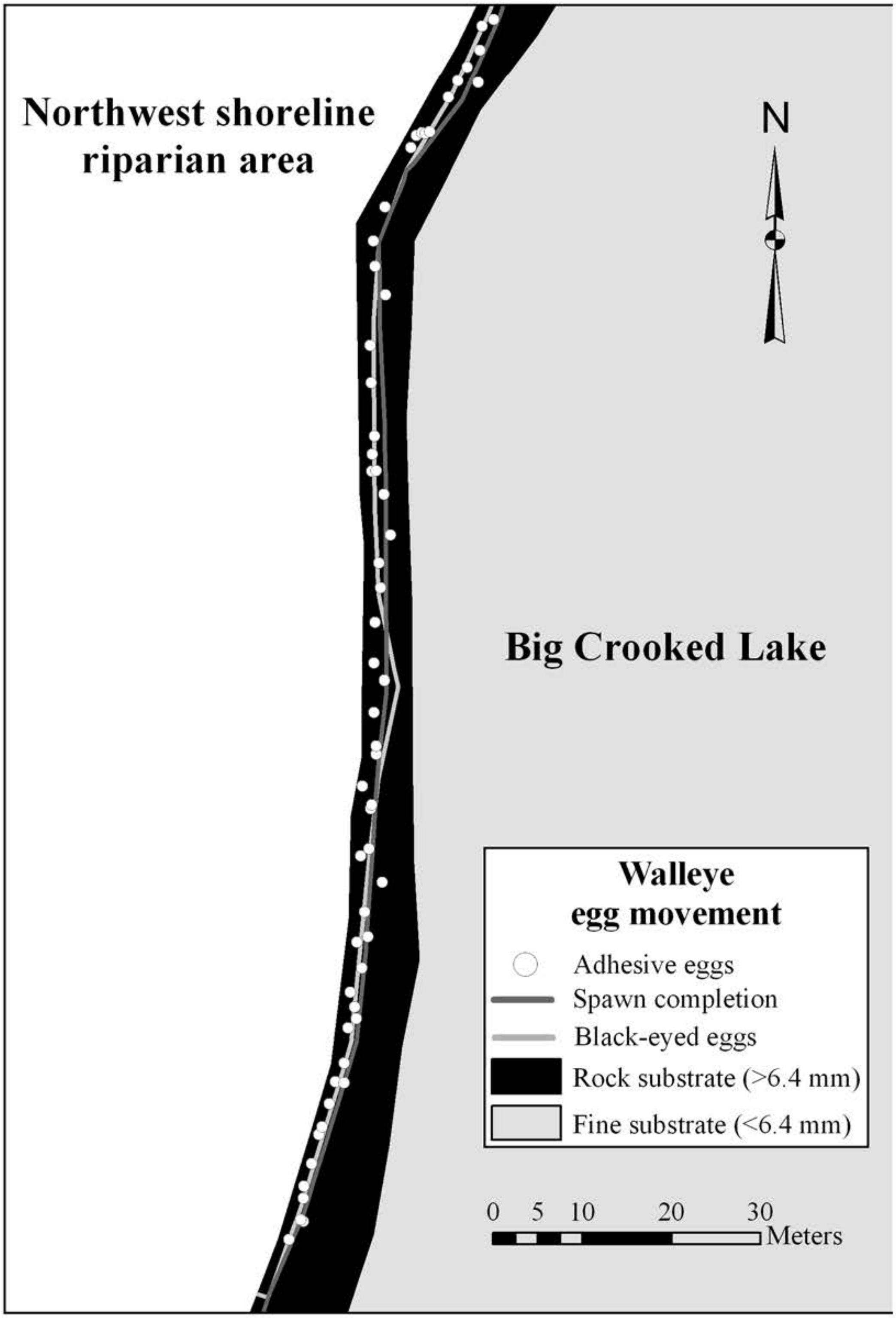


Figure 1-5. Locations of adhesive walleye eggs on the southern section (40-195 m) of the shoreline study reef in Big Crooked Lake. A total of 59 adhesive egg areas were found over this 155 m stretch. Adhesive eggs were present from the beginning of the egg deposition zone (0 m), but daily egg collections occurred from 0 to 40 m.

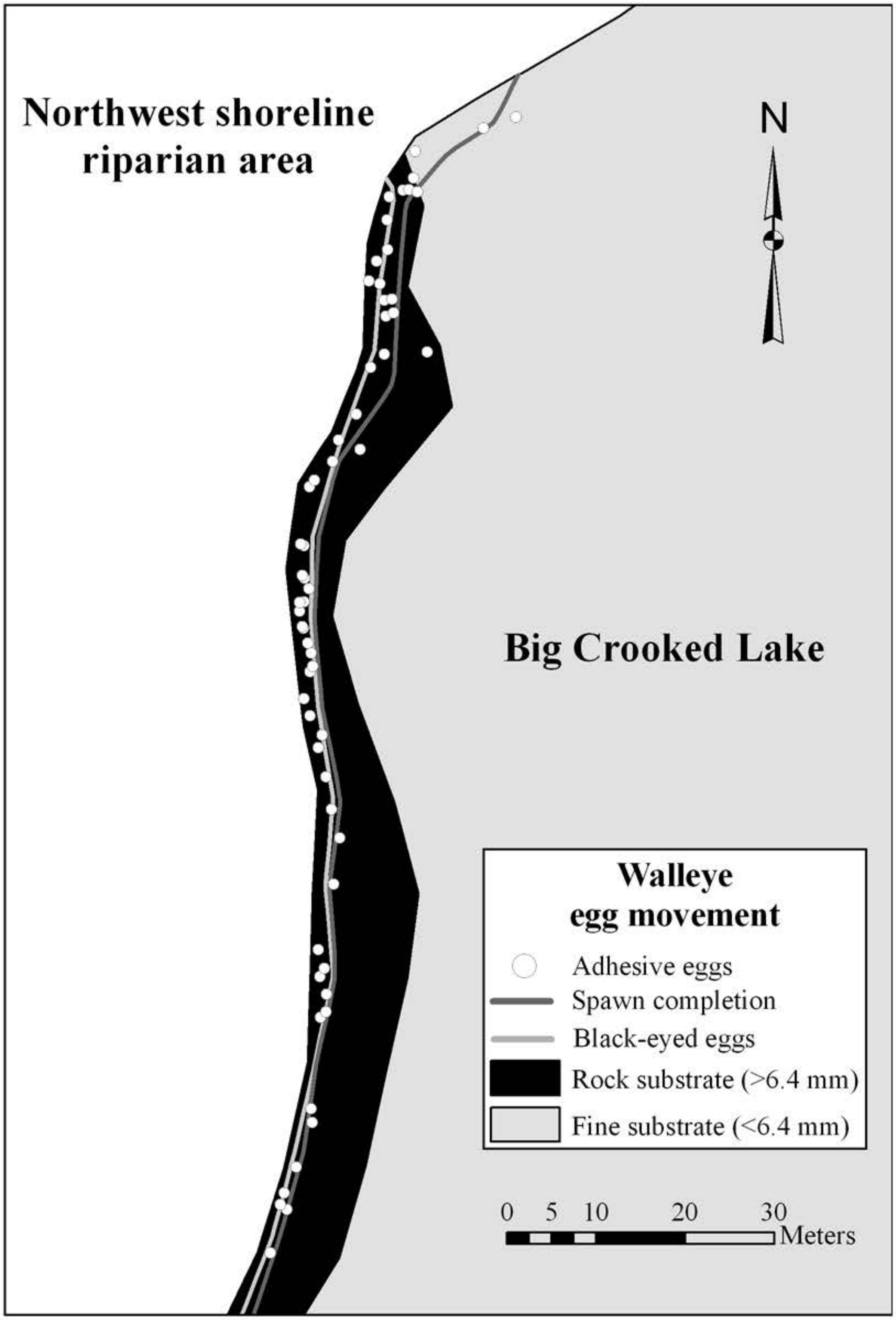


Figure 1-6. Locations of adhesive walleye eggs on the northern section (200-350 m) of the shoreline study reef in Big Crooked Lake in 2005. A total of 62 adhesive egg areas were present, including three areas in pure sand substrate.

was the only substrate present (Figure 1-6). At adhesive sites, rubble was as common as coarse organic material, that was primarily pine needles and some leaves. Small boulders and wood were not common and fine organic matter, silt, and large boulders were never more than just present at the selected habitat (Table 1-4). The selected rock habitat had fairly low embeddedness, with a mean value of 1.43. However, there were only 10 sites where the embeddedness was zero, or at least two layers of clean rock substrate.

Adhesive egg areas were found throughout the shoreline spawning reef during the entire spawning period, but certain areas were used more extensively or during certain time periods. Adhesive sites were found near the start of the egg deposition zone (0 m) and throughout the reef (Figures 1-5, 1-6). However, the first 40.0 m of the reef were not included as this was used for daily egg collections for monitoring embryo development. The northern and southern stretches had the highest density of adhesive egg areas, while the center had the lowest densities of sites. From south (0 m) to north (344 m) along the shoreline reef, the densities of adhesive egg polygons in each segment were: 24 sites (40-99 m), 18 sites (100-149 m), 17 sites (150-199 m), 14 sites (200-249 m), 26 sites (250-299 m), and 22 sites (300-344 m)(Figures 1-5, 1-6). In addition to slight differences in densities throughout the shoreline reef, areas were used more extensively during certain time periods. The most obvious example was the northern reaches (250-344 m) that were used extensively in the beginning of the spawning period. The southern section (40-100 m) was utilized throughout the season, but most often during the middle to end, while a center reach (150-199 m) was utilized more often towards the end of the spawning period. Repeated use of certain areas throughout the spawning period is depicted by clusters on the two-dimensional diagrams (Figures 1-5, 1-6).

When looking at spawning sites throughout the lake, walleye selected habitat close to shore, in shallow water, and over fairly gradual slopes. Over both years, eggs were located on average within 2.7 m of the shoreline but were often clustered closer or adjacent to the shoreline (Table 1-3). The furthest live eggs were observed was 12.0 m from the shoreline at the point study reef. The mean distance for the outer boundary of eggs along transects was 3.8 m in 2004 and 2.3 m 2005 (Table 1-3). Concurrent with the observations of walleye spawning close the shoreline, eggs were observed in shallow water. For both years combined, the mean maximum depth of egg polygons was only 0.29 m ($\bar{x}$ = 0.42 m in 2004, $\bar{x}$ = 0.25 m in 2005) and the deepest point along transects eggs were found was 1.04 m (Table 1-3). The mean slope for spawning reefs was fairly gradual, with slopes of 0.07 in 2004 and 0.08 in 2005.

The nearshore, shallow areas used by walleye for spawning habitat were dominated by gravel substrate with low embeddedness. For both years, gravel covered 64.3% ($\bar{x}$ = 62.4% in 2004, $\bar{x}$ = 65.2% in 2005) of all spawning habitat (Table 1-3). Cobble, sand, and rubble were the other most abundant spawning substrates, with means of 14.2, 12.8, and 3.7%, respectively. Cobble was slightly more abundant at spawning sites in 2005, with a mean of 15.0% compared to 12.9% in 2004, while sand (13.4, 12.4%) and cobble (3.8, 3.7%) covered similar mean percents of the spawning habitat in 2004 and 2005, respectively. Coarse organic material and wood were present at spawning sites at low rates, while small and larger boulders were not common. Very little fine organic material and no silt were found at the utilized portions of spawning reefs. Sand was the main embedding substrate, but the abundance of gravel resulted in a low, overall mean rock substrate embeddedness value of 1.30. The embeddedness value of the spawning habitat rock substrates was 1.17 in 2005, lower than the 1.53 value in 2004 (Table 1-3).

Not only did walleye select habitat across the lake, walleye also selected habitat within the utilized spawning reef sites proper. Eggs were often deposited or observed incubating close to shore and shallow relative to the entire rock reef structure. For example, although the rock substrate of reefs extended out to a mean of 5.39 m from the shoreline, eggs were found within a mean of 2.34 m from the shoreline in 2005. As a result, walleye used only 25.6% of the available 9.38 km^2 of rock substrate at reef sites. Structurally, the mean water depth and slopes were significantly lower over the utilized habitat (0.14 m, 0.08) compared to the unutilized portion (0.50 m, 0.15) of the reefs in 2005 (Table 1-5). There also were significant differences ($p < 0.05$) between the substrates, with gravel and coarse organic matter present at higher rates at the used spawning habitat in 2005 (Table 1-5). On the other hand, sand, cobble, large boulders and fine organic matter were all more common at the unused portions of the reefs (Table 1-5). Dominant substrate embeddedness and gravel embeddedness were lower at utilized portions of the spawning reefs. However, there was no difference between reef sections (used-unused) for percent of rubble and small boulders, both uncommon (Table 1-5).

In both study years, lake-wide resource selection functions determined that distance to shoreline was an important variable for habitat selection. In fact, it was the single best univariate model predicting used walleye spawning habitat, whereas the highest overall correct classification rates for univariate models was the dominant substrate model (Appendix B). The percent of gravel substrate alone was a solid predictor of spawning habitat in both years whereas other substrates were not as reliable

Table 1-5. Differences in habitat characteristics between used (egg deposition) and unused (no egg deposition) portions of rock spawning reefs in Big Crooked Lake in 2005. Means with standard error are presented for each characteristic, along with the results of two-sample t-tests comparing the used and unused portions of the spawning reefs. (Note: used N = 1284, unused N = 1053).

	Spawning Reef		
Habitat Characteristics	Used	Unused	P
Distance to shore (m)	1.46 ± 0.047	5.53 ± 0.131	<0.001
Depth (m)	0.14 ± 0.003	0.50 ± 0.012	<0.001
Slope	0.08 ± 0.002	0.14 ± 0.013	<0.001
Sand (%)	12.43 ± 0.547	22.92 ± 0.745	<0.001
Gravel (%)	65.25 ± 0.716	53.09 ± 0.793	<0.001
Cobble (%)	14.97 ± 0.455	16.49 ± 0.553	0.030
Rubble (%)	3.66 ± 0.279	3.75 ± 0.304	0.819
Small boulder (%)	0.27 ± 0.090	0.40 ± 0.120	0.378
Large boulder (%)	0.85 ± 0.205	2.17 ± 0.422	0.003
Coarse organic matter (%)	1.89 ± 0.179	0.56 ± 0.131	<0.001
Dominant substrate present	4.12 ± 0.021	4.04 ± 0.299	0.018
Dominant substrate embeddedness	1.37 ± 0.029	1.87 ± 0.042	<0.001
Gravel embeddedness	1.22 ± 0.022	1.48 ± 0.028	<0.001

(Appendix B). Correct classification rates and AIC values improved substantially for bivariate models and continued to improve, but at a lesser degree for three-, four-, and five-variable (Appendix B). The most parsimonious model consisted of distance to shoreline with percent of gravel and cobble substrate and had high correct classification rates of 96.6 and 97.1% in 2004 and 2005, respectively (Table 1-6). The 2005 model containing distance to shoreline, dominant substrate embeddedness, and the percent of gravel, fine organic matter, and cobble substrates was the best resource selection function (Table 1-6). This model had the highest overall correct classification rate (97.6%) and lowest AIC value (307.8) of all developed models in either year. A difference of 2.0 in AIC values did not occur with other models, therefore there were no alternative models. Compared to the best 2005 model, the top model in 2004 had lower correct classification rates and AIC values and substituted dominant substrate embeddedness with the percent of sand substrate (Table 1-6).

To better evaluate spawning habitat selection by walleye excluding wide open sand flats, a second set of resource selection functions were developed with only nearshore (< 13.0 m) littoral habitat used in the analyses. Substrate characteristics were better predictors than structural variables for nearshore models as the top univariate models were the dominant substrate, and percent of gravel and sand substrates (Appendix C). The best nearshore model was from 2005 and contained the variables percent of gravel, sand, and coarse and fine organic matter substrates with water depth, for an overall correct classification rate of 91.9% and an AIC value of 609.6 (Table 1-7). No alternative models occurred, but the best model in 2004 was percent of sand, gravel, and fine organic matter substrates combined with distance to shore and the dominant substrate

Table 1-6. The most parsimonious and best resource selection functions developed for utilized habitat compared to lake-wide available littoral habitat of Big Crooked Lake in 2004 and 2005 (total sample points for lake-wide available N = 1,000, and used N = 775 in 2004 and 1,000 in 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P	Coefficient	P	-2 Log	AIC	Presence	Absence	Overall
2004									
Distance to shoreline	-0.364	<0.0001	-0.061	0.8009	353.8	361.8	97.1	96.3	96.6
Gravel substrate (%)	0.064	<0.0001							
Cobble substrate (%)	0.064	<0.0001							
Distance to shoreline	-0.306	<0.0001	1.930	<0.0001	317.8	329.8	97.2	96.4	96.8
Sand substrate (%)	-0.030	<0.0001							
Gravel substrate (%)	0.046	<0.0001							
Fine organic matter (%)	-0.081	0.0395							
Cobble substrate (%)	0.030	0.0336							
2005									
Distance to shoreline	-0.542	<0.0001	0.450	0.0807	318.5	326.5	98.1	96.0	97.1
Gravel substrate (%)	0.053	<0.0001							
Cobble substrate (%)	0.091	<0.0001							
Distance to shoreline	-0.449	<0.0001	2.551	0.0039	295.8	307.8	98.5	96.6	97.6
Dominant embeddedness	-0.492	0.0150							
Gravel substate (%)	-0.295	0.0040							
Fine organic matter (%)	0.039	<0.0001							
Cobble substrate (%)	0.051	0.0020							

Table 1-7. The most parsimonious and best resource selection functions developed for utilized habitat compared to nearshore available littoral habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 662, utilized sites N = 662 in 2004 and 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P	Coefficient	P	-2 Log	AIC	Presence	Absence	Overall
2004									
Sand substrate (%)	-0.036	<0.0001	0.732	0.0051	850.8	858.8	90.5	82.9	86.7
Gravel substrate (%)	0.033	<0.0001							
Distance to shoreline	-0.198	<0.0001							
Sand substrate (%)	-0.045	<0.0001	-0.469	0.1999	811.2	823.1	90.8	82.6	86.7
Gravel substrate (%)	0.044	<0.0001							
Distance to shoreline	-0.157	<0.0001							
Fine organic matter (%)	-0.045	<0.0001							
Dominant embeddedness	0.437	<0.0001							
2005									
Gravel substrate (%)	0.045	<0.0001	-0.425	0.0910	672.2	680.2	93.4	86.7	90.0
Fine organic matter (%)	-0.973	<0.0001							
Sand substrate (%)	-0.027	<0.0001							
Gravel substrate (%)	0.030	<0.0001	1.686	<0.0001	597.6	609.6	94.7	89.1	91.9
Fine organic matter (%)	-0.892	<0.0001							
Sand substrate (%)	-0.036	<0.0001							
Depth	-4.917	<0.0001							
Coarse organic matter (%)	-0.069	<0.0001							

embeddedness (Table 1-7). When the best three- and five-variable models from the lake-wide and nearshore sets were compared, the correct classification rates and AIC values were poorer in the 2004 models and in the nearshore models (Tables 1-6, 1-7; Appendices B, C).

To evaluate site-specific habitat selection within a spawning reef, attempts were made to develop resource selection functions predicting use (i.e. adhesive egg polygons) compared to the available habitat at the shoreline spawning reef in 2005. However, logistic regression could not adequately separate the used adhesive sites versus the available shoreline rock habitat. This resulted in highly skewed correct classification rates, such as 100.0% available and 0.0% used. Logistic regression most likely could not adequately separate due to similarities in the unused, nearshore habitat that was included in the available rock habitat and also was incubation habitat once eggs settled out. Therefore, unlike the lake-wide and nearshore analyses that had multiple significant, usable models, there were no usable adhesive egg models.

Habitat quality

Walleye deposited more eggs in 2004, but had higher survival in 2005, and in both years eggs clearly incubated close to shore and in shallow water. An estimated total of 19,031,064 eggs were deposited at the three study reefs in 2004 (Table 1-8). For the three reefs combined, the mean egg survival rate was 12.6% in 2004. Therefore, an estimated 2,400,698 fry hatched from the three study reefs. Egg densities were significantly lower in 2005 at all three study reefs, with an estimated deposition total of 258,730 eggs (Table 1-8). However, the percent survival was higher at 25.1%, with an estimated 64,845 fry produced in 2005 from the three study reefs. Over both years, the

Table 1-8. Estimated number of live and total walleye eggs with percent egg survival in 2004 and 2005 at the shoreline, point, island reefs and the reefs combined.

	2004				2005			
	Shoreline	Point	Island	Combined	Shoreline	Point	Island	Combined
Live Eggs	1650753	468584	335642	2400698	385836	96204	34867	64845
Total Eggs	11362447	6671229	997390	19031065	1663676	258730	186473	258730
Egg Survival (%)	14.5	7.0	33.7	12.6	23.2	37.2	18.7	25.1

number of live eggs and total eggs was highest in chambers located 0.0 to 1.0 m from shore and the density of eggs then decreased drastically with distance from the shoreline (Table 1-9). A similar trend was seen with water depth, as the highest densities of live and total eggs were in chambers ranging from 0.0 to 0.29 m in depth, and also decreasing dramatically as water depth increased (Table 1-9). The impact of distance to shore and water depth on percent egg survival was not as evident as overall densities (Table 1-9)

Walleye egg deposition and survival rates differed between the study reefs and also differed between years at the individual reefs. The shoreline study reef had the highest estimated live and total egg deposition of the three study reefs, with the intermediate survival rate both years at 14.5 and 23.2% in 2004 and 2005, respectively (Table 1-8). In 2004, the highest egg survival (33.7%) was at the island study reef, but the reef also had the lowest survival (18.7%) in 2005 and lowest egg densities in both years (Table 1-8). At the point study reef, the survival was very poor in 2004, with only 7.0% of eggs surviving, but the highest in 2005 with a survival rate of 37.2% (Table 1-8). depth (Table 1-10).

Gravel, cobble, and sand were the only substrates in collection chambers, and there was no significant relationships between live eggs and the percent of these three substrates or the dominant substrate in each chamber. However, there was a positive relationship between percent egg survival and cobble substrate. The number of live eggs decreased with distance to shore and water depth, and there were no significant models containing embeddedness. Multiple regression analyses yielded one significant model; the number of live eggs was negatively related to distance to shore and sand substrate

Table 1-9. Mean number (standard error) of live and total walleye eggs with percent survival for egg collection chambers located in different ranges of distance to shore (m) and water depth (m) in 2004 and 2005.

Chamber Locations	Live Eggs	Total Eggs	% Egg Survival
2004 Distance			
0-1 m	174.9 ± 47.71	1582.4 ± 528.54	11.1
2-4 m	23.5 ± 13.36	61.8 ± 26.87	38.0
6-8 m	3.7 ± 1.58	7.7 ± 4.06	48.1
2005 Distance			
0-1 m	37.0 ± 26.95	160.4 ± 81.35	23.1
2-4 m	18.2 ± 10.63	67.1 ± 27.11	27.2
6-10 m	3.8 ± 2.09	9.4 ± 5.19	41.0
2005 Depth			
0-0.29 m	183.2 ± 49.65	1582.4 ± 528.54	11.6
0.3-0.49 m	25.7 ± 14.14	67.5 ± 30.16	38.1
0.5-1.12 m	4.3 ± 1.86	9.6 ± 4.76	44.3
2005 Depth			
0-0.29 m	37.1 ± 18.69	135.5 ± 54.62	27.4
0.3-0.49 m	4.9 ± 2.25	44.6 ± 22.74	11.0
0.5-1.12 m	1.8 ± 0.95	5.4 ± 3.60	33.9

Table 1-10. Regression models evaluating the relationship between habitat variables and both the number of live eggs and percent survival of eggs in collection chambers in 2004 and 2005 combined. Additional habitat characteristics were determined to be not significant (NS).

Model	N	r^2	Intercept Coefficient	Intercept P	Slope Coefficient	Slope P
Live eggs						
Distance to shoreline (m)	90	0.093	94.519	<0.001	-13.410	0.004
Depth (m)	90	0.054	90.912	<0.001	-100.928	0.027
Distance to shoreline (m)	89	0.114	118.912	<0.001	-13.607	0.003
Sand substrate (%)					-0.939	0.032
Sand substrate (%)	90					NS
Gravel substrate (%)	90					NS
Cobble substrate (%)	90					NS
Dominant substrate	90					NS
Dominant substrate embeddedness	90					NS
Percent survival						
Cobble substrate (%)	41	0.145	16.851	0.001	0.508	0.014
Distance to shoreline (m)	41					NS
Depth (m)	41					NS
Sand substrate (%)	41					NS
Gravel substrate (%)	41					NS
Cobble substrate (%)	41					NS
Dominant substrate	41					NS
Dominant substrate embeddedness	41					NS

(Table 1-10). This model indicated that less live eggs were collected further from shore and with higher percentage of sand substrate.

Quantitative Description of Spawning Habitat

Detailed descriptions and two-dimensional blueprints from the 2005 spawning period were completed for each reef (Appendix D) because there were differences and unique situations among the six main spawning reefs (Figure 1-4). In addition to Appendix D, a general summary of differences between reefs and a three-dimensional blueprint of the shoreline spawning reef were also completed (Table 1-11, Figure 1-7). Two spawning sites were located on the western side of the lake and had similar characteristics. The “shoreline” spawning reef was the northern most reef and was fairly shallow with a clear transition into sand both laterally and deep (Figures 1-4, 1-7, Appendix D). Walleye utilized the entire length of the reef, including spawning in a sand substrate area (Figure 1-7, Appendix D). Organic material, especially pine needles and leaves, was relatively high at this spawning site, particularly in the nearshore region (Table 1-11). Walleye spawning activity was high at the shoreline reef, including observed egg deposition events during the day. In 2004, eggs were observed over similar portions of the reef except no eggs were present after the southern most bend, that was covered with coarse organic material; leaves in particular. The “west” spawning reef was located in the west-central portion of the lake, was the longest reef but very narrow, and had walleye eggs located extremely close to the shoreline and in shallow water (Figure 1-4, Table 1-11, Appendix D). Walleye used the majority of the narrow row of rock substrate and at a few locations also spawned in sand after the reef transition. The

Table 1-11. Reef structural components for the used, egg deposition portion and overall available rock reefs areas at the utilized spawning reefs in Big Crooked Lake in 2005. Means are presented for distance to shoreline (m), depth (m), slope, rock embeddedness, and percent composition for present substrate size classes, along with actual lengths and areas. Note: shore = shoreline.

	Reef characteristics					Substrate characteristics							
Reef	Distance	Depth	Slope	Length	Area	Embed	Sand	Gravel	Cobble	Rubble	Sm. Bld	La. Bld	COM
Shore. (Used)	2.45	0.27	0.10	346.50	801.49	1.27	18.4	57.6	17.5	2.4	0.2	0.0	3.9
Shore. (Available)	9.24	0.70	0.13	350.09	2464.99	1.58	32.6	51.5	10.8	2.8	0.0	0.0	2.2
West (Used)	1.58	0.21	0.07	371.62	586.70	1.16	13.4	69.8	12.7	2.6	0.0	0.0	1.4
West (Available)	2.17	0.28	0.08	514.81	1021.35	1.18	15.5	68.3	12.1	2.7	0.0	0.0	1.0
Bay (Used)	1.96	0.21	0.05	104.68	103.98	1.28	11.8	82.5	3.4	0.4	0.0	0.0	1.8
Bay (Available)	3.98	0.38	0.07	310.53	1839.89	1.40	14.6	77.6	5.0	1.4	0.0	0.0	1.2
Point (Used)	5.86	0.36	0.07	58.80	355.65	1.44	20.6	53.6	18.0	5.1	0.0	0.0	2.8
Point (Available)	15.21	1.04	0.08	63.76	969.32	1.33	19.9	54.2	17.9	5.2	0.3	0.8	1.9
South (Used)	1.74	0.21	0.09	214.00	367.34	1.03	3.3	61.4	23.1	6.9	0.0	0.0	5.4
South (Available)	5.89	0.86	0.12	216.30	1116.14	0.97	5.4	60.0	26.3	5.1	0.1	0.0	2.9
Island (Used)	3.81	0.36	0.10	51.60	183.36	0.78	6.3	66.6	15.5	4.8	1.4	5.2	0.2
Island (Available)	8.77	1.29	0.14	164.55	1977.11	0.81	7.4	57.8	18.1	6.0	1.6	8.8	0.3

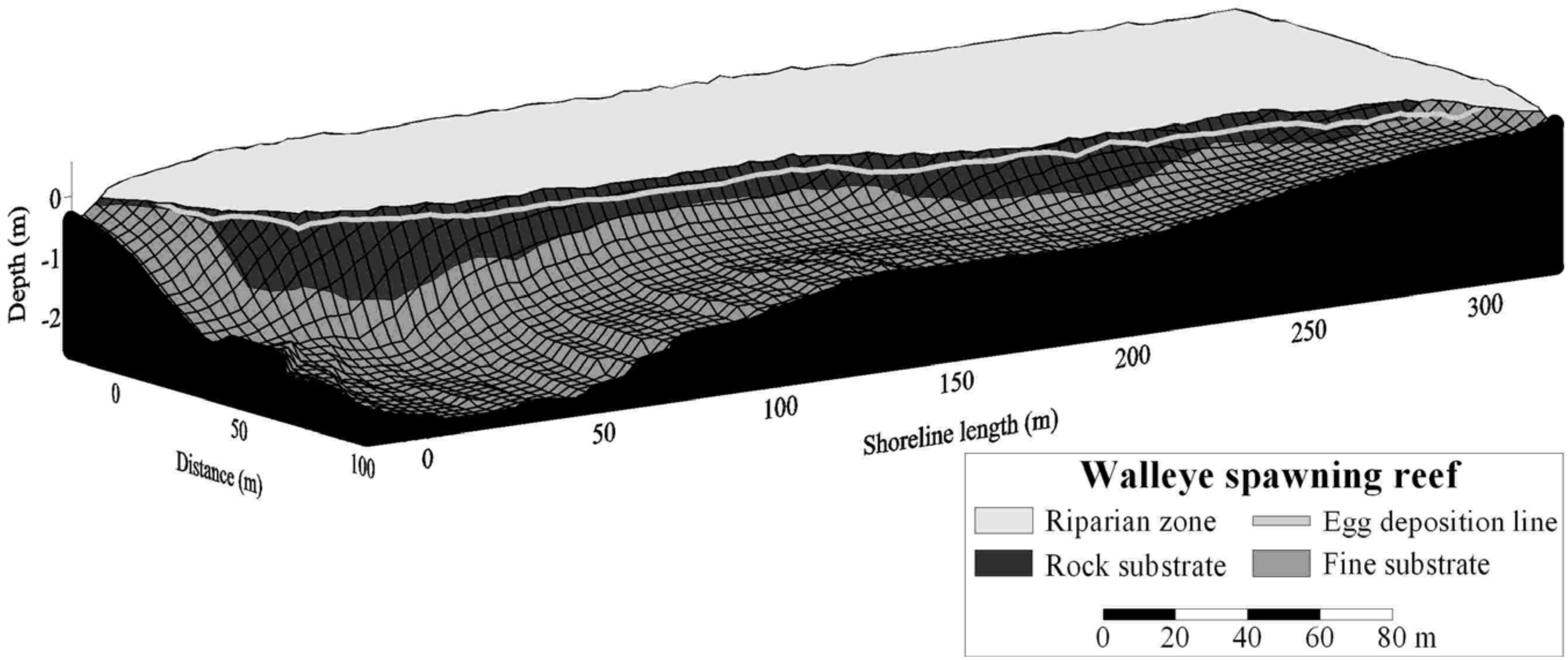


Figure 1-7. Three-dimensional blueprint of the northwest shoreline study reef illustrating the extent of walleye egg deposition relative to the rock substrate reef in Big Crooked Lake. Eggs were consistently observed between the shoreline and the egg deposition line along the entire rock reef and in a sand area to the north (right side). Note: The x-axis is the distance in m from an arbitrary point and measurements were not taken in the riparian zone.

utilized southern stretch was near a large patch of reeds to the east, while the northern stretch was tucked within a large fallen tree (Appendix D).

