

Wetland Wildlife Populations and Research Group

102 – 23rd Street Northeast

Bemidji, Minnesota 56601

(218) 308-2282

EVALUATION OF THE EFFECT OF GRAZING ON SELECTED GRASSLAND VARIABLES

David Rave, Kevin Kotts, and John Fieberg

SUMMARY OF FINDINGS

In 2011, we began a study in or near Working Land Initiative Areas to determine the effects of grazing on habitat metrics thought to be associated with the abundance of grassland bird communities. Specifically, we wanted to look at grazing impacts on woody vegetation, white lady slippers (*Cypripedium candidum*), and the diversity of plant species in upland and wetland areas. Preliminary sites were selected and initial data collection began in 2011.

INTRODUCTION

The Minnesota Department of Natural Resources acquires and manages Wildlife Management Areas primarily to establish and maintain optimal population levels of wildlife while maintaining ecological diversity; maintaining or restoring natural communities and ecological processes; and maintaining or enhancing populations of native species (including uncommon species and state- and federally-listed species). Prior to settlement and implementation of agriculture, natural disturbance in the form of fire and grazing maintained native grassland diversity and productivity (Anderson 1990). Wildlife managers have traditionally used spring prescribed burns to simulate these natural disturbances (K. Kotts, personal communication). Although burns can be effective, they are weather dependent, and require a large investment in personnel time, often making it difficult to attain habitat management goals. A variety of other options for creating disturbances in native grass stands are available to wildlife managers (e.g., grazing, haying, biomass harvest), but less is known about the response of native grass stands to these treatments. In particular, several managers have expressed interest in using grazing to help manage grasslands, but grazing has seen limited use due to questions surrounding its effectiveness as a management tool.

Historically, the major factors influencing grassland ecosystems were fire, grazing by herbivores, and climatic variations (Kirsch et al. 1978). Wildlife managers attempt to simulate these effects by manipulating vegetation. Grazing and mowing (Kirsch et al. 1978) and prescribed burning (Kirsch and Kruse 1972) are used to set back succession on managed areas. The suppression of these types of disturbances in prairie grasslands results in the invasion of woody species (Sauer 1950; Stewart 1956). Kirsch and Kruse (1972) found that species diversity of bird and vegetative species, as well as nest success, increased in managed versus non-managed grass fields in North Dakota.

Many species of upland nesting birds utilize residual vegetation as nest sites. Leopold (1933) noted that most waterfowl and gallinaceous birds depend upon residual vegetation for initial nesting attempts. Further, Bue et al. (1952) determined that ducks nesting in western South Dakota chose the tallest, most dense nesting cover available. Many studies have detected a positive relationship between upland nesting birds and grassland disturbance accomplished using grazing (Mundinger 1976, Brown 1978, Duebbert et al. 1986), prescribed burning (Kirsch and Kruse 1972, Tucker et al. 2004, Thatcher et al. 2006), and both treatments in combination (Fuhlendorf and Engle 2004, Trager et al. 2004, Powell 2006). Evaluating treatment response over time is also important as Powell (2006) found that the effects of prescribed burning and grazing on habitats of grassland nesting birds benefited different species depending upon number of years post treatment.

Appropriate response measures will be necessary to evaluate the effectiveness of grazing as a management tool. Sample and Mossman (1997) found that differences in habitat structure are likely more important to bird communities than differences in vegetative species composition. They suggest the following features of grassland habitat are important to grassland nesting birds: 1) vegetation height and density, 2) height and cover of woody

vegetation, 3) litter depth and cover, 4) standing residual (dead) and live herbaceous cover, and 5) ratio of grass vs. forb cover.

This study will attempt to determine if grazing has positive (or negative) impacts on habitat metrics thought to be associated with the abundance of grassland bird communities. Specifically, we will conduct tests of the following null hypotheses:

1. Grazing does not affect the density of woody vegetation.
2. Grazing does not influence the abundance of small white ladies slippers (*Cypripedium candidum*).
3. Grazing does not influence the plant species diversity in upland areas.
4. Grazing does not influence plant species composition in temporary and seasonal wetlands.

STUDY AREA

The study will be conducted in Chippewa, Grant, Kandiyohi, Lac Qui Parle, Renville, Stevens, and Swift counties, within the prairie portion of Minnesota (Figure 1), and will be targeted at Working Lands Initiative (MNDNR unpublished brochure <http://files.dnr.state.mn.us/assistance/backyard/privatelandsprogram/working-lands-ini.pdf>) Focus Areas. Fields sampled will all be located on state managed WMAs or federally managed WPAs.

METHODS

Managed grasslands will be non-randomly selected from fields that will be grazed in 2011 or 2012. Paired subplots of equal size (30 ft²) will be delineated at each site, and one subplot of each pair will be randomly assigned to the “grazing” treatment; the other, the control, will be enclosed using cattle exclusion fencing, and thus protected from grazing. We will attempt to minimize differences between paired subplots when choosing areas for inclusion in the study. Paired subplots will be erected in each of FY12 and FY13, then subplots will be monitored through the end of the growing season 2014 to determine grazing effects.

For each response variable; stem density of woody plant species, blossom densities of small white lady’s slippers (*Cypripedium candidum*), species composition in upland areas, and species composition in seasonal/temporary wetlands; we will select paired subplots, for a total of 12 - 16 paired subplots.

Visual obstruction measurements (VOMs, Robel et al. 1970) will be taken every month from May through August in grazed and control subplots of each field following methods described by Zicus et al. (2006). Three VOM readings will be taken at the 3 quarter points along the longest straight-line transect across each subplot. At each field sampling point, VOMs will be measured in each cardinal direction. This will provide 12 VOMs for each subplot on a given date.

A Daubenmire square (Daubenmire 1959) will be used to determine coverage by various species across grazed and control subplots. We will sample at 3 locations along the transect in all subplots of each field every month from May - August. The 1m² Daubenmire frame will be placed on the ground in 3 locations in each subplot. Each plant species (and % coverage) within the frame will be recorded.

RESULTS

We selected 3 Wildlife Management Areas (WMA) to work on in 2011. The Bjornson WMA was selected because it was scheduled to be grazed and there is a high density of white ladies slippers on the area. We expected high annual variability in the blossom density of lady’s slippers, thus, in June 2011 we erected 3 paired subplots in a single pasture to examine the grazing response of small white ladies slippers. Prior to cattle grazing the unit we counted the

blossoms within each of the grazed and control subplots. In August 2011, we erected 3 paired subplots in 3 pastures on the Simon Lake WMA, and 2 paired subplots on the Helcene WMA. Because of the July, 2011 Minnesota state government shutdown, we were unable to erect all the subplots we had hoped in summer 2011. In FY 2012 we plan to erect another 12 paired subplots in several pastures to examine the grazing response of woody vegetation, and begin to examine species composition changes in uplands and seasonal/temporary wetlands.

DISCUSSION

Management of native grass stands has become an important component of wildlife management in prairie portions of Minnesota (K. Kotts, personal communication). Historically, spring prescribed burning has been the preferred management option used to create disturbances in these fields. However, the amount of habitat manipulated by spring burns is often dictated by spring weather conditions. Knowledge of the response of native grasses to management treatments other than spring burning may allow managers to treat additional acres, or manage grasslands in a more efficient manner.

Further, determining alternate management scenarios for grasslands, particularly those that may have a financial incentive for the landowner (e.g. biofuel harvest, haying, or grazing), may entice some landowners to maintain their land in a grassland program such as CRP, WRP, or managed pasture rather than convert the land into cropland. This would have landscape wide benefits for wildlife, erosion control, and clean water.

Standardizing the many variables associated with grazing (e.g. stocking rates, grazing period), among grazing treatment fields will be challenging. Variation in the implementation of the grazing treatment will add variability to the response measures, and will likely reduce statistical power to detect treatment effects.

ACKNOWLEDGMENTS

Funding for this study was provided by a Working Lands Initiative grant. R. Olsen, J. Strege, C. Vacek, and J. Zajac helped with study logistics.

LITERATURE CITED

- Anderson, R. C. 1990. The historic role of fire in the North American grassland. Pages 8-18 *in* Fire in North American Tallgrass Prairies (S. L. Collins and L. L. Wallace, Eds). University of Oklahoma Press, Norman.
- Brown, D. E. 1978. Grazing, grassland cover and gamebirds. North American Wildlife and Natural Resources Conference Transactions 43:477-485.
- Bue, I. G., L. Blankenship, and W. H. Marshall. 1952. The relationship of grazing practices to waterfowl breeding populations and production on stock ponds in western South Dakota. Transactions North American Wildlife Conference 17:396-414.
- Daubenmire, R.F. 1959. A canopy-cover method of vegetational analysis. Northwest Science 33:43-46.
- Duebber, H. F., J. T. Lokemoen, and D. E. Sharp. 1986. Nest sites of ducks in grazed mixed-grass prairie in North Dakota. The Prairie Naturalist 18(2): 99-108. 1986.
- Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604-614.

- Kirsch, L. M., H. F. Duebbert, and A. D. Kruse. 1978. Grazing and haying effects on habitats of upland nesting birds. North American Wildlife and Natural Resources Conference. Transactions 43:486-497.
- Kirsch, L. M., and A. D. Kruse. 1972. Prairie Fires and Wildlife. Pages 289–303 *in* Proceedings Annual Tall Timbers Fire Ecology Conference.
- Leopold, A. 1933. Game management. Charles Scribner's Sons, New York. 481 pages.
- Mundinger, J. G. 1976. Waterfowl response to rest-rotation grazing. Journal of Wildlife Management 40:60-68.
- Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. The Auk 123:183-197.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-297.
- Sample, D. W., and M. J. Mossman. 1997. Managing Habitat for Grassland Birds. A Guide for Wisconsin. Department of Natural Resources, Madison, Wisconsin 154 pages.
- Sauer, C. O. 1950. Grassland climax, fire and man. Journal of Range Management 3:16-21.
- Stewart, O. C. 1956. Fire as the first great force employed by man. Pages 115-129 *in* Man's role in changing the face of the earth. University of Chicago Press, Chicago and London.
- Thatcher, B. S., D. G. Krementz, and M. S. Woodrey. 2006. Henslow's sparrow winter-survival estimates and response to prescribed burning. Journal of Wildlife Management 70(1): 198-206.
- Trager, M. D., G. W. Wilson, and D. C. Hartnett. 2004. Concurrent effects of fire regime, grazing and bison wallowing on tallgrass prairie vegetation. American Midland Naturalist 152:237-247.
- Tucker, J. W. Jr, W. D. Robinson, J. B. Grand. 2004. Influence of fire on Bachman's sparrow, an endemic North American songbird. Journal of Wildlife Management 68:1114-1123.
- Zicus, M. C., D. P. Rave, A. Das, M. R. Riggs, and M. L. Buitenwerf. 2006. Influence of land use on mallard nest-structure occupancy. Journal of Wildlife Management 70(5):1325-1333.

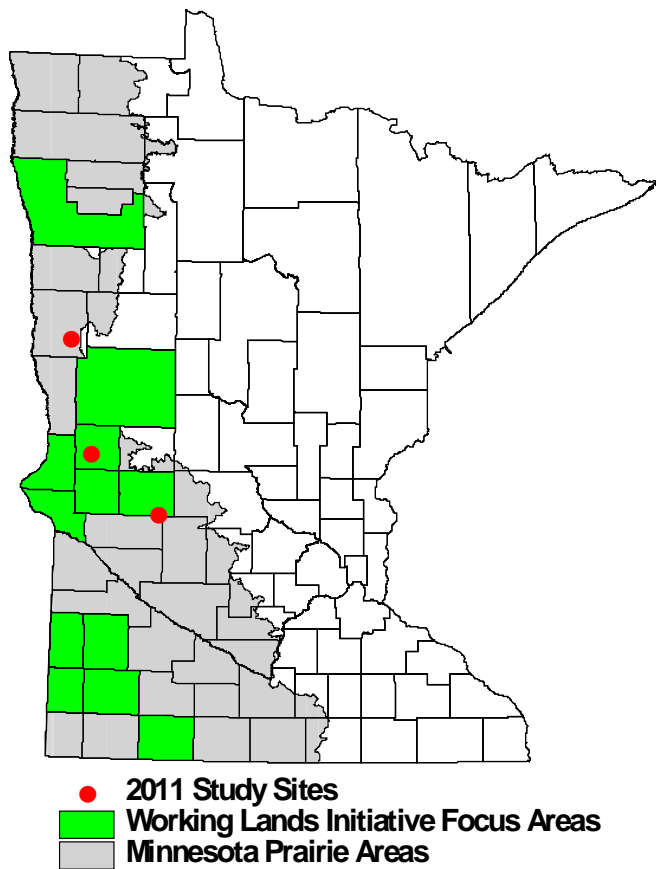


Figure 1. Minnesota counties showing 2011 study sites, Minnesota prairie areas and Working Lands Initiative focus areas, 2011.

NESTING ECOLOGY OF RING-NECKED DUCKS IN THE BOREAL FOREST OF NORTHERN MINNESOTA

Charlotte Roy and Christine Herwig

SUMMARY OF FINDINGS

We have completed 4 years of fieldwork on this research project. Thus far, we have searched 118 wetlands, located 88 ring-necked duck (*Aythya collaris*) nests, marked 50 hens, and followed 22 broods. Nest success during this study has ranged from 0.12-0.46, with high success in a wet year, lower success in dry years, and the lowest success in a year with extreme flooding of nesting habitat. Hen survival during the breeding season has not been previously estimated in Minnesota, and ranged 0.54-0.88, again with high survival in a wet year and low survival in a dry year. Brood survival also has not been estimated previously in Minnesota and was 0.23 for 2008-2010 combined. Additional data collection will enable more robust estimates of these parameters.

INTRODUCTION

The ring-necked duck is a characteristic and important species for the Laurentian Mixed Forest province of Minnesota (Minnesota Department of Natural Resources [MNDNR] 2006), also known as the Boreal or Coniferous Forest biome. Recent surveys near Bemidji have indicated declines in ring-necked duck numbers, despite increases elsewhere in their breeding range (Zicus et al. 2005). Unfortunately, basic information on nest success, hen survival, and brood survival in north-central Minnesota are unavailable, limiting informed interpretation of these local survey data and our understanding of how vital rates affect population growth of ring-necked ducks in the forest. These data are particularly pertinent given the increasing development and recreational use in the forest (MNDNR 2006) and predictions that the spruce-fir forest will shift north of Minnesota as a result of global climate change (Iverson and Prasad 2001).

Nest success, hen survival, and brood survival in the boreal forest are largely unknown. Some data are available for nest success and brood survival in north-central Minnesota (Hohman and Eberhardt 1998) and Maine (McAuley and Longcore 1988, 1989), but data for the boreal forest of the upper Midwest dates back to the early 1970s (Sarvis 1972). Limited data are available for nest success outside the forest; Maxson and Riggs (1996) studied nest success of ring-necked ducks in the forest-prairie transition during 1985–1987, and Koons and Rotella (2003) compared nest success of ring-necked ducks to that of lesser scaup (*Aythya affinis*) in the parkland of Manitoba. However, neither study examined hen or brood survival during the breeding season. In general, nesting and brood-rearing information for diving ducks are limited in comparison to the data available for dabbling ducks (Yerkes 2000).

Gathering information on vital rates during the breeding season is an important first step to understanding recent population patterns of ring-necked ducks in Minnesota. Although sensitivity analyses of vital rates on population growth rates are not available for ring-necked ducks, sensitivity analyses for mid-continent mallards indicated that nest success explained the most variation (43%) in population growth rates (Hoekman et al. 2002). A similar analysis for the Great Lakes Region indicated that duckling survival (32%) and nest success (16%) accounted for the greatest variation in mallard population growth rates during the breeding season (Coluccy et al. 2008).

OBJECTIVES

1. To obtain baseline information on ring-necked duck nest success, hen survival, and brood survival before fledging in the forest.

2. To examine how these vital rates vary along a gradient of development and recreational use (e.g., number of dwellings, boat access, proximity to roads).

METHODS

We used multiple methods and data sources to identify lakes to search, including locations of pairs and lone males from a ring-necked duck helicopter survey conducted during 2004–2010 and ground surveys conducted on 10–14 lakes in the Bemidji area beginning in 1969. The survey data were used to identify land cover attributes of wetlands that ring-necked ducks used (US Geological Survey Gap Analysis Program [GAP] types 12 and 13 surrounded by GAP types 10, 14, and 15). We identified 103 lakes within a 40-km (25-mile) radius of Bemidji with land cover attributes similar to those used in the 2 surveys. In 2009, we scouted wetlands in early spring and focused nest-searching efforts on the wetlands where ring-necked ducks had been seen. In 2010, we used scouting data from 2007 to 2009 to identify lakes where ring-necked ducks had been observed. We excluded lakes considered unsafe to search or where we had been denied access. This process resulted in 95 basins as potential targets for nest-searching in 2010 and 2011. In 2011, 8 more wetlands were added due to preseason scouting and the location of a radio-marked hen on 1 wetland.

We searched for ring-necked duck nests in the springs and summers of 2008–2011. To locate nests, we searched emergent vegetation on floating bog mats and along wetland margins using bamboo poles and nest drags. When a nest was located, we determined the stage of incubation by candling eggs (Weller 1956) and from the appearance of new eggs in the nest. We determined water depth and distance to open water at each nest after it hatched or failed.

Late in incubation, we trapped hens on nests with Weller traps (Weller 1957) to attach radio-transmitters. Because we were initially concerned that a surgical transmitter attachment method might be too disruptive to incubating hens, we tried a bib-type transmitter attachment method, which had been used with previous success in wood ducks (Montgomery 1985). This attachment method was faster and less invasive than surgical methods. Hens received a transmitter fastened to a Herculite[®] fabric bib with dental floss and superglue (total weight of approximately 11 g). We modified the method used unsuccessfully with redheads (*Aythya americana*) by Sorenson (1989) by securing the bib more tightly and by preening the bib into the breast feathers as in Montgomery (1985). After the transmitter was in place, we trimmed any excess fabric so that feathers concealed the transmitter. Due to concerns about low hen survival in 2009 and low brood survival during 2008 and 2009, we changed the transmitter attachment method in 2010. We tried the surgical transmitter attachment method that we had been using for the MNDNR-funded study on post-fledging ring-necked ducks (Korschgen et al. 1996). However, we used a local anesthetic (i.e., lidocaine) instead of isoflurane so that we could do surgeries in the field (Corcoran et al. 2007). We also used propofol, injected intravenously, to reduce nest abandonment (Rotella and Ratti 1990, Machin and Caulkett 2000) on 6 hens in 2010 and on all hens in 2011. When propofol was used, hens were placed on nests rather than being released from the edge of the wetland.

Nests were monitored every 4–7 days to determine fate (abandoned, depredated, or successful) and Mayfield nest success (Mendall 1958, Mayfield 1975). After nests hatched, we attempted to monitor broods every 3–7 days. At each observation, we counted the ducklings present, and when possible, aged them from a distance based on plumage characteristics (Gollop and Marshall 1954). Broods were monitored until ducklings reached age Class III (39–49 days old) or until total brood loss occurred. We considered hens to have lost their entire brood when hens were observed without any ducklings for 3 consecutive observations or if the hen was found >16 km (10 miles) from the nesting lake. We continued to monitor hens after the brood-rearing period for as long as they could be tracked before migration to examine their survival using the Kaplan-Meier method (Kaplan and Meier 1958).

In 2011, the state government shutdown occurred 1 July to 20 July, during peak weeks

of ring-necked duck hatching. We were still finding nests at the time of the shutdown (2 nests were located 2 days before the shutdown) and 5 nests were still active when the shutdown began. We attempted to check nests that had been active and locate broods when state government activities resumed. However, the shutdown precluded data collection according to the methods described above.

RESULTS

Thus far, we have searched 118 wetlands (Figure 1), located 88 active nests, marked 50 hens, and followed 22 broods. We searched for nests on 37 wetlands for a total of 73 searches (17 wetlands searched once and 20 wetlands searched >1 time) between 22 May and 22 July 2008, 37 wetlands searched 54 times (21 wetlands once and 16 wetlands searched >1 time) between 29 May and 22 July 2009, 73 wetlands searched 128 times (35 wetlands once and 38 wetlands searched >1 time) between 19 May and 12 July 2010, and 76 wetlands were searched 107 times (54 wetlands once and 22 wetlands searched >1 time) between 23 May and 30 June 2011.

