

WALLEYE AND MUSKELLUNGE MOVEMENT IN  
THE MANITOWISH CHAIN OF LAKES, VILAS COUNTY, WISCONSIN

By

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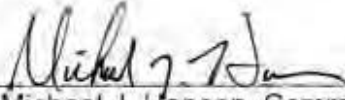
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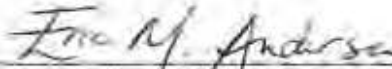
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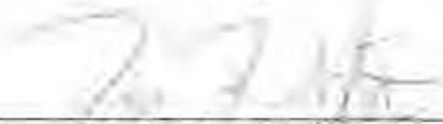
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ABSTRACT. —I quantified movement and spawning-lake fidelity for walleye *Sander vitreus* and muskellunge *Esox masquinongy* in the Manitowish Chain of 10 interconnected lakes in Vilas County, Wisconsin. I marked 7,427 walleye (55–2,720 per lake) and 491 muskellunge (24–99 per lake) with T-bar anchor tags and 34 walleye and 36 muskellunge with radio-tags. Tags were recovered from catches in electrofishing, trap netting, voluntary angler returns, tribal spearing, and angler creel surveys. From May 2004 to October 2005, 23% of all walleye tagged and 19% of all muskellunge tagged were recovered. During that period, 85% of walleye (17–95% per lake, 1,710 tags, 19–555 tags per lake) and 59% of muskellunge (0–92% per lake; 92 tags, 1–18 per lake) were recovered in the same lake in which they were tagged. Of 1,152 tag returns (2–302 per lake) for walleye and 58 tag returns (0–11 per lake) for muskellunge, 87% of walleye (33–97% per lake) and 55% of muskellunge (0–91% per lake) spawned in the same lake in 2004 and 2005. Walleye movement rate increased with the number of outlets that connected each lake to other lakes in the chain: 11% in lakes with one connection, 21% in lakes with two connections, and 50% in lakes with three connections. Muskellunge movement rate also varied with the number of outlets that connected each lake to other lakes in the chain: 74% from lakes with one connection to other lakes, 26% from lakes with two connections, and 50% from lakes with three connections. My results indicate that most walleye spawned and stayed in the same lake, but that many muskellunge did not spawn or stay in the same lake in the Manitowish Chain in 2004 and 2005. I recommend that angling and spearing fisheries be managed for individual lakes for walleye and entire lake chains for muskellunge.

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## INTRODUCTION

Many fish species move daily or seasonally within and among water bodies to fulfill their life history needs. Management of fisheries for such mobile populations is often hindered by lack of knowledge of their patterns and rates of movement (Rasmussen et al. 2002). Fisheries biologists must know if different spawning runs mix freely in lakes or maintain discrete populations (Rawson 1957). Despite widespread knowledge that fish move, movement patterns are usually only qualitatively known (Rasmussen 2002). For example, movement rate and spawning site fidelity of walleye and muskellunge in lake chains have rarely been quantified. Studies of movement rate may quantify previously qualitative knowledge of fish movement (Schwartz et al. 1993), assess interactions between spatially distinct fisheries, or define discreteness of fish stocks (Hilborn 1990). Such estimates of movement rate and spawning site fidelity can thereby aid in determining if mobile populations should be managed as separate discrete populations or as a single population (Schwartz et al. 1993).

The Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) cooperatively manage angling and spearing fisheries for walleye and muskellunge in the northern third of Wisconsin (i.e. the ceded territory; BIA 1991, BIA 2003; Figure 1). Within the ceded territory, walleye occur in 919 lakes and muskellunge occur in 623 lakes. During 1980–1989, angling accounted for 75–85% of all walleye harvested in northern Wisconsin, whereas spearing accounted for only 15–22% (Staggs 1989). The management system for walleye and muskellunge fisheries in the



ceded territory of Wisconsin grew from a federal court decision that specified methods by which "safe harvest" levels should be set for spearing (Hansen 1989, Staggs 1989; Staggs et al. 1990; Hansen et al. 1991). The angling fishery is regulated with daily bag and minimum length limits, within a season that runs from the first Saturday in May through February for walleye and from the last Saturday in May through November for muskellunge. The spearing fishery is regulated with individual nightly bag limits that account for the allowable spearing harvest on each lake each night with a season focused in April (Staggs 1989; Staggs et al. 1990). Winter ice spearing of muskellunge is currently regulated by a length limit (1 muskellunge may be of any size, and thereafter, half of the muskellunge speared must be longer than 32 inches; no bag limit).

Walleye and muskellunge are popular sport-fish in Wisconsin. At present, the literature contains little basic behavioral information on either species, thereby resulting in much speculation about habits (Dombeck 1979). Biologists need to know behavioral information to make intelligent management decisions, such as setting stocking and harvest quotas, and identifying and protecting spawning areas. Tagging and mark-recapture studies provide useful methods for answering fisheries management questions. Yet, knowledge of the life history of these species remains incomplete, especially regarding movement and spawning within chains of lakes.

Wisconsin has many lake chains that vary in total acreage, number of lakes, and degree of connectivity. Fish may or may not use all lakes in the chain. Walleye and muskellunge populations require species-specific spawning

habitats, and therefore, differ in the distance they move to reach historic spawning areas (Colby et al. 1979). Knowledge of fish movement and spawning lake fidelity are important because one lake in a chain may have excellent spawning habitat whereas other lakes in the chain may have excellent feeding habitat. Furthermore, the degree to which fish move from spawning areas to feeding areas among lakes varies in relation to the distribution of spawning and feeding areas among lakes (Rasmussen et al. 2002).

Tribal spearing takes place on spawning grounds, where adult walleye and muskellunge are often harvested. Tagging studies have generally shown that walleye and muskellunge disperse widely after spawning (Stroudt and Eddy 1939; Eschmeyer 1950; Smith et al. 1952; Fomey 1963; Minor and Crossman 1978; Dombeck 1979; Strand 1986). Therefore, angler harvest is not focused only on spawning areas, but rather, includes the entire lake and encompasses both mature and immature fish. Because spearing and angling differ, movement of fish after spawning further complicates fishery management in lake chains.

Successful management of lake chains relies on an understanding of species-specific fish movement within and among lakes and years. If walleye and muskellunge move seasonally among lakes, the number of each species in a lake at a particular time may not be related to lake area or the spawning population of that lake. In such systems, quotas based on lake-specific population estimates may not effectively regulate harvest for all sub-populations, so should be set based on sub-populations within groups of lakes or overall for some combination of lakes (Rasmussen et al. 2002).

Walleye and muskellunge movement after spawning can be extensive in lake chains. If walleye move seasonally among lakes, the number of walleye in a lake at a particular time may not be related to lake area or the spawning population of that lake. Rasmussen et al. (2002) found up to 29% of walleye marked during spawning in four small lake chains (2–5 lakes per chain) in northern Wisconsin moved to other lakes within the chain after spawning. Muskellunge also move extensively during parts of the season in large lakes, and presumably, lake chains (Minor and Crossman 1978; Dornbeck 1979; Miller and Menzel 1986a; and Strand 1986). Miller and Menzel (1986b) found that after spawning, muskellunge moved from littoral areas into pelagic water as the season progressed. This suggests that mark-recapture estimates of adult abundance at spawning are appropriate for setting lake-specific spearing quotas but not for setting lake-specific angling regulations.

My objectives were to determine (1) if walleye and muskellunge use multiple lakes in the chain for spawning and feeding, and (2) if walleye and muskellunge spawn in the same lake in a chain in successive years. These objectives were accomplished through a mark-recapture study from spring 2004 through spring 2005 in which walleye and muskellunge were marked with individually-colored and numbered T-bar anchor tags to monitor long-term movement and a sub-sample were fitted with radio transmitters to quantify short-term movements. I quantified movement from spawning lakes to other lakes in the chain from recaptures of T-bar and radio-tagged walleye and muskellunge

during the year and spawning-lake fidelity from recaptures of tagged walleye and muskellunge in successive spawning runs in 2004 and 2005.