Walleye utilized two reefs in the south-central portion of Big Crooked Lake. The "bay" spawning reef, located south and west of the "point" study reef, was unique as it had the highest concentration of gravel substrate (82.5%) and because walleye used the northern portion of the reef but did not spawn over entire reef (Figure 1-4, Table 1-11, Appendix D). Walleye used approximately a third of the available shoreline as they only spawned on a short section of the southern reach. Water depth was shallow over the entire reef and very shallow in the utilized portions (Table 1-11). Walleye spawned the furthest from shore (outer boundary $\bar{x}$ distance = 5.86) at the "point" study reef that differed both in structure and substrate composition from the other spawning sites (Figure 1-4, Table 1-11, Appendix D). The western side of the reef was quite shallow with rock substrates having high embeddedness due to sand. Rock substrate increased at the northwest and northern portion of the reef, although sand and reeds were located near shore (Appendix D). The northeast rockbar was made up of various rock substrate including rubble and boulders and extended up to 33.25 m from the shoreline. Nearshore, the northeast side of the reef was primarily gravel that dissipated into a small row of gravel along the east side (Appendix D). Walleye utilized a similar portion of the point reef in 2004.

Walleye utilized an island and a rock shoreline in the southern bay of Big Crooked Lake. The furthest southern and eastern spawning site was the "south" reef, where walleye spawned over the entire length of the reef (Figure 1-4, Table 1-11, Appendix D). The south reef ran in a semi-circle from the northeast, that was primarily sand substrate, to the southwest bay, that had a high content of fine organic matter and silt. Walleye spawned over the majority (98.98%) of available shoreline, but did not use rock that extended further from shore and in deeper water. In addition, eggs were not observed at a gravel/cobble/rubble offshore rockbar to the northwest or when the rock resumed to the south. At the utilized portion of the reef gravel was the dominant substrate but the highest concentration of cobble (23.1%) was also at the south reef, along with the lowest rock embeddedness due to the lowest concentration of sand at all spawning sites (Table 1-11). The "island" study reef was unique, as it was the only island habitat utilized by walleye for spawning and had the highest concentration of boulders (Figure 1-4, Table 1-11, Appendix D). Despite gravel and other rock substrate being present on the northern face of the southern island (Figure 1-1), walleye did not deposit eggs at that location. In 2005, walleye only deposited eggs on the northern face of the island spawning reef, stopping abruptly at boulders located to the northwest (Appendix D). Boulders and trees were located to the northeast, while rock substrate was closer to shore and at lower concentrations on the southern side of the island. The utilized spawning substrate at the island reef was again dominated by gravel and followed by cobble, but also had the highest concentrations of large and small boulders of all spawning sites and an overall low percentage of sand (Table 1-11). Eggs were observed over an additional 20.9 m in 2004, but the main spawning habitat was again the northern face of the island.

DISCUSSION

The results of this study supplement past studies on walleye spawning, providing more detailed insight into habitat selection, quantity, and quality. In this study, walleye clearly selected for habitat that was particularly close to the shore and in shallow water. Offshore (i.e., deeper or further from shore) rock reefs were not utilized for spawning and eggs were found at their highest densities very near the shoreline; egg distributions often stopped well before the transition from rock to sand at most of the spawning sites. Distance to shoreline was likely the most important variable in lake-wide models predicting spawning habitat and appeared more influential than water depth. Previous studies mentioned that walleye spawning activity was focused nearshore (Eschmeyer 1950, Ellis and Giles 1965, Priegel 1961). However, these studies indicated that water depth was the important habitat component. In Lake Gogebic, Michigan, nearly all spawning activity occurred nearshore and in water less than 61.0 cm, with a few eggs collected in 122.0 cm of water (Eschmeyer 1950). Johnson (1961) noted that walleye typically spawned in water between 30.5 and 76.0 cm in depth, but eggs were found as shallow as 5.0 cm and the deepest eggs were estimated at 122.0 cm in Lake Winnibigoshish, Minnesota. In Big Crooked Lake, eggs were deposited or observed incubating towards the lower depth range indicated in these studies, as the outer boundary of eggs had a mean water depth of 0.35 m for the two years combined.

Gravel was the dominant substrate at all of the utilized spawning reefs in Big Crooked Lake, but was commonly combined with sand and cobble, along with lower amounts of rubble, boulders, and coarse organic material. These results are more detailed, but similar to past studies that described spawning substrates in general terms, such as gravel/rubble or gravel/sand (Eschmeyer 1950, Johnson 1961, Priegel 1970). In Big Crooked Lake, the embeddedness of rock substrate was low at all of the spawning sites showing that interstitial spaces were present with a mixture of gravel and cobble, not just with larger substrates. The relative probability of egg deposition decreased with higher rock embeddedness, suggesting that walleye select for lower embeddedness at spawning sites, as eggs settle into interstitial spaces and find protection from scouring or transport by wave energy (Johnson 1961) and allow for higher water movement and dissolved oxygen flow (Daykin 1965). Moreover, the spawning reefs were fairly "clean" in this study as no silt and very little fine organic matter was present at the spawning reefs. Silt and fine organic matter can cover eggs, restricting oxygen flow to developing embryos (Daykin 1965). Interestingly, coarse organic matter was present to relatively common at many of the spawning sites with concentrations increasing closer to shore.

In Big Crooked Lake, walleye annually produce strong year-classes (e.g., 22.0/ha in fall 2004, 20.0/ha in fall 2005) and do not appear limited by spawning habitat as only 39% of available rock shoreline habitat was used during 2005. No other studies have attempted to quantify available spawning habitat, but Nate et al. (2003) used substrate as a variable in modeling walleye presence in lakes. This study found that both percentage of sand and muck substrate, considered intermediate to poor spawning substrates (Johnson 1961, Priegel 1970), were inversely related to adult walleye abundance. According to models developed in the study by Nate et al. (2003), Big Crooked Lake would not be considered a good walleye lake as it has an extensive region of sand, while rock substrates comprised only 7.5% of the entire littoral zone habitat. Walleye only sporadically used the sand region for spawning and just 10% of the total area of rock substrate in the littoral zone. Approximately three kilometers of the shoreline was comprised of consistent rock substrate with walleye utilizing less than half of this habitat (39%) and only 14% of the total shoreline habitat.

Walleye spawning habits and habitat were fairly similar between reefs in Big Crooked Lake, but there were a few unique situations. The mean distance to shoreline of the furthest observed eggs was similar for the three study reefs in 2004 and 2005. However, the other three reefs studied in 2005 had eggs very close to shoreline, resulting in an overall lower mean in 2005. In both years, eggs were located the furthest out at the point study reef. The unique situation at the point study reef probably was a result of the northern, nearshore habitat being very shallow and with a higher content of sand. As the shallow area sloped into deeper water, the rock habitat also was more consistent with the other study reefs, and was the area where a high concentration of spawning activity occurred. Although primarily rock substrate was used as spawning habitat, walleye did deposit eggs in areas of pure sand substrate at the shoreline reef in both 2004 and 2005. However, the north and eastern sandbar region was used more extensively in 2004.

Walleye are believed to home (Crowe 1962), either due to genetics (Jennings et al. 1996) or as a learned behavior (Olson et al. 1978). Walleye are a schooling fish and may "learn" their spawning habitat by following mature individuals to the spawning grounds (Olson et al. 1978). While walleye are not considered territorial or protective, they do exhibit courtship activities including circling and physical contact (Ellis and Miles 1965). It is possible that more mature or aggressive females are establishing their selected habitat by this circling action and force "following" younger or less aggressive females to other habitat that may be potentially less desirable. For example, four adhesive egg polygons locations had a sand concentration of 95 or 100% and were deposited over the same night, possibly by the "following" females. There were additional adhesive polygons from the same night that were located slightly south of these four areas and the habitat was primarily gravel with low embeddedness, a preferred habitat. Another hypothesis to explain spawning over less desirable substrates is that the preferred habitat was saturated with deposited eggs. For instance, in 2004 the egg density was higher at the three studies reefs and more areas in the extensive sand regions were utilized than in 2005 that had much lower egg densities and little sand region use.

Walleye spawned close to the shoreline, in shallow water and over primarily gravel substrates, suggesting that this is the highest quality habitat, particularly because there were other substrates sizes, both larger and smaller, to spawn over. According to regression analyses on egg densities in collection chambers, the density of live eggs in Big Crooked Lake increased closer to the shore and with shallow water depth. Also, the number of live eggs was inversely related to the percent of sand when combined with distance to shoreline. Yet, percent survival was not correlated with distance to shore or water depth. No significant correlations were found with the percent of gravel substrate and the number of live eggs or percent survival. The lack of a relationship is most likely due to the fact that gravel was the most common substrate at spawning reefs, even in the further, deeper areas that were not utilized less by walleye as spawning habitat. The percent of cobble was the only single substrate to positively correlate with egg survival rates. It should be noted that the highest concentration of cobble in chambers was 50%, so a mixture of cobble with gravel or even sand may be ideal as the larger substrate can increase the interstitial spaces.

Eggs incubated in gravel, cobble, and sand mixtures in Big Crooked Lake and survival ranged between 7.0 to 37.2% over both years. Johnson (1961) determined survival rates of 17.5 to 34.3% on gravel and rubble spawning reefs, while a 60% gravel, 40% sand spawning area had a survival rate of 17.4%. Egg survival rates were intermediate (2.7 to 13.2%) for eggs incubating on firm, fine sand but eggs were easily removed by wave activity from the sand areas (Johnson 1961), that also was observed by Priegel (1970). Eggs incubating in soft muck-detritus substrate, including undecomposed aquatic plants, had the poorest survival rates, ranging from 0.6 to 4.5%. This is similar to other studies that have observed or suggested high egg mortality when eggs are deposited or carried onto muck-detritus substrate (Eschmeyer 1950, Priegel 1970, Busch et al. 1975). In Big Crooked Lake, walleye occasionally used sand substrates but did not utilize muck-detritus habitat, perhaps because rock and sand substrates were prevalent.

The question arises of why walleye are selecting for rock habitat near the shoreline and in shallow water if these variables did not relate to the percent survival of eggs and when similar rock substrates were available further from shore and in deeper water. Habitat close to shore is the location where waves break and the energy is highest. This energy can both "clean" the habitat of fine organic matter or silt that can suffocate eggs and provide higher dissolved oxygen flow across eggs. Dissolved oxygen was not measured in this study as it typically is sufficient during the spring due to mixing, lake turnover, surface runoff, and because cold water can retain more dissolved oxygen. However, the utilized spawning areas were "clean," as fine organic matter and silt content was very low. Another possibility is that there is a thermal advantage in the shallower water. This area may warm more sooner, triggering walleye spawning activity. The nearshore area may also warm at a higher rate or stay warmer, accelerating embryo development; shortening the incubation period (Johnson 1961, Koenst and Smith 1976, Hokanson, Koonce et al. 1977).

Another explanation for why walleye spawned near the shoreline and in shallow water is provided through the river habitat hypothesis presented by Kitchell et al. (1977). The authors hypothesized that walleye were most successful in lakes that have littoral habitat similar to large river systems. Walleye were originally native and appear best adapted to riverine systems (Scott and Crossman 1973, Colby et al. 1979, Becker 1983), so their invasions of lentic systems may have been most successful in habitat that represented similar conditions and habitat (Kitchell et al. 1977). Large lakes with extensive shallow areas tend to have habitat similar to large moderate-to-low gradient rivers, such as oxbows and backwaters, that provide habitat for all life stages of walleye (Kitchell et al. 1977).

Big Crooked Lake appears to have a high degree of habitat, including spawning habitat, similar to large river systems. The littoral habitat is shallow and extensive, but also has nearshore rock substrate for spawning. Similar to walleye spawning habitat in lakes, few quantitative studies have been conducted for river walleye spawning habitat. The most extensive study was by Corbett and Powles (1986) on two rivers in southeastern Ontario, Canada. They clearly documented that walleye selected for slower velocity “backwater” and “quiet border zones.” Egg densities were high in these areas, while riffle zones had low densities or no eggs present. It was hypothesized that walleye selected these slower velocities areas so they could deposit eggs at the desired, rock habitat. They determined that survival was higher on “sand-gravel-rock” substrates than on “mud-detritus” bottoms (Corbett and Powles 1986). Spawning walleye were in areas of gravel and rubble substrates in four Wisconsin rivers and at one of these rivers gravel was dominant with some sand at the egg incubation site (Stevens 1990). Based on these studies and the river habitat hypothesis, walleye may be adapted to spawning near shore and over predominantly gravel substrates, the same situation observed in Big Crooked Lake. In addition, water movement or velocity is lower in deeper lake water zones, but common in shallower water. In rivers, the slower velocity of backwater and quiet border water zones is ideal for specific habitat selection, but also for dissolved oxygen and transportation of fry (Priegel 1970, Corbett and Powles 1986). In the Lake Winnebago, system (Wisconsin), walleye spawned in flooded marshes with consistent flows and eggs that remained in vegetation had high hatching success (Priegel 1970). The highest concentration of dead vegetation or coarse organic matter was found close to the shoreline in Big Crooked Lake. While percent survival did not correlate with organic matter, it is possible that walleye are adapted and select for that type of spawning habitat.

The research in this study presents various management implications for walleye populations and spawning habitat. First, the river habitat hypothesis (Kitchell et al. 1977) and supporting walleye river life history and habitat studies should be considered when deciding if an inland lake and spawning habitat should be managed for natural reproduction of walleye. Second, the quantified spawning habitat information, predictive models, and visual maps can be utilized to identify and protect successful natural walleye spawning habitat. While each system may be unique, the nearshore habitat should be evaluated first as it was the primary spawning habitat in Big Crooked Lake and also is the most vulnerable to human lakeshore development. Protection of this habitat would benefit walleye along with other fish species, such as cyprinids or darters (Becker 1983, Lyons and Magnuson 1987), invertebrates (Tolonen et al. 2001), and any organisms that reside in similar littoral habitat. Lake-specific evaluations are necessary to determine if spawning habitat is a limiting factor towards self-sustaining walleye populations. In Big Crooked Lake, that annually produces year-classes of walleye, walleye utilized 14% of the total shoreline and only 39% of the available rock shoreline.

This research should be considered prior to spawning habitat restoration or enhancement projects that have been largely unsuccessful. Johnson (1961) added gravel substrate (2.54 to 40.64 cm diameter) to a firm sand area in Little Cutfoot Sioux in the Lake Winnibigoshish system (Minnesota) that was previously utilized by walleye. He determined that egg abundance was more than 10 times greater and egg survival improved by more than 100 times when compared to data from egg survival on the former sandy bottom. However, it was not determined if this area significantly increased overall recruitment in the system. In other projects, walleye have utilized artificially constructed reefs with apparent embryo development and hatching, but a significant input to young or adult populations again has not been observed (Weber and Imler 1974, McKnight 1975, Newburg 1975, Wagner 1990, Geiling et al. 1996, Neuswanger and Bozek 2004). For example, Neuswanger and Bozek (2004) evaluated 20 different reef projects in northern Wisconsin and no project that constructed an artificial reef showed a significant increase in the adult walleye population without other management applications. In a survey of walleye habitat enhancement projects in Ontario, Canada, most evaluations were subjective (e.g., an opinion from the biologist, not concrete data) or preliminary, but determined that success was low for supplementing a self-sustaining population and did not work when reproduction was limited (Geiling et al. 1996). Therefore, the goal of increasing recruitment was not achieved in numerous artificial reef projects, potentially because spawning habitat was not the limiting factor in these systems, because the extent of the project was too small, or the structural components and placement were not conducive to successful reproduction. Based on this study, restoration or enhancement should consider the potential total amount of spawning habitat needed to increase recruitment, placed nearshore and in shallow water, and composed of gravel, cobble, and sand substrates with low rock embeddedness.

Although this study began to close the knowledge gap on successful walleye spawning habitat, additional quantitative research would further increase our understanding of this important area of walleye reproduction. First, Big Crooked Lake is only one self-sustaining walleye population. Reproductive success may vary annually and between systems and walleye have been shown to be variable in their spawning habits. Therefore, evaluating different systems would be highly beneficial to the understanding of what comprises quality spawning habitat. A more detailed or controlled study of egg survival based on habitat variables such as depth, distance to shoreline, substrates, and embeddedness would also offer further define what comprises quality habitat. Similarly, the quantity of spawning habitat necessary for a self-sustaining population in any given lake is still relatively unclear. Additional studies would provide insight into whether a lake is limited by spawning habitat and a candidate for restoration or enhancement projects. Future study of adhesive eggs can further clarify specific habitat selection, and also spawning timing, egg survival, habitat saturation, and general spawning behavior. Lastly, if a lake is determined to be a candidate for a spawning habitat project, both pre- and post-evaluations should be conducted to determine if the project was successful in reaching the goal of increasing reproductive success and moving towards a self-sustaining population.

CHAPTER 2: Thermal conditions on walleye spawning reefs during two spawning seasons in a north temperate lake; implications for reproductive success

ABSTRACT

Variations in spring water temperatures can strongly influence walleye populations by directly and indirectly affecting reproductive success. As a key component of high quality spawning habitat, differences in water temperatures on spawning reefs may help explain why fish select specific locations for spawning. To understand thermal conditions at spawning reefs in Big Crooked Lake, a north temperate Wisconsin lake, thermal variability between 2004 and 2005, among different sites, and at locations within sites (reefs) were evaluated and the potential impact on incubating eggs was considered. In 2004, water temperature gradually rose but began below optimal fertilization and lethal limits (6°C), concurrent with lower egg survival rates. In 2005, thermal conditions fluctuated, but stayed above 6°C, resulting in higher hatching rates. In 2004, significant differences ($p < 0.05$) in mean daily water temperature throughout the spawning period occurred among three spawning reefs, apparently due to the water depth adjacent to each reef and their locations in the lake. Overall, shallow water (<0.25 m) adjacent to shore, where walleye egg densities were highest, responded more to fluctuations in air temperatures and also tended to be cooler than the more stable, deeper water (>0.60 m) at all reefs, but this difference was not always significant ($p < 0.05$). The results of this study demonstrate that walleye are subjected to varying thermal conditions across years, among sites within years, and even within sites. These differences may directly affect egg survival through success of fertilization and lethal limits, and also indirectly through embryo development rates, predisposing eggs to other factors influencing egg survival for longer periods of time.

INTRODUCTION

Annual spring water temperatures have been considered a dominant factor in reproductive success and formation of year-classes in walleye (*Sander vitreus*) populations (Busch et al. 1975, Madenjian et al. 1996, Hansen et al. 1998). Water temperatures, and especially spring warming water rates, provide a physical cue for adult walleye to initiate spawning activity and deposit eggs (Priegel 1970, Hokanson 1977). In north temperate lakes, walleye migrate towards spawning areas before or at ice-out and congregate until thermal conditions are desirable (Eschmeyer 1950, Ellis and Giles 1965, Priegel 1970). Physical deposition of eggs typically occurs with warming water rates (Priegel 1970, Hokanson 1977). On the other hand, fluctuating, especially descending, water temperatures may prolong spawning (Priegel 1970, Hokanson 1977) or result in females retaining eggs as suggested by Derback (1947), although egg retention or resorbtion appears relatively unstudied. Thus the duration of annual spawning periods are influenced by thermal conditions (Priegel 1970, Hokanson 1977).

Spring water temperatures may also influence hatching success during egg fertilization and determine the rate of embryo development. In the laboratory, optimum fertilization of walleye eggs occurs at temperatures between 6 and 12°C (Koenst and Smith 1976). Hatching success decreases above these temperatures and temperatures below 6°C can be lethal to embryos (Koenst and Smith 1976). In both the laboratory and the field, egg development declines with lower temperatures, thus increasing the days to hatch and the length of the overall incubation period (Johnson 1961, Priegel 1970, Koenst and Smith 1976). While walleye eggs are fairly robust to relatively high temperature fluctuations, stress or mortality can occur with drastic fluctuations or prolonged extreme water temperatures. Walleye eggs have been shown to develop to the black-eyed stage with temperature fluctuations as great as 21.1°C and hatching success was not influenced by temperature fluctuations up to 13.6°C over 12 hours (Albaugh and Manz 1964, Schneider et al. 2002). However, prolonged extreme water temperatures may stress developing embryos and increase the percentage of abnormal fry (Koenst and Smith 1975, Schneider et al. 2002). For example, Koenst and Smith (1975) recorded 1.0% and 3.8% abnormal fry for eggs incubated from 6 to 15°C, respectively, while the number of abnormal fry increased to 15% and 18% for eggs incubated at 18°C and 21°C, respectively. In addition, extended or consistent incubation intervals below 6°C and above 19 to 21°C proved lethal to walleye embryos (Koenst and Smith 1975, Schneider et al. 2002).

The affects of spring water temperatures on year-class strength of walleye have been equivocal. Some studies have shown correlations between year-class strength of walleye and spring water temperatures (Johnson 1961, Busch et al. 1975), while others have found weak or no relationships (Kempinger and Carline 1977, Serns 1982b, Madenjian et al. 1996). Based on egg survival rates, Johnson (1961) felt that walleye reproductive success was higher in years with stable, rising water temperatures. In Lake Erie, Busch et al. (1975) found year-class strength was most related to the rate of water warming whereas Madenjian et al. (1996) found spring water temperature had a positive, but weak relationship to walleye recruitment. In Escanaba Lake, Wisconsin, the variation of spring water temperatures correlated with walleye year-class strength (Serns 1982b, Hansen et al. 1998). In contrast, Kempinger and Carline (1977) did not find a relation between walleye recruitment and temperatures during incubation in Escanaba Lake.

Although studies have correlated the importance of fluctuating water temperature to walleye year-class strength, specific studies on thermal conditions of spawning reefs is unclear. In particular, how thermal differences between years may impact survival (e.g., how often lethal limits are exceeded) and whether eggs incubating at different locations in the lake (i.e. different spawning reefs) or within a reef (i.e., water depth, distance to shore) attain a thermal developmental advantage or are buffered from thermal stresses. Thus, there is a need to assess thermal conditions present at spawning sites to further understand relations between annual thermal conditions and walleye year-class-strength. Therefore, the specific objectives of this study were to evaluate thermal conditions and the potential impact on walleye reproductive success:

1) between years (inter-annual),
2) between three geomorphically different spawning areas (inter-reef), and
3) at different locations within spawning reefs (intra-reef).

METHODS

Study site

This study was conducted on Big Crooked Lake, Vilas County, Wisconsin, in 2004 and 2005. Big Crooked Lake is entirely surrounded by land owned by Dairymen's Incorporated, a private resort near Boulder Junction. The riparian area is forested, with development along the 8.1 km of shoreline limited to a lodge and several cabins on a stretch of the north shore. The lake is oligotrophic, 276 ha in size, and has a maximum depth of 11.6 m. The fish community consists of walleye, smallmouth bass (*Micropterus dolomieu*), muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), yellow perch

(*Perca flavescens*), rock bass (*Ambloplites rupestris*), white sucker (*Catostomus commersoni*) and various minnows (*Cyprinida*e) and darters (*Percidae*).

Big Crooked Lake has a naturally reproducing and self-sustaining walleye population. Walleye may have initially been introduced to the lake, but reliable historical records of introduction are absent. Currently, the lake is one of four lakes in the ceded territory of northern Wisconsin utilized by the Wisconsin Department of Natural Resources (WDNR) for walleye exploitation rates research (S.P. Newman, WDNR, personal communication).

The lake contains three classical walleye spawning habitat types: rock shorelines, point bars, and islands. One of each type was selected for detailed study of their thermal properties during walleye spawning and egg incubation: a relatively linear rock shoreline in the northwest corner of the lake ("shoreline"), a point rockbar in the south-central portion of the lake ("point"), and an island located in the southeastern bay ("island")(Figure 2-1). These three study reefs were each used by walleye for spawning during this study and were described in detail in Chapter 1.

Spawning Chronology

The spawning chronology of adult walleye was followed throughout the 2004 and 2005 spawning seasons in Big Crooked Lake. In order to track spawning adult walleye, six standard WDNR fyke-nets were installed perpendicular from the shore immediately upon lake-wide ice-out and were checked each morning. Each sampled walleye was fin clipped until an adequate number of fish were marked (approximately 10% of the population). The point at which 85% of adults spawned and the peak of spawning were estimated by nightly catch numbers and reproductive status determined upon handling.

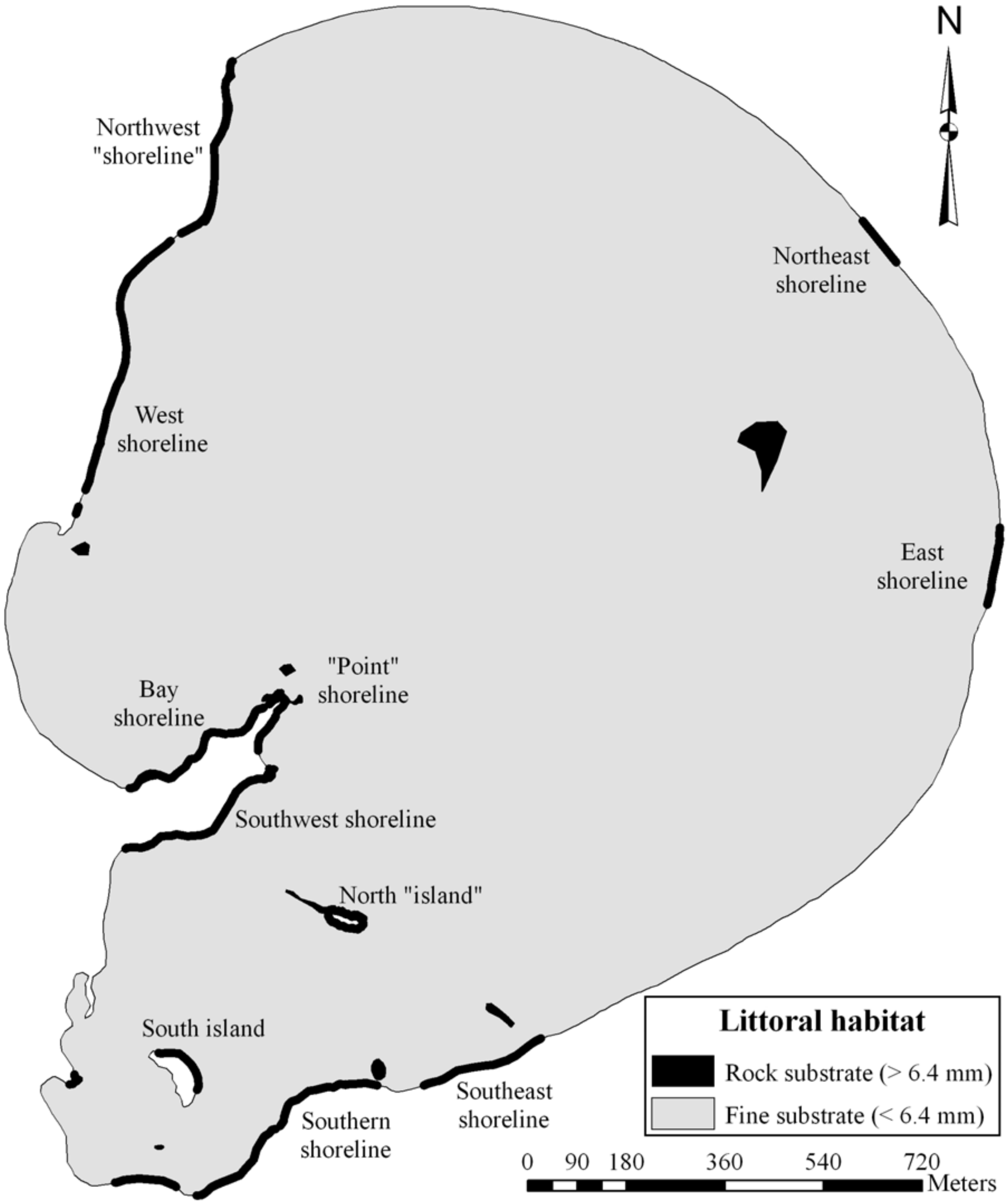


Figure 2-1. Locations of rock substrates (gravel, cobble, rubble, etc.)(any material ≥ 6.4 mm) including the three study reefs compared to fine substrates in the Big Crooked Lake littoral zone (<3.0 m of water depth). Sand substrate dominated the littoral habitat, while rock substrate was primarily nearshore and in the western half of the lake.

Individual walleye were recaptured using a standardized AC, WDNR boom electrofishing boat and population estimates were conducted using the Peterson method (Ricker 1975) in order to estimate the walleye stock size:

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

Where: N = size of population at time of marking

M = number of walleye marked

C = sample taken for census (catch)

R = number of recaptured walleye in sample

Upon egg deposition, thirty live eggs were collected daily from spawning areas to determine embryo development and larval emergence. In particular, the development of black-eye pigment and then later, the physical movement of the embryo within the chorion were considered two separate, late stages of development. Eggs were collected at the point study reef in 2004 and the shoreline study reef in 2005. To collect these eggs, the bottom substrate was agitated by foot and a mesh collector was brought through the turbulent water to collect suspended eggs. Using forceps, viable eggs were removed from the collector and placed into a labeled vial containing 10% formalin. Field observations of embryo development were recorded along with laboratory observations using a dissecting microscope. The start of hatching was determined by visual observations of embryos in collection chambers and through collection of walleye in night boat tow-net surveys.

