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[Management Brief]

Mixed-Stock Analysis of Lake Sturgeon in the Menominee River Sport Harvest and Adjoining Waters of Lake Michigan

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Abstract.—Lack of information about the rates and sources of population-specific mortality and habitat use during nonspawning periods has impeded the restoration of lake sturgeon *Acipenser fulvescens*. Using eight microsatellite loci and mixed-stock analyses, we estimated the proportional contributions of spawning populations from throughout the Lake Michigan basin ($n = 5$) to the fall sport fishery in the lower Menominee River, Wisconsin. We compared estimates of harvest composition with estimates from collections made in adjacent open-water habitats in Green Bay. The analyses revealed that 81% (90% confidence interval [CI] = 72.9–89.3%; $N = 104$) of harvested individuals originated from the Menominee River; all of the bycaught fish originated in adjacent streams. The harvest composition estimates differed significantly from those of open waters immediately offshore (26.7% Menominee River; 90% CI = 9.7–44.8%; $N = 36$) and across Green Bay (27% Menominee River; 90% CI = 19.5–34.7%; $N = 214$), indicating that the harvest was not a random sample from across the basin. The harvest composition estimates were not consistent with the estimates of individuals in prespawning condition (females = 50%; males = 83%), suggesting that not all of the harvested fish were staging for spring spawning. The contributions of nontargeted and numerically depressed populations to the fishery are of management concern given efforts to rehabilitate populations. Spatially restricted harvests during nonbreeding periods may not protect numerically depressed populations originating in nearby streams.

Fisheries management has benefited from development of quantitative methods to predict fish population abundance, recruitment, and rates of mortality. Such information allows managers to estimate probabilities of population persistence, and in situations of adequate abundance, to set allowable harvest quotas. Individuals of numerous fish species are structured spatially into genetically distinct breeding populations but share common habitats during nonbreeding periods. Nonspawning individuals may not be randomly distributed and thus populations may not be equally affected by environmental disturbances (Seeb et al. 2000) or may be differentially susceptible to harvest (Beacham et al. 2004; Seeb et al. 2004). Managers need techniques to assess population risk, both in terms of harvest and of exposure to environmental perturbations or catastrophes.

Harvest can represent a major source of mortality (Shuter et al. 1979; Myer et al. 1997; Julliard et al. 2001). Management complications arise when multiple populations share a common environment in which harvest occurs. Managers may base harvest prescriptions on untested assumptions pertaining to degree of population co-occurrence and susceptibility to harvest. Such management decisions can negatively impact nontarget populations, especially when populations share a common environment and vary greatly in numerical abundance (Policansky and Magnuson 1998).

Molecular genetic markers and established methods of statistical inference have been widely used in fisheries management (Carvalho and Hauser 2004; Pella and Masuda 2004) and in other basic and applied sciences (Manel et al. 2005). Specifically, mixed-stock analysis has been widely used to provide compositional estimates of harvests from population mixtures in both marine (e.g., Beacham and Wood 1999; Ruzzante et al. 2000; Seeb et al. 2004) and freshwater (e.g., Gatt et al. 2003) realms as well as to quantify spatiotemporal

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TABLE 1.—Results of simulation analysis assessing the accuracy of the assignment of lake sturgeon based on resampling from baseline populations with SPAM. Averages and 90% symmetric confidence intervals (parentheses) of the posterior probabilities of assignment over 1,000 Monte Carlo–Markov chain replicates are provided for four baseline population groups.

	Assignment			
Source (*n*)	Fox	Menominee	Oconto–Peshtigo	Manistee
Fox (71)	0.89 (0.800–0.966)	0.009 (0–0.028)	0.054 (0–0.121)	0.015 (0–0.055)
Menominee (41)	0.024 (0–0.063)	0.873 (0.763–0.958)	0.055 (0–0.122)	0.030 (0–0.066)
Oconto–Peshtigo (91)	0.052 (0.008–0.112)	0.006 (0–0.023)	0.927 (0.858–0.989)	0.009 (0–0.038)
Manistee (80)	0.008 (0–0.031)	0.001 (0–0.006)	0.007 (0–0.024)	0.977 (0.935–0.999)

variation in population contributions in habitats occupied during nonspawning periods (Potvin and Bernatchez 2001). While the majority of studies have focused on species of economic importance, increasing attention has been directed towards species of conservation concern (e.g., sturgeon; Waldman et al. 1996).

