WALLEYE HABITAT USE, SPAWNING BEHAVIOR, AND EGG DEPOSITION IN SANDUSKY BAY, LAKE ERIE

Thesis

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ABSTRACT

Understanding habitat selection in fish can reveal areas critical for a population’s continuation in the ecosystem. In systems experiencing habitat alterations or reductions in population sizes, identifying habitat use takes on increased importance. To facilitate our understanding of potential factors limiting the success of walleye (*Sander vitreus*) in Sandusky Bay, Lake Erie, we combined walleye locations determined from radio telemetry with habitat predictor variables to model habitat use and reveal sex-specific patterns of habitat use throughout the spawning season (Chapter 2). Models revealed that the presence of preferred walleye spawning substrate, gravel and cobble, was an important predictor of walleye locations during the entire spawning season, and depth and distance from shore were important particularly prior to the spawn. In examining sex-specific patterns of habitat use, we discovered that males were more likely to occur over gravel and cobble substrates than females. We hypothesize that males establish position in these areas in anticipation of spawning females. Only a small proportion of walleye tagged in Sandusky Bay migrated to upstream spawning grounds (2 of 197; 1%). To confirm whether
walleye spawning occurs in Sandusky Bay and to analyze how spawning substrate might affect egg deposition rates and viability, we compared eggs collected using spawning mats from gravel/cobble and sand/silt substrates (Chapter 3). Egg deposition and egg viability were not significantly different between substrates, and the majority of walleye eggs were collected from one site that contained gravel and cobble. The combined results of this investigation reveal that the Sandusky Bay is a spawning ground for walleye and that preferred spawning substrate is an important factor predicting the location of walleye during the spawn. Because the amount of spawning habitat in this system has declined by an estimated 92% during the past century, we recommend that conservation and restoration steps be taken to preserve this walleye spawning population.
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CHAPTER 1

INTRODUCTION

Understanding how an organism relates to its abiotic environment is a primary goal in ecology (Rosenzweig 1981; Morris 1987). In fishes, identifying habitat use can reveal insight into habitat preferences and mechanisms driving survival (Baxter and Hauer 2000; Olden and Jackson 2001). Further, understanding habitat use becomes essential in systems that have undergone habitat degradation in order to predict how populations might respond to additional change (e.g., Gross 1991).

Historically, Lake Erie has experienced many forms of habitat degradation including nutrient loading (Ludsin et al. 2001), invasive species (e.g., Berkman et al. 1998), and pollution (Koonce et al. 1996). Understanding the impact of these changes on fish populations will ultimately lead to better conservation and management practices. In the Sandusky River, a reduction in spawning substrate due to dams and channel modifications is thought to be responsible for recent declines in walleye (Sander vitreus) harvest (Ohio Division of Wildlife
Further, it is believed that this reduction in habitat has caused some walleye to spawn in less preferred areas throughout Sandusky Bay.

In response to these hypotheses, a recent pilot study was launched to study the movements of walleye in the Sandusky River and Sandusky Bay using radio telemetry. Results from this study revealed that very few walleye tagged in or near Sandusky Bay migrated up the Sandusky River (4 of 50; 8%), and most fish remained in Sandusky Bay (Ohio Division of Wildlife 2008). This result highlights the need for a greater understanding of what drives the habitat use and behavior of walleye during the spawn to protect this spawning population from further reductions in population sizes.

In an effort to identify potential mechanisms surrounding recent spawner declines, we conducted the following investigation to gain insight into the habitat use and reproductive behavior of walleye in this system. In Chapter 2, we modeled the locations of walleye in Sandusky Bay in relation to habitat features (i.e., substrate, depth, and distance from shore) throughout the spawning season to reveal important habitats for walleye. We also modeled the predicted probability of a walleye occurrence over gravel and cobble substrate in relation to the traits of an individual (i.e., sex, length, weight, condition) to tease apart patterns in habitat use. Finally, in Chapter 3, we asked the question of whether walleye spawn in Sandusky Bay and, if so, how egg deposition rates and viability differed between substrate types.
CHAPTER 2: HABITAT USE AND SPAWNING BEHAVIOR OF WALLEYE IN SANDUSKY BAY, LAKE ERIE

INTRODUCTION

Habitat use in fish is driven primarily by demands for growth, survival, and reproduction (Werner et al. 1983; Fausch 1984; Kramer et al. 1997). During reproduction, individuals are expected to select habitats that will maximize reproductive output and the success of their offspring (Potts and Wootton 1984; Itzkowitz 1991; Fleming 1998; Hendry et al. 2001). Consequently, understanding the habitat use of spawners can reveal which areas are critical for a population’s continuation in the ecosystem (Baxter and Hauer 2000). Identifying habitat use takes on increased importance throughout systems that have experienced habitat degradation or reductions in population sizes (Hayes et al. 1996; Olden and Jackson 2001). Reliable habitat use models that predict the importance of specific habitats for declining populations, therefore, are essential in making appropriate fisheries conservation and management decisions.

The traits of an individual (e.g., sex and size) can influence spawning habitat use and behavior (Quinn and Foote 1994; Slotte and Fiksen 2000). For
example, large spawning male and female sockeye salmon (*Oncorhynchus nerka*) selected deeper water spawning sites than smaller individuals (Hendry et al. 2001). Additionally, male brook trout (*Salvelinus fontinalis*) remained over spawning grounds for longer durations than females (Blanchfield and Ridgway 1997). State-dependent spawning behavior also has been documented in walleye (*Sander vitreus*), with the earliest arrivals to the spawning grounds biased towards the largest individuals (J. J. Van Tassell, The Ohio State University, unpublished data). Here, we predict the habitat use of walleye to reveal critical habitats affecting reproductive success and examine how the traits of an individual affect its habitat use.

