Yellow perch (*Perca flavescens*) stock structure in Lake Michigan: an analysis using mark–recapture data

David C. Glover, John M. Dettmers, David H. Wahl, and David F. Clapp

Abstract: To evaluate the stock structure of yellow perch (*Perca flavescens*) in the southern basin of Lake Michigan and in Green Bay, we analyzed recaptures from a lake-wide mark–recapture study implemented from 1996 to 2001 to infer the range and pattern of movement and spawning-site fidelity. Yellow perch generally moved south along the western shoreline, west along the southern shoreline, and north along the eastern shoreline during summer and non-summer months; the magnitude of movement was greater after spawning. Spawning yellow perch frequently returned to the same site, with 35%–80% of recaptured individuals returning to their marking site. Results from multiple tagging sites within Illinois indicated that spawners may return to larger areas rather than to specific sites, suggesting that large spawning complexes exist. Despite strong fidelity in some areas, straying was evident from all sites during spawning, resulting in mixing throughout the southern basin. Such mixing could promote gene flow and diminish stock differentiation. Dispersal of yellow perch within the southern basin of Lake Michigan occurred regularly across adjacent management boundaries. Therefore, adjacent jurisdictions may wish to consider re-examining their regulations based on this information to ensure consistent, complementary regulations that incorporate the movement patterns of yellow perch.

Résumé : Afin d'évaluer la structure du stock de perchaudes (*Perca flavescens*) dans le bassin sud du lac Michigan et dans Green Bay, nous avons analysé les recaptures provenant d'une étude de marquage et de recapture menée sur l'ensemble du lac en 1996–2001; nous en avons déduit l'étendue de la répartition et les patrons de déplacement, ainsi que la fidélité au site de fraye. Les perchaudes se déplacent généralement vers le sud le long de la rive ouest, vers l'ouest le long de la rive sud et vers le nord le long de la rive est durant les mois d'été et durant les autres mois; l'amplitude des déplacements est plus grande après la fraye. Les perchaudes en reproduction retournent souvent au même site de fraye, 35–80% des individus recapturés étant retournés à leur site de marquage. Les résultats obtenus dans des sites multiples de marquage en Illinois indiquent que les reproducteurs peuvent retourner vers des endroits plus étendus que les sites spécifiques, ce qui laisse croire qu'il existe des complexes élargis de fraye. Malgré la forte fidélité à certains régions, il y a des indications d'errance dans tous les sites durant la fraye, ce qui cause des mélanges dans tout le bassin sud. Ce mélange pourrait favoriser le flux génique et réduire la différenciation des stocks. Il y a une dispersion régulière des perchaudes au sein du bassin sud entre les limites des différentes zones adjacentes de gestion. C'est pourquoi d'après ces renseignements, les administrations adjacentes pourraient vouloir réexaminer leurs règlements afin de s'assurer d'avoir des réglementations compatibles et complémentaires qui tiennent compte des déplacements des perchaudes.

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Introduction

Stock identification and discrimination are fundamental issues in fisheries management that are used for a variety of purposes, including conservation of biodiversity, recovery of endangered species, the spatial allocation of harvest among competing fisheries, recognition and protection of critical spawning habitat, and development of optimal monitoring strategies (Waples 1995; Begg et al. 1999a; Stephenson 1999). Stocks are distinguished by differences in characteristics that could represent differing adaptations to variation in local environments, including life history and population parameters, morphometrics, meristics, physiology, behavior, calcified structures, and genetics (Ihssen et al. 1981; Pawson and Jennings 1996; Begg et al. 1999b). Divergence among these characters depends upon the degree of spatial and temporal isolation between stocks. Divergence is measured relative to the difference between the local environments that

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individual stocks experience (Ihssen et al. 1981; Pawson and Jennings 1996; Swain and Foote 1999). Disparities in these characteristics cause individual stocks to respond differently to exploitation. Therefore, stocks should be treated as separate biological units for management purposes (Ricker 1981; Gulland 1983; Stephenson 1999). Delineation of stocks has been recognized as a critical issue for management in the Great Lakes because of the decline of many ecologically and economically important fish species and the multijurisdictional challenges faced in these systems (Kutkuhn 1981).

Before 1997, yellow perch (*Perca flavescens*) was one of the most important, commercially fished species in Lake Michigan and contributed as much as 85% of the recreational harvest by number (Francis et al. 1996). However, estimated abundances of adult yellow perch in 2002 were approximately 8% and 20% of 1986 abundance in Wisconsin and Illinois, respectively (Wilberg et al. 2005). This reduction resulted partly from extremely poor recruitment since 1988 (Francis et al. 1996; Madenjian et al. 2002; Marsden and Robillard 2004) that was exacerbated by high fishing mortality and size-selective removal of larger fish (i.e., mature females; Heyer et al. 2001; Wilberg et al. 2005). Similar declines of yellow perch abundance occurred lake-wide, although declines were less drastic in Green Bay (Francis et al. 1996). Continued poor recruitment led to strict harvest regulations on the recreational fishery and a moratorium on commercial fishing in Lake Michigan (Francis et al. 1996; Marsden and Robillard 2004), although a limited commercial fishery remains active in Wisconsin waters of Green Bay (Clapp and Dettmers 2004), and a limited tribal commercial fishery is active in northeastern Lake Michigan. Predicting population responses to changes in fishing pressure is difficult, however, because the stock structure is poorly defined.

Determining whether multiple genetic stocks of yellow perch exist within Lake Michigan has proven difficult because of low levels of genetic variability observed with protein and mitochondrial DNA characters (Leary and Booke 1982; Billington 1996). Recent genetic research using hypervariable microsatellite DNA indicated that at least three genetically distinct groups of yellow perch exist in Lake Michigan: Green Bay, northern basin, and southern basin (Miller 2003). Yet, other work suggests that sympatric stocks may occur within these three genetic groups (Horns 2001). Length and condition of adult yellow perch along the western shoreline of southern Lake Michigan (i.e., Wisconsin and Illinois) were more similar to each other than to fish from Indiana and Michigan, suggesting an east–west spatial segregation within the population (Horns 2001).

