AN EVALUATION OF WALLEYE (*SANDER VITREUS*) SPAWNING POTENTIAL IN A NORTH TEMPERATE WISCONSIN LAKE

By

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Abstract

Poor spawning habitat can limit walleye (*Sander vitreus*) reproduction in north temperate lakes and therefore the need to understand and quantify high quality spawning habitat is essential in managing walleye populations. To address this issue, artificial spawning reefs have been constructed in an attempt to augment recruitment, but with limited success. The objectives of this study were to: 1) quantify physical characteristics of high quality walleye spawning reefs in lakes with high natural recruitment, 2) develop a model that predicts spawning habitat potential in lakes, and 3) use the models to evaluate spawning habitat in a lake with low recruitment and predict the potential success of constructing an artificial spawning reef there. Red Cedar and Big Crooked Lakes, both north-temperate Wisconsin lakes with high natural recruitment of walleye, were used to evaluate habitat characteristics of high quality spawning sites and develop resource selection functions of walleye spawning habitat. The modeling results obtained from both lakes were applied to a third lake, Beaver Dam Lake, Wisconsin, which has low/intermittent recruitment of walleye and a pre-existing artificial spawning reef. Spotlighting and SCUBA surveys were conducted in study lakes immediately after ice-out to determine the extent of egg deposition by walleye in lake littoral zones. Egg collection chambers were also buried in "suitable" substrates just prior to the spawning period to determine egg survival at different locations within Red Cedar and Beaver Dam Lakes. Survey quadrats were placed along transects within egg deposition zones to characterize habitat on spawning reefs and 100 transects were placed randomly in sample lakes to quantify available habitat. Habitat variables measured at each quadrat included depth, distance from shore, substrate, embeddedness and organic material. The best

logistic regression models (i.e., best individual model and alternate models) created from Red Cedar and Big Crooked Lakes were chosen based on AIC values and correct classification rates. Final models were evaluated using actual used and available habitat data from each study lake; each model had high accuracy rates when used to classify sites. Models were then used to evaluate relative spawning potential of walleye in the littoral zone habitats of Beaver Dam Lake. Walleye spawned primarily within 2 m from shore in water less than 0.35 m deep, on larger substrates (gravel and cobble) that had low embeddedness values (mean = 1.5). As a result, the best resource selection function from Red Cedar Lake (overall correct classification = 90.5%) predicted that the relative probability of egg deposition increased on sites closer to shore, at shallower depths, with increasing percentages of gravel and cobble and higher embeddedness values. The best resource selection function from Big Crooked Lake (overall correct classification = 97.4%) predicted that the relative probability of egg deposition increased on sites closer to shore, with increasing percentages of gravel and cobble, and on sites with lower embeddedness values. An additional simplified model consisting of gravel and cobble was also created and applied to shallow, near-shore habitat in Beaver Dam Lake. When models were applied to Beaver Dam Lake, the majority of the littoral zone of the lake as well as the artificial spawning reef had a low relative probability of egg deposition (< 0.5) (i.e., habitat that was not suitable). Based on the accuracy of models when tested on data collected from study lakes, models were highly transferable across systems. Therefore, these models can be used to predict the characteristics of high quality spawning sites as well as the use of an artificial spawning reef by walleye, aiding in both the protection of natural spawning sites as well as determining the need for potential habitat restoration.

Introduction

Little is known about the environmental effects of artificial spawning reefs on walleye or other species and yet many artificial spawning reefs are constructed without assessing whether spawning habitat is the limiting factor precluding walleye recruitment. Because walleye recruitment can be affected by many factors such as climate (Madenjian et al. 1996; Hansen et al. 1998; Pitlo 2002; Beard et al. 2003), unfavorable lake basin morphometry, poor spring weather conditions, poor water quality, low productivity (Neuswanger and Bozek 2004), stock size (Madenjian et al. 1996), water level (Johnson 1961; Priegel 1970b; Chevalier 1977; Kallemeyn 1987), fish community structure (Neuswanger and Bozek 2004), prey availability (Forney 1976; Ritchie and Colby 1988; Johnson et al. 1996; Madenjian et al. 1996), predation (Forney 1976; Johnson et al. 1996) and stocking programs (Johnson et al. 1996; Li et al. 1996; Beard et al. 2003), simply constructing artificial spawning reefs is no guarantee of success.

Many studies evaluating the effects of artificial spawning reefs on walleye populations have found little to no evidence of success. A study that evaluated the effects of artificial spawning reefs constructed in 20 northern Wisconsin lakes found that walleye recruitment did not increase in 85% of the study lakes (Neuswanger and Bozek 2004). In the remaining study lakes, the results were not encouraging because several management techniques were implemented simultaneously, so whether the artificial spawning reef enhanced reproduction or recruitment is uncertain (Neuswanger and Bozek 2004). An evaluation of an artificial spawning reef in a Colorado reservoir found no significant increase in the adult walleye population (Weber and Imler 1974) and a study in Lake Osakis, Minnesota, found that an artificial spawning reef added less than 10% to the annual walleye fry production (Newburg 1976). In two out of three North Dakota Reservoirs with artificial spawning reefs, water levels dropped which resulted in reefs being completely out of the water, and in the third reservoir, the number of live eggs collected off artificial spawning reef were low (517 eggs over two study years) and no survival beyond the egg stage was observed (Sprague 1963). McKnight (1975) recorded eyed walleye eggs on artificial spawning reefs in Jennie Webber Lake, Wisconsin; however, no fry, fingerlings, or adult walleye were taken during subsequent meter netting, seining, or electrofishing surveys. A riverine study, conducted in the Current River, Ontario, found similar results (Geiling 1996). After a five-fold increase in the amount of walleye spawning habitat constructed by adding gravel, cobble, and boulders in three shallow water areas of the river, neither total walleye egg deposition or adult walleye abundance were increased (Geiling 1996).

In addition to the limited success of artificial spawning reefs, constructing these reefs is generally believed to be less cost-effective than stocking walleye (Newburg 1975). In an evaluation of an artificial spawning reef by Newburg (1975), it was estimated that only 10% of potential walleye fry were hatched on the artificial spawning reef in Lake Osakis, Minnesota. A cost-benefit analysis at that time concluded that stocking fry would be cheaper than attempts to produce fry on an artificial spawning reef; an analysis suggested it would take between 37 and 65 years of fry production for the construction of the artificial spawning reef to be more cost-effective than yearly stocking (Newburg 1975).

While stocking may be more cost effective than building artificial spawning reefs, many factors may also limit the success of stocking, such as the negative effects it has on adjacent year-class strength (Li et. al 1996). Based on data from populations estimates conducted by the Minnesota Department of Natural Resources, Li et al. (1996) found that stocking in lakes with natural walleye recruitment decreased the abundance of the year classes one year older and one year younger than the stocked year class. Stocking can also be ineffective when introducing walleye that lack the suitable genetically based behavior (Jennings et al. 1996) or physiological characteristics (Galarowicz and Wahl 2003) for the system into which they are stocked. Jennings et al. (1996) believed that spawning site selection is a heritable trait, and the type of spawning habitat utilized is different between walleye populations (lacustrine versus riverine). Therefore the type of habitat available in any system where walleye are stocked may affect their potential for reproductive success depending upon the source population. When walleye broodstocks from two different habitats, one from lacustrine and one from riverine, were tagged and stocked into Saylorville Lake, Iowa (which is connected to the Des Moines River), sampling efforts several years later found that the fish returned to their respective spawning grounds based on their genetically inherited traits (Jennings et al. 1996). In addition, Galarowicz and Wahl (2003) found that walleye from across latitudinal gradients of North America (Canada and Wisconsin versus Missouri and Arkansas) are adapted to different thermal regimes based on metabolic rate, growth, food consumption and conversion efficiencies; therefore, these differences may play a critical role in the survival of stocked walleye.

Based on previous studies, it is clear that artificial spawning reefs have not been successful overall. However, exactly why artificial spawning reefs have faired so poorly is not well understood. In general, artificial spawning reefs have been designed and constructed based on general information published in the literature describing natural spawning areas (e.g., shallow, large material) (Eschmeyer 1950; Niemuth et al. 1959; Johnson 1961; Corbett and Powles 1986; Pitlo 1989). However, quantifying general and specific features of natural spawning reefs is essential in evaluating the success of artificial spawning reefs, and in addition to being able to protect natural spawning habitat, quantification of natural walleye spawning reefs is crucial in the design and placement of artificial spawning reefs in the future. Moreover, the development of an across-lake model that predicts relative spawning potential of walleye may be beneficial to lake managers when deciding on the best possible options for enhancing reproduction in a lake system with low natural recruitment.

Objectives

The objectives of this study were to:

1) quantify physical characteristics of high quality walleye spawning reefs in lakes with high natural recruitment,

2) develop models that predict spawning habitat potential in lakes, and

3) evaluate walleye spawning habitat and predict the potential success of adding an additional artificial spawning reef in Beaver Dam Lake, a lake with low walleye recruitment.

Literature Review

Background

The walleye (*Sander vitreus*) is one of the most popular game fish in Wisconsin (Mraz 1968). Total angling activities in Wisconsin generate over 2 million dollars annually (American Sportfishing Association 2002), and walleye angling accounts for a significant portion of this amount (Staggs et al. 1990). According to a study conducted by Staggs et al. (1990), anglers in Wisconsin harvested an average of 670,000 adult and juvenile walleye annually from 1980 to 1987.

Due to their popularity as a sport fish, walleye are an intensely managed fish species in Wisconsin (Mraz 1968) as well as throughout North America (Jennings et al. 1996). Many management strategies are employed including stocking, regulations, and habitat protection and restoration. Due to poor natural walleye recruitment in some Wisconsin lakes, the Wisconsin Department of Natural Resources (WDNR) along with lake associations and walleye organizations have built artificial spawning reefs throughout the state in attempts to increase walleye productivity (Neuswanger and Bozek 2004). However, as with many habitat improvement projects, little research has been conducted on the success or cost-effectiveness of using artificial walleye spawning reefs to create habitat that increases walleye production.

Range

Walleye are native to freshwater lakes and rivers of the United States and Canada (Scott and Crossman 1973) and are considered a coolwater species (Nelson 1978). The boundaries for distribution of walleye throughout North America are Great Slave Lake in the northwest and Labrador in the northeast, south to northern Arkansas and Alabama and west into Nebraska (Niemuth et al. 1959; Scott and Crossman 1973). However, this range of walleye throughout North America has been increased due to stocking efforts, especially throughout the northwestern United States (e.g., Columbia, Snake, Missouri, Yellowstone, and North Platte River drainages) (McMahon and Bennett 1996). Walleye have also been introduced into other parts of the United States, including the Atlantic drainages, Gulf of Mexico drainages in Texas and Mississippi, and impoundments along the Mississippi River (Carlander et al. 1978).

While walleye are native to river systems, large, shallow lakes provide analogous littoral zone habitat necessary to sustain walleye populations (Kitchell et al. 1977). Walleye tend to occur in mesotrophic lakes but can occur in a range of lakes having different trophic conditions (Niemuth et al. 1959; Kitchell et al. 1977; Leach et al. 1977). However, reproduction may be sporadic in more fertile waters (Niemuth et al. 1959), because as lakes become more eutrophic, turbidity and nutrient loading increase and habitat diversity and suitable walleye spawning substrate decrease (Kitchell et al. 1977).

Behavior

The primary habitat used and foraging behavior exhibited by adult walleye changes based on time of day due to light sensitivity of adult walleye (Ryder 1977; Lester et al. 2004). Walleye seek shelter from the light by retiring to deeper, darker waters during the daytime (Niemuth et al. 1959). This behavior occurs because adult walleye are negatively phototactic and prefer low light environments that provide reduced light conditions during the daylight hours such as deeper water, submerged debris, weed beds, and boulders (Ryder 1977). During the daytime, adult walleye may also form loose aggregates in open water (Niemuth et al. 1959). Foraging generally occurs in the evening with walleye often moving from open water to offshore bars and shoals near windswept points of land to feed (Kerr et al. 1997). The physiological adaptation of walleye allows them to feed in low light, reducing competition with other predators (Ryder 1977). However, while walleye tend to be nocturnal and crepuscular feeders in clear lakes, they can also be diurnal feeders in more turbid environments (Ali et al. 1977).

Diet

Adult walleye are opportunistic feeders, and will often consume prey species based on their abundance in particular systems. Adult walleye will eat large aquatic invertebrates if available, however they feed primarily on fish in many systems (Eschmeyer 1950; Niemuth et al. 1959; Frey et al. 2003). A study conducted in Big Crooked Lake, Wisconsin found crayfish (*Orconectes* sp.) to be the most important diet item of walleye in June, followed by Ephemeroptera and yellow perch (*Perca flavescens*) in importance (Frey et al. 2003). After June (July through the following March), yellow perch were an important diet item while Ephemeroptera and crayfish declined (Frey et al. 2003). In a study of several lakes throughout Michigan, the primary prey items for walleye were yellow perch and suckers (*Catostomus* spp.) (Eschmeyer 1950). In northern Saskatchewan, cisco (*Coregonus artedii*) were the primary prey item of walleye, followed by ninespine sticklebacks (*Pungitius pungitius*), suckers and yellow perch (Rawson 1957). Walleye also eat other fish species when available, including trout-perch (*Percopsis omiscomaycus*), topminnows (*Fundulus* spp.) and Iowa darters (*Etheostoma exile*) (Eschmeyer 1950). In systems where gizzard shad (*Dorosoma cepedianum*) are abundant, shad may be a primary food source (Quist et al. 2003; Hartman and Margraf 1992); Quist et al. (2003) conducted their study in a warm water system in Kansas, whereas Hartman and Margraf (1992) found a significant correlation between walleye growth and shad abundance in Lake Erie.

While walleye will feed on other fishes based on availability, they will also forage on other walleye (Kerr et al. 1997) although cannibalism occurs infrequently (Eschmeyer 1950; Rawson 1957). In a food habits study conducted on adult walleye by Rawson (1957) on Lac la Ronge in northern Saskatchwan, less than 5% of the fish material present in stomachs consisted of walleye. However, the tendency of adult walleye to feed on juvenile walleye increases as adult walleye density and competition for prey increases (Chevalier 1973; Forney 1976; Hansen et al. 1998). Two separate studies conducted in Lake Oneida, New York, found that cannibalism increased when numbers of young walleyes increased (Chevalier 1973) or when numbers of the primary prey item, yellow perch, declined (Forney 1976). In addition, Hansen et al. (1998) found that in Escanaba Lake, Wisconsin, walleye recruitment may have been affected by cannibalism and intraspecific competition.

Walleye fry feed on a variety of different prey items and are size- and gape-limited. Fry will feed on planktonic crustaceans such as *Daphnia* spp. (Eschmeyer 1950, Mathias and Li 1982), then on larger insect larvae before moving onto forage fishes as their size increases (Becker 1983). In Lake Gogebic, located in the Upper Peninsula of Michigan, fry approximately 28 mm in length were captured in early July and were found to have eaten sucker fry of similar size (Eschmeyer 1950). In Wisconsin lakes, the greatest growth recorded by walleye fry occurs from July to August, due to a change in diet from zooplankton to invertebrate larvae and forage fishes (Priegel 1970a). According to the stomach content analysis of a study conducted by Pratt and Fox (2001) in Big Clear Lake, Ontario, walleye become completely piscivorous during the first month after they become demersal. Young-of-year (YOY) bluntnose minnow (*Pimephales notatus*), mimic shiner (*Notropis volucellus*), and yellow perch were identified as primary prey items of YOY walleye (Pratt and Fox 2001). In Lake Gogebic, fish constituted 88% of the volume of YOY walleye stomach contents and yellow perch were found to be the primary prey item (Eschmeyer 1950). Young-of-year walleye were also found to be cannibalistic; however, this occurred relatively infrequently compared to the consumption of other prey items (Eschmeyer 1950; Mathias and Li 1982).

<u>Growth</u>

Growth rates of walleye are affected by many factors, including thermal conditions, adult density, and prey abundance. Adult walleye generally mature earlier, exhibit greater growth, and have shorter life spans in lower latitudes which have longer growing seasons (Colby and Nepszy 1981; Galarowicz and Wahl 2003). In a study that evaluated physiological differences in walleye based on regional temperatures across the United States, Galarowicz and Wahl (2003) found that walleye in southern latitudes had higher metabolic rates than northern populations. In Lake Winnebago, Wisconsin, Staggs and Otis (1996) found that spring and summer temperatures seemed to be the most important variable influencing age-0 walleye growth.

Density-dependence can also be a factor affecting growth, especially in juvenile walleye. Fox and Flowers (1990) monitored growth, consumption, and prey density in rearing ponds; mean length and weight of walleye at harvest were found to be inversely related to initial walleye stocking density. In the ceded territory of Wisconsin, Sass et al.

(2004) found that increased density of walleye within lakes contributed to lower growth patterns and lower growth rates of juveniles.

Biotic factors such as abundance and size of prey within a system can also affect growth. In Oneida Lake, New York, fluctuations of the primary prey item of walleye, yellow perch, were correlated to the abundance of adult walleye (Forney 1974), and a later study in the same lake found that growth of YOY walleyes was correlated to the vulnerability of YOY prey species (Madenjian and Carpenter 1991). A study conducted by Staggs and Otis (1996) found that in Lake Winnebago, walleye growth was greater in years when the primary prey items of walleye, freshwater drum (*Aplondinotus grunniens*) and trout-perch (*Percopsis omiscomaycus*) were more abundant.

In addition to conditions affecting lake-wide growth rates such as thermal patterns and community dynamics, the growth of walleye in a given water body varies among individual fish of the same age (Eschmeyer 1950). In Lake Gogebic, Michigan, YOY walleye cannot be distinguished from older fish on the basis on length alone, because some yearlings are smaller than the largest YOY (Eschmeyer 1950). The study conducted by Eschmeyer (1950) in Lake Gogebic also found that females grow faster than males, particularly after two years of age, which appears to be a general trend for the species (Scott and Crossman 1973; Becker 1983).

<u>Maturation</u>

The average life span of walleye in Wisconsin and Minnesota is approximately seven years, however many walleye exceed this age, especially females (Niemuth et al. 1959). Female walleye mature in approximately four to five years, at a length of 38 to 43 cm, whereas males mature in two to three years at a length of 31 to 34 cm (Niemuth et al.

1959). Young-of-year walleye in these states typically reach lengths of 13 to 15 cm by fall (Niemuth et al. 1959). However, density affects growth and thus maturation. A study on Big Crooked Lake, Wisconsin, found that as the walleye population increased, age-at-maturity decreased (Schueller et al. 2005). Maturation and fecundity of female walleye can vary greatly based on factors such as food availability and adult densities (Serns 1982; Baccante and Reid 1988). Serns (1982) estimated that fecundity in Escanaba Lake, Wisconsin, ranged from 12,458 to 14,270 eggs per kg (27,500 to 31,500 eggs per lb) from 1979 to 1981 and was correlated to female weight in 1979 and 1980 and female length in 1981, which may be due to differences in food supply and/or competition among adult walleye between years (Serns 1982). This corresponds to a study conducted by Baccante and Reid (1988) that found increased fecundity of walleye in Henderson and Savanne Lakes, Ontario, resulted from improved feeding conditions due to reduced intraspecific competition (i.e., density).

Spawning Habitat and Behavior

Spawning occurs immediately following ice-out in most north temperate systems (Eschmeyer 1950; Niemuth et al. 1959; Scott and Crossman 1973; Becker 1983), generally when water temperatures are in the range of 3.3 to 6.7°C (Becker 1983). Pre-spawning behavior and courtship may begin much earlier, when water temperature is as low as 1.1°C (Scott and Crossman 1973). In Wisconsin, spawning usually occurs mid-April and lasts into May, with extremes ranging from late March to late June (Jovanovic 1970).

Walleye are nocturnal spawners (Eschmeyer 1950; Niemuth et al. 1959; Ellis and Giles 1965; Scott and Crossman 1973), do not build nests, and are not territorial (Ellis and Giles 1965; Becker 1983). They are broadcast spawners, releasing gametes into the water column and allowing fertilized eggs to settle into the interstitial spaces between rocks (Eschmeyer 1950; Kerr et al. 1997). Males are generally the first to arrive at the spawning grounds and remain after the females have left (Eschmeyer 1950; Rawson 1957; Niemuth et al. 1959). Females may spawn out completely in one night; however males have the potential to spawn over a longer period of time (Eschmeyer 1950; Ellis and Giles 1965). The act of spawning usually involves one female with one to two males; however, larger groups with two females and two to six males can also occur, in which pursuit, pushing, and circular swimming activity occurs near the shoreline, and ends with a rush to the surface where the eggs and sperm are released (Ellis and Giles 1965). After release, eggs are initially adhesive and adhere to both one another and other objects until water hardens the outer membrane, at which time the adhesive properties are lost (Becker 1983). The amount of time eggs are adhesive is variable, usually for one to two hours after release (Priegel 1970b; Becker 1983). However, in hatchery experiments, eggs have remained adhesive for up to four days (Krise et al. 1986). After spawning, no protection of eggs is provided (Jovanovic 1970; Marshall 1977).

Several different spawning site characteristics influence egg survival, such as substrate size, water movement, and depth. Walleye generally spawn on large rocky substrate, which is believed to be most conducive to egg viability (Eschmeyer 1950; Johnson 1961; Corbett and Powles 1986; Pitlo 1989; Kerr 1997). However, in some cases, walleye have been know to spawn over sand, muck, and detritus bottoms (Johnson 1961), and flooded wetland vegetation and “marsh grass” (Priegel 1970b; Becker 1983). Egg survival is believed to be greatest when eggs are deposited over rocky substrate due to the presence of interstitial spaces for protection, as opposed to muck and sand, on which eggs experience higher mortality rates (Eschmeyer 1950; Johnson 1961). Rocky substrate provides protection from entanglement due to less debris present, and also protection from scouring due to wave action (Johnson 1961). On Lake Winnibigoshish in Minnesota, Johnson (1961) found that average egg survival on gravel-rubble substrate was 22.0%, compared to 8.6% on fine sand and only 2.5% on muck-detritus substrates. A model created by Nate et al. (2001) from several northern Wisconsin lakes showed that the percentage of sand and muck substrate present in a lake was inversely related to walleye abundance.

Another feature of spawning sites critical to the viability of walleye eggs is the availability of oxygen, which is increased with a supply of moving water (Niemuth et al. 1959) and shallower water (Eschmeyer 1950; Johnson 1961; Kerr 1997). In lakes, spawning sites orientated to prevailing winds may help to ensure adequate wave action to keep substrate clean of debris and sediment and provide sufficient oxygen to incubating eggs (Eschmeyer 1950; Kerr et al. 1997). In addition to the presence of moving water, lower water depths also correlate to increased oxygen available for incubating eggs because oxygen can easily circulate due to wave action. A study on Lake Erie found that walleye eggs deposited on sites with deeper water, lower dissolved oxygen levels, and silt substrate led to suffocation of the eggs (Roseman et al. 1996).