Inter-annual Thermal Variation

Thermal conditions during the two walleye spawning seasons in Big Crooked Lake were recorded using temperature data loggers (Richard Brancker Research, Model XL-800)(Accuracy = $\pm$0.07 °C) installed at the three study reefs in Big Crooked Lake. The data loggers were installed immediately upon lake-wide ice-out and each unit had eight probes that measured hourly air and water temperature across each reef. To record air temperature, the first probe was suspended in the air approximately 25 cm from land using a metal wire, while a second probe was placed in the water at the land-water interface (0 m). Additional probes were placed 1.0 m and 2.0 m from shore, and the remaining four probes were positioned along a transect running perpendicular from the shoreline and equidistantly to cover the entire rock reef. Therefore, the locations of probes were different between the three reefs. Probes were placed relative to their distance to shoreline to standardize comparisons and because water depth potentially could fluctuate. Data was downloaded from each temperature logger after all eggs had hatched. For inter-annual comparisons, the mean daily water temperature was determined as the mean of the three temperature data loggers located at the study reefs in 2004. In 2005, the temperature data loggers at the point and island study reefs did not work properly throughout the spawning season. Therefore, the daily mean water temperature was the mean at the shoreline study reef only. To visually compare the two years, charts of the daily mean water temperature throughout the entire spawning periods were constructed in Microsoft Excel (Microsoft Corporation 2001).

Thermal units were calculated to compare thermal conditions and embryo development between years, between reefs, and within reefs were studied. Two different thermal indices were calculated for each spawning period. The first method, basic thermal units (BTU), was the cumulative sum of the mean daily water temperature above 0°C for each day post-fertilization (McElman and Balon 1979). The second method, quadratic thermal units (QTU), used a quadratic regression equation developed by Jones et al (2003):

$$Y = 0.0479T^2 - 0.2385T + 2.499$$

Where: Y = predicted % ("units") of development / day

T = mean daily water temperature (°C).

Development units were successively summed each day during the spawning period and Jones et al. (2003) assumed eggs hatched once 100 egg development units was reached.

Inter-reef Thermal Variation

Thermal conditions can vary within a lake, potentially influencing embryo development rates at different spawning sites. Therefore, descriptive statistics, thermal units, and paired t-tests analyses were evaluated to compare differences in water temperature among the three spawning sites. Inter-reef comparisons were conducted for 2004 but could not be completed for 2005 as data was only available from the shoreline reef. Hourly water temperature means were determined from the first four (0-3 m) water probes that were placed at the same distance from shoreline at each reef. Paired t-tests were conducted in Number Cruncher Statistical Systems (NCSS)(Hintz 2004) to determine any differences in daily mean water temperature between reefs. Paired t-tests were used because the data (daily mean water temperatures for the entire spawning period) was continuous (i.e., repeated measures). For consistency, BTU were compared between years using data from the probe 2.0 m from shore at the shoreline study reef.

Intra-reef Thermal Variation

Thermal conditions may differ within individual reefs, potentially providing a thermal advantage towards incubating at a certain reef location (e.g., relative to water depth). To test for thermal differences within the reefs, descriptive statistics, thermal units, and paired t-tests analyses were evaluated for various distances to shore and water depths. At each study reef, three paired t-tests in NCSS evaluated differences in daily mean water temperature relative to location on the reef. The first set of tests evaluated the two extreme probe locations (i.e., closest and furthest probe), the second set evaluated the next extremes (i.e., second closest and second furthest probe), and the third set evaluated two middle locations. Regular t-tests were also conducted in NCSS between different reef locations and water temperatures over the course of 24 hours to evaluate daily thermal differences.

Egg Density and Survival

Egg density and percent survival were quantified at the three study reefs to evaluate potential impacts of thermal conditions. Thirty egg collection chambers (diameter = 0.25 m) were installed on each of three spawning reefs immediately upon ice-out. Five transects along each reef had six chambers, with the first chamber placed at the shoreline-water interface, the second chamber at 1.0 m from the shoreline, and the third at 2.0 m from the shoreline. The remaining three were placed equidistantly across the remainder of the reef, therefore differing according to each study reef. The water depth, distance from shoreline, percent substrate composition and substrate embeddedness were recorded or estimated for each collector. Upon completion (100%) of spawning activity and egg deposition, half (15) of the collectors were carefully removed from the substrate to assess distribution of eggs across the reef. The remaining 15 chambers were fitted with mesh and removed after hatching to assess success to fry swim-up. However, very few fry were recorded in either year. Therefore, the total number of eggs deposited and fry produced was estimated for each reef according to eggs deposition, survival rates and linear regression, described in further detail in Chapter 1.

RESULTS

Spawning Chronology

Walleye spawning chronology differed between the 2004 and 2005 spawning periods in Big Crooked Lake. In 2004, walleye eggs were deposited on April 22, the first day of complete ice-out (Figure 2-2, Table 2-1). By April 29, 85% of egg deposition had occurred. During the spawning period, there was an estimated adult population of 1,992 ± 425 individuals (95% C.I.); it is possible that a few juvenile males may have been in spawning areas. Incubating eggs began to develop black eyes around May 8; 17 days after the first deposited eggs. Movement was observed within the chorion five days later on May 13, and hatching began two days later on May 15. No live eggs were observed on the spawning reefs after May 23 (Figure 2-2, Table 2-1). Therefore, hatching lasted approximately eight days, with the total spawning period (first spawn to last swim-up fry) lasting 32 days.

In 2005, the spawning period was longer, lasting a total of 38 days. Deposited eggs were first observed on April 16, one day after lake-wide ice-out (Figures 2-2, Table 2-1). Peak spawning appeared to occur on April 20 and by April 23 an estimated 85% of adults had spawned. Egg deposition was completed by April 26 as adhesive eggs were not found after this date, with one exception. On May 5 a patch of adhesive eggs was

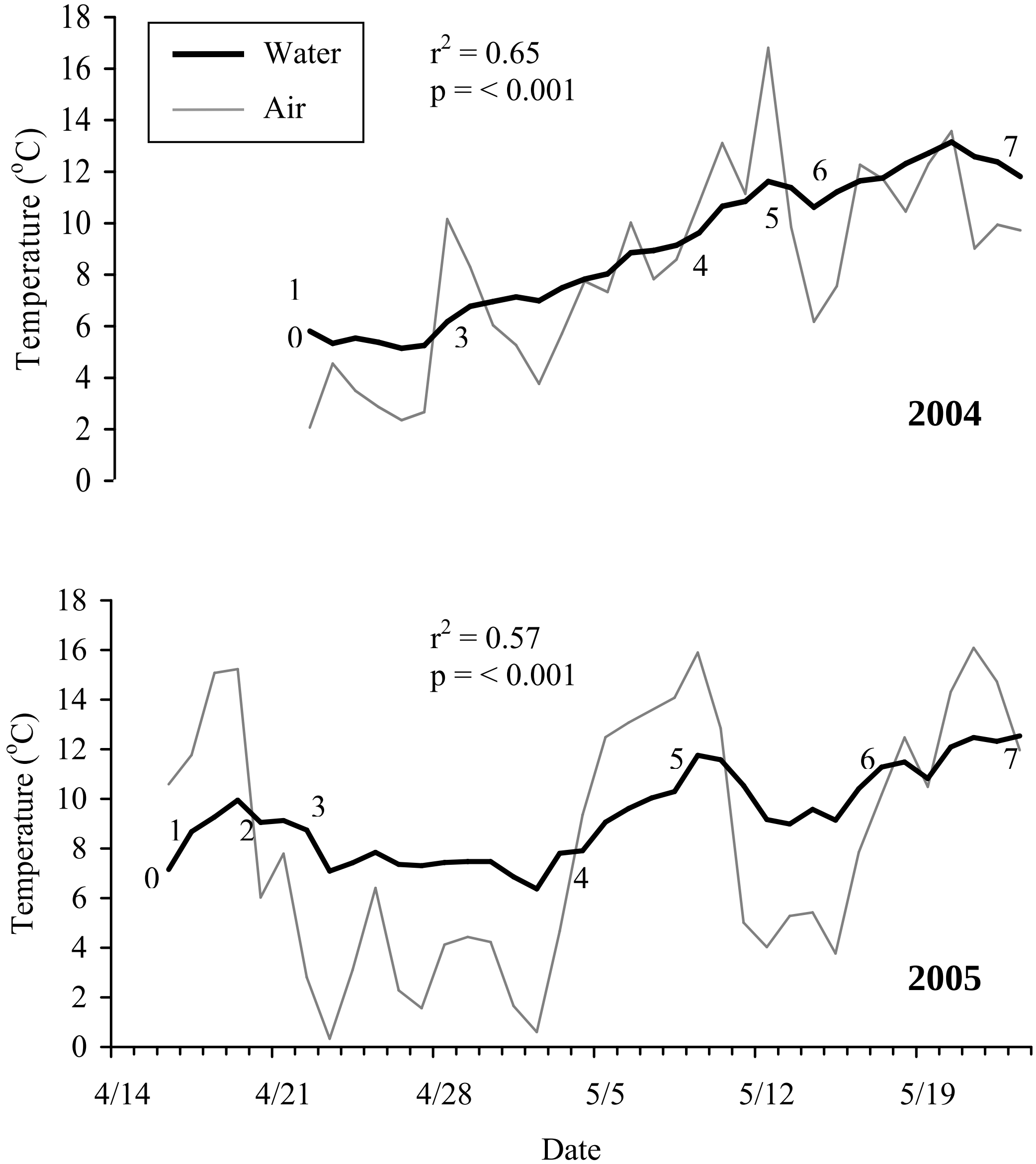


Figure 2-2. Mean daily water and air temperatures during the walleye spawning seasons in 2004 and 2005 in Big Crooked Lake. Spawning chronology stages were: 0 = lake-wide ice-out, 1 = egg deposition commencement, 2 = peak spawning, 3 = 85% female spawned, 4 = black-eyed stage, 5 = embryo movement stage, 6 = hatching commencement, 7 = hatching completion. Coefficients of determination tested the extent that air and water temperatures are synchronous (2004: $T_{water} = -1.83 + 1.11T_{air}$, p = <0.001, $r^2 = 0.65$; 2005: $T_{water} = 7.07 + 0.27T_{air}$, p = <0.001, $r^2 = 0.57$).

observed, however all eggs died, most likely due to a lack of fertilization or poor egg viability. The adult walleye population was estimated at 1,174 $\pm$ 291 individuals (95% C.I.); again, a few juvenile males may have been present. The black-eyed embryo stage was first observed on May 4, 19 days after the first deposited eggs. Embryo movement was observed five days later on May 9, but hatching did not occur for eight more days on May 17 (Figures 2-2, Table 2-1). Hatching lasted for approximately six days, as no live eggs were found on the spawning reefs after May 23; the total spawning period lasted 38 days.

Inter-annual Thermal Variation

Thermal conditions were noticeably different between the two years that may have influenced the spawning chronologies. The year 2004 was characterized as stable, with steadily rising water temperatures during the spawning and incubation periods (Figure 2-2). Immediately after ice-out, the mean daily water temperature cooled or stayed between 5.3 and 5.5°C for the first five days as walleye were depositing eggs (Figure 2-2, Table 2-1). By April 28, water temperature began to rise above 6.0°C when walleye completed egg deposition and continued to rise throughout the incubation period for two more weeks (April 30-May 12). Eggs developed black eyes by May 8, when the mean daily water temperature was 9.1°C (Figure 2-2, Table 2-1). Despite a minor cooling period from May 13 to 15, embryo movement was observed within the chorion on May 13 and hatching began two days later on May 15 at 12.2°C. The water temperature continued to rise for the next three days of hatching (May 16 - 18), but cooled slightly during the final days of larval emergence that was completed by May 23 (Figure 2-2, Table 2-1).

Table 2-1. Chronology of the walleye spawning periods in 2004 and 2005 in Big Crooked Lake. The date, number of days, mean temperature (mean T), and quadratic (QTU) and basic (BTU) thermal units presented for seven different stages of development from the beginning of spawning through hatching completion.

	2004					2005				
Spawning stage	Date	# of Days	Mean T	QTU	BTU	Date	# of Days	Mean T	QTU	BTU
Ice-Out	4/22	1	-	-	-	4/15	0	-	-	-
Spawning	4/22	1				4/16	1	7.16	3.3	7.2
Peak spawning	-	-	-	-	-	4/20	5	9.06	21.1	44.5
85% spawned	4/29	8	6.77	19.7	42.1	4/23	8	7.09	32.6	69.3
Eyed eggs	5/8	17	9.14	53.7	115.6	5/4	19	10.29	69.6	150.6
Movement	5/13	22	11.37	82.6	171.1	5/9	24	8.98	95.2	201.7
Hatching	5/15	24	11.21	94.2	193.4	5/17	32	11.29	134.8	281.7
Completion	5/23	32	11.81	149.8	292.9	5/23	38	12.54	173.7	353.3

A longer spawning period in 2005 was likely a result of fluctuating and prolonged cool water temperatures. Ice-out occurred on April 15 and the mean daily water temperature rose drastically from 7.2°C on April 16 to 9.95°C on April 19 (Figure 2-2, Table 2-1). Water temperature cooled on April 20 and continued to decrease or stay cool until May 2, for a total cool period of 14 days. The majority, but not all adult walleye spawned during the warming period as peak spawning was estimated to occur on April 20 and by April 23 an estimated 85% of adults had spawned. The lowest daily mean water temperature of the 2005 spawning period (6.4°C) was reached on May 2, and then warmed stably to 11.8°C by May 9 (Figure 2-2, Table 2-1). The embryos eventually reached the black-eyed stage (May 4) after the prolonged cooling period. Embryo movement occurred on May 9, but a cooling period from May 10 to 16 having a low of 9.0°C appeared to delay larval emergence; hatching did not occur until May 17 when water temperatures rose again. The water temperature then rose until the end of the spawning and incubation period on May 23, when larval emergence was completed (Figure 2-2, Table 2-1).

In both years, water temperatures tracked air temperatures (2004: $T_{water} = -1.83 + 1.11T_{air}$, $p = <0.001$, $r^2 = 0.65$; 2005: $T_{water} = 7.07 + 0.27T_{air}$, $p = <0.001$, $r^2 = 0.57$). Air temperatures were more variable and water temperatures showed less fluctuations relative to air temperature swings. Thermal units depicted similar differences between the spawning seasons. In 2004, an estimated 85% of walleye spawned at 42.1 BTU (19.7 QTU), while in 2005 this stage occurred at 69.3 BTU (32.6 QTU)(Table 2-1). The black-eyed embryo stage was reached faster in 2004 at 115.6 BTU (53.7 QTU) compared to 150.6 BTU (69.6 QTU) in 2005. Movement within the chorion was observed at 171.1

BTU (82.6 QTU) in 2004 and at 201.7 (95.2 QTU) in 2005. Actual hatching began at 194.3 BTU (94.2 QTU) in 2004 but not until 281.7 BTU (134.8 QTU) in 2005. In 2004, all eggs had hatched by 292.9 BTU (149.8 QTU) compared to 353.3 BTU (134.8 QTU) in 2005. By hatching completion, thermal units in 2005 surpassed 2004 thermal units due to thermal warming at the end of the spawning period (Table 2-1).

In both spawning periods at the shoreline study reef (2.0 m from shore, water depth = 0.29 m in 2004, 0.27 m in 2005), minimum lethal thermal limits were exceeded but maximum lethal thermal limits never were exceeded (Figure 2-3). In 2004, the minimum and maximum hourly water temperatures were 4.2°C and 14.6°C, respectively, compared to 5.2°C and 14.8°C, respectively, in 2005. In 2004, the first six days of the spawning period had minimum water temperatures below 6°C, and eight days had minimum water temperatures below 6°C (Figures 2-2, 2-3). In 2005, no day had a mean temperature below 6°C and only four days had a hourly water temperatures below 6°C (Figures 2-2, 2-3).

Inter-reef Thermal Variation

There were significant differences ($p < 0.05$) in water temperatures among spawning reefs in Big Crooked Lake during the 2004 spawning and incubation periods. In 2004, the shoreline spawning reef had the warmest mean water temperature of the three study reefs at 9.5 $\pm$ 0.47°C (standard error) for the entire spawning period. In comparison, the point reef had a mean water temperature of 9.2 $\pm$ 0.49°C (standard error) and the island was the coolest spawning reef with a mean water temperature of 8.9 $\pm$ 0.48°C (standard error). The shoreline study reef also accumulated the highest total of

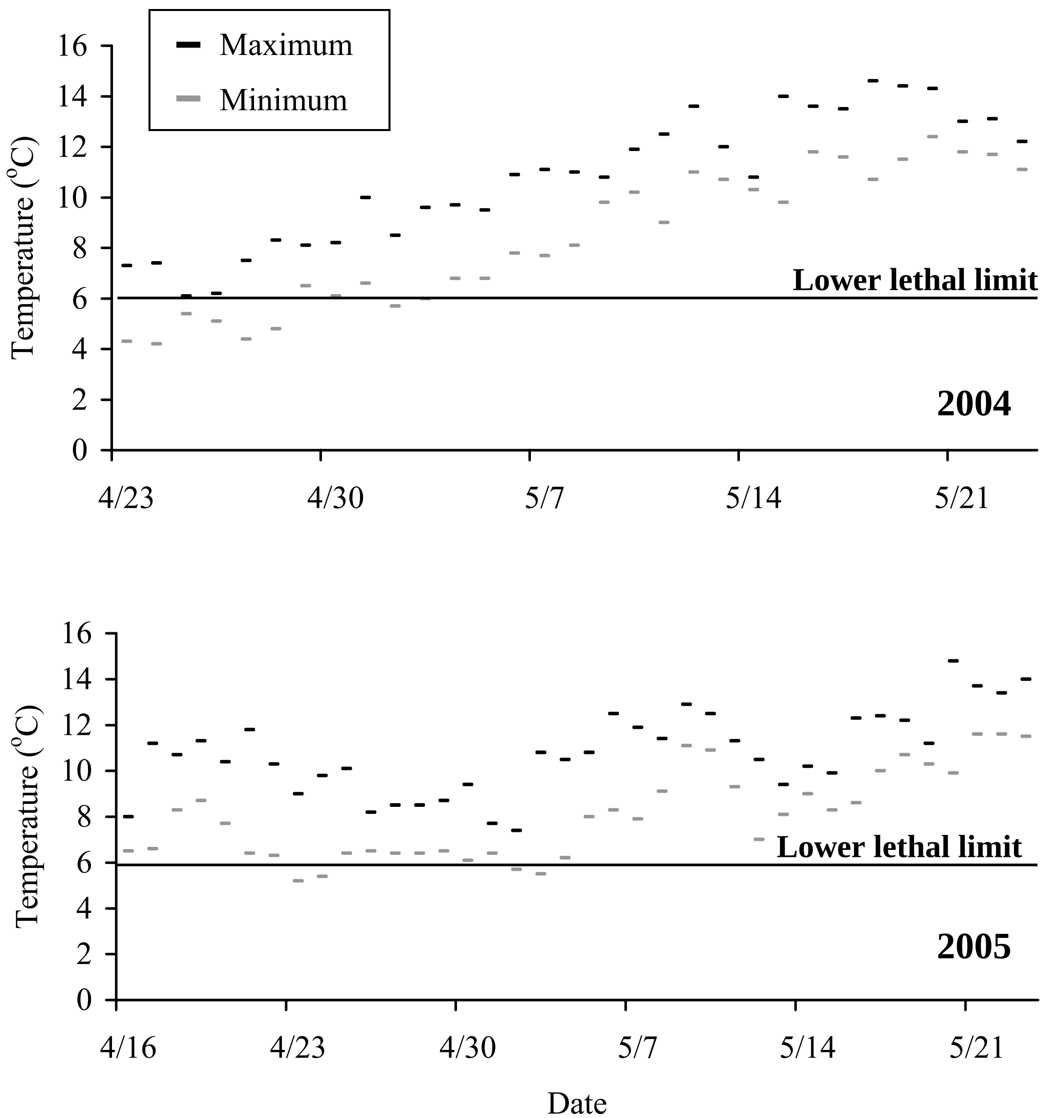


Figure 2-3. Daily minimum and maximum water temperatures at 2.0 m from the shoreline (water depth = 0.29 m in 2004, 0.27 in 2005) at the shoreline study reef during the 2004 and 2005 walleye spawning periods in Big Crooked Lake. The black line represents the potential lower lethal minimum temperature (6°C) for developing embryos. Minimum temperatures fell below this limit 7 times in 2004 and 3 times in 2005. Note: the first day (ice-out) was not included as temperature data loggers were installed in the afternoon.

BTU at 293.6 (150.6 QTU), compared to 285.6 BTU (145.9 QTU) at the point study reef and 277.8 BTU (140.7 QTU) at the island study reef.

Intra-reef Thermal Variation

Among seven thermal probes at each reef, there was a general pattern of shallower probes being more responsive to changes in air temperature than deeper water probes. In testing differences throughout each reef, there was a significant difference ($p < 0.001$) between the deepest and shallowest probes at the shoreline reef in 2004 (Table 2-2, Figure 2-4). Interestingly, there were significant thermal differences ($p < 0.001$) throughout the island reef in 2004 (Table 2-2, Figure 2-4). There were no significant thermal differences ($p > 0.05$) at the point reef in 2004 (Figure 2-4) or the shoreline reef in 2005 (Figure 2-5). While there were significant differences within the reefs, the differences were relatively small, with the greatest difference only 0.22°C in mean daily water temperature for the entire spawning period (Table 2-2). In addition, only minor differences were seen in the cumulative thermal units (Table 2-2).

Although the degree of difference throughout the spawning period varied for mean daily water temperature within the reefs, it was clear that the shallow water was more responsive. As expected, air temperatures had diel fluctuations, with the coolest air temperatures typically at night and warmest air temperature typically during the mid-day. Water temperatures followed this diel trend in air temperatures (shoreline reef, 2.0 m from shore, 2004: $T_{water} = 8.11 + 0.14T_{air}$, $p = <0.001$, $r^2 = 0.14$; 2005: $T_{water} = 7.23 + 0.24T_{air}$, $p = <0.001$, $r^2 = 0.54$), but due to the higher specific heat of water, it was less variable. Water close to the shoreline and in shallow water also had a response time, but was more responsive to changes in air temperature than water further from shoreline and

Table 2-2. Paired t-tests evaluating potential differences in mean water temperature (standard error) within spawning reefs for the 2004 and 2005 walleye spawning periods in Big Crooked Lake. For additional comparisons, the quadratic thermal units (QTU) at the completion of fry hatching are also presented.

Location	Distance to shore (m)	Water depth (m)	Mean Temp (°C)	Δ Temp (°C)	P	QTU
2004						
Shoreline	0.0	<0.10	9.4 ± 0.47	-0.121	<0.001	149.8
	6.0	0.66	9.6 ± 0.47			152.2
Shoreline	1.0	0.19	9.5 ± 0.47	0.049	0.291	151.0
	4.0	0.47	9.4 ± 0.47			149.6
Shoreline	2.0	0.29	9.4 ± 0.47	-0.029	0.274	149.8
	3.0	0.41	9.5 ± 0.47			150.4
Point	0.0	<0.10	9.2 ± 0.48	0.053	0.294	144.9
	10.0	0.73	9.1 ± 0.48			143.9
Point	1.0	0.19	9.2 ± 0.49	0.008	0.835	145.7
	8.0	0.60	9.2 ± 0.49			145.1
Point	2.0	0.33	9.3 ± 0.48	0.021	0.125	147.0
	5.0	0.30	9.3 ± 0.49			146.7
Island	0.0	<0.10	8.8 ± 0.49	-0.221	<0.001	138.5
	8.0	0.91	9.1 ± 0.48			142.1
Island	1.0	0.17	8.9 ± 0.48	-0.156	<0.001	139.3
	6.0	0.55	9.0 ± 0.48			142.1
Island	2.0	0.31	8.9 ± 0.48	-0.099	<0.001	139.7
	4.0	0.44	9.0 ± 0.48			141.4
2005						
Shoreline	0.0	0.05	9.2 ± 0.33	-0.111	0.377	173.8
	10.0	0.88	9.3 ± 0.27			173.7
Shoreline	1.0	0.15	9.3 ± 0.30	-0.012	0.880	174.3
	8.0	0.71	9.3 ± 0.27			173.2
Shoreline	2.0	0.27	9.3 ± 0.29	-0.016	0.711	173.7
	6.0	0.57	9.3 ± 0.28			173.6

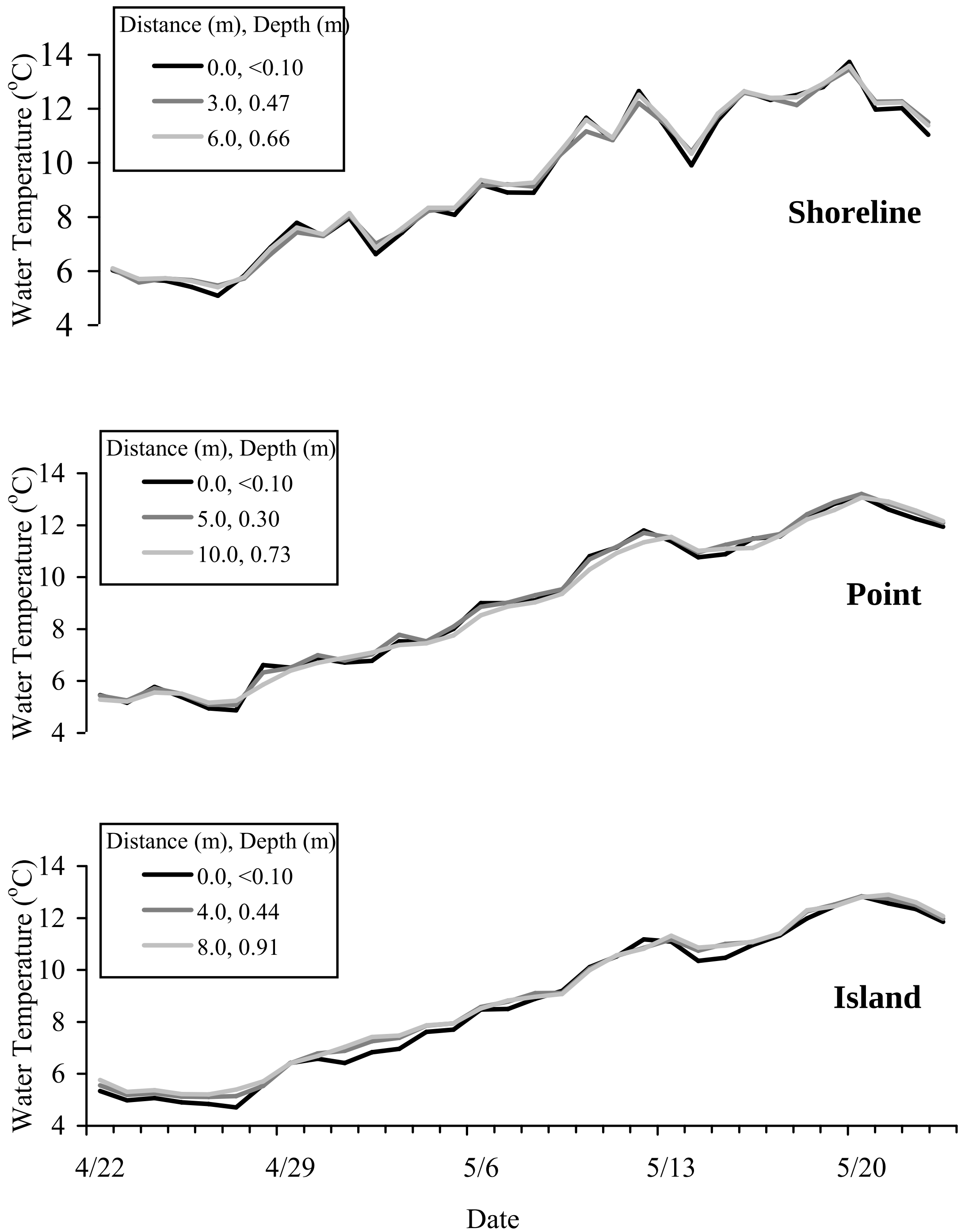


Figure 2-4. Daily mean water temperatures at three locations on each study reef during the 2004 walleye spawning period in Big Crooked Lake. The probes at the closest distance to shore and shallowest water tended to respond more to fluctuations in air temperatures than further, deeper water that was more stable. These differences were sometimes significant ($p < 0.05$), but were relatively small.

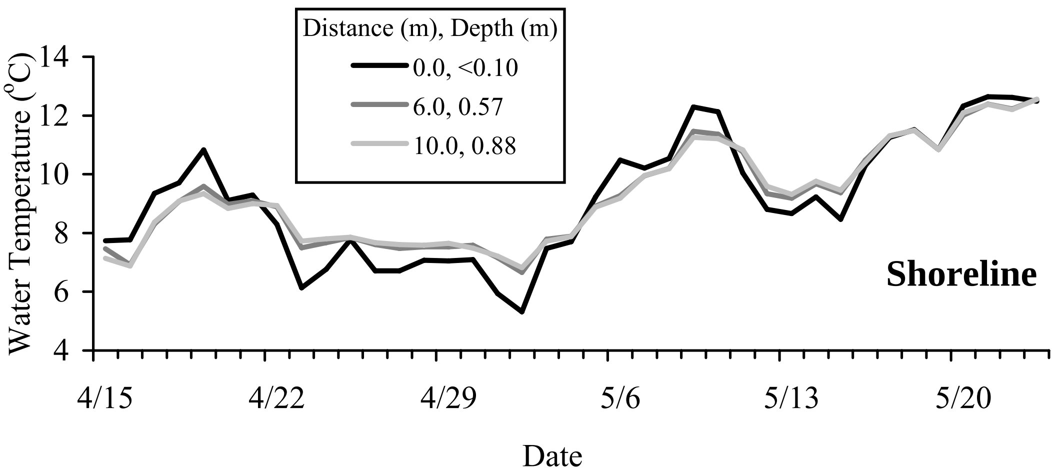


Figure 2-5. Daily mean water temperatures at three locations on the shoreline study reef during the 2005 walleye spawning period in Big Crooked Lake. The probes at the closest distance to shore and shallowest water tended to respond more to fluctuations in air temperatures than further, deeper water that was more stable. However, these differences were not significant ($p > 0.05$) and were relatively small.

deeper (Figures 2-4, 2-5, 2-6). On days with higher air temperature fluctuations, the differences in changing water temperatures were tended to be significantly different between locations on the reef while days with minor air fluctuations resulted in water temperature fluctuations that tended to not be significant within the reefs. For example, during the egg deposition period on April 19, 2005, air temperature remained relatively warm ($\bar{x}$ = 15.2°C) and water temperatures at 1.0 m from the shoreline remained significantly ($p < 0.001$) warmer (10.5 $\pm$ 0.15°C, S.E.) than water at 8.0 m from the shoreline (9.4 $\pm$ 0.17°C, S.E.) according to two-sample t-tests for temperatures tested on that day (Figure 2-6). However, during the egg incubation period on April 29, 2005 ($\bar{x}$ = 4.4°C), water 1.0 m from the shoreline (7.4 $\pm$ 0.20°C, S.E.) followed minor fluctuations in air temperature more closely than the 8.0 m from shoreline water (7.6 $\pm$ 0.12°C, S.E.), but these differences in water temperature between distances from shore were not significant ($p > 0.05$)(Figure 2-6).