Lake sturgeon *Acipenser fulvescens* are of conservation concern across their range (Welsh 2004). Prior to the late 1800s, lake sturgeon were abundant throughout the Great Lakes basin (Harkness and Dymond 1961). Since the late 1800s, overharvest, habitat loss, and the construction of dams that block access to spawning grounds have led to severe population declines (Harkness and Dymond 1961; Houston 1987; Auer 1999).

Current impediments to lake sturgeon restoration include sensitivity to anthropogenic factors such as overharvest, degradation in water quality and spawning habitat, and loss of connectivity of habitat because of impoundment (Holey et al. 2000). These factors, combined with low spawner abundance and the species' unique life history characteristics (late age at maturity, infrequent spawning, and low recruitment rate; Houston 1987; Kempinger 1988) further complicate recovery efforts because fish use stream habitats where individuals are readily detectable for only brief periods.

One goal of lake sturgeon rehabilitation is to restore populations to self-sustaining levels and to abundance that could support sustained exploitation and allow survival if exposed to environmental catastrophes. Harvests and other sources of mortality often occur during nonspawning periods. Since managers lack detailed information on habitat occupancy relative to population of origin, considerable uncertainty exists when describing risks to remnant populations during nonspawning periods.

Fishing-induced mortality has been tied to declines in populations of multiple species of sturgeon throughout North America (Boreman 1997). Populations of lake sturgeon throughout the Great Lakes have been similarly affected by past commercial harvests (Baldwin et al. 1979). Only a few populations of lake sturgeon have persisted or recovered to levels capable of sustaining harvest. The Menominee River, which forms the border between Wisconsin and the Upper Peninsula of Michigan, has supported a recreational fishery for lake sturgeon in Lake Michigan since 1946.

Our objectives were to estimate proportional contributions of different breeding populations of lake sturgeon in the Menominee River harvest and to compare these harvest estimates with compositional estimates from collections of lake sturgeon during nonspawning periods in open-water habitats of Lake Michigan in proximity to the area of harvest. The null hypothesis was that lake sturgeon during nonspawning periods of the year were completely admixed in stream habitats, as well as in nearshore and open-water Great Lakes habitats, and thus equally susceptible to harvest. The working hypothesis, which informed management decisions of total allowable harvest, was that all individuals targeted in this harvest originated in the Menominee River.

Methods

Breeding populations.—We used samples of fin tissue (approximately a 1-cm^2 clip of the dorsal fin) collected from spawning adult lake sturgeon from five remnant populations spawning in tributaries throughout the Lake Michigan basin. Fin clips were dried and stored in envelopes at room temperature (DeHaan et al. 2006; Elliott and Gunderman 2008). Collections included the lower Fox River ($n = 71$), the Peshtigo and Oconto rivers ($n = 91$), the Manistee River ($n = 80$), and the Menominee River ($n = 41$; Table 1). Estimation of mixture composition can be affected when databases from breeding populations are incomplete (Pella and Masuda 2006). DeHaan et al. (2006) and Welsh et al. (2008) found comparatively low levels of genetic differentiation in allelic and haplotypic frequency among other Lake Michigan eastern basin, Lake Huron western basin, and Lake St. Clair remnant populations. For analyses reported herein, because of similarities in allele frequency between lake sturgeon from the Manistee River and other populations in the eastern Lake Michigan basin, the Manistee River population was selected to represent breeding populations from throughout this region that might be at potential risk of harvest. Individuals from the Peshtigo and Oconto rivers also were combined into a single composite baseline population because of similarities in allelic frequency (DeHaan et al. 2006). Similarly, allelic frequency of the lower Fox River spawners was indistinguishable from that of the Wolf River (Lake Winnebago) spawning population located upstream, as was the lower Menominee River indistinguishable from the upper Menominee River spawning populations (DeHaan et al. 2006).