During the past few decades, Lake Erie habitat has undergone considerable changes due to nutrient loading (Ludsin et al. 2001), invasive species (Berkman et al. 1998), and pollution (Koonce et al. 1996). The availability of spawning substrate has also changed throughout the past, as in the case of the Sandusky River and Sandusky Bay. First, the Ballville Dam was built in 1911, blocking access to upstream areas that contain large areas of preferred walleye spawning substrate (i.e., gravel and cobble; Cheng et al. 2006). Further, in 1972, a large section of the Sandusky River downstream of the dam was modified for flood control, removing areas of natural spawning habitat (Plott 2000; Gillenwater et al. 2006). Finally, fine sedimentation from river inputs and shoreline erosion (Carter et al. 1975) has reduced the amount of gravel and cobble throughout Sandusky Bay by an estimated 92% during the past century.
Many believe that the combined effects of habitat degradation in this system have caused walleye to spawn over unsuitable substrates, thus compromising egg survival and, in turn, reducing recruitment into the adult population. With walleye harvest in this system in decline (Ohio Division of Wildlife 2008), understanding habitat use and spawning behavior becomes a great priority to protect this historically important walleye spawning population. In this study, our objectives were to understand how habitat affects the probability of a walleye occurrence in Sandusky Bay and to determine how an individual’s traits affect its probability of using preferred spawning substrate.
METHODS

Study site

The Sandusky Bay is a 14,692 ha eutrophic bay with a mean depth of 1.6 m located in the Ohio waters of Lake Erie (Figure 1). The Sandusky River is a 210-km tributary situated in a 3,680-km² watershed (Evans et al. 2002) dominated by agricultural land use (84%). Constructed along river kilometer (rkm) 29, the Ballville Dam blocks the upstream migration of fish into an additional 35-km stretch of river containing large areas of walleye spawning substrate (Cheng et al. 2006). In an attempt to increase the availability of upstream habitat, and to avoid various safety issues (Evans et al. 2002), the Ballville Dam is scheduled to be removed by 2012.

Study species

Walleye are iteroparous, broadcast-spawners native throughout large parts of the United States and Canada. Walleye spawn in the spring, depending on latitude, at water temperatures of 6-11°C (Johnston and Leggett 2002). Peak spawning activity typically occurs during the evening and night (Ellis and Giles 1965). Walleye exhibit site fidelity to their natal spawning grounds (Crowe 1962;
Olson and Scidmore 1962; Bigrigg 2006), although some straying is thought to occur (Strange and Stepien 2007). Throughout Lake Erie and surrounding waters, distinct spawning groups are believed to exist (Todd and Haas 1993; Merker and Woodruff 1996), with each group contributing differentially to the lake-wide fishery (Bigrigg 2006). Most walleye spawning occurs in the productive, western basin of Lake Erie, particularly in the Maumee River and on open-water reefs (Goodyear et al. 1982). The Sandusky River historically has supported large spawning runs of walleye (Regier et al. 1969; Goodyear et al. 1982); however, the number of spawners in this system has recently declined (Ohio Division of Wildlife 2008).

Capture and tagging

During late March through mid-April, we used gillnets and seines to collect walleye ($n = 197$) from alleged staging areas in eastern Sandusky Bay for the external attachment of radio transmitters (Figure 1). Gillnets (varied mesh sizes) were set either during the day or overnight for maximum durations of 6 and 12 h, respectively. Given the low water temperatures (4-8°C) and short set times, this collection method had only a minimal impact on the physical condition of the fish. Seining was conducted by a commercial seining operation for rough-fish (Buehler Fisheries), which routinely captures walleye as bycatch during this time of year. We transferred walleye to net pens along a shore site for recovery after capture.
Prior to surgery, we anesthetized fish in a solution of 2.66 g/L sodium bicarbonate according to Peake (1998).

We measured total length (TL; nearest 1 mm) and mass (nearest 0.5 g) for each captured walleye. We determined sex by checking for the presence of eggs or milt; fish were classified as ‘unknown’ if these cues were unavailable. We used the residuals of the ln(mass) versus total length relationship based on sex-specific slopes and intercepts as a proxy for condition (Kaufman et al. 2007).

We attached external radio transmitters (model MCFT-7A, Lotek Wireless, Newmarket, Ontario) beneath the dorsal fin. Surgically implanted radio transmitters are commonly used in fish movement studies (reviewed in Jepsen et al. 2002), although we chose to use an external transmitter to minimize surgery and invasiveness of the tagging procedure. Each transmitter contained a unique code between 164.420 and 164.820 MHz, weighed 32 g (in air), and had an expected battery life of 339 d. Transmitters were equipped with return information and signs were posted throughout the study area for public notification. Transmitters were attached by puncturing the dorsal musculature with a surgical biopsy needle, threading wires through the tissue, and tying the two ends together on the opposite side of the fish. Foam backing plates were installed between the fish and the wires to reduce abrasion. Heat-shrink tubing was applied to the knot to reduce the risk of tag loss. Gills were flushed with lake water during surgery. For most fish (n = 152) tag weight did not exceed 2% of the weight of the fish (Winter 1996); for some smaller individuals (n = 45) the tag
to body weight ratio did not exceed 3%. Because tag sizes that exceed 3% of the weight of the fish can have little or no effect on fish behavior (Brown et al. 1999; Jepsen et al. 2001), we felt confident in using 3% as a guideline. After surgery was complete, we transferred fish to a flow-through recovery tank until fish recovered. Fish were released either in a central location within Sandusky Bay or from shore when weather and equipment did not permit releases to occur centrally (Figure 1).