Walleye have a high degree of fidelity to general spawning locations and may return to the same spawning site in subsequent years (Crowe 1962; Olson et al. 1978; Jennings et al. 1996). According to a study conducted on Saylorville Lake and the Des Moines River in Iowa, walleye may choose general spawning location, such as riverine and lacustrine habitats, based on genetics (Jennings et al. 1996). Other studies by Rawson (1957) and Priegel (1968) found spawning walleye that were previously marked on a spawning site were recaptured on that same spawning site in subsequent years, even when other suitable spawning habitat was available. Rawson (1957) found that in Lac la Ronge, Saskatchewan, 67% of walleye marked on specific spawning grounds were recaptured in the same area in subsequent years, and in a study conducted in Lake Winnebago, 69% of the walleye recaptured at one site had been marked on that same site during previous spawning seasons (Priegel 1968).

Egg Incubation

During the incubation period, eggs are susceptible to high mortality rates. In Oneida Lake, New York, 99% of walleye mortality occurred before larvae reached a length of 9 to10 mm; however, it was estimated that the majority of the loss was sustained in the egg phase (Forney 1976). On two large reefs in western Lake Erie, Roseman et al. (1996) found egg survival rates ranging from 41 to 74% in the first study year and from 6 to 76% in the second study year. On Lake Winnibigoshish, Minnesota, egg survival rates were estimated as low as 0.6 to 35.7% (Johnson 1961).

Water temperature is important during the egg phase and can affect fertilization, incubation time, and mortality (Busch et al. 1975; Smith and Koenst 1975; Roseman et al. 1996). A laboratory study conducted by Smith and Koenst (1975) evaluated the effects of different water temperatures during fertilization and incubation of walleye eggs. The highest fertilization rate occurred between 6 and 12°C, and as temperature increased, fertilization rates decreased, with the lowest fertilization rate occurring at 21°C (Smith and Koenst 1975). Incubation temperatures between 9 and 15°C resulted in the greatest hatch rate, and the mean fry size was also greatest between 9 and 18°C (Smith and Koenst 1975). In addition, incubation periods were longest at lower temperatures and increased exponentially with increased temperatures (Smith and Koenst 1975). However, it was the absolute temperatures, not temperature fluctuations that influenced development (Smith and Koenst 1975). Laboratory experiments conducted by Schneider et al. (2002) found that developing eggs had a remarkable tolerance to temperature fluctuations and that minimum temperature fluctuations of ± 14-19°C over several days were necessary to reduce hatching success. However, these temperature fluctuations are unlikely to occur on natural spawning grounds *in situ*.

Although walleye eggs and fry are thought to be relatively tolerant to large and rapid temperature changes, low egg survival rates can sometimes be attributed to slow warming rates, cold weather, or cold water discharges (Johnson 1961; Roseman et al. 1996; Kerr et al. 1997). In Lake Winnibigoshish, Minnesota, water temperatures and walleye egg incubation times were measured; increased embryo development and decreased incubation time were associated with higher water temperatures (Johnson 1961). The decreased incubation time was also correlated to increased egg survival (Johnson 1961); increased incubation time may increase egg vulnerability to environmental stress and predation (Busch et al. 1975; Roseman et al. 1996). In Lake Erie, walleye year class strength was strongly related to the rate of increasing water temperature (Busch et al. 1975) and prolonged incubation periods may increase the potential for predation. A predator diet analysis in Lake Erie found walleye eggs in 86% of white perch (*Morone americana*) stomachs with an average of 349 eggs per stomach (Roseman et al. 1996). In addition, Corbett and Powles (1986) found that yellow perch and spottail shiners (*Notropis hudsonius*) also preyed on walleye eggs in an Ontario stream. During this study, 7 out of 11 yellow perch stomach contents contained an average of 44 walleye eggs and 4 out of 10 spottail shiner stomach contents contained an average of 13 walleye eggs (Corbett and Powles 1986).

Water level fluctuations are also thought to affect egg mortality by reducing the amount of suitable spawning habitat, forcing adult walleye to spawn on habitat less conducive to egg viability or by stranding walleye eggs once they are deposited (Johnson 1961; Priegel 1970b; Chevalier 1977). A low water year in Lake Winnibigoshish left former spawning sites dry, thereby forcing walleye to spawn on less suitable substrate resulting in a weaker year class (Johnson 1961). In the Lake Winnebago region of Wisconsin, a rapid drop in water levels desiccated many walleye eggs deposited along the shoreline (Priegel 1970b).

Young-of-Year Habitat and Behavior

The movements of walleye fry are generally not well documented. It is believed that newly hatched fry are restricted to erratic vertical movements due to the lack of well-developed paired fins at hatching and that fry use vigorous tail motions to move vertically to the surface, then sink in the water approximately 15 to 20 cm before moving to the surface again (Becker 1983). Eschmeyer (1950) conducted a study in rearing ponds to determine the movement of newly hatched walleye and observed and collected fry at different times and locations throughout the pond. During each collection period, the majority of the fry were captured in the open waters of the rearing ponds as opposed to "inshore" areas (Eschmeyer 1950). After the development of paired fins, fry are thought move into the open water until they reach a length of approximately 2.5 to 3.75 cm, at which time fry then move back to inshore areas of the lake (Eschmeyer 1950). In the same study, both in rearing ponds and in observation tanks, walleye fry were observed neither seeking the bottom nor the surface of the water and generally remained in the middle of the water column (Eschmeyer 1950).

Ontogeny affects habitat selection of young-of-year (YOY) walleye (Eschmeyer 1950, Pratt and Fox 2001). In Lake Gogebic, Michigan, YOY walleye moved back to the inshore areas of the lake, had a strong tendency to school with YOY yellow perch, and were generally found between the bottom and the middle of the water column Eschmeyer (1950). Young-of-year walleye become demersal sometime in their first year of life, and a study conducted by Pratt and Fox (2001) found that in the first month of the demersal period, YOY were found in heavily vegetated, medium-depth habitats (2-5 m), whereas after the first month, shallower habitats with moderate cover showed higher levels of use.

<u>Recruitment</u>

Many factors affect walleye recruitment including stock size, prey, stocking efforts, and competition; however, many studies have found that climate is one of the most important factors influencing year-class strength (Madenjian et al. 1996; Hansen et al. 1998; Pitlo 2002; Beard et al. 2003). However, despite several correlative studies, the causal factors for this phenomenon are still unknown. Spring warming rate was found to be an important factor and was included in a model that predicts high walleye recruitment in Lake Erie (Madenjian et al. 1996). Beard et al. (2003) suggested that walleye recruitment was synchronous in small lakes across a large region due to broad-scale climate patterns that affect all lakes in a region similarly. A study conducted in a reservoir on the upper Mississippi River found that 79% of the variation in walleye recruitment from 1992 to 2000 was explained by spring warming rates (Pitlo 2002). Temperature may be correlated to or act synergistically with spawning behavior, prey availability, cannibalism, predation and mortality of adults, therefore increasing the effects of temperature and climate changes on walleye recruitment (Koonce et al. 1977).

Prey availability also affects walleye recruitment (Forney 1976; Ritchie and Colby 1988; Johnson et al. 1996; Madenjian et al. 1996). High fall age-0 gizzard shad abundance, a primary prey item of walleye in Lake Erie, resulted in high walleye recruitment (Madenjian et al. 1996), and age-0 walleye abundance and subsequent year-class strength coincided with the pulse production of the mayfly (*Hexagenia limbata*) in an Ontario lake (Ritchie and Colby 1988). High prey abundance may increase the consumption of these prey items by juvenile walleye allowing them to grow out of their vulnerable size quicker, making them less susceptible to predation, thus increasing year classes (Johnson et al. 1996). In contrast, low abundance of prey has a negative effect on walleye recruitment by leading to an increase in predation and cannibalism (Forney 1976). In Oneida Lake, New York, Forney (1976) found that a decrease in the primary prey item, yellow perch, led to an increase in cannibalism, and that cannibalism was responsible for much of the variation in year classes.

In addition to prey availability, predation also affects walleye recruitment (Forney 1976; Johnson et al. 1996; Hansen et al. 1998). Throughout eight successive walleye year classes in Oneida Lake, the majority of larval walleye mortality was due to predation by yellow perch and older walleye, and a decrease in the number of walleye fingerlings was due to predation by older walleye (Forney 1976). On Lake Mendota, in south-central Wisconsin, predation appeared to be an important factor in recruitment, and as predator biomass increased, the consumption of young walleye also increased (Johnson et al. 1996). Another study found that cannibalism or intraspecific competition with walleye and predation or interspecific competition with yellow perch influenced the number of age-0 walleye present after their first summer in Escanaba Lake, Wisconsin (Hansen et al. 1998).

Other factors such as stock size, water level, and spawning habitat also affect walleye recruitment. Spawning-stock size is directly correlated to high walleye recruitment (Madenjian et al. 1996) and year-class strength was found to be significantly correlated to water levels in several lakes on the Minnesota-Canadian border because higher lake levels increase the quantity and quality of available spawning habitat (Kallemeyn 1987). In addition, a study conducted by Nate et al. (2001) on several northern Wisconsin lakes found that large amounts of sandy substrate in the littoral zones of lakes, which is unfavorable to egg survival, may limit walleye recruitment. This corresponds to several other studies previously mentioned documenting decreased egg survival on unfavorable substrate, therefore limiting walleye recruitment (Eschmeyer 1950; Johnson 1961; Corbett and Powles 1986; Pitlo 1989; Roseman et al. 1996; Kerr et al. 1997).

Stocking walleye, a common management practice, might also reduce natural walleye recruitment within a system (Johnson et al. 1996; Li et al. 1996; Beard et al. 2003). When walleye are stocked into a system, resource limitation and density dependence can reduce the abundance and growth of the natural recruiting year classes (Li et al. 1996; Beard et al. 2003). Li et al. (1996) found that in many Minnesota lakes, stocking walleye increased the year class strength index (YCSI) of the stocked year class, but significantly decreased the YCSI of the preceding year class by 26.8% and the succeeding year class by 24.5%. In addition, stocking programs increase predator biomass which may lead to an increase in the consumption of juvenile walleye (Johnson et al. 1996). Johnson et al. (1996) found that in Lake Mendota, Wisconsin, where extensive walleye stocking took place, the increase in walleye biomass may have led to increased cannibalism, therefore reducing the survival of subsequent stocking efforts.

Competition

Species associations may play a role in regulating walleye abundance in a given water body. In larger lakes, walleye can coexist with smallmouth bass (*Micropterus dolomieui*), lake trout (*Salvelinus namaycush*), and northern pike (*Esox lucius*) presumably due to increased abundances of food and habitat resources associated with larger bodies of water (Johnson et al. 1977). However, walleye and northern pike do not generally coexist at high densities in smaller lakes (Johnson et al. 1977). This may be due to northern pike reducing the preferred prey of walleyes: yellow perch, therefore causing walleye populations to decline (Colby et al. 1987). Largemouth bass (*Micropterus salmoides*) also appear to affect walleye populations and can limit the success of stocked walleye due to predation (Fayram et al. 2005). Fayram et al. (2005) determined that if a largemouth bass population is limited by prey availability, stocking walleye into that system may increase largemouth bass abundance, therefore reducing the success of future walleye stocking efforts. Conversely, in a system where walleye are dominant, smallmouth bass may eventually disappear from the lake due to walleye predation, and the system may then shift to a walleye-dominated lake (Becker 1983). A study conducted on Big Crooked Lake, Wisconsin, found that YOY walleye affected survivorship of YOY smallmouth bass due to predation (Frey 2003).

Artificial Spawning Reefs

Characteristics of fish populations such as growth, reproduction, and recruitment in lakes are believed to be attributed in part to the structural and functional aspects of the littoral zone (Tonn and Magnuson 1982). Most North American lake-dwelling fish species rely on the littoral zone for foraging, spawning, and rearing; however, little is known quantitatively about the specific features of the littoral zone and how those features affect fish communities and populations (Neuswanger and Bozek 2004). Because the quantity and quality of spawning habitat in the littoral zone appears to be related to walleye recruitment (Nate et al. 2001), habitat restoration in the form of artificial spawning reefs has been frequently used since the 1930's in an attempt to increase recruitment (Stuart 1963; McKnight 1975; Newburg 1975; Wagner 1990; Geiling et al. 1996; Neuswanger and Bozek 2004).

The construction of artificial spawning reefs remains common despite evidence of their ineffectiveness and the lack of scientific study or design, and interest in and construction of artificial spawning reefs has increased greatly in Wisconsin in recent years (Neuswanger and Bozek 2004). Artificial spawning reefs constructed in Wisconsin lakes generally consist of large, rocky substrates such as gravel, cobble, and rubble and are placed over the ice in shallow areas of a lake during the winter and drop into place when the ice melts in the spring (Neuswanger and Bozek 2004). Reef design follows several forms, including: rock blankets, which are low-profile structures consisting of 5-30 cm diameter washed field stone, generally 15-30 cm thick and built on existing contours, and rock reefs, which are ridges or mounds of 5-30 cm diameter washed field stone, generally surrounded by shallow water and constructed with a greater vertical profile and side slopes than rock blankets (Neuswanger and Bozek 2004). Several other reef types exist, which are categorized based on their location within the lake, such as shore, mid-lake, inlet, point, island, etc. (Neuswanger and Bozek 2004).

Methods

Study Sites

This study was conducted on three northern Wisconsin lakes: Beaver Dam, Red Cedar and Big Crooked Lakes. Beaver Dam Lake is located in the Red Cedar River drainage in northwestern Barron County, near Cumberland, Wisconsin. Shoreline development is extensive, with private housing developments surrounding the lake. Total shoreline length is 29 km. Beaver Dam Lake is separated into two primary basins: the west basin and the east basin. The east basin of Beaver Dam Lake is 124 ha with a maximum depth of 27 m. The east basin is eutrophic with dense macrophyte growth and frequent algal blooms. The average summer secchi disk reading is 0.5 m. Since the removal of the City of Cumberland sewage disposal plant, which was previously discharged into the east basin, water quality has substantially improved (Wisconsin Department of Natural Resources 1995). The surface area of the west basin of Beaver Dam Lake is 326 ha with a maximum depth of 32 m, and the summer secchi disk average is 3.75 m. The west basin is mesotrophic, with a small littoral zone and limited productivity. The hypolimnion is mostly anoxic due to incomplete fall and spring turnovers. Macrophyte growth is confined to shallow bays.

An artificial spawning reef was constructed in the west basin of Beaver Dam Lake in 2001 in an attempt to increase available walleye spawning habitat. Funding for the construction of the artificial spawning reef was provided by the Beaver Dam Lake Management District. This reef is located directly on the southeast shoreline, and northeast of Eagle Point Park and the main boat launch in the west basin. It is considered a shoreline blanket reef because it abuts and runs parallel to the shoreline. The reef is 268 m in length and extends from the shoreline an average of 11 m. It is approximately 2,948 m^2 and its length comprises about 1% of the total shoreline of Beaver Dam Lake. The building materials comprised mostly of "gravel, cobble, and rubble" (Wisconsin Department of Natural Resources 2000), although specific material size was not quantitatively prescribed.

Because the east and west basins of Beaver Dam Lake are separated by a box culvert, the fisheries of the two basins are thought to be discrete due to perceived limited fish movement (Wisconsin Department of Natural Resources 1995). The main fish species in Beaver Dam Lake are walleye, northern pike, largemouth bass, smallmouth bass, bluegill (*Lepomis macrochirus*), and black crappie (*Pomoxis nigromaculatus*) (Table 1). The Wisconsin Department of Natural Resources currently manages lakes that are maintained through stocking at approximately five adult walleye per ha (Wisconsin Department of Natural Resources 2005). The primary source of walleye recruitment in Beaver Dam Lake is stocking, and the lake is considered a Category A lake (i.e., a fishery maintained through stocking) in the Wisconsin Department of Natural Resources Walleye Management Classification System (Appendix A). Walleye have been stocked in Beaver Dam Lake since 1933 and the walleye population has been in a steady decline since 1970

Table 1. Common fish species present in Beaver Dam, Red Cedar and Big Crooked Lakes. Species have been surveyed by the Wisconsin Department of Natural Resources in Beaver Dam Lake (Wisconsin Department of Natural Resources 1995) and Red Cedar Lake (Wisconsin Department of Natural Resources 2005). Big Crooked species presence provided by Musch (2007). Note: some species such as white sucker are likely to occur across all study lakes but have not been noted in previous surveys.

Common name	**Scientific name**	**Beaver Dam**	**Red Cedar**	**Big Crooked**
Black crappie	*Pomoxis nigromaculatus*	●	●	
Bluegill	*Lepomis macrochirus*	●	●	●
Bowfin	*Amia calva*		●	
Bullhead	*Ameiurus sp.*	●	●	
Burbot	*Lota lota*			●
Carp	*Cyprinus carpio*	●		
Cisco	*Coregonus artedii*	●	●	
Creek chub	*Semotilus atromaculatus*		●	
Golden shiner	*Notemigonus chrysoleucas*		●	
Green sunfish	*Lepomis cyanellus*	●		
Largemouth bass	*Micropterus salmoides*	●	●	
Muskellunge	*Esox masquinongy*			●
Mottled sculpin	*Cottus bairdi*		●	
Northern pike	*Esox lucius*	●	●	●
Pumpkinseed	*Lepomis gibbosus*	●	●	●
Rainbow smelt	*Osmerus mordax*	●		
Rock bass	*Ambloplites rupestris*	●	●	●
Smallmouth bass	*Micropterus dolomieui*	●	●	●
Trout perch	*Percopsis omiscomaycus*		●	
Walleye	*Sander vitreus*	●	●	●
Warmouth	*Lepomis gulosus*		●	
White sucker	*Catostomus commersoni*		●	●
Yellow perch	*Perca flavescens*	●	●	●

(Wisconsin Department of Natural Resources 1995). Approximately 124 walleye fingerlings per ha have been stocked in alternate years since 1978 (Wisconsin Department of Natural Resources 1995). The second lake in this study is Red Cedar Lake, also located in the Red Cedar River drainage, in northeastern Barron County, near Mikana, Wisconsin. Red Cedar Lake is the largest in a chain of three lakes with a surface area of 745 ha and 26 km of shoreline and maximum depth of 17 m. Navigable waters connect Red Cedar Lake to the other two lakes in the chain, Balsam Lake to the north and Hemlock Lake to the south. Red Cedar Lake flows into the Red Cedar River, with a 3.4 m high dam located at the outlet. Residential development is extensive on the shoreline, as well as hotel and golf course development. The most common fish species present in Red Cedar Lake are walleye, northern pike, smallmouth bass, largemouth bass, bluegill and black crappie (Table 1).

Walleye fry and/or fingerlings were stocked in Red Cedar Lake from 1933 to 1973, but based on a positive walleye survey in 1973, stocking was discontinued. Surveys conducted in 1977, 1980, 1986 and 1990 also indicated a good walleye population. However, a survey conducted in 1992 found that the walleye population was declining and stocking resumed at a rate of 124 small fingerlings per ha every other year (Wisconsin Department of Natural Resources 2001). In 2004, the Indianhead Chapter of Walleyes for Tomorrow established a portable walleye hatchery on the shoreline of Red Cedar Lake. In 2005, the hatch rate of the eggs was 90% in the portable walleye hatchery and approximately 3.15 million fry were stocked into the lake from that effort (Indianhead Chapter Walleyes for Tomorrow 2005). Currently, the walleye population in Red Cedar Lake is stable or slightly increasing and the primary source of walleye recruitment in Red Cedar Lake is natural reproduction and has been categorized as such as recently as 2001 (Wisconsin Department of Natural Resources 2001). Therefore, it is considered a Category 2 lake (i.e., a naturally reproducing population) in the Wisconsin Department of Natural Resources Walleye Management Classification System (Appendix A). A more recent classification based on new data or the presence of the portable walleye hatchery is not available.

The third lake in this study is Big Crooked Lake, located in Vilas County, Wisconsin. Big Crooked Lake is surrounded by land owned by Dairymen's Inc., a private resort near Boulder Junction. The lake has a surface area of 276 ha with 8.1 km of shoreline and a maximum depth of 11.6 m. The shoreline is primarily forested, with development limited to a lodge and several cabins on a stretch of the north shoreline. Big Crooked Lake is considered oligotrophic. The fish community consists of walleye, smallmouth bass, muskellunge, northern pike, yellow perch, rock bass (*Ambloplites rupestris*), white sucker, and various minnows and darters (Table 1).

Big Crooked Lake has a naturally reproducing and self-sustaining walleye population. Walleye may have initially been stocked into the lake (i.e., were not native), but reliable historical records of any such 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 for research on maximum walleye exploitation rates. The primary source of walleye recruitment in Big Crooked Lake is natural reproduction and it is considered to be a Category 3 lake (i.e., a naturally reproducing population) in the Wisconsin Department of Natural Resources Walleye Management Classification System. Therefore, the walleye population is classified as "sustainable" (Appendix A).

Demographics

To determine recruitment success of young-of-year and the adult walleye stock size producing those young on available spawning habitat, population estimates were conducted on each study lake. Population estimates of adult walleye were conducted by the Wisconsin Department of Natural Resources using standardized procedures: adult walleye were captured using fyke nets after ice-out and marked and then recaptured one week later using pulsed direct current (DC) electrofishing. The population estimates for adult walleye were obtained on Red Cedar Lake in 2005 and on Beaver Dam Lake in 2006; the same years that available habitat was evaluated. Young-of-year walleye sampling was conducted in the fall using electrofishing on each lake in both study years. Electrofishing for YOY took place after dark on multiple occasions with pulsed DC. An attempt was made to cover the total shoreline of each lake on each occasion. Walleye less than 22.9 cm in length were considered YOY based on the Wisconsin Department of Natural Resources standardized procedures; each was marked with a fin clip (Appendix B). During each survey, a different fin was clipped to mark the fish and differentiate between marking runs. All recaptures were recorded.

To attain a population estimate reflecting only wild YOY, scales were aged and the presence of oxytetracycline (OTC) marks on otoliths were examined from a subsample of YOY captured. Total length was measured and scale samples were obtained from walleye under 22.9 cm; 50 samples from Beaver Dam Lake in 2005 and 20 samples from Red Cedar Lake in 2006 were collected (Appendix C). Scales were aged to determine the percentage of walleye under 22.9 cm that were age-0, and 87% of the walleye less than 22.9 cm sampled were found to be age-0. In addition, approximately 50

YOY walleye were sampled by the Wisconsin Department of Natural Resources (WDNR) from Beaver Dam Lake in 2005 and Red Cedar Lake in 2005 and 2006 to determine the percentage of YOY that were stocked based on the presence or absence of (OTC) marks on otoliths (Appendix C). Approximately 8% of the YOY walleye in Beaver Dam Lake (2005), and 92% (2005) and 27% (2006) in Red Cedar Lake were found to be wild (not stocked). Therefore, population estimates represent only age-0 wild walleye; estimates were corrected for age and stocking (Appendix D). A Schnabel (1938) population estimate was used to estimate the number of walleye YOY in each study lake:

$$\hat{N} = \left(\sum_{t=1}^{n} C_t M_t\right) \Bigg/ \left(\sum_{t=1}^{n} R_t\right)$$

Where:

N = population size,

C = total number of fish captured,

M = number of fish marked and released prior to sample period,

R = number of marked fish captured,

t = the individual sample period, and

n = the number of periods.