Additional information about movement of yellow perch among areas of Lake Michigan would aid in managing this important fishery. Existing information relating to the movement of yellow perch in the Great Lakes is scarce, dated, and based on very few recaptures. A tagging study conducted in Green Bay indicated that most yellow perch were recaptured within 32 km of their release site, yet some individuals were recorded up to 81 km away (Mraz 1951). Similarly, 60% of all recaptured yellow perch released from Port Washington, Wisconsin, were recaptured within 16 km, with some straying up to 92 km (Smith and Van Oosten 1939). Tagging studies conducted in smaller systems also suggest that most yellow perch do not move far from their release location (Mansueti 1960; Fortin and Magnin 1972; Clady 1977) and demonstrate a high degree of site fidelity (Mansueti 1960; Muncy 1962; Aalto and Newsome 1990), which could provide a mechanism for spatial segregation. However, the movement of adult yellow perch has not been evaluated on a lake-wide scale in Lake Michigan. Strong site fidelity and limited movement by many individuals within Lake Michigan, coupled with a few rogue individuals traveling extreme distances, might maintain differences observed in population parameters in the southern basin of Lake Michigan (Horns 2001) but promote gene flow to reduce genetic variability over large areas (Slatkin 1987; Miller 2003).

Currently, yellow perch management units in the southern basin of Lake Michigan are delimited by state boundaries because the stock structure is poorly defined. Consequently, several stocks may be exploited within a state. Stocks that move across state lines or are located transboundary may be subjected to different fishing pressures. Thus, determining the movement of these putative stocks is imperative from a management perspective to facilitate the allocation of harvest among the four states that share the yellow perch fishery (Kutkuhn 1981; Horns 2001; Fu and Fanning 2004). We analyzed data from a mark–recapture study conducted from 1996 to 2001 in the southern basin of Lake Michigan and southern Green Bay to (*i*) describe the range and pattern of adult yellow perch movements and (*ii*) determine the extent to which yellow perch exhibit spawning-site fidelity. We used all information to determine the potential for the existence of sympatric stocks as well as evaluate current management boundaries.

Materials and methods

Yellow perch capture, marking, and recapture

Adult yellow perch were captured, marked, and released concurrently with annual assessments of spawning adults at nine locations in the southern basin of Lake Michigan and one location in the southern portion of Green Bay (Table 1; Fig. 1). Tagging was conducted during May and June from 1996 to 2000 in Illinois and from 1997 to 1999 in Indiana, Michigan, and Wisconsin waters. Yellow perch were tagged in Green Bay during April from 1997 to 1999. Tagging was conducted during the spring because yellow perch congregate in large numbers nearshore during spawning, making them more susceptible to capture.

Yellow perch were collected with a variety of gear types suitable for capturing fish >150 mm total length, including double-ended fyke nets, gill nets, and trap nets. All gear types were set in suitable habitat for capturing yellow perch during spawning and were retrieved within 24 h when possible. Rarely, unfavorable weather prevented their retrieval for up to 8 days (3 of 363 sets). The Illinois Natural History Survey (INHS) tagged fish at five sites in Illinois, including Waukegan Wiremill (IL-1), Lake Bluff (IL-2), North Lake Forest (IL-3), South Lake Forest (IL-4), and Fort Sheridan (IL-5; Table 1; Fig. 1). Yellow perch were captured at Mt. Baldy, Indiana (IN-1) by the Indiana Department of Natural Resources (INDNR) (Table 1; Fig. 1). Michigan Department of Natural Resources (MDNR) tagged fish at North St. Jo-

Table 1. Location identifier, latitude (Lat.) and longitude (Long.) of each tagging location, years sampled, number of adult yellow perch (*Perca flavescens*) tagged, mean size (mm) at tagging with standard error (SE) in parentheses, and number of recaptures by source.

					Recaptures		
Location identifier	Tagging location (Lat., Long.)	Years sampled	No. tagged	Mean size (mm) at tagging (SE)	Agency	Sport	Commercial
GB-1	44°39.384′N, 87°59.571′W	1997–1999	7 198	171 (0.32)[h]	413	52	104
WI-1	42°59.035′N, 87°50.250′W	1997–1999	9 615	239 (0.23)[c]	543	53	0
IL-1	42°20.244′N, 87°49.462′W	1997–2000	4 633	244 (0.46)[a]	410	59	0
IL-2	42°16.772′N, 87°49.502′W	1996	4 210	231 (0.38)[d]	424	124	57
IL-3	42°15.280′N, 87°49.015′W	1996–2000	11 167	241 (0.27)[b]	658	83	35
IL-4	42°13.950′N, 87°48.435′W	1997–1999	1 766	238 (0.63)[c]	123	25	9
IL-5	42°12.789′N, 87°47.792′W	1996–2000	10 952	240 (0.28)[b]	522	142	75
IN-1	41°42.912′N, 86°56.095′W	1997–1999	6 410	185 (0.41)[g]	233	115	0
MI-1	42°8.166′N, 86°28.454′W	1997–1999	5 240	217 (0.45)[e]	312	187	0
MI-2	42°6.154′N, 86°30.200′W	1997–1999	2 757	216 (0.59)[f]	163	104	0
Total			63 948		3 801	944	280

Note: Recaptures are from 1996 to 2001 for Illinois tagging locations and from 1997 to 2001 for all other locations. Mean sizes at tagging with similar letters did not significantly differ (α = 0.05).

seph (MI-1) and South St. Joseph (MI-2; Table 1; Fig. 1). Wisconsin Department of Natural Resources (WDNR) captured and tagged fish at Green Can Reef (WI-1), as well as at Little Tail Point (GB-1; Table 1; Fig. 1).

All yellow perch were measured (nearest mm, total length), and sex was determined by discharge of milt or eggs. Fish over 150 mm (120 mm in Green Bay) and in good condition were tagged and immediately released. Individually numbered Floy FD-94 anchor tags were inserted on the left side, above the lateral line and below the soft rays of the dorsal fin. The INHS address and phone number was also imprinted on all tags to facilitate returns.

Tagged fish were recaptured by commercial fishermen, recreational anglers, and state fisheries agencies from 1996 to 2001. The tag number, date, recapture location, sex, and total length (nearest mm) were recorded for each yellow perch recaptured. For yellow perch recaptured by commercial and recreational sources, information was requested for the tag number, date, and location. Details about the project and information specific to the recaptured yellow perch (e.g., length, sex, date, and location tagged) were sent to anglers that supplied contact information. Occasionally, inconsistencies were found with a reported tag recaptured by recreational anglers (e.g., INHS zip code reported as tag number). Unless inconsistencies could be verified with the original tag, these recaptures were omitted from analyses.