**Tracking**

The spatial distribution of walleye in Sandusky Bay and Sandusky River was determined by airplane and boat tracking during late March until early May, 2008. Airplane tracking was conducted 1-2 times weekly along predetermined transects such that the entire study area was covered in a single sampling date. All areas within the bay and river were sampled with equal effort; therefore, we assumed that all fish had an equal probability of being detected by airplane. Our ability to detect fish decreased over depths greater than 5 m; however, these areas constituted a small proportion of our study area (Appendix B). Aerial tracking also was periodically conducted across shallow, open reefs and shoals adjacent to Sandusky Bay where walleye have historically spawned (US waters only; Goodyear et al. 1982), to gain insight into whether fish migrated to other areas during the spawn and whether the bay might be used as a staging area for multiple spawning groups.
Boat tracking was conducted 2-3 times weekly. Owing to logistical constraints, we were unable to track the entire study area in a single day. Therefore, we parsed the study area into three discrete sampling units (Sandusky River, western Sandusky Bay, and eastern Sandusky Bay) that could be covered in a single day such that we covered all or most of the study area each week by boat. Using a global positioning system (GPS), we recorded the coordinates of individually coded walleye once they were detected by the mobile receivers. All tracking was conducted during the day; night tracking was not conducted due to logistical concerns.

In addition to mobile tracking, we placed three stationary receivers (model SRX400, Lotek Wireless, Newmarket, Ontario) along the Sandusky River to continuously monitor the movement of walleye upstream from early March until late May. Receivers were placed (1) at the river mouth to document the entrance of fish into the river, (2) along existing spawning grounds in Fremont, and (3) at the Ballville Dam to reveal whether fish attempted to access upstream spawning sites (Figure 1). Detection probabilities at our second and third sites were high; some fish were able to evade detection at the river mouth site because of deeper water during high discharge events.

Habitat variables

We compiled data for three features of the abiotic habitat: substrate, depth, and distance from shore. A map of the substrate was created using a
Voronoi diagram (Aurenhammer 1991) in ArcGIS 9.3 (ESRI 2008) using substrate composition data collected at regular 300-m intervals (Appendix B). Substrate data were categorized in the following way: 1 = walleye spawning habitat (i.e., gravel and cobble) present; 0 = walleye spawning habitat absent (Figure 12). Depth data were interpolated from National Oceanic and Atmospheric Administration (NOAA) digital sounding data (Figure 13; Appendix B). Finally, the distance from shore that a walleye was located was determined using the Spatial Analyst Toolbar in ArcGIS 9.3 (ESRI 2008; Figure 14; Appendix B). We assumed habitats to be independent because correlation coefficients ($r^2$) for habitat variables were close to zero (Table 1). A cell size of 5 m x 5 m was used for all habitat layers to eliminate the potential of having multiple fish in the same cell, resulting in $n = 5,771,962$ individual cells. The study area for modeling purposes is shown in Figure 1.

Model development

We developed two models to address questions related to walleye habitat use in Sandusky Bay. First, how important was the abiotic habitat in explaining the probability of a walleye occurrence throughout the spawning season? Second, looking just at where walleye were observed, how did an individual’s biological characteristics affect its likelihood of being found over gravel and cobble substrates?
Abiotic habitat model

To address our first question, we used binary logistic regression (McCullagh and Nelder 1989) to relate the presence/absence of a transmitter-bearing walleye in an individual 5 m x 5 m cell in Sandusky Bay (response variable) to three habitat predictor variables through the logistic link function (i.e., logit, \( y_i \)):

\[
y_i = \ln \left( \frac{\pi_i}{1 - \pi_i} \right) = \beta_0 + \beta_{1,i}x_{1,i} + \beta_{2,i}x_{2,i} + \ldots + \beta_{m,i}x_{m,i}
\]

where \( \pi_i \) is the probability of a walleye occurrence in cell \( i \), \( \beta_0 \) is the regression constant, and \( \beta_j \) are the regression coefficients associated with the predictor variables \( x_{j,i} \) (i.e., substrate, depth, and distance from shore). Stata 10.0 (StataCorp LP 2007) was used to fit the logistic regression and provide significance values for the regression coefficients.

We modeled walleye habitat use over three distinct time periods: pre-spawn, peak-spawn, and post-spawn. Time periods corresponded to water temperatures at which walleye have been observed to spawn in the Sandusky River during 2004-2005 (J. J. Van Tassell, The Ohio State University, unpublished data). Specific temperatures for pre-spawn, peak-spawn, and post-spawn periods were <8°C, 8-11°C, and >11°C, respectively. Although we recorded walleye locations by boat and airplane, for this analysis we chose to model only the locations recorded by airplane because of the universal coverage
of our study area achieved during each sampling event. Finally, to interpret our results in terms of the probability of a walleye occurrence, we applied the inverse logit link function:

\[ \pi_i = \frac{1}{1 + e^{-y_i}} \]

and plotted predicted probabilities of walleye occurrences during each time period using ArcGIS 9.3 (ESRI 2008).

**Individual traits model**

The model used for our first analysis predicted the probability of walleye occurrence in relation to the abiotic habitat; however, it was not designed to test for differences in habitat use based on an individual’s traits. Therefore, to address our second question, we used binary logistic regression to examine how the characteristics of an individual affected its likelihood of being found over gravel and cobble substrates. Specifically, we predicted the presence/absence of transmitter-bearing walleye over gravel and cobble (response variable) in relation to individual traits (i.e., sex, length, mass, and condition) through the logistic link function (McCullagh and Nelder 1989). Continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation. We used only the data from cells in which walleye were present (airplane and boat tracking). Observations from fish with unknown sex \((n = 12)\) were excluded from analyses.
We examined relationships between predictor variables using a one-way analysis of variance (one-way ANOVA) to assess independence. Sex was highly correlated with length ($p < 0.001$) and mass ($p < 0.001$; Figures 2 and 3). Residual mass was a composite metric and thus not comparable with sex. When residual mass was included in the model, results revealed it was not a significant predictor of walleye locations ($p = 0.58$); thus, we used sex as the only predictor variable. To account for having multiple observations on the same fish, a random intercept was assigned to each fish using the lme4 library package (Bates et al. 2008) in R (R 2008). Results were qualitatively the same regardless of whether the random intercept was included, suggesting that an individual's preference for specific habitats was not significantly biasing model results.