Egg Density and Survival

Egg densities across spawning reefs were higher in 2004, but the survival rates were lower when compared to 2005. An estimated total of 19,031,064 eggs were deposited at the three study reefs in 2004 (Table 2-3). For the three reefs combined, the mean egg survival rate was 12.6% with an estimated 2,400,698 fry (live eggs) emerging from the reefs. Egg densities were significantly lower in 2005 at all three study reefs, with an estimated total deposition of 258,730 eggs (Table 2-3). However, the egg survival was higher at 25.1%, with an estimated 64,845 fry (live eggs) produced in 2005 from the reefs. In both 2004 and 2005, the highest density of eggs was located in collection chambers close to shore (0-1 m) and in shallow water (0.0-0.29 m)(Table 2-4).

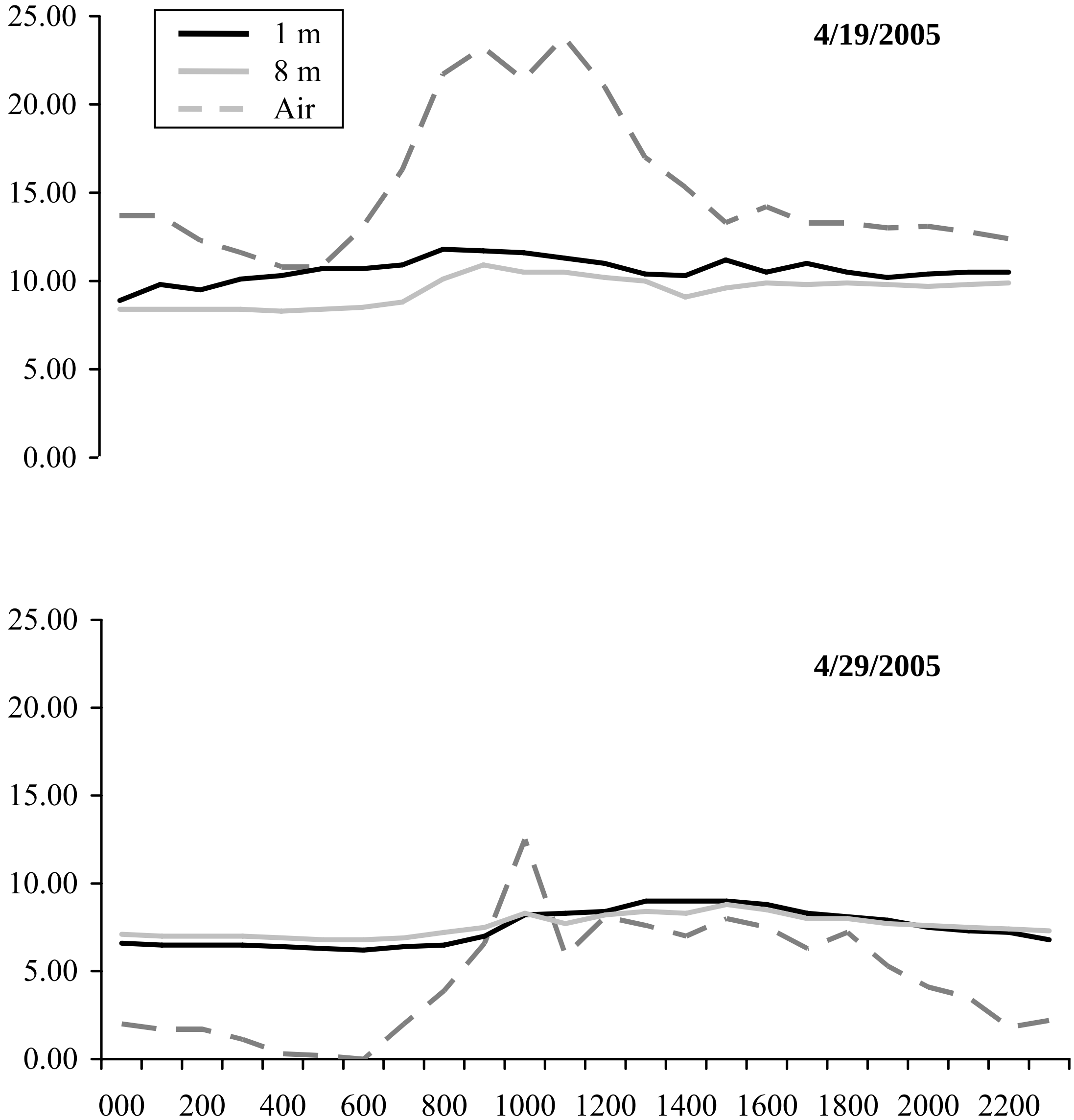


Figure 2-6. Example of daily fluctuations of water temperatures at 1 and 8 m from the shoreline relative to air temperature at the shoreline study reef in Big Crooked Lake in 2005. The closer to shore (and shallower) water was more responsive to changes in air temperature than the further, deeper water. (Note: differences in water temperature were significant ($p < 0.001$) on 4/19/2005 but were not significant ($p > 0.05$) on 4/29/2005.)

Table 2-3. Estimated number of live and total walleye eggs with percent egg survival in 2004 and 2005 at the shoreline, point, island reefs and the reefs combined. (Note: N = 15 for each spawning reef, N = 45 for three spawning reefs combined).

	2004				2005			
	Shoreline	Point	Island	Combined	Shoreline	Point	Island	Combined
Live Eggs	1,650,753	468,584	335,642	2,400,698	385,836	96,204	34867,	64,845
Total Eggs	11,362,447	6,671,229	997,390	19,031,065	1,663,676	258,730	186,473	258,730
Egg Survival (%)	14.5	7.0	33.7	12.6	23.2	37.2	18.7	25.1

Table 2-4. Mean number (standard error) of live and total walleye eggs with percent survival for egg collection chambers located in different ranges of distance to shore (m) and water depth (m) in 2004 and 2005.

Chamber Locations	Live Eggs	Total Eggs	% Egg Survival
2004			
Distance			
0-1 m	174.9 ± 47.71	1582.4 ± 528.54	11.1
2-4 m	23.5 ± 13.36	61.8 ± 26.87	38.0
6-8 m	3.7 ± 1.58	7.7 ± 4.06	48.1
Depth			
0-0.29 m	183.2 ± 49.65	1582.4 ± 528.54	11.6
0.3-0.49 m	25.7 ± 14.14	67.5 ± 30.16	38.1
0.5-1.12 m	4.3 ± 1.86	9.6 ± 4.76	44.3
2005			
Distance			
0-1 m	37.0 ± 26.95	160.4 ± 81.35	23.1
2-4 m	18.2 ± 10.63	67.1 ± 27.11	27.2
6-10 m	3.8 ± 2.09	9.4 ± 5.19	41.0
Depth			
0-0.29 m	37.1 ± 18.69	135.5 ± 54.62	27.4
0.3-0.49 m	4.9 ± 2.25	44.6 ± 22.74	11.0
0.5-1.12 m	1.8 ± 0.95	5.4 ± 3.60	33.9

There was a similar inverse correlation where live egg densities decreased with distance to shoreline and water depth, with very few eggs in the furthest, deepest egg collection chambers (Table 2-4).

Although the physical habitat stayed relatively constant between the years, the walleye egg deposition and survival rates differed among study reefs and among years at the individual reefs (Table 2-3). The shoreline study reef had the highest estimated live and total egg deposition of the three study reefs, with the intermediate survival rate both years. The island reef had the lowest densities of total and live eggs both years, but had the highest survival rate in 2004 and the lowest survival rate in 2005. The point study reef had the intermediate densities of total and live eggs both years and the survival was very poor in 2004, but then was the highest in 2005 (Table 2-3).

DISCUSSION

Thermal differences occurred between the two spawning periods in Big Crooked Lake. Water temperatures began low in 2004 and then steadily rose throughout the rest of the spawning period. Ice-out occurred earlier in 2005 and water temperatures rose initially, but then cooled and fluctuated throughout the remainder of the spawning period. Despite differences between ice-out dates and thermal fluctuations, adult walleye deposited eggs over a similar time-span as an estimated 85% of walleye spawned after eight days in both 2004 and 2005 and within the range of previously reported water temperatures of 2.2 to 15.6°C in both years (Priegel 1970, Hokanson 1977). Peak spawning occurred at a mean daily water temperature of 9.1°C in 2005, also falling into the range of 5.6 to 10°C from past studies (Niemuth et al. 1959, Becker 1983). In 2004, water temperature consistently rose during the incubation period in 2004 whereas in 2005 it cooled during portions of the incubation period. Despite these differences, the black-eyed egg stage was reached only a few days earlier in 2004 compared to 2005. Using standardized thermal units, eggs in Big Crooked Lake reached the black-eyed stage at 115.6 BTU and 150.6 BTU in 2004 and 2005, respectively. This is longer than the 76.2 BTU reported by McElman and Balon (1979) but before 152.2 BTU reported by Hurley for the black-eyed egg stage (1972). Movement of embryos within the chorion in Big Crooked Lake occurred at 171.1 BTU and 201.7 BTU in 2004 and 2005, respectively. This was much later than the observed movement at 81.2 BTU recorded by McElman and Balon (1979). The hatching of fry also occurred more rapidly in 2004 at 193.4 to 292.4 BTU, only two days after embryo movement was observed, possibly due to rising water temperatures. On the other hand, the cooling of water in 2005 resulted in major hatching being delayed for eight days past this same observed movement and between 281.7 and 353.3 BTU. Hurley (1972) observed a small prehatch at 194.9 BTU, but the majority of hatching was from 257.7 to 265.5 BTU; similar to 2004 but lower than 2005 in Big Crooked Lake. In 2004, eggs began to hatch at 94.2 QTU, below the 100 QTU suggested by Jones et al. (2003), while in 2005 eggs began to hatch at 134.8 QTU. Peak hatching also occurred at lower water temperatures (11.2-12.5°C) in both years than previously recorded temperatures of around 15°C (Koenst and Smith 1976, Engel et al. 2000). Due to the delayed hatching of fry, the 2005 spawning period lasted six days longer (38 days) than the 2004 spawning period (32 days). Both spawning periods lasted slightly longer than past studies that have recorded incubation to swim-up fry periods ranging from 10 to 27 days in the wild (Niemuth et al. 1959, Johnson 1961, Priegel 1970, Engel et al. 2000) and from 5 to 30 days in a laboratory setting (Hurley 1972, Koenst and Smith 1976, McElman and Balon 1979).

Thermal conditions during egg deposition and incubation may not have been ideal in either year of this study for recruiting young walleyes. In 2004, more adult walleye spawned, broadcasting more eggs, but survival was reduced, whereas fewer walleye spawned in 2005, broadcasting fewer eggs, but survival was higher. Although 2004 had steadily warming water temperatures, the first five days of the spawning season were below the lethal temperature limits of walleye egg survival. These temperatures also fell below the optimal fertilization thermal ranges for walleye eggs, potentially resulting in direct egg mortality (Koenst and Smith 1976, Schneider et al. 2002). In 2005, temperatures were reduced during portions of incubation and the overall incubation period was longer, but did not appear to directly impact egg mortality. This finding is consistent with studies indicating that walleye eggs are fairly robust to temperature fluctuations; developing to the black-eyed stage with fluctuations as great as 20.2 to 21.1°C (Albaugh and Manz 1964, Schneider et al. 2002). In addition, percent hatching success was not significantly affected by swings up to 13.6°C over 12 hours compared to eggs incubated with minimal or no temperature fluctuations (Schneider et al. 2002). Over both study years, the greatest daily temperature fluctuation was 5.4°C in 2005, well below the experimental swings that did not affect development or hatching. Large temperature fluctuations have been shown to stress developing embryos and increase the percentage of abnormal fry (Koenst and Smith 1975, Schneider et al. 2002), but the fluctuations experienced in Big Crooked Lake were relatively minor and most likely did not result in abnormal fry. Koenst and Smith (1975) recorded 1.0 to 3.8% abnormal fry for eggs incubated from 6 to 15°C, respectively, and both incubation periods were primarily in this range. Overall, the prolonging of the incubation period in 2005 did not appear to result in higher mortality by environmental factors such as wave energy or predation, as implied by Busch et al. (1975), while the initial thermal conditions below 6°C may have strongly impacted the egg survival in 2004.

The influence of inter-annual thermal conditions on egg survival in this study were not definitive (i.e., not tested directly), but other studies have found a relation between annual water temperatures and year-class strength. Based on egg survival rates, Johnson (1961) felt that reproductive success in walleye was higher in years with stable, rising water temperatures, such as 2004 in Big Crooked Lake. In Lake Erie, one study found year-class strength was most related to the rate of water warming (Busch et al. 1975) and in another study water temperature showed a positive, but weak relationship with walleye recruitment (Madenjian et al. 1996). Variations in spring water temperature explained variation in walleye year-classes in Escanaba Lake, Wisconsin (Serns 1982b, Hansen et al. 1998). Busch et al. (1975) believed that hatching success increased with warming water by accelerating embryo development, thus limiting the period that eggs are subjected to environmental stresses or predation. Serns (1982b) likewise thought the thermal conditions during both incubation and post-swim up periods were critical for walleye recruitment.

Unlike thermal differences between years, differences in water temperatures among reefs were low. While paired t-tests determined that the temperature differences between each study reef were significant in 2004, the overall differences in cumulative thermal units through hatching was small. Overall the shoreline was the warmest reef, the point intermediate, and the island coolest. Water depth and deeper water upwelling around the spawning reefs may have impacted water temperatures on the reefs; water surrounding the shoreline reef was the shallowest and most likely warmest, intermediate at the point reef, and deepest and most likely coolest at the offshore island reef. The location within the lake likely affects water temperatures. For instance, the northwest shoreline would receive extended thermal radiation due to longer direct exposure to sunlight. However, the differences between reefs did not necessarily translate into the expected thermal advantages for embryo development and hatching success. The cool temperatures at the island reef resulted in the highest egg survival rate while the warm shoreline reef had intermediate survival rates and the intermediate temperatures at the point reef had the lowest egg survival in 2004. Johnson (1961) followed minimum, maximum, and mean water temperature at different spawning reefs, but felt that annual thermal conditions, not thermal differences at reefs, were more critical to egg survival, suggesting other factors besides physical habitat or temperature may influence egg survival rates. A large number of eggs were buried in sand at the point study reef, so wave energy may be another critical factor towards annual reproductive success (Johnson 1961, Priegel 1970, Busch et al. 1975) and may differ between individual reefs.

While walleye specifically selected shallow water (<0.3 m) to spawn in and thermal differences existed among depths in reefs, the difference was small and probably did not affect this habitat choice or egg survival. In 2004, significant thermal differences occurred at the two extreme locations at the shoreline reef and throughout the island reef, but the maximum difference for the mean spawning period temperature was only 0.221°C. Overall, the nearshore regions at spawning sites were more sensitive to fluctuations in air temperature and due to air temperatures also were cooler than deeper, more stable water. Although the highest density of eggs was in shallow water and close to shore, these results suggest that there would not be a thermal advantage towards depositing eggs in these regions. In addition, regression analyses in Chapter 1 showed that there were no correlations with egg survival and distance to shoreline or water depth. Therefore, the differences in thermal conditions within reefs appeared to be so minimal that they did not impact egg survival.

The results of this study provide insights into the thermal conditions present at natural walleye spawning reefs during spawning periods and the potential impacts on reproductive success. Annual thermal conditions may have an affect on the reproductive success of walleye eggs, but the rising water temperature in 2004 did not have the expected results suggested by past studies (Johnson 1961, Busch et al. 1975, Madenjian et al. 1996), but additional data across years is necessary to establish this relation. Water temperature during incubation is likely not the only important thermal condition towards annual reproductive success. In Escanaba Lake, Wisconsin, (Serns 1982b, Hansen et al. 1998) found that year-class strength correlated more with variation in May (after emergence) water temperature than variation in water temperature during the first 30 days after ice-out. Other temperature variables, such as the mean, standard deviation, and warming rates were less descriptive (Hansen et al. 1998). The negative correlation of May water temperature to year-class strength might be attributed to influences on not only egg incubation and hatching, but also on the early stages of fry survival and development (Serns 1982b). For instance, temperature affects the timing of zooplankton blooms, a primary food source for walleye fry and fingerlings (Priegel 1970, Serns

1982b, Frey 2003). Other studies have shown that fry survival and development can be directly influenced by water temperatures, such as high temperatures increasing respiration or metabolism, leading towards stress in young walleye (Koenst and Smith 1976, Hokanson 1977, Clapp et al. 1997). Overall, water temperature is most likely influential in survival because it may affect a combination of factors including adults during the spawning period, slow embryo development rates, and influence egg or fry mortality rates either directly or indirectly through other factors such as prey abundance, metabolism and growth rates (Chevalier 1973, Hokanson 1977, Koonce et al. 1977).

Additional quantitative research on annual water temperatures should be conducted and other habitat factors considered that may influence year-class strength of walleye should also be considered. The results of this study show that development and reproductive success in the wild does not always correlate with development and hatching in laboratory studies. Additional research in the wild should focus on when the highest egg mortality actually occurs and determine if there is a correlation with optimal fertilization ranges and thermal lethal limits. An increase in the number of egg collection chambers and temperature data loggers would provide a better understanding of reproductive success at different locations within and between spawning reefs. Questions about how thermal conditions impact walleye throughout the first year need to be answered. Water temperature should be followed closely from the spawning period until ice cover and different methods should be conducted to follow the survival of not only embryos, but also fry and fingerlings. If all of this data is available for multiple years, statistical modeling could determine potential critical thermal periods during the development of walleye year-classes. Wind and wave energy is another factor that should be considered in recruitment of year-classes as it can influence water temperatures, dissolved oxygen, egg movement and entrainment (Johnson 1961, Priegel 1970, Busch et al. 1975). Water levels, especially receding, can also influence the amount of available habitat and potentially result in desiccation of eggs (Johnson 1961, Priegel 1970).

CHAPTER 3: Wind, wave energy, and water level dynamics on a walleye spawning reef in a north temperate lake

ABSTRACT

Wind activity, wave energy, and water levels are functional processes that affect nearshore areas of littoral zones in lakes. The processes are influenced by spring thermal conditions that can, in turn impact walleye egg survival through transportation, exposure to predation or desiccation, abrasion, and burial in spring. The objectives of this study were to: 1) determine wind and wave patterns in a walleye spawning area and how often critical wave velocities were exceeded for egg and substrate transport in spawning areas, 2) evaluate subsequent egg movement due to wave energy, and 3) determine if fluctuations in water levels impacted available habitat and egg survival. A wind anemometer and a tri-directional velocimeter were installed to monitor wind and wave activity while a staff gauge was used to assess fluctuations in water level. Egg movement was evaluated by delineating eggs at three different stages: adhesive, spawn completion, and black-eyed egg stage along with surveys of stranded eggs on the shoreline. Wind velocities showed a positive, significant ($p < 0.001$) correlation to wave velocities in the spawning area. Periods of wave energy were sufficient to initiate movement of walleye eggs (19.0%), sand (7.2%), and gravel (0.3%) during the incubation period. Stranded eggs were typically found at higher densities over a large sandbar region compared to the utilized reefs that had larger substrates and steeper shorelines. Water level fluctuations were minimal ($\pm$1.20 cm) and most likely did not impact the amount of available habitat or strand and desiccate eggs. These results clearly document that wind and wave activity can potentially have a negative impact on egg survival and should be considered as a factor critical to annual walleye year-class strength.

INTRODUCTION

Walleye (*Sander vitreus*) naturally experience cycles in population size, often attributed to differences in annual recruitment or year-class strength. Studies have evaluated a suite of both biotic and abiotic factors that may influence annual year-class strength and the most common significant factors have been stock size, available prey, and spring water temperature (Forney 1976, Madenjian et al. 1996, Hansen et al. 1998). Of these, water temperature has been suggested to be the most influential as it can directly and indirectly impact factors important to all life stages of walleye (Hokanson 1977, Koonce et al. 1977). During the reproductive stage, water temperature can directly influence the timing of egg deposition by female walleye, fertilization success, and mortality of embryos if lethal limits are exceeded (Priegel 1970, Hokanson 1977, Koenst and Smith 1976). However, water temperature can also indirectly impact egg survival as stable, warm or rising water temperatures increase the development rate of walleye embryos, thus decreasing the incubation period (Hokanson 1977, Koenst and Smith 1976). A shorter incubation period may increase survival by limiting the duration eggs are vulnerable to environmental stresses (Johnson 1961, Priegel 1970, Busch et al. 1975).

Environmental stresses, such as functional dynamic wave energy, can also be influenced by air temperature that is a main causal factor influencing water temperature. Wave activity is considered important to walleye reproduction as it can keep spawning areas clear of silt and organic matter that can bury eggs and also provides adequate dissolved oxygen flow over eggs (Johnson 1961, Daykin 1965). However, the occurrence and severity of storms each year that track changes in temperature due to thermal fronts, and the resulting wind activity and wave energy, may negatively affect hatching success. Live walleye eggs have been observed on shorelines, apparently washed up by heavy wave activity that would ultimately lead to mortality through predation or desiccation (Eschmeyer 1950, Johnson 1961, Priegel 1970). In other situations, heavy wave activity has resulted in egg mortality by carrying eggs to deeper, less suitable spawning habitat such as silt and detritus (Johnson 1961, Busch et al. 1975, Roseman et al. 1996, 2001). Fish egg survival can also be impacted by moving substrates that can lead to egg burial or abrasion (Ventling-Schwank and Livingstone 1994). Therefore, the critical velocity, or the velocity that initiates movement of an object (USBR 1977), is important for both walleye eggs and substrates.

Fluctuations in water level during spawning and incubation periods are another functional dynamic that may affect reproductive success of walleye. Receding water levels may limit the amount of available spawning habitat, forcing walleye to utilize lower quality spawning habitat or may strand and desiccate eggs deposited in shallow water (Johnson 1961, Priegel 1970, Chevalier 1977). For instance, in the Lake Winnibigoshish system, Minnesota, low water levels in certain years led walleye to deposit eggs in areas that previously receive little use (Johnson 1961). In another example, walleye were unable to use a preferred marsh habitat for spawning due to extremely low water levels in certain years in the Lake Winnebago system (Wisconsin), and also appeared to affect egg mortality in the marsh and on lake rock shoals through egg desiccation (Priegel 1970).

Both wave energy and water level fluctuations are especially important to walleye as they tend to broadcast spawn eggs near shore and in relatively shallow water (Eschmeyer 1950, Johnson 1961, Ellis and Giles 1965, Priegel 1970). Previous studies have provided information on water depth, but distance to shore may be more important. Depth of egg deposition has typically ranged from 30.5 to 76.0 cm, and rarely deeper than 122.0 cm (Eschmeyer 1950, Johnson 1961, Priegel 1970). In fact for inland lakes, no study has clearly recorded walleye spawning in water over 1.5 m or on offshore reefs. In Big Crooked Lake, Wisconsin, walleye egg boundaries had a mean maximum depth of 0.35 m and eggs were contained within a mean of 3.10 m from the shoreline (Chapter 1). These areas are the most susceptible to wave energy and fluctuations in water level.

Studies of wind activity and egg movement has occurred in Lake Erie (Busch et al. 1975, Roseman et al. 1996, 2001) but limited study of wind activity, wave energy, and water levels in inland lakes has been conducted (Roseman et al. 1996, 2001). Therefore, the goal of this study was to assess the potential impacts of functional dynamics during the walleye spawning period, with the specific objectives to:

1) determine the percent of time critical wave velocity was exceeded for eggs and various substrates,
2) evaluate subsequent egg movement due to wave energy, and
3) determine if fluctuations in water levels impacted available habitat and egg survival.

METHODS

Study site

This study was conducted on Big Crooked Lake, Vilas County, Wisconsin, in 2004 and 2005; wind and wave data were only collected in 2005. Big Crooked Lake is entirely surrounded by land owned by Dairymen's Incorporated, a private resort near Boulder Junction. The riparian area is forested, with development along the 8.1 km of shoreline limited to a lodge and several cabins on a stretch of the north shore. The lake is oligotrophic, 276 ha in size, and has a maximum depth of 11.6 m. The fish community consists of walleye, smallmouth bass (*Micropterus dolomieu*), muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), white sucker (*Catostomus commersoni*) and various minnows (*Cyprinidae*) and darters (*Percidae*).

Big Crooked Lake has a naturally reproducing and self-sustaining walleye population. Walleye may have initially been introduced to the lake, but reliable historical records of introduction are absent. Currently, the lake is one of four lakes in the ceded territory of northern Wisconsin utilized by the Wisconsin Department of Natural Resources (WDNR) for walleye exploitation rates research (S.P. Newman, WDNR, personal communication). The lake contains three classical walleye spawning habitat types: rock shorelines, point bars, and islands and three specific spawning areas were selected for detailed study of egg movement: a relatively linear rock shoreline in the northwest corner of the lake (“shoreline”), a point rock bar in the south-central portion of the lake (“point”), and an island located in the southeastern bay (“island”)(Figure 3-1). Chapter 1 contains additional detailed description of these three study reefs.

Spawning Chronology

The spawning chronology of adult walleye and embryos was followed throughout the 2005 spawning season in Big Crooked Lake. Temperature data loggers (Richard Brancker Research, Model XL-800)(Accuracy = $\pm$0.07 °C) were installed at the three study reefs in Big Crooked Lake to monitor air and water thermal conditions. However, only the temperature data logger at the shoreline reef functioned properly so the mean

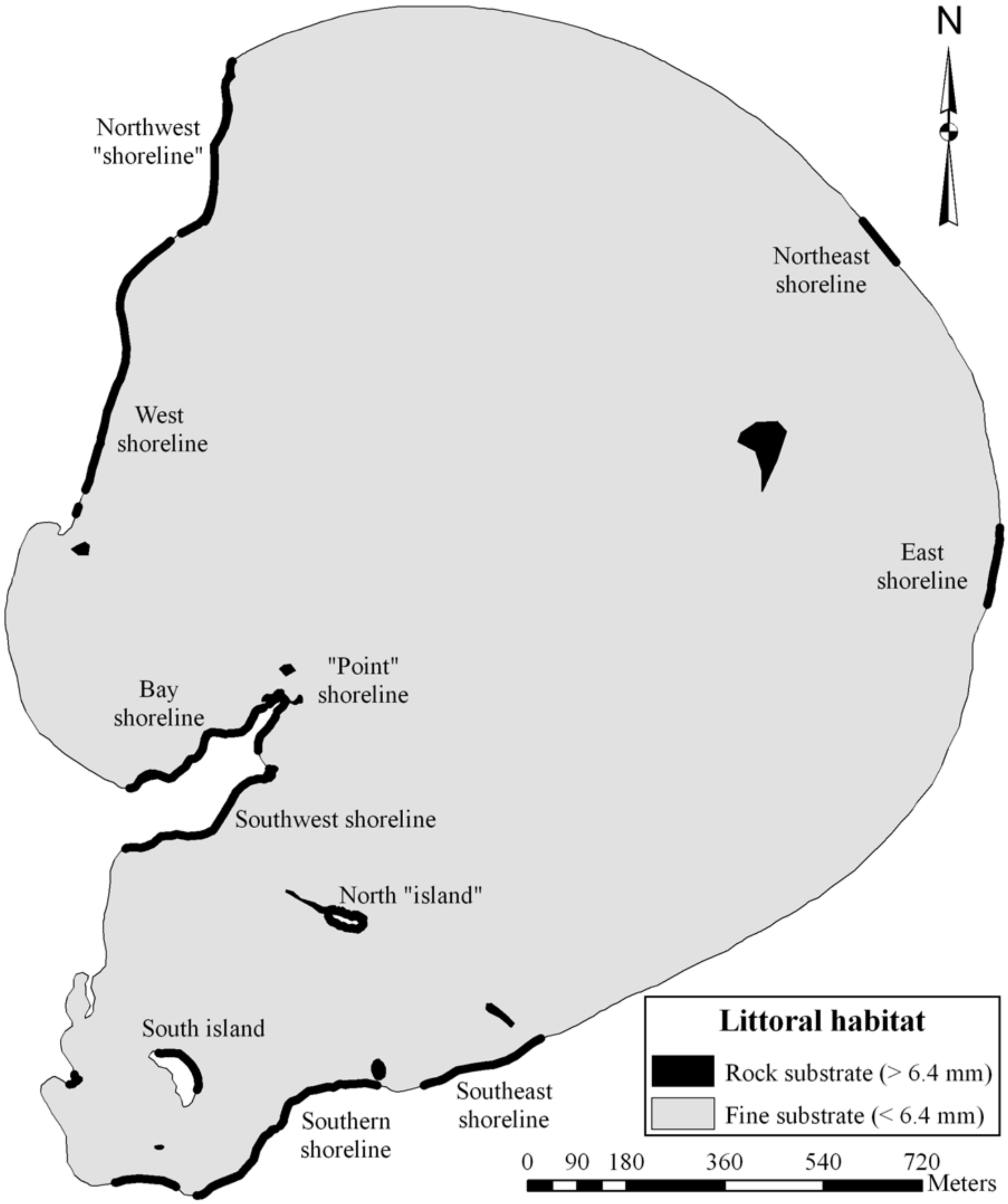


Figure 3-1. Locations of rock substrates (gravel, cobble, rubble, etc.)(any material $\geq$ 6.4 mm) including the three study reefs compared to fine substrates in the Big Crooked Lake littoral zone (<3.0 m of water depth). Sand substrate dominated the littoral habitat, while rock substrate was primarily nearshore and in the western half of the lake.

was taken from that location. In order to follow spawning adult walleye, standard Wisconsin Department of Natural Resources fyke-nets were installed immediately upon ice-out and were checked each morning. The total length, sex, and general reproductive condition (i.e., ripe, spent) were recorded for all captured walleye. The point that 85% of adults spawned and the peak of spawning were estimated by nightly catch numbers and reproductive status during handling. Population estimates were also conducted in the spring using the Peterson method (Ricker 1975) in order to estimate the walleye stock size, with methods described in further detail in Chapter 1.