Harvest mixtures and open-water samples.—Samples of fin tissue were collected by Wisconsin Department of Natural Resources (WDNR) personnel from all individuals harvested from the lower Menominee River in the 2001 hook-and-line recreational fishery ($n = 104$). Samples were dried and stored at ambient temperature. Sex and stage of gonadal development was assessed in a subset of fish that were provided to WDNR personnel (see Bruch et al. 1993).

Lake sturgeon were sampled in open waters throughout Green Bay, Lake Michigan, including sites in close proximity to the Menominee River, during nonspawning periods from 2002 to 2006 (Figure 1). In Green Bay, lake sturgeon were sampled by the U.S. Fish and Wildlife Service (USFWS), Michigan Department of Natural Resources (MiDNR), Michigan Technological University, and WDNR field researchers working with commercial fishers using trap nets and gill nets. The majority of samples were collected in the late spring and early summer in most areas of the lake, although additional samples were collected during fall and winter in other areas. Live individuals were marked with an external Floy tag and an internal passive integrated transponder tag (Auer and Baker 2007; Elliott and Gunderman 2008) prior to release in order to identify recaptures during sampling. The entire Green Bay sampling area was used to represent the pool of nonspawning individuals that could be represented in the harvest (Bott 2006). Samples from the two open-water sampling locations in closest proximity to the mouth of the river were also selected for comparison.

Genetic analyses.—We extracted DNA from samples using QIAGEN DNeasy kits (QIAGEN, Inc.) according to manufacturers' protocols. We used DNA concentrations of 20 ng/μL in polymerase chain reactions (PCR). Individuals were genotyped at eight microsatellite loci: *LS-68* (May et al. 1997); *Afu68b* (McQuown et al. 2002); *Spl120* (McQuown et al. 2000); *Aox27* (King et al. 2001); *AfuG9*, *AfuG63*, *AfuG74*, and *AfuG112* (Welsh et al. 2003). Amplification reactions (PCR) were conducted in 25-μL volumes as described by DeHaan et al. (2006). Products from PCR reactions were run on 6% denaturing polyacrylamide gels and visualized on a Hitachi FMBIOII scanner. Allele sizes were determined using commercially available size standards (MapMarkerTM; BioVentures, Inc.) and based on standard samples of known genotype. Genotypes were independently scored by two experienced laboratory personnel and verified after data were entered into electronic databases.

Statistical analyses.—Estimates of allele frequency and measures of genetic diversity were described in DeHaan et al. (2006) for all breeding populations at risk of harvest and with access to the western Lake Michigan basin. Mixture analyses were conducted using SPAM (Debevec et al. 2000), using the Bayesian option (Pella and Masuda 2001). We used SPAM to conduct simulations to determine accuracy, precision, and allocation bias of compositional estimates. The magnitude of misallocation largely reflects the degree of genetic differentiation among baseline populations (Kalinowski 2004). Simulation analyses were based on 1,000 Monte Carlo–Markov chain (MCMC) replicates, with both the mixtures and the baselines being resampled each iteration. Individuals from the harvest ($N = 104$) and open-water collections ($N = 214$) were assigned to populations of origin based on 1,000 MCMC replicates, both the mixtures and the baselines being resampled each iteration. Only fish of length greater than or equal to 50 in were included in the analysis of open-water samples ($N = 36$ for the two closest open-water locations, $N = 214$ for all open-water locations).

Results

Mixture Analysis

Simulations.—Simulation analyses support a high level of accuracy and precision in assignment to breeding populations. Assignments to simulated 100% mixtures ranged from 0.89 to 0.97 (Table 1). Allocation bias was not evident as documented by off-diagonal estimates of misallocation with confidence intervals (CIs) including zero.