Egg Density and Survival

To better understand successful use of spawning reefs by walleye, egg densities and survival on spawning reefs along shorelines were assessed. Reefs thought to have the highest use by walleye based on visual observations of spawning activity immediately after ice-out were chosen as study reefs (Table 2, Appendix D). Two sites (i.e., spawning

Table 2. Location of egg collection chambers on Red Cedar and Beaver Dam Lakes, 2005 and 2006. See Appendix D.

Lake	**Site name**	**Year**	**Latitude (°)**	**Longitude (°)**	**Description**
Beaver Dam Lake	"Artificial Reef"	2005, 2006	45.54712	-92.02895	Artificial spawning reef, located in west basin.
	"Arm"	2006	45.56228	-92.06926	In west basin, in northwest portion of lake.
Red Cedar Lake	"Cove"	2005	45.63428	-91.59227	In small cove on northwest shoreline of lake.
	"Island"	2006	45.62158	-91.59087	Western point of small island in center of lake.
	"River"	2006	45.59189	-91.59255	North of river mouth, on southwest shoreline.

reefs) within each lake were studied each year (2005 and 2006). The artificial spawning reef located in Beaver Dam Lake was chosen as one of the two study reefs in that lake for both years of the study. At each study reef, quantification of egg density and survival was attempted using thirty egg collection chambers installed immediately following the lake-wide ice-out (Table 2, Appendix E).

At each study reef, five transects were set up perpendicular to the shore and were spaced evenly along the length of the reef (i.e., length of larger substrate). Six egg collection chambers were placed along each transect at equal distances, beginning at the shoreline-water interface and ending 1 m past where the rocky reef. Round (0.25 material ended m diameter, 0.15 m deep) plastic chambers were used to collect eggs during the spawning period. Each chamber was buried in the sediment so the rim of the chamber was flush with the substrate. The extracted sediment was then immediately placed back in the chamber. The depth, distance from shoreline, substrate composition (Table 3), substrate embeddedness (Table 4, Figure 1), organic material and position (Table 5), and periphyton was recorded for each egg collection chamber.

To quantify egg deposition on each reef, half of all egg collection chambers were removed after spawning activity had ceased in 2005 and all were removed in 2006. Eggs were separated from the substrate, counted, and recorded as live or dead based on the criteria described by Newburg (1975): "an egg was considered to be dead if a small white speck (dead blastodisc) was present or if the egg was milky white, gray black or yellowish and completely opaque. Live eggs are hyaline and turgid early in development but become soft when eyed."

Table 3. Classification of substrate sizes used to evaluate habitat conditions, modified from Wentworth (1922) and Platts et al. (1983).

Substrate	Code	Dimensions
Fine Organic	1	Fine particulate organic matter is discernible, but unidentifiable
Silt	2	< 0.2 mm
Sand	3	0.2 – 6.3 mm
Gravel	4	6.4 – 76.0 mm
Cobble	5	76.1 – 149.9 mm
Rubble	6	150.0 – 303.9 mm
Small Boulder	7	304.0 – 609.9 mm
Large Boulder	8	≥ 610.0 mm
Bedrock	9	Consolidated parent material
Coarse Organic	10	Coarse particulate organic matter is discernible and identifiable (e.g., leaves, pine needles)
Wood 1	W1	< 20.5 mm diameter and any length
Wood 2	W2	20.6 – 50.8 mm diameter and any length, or > 50.9 mm diameter and < 1.0 m length
Wood 3	W3	≥ 50.9 mm diameter, > 1.0 m length

Table 4. Substrate embeddedness typology based on layers of substrate and its effects on egg movement in the matrix. Also see Figure 1. Developed by Raabe (2006).

Embeddedness	Description	Functional Effects
0	2 clean layers of substrate	Eggs can fall into first or second layer of interstitial spaces
1	1 – 1.5 clean layers of substrate	Eggs can fall into first layer of interstitial spaces
2	Substrate embedded half way or less	"Overhang" of first layer of substrate protects eggs from direct overhead observation
3	Substrate embedded over half way	Substrate profile creates boundary layer resistant to free movement of eggs
4	Only top of substrate showing	Substrate exposed but provides little resistance (shear) to movement

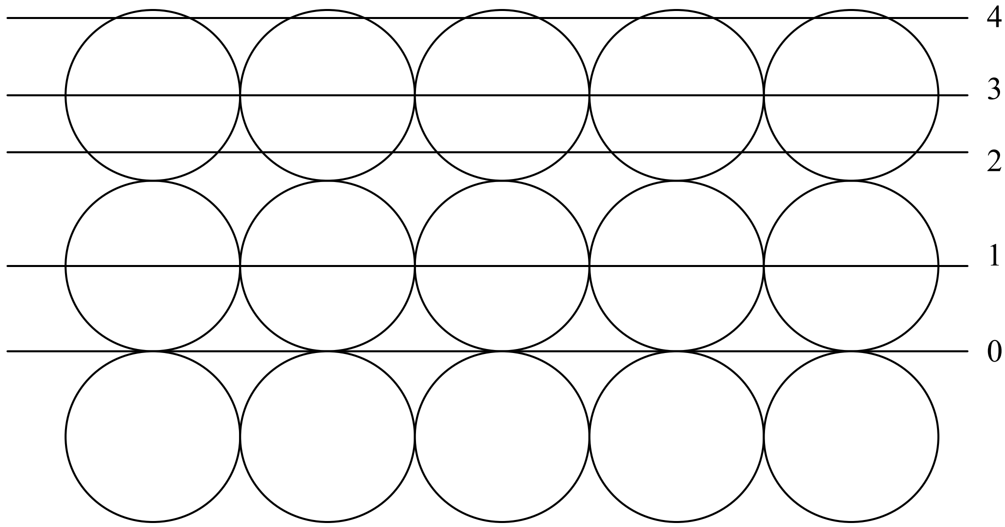


Figure 1. Substrate embeddedness. Horizontal lines indicate the level to which fine particles fill the space between areas of larger substrate. Zero to four represents assigned score. See Table 4 for descriptions of each score. Developed by Raabe (2006).

Table 5. Type of organic material and position of material present in the substrate matrix at each spawning site with corresponding code. Codes are from Raabe (2006).

Code	Type	Description
	Material	
1	Pine/spruce needle	
2	Deciduous leaf	
3	Root mass	
4	Fine organic material	Fine particulate matter is discernible
5	Misc. coarse organic material	Coarse particulate matter is discernible
6	Wood 1	< 20.5 mm diameter, <1.0 m length (diameter higher priority)
7	Wood 2	20.6 – 50.8 mm diameter, <1.0 m length (diameter higher priority)
8	Wood 3	$\geq$ 50.9 mm diameter, > 1.0 m length (diameter higher priority)
	Position	
1	Embedded within matrix	
2	Resting on substrate	
3	Floating or moving	
4	Above substrate (not touching)	

To assess survival across each study reef, the remaining half of the egg collection chambers were covered to trap walleye fry in 2005 once spawning ended. A Nitex mesh cover (10.9 threads/cm) was secured over the top of each of the remaining collection chambers. After the hatch, the collection chambers were removed and the substrate was sorted through to find fry and any remaining eggs. However, no eggs or fry were present in these collection chambers at the time of sorting, possibly due to fry escaping through the mesh or decomposition within the egg collection chamber prior to hatch. In 2006, all egg collection chambers were removed to assess egg densities across study reefs after spawning activity had ceased. Quantification of fry survival rates was not attempted.

The density of eggs deposited and survival rates on all study reefs (grouped together by lake and by year) were analyzed relative to specific habitat characteristics such as depth, distance to shore, substrate composition, embeddedness, vegetation and organic material present. T-tests were used to determine differences in egg densities and survival rates between study reefs.

General Habitat

Models of spawning habitat were developed for walleye on Red Cedar and Big Crooked Lakes where natural walleye recruitment is high. These models were then used to assess spawning habitat potential in Beaver Dam Lake, where natural recruitment is low to non-existent. All data used for model development collected from Big Crooked Lake was obtained during a previous study conducted by Raabe (2006). Data collection methods in all three study lakes were standardized per Raabe (2006).

To determine spawning locations, spotlighting surveys were conducted at night during the spawning season to locate walleye spawning sites. Surveys were conducted beginning at dusk every evening for the first week of the spawning period (coinciding with ice-out) from a boat at low speeds with a spotlight. Because walleye eyes reflect light, detecting the presence of walleye in spawning areas was relatively straightforward. Once spotted, the approximate number of walleye present was counted, time of day recorded, and approximate average depth visually estimated. “Paired walleye” (i.e., potentially spawning fish) and spawning activity were also recorded. Exact spawning locations were recorded using a hand-held Garmin GPSmap© unit and general spawning areas were marked on a lake map.

In addition to spotlighting surveys, snorkel surveys were conducted during the daytime throughout the spawning period along the perimeter of each lake to specifically identify and delineate spawning locations based on the actual presence of walleye eggs. First, sites that were identified during spotlighting surveys were snorkeled and delineated based on the distribution of eggs in those areas. Once these sites were surveyed, additional random 0.81 km increments of the shoreline were snorkeled to identify other spawning areas not detected during the spotlighting surveys. The entire shoreline of all study lakes could not be surveyed due to length of shoreline.

When walleye eggs were found and positively identified, washers were placed to mark the perimeter, herein referred to as the egg deposition zone. Each egg deposition zone was delineated as a polygon; therefore the entire area within the polygon represents the area of egg deposition. The actual polygon was created for each egg deposition zone by swimming perpendicular to the shore until the deepest area of egg deposition was observed (with a minimum of ten eggs) and a washer was placed to mark this point in the polygon. The surveyor then swam 2 to 4 m outside the egg deposition zone, made a 45 degree turn towards the shoreline, and swam until the deepest eggs were observed again, and another washer was placed. This continued with washers being placed approximately every 5 m until the lateral ends of the polygon were identified (i.e., no more eggs were observed). The beginning and end (i.e., lateral ends) of egg deposition zones (i.e., the polygons) were also marked with flagging tape on shore and recorded with a hand-held GPS unit.

Spawning Chronology

Throughout the spawning season, water temperature and egg ontogeny were monitored to determine rate of egg development within each egg deposition zone. Onset© temperature data loggers were installed near the substrate-water interface on each study reef in each lake immediately after ice-out to record water temperature at one hour increments throughout the spawning and egg incubation periods. In addition, temperature data loggers were placed on each of the four cardinal points (north, south, east, and west) on each lake to record temperature differences within and between the lakes. Water levels were also recorded in each lake to monitor fluctuations in depth to the nearest 0.5 cm daily using rebar installed at one location in each lake.

To track the chronology of the spawning season, eggs were collected daily throughout the spawning and incubation periods using a hand-held strainer. Egg collection locations were randomly selected on spawning reefs within each study lake daily and strained until approximately 100 eggs were collected from each study lake. The straining technique temporarily suspended the eggs in the water column so they could be collected with the net of the strainer. Three stages of development were identified: pre-eyed, eyed, and hatched. The pre-eyed stage was determined by the absence of the eyes; the eyed stage of development was determined by the presence of the eyes (either pigmented or not) and body movement within the egg. Because walleye swim up soon after hatch and are then difficult to collect, hatching was determined by the notable absence of live eggs on the reefs relative to prior day's presence.

To determine significant temperature differences across study reefs and across lake locations (north, south, east, and west), repeated-measures ANOVA were used. Alpha was set at 0.05. To illustrate the spawning chronology in each lake, the mean daily water temperatures on one study reef per lake per year were graphed and compared to egg-related events. Four events were delineated: ice-out, onset of egg deposition, presence of eyed eggs, and onset of hatching.

Spawning Habitat

After all walleye eggs had hatched, habitat characteristics within egg deposition zones were evaluated using transects placed perpendicular to the shoreline and spaced equally throughout the zones. Habitat characteristics were then measured at sample points along each transect. Within egg deposition zones, a minimum of 200 sample points were collected to ensure that suitable sample sizes were obtained for statistical analyses. To obtain the number of transects needed within each egg deposition zone to obtain 200 sample points, the length (from lateral end to lateral end) of the egg deposition zone (polygon) was measured and the average distance from each washer to the shoreline-water interface was measured. The number of transects necessary to obtain 200 sample points within each egg deposition zone was then determined:

$$T = \frac{200}{\left[1 + \left(x/0.5\right)\right]}$$

Where:

T = the number of transects necessary, and

x = the mean distance from each washer (i.e., boundary of the egg deposition zone polygon) to the shoreline-water interface.

Once the number of transects necessary had been determined, the distance between each transect was determined with the following equation:

$$D = L/T$$

Where:

D = the distance between transects, and

L = the total reef length where eggs were deposited.

Once the number of transects needed and the distance between transects was determined, sample points were taken along each transect within each egg deposition zone in all study lakes to quantify spawning habitat. To assess differences between spawning habitat (i.e., egg deposition locations) and nearby non-spawning habitat, two transects were constructed outside the egg deposition zone polygon on both lateral ends, representing habitat directly adjacent to the egg deposition zone. These data were not used to develop habitat models.

Along each transect, a sample point was placed every 0.5 m starting at the shoreline-water interface and proceeding perpendicular from the shoreline until the edge of the polygon (i.e., transition point) was reached. The transition point was defined as the point where the deepest eggs were found (i.e., the boundary of the egg deposition zone polygon). Once the transition point was reached, additional sample points were taken every meter along each transect until the end of the reef was reached (i.e., where the dominant substrate changed from rock to smaller substrate such as silt and/or sand). Each sample point along all transects were classified based on where it fell relative to where eggs were deposited based on protocol developed by Raabe (2006) (Table 6). egg deposition zone (adhesive eggs), 2) within the egg deposition zone (non-adhesive eggs), 3) transition point (adhesive or non-adhesive eggs), 4) outside the egg deposition zone (no eggs), and 5) off the reef (no eggs). Once sand (or other non-reef material such as silt, muck or detritus) was reached, three more sample points, continuing at every meter along the transect, were assessed. These sample points represented the habitat directly surrounding the reef.

At each sample point, a 0.3 m^2 quadrat was used to estimate habitat characteristics. Depth and distance to the shoreline were measured in the center of each quadrat. Slope of the reef was determined as the difference between the depths of the first quadrat of the transect and the last quadrat of the transect divided by distance. Slope was also calculated for the egg deposition zone portion of the reef only, and was determined by finding the difference between the depths of the first quadrat of the transect and the last quadrat that fell within the egg deposition zone by distance. When the egg deposition zone fell within 0.5 m from shore, and therefore only one quadrat was evaluated, slope was not calculated. Within each quadrat, substrate composition (Table 3) and substrate embeddedness (Table 4, Figure 1) were visually estimated to the nearest 5%. Percent composition and dominant position of organic material was also recorded in each quadrat (Table 5). Percentage of periphyton on substrate within each quadrat was estimated to the nearest 5% and average length of periphyton was measured to the nearest mm and recorded.

Table 6. Egg deposition zone categories, definitions and codes for walleye spawning reefs and adjacent areas. Developed by Raabe (2006).

Egg Deposition Zone	Definition	Code
Adhesive within	Adhesive eggs were present during the spawning period within the egg deposition zone	1
Non-adhesive within	Non-adhesive eggs were present during the spawning period within the egg deposition zone	2
Transition	Eggs located on the transition point (i.e., boundary of the egg deposition zone polygon)	3
Outside	On the reef but outside the egg deposition zone (no eggs deposited here)	4
Non-reef	Of the reef material completely and into sand, muck or detritus (no eggs deposited here)	5

Available Habitat

Available habitat was assessed in each lake in order to develop the resource selection models. One hundred random transects were chosen around the shoreline of each study lake. Location of the transects was determined by generating 100 random numbers between 0 and 360. These numbers were then identified from compass bearings; from the center of the lake the boat motored directly to each bearing. That location was marked on the shoreline with flagging tape and recorded using a handheld GPS unit. Each transect was set up perpendicular to the shoreline and a sample point was placed every other meter along the transect using a 1 m^2 quadrat, starting from the shoreline-water interface and ending at a depth of three meters. SCUBA was used to survey the deeper portions of each transect. At each quadrat, the same variables used to evaluate the egg deposition zones were used: depth, distance from shoreline, slope, substrate composition (Table 3), substrate embeddedness (Table 4, Figure 1), organic matter and percent composition (Table 5). In addition to the previous variables, distance to cover was also determined. Substrate categorized as large boulders ($\geq$ 610.0 mm) or wood 3 ($\geq$ 50.9 mm in diameter and > 1.0 m in length) was considered potential cover. If cover was located within 10 m of quadrat, distance, length and width of the structure was recorded.

Model Development

Physical habitat characteristics for each egg deposition zone found during surveys and the available habitat of Red Cedar and Beaver Dam Lakes were illustrated graphically using histograms. Selection of spawning habitat by walleye was analyzed using logistic regression models; Statistical Analysis System 8.2 (SAS, Cary, NC) was used to create logistic regression models and Number Cruncher Statistical Systems 2004 (NCSS, Kaysville, UT) and legacy routines within NCSS (2004) from a previous version (1997) were used to generate univariate models and to determine overall correct classification rates for each logistic regression model. Logistic regression was used because two classes of response variables (used versus available sites) were available to determine resource selection (Press and Wilson 1978, Manly et al. 1993). Before multiple logistic regression models were created, univariate models were created for each variable. A stepwise method was then used to create the logistic regression models, which uses both the addition and the elimination of independent variables (Zar 1996). Alpha was set at 0.05 to determine inclusion into the model. The independent variable was binary; and the presence and availability of habitat was used (Press and Wilson 1978, Manly et al. 1993). The logistic regression equation used was:

$$\Pi = e^{u}/\left(1+e^{u}\right)$$

Where:

Π = relative probability of egg deposition,

e = inverse of natural logarithm of 1 (exponent constant), and

$u = k + m_1x_1 + m_2x_2 + \ldots m_jx_j$.

Where:

k = constant,

m_j = regression coefficients, and

x_j = values of other independent variables.

A series of logistic regression models, including a global model, were created and compared; Akaike's Information Criterion (AIC) was used to determine the best model, which was the model with the minimum AIC value (Burnham and Anderson 1998). All models within two AIC units were considered alternate models, although models within four AIC units may have had some limited empirical support (Burnham and Anderson 1998). Models were also ranked from best to worst using AIC and using the principle of parsimony; if multiple models fit equally well, the model with the fewest variables was used (Burnham and Anderson 1998). Models selected using AIC were compared with more traditional approaches (e.g., significance and correct classification rates) to assess differences.

The final models were then tested to determine correct classification rates using actual used and available habitat data from Red Cedar, Beaver Dam and Big Crooked Lakes. To determine actual correct classification rates, points (i.e., quadrats) with a relative probability of egg deposition of $\geq$ 0.50 as predicted by each model were compared to actual sites with egg deposition in both lakes. Points with a relative probability of egg deposition of < 0.50 were compared to actual available habitat sites in both lakes. When the predicted occurrence matched the actual occurrence, the model was considered correct.

Once all models were tested, a final "best" model (based on AIC) was then used to predict the relative probability of egg deposition in Beaver Dam Lake based on the available habitat data collected (Appendix F). Relative probability of egg deposition was determined for Beaver Dam Lake as a whole, separated by basins, and by individual spawning reefs to determine differences between locations.

Although the previous best models were chosen based on highest correct classification rates and lowest AIC values, all final models contained variables that were similar in each study lake: distance from shore and/or water depth. Therefore a series of additional resource selection models were tested to determine 1) which variables best elucidated differences between lakes and 2) to determine how distance from shore and water depth affected results (Appendix G). Because quadrat locations were chosen based on the same, predetermined transect layout (therefore reflecting the same distance from shore increments), the variable "distance from shore" was removed from the Red Cedar Lake Model 2. Dominant embeddedness was also removed because it did not greatly affect correct classification results (Appendix G) and to aid in the ease in which variables can be collected in the field. After these variables were removed, the model created from Red Cedar Lake data contained only two variables: percentage of gravel and cobble present at a given site (Red Cedar Lake Model 3); the same variables were in the Big Crooked Lake Model.

Univariate models showed that the relative probability of use was 0.5 at ($\leq$ 0.485 m) deep and within ($\leq$ 2.0 m) to shore, these variables were not very diagnostic in identifying walleye spawning areas because the entire lake had these conditions thereby, inflating the relative probability of use for all shallow and close quadrats regardless of substrates present. To eliminate this effect of water depth and distance from shore, models containing only gravel and cobble were then applied to each dataset for quadrats $\leq$ 0.5 m deep and $\leq$ 2.0 m from shore.

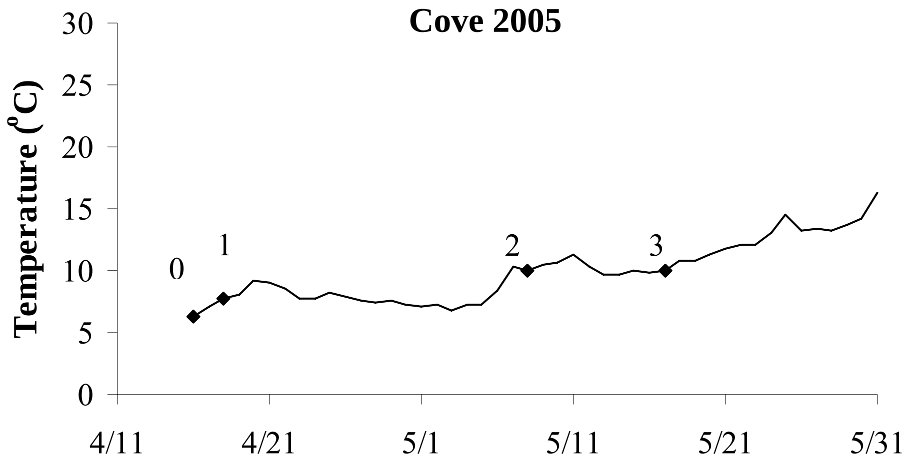
Results

Demographics

In 2005, Wisconsin Department of Natural Resources population surveys estimated 3,733 adult walleye (7.41/ha) in Red Cedar Lake. In 2006, surveys estimated 761 adult walleye (1.73/ha) in Beaver Dam Lake. Naturally recruited YOY walleye in Red Cedar Lake were estimated at 1,678 individuals (95% C.I.: 1,121-2,642) in 2006 and 3,269 individuals (95% C.I.: 2,740-4,052) in 2005. Surveys estimated 82 naturally recruited YOY walleye (95% C.I.: 51-143) in the west basin of Beaver Dam Lake in 2005 (Appendix C). No YOY population estimate was obtained for the east basin of Beaver Dam Lake in 2005 and 2006, or the west basin of Beaver Dam Lake in 2006 due to small sample size (< 15 fish captured throughout the basin and zero recaptures over several electrofishing efforts).