Thirty live eggs were collected daily from the shoreline spawning reef to track embryo development and larval emergence (see McElman and Balon 1979). In particular, the initial development of black pigment in the eyes and later physical movement of individual embryos within the egg chorion were considered two separate, late stages of development. To collect eggs, bottom substrates were agitated by foot and a mesh collector was brought through the turbulent water to collect suspended eggs. Using forceps, viable eggs were removed from the collector and placed into a labeled vial containing 10% formalin. Field observations of embryo development were recorded along with laboratory observations using a dissecting microscope. The commencement of fry hatching was determined by visual observations of hatching in collection chambers and through collections of walleye fry during night boat tow-net surveys.

Water Level

Water levels were recorded daily using a staff gauge starting the first day after ice-out. All future depth measurements taken for habitat assessment were standardized (i.e., converted) to this initial ice-out water level. A chart following water level fluctuations was constructed in Microsoft Excel (Microsoft Corporation 2001).

Wind Activity and Wave Energy

An Onset Computer Corporation Wind Speed/Direction Smart Sensor, Model S-WCA anemometer (velocity: range = 0 – 44 m/s, accuracy ± 0.5 m/s; direction: range = 0 to 358°, accuracy ± 5°) was installed to monitor wind velocity, gust velocity, and wind direction. This device was installed upon lake ice-out at the shoreline study reef. The velocimeter was located 4.0 m from the shoreline, in 0.46 m of water, and with the wind cup located 1.0 m from the water. The wind sensor was connected to a data logger (Onset Computer Corporation HOBO Micro Station) and recorded data every one hour for intervals lasting 120 seconds. Data was downloaded into BoxCar Pro Version 4.3 software (Onset Computer Corporation 2002) and hourly means were calculated.

To monitor wave energy, a tri-directional velocimeter (Alec Electronics Electromagnetic Current Meter, Model ACM 16M-338)(range = 0 - ± 250 cm/s, accuracy = ± 1.00 cm/s) measured three-dimensional (X,Y,Z) wave velocity at the shoreline study reef throughout the spawning season. From April 15 to April 24, the velocimeter was located 4.6 m from the shoreline, in water 0.51 m deep, with the sensor 0.17 m from the lake bottom. On the afternoon of April 24 the velocimeter was moved to 2.0 m from the shoreline, a water depth of 0.28 m, and the sensor was 0.10 m from the lake bottom. In both locations, the velocimeter was located adjacent to the anemometer. Data was downloaded into ACM16-338 Data Processing software (Alec Electronics Company, Ltd. 2002) that computed hourly mean velocity, calculated as the vector velocity of the X and Y coordinates. In addition to hourly means, 120 sample points of the vector and vertical

(Z) velocities from each hour were available for analyses. The hourly mean of wind velocity and wave vector velocities were utilized in regression analyses to determine if wave activity and wind energy were correlated, with wave energy as the dependent variable. Two separate regression analyses were conducted in Number Cruncher Statistical Systems (NCSS)(Hintz 2004), one evaluating the period during the first velocimeter location and one for the second velocimeter location. Two-sample t-tests were conducted in NCSS to compare differences in wind activity and wave energy between the two periods.

Critical Velocity

The critical velocity (C_v), or the velocity that initiates motion of a specific object, needed to be determined for both substrates and walleye eggs. The critical velocity for each substrate size class was determined according to a model developed by the United State Bureau of Reclamation (1977):

$$Cv = 0.155 * \sqrt{diameter} \text{ (mm)}$$

The diameter of each substrate was entered in mm and the resulting critical velocity was calculated in m/s. Since wave velocity was recorded in cm/s, the critical velocity determined by the model was multiplied by 100. The critical velocity was calculated for both the minimum and median of each substrate size class (Table 3-1).

The critical velocity of walleye eggs was based on a model developed by Ventling-Schwank and Livingstone (1994) that focused on the egg movement threshold of whitefish eggs in Lake Sempach, Switzerland. Whitefish eggs utilized in this study ranged in diameter from 2.00 to 2.50 mm. In comparison, walleye eggs have been measured between 1.63 mm and 1.73 mm in diameter (Wolfert 1969, Serns 1982a).

Table 3-1. Critical velocity values for each substrate size class and walleye eggs. The critical velocity was determined for the minimum and median particle size of each substrate size class while the walleye egg critical velocity was based on a model by Ventling-Schwank and Livingstone (1994).

	Substrate size (mm)		Critical velocity (m/s)	
	Minimum	Median	Minimum	Median
Sand	0.20	3.25	6.93	27.94
Gravel	6.40	41.20	39.21	99.49
Cobble	76.10	113.00	135.21	164.77
Rubble	150.00	226.95	189.84	233.51
Small boulder	304.00	456.95	270.25	331.33
Large boulder	610.00	n/a	382.82	n/a
Walleye egg	n/a	n/a	10.00	12.50

Although walleye eggs are slightly smaller, Ventling-Schwank and Livingstone (1994) noted that egg diameter was not important in their determination of critical shear and stress. The authors determined that the critical velocity for whitefish eggs was between 10.0 and 15.0 cm/s. To test this range, they studied eggs placed 6.0 m from the water surface and believed it was accurate. While walleye do not deposit eggs at this water depth, the wave velocities were recorded 0.5 m from the bottom substrate (Ventling-Schwank and Livingstone 1994). Therefore, this study was relatively comparable to walleye eggs and the critical velocities for walleye eggs were determined to be 10.0 cm/s for the minimum and the median at 12.5 cm/s (Table 3-1).

Egg Movement

In order to monitor egg movement, delineations of egg locations occurred at three different egg stages. The first delineation of the "adhesive egg" stage, or recently deposited eggs, occurred only at the shoreline study reef. To delineate these areas, a snorkeler moved along the entire reef in search of adhesive eggs immediately upon ice-out and each morning thereafter. Areas of adhesive eggs were delineated by placing colored metal washers around the entire perimeter of the area. This process was continued daily until egg deposition ceased. Once eggs hatched, the depth, distance from shoreline, and overall reef location was recorded from the center of the washer polygon. The reef location was recorded as the shoreline distance from the start of the egg deposition on the reef (southern end).

The location of eggs after the completion of egg deposition ("post-spawn") and closer to hatching ("black-eyed"eggs) was also delineated at each of the three study reefs. In laboratory studies, eggs have remained adhesive for five hours under constant stirring

(Waltmeyer 1976) and clumped together up to four days (Krise et al. 1986) before losing adhesive characteristics and settling into the substrate or moving with wave energy. In this study, eggs were adhesive for approximately 15 to 24 hours. For the post-spawn stage, egg locations were delineated once an estimated 85% of females spawned and most eggs would no longer be adhesive. The boundaries of egg deposition were delineated by the continuous placement of metal washers along the perimeter of observed eggs. The snorkeler began at the start of observed eggs on one end of a spawning reef and moved perpendicular from the shoreline and then progressed in a 90° zig-zag motion. Washers were placed at the deepest, furthest point from shoreline that eggs were observed; points had to have a minimum of ten live eggs in approximately a 0.5 x 0.5 m area to be considered. The surveyor also searched deeper water and past the transition from rock to sand substrate to assure eggs were not present in those locations. At times, eggs were visible on top of the substrate, and other times the substrate was slightly moved or agitated to temporarily suspend eggs. This method continued across the reefs, with washers being placed approximately every five m along the egg perimeter. For the black-eyed stage, this process was repeated once the majority of eggs reached the black-eyed egg stage with the placement of different colored washers. After the eggs hatched, transects were established within each study reef to quantify physical characteristics of reefs as described in Chapter 1.

Two-dimensional blueprints were constructed to represent the movement of eggs at the three study reefs. These blueprints were constructed in ArcGIS Version 9.1 (ESRI 2004) using GPS data points and raw field data measurements. Included on the blueprints were the locations of adhesive egg areas (shoreline reef only), lines representing the post-spawn and black-eyed egg stages, the rock reef, and the surrounding fine substrate (e.g., sand) area.

Quantitative counts of stranded eggs on shore were also conducted to evaluate egg movement and potential desiccation. Sample were collected at five shoreline locations for each study reef and at 16 random locations throughout eastern and northern sandbar portion of the lake. Immediately at the onshore portion of the shoreline-water interface, a 0.25 m diameter ring was placed and any substrates within the ring were excavated. Eggs were sorted from the collections, the total number of live and dead eggs was recorded, and ANOVA analyses were conducted in NCSS to compare egg densities between the four sites.

RESULTS

Spawning Chronology

The spawning period in 2005 lasted a total of 38 days and appeared prolonged by fluctuating air temperatures. Deposited eggs were first observed on April 16, one day after ice-out (Figure 3-2); peak spawning occurred following a warming period on April 20 and 85% of walleye spawned by April 23 (Figures 3-2). Egg deposition appeared to be completed by April 26 as adhesive eggs were not found after this date, except for one event. On May 5 a patch of adhesive eggs was observed, however all eggs died, most likely due to a lack of fertilization or poor egg viability. The adult walleye population was estimated at 1,174 $\pm$ 291 individuals (95% C.I.), a few juvenile males may have been present. A cool period lasted for 14 days as water temperature cooled on April 20 and continued to decrease or stay cool until May 2 (Figure 3-2). The black-eyed embryo stage was first observed on May 4, 19 days after the first deposited eggs. Embryo

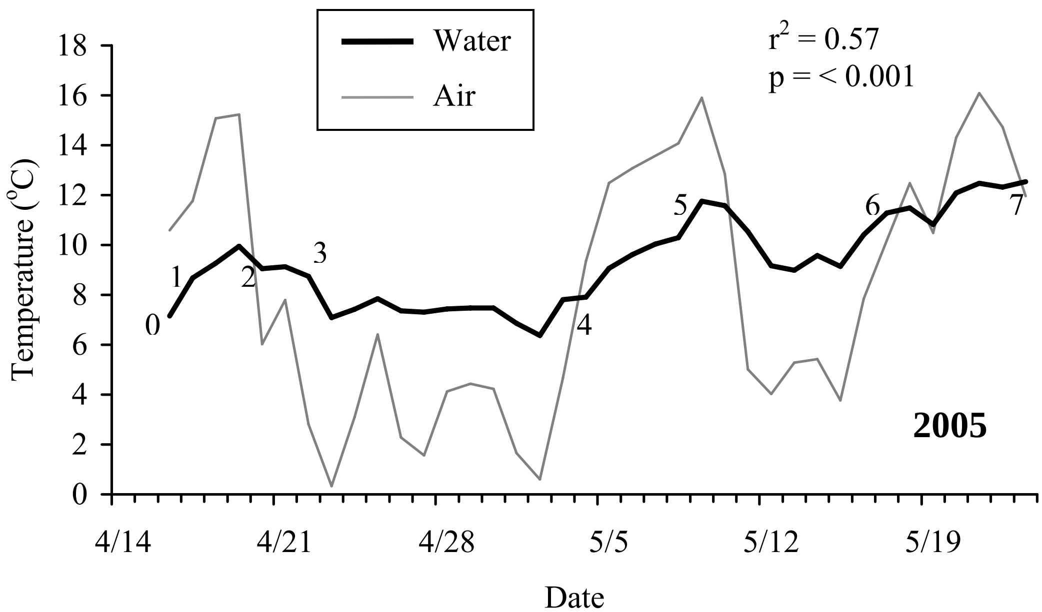


Figure 3-2. Mean daily water and air temperatures during the 2005 walleye spawning season in Big Crooked Lake. Spawning chronology stages were: 0 = lake-wide ice-out, 1 = egg deposition commencement, 2 = peak spawning, 3 = 85% female spawned, 4 = black-eyed stage, 5 = embryo movement stage, 6 = hatching commencement, 7 = hatching completion. Coefficients of determination tested the extent that air and water temperatures are synchronous ($T_{water} = 7.07 + 0.27T_{air}$, $p = <0.001$, $r^2 = 0.57$).

movement was observed five days later on May 9, but obvious hatching did not occur for eight more days on May 17, most likely due to another cooling period (Figure 3-2). Hatching lasted for approximately six days, as no live eggs were found on the spawning reefs after May 23.

Water Level

Water level fluctuations throughout the walleye spawning period in Big Crooked Lake were small (Figure 3-3). The water level initially rose during the egg deposition period to a maximum of 1.20 cm compared to the ice-out water level. The water level then dropped and fluctuated during the incubation period, with a low of 1.10 cm below the ice-out water level (Figure 3-3). Therefore, the greatest total difference in water levels was 2.30 cm. The water level was lower then the ice-out level when fry hatching commenced but rose above the ice-out level by the end of the hatching period.

Wind Activity and Wave Energy

Wind activity varied throughout the spawning period but typically showed a diel pattern (Figure 3-4). The mean hourly wind velocity for the entire walleye spawning period was 1.37 m/s, with a maximum hourly mean of 4.82 m/s. High wind periods typically occurred between hours 1000 and 1400, but with some variability and exceptions. Gust velocities tended to be higher, with a spawning period mean of 4.03 m/s and a maximum of 11.50 m/s. The calmest period occurred from April 25 to May 6, while May 8 to 13 was particularly windy (Figure 3-4). The wind direction also varied greatly throughout the spawning period, but was most often headed in a south-southeast (20.3%) or south-southwest (18.3%) direction (Table 3-2). West-northwest and north-

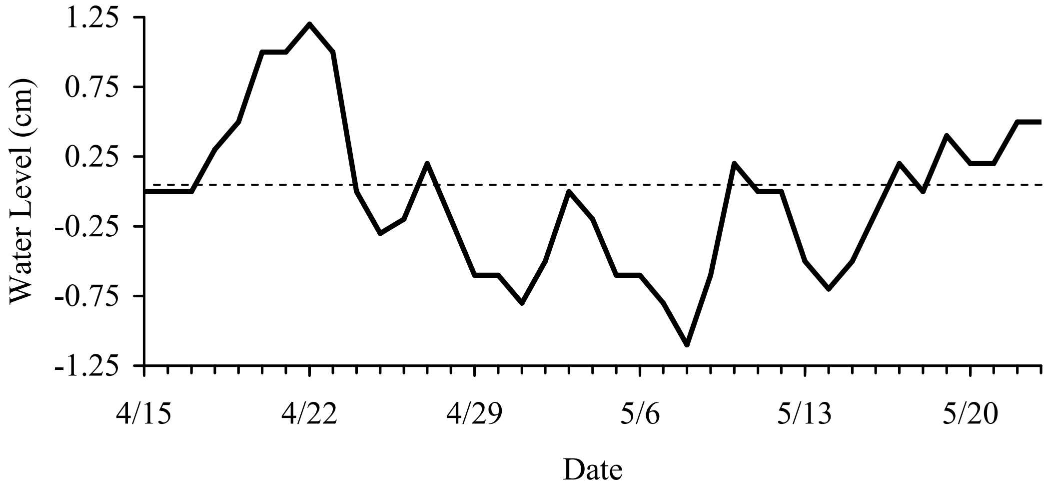


Figure 3-3. Water level fluctuations during the 2005 walleye spawning period in Big Crooked Lake. Ice-out occurred on April 15 and the ice-out water level is represented by the dotted black line.

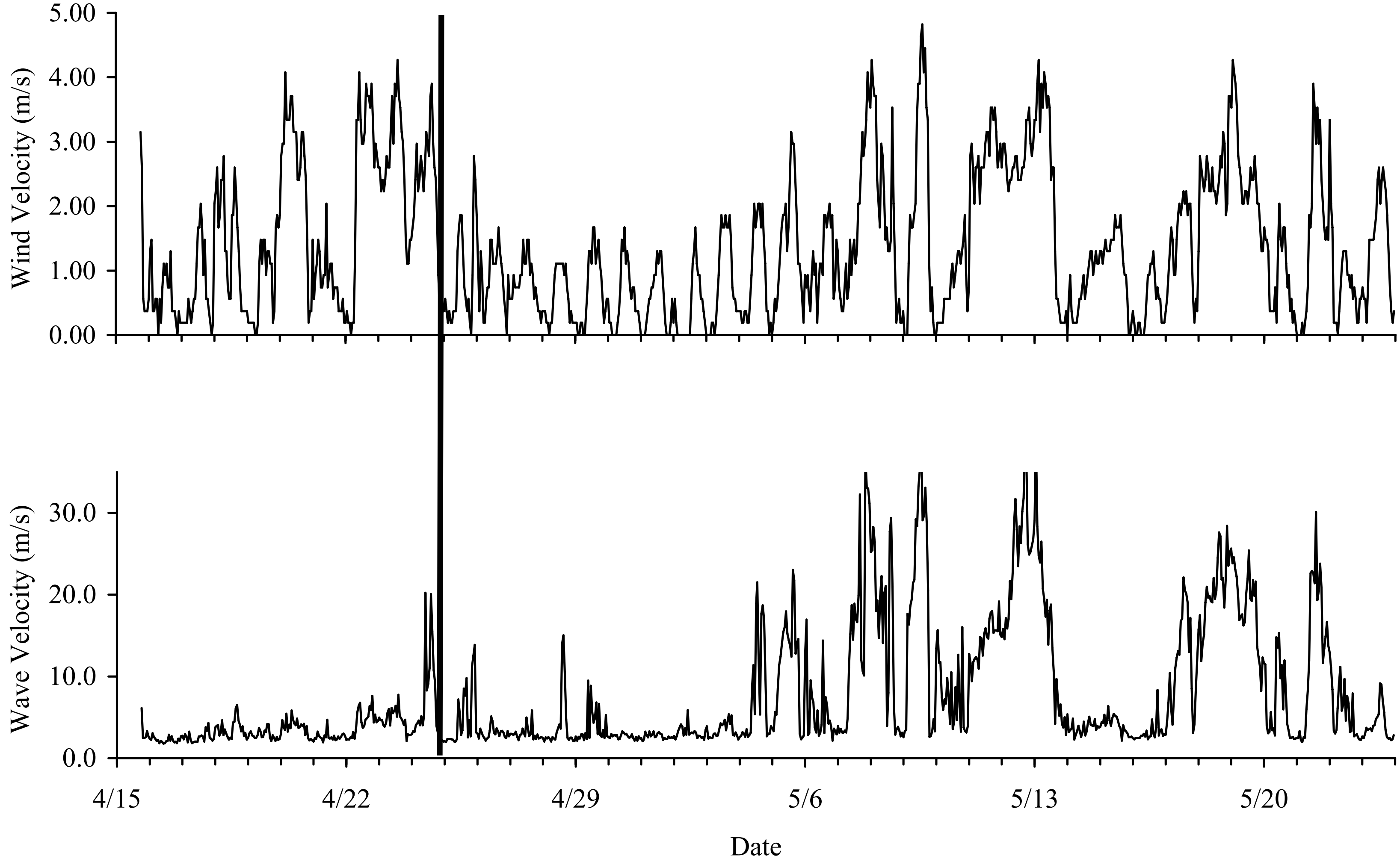


Figure 3-4. Wind (upper) and wave velocity (lower) profiles during the 2005 walleye spawning period in Big Crooked Lake. The black gray line separates the two evaluation periods based on velocimeter location: April 15-24 and April 25-May 23.

Table 3-2. The percent of the 2005 walleye spawning period that wind headed in each of eight directions that were determined according to 45° ranges.

Direction	Range (°)	Wind (%)
N-NE	0-45	19.3
NE-E	45-90	10.8
E-SE	90-135	9.7
SE-S	135-180	20.3
S-SW	180-225	18.3
SW-W	225-270	4.4
W-NW	270-315	14.5
NW-N	315-360	2.8

northwest winds likely would have the most influence on the northwest shoreline study reef and occurred at 14.5% and 2.8% of the spawning period, respectively (Table 3-2).

Wave energy in Big Crooked Lake followed similar patterns to wind speed patterns, but did not necessarily track the diel pattern observed with the wind activity (Figure 3-4). The mean wave velocity was 7.82 cm/s for the entire spawning period. The maximum hourly mean wave velocity was 39.01 cm/s for the entire spawning period while the maximum individual sample point velocity was 328.70 cm/s. The wave energy from April 25 through May 3 was quite calm, while May 4 to 13 had considerable wave energy (Figure 3-4).

Wave energy showed positive correlation with wind activity but the correlation was weaker during the first period (April 15-24) compared to the second period (April 25-May 23). The first period model was $V_{wave} = 1.820 + 1.188(V_{wind})$($r^2 = 0.37$, $p < 0.001$) while the second period model was $V_{wave} = 0.956 + 6.126(V_{wind})$($r^2 = 0.62$, $p < 0.001$). The weaker relation for the first period model was a result of a significantly lower hourly wave velocity ($\bar{x} = 3.71$ cm/s, $p < 0.001$) but a significantly higher hourly wind velocity ($\bar{x} = 1.59$ m/s, $p < 0.001$) compared to the second period ($\bar{x}$ hourly wind velocity = 1.30 m/s, $\bar{x}$ hourly wave velocity = 8.91 cm/s). This result implies that the wave velocity in deeper water was impacted less by wind activity than the shallower water during the second period.

Critical Shear

Periods of wave energy were sufficient to transport both walleye eggs and various substrates in the shoreline spawning reef during the 2005 walleye spawning period. Of particular interest was the amount of time the critical velocity was exceeded throughout

the spawning period. During the first period, when the wave velocimeter was located further from shore (4.6 m) and in deeper water (0.51 m), the recorded wave energy was much lower, and thus the percent of time critical velocity was exceeded was also much lower compared to the second period (Table 3-3). The minimum size of sand (0.20 mm) would have been in motion around 8% of the first period according to the horizontal X-Y vector velocity and less than 0.4% for the median size (3.25 mm). In comparison, the minimum and median size sand closer to shore (2.0 m) and in shallower water (0.28 m) was in motion over 28% and 7%, respectively, during the second period (Table 3-3). Also, gravel and even some cobble and rubble, all components of the reef substrate matrices, were in motion a substantial amount of the second period (Table 3-3)
Similar trends between the two periods were observed with the walleye eggs. The minimum and median eggs were in motion around 2.5% and 1.5%, respectively, for the first period and over 23% and 19% for the second period (Table 3-3). The critical Z velocity for walleye eggs was exceeded between 1 and 3% of the first period and 12 and 15% of the second period (Table 3-3). Based on regression equations, the wind velocity necessary to move minimum and median eggs during the first period was 6.9 m/s and 8.8 m/s, respectively. The wind velocities required to move eggs was much lower for the second period at 1.5 m/s and 1.9 m/s for the minimum and median eggs, respectively.

Egg Movement

Walleye eggs were observed suspended and moving with waves during periods of high wave activity, often with coarse and fine organic matter. A lake-wide survey for egg deposition resulted in observations of eggs fairly consistently washed onto shore along the north and eastern sand region of Big Crooked Lake and mixed in with

Table 3-3. The percent of time wave energy exceeded the critical velocity for five substrate size classes and walleye eggs during the first period (April 15-24, N = 26,520), second period (April 25-May 23, N = 83,520), and the total spawning period (May 15-23, N = 110,040). The wave velocimeter was located further from shore (4.6 m) and in deeper water (0.51 m) during the first period than the second period (distance from shore = 2.0 m, water depth = 0.28 m).

	FIRST PERIOD				SECOND PERIOD				TOTAL PERIOD			
	X-Y Vector		Z		X-Y Vector		Z		X-Y Vector		Z	
	Min.	Median	Min.	Median	Min.	Median	Min.	Median	Min.	Median	Min.	Median
Sand	7.99	0.38	6.44	0.56	28.09	7.19	33.87	9.29	23.24	5.55	35.69	9.42
Gravel	0.19	0.04	0.31	0.04	3.92	0.33	5.95	0.87	3.02	0.26	5.99	0.82
Cobble	0.01	<0.01	0.02	0.02	0.11	0.04	0.28	0.14	0.09	0.03	0.26	0.14
Rubble	<0.01	<0.01	0.02	0.02	0.03	<0.01	0.08	0.04	0.02	<0.01	0.07	0.04
Small boulder	<0.01	0.00	0.02	0.00	<0.01	0.00	0.02	0.00	<0.01	0.00	0.02	0.00
Egg	2.55	1.53	2.22	1.67	22.67	18.99	14.90	12.62	17.82	14.78	11.84	9.98

organic matter. Examinations of the shoreline at the utilized reefs also revealed eggs stranded out of water.

The first quantitative measure of egg movement was the physical delineation of eggs located furthest from the shoreline. A total of 121 adhesive, recently deposited egg polygons were observed throughout the shoreline rock reef and also in three areas north of the rock reef that were pure sand (Figures 3-5, 3-6). The mean distance to shore from the center of each adhesive polygon was 1.74 $\pm$ 0.08 m (S.E.)(Table 3-4). As the eggs lost their adhesive characteristics after spawning completion, they settled out to a mean maximum distance to shore of 2.45 $\pm$ 0.12 m (S.E)(Table 3-4). Eggs were still present after spawning completion in the sand area north of the rock reef (Figures 3-5, 3-6). However, immediately before hatching at the black-eyed egg stage the viable eggs were again quite close to the shoreline, with a maximum mean of 1.64 $\pm$ 0.10 m (S.E)(Table 3-4). In addition, eggs were no longer present in the sand region (Figures 3-5, 3-6).

Adhesive egg areas were not delineated at the other two study reefs but movement between post-spawn and black-eyed stages were compared. At the point reef, very little movement for the furthest eggs was recorded, as the mean distance from shore was 5.86 $\pm$ 0.73 m (S.E.) and 5.93 $\pm$ 0.84 m (S.E.) for the post-spawn and black-eyed stage, respectively (Table 3-4). However, eggs that were present in a sandy region on the west portion of the reef after spawning completion were no longer observed by the time of the black-eyed egg stage (Figure 3-7). A slight movement towards shore was recorded at the island reef as the eggs were located at a mean of 3.81 $\pm$ 0.29 m (S.E.) after spawning completion and then at a mean of 3.47 $\pm$ 0.29 m (S.E.) at the eyed egg stage (Table 3-4,

Table 3-4. Two measures of walleye egg movement during the 2005 spawning period in Big Crooked Lake at three spawning reefs and the north to east sandbar portion of the lake. The egg stage measure evaluated the location of the mean (standard error) furthest eggs from shore (m) for the adhesive, post-spawn, and black-eyed stage. The egg density measure evaluated the mean (standard error) number of eggs stranded on the shoreline. (Note: For the egg density measure, N = 5 for the three reefs and N = 16 for the sandbar).

	Shoreline Reef		Point Reef		Island Reef		Sandbar	
	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.
Egg Stage								
Adhesive	1.74 ± 0.08	7.20	n/a	n/a	n/a	n/a	n/a	n/a
Post-spawn	2.45 ± 0.12	4.62	5.86 ± 0.73	9.99	3.81 ± 0.29	5.89	n/a	n/a
Black-eyed	1.64 ± 0.10	3.90	5.93 ± 0.84	9.90	3.47 ± 0.29	5.87	n/a	n/a
Egg Density								
Live	11.6 ± 5.90	34	6.2 ± 5.70	29	1 ± 1.00	5	40.6 ± 32.30	519
Dead	23.8 ± 4.35	37	10.0 ± 8.51	44	0.4 ± 0.24	1	116.6 ± 74.30	1214
Total	35.4 ± 10.04	71	16.2 ± 14.21	73	1.4 ± 1.17	6	157.2 ± 106.34	1733

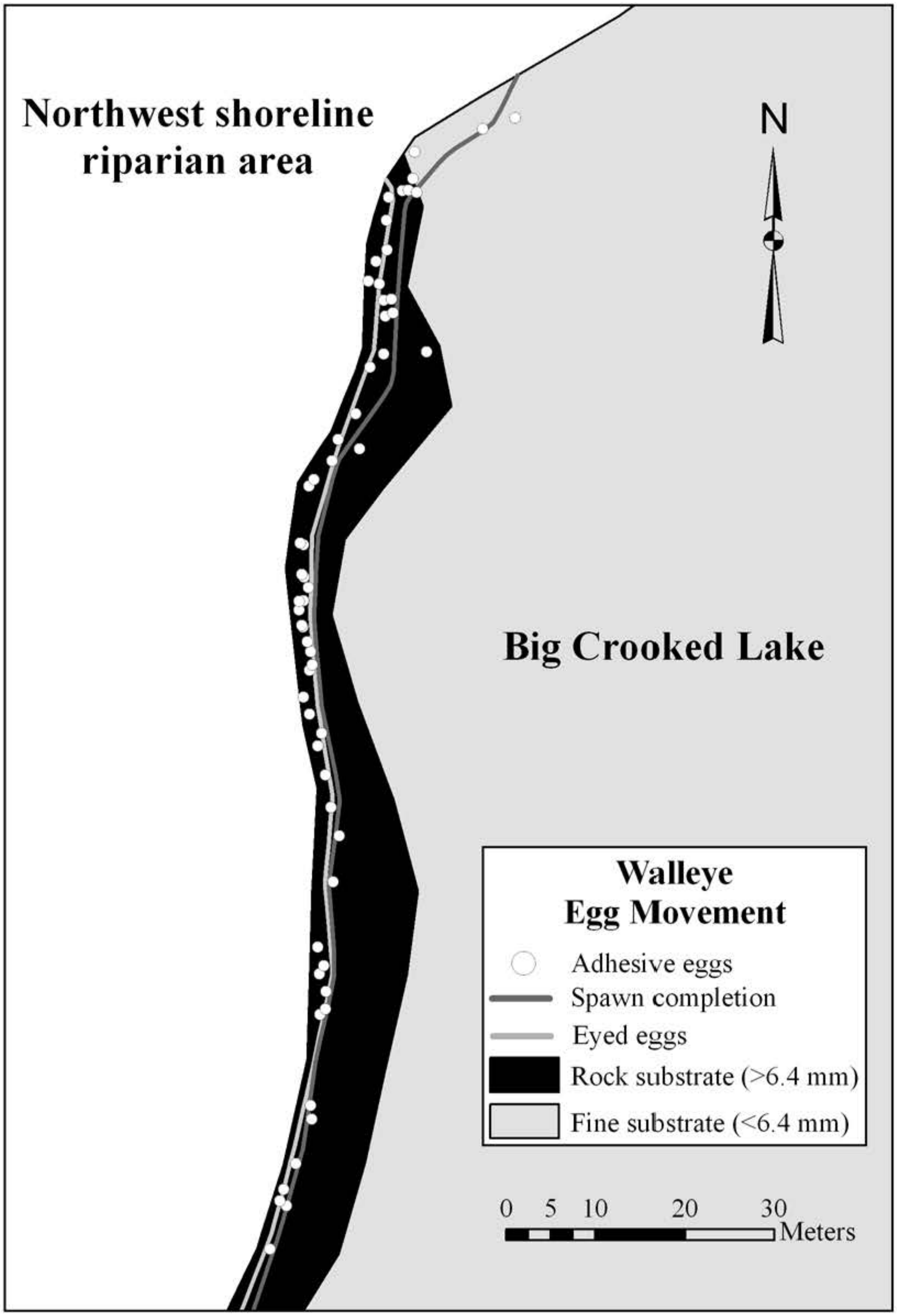


Figure 3-5. Northern portion of the shoreline study reef in Big Crooked Lake depicting the location of walleye eggs during three different stages. Eggs were deposited close to shore, settle outward slightly, and then were again close to shore prior to hatching.