Nest Survival

We located 18 (14 active, 4 depredated when found) ring-necked duck nests on 10 wetlands in 2008, 20 active nests on 11 wetlands in 2009, 32 active nests on 17 wetlands in 2010, and 22 active nests on 16 wetlands in 2011. In 2008, 8 nests hatched, 4 were depredated when found, 3 were depredated after they were found, and 3 nests were flooded by rising water levels following rain events. Average clutch size for nests that were incubated was 9.1 ± 0.6 (mean \pm SE, range = 7–15, $n = 12$ nests with 109 eggs) and $86.6 \pm 0.1\%$ of eggs hatched in nests that hatched. In 2009, 7 nests hatched, 9 were depredated, and 4 were abandoned, with at least 2 cases of abandonment likely due to trapping. The average clutch size for incubated nests was 8.3 ± 0.3 (range = 7–11, $n = 19$ nests with 158 eggs) and $89.5 \pm 0.6\%$ of the eggs hatched in nests that were successful. In 2010, 13 nests hatched, 9 were depredated, 6 were abandoned after trapping and transmitter attachment, 2 were abandoned for other reasons, 1 had an unknown fate because we could not determine the outcome based on evidence at the nest site, and 1 failed because the hen died during transmitter-implantation surgery. We began using propofol on all hens captured later in the field season because 5 of 13 hens marked without propofol had abandoned their nests. Average clutch size for incubated nests was 8.3 ± 0.3 (range = 5–10, $n = 30$ nests with 250 eggs) and $84.5 \pm 0.1\%$ of eggs hatched. In 2011, 6 nests hatched, 3 were abandoned (2 to investigator disturbance and 1 for unknown reasons), and 13 were depredated. Average clutch size was 8.8 ± 0.4 (range = 4–11, $n = 19$ nests with 166 eggs) and hatching success was $85.0 \pm 0.2\%$. Mayfield nest success for a 35-day period of laying and incubation was 30% in 2008, 27% in 2009, 46% in 2010, and 12% in 2011.

Hen Survival

We put transmitters on 8 hens in 2008, 14 hens in 2009, 19 hens in 2010, and 9 hens in 2011. In 2008, 2 hens died due to predation during the tracking season; 1 lost her nest late in incubation and the other had a brood. Both of these birds had been observed preening more than other birds with transmitters, although this behavior occurred during the first 2 weeks after marking and then subsided. Both deaths occurred after this period, one 3 weeks post-marking and the other 4 weeks post-marking. All birds in 2008 continued to nest and rear broods after transmitter attachment, with the exception of birds that lost their nests to flooding. In 2009, 6 hens died during the monitoring period (17, 20, 32, 33, 55, and 84 days post-marking). Evidence obtained at the recovery sites indicated that radioed birds were either depredated or scavenged by avian predators (3) or by mammalian predators (1). Additionally, there were 2

cases in which a probable cause of death could not be determined, because the transmitter was underwater and no carcass was found. All of the hens that died did not have broods at the time of death; 3 lost their nest late in incubation, 1 abandoned her nest due to trapping, and 2 lost broods early after hatching. In 2010, only 1 hen died during the monitoring period. She died 17 days after marking and appeared to have been killed by a mammalian predator. She did not have a brood. Twelve of 19 transmitters dehiscence 55.1 ± 6.0 days (range = 30–121 days) after attachment. In 2011, 2 hens were depredated, one by a mink and the other by an unknown predator. One hen did not recover from anesthesia and her nest was censored. One hen dehiscence her transmitter in mid-August, 53 days after marking. Hen survival through mid-September was 0.80 ± 0.18 for 2008, 0.54 ± 0.08 for 2009, 0.88 ± 0.11 for 2010, 0.69 ± 0.19 for 2011 (through 19 August because too few hens were marked to justify tracking through September).

Brood and Duckling Data

In 2008, 7 radiomarked hens had broods ($n = 57$ ducklings). One brood survived to fledge 5 ducklings. Other broods dwindled slowly, with total brood loss at the IA (1), IB (1), IC (1), and IIA (2) age classes (Gollop and Marshall 1954). The fate of 1 brood could not be determined, because the hen died when the brood was at the IIA stage, and we could no longer relocate the ducklings without the marked hen. We also monitored the brood of 1 unmarked hen that was not trapped in time to give her a transmitter. Her brood made it to the IC stage, but they were not observed again and their fate was uncertain.

Seven broods were monitored in 2009 ($n = 56$ ducklings). Total brood losses occurred at IA (3), IB (1), and IC (1) age classes. One brood fledged 2 young. Another brood matured to IIA before the hen left the wetland, after which time 1 duckling was seen on the wetland and no hens were present.

We observed 6 broods in 2010 ($n = 40$ ducklings); 3 broods survived to age Class III and likely fledged 14 ducklings, 1 brood was located as Class IA ducklings, but the hen was not located again, 1 brood survived until age Class 1A, and another brood survived to age Class IB. Seven marked hens were believed to have hatched ducklings, but were not located with broods before total brood loss.

In 2011, following the government shutdown, we were able to locate 5 hens and follow 2 broods that were still alive. Both broods fledged; one brood of 3 ducklings made it to flight (50 days) and the other had 6 ducklings survive until at least class III (42 days, and most likely flight). Thus, excluding 2011, brood survival to fledging was 0.23 ± 0.09 .

Brood movements also were observed. In 2009, for example, a hen moved her 3 (IC) young from the nesting wetland to another wetland (~1,205 m) from which they fledged. In another instance, a hen and her brood of 6 (IB) were seen walking to another wetland ~365 m from their nesting wetland. In 2010, 4 hens moved their broods to nearby wetlands at various ages (i.e., IA, IC, IIA, IIB). One of these hens later returned with her brood to the wetland where they hatched and her brood later fledged.

DISCUSSION

Our success finding nests has been comparable to that in other studies that found ring-necked duck nests (45 nests in 3 years, Maxson and Riggs 1996; 35 nests in 2 years, Koons and Rotella 2003, 188 nests in 6 years by R. T. Eberhardt). Thus far, our results have been similar to findings by R. T. Eberhardt in northern Minnesota during 1978–1984 (Hohman and Eberhardt 1998). Our nest survival rates are comparable to his estimates of 44% based on 188 nests. The causes of nest failure in our study (17% flooding, 70% depredation, and 13% abandonment) were similar to those of other studies (16–24% flooding, 67–80% depredation, and 5% abandonment; Mendall 1958, McAuley and Longcore 1989), if we exclude nests where abandonment was attributed to investigator disturbance. Early estimates of hatching success

appeared to be lower than those of Eberhardt's previous study in north-central Minnesota (94%, Hohman and Eberhardt 1998), but the springs and summers of 2008 and 2009 were very cool and rainy, and early summer 2010 was very rainy as well, which may have chilled eggs and flooded nests. The spring of 2011 was unusually wet and we noticed unusually high depredation rates of nests, which we hypothesize may have been due to contraction of available nesting habitat due to extremely high water levels.

Our hen survival rates for the period June–mid-September were comparable to reports for hen mallards during April–September (0.80, Cowardin et al. 1985; 0.60, Blohm et al. 1987; 0.67, Brasher et al. 2006). This was unexpected because we marked hens late in incubation, and incubation is a period when hen mortality is expected to be greatest. Brood survival rates also seemed low. Brood survival in ring-necked ducks has only been examined previously in Maine (77% to 45 days, $n = 64$, McAuley and Longcore 1988). Duckling survival in the same study was 37% ($n = 381$). Further investigation is necessary to get better estimates of hen survival and brood survival in ring-necked ducks in Minnesota.

This study is planned to continue through 2012. Results should be viewed as preliminary and are subject to change with further data collection.

LITERATURE CITED

- Blohm, R. J., R. E. Reynolds, J. P. Bladen, J. D. Nichols, J. E. Hines, K. H. Pollock, and R. T. Eberhardt. 1987. Mallard mortality rates on key breeding and wintering areas. Transactions of the North American Wildlife and Natural Resources Conference. 52:246-257.
- Brasher, M. G., T. W. Arnold, J. H. Devries, and R. M. Kaminski. 2006. Breeding-season survival of male and female mallards in Canada's prairie-parklands. Journal of Wildlife Management 70:805-811.
- Coluccy, J. M., T. Yerkes, R. Simpson, J. W. Simpson, L. Armstrong, and J. Davis. 2008. Population dynamics of breeding mallards in the Great Lakes states. Journal of Wildlife Management 72:1181-1187.
- Corcoran, R. M., J. R. Lovvorn, M. R. Bertram, and M. T. Vivion. 2007. Lesser scaup nest success and duckling survival on the Yukon flats, Alaska. Journal of Wildlife Management 71:127-134.
- Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92. 37pp.
- Gollop, J. B., and W. H. Marshall. 1954. A guide to aging duck broods in the field. Unpublished report. Mississippi Flyway Council Technical Section,
Online. <http://www.npwrc.usgs.gov/resource/birds/ageduck/index.htm> last accessed 10/14/11.
- Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, I. J. Ball. 2002. Sensitivity analyses of the life cycle of mid-continent mallards. Journal of Wildlife Management 66:883-900.
- Hohman, W. L., and R. T. Eberhardt. 1998. Ring-necked Duck (*Aythya collaris*). In The Birds of North America, No. 329 A. Poole and F. Gill, eds. The Birds of North America, Inc., Philadelphia, Pennsylvania. 32 pp.
- Iverson, L. R., and A. M. Prasad. 2001. Potential changes in tree species richness and forest community types following climate change. Ecosystems 4:186-199.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457-481.
- Koons, D. N., and J. J. Rotella. 2003. Comparative nesting success of sympatric lesser scaup and ring-necked ducks. Journal of Field Ornithology 74:222-229.
- Korschgen, C. E., K. P. Kenow, W. L. Green, M. D. Samuel, and L. Sileo. 1996. Technique for implanting radiotransmitters subcutaneously in day-old ducklings. Journal of Field Ornithology 67:392-397.
- Machin, K. L., and N. A. Caulkett. 2000. Evaluation of isoflurane and propofol anesthesia for intra-abdominal transmitter placement in nesting female canvasback ducks. Journal of Wildlife Diseases 36:324-334.
- Maxson, S. J., and M. R. Riggs. 1996. Habitat use and nest success of overwater nesting ducks in westcentral Minnesota. Journal of Wildlife Management 60:108-119.

- Mayfield, H. F. 1975. Suggestions for calculating nest success. *The Wilson Bulletin* 87:456-466.
- Mendall, H. L. 1958. Ring-necked duck in the Northeast. University of Maine Orono, study no. 73, *Bulletin* 60(16): 317 pp.
- McAuley, D. G., and J. R. Longcore. 1988. Survival of juvenile ring-necked ducks on wetlands of different pH. *Journal of Wildlife Management* 52:169-176.
- McAuley, D. G., and J. R. Longcore. 1989. Nesting phenology and success of ring-necked ducks in east-central Maine. *Journal of Field Ornithology* 60:112-119.
- Minnesota Department of Natural Resources. 2006. A vision for wildlife and its use – goals and outcomes 2006–2012. Minnesota Department of Natural Resources, St. Paul. <http://files.dnr.state.mn.us/aboutdnr/reports/strategic-documents/wildlife-strategic-plan05-12.pdf> Last accessed 17 February 2010.
- Montgomery, J. 1985. A collar radio-transmitter attachment for wood ducks and other avian species. *Proceedings of the International Conference on Wildlife Biotelemetry* 5:19-27.
- Rotella, J. J., and J. T. Ratti. 1990. Use of methoxyflurane to reduce nest abandonment in mallards. *Journal of Wildlife Management* 54:627-628.
- Sarvis, J. E. 1972. The breeding biology and ecology of ring-necked ducks in northern Michigan. M. S. thesis, Utah State University, Logan.
- Sorenson, M. D. 1989. Effects of neck collars on female redheads. *Journal of Field Ornithology* 60:523-528.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- Weller, M. W. 1957. An automatic nest-trap for waterfowl. *Journal of Wildlife Management* 21:456-458.
- Yerkes, T. 2000. Nest-site characteristics and brood-habitat selection of redheads: an association between wetland characteristics and success. *Wetlands* 20:575-580.
- Zicus, M. C., D. P. Rave, J. Fieberg, J. Giudice, and R. Wright. 2005. Minnesota's ring-necked ducks: a pilot breeding pair survey. Pages 137–158 in P. J. Wingate, R. O. Kimmel, J. S. Lawrence, and M. S. Lenarz, eds. *Summaries of wildlife research findings, 2004*. Minnesota Department of Natural Resources, Wildlife Populations and Research Group, St. Paul.

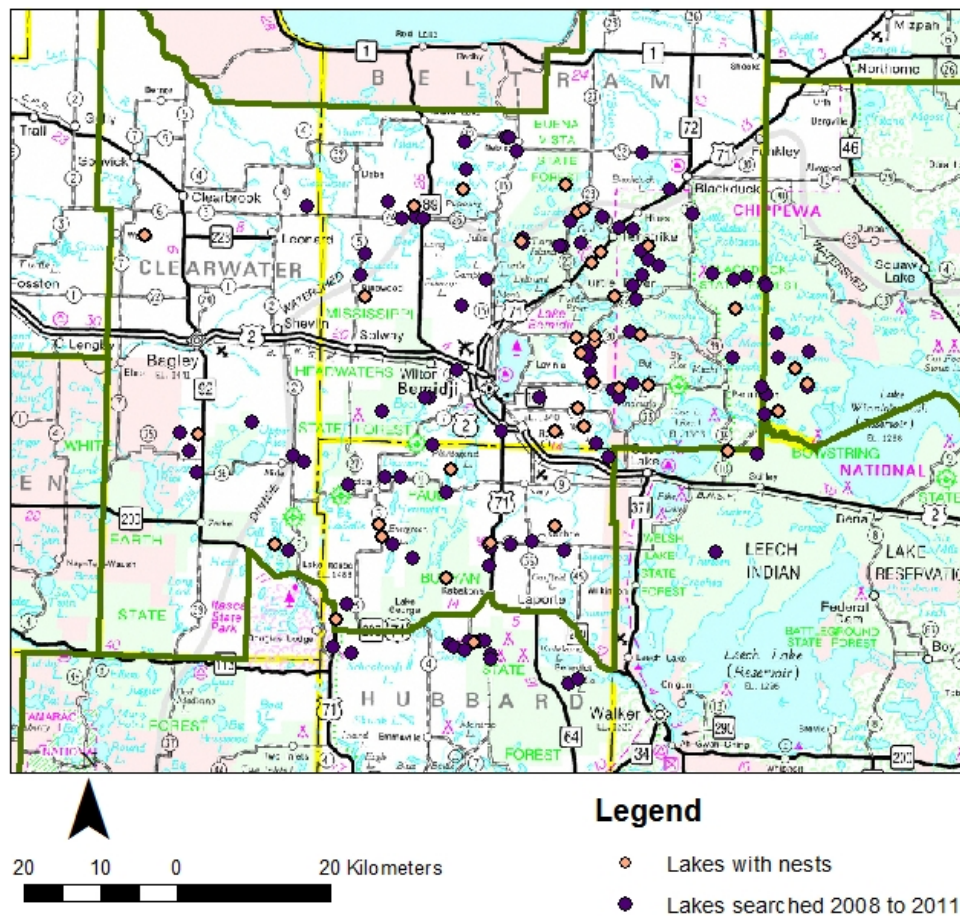


Figure 1. Wetlands searched for ring-necked duck nests in north-central Minnesota during 2008–2011.

INVESTIGATION OF TREMATODES AND FAUCET SNAILS RESPONSIBLE FOR LESSER SCAUP AND AMERICAN COOT DIE-OFFS

Charlotte Roy and Christine Herwig

SUMMARY OF FINDINGS

Two waterfowl die-offs occurred on Lake Winnibigoshish in 2011. During spring 2011, several hundred Lesser Scaup scaup (*Aythya affinis*) were observed moribund, unable to fly and/or keep their heads up, and necropsy later confirmed trematodiasis. Later in the fall of 2011, 5-10% of a raft of 800-1,000 Lesser Scaup appeared sick near Third River Flowage. Trematodiasis was again confirmed through necropsy of dead individuals. Additionally, a few sick birds were observed at Bowstring and Round lakes, but whether they were infected with trematodes and the origin of the disease was unknown.

The invasive faucet snail is the only known first host of the trematodes, so we sampled faucet snails where they are known to occur in Minnesota; Lake Winnibigoshish, Upper and Lower Twin lakes, the Shell River, First Crow Wing Lake, and Crow Wing River. We detected the trematodes *Cyathocotyle bushiensis* and *Sphaeridiotrema globules* in all sites, with the exception of Upper Twin Lake where we only found *S. globules*. We also sampled Bowstring and Round lakes for faucet snails, because these lakes are known to be important to migrating Lesser Scaup. We report the first detection of faucet snails in Round Lake, although we have not yet detected the trematodes there. We still have not detected faucet snails or the trematodes at Bowstring Lake.

INTRODUCTION

During the autumn of 2007, 7,000 Lesser Scaup (*Aythya affinis*) and hundreds of American Coots (*Fulica americana*) died on Lake Winnibigoshish in north-central Minnesota (Lawrence et al. 2008). In 2008, 2,000 more birds died (Lawrence et al. 2009). These deaths were attributed to trematodiasis caused by non-native intestinal trematodes (*Cyathocotyle bushiensis*, *Sphaeridiotrema globules*, and *Leyogonimus polyoon*).

The trematode species responsible for the die-offs have a complex life cycle that involves two intermediate hosts. The faucet snail (*Bithynia tentaculata*), a non-native species from Europe (Sauer et al. 2007), is the only known first intermediate host of these trematodes in the Midwest and also serves as the second host for *C. bushiensis* and *S. globules*. The second host of *L. polyoon* is one of a variety of larval aquatic insects, including damselflies (Zygoptera) and dragonflies (Odonata) (National Wildlife Health Center, unpubl. data). Adult trematodes develop in waterfowl after they consume infected snails and in American Coots (*Fulica americana*) and Common Moorhens (*Gallinula chloropus*) after consumption of infected insects. Parasite eggs are then defecated by sick birds and later ingested by snails, continuing the cycle. Because of this complex life cycle, the dynamics of faucet snail distribution and transmission of these parasites to Lesser Scaup and other birds are poorly understood.

The faucet snail was first detected in Lake Winnibigoshish in the spring of 2008, following the waterfowl die-off the previous fall. The faucet snail was detected in Upper and Lower Twin lakes and the Shell River in Minnesota in 2009. In 2010, the Crow Wing River was designated as infested with faucet snails, and in 2011, First Crow Wing Lake and Second Crow Wing Lake were added to the list of waters infested with faucet snails. These new infestation sites may afford us additional opportunities to learn about this disease cycle. We will examine the factors associated with faucet snail abundance and distribution, parasite prevalence within

snails, and the influence of snail densities and site attributes (e.g., water depth, distance from shore, substrate composition) on Lesser Scaup foraging.

OBJECTIVES

1. Improve understanding of Lesser Scaup foraging as it relates to faucet snail and other food source distribution and density, including water depth, distance from shore, and substrate composition
2. Examine factors (e.g., temperature, substrate, vegetation, other snail species) that are associated with the distribution and movement of faucet snails
3. Examine the factors that influence the prevalence of the parasites in faucet snails (e.g., snail density, temperature, microhabitat, time of year)
4. Examine how faucet snail distribution varies during spring, summer, and fall

METHODS

During 2011, we sampled faucet snails during spring, summer, and fall at the same points within a lake or river (Table 1a,b). In small lakes (<1000 acres/404 hectares), we used transects that traversed the entire length of the lake and across a range of depths. In large lakes, we used index areas with points stratified by depth for sampling. In Lake Winnibigoshish, we had 2 index areas, the West Winni Index Area and the East Winni Index Area, which were 5-6 km along the longest dimension and approximately 2 km in width (Fig. 1). In rivers, we sampled points at regular intervals (500 m) along the infested corridor for a maximum length of 10 km.

We used 2 sampling methods; we used a bottomless sampling cylinder (0.2 m²) at 30 and 60 cm depths for comparisons with an ongoing study on the Upper Mississippi River, and we also sampled with a benthic sled to standardize our protocol for all depths. We dragged the sled a distance of 1.2 m at deeper depths to examine how snail distribution varied within a water body. We collected data on microhabitat variables at each point to examine relationships to snail distribution, the snail community, and parasite prevalence. These included substrate (e.g., silt, rock, sand, vegetated, muck, etc.), temperature (C°), water depth (cm), and a secchi depth (cm) reading was taken 8 times (4 times on the way down and 4 times on the way up) from the shaded side of the boat and averaged. At each snail collection site, we determined pH, dissolved oxygen (mg/L), conductivity (µS/cm), and salinity (‰) with a Hach Company (Loveland, Colorado) HQd portable meter that was calibrated daily for pH and weekly for conductivity. Flow (mps) was measured at 60% of the total depth (from the surface) with a Global Water Instrumentation (Gold River, California) flow probe when flow was detectable and averaged over a 40 s interval (the USGS “6 tens method”).

Invertebrate samples were stored in the refrigerator until processed. We used a magnifying lens and microscope as needed to identify all invertebrates to Order and noted their presence in each sample. We identified all snails to genus and counted their numbers in each sample. We determined the size of *B. tentaculata* and similarly sized *Amnicola* spp. with calipers, as measured along the central axis from the apex. Parasite prevalence was determined for all samples possessing at least 50 *B. tentaculata* (R. Cole, NWHC, unpubl. data). For samples possessing 10-49 *B. tentaculata*, we collected additional snails while in the field from the same location at the same time to increase the number of samples for which we could do prevalence. These additional snails were not used in the determination of snail abundance at the site. Trematode stages (cercariae or metacercariae), species (*C. bushiensis*, *S. globulus*, *L. polyoon*), and numbers were also recorded in the lab.