Finally, we included time period as a factor in the model to examine how substrate use by males and females changed through time. Walleye habitat preference was inferred based on the sign (positive or negative) of the parameter coefficients. A positive sign for the depth coefficient, for example, would indicate preference for deeper depths.
RESULTS

Walleye locations

We recorded 322 locations for 111 walleye from mobile tracking efforts conducted during 2008 (\(n = 167\) by airplane; \(n = 155\) by boat). Of the 197 walleye tagged in Sandusky Bay, only two fish (1%) ascended the Sandusky River; neither fish were detected at the Ballville Dam. The remaining 109 fish were located in Sandusky Bay. A total of 86 walleye were never detected; no apparent differences in fish lengths or sexes existed between fish detected and those not detected. From our aerial surveys conducted throughout the adjacent reefs we detected two fish; neither fish were ever detected in the Sandusky River or Sandusky Bay.

Abiotic habitat model

Substrate was an important predictor of walleye locations throughout all three time periods (Table 2). Depth and distance from shore were important predictors only during certain time periods (Table 2). According to the sign of parameter coefficients, the highest probabilities of a walleye occurrence in an
individual cell were related to the presence of gravel and cobble, deeper depths, and closeness to shore (Table 2; Figures 4-6).

Examining results by time periods, we found that during the pre-spawn period, the probability of a walleye occurrence increased significantly with deeper depths and closeness to shore; the presence of gravel and cobble was nearly significant (Table 2). During the peak-spawn period, the probability of locating a walleye increased significantly with the presence of gravel and cobble and closeness to shore (Table 2). Finally, during the post-spawn period, the probability of a walleye occurrence was significantly correlated only with the presence of gravel and cobble (Table 2).

**Individual traits model**

We used logistic regression to test whether males and females differed in their habitat use. Model results revealed that males were significantly more likely to be present over gravel and cobble than females (Table 3). The proportions of males and females found over gravel and cobble substrates were 0.18 and 0.07, respectively, even though gravel and cobble constituted only 0.03 proportion of the total study area (Figure 7; Appendix C). The likelihood of males occurring over gravel and cobble did not significantly vary through time ($p > 0.05$).
Habitat selection models contributed to our understanding of walleye habitat preferences and spawning behavior. First, the presence of spawning substrate (i.e., gravel and cobble) proved to be an important predictor of walleye locations throughout the spawning season. This finding is supported by previous studies that have shown spawning walleye to prefer gravel and cobble substrates (McMahon et al. 1984; Liaw 1991). Differential egg survival can likely explain the selection for substrates, as walleye egg survival is generally much higher over gravel and cobble (31-80%) as opposed to sand or silt (2-14%; Johnson 1961; Corbett and Powles 1986). Therefore, substrate selection in walleye could be viewed as a reproductive tactic to maximize offspring survival (Fleming 1998).

In addition to presence of gravel and cobble, deeper depths and closeness to shore helped to explain the locations of walleye. Although this combination of habitats may seem incongruent, areas containing deep water close to shore were characterized by steep slopes and were exemplified by a shipping canal in the eastern bay and a set of bridges in the bay center. We hypothesize that fish may be attracted to the faster flows in these regions, rather than to closeness to shore per se, given the geomorphology of the areas. Other
studies have found flow to be an important factor for spawning walleye (McMahon et al. 1984; Liaw 1991; Gillenwater et al. 2006).

Habitat selection differed slightly among pre-, peak-, and post-spawning periods. The probability of a walleye occurrence was significantly related to deeper depths and closeness to shore during the pre-spawn period, with the presence of gravel and cobble substrates not quite significant. Because pre-spawn temperatures are characteristically below those temperatures that are optimal for fertilization and embryo incubation (Koenst and Smith 1976), we suspect that habitat use during this time may be related more to staging or foraging than to reproduction (Ickes et al. 1999). During the peak-spawn period, a high probability of walleye occurrence was related to presence of gravel and cobble substrate and closeness to shore, habitats typically associated with spawning (e.g., McMahon et al. 1984). Finally, during the post-spawn period, only substrate was significant in predicting the occurrence of walleye. The temperatures that corresponded to the post-spawn period (>11°C) could continue to be favorable for walleye egg deposition, evidenced by the regional variability in peak spawning activity related to water temperature (reviewed by Kerr et al. 1997). In our study, spawning individuals could have been present when water temperatures exceeded 11°C, thus explaining the importance of gravel and cobble during this time period.

Male walleye had a higher probability of occurring over preferred substrate types than females. We hypothesize that males maintain position on spawning
grounds in anticipation of spawning females. This tactic has been observed in kokanee salmon (*Oncorhynchus nerka*) in which males establish positions on spawning grounds before arrival of females (Foote 1990). Although territories are typically defended aggressively in male salmonids (Foote 1990), the degree to which male walleye exhibit this behavior remains less certain. The low proportion of females over gravel and cobble could be explained by the fact that the majority of our sampling was conducted during the day, whereas peak spawning activity in walleye generally occurs during the evening and night (Ellis and Giles 1965; Kerr et al. 1997). Using telemetry to directly detect spawning over a large sample area would be difficult because spawning usually takes place over only a brief time interval (Ellis and Giles 1965; Paragamian 1989). Our data are consistent with the idea that females reside in unsuitable spawning areas during the day before migrating to spawning grounds at night.