## METHODS

### *Study Area*

Wisconsin has 18 chains of lakes that vary in acreage (289–2587 ha), numbers of lakes (2–16 lakes), and degree of connectivity (number of connections to other lakes). The Manitowish Chain is one of the larger chains in both acreage (1649 ha) and number of lakes (10 lakes). The Manitowish Chain includes Alder (111 ha), Clear (225 ha), Fawn (30 ha), Island (414 ha), Little Star (99 ha), Manitowish (205 ha), Rest (246 ha), Spider (110 ha), Stone (56 ha) and Wild Rice (153 ha) lakes (Schneberger 1963; Table 1; Figure 1). The Manitowish Chain has four inlets and one outlet. Inlets include Rice Creek and the Manitowish River flowing into Island Lake, Trout River flowing into Wild Rice Lake, and Papoose Creek flowing into Rest Lake. Water flows northeast toward Rest Lake, where a small low-head dam forms the chain. The outlet is the Manitowish River that flows to the Turtle-Flambeau Flowage.

### *Marking*

Immediately after ice out on 20 April 2004, fyke nets were set to capture walleye for marking. Fyke nets were fished through the peak of walleye spawning (25 April 2004), when the water temperature was approximately 45°F. Sampling effort included 56 nets fished for 6 nights (336 net nights) in 2004 on known walleye spawning habitat.

For each walleye captured, gender was determined by extrusion of gametes, total length was measured to the nearest 0.254 cm, a T-bar anchor tag was affixed below the spiny dorsal fin, and a fin was marked by partial removal. Each lake was assigned a specific primary fin clip(s) and each T-bar anchor tag was individually numbered and colored according to lake (Table 1). Adult walleye were defined as sexually mature fish (by extrusion of gametes) or fish of unknown sex longer than 38.1 cm (Beard et al. 1997). Only walleye longer than 25.4 cm and of known sex were tagged and marked with the primary fin clip specified for each lake. All walleye of unknown sex longer than 25.4 cm but shorter than 38.1 cm, were tagged and marked with the secondary fin clip (top caudal clip). After marking, fish were released away from the capture site in the same lake to avoid recapture bias.

A sub-sample of walleye ( $N = 34$ ) were fitted with radio transmitters that were implanted in the body cavity after anaesthetization with carbon dioxide. Five female and nine male walleye were radio-tagged in Clear Lake and eight female and 12 male walleye were radio-tagged in Island Lake. Surgical procedures followed methods described by Hart and Summerfelt (1975).

Fyke nets were also used to capture muskellunge for marking. Fyke nets were fished, and muskellunge were marked, from ice out on 20 April 2004 through the peak of muskellunge spawning on 13 May 2004, when the water temperature was approximately 55°F. Sampling effort included 56 nets fished for 11 nights (616 net nights) in 2004 on known muskellunge spawning habitat.

Muskellunge were marked in a fashion similar to walleye. For each muskellunge captured, gender was determined by extrusion of gametes, total length was measured to the nearest 0.254 cm, a T-bar anchor tag was inserted near the dorsal fin, and a fin was marked by partial removal. Each lake was assigned a specific primary fin clip(s) and each T-bar anchor tag was individually numbered and colored according to lake (Table 1). Adult muskellunge were defined as sexually mature fish (by extrusion of gametes) or fish of unknown sex longer than 50.8 cm. Only muskellunge longer than 50.8 cm and of known sex were marked with the primary fin clip specified for each lake. All muskellunge of unknown sex shorter than 76.2 cm were tagged and given the secondary fin clip (top caudal clip).

A sub-sample of muskellunge ( $N = 36$ ) was fitted with radio transmitters implanted in the body cavity after anaesthetization with carbon dioxide. Seventeen female and 19 male muskellunge were radio tagged in the chain. Surgical procedures followed methods described by Hart and Summerfelt (1975). After marking, fish were released away from the capture site in the same lake to avoid recapture bias. Two tag types, (T-bar and radio) were used to avoid any bias related to tag returns.

### *Recapture*

On 25 April 2004, at the peak of walleye spawning, fyke nets were removed for one night from all lakes in the chain and electrofishing was used to sample all lakes for recaptures. This electrofishing run was also used to mark additional walleye and muskellunge and to estimate initial movement of marked

fish. During this run, all walleye and muskellunge collected were examined for tags and marks. Each unmarked fish was marked using the protocol described above. Tag number, tag color, lake location and date were recorded for all marked fish recaptured.

After the first recapture run, fyke nets were reset and fished until 13 May 2004, to mark additional walleye and muskellunge. Each new unmarked walleye or muskellunge was marked using the protocol described above. Fyke netting, electrofishing, angling, tribal spearing, and creel surveys that ran from the first Saturday in May 2004 through 1 October 2005 were used to recapture marked fish and estimate if walleye and muskellunge use multiple lakes in the chain for spawning and feeding.

In 2005 fyke nets were set immediately after ice out on 14 April, to determine if walleye and muskellunge spawn in the same lake in successive years. Fyke nets were fished for seven nights, through the peak of walleye and muskellunge spawning (20 April 2005), when the water temperature was approximately 55°F. Sampling effort included 48 nets fished for 7 nights (336 net nights). All nets were set on the same sites in 2005 as in 2004, on known spawning habitat.

Radio-tagged fish were located weekly by boat during the open-water season. Each lake in the chain was searched at least once each week during June, July, and August 2004. Locations of radio-tagged fish were marked with Global Positioning System (GPS). At each location, date, time of day (24 hour

clock), water depth, temperature, bottom type, presence or absence of vegetation, and presence or absence of baitfish was noted if possible.

To aid in tag recovery, signs were posted at boat landings and information was spread by creel clerks. Tags were also recovered and voluntarily returned by anglers. This tag-return system was advertised and coordinated through local bait shops, guides, chambers of commerce, resorts, marinas, and word of mouth. Tags were labeled with a mailing address to facilitate their return. No reward was offered for tag returns.

### *Data Analysis*

I used recoveries of T-bar anchor tags and radio-tagged fish location to estimate (1) the probability that fish moved from marking locations (spawning lakes) to other lakes in the chain during the same open-water year; and (2) the probability that fish were recaptured in the same marking lake (spawning lakes) during the course of one year (spawning lake fidelity). Spawning lake fidelity is defined as fish marked during the spawn in lake  $x$  in year 1 (2004) and recaptured during the spawn in lake  $x$  in year 2 (2005). Measurement error of each movement probability was estimated using approximate binomial confidence limits described by Agresti and Coull (1998).

Tag loss was estimated for walleye and muskellunge captured in April 2005 as the fraction of fish that lost a tag (retained a fin clip) of the total number of fish captured in 2005, similar to a study by Newman and Hoff (1998). Only fish captured by researchers were used to estimate tag loss to avoid non-recognition



by untrained personnel. Estimates were not available for fish captured in Rest and Stone Lakes because lost tags were not reported by work crews (Table 1).

Lakes were grouped by the number of outlets that connected each lake to other lakes in the chain, to estimate the probability that fish movement differed among lakes with varying numbers of connections. Probabilities were estimated in a matrix with elements  $P_{mr}$  = the probability of a fish marked in lake  $m$  at time  $t$ , and recaptured later in lake  $r$  at time  $t+1$  (Rasmussen et al. 2002; Table 2). A matrix was estimated to quantify: (1) movement rates from spawning lakes to other lakes during the year, but before spawning in the next year; and (2) movement rates from spawning lakes in one year to spawning lakes in the next year. I did not estimate mortality because interest was solely on movement rates among lakes in the chain. Movement rates for models without mortality are the probability that a fish in lake  $m$  at a given time was in lake  $r$  at the next time (Rasmussen 2002)

## RESULTS

### *Walleye*

I recovered 23% of all tagged walleye in the Manitowish Chain through September 2005 (1,710 of 7,427). Of 7,427 walleye marked (55–2,720 per lake) in the Manitowish Chain during the two-year study, more fish were recaptured in May and early June in both 2004 and 2005 than in any other months (Figure 2). Tag returns were mostly from males (1,075), followed by females (391), and those of unknown sex (244), and were proportional to the numbers of each sex marked and released (4,834 males, 1,640 females, and 949 of unknown sex).