Each season, we collected a water sample at each sample lake or river and sent it to the Minnesota Department of Agriculture for analysis. Total phosphorus (ppm), nitrite plus nitrate

nitrogen (ppm), chlorophyll a (ppb), total alkalinity (ppm), ammonia nitrogen (ppm), and calcium (ppm) were quantified but have not yet been interpreted.

We also identified sites where Lesser scaup foraged and collected benthic samples at these locations. These sites were identified through observations of birds from shore or from a boat. We determined the location of rafts of scaup using a compass from 2-3 observation points, which was plotted in ArcMap version 10 (Environmental Systems Research Institute, Inc., Redlands, California) to determine the area occupied by the birds. We then sampled at 100 m intervals along a transect through this area. Food densities, water depths, distance from shore, lake size, and substrate composition at these foraging locations were recorded using the same techniques as snail sampling.

We also collected scaup carcasses during die-offs at study lakes (Fig. 1) for confirmation of trematodiasis by the NWHC in Madison, Wisconsin. Additionally, Bowstring and Round lakes are known for having large number of scaup, particularly in the fall, and have been the sites of trematodiasis die-offs in the past. We monitored Bowstring and Round lakes for scaup die-offs during the spring and fall and collected benthic samples during the summer of 2011 to search for faucet snails which have not previously been detected at these lakes.

RESULTS

Faucet snails

We detected faucet snails at both index areas on Lake Winnibigoshish, Upper and Lower Twin lakes, the Shell River, First Crow Wing Lake, and Crow Wing River (Table 1). We also report the first detection of faucet snails in Round Lake (Fig. 1).

We did not find faucet snails on Bowstring Lake, but we did detect metacercarial stages of the trematodes in banded mystery snails (*Viviparus georgianus*) collected from Bowstring, suggesting that either the faucet snail is present but not yet detected here, or that another snail species is serving as the first intermediate host. Samples of *V. georgianus* were sent to University of Wisconsin-LaCrosse for experimental challenges with miracidial stages of trematodes to determine whether it can serve as the primary host of these trematodes.

Preliminary analysis indicates that faucet snails are more abundant during the summer than during fall or spring. Faucet snails also appear to move into shallower depths in the summer, perhaps to reproduce on vegetation, with a return to deeper depths in fall and spring. Additional data collection will help determine whether this is a robust seasonal pattern. At the Twin lakes, populations of faucet snails may be expanding and increasing; further data collection will be necessary to determine whether separation of population growth and expansion from seasonal patterns is possible. More formal analyses will be included in subsequent reports.

Trematodes

Both *C. bushiensis* and *S. globulus* were detected on Lake Winnibigoshish, Lower Twin Lake, the Shell River, Bowstring Lake, and the Crow Wing River. Only *S. globulus* was detected in samples from Upper Twin Lake. Faucet snails collected from Round Lake were not infected with trematodes, but we only found snails at one location which likely limited our ability to detect infections. Prevalence (proportion of snails infected) of *C. bushiensis* was generally higher than that of *S. globulus* within a water body. Among water bodies, the West Winni Index Area and Shell River had very high prevalence relative to that of the Twin lakes and East Winni Index Area. Prevalence was generally highest in the spring and fall, and lowest in the summer, but some exceptions did occur. Intensity (number of parasites in infected snails) of parasites also appeared highest in the spring and fall, but the highest intensity observed was of *S.*

globulus in the summer at West Winni Index Area. Intensities of both *C. bushiensis* and *S. globulus* were highest at West Winni Index Area and were consistently high enough to result in mortality of waterfowl within 8-10 days after consumption of 4-20 snails (Mucha and Huffman 1991). Not coincidentally, this is where the waterfowl die-offs have been occurring on Lake Winnibigoshish (Fig. 1).

Scaup

We also collected benthic samples from below rafts of foraging scaup (Table 1). Foraging could only be confirmed in the spring, as we could not get close enough to the raft during hunting season to evaluate whether they were foraging. We observed large rafts of scaup during our visits to Bowstring, Round, and Winnibigoshish lakes (Table 2). Staff from the Minnesota Department of Natural Resources-Grand Rapids office also made regular visits to Winnibigoshish, Round, and Bowstring lakes throughout the season to check for sick birds (Table 2).

Two die-offs occurred on Lake Winnibigoshish in 2011; during spring 2011 a raft of 2,000 birds were observed on the west side and several hundred sick birds were documented (Table 2). Nine birds (2 Greater Scaup, 7 Lesser Scaup) were collected and sent to the NWHC. Trematodiasis was confirmed. During fall 2011, a raft of 800-1,000 Lesser Scaup was observed near Third River Flowage at Lake Winnibigoshish, with 5-10% of the raft exhibiting symptoms of trematodiasis. Five Lesser Scaup were collected from this die-off and sent to the NWHC for confirmation of trematodiasis and it was confirmed. We also collected benthic samples from below the raft of sick scaup. A few sick birds were also observed at Bowstring and Round lakes (Table 2).

DISCUSSION

This report summarizes activities for the first full year of field work (spring, summer and fall 2011). Fall 2010, a pilot season, was included in an earlier report. Data entry and analysis is preliminary and still underway. More formal analyses will be included in subsequent reports. We plan to continue using the same methodology, adding additional lakes with faucet snails as they become known, through fall 2012.

LITERATURE CITED

- Lawrence, J. S., S. D. Cordts, R. A. Cole, and P. Loegering. 2008. Determining gastropod hosts of trematodes and monitoring lesser scaup and coot mortality in north central Minnesota. Unpublished Phase 1 Proposal, Minnesota Department of Natural Resources, Wildlife Research.
- Lawrence, J. S., P. Loegering, R. A. Cole, and S. D. Cordts. 2009. Scaup and coot die-off at Lake Winnibigoshish-2008 Update. Minnesota Department of Natural Resources, Section of Wildlife, unpublished report, Minnesota Department of Natural Resources, Wildlife Research.
- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Seacor. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19(1):1-54.
- Mucha, K. H., and J. E. Huffman. 1991. Inflammatory cell stimulation and wound healing in *Sphaeridiotrema globulus* experimentally infected mallard ducks (*Anas platyrhynchos*). *Journal of Wildlife Diseases* 27(3):428-434.

Table 1a. Sampling sites for faucet snails in northern Minnesota water bodies during spring, summer, and fall 2011. Number of points refers to the number of points sampled each season of sampling.

Location	No. seasons sampled	No. sample points	Faucet snails detected
East Winni Index Area	3	80	Yes
West Winni Index Area	3	80	Yes
Bowstring Lake	1 (Summer)	61	No
Round Lake	1 (Summer)	42	Yes
Upper Twin Lake	3	24	Yes
Lower Twin Lake	3	39	Yes
First Crow Wing Lake /River	1 (Fall)	18	Yes
Shell River	3	22	Yes
Total		874	

Table 1b. Sampling sites for faucet snails associated with Lesser Scaup in northern Minnesota water bodies during spring and fall 2011. Number of points refers to the number of points sampled each season of sampling.

Location	Season sampled	No. sample points	Faucet snails detected
Lake Winnibigoshish	Spring/Fall	2/3	Yes
Sugar Lake	Fall	2	No
Bowstring Lake	Fall	8	No
Round Lake	Fall	6	Yes
Total		21	

Table 2. Reports of scaup observed by Minnesota Department of Natural Resources staff on lakes in northern Minnesota during spring and fall 2011. Scaup that failed to escape approach or had drooping heads were considered to be sick; dead birds were typically found along the shoreline.

Location	Date	Total no. of scaup observed	No. of sick or dead scaup observed
SPRING			
Winnibigoshish	4/19/11	1,800	None
Winnibigoshish	4/20/11	1,600 ^a	200 sick
Winnibigoshish	4/22/11	1,500	None
Winnibigoshish	4/25/11	2,000	None
Bowstring	5/3/11	1,200-2,500	None
Round	5/3/11	200-400	None
Winnibigoshish	5/5/11	7,200	6-12 sick, 1 collected ^b
Winnibigoshish	5/6/11	9,000	300 sick, 6 collected
Winnibigoshish	5/11/11	900-1,000	~20% suspected sick
Winnibigoshish	5/19/11	Not reported	3 sick, 10 dead
FALL			
Bowstring	10/4/11	10	None
Round	10/4/11	0	None
Winnibigoshish	10/4/11	0	None
Round	10/13/11	100-1,000	None
Bowstring	10/19/11	5,000	None sick, 1 dead
Winnibigoshish	10/20/11	2,000	2 dead near Third River Flowage
Round	10/24/11	5,000-7,000	5 suspected sick
Winnibigoshish	10/24/11	200-300	Not assessed
Bowstring	10/25/11	2,000-3,000	1 suspected sick, 1 dead
Winnibigoshish	10/26/11	800-1,000	10-20 suspected sick, 40-60 dead, 5-10% mortality of raft
Bowstring	10/27/11	300-400 ^a	25 sick
Winnibigoshish	10/31/11	Not reported	42 dead near Third River Flowage

Round	11/1/11	10,000	1 sick, 2 dead
Bowstring	11/1/11	20,000	None
Winnibigoshish	11/2/11	Not reported	3 sick, 20 dead
Round	11/8/11	5,000-10,000 ^a	None
Bowstring	11/8/11	20,000-30,000 ^a	225 sick
Winnibigoshish	11/10/11	200-300	2 suspected sick, 1 dead
Winnibigoshish	11/12/11	400-500 (Sugar) ^a	6 sick near Third River Flowage
Round	11/14/11	3,000-5,000	None
Bowstring	11/14/11	10,000-15,000	None
Winnibigoshish	11/18/11	Few scaup- freezing up	None

^a Benthic samples collected below scaup.

^b Scaup were collected and sent to the NWHC to be tested for trematodiasis.

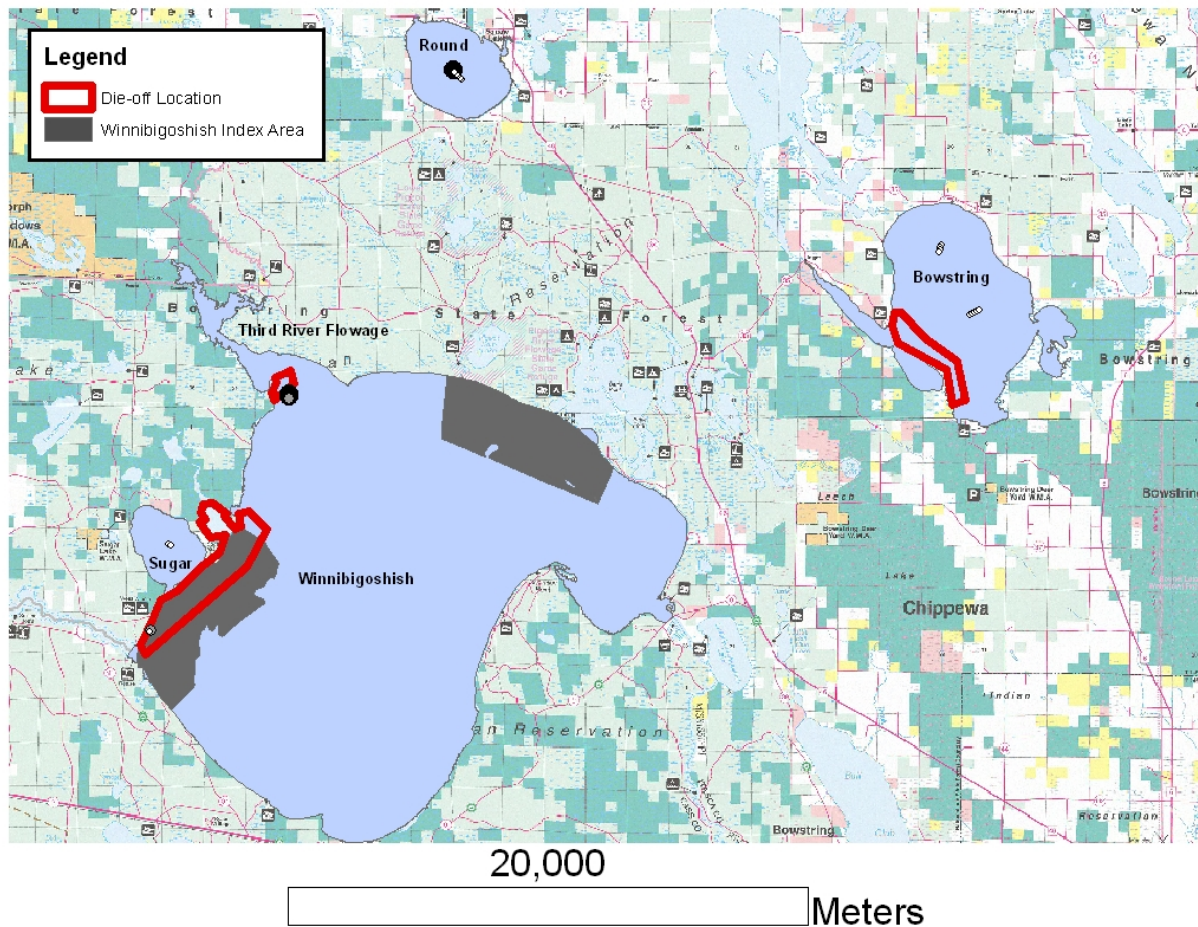


Figure 1. Relative locations of the index areas on Winnibigoshish and the other lakes where birds with trematodiasis were observed. Locations of waterfowl die-offs in Minnesota during spring and fall 2011 are also depicted, along with points sampled under Lesser Scaup rafts on each water body.

CHARACTERISTICS OF SHALLOW LAKES IN MINNESOTA: REGIONAL COMPARISONS AND RELATIONSHIPS AMONG LANDSCAPE SETTING, AMBIENT NUTRIENTS, AND FISH COMMUNITIES

Mark A. Hanson, Brian R. Herwig¹, Kyle D. Zimmer², Shane Bowe³, Jim Cotner⁴, Sean R. Vaughn⁵, Patrick G. Welle⁶, Robert W. Wright⁷, John Fieberg⁸, and Jerry A. Young¹

SUMMARY OF FINDINGS

Minnesota's shallow lakes provide numerous direct human benefits such as clean water, hydrologic storage to limit flooding, recreational opportunities, and access to unique wild areas. They also contribute valuable ecosystem services including carbon sequestration and habitat for native species. Unfortunately, water and habitat quality of Minnesota's shallow lakes have deteriorated dramatically during the past century. We are studying factors influencing ecological features and causes for deterioration of these sites, comparing costs of possible rehabilitation strategies, and synthesizing results to provide guidance for future shallow lake management. We evaluated approximately 130 shallow lakes in 5 ecological regions of Minnesota. Efforts include extensive sampling of shallow lakes to identify direct and indirect causes of deterioration, evaluation of responses of 12 lakes currently undergoing rehabilitation, and an economic analysis to identify enhancement strategies most likely to produce the greatest improvements in water quality per unit cost. Ultimately, our results will provide guidance to municipalities, state, county, and local governments, and private organizations in identifying cost-effective approaches for maintaining and restoring ecological integrity of shallow lakes throughout Minnesota.

¹Fisheries Research, Populations and Community Ecology Group, Minnesota Department of Natural Resources, 2114 Bemidji Avenue, Bemidji, MN 56601

²Department of Biology, University of St. Thomas, 2115 Summit Avenue, St. Paul, MN 55105

³Red Lake Department of Natural Resources, 15761 High School Drive, Red Lake, MN 56671

⁴Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, MN 55108

⁵Division of Waters, Minnesota Department of Natural Resources, 800 Oak Savanna Lane SW, Cambridge, MN 55008

⁶Department of Economics, Bemidji State University, 1500 Birchmont Drive NE # 30, Bemidji, MN 56601

⁷Wildlife GIS/IT Unit, Minnesota Department of Natural Resources, Carlo-Avery Game Farm, 5463-C West Broadway, Forest Lake, MN 55025

⁸Biometric Unit, Minnesota Department of Natural Resources, 5463 W. Broadway, Forest Lake, Minnesota 55025

BACKGROUND

Minnesota has approximately 4,000 lakes characterized by mean depth ≤ 15 ft and surface area > 40 acres (Nicole Hansel-Welch, personal comm.) and many thousands of smaller waters technically classified as “prairie wetlands”; the latter are functionally indistinguishable from the larger analogues. Collectively, these shallow lakes represent an international resource, providing critical waterfowl habitat and ecological benefits within Minnesota and the Mississippi Flyway. Currently, only about 40 of these lakes > 40 acres are formally designated for wildlife management, however many others are focus areas for various wildlife habitat and conservation practices. Due to concerns over shallow lake water quality, seasonal duck abundance and habitat use, and hunter satisfaction, MN DNR recently proposed a collaborative plan to Recover Ducks, Wetlands, and Shallow Lakes (http://files.dnr.state.mn.us/outdoor_activities/hunting/waterfowl/duck_plan_highlights.pdf). This plan targets restoration of 1,800 shallow lakes in Minnesota. Rehabilitation strategies available to shallow lake managers remain limited and often ineffective; in addition, reliable data on baseline conditions of shallow lake characteristics and regional patterns of variability are often unavailable, especially for northern areas. This means that lake and wildlife managers are frequently unsure of the current status of lakes they manage, and whether ecological characteristics of these areas may be limiting use by waterfowl and other wildlife. In general, managers receive little technical guidance useful for management and restoration of these lakes, or for implementation of rules for managing increased development and other anthropogenic influences in these areas.

Ecological characteristics of shallow lakes, along with their suitability for ducks and other wetland wildlife species, result from integrated influences of within-site and landscape-mediated processes. Effects of key variables operate at multiple spatial scales, sometimes result from off-site influences, and no doubt vary regionally throughout the state. Ecologists have long held that prairie wetlands (including our “shallow lakes”) are strongly influenced by gradients of hydrology (or hydrogeomorphic setting) and climate (especially precipitation) (Euliss et al. 2004). However, within boundaries established by hydrology and climate, biological interactions, especially wetland fish communities, also exert major structuring influences on communities and characteristics of shallow lakes (Hanson et al. 2005). This is not surprising given robust improvements known to follow removal of undesirable fishes from shallow Minnesota lakes such as Christina (Hanson and Butler 1994), and smaller “prairie pothole” wetlands (Zimmer et al. 2001).

As evidenced by whole-lake fish removals such as those summarized above, shallow lake food webs often differ dramatically in response to density and community structure of associated fish populations. Fish-mediated influences on invertebrate community structure and water transparency are often pronounced (Bendell and McNicol 1987; Zimmer et al. 2000, 2001). Recent studies in Minnesota’s Prairie Pothole Region (PPR) documented the strong negative influences of fathead minnows on invertebrate populations (Zimmer et al. 2000, 2001, 2002). Consequent reductions in herbivorous zooplankton (resulting from fish predation) allowed increases in phytoplankton densities and turbidity consistent with predictions of the models of Scheffer et al. (1993) and Scheffer (1998). These models propose that shallow-water ecosystems exist in one of two alternative conditions, either a clear-water, macrophyte-dominated state, or a turbid-water, phytoplankton-dominated state (Scheffer et al. 1993). Minnesota PPR wetlands largely conform to a binomial distribution (clear or turbid), rather than a normal distribution of features along a theoretical continuum (Zimmer et al. 2001; Herwig et al. 2004; Zimmer et al. 2009).

Composition of fish assemblages may also mitigate the relative influence of fish on shallow lake communities, and may dictate the success of remediation efforts. For example, stocking of piscivorous fish sometimes results in a reduction of planktivorous fish (especially

soft-rayed minnows), which may indirectly increase water transparency (Walker and Applegate 1976; Spencer and King 1984; Herwig et al. 2004). Similarly, in small lakes in northern Wisconsin containing natural fish communities, piscivores (largemouth bass *Micropterus salmoides* or northern pike *Esox lucius*) and cyprinids often occupy unique and separate assemblages. This pattern is thought to reflect the elimination of minnows via predation, and further suggests that biotic interactions can be important in structuring fish assemblages (Tonn and Magnuson 1982; Rahel 1984). In contrast, populations of large-bodied benthivorous fish species (e.g., black bullhead *Ameiurus melas*, white sucker *Catostomus commersoni*, and common carp *Cyprinus carpio*) are often resistant to predation, and are frequently associated with high turbidity and loss of rooted aquatic plants (Hanson and Butler 1994; Braig and Johnson 2003; Parkos et al. 2003). Due to the important but very different influences of planktivorous and benthivorous fishes on water quality, and the potential for restoration success given different fish assemblages, managers would benefit from tools that linked fish assemblages to landscape features and shallow lake characteristics.