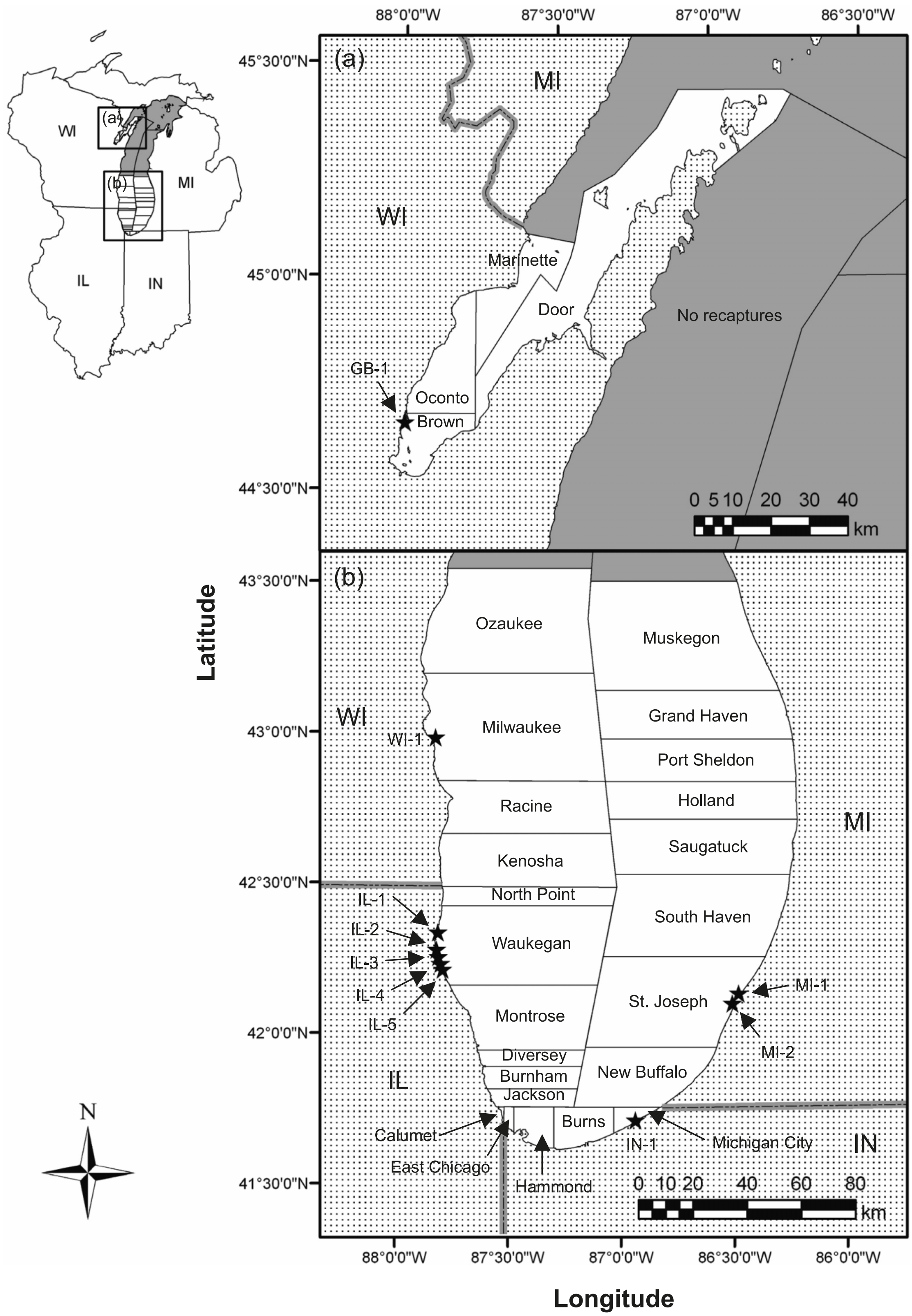
Data analysis

To describe the range and pattern of adult yellow perch movements, the spatial distribution of sport recaptures was analyzed from each release site. Sport recaptures were used because they exhibited greater spatial and temporal variation than agency recaptures. The ban on commercial fishing in Lake Michigan proper during most of the tagging study limited the utility of commercial recaptures for movement analyses. However, all sources of recapture were used later in spawning-site fidelity analyses.

Data standardization

To account for spatially disproportionate angling effort that can bias movement analyses (Hilborn 1990), estimates of directed angler effort (h) for yellow perch were incorporated. Annual creel surveys were conducted for each port or county within each state. Monthly estimates of harvest were pooled by Lake Michigan management units for each species by fishery type (i.e., boat, charter, shore, and stream anglers). Specific information regarding the estimation of angler effort can be obtained from creel surveys conducted within Wisconsin (Peterson and Eggold 2003), Illinois (Brofka and Dettmers 2004), Indiana (Palla 2003), and Michigan (Lockwood 1999; Lockwood et al. 1999). To account for spatial differences in angler effort at the smallest scale possible, we obtained these estimates separated by port for Illinois (W. Brofka, INHS, Lake Michigan Biological Station, 400 17th Street, Zion, IL 60099, USA, unpublished data), Indiana (J. Palla, INDNR, Lake Michigan Fisheries Office, 100 W. Water Street, Michigan City, IN 46360, USA, unpublished data), and Michigan waters (D. Clapp, MDNR, Charlevoix Fisheries Research Station, 96 Grant Street, Charlevoix, MI 49720, USA, unpublished data) and by county for Wisconsin waters (B. Eggold, WDNR, 600 East Greenfield Avenue, Milwaukee, WI 53204, USA, unpublished data) for each year of the tagging study (1996–2001; Fig. 1). Michigan did not separate effort directed at a specific species until 1997. To obtain angling effort directed at yellow perch during 1996 in Michigan waters, the ratio between effort directed at yellow perch and effort directed at all species for 1997 to 2001 (0.14) was multiplied by the effort directed at all species in 1996. Creel surveys were conducted in Wisconsin from March to October (March–April and September–October were combined into two single estimates), but no county was consistently surveyed during March and April throughout the tagging study. All ports in Illinois were surveyed from April to September each year. Ports in Indiana and Michigan were sampled from April to October, with the exception of St. Jo-

Fig. 1. Map of Lake Michigan with inset sections of Green Bay (*a*) and southern Lake Michigan (*b*), tagging sites (stars), and creel survey sampling areas. Creel units for each port were derived by drawing straight lines from the midpoint between ports to their respective state line. Existing county lines were used to delineate creel units in Wisconsin waters of Lake Michigan and Green Bay. No recaptures occurred in the gray-shaded waters.



seph, Michigan, and New Buffalo, Michigan, which were also sampled in March. For analyses concerning fish released in Illinois, angler effort was summed across 1996 to 2001 into two recapture periods: summer (June–August) and non-summer (March–May and September–October). Additionally, angler effort was summed across both recapture periods (March–October) when there were too few recaptures during the non-summer recapture period to provide a depiction of overall movement across the study period. For all other areas, angler effort was summed from 1997 to 2001 into the same recapture periods because tagging commenced 1 year after tagging began in Illinois. Rare recaptures that occurred from November through February were omitted because no estimates of angler effort directed at yellow perch were available.