Radio telemetry revealed that only 1% of walleye tagged in Sandusky Bay migrated upstream to historical spawning grounds, a finding similar to a pilot study that discovered few adult walleye tagged in or near Sandusky Bay (4 of 50; 8%) ascended the Sandusky River during spring 2006 (Ohio Division of Wildlife 2008). We considered that this low proportion of tagged fish ascending the river to spawn may have been the result of stress due to capture and tagging so soon before the spawning period. To test this, we compared our results with the multiple-year pilot study, and found that even several years after tagging, similar proportions of walleye ascended the river (Ohio Division of Wildlife 2008). Thus,
we rejected the argument that a handling and tagging effect was responsible for the limited upstream migrations in our study.

The small proportion of walleye traveling upriver could be explained in terms of conditional reproductive strategies (Maynard Smith 1982; Gross 1996) in response to environmental change. That spawning individuals can adaptively respond to change by substituting habitats is not a new concept. McAughey and Gunn (1995) demonstrated that lake trout (Salvelinus namaycush) used new spawning habitats when historical grounds were experimentally covered. In addition, Atlantic salmon (Salmo salar) explored different spawning areas when confronted with an impassable dam (Gerlier and Roche 1998). In our study, walleye could be responding adaptively to habitat reductions in the Sandusky River by choosing alternate spawning locations in Sandusky Bay. However, with gravel and cobble in Sandusky Bay decreasing as well, the fitness of these two reproductive strategies (i.e., bay spawning versus river spawning) may be equally poor and thus partially responsible for recent reductions in walleye harvest in the Sandusky River (Ohio Division of Wildlife 2008).

This research has several implications for habitat restoration. First, dams have a long history of degrading habitats by altering downstream flow regimes and restricting fish migrations (reviewed by Ligon et al. 1995). Consequently, a growing interest in dam removal has emerged as a means to restore river habitats. In the Sandusky River, the upcoming removal of the Ballville Dam will increase the availability of suitable spawning habitat in sections where
experimentally relocated individuals demonstrated successful reproduction (Plott 2000). Removing the dam is predicted to have a positive impact on walleye larval production (Jones et al. 2003; Cheng et al. 2006); however, the question of whether adult walleye will use these sites remains unknown (Jones et al. 2003).

Second, the negative effects of siltation on fish spawning habitat is well documented (Cederholm et al. 1981; Berkman and Rabeni 1987; Soulsby et al. 2001). In Sandusky Bay, siltation from river inputs and shoreline erosion has covered large areas of gravel and cobble over the past century (Carter et al. 1975; Appendix C). Steps to preserve remaining habitat could include incorporating sustainable agricultural practices in upstream regions, installing riparian buffers, and protecting coastal areas (e.g., Koonce et al. 1996; Wichert and Rapport 1998). Many programs are currently in place to address these issues (see Lake Erie LaMP 2000).

Finally, the addition of spawning habitat as a restoration technique could have beneficial effects on walleye egg deposition and survival (Johnson 1961; Newburg 1975; but see Radomski 1991; Geiling et al. 1996). However, habitat additions may have little or no effect on fish populations if the original habitat structural complexity is not restored (Lepori et al. 2005) or if habitat is not a limiting factor affecting the population (Radomski 1991; Jones et al. 2003). Because our research revealed a large proportion of walleye remain in Sandusky Bay where suitable spawning habitat is scarce, the above habitat restoration
efforts could be an important step towards protecting this valuable spawning population.
INTRODUCTION

The abiotic habitat plays an important role during each stage of a fish’s development. The embryonic stage is especially sensitive to the abiotic habitat because of the direct impact it can have on development (e.g., Giorgi and Congleton 1984; Pepin 1991). While egg development and survival are influenced by a variety of different habitat features, the presence of interstitial spaces in the substrate can have a considerable effect by creating oxygenated incubation spaces and a safeguard against predation (Kerr et al. 1997). In walleye (Sander vitreus), spawning substrate has been shown to influence egg deposition (Johnson 1961, but see Geiling et al. 1996) and egg survival (Johnson 1961; Corbett and Powles 1986; Auer and Auer 1990). “Suitable” walleye spawning substrates are gravel and cobble mixtures because they provide ideal habitats for developing eggs (McMahon et al. 1984; Liaw 1991). Fine substrates such as sand and silt are deemed “unsuitable” because they typically contain
lower concentrations of dissolved oxygen and more contaminants, leading to decreased egg survival (Colby and Smith 1967; Auer and Auer 1990). Here, we investigate how spawning substrate affects walleye egg deposition and viability.

Throughout Lake Erie, walleye spawn in a variety of areas including river tributaries and mid-lake reefs (Goodyear et al. 1982). Located in southwestern Lake Erie, the Sandusky River is an historical spawning area for walleye. The role of the connecting Sandusky Bay is less clear, although it is believed to be a staging area for the Sandusky River walleye spawning population. Results from Chapter 1 revealed that many walleye remain in the bay throughout the duration of the spawn. Therefore, the role of the bay might include a spawning area as well a staging area. Given that the amount of suitable substrate in this system has undergone marked reductions throughout the past century (Appendix C), discovering that walleye spawn in the bay could have important implications on the survival of their eggs and, in turn, the year-class strength of the Sandusky spawning population. In this study, our objectives were to answer the question of whether walleye spawn in Sandusky Bay and, if they do, how deposition rates and viability differed between substrate types. We hypothesized that both deposition and viability would be higher among gravel and cobble substrates.
METHODS

Egg collections

We used spawning mats (Manny et al. 2007) to determine whether walleye spawned in Sandusky Bay during 2009. Spawning mats consisted of a cement block (39 x 20 x 9 cm) wrapped with furnace filter material on all four sides. Furnace filter material was held in place with two elastic cords. A gang of spawning mats was formed by connecting 3-4 mats together using rope. During early spring 2009, we placed 10 gangs over naturally occurring gravel and cobble mixtures of substrate (hereafter ‘gravel/cobble’) and 10 gangs over naturally occurring sand and silt (hereafter ‘sand/silt’) to examine how walleye egg deposition and viability differed between substrate types (Figure 8). The dominant substrate type at each site was determined using a petite Ponar grab and probing the lake bottom with a long-handled pole (Sarkar and Bain 2007).