Many lake and wetland studies have reported that landscape setting directly influences characteristics of embedded waters. For example, the watershed position sets boundaries on a variety of physical, chemical, and biological attributes of both deep lakes (Kratz et al. 1997) and prairie wetlands (Euliss et al. 2004). These lake properties include potential responses to drought, predominant groundwater interactions, water chemistry and concentrations of dissolved constituents, and biological communities. Other landscape features that have been found to influence lake water quality are wetland extent in the lake watershed (Detenbeck et al. 1993; Prepas et al. 2001), and extent of agricultural land use, the latter being correlated with higher trophic state index in associated lakes (Detenbeck et al. 1993). In many cases, off-site influences probably interact with site-level wetland features and processes so that observed community characteristics reflect simultaneous influences operating within the local context of lake nutrient status (Scheffer et al. 1993; Bayley and Prather 2003; Jackson 2003), surface area (Hobæk et al. 2002), depth (Scheffer et al. 1993), and biological properties such as abundance of macrophytes (Scheffer et al. 1993; Paukert and Willis 2003; Zimmer et al. 2003).

Our previous work (2005-06) confirmed that landscape characteristics can influence lake communities, interact with within-basin processes, and may be important determinants of shallow lake characteristics in Minnesota. These landscape effects are direct and indirect. For example, both presence of downstream fish sources and depth were useful for predicting fish presence/absence (Herwig et al. 2010), and landscape control on distribution of fish species limited the ability of predatory fish to control prey fish and improve water quality conditions (Friederichs et al. 2010). Extent of agriculture in upstream lake watersheds interacted with fish mass in our best models and together these attributes were useful for predicting algal biomass in adjacent shallow lakes (Gorman et al. In prep.), and fish variables were always included in best models for predicting amphibian site occupancy and abundance in shallow lakes (Herwig et al. 2012). In addition, results from our previous study helped elucidate mechanisms associated with important in-lake processes such as identifying thresholds at which shallow lakes shift from turbid- to clear-water regimes, and clarifying roles of benthivorous fish in these well-known lake dynamics (Zimmer et al. 2009). Results from our earlier work indicate that fish abundance and community structure exert major influences on shallow lake invertebrates, yet this relationship varies widely across ecological regions. We are also comparing relative influences of fish communities, lake isolation, and watershed size and composition on shallow lake invertebrate communities. Contributions from Sean Vaughn (Division of Waters, MDNR) and Robert Wright (Section of Wildlife, MDNR) provided new spatial analysis tools (delineating lake watershed boundaries, spatial analysis, etc.) that were not only critical for the recently-completed study, but will have direct application to questions and hypotheses posed in this current effort.

We plan to develop conceptual and empirical models linking landscape features, environmental influences and wetland fish assemblages, to assess influences of these factors

on the community characteristics in shallow lakes, and to clarify specific influences of within-lake processes that modify ecological characteristics of shallow lakes. An overarching finding of the prior work was that regional differences often constituted the largest source of variance in characteristics of shallow Minnesota lakes. This is not unexpected given findings of others studying deeper lakes (Carpenter et al. 2007), or perceptions of staff from the MDNR shallow lakes program indicating that baseline characteristics of shallow lakes differ dramatically across regions of the state (Nicole Hansel-Welch, pers. comm.). Regional differences not only contribute to major variability in obvious lake characteristics such as water clarity, but they probably influence extent and nature of lake responses to landscape constraints such as surface-water connectivity, as well as within-lake processes in regime responses to thresholds of phytoplankton and fish mass. For example, it is likely that combinations of increased benthivorous fish mass and/or decreased macrophytes will often induce regime shifts to turbid-water states in prairie lakes. We need to understand extent and patterns of regional variation, and to assess how it influences key structuring mechanisms such as surface connectivity, fish community characteristics, stability of phytoplankton- and macrophyte-dominated states, and proportion of lakes in clear- vs. turbid-water states.

Working Hypotheses

We hypothesize that fundamental drivers are ultimately responsible for most of the variation in ecosystem characteristics of Minnesota's shallow lakes: climate, ambient nutrient levels, fish abundance and community type, landscape features, land use, and morphometric features of individual lakes. These factors, in turn, are expected to induce strong, predictable spatial gradients in shallow lake characteristics across Minnesota. Thus, shallow lakes should exhibit wide ranges of features (and responses to lake management) at a statewide scale as the influence of some drivers increase while others decrease. Additionally, inter-annual and regional variability in precipitation and temperature will have strong influences on shallow lakes. Thus, we hypothesize these drivers generate predictable spatial and temporal patterns in shallow lakes across the state of Minnesota. Overall, we believe that understanding and predicting ecosystem characteristics of shallow lakes (fish, plant and invertebrate communities, water quality, carbon cycling, etc.), along with lake responses to rehabilitation efforts, requires understanding influence of these drivers, as well as synergistic combinations of two or more drivers. Within-lake interactions, such as those associated with fish, have strong influences on shallow lakes (Scheffer et al. 2006; Verant et al. 2007; Potthoff et al. 2008). However, we hypothesize that strengths of these interactions are also a function of our fundamental drivers such that within-lake interactions will also contribute to observed spatial and temporal patterns.

We believe it is also especially important to test further hypotheses regarding stability regimes in shallow lakes. Previous work (Hanson and Butler 1994) suggests that shallow lakes in MN conform to general models of alternative states developed for European lakes (Scheffer et al. 1993, Scheffer 1998) and these relationships have recently been confirmed from our prior work on Minnesota lakes (Zimmer et al. 2009). However, in Minnesota, it is likely that regime dynamics and stability thresholds will vary along regional gradients. We expect that companion models may need to be developed that extend concepts of lake regimes to include patterns of variance in invertebrate communities and other lake characteristics. Results from all study lakes will be used to estimate the magnitude of major factors responsible for deterioration of shallow lakes within the 6 study regions. Comparisons among management outcomes on 8 Intensive lakes will allow generalizations about relative usefulness of these lake rehabilitation approaches. Using a combination of data and outcomes from Extensive and Intensive lakes, our economic analysis will compare cost-effectiveness of various management approaches and will provide guidelines useful for maximizing future lake restoration and management decisions, including suggestions for cost-effective approaches in different regions of the state.

APPROACH AND METHODS

Our research has 3 general objectives; approaches and specific methods for each objective are summarized below.

Objective 1: Extensive Lakes - Identify and estimate major factors responsible for deterioration of shallow lakes in 6 areas of Minnesota (hereafter Extensive Lakes).

We selected study lakes in 6 areas among 5 Ecoregions of Minnesota. The following numbers of lakes were sampled during 2010 and 2011 (Figure 1): Twin Cities 22, Windom 22, Alexandria 23, Itasca 22, Chippewa 15, and Red Lake 23. We sampled a total of 127 lakes for this extensive aspect of our study. We had planned to sample approximately 17 more lakes during 2010, but this was not practical due to low-water conditions, unexpected characteristics of lakes (such as alteration due to damming by beavers, extreme depth, or other features not noted until field visits), and because in at least one case land ownership changed before onset of our study.

Lakes were sampled to assess general ecological features and to determine whether basins exhibit characteristics of clear- or turbid-water regimes. Lake watershed characteristics associated with each study lake were also determined. Resulting data will be used to develop models to identify combinations of variables that explain most variability in shallow lake characteristics, especially water quality features and lake regime status (turbid or clear). Special attention will be given to assessing influences of resident fish populations, extent of surface-water connectivity associated with study lakes, and proportion of agriculture in lake watersheds because these are believed to be major determinants of water quality in Minnesota's shallow lakes. Resulting data will help identify and estimate magnitude of major factors responsible for deterioration of water quality and ecological characteristics in our regional subsets of study lakes.

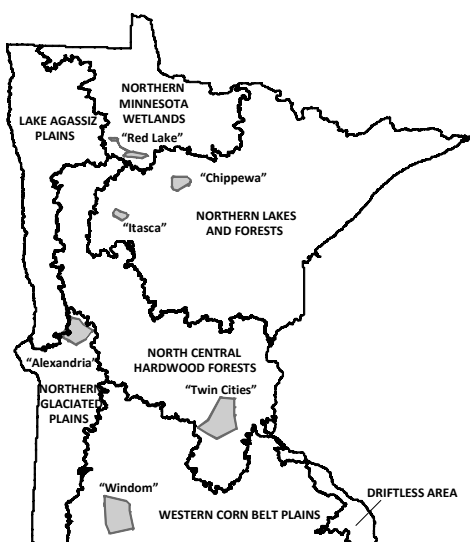


Figure 1. Map showing locations of study areas (shaded gray) in relationship to Minnesota's aquatic ecoregions (thick black lines).

All sites were visited during July-early August 2010 and 2011. At each study lake, we sampled fish populations, abundance of submerged aquatic plants, aquatic invertebrates, water

transparency, and a suite of chemical constituents in lake waters (Table 1). Water samples were collected in the field and are being tested for turbidity and concentrations of dissolved inorganic and total nitrogen, dissolved and total phosphorus, dissolved inorganic and organic carbon, chlorophyll *a* (chl_a; as a proxy for phytoplankton biomass). Additional laboratory analyses are being conducted on water column particulate matter (seston) to determine concentrations of carbon, nitrogen, and phosphorus suspended in lake water columns. Field crews collected approximately >2,500 samples of aquatic invertebrates from study lakes. Samples are currently being processed and we expect that resulting electronic data sets will be developed by summer 2013.

Table 1. Summary of lake variables sampled during summer 2010 and 2011. Similar data were gathered from Extensive (N=127) and Intensive (N=8) lakes except that Intensive lakes were sampled once monthly during June, July, and August. Extensive lakes were sampled a single time during July (2010) or August (2011).

Biological	Physical	Chemical
Fish abundance (gill and trap nets)	Turbidity	Total Nitrogen
Submerged aquatic plants (rake and mass) methods	Specific Conductivity	Dissolved Inorganic Nitrogen
Aquatic invertebrates (sweep nets, column samplers)		Total Phosphorus
Phytoplankton abundance (chlorophyll <i>a</i>)		Dissolved Phosphorus
		Dissolved Inorganic Carbon
		Dissolved Organic Carbon
		Seston Phosphorus
		Seston Carbon
		Seston Nitrogen

We are also investigating influences of earthworms on lake productivity and soil properties in 10 small watersheds within or near Itasca State Park, Minnesota. Worms were extracted from soils to measure biomass, and soil properties and lake properties characterized.

Objective 2: Intensive Lakes - evaluate and refine specific strategies for improving water quality and ecological characteristics of shallow lakes across Minnesota (hereafter intensive lakes).

We are evaluating responses of 12 shallow lakes (hereafter Intensive lakes) following recent lake restoration treatments such as draw downs or fish community manipulations. Treatments and timing varied, but generally included combinations of either partial or full drawdown, rotenone additions, and in some cases stocking of piscivorous fish (e.g. walleye) (Table 2).

Ecological characteristics of Intensive lakes were sampled during spring and summer 2010 and 2011 including parameters comparable to those measured in the Extensive sites. Landscape-level analyses are being conducted on these areas to determine upland cover and surface-water connectivity in lake watersheds using GIS analysis and interpretation of aerial photographs. Combining results and data from Intensive and Extensive lakes, we will estimate water quality improvements in response to various combinations of rehabilitation treatments

including upland restoration and within-lake-basin measures such as fish manipulation. Specific efforts will be directed to evaluating responses of the Intensive lakes to management efforts at each lake in a case-study format.

Table 2. Shallow lake enhancement strategies implemented on selected Intensive case study lakes.

Lake	County	Size (acres)	Enhancement Strategy	Years Post-Treatment in 2011
Nora	Pope	60	Full drawdown implemented in 2007. Began to refill in 2008, 40-50% open water by 2009. Metal half-riser structure with stoplogs functions as a fish barrier.	4 yrs
Sedan	Pope	62	Partial drawdown began in 2007, with a full drawdown occurring in 2008. Began to refill in 2009. Concrete variable crust structure with stoplogs regulates water level.	3 yrs
Wilts	Grant	55	Water levels were low in 2008 and lake is isolated, thus a decision was made to rotenone-treat the lake in fall 2008. Isolated basin.	3 yrs
Augusta	Cottonwood	499	This lake has a long history of drawdown to achieve wildlife benefits (pre-2004), but the most recent full drawdown occurred in 2008. Lake was re-flooded in 2009. Water control structure exists on lake outlet; control structures and high-velocity fish barrier installed on other adjacent waters within immediate watershed.	3 yrs
Hjermstad	Murray	60	Partial drawdown implemented in 2008, and lake was rotenone-treated under the ice during 2008-09. Fathead minnows persisted, so the lake was stocked with piscivores (walleye fry) in 2009 to attempt to suppress antecedent minnow populations. Water control via weir with stop logs; hanging finger fish barrier in place.	3 yrs
Maria	Murray	425	Full drawdown implemented from fall 2006 through fall 2007. Electric fish barrier was placed at lake outlet. Lake was rotenone-treated under the ice in February 2007. As of 2010, water levels remain low, much of lake remains covered with very dense stands of emergent cattail and fish persist in basin. Water control via weir with stop logs.	4 yrs
Spellman	Yellow Medicine	300	A managed drawdown occurred on this basin from 2006-08. 2009 was the first year with full water in the south basin. Box inlet culvert, outlet pipe, and finger-gate fish barrier in place.	3 yrs
Teal	Jackson	91	Partial drawdown implemented in 2008, and	3 yrs

			lake was rotenone-treated under the ice during winter 2008-09. Water control structure allows partial drawdown; no fish barrier in place at present.	
Froland	Pope	14	Fish removal via rotenone Oct 2010	1 yr
Leverson	Grant	20	Fish removal via rotenone Oct 2010	1 yr
Todd North	Grant	28	Fish removal via rotenone Oct 2010	1 yr
Todd South	Grant	22	Fish removal via rotenone Oct 2010	1 yr

Objective 3: Assess cost-effectiveness of alternative lake management methods - develop region-specific guidelines useful for identifying cost effective reclamation approaches

An economic analysis is being conducted using results from Extensive and Intensive Lakes to assess costs of water quality improvements (such as cost per unit of algae reduced [$\mu\text{g/L chl}a$]) following application of various management options being used in Minnesota. We plan to contrast cost effectiveness of combinations of upland vegetation restoration (conversion of agriculture to grass) and in-lake habitat enhancements (fish removal, installation of barriers, etc.) required to achieve given levels of lake water quality improvement. We expect that costs of management options will vary widely among ecological regions due to variability in lake characteristics, lake watersheds, upland easement costs, property values, and other attributes of lakes and adjacent uplands.

Comparison of restoration costs will be informative and will help elucidate trade-offs on temporal and spatial scales. Some options may generate quick results but may need to be repeated frequently, so that variations in long-run costs (over multiple decades) will be important to consider. Easement costs for land to be restored to vegetative buffers are known to vary across regions of the state. Cost data for the management options being studied are known to be currently available or obtainable.

RESULTS AND DISCUSSION

During 2010 and 2011, we completed sampling of all Extensive and Intensive Lakes and most laboratory work. Here we show preliminary trends in water quality, submerged aquatic plants, and fish populations in Extensive sites. We also show data illustrating patterns in Intensive Lakes and compare these trends to values observed in Extensive sites. Results shown are preliminary and are subject to change after additional data analysis and interpretation.

Regional patterns in total phosphorus (TP) – In 2010, TP values in study lakes showed an increasing trend along a general north-south gradient from Red Lake to Windom areas, with highest median values recorded for lakes within the Windom core (Figure 2). Smallest variation in TP among lakes was observed within the Red Lake and Itasca study areas, where mean and range values were $< 5 \mu\text{m L}^{-1}$. Median values in the Metro were comparable to those observed in other areas, but showed greater variability due to one record of extremely high TP ($>20 \mu\text{m L}^{-1}$). Final TP values for 2011 are not yet available, but are expected soon.

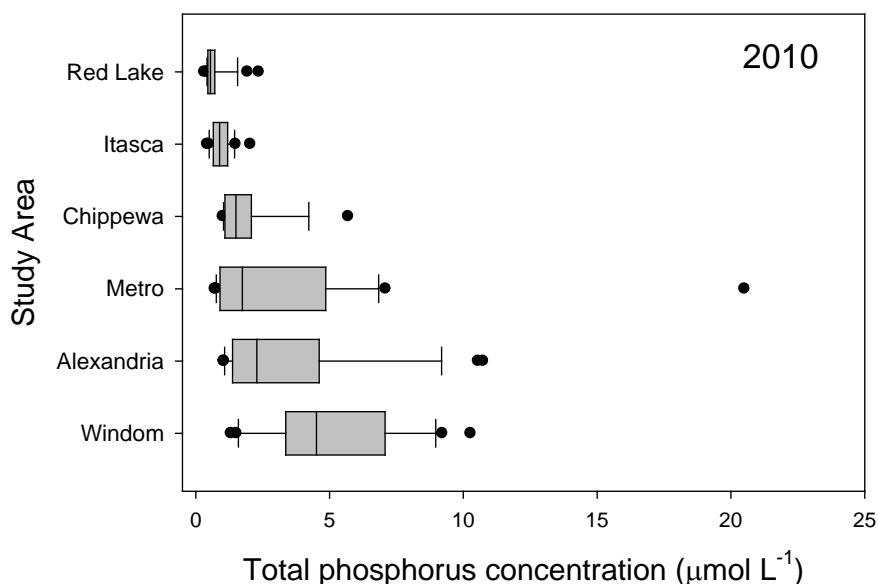


Figure 2 Box plots showing mean abundance of total phosphorus (TP) for shallow lakes sampled within 6 study regions during 2010. Vertical lines within boxes depict median TP values for each study region; extent of boxes depict 25th and 75th percentiles. Whiskers show 10th and 90th percentiles, with dots indicating more extreme values.

Submerged aquatic plants, phytoplankton, and regime implications – In general, phytoplankton abundance was higher in lakes in west-central and southern study areas, especially in Windom lakes, where values for chl_a often exceeded 100 $\mu\text{g L}^{-1}$. Other recent research on shallow Minnesota lakes suggests that sites where summer chl_a > 31 $\mu\text{g L}^{-1}$ most often showed characteristics of turbid-regimes (Zimmer et al. 2009). Many lakes in Red Lake, Itasca, Chippewa, and Metro study areas were characterized by phytoplankton levels falling in a range expected for clear-regimes. In contrast, many Alexandria and Windom lakes showed phytoplankton levels in excess of thresholds expected for turbid-regime lakes (Figure 3). This indicates higher probability for lakes in Alexandria and Windom to show characteristics of turbid regimes.

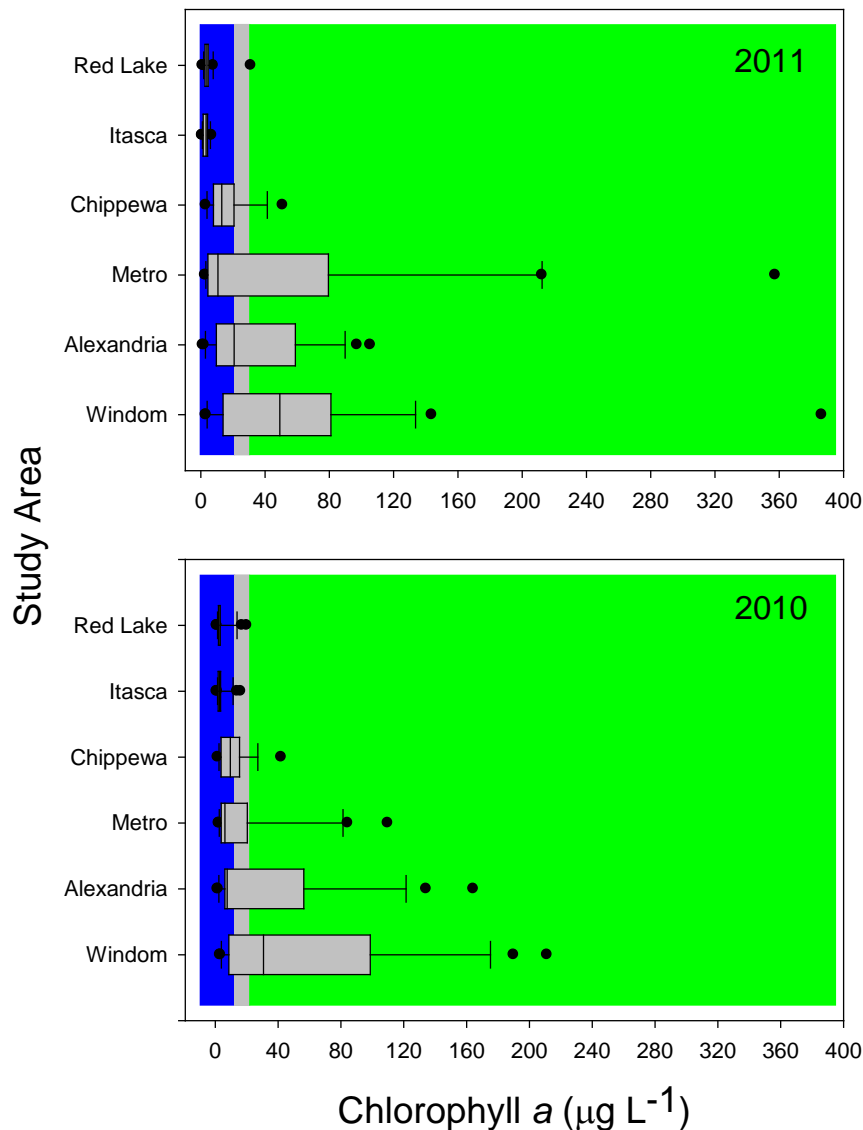


Figure 3 Box plots showing mean abundance of phytoplankton (chlorophyll a concentration) for shallow lakes sampled within 6 study regions during 2010 and 2011. Background colors depict expected chlorophyll a regions for clear- (blue), transition (grey), and turbid-regimes (green) based on threshold values after Zimmer et al. (2009).