Each recaptured yellow perch was assigned the amount of estimated angler effort from the creel unit in which it was recaptured. Creel units for each port were derived by drawing straight lines from the midpoint between ports to their respective state boundary within the lake. Existing county lines were extended into the lake to delineate creel units in Wisconsin waters of Lake Michigan and Green Bay. Distance moved was calculated as the straight-line distance from the tagging location to the closest possible location of reported recapture (e.g., street names of cities and towns, harbors, piers, beaches, power plants, water filtration plants). To determine the direction moved, we assigned directional movement for each fish as follows: north (315°–45°), south (135°–225°), east (45°–135°), or west (225°–315°). Fish recaptured at the original tagging location were omitted from the directional analyses to reduce the potential of underestimating mean movement in a particular direction. Fish that moved toward the shoreline from recapture sites (i.e., in small creeks or harbors) were assumed to represent no movement and were also omitted. These scenarios were extremely rare for sport recaptures and did not change the interpretation of the results.

Dispersal distance

Dispersal distance, which we defined as the distance within which 90% of the recaptures per effort (RPE) occurred (Schmalz et al. 2002), was used as an index of home range for a group of individuals. The RPE for each recapture location was calculated as the number of recaptures per 10 000 angler hours directed at yellow perch. We assumed that angler effort was uniformly distributed within each port and county, which allowed us to assign several recapture locations within each area with identical estimates of angler effort. We feel that this is a reasonable assumption given the resolution of angler effort we were able to obtain. The cumulative proportion of RPE (y) was fit to an exponential sigmoid function of distance from each tagging location:

$$(1) \qquad y = \frac{\alpha}{\left(1 + \beta\ \mathrm{e}^{Kx}\right)}$$

where α is the maximum cumulative proportion of RPE that can be obtained (theoretically 1.0 or 100%), β is a parameter that scales the function toward zero, and K is the rate at which RPE increases with distance (x). The modified Gauss–Newton iterative method that relies on exact derivatives was used to determine the parameters that produce the lowest residual sum of squares for each tagging location (PROC NLIN; SAS Institute Inc. 1999). Using derived parameters, the distance (x) at which the cumulative proportion of RPE (y) was equal to 0.90 (90%) was estimated for each tagging location and recapture period. We applied this analysis to recaptures during summer and to total time periods (summer and non-summer time periods combined). Although the summer and total time periods are not independent, insufficient recaptures occurred during the non-summer period to allow numerical convergence when considered alone. Therefore, it was necessary to estimate dispersal during the total time period to provide information about the range of non-summer movement that would otherwise not be displayed.

ArcView, version 3.2 (Environmental Systems Research Institute 1998) was used to develop a linear scale for shoreline distance in the southern basin of Lake Michigan to assess dispersal across management boundaries and overlap among fish released from the various tagging locations (shoreline data provided by E. Marshall, University of Michigan, Institute for Fisheries Research, 1109 North University Street, Museum Annex Building, Ann Arbor, MI 48103, USA). Shoreline distance was used because all recaptures occurred nearshore throughout the study except in Green Bay. The shoreline distance scale began at the northern border of Ozaukee County, Wisconsin (43°32.528′N, 87°47.607′W; Fig. 1) and continued counterclockwise around the southern basin, ending at the northern border of the Muskegon creel unit, Michigan (43°30.233′N, 86°26.714′W; Fig. 1). Dispersal was expressed in terms of shoreline distance by creating 90% dispersal buffers around each tagging location for each recapture period and determining the point at which the buffer crossed the shoreline. All recaptures, tagging sites, and management boundaries were similarly translated into shoreline distance.

Directional movement

To describe directional movement of adult yellow perch, we used separate weighted analyses of variance (ANOVA; PROC MIXED; SAS Institute Inc. 1999) for each major tagging area (i.e., Green Bay, Wisconsin, Illinois, Indiana, and Michigan). We examined the effect of tagging sites (T), recapture periods (R; summer and non-summer), the interaction between tagging sites and recapture periods (TR), direction nested within recapture periods ($D(R)$), and the interaction between tagging sites and distance nested within recapture periods ($TD(R)$) on mean movement. Time-at-liberty (L) was also included to test whether the variance of movement distance increased with time. To correct for disproportionate angler effort, each recaptured yellow perch was weighted by the reciprocal of the appropriate angler effort (h). We did not include the effect of T and its interactions for models that had only one tagging location (i.e., Green Bay, Wisconsin, and Indiana). To evaluate whether similar trends occurred at closely spaced tagging locations, T was included in the Illinois and Michigan models. Directions in which few recaptures (three or less) occurred in the specific recapture period were omitted from the analysis. Residuals were assessed for normality.

If F tests were significant at $\alpha = 0.05$, we minimized the type I experiment-wise error using post hoc one-tailed t tests at the $\alpha = 0.025$ level to determine whether (*i*) there was directional preference from each tagging location by determining whether the largest directional mean distance traveled was statistically larger than the distance traveled in all other directions, (*ii*) the magnitude of directional movement was greater in summer as compared with non-summer periods when the preferred direction of movement was similar between periods, and (*iii*) mean movement was greater during the non-summer recapture period.

Fidelity and movement

We used separate baseline-category logit models for each tagging site to determine the probability of fish being recaptured at their release site as well as the probability of being recaptured at other sites or areas for the entire study. Probabilities were transformed from odds ratio estimates calculated using maximum likelihood procedures (PROC LOGISTIC; SAS Institute Inc. 1999) and were then converted to percentages by multiplying by 100. Analysis of recaptures was limited to spawning seasons (May–July in Lake Michigan; April–June in Green Bay) at least 1 year after tagging. Estimating the probability of movement to areas other than the tagging site allowed us to determine (*i*) whether fidelity occurred at a larger scale (i.e., nearby tagging locations within the same region), (*ii*) if some areas represented transition zones in which fish were caught en route to more preferred spawning areas, and (*iii*) the percentage of fish moving across jurisdictional boundaries. Wald χ^2 statistics were used to test whether the observed probability of fish being caught at the tagging site was greater than that observed at other locations. In Illinois, IL-2 and IL-4 were excluded from the fidelity analysis, because no or low effort was expended to recapture yellow perch at these sites after initial tagging. Rather than omitting fish recaptured at IL-2 and IL-4 that were released from other sites, they were pooled into our analysis of all Illinois waters (IL).