Estimation.—Mixture analysis of the 2001 Menominee harvest fishery shows that the majority of the fish present in the lower section of the Menominee River are of Menominee River origin (estimate = 0.810, 90% CI = 0.749–0.899; Table 2). However, significant and nonzero contributions from the neighboring Peshtigo and Oconto River populations were also present (estimate = 0.190; 90% CI = 0.111–0.269). No evidence of lake sturgeon originating from the Fox River or from the eastern basin of Lake Michigan was documented (Table 2).

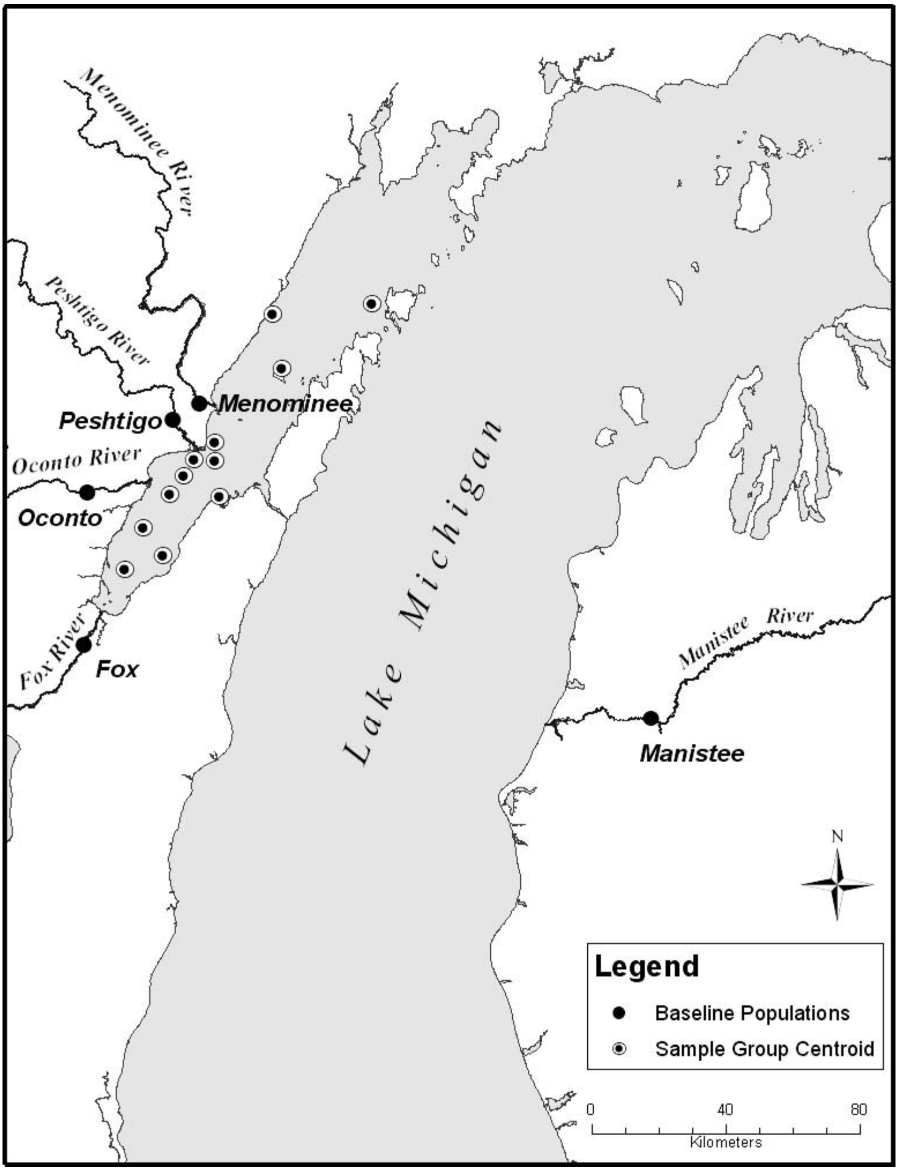

FIGURE 1.—Locations of the baseline populations of lake sturgeon used in this study (the Fox, Oconto–Peshtigo, Menominee, and Manistee rivers, the last representing populations in the eastern Lake Michigan basin) and the sampling sites in open-water habitats of Lake Michigan. The points on the map represent the centroids of all collection points (samples) for each collection area. The centroids were determined by calculating the nonweighted mean of the latitude–longitude coordinates for each sample in the group.