Submerged aquatic plants are key ecosystem components of lakes and dense plant communities are known to favor clear-water regimes in Minnesota's shallow lakes. Our preliminary data show that abundance of submerged plants varies widely from lake-to-lake and among study areas in Minnesota. In general, lakes supporting high mass of submerged plants showed relatively low abundance of phytoplankton (chl_a). Alternatively, lakes with chl_a concentrations above 31 µg L⁻¹ showed lower abundance of submerged macrophytes (Figure 4). This pattern was especially obvious during 2010, but more lakes showed transitional characteristics in 2011 (with higher chl_a and submerged plants). Preliminary data also suggested that these patterns vary considerably among study areas. For example, most Windom, Alexandria, and Metro-area lakes showed high abundance of either macrophytes or phytoplankton (but not both). In contrast, lakes in our Red Lake, Itasca, and Chippewa study areas were dominated by macrophytes, but abundance of macrophytes and phytoplankton were

much lower than in other ecoregions. This seems to suggest that primary producers in Itasca and Chippewa lakes were limited by factors other than light limitation.

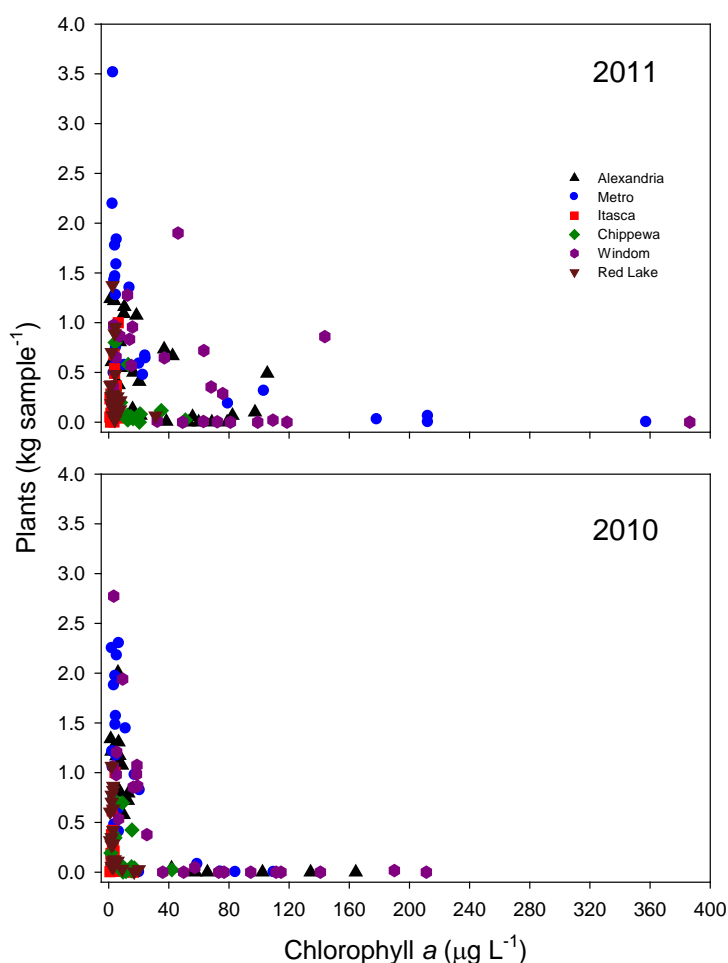


Figure 4 Abundance of phytoplankton (chlorophyll *a* concentration) and submerged macrophyte biomass for shallow lakes in 5 study regions during 2010 and 2011. Plant mass indicates average wet weight of plants collected on rake casts in each lake. Colors depict study area as indicated in caption.

Regional patterns in fish communities – Complex fish communities were found in lakes of all study areas. We observed no fishless lakes in our Chippewa study area, but we sampled 7 fishless sites in our Itasca study area; smaller numbers of fishless sites were observed in all other areas (Figure 5). Highest fish species richness (13) was observed in Windom lakes during 2011. Common carp (*Cyprinus carpio*) were less widely distributed among our lakes than we expected. During 2010, we collected carp from 23, 14, and 14 % of lakes in Windom, Metro, and Alexandria areas, respectively. In 2011, carp were sampled in 30, 13, and 29 % of Windom, Metro, and Alexandria lakes. Carp were not collected from lakes in Chippewa, Itasca, or Red Lake study areas during 2010 or 2011. In contrast, bullheads were ubiquitous and were collected from lakes in all study areas during 2010 and 2011. Bullhead abundance was highest in Windom, Metro, and Alexandria areas (> 46% in 2010 and \geq 60% during 2011). Still, bullheads were collected in only 9% of Itasca lakes during both study years.

We also summarized relative abundance (mean total mass sampled) of predominant fish feeding guilds (planktivores [e.g. fathead minnows, shiners, yellow perch], benthivores [e.g. bullheads, common carp], piscivores [e.g. northern pike, walleye, largemouth bass]) for lakes within each study area (Figure 6). In general fish mass was roughly comparable among Alexandria, Chippewa, Metro, and Windom lakes, but showed a trend toward lower abundance in Itasca and Red Lake areas during both study years. Highest mass of planktivorous fishes was collected from lakes in Chippewa and Windom areas; piscivores were usually collected in lower numbers than other guilds, but were sampled at higher levels than benthivorous species in Itasca lakes. Piscivore abundance was also relatively high in Chippewa lakes. Dense populations of planktivores (shiners, yellow perch) and benthivores (bullheads) were evident in Chippewa lakes, although conventional wisdom suggests that these species are more abundant in prairie regions.

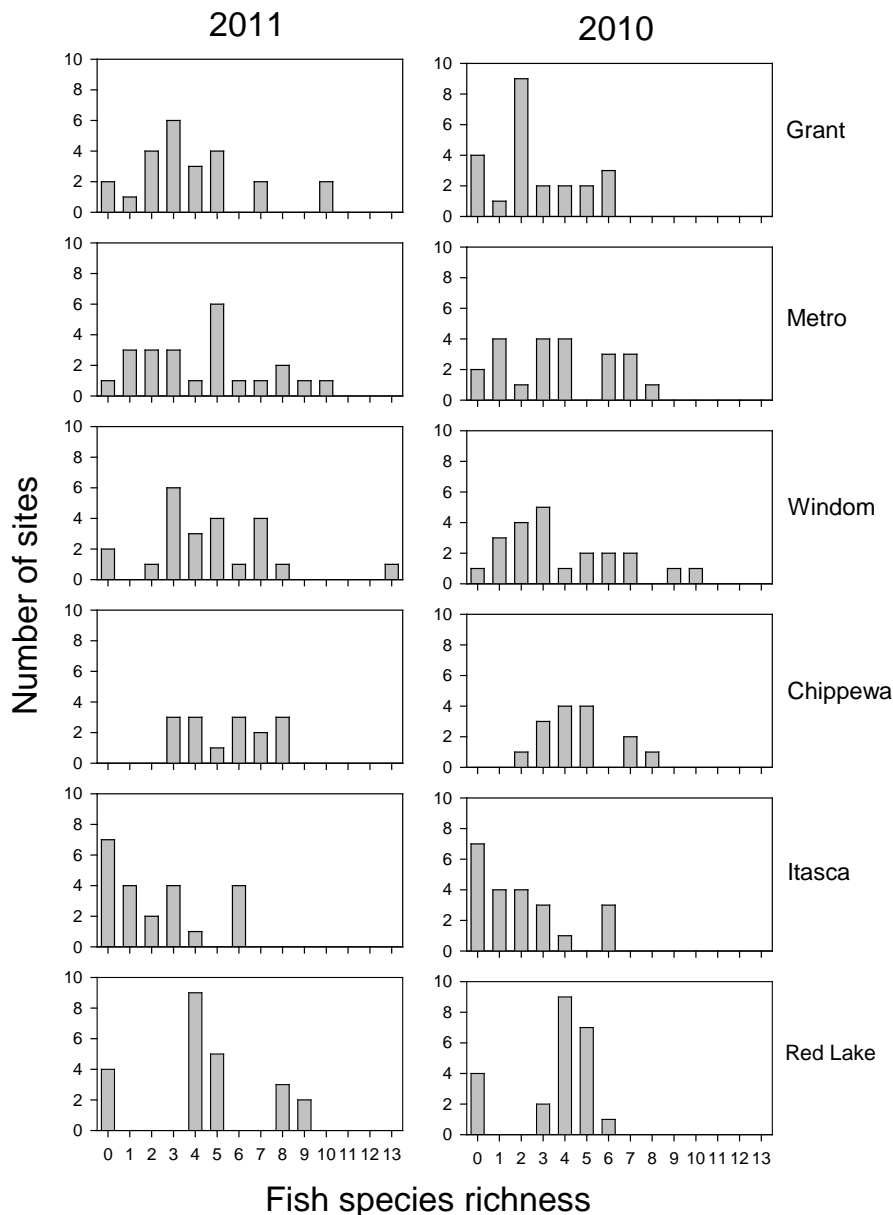


Figure 5. Fish species richness for shallow lakes in 6 study regions during 2010 and 2011, respectively. Height of bars on x-axis depicts number of lakes in which corresponding number of fish species were collected.

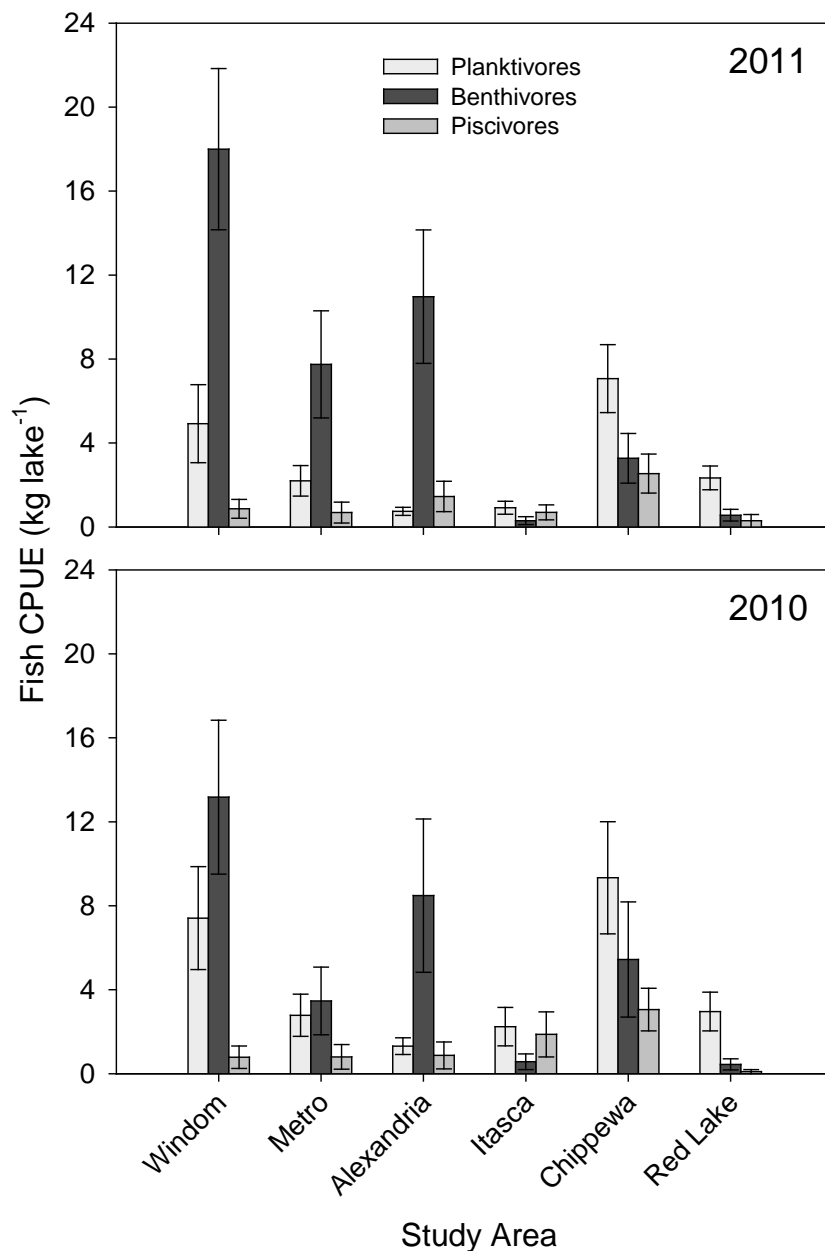


Figure 6 Summary of fish relative abundance for shallow lakes in 6 study regions during 2010 and 2011, respectively. Height of bars on x-axis depicts average weight (mass) for each of 3 major fish feeding guilds common in these lakes (planktivores, benthivores, piscivores).

Earthworm Sampling in Itasca study area - We continued investigating the influence of earthworms on lake productivity and soil properties in ten small watersheds within or near Itasca State Park, Minnesota. In addition to field work, we conducted experiments where we manipulated worm biomass and examined effects on dissolved organic phosphorus (DOP), dissolved organic carbon (DOC), and total nitrogen (TN). The results of these experiments suggested that the presence of earthworms increased the availability of organic carbon and nitrogen in soils. One of the important implications of these results is that watersheds with

abundant anecic worms are likely to have depleted organic carbon and nitrogen pools due to increased lability of organic matter and increased leaching into surrounding water bodies.

Evaluation of Intensive Lakes - We have begun compiling data on aquatic plants, fish communities, and other characteristics of intensive sites so lake responses can be assessed.

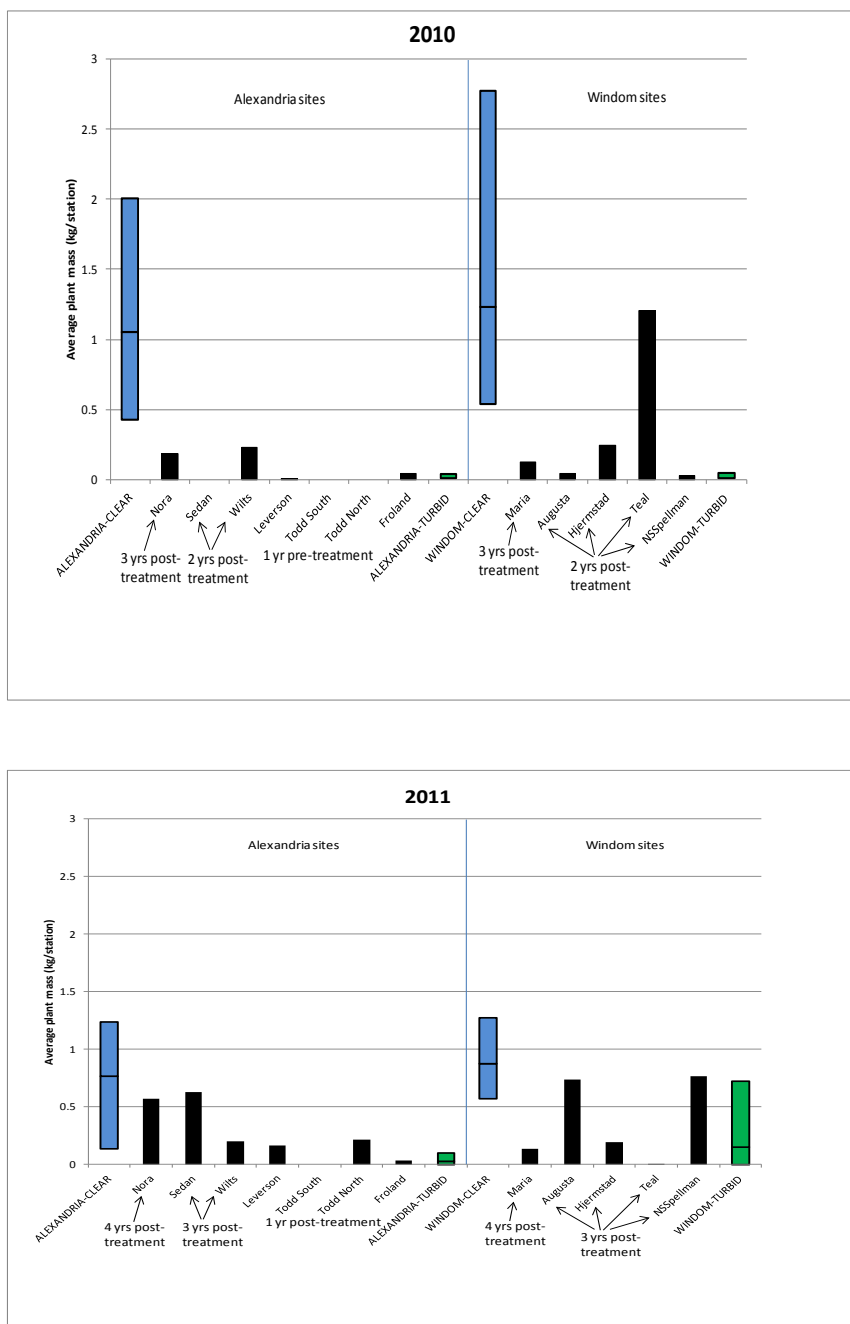


Figure 7. Black bars indicate relative abundance of submerged aquatic plants (average mass per sampling station) in Intensive Lakes in Alexandria and Windom study regions during 2010 (top panel) and 2011 (bottom panel). Blue bars indicate means and ranges of regional Extensive Lakes in clear-water regime; green bars indicate means and ranges of regional Extensive sites in turbid-water regime (based on threshold values of Zimmer et al. 2009).

We depicted relative abundances of plants and fish to allow comparisons between individual Intensive Lakes and Extensive Lakes within the same study region (Windom or Alexandria). We included Extensive Lake data averages and ranges of clear and turbid sites as a basis for comparisons. Resulting patterns indicated that plant communities were less extensive in Alexandria Intensive Lakes than in most regional Extensive sites in 2010 (Figure 7). By 2011, 2 of Alexandria 3 lakes rehabilitated 3 or more years earlier showed improvement in submerged macrophytes, while $\frac{1}{2}$ of the sites treated the year previous with rotenone application showed improvement. Plant communities in Windom Intensive Lakes showed variable improvements relative to regional data ranges. Initial improvements in one lake (Teal) faded between 2010 and 2011; 2 lakes improved with an additional year post-treatment (cf. Augusta and NS Spellman in 2010 and 2011), and one lake (Maria) had plant biomass similar to regional turbid lakes throughout 2010-11 (Figure 7). Overall, these results seem to indicate both initial improvements and extreme variability in responses following rehabilitation efforts. For example, Teal Lake (Windom) showed high submerged plant abundance during 2010, but plants disappeared by 2011, just 3 years following rotenone treatment.

Relative abundance of planktivorous and benthivorous fishes was variable, but often high in Intensive Lakes, especially in Windom (Figure 8). Fish abundance was also extremely variable in Extensive Lakes in both regions, so comparisons between Intensive and Extensive Lakes may be less informative than expected. Still, Windom sites showed a trend toward higher abundance of planktivorous and benthivorous fishes than did Alexandria lakes and this was evident during 2010 and 2011. High fish abundance in 3 or 4 Windom sites was well within the range indicated for regional turbid lakes, probably indicating that fish successfully repopulated these lakes during 2 or 3 years following drawdown and reflooding. Interestingly, one of the Windom sites (Teal) had consistently low fish abundance, and yet water quality (as measured by plants – Figure 7) remains low, suggesting something other than fish is influencing the regime status of this lake, perhaps watershed land use, internal nutrient loading, or both.

Relatively low plant and high fish abundance indicated that 3 or 4 Windom Intensive Lakes showed characteristics of turbid regimes. Using our data, is not possible to determine whether these sites failed to respond to rehabilitation (via drawdown and reflooding) or if fish quickly recolonized and caused trends back towards turbid conditions prior to onset of our study. It is possible that abundance of submerged plants and fishes may not reflect regime characteristics of Intensive sites. This is because shallow lakes exhibit stability in both turbid and clear regime conditions, so fish or plants may not be closely correlated with regime conditions in any single year.