Results

Yellow perch capture, marking, and recapture

Throughout the study, 63 948 adult yellow perch were tagged (Table 1). The mean size at tagging ranged from 171 to 244 mm and differed among tagging sites ($F_{[9,\,63\,807]} = 5578.45$; $P < 0.001$; Table 1). Sometimes disparities in size at tagging among tagging sites may represent biologically meaningful differences (e.g., fish tagged at Green Bay were smaller than fish tagged in the open lake). However, large sample sizes increased the power to detect small differences among locations and may not always represent biologically meaningful differences (e.g., between MI-1 and MI-2). The sex ratio of tagged individuals was highly skewed toward males (18:1), and only about 4% of all tagged individuals could not be sexed. A total of 5025 yellow perch were recaptured between 1996 and 2001 (Table 1), which represented an overall recapture rate of 7.9%. Agency, sport, and commercial returns accounted for 75.6%, 18.8%, and 5.6% of all recaptures, respectively. Mean time-at-liberty was 224 days and ranged from 0 to 2004 days (5.5 years), with 92% of all recaptures occurring within 2 years of release.

Dispersal distance

The proportion of total variability explained (R^2) by the dispersal distance models ranged from 0.94 to 0.99, indicating that describing the cumulative proportion of RPE as an exponential sigmoid function of distance fit the data very well for both summer and total recapture periods. During summer, 90% dispersal distance from GB-1 was 28.7 km, which remained within the Wisconsin waters of Green Bay. In the southern basin, dispersal distance averaged 60.4 km (all sites combined) but was quite variable among sites, ranging from 12.8 to 101.4 km. Ninety percent of the recaptures from WI-1 occurred within the Wisconsin waters of Lake Michigan. However, dispersal distances from four out of five Illinois tagging sites crossed the Illinois border into Wisconsin waters. The 90% dispersal distance from IL-3 also crossed into Indiana waters. For the fish released at site IN-1, 90% of the recaptures were reported within 44.3 km, resulting in overlap into Michigan waters. Dispersal from MI-2 crossed into Indiana waters, whereas dispersal from MI-1 extended 101.4 km, well into Illinois waters.

Considerable amounts of mixing by tagged fish within and among jurisdictions occurred during summer (Fig. 2). Dispersers from Illinois and Michigan waters overlapped considerably among nearby sites, many being completely within the dispersal area of another site, indicating little potential for isolation by distance within states (Fig. 2). Mixing among states occurred between adjacent states, with the exception of Michigan and Illinois.

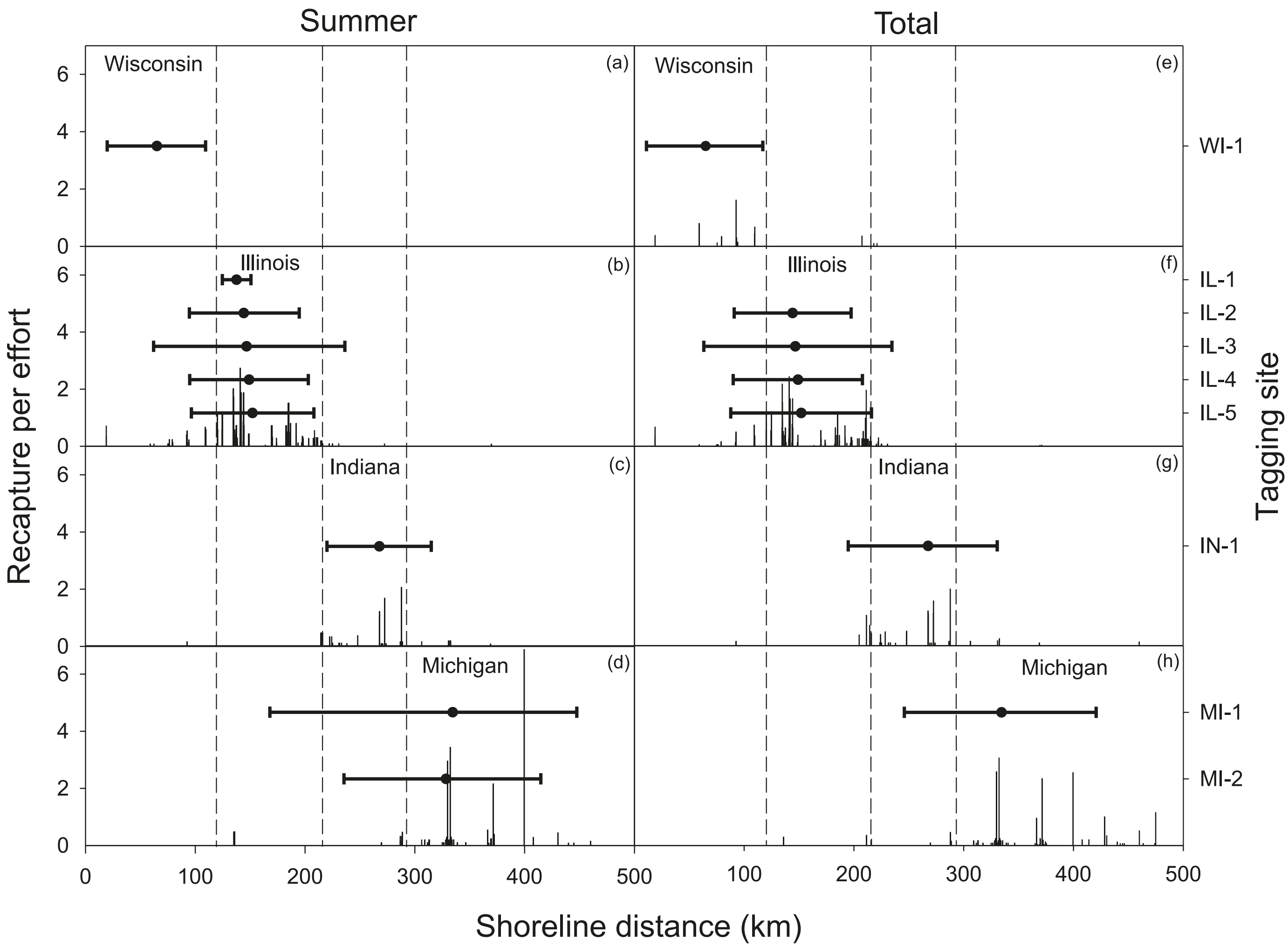
Dispersal distances for the total recapture period exceeded those of summer for all sites except for fish from IL-3 and MI-1. Dispersal distance could not be estimated for IL-1 and MI-2 because the estimated maximum cumulative proportion of RPE (α) was below 0.90, likely because too few recaptures occurred far from the release site. Although the dispersal distance increased when considering the entire time period, movement from GB-1 and WI-1 remained within the local management jurisdiction. Dispersal from four sites in Illinois waters crossed into Wisconsin waters (Fig. 2). Dispersal from two sites in Illinois crossed into Indiana waters. Ninety percent of the fish from IN-1 were recaptured within 58.8 km, resulting in movement into both Illinois and Michigan waters. Dispersal from MI-1 extended 80.5 km, crossing into Indiana waters.