Tag loss ranged from 0% to 10.5% per lake for T-bar anchor tags from May 2004 to April 2005 (Table 1).

The average overall movement rate for walleye was 15% (95% confidence interval = 13.4–16.8%) for the entire Manitowish Chain, varied among lakes, and increased with the number of outlets that connected each lake to other lakes in the chain. Based on recoveries of anchor-tagged and radio-tagged walleye, 85% (83.2–86.6%) of walleye remained in the same lake in which they were marked during 2004 and 2005 (Figure 3; Table 3). The average movement rate was 11% (7.7–14.0%) for walleye in lakes with one connection to the rest of the chain (Clear, Island, Little Star, Rest and Wild Rice), 21% (14.9–27.1%) for walleye in lakes with two connections (Alder and Fawn), and 50% (48.4–50.8%) for walleye in lakes with three connections (Manitowish, Spider and Stone, Figure 4). Radio-tagged fish (N = 34) moved at a rate of 15% (11.5–19.3%) for fish marked and released in the chain. Over all lakes, 87% (84.7–88.6%; 1,000 returns of 1,152 tagged and released) of all tagged sexually-mature walleye were recaptured during the spawning season in the same lake in the Manitowish Chain in 2004 and 2005 (Figure 5; Table 4).

### *Muskellunge*

Of 491 muskellunge marked (24–99 per lake) in the Manitowish Chain during the two year study (Table 1), 92 (19%) were voluntarily returned by anglers and tribal members through September 2005. Anglers returned more tags in June of both 2004 and 2005, whereas fishery surveys captured most fish in May of 2004 and June of 2005 (Figure 6). Tag returns were mostly from males

(58), followed by females (26) and those of unknown sex (8), and were proportional to the numbers of each sex marked and released (256 males, 163 females, and 72 of unknown sex). Tag loss was 6.5% in Clear Lake and 4.1% in Manitowish Lake for T-bar anchor tags from May 2004 to April 2005 (tag loss could not be estimated for other lakes in the chain; Table 1).

The average overall movement rate for muskellunge was 41% (95% confidence interval = 31.7–51.5%) for the entire Manitowish Chain, and varied among lakes (8–100% per lake; Figure 7; Table 5). The average movement rate was 26% (16.8–34.2%) for muskellunge marked in lakes with one connection to the rest of the chain (Clear, Island, Little Star, Rest and Wild Rice), 73% (53.1–93.5%) for muskellunge marked in lakes with two connections (Alder and Fawn), and 50% (38.5–61.5%) for muskellunge marked in lakes with three connections (Manitowish, Spider, and Stone; Figure 8). Radio-tagged fish (N = 36) moved at a rate of 45% (39.7–50.9%) for fish marked and released in the chain (Figure 7). Over all lakes, 55% (42.5–67.3%; 32 returns of 58 tagged and released) of all tagged sexually-mature muskellunge were recaptured during the spawning season in the same lake in the Manitowish Chain in 2004 and 2005 (Figure 9; Table 6).

## DISCUSSION

### *Tag recovery*

My results showed that tag-return rates of walleye declined through the year, from spring 2004 to spring 2005, probably because tagged walleye were being harvested, dying of natural causes, and losing their tags. Walleye angling

on the Manitowish Chain was most intense during May, so most tags were returned in May. In addition, many tags were returned after first ice in December, when winter ice-fishing pressure increased. I found that tag loss was negligible, but other studies found that tag loss was much higher for white bass *Morone chrysops* (24.8%), striped bass *Morone saxatilis* (58%), and lake trout *Salvelinus namaycush* (64%), which could account for fewer tags recovered over time (Waldman et al. 1991; Muoneke 1992; Fabrizio et al. 1996).

I found that more tagged walleye were recaptured in 2004 than in 2005, which was counter-intuitive because more marked fish were at large in 2005 than in 2004. Fewer tags were returned perhaps because walleye become less vulnerable to capture by anglers and researchers as they move from shallow areas in spring to deeper areas later in the year. Rasmussen et al. (2002) attributed similar results to reduced vulnerability and individual mortality. Therefore, reducing the time at large, minimizing the number of fish moving between lakes, increasing recapture effort, and double-tagging could assist in monitoring these mobile populations. Although walleye tag returns decreased through time, so did public relations around the study area. Increased effort by researchers to inform the public of the tagging study influences tag return rates. In 2004, I attended many public meetings to advertise the project and to solicit tag returns, whereas in 2005, my effort was greatly reduced, thereby possibly reducing voluntary tag returns.

My results showed that muskellunge tag-return rates declined through the year. Most fish were captured by researchers in spring of both 2004 and 2005.

Tag returns from other sources declined throughout the year, probably because muskellunge were losing tags, dying of natural causes, being harvested, or were targeted by anglers at a reduced level. Muskellunge angling on the Manitowish Chain was most intense in June, so most tags were returned in June. Tag returns decreased into the fall, which is unexpected because muskellunge angler activity was high in fall. No tags were returned in November or December 2004. Many tagged fish (49) were observed during spring surveys in 2005. Similarly, 27% of tags were returned in April and 18% in May in a West Virginia river (Miles 1978). Haas (1978) found a similar tag-return rate (14.0 %) in Lake St. Clair. Further, some tags from harvest or capture of tagged fish are not reported (Schwarz and Arnason 1990).

More tagged muskellunge were recaptured in 2005 than in 2004, perhaps because netting effort was greater in 2005 than in 2004. Muskellunge may be less vulnerable to capture by angling than by other sampling methods or fish may move from shallow areas where they were more easily captured, to deep areas where they were more difficult to catch over time. A high percentage of angler tag returns (35.0 %) in Middle Island Creek, West Virginia suggested that muskellunge were easily and effectively harvested (Miles 1978). Initial recaptures for northern pike *Esox lucius* were greatest in the year after marking, but in some cases, the first recapture did not occur until 3–4 years after marking (Miller et al. 2001). Similarly, muskellunge in the Manitowish Chain may have strayed to un-sampled spawning sites, not spawned in some years, or been missed because the entire spawning populations were not sampled. Therefore,

longer study periods, closer monitoring, increasing recapture effort by researchers, double tagging, and increased public relations could assist in monitoring these mobile populations.

#### *Movement Rate*

I found that walleye moved little between lakes in the Manitowish Chain, which is consistent with other studies of walleye populations in lake chains and large inland lakes. Adult walleye migrations to home feeding areas are likely learned (Olson et al. 1978). After spawning, walleye disperse from shallow spawning areas into deeper water and may return to the same feeding areas year after year (Forney 1963; Olson et al. 1978). The rate of dispersal may be up to 1 km/d (Spangler et al. 1977). In lake chains, movement from spawning areas to summer feeding areas results in movement in or among lakes that depends on the distribution of spawning areas, prey, suitable habitat, and ease of movement between lakes in each chain (Rasmussen et al. 2002).

I found that walleye tagged in lakes with one connection in the Manitowish Chain moved less than walleye tagged in lakes with two or three connections. Partial barriers may restrict walleye movement (Holt et al. 1977), whereas in more open systems, fish have greater opportunity to move among lakes or within systems with distinctly different habitats (suitable spawning sites versus feeding sites). For example, I found that some tagged walleye from Rest Lake, the most separated lake in the Manitowish Chain, moved to all other lakes in the chain, thereby showing that some walleye ranged widely, while most did not. Similarly, movement rates by walleye varied greatly among lakes in chains, up to 50% for

some lake populations (Rasmussen et al. 2002). Rasmussen et al. (2002) attributed variation in movement rates to distributions of spawning and feeding areas, though my findings suggest that the degree of connectivity (number of connections) to other lakes in the chain also influenced movement rate.