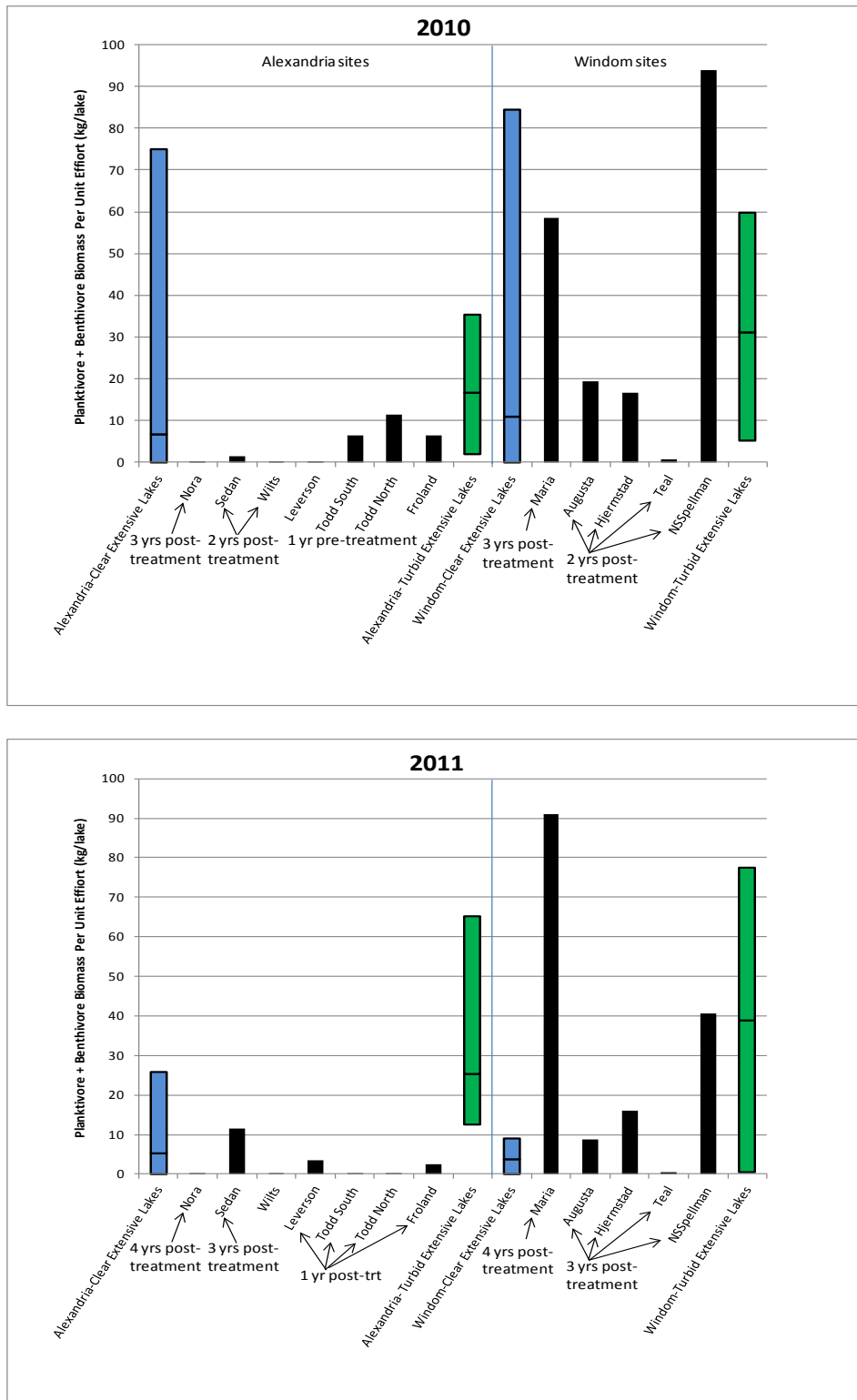


Figure 8. Black bars indicate relative abundance of planktivorous and benthivorous fishes (average mass per lake) in Intensive Lakes in Alexandria and Windom study regions during 2010 (top panel) and 2011 (bottom panel). Blue bars indicate means and ranges of regional Extensive Lakes in clear-water regime; green bars indicate means and ranges of regional Extensive sites in turbid-water regime (based on threshold values of Zimmer et al. 2009).

Cost-effectiveness – A cost-effectiveness assessment is being developed in two stages. First, using data from 2010, we identified high and low fish mass levels (planktivores and benthivores), and high and low agriculture sites (as a % of watershed area), by selecting 75th and 25th percentile values from Extensive Lakes in Alexandria and Windom study regions. We assumed in-lake rehabilitation would reduce fish abundance by 50% and 90% (lakes with low fish abundance are unlikely to be rehabilitated). Next, we used regression models to predict chl_a from combinations of fish mass (planktivores + benthivores) or extent (%) of watershed agriculture for these Extensive Lakes. Finally, we simulated likelihoods that lake rehabilitation by fish removal would reduce fish mass and chl_a to levels associated with clear-water regimes in our Minnesota study lakes (37 chl_a ug L⁻¹, updated threshold value from most recent analysis of present study data). Simulations identify the proportion of outcomes for which ending chl_a values (following lake management) were ≤ thresholds known for clear-water shallow lakes in Minnesota (Figure 9).

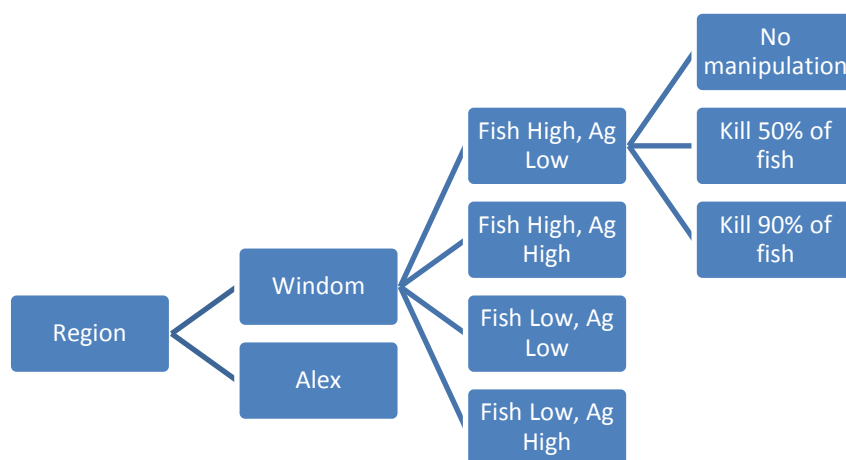


Figure 9: We considered a total of 24 scenarios (12 for each Region showing high fish mass and high proportions of agriculture in study landscapes). These scenarios capture 2 different values of %Ag (25th and 75th percentiles from within each region), 2 different starting levels of fish biomass, and 3 possible management scenarios (no reduction in fish biomass, 50% reduction, 90% reduction).

Results allow comparisons of likely water quality improvements (chl_a reductions) following lake rehabilitation via drawdown or rotenone (reducing benthivorous and planktivorous fish) or by restoration of upland cover (such as replacing row crops with grass). For example, results indicate that fish removal to 10 kg has approximately 70% likelihood of reducing chl_a levels to 37 ug L⁻¹, a level observed to be associated with clear-water regimes in Extensive Lakes (Figure 10). Results also indicate that a wide range of chl_a responses are likely in response to reductions in watershed agriculture. Comparing such patterns seems to suggest that within-lake rehabilitation has higher potential for reducing chl_a in shallow lakes than does conversion of watershed cover types. Still, we caution that presents results reflect short-term reductions in chl_a. Lake rehabilitation by drawdown or rotenone application often induces only brief increases in lake water quality. Most likely, restoration of grass in lake watersheds will ultimately favor long-term, sustainable reductions in chl_a and other water quality improvements, but improvements following watershed-scale enhancements may be delayed due to nutrient accumulation in lake sediments or other factors (Hobbs et al. 2012).

Probability clear (chla < 37)

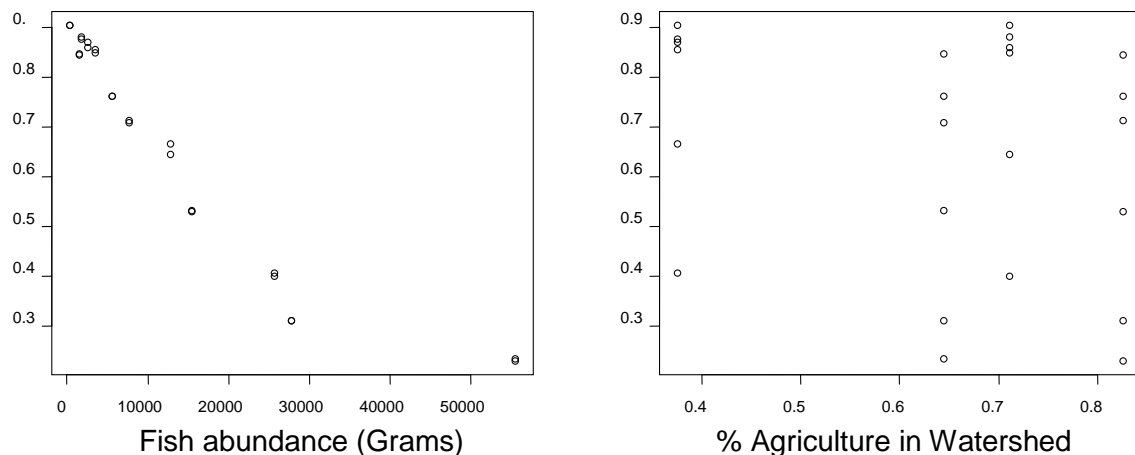


Figure 10. Summary of simulation results (probability of clear state [chla < 37] as a function of ending fish abundance [planktivore + benthivore fish mass] and % Agriculture in Lake Watersheds.

A second stage involves summarizing physical costs and results associated with each of our Intensive lakes and using these to value benefits to lakes. Through assistance of project collaborators (Ducks Unlimited, Minnesota DNR Shallow Lakes Program, USFWS, and others), we have secured data to support this larger cost-effectiveness analysis. Collaborators are also providing lake-specific costs of fish removal methods, installation and maintenance of water level control structures, seasonal water level drawdown, conservation easements, staff time, and other various physical and operational needs required for completion of these rehabilitation projects. Costs and results of lake rehabilitation will be evaluated in case study manner. We believe this combined approach (results from Extensive and Intensive lakes) has the best potential for reflecting cost details associated with lake rehabilitation, and should ultimately allow cost-effectiveness comparisons of lake- vs. watershed-scale approaches.

LITERATURE CITED

- Bayley, S.E., and Prather, C.M. 2003. Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. *Limnology and Oceanography* 48: 2335-2345.
- Bendell, B.E., and McNicol, D.K. 1987. Fish predation, lake acidity and the composition of aquatic insect assemblages. *Hydrobiologia* 150: 193-202.
- Braig, E.C., and Johnson, D.L. 2003. Impact of black bullhead (*Ameiurus melas*) on turbidity in a diked wetland. *Hydrobiologia* 490: 11-21.
- Carpenter, S.R., Benson, B.J., Biggs, R., Chipman, J.W., Foley, J.A., Golding, S.A., Hammer, R.B., Hanson, P.C., Johnson, P.T.J., Kamarainen, A.M., Kratz, T.K., Lathrop, R.C., McMahon, K.D., Povencher, B., Rusak, J.A., Solomon, C.T., Stanley, E.H., Turner, M.G., Vander Zanden, M.J., Wu, C.-H., and Yuan, H. 2007. Understanding regional change: a comparison of two lake districts. *BioScience* 57: 323-335.
- Detenbeck, N.E., Johnston, C.A., and Niemi, G.J. 1993. Wetland effects on lake water quality in the Minneapolis/St. Paul metropolitan area. *Landscape Ecology* 8: 39-61.

- Euliss, N.H., Jr., LaBaugh, J.W., Fredrickson, L.H., Mushet, D.M., Laubhan, M.K., Swanson, G.A., Winter, T.C., Rosenberry, D.O., and Nelson, R.D. 2004. The wetland continuum: a conceptual framework for interpreting biological studies in the prairie pothole region. *Wetlands* 24: 448-458.
- Friederichs, S.J., K.D. Zimmer, B.R. Herwig, M.A. Hanson, and J.R. Fieberg. 2010. Total phosphorus and piscivore mass as drivers of food web characteristics in shallow lakes. *Oikos* 120: 756-765.
- Gorman, M.W., Zimmer, K.D., Herwig, B.R., Hanson, M.A., Wright, R.G., Vaughn, S.R., and Younk, J.A. In prep. Ambient nutrient levels, fish communities, and watershed characteristics as drivers of phytoplankton abundance in shallow lakes. (Target journal: *Ecological Applications*)
- Hanson, M.A., and Butler, M.G. 1994. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1180-1188.
- Hanson, M.A., Zimmer, K.D., Butler, M.G., Tangen, B.A., Herwig, B.R., and Euliss, N.H., Jr. 2005. Biotic interactions as determinants of ecosystem structure in prairie wetlands: an example using fish. *Wetlands* 25: 764-775.
- Herwig, B.R., Hanson, M.A., Reed, J.R., Parsons, B.G., Potthoff, A.J., Ward, M.C., Zimmer, K.D., Butler, M.G., Willis, D.W., and Snook, V.A. 2004. Walleye stocking as a tool to suppress fathead minnows and improve habitat quality in semipermanent and permanent wetlands in the prairie pothole region of Minnesota. Minnesota Department of Natural Resources, Division of Fisheries and Wildlife, Special Publication 159, St. Paul, MN.
- Herwig, B.R., L.W. Schroeder, K.D. Zimmer, M.A. Hanson, D.F. Staples, R.W. Wright, and J.A. Younk. 2012. Fish Influences on Amphibian Presence and Abundance in Prairie and Parkland Landscapes of Minnesota, U.S.A. *Journal of Herpetology*: *in press*.
- Herwig, B.R., K.D. Zimmer, M.A. Hanson, M.L. Konsti, J.A. Younk, R.W. Wright, S.R. Vaughn, and M.D. Haustein. 2010. Factors influencing fish distributions and community structure in shallow lakes in prairie and prairie-parkland regions of Minnesota, USA. *Wetlands* 30: 609-619.
- Hobaek, A., Manca, M., and Andersen, T. 2002. Factors influencing species richness in lacustrine zooplankton. *Acta Oecologia* 23: 155-163.
- Hobbs, W.O., Ramstack Hobbs, J.M., LaFrancois, T., Zimmer, K.D., Theissen, K. B., Edlund, M. B., Michelutti, N. Butler, M.G., Hanson, M.A., Carlson, T.J. 2012. A 200-year perspective on alternative stable state theory and lake management from a biomanipulated shallow lake. *Ecological Applications* *In press*.
- Jackson, L.J. 2003. Macrophyte-dominated and turbid states of shallow lakes: evidence from Alberta lakes. *Ecosystems* 6: 213-223.
- Kratz, T.K., Webster, K.E., Bowser, C.J., Magnuson, J.J., and Benson, B.J. 1997. The influence of landscape position on lakes in northern Wisconsin. *Freshwater Biology* 37: 209-217.

- Parkos III, J.J., Santucci, V.J., Jr., and Wahl, D.H. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 182-192.
- Paukert, C.P., and Willis, D.W. 2003. Aquatic invertebrate assemblages in shallow prairie lakes: fish and environmental influences. *Journal of Freshwater Ecology* 18: 523-536.
- Potthoff, A.J., Herwig, B.R., Hanson, M.A., Zimmer, K.D., Butler, M.G., Reed, J.R., Parsons, B.G., and Ward, M.C. 2008. Cascading food-web effects of piscivore introductions in shallow lakes. *Journal of Applied Ecology* 45:1170-1179.
- Prepas, E.E., Planas, D., Gibson, J.J., Vitt, D.H., Prowse, T.D., Dinsmore, W.P., Halsey, L.A., McEachern, P.M., Paquet, S., Scrimgeour, G.J., Tonn, W.M., Paszkowski, C.A., and Wolfstein, K. 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1286-1299.
- Rahel, F.J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. *Ecology* 65: 1276-1289.
- Scheffer, M. 1998. *Ecology of Shallow Lakes*. Chapman and Hall, London, UK.
- Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B., and Jeppesen, E. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8: 275-279.
- Scheffer, M., vanGeest, G.J., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M.G., Hanson, M.A., Declerck, S., De Meester, L. 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* 112: 227-231.
- Spencer, C.N., and King, D.L. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1851-1855.
- Tonn, W.M., and Magnuson, J.J. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63: 1149-1166.
- Verant, M.L., Konsti, M.L., Zimmer, K.D., and Deans, C.A. 2007. Factors influencing nitrogen and phosphorus excretion rates of fish in a shallow lake. *Freshwater Biology* 52:1968-1981.
- Walker, R.E., and Applegate, R.L. 1976. Growth, food, and possible ecological effects of young-of-the-year walleyes in a South Dakota prairie pothole. *The Progressive Fish-Culturist* 38: 217-220.
- Zimmer, K.D., Hanson, M.A., and Butler, M.G. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 76-85.
- Zimmer, K.D., Hanson, M.A., and Butler, M.G. 2001. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. *Ecosystems* 4: 346-357.

- Zimmer, K.D., Hanson, M.A., and Butler, M.G. 2002. Effects of fathead minnows and restoration on prairie wetland ecosystems. *Freshwater Biology* 47: 2071-2086.
- Zimmer, K.D., Hanson, M.A., and Butler, M.G. 2003. Relationships among nutrients, phytoplankton, macrophytes, and fish in prairie wetlands. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 721-730.
- Zimmer, K.D., M.A. Hanson, B.R. Herwig, and M.L. Konsti. 2009. Thresholds and stability of alternative regimes in shallow prairie-parkland lakes of central North America. *Ecosystems* 12:843-852.

MODELING AND ESTIMATION OF HARVEST PARAMETERS AND ANNUAL SURVIVAL RATES OF WOOD DUCKS IN MINNESOTA, 1996–2010

James B. Berdeen

SUMMARY OF FINDINGS

Knowledge of the variables that influence harvest parameters and demographic vital rates is important for the management of game species. Harvest regulations are thought to have influenced the harvest parameters (e.g., Conroy et al. 2005) and demographic vital rates (e.g., Sheaffer et al. 2005) of some gamebird species. Consequently, there has been some concern regarding the increase in the daily bag limit of wood ducks (*Aix sponsa*) from 2 to 3 in the Mississippi Flyway (2008) and Minnesota (2011). The predicted harvest rates of adult males when the daily bag limits were 2 (0.087 [95% CI: 0.078–0.096]) and 3 (0.093 [95% CI: 0.077–0.109]) during a 60-day hunting season (Balkcom et al. 2010) suggest that the increase in hunting mortality would be slight, but this prediction has not been examined with empirical data.

To better understand the population biology and harvest dynamics of wood ducks, I conducted preliminary analyses on wood duck band and recovery data collected in Minnesota during 1996–2010. The specific objectives of these analyses were to (1) develop and evaluate band and recovery models of direct-recovery, recovery, and annual survival rates, (2) generate estimates of these parameters from the best approximating models, (3) convert estimates of direct-recovery rates to estimates of harvest rates, and (4) estimate the cohort-specific sample sizes of marked individuals needed to generate precise estimates of parameters of interest.

I developed and evaluated 44 approximating models to determine the influence of the predictors age, sex, time (year, aggregations of years corresponding to the periods during which there were 2- and 3-bird daily bag limits), and geographic strata of capture (ecological provinces, statewide) on recovery rates and annual survival rates. I conducted analyses using the Brownie et al. Recoveries option in Program MARK (Brownie et al. 1985, White and Burnham 1999) and evaluated the support for each model based on QAICc-values (Burnham and Anderson 2002).

I also developed and evaluated 39 logistic regression models to ascertain the influence of age, sex, time (year, aggregations of years corresponding to the periods during which there were 2- and 3-bird daily bag limits), and geographic strata of capture (ecological provinces, statewide) on direct-recovery rates (see Otis and White 2002). I analyzed data using the Known Fate option in Program MARK and evaluated the support for each model based on AICc-values (Burnham and Anderson 2002). I converted the direct-recovery rate estimates associated with the best approximating logistic regression model to harvest rate estimates using the equation of Henny and Burnham (1976).

To guide future banding efforts, I estimated the sample size of banded individuals in each age-sex cohort needed to generate precise estimates of harvest rates. I first fitted exponential curves to the relationship between the sample size of banded wood ducks in each age-sex-year cohort and the corresponding estimated coefficients of variation of harvest rates $CV(\hat{H})$ associated with the best approximating model. I then solved these equations to estimate sample sizes necessary to achieve $CV(H)$ -values of 0.05 and 0.10.

The best approximating Brownie et al. (1985) model suggested that recovery rates and annual survival rates varied by age, sex, and ecological provinces in additive relationships. This model had 76% of total weight. The parameter estimates associated with this model indicate

that within each ecological province, the AHY-M cohort had the greatest annual survival rate estimate, followed by the HY-M, AHY-F, and HY-F cohorts. Further, the greatest annual survival rate estimates were associated with the Forest ecological province, followed by the Prairie, Aspen Parkland, and Transition ecological provinces.

The best approximating logistic regression model indicated that direct-recovery rates of wood ducks varied by age, sex, and time (year) in an additive relationship, and had 52% of model weight. The direct-recovery rate estimates associated with this model are greatest for the HY-M cohort, followed by the HY-F, AHY-M, and AHY-F cohorts. There is little evidence that the temporal variation of direct-recovery rates varied is attributable to the change in daily bag limit in the Mississippi Flyway. Further, the harvest rate estimates of the AHY-M cohort during the years in which daily bag limits were 2 and 3 were not significantly different than those predicted by Balkcom et al. (2010) during 13 of 15 years, as indicated by overlapping 95% CIs.