Mixing among dispersers during the total time period was limited to mixing among fish released from adjacent states (Fig. 2). However, as a result of increased dispersal distances during the total time period, the mixing that occurred between Illinois and Wisconsin and between Illinois and Indiana increased slightly compared with summer. Dispersal among all sites within Illinois was completely overlapped.

Directional movement

Time-at-liberty affected the variability of distance traveled from Illinois, Indiana, and Michigan tagging areas but not from Green Bay or Wisconsin (Table 2). Thus, we omitted this term from the Wisconsin and Green Bay models. Recapture period affected the mean distance traveled for all tagging areas except Green Bay (Table 2). Specifically, non-summer movement was greater than summer movement in Illinois, Indiana, and Michigan waters ($t \geq 6.30$, $P < 0.001$),

Fig. 2. Number of recaptures per effort (vertical bars) during the summer and total time periods at specific locations expressed as shoreline distance (km) for yellow perch (*Perca flavescens*) released from Wisconsin (*a* and *e*), Illinois (*b* and *f*), Indiana (*c* and *g*), and Michigan (*d* and *h*). Tagging sites are indicated with solid circles; 90% dispersal distance from each tagging site is shown by horizontal bars and is expressed in shoreline distance rather than straight-line distance (i.e., the point at which the 90% straight-line buffer transected the shoreline). The shoreline distance scale begins at the northern border of Ozaukee County, Wisconsin, and continues counterclockwise around the southern basin, ending approximately at the northern border of the Muskegon Fishery creel unit, Michigan, and corresponding to the unshaded portion of Fig. 1*b*. Vertical broken lines represent the point on the scale at which state boundaries occur.



but less than summer movement for fish released from Wisconsin waters (t = 4.12, df = 44, P < 0.001).

Directional preference by yellow perch was evident at all tagging sites in at least one recapture period, as the direction within recapture period was significant for Green Bay, Wisconsin, and Indiana waters, and an interaction with tagging sites was observed for returns from Illinois and Michigan sites (Table 2). During summer months, yellow perch traveled farther south than north from WI-1, IL-2, IL-3, IL-4, and IL-5 (Table 3). Fish from IN-1 and MI-1 moved at greater distances westward and northward, respectively, than any other direction observed from these sites during the summer (Table 3).

During non-summer months, yellow perch traveled farther east than south from GB-1 (Table 3). The distance traveled southward was greater than northward for all Illinois sites during the non-summer recapture period (Table 3). The magnitude of southward movement increased during non-summer months compared with summer months for IL-2 (t = 5.67, df = 399, P < 0.001), IL-3 (t = 2.25, df = 399, P = 0.01), and IL-5 (t = 4.60, df = 399, P < 0.01). During non-summer months, yellow perch only moved westward from IN-1 (Table 3) for greater distances compared with summer (t = 2.28, df = 82, P = 0.01). Only northward movement from MI-1 and MI-2 was observed during the non-summer recapture period (Table 3). This movement northward was greater during non-summer months when compared with summer (t = 5.21, df = 268, P < 0.001).

Fidelity and movement

The percentage of yellow perch recaptured in at least one spawning season after release was greatest at the site of release for GB-1 ($\chi^2_1 = 4.61$, P = 0.03), WI-1 ($\chi^2_1 > 13.46$, P < 0.001), IL-1 ($\chi^2_1 > 26.76$, P < 0.001), IL-3 ($\chi^2_1 > 26.82$, P < 0.001), and IN-1 ($\chi^2_1 > 7.25$, P < 0.01) (Fig. 3). Fish released from IL-5 showed higher fidelity for the release site

Table 2. Analysis of variance results for directional preference for each tagging area, comparing movement distance between recapture periods (*R*; summer, non-summer), direction nested within recapture periods (*D*(*R*)), tagging sites (*T*), tagging sites between recapture periods (*TR*), and the interaction between tagging sites and distance nested within recapture periods (*TD*(*R*)).

	Green Bay			Wisconsin			Illinois			Indiana			Michigan		
Factor	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
L	0.64	1, 40	0.43	1.36	1, 43	0.25	28.4	1, 399	<0.001	7.69	1, 82	0.01	20.62	1, 268	<0.001
R	0.87	1, 41*	0.36	16.96	1, 44*	<0.001	39.63	1, 399	<0.001	161.68	1, 82	<0.001	53.29	1, 268	<0.001
D(*R*)	11.01	3, 41*	<0.001	5.33	1, 44*	0.03	68.78	2, 399	<0.001	34.72	2, 82	<0.001	8.99	1, 268	<0.01
T	—	—	—	—	—	—	5.06	4, 399	<0.001	—	—	—	3.82	1, 268	0.05
TR	—	—	—	—	—	—	6.51	4, 399	<0.001	—	—	—	3.94	1, 268	0.05
TD(*R*)	—	—	—	—	—	—	3.69	8, 399	<0.001	—	—	—	9.67	1, 268	<0.01

Note: Time-at-liberty (*L*) tested whether the variance of movement distance increased with time. The effect of tagging location and its interactions was tested at Illinois and Michigan only because these areas contained multiple tagging sites.

*These statistical results were determined after the removal of the insignificant time-at-liberty (*L*) term from the directional preference model.

Table 3. Mean distance traveled (km) by yellow perch (*Perca flavescens*) determined from sport recaptures, adjusted by directed angler effort (h) for yellow perch in each direction relative to the tagging location (standard error, SE, in parentheses) during summer and non-summer recapture periods.