Spawning Chronology

In 2005, ice-out occurred on Red Cedar Lake on April 16, and the first walleye eggs were found during visual snorkel surveys approximately two days later, when water temperature was 7.8 °C (Figure 2). The incubation period lasted approximately 29 days. In 2006, ice-out occurred on Red Cedar Lake on April 15, and the first walleye eggs were found four days later, when water temperature reached 8.8 °C; egg incubation lasted approximately 21 days (Figure 2). Within Red Cedar Lake, temperatures at each of the four cardinal "points" were thermally different from each other in both years (Table 7). In 2006, spawning sites were significantly cooler than sites where no eggs were found when hourly temperatures were averaged over the duration of the egg incubation period



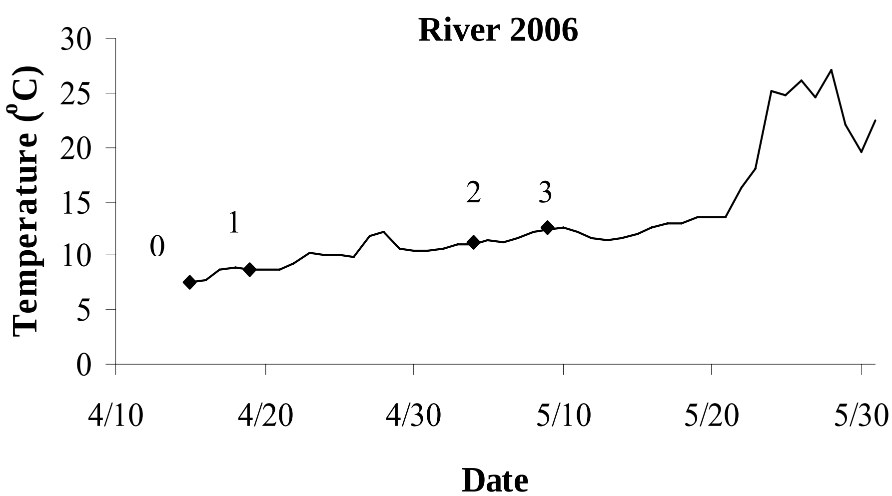


Figure 2. Water temperatures in Red Cedar Lake (2005 and 2006) at egg collection chamber sites ("cove" and "river", respectively). Spawning chronology stages were: 0 = lake-wide ice-out, 1 = onset of egg deposition, 2 = eyed stage, and 3 = onset of hatching.

Table 7. Differences in water temperatures across Red Cedar Lake beginning from the onset of the spawning period through swim-up periods in 2005 and 2006. “Spawning reef” indicates water temperature was recorded on study reefs (e.g., sites with egg collection chambers). Cardinal point locations (north, south, east, and west) were sites without walleye egg deposition, and were pooled together as “non-spawning sites”. Comparisons were made using two-sample t-test (alpha ≤ 0.05). “[1]” and “[2]” refer to corresponding columns ($\bar{x}$ (± 1 se)).

Year	**Comparison**			**$\bar{x}$ (± 1 se)[1]**	**$\bar{x}$ (± 1 se)[2]**	**F ratio**	**P**
2005	Spawning reef[1]	vs.	Non-spawning reef[2]	10.35 (0.096)	10.09 (0.096)	3.75	0.053
	North[1]	vs.	East[2]	10.09 (0.058)	9.64 (0.058)	29.09	<0.001
	North[1]	vs.	South[2]	10.09 (0.053)	9.28 (0.053)	119.42	<0.001
	North[1]	vs.	West[2]	10.09 (0.050)	9.09 (0.050)	202.91	<0.001
	South[1]	vs.	East[2]	9.28 (0.060)	9.64 (0.060)	19.07	<0.001
	South[1]	vs.	West[2]	9.28 (0.051)	9.09 (0.051)	6.92	0.009
	East[1]	vs.	West[2]	9.64 (0.057)	9.09 (0.057)	47.79	<0.001
2006	Spawning reef[1]	vs.	Non-spawning reef[2]	9.96 (0.049)	10.83 (0.070)	102.22	<0.001
	Islands[1]	vs.	Non-islands[2]	10.10 (0.056)	10.28 (0.040)	6.85	0.009
	Island site[1]	vs.	River site[2]	9.87 (0.075)	10.05 (0.075)	2.87	0.090
	North[1]	vs.	East[2]	10.83 (0.074)	10.03 (0.074)	58.78	<0.001
	North[1]	vs.	South[2]	10.83 (0.075)	10.32 (0.075)	22.75	<0.001
	North[1]	vs.	West[2]	10.83 (0.070)	10.20 (0.070)	39.59	<0.001
	South[1]	vs.	East[2]	10.32 (0.087)	10.03 (0.087)	5.84	0.016
	South[1]	vs.	West[2]	10.32 (0.084)	10.20 (0.084)	1.00	0.317
	East[1]	vs.	West[2]	10.03 (0.083)	10.20 (0.083)	2.32	0.128

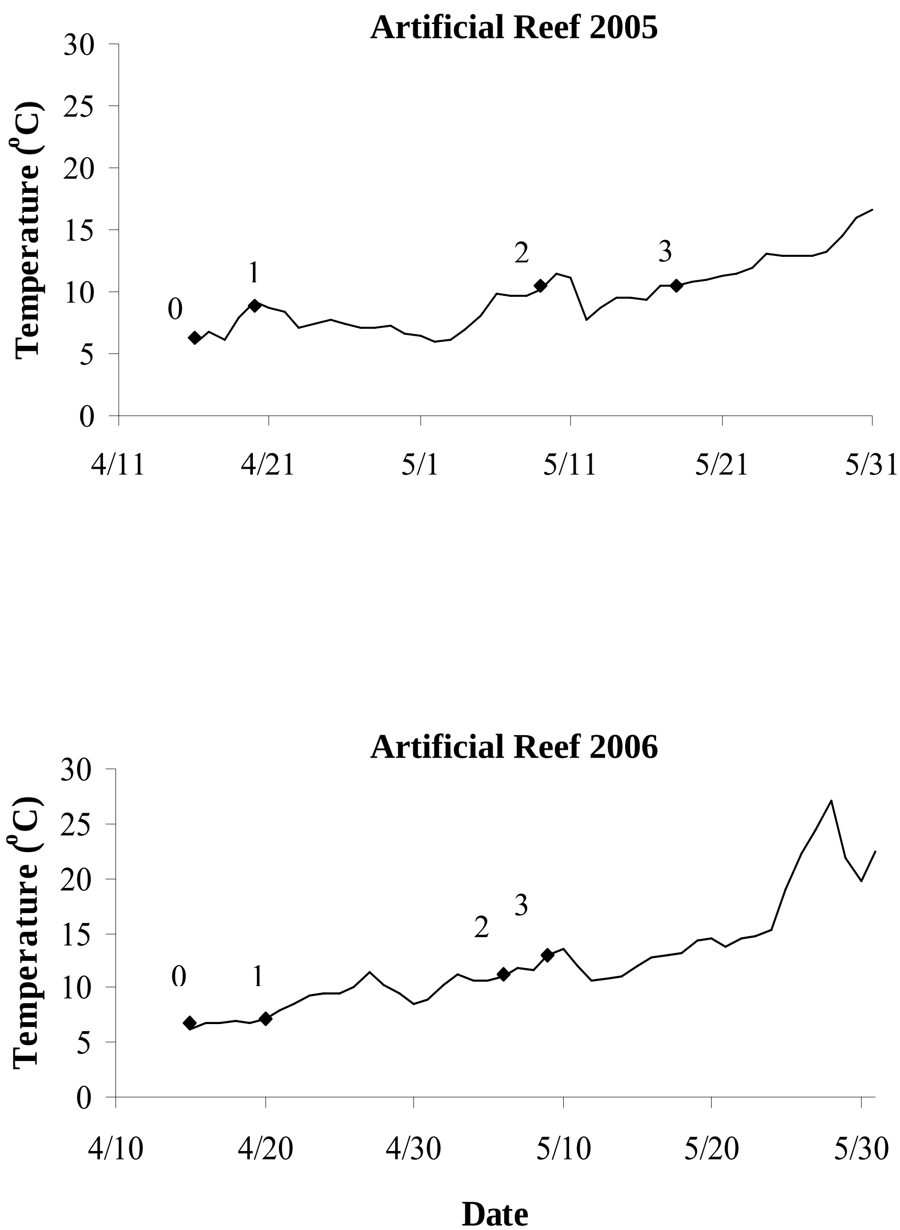


Figure 3. Water temperatures in Beaver Dam Lake (2005 and 2006) at egg collection chamber site ("artificial reef"). Spawning chronology stages were: 0 = lake-wide ice-out, 1 = onset of egg deposition, 2 = eyed stage, and 3 = onset of hatching.

(spawning sites: $\overline{x}$ = 9.96 °C, non-spawning sites: $\overline{x}$ =10.83 °C); site temperatures did not significantly differ in 2005 (Table 7).

In 2005, ice-out occurred on Beaver Dam Lake on April 16, and walleye eggs were found four days later, when water temperature reached 8.9 °C; incubation lasted approximately 28 days (Figure 3). In 2006, ice-out occurred on April 15, and the first eggs were found four days later, when water temperature reached 7.7 °C (Figure 3); incubation lasted approximately 19 days. Within Beaver Dam Lake, temperatures at each of the four cardinal "points" on each shoreline within in each basin were significantly different from each other in 2005 and 2006 (Tables 8 and 9). The artificial spawning reef, where walleye eggs were found in both study years, was significantly cooler than non-spawning sites combined (spawning reef: $\overline{x}$ =8.81 °C, non-spawning sites: $\overline{x}$ =9.33 °C (2005); spawning reef: $\overline{x}$ =9.09 °C, non-spawning sites: $\overline{x}$ =9.58 °C (2006)), as well as all other temperature monitoring locations across the lake, with the exception of the eastern shoreline of the west basin; however, this location is closest spatially (Table 8). No temperatures were available for the east basin north site in 2005 or the west basin south site in 2006 due to the loss of data loggers.

<u>Egg and Fry Density and Survival</u>

The majority (63%) of egg collection chambers did not contain eggs, whereas those that did were generally located within 4 m from shore at a depth of less than 0.5 m (Figure 4, Appendix E). The majority of live eggs were present in chambers comprised of gravel and cobble as the dominant substrates, while some chambers with eggs present contained a range of substrate sizes (Figure 2, Appendix E).

Table 8. Differences in water temperatures across the west basin of Beaver Dam Lake beginning from the onset of the spawning period through swim-up periods in 2005 and 2006. “Artificial reef” indicates water temperature was recorded on artificial spawning reef, also a study reef (e.g., site with egg collection chambers). Cardinal point locations (north, south, east, and west) were sites without walleye egg deposition, and were pooled together as “non-spawning sites”. Comparisons were made using two-sample t-test (alpha $\leq$ 0.05). “[1]” and “[2]” refer to corresponding columns ($\bar{x}$ ($\pm$ 1 se)).

Year	**Comparison**			**$\bar{x}$ (± 1 se)[1]**	**$\bar{x}$ (± 1 se)[2]**	**F ratio**	**P**
2005	Artificial reef[1]	vs.	Non-spawning sites[2]	8.81 (0.079)	9.33 (0.039)	170.92	<0.001
	Artificial reef[1]	vs.	North[2]	8.18 (0.066)	9.20 (0.066)	119.64	<0.001
	Artificial reef[1]	vs.	South[2]	8.18 (0.073)	10.52 (0.073)	508.08	<0.001
	Artificial reef[1]	vs.	East[2]	8.18 (0.068)	8.68 (0.068)	26.82	<0.001
	Artificial reef[1]	vs.	West[2]	8.18 (0.077)	8.90 (0.077)	42.67	<0.001
	North[1]	vs.	South[2]	9.20 (0.074)	10.52 (0.074)	157.42	<0.001
	North[1]	vs.	East[2]	9.20 (0.069)	8.68 (0.069)	29.25	<0.001
	North[1]	vs.	West[2]	9.20 (0.078)	8.90 (0.78)	7.66	0.006
	South[1]	vs.	East[2]	10.52 (0.076)	8.68 (0.76)	295.65	<0.001
	South[1]	vs.	West[2]	10.52 (0.084)	8.90 (0.084)	184.26	<0.001
	East[1]	vs.	West[2]	8.68 (0.080)	8.90 (0.080)	3.77	0.052
2006	Artificial reef[1]	vs.	Non-spawning sites[2]	9.09 (0.109)	9.58 (0.063)	14.64	<0.001
	Artificial reef[1]	vs.	North[2]	9.09 (0.102)	9.61 (0.102)	12.69	<0.001
	Artificial reef[1]	vs.	East[2]	9.09 (0.114)	9.37 (0.114)	3.01	0.083
	Artificial reef[1]	vs.	West[2]	9.09 (0.097)	9.75 (0.098)	22.57	<0.001
	North[1]	vs.	East[2]	9.61 (0.120)	9.37 (0.120)	1.91	0.167
	North[1]	vs.	West[2]	9.61 (0.104)	9.75 (0.104)	0.88	0.349
	East[1]	vs.	West[2]	9.37 (0.116)	9.75 (0.116)	5.17	0.023

Table 9. Differences in water temperatures across the east basin of Beaver Dam Lake beginning from the onset of the spawning period through swim-up periods in 2005 and 2006. Cardinal point locations (north, south, east, and west) were sites without walleye egg deposition. Comparisons were made using a paired t-test (alpha $\leq$ 0.05). "[1]" and "[2]" refer to corresponding columns ($\bar{x}$ (± 1 se)).

Year	**Comparison**			**$\bar{x}$ (± 1 se)[1]**	**$\bar{x}$ (± 1 se)[2]**	**F ratio**	**P**
2005	South[1]	vs.	East[2]	11.61 (0.090)	9.94 (0.090)	173.98	<0.001
	South[1]	vs.	West[2]	11.61 (0.097)	10.19 (0.097)	106.95	<0.001
	East[1]	vs.	West[2]	9.94 (0.087)	10.19 (0.087)	4.25	0.039
2006	North[1]	vs.	South[2]	13.05 (0.090)	11.32 (0.090)	185.92	<0.001
	North[1]	vs.	East[2]	13.05 (0.096)	11.59 (0.096)	114.97	<0.001
	North[1]	vs.	West[2]	13.05 (0.100)	10.96 (0.100)	218.62	<0.001
	South[1]	vs.	East[2]	11.32 (0.094)	11.59 (0.094)	4.09	0.043
	South[1]	vs.	West[2]	11.32 (0.098)	10.96 (0.098)	6.89	0.009
	East[1]	vs.	West[2]	11.59 (0.104)	10.96 (0.104)	18.52	<0.001

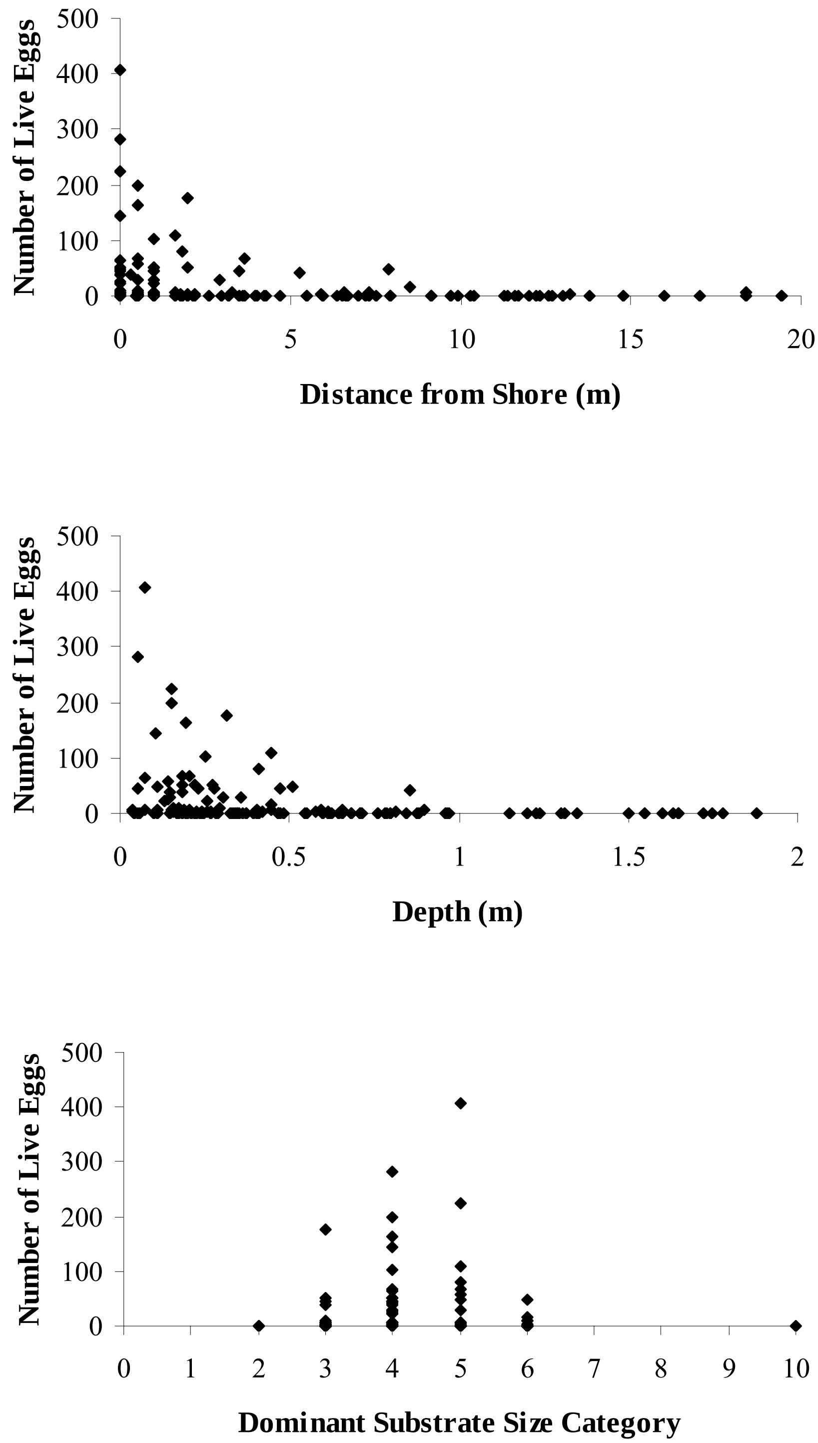


Figure 4. Number of live eggs in all egg collection chambers from the littoral zones of Red Cedar and Beaver Dam Lakes, 2005 and 2006, combined relative to distance from shore, depth, and dominant substrate. See Table 3 for substrate sizes.

Table10. Differences in egg survival rates and total number of eggs present in the egg collection chambers between study sites, lakes, and years. Comparisons were made using a paired t-test (alpha $\leq$ 0.05). “1” and “2” (identified in the “Comparison” column) refer to corresponding columns ($\bar{x}$ ($\pm$ 1 se)). (BDL = Beaver Dam Lake and RCL = Red Cedar Lake).

Relationship	**Comparison**			**$\bar{x}$ (± 1 se)[1]**	**$\bar{x}$ (± 1 se)[2]**	**P**
	Survival Rates (%)					
Across lakes-	BDL Artificial Reef 2005[1]	vs.	RCL Cove 2005[2]	40.7 (14.61)	37.0 (13.51)	0.424
within years	BDL (total) 2006[1]	vs.	RCL (total) 2006[2]	49.7 (3.48)	17.7 (4.03)	0.000
Within lakes-	BDL Artificial Reef 2006[1]	vs.	BDL Arm 2006[2]	48.7 (11.14)	50.1 (2.59)	0.295
within years	RCL Island 2006[1]	vs.	RCL River 2006[2]	33.2 (10.80)	11.8 (3.08)	0.047
	Total Eggs (#)					
Across lakes-	BDL Artificial Reef 2005[1]	vs.	RCL Cove 2005[2]	42.2 (26.34)	66.2 (62.92)	0.367
within years	BDL (total) 2006[1]	vs.	RCL (total) 2006[2]	106.9 (42.05)	66.5 (29.99)	0.210
Within lakes-	BDL Artificial Reef 2006[1]	vs.	BDL Arm 2006[2]	102.7 (78.25)	111.1 (32.70)	0.461
within years	RCL Island 2006[1]	vs.	RCL River 2006[2]	12.4 (5.22)	120.6 (52.30)	0.022

In 2005, egg survival rates in the egg collection chambers did not differ between lakes (Table 10). However, in 2006 the survival rate was statistically higher in Beaver Dam Lake (50%) versus Red Cedar Lake (18%) (Table 10). Within lakes, survival rates did not statistically differ between most sites. However, survival rates of eggs deposited in the egg collection chambers located at the island site in Red Cedar Lake in 2006 had a higher survival rate (33%) than those located at the river site in the same lake (13%) yet the mean number of eggs per egg collection chamber was significantly lower at the island site relative to the river site (12 eggs and 121 eggs, respectively). While the total number of eggs collected was variable among years, the highest number of eggs collected in a given bucket was 2,349 eggs on the artificial reef in Beaver Dam Lake in 2006 and 1,403 eggs at the river site in Red Cedar Lake in 2005, the total number of eggs present in collection chambers did not differ significantly between lakes. In addition to comparing egg survival between sites, egg survival was also evaluated relative to dominant substrate within the egg collection chamber. Eggs were present in buckets containing sand, gravel, cobble, and rubble, and survival rates ranged from 0 to 94%. However, survival rates did not differ significantly among substrate types across study lakes (alpha=0.05, p=0.183).

General Habitat

In both Red Cedar and Beaver Dam Lakes, the majority of the dominant substrate sizes found in the littoral zone were small overall (e.g., silt and sand), whereas the dominant substrate present in the egg deposition zones was larger (e.g., gravel and cobble) (Figure 5). Similarly, the second most common substrate size (i.e., subdominant substrate) throughout the available habitat was also small compared to the subdominant substrate present within the egg deposition zones. However, more overlap in the sizes of

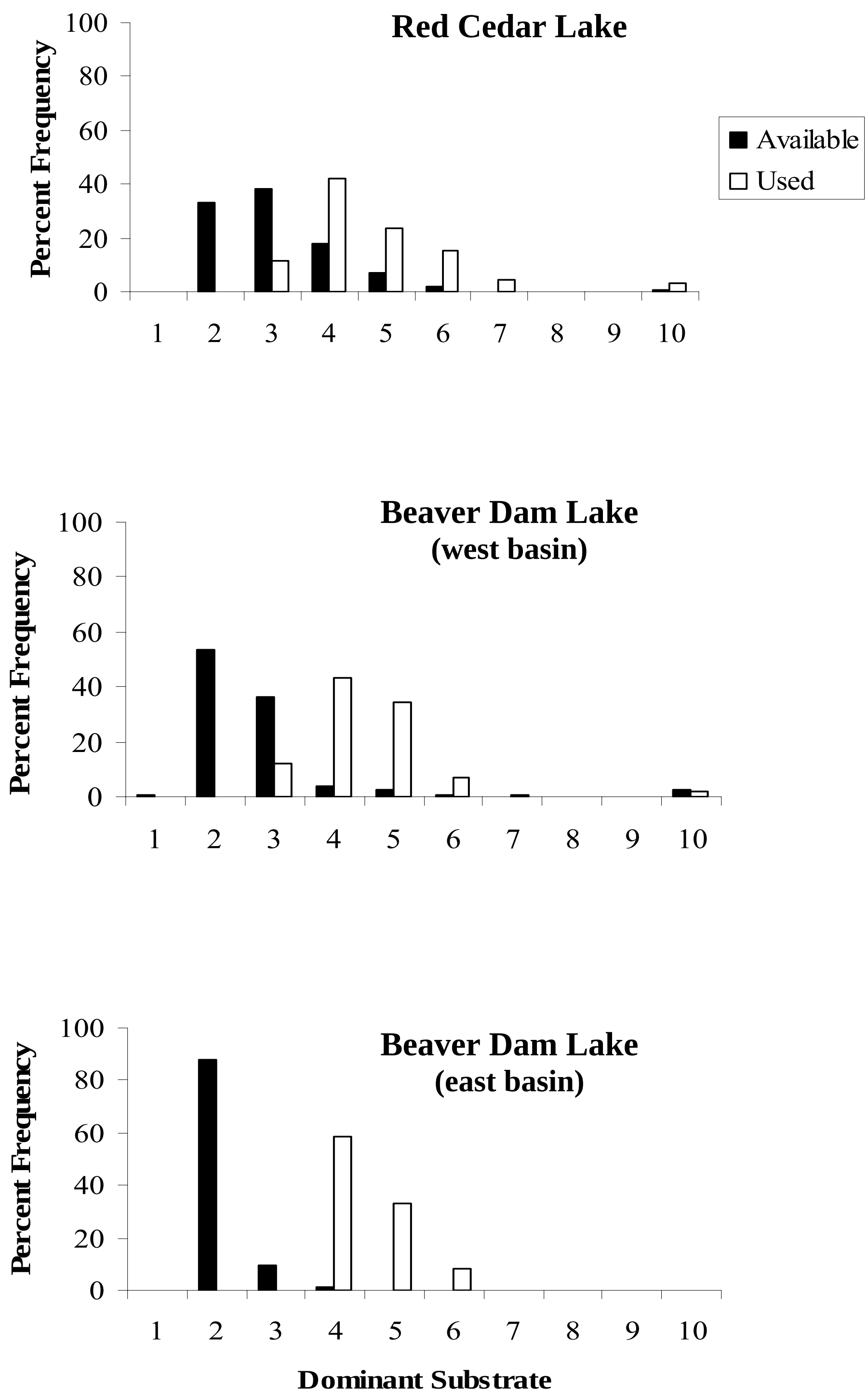


Figure 5. A comparison between the frequency of dominant substrates in sites with egg deposition (used) versus the overall lake (available habitat) in Red Cedar and Beaver Dam Lakes.

the subdominant substrate occurred between the egg deposition zones and the available habitat.