These best approximating models suggest that mortality rate estimates ($1 - \text{annual survival rate estimate}$) vary at the spatial scale of ecological provinces but direct-recovery rates vary at a statewide scale. These models also suggest that annual survival was constant but direct-recovery rates varied annually during 1996–2010. Thus, the spatiotemporal characteristics of mortality of wood ducks in Minnesota appear complex. Further research is needed to develop a better understanding of the influence of harvest regulations and habitat characteristics on harvest parameters and demographic vital rates.

Preliminary estimation of sample size needs indicate that 952 AHY-M, 209 AHY-F, 259 HY-M, and 276 HY-F should be banded to achieve $CV(H)$ -values of 0.10. If a $CV(H)$ -value of 0.05 is desired, 2107 adult males, 440 AHY-F, 605 HY-M, and 622 HY-F should be banded. The cohort-specific sample sizes seem attainable, especially if $CV(H)$ -values of 0.10 are desired.

INTRODUCTION

Reliable knowledge of harvest parameters and demographic vital rates are necessary for the management of populations of game species. Harvest regulations are thought to have influenced the harvest parameters (e.g., Conroy et al. 2005) and demographic vital rates (e.g., Sheaffer et al. 2005) of some gamebird species. Data from reencounters of banded gamebirds can be used to estimate several of these parameters, including direct-recovery, recovery, and annual survival rates (Brownie et al. 1985). Harvest rates can be estimated if both direct-recovery rate and band-reporting rate estimates are available (Henny and Burnham 1976).

There has been some concern regarding the increase in the daily bag limit from 2 to 3 for wood ducks (*Aix sponsa*) in the Mississippi Flyway (2008) and Minnesota (2011). During a 60-day hunting season, the predicted harvest rates of adult males are 0.087 (95% confidence interval [CI]: 0.078–0.096) and 0.093 (95% CI: 0.077–0.109) when the daily bag limits are 2 and 3, respectively (Balkcom et al. 2010). Unfortunately, an examination of these predictions have not been performed on empirical data and published. Further, harvest rates for other age-sex cohorts were not predicted by Balkcom et al. (2010) and changes in cohort-specific annual survival rates in response to this regulatory change have not been examined.

To better understand the population biology and harvest dynamics of wood ducks, I performed analyses on band and recovery data from wood ducks captured in Minnesota during 1996–2010. The results of these analyses can be used to improve the understanding of the sources of variation of harvest parameters and annual survival rates, identify information gaps,

and provide the information needed to improve the existing Minnesota Department of Natural Resources (MNDNR) banding program.

The specific objectives of these analyses were to:

- (1) Develop and evaluate band and recovery models of direct-recovery, recovery, and annual survival rates,
- (2) Generate estimates of these parameters from the best approximating models,
- (3) Convert estimates of direct-recovery rates to estimates of harvest rates, and
- (4) Estimate the cohort-specific sample sizes of marked individuals needed to generate precise estimates of parameters of interest.

METHODS

I used the banding data from (1) normal, wild, and flighted wood ducks of known age and sex that were captured in Minnesota during July – mid-September (i.e., pre hunting season) 1996–2010, (2) marked with a standard U.S. Geological Survey (USGS) leg band on which a toll-free telephone number or website at which reencountered bands could be reported, and (3) captured via standard methods (e.g., rocketnetting [Wunz 1984], baited swim-in traps [Mauser and Mensick 1992]) or nightlighting (Lindmeier and Jessen 1961) and held <24 h. I used recovery data from (4) unsolicited bands that were reencountered during the 1996–1997 to 2010–2011 hunting seasons. There were 12,220 bandings, 994 direct recoveries, and 860 indirect recoveries that met these criteria.

I initially stratified capture and recovery data by age class (2 levels: after hatch-year [AHY] or hatch-year [HY]), sex (M or F), time (years of capture and recovery), and ecological province of capture (4 levels: Tallgrass Aspen Parkland [Aspen Parkland], Prairie Parkland [Prairie], Eastern Broadleaf Forest [Transition], Laurentian Mixed Forest [Forest]; Hanson and Hargrave 1996). Unfortunately, birds were banded in the Forest ecological province during only 2004–2010.

Estimation of Recovery and Annual Survival Rates

I used maximum likelihood methods to model and estimate the recovery rate (f) and annual survival rate (S) of wood ducks. Recovery rate is defined as the probability that a banded duck is shot or found dead during the hunting season, retrieved, and reported (Williams et al. 2001). Annual survival rate is defined as the probability that a banded duck alive at the time of banding in year t survives until the banding period in year $t + 1$ (Williams et al. 2001).

I developed and examined the support for the global model, $f_{age*sex*time*ecological\ province}$ $S_{age*sex*time*ecological\ province}$, in which f and S varied by age, sex, time (year), and ecological province of capture in an interactive relationship. I also developed 43 reduced models in which these variables in different combinations and structural relationships were used as predictors. To ascertain whether a regulatory change influenced f and S , I developed some reduced models in which time (years of capture and recovery) was aggregated into 2 time periods that corresponded with the years during which there were 2- and 3-bird daily bag limits. I also developed a subset of models in which there were 2 different spatial aggregations of the capture locations (i.e.; ecological provinces, statewide). The relative support for models with spatially

aggregated capture data was used to make inferences about the sources of spatial variation of f and S .

I used the Brownie et al. Recoveries option in Program MARK (Brownie et al. 1985, White and Burnham 1999) to fit each model to the band and recovery data, generate parameter estimates and associated 95% CIs, calculate the Akaike Information Criterion (QAICc) adjusted for overdispersion and small sample size, and perform a bootstrap simulation to estimate a median \hat{c} -value associated with the global model. I evaluated the relative support for each model based on the QAICc-values (Burnham and Anderson 2002).

Recovery rate estimates generated in this analyses could be used as an index of harvest rates, but (1) there is covariance between this parameter and S (Brownie et al. 1985), and (2) the parameterization of both S and f have some influence on the likelihood function associated with each model (see Brownie et al. 1985:12). Thus, the parameterization of S has some influence on maximum likelihood estimates and consequently f in Brownie models. The parameterization and estimation of S is of primary interest in this analysis because of the need to understand the sources of variation of this parameter; specifically whether the change in the daily bag limit in the Mississippi Flyway had some effect on the annual survival of wood ducks. Consequently, I report the values of \hat{S} but not \hat{f} associated with the best approximating Brownie model. I estimate direct-recovery rates (f^*) in a separate analysis to avoid the influence of S .

Estimation of Direct-Recovery and Harvest Rates

I modeled and estimate f^* using logistic regression methods (Otis and White 2002). This parameter is defined as the proportion of wood ducks banded in year t that is shot and retrieved during the first hunting season after banding, and reported to the BBL (Williams et al. 2001). I used the Known Fate option of Program MARK (White and Burnham 1999) to fit candidate models to the data, generate parameter estimates, calculate AICc-values, and rank the models based on these values (Burnham and Anderson 2002). The global model, $f^*_{age*sex*ecological\ province*time}$, used the variables age, sex, year, ecological province of capture, and time in an interactive relationship as predictors of f^* . The 38 reduced models used different combinations of these predictors in interactive and additive relationships.

I converted \hat{f}^* -values from my best approximating logistic regression model to \hat{H} with the equation of Henny and Burnham (1976):

$$f^* = H \lambda,$$

in which the value of band-reporting rate estimate ($\hat{\lambda}$) was 0.73 ($1\ SE\hat{E} = 0.026$; Zimmerman et al. 2010). I used the delta method (Seber 1982) to estimate the variance (\hat{var}) of \hat{H} .

Estimation of Sample Size

Although Program Band2 (Wilson et al. 1989) can be used to estimate cohort-specific sample sizes necessary to precisely estimate annual survival rates, a sample size of 300 individuals per cohort generally is required to estimate this parameter (Brownie et al. 1985). However, this sample size guideline now may be <300 because (1) modern analytical software

has greater capabilities than the program used when the original sample size recommendation was made, and (2) there has been an increase in $\hat{\lambda}$ from 0.32 ($1\ SE\hat{E} = 0.020$) when the original guidelines were established to 0.73 ($1\ SE\hat{E} = 0.026$) during the contemporary period (Zimmerman et al. 2010).

To ascertain the sample size of each age-sex cohort that must be banded to generate precise estimates of harvest rates, I fit an exponential curve to the relationship between the sample size of banded wood ducks of each age-sex-year cohort and the corresponding $CV(\hat{H})$ value. I solved the exponential equation associated with the curve of each age-sex cohort in a manner that the sample sizes necessary to achieve $CV(H)$ -values of 0.05 and 0.10 were estimated.

RESULTS

Recovery and Annual Survival Rate Estimates

The values of AICc associated with all models and variances associated with parameter estimates were adjusted with the median \hat{c} -value of the global model, 1.065. Four Brownie et al. (1985) models have weights of $\geq 0.5\%$ (Table 1). Models in which annual survival varies by age, sex, ecological province, time (year or Flyway bag limit) have 81.8, 99.8, 76.1, 0, and 0%, respectively, of model weight.

The best approximating Brownie et al. (1985) model of recovery and annual survival rates, $f_{age+sex+ecological\ province} S_{age+sex+ecological\ province}$, uses age, sex, and ecological province in an additive relationship as predictors of f and S , and has 76.1% of model weight (Table 1). The parameter estimates associated with this model indicate that in general, the AHY-M cohort had the greatest annual survival rates, followed by the HY-M, AHY-F, and HY-F cohorts in each ecological province (Table 2). Within each age-sex cohort, the annual survival rate estimates associated with the Forest ecological province are greatest, followed by Prairie, Aspen Parkland, and Transition ecological provinces (Table 2). Overlapping 95% CIs associated with some pairs of age-sex-ecological province cohorts suggest that differences are not significant. However, nonoverlapping 95% CIs indicate that the annual survival rate estimates of AHY-M birds captured in the Prairie, Transition, and Aspen Parkland ecological provinces are significantly greater than the AHY-F and HY-F cohorts captured in the same geographical strata (Table 2).

Direct-recovery and Harvest Rate Estimates

Nine logistic regression models have weights of $\geq 0.5\%$ (Table 3). Approximating models in which age, sex, time (year), time (Flyway bag limit), and ecological province of capture were predictors of direct-recovery rates have 98.5, 78.3, 68.7, 3.8, and 26.0% of model weight, respectively (Table 3). The best approximating model, $f^*_{age+sex+time}$, includes age, sex, and time (year) in an additive relationship as predictors and has 52.1% of the model weight.

I used a band-reporting rate of a single value to convert \hat{f}^* from the best approximating logistic regression model to \hat{H} (Figure 1a–d). Consequently, the relationships among \hat{H} associated with each age-sex-year cohort are the same as those of \hat{f}^* from the best approximating model.

Sample Size Estimates

Only 7 of 240 age-sex-year-ecological province cohorts have sample sizes of banded birds that met the recommended guideline of 300 marked individuals (see Brownie et al. 1985). However, 11 of 16 estimated coefficients of variation associated with annual survival rate estimates ($CV[\hat{S}]$) of age-sex-ecological province cohorts generated in the best approximating Brownie model are <0.10 , and 3 of 16 are <0.05 . All age-sex cohorts captured in the Forest ecological province and HY-F cohort captured in the Aspen Parkland ecological province have associated $CV(\hat{S})$ -values >0.10 . In contrast, only AHY-M captured in the Prairie, Transition, and Aspen Parkland ecological provinces are the only cohorts with $CV(\hat{S})$ -values <0.05 .

Generally, the $CV(\hat{H})$ -values are greatest for the AHY-F cohort and lowest for the AHY-M cohort. However, only 1 of 60 age-sex-year cohorts has a $CV(\hat{H})$ -value of <0.10 . I used the equations in Figure 2a–d to estimate sample sizes of each age-sex cohort that are necessary to generate $CV(H)$ -values of 0.05 and 0.10. I present these estimates in Table 4.

DISCUSSION

Modeling and Estimation of Annual Survival Rates

Age, sex, and ecological province of capture appear to be important predictors of the annual survival rates of wood ducks banded in Minnesota during 1996–2010. Variation among age-sex cohorts is somewhat consistent to those of other analyses of wood ducks banded in the northern portion of the Mississippi Flyway during earlier periods (Nichols and Johnson 1990, Bellrose et al. 1994). In each of these studies, the AHY-M cohort had the greatest annual survival rate estimates, followed by HY-M, AHY-F, and HY-F (Table 2).

This and other studies have detected geographic variation of annual survival rates, but the different spatial scale at which these analyses were conducted restricts the ability to make comparisons. Previous studies indicated that wood ducks banded in the southern U.S. generally had greater annual survival rate estimates than did those banded in northern states (Nichols and Johnson 1990, Bellrose et al. 1994). My preliminary results suggest that variation of annual survival is better explained at the spatial scale of ecological provinces in Minnesota than at that of this state. It may be that habitat characteristics associated with ecological provinces influenced survival. Alternatively, annual survival rates may have been influenced by some characteristic unrelated to habitat but associated with capture areas.

There was a lack of support for any Brownie et al. (1985) models in which annual survival varied either annually or by groups of years that corresponded to the daily bag limits in the Mississippi Flyway. These results suggest that annual survival was relatively constant during 1996–2010, and was not influenced by the liberalization of this hunting regulation in the Mississippi Flyway. Temporal variation of this parameter also was not observed in either the northcentral U.S. during 1966–1985 (Nichols and Johnson 1990) or the northern Mississippi Flyway during 1960–1985 (Bellrose et al. 1994). However, increasing trends in annual survival rates were detected in 9 of 10 sex-geographic area cohorts during 1959–1996 (Franklin et al. 2002). It may be that the sample sizes of banded wood ducks were insufficient to detect temporal changes in annual survival rates in some of these studies. Thus, it is important to mark an adequate sample size of individuals in each cohort if it is a priority to monitor the demographic response to changes in hunting regulations.

Although it is difficult to compare results of studies conducted at different spatiotemporal scales, an examination of the annual survival rate estimates of each age-sex cohort could provide direction for future investigations and population management. The annual survival rate estimates of the AHY-M, HY-M, and HY-F birds banded in Minnesota during 1996–2010 were at least slightly greater than the corresponding cohorts banded in Illinois, Iowa, Minnesota, Missouri, and Wisconsin during 1966–1985 (hereafter, northcentral U.S.; Nichols and Johnson 1990) and in portions of the eastern Dakotas, Manitoba, Michigan, Minnesota, Ontario, and Wisconsin (hereafter, northern Mississippi Flyway) during 1960–1985 (Bellrose et al. 1994, Table 2). The annual survival rate estimate of the AHY-M cohort captured in the Prairie ecological province during 1996–2010 is significantly greater than this age-sex cohort banded in both the northcentral U.S. during 1966–1985 and the northern Mississippi Flyway during 1960–1985 (Table 2). Similarly, estimates of the annual survival rate of HY-M birds captured in the Prairie, Transition, and Aspen Parklands ecological province during 1996–2010 are significantly greater than the same age-sex cohort in both the northcentral U.S. during 1966–1985 and the northern Mississippi Flyway during 1960–1985 (Table 2). The apparent spatiotemporal variation of the annual survival rates in 3 investigations (Nichols and Johnson 1990, Bellrose et al. 1994, this study) indicates a need to better understand why such differences existed.

Demographic vital rates of females often are used to estimate rates of population change in population projection matrices (e.g., Case 2000). In some species, survival especially influences the finite rate of population growth (Crone 2001). Juvenile survival may have the greatest value of elasticity in increasing populations and short-lived species, but the survival rates of the oldest age class generally have the greatest elasticity value in decreasing populations and long-lived species (see Sandercock 2006). Thus, it is particularly important to ascertain whether annual survival rates of the AHY-F or HY-F cohorts have the greatest influence on the rate of population growth.

Estimation of Direct-Recovery Rates and Harvest Rates

Age, sex, and time (year) appear to be important predictors of the direct-recovery rates of wood ducks in Minnesota during 1996–2010. Based on estimates of direct-recovery rates, it appears that the HY-M cohort was most susceptible to hunting mortality, followed by the HY-F, AHY-M, and AHY-F cohorts. This cohort-specific order of susceptibility is the same as that observed in the northern Mississippi Flyway during 1960–1985 (Bellrose et al. 1994) and in the northcentral U.S. during 1966–1985 (Nichols and Johnson 1990).

Models in which time (year) was a predictor of direct-recovery rates had 68.7% of model weight, but models in which time (Flyway bag limit) was a predictor had 3.8% of model weight. Thus, there is little evidence that the temporal variation of harvest parameters was attributable to a change in the daily bag limit in the Mississippi Flyway. Unexamined variables (e.g., hunter effort) probably had a greater influence on the likelihood of a banded wood duck being harvested than did the change in daily bag limit. The harvest rate estimates of AHY-M banded in Minnesota during periods in which there were a 2- and 3-bird daily bag limits 1996–2010 were not significantly different than those predicted by Balkcom et al. (2010) during 13 of 15 years, as indicated by overlapping 95% CIs. However, the effects of the 3-bird daily bag limit on harvest rates should continue to be monitored in both Minnesota and the Mississippi Flyway, given that (1) Minnesota enacted a 3-bird daily bag limit after the period of analyses, (2) the majority of direct recoveries of the female age-sex cohorts occurred in-state during the study (MNDNR, unpublished data), and (3) the observed temporal variation of this parameter estimate.

The best approximating models suggest that annual mortality rates ($M = 1 - S$) varied at the spatial scale of ecological provinces within Minnesota, but direct-recovery rates varied at a statewide scale. Thus, habitat characteristics associated with the ecological province of capture appeared to have influenced overall mortality rates but not one source of mortality (i.e., hunting). Alternatively, it may be that the spatial variation of direct-recovery rates is better explained by another habitat classification system, or that the sample size of banded individuals was insufficient to detect geographic variation. These approximating models also suggest that annual mortality rates were constant but hunting mortality rates varied annually during 1996–2010. Such results suggest that the spatiotemporal characteristics of mortality of wood ducks in Minnesota are complex. Further research is needed to develop a better understanding of the variables (e.g., harvest regulations, habitat characteristics) that influence harvest parameters and demographic vital rates.

Relationship between Harvest and Annual Survival Rates

The differences among age-sex cohorts with regard to estimates of harvest rates and overall mortality rates suggest that these cohorts are differently affected by hunting and other sources of mortality. I examined the associated harvest rate estimates in relation to mortality rate estimates (\hat{H} / \hat{M} , with parameter estimates generated in the best approximating models) to better understand the magnitude of hunting mortality of these cohorts. The values of these proportions are 13.7 – 39.7, 9.3 – 25.9, 19.4 – 53.3, and 13.3 – 35.5% for the AHY-M, AHY-F, HY-M, and HY-F cohorts, respectively. These estimates suggest that there was not an inverse relationship between harvest rate estimates and annual survival rate estimates among cohorts (e.g., the cohort with the lowest survival rate estimate [HY-F] did not have the greatest harvest rate estimate and the cohort with the greatest survival rate estimate [AHY-M] did not have the lowest harvest rate estimate) in Minnesota during 1996–2010. However, an inverse relationship detected between the recovery and annual survival rates of wood ducks during 1966–1984 suggests that hunting mortality had a negative influence on survival during that period (Trost 1990).

The spatiotemporal variability of annual survival in the northern Mississippi Flyway, significant temporal variation of contemporary harvest rate estimates of Minnesota-banded birds (Figure 1a–d), substantial variability of harvest rate estimates in relation to the overall mortality rate estimates, and lack of knowledge about both the point at which hunting mortality becomes additive and the contemporary relationship between harvest and annual survival rates indicate that a better understanding of the population ecology of wood ducks is needed. These topics should be addressed formally in well-designed studies using modern analytical methods; e.g., the Pollock et al. (1994) method to apportion overall mortality rates into hunting and natural mortality rates, and the Otis and White (2004) or Sedinger et al. (2010) method to examine the relationship between the harvest and annual survival rates of each cohort.

Sample Size Estimates

Future studies that address gaps in current knowledge of the population dynamics of wood ducks will require a representative sample of a sufficient number of banded individuals in each cohort of interest (e.g., age, sex, geographic area, time). An adequate sample size of banded individuals will permit the development of reliable models, generation of precise estimates of harvest parameters and annual survival rates, increase the likelihood of detecting significant differences among parameters estimates, and facilitate the evaluation of the effects of regulatory change on harvest parameters and annual survival rates. It is especially important

to band an adequate sample size of those cohorts which (1) may be most important in influencing the rate of population change (e.g., females), (2) have relatively great \hat{CV} -values, and (3) traditionally have had relatively small samples sizes of banded individuals.

\hat{CV} -values >0.10 may indicate that the sample size of marked birds is too small or that the model structure does not describe the system well. Generally, the $\hat{CV}(\hat{S})$ -values associated with the HY-F cohort were greatest and those associated with the AHY-M cohort were lowest, and those associated with the Forest ecological province were greatest and those captured in the Prairie ecological province were lowest in this study. Further, 11 of 16 $\hat{CV}(\hat{S})$ -values associated with the best approximating Brownie model are <0.10 . Thus, it appears that the sample size of banded birds and fit of the best approximating Brownie et al. (1985) model were sufficient to generate precise estimates of annual survival rates for all cohorts except HY-F captured in the Aspen Parkland ecological province and all age-sex cohorts captured in the Forest ecological province.