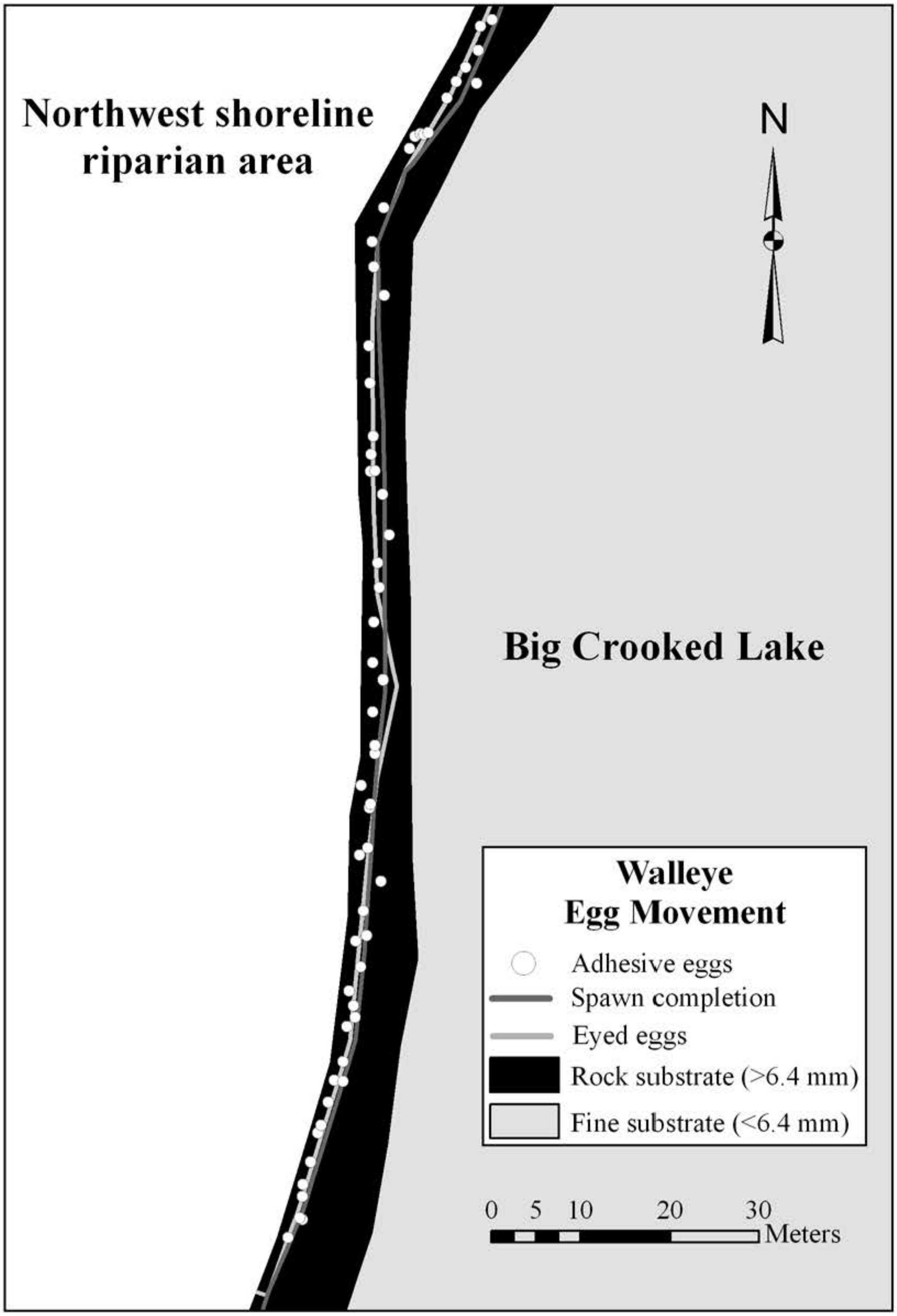


Figure 3-6. Southern portion of the shoreline study reef in Big Crooked Lake depicting the location of walleye eggs during three different stages. Eggs were deposited close to shore, settle outward slightly, and then were again close to shore prior to hatching.

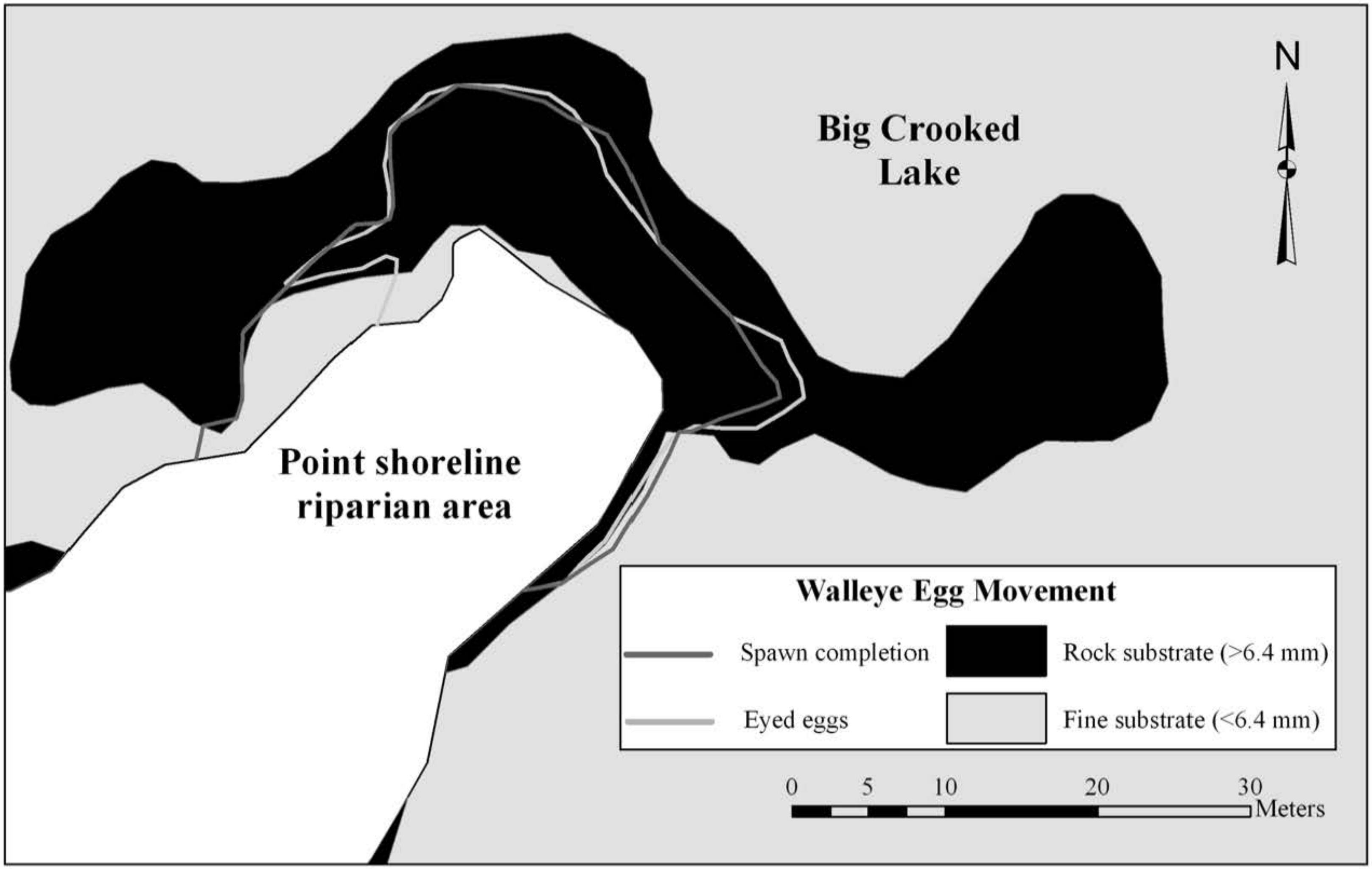


Figure 3-7. Point study reef in Big Crooked Lake depicting the location of walleye eggs after spawn completion and at the eyed egg stage. Minimal egg movement was observed at the rock portions of the reef, but eggs did move from the western sand region.

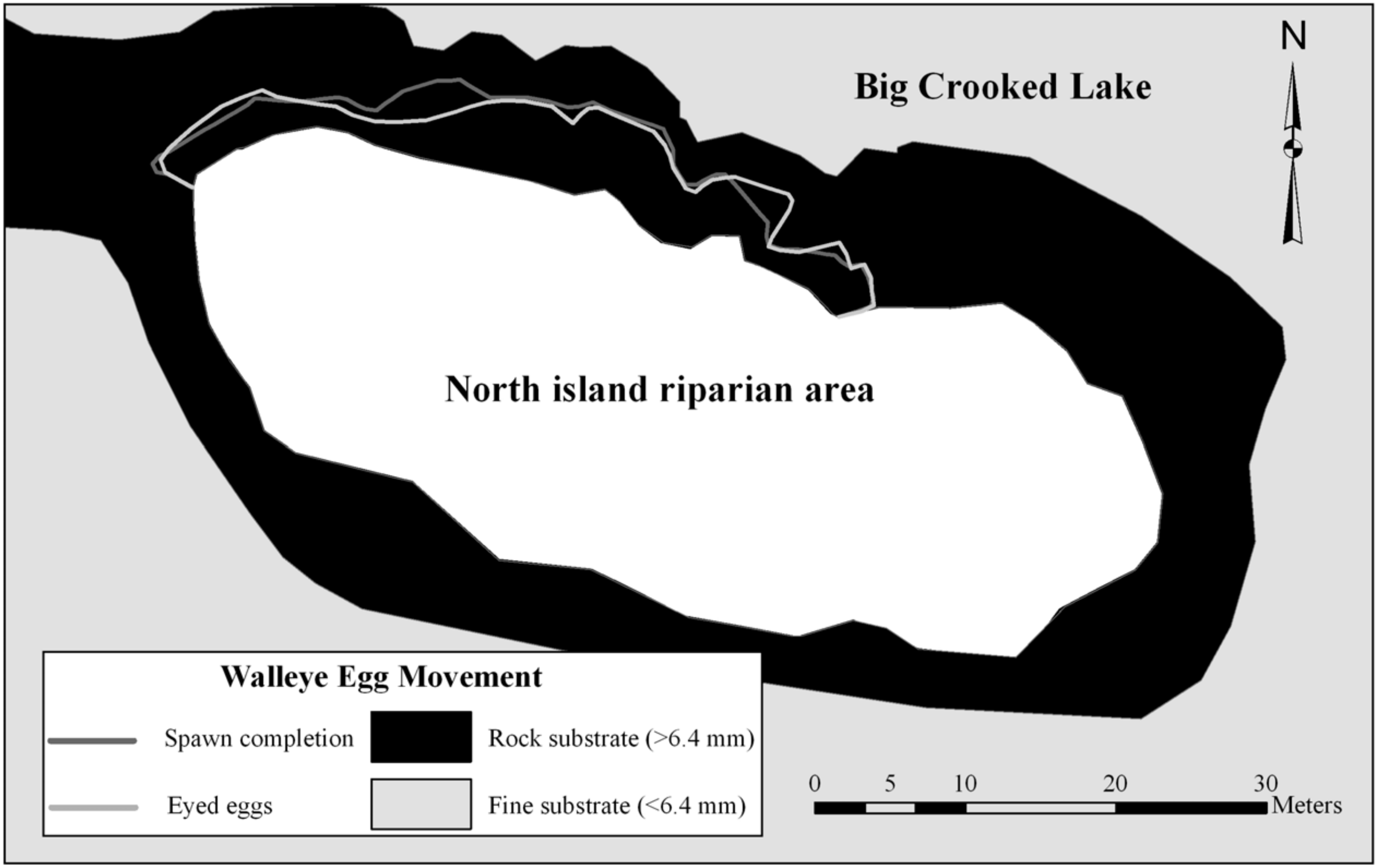


Figure 3-8. Island study reef in Big Crooked Lake depicting the location of walleye eggs after spawn completion and at the eyed egg stage. Minimal egg movement was observed, although the mean distance to shore was lower for the eyed egg stage.

Figure 3-8). Eggs delineations did not occur at the sandbar regions since very few eggs were observed incubating in the water.

The second quantitative measure of egg movement was the density of eggs stranded on shore. The highest density of stranded eggs for the three walleye spawning sites was at the shoreline reef ($\bar{x}$ = 35.4 $\pm$ 10.04 S.E.), while the point was intermediate ($\bar{x}$ = 16.2 $\pm$ 14.21 S.E) and the island had very few eggs stranded on shore ($\bar{x}$ = 1.4 $\pm$ 1.4 S.E)(Table 3-4). Eggs were found most consistently at the shoreline site, while the point had a few collections with a high number of stranded eggs. The density of stranded eggs at the sandbar region was noticeably higher than at the three spawning reefs with a mean of 157.2 eggs ($\pm$ 106.34 S.E)(Table 3-4). However, samples with few or no eggs resulted in high variation and no significant differences ($p > 0.05$) in the density of stranded eggs between the sites. Nevertheless, at certain collection points, the number of stranded eggs at the sandbar was very high, with a maximum of 1,733 total eggs in one 0.25 m diameter sample (Table 3-4). This particular location also had a high concentration of organic matter, especially leaves and pine needles, apparently carried and deposited onto shore by wave energy. Interestingly, there was a relatively high ratio of live to dead eggs at the

sites (Table 3-4). The duration that the eggs were stranded on shore was unknown, but it appeared that eggs remained viable when mixed with moist organic material.

DISCUSSION

The results from this study in Big Crooked Lake imply that functional wind and wave dynamics should be considered with spring air and water temperature when evaluating factors important in influencing annual walleye year-class strength. Studies have shown correlations between year-class strength and spring water temperatures (Johnson 1961, Busch et al. 1975), yet others have found weak or no relation (Kempinger and Carline 1977, Serns 1982b, Madenjian et al. 1996). For example, in Lake Erie spring water temperature was able to explain 21% of the variation in walleye recruitment and the relationship was positive, but weak (Madenjian et al. 1996). The variation in May water temperatures was also included in a model by Hansen et al. (1998), with increased variation equaling fewer recruits in Escanaba Lake, Wisconsin. However, Kempinger and Carline (1977) did not find a relation between walleye recruitment and temperatures during incubation in Escanaba Lake, Wisconsin. In 2005, the thermal conditions in Big Crooked Lake did not result in direct egg mortality as lethal limits were not exceeded, but temperature fluctuations did prolong the overall spawning period (Chapter 2).

Although water temperature is considered a main physical factor affecting reproduction and recruitment its direct causality is unclear and other indirect thermal factors, such as wind and wave activity may also be important. In Big Crooked Lake, wind and wave activity showed a positive, significant correlation. While no known previous studies have quantified wave energy, studies have looked at wind activity relative to walleye egg survival and movement (Johnson 1961, Busch et al. 1975, Roseman et al. 2001). In Lake Winnibigoshish, Minnesota, Johnson (1961) observed dead eggs washed onto shore after three days of 6.7-11.1 m/s ("moderate") easterly winds (Johnson 1961). Johnson (1961) also recorded a mean decrease of egg abundance from 93 to 46 eggs per 0.09 m^2 after "very strong winds during the night." Busch et al. (1975) believed that any storm and wind activity in western Lake Erie resulting in turbulence and daily water temperature reversals of greater than or equal to 0.5°C would be detrimental to walleye eggs. The wind velocity capable of creating this effect ranged from 4.0 to 5.7 m/s, depending on wind direction. Also in Lake Erie, a severe storm with winds in excess of 22.2 m/s and surface waves in excess of 4 m high, resulted in an 80% decrease of eggs on a spawning reef, apparently transported due to wave energy (Roseman et al. 2001). In Big Crooked Lake, the maximum hourly mean (4.82 m/s) fell within the range stated by Busch et al. (1975), but the overall spawning period mean (1.37 m/s) was lower than all of the other study ranges; the fetch of Big Crooked Lake is considerably smaller than Lake Erie. However, in Big Crooked Lake wind velocities of only 1.5 m/s to 1.9 m/s were necessary to generate wave velocity sufficient to move eggs located 2.0 m from the shoreline compared to wind velocities from 6.9 m/s to 8.8 m/s to generate wave velocities that would move eggs located 4.6 m from the shoreline.

Lateral egg movement within reefs and eggs stranded onto shore verified egg movements off reefs due to critical wave velocities attained during the spawning period. Wave energy exceeded the critical velocity for eggs over 28% of the second evaluation period that measured wave energy 2.0 m from the shore; a common distance from shore for incubating eggs to be located. Eggs moved closer to shore ($\bar{x}$ = 0.4 m) along portions of each reef, but very little outward movement was observed. The shoreline study reef showed the highest amount of lateral egg movement and highest stranded egg densities compared to the other two reefs (Table 3-4). The adjacent area and the actual reef were shallowest at the shoreline site, perhaps allowing greater wave energy to accumulate and transport eggs. The shoreline reef also had higher rock embeddedness than the island reef (Chapter 1), meaning it had less complex interstitial spaces that provide protection from wave energy for incubating eggs. Compared to the point reef, the shoreline reef was comprised of smaller substrates as less cobble and rubble were present (Chapter 1). These larger substrates often provide more interstitial spaces and require more wave energy to move, both potentially limiting egg transport.

The most obvious impact of wave energy was transport of eggs to the north and east sandbar shorelines. Priegel (1970) noted that eggs were easily removed from sand substrates and both live and dead eggs have been observed washed onto shore in other lake systems (Eschmeyer 1950, Johnson 1961, Priegel 1970). It has been suggested that dead eggs are more susceptible to wave activity (Eschmeyer 1950, Johnson 1961) and this was also the case in Big Crooked Lake. However, a high percentage of stranded eggs were still viable during the collections. As suggested by others (Johnson 1961, Busch et al. 1975, Roseman et al. 1996, 2001), the eggs were moved to less desirable habitat (i.e., sand) that ultimately led to stranding onshore. The higher density of eggs along the sandbar shoreline was most likely a result of the low concentration of rock substrates and vertical banks that were present at the rock reefs. These two features appeared to prevent stranding eggs along the rock reef shorelines while an absence of these features allowed wave energy to force eggs onto the shoreline at the sandbar region.

In 2005, water level did not appear to have a major impact on walleye reproductive success in Big Crooked Lake. The water level initially rose 1.20 cm during the egg deposition period so available spawning habitat was not reduced like it was in other systems (Johnson 1961, Priegel 1970, Chevalier 1977). For instance, over a four year study on Lake Winnibigoshish, Minnesota, the water level in 1958 was more than 60.0 cm lower than other years (Johnson 1961). The low water level forced walleye to utilize habitat that previously used sparingly and the resulting year-class appeared less abundant in summer seine and trawl catches. While fluctuations occurred in Big Crooked Lake the greatest difference was fairly minimal at 2.30 cm. Therefore, the stranded eggs were more likely a result of wave energy than receding water levels. In 1963 in the Lake Winnebago system (Wisconsin), water levels were sufficient for spawning but then receded rapidly, which resulted in complete mortality of deposited eggs (Priegel 1970). Additional studies have stated that water level fluctuations appeared to affect egg mortality in shallow water areas as it resulted in desiccation (Johnson 1961, Priegel 1970, Chevalier 1977). The water level in Big Crooked Lake rose slightly during the hatching period. A high number of stranded eggs were still viable and a larger rise in water level potentially could allow those eggs to survive and hatch within the lake.

It is perplexing that walleye deposit their eggs in locations (e.g., shallow, close to shore) that are the most vulnerable to wave energy and water level fluctuations, but one possible explanation is the river hypothesis presented by Kitchell et al. (1977). The authors hypothesized that walleye were most successful in lakes that have littoral habitat similar to large river systems. Walleye were originally native and appear best adapted to riverine systems (Scott and Crossman 1973, Colby et al. 1979, Becker 1983) so their invasions of lentic systems may have been most successful in habitat that represented similar conditions and habitat (Kitchell et al. 1977). Along with being most successful in riverine type habitats, they also may function in lakes in a similar fashion as in rivers, including during the reproductive stage. River velocity can provide sufficient dissolved oxygen, remove organic material, and also transport recently hatched fry that are initially poor swimmers to food sources (Priegel 1970 Corbett and Powles 1986). In fact, Nelson (1978) found that 55% of the variation in walleye year-class strength in Lake Oahe, a

Missouri River reservoir, was attributed to mean river flows and air temperatures during the spawning period. Corbett and Powles (1986) worked on two rivers in southeastern Ontario, Canada, and clearly documented that walleye selected for "backwater" and "quiet border water zones" close to the shoreline during egg deposition. Egg densities were high in these areas, while riffle zones had low densities to no eggs present. It was hypothesized that walleye selected these slower velocities areas so they could deposit eggs at the desired rock habitat (Corbett and Powles 1986). In Pool 13 of the Upper Mississippi River, walleye spawning sites were located at the nearshore border habitat of main-channels and river bends comprised of sand, gravel, cobble, and even a freshwater mussel bed (Pitlo 1989). The water depth ranged from 0.6 to 6.1 m, and current velocities ranging 42.7 to 115.8 cm/s at these sites (Pitlo 1989). The current velocity ranged from 35.0 to 75.0 cm/s at gravel, rubble and sand walleye spawning areas in four Wisconsin rivers (Stevens 1990). These descriptions of river spawning habitats appear to be quite similar to the utilized spawning habitat in Big Crooked Lake (Chapter 1). In addition, the mean hourly wave velocity (7.82 cm/s) for the entire spawning period in Big Crooked Lake was much lower than the mean current velocities at the river spawning sites. Therefore, the walleye may not be deterred by wave velocity, but actually select for areas with wave energy and close to the shoreline; similar to spawning habits in rivers.

This study did not determine the actual impact of wind activity, wave energy, and water levels on walleye recruitment, but provided a case study to more closely investigate results of studies that have examined these relationships. Roseman et al. (1996, 2001) found that larvae production was higher in years of low storm activity in Lake Erie than in years of reoccurring or severe storms, such as a storm with wind velocities of 22.2 m/s and waves in excess of 4.0 m (Roseman et al. 1996, 2001). Busch et al (1975) felt that spring water temperatures in Lake Erie were critical as they determined the duration eggs were vulnerable to wave energy, but did not find a correlation between wind activity and year-class strength. Serns (1982b) also did find not any direct correlation between wind activity and walleye year-class strength in Escanaba Lake, Wisconsin. However, the severity of wind and resulting waves may be dissipated by the short fetch (maximum 1.7 km) and a heavily forested riparian area found at the lake (Serns 1982b).

Receding or low waters levels, that may decrease available spawning habitat, was considered a factor in weak year-classes in several lakes (Johnson 1961, Chevalier 1977). For example, spring water levels correlated with variation in the commercial catch-per-effort of walleye five years later in Rainy Lake. After five years, walleye from that year-class would all be recruited into the adult population and susceptible to harvest (Chevalier 1977). However, annual recruitment in others lakes did not appear affected by decreased water levels (Priegel 1970, Busch et al. 1975). Water level fluctuations during the 2005 spawning period in Big Crooked Lake were minimal and most likely did not affect egg survival. While the actual impact of functional dynamics on walleye reproductive success was not determined, the results did provide insight to the potential impact on reproductive success of walleye and why these factors were important in different studies. Further comparisons of wind-wave energy, water levels, and eggs stranded on shore with annual recruitment between years and aquatic systems would provide a better insight into how functional dynamics factor into annual walleye year-class strength.

LITERATURE CITED

Alec Electronics Company, Ltd. 2002. ACM16-338 Data Processing. Kobe, Japan.

Allbaugh, C.A., and J.V. Manz. 1964. Preliminary study on the effects of temperature fluctuations on developing walleye eggs and fry. Progressive Fish Culturist 26:175-180.

Auer, M.T., and N.A. Auer. 1990. Chemical suitability of substrates for walleye egg development in the Lower Fox River, Wisconsin. Transactions of the American Fisheries Society 119:871-876.

ASA. 2002. Sportfishing in America. American Sportfishing Association, Alexandria, Virginia. 12 p.

Becker, G.C. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin. 1952 p.

Beard, T.D., Jr., S.P. Cox, and S.R. Carpenter. 2003. Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. North American Journal of Fisheries Management 23:1283-1293.

Bergerhouse, D.L. 1992. Lethal effects of elevated pH and ammonia on early life stages of walleye. North American Journal of Fisheries Management 12:356-366.

Brousseau, C.S., and E.R. Armstrong. 1987. The role of size limits in walleye management. *Fisheries* 12:2-5.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, Inc., New York. 353 p.

Busch, W.-D.N., R.L. Scholl, and W.L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-1970. Journal of the Fisheries Research Board of Canada 32:1733-1743.

Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake, 1973. Transactions of the American Fisheries Society 102:739-744.

Chevalier, J.R. 1977. Changes in walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance. Journal of the Fisheries Research Board of Canada 34:1696-1702.

Clapp, D.F., Y. Bhagwat, and D.H. Wahl. 1997. The effect of thermal stress on walleye fry and fingerling mortality. North American Journal of Fisheries Management 17:429-437.

Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye. Fisheries Synopsis No. 119, Food and Agriculture Organization, Rome, Italy. 139 p.

Corbett, B.W., and P.M. Powles. 1986. Spawning and larval drift of sympatric walleyes and white suckers in an Ontario stream. Transactions of the American Fisheries Society 115:41-46.

Cox, D.R., and E.J. Snell. 1989. Analysis of binary data. Chapman and Hall, New York. 142 p.

Crowe, W.R. 1962. Homing behaviors of walleyes. Transactions of the American Fisheries Society 91:350-354.

Daykin, P.N. 1965. Application of mass transfer theory to the problem of respiration of fish eggs. Journal of the Fisheries Research Board of Canada 22:159-171.

Derback, B. 1947. The adverse effect of cold weather upon the successful reproduction of pickerel, *Stizostedion vitreum*, at Heming Lake, Manitoba in 1947. Canadian Fish Culturist 2:22-23.

Ellis, D.V., and M.A. Giles. 1965. The spawning behavior of the walleye, *Stizostedion vitreum* (Mitchill). Transactions of the American Fisheries Society 94:358-362.

Ellison, D.G., and W.G. Franzin. 1992. Overview of the symposium on walleye stocks and stocking. North American Journal of Fisheries Management 12:271-275.

Engel, S., M.H. Hoff, and S.P. Newman. 2000. Walleye fry hatching, diet, growth, and abundance in Escanaba Lake, Wisconsin, 1985-1982. Wisconsin Department of Natural Resources Research Report 184, Madison, Wisconsin. 17 p.

Eschmeyer, P.H. 1950. The life history of the walleye, *Stizostedion vitreum vitreum*, in Michigan. Michigan Department of Conservation, Bulletin of the Institute of Fisheries Research No. 3, Ann Arbor, Michigan. 99 p.

ESRI. 2004. ArcGIS Version 9.1. Redlands, California.

Forney, J.L. 1974. Interactions between yellow perch abundance, walleye predation and survival of alternate prey in Oneida Lake, New York. Transactions of the American Fisheries Society 103:15-24.

Forney, J.L. 1976. Year-class formation in the walleye population of Oneida Lake, New York 1966-73. Journal of the Fisheries Research Board of Canada 33:783-792.

Forney, J.L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. Journal of the Fisheries Research Board of Canada 34:1812-1820.

Fox, M.G. 1993. A comparison of zygote survival of native and non-native walleye stocks in two Georgian Bay rivers. Environmental Biology of Fishes 38:379-383.

Frey, A.P. 2003. Trophic interactions between walleye and smallmouth bass in a north temperate lake. M.S. thesis. University of Wisconsin – Stevens Point. 116 p.

Geiling, W.D., J.R.M. Kelso, and E. Iwachewski. 1996. Benefits from incremental additions to walleye spawning habitat in the Current River, with reference to habitat modification as a walleye management tool in Ontario. Canadian Journal of Fisheries and Aquatic Sciences 53(S1):79-87.

Golden Software, Incorporated. 2002. Surfer Version 8. Golden, Colorado.

Hansen, M.J., M.A. Bozek, J.R. Newby, S.P. Newman, and M.D. Staggs. 1998. Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958-1995. North American Journal of Fisheries Management 18:764-774.

Heidinger, R.C., R.C. Brooks, D. Leitner, and I. Soderstrom. 1997. Prediction of walleye egg and embryo survival at two stages of development. The Progressive Fish-Culturist 59:64-67.

Henderson, B.A., and S.J. Nepszy. 1994. Reproductive tactics of walleye (*Stizostedion vitreum*) in Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 51:986-997.

Hintz, J. 2004. NCSS and PASS. Number Cruncher Statistical Systems, Kaysville, Utah.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34:1524-1550.

Holtze, K.E. and N.J. Hutchinson. 1989. Lethality of low pH and Al to early life stages of six fish species inhabiting Precambrian shield waters in Ontario. Canadian Journal of Fisheries and Aquatic Sciences 46:1188-1202

Hosmer, D. W. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons Inc., New York. 307 p.

Hulsman, P.F., P.M. Powles, and J.M. Gunn. 1983. Mortality of walleye eggs and rainbow trout yolk sac larvae in low pH waters of the La Cloche Mountain area, Ontario. Transactions of the American Fisheries Society 112:680-688.

Hurley, D.A. 1972. Observations on incubating walleye eggs. The Progressive Fish-Culturist 34:49-54.

Jennings, M.J., J.E. Claussen, and D.P. Philipp. 1996. Evidence for heritable preferences for spawning habitat between two walleye populations. Transactions of the American Fisheries Society 125:978-982.

Johnson, F.H. 1961. Walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and connecting waters. Transactions of the American Fisheries Society 90:312-322.