Compositional estimates of breeding populations contributing to collections in open-water habitats closest to the Menominee River and across Green Bay differed greatly from estimates based on the 2001 harvest (Table 2). Estimates of contributions of the Menominee River population to open-water collections were 0.267 (90% CI = 0.097–0.448; Table 2) for locations closest to the river mouth and 0.270 across Green Bay (90% CI = 0.195–0.347).

Discussion

The fall lake sturgeon sport fishery on the Menominee River has been managed under the assumption that individuals in the lower river were

TABLE 2.—Population compositional estimates based on a Bayesian estimator (Pella and Masuda 2001) for the 2001 lake sturgeon sport harvest ($N = 104$) in the Menominee River and open-water collections closest to the mouth of the river ($N = 36$) and in all of Green Bay ($N = 214$). See Table 1 for additional details.

	Assignment			
Population	Fox	Menominee	Oconto–Peshtigo	Manistee
Harvest	0.002 (0.000)	0.809 (0.729–0.893)	0.189 (0.110–0.268)	0.001 (0.000)
Open-water (adjacent)	0.294 (0.96–0.498)	0.267 (9.7–0.448)	0.420 (0.176–0.650)	0.020 (0.000–0.106)
Open-water (entire bay)	0.315 (0.226–0.406)	0.270 (0.195–0.347)	0.397 (0.298–0.500)	0.018 (0.000–0.049)

predominantly residents staging during the fall for spring spawning. Straying of adults from other populations was expected to be infrequent, given recent evidence showing significant differences in microsatellite allele and mitochondrial DNA haplotype frequencies among Lake Michigan spawning populations (DeHaan et al. 2006) that suggest a high degree of spawning site fidelity. Further, visual assessments of many harvested fish found that large proportions of individuals had gonads in developmental stages, suggesting the ability to spawn the following spring. However, without knowledge of lake sturgeon habitat use and movements during nonspawning periods, managers were not able to estimate occupancy rates and the potential for unintentional harvest from smaller, nontargeted populations of relatively lower numerical abundance (Holey et al. 2000; Elliott 2008; Elliott and Gunderman 2008).

Impacts of Harvests on Target and Nontarget Populations

Results support the assumption that the majority of individuals present in the lower Menominee River in the fall, and therefore at risk of harvest, originated from the Menominee River. Mixed-stock analysis shows that the majority of fish in the lower section of the river—approximately 84 of 104 individuals—originated from the Menominee River (estimate = 0.810, 90% CI = 0.729–0.891; Table 2). Results also show a significant nonzero contribution of approximately 20 of 104 individuals from the neighboring Peshtigo and Oconto rivers (estimate = 0.190, 90% CI = 0.111–0.269; Table 2).

Harvest in the Menominee River has occurred since 1946 and has been monitored through mandatory registration since 1983 in Wisconsin and 1986 in Michigan. Fishing has increased most substantially within the lowest section of the Menominee River, where fish have access to Green Bay (Kornely and Meronek 2004). Lake sturgeon harvested from the lowest river section averaged 40 individuals per year from 1983 to 2005. Although harvest numbers are modest and individual lake sturgeon are targeted only once a year at a single location, the potential impact of this harvest on target and nontarget lake sturgeon populations is large. Over the period of harvest 1983–2004, 792 individuals have been harvested from the downstream section of the Menominee River, the majority of fish being harvested in more recent years (Kornely and Meronek 2004). If the results from the 2001 harvest are representative of harvest for all years, 150 Peshtigo and Oconto River fish may have been harvested during this time period. Further analysis of individuals harvested in additional years would better gauge the degree to which different populations have been affected by the Menominee harvest and whether environmental or other factors contribute to variance in harvest composition from year to year. Since lake sturgeon are long-lived and mature late in life, the potential effects of this fishery on recruitment from nontarget populations may persist for many years.