Unfortunately, 59 of 60 $\hat{CV}(\hat{H})$ -values were >0.10 . The lack of precision of these estimates may be attributed to (1) the use of variances associated with both direct-recovery rates and band-reporting rates in the estimation of $CV(H)$, (2) the likelihood that another logistic regression model would better describe the system of interest, and (3) an insufficient sample size of banded individuals in most cohorts. More specifically, the mean sample size of each age-sex cohort banded annually in Minnesota during 1996–2010 was: AHY-M = 478.6 (range: 238–952), AHY-F = 75.3 (range: 42–142), HY-M = 146.9 (range: 28–297), and HY-F = 113.7 (range: 26–237). Thus, it appears necessary to increase the sample size of banded individuals in most cohorts.

The cohort-specific sample size estimates necessary to generate precise harvest rate estimates (Table 4) and annual survival rate estimates (300 per cohort, Brownie et al. 1985) in general seem attainable. However, the low sample sizes associated with some cohorts banded during 1996–2010 suggest that it has been difficult to obtain adequate samples via standard capture methods. It may be necessary to use alternative capture methods in a more focused effort than the MNDNR has previously employed in their general banding program.

ACKNOWLEDGMENTS

This project was funded in part by the Wildlife Restoration Program (Pittman-Robertson).

I thank personnel from the U.S. Fish and Wildlife Service and White Earth Band for their efforts in banding wood ducks in Minnesota. C. Herwig provided GIS assistance. J. Fieberg and J. Lawrence reviewed earlier versions of this manuscript. This project was funded in part by the Wildlife Restoration (Pittman-Robertson) Program. Progress Report, Study 3, PR Project W-69-S Minnesota.

LITERATURE CITED

- Balkcom, G. D., P. R. Garretson, and P. I. Padding. 2010. Predicting wood duck harvest rates in eastern North America. *Journal of Wildlife Management* 74:1575–1579.
- Bellrose, F. C., D. J. Holm, and R. Kasul. 1994. Population dynamics. Pages 437–459 in F. C. Bellrose and D. J. Holm, authors. *Ecology and management of the wood duck*. Stackpole, Mechanicsburg, Pennsylvania, USA.

- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data – a handbook. Second edition. U.S. Fish and Wildlife Service Resource Publication 156, Washington, D.C., USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer, New York, New York, USA.
- Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, New York, New York, USA.
- Conroy, M. J., C. J. Fonnesebeck, and N. L. Zimpfer. 2005. Modeling regional waterfowl harvest rates using Markov Chain Monte Carlo. *Journal of Wildlife Management* 69:77–90.
- Crone, E. E. 2001. Is survivorship a better fitness surrogate than fecundity? *Evolution* 55:2611–2614.
- Franklin, A. B., D. R. Anderson, and K. P. Burnham. 2002. Estimation of long-term trends and variation in avian survival probabilities using random effects models. *Journal of Applied Statistics* 1–4:267–287.
- Hanson, D. S., and B. Hargrave. 1996. Development of a multilevel Ecological Classification System for the state of Minnesota. *Environmental Monitoring and Assessment* 39:75–84.
- Henny, C. J. and K. P. Burnham. 1976. A reward band study of mallards to estimate band reporting rates. *Journal of Wildlife Management* 40:1–14.
- Lindmeier, J. P., and R. L. Jessen. 1961. Results of capturing waterfowl in Minnesota by spotlighting. *Journal of Wildlife Management* 25:430–431.
- Mausser, D. M., and J. G. Mensick. 1992. A portable trap for ducks. *Wildlife Society Bulletin* 20:299–302.
- Nichols, J. D., and F. A. Johnson. 1990. Wood duck population dynamics: a review. Pages 83–105 in L. H. Frederickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. *Proceedings of the 1988 North American wood duck symposium*, 20–22 February 1988, St. Louis, Missouri, USA.
- Otis, D. L., and G. C. White. 2002. Re-analysis of a banding study to test effects of an experimental increase in bag limits of mourning doves. *Journal of Applied Statistics* 29:479–495.
- Otis, D. L., and G. C. White. 2004. Evaluation of ultrastructural and random effects band recovery models for estimating relationships between survival and harvest rates in exploited populations. *Animal Biodiversity and Conservation* 27:157–173.
- Pollock, K. H., K. Tsai, and J. M. Hoenig. 1994. Band return models: use of solicited bands and separation of hunting and natural mortality. *Journal of Wildlife Management* 58:193–198.
- Sandercock, B. K. 2006. Estimation of demographic parameters from live–encounter data: a summary review. *Journal of Wildlife Management* 70:1504–1520.
- Sedinger, J. S., G. C. White, S. Espinosa, E. T. Partee, and C. E. Braun. 2010. Assessing compensatory versus additive mortality: an example using greater sage-grouse. *Journal of Wildlife Management* 74:326–332.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second Edition. MacMillan, New York, New York, USA.
- Sheaffer, S. E., W. L. Kendall, and E. F. Bower. 2005. Impact of special early harvest seasons on subarctic-nesting and temperate nesting Canada geese. *Journal of Wildlife Management* 69:1494–1507.
- Trost, R. E. 1990. Relationship between harvest and annual survival rates of wood ducks in eastern North America, 1966–1984. Pages 367–370 in L. H. Frederickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, editors. *Proceedings of the*

- 1988 North American wood duck symposium, 20–22 February 1988, St. Louis, Missouri, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–138.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA.
- Wilson, K. R., J. D. Nichols, and J. E. Hines. 1989. A computer program for sample size computations for banding studies. U.S. Fish and Wildlife Service Technical Report 23.
- Wunz, G. A. 1984. Rocket net innovations for capturing wild turkeys and waterfowl. *Transactions of the Northeast Section of The Wildlife Society* 41:219.
- Zimmerman, G., P. Garrettson, M. Koneff, and N. Zimpfer. 2010. Guidance on the estimation and application of reporting rates of waterfowl leg bands. U.S. Fish and Wildlife Service, unpublished report.

Table 1. Model selection statistics for Brownie et al. (1985) models used to estimate the recovery (f) and annual survival rates (S) of wood ducks banded in Minnesota, 1996–2010.

Model	K	QAICc	Δ QAICc	ω_i
$f_{age+sex+ecological\ province} \quad S_{age+sex+ecological\ province}$	13	14,093.684	0	0.761
$f_{age+sex} \quad S_{sex}$	5	14,097.251	3.567	0.128
$f_{age+sex} \quad S_{age+sex}$	6	14,098.876	5.192	0.057
$f_{age \times sex} \quad S_{sex}$	6	14,099.035	5.350	0.052

Table 2. Annual survival rate estimates of wood ducks banded in the northern Mississippi Flyway generated in 3 studies.

Period ^a	Geographic area ^b	Annual survival rate estimates (95% CI) of each age-sex cohort ^c			
		AHY-M	AHY-F	HY-M	HY-F
1996–2010	Prairie	0.607 (0.579–0.634)	0.494 (0.439–0.548)	0.572 (0.492–0.649)	0.458 (0.376–0.542)
	Transition	0.556 (0.510–0.600)	0.441 (0.380–0.504)	0.520 (0.440–0.599)	0.406 (0.330–0.487)
	Aspen Parkland	0.567 (0.529–0.605)	0.453 (0.390–0.518)	0.532 (0.444–0.617)	0.418 (0.330–0.511)
	Forest	0.640 (0.469–0.781)	0.529 (0.356–0.695)	0.606 (0.420–0.767)	0.493 (0.315–0.673)
1960–1985	Northern Mississippi Flyway	0.543 (0.529–0.557)	0.472 (0.440–0.504)	0.411 (0.383–0.439)	0.398 (0.355–0.441)
1966–1985	Northcentral U.S. ^j	0.544 (0.530–0.558)	0.496 (0.469–0.523)	0.416 (0.392–0.440)	0.363 (0.332–0.394)

^a Estimates from 1996–2010 were generated in this study, 1960–1985 estimates are from Bellrose et al. (1994), and 1966–1985 estimates are from Nichols and Johnson (1990).

^b Geographic areas are as follows: Prairie = Prairie Parkland ecological province, Transition = Eastern Broadleaf Forest ecological province, Aspen Parkland = Tallgrass Aspen Parkland ecological province, Forest = Laurentian Mixed Forest ecological province (Hanson and Hargrave 1996) all within Minnesota; Northern Mississippi Flyway = portions of the eastern Dakotas, Manitoba, Michigan, Minnesota, Ontario, and Wisconsin; Northcentral U.S. = Illinois, Iowa, Minnesota, Missouri, and Wisconsin.

^c Age-sex cohorts are AHY-M = adult male, AHY-F = adult female, HY-M = juvenile male, HY-F = juvenile female.

Table 3. Model selection statistics for logistic regression models used to estimate the direct-recovery rates (f^*) of wood ducks banded in Minnesota, 1996–2010.

Model	K	AICc	Δ AICc	ω_i
$f^* \text{ age} + \text{sex} + \text{time}$	17	6848.973	0	0.521
$f^* \text{ age} \times \text{sex} \times \text{ecological province}$	16	6851.389	2.416	0.156
$f^* \text{ age} + \text{time}$	16	6851.422	2.449	0.153
$f^* \text{ age} + \text{sex} + \text{ecological province}$	6	6852.828	3.854	0.076
$f^* \text{ age} + \text{sex} + \text{flyway bag limit}$	4	6854.690	5.717	0.030
$f^* \text{ age} + \text{ecological province}$	5	6856.002	7.029	0.016
$f^* \text{ age} \times \text{time}$	30	6856.309	7.336	0.013
$f^* \text{ age} \times \text{ecological province}$	8	6856.463	7.490	0.012
$f^* \text{ age} + \text{flyway bag limit}$	3	6857.426	8.453	0.008

Table 4. Estimates of the sample size of banded wood ducks needed to generate harvest rate (H) estimates with coefficients of variation (CV)—values of 0.05 and 0.10.

Age-sex cohort	$CV(H)$	
	0.05	0.10
AHY-M	2107	952
AHY-F	440	209
HY-M	605	259
HY-F	622	276

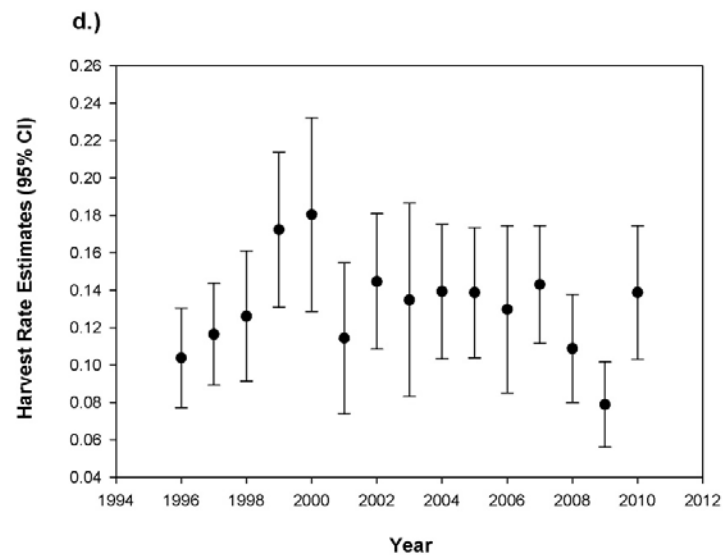
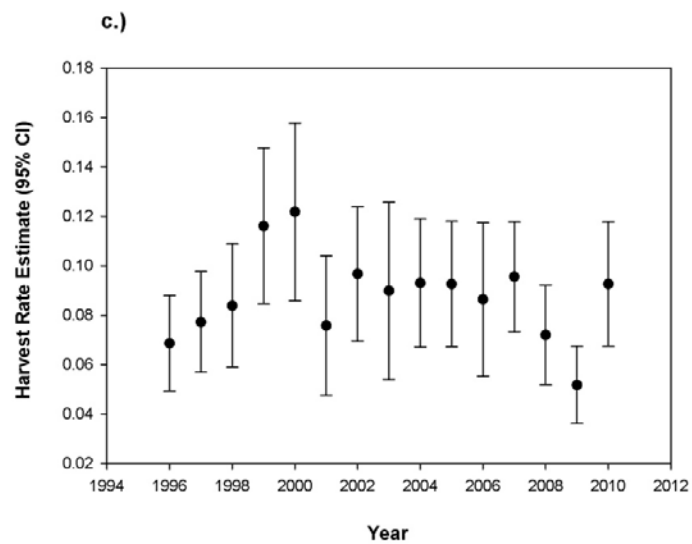
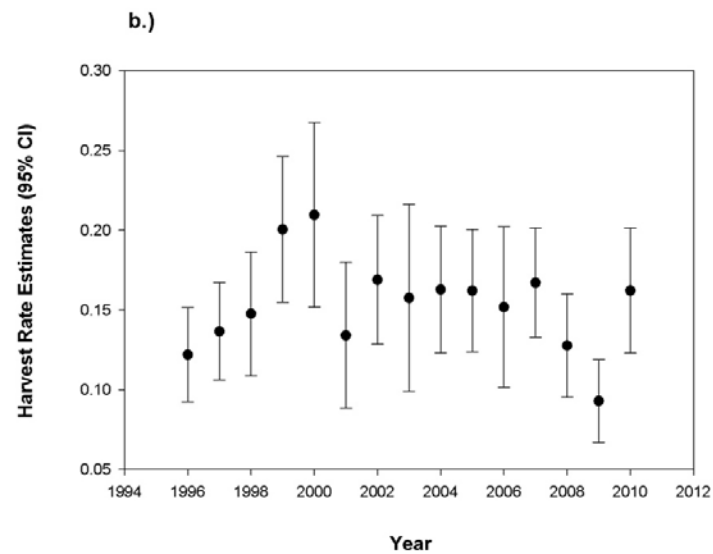
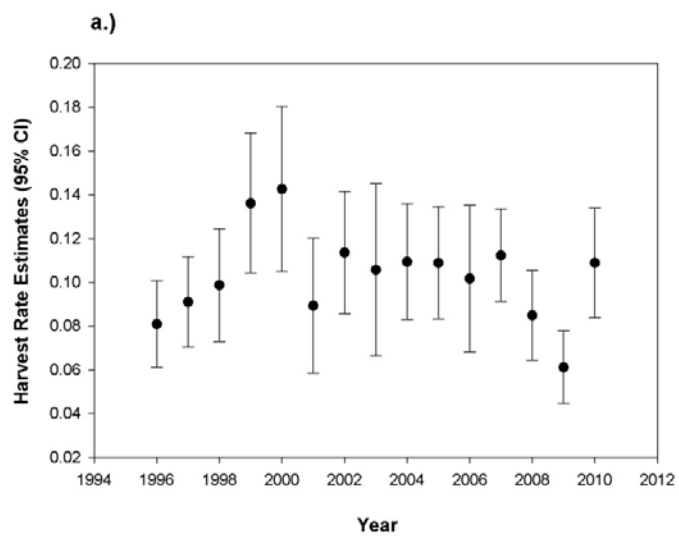


Figure 1a–d. Harvest rate estimates of a.) AHY-M, b.) HY-M, c.) AHY-F, and d.) HY-F wood ducks banded in Minnesota, 1996–2010.

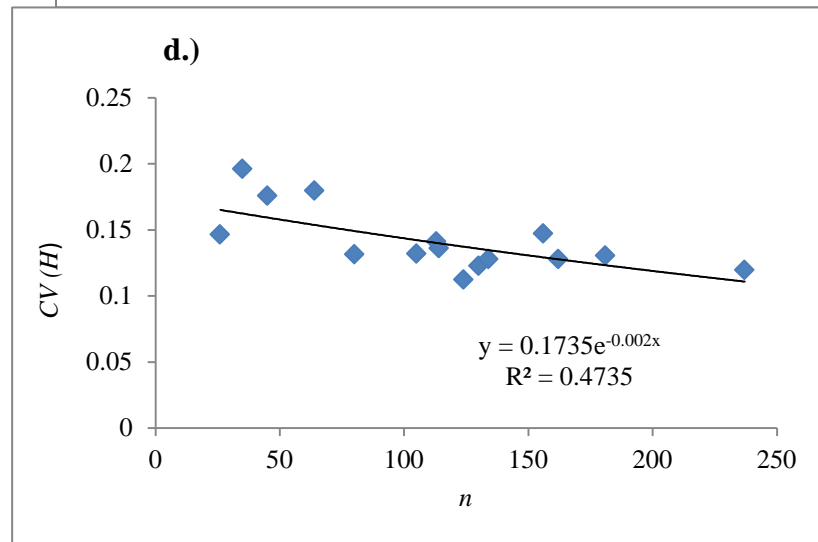
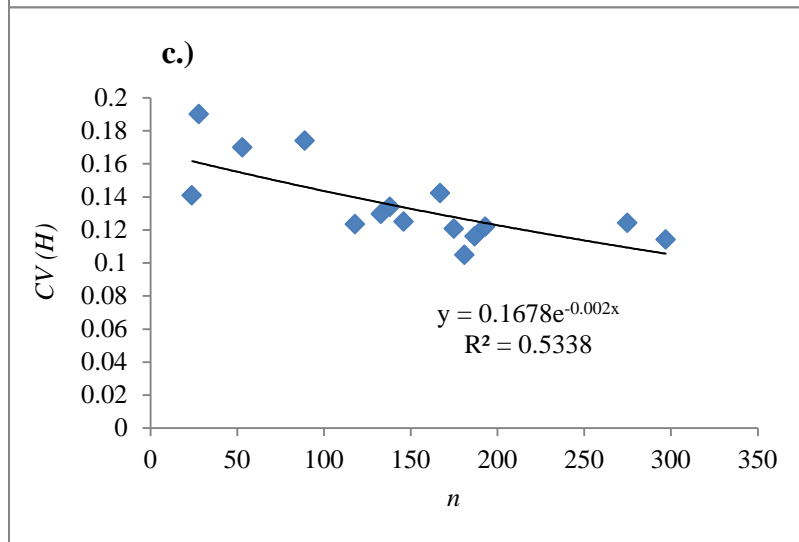
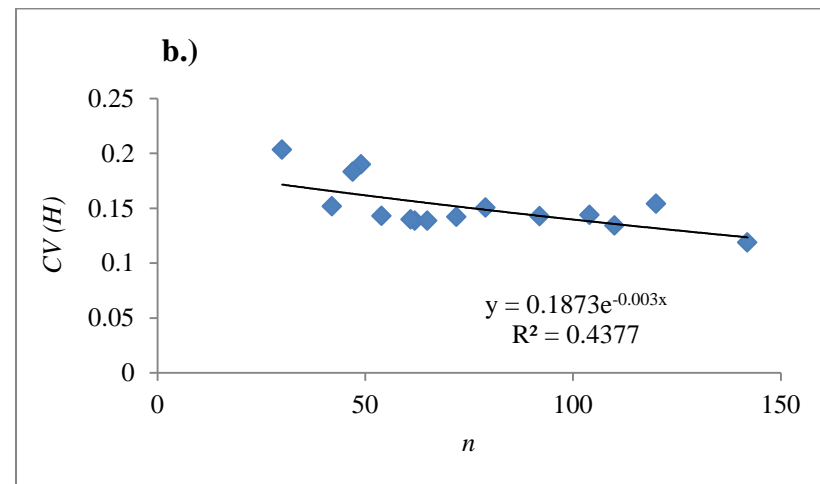
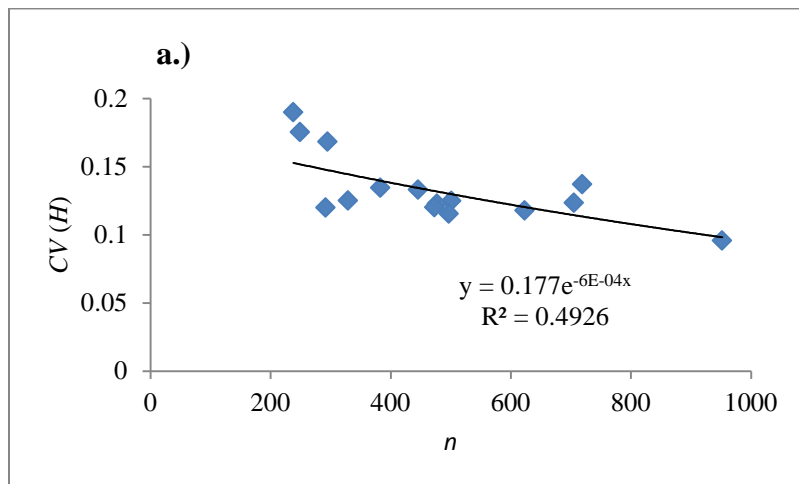


Figure 2a–d. The exponential relationship between the estimated coefficient of variation ($CV[\hat{H}]$) and sample size (n) of a.) AHY-M, b.) AHY-F, c.) HY-M, and d.) HY-F wood ducks banded in Minnesota, 1996–2010.