I found that muskellunge moved significantly among lakes in the Manitowish Chain, which is similar to other studies of muskellunge. After spawning, muskellunge disperse from shallow spawning areas into deeper water and may return to the same feeding areas year after year. The rate of dispersal may be quite rapid. For example, activity of muskellunge increased greatly soon after ice went out (Dombeck 1979). Muskellunge movement in spring and fall coincided with travel to and from spawning and over-wintering areas, which resulted in larger mean movements during this period, and possibly the rest of the year (Younk et al. 1996). In lake chains, movement from spawning areas to summer feeding areas may result in movement within or among lakes, depending on the distribution of spawning areas, prey, suitable habitat, and ease of movement among lakes in each chain (Rasmussen et al. 2002). However, tagged muskellunge moved little during summer and had highly variable movements in the fall in an Ontario river (Crossman 1956).

I found that muskellunge tagged in lakes with one connection in the Manitowish Chain moved less than muskellunge tagged in lakes with two or three connections. Partial barriers can restrict fish movement (Holt et al. 1977). In more open systems, fish have greater opportunity to move among lakes or within systems with distinctly different habitats (suitable spawning sites versus feeding

sites). Movements from spawning grounds to summer home ranges may be characterized by directed movements that frequently cross large open stretches of lake (Strand 1986). Johnson (1963) claimed that availability of food was a factor that likely influenced home range size of muskellunge. Peak movement is in fall, followed by minimal movement during winter and intermediate movement during summer (Dombeck 1979). For example, tagged muskellunge from each lake in the Manitowish Chain were found in at least one other lake in the chain, thereby showing that muskellunge can range widely given the opportunity. I also found that fish tagged in lakes with more than one connection were more often found in other lakes in the chain than fish tagged in lakes with only one connection. This could be caused by factors such as distribution of spawning and feeding areas, and number and degree of connectivity (length of channels between lakes). Activity of muskellunge is related to water temperature (Dombeck 1979), which can cause increased movement at certain times of the year, within seasons, and across years. Alternatively, muskellunge migration to home feeding areas may be learned (Miller and Menzel 1986a).

#### *Spawning Lake Fidelity*

I found that most walleye spawned in the same lake in successive years in the Manitowish Chain, which was consistent with other studies and indicated that the choice of spawning habitat was likely a genetically heritable trait. Numerous tagging studies of walleye confirmed that walleye returned to the same spawning site each year (Stoudt 1939; Eddy and Surber 1947; Eschmeyer 1950; Eschmeyer and Crowe 1955; Crowe et al. 1963; Forney 1963). Walleye appear



to have a genetically-based environmental cue that guides them to preferred spawning habitat (Jennings et al. 1996). In Many Point Lake, Minnesota, many walleye marked during their spawning runs returned to spawn at the same site, despite the availability of other spawning areas (Olson and Scidmore 1962). In Oneida Lake, New York, only two individual walleye changed spawning location during the season (Forney 1963). From the evidence available, I conclude that returns of most walleye to the same spawning lake are non-random. Considering the factors that account for non-random return, I also conclude that this return is likely a homing behavior (Olson and Scidmore 1962).

I found that some walleye ranged great distances to and from spawning lakes, but that most post-spawning movement was not extensive, as was also true of walleye in Leech Lake, Minnesota (Olson et al. 1978). In Leech Lake, some walleye appeared to select the same general location for feeding in successive years (Olson et al. 1978). Olson (1978) proposed that walleye homing is an adult learned behavior that is more strongly displayed by fish with a home feeding area near a particular spawning site or that is reinforced by repeated migrations. Spawning migrations from home feeding areas are likely to the nearest spawning site, though migrations of greater distance may also occur (Olson et al. 1978). Home range is often defined as the area in which an animal tends to stay (Clarke 1954) and is often quantified as the area within which an animal spends 90% of its time (Tufto et al. 1996). I conclude that walleye in the Manitowish chain likely spawn within or near preferred feeding sites within their home range.

I found that walleye moved little in the Manitowish Chain, similar to other studies. For example, the average distance between the tagging site and the point of recovery for walleye in Lac la Ronge was only 3.5 miles (Rawson 1957). Variation in strength of environmental stimuli among years or variation in individuals to perceive stimuli may also explain variation in tag-return rates among years (Olson and Scidmore 1962). Most walleye tagged in Lac la Ronge were recaptured close to the point of tagging: of 281 recaptures, 190 (67.5%) were within two miles of the tagging site, 43 (15.3%) were within 2–5 miles, 35 (12.5%) were within 5–10 miles, 8 (2.9%) were within 10–20 miles, and 5 (1.8%) were within 20–65 miles (Rawson 1957).

I found that most muskellunge did not spawn in the same lake in successive years in the Manitowish Chain, which is inconsistent with other studies that indicate the choice of spawning habitat is a genetic trait. For example, all muskellunge in the Mississippi River returned to the same spawning site in consecutive years, and several fish bypassed other suitable spawning sites to return to previously-used sites (Younk et al. 1996). Some muskellunge move great distances to and from spawning areas and some appear to select the same general location for feeding in successive years. Muskellunge formed two distinct groups in Lake St. Clair (Haas 1978). Most (61%) muskellunge tracked in Middle Island Creek, West Virginia, moved at least 0.3 km from the initial tagging site and 40% moved out of the pool in which they had been released (Miles 1978). In West Okoboji Lake, Iowa, four of nine muskellunge were found at the same location in two consecutive spawning seasons (Miller and Menzel

1986a). Some muskellunge tagging studies suggest that muskellunge return to the same spawning site each year (Strand 1986; Crossman 1956; Johnson 1963; Miles 1978; Farrell in press), whereas others suggest non-homing behavior (Miller and Menzel 1986a, Strand 1986). Homing here refers to the annual return of spawning muskellunge to a particular spawning site, in this case lake, rather than any suitable spawning area (Crowe 1962).

I found substantial movement by muskellunge among lakes in the same season, which is consistent with other studies in which muskellunge moved significant distances after spawning (Miller and Menzel 1986b; Dombeck 1979; Crossman 1956). Several other studies have shown that movement increased with higher water temperatures (Minor and Crossman 1978). Although spawning site fidelity has been shown in other studies, mixing may be essentially random in spawning populations in the Manitowish Chain. Movement was highest for muskellunge in the months of April and October, which may explain low spawning lake fidelity (Dombeck 1979).

#### MANAGEMENT IMPLICATIONS

For walleye, I conclude that current lake-by-lake management of angling and spearing fisheries are appropriate for protecting populations from over-harvest in chains of lakes. My conclusion is based on my estimates of low overall movement rates among lakes (15%) and high spawning-lake fidelity (87%) of walleye in the Manitowish Chain of lakes. Management of spearing and angling fisheries for walleye in northern Wisconsin is based on mark-recapture population estimates that assume fish populations in individual lakes are discrete

sampling units. Based on my findings, this approach seems justified in interconnected chains of lakes.

For muskellunge, I conclude that current lake-by-lake management of angling and spearing fisheries may not be necessary to protect populations from over-harvest in chains of lakes. My conclusion is based on my estimates of high overall movement rates among lakes (41%) and low spawning-lake fidelity (55%) of muskellunge in the Manitowish chain of lakes. Management of spearing and angling fisheries for muskellunge in northern Wisconsin is based on population estimates that assume populations are discrete sampling units. Based on my findings, this approach does not seem justified in interconnected chains of lakes, so abundance and resulting harvest quotas should be estimated by a method that accounts for fish movement (Plante et al. 1998, Schwarz and Taylor 1998) or abundance should be estimated over the entire chain of lakes as a single unit, rather than separately for each individual lake within the chain.

Table 1. Lake name, size, number of walleye and muskellunge marked and recovered, tag loss, and T-bar anchor-tag color in each lake in the Manitowish Chain of lakes from April 2004 through October 2005.