	Distance moved relative to tagging location			
Location identifier	North	South	East	West
Summer				
GB-1	12.6 (2.7)	5.0 (4.5)	11.6 (3.4)	—
WI-1	20.5 (4.2)	31.3 (2.1)*	—	—
IL-1	10.7 (3.0)	11.4 (3.2)	—	—
IL-2	10.9 (2.1)	28.7 (2.7)*	—	—
IL-3	19.1 (3.4)	39.6 (4.3)*	—	—
IL-4	22.7 (4.4)	44.2 (5.9)*	—	—
IL-5	24.4 (2.4)	35.1 (2.4)*	—	—
IN-1	—	1.1 (4.5)	9.1 (2.2)	40.5 (3.5)*
MI-1	38.8 (4.5)*	1.0 (5.0)	—	—
MI-2	18.3 (5.1)	19.1 (10.0)	—	—
Non-summer				
GB-1	—	3.9 (2.3)	20.2 (1.9)*	—
WI-1	6.0 (4.2)	—	—	—
IL-1	23.2 (8.6)	64.6 (4.1)*	—	—
IL-2	11.6 (3.0)	55.2 (3.9)*	—	—
IL-3	33.9 (8.6)	50.6 (2.5)*	—	—
IL-4	12.5 (4.1)	51.2 (4.8)*	—	—
IL-5	27.1 (4.2)	50.0 (1.9)*	—	—
IN-1	—	—	—	49.0 (1.8)
MI-1	62.1 (6.6)	—	—	—
MI-2	43.3 (6.6)	—	—	—

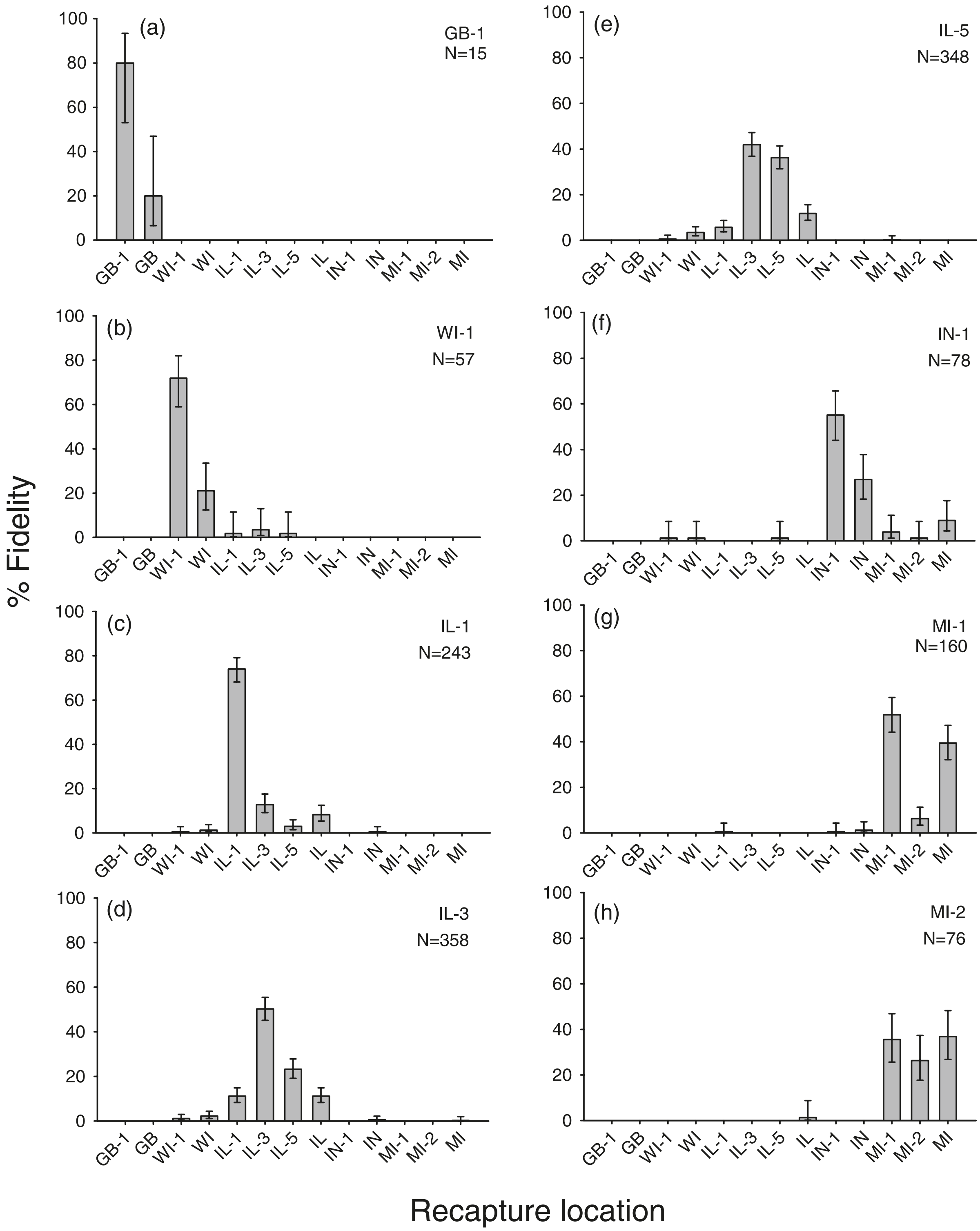
Note: An asterisk (*) represents the preferred direction from a site (α = 0.025). A dash (—) indicates that no yellow perch were recaptured in that respective direction.

compared with all other recapture locations ($\chi_1^2 > 23.21$, $P <$ 0.001), with the exception of IL-3 ($\chi_1^2 = 1.47$; $P = 0.27$). Fish released from MI-1 were 8.3 times more likely to be recaptured at their release site than at MI-2 ($\chi_1^2 = 39.97$, $P < 0.001$), but were only slightly less likely to be caught anywhere within Michigan waters ($\chi_1^2 = 2.72$, $P = 0.10$). Fish recaptured from MI-2 did not display greater fidelity to any area within Michigan ($\chi_1^2 < 1.32$, $P > 0.31$; Fig. 3). Although the majority of recaptures occurred at nearby sites within the state released, some yellow perch ventured across adjacent state lines (i.e., WI-1, IL-1, and MI-2) and even multiple state lines (i.e., IL-3, IL-5, IN-1, MI-1, and MI-2) (Fig. 3).

Discussion

In the southern basin of Lake Michigan, tagged adult yellow perch generally moved south along the west side of the lake, west along the south side of the lake, and north along the east side of the lake. Movement direction was largely consistent across time periods. The magnitude of these movements was typically small during summer, ranging between 13 and 101 km, but increased during non-summer months. In addition, the proportion of yellow perch returning to the identical or nearby locations in subsequent spawn-

Fig. 3. Percentage of tagged yellow perch (*Perca flavescens*) from each tagging site ((*a*) GB-1, (*b*) WI-1, (*c*) IL-1, (*d*) IL-3, (*e*) IL-5, (*f*) IN-1, (*g*) MI-1, (*h*) MI-2) that were recaptured at various locations during subsequent spawning seasons. Error bars represent the 95% confidence intervals. *N* is the total number of recaptures that occurred during spawning seasons subsequent to tagging, which include agency, sport, and commercial sources.



ing seasons was high (35%–80%), particularly along the west shoreline of southern Lake Michigan and in Wisconsin waters of Green Bay. Yet, fish released from Illinois were recaptured at all other sites within Illinois, suggesting that yellow perch in these waters were not faithful to an exact spawning location, but remained faithful to a much larger area. This contrasts with studies in much smaller systems such as Long Lake, Michigan, where homing by displaced yellow perch to an exact location was documented (Hodgson et al. 1998). Nevertheless, faithfulness to certain spawning areas throughout the southern basin of Lake Michigan could provide a mechanism to isolate groups of yellow perch for the formation of sympatric stocks.