Comparisons of Compositional Estimates between River and Open-Water Habitats

Seasonal variation in patterns of habitat occupancy and movement will affect probability of harvest. If individuals tend to stay closer to natal tributaries and harvest occurs in rivers, then individuals originating from a river subject to harvest are more likely to be affected. Conversely, if individuals move among rivers, nontargeted populations may be subject to incidental harvest.

Our results show that the fall harvest on the lower Menominee River differed greatly in composition (population of probable origin) from adult lake sturgeon of similar size (at least 50 in in total length) sampled during the summer and fall from open-water habitats of Green Bay (Table 2; Bott 2006). Mixture analyses revealed that lake sturgeon occupying open-water habitats across Green Bay included fish from all four breeding population-groups. We estimate that 27.0% of the fish we sampled in Green Bay originated from the Menominee River, and that 26.7% of the fish we sampled from waters closest to the Menominee River were of Menominee River origin (Table 2).

Harvest of other sturgeon species (e.g., shovelnose sturgeon *Scaphirhynchus platorynchus*) has negatively affected recruitment and depleted size-classes, particularly when large (sexually mature) females are harvested (Colombo et al. 2007). Similar patterns have been seen in Atlantic sturgeon *A. oxyrinchus*, where low levels of recruitment are likely tied to population depletion from overfishing (Trencia et al. 2002). Given common life history characteristics of sturgeon species, it is not unreasonable to predict similar negative effects on lake sturgeon populations that are subject to harvest.

In recognition of the potential negative affects of harvest on lake sturgeon populations, an effort has been made to reduce fishing pressure on lake sturgeon in the Menominee River. The management agencies (WDNR and MiDNR) implemented new regulations beginning in 2000, alternating between a 70-in minimum length in the even-numbered years and a 50-in minimum length in the odd-numbered years. Although no fish were harvested in 2000, 2002, or 2004, the harvest increased in the odd-numbered years—from 118 in 2001 to 155 in 2003. The new regulations did not have the desired effect of significantly reducing harvest in the lower Menominee River (Kornely and Meronek 2004). Since the new limits were put in place, harvest was eliminated in the even-numbered years (2000, 2002, 2004; 70-in limit); however, harvest increased in alternate years, to 118 in 2001 and 155 in 2003 (50-in limit). This alternating increase and decrease in both harvest and effort has effectively maintained or increased, rather than decreased, fishing pressure (Kornely and Meronek 2004). The lake sturgeon fishery in the lower Menominee River was completely closed in 2006, based in part on findings reported herein.

In other species of sturgeon (e.g., Gulf sturgeon *A. o. desotoi*), movement patterns differ based on reproductive status (i.e., adults versus subadults; Rogillio et al. 2007). Gulf sturgeon exhibit differences in migration times based on sex and reproductive status (Fox et al. 2000), and also remain near spawning sites during nonspawning periods (Heise et al. 2004). However, estimates from the 2001 Menominee harvest were not consistent with the number of individuals assigned to prespawning condition (as per Bruch et al. 1993). Rather, results from condition assessment for both males and females (83% and 50%, respectively) suggest that all harvested fish were not staging for spring spawning. Instead, some individuals were using riverine habitats for other purposes.

Studies from several species have reported nonuniform distributions of individuals across different regions or habitats (e.g., brook trout *Salvelinus fontinalis* [Frazer et al. 2004, 2005]; brown trout *Salmo trutta* [Potvin and Bernatchez 2001]). Factors affecting habitat occupancy, movements, and dispersal may include kin relationships (Frazer et al. 2005), genetic affinities among populations (Potvin and Bernatchez 2001), sex (Frazer et al. 2004), and different migratory tendencies (e.g., chum salmon *Oncorhynchus keta* [Seeb et al. 2004]). Understanding the migratory tendencies and seasonal and temporal patterns of habitat occupancy during nonspawning seasons will inform management decisions for other remnant populations of lake sturgeon throughout the Great Lakes, including prioritizing habitat restoration and population rehabilitation efforts, and setting harvest quotas, where applicable.

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