Lake	Area (ha)	Walleye			Muskellunge			Color
		Marked	Recovered	Tag Loss	Marked	Recovered	Tag Loss	
Alder	110.9	853	164	1.0%	24	7	0.0%	Yellow
Clear	224.6	1186	337	10.5%	99	18	6.5%	Green
Fawn	29.9	55	19	0.0%	41	6	0.0%	White/Red
Island	414.0	2720	555	1.5%	32	1	0.0%	Orange
Little Star	95.7	399	104	2.6%	37	13	0.0%	Red
Manitowish	204.6	289	65	2.4%	58	17	4.2%	White
Rest	246.1	1150	308	NA	81	13	0.0%	Grey
Spider	110.1	379	82	2.9%	49	8	0.0%	Purple
Stone	56.3	75	23	NA	28	7	0.0%	Blue
Wild Rice	153.4	221	55	2.8%	42	2	0.0%	White/Blue
<b>Total</b>	<b>1648.7</b>	<b>7427</b>	<b>1710</b>		<b>491</b>	<b>92</b>		

Table 2. Probability (P) of recapture in each lake in the Manitowish Chain from April 2004 through October 2005.  $P_{1,1}$  indicates the probability that a fish marked in a lake was recaptured later in another lake.

Recapture Lake	Marking Lake									
	Alder (1)	Clear (2)	Fawn (3)	Island (4)	Little Star (5)	Manitowish (6)	Rest (7)	Spider (8)	Stone (9)	Wild Rice (10)
Alder (1)	$P_{1,1}$	$P_{2,1}$	$P_{3,1}$	$P_{4,1}$	$P_{5,1}$	$P_{6,1}$	$P_{7,1}$	$P_{8,1}$	$P_{9,1}$	$P_{10,1}$
Clear (2)	$P_{1,2}$	$P_{2,2}$	$P_{3,2}$	$P_{4,2}$	$P_{5,2}$	$P_{6,2}$	$P_{7,2}$	$P_{8,2}$	$P_{9,2}$	$P_{10,2}$
Fawn (3)	$P_{1,3}$	$P_{2,3}$	$P_{3,3}$	$P_{4,3}$	$P_{5,3}$	$P_{6,3}$	$P_{7,3}$	$P_{8,3}$	$P_{9,3}$	$P_{10,3}$
Island (4)	$P_{1,4}$	$P_{2,4}$	$P_{3,4}$	$P_{4,4}$	$P_{5,4}$	$P_{6,4}$	$P_{7,4}$	$P_{8,4}$	$P_{9,4}$	$P_{10,4}$
Little Star (5)	$P_{1,5}$	$P_{2,5}$	$P_{3,5}$	$P_{4,5}$	$P_{5,5}$	$P_{6,5}$	$P_{7,5}$	$P_{8,5}$	$P_{9,5}$	$P_{10,5}$
Manitowish (6)	$P_{1,6}$	$P_{2,6}$	$P_{3,6}$	$P_{4,6}$	$P_{5,6}$	$P_{6,6}$	$P_{7,6}$	$P_{8,6}$	$P_{9,6}$	$P_{10,6}$
Rest (7)	$P_{1,7}$	$P_{2,7}$	$P_{3,7}$	$P_{4,7}$	$P_{5,7}$	$P_{6,7}$	$P_{7,7}$	$P_{8,7}$	$P_{9,7}$	$P_{10,7}$
Spider (8)	$P_{1,8}$	$P_{2,8}$	$P_{3,8}$	$P_{4,8}$	$P_{5,8}$	$P_{6,8}$	$P_{7,8}$	$P_{8,8}$	$P_{9,8}$	$P_{10,8}$
Stone (9)	$P_{1,9}$	$P_{2,9}$	$P_{3,9}$	$P_{4,9}$	$P_{5,9}$	$P_{6,9}$	$P_{7,9}$	$P_{8,9}$	$P_{9,9}$	$P_{10,9}$
Wild Rice (10)	$P_{1,10}$	$P_{2,10}$	$P_{3,10}$	$P_{4,10}$	$P_{5,10}$	$P_{6,10}$	$P_{7,10}$	$P_{8,10}$	$P_{9,10}$	$P_{10,10}$

Table 3. The proportion of walleye that were tagged in April 2004 and recaptured through October 2005 in each lake in the Manitowish Chain of ten interconnected lakes, Vilas County, Wisconsin. Numbers of walleye tagged in each lake are shown in Table 1.

Recapture Lake	Marking Lake									
	Alder	Clear	Fawn	Island	Little Star	Manitowish	Rest	Spider	Stone	Wild Rice
Alder	0.7683			0.0018	0.0192	0.1385	0.0033	0.0122		0.2545
Clear		0.9169	0.1579	0.0018		0.0154	0.0131	0.0244	0.0435	0.0182
Fawn		0.0059	0.4737	0.0018			0.0033	0.0244	0.0870	
Island		0.0237	0.1053	0.9405	0.0288	0.3846	0.0196	0.0659		
Little Star	0.0122	0.0059			0.8558	0.0154		0.0244	0.0435	0.0182
Manitowish	0.0732			0.0054	0.0673	0.3846		0.0244	0.0435	0.0182
Rest		0.0356	0.1053	0.0144		0.0154	0.9510	0.0365	0.2609	
Spider	0.0061	0.0030	0.1053	0.0306	0.0192	0.0462	0.0098	0.4878	0.3478	
Stone		0.0089	0.0526	0.0018					0.1739	
Wild Rice	0.1402			0.0018	0.0096					0.6909

Table 4. The proportion of walleye that were tagged in April 2004 and recaptured while spawning in April 2005 in each lake in the Manitowish Chain of ten interconnected lakes, Vilas County, Wisconsin. Numbers of walleye tagged in each lake are shown in Table 1.

Recapture Lake	Marking Lake									
	Alder	Clear	Fawn	Island	Little Star	Manitowish	Rest	Spider	Stone	Wild Rice
Alder	0.9231				0.0244	0.2941		0.0233		0.3962
Clear		0.9698	0.1818	0.0147			0.0403	0.0233	0.5000	
Fawn		0.0129	0.4545							
Island			0.0909	0.8882		0.0588	0.0202	0.3256	0.1667	0.0189
Little Star	0.0192			0.0059	0.9268	0.1765				
Manitowish	0.0192			0.0529		0.4118	0.0040	0.0465		
Rest		0.0043	0.0909	0.0118			0.9274	0.0698		
Spider		0.0043	0.0909	0.0265	0.0244	0.0588	0.0040	0.4681		
Stone		0.0043	0.0909		0.0122		0.0040	0.0465	0.3333	
Wild Rice	0.0385	0.0043			0.0122					0.5849



Table 5. The proportion of muskellunge that were tagged in April 2004 and recaptured through October 2005 in each lake in the Manitowish Chain of ten interconnected lakes, Vilas County, Wisconsin. Numbers of muskellunge tagged in each lake are shown in Table 1.