The embeddedness of the dominant substrate that was present was also different between egg deposition zones relative to the overall lake. The majority of the egg deposition zones had lower embeddedness values, ranging in value from 0 to 3, whereas the majority of the sites in both Red Cedar and Beaver Dam Lake had the highest embeddedness value possible (4) (Figure 6). Bottom slope also differed between egg deposition zones and the overall lake. In both Red Cedar and Beaver Dam Lakes, average slope was significantly lower in the available habitat sites (Red Cedar Lake at 12% and Beaver Dam Lake at 9%) compared to egg deposition zones, where slope was significantly greater (Red Cedar Lake at 20% and Beaver Dam Lake 23%). Within Beaver Dam Lake, the slope of the natural spawning reef was higher (18%) than that of the artificial spawning reef (6%). In addition, larger-scale habitat features also differed between the natural and artificial spawning reefs; both water depth and distance from shore at the outer edge of each reef was greater at the artificial spawning reef compared to the natural spawning reef (Figure 7).

Model Development

Three resource selection models were developed, two from Red Cedar Lake and one from Big Crooked Lake; all were similar and contained a variable indicating distance from shore or depth, substrate size and embeddedness (Table 11). One model created from Red Cedar Lake data (Red Cedar Model 1) was chosen as the best model because it ranked best using AIC and also had the highest correct classification rate of all other

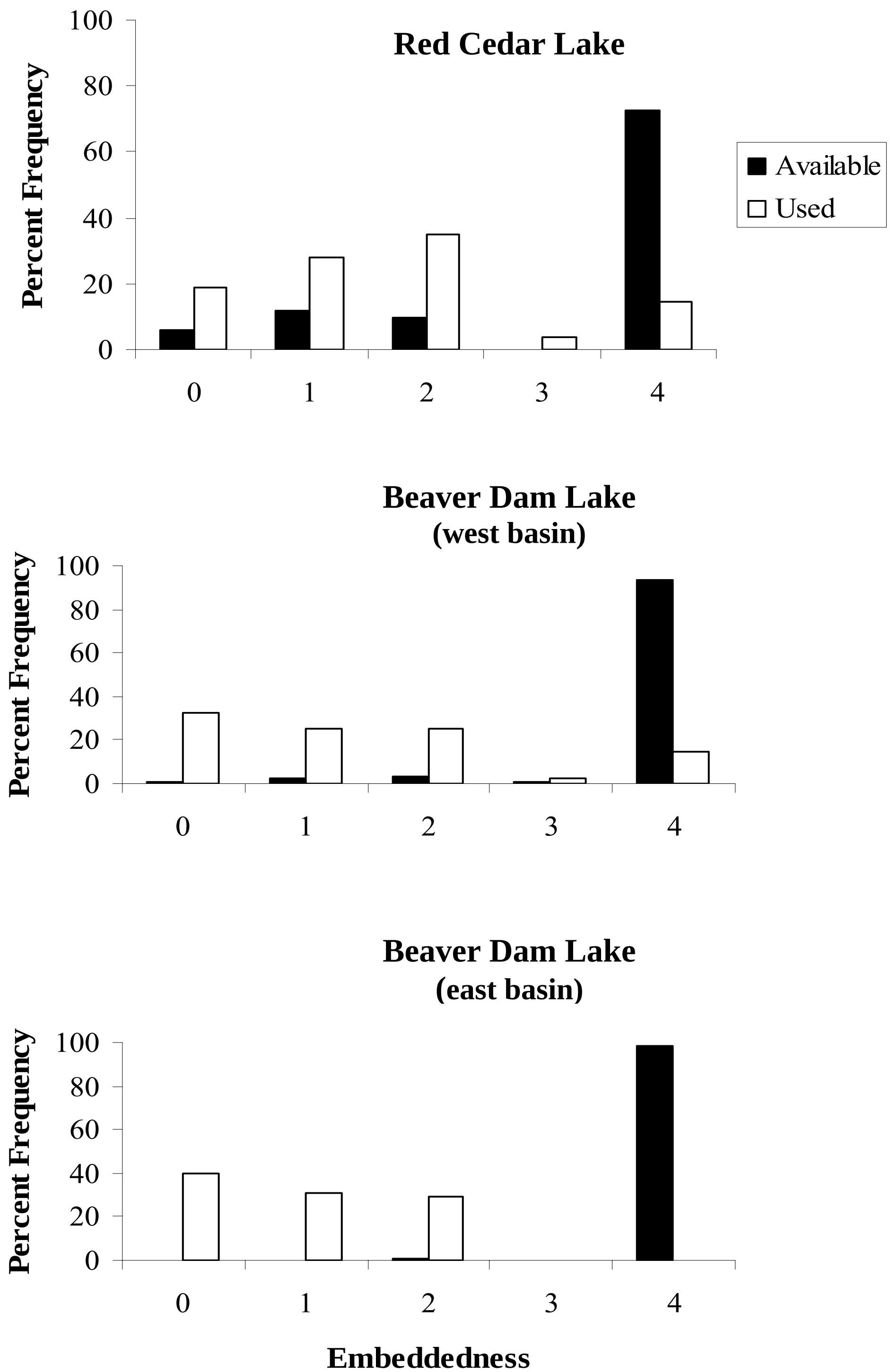


Figure 6. A comparison between the embeddedness of the dominant substrate in sites with egg deposition (used) versus the overall lake (available habitat) in Red Cedar and Beaver Dam Lakes.

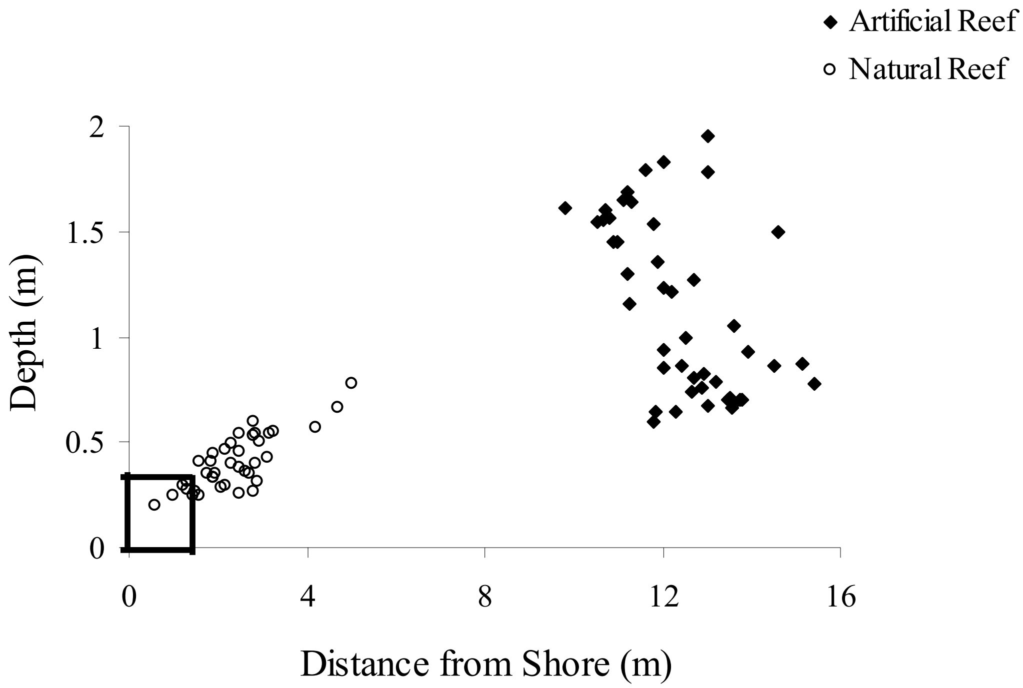


Figure 7. Comparison of the deep-water edge of rocky reef material relative to both distance from shore and water depth for the artificial spawning reef versus the natural spawning reef in Beaver Dam Lake. The black square represents the depth and distance from shore where approximately 90% of the walleye eggs were deposited on the natural spawning reef (< 1.0 m from shore and < 0.3 m depth).

Table 11. The best resource selection functions developed from used spawning habitat for walleye compared to available habitat in Red Cedar (RCL) and Big Crooked Lakes (BCL) (RCL available sites N = 1,642, used sites N = 882; BCL available sites N = 1,000, used sites N = 1,000).

							Predicted	% Classification	
Model Name	**Variables**	**Coefficient**	**Wald Chi Sq**	**P**	**AIC**	**Log L**	**Presence**	**Absence**	**Overall**
RCL Model 1	Intercept	0.605	2.036	0.154	1204.556	1194.556	93.2	89.0	90.5
	Distance from Shore	-0.198	12.193	<0.001					
	Depth	-4.607	75.908	<0.001					
	Dominant Substrate	0.389	23.464	<0.001					
	Dominant Embeddedness	0.313	22.412	<0.001					
RCL Model 2	Intercept	0.685	6.092	0.014	1299.096	1289.096	93.1	87.8	89.7
	Distance from Shore	-0.708	288.100	<0.001					
	Percent Gravel	0.014	15.576	<0.001					
	Percent Cobble	0.013	9.394	0.002					
	Dominant Embeddedness	0.317	20.546	<0.001					
BCL Model	Intercept	2.937	11.388	<0.001	318.433	308.433	98.2	96.5	97.4
	Distance from Shore	-0.550	71.827	<0.001					
	Percent Gravel	0.037	25.109	<0.001					
	Percent Cobble	0.060	13.127	<0.001					
	Dominant Embeddedness	-0.611	9.365	0.002					

models created (Table 11). This model indicated that the relative probability of spawning by walleye was related to distance from shore (-), depth (-), dominant substrate (+), and the embeddedness of the dominant substrate (+). Therefore, this model predicted that walleye will spawn on sites closer to shore, at shallower depths, with larger sized substrate, and higher embeddedness values.

The two other models evaluated (one from Big Crooked Lake and one from Red Cedar Lake) were also similar; the Big Crooked Model indicated that the relative probability of spawning by walleye was related to distance from shore (-), percent gravel (+), percent cobble (+), and embeddedness of the dominant substrate (-) (Table 11). The Red Cedar Model 2 indicated that the relative probability of spawning by walleye was related to distance from shore (-), percentage of gravel (+), percentage of cobble (+), and embeddedness of the dominant substrate (+) (Table 11). Therefore, both models predicted that walleye will spawn on sites closer to shore, with increasing percentages of gravel and cobble. However, the Big Crooked Model predicted walleye would spawn on sites with lower embeddedness (i.e., less fines; whereas the Red Cedar Model 2 predicted the opposite. All models had a high correct classification rate, both within lakes and across lakes (Table 12). Both models created from Red Cedar Lake correctly classified sites as used or available approximately 90% of the time when compared to actual data collected from Beaver Dam and Big Crooked Lakes. The model created from Big Crooked Lake correctly classified sites as used or available approximately 85% of the time when compared to actual data collected on Red Cedar Lake and 93% of the time from Beaver Dam Lake data.

Table 12. Transferability of resource selection models across study lakes; classification rates of each model based on actual used and available habitat data collected from Beaver Dam, Red Cedar and Big Crooked Lakes during field sampling. Values underlined indicate the correct classification rates when the model was applied to the lake where the model was developed.

		Big Crooked Lake			**Red Cedar Lake**			**Beaver Dam Lake**		
Model Name	**Variables**	**Presence**	**Absence**	**Overall**	**Presence**	**Absence**	**Overall**	**Presence**	**Absence**	**Overall**
Big Crooked Lake Model	Intercept Distance from Shore Percent Gravel Percent Cobble Dominant Embeddedness	98.20	96.50	97.40	95.90	78.70	84.50	95.80	92.30	93.20
Red Cedar Lake Model 2	Intercept Distance from Shore Percent Gravel Percent Cobble Dominant Embeddedness	86.60	95.00	92.90	93.10	87.80	89.70	91.10	91.90	91.70
Red Cedar Lake Model 1	Intercept Distance from Shore Depth Dominant Substrate Dominant Embeddedness	94.40	90.50	91.40	93.20	89.00	90.50	89.50	90.80	90.40

The best model from Red Cedar Lake (Model 1) was chosen as the final model due to the highest correct classification rates, lowest AIC value, and the ease at which variables are measured in the field compared to other variables that were measured. No models were within two to four AIC units of the Red Cedar Model 1 and therefore no alternative models were selected. When this model was applied to Beaver Dam Lake, the model predicted that the majority of the shoreline had a relatively low probability of egg deposition (Appendix F). The Red Cedar Model 1 predicted that over 80% of the littoral zone of Beaver Dam Lake had relative probability of egg deposition of only 0.1 (Figure 8). Broken down by basin, the majority (89%) of the littoral zone of the east basin had a relative low probability of egg deposition of only 0.1, with less than 6% above 0.5 (Figure 8). However, the west basin had higher probabilities of egg deposition than the east, with 77% of the littoral zone at 0.1, and approximately 15% above 0.5 (Figure 8). Approximately 70% of the natural spawning reef had a relative probability of egg deposition greater than 0.5, whereas only 8% of the total reef had a low probability of 0.1. In contrast, only 43% of the artificial spawning reef had a relative probability of egg deposition of greater than 0.5, and 37% had a low probability of only 0.1 (Figure 9).

Model Application

The Red Cedar Lake Model 3, created from Red Cedar Lake data using only gravel and cobble, was applied to the littoral zone ($\leq$ 0.485 m depth) of each study lake (Table 13). Using that model, Red Cedar Lake had the most suitable habitat for walleye (70.6% of the littoral zone at $\geq$ 0.5 relative probability of use), followed by Beaver Dam Lake (20.7%), and then Big Crooked Lake (8%) (Figure 10, Appendix H). Therefore, Beaver Dam Lake has approximately 2.5 times the spawning habitat as Big Crooked

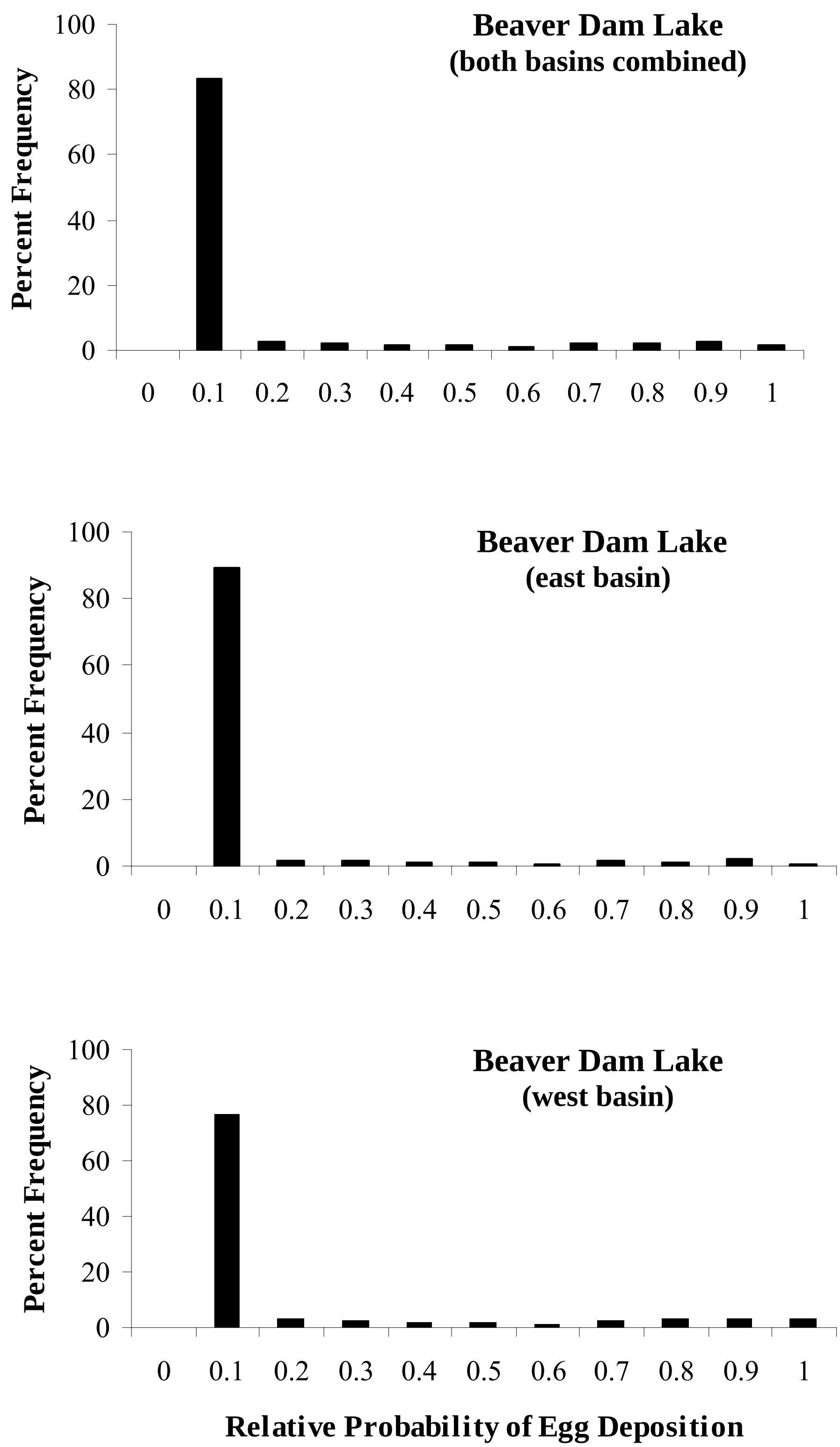


Figure 8. Relative probability of egg deposition by walleye in the littoral zone of Beaver Dam Lake as predicted by the Red Cedar Lake Model 1.

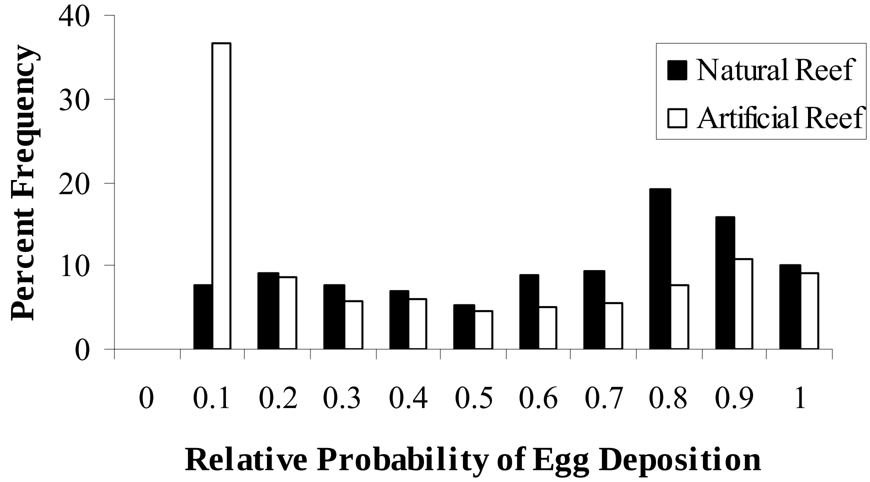


Figure 9. Relative probability of egg deposition by walleye on the artificial and natural spawning reefs located in the west basin of Beaver Dam Lake as predicted by the Red Cedar Lake Model 1.

Table 13. Application of Red Cedar Lake resource selection model containing gravel and cobble variables across study lakes; probability of use (%) calculated from actual used and available habitat data collected from Beaver Dam, Red Cedar and Big Crooked Lakes during field sampling. Models assessed only available habitat ≤0.485 m in depth based on the depth cut-off point for egg deposition (≥0.5). The same models were then applied only to available habitat ≤ 2 m from shore based on the distance cut-off point for egg deposition (≥0.5).