Once per week from 9 April until 6 May 2009, spawning mats were brought onto a boat and were visually inspected for the presence of eggs. We assumed that an equal proportion of eggs were lost from each sample in the process of bringing the mats onto the boat. On spawning mats that contained a low number of eggs (less than 100), eggs were removed with a forceps from the
exposed top surface and placed into plastic bottles containing ambient water. We employed two different methods when egg densities were too high to efficiently remove by hand. We detached the furnace filters and stirred the top surface in a 400 mg/l solution of tannic acid for 2 min to reduce the adhesiveness of the eggs (Waltemyer 1976). Eggs were then strained using a 0.84-mm sieve and transferred into plastic bottles containing ambient water. Alternatively, we removed the furnace filters and placed them in coolers containing ambient water for subsequent processing. All eggs were sorted within 6 h in the laboratory, although a previous study reported that delays in processing of up to 24 h had no effect on egg viability (Roseman et al. 1996). Sampling was concluded when walleye eggs were completely absent from the spawning mats and when water temperatures approached 16°C.

Sample processing and statistical treatment

Using a dissecting microscope, we counted the total number of eggs and the proportion of viable eggs in each sample where eggs were found. Dead eggs were opaque and were often covered with fungus (Johnson 1961). We identified eggs as belonging to walleye based on egg color and size (Auer 1982). Species assessments were validated with a subsample of eggs using restriction fragment length polymorphism (RFLP) to reveal mitochondrial DNA sequences diagnostic for walleye (Ivanova et al. 2007). Results revealed that initial species assessments based on egg color and size were 100% accurate.
To test for differences in walleye egg deposition and viability between substrate types, we calculated the proportion of sites that had eggs present, and the average viability of eggs over gravel/cobble and sand/silt substrates, for each sampling date. Proportional data were arcsine-square root transformed. Differences were analyzed using a two-way analysis of variance (two-way ANOVA). All statistical tests were evaluated at the significance level of $p < 0.05$ using JMP 8 (SAS Institute 2008).
RESULTS

The presence of walleye eggs at various sampling sites revealed that walleye spawned in Sandusky Bay during 2009. The proportion of sites that contained walleye eggs appeared to be higher for gravel/cobble sites (Figure 9); however, these differences were not significant ($F = 3.74, p = 0.13$). Further, average walleye egg viability appeared higher for gravel/cobble sites (Figure 10), yet again, these differences were not significantly different ($F = 4.97, p = 0.16$). The majority of walleye eggs (2,805 of 3023; 93%) came from one site that contained gravel/cobble (Figure 11).
DISCUSSION

The majority of walleye eggs (2,987 of 3,023; 99%) were collected over gravel/cobble substrates; however, the proportions of sites containing eggs were not significantly different between substrate types. This result could be explained in terms of overall site suitability. Specifically, some gravel/cobble sites could have contained suitable substrates, yet were unsuitable with regard to other factors such as water velocity or depth (McMahon et al. 1984; Cheng et al. 2006). Additionally, from qualitative assessments at the time of collection, we noticed that several sites had accumulated deposits of silt, possibly decreasing their suitability for spawning.

No significant differences in walleye egg viability were found between substrates. This is likely due to the high variation of viability within substrates and the absence of eggs at sand/silt sites during some days. Overall, walleye egg viability from gravel/cobble was similar to eggs collected from Niagara Reef (Roseman et al. 1996) and Sunken Chicken Reef (Fitzsimons et al. 1995), both located in western Lake Erie. The drop in egg viability during April 23-24 could be related to a series of storms and high wind events which can contribute to walleye egg mortality (Busch et al. 1975; Roseman et al. 2001).
The result that walleye egg deposition occurred over sand and silt was somewhat surprising given that egg survival over these substrates is generally lower than gravel and cobble (Johnson 1961; Corbett and Powles 1986). Several hypotheses could explain this phenomenon. First, in terms of egg success, spawning over sand and silt may be a suitable tactic because no significant differences were found in the viability of walleye eggs between substrates. Second, eggs could have been transported to these sites from adjacent spawning areas. Severe storms and waves during the spring can dislodge eggs from rocky habitats, especially in shallow water (Busch et al. 1975; Roseman et al. 1996). In our study, high wind events were common throughout the sampling period; therefore, this hypothesis could likely explain the presence of eggs over less preferred substrates. Finally, representing only 3% of the entire study area (Appendix C), gravel and cobble spawning habitat could be a limiting resource, forcing some fish to spawn over less preferred areas. Johnson (1961) stated that walleye will deposit eggs over unsuitable substrates in systems where spawning habitat is scarce. If true, this could help explain recent reductions in walleye harvest in this system (Ohio Division of Wildlife 2008).

Understanding where walleye spawn throughout Lake Erie is important for fisheries management and conservation. Recently, additional walleye spawning grounds were documented in the Maumee Bay (Roseman et al. 2002) and the Detroit River (Manny et al. 2007), revealing that the role of these areas is broader than previously thought. Similarly, discovering that walleye spawn in Sandusky
Bay highlights the importance of the bay as a staging area and a spawning area. Therefore, future management strategies should account for multiple uses of these areas, particularly in the Sandusky Bay where walleye populations are believed to be declining.