Recapture Lake	Marking Lake									
	Alder	Clear	Fawn	Island	Little Star	Manitowish	Rest	Spider	Stone	Wild Rice
Alder	0.5714					0.1111				0.2500
Clear		0.7143	0.6667	0.5000						
Fawn		0.2381							0.7500	
Island				0.5000						
Little Star					0.5455	0.2778	0.0769			0.2500
Manitowish	0.2857				0.4545	0.5556				
Rest							0.9231	0.1111		
Spider		0.0476				0.0556		0.4444		
Stone			0.3333					0.4444	0.2500	0.2500
Wild Rice	0.1429									0.3500

Table 6. The proportion of muskellunge that were tagged in April 2004 and recaptured while spawning in April 2005 in each lake in the Manitowish Chain of ten interconnected lakes, Vilas County, Wisconsin. Numbers of muskellunge tagged in each lake are shown in Table 1

Recapture Lake	Marking Lake									
	Alder	Clear	Fawn	Island	Little Star	Manitowish	Rest	Spider	Stone	Wild Rice
Alder	0.5000					0.2857				1.0000
Clear		1.0000	0.7143					0.1667		
Fawn									0.3333	
Island				1.0000						
Little Star					0.2500	0.4286				
Manitowish	0.5000				0.6250	0.2857		0.1667		
Rest					0.1250		0.9167			
Spider							0.0833	0.6667	0.8571	
Stone			0.2857							
Wild Rice										



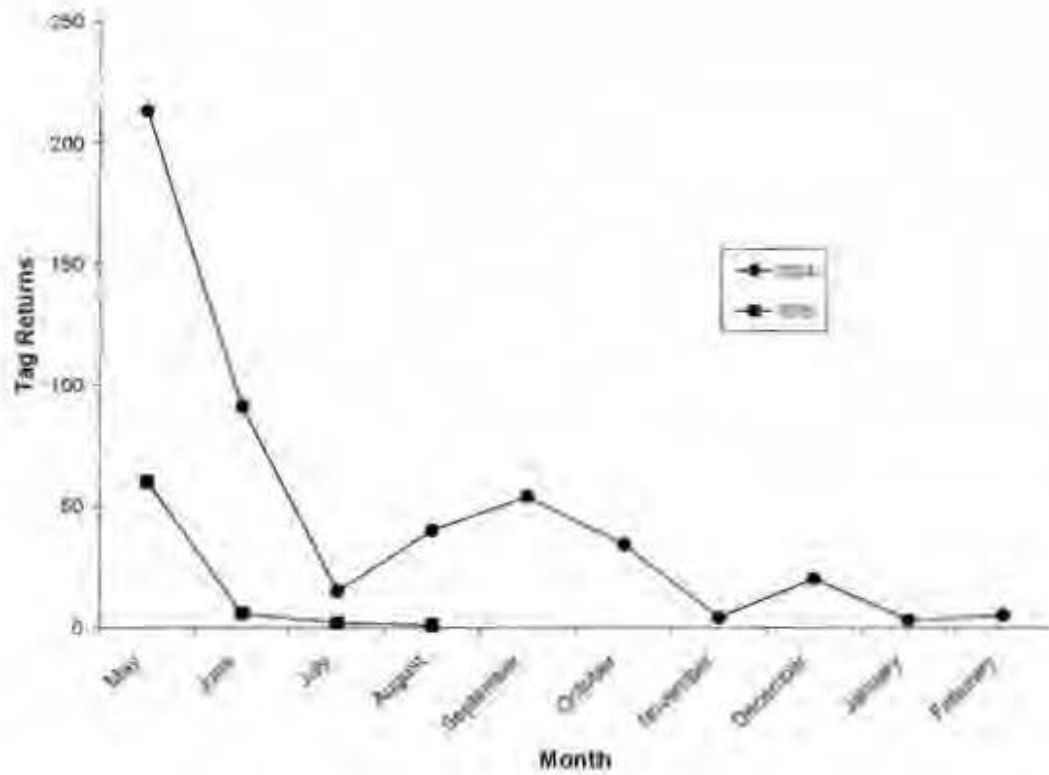


Figure 2. Number of T-bar anchor-tag returns for all capture methods of walleye in the Manitowish Chain, Vilas County, Wisconsin from May 2004 through February 2005.

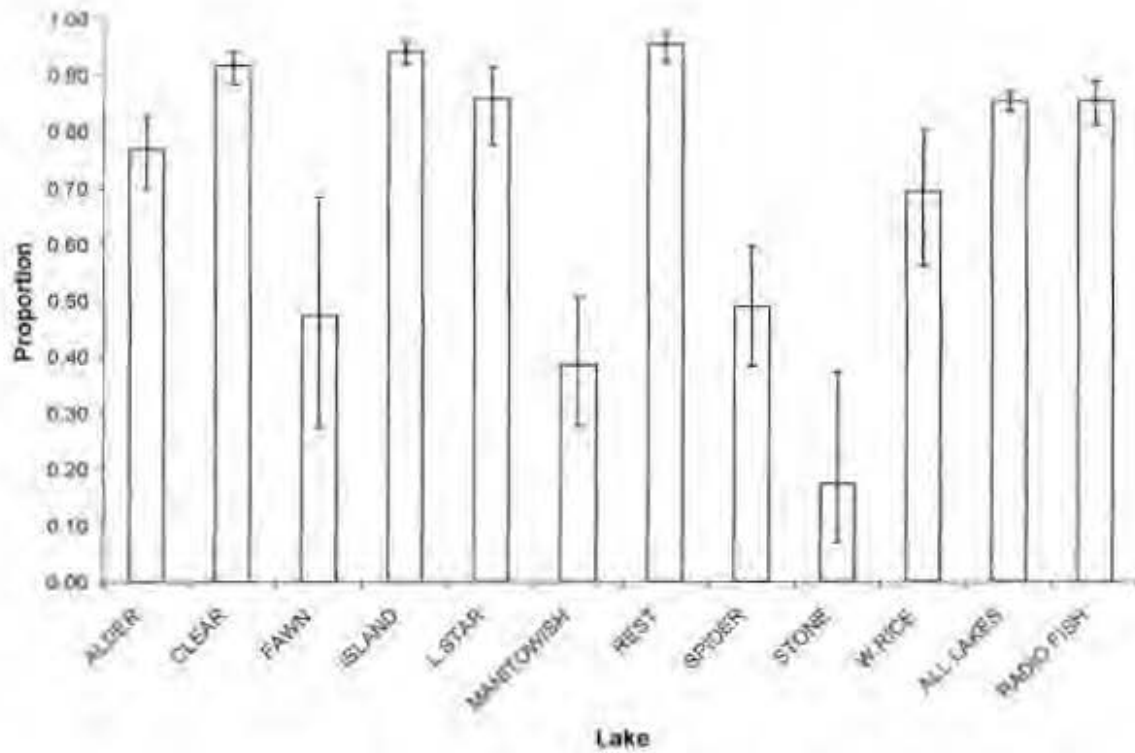


Figure 3. Proportion of walleye remaining in each marking (spawning) lake in the Manitowish Chain, Vilas, County, Wisconsin during 2004 and 2005. Error bars indicate 95% confidence limits.

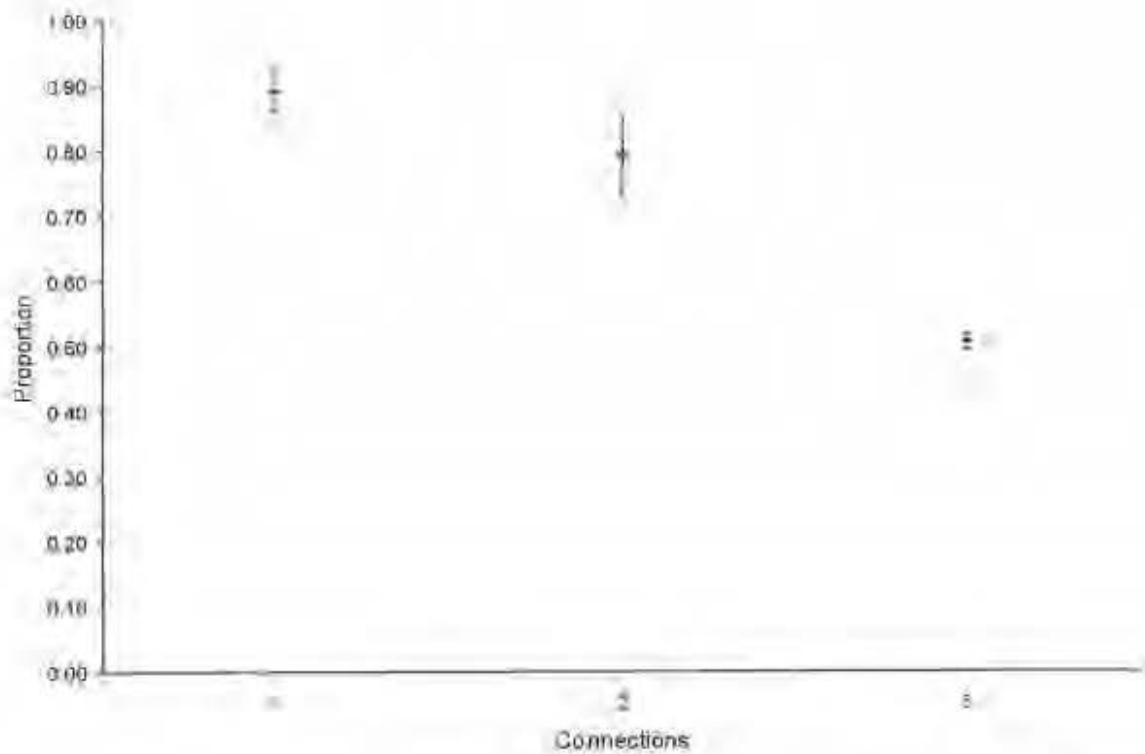


Figure 4 Proportion of walleye recaptured in marking (spawning) lake versus number of connections (channels) to other lakes in the Manitowish Chain, Vilas County, Wisconsin during 2004 and 2005. Error bars indicate 95% confidence limits.