					Probability of Use (%)					
					Big Crooked Lake		**Red Cedar Lake**		**Beaver Dam Lake**	
Variables	**Coefficient**	**Wald Chi Sq**	**P**	**Model P**	**≥0.5**	**≥0.75**	**≥0.5**	**≥0.75**	**≥0.5**	**≥0.75**
Reduced based on depth (≤0.485 m):										
Intercept	-2.243	643.640	<0.001	<0.001	8.0	0.6	70.6	13.0	20.7	5.5
Percent Gravel	0.031	208.057	<0.001							
Percent Cobble	0.049	318.311	<0.001							
Intercept	-0.492	740.644	<0.001	<0.001	7.7	1.0	67.9	14.7	16.4	4.3
Percent Gravel	0.015	30.378	<0.001							
Percent Cobble	0.030	83.037	<0.001							
Dominant Embed.	-0.459	97.004	<0.001							
Reduced based on distance from shore (≤2 m):										
Intercept	-2.243	643.640	<0.001	<0.001	24.5	1.0	69.5	14.0	33.0	1.5
Percent Gravel	0.031	208.057	<0.001							
Percent Cobble	0.049	318.311	<0.001							
Intercept	-0.492	740.644	<0.001	<0.001	25.0	2.0	71.0	21.5	20.0	5.0
Percent Gravel	0.015	30.378	<0.001							
Percent Cobble	0.030	83.037	<0.001							
Dominant Embed.	-0.459	97.004	<0.001							

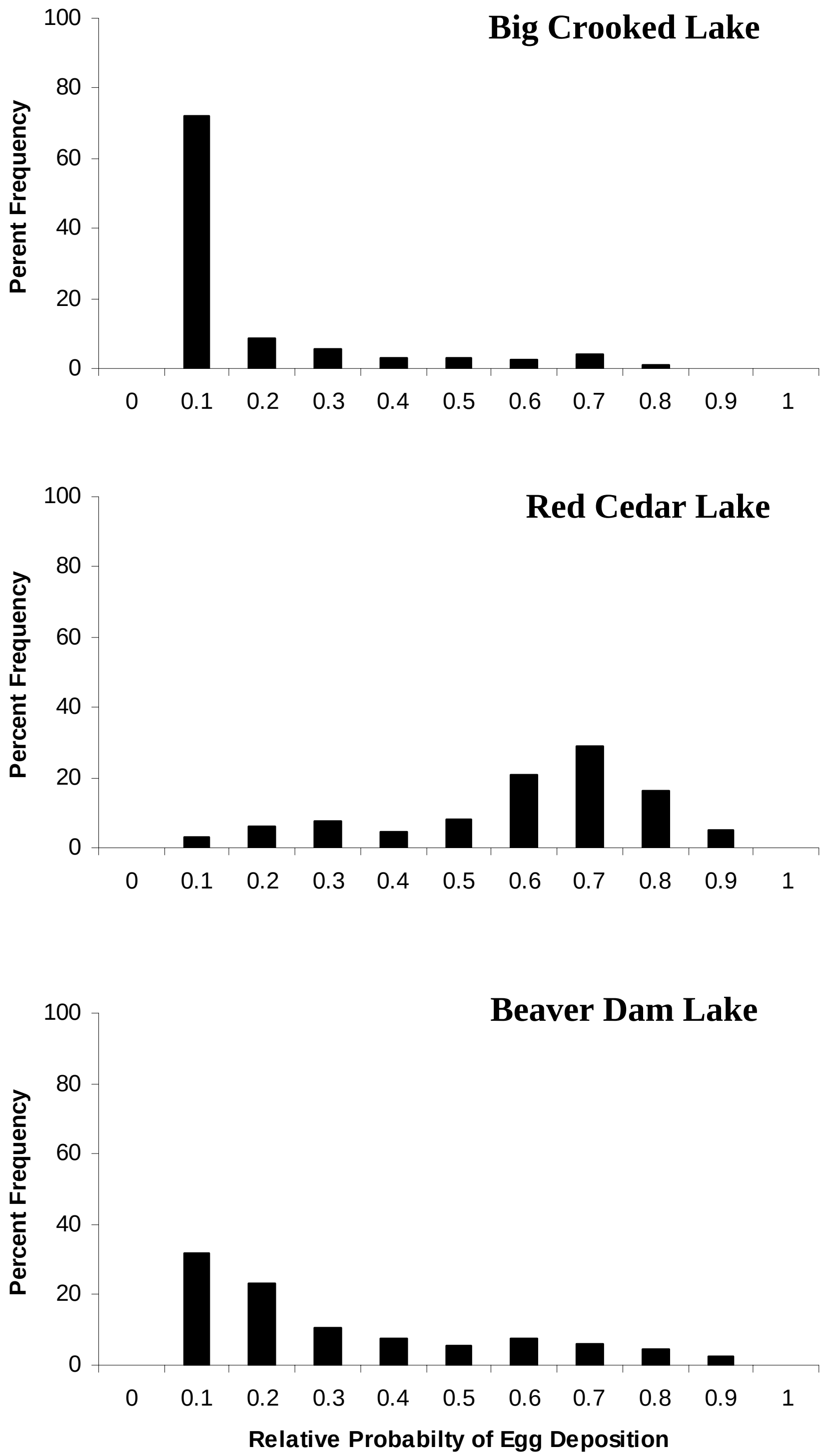


Figure 10. Relative probability of egg deposition by walleye in the littoral zone ($\leq$0.485 m depth) of Big Crooked, Red Cedar and Beaver Lakes as predicted by the Red Cedar Lake Model 3 (containing gravel and cobble variables).

Lake, and Red Cedar Lake has approximately 3.5 times the relative amount of spawning habitat in Beaver Dam Lake. The lakes rank similarly when comparing the quantity of even higher quality habitat ($\geq$ 0.75 relative probability of use); Red Cedar Lake has the most suitable spawning habitat throughout the lake (13%), followed by Beaver Dam Lake (5.5%), and then Big Crooked Lake (0.6%).

Discussion

This study found that walleye selected spawning locations close to shore and in shallow water, with steeper, rocky bottoms with greater interstitial spaces. These findings support many previous studies; Eschmeyer (1950) found that the primary spawning grounds of walleye in Lake Gogebic, Michigan, were located in the shallow water areas around the shoreline, over gravel, rubble, and boulder substrates. In Lake Winnebigoshish, Minnesota, Johnson (1961) reported walleye spawning primarily over gravel-rubble substrates and in water ranging from 0.31 to 0.76 m in depth; however, eggs were found as shallow as 0.05 m. Roseman et al. (1996) found that walleye spawning sites in Lake Erie were located in water < 3 m deep and were comprised of gravel and cobble, with little to no sand or silt; however, deeper spawning sites had higher percentages of smaller substrates. In addition, a walleye spawning study conducted on Lake Ashtabula, North Dakota, found walleye eggs only over gravel substrate, in water ranging from 0.61 to 0.76 m (Sprague 1963). Raabe (2006) found similar results in Big Crooked Lake, with walleye spawning on gravel, close to the shore and in shallow water; however, slope was relatively gradual (4%). In Big Crooked Lake walleye eggs were found within 2.7 m from shore and in water 0.29 m deep on average (Raabe 2006).

The habitat characteristics of walleye spawning sites were similar in both Beaver Dam and Red Cedar Lakes. Walleye eggs were deposited within 2 m from shore in water less than 0.35 m deep in both lakes. Egg deposition zones had a higher slope (21%) compared to the non-egg deposition sites (11%). The majority of the habitat throughout the littoral zone (out to a depth of 3 m) of both lakes consisted of small substrate (silt and sand) with high degrees of embeddedness (mean: 3.6), whereas the sites with egg deposition consisted of larger, rocky material (gravel and cobble) with lower embeddedness values (mean: 1.5). The egg collection chambers with live eggs were also located closest to shore and in the shallower water areas of the reef and contained larger substrates such as gravel, cobble and rubble. Only 12% of egg collection chambers with live eggs were dominated by smaller substrates (sand or silt), compared to the remainder of the chambers, which consisted of substrates gravel sized or larger. This may be due to the nature of broadcast spawning employed by walleye; eggs not only are deposited on gravel-cobble shoreline, but are also deposited on areas adjacent to primary spawning sites which may be comprised of less desirable substrates. However, other studies found survival rates to be greatest when eggs are deposited over rocky substrate as opposed to muck and sand (Eschmeyer 1950; Johnson 1961; Corbett and Powles 1986; Pitlo 1989; Kerr 1997). This may be due to the protection provided by rocky substrate from wave action as well as protection from entanglement in debris associated with softer substrates (Johnson 1961). In addition, walleye selected sites very close to shore in this study, which may be due to the higher oxygen levels associated with shallower water, which is correlated with increased egg survival rates (Eschmeyer 1950; Johnson 1961; Kerr 1997). The selection of spawning habitat by walleye in this study, as well as many previous studies may be related to the riverine ancestry of walleye, and that walleye may be more successful in large, shallow lakes due to increased littoral areas, which are analogous to the many oxbows, sloughs, and embayments found on large rivers (Kitchell et al. 1977).

Egg survival rates and the total number of walleye eggs collected in our egg collection chambers did not differ between lakes in 2005, but were higher on Beaver Dam Lake, the lake with low natural recruitment, compared to Red Cedar Lake, the lake with high natural recruitment in 2006. This could be an artifact of poor bucket placement in 2006 relative to the abundance of spawning habitat in Red Cedar Lake. One site chosen in Red Cedar Lake in 2006 was thought to be a site of high use by spawning walleye based on visual observations in 2005; however, this was not the case in 2006. Because approximately 70% of the near-shore sites ($\leq$ 0.485 m depth) of Red Cedar Lake are suitable for walleye to spawn on, there are greater potential spawning sites on which walleye may spawn relative to stock size. Therefore, spawning habitat is not saturated and selecting areas for egg collection chamber placement where eggs will be deposited is dependent on the density of spawning walleye. Under such conditions, a large number of egg collection chambers would be required to find more used sites. In contrast, Beaver Dam Lake has a limited area of suitable spawning habitat (20%), thus concentrating spawning walleye. Therefore, the chance of choosing potential spawning sites for egg collection chambers placement was greater.

The best models created in this study were comprised of factors expected to influence spawning site selection based on previous studies regarding spawning characteristics: shallow water, close to shore, and high amounts of gravel and cobble. Embeddedness was also an important factor in our models, however, whether higher or lower embeddedness values helped to predict site selection varied between models. Two models developed from Red Cedar Lake (e.g., Red Cedar Lake Models 1 and 2) both predicted that higher embeddedness values would increase the probability of walleye spawning on a given site. Interestingly, the resource selection function for Red Cedar Lake showed walleye selected for substrates with higher embeddedness whereas in Big Crooked Lake they selected for sites with lower embeddedness. This phenomenon is an artifact of modeling habitat selection. While walleye spawn on gravel and cobble with low embeddedness overall, the availability of these habitats dictate the actual selection. In Red Cedar Lake, most available sites had lower embeddedness values overall whereas Big Crooked available sites had higher embeddedness overall, thus suggesting that walleye in Big Crooked Lake spawned on lower quality sites because that is what was most available. It may also suggest that walleye choose substrate based on the primary substrate size present. Survival may depend on level of embeddedness but not selection.

All three models used in this study had high overall rates of correct classification ($\geq$ 90%) and were highly transferable; they correctly classified walleye spawning sites when applied to the other two study lakes $\geq$ 87% of the time. These results illustrate both the applicability of these models to other systems as well as the accuracy of the predicted spawning probabilities throughout Beaver Dam Lake. When the best model created from Red Cedar Lake was applied to Beaver Dam Lake, the majority of the littoral zone was unsuitable for walleye spawning. In the west basin, the “better” of the two basins, the majority of sites had a relative probability of egg deposition of less than 0.5 (usually

≤ 0.1). The east basin was found to be even less suitable than the west basin, with $\geq 90\%$ of the littoral zone having a relative probability of egg deposition of less than 0.5.

It is unknown specifically what area or percentage of suitable spawning habitat is necessary to support natural walleye recruitment in north temperate lakes. However, comparing habitat characteristics of Red Cedar and Big Crooked Lakes, lakes both having high natural walleye recruitment, to Beaver Dam Lake, can provide insight into the differences driving recruitment between lakes. Using the reduced gravel-cobble model created from Red Cedar Lake and applied only to quadrats ≤ 0.485 m in depth, (where the probability of use is high at ≥ 0.5) approximately 70% of the littoral zone of Red Cedar Lake was suitable, compared to 20% on Beaver Dam Lake. In contrast, Big Crooked Lake had a relative probability of use ≥ 0.5 in only 8% of the littoral zone. Comparatively, there is much more suitable spawning habitat available to walleye in Beaver Dam Lake when compared to Big Crooked Lake, yet the 8% of suitable habitat in Big Crooked Lake is sufficient to sustain a high naturally recruiting walleye population. Moreover, 20% of the habitat in Beaver Dam Lake has relative probability of use of ≥ 0.5, most of it occurs along a narrow margin of the lake which is the egg deposition area of walleye. However, because this area is narrow, slight fluctuations in water elevation might render this habitat inaccessible at times. In fact, the water level in Beaver Dam Lake dropped during the 2005 spawning season drying much of the higher quality sites. While we cannot determine exactly how much suitable habitat is necessary to sustain natural reproduction, 8% is clearly enough in Big Crooked Lake. And because the littoral zone of Beaver Dam Lake has over twice that of Big Crooked Lake, there clearly are other factors affecting the walleye population in the lake besides habitat availability, therefore constructing additional spawning reefs would likely not increase walleye recruitment.

The existing artificial spawning reef in Beaver Dam Lake was also evaluated to determine the use by walleye and to assess overall suitability of Beaver Dam Lake for walleye spawning. The best model from Red Cedar Lake predicted that the majority (70%) of the natural spawning reef in Beaver Dam Lake had a relative probability of egg deposition of 0.5 or greater and therefore the probability of walleye spawning on this reef was relatively high. In addition, 60% of the egg collection chambers buried on the natural spawning reef contained at least 10 walleye eggs. This reef is primarily comprised on gravel and cobble and is located in depths ranging from 0 to 0.8 m. When the same model was applied to the artificial spawning reef (comprised primarily of sand, gravel and cobble, located in depths ranging from 0 to 2 m) only 43% of the artificial spawning reef had a relative probability of use of > 0.5 and less than 25% of the egg collection chambers buried on the artificial spawning reef contained $\geq$ 10 eggs in both years.

And while the artificial spawning reef was utilized by walleye during the spawning season, the reef was constructed in a manner that does not mimic natural spawning habitat within either Beaver Dam or Red Cedar or Big Crooked Lakes; moreover the majority of the reef is unsuitable for walleye spawning. The size and location of the artificial spawning reef relative to the natural spawning reef in Beaver Dam Lake were considerably different. These differences correspond to two of the major variables in our model used to predict spawning potential: distance from shore and water depth. On the natural spawning reef in Beaver Dam Lake, rocky (gravel-cobble) substrate was present beginning at the shoreline-water interface (i.e., there was no space between the shoreline-water interface and the beginning of the reef). This shallow, near-shore area was used most frequently by spawning walleye in all study lakes. Many previous studies also found the primary spawning sites of walleye to be located in these shallow water areas (Eshcmeyer 1950; Johnson 1961; Sprague 1963). The artificial spawning reef had many “gaps”; when the artificial spawning reef was constructed along the shoreline; however there were many points were the rocky reef material did not abut the shoreline resulting in pockets of silt and sand. These gaps have also filled with additional sediment and detritus, potentially decreasing the survival of any eggs that were deposited on the rocky portions of the reef, then brought in closer to shore due to wave action. This phenomenon has been documented in several previous studies; intense wind and wave action can cause walleye eggs to be washed into less desirable habitats (Eschmeyer 1950; Johnson 1961; Roseman et. al 2001; Raabe 2006). This perhaps emphasizes the importance of the steeper slopes of natural spawning areas; steeper slopes allow finer materials to be carried offshore. The deep-water or outer edges of the natural spawning reef fall within 4 m from the shore and in water less than 0.80 m deep. In contrast, the majority of the outer edge of the artificial spawning reef was located between 12 and 16 m from the shore and in water ranging from 0.60 to1.85 m in depth. The majority of this reef was constructed in a location that is predicted by our model to have low spawning probabilities (relative probability of use ≤ 0.5). In addition, the majority of the artificial spawning reef was not utilized by walleye during either study year. Approximately 90% of the walleye eggs deposited on the artificial spawning reef were located within 2 m from shore and in water less than 0.32 m deep. This is similar to the location of approximately 90% of the eggs on the natural spawning reef in Beaver Dam Lake, which were also deposited within 2 m from shore, in water less than 0.50 m deep. Therefore, the artificial spawning reef constructed in Beaver Dam Lake did not mimic natural spawning habitat within the same lake and the majority of the reef can be categorized as poor walleye spawning habitat.

Previous studies support our findings on the overall ineffectiveness of artificial walleye spawning reefs. A study conducted by Neuswanger and Bozek (2004) evaluated artificial spawning reefs in 20 northern Wisconsin lakes and found that walleye reproduction did not increase in 17 of the 20 study lakes. In the remaining three study lakes, the results were inconclusive; therefore the success of those artificial spawning reefs was also inconclusive. In Lake Osakis, Minnesota, an evaluation found that egg survival and fry production on an artificial spawning reef in the lake was lower than that of the main natural spawning reef in the same lake, and that the artificial spawning reef did not lead to a significant increase in production (Newburg 1976). A study on three North Dakota reservoirs found that in two of the reservoirs with artificial spawning reefs, water levels dropped which resulted in reefs being completely out of the water, and in the third reservoir, live walleye eggs were collected on the artificial spawning reef. However, numbers were low (517 eggs over two study years) and no survival beyond the egg stage was observed (Sprague 1963). McKnight (1975) recorded eyed walleye eggs on artificial spawning reefs in Jennie Webber Lake, Wisconsin; however, no fry, fingerlings, or adult walleye were taken during meter netting, seining, and electrofishing surveys. A riverine study, conducted in the Current River, Ontario, found similar results; after a five-fold increase in the amount of walleye spawning habitat was constructed by adding gravel, cobble and boulders in three shallow water areas of the river, neither total walleye egg deposition or adult walleye abundance were increased (Geiling 1996).

The poor success rate of artificial spawning reefs may be due in part to construction that may not mimic natural spawning areas; this is part of the reason why the artificial spawning reef in Beaver Dam Lake does not do well. But poor success may also be due to other factors in lakes that may limit recruitment such as poor water quality, poor spring weather conditions, unfavorable lake basin morphometry, low productivity, prey availability and fish community structure (Neuswanger and Bozek 2004). A study conducted by Nate et al. (2003) identified physical features in northern Wisconsin lakes that were conducive to self-sustaining walleye populations, which included surface area, fetch and mean depth, in addition to features that precluded recruitment such as the amount of sand and muck present.

Fish community structure may also affect the success of walleye in a system. High walleye and muskellunge densities were features that were conducive to self-sustaining walleye populations (Nate et al. 2003). According to Nate et al. (2003) successful walleye stocking may depend on both the physical features of a lake (large, deep, with gravel bottom) and favorable fish communities (muskellunge, but not largemouth bass or northern pike). Walleye and northern pike do not generally coexist at high densities in smaller lakes (Johnson et al. 1977), possibly due to northern pike reducing the prey of walleyes (Colby et al. 1987). Largemouth bass also appear to negatively affect walleye populations and can limit the success of stocked walleye due to predation (Fayram et al. 2005).

Prey availability also affects walleye recruitment (Forney 1976; Ritchie and Colby 1988; Johnson et al. 1996; Madenjian et al. 1996). High abundance of a primary prey item of walleye can result in high walleye recruitment (Madenjian et al. 1996), as well as age-0 walleye abundance and subsequent year-class strength (Ritchie and Colby 1988). High prey abundance may also increase the consumption of these prey items by juvenile walleye allowing them to grow out of their vulnerable size quicker, making them less susceptible to predation, thus increasing year classes (Johnson et al. 1996). In contrast, low abundance of prey can negatively affect recruitment by leading to an increase in predation and cannibalism (Forney 1976). In addition to prey availability, predation also affects recruitment; the majority of larval walleye mortality in Oneida Lake was due to predation by yellow perch and older walleye (Forney 1976). On Lake Mendota, in south-central Wisconsin, predation also appeared to be an important factor in recruitment, and as predator biomass increased, the consumption of young walleye also increased (Johnson et al. 1996). In Escanaba Lake, Wisconsin, both intraspecific competition with walleye and interspecific competition with yellow perch influenced the number of age-0 walleye present after their first summer (Hansen et al. 1998).

Management Summary

This study showed that the majority of the substrate in the littoral zone of Beaver Dam Lake is not rocky; rather it's comprised primarily of sand and muck. To facilitate natural reproduction of walleye, the Beaver Dam Lake Management District built an artificial spawning reef and sought advice regarding the placement of an additional reef. However, even with the limited spawning habitat Beaver Dam Lake has, it contains more than twice the amount of suitable spawning habitat than Big Crooked Lake, a lake with consistently high natural walleye reproduction and recruitment. Therefore, increasing the amount of suitable spawning habitat by adding additional artificial spawning reefs in Beaver Dam Lake would likely still not result in a successful naturally reproducing walleye population. Artificial spawning reefs should not be expected to increase walleye reproduction in lakes where increase walleye recruitment after stocking was not overly successful. In these cases, other factors besides spawning habitat are affecting survival beyond the egg stage. According to our base models, only 8% of the shoreline of Big Crooked Lake is suitable for walleye spawning; however, this lake has consistent and high walleye recruitment. Beaver Dam Lake has 2.5 times more suitable spawning habitat than Big Crooked Lake yet has little to no natural recruitment. Therefore, when attempting to manage for walleye, all factors should be considered because spawning habitat may not be the limiting factor and simply constructing artificial spawning reefs is no guarantee of success. Other factors clearly can affect recruitment of walleye in Beaver Dam Lake including perhaps spring water level fluctuations that may strand spawning areas and the fish community already present in the lake. The adult walleye population in Beaver Dam Lake is relatively low (1.73/ha), and the fish community contains largemouth bass and northern pike, species shown to be detrimental to walleye populations (Johnson et al. 1977; Colby et al. 1987; Fayram et al. 2005). In these cited studies, smaller lakes with these species compositions often make them incompatible for the successful establishment and sustained recruitment of walleye, which may be occurring in Beaver Dam Lake. Due to current evidence supporting the lack of success of artificial spawning reefs, it is recommended that construction of these reefs be suspended. Identifying the precise factors limiting walleye survival and recruitment would be beneficial, but changes in fish community structure can be difficult, and if achieved may have other unwanted consequences.

This study provides quantitative data useful for evaluating walleye spawning habitat in north-central Wisconsin lakes. Walleye selected sites comprised of primarily gravel and cobble in shallow near-shore areas in all study lakes and resulting models are transferable to other systems, and can accurately predict the relative quality of spawning sites in a lake. Individual components of these models are useful in helping lake managers make informed decisions about the quality of spawning habitat in a lake and also aid in the understanding and identification of natural walleye habitat, which can help protect natural spawning sites within a system. These models can also aid in decisions regarding the potential need for artificial spawning reefs as a walleye management tool, and in the future, be used as a tool to construct artificial spawning reefs more precisely to reflect natural spawning habitat, thereby maximizing both their potential for use by spawning walleyes and their cost effectiveness.