Finally, this research raises the question of whether fish that spawn in the Sandusky River and Sandusky Bay represent two distinct spawning populations. The coexistence of fish that use different spawning sites in the same system has been documented in a variety of species including brown trout (Salmo trutta; Jonsson 1985) and roach (Rutilus rutilus; Brodersen et al. 2008). Walleye also have been shown to demonstrate this behavior, where intermixed fish routinely spawn either in a river or lake environment (Jennings et al. 1996; Palmer et al. 2005). While the selection of spawning sites in walleye is known to have a genetic component (Jennings et al. 1996; Strange and Stepien 2007), various biological and environmental mechanisms, such as overcrowding on the spawning grounds, may play a role as well (Olson and Scidmore 1962; Strange and Stepien 2007). Until it is clear as to whether bay and river spawners constitute distinct populations, walleye throughout the Sandusky system should be conserved to maintain genetic diversity for the collective Lake Erie population.
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APPENDIX A

TABLES AND FIGURES
Table 1. Correlation coefficients ($r^2$) of model parameters: depth (m), distance from shore (m; “distance”), and substrate (1 = gravel and cobble present; 0 = gravel and cobble absent).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>depth</th>
<th>distance</th>
<th>substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>depth</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>distance</td>
<td>0.19</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>substrate</td>
<td>-0.11</td>
<td>-0.16</td>
<td>–</td>
</tr>
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</table>
Table 2. Parameter coefficients and corresponding \( p \)-values from logistic regression for pre-spawn, peak-spawn, and post-spawn time periods. The model predicted the presence/absence of walleye in an individual cell in relation to depth (m), distance from shore (m), and substrate (1 = gravel and cobble present; 0 = gravel and cobble absent).

**Pre-spawn**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
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<tr>
<td>Substrate</td>
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<td>0.071</td>
</tr>
<tr>
<td>Depth</td>
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<td>0.006</td>
</tr>
<tr>
<td>Distance</td>
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<td>0.048</td>
</tr>
<tr>
<td>Constant</td>
<td>-12.002</td>
<td>&lt;0.001</td>
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**Peak-spawn**

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<tr>
<td>Substrate</td>
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<tr>
<td>Depth</td>
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<td>0.522</td>
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<tr>
<td>Distance</td>
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<td>0.047</td>
</tr>
<tr>
<td>Constant</td>
<td>-11.273</td>
<td>&lt;0.001</td>
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</table>

**Post-spawn**

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<th>( p )</th>
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</thead>
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<tr>
<td>Substrate</td>
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<tr>
<td>Depth</td>
<td>0.041</td>
<td>0.664</td>
</tr>
<tr>
<td>Distance</td>
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<tr>
<td>Constant</td>
<td>-12.060</td>
<td>&lt;0.001</td>
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Table 3. Parameter coefficients and corresponding $p$-values from logistic regression taken across all time periods. The model predicted the presence/absence of walleye over gravel and cobble in relation to an individual’s sex (1 = male; 0 = female).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
<th>$p$</th>
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</thead>
<tbody>
<tr>
<td>Sex</td>
<td>1.179</td>
<td>0.009</td>
</tr>
<tr>
<td>Constant</td>
<td>-2.871</td>
<td>&lt;0.001</td>
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</table>
Table 4. Area, proportion, and percent change of substrate throughout Sandusky Bay, Lake Erie assessed during historical (1872, 1905) and current (2009) time periods.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Area (km²)</th>
<th>Proportion</th>
<th>Area (km²)</th>
<th>Proportion</th>
<th>Percent change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock present</td>
<td>54.7</td>
<td>0.38</td>
<td>4.59</td>
<td>0.03</td>
<td>-91.6%</td>
</tr>
<tr>
<td>Rock absent</td>
<td>89.6</td>
<td>0.62</td>
<td>139.64</td>
<td>0.97</td>
<td>+55.9%</td>
</tr>
</tbody>
</table>
Figure 1. Map of the Sandusky River and Sandusky Bay situated in the southwest portion of Lake Erie, Ohio. The Ballville Dam (gray square) is located on the Sandusky River at river kilometer (rkm) 29. Stationary receivers to monitor the movements of walleye upstream were located (from left to right) at the Ballville Dam, along existing spawning grounds in Fremont, and near the river mouth (black circles). Walleye were captured from gillnets (black squares) and a commercial seiner (black triangle) and released back into the eastern portion of the bay (black cross). Cross-hatching in the bay indicates areas used for habitat modeling.
Figure 2. Boxplots of ln(total length) for transmitter-bearing walleye located throughout Sandusky Bay, Lake Erie, Ohio during 2008. Females were significantly larger than males ($p < 0.001$). Boxplot marks represent (from bottom to top) 10$^{th}$ and 25$^{th}$ percentiles, median, and 75$^{th}$ and 90$^{th}$ percentiles.
Figure 3. Boxplots of ln(weight) for transmitter-bearing walleye located throughout Sandusky Bay, Lake Erie, Ohio during 2008. Females were significantly heavier than males ($p < 0.001$). Boxplot marks represent (from bottom to top) 10th and 25th percentiles, median, and 75th and 90th percentiles.
Figure 4. Map of probability of walleye occurrences throughout Sandusky Bay, Lake Erie, Ohio during the pre-spawn time period. Probabilities were calculated using logistic regression using substrate, depth, and distance from shore as predictor variables. Walleye observations refer to locations where transmitter-bearing walleye were located during the pre-spawn period, 2008.
Figure 5. Map of probability of walleye occurrences throughout Sandusky Bay, Lake Erie, Ohio during the peak-spawn time period. Probabilities were calculated using logistic regression using substrate, depth, and distance from shore as predictor variables. Walleye observations refer to locations where transmitter-bearing walleye were located during the peak-spawn period, 2008.
Figure 6. Map of probability of walleye occurrences throughout Sandusky Bay, Lake Erie, Ohio during the post-spawn time period. Probabilities were calculated using logistic regression using substrate, depth, and distance from shore as predictor variables. Walleye observations refer to locations where transmitter-bearing walleye were located during the post-spawn period, 2008.
Figure 7. The proportion of walleye found over different substrate types throughout Sandusky Bay, Lake Erie, Ohio during 2008 (primary y-axis) as a function of sex. Included also is the proportion of each substrate type throughout Sandusky Bay (secondary y-axis; see Appendix B).
Figure 8. Fixed locations of spawning mats used to document the occurrence of walleye spawning over gravel/cobble (●) and sand/silt (▲) throughout Sandusky Bay, Lake Erie, Ohio from April 9 until May 6, 2009.
Figure 9. Proportion of sampling sites where walleye eggs were present by substrate type. Values were determined from egg samples collected using spawning mats in Sandusky Bay, Lake Erie, Ohio from April 9 until May 6, 2009. Sampling was conducted over two days during April 23-24 because high waves prevented access to some sites.
Figure 10. Average viability (% alive) of walleye eggs collected over gravel/cobble and sand/silt substrates in Sandusky Bay, Lake Erie, Ohio from April 9 until May 6, 2009 using spawning mats. Error bars denote standard error (SE). Sampling was conducted over two days during April 23-24 because high waves prevented access to some sites. No viability data are available for those dates on which no eggs were found.
Figure 11. Site-specific numbers of walleye eggs collected over gravel/cobble (●) and sand/silt (▲) throughout Sandusky Bay, Lake Erie, Ohio from April 9 until May 6, 2009 using spawning mats.
Figure 12. Substrate composition of Sandusky Bay, Lake Erie, Ohio created using a Voronoi diagram of substrate point data.
Figure 13. Distribution of depths throughout Sandusky Bay, Lake Erie, Ohio interpolated from digital sounding data collected during 1979 (NGDC 2009).
Figure 14. Distance from shore map of Sandusky Bay, Lake Erie, Ohio calculated using Spatial Analyst Toolbar in ArcGIS 9.3 (ESRI 2008).
Figure 15. Historical substrate composition of Sandusky Bay, Lake Erie, Ohio created using a Voronoi diagram of substrate data collected during 1905 (eastern half; Lydecker et al. 1905a; Lydecker et al. 1905b) and 1872 (western half; Lamson et al. 1872a; Lamson et al. 1872b).
APPENDIX B