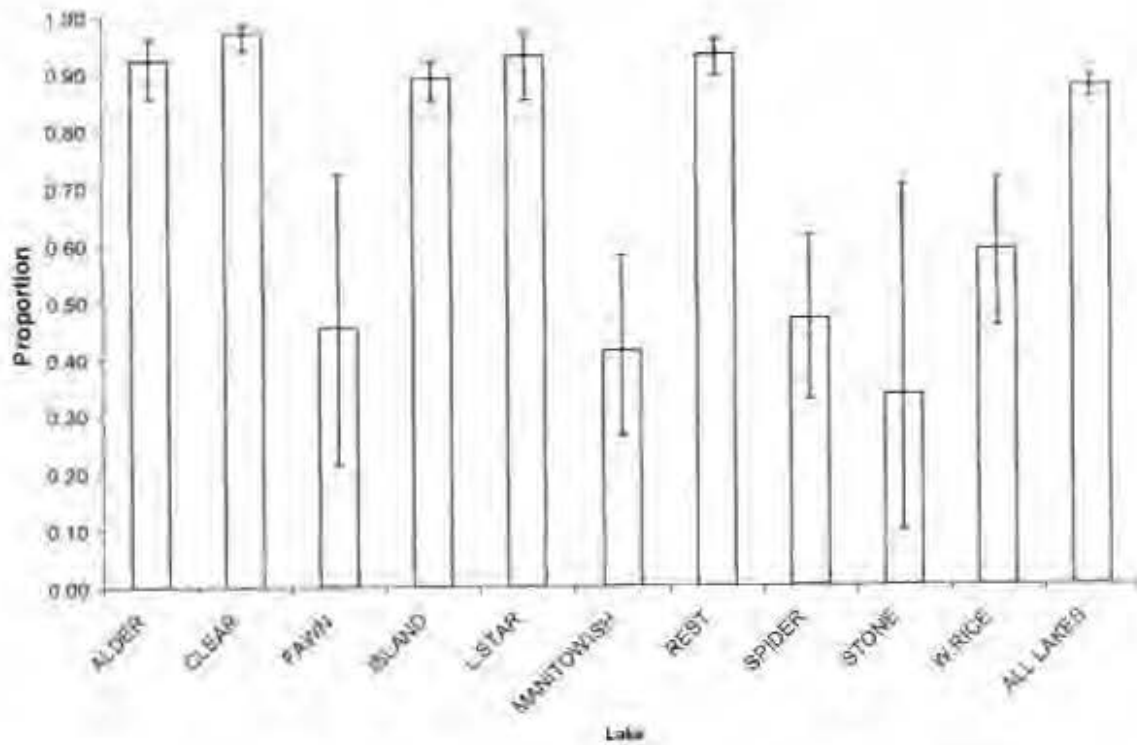


Figure 5. Proportion of walleye spawning in the same lake in both 2004 and 2005 in the Manitowish Chain, Vilas County, Wisconsin. Error bars indicate 95% confidence limits.

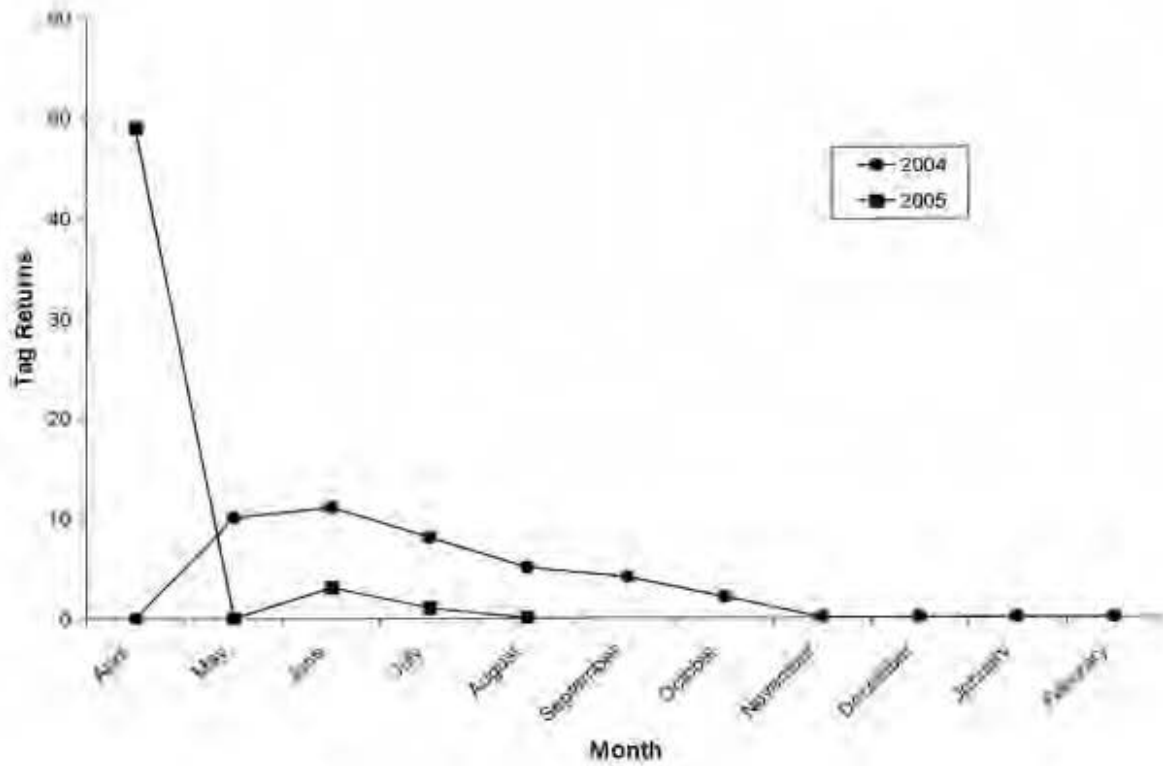


Figure 6 Number of T-bar anchor-tag returns using all gears for muskellunge in the Manitowish Chain, Vilas County, Wisconsin from April 2004 through February 2005.