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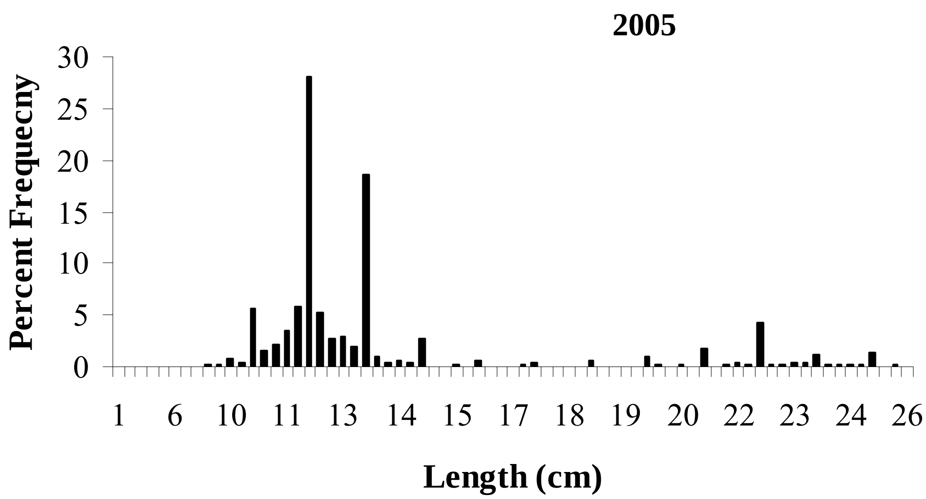
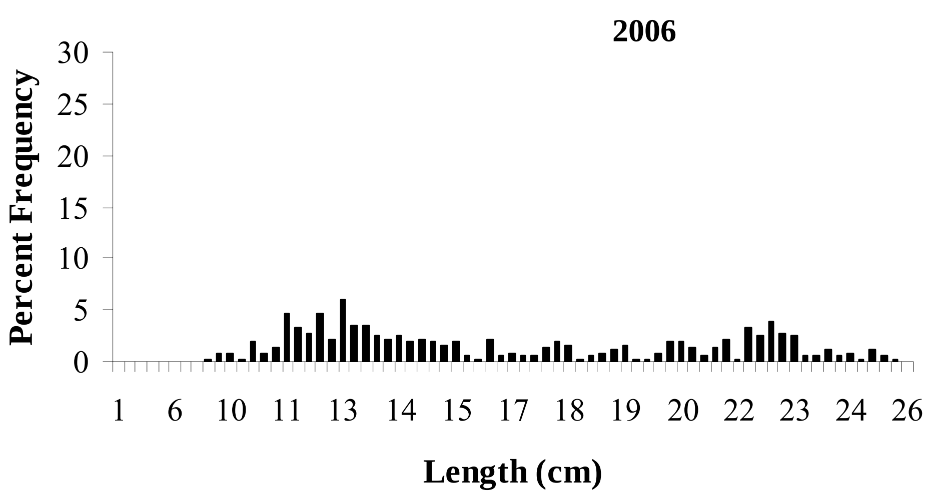
Appendix A. Wisconsin Department of Natural Resources Walleye Management Classification System (Hewett and Simonson 1998). "Possible Regulation Options" are management options suggested by the Wisconsin Department of Natural Resources based on lake category and "Predicted Outcome" is what is expected to occur based on management options implemented.

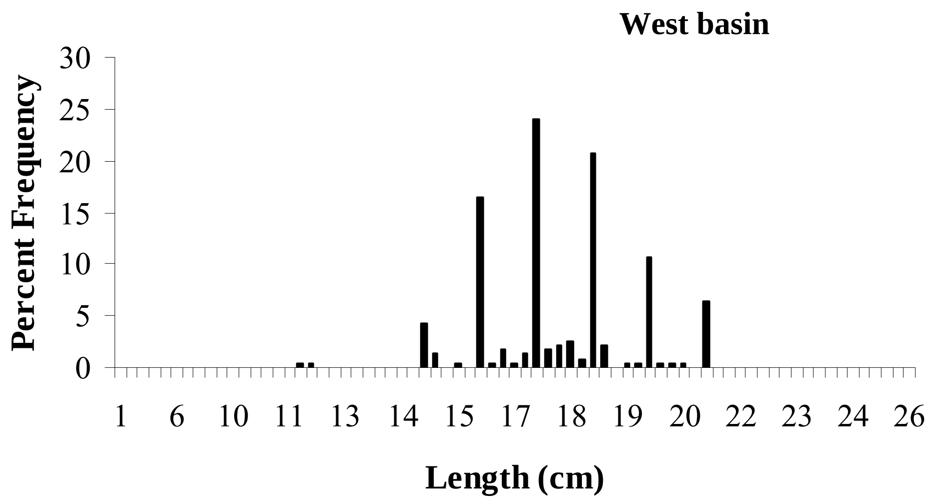
Category	**Classification**	**Possible Regulation Options**	**Predicted Outcome**
Natural Reproduction Waters			
1	Remnant, low density	-Discontinue walleye management -28" minimum length limit, 1 bag	-Shift in top predator -Increase adult density
2	Recovering/ Declining	-15" minimum length limit, 3 bag -18" minimum length limit, 3 bag	-Increase adult density, catch rates and harvest quality of fish
3	Sustainable	-No minimum length limit, 5 bag -1 over 14", 3 bag -14"-18" protected slot, 3 bag but only 1 over 18"	-Optimize harvest and maintain adult density
4	Trophy, low density, community restoration	-28" minimum length limit, 1 bag	-Improve/maintain adult density and size structure -Increase predator density to help restore balance community
Stocked Waters			
A	Stocked fishery	-15" minimum length limit, 3 bag -18 minimum length limit, 3 bag	-Maintain stocked fishery
B	-Community restoration -Establish self-sustaining fishery -or trophy	-28" minimum length limit, 1 bag	-Increase predator density -Increase adult density to maximize potential for natural reproduction

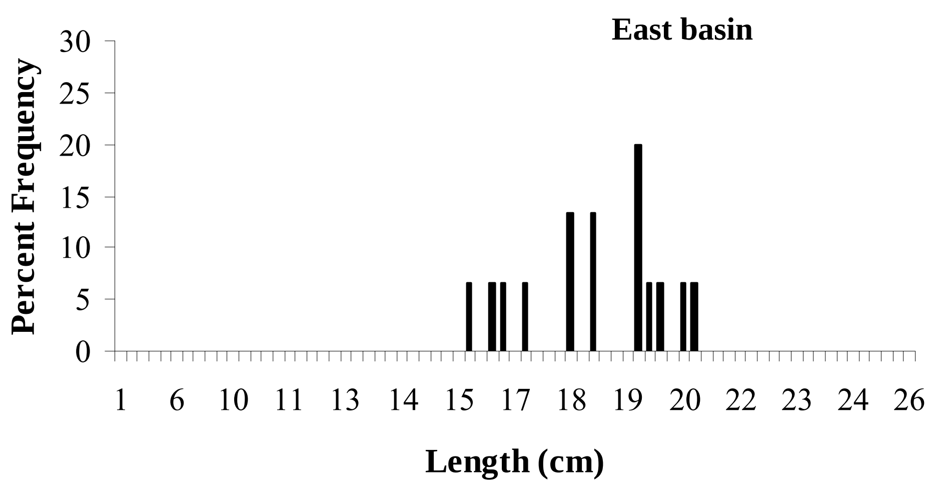
Appendix B1. Length Frequencies.
Length frequencies of walleye electrofished in Red Cedar Lake, September-October, 2005 and 2006 (2005, n=2217; 2006, n=365). Note the bimodal length distribution separating the two year classes.





Appendix B2. Length Frequencies.
Length frequencies of walleye electrofished in Beaver Dam Lake, September-October, 2005 (west basin of Beaver Dam 2005, n=237; east basin of Beaver Dam 2005, n=15). No young-of-year walleye were electrofished in either basin of Beaver Dam Lake in 2006. Note the lack of a bimodal length distribution separating year classes.





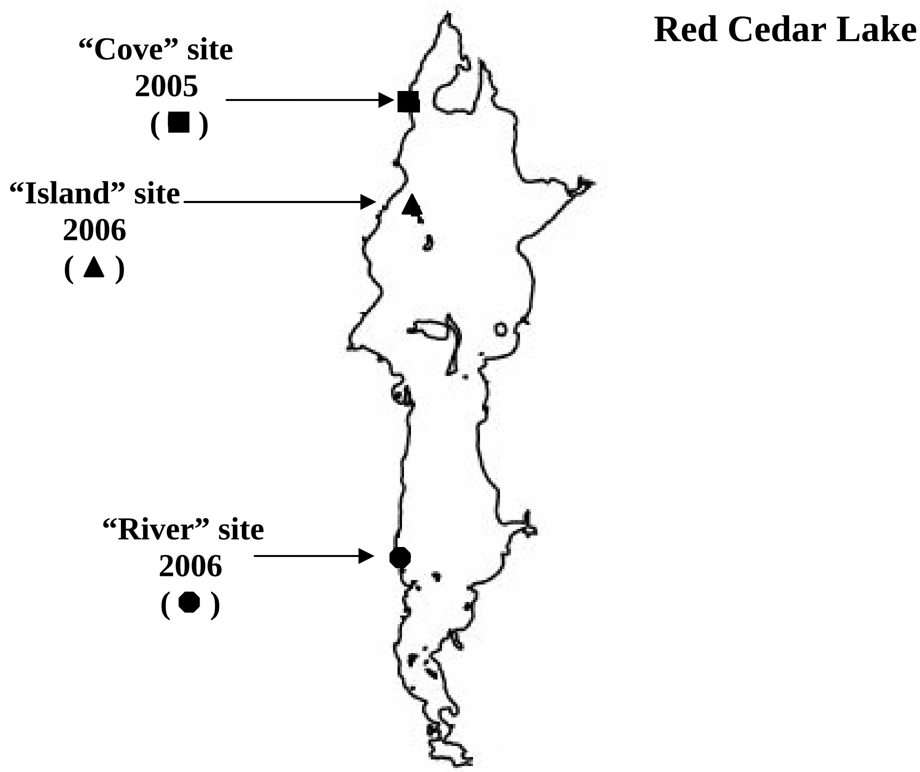
Appendix C1. Young-of-year Population Estimates.
Percentage of actual YOY walleye that were produced from natural reproduction in study lakes. Approximately 50 young-of-year walleye were sampled by the Wisconsin Department of Natural Resources (WDNR) from several lakes throughout Barron County, including Beaver Dam and Red Cedar Lakes, to determine the percentage of stocked fish based on the presence or absence of oxytetracycline (OTC) marks on otoliths. Walleye with OTC marks in Beaver Dam Lake were the result of a fall stocking event by the WDNR and walleye with OTC marks in Red Cedar Lake were the result of a portable walleye hatchery on-site at the lake. No young-of-year walleye were electrofished in either basin of Beaver Dam Lake in 2006.

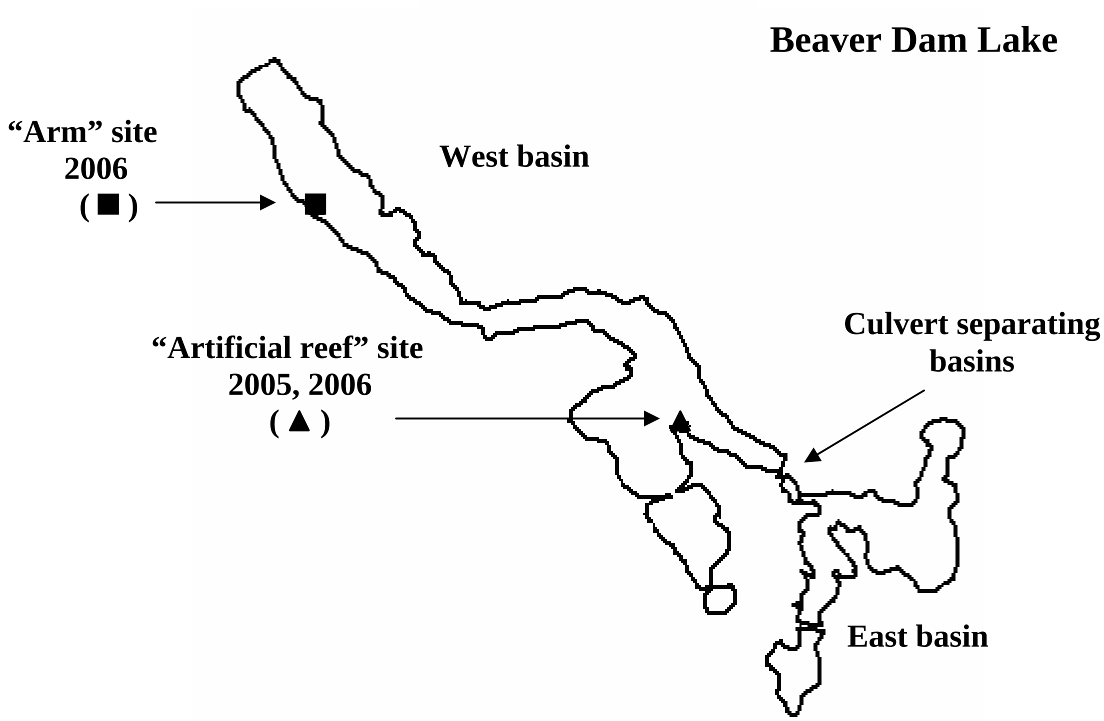
Lake	**Year**	**# Read**	**# Marked (Stocked)**	**# Unmarked (wild)**	**% Wild**
Red Cedar Lake	2005	49	4	45	91.84
Red Cedar Lake	2006	51	37	14	27.45
Beaver Dam Lake	2005	37	34	3	8.11

Appendix C2. Young-of-year Population Estimates.
Walleye young-of-year population estimates for Red Cedar and Beaver Dam Lakes. Initial population estimate, 95% confidence intervals, proportion of age 0 walleye based on scale readings and proportion of wild walleye based on presence of oxytetracycline marks also reported.

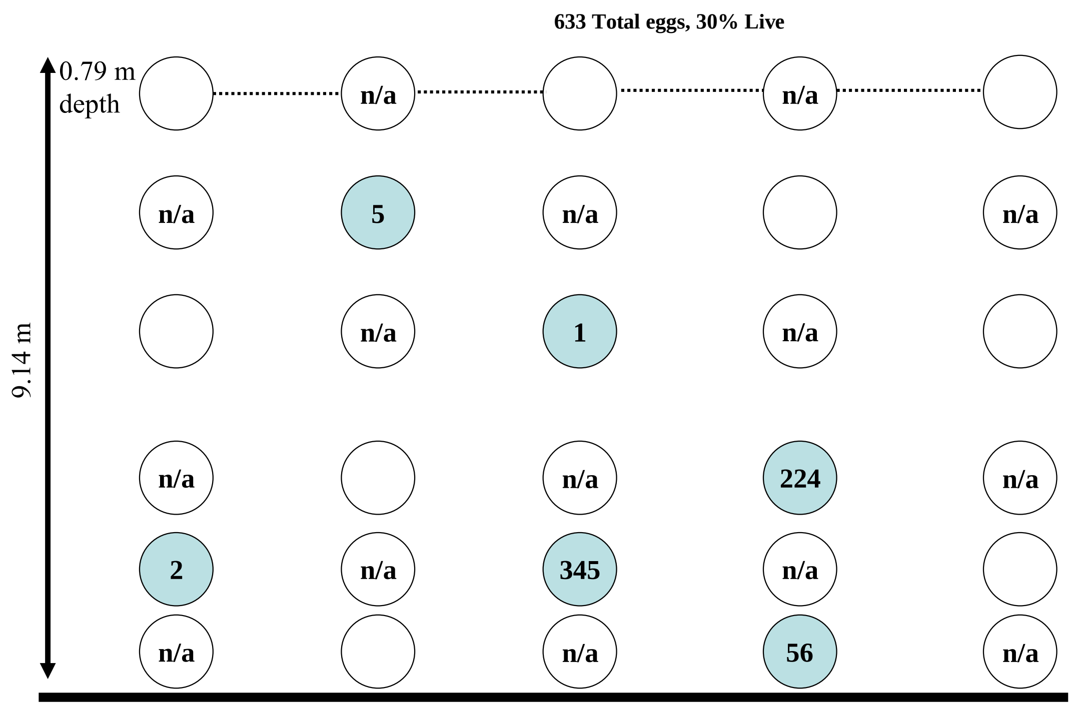
Lake	**Year**	**Population Estimate (< 228 mm)**	**95% Confidence Interval**		**Proportion of Age 0**	**Proportion of Wild , Age 0 (Final Estimate)**
			Lower	**Upper**		
Red Cedar Lake	2006	2,104	1,406	3,314	1,823	1,678
Red Cedar Lake	2005	13,971	11,710	17,315	3,269	11,140
Beaver Dam Lake (both basins)	2006	N/A	N/A	N/A	N/A	N/A
Beaver Dam Lake (west basin)	2005	1,188	731	2,066	1,030	82
Beaver Dam Lake (east basin)	2005	N/A	N/A	N/A	N/A	N/A

Appendix D. Egg Collection Chamber Locations.
Locations of egg collection chambers and corresponding site names. Reefs on which egg collection chambers were buried are indicated by circles on map.

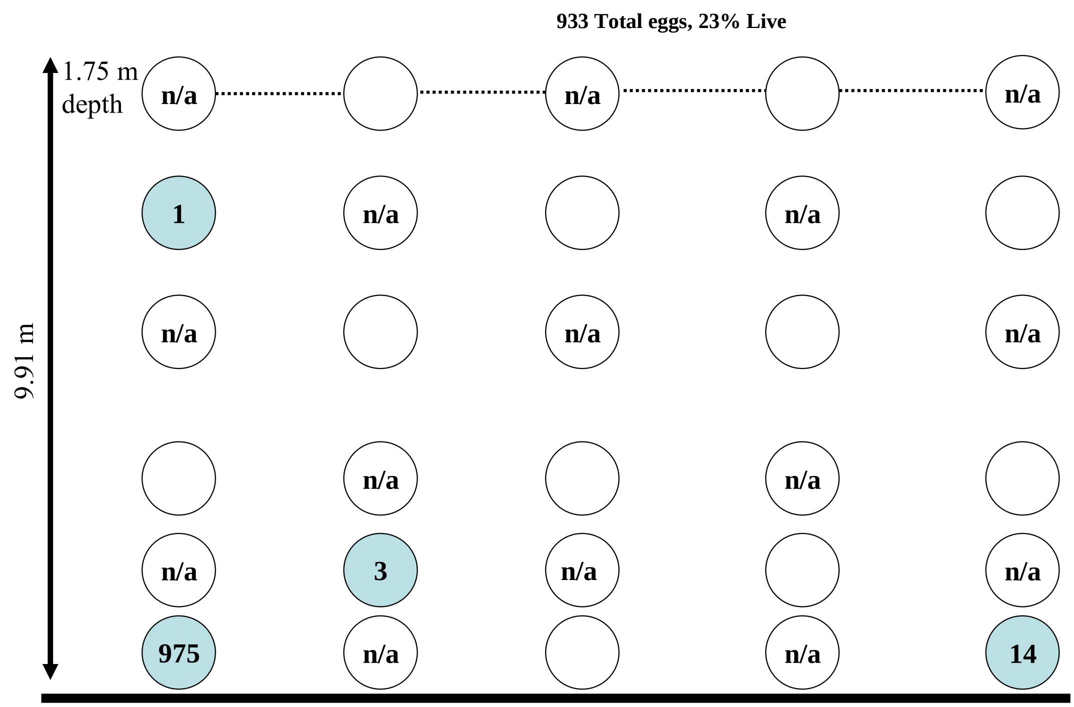




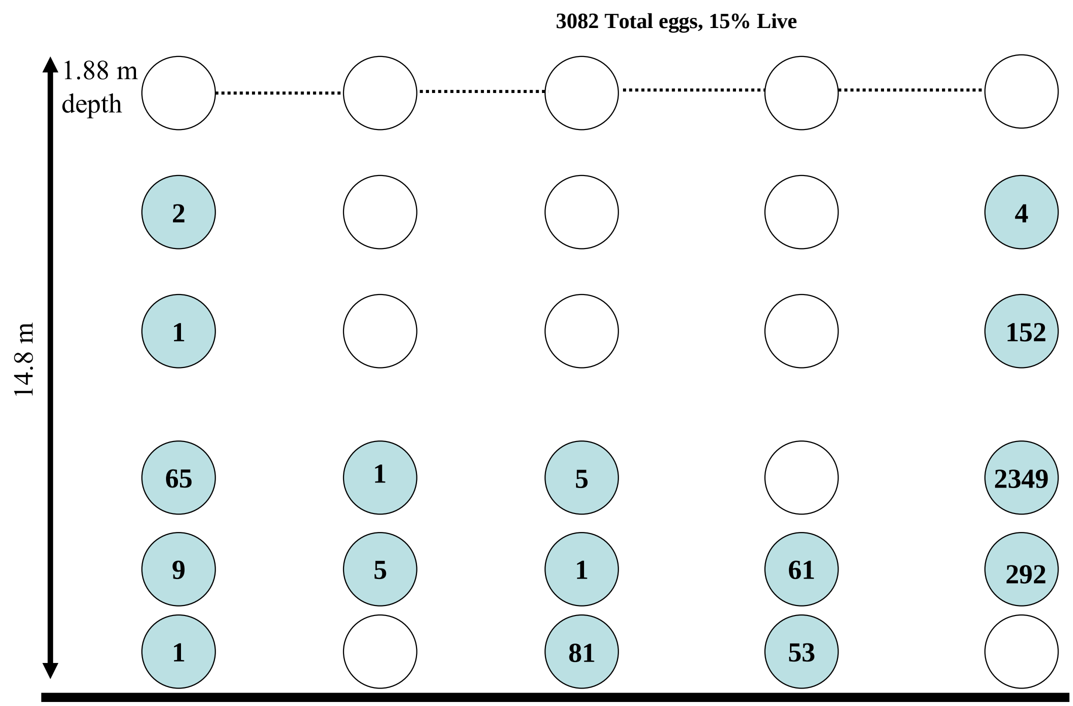
Appendix E1. Egg Collection Chambers.
Configuration of egg collection chambers buried in the substrate on the artificial spawning reef in Beaver Dam Lake, 2005. In 2005, half of the egg collection chambers were covered in an attempt to quantify fry. Because those egg collection chambers were covered and left in place, the numbers of eggs as well as egg survival rates were not quantified (labeled "n/a"). The numbers in the egg collection chambers are of the total live eggs present at the time of counting (also indicated by the darker shade). Egg collection chambers without numbers did not contain any eggs (live or dead).



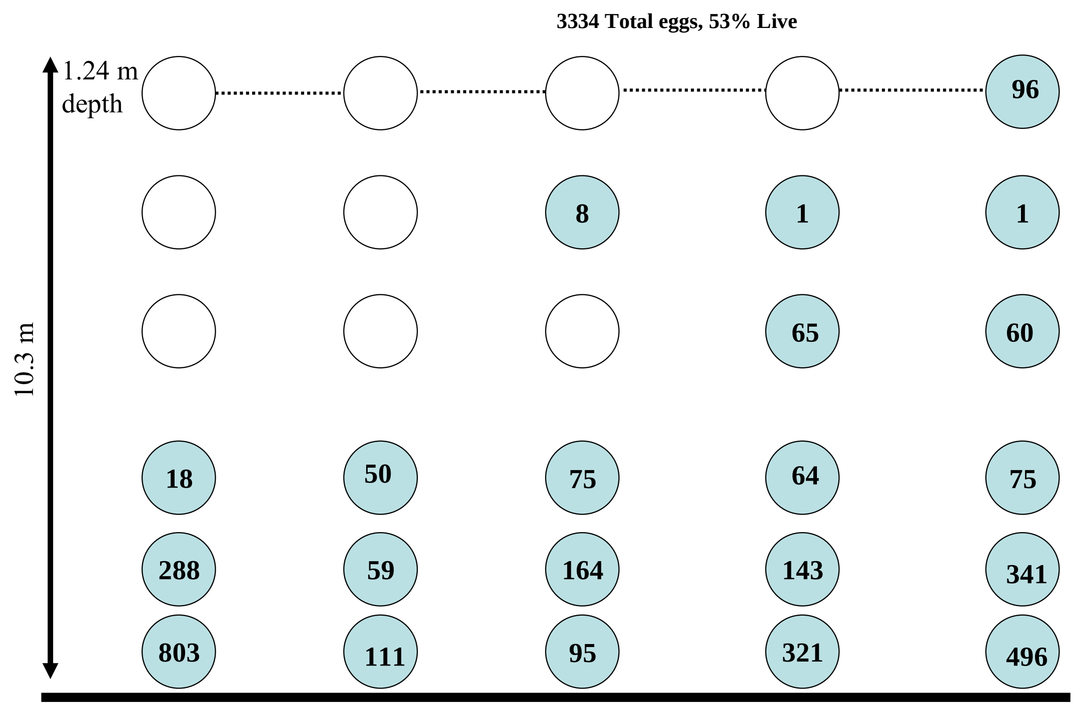
Appendix E2. Egg Collection Chambers.
Configuration of egg collection chambers buried in the substrate at the cove site in Red Cedar Lake in 2005. In 2005, half of the egg collection chambers were covered in an attempt to quantify fry. Because those egg collection chambers were covered and left in place, the numbers of eggs as well as egg survival rates were not quantified (labeled "n/a"). The numbers in the egg collection chambers are of the total live eggs present at the time of counting (also indicated by the darker shade). Egg collection chambers without numbers did not contain any eggs (live or dead).