COMPILATION OF HABITAT DATA
We compiled data for substrate, bathymetry, and distance from shore throughout Sandusky Bay for use in habitat models. The bottom substrate of Sandusky Bay was compiled using a Voronoi diagram of substrate composition data in ArcGIS 9.3 (ESRI 2008). Specifically, a Voronoi diagram creates a series of polygons around a set of points according to the nearest-neighbor rule (Aurenhammer 1991). A reliable experimental variogram could not be calculated from the data because no discernable pattern in the substrate existed (E. Venteris, Ohio Department of Natural Resources, Division of Geological Survey, personal communication). Substrate composition was measured at regular 300-m intervals throughout Sandusky Bay using a petite Ponar and a long-handled pole (Sarkar and Bain 2006). Sampling was carried out only in areas that historically contained rocky substrates (Lamson et al. 1872a; Lamson et al. 1872b; Lydecker et al. 1905a; Lydecker et al. 1905b). We assumed that the area of rock did not increase through time, a probable assumption given that the Sandusky Bay has experienced sedimentation rates as high as 2.0 cm/yr (Walters 1975). Sampling in this manner also allowed us to assess changes in habitat throughout the past century (Appendix C). Substrate data were reclassified into one of two categories: 1, if preferred walleye spawning habitat (i.e., gravel and cobble) was present or 0, if preferred walleye spawning habitat was absent (i.e., sand and silt; Figure 12). Muddy Creek Bay, located at the far
western end of Sandusky Bay, was not sampled because most areas were inaccessible by boat.

Bathymetry data were compiled from digital National Oceanic and Atmospheric Administration (NOAA) National Ocean Service digital soundings collected during 1979 (NGDC 2009). These data constituted the best available source of depth data for the Sandusky Bay region. Sounding point data were interpolated using an ordinary kriging method in ArcGIS 9.3 (ESRI 2008) to generate a vector polygon map (Figure 13). Finally, the distance from shore that a walleye was located was depicted using the Spatial Analyst Toolbar in ArcGIS 9.3 (ESRI 2008; Figure 14). All files were converted to a raster format. A cell size of 5 m x 5 m was used for all habitat layers resulting in \( n = 5,771,962 \) individual cells.
APPENDIX C

HISTORICAL SUBSTRATE OF SANDUSKY BAY
We compiled historical substrate composition data in Sandusky Bay to assess how the substrate has changed through time. Specifically, historical substrate maps of the western (Lydecker et al. 1905a; Lydecker et al. 1905b) and eastern (Lamson et al. 1872a; Lamson et al. 1872b) Sandusky Bay were obtained from the Ohio Geological Survey (OGS) and scanned using large flatbed scanner to create high-resolution images. Using ArcGIS 9.3 (ESRI 2008), images were georeferenced, digitized by creating a series of points over each substrate label, and converted to polygons using a Voronoi diagram (Aurenhammer 1991). Data were categorized whether rock (i.e., gravel or cobble) was present or absent (Figure 15).

We compared the substrate composition from historical (1872, 1905) and current (2009; Appendix B) time periods by assessing changes in the area and proportion of each substrate category (Table 4). The percent change (increase or decrease) in substrate was calculated by subtracting the current area from the historical area and dividing by the historical area. Results revealed that areas containing rock have decreased by 92%, while areas with rock absent (i.e., sand and silt) have increased by 56% (Table 4).