Johnson, M.G., J.H. Leach, C.K. Minns, and C.H. Oliver. 1977. Limnological characteristics of Ontario lakes in relation to association of walleye (*Stizostedion vitreum vitreum*), northern pike (*Exox lucius*), lake trout (*Salvelinus namaycush*), and smallmouth bass (*Micropterus dolomieui)*. Journal of the Fisheries Research Board of Canada 34:1952-1601.

Jones, M. L., J.K. Netto, J.D. Stockwell, and J.B. Mion. 2003. Does the value of newly accessible spawning habitat for walleye (*Stizostedion vitreum*) depend on its location relative to nursery habitat? Canadian Journal of Fisheries and Aquatic Sciences 60:1527-1538.

Kempinger, J.J., and W.S. Churchill. 1972. Contribution of native and stocked walleye fingerlings to the angler's catch, Escanaba Lake, Wisconsin. Transactions of American Fisheries Society 101:644–649.

Kempinger, J. J., and R. F. Carline. 1977. Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955–72. Journal of the Fisheries Research Board of Canada 34:1800–1811.

Kerr, S.J. 1993. A bibliography of selected fish habitat protection guidelines and references. Volume 1: Aquatic habitat. Ontario Ministry of Natural Resources Publication 50408, Ontario, Canada. 187 p.

Kitchell, J.F., M.G. Johnson, C.K. Minns, K.H. Loftus, L. Greig, and C.H. Olver. 1977. Percid habitat: the river analogy. Journal of the Fisheries Research Board of Canada 34:1936-1940.

Koenst, W.M., and L.L. Smith, Jr. 1976. Thermal requirements of the early life history stages of walleye, *Stizostedion vitreum vitreum,* and sauger, *Stizostedion canadense*. Journal of the Fisheries Research Board of Canada 33:1130-1138.

Kohler, C.C., and W.A. Hubert. 1999. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland. 718 p.

Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokanson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: A summary and model of temperature effects. Journal of the Fisheries Research Board Canada 34:1900-909.

Krise, W.F., L. Bulkowski-Cummings, A.D. Shellman, K.A. Kraus, and R.W. Gould. 1986. Increased walleye egg hatch and larval survival after protease treatment of eggs. The Progressive Fish-Culturist 48:95-100.

Leach, J.H., M.G. Johnson, J.R.M. Kelso, J. Hartman, W. Nomann, and B. Entz. 1977. Responses of percid fishes and their habitats to eutrophication. Journal of the Fisheries Research Board of Canada 34:1964-1971.

Li, J., Y. Cohen, D.H. Schupp, and I.R. Adelman. 1996a. Effects of walleye stocking on population abundance and fish size. North American Journal of Fisheries Management 16:830-839.

Li, J., Y. Cohen, D.H. Schupp, and I.R. Adelman. 1996b. Effects of walleye stocking on year-class strength. North American Journal of Fisheries Management 16:840-850.

Lyons, J., and J.J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Transactions of the American Fisheries Society 116:29-39.

Madenjian, C.P., J.T. Tyson, R.L. Knight, M.W. Kershner, and M.J. Hansen. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. Transactions of the American Fisheries Society 125:821-830.

Manly, B.F.J, L.L. McDonald, and D.L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies, 2nd edition. Chapman and Hall, New York. 175 p.

Mathias, J.A., and S. Li. 1982. Feeding habits of walleye larvae and juveniles: comparative laboratory and field studies. Transactions of the American Fisheries Society 111:722-735.

McClanahan, D.R. 2003. A statewide mail survey to estimate 2000-2001 angler catch, harvest, and effort in Wisconsin. M.S. Thesis. University of Wisconsin - Stevens Point. 98 p.

McElman, J.F., and E.K. Balon. 1979. Early ontogeny of walleye, *Stizostedion vitreum*, with steps of salutatory development. Environmental Biology of Fishes 4:309-348.

McKnight, T.C. 1975. Artificial walleye spawning reefs in Jennie Webber Lake, Oneida County. Wisconsin Department of Natural Resources Fish Management Section Report No. 81, Madison, Wisconsin. 16 p.

Microsoft Corporation. 2001. Microsoft Excel 2002. Redmond, Washington.

Moore, A.A. 2003. Manipulation of fertilization procedures to improve hatchery walleye egg fertility and survival. North American Journal of Aquaculture 65:56-59.

Mraz, D. 1968. Recruitment, growth, exploitation and management of walleyes in a southeastern Wisconsin lake. Wisconsin Department of Natural Resources Technical Bulletin 40, Madison, Wisconsin. 38 p.

Nate, N.A., M.A. Bozek, M.J. Hansen, and S.W. Hewett. 2001. Variation of adult walleye abundance in relation to recruitment and limnological variables in northern Wisconsin lakes. North American Journal of Fisheries Management 21:441-447.

Nate, N.A., M.A. Bozek, M.J. Hansen, C.W. Ramm, M.T. Bremigan, and S.W. Hewett. 2003. Predicting the occurrence and success of walleye populations from physical and biological features of northern Wisconsin lakes. North American Journal of Fisheries Management 23:1207-1214.

Nelson, W.R. 1978. Implications of water management in Lake Oahe for the spawning success of coolwater fishes. Pages 154-158 *in* R.L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland. 437 p.

Neuswanger, D., and M.A. Bozek. 2004. Preliminary assessment of effects of rock habitat projects on walleye reproduction in 20 northern Wisconsin lakes: a summary of case histories as of March 2004. Wisconsin Department of Natural Resources, Hayward, Wisconsin. 10 p.

Newburg, H.J. 1975. Evaluation of an improved walleye (*Stizostedion vitreum*) spawning shoal with criteria for design and placement. Minnesota Department of Natural Resources Investigational Report No. 340, St. Paul, Minnesota. 40 p.

Niemuth, W., W. Helm, and V. Hacker. 1959. The walleye, its life history, ecology and management. Wisconsin Conservation Department Publication No. 227, Madison, Wisconsin. 14 p.

Olson, D., D.H. Schupp, and V. Macins. 1978. An hypothesis of homing behavior of walleye as related to observed patterns of passive and active movements. Pages 52-57 *in* R.L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland. 437 p.

Onset Computer Corporation. 2002. BoxCar Pro Version 4.3. Bourne, Massachusetts.

Oseid, D.M., and L.L. Smith, Jr. 1971. Survival and hatching of walleye eggs at various dissolved oxygen levels. Progressive Fish-Culturist 33:81-85.

Pitlo, J., Jr. 1989. Walleye spawning habitat in pool 13 of the Upper Mississippi River. North American Journal of Fisheries Management 9:303–308

Potter, D.F. 1995. Relations of angler catch per unit effort and yield to limnological variables in Wisconsin lakes. M.S. Thesis. University of Wisconsin - Stevens Point. 328 p.

Press, S.J., and S. Wilson. 1978. Choosing between logistic regression and discriminant analysis. Journal of American Statistics Association 73:699-705.

Priegel, G.R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago region. Wisconsin Department of Natural Resources Technical Bulletin 45, Madison, Wisconsin. 105 p.

Quinn, S.P. 1992. Angler perspective on walleye management. North American Journal of Fisheries Management 12:367-378.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191. 382 p.

Roseman, E.F., W.W. Taylor, D.B. Hayes, R.C. Haas, R.L. Knight and K.O. Paxton. 1996. Walleye egg deposition and survival on reefs in Western Lake Erie (USA). Annales Zoologici Fennici 33:341-351.

Roseman, E.F., W.W. Taylor, D.B. Hayes, R.L. Knight, and R.C. Haas. 2001. Removal of walleye eggs from reefs in western Lake Erie by a catastrophic storm. Transactions of the American Fisheries Society 130:341-346.

SAS Institute, Incorporated. 2001. SAS Version 8.2. Cary, North Carolina.

Schneider, J.C., J. Copeland, and M. Wolgamood. 2002. Tolerance of incubating walleye eggs to temperature fluctuation. North American Journal of Aquaculture 64:75-78.

Schupp, D.H., and V. Macins. 1977. Trends in percid yields from Lake of the Woods, 1888-1973. Journal of the Fisheries Research Board of Canada 34:1784-1791.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184, Ottawa, Ontario. 966 p.

Serns, S.L. 1978. Effects of a minimum size limit on the walleye population of a northern Wisconsin lake. Pages 390–397 *in* R. L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland. 437 p.

Serns, S.L. 1982a. Walleye fecundity, potential egg deposition, and survival from egg to fall young-of-year in Escanaba Lake, Wisconsin, 1979-1981. North American Journal of Fisheries Management 4:388-394.

Serns, S.L. 1982b. Influence of various factors on the density and first year growth of age-0 walleye in Escanaba Lake, Wisconsin, 1958-80. Transactions of the American Fisheries Society 111:299-306.

Serns, S.L. 1986. Cohort analysis as an indicator of walleye year-class strength in Escanaba Lake, Wisconsin, 1956-1974. Transactions of the American Fisheries Society 115:849-852.

Smith, L.L., Koenst, W.M., and K.E.H. Hokanson. 1975. Temperature effects on eggs and fry of percoid fishes. United States Environmental Protection Agency, National Environmental Research Center, Corvallis, Oregon. 91 p.

Staggs, M.D., R.C. Moody, M.J. Hansen, and M.H. Hoff. 1990. Spearing and sport angling for walleye in Wisconsin's ceded territory. Wisconsin Department of Natural Resources, Fisheries Management Administrative Report 31, Madison, Wisconsin. 34 p.

Stevens, A.G. 1990. Physical habitat preferences of walleyes in streams in Wisconsin. M.S. Thesis. University of Wisconsin - Stevens Point. 282 p.

Sullivan, M.G. 2003. Active management of walleye fisheries in Alberta: Dilemmas of managing recovering fisheries. North American Journal of Fisheries Management 23:1343-1358.

Tolonen, K.T., H. Hamalainen, I.J. Holopainen, and J. Karjalainen. 2001. Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. Archiv fuer Hydrobiologie 152:39-67.

USBR. 1977. Design of small dams. United State Bureau of Reclamation, Washington, D.C. 816 p.

Ventling-Schwank, A.R, and D.M. Livingstone. 1994. Transport and burial as a cause of whitefish (*Coregonus* sp.) egg mortality in a eutrophic lake. Canadian Journal of Fisheries and Aquatic Sciences 51:1908-1919.

Wagner, W.C. 1990. Evaluation of a man-made walleye spawning reef. Michigan Department of Natural Resources Fisheries Research Report 1959, Marquette, Michigan. 22 p.

Waltemeyer, D.L. 1975. The effect of tannin on the motility of walleye, *Stizostedion vitreum vitreum*, spermatozoa. Transactions of the American Fisheries Society 104:818-810.

Waltemeyer, D.L. 1976. Tannin as an agent to eliminate adhesiveness of walleye eggs during artificial propagation. Transactions of the American Fisheries Society 105:731-736.

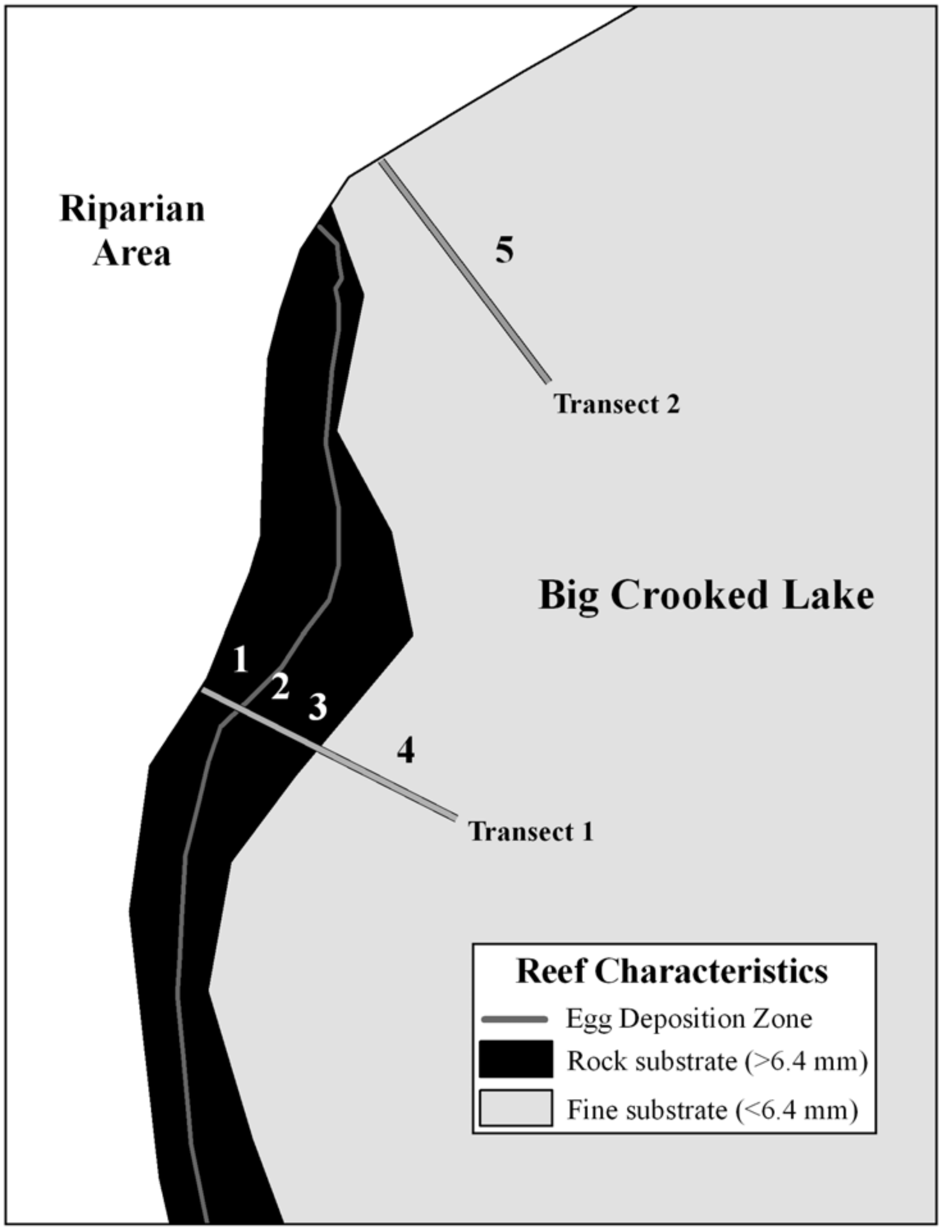
Weber, D.T., and R.L. Imler. 1974. An evaluation of artificial spawning beds for walleye. Colorado Division of Wildlife, Fisheries Research Section, Special Report No. 34, Fort Collins, Colorado. 17 p.

Wentworth, C.K. 1922. A scale of grade and class terms for classic sediments. Journal of Geology 30:377-392.

Wolfert, D.R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. Journal of the Fisheries Research Board of Canada 26:1877-1888.

Wolfert, D.R., W.D.N. Busch, and C.T. Baker. 1975. Predation by fish on walleye eggs on a spawning reef in western Lake Erie, 1969-1971. Ohio Journal of Science 75:118-125.

Appendix A. Diagram of the sample point classification system used for quantification of spawning habitat features.



Sample point classification relative to egg deposition zone and reef characteristics. Along snorkeling transect 1: region 1 was sample points contained within the egg deposition zone, region 2 was the "transition" sample point from the egg deposition zone to the area where no eggs were observed, region 3 were sample points within the rock reef but where no eggs were observed, and region 4 were sample points outside of the rock reef and in fine substrates. Along snorkeling transect 2 all sample points were adjacent to the rock reef and eggs were never observed in the region.

Appendix B. Additional lake-wide available habitat resource selection functions of Big Crooked Lake in 2004 and 2005.

Top eight univariate resource selection functions for utilized spawning habitat compared to available littoral habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 1,000, utilized sites N = 775 in 2004 and 1,000 in 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P-value	Coefficient	P-value	-2 Log	AIC	Presence	Absence	Overall
2004									
Distance to shoreline	-0.400	<0.0001	3.081	<0.0001	684.3	688.3	95.9	90.8	92.9
Gravel substrate (%)	0.094	<0.0001	-2.868	<0.0001	829.2	833.2	85.8	93.5	90.3
Dominant substrate	4.871	<0.0001	-17.250	<0.0001	834.6	838.6	93.2	95.1	94.3
Dominant embed.	-2.140	<0.0001	6.409	<0.0001	1021.4	1025.4	76.4	95.9	87.7
Depth	-7.780	0.1473	3.460	0.7958	1098.0	1102.0	89.2	82.6	85.4
Sand substrate (%)	-0.061	<0.0001	2.108	<0.0001	1170.8	1174.8	88.6	86.6	87.4
Fine organic matter (%)	-0.403	<0.0001	0.935	<0.0001	1513.4	1517.4	87.3	75.6	80.5
Cobble substrate (%)	0.169	<0.0001	-1.074	<0.0001	1801.3	1805.3	55.0	95.0	78.2
2005									
Distance to shoreline	-0.560	<0.0001	3.614	<0.0001	615.7	619.7	97.0	90.8	93.9
Depth	-13.121	<0.0001	4.527	<0.0001	772.9	776.9	93.5	91.0	92.3
Gravel substrate (%)	0.094	<0.0001	-2.696	<0.0001	926.0	930.0	91.1	92.1	91.6
Dominant embed.	-2.175	<0.0001	6.329	<0.0001	926.1	930.1	88.3	95.9	92.1
Dominant substrate	4.969	<0.0001	-17.267	<0.0001	979.1	979.1	93.2	95.1	94.2
Fine organic matter (%)	-0.969	<0.0001	1.395	<0.0001	1305.9	1309.9	99.4	75.6	87.5
Sand Substrate (%)	-0.060	<0.0001	2.311	<0.0001	1373.1	1377.1	91.5	85.9	88.7
Cobble substrate (%)	0.170	<0.0001	-0.848	<0.0001	2044.5	2048.5	67.9	91.4	79.7

Top three bivariate and best three-variable resource selection functions for used spawning habitat compared to available littoral habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 1,000, utilized sites N = 775 in 2004 and 1,000 in 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P-value	Coefficient	P-value	-2 Log	AIC	Presence	Absence	Overall
2004									
Distance to shoreline	-0.366	<0.0001	0.322	0.1520	390.7	396.7	96.4	95.3	95.8
Gravel substrate (%)	0.072	<0.0001							
Distance to shoreline	-0.305	<0.0001	-10.438	<0.0001	397.5	403.5	96.4	96.3	96.3
Dominant substrate	3.639	<0.0001							
Distance to shoreline	-0.336	<0.0001	6.993	<0.0001	450.5	456.5	96.3	95.0	95.5
Dominant embed.	-1.477	<0.0001							
Distance to shoreline	-0.364	<0.0001	-0.061	0.8009	353.8	361.8	97.1	96.3	96.6
Gravel substrate (%)	0.064	<0.0001							
Cobble substrate (%)	0.064	<0.0001							
2005									
Distance to shoreline	-0.564	<0.0001	7.573	<0.0001	340.9	346.9	98.3	95.3	96.8
Dominant embed.	-1.565	<0.0001							
Distance to shoreline	-0.543	<0.0001	-9.411	<0.0001	356.9	362.9	98.1	95.2	96.7
Dominant substrate	3.570	<0.0001							
Distance to shoreline	-0.438	<0.0001	0.778	0.0007	394.2	400.2	97.6	95.2	96.4
Gravel substrate (%)	0.065	<0.0001							
Distance to shoreline	-0.542	<0.0001	0.450	0.0807	318.5	326.5	98.1	96.0	97.1
Gravel substrate (%)	0.053	<0.0001							
Cobble substrate (%)	0.091	<0.0001							

Best four- and five-variable resource selection functions for utilized spawning habitat compared to available littoral habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 1,000, utilized sites N = 775 in 2004 and 1,000 in 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P-value	Coefficient	P-value	-2 Log	AIC	Presence	Absence	Overall
2004									
Distance to shoreline	-0.304	<0.0001	2.485	<0.0001	323.2	333.2	97.1	96.2	96.6
Sand substrate (%)	-0.036	<0.0001							
Gravel substrate (%)	0.045	<0.0001							
Fine organic matter (%)	-0.096	0.0099							
Distance to shoreline	-0.306	<0.0001	1.930	<0.0001	317.8	329.8	97.2	96.4	96.8
Sand substrate (%)	-0.030	<0.0001							
Gravel substrate (%)	0.046	<0.0001							
Fine organic matter (%)	-0.081	0.0395							
Cobble substrate (%)	0.030	0.0336							
2005									
Distance to shoreline	-0.415	<0.0001	4.426	<0.0001	306.9	316.9	98.5	96.4	97.5
Dominant embed.	-0.922	<0.0001							
Gravel substate (%)	0.032	<0.0001							
Fine organic matter (%)	-0.333	0.0014							
Distance to shoreline	-0.449	<0.0001	2.551	0.0039	295.8	307.8	98.5	96.6	97.6
Dominant embed.	-0.492	0.0150							
Gravel substate (%)	-0.295	0.0040							
Fine organic matter (%)	0.039	<0.0001							
Cobble substrate (%)	0.051	0.0020							

Appendix C. Additional nearshore available habitat resource selection functions of Big Crooked Lake in 2004 and 2005.

Top eight univariate resource selection functions for utilized spawning habitat compared to available nearshore habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 662, utilized sites N = 662 in 2004 and 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P-value	Coefficient	P-value	-2 Log	AIC	Presence	Absence	Overall
2004									
Sand substrate (%)	-0.057	<0.0001	2.106	<0.0001	1010.9	1014.9	90.0	78.9	84.4
Dominant substrate	3.488	<0.0001	-12.644	<0.0001	1032.8	1036.5	93.0	81.0	86.7
Gravel substrate (%)	0.062	<0.0001	-2.345	<0.0001	1053.8	1057.8	81.7	79.9	80.8
Dominant embed.	-1.109	<0.0001	2.996	<0.0001	1265.3	1269.3	75.8	83.1	79.5
Distance to shoreline	-0.320	<0.0001	1.261	<0.0001	1498.0	1502.0	78.4	71.1	74.8
Fine organic matter (%)	-0.258	<0.0001	0.462	<0.0001	1633.3	1637.3	86.9	45.9	66.4
Cobble substrate (%)	0.067	<0.0001	-0.485	<0.0001	1668.7	1672.7	54.4	84.0	69.2
Depth	-2.446	<0.0001	0.780	<0.0001	1754.6	1754.6	69.8	52.6	61.2
2005									
Gravel substrate (%)	0.065	<0.0001	-2.649	<0.0001	958.2	962.2	82.9	83.1	83.0
Sand substrate (%)	-0.059	<0.0001	2.038	<0.0001	972.8	976.8	90.0	80.8	85.4
Dominant substrate	3.786	<0.0001	-13.775	<0.0001	991.4	995.4	94.9	81.0	87.9
Dominant embed.	-1.353	<0.0001	3.279	<0.0001	1017.5	1021.5	89.4	83.1	86.3
Distance to shoreline	-0.484	<0.0001	1.531	<0.0001	1272.8	1276.8	86.1	71.1	78.6
Fine organic matter (%)	-1.027	<0.0001	0.612	<0.0001	1342.4	1346.4	99.7	45.9	72.8
Depth	-8.866	<0.0001	1.957	<0.0001	1348.6	1352.6	83.4	72.4	77.9
Cobble substrate (%)	0.072	<0.0001	-0.581	<0.0001	1614.7	1618.7	57.7	84.0	70.5

Top three bivariate and best three-variable resource selection functions for utilized spawning habitat compared to available nearshore habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 662, utilized sites N = 662 in 2004 and 2005).

Model	Variable		Intercept		-2 Log	AIC	% Correct Classification		
	Coefficient	P-value	Coefficient	P-value			Presence	Absence	Overall
2004									
Sand substrate (%)	-0.038	<0.0001	-0.061	0.7836	904.8	910.8	89.6	81.6	85.6
Gravel substrate (%)	0.036	<0.0001							
Sand substrate (%)	-0.053	<0.0001	2.815	<0.0001	929.8	935.8	89.3	80.5	84.9
Distance to shoreline	-0.229	<0.0001							
Dominant substrate	3.334	<0.0001	-11.702	<0.0001	959.5	965.5	92.3	82.9	87.6
Fine organic matter (%)	-0.216	<0.0001							
Sand substrate (%)	-0.036	<0.0001	0.732	0.0051	850.8	858.8	90.5	82.9	86.7
Gravel substrate (%)	0.033	<0.0001							
Distance to shoreline	-0.198	<0.0001							
2005									
Gravel substrate (%)	0.065	<0.0001	-2.039	<0.0001	732.6	738.6	89.1	86.6	87.8
Fine organic matter (%)	-1.028	<0.0001							
Dominant substrate	3.608	<0.0001	-12.589	<0.0001	756.9	762.9	94.6	88.4	91.5
Fine organic matter (%)	-1.096	<0.0001							
Sand substrate (%)	-0.551	<0.0001	-12.589	<0.0001	784.3	790.3	92.4	85.7	89.0
Depth	-6.998	<0.0001							
Gravel substrate (%)	0.045	<0.0001	-0.425	0.0910	672.2	680.2	93.4	86.7	90.0
Fine organic matter (%)	-0.973	<0.0001							
Sand substrate (%)	-0.027	<0.0001							

Best four- and five-variable resource selection functions for utilized spawning habitat compared to available nearshore habitat of Big Crooked Lake in 2004 and 2005 (available sites N = 662, utilized sites N = 662 in 2004 and 2005).

	Variable		Intercept				% Correct Classification		
Model	Coefficient	P-value	Coefficient	P-value	-2 Log	AIC	Presence	Absence	Overall
2004									
Sand substrate (%)	-0.045	<0.0001	-0.199	0.5758	836.3	846.3	91.1	81.4	86.3
Gravel substrate (%)	0.040	<0.0001							
Distance to shoreline	-0.206	<0.0001							
Dominant embed.	0.366	0.0002							
Sand substrate (%)	-0.045	<0.0001	-0.469	0.1999	811.2	823.1	90.8	82.6	86.7
Gravel substrate (%)	0.044	<0.0001							
Distance to shoreline	-0.157	<0.0001							
Fine organic matter (%)	-0.045	<0.0001							
Dominant embed.	0.437	<0.0001							
2005									
Gravel substrate (%)	0.039	<0.0001	0.755	0.0201	618.8	628.8	94.0	88.1	91.0
Fine organic matter (%)	-0.891	<0.0001							
Sand substrate (%)	-0.030	<0.0001							
Depth	-4.186	<0.0001							
Gravel substrate (%)	0.030	<0.0001	1.686	<0.0001	597.6	609.6	94.7	89.1	91.9
Fine organic matter (%)	-0.892	<0.0001							
Sand substrate (%)	-0.036	<0.0001							
Depth	-4.917	<0.0001							
Coarse organic matter (%)	-0.069	<0.0001							

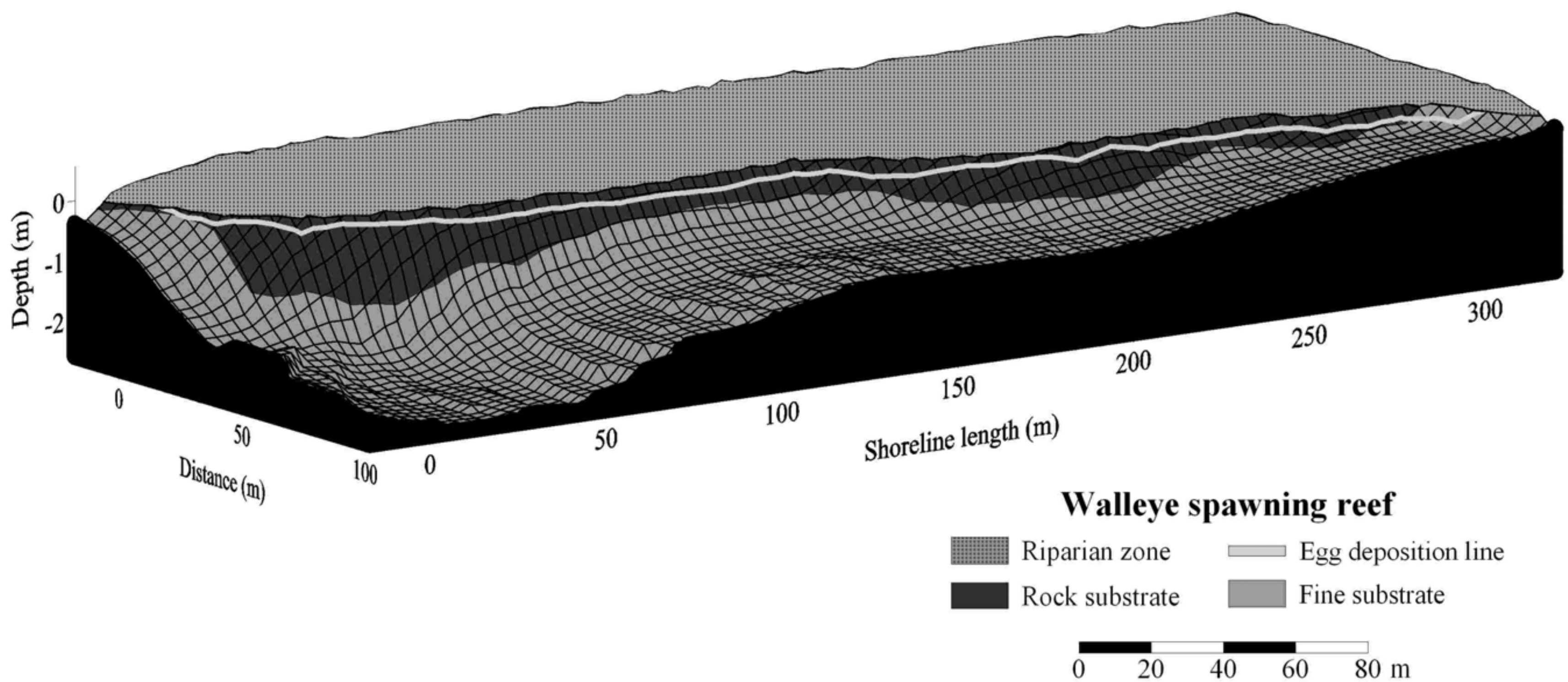
Appendix D. Additional quantitative descriptions and two-dimensional blueprints of the utilized spawning sites in Big Crooked Lake.

The "shoreline" spawning reef was the northern most reef and walleye utilized the entire length of the reef, including spawning in a sand substrate area. The water depth over the entire rock reef was fairly shallow and the rock reef often had a clear transition into sand. Walleye spawned tight to the shoreline and in shallow water, often well before the distinct reef transition. Gravel was the dominant substrate at both the utilized and unutilized portions of the rock reef, while sand and cobble were also common. Organic material, especially pine needles and leaves, was relatively high at this utilized spawning habitat, especially closer to the shoreline. Walleye spawning activity was high at the shoreline reef, including observed egg deposition events during the day. Interestingly, walleye spawned in exclusively sand substrate north of the rock reef in both 2004 and 2005. In 2004, eggs were observed over similar portions of the reef except no eggs were present after the southern most bend, that was covered with coarse organic material; leaves in particular.