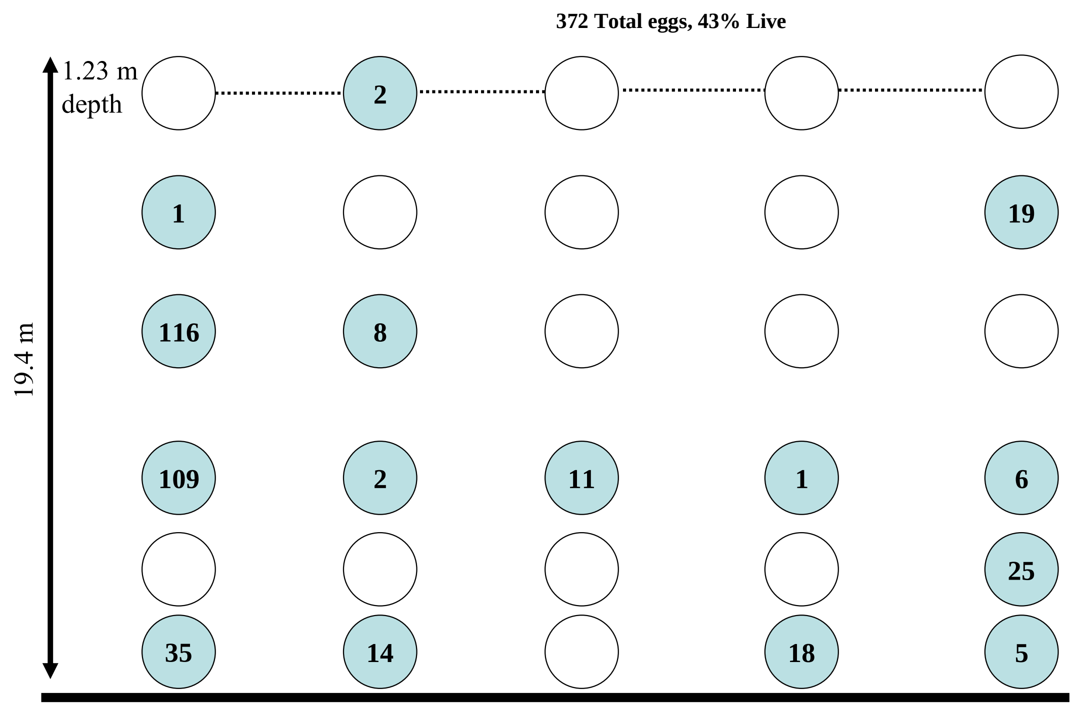
Appendix E3. Egg Collection Chambers.
Configuration of egg collection chambers buried in the substrate on the artificial spawning reef in Beaver Dam Lake, 2006. The numbers in the egg collection chambers are of the total live eggs present at the time of counting (also indicated by the darker shade). Egg collection chambers without numbers did not contain any eggs (live or dead).



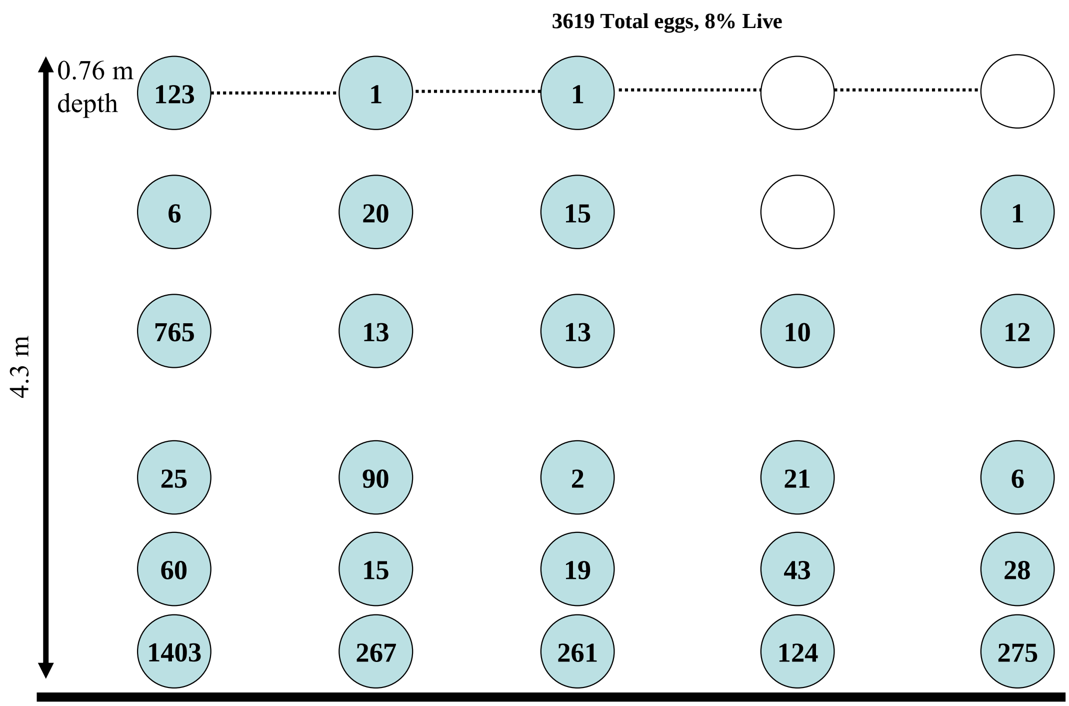
Appendix E4. Egg Collection Chambers.
Diagram of egg collection chambers buried in the substrate at the arm site in Beaver Dam Lake, 2006. The numbers in the egg collection chambers are of the total live eggs present at the time of counting (also indicated by the darker shade). Egg collection chambers without numbers did not contain any eggs (live or dead).



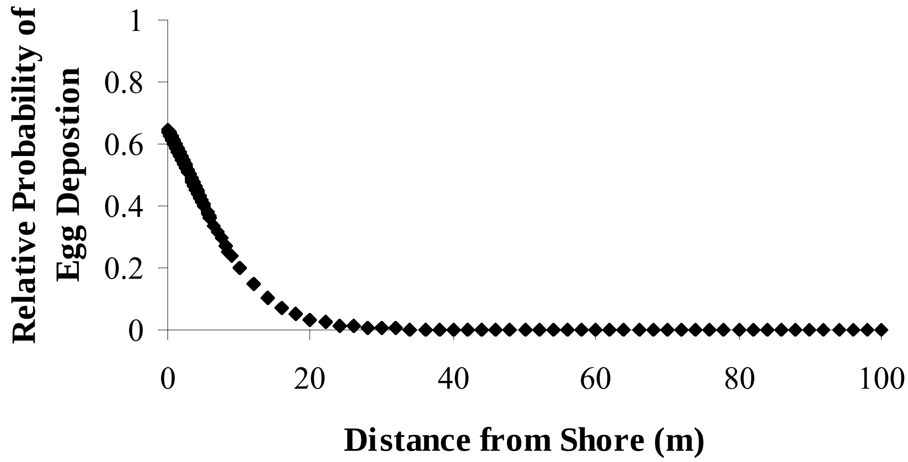
Appendix E5. Egg Collection Chambers.
Configuration of egg collection chambers buried in the substrate at the island site in Red Cedar Lake, 2006. The numbers in the egg collection chambers are of the total live eggs present at the time of counting (also indicated by the darker shade). Egg collection chambers without numbers did not contain any eggs (live or dead).

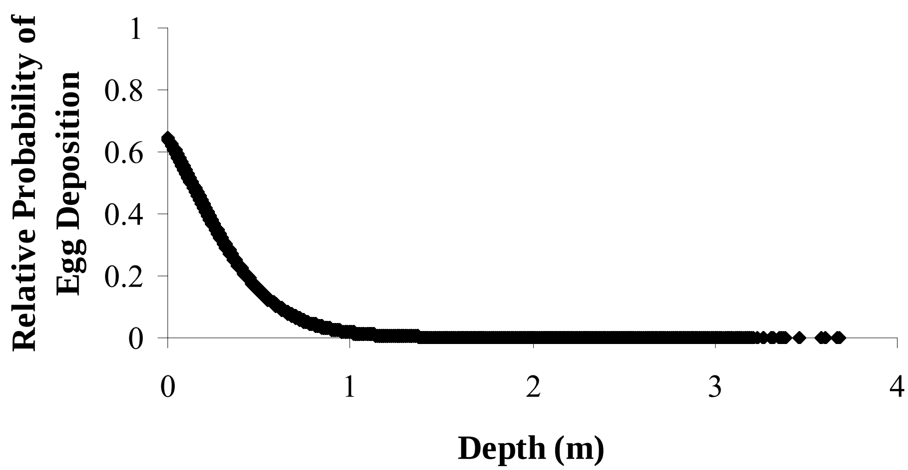


Appendix E6. Egg Collection Chambers.
Configuration of egg collection chambers buried in the substrate at the river site in Red Cedar Lake, 2006. The numbers in the egg collection chambers are of the total live eggs present at the time of counting (also indicated by the darker shade). Egg collection chambers without numbers did not contain any eggs (live or dead).

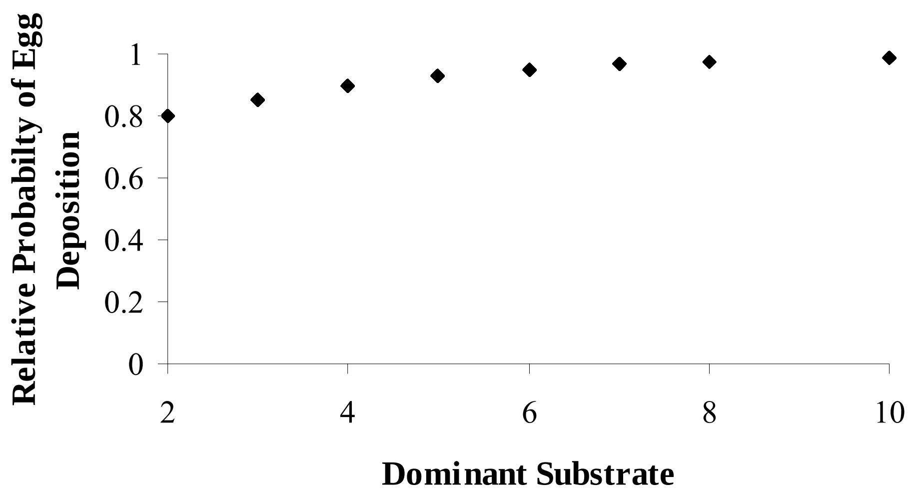


Appendix F1. Model Development.
Relative probability of egg deposition based on first two variables from the Red Cedar Lake Model 1; distance from shore and water depth.





Appendix F2. Model Development.
Relative probability of egg deposition based on second two variables from the Red Cedar Lake Model 1; dominant substrate and embeddedness of the dominant substrate at a given site.



Appendix G1. Model Application.

To determine the effect of depth and distance to shore in each of the resource selection functions, as well as to determine the influence of each variable on the results, models were created in addition to the "final" models. The best models are included below, then the final models with depth and distance from shore removed, to eliminate variables that were similar between study lakes. Dominant embeddeness was also removed from the final models to examine the models with only substrate variables included. Univariate models were created from each significant variable collected in the field, and additional significant models (not based on final models) were created to further examine the affects of each variable.

								Predicted % Classification		
Model Name	**Variables**	**Coefficient**	**Chi Sq**	**P**	**Model P**	**AIC**	**Log L**	**Presence**	**Absence**	**Overall**
Final models										
RCL Model 1	Intercept	0.605	2.036	0.154	<0.001	1204.556	1194.556	93.2	89.0	90.5
	Distance from Shore	-0.198	12.193	<0.001						
	Depth	-4.607	75.908	<0.001						
	Dominant Substrate	0.389	23.464	<0.001						
	Dominant Embed.	0.313	22.412	<0.001						
RCL Model 2	Intercept	0.685	6.092	0.014	<0.001	1299.096	1289.096	93.1	87.8	89.7
	Distance from Shore	-0.708	288.100	<0.001						
	Percent Gravel	0.014	15.576	<0.001						
	Percent Cobble	0.013	9.394	0.002						
	Dominant Embed.	0.317	20.546	<0.001						
BCL Model	Intercept	2.937	11.388	<0.001	<0.001	318.433	308.433	98.2	96.5	97.4
	Distance from Shore	-0.550	71.827	<0.001						
	Percent Gravel	0.037	25.109	<0.001						
	Percent Cobble	0.060	13.127	<0.001						
	Dominant Embed.	-0.611	9.365	0.002						

								Predicted % Classification		
Model Name	**Variables**	**Coefficient**	**Chi Sq**	**P**	**Model P**	**AIC**	**Log L**	**Presence**	**Absence**	**Overall**
Bivariates based on final models										
RCL Model 1	Intercept	-2.204	911.324	<0.001	<0.001	2361.249	2355.250	70.5	77.3	75.3
	Dominant Substrate	0.683	104.692	<0.001						
	Dominant Embed.	-0.453	266.270	<0.001						
RCL Model 2	Intercept	-2.243	643.640	<0.001	<0.001	2628.933	2622.930	56.6	83.4	70.1
	Percent Gravel	0.031	208.057	<0.001						
	Percent Cobble	0.049	318.311	<0.001						
BCL Model	Intercept	-3.163	1993.945	<0.001	<0.001	784.644	778.644	93.1	92.6	92.9
	Percent Gravel	0.079	1265.875	<0.001						
	Percent Cobble	0.079	147.341	<0.001						
Trivariates based on final models										
RCL Model 1	Intercept	0.712	2049.509	0.087	<0.001	1246.884	1217.065	92.5	88.8	90.1
	Depth	-6.082	1138.185	<0.001						
	Dominant Substrate	0.274	19.166	<0.001						
	Dominant Embed.	0.410	32.009	<0.001						
RCL Model 2	Intercept	0.024	1984.888	0.950	<0.001	1289.686	1281.686	92.4	87.6	89.3
	Distance from Shore	-0.652	1073.563	<0.001						
	Dominant Substrate	0.358	15.076	<0.001						
	Dominant Embed.	0.235	26.474	<0.001						

								Predicted % Classification		
Model Name	**Variables**	**Coefficient**	**Chi Sq**	**P**	**Model P**	**AIC**	**Log L**	**Presence**	**Absence**	**Overall**
RCL Model 2	Intercept	-0.492	740.644	<0.001	<0.001	2533.930	2525.930	60.0	79.7	72.8
	Percent Gravel	0.015	30.378	<0.001						
	Percent Cobble	0.030	83.037	<0.001						
	Dominant Embed.	-0.459	97.004	<0.001						
BCL Model	Intercept	-0.417	2024.813	<0.001	<0.001	755.776	747.776	95.3	92.6	94.0
	Percent Gravel	0.062	172.055	<0.001						
	Percent Cobble	0.048	26.230	<0.001						
	Dominant Embed.	-0.672	30.868	<0.001						
Other models (not based on final models)										
Univariates	Intercept	2.000	402.340	<0.001		1318.387	1314.390	93.0	87.8	89.6
	Distance from Shore	-0.654	348.210	<0.001						
	Intercept	2.970	436.270	<0.001		1282.655	1256.140	92.3	88.8	90.0
	Depth	-6.068	353.060	<0.001						
	Intercept	-4.700	601.860	<0.001		2463.941	2459.940	46.3	89.5	74.4
	Dominant Substrate	1.071	499.360	<0.001						
	Intercept	1.270	194.380	<0.001		2625.519	2621.520	47.2	82.0	69.8
	Dominant Embed.	-0.768	523.460	<0.001						
	Intercept	-1.620	448.050	<0.001		2945.245	2941.240	31.6	90.6	70.0
	Percent Gravel	0.035	277.030	<0.001						

								Predicted % Classification		
Model Name	**Variables**	**Coefficient**	**Chi Sq**	**P**	**Model P**	**AIC**	**Log L**	**Presence**	**Absence**	**Overall**
Univariates (cont.)	Intercept	-1.600	512.450	<0.001		2834.991	2830.990	41.4	86.2	70.6
	Percent Cobble	0.055	343.620	<0.001						
	Intercept	-0.124	5.240	0.022		3070.103	3066.100	0.0	100.0	65.1
	Percent Sand	-0.023	165.770	<0.001						
	Intercept	-1.170	466.310	<0.001		2874.324	2870.320	41.8	90.6	73.5
	Percent Rubble	0.063	282.880	<0.001						
	Intercept	-1.066	479.820	<0.001	<0.001	2792.753	2786.754	40.0	88.2	71.4
	Sand	-0.023	154.491	<0.001						
	Gravel	0.033	279.350	<0.001						
Bivariates (cont.)	Intercept	-1.098	528.942	<0.001	<0.001	2743.632	2737.632	44.0	86.8	71.8
	Sand	-0.018	93.359	<0.001						
	Cobble	0.049	328.471	<0.001						
Trivariates	Intercept	-3.322	1001.938	<0.001	<0.001	2272.636	2264.636	70.5	83.4	78.9
	Gravel	0.042	323.064	<0.001						
	Cobble	0.041	195.854	<0.001						
	Rubble	0.061	358.297	<0.001						

								Predicted	% Classification	
Model Name	**Variables**	**Coefficient**	**Chi Sq**	**P**	**Model P**	**AIC**	**Log L**	**Presence**	**Absence**	**Overall**
Trivariates (cont.)	Intercept	-1.856	707.162	<0.001	<0.001	2567.410	2559.412	59.4	84.2	75.6
	Sand	-0.017	63.522	<0.001						
	Gravel	0.028	178.221	<0.001						
	Cobble	0.042	227.342	<0.001						
	Intercept	0.732	675.166	<0.001	<0.001	2599.408	2591.408	52.7	81.2	71.3
	Sand	-0.009	17.559	<0.001						
	Gravel	0.011	17.916	<0.001						
	Dominant Embed.	-0.598	195.346	<0.001						

Appendix G2. Model Application.
To determine the effect of depth and distance to shore in each of the resource selection functions, as well as to determine the influence of each variable on the results, models were created in addition to the "final" models. Each additional model created was applied to each study lake to determine the percentage of shoreline with suitable spawning habitat (probability of use $\geq$0.5).

		Probability of Use (%)					
		Big Crooked Lake		**Red Cedar Lake**		**Beaver Dam Lake**	
Model Name	**Variables**	**<0.5**	**$\geq$0.5**	**<0.5**	**$\geq$0.5**	**<0.5**	**$\geq$0.5**
Final models							
RCL Model 1	Intercept Distance from Shore Depth Dominant Substrate Dominant Embed.	90.5	9.5	89.0	11.0	90.8	9.2
RCL Model 2	Intercept Distance from Shore Percent Gravel Percent Cobble Dominant Embed.	95.0	5.0	87.9	12.1	91.1	9.2
BCL Model	Intercept Distance from Shore Percent Gravel Percent Cobble Dominant Embed.	95.4	4.6	78.8	21.2	92.4	7.6

		Big Crooked Lake		Red Cedar Lake		Beaver Dam Lake	
Model Name	**Variables**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**
Bivariates based on final models							
RCL Model 1	Intercept Dominant Substrate Dominant Embed.	95.6	4.4	77.8	22.2	96.3	3.7
RCL Model 1	Intercept Percent Gravel Percent Cobble	96.2	3.8	78.3	21.7	96.9	3.1
BCL Model	Intercept Percent Gravel Percent Cobble	99.5	0.5	65.7	34.3	99.0	1.0
Trivariates based on final models							
RCL Model 1	Intercept Depth Dominant Substrate Dominant Embed.	77.6	22.4	90.1	9.9	89.4	10.6
RCL Model 1	Intercept Distance from Shore Dominant Substrate Dominant Embed.	95.3	4.7	87.6	12.4	91.8	8.2

Model Name	Variables	Big Crooked Lake		Red Cedar Lake		Beaver Dam Lake	
		<0.5	**≥0.5**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**
Trivariates based on final models (cont.)							
RCL Model 2	Intercept	96.7	3.3	79.6	20.4	97.7	2.3
	Percent Gravel						
	Percent Cobble						
	Dominant Embed.						
BCL Model	Intercept	95.4	4.6	78.8	21.2	92.4	7.6
	Percent Gravel						
	Percent Cobble						
	Dominant Embed.						
Other models (not based on finals models)							
Univariates	Intercept	95.0	5.0	87.8	12.2	92.0	8.0
	Distance from Shore						
	Intercept	79.8	20.2	88.8	11.2	89.7	10.3
	Depth						
	Intercept	98.1	1.9	89.5	10.5	97.0	3.0
	Dominant Substrate						
	Intercept	97.0	3.0	82.0	18.0	98.0	2.0
	Dominant Embed.						
	Intercept	96.4	3.6	90.6	9.4	98.3	1.7
	Percent Gravel						

		Big Crooked Lake		Red Cedar Lake		Beaver Dam Lake	
Model Name	**Variables**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**
Univariates (cont.)	Intercept Percent Cobble	98.4	1.6	86.2	13.8	97.9	2.1
	Intercept Percent Sand	100.0	0.0	100.0	0.0	100.0	0.0
	Intercept Percent Rubble	99.0	1.0	90.6	9.4	98.9	1.1
Bivariates	Intercept Sand Gravel	96.5	3.5	88.3	11.7	98.3	1.7
	Intercept Sand Cobble	98.7	1.3	86.8	13.2	98.4	1.6
Trivariates	Intercept Gravel Cobble Rubble	97.6	2.4	83.2	16.8	98.2	1.8
	Intercept Sand Gravel Cobble	97.4	2.6	85.4	14.6	98.1	1.9

		Big Crooked Lake		Red Cedar Lake		Beaver Dam Lake	
Model Name	**Variables**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**	**<0.5**	**≥0.5**
Trivariates (cont.)	Intercept	96.5	3.5	81.2	18.8	97.8	2.2
	Sand						
	Gravel						
	Dominant Embed.						

Appendix H. Shoreline Area Calculations.
The total area (m^2) of the littoral zone was calculated for each lake, then percentage of suitable habitat for walleye spawning based on the Red Cedar Lake Model 3 (relative probability of egg deposition > 0.5) was used to determine the corresponding area (m^2) of the shoreline with suitable habitat.

		Suitable Habitat	
Lake	**Littoral Zone Area (m2)**	**Percent (%)**	**Area (m2)**
Red Cedar Lake	52,000	70	36,400
Big Crooked Lake	16,200	8	1,296
Beaver Dam Lake	58,000	20	11,600