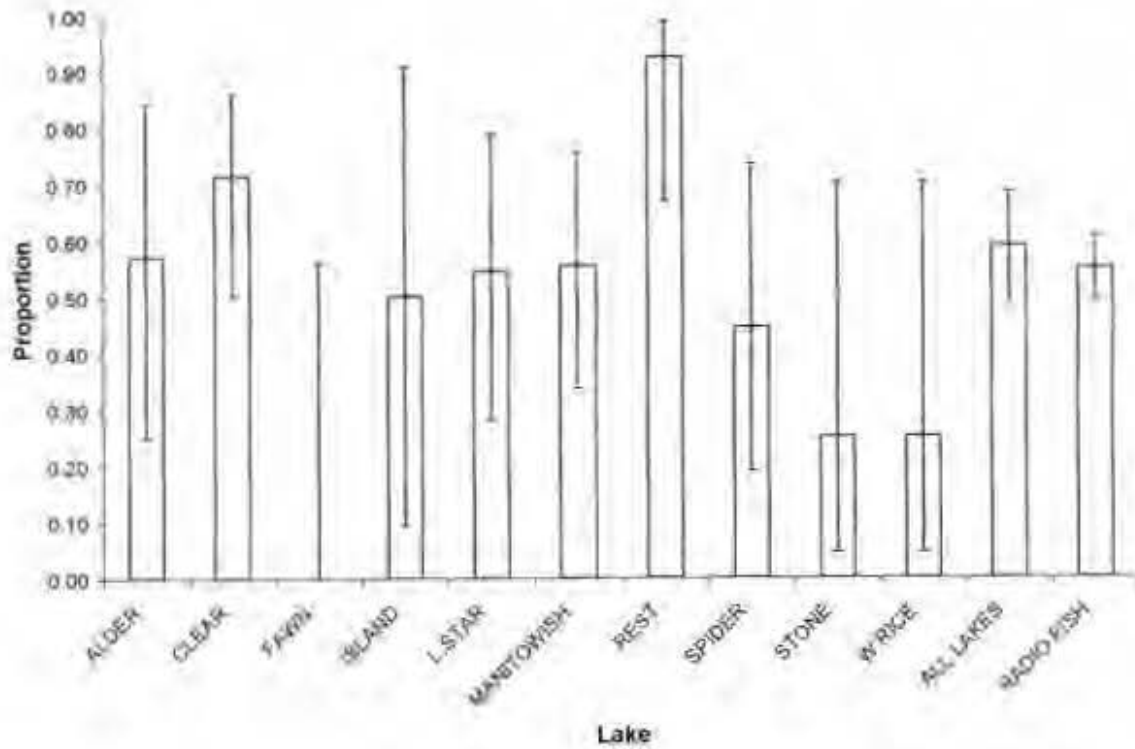


Figure 7. Proportion of muskellunge remaining in each marking (spawning) lake in the Manitowish Chain, Vilas, County, Wisconsin during 2004 and 2005. Error bars indicate 95% confidence limits.

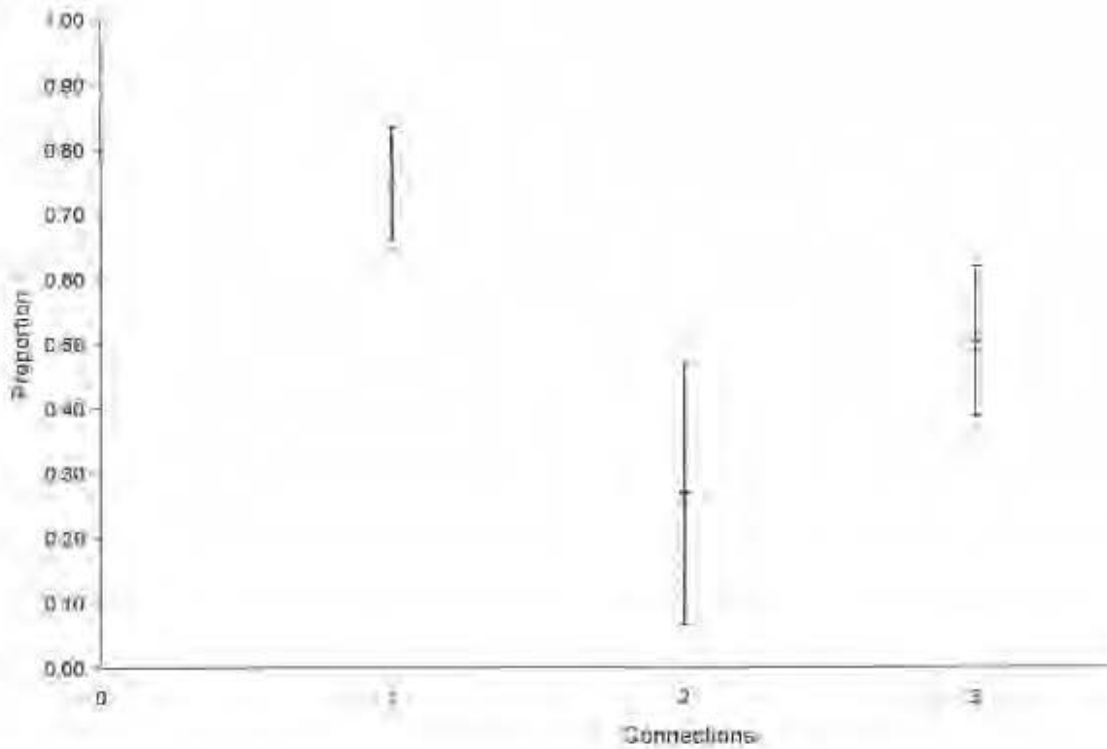


Figure 8 Proportion of muskellunge recaptured in marking (spawning) lake versus number of connections (channels) to other lakes in the Manitowish Chain, Vilas County, Wisconsin during 2004 and 2005. Error bars indicate 95% confidence limits.

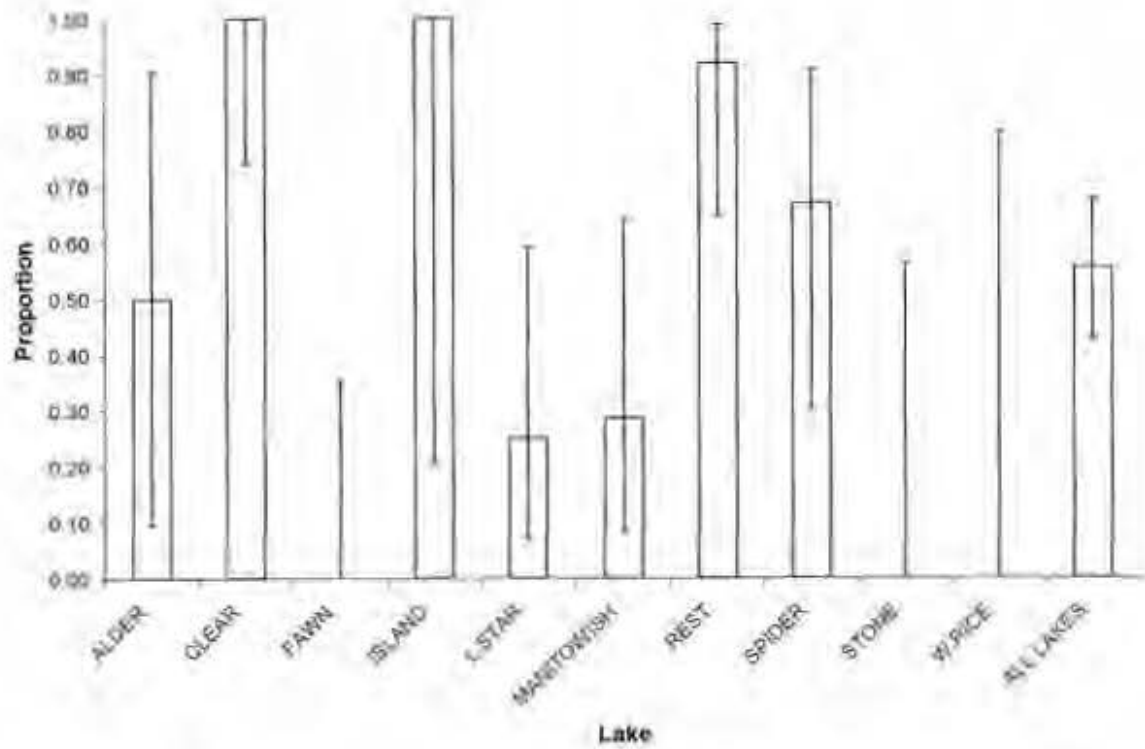


Figure 9. Proportion of muskellunge spawning in the same lake in both 2004 and 2005 in the Manitowish Chain, Vilas County, Wisconsin. Error bars indicate 95% confidence limits.

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