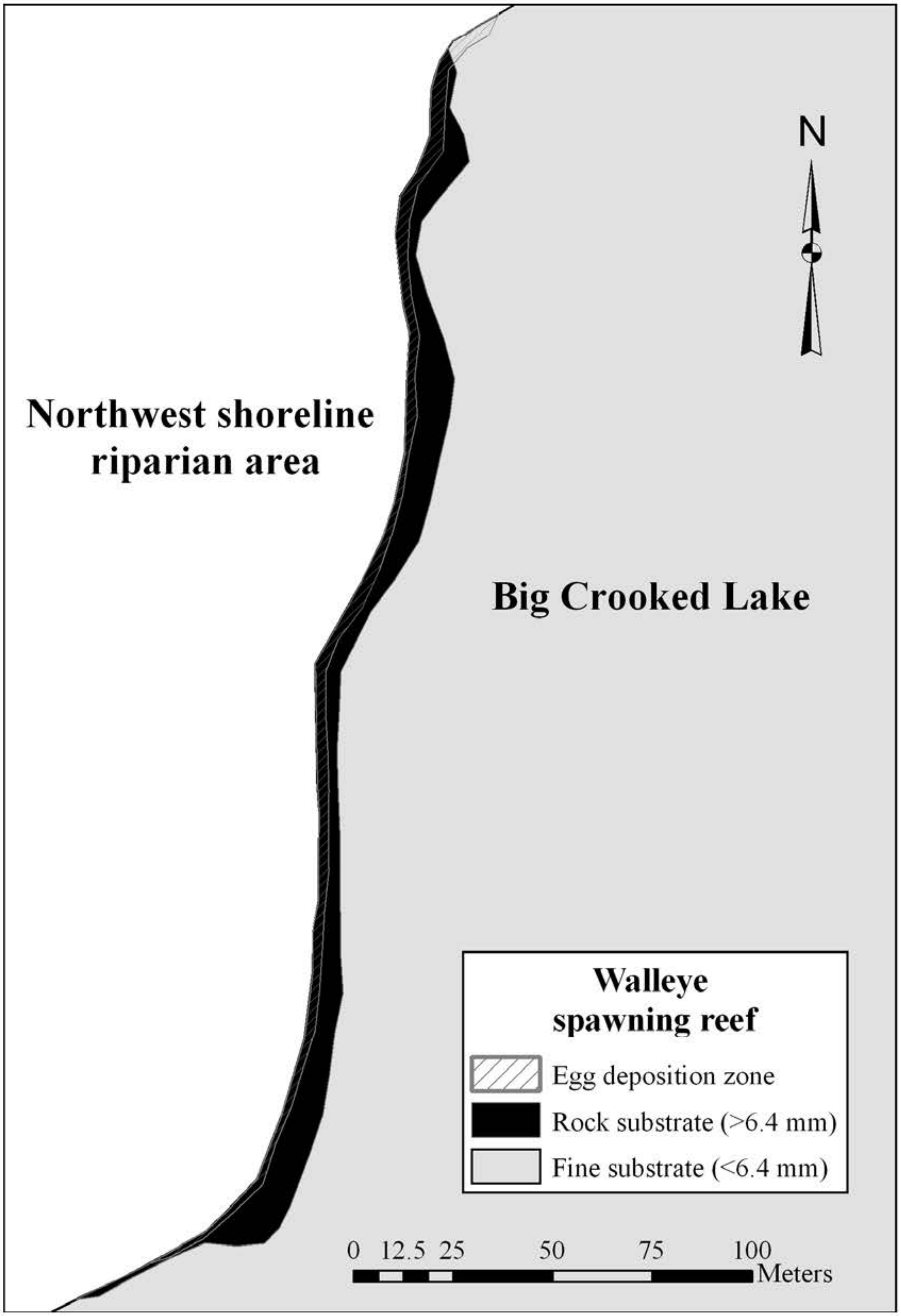
The "west" spawning reef was located in the west-central portion of the lake, was very narrow, and had walleye eggs located extremely close to the shoreline and in shallow water. While the rock reef was very narrow, it was the longest reef, with a main center reach and two shorter sections north and south. The west reef was composed of primarily gravel with low embeddedness along with sand, cobble, and small amounts of rubble. No small or large boulders were present, and fine and organic matter were both rare. Walleye used the majority of the available rock substrate and at a few locations also spawned in primarily sand after the rock transition. The utilized southern stretch was near a large patch of reeds to the east, while the northern stretch was tucked

Reef and substrate characteristics for the used egg deposition habitat and overall available rock substrate at the utilized spawning reefs in Big Crooked Lake. Means are presented for distance to shoreline, depth, slope, rock embeddedness, and percent composition for present substrate size classes, along with actual lengths and areas.

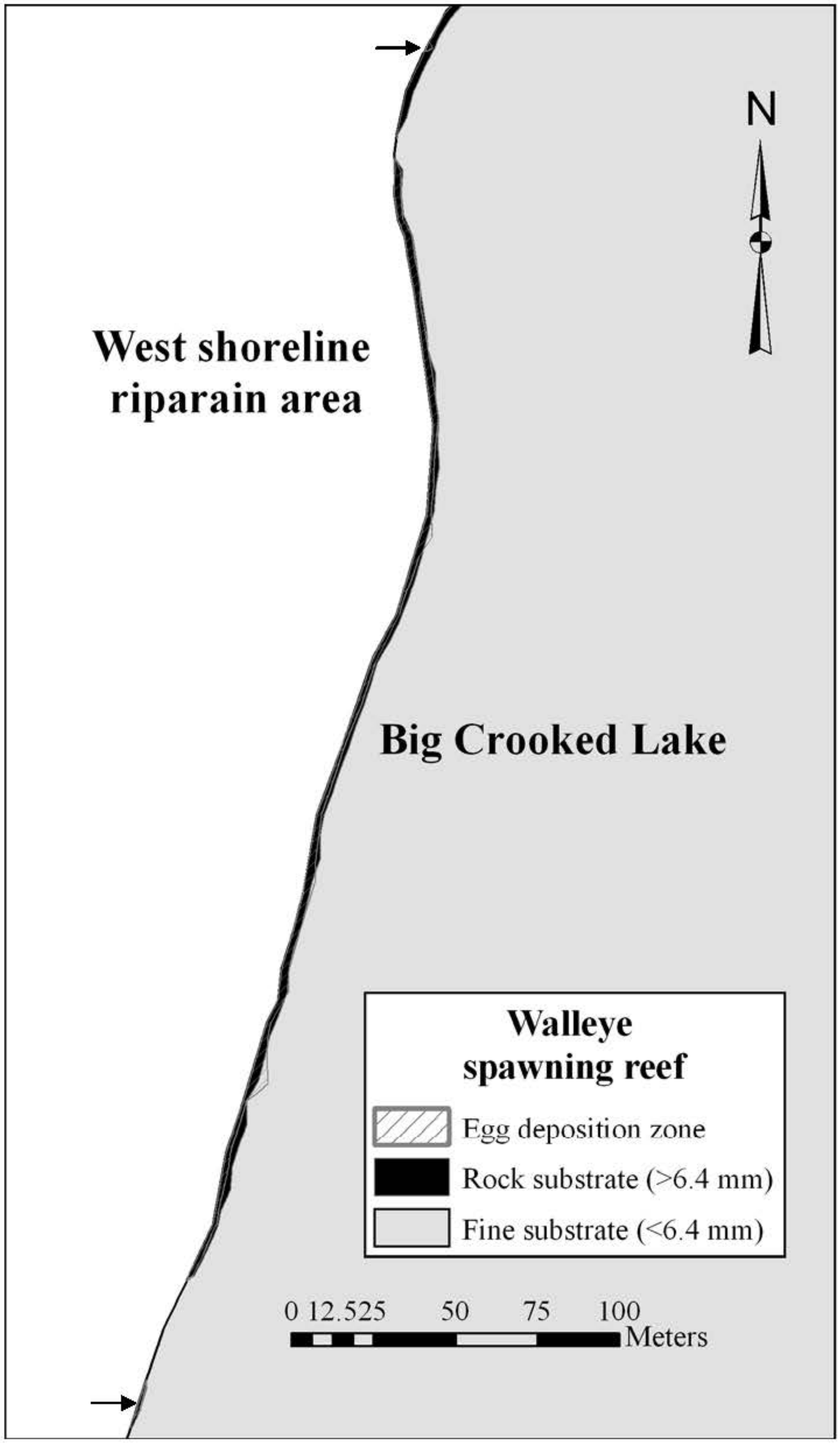
	Reef characteristics					Substrate characteristics							
	Distance	Depth	Slope	Length	Area	Embed	Sand	Gravel	Cobble	Rubble	Sm. Bld	La. Bld	COM
Shore Used	2.45	0.27	0.10	346.50	801.49	1.27	18.4	57.6	17.5	2.4	0.2	0.0	3.9
Shore Available	9.24	0.70	0.13	350.09	2464.99	1.58	32.6	51.5	10.8	2.8	0.0	0.0	2.2
West Used	1.58	0.21	0.07	371.62	586.70	1.16	13.4	69.8	12.7	2.6	0.0	0.0	1.4
West Available	2.17	0.28	0.08	514.81	1021.35	1.18	15.5	68.3	12.1	2.7	0.0	0.0	1.0
Bay Used	1.96	0.21	0.05	104.68	103.98	1.28	11.8	82.5	3.4	0.4	0.0	0.0	1.8
Bay Available	3.98	0.38	0.07	310.53	1839.89	1.40	14.6	77.6	5.0	1.4	0.0	0.0	1.2
Point Used	5.86	0.36	0.07	58.80	355.65	1.44	20.6	53.6	18.0	5.1	0.0	0.0	2.8
Point Available	15.21	1.04	0.08	63.76	969.32	1.33	19.9	54.2	17.9	5.2	0.3	0.8	1.9
South Used	1.74	0.21	0.09	214.00	367.34	1.03	3.3	61.4	23.1	6.9	0.0	0.0	5.4
South Available	5.89	0.86	0.12	216.30	1116.14	0.97	5.4	60.0	26.3	5.1	0.1	0.0	2.9
Island Used	3.81	0.36	0.10	51.60	183.36	0.78	6.3	66.6	15.5	4.8	1.4	5.2	0.2
Island Available	8.77	1.29	0.14	164.55	1977.11	0.81	7.4	57.8	18.1	6.0	1.6	8.8	0.3



Three-dimensional blueprint of the northeast shoreline study reef illustrating the extent of walleye egg deposition relative to the rock substrate reef in Big Crooked Lake. Eggs were consistently observed between the shoreline and the egg deposition line along the entire rock reef and in a sand area to the north (right side). Note: The x-axis is the distance in m from an arbitrary point and measurements were not taken in the riparian zone.



Section of the northwest shoreline utilized by walleye as spawning habitat. Eggs were contained within the rock substrate, but eggs were observed in fine substrate north of the rock reef.

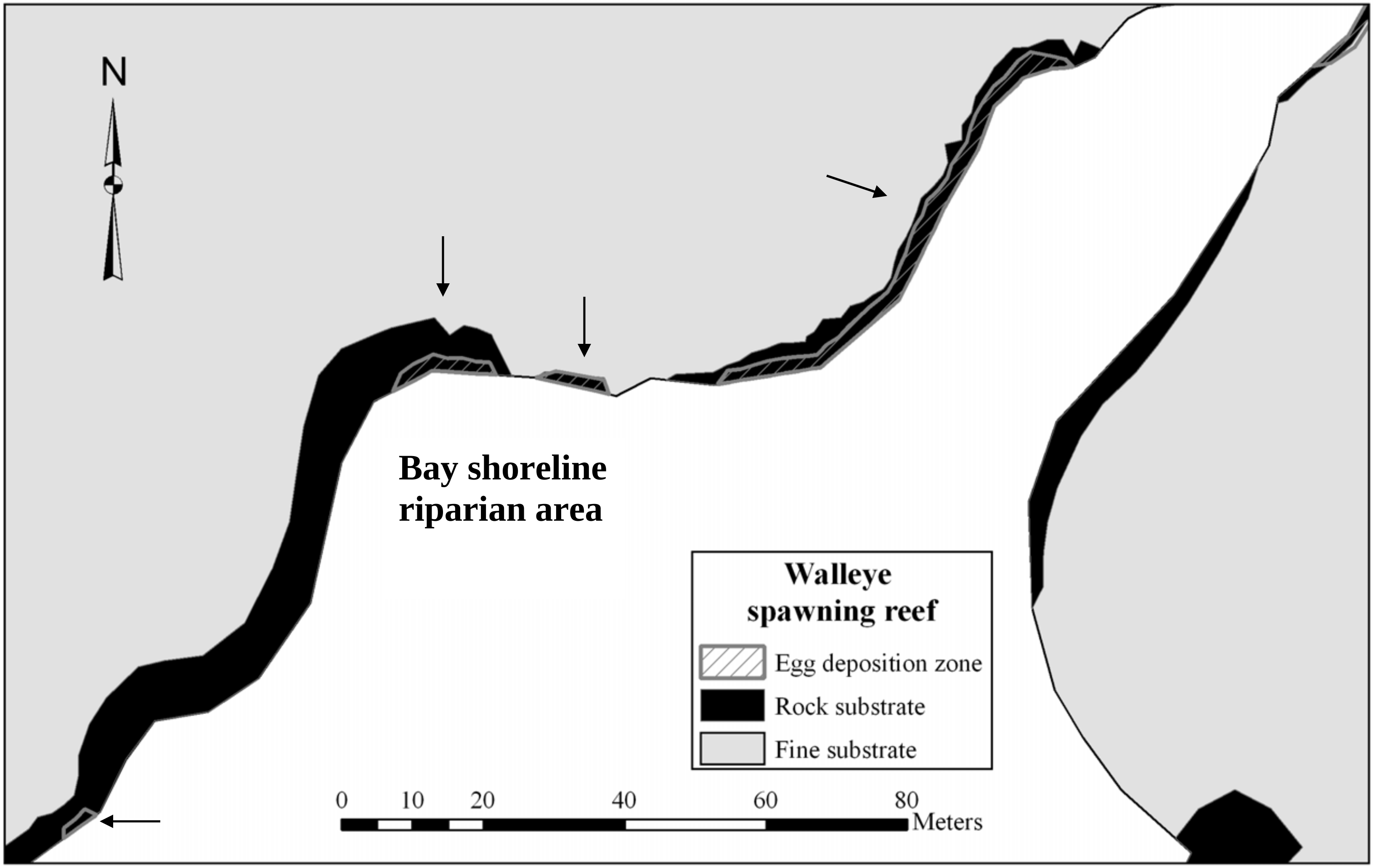


Section of the western shoreline utilized by walleye as spawning habitat. At this narrow rock reef, eggs were observed over two small stretches (arrows) and into fine substrate at portions of the main reef.

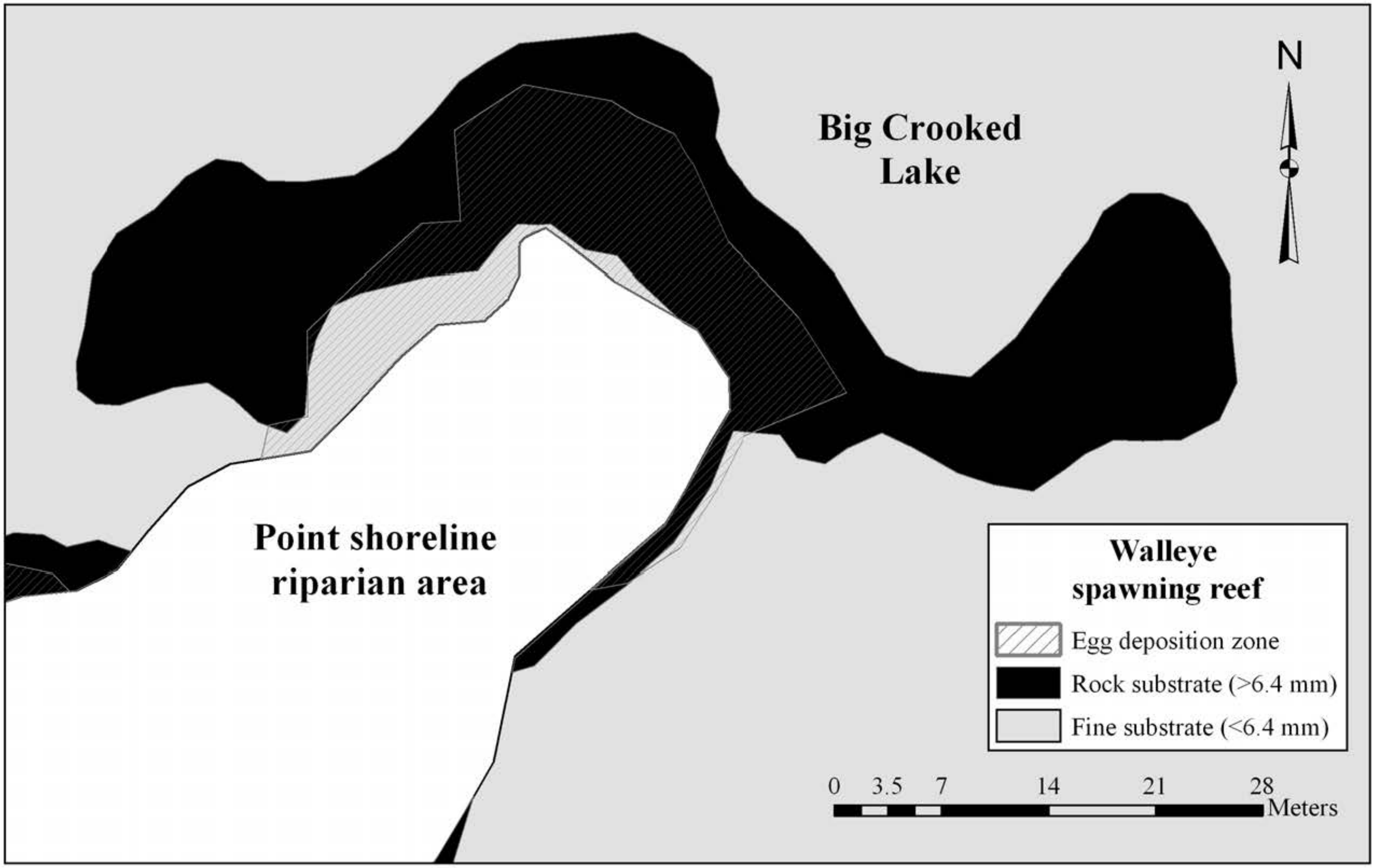
within a large fallen tree. Eggs were observed over a portion of the west spawning reef in 2004, but the extent was not delineated nor the entire reef surveyed.

The "bay" spawning reef, located south and west of the "point" study reef, was unique as it had the highest concentration of gravels substrate and because walleye used the northern portion of the reef but did not spawn over the majority of the southern reach. Rock substrate extended from the northeast starting point until it reached the northwest angled sandbar, except for two short sand breaks in the northern half of the reef. However, walleye used approximately a third of the available shoreline as they only spawned on a short section of the southern reach. Water depth was shallow over the entire reef and very shallow in the utilized portions. The west spawning reef had the highest percentage of gravel (82.5%) of all reefs, with sand and some cobble and coarse organic material also present.

Walleye spawned the furthest from shore at the "point" study reef that differed both in structure and substrate composition from the other spawning sites. The western side of the reef was quite shallow with rock substrates having high embeddedness due to sand. Rock substrate increased at the northwest portion of the reef, but sand and reeds were located nearshore. The northern face was quite shallow and primarily gravel until approximately 7.0 to 9.0 m from the shoreline, where a dropoff and larger substrates occurred. The northeast rockbar was made up of various rock substrate including rubble and boulders, extended up to 33.25 m from the shoreline, increased in depth to the west, but was shallow along the rockbar and to the east and southeast. Nearshore, the northeast side of the reef was primarily gravel and the east side dissipated into a small row of



Section of the western bay shoreline utilized by walleye as spawning habitat. Eggs were observed over four stretches (arrows) and within rock substrate, while a large section of the rock reef was not utilized.

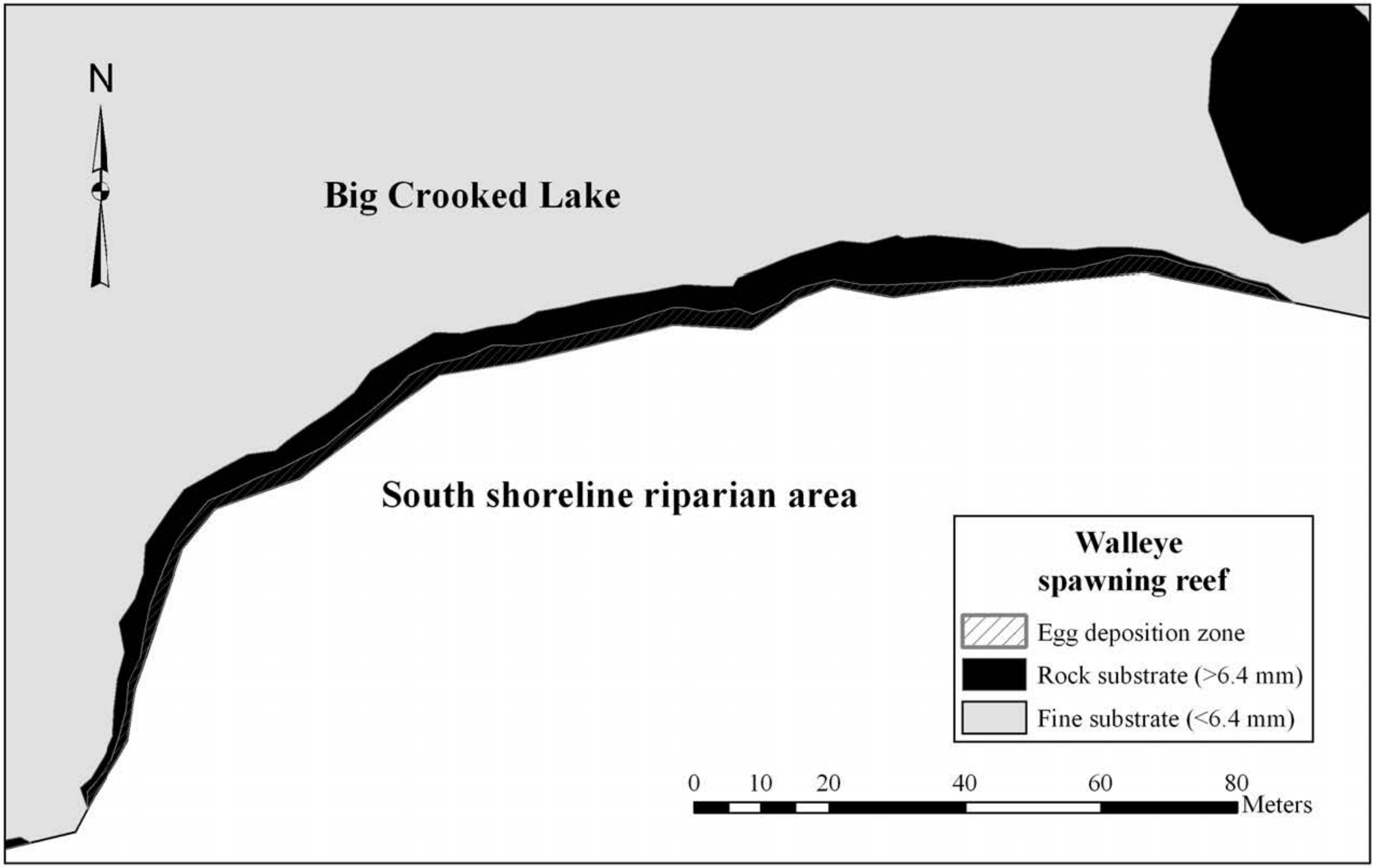


Section of the western bay shoreline utilized by walleye as spawning habitat. Eggs were located at the nearshore habitat, even in sections that were predominantly fine substrate while offshore rock substrate was not utilized.

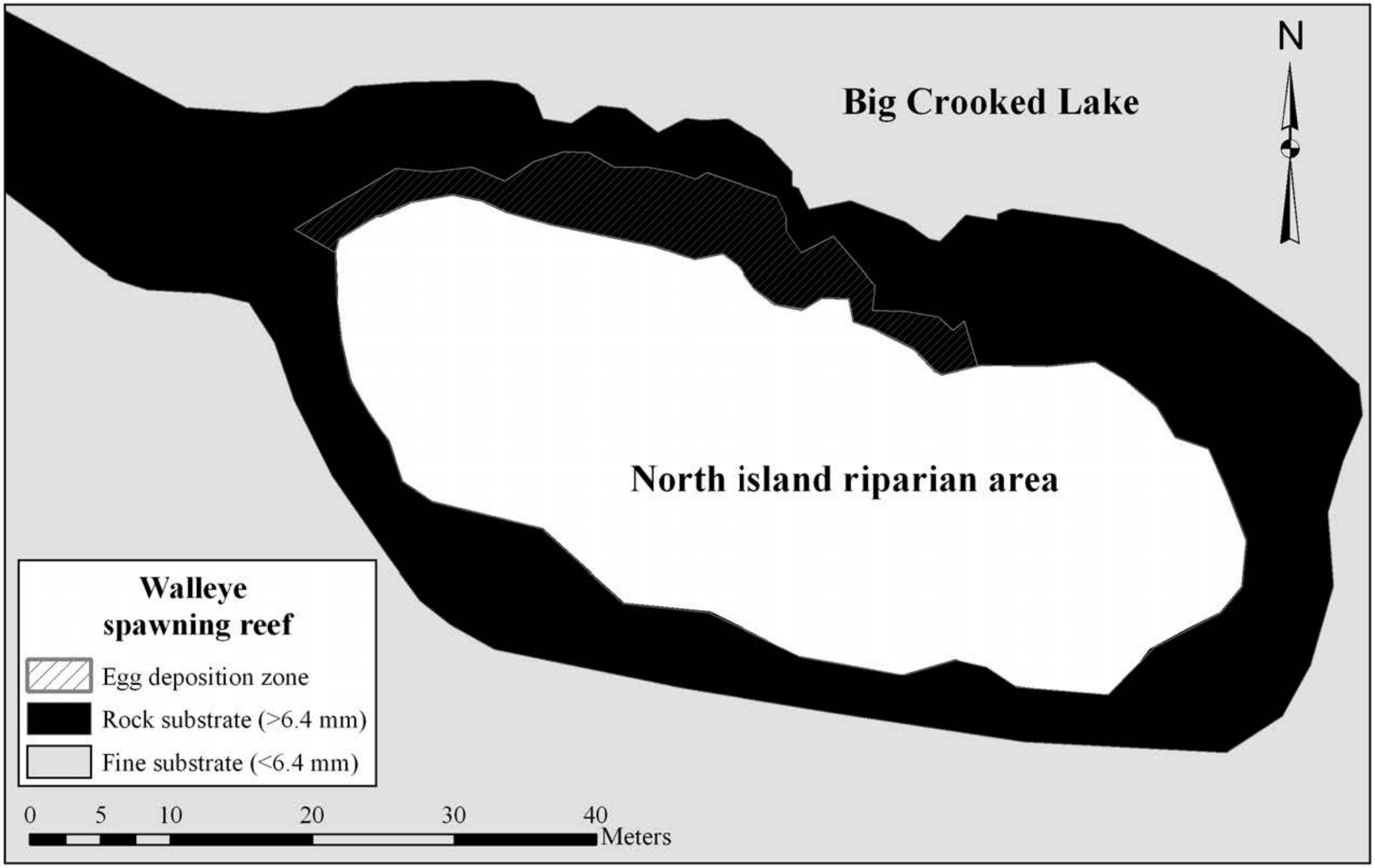
gravel and then sand. At the point study reef, walleye spawned the furthest from shore of all utilized habitat but still in shallow water and did not utilized rock available much further from shore. Gravel was the most common substrate of the utilized habitat at 53.6%, but sand (20.6%), cobble (18.0%) and rubble (5.1%) were also prevalent. The high percentage of sand was a result of the eggs being present over sand on the western and northwestern portion of the reef that also lowered the overall mean rock embeddedness. Walleye utilized a similar portion of the point reef in 2004.

The furthest southern and eastern utilized spawning habitat was the "south" reef that was a consistent reach of rock substrate where walleye spawned over the entire length of the reef. The south reef ran in a semi-circle from the northeast, that was primarily sand substrate, to the southwest bay that had a high content of fine organic matter and silt. The transition from rock to sand was quite distinct into a mixture of sand substrate and a relatively high content of fine organic matter. Walleye spawned over the majority (98.98%) of available shoreline, but did not use rock that extended further from shore and in deeper water. In addition, eggs were not observed at a gravel/cobble/rubble offshore rock bar to the northwest or when the rock resumed to the south. At the utilized portion of the reef gravel was the dominant substrate but the highest concentration of cobble (23.1%) was at the south reef, along with the lowest rock embeddedness due to the lowest concentration of sand at all spawning sites. No boulders were present, but rubble and fine organic matter were present at a few locations. Eggs were found at a similar starting point in 2004, but the actual extent of egg deposition was not quantified.

The "island" study reef was unique, as it was the only island habitat utilized by walleye for spawning and had the highest concentration of boulders. Despite gravel and



Section of the southern shoreline utilized by walleye as spawning habitat. Eggs were observed consistently along and within the entire rock reef. A rock bar to the northeast was not utilized by walleye.



Section of the north island utilized by walleye as spawning habitat. Eggs were observed only on the northwest portion of the island and were contained within the rock reef.

other rock substrate being present on the northern face of the southern island, walleye did not deposit eggs at that location. In 2005, walleye only deposited eggs on the northern face of the island spawning reef, stopping abruptly at boulders located to the northwest. Boulders and trees were located to the northeast, while rock substrate was closer to shore and at lower concentrations on the southern side of the island. Gravel and cobble dominated the northern side of the island until approximately 6.0 to 9.0 m, where the depth increased and the substrates size also increased at certain sections. Eggs were found well before the transition from rock to fine substrates and in shallow water. The utilized spawning substrate at the island reef was again dominated by gravel and followed by cobble, but also had the highest concentrations of large and small boulders of all spawning sites and an overall low percentage of sand (Table 1-8). Eggs were observed over an additional 20.9 m in 2004, but the main spawning habitat was the northern face of the island.