Despite high fidelity to certain sites, straying occurred from all sites, resulting in mixing among all areas in the southern basin except between Michigan and Wisconsin waters. Further, no fish tagged in the southern basin were caught within the northern basin. Because this straying occurred during spawning seasons, it increases the chance for gene flow among areas (Slatkin 1987), supporting the conclusion that a homogenous genetic population exists within the southern basin (Miller 2003). In addition, our results are based on nearshore recaptures of adult yellow perch. Therefore, the estimated mixing within the southern basin is conservative considering that any potential offshore movement and mixing is underrepresented in this study. These results demonstrate that movement of adult yellow perch can contribute to the genetic homogeneity within the southern basin, whereas Miller (2003) speculated the homogeneity to be mainly from larval mixing via ocean-like currents (Beletsky et al. 1999). Also, a single yellow perch from Fort Sheridan, Illinois, was recaptured in Green Bay, which we considered an outlier in both directional and dispersal models. This type of large-scale movement by a few individuals can contribute to low genetic variability within Lake Michigan.

Offshore advection of larval yellow perch via wind-induced currents (Dettmers et al. 2005), combined with counterclockwise, ocean-like gyres (Beletsky et al. 1999), likely transfers larval fish large distances within each basin, further decreasing the likelihood of genetic differentiation. The transfer of a single dispersing age-0 fish per generation has the potential to diminish the effects of local adaptation and maintain basin-wide genetic homogeneity (Slatkin 1987; Taylor 2003). Characteristics of smaller systems than Lake Michigan may increase the potential for larval retention within spawning areas, increasing the probability of forming sympatric stocks (e.g., Aalto and Newsome 1993). In Lochaber Lake, Nova Scotia, Canada, indirect evidence suggested that larval yellow perch became acquainted with the spawning area to allow later homing (Aalto and Newsome 1990). Mixing at both the larval and adult life stages within the southern basin of Lake Michigan therefore decreases the likelihood of sympatric yellow perch stock formation.

Although we could not directly associate patterns of movement with habitat characteristics, our data suggest interesting relationships that deserve further investigation. Previous work has indicated that substrate type and availability is important to the spawning and feeding of yellow perch in Lake Michigan. Yellow perch select cobble substrate for spawning in Lake Michigan (Robillard and Marsden 2001), but also select these areas during other time periods because preferred prey, such as crayfish, sculpins (*Cottus* spp.), and alewife (*Alosa pseudoharengus*) (Powers and Robertson 1968; Janssen and Quinn 1985; Janssen and Luebke 2004) typically favor rocky habitat. Abundant zebra mussels (*Dreissena polymorpha*) in rocky areas of Lake Michigan (Fleischer et al. 2001) also increase abundance of other invertebrates important in the diet of yellow perch (Stewart et al. 1998; Kuhns and Berg 1999; Cobb and Watzin 2002). Further investigation may therefore be warranted to determine the role of substrate type and availability in regulating movement of individual yellow perch and the structure of the population.

Our estimates of dispersal distance and direction were based on an accepted technique to estimate movements of fish that corrects for nonuniform distribution of spatial and temporal fishing effort (Schmalz et al. 2002). Complete removal of bias from spatially disproportionate effort may be impossible, but this technique offers the best available tool to remove bias. Differences in harvest policies among states, particularly bag limits, are considered reflected in the angling effort that was estimated from the creel surveys; as a result, these differences should be accounted for using this data standardization technique. Only the size distribution of yellow perch being harvested should be affected, not the size of yellow perch caught by anglers. Thus, size limits impose a bias only if they affect the reporting rate of anglers. During our study, a size limit to keep 200–250 mm yellow perch was in effect only in Illinois waters. The number of recaptures from Illinois waters was sufficiently high to indicate that the slot limit did not appreciably affect tag reporting rate.

Dispersal of yellow perch within the southern basin of Lake Michigan always crossed management boundaries (particularly between adjacent states). The summer movement period includes spawning, during which many males tend to linger in spawning areas (Muncy 1958). Because the population was largely skewed toward males at the time of tagging, this may have increased the probability of recovering fish close to spawning areas. Additionally, our models of dispersal distance indicated that only fish from Green Bay and Wisconsin waters stayed within local management boundaries during both time periods. However, yellow perch exhibited directional preference during summer and non-summer time periods. Although fish from four of five Illinois sites moved into Wisconsin waters during summer, the preferred directional movement was southward from these sites during this time period, thus decreasing the number of fish likely crossing into Wisconsin as well as the amount of mixing with fish in Wisconsin waters. This argument could be extended to dispersal during total recapture periods when directional preference was similar between the two recapture periods (e.g., Illinois, Indiana, and Michigan), increasing the likelihood of mixing between fish from Illinois and Indiana waters, but decreasing the likelihood of mixing between fish from Indiana and Michigan waters. Therefore, both dispersal distance and directional preference should be considered when evaluating movement of yellow perch.

Horns (2001) documented similarities in length and condition of adults and their size at age-1 between fish from Wisconsin and Illinois waters. Fish from Indiana waters were greater in size at age-1 than fish from all other areas, but were smaller and in poorer condition compared with adults. His results suggested a separation for management between Indiana and Illinois–Wisconsin. However, our results suggest that mixing is strong among fish from Wisconsin, Illinois, and Indiana waters, suggesting that fish in Indiana waters were not a separate stock. Yet, our results do suggest that fish from Michigan waters may be spatially segregated because they tend to move away from fish released in waters of the other three states. While our results support the assignment of a single genetic stock within the southern basin of Lake Michigan, environmentally induced phenotypic expressions of local environments will still cause groups to respond differently to exploitation (Pawson and Jennings 1996; Swain and Foote 1999). Therefore, managers should carefully consider the delineation of biologically significant management boundaries that not only encompass the directed range of yellow perch movements, but also consider differences in population characteristics such as growth rates. Further, most tagged yellow perch remained within their respective management unit, indicating the current delineation of management units is reasonable. Nevertheless, because movement occurred across management boundaries between adjacent states based on these nearshore recaptures, we recommend that adjacent states consider re-examining their regulations based on this information to ensure consistent, complementary regulations that incorporate the movement patterns of yellow perch.

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