Muskellunge and Northern Pike Ecology and Management: Important Issues and Research Needs

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Image for cover of *Fisheries*. Former SUNY-ESF graduate student Brian Henning prepares to release a large female Muskellunge collected during the annual spring Muskellunge trap-net survey, conducted by staff from SUNY-ESF's Thousand Islands Biological Station on the upper St. Lawrence River. Photo credit: Natalie Scheibel

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ABSTRACT

New research techniques and changing Muskellunge *Esox masquinongy* and Northern Pike *E. lucius* fisheries have contributed to paradigm shifts in the science and management of these species. A symposium on Muskellunge and Northern Pike biology, ecology, and management was held at the American Fisheries Society Annual Meeting in Little Rock, Arkansas, and a panel discussion following the symposium identified several research and management priorities, including spawning habitat identification, habitat and population restoration, genetics, and selective mortality and exploitation. Future Muskellunge and Northern Pike research should focus on quantifying egg and age-0 survival based on habitat characteristics, rigorously evaluating habitat restoration efforts using statistically sound study designs, describing range-wide genetic structure of populations, and developing a better understanding of how selective mortality and exploitation can alter population size structure, sex ratios, and life history characteristics. Information and outcomes from the proposed research and management priorities will be critical for conserving and restoring self-sustaining populations of Muskellunge and Northern Pike.

INTRODUCTION

A recent American Fisheries Society symposium focused on Muskellunge *Esox masquinongy* and Northern Pike *E. lucius* science and management and illustrated the need for review of this evolving field. Despite their importance as apex predators and value to fisheries, many populations of Muskellunge and Northern Pike face an uncertain future because they are subject to an increasing array of challenges and information gaps preclude development of comprehensive management programs. Here, we focus on the topics of Muskellunge and Northern Pike spawning habitat identification, habitat and population restoration, genetics, and selective mortality and exploitation because increased knowledge of these topics is necessary to manage for self-sustaining fisheries. The goals of this paper are to (1) provide an update on the status of Muskellunge and Northern Pike research, (2) suggest future research and management priorities, and (3) stimulate novel, collaborative research on Muskellunge and Northern Pike.

SPAWNING HABITAT IDENTIFICATION

Conserving and restoring spawning habitat is a top priority for Muskellunge and Northern Pike management. To conserve these habitats, managers must first know spawning locations and what features characterize optimal spawning habitat. Spawning site selection by Muskellunge and Northern Pike has been evaluated by a variety of methods, including telemetry, visual observation, and egg collection. Telemetry observations demonstrate that both species typically show large annual movements but focus on limited areas during spawning periods (Diana et al. 1977; Strand 1986). Although localized movements during spawning have helped to roughly identify spawning locations, in particular when followed with sampling for age-0 progeny (LaPan et al. 1996), these observations do not result in confirmation of actual spawning sites or their micro-habitat characteristics. Behavioral observations of spawning Muskellunge at night using spotlights (Zorn et al. 1998; Figure 1) provide a better method to locate specific spawning sites, especially when they are coupled with collections that verify egg deposition. A weakness of this method is that it can be used only in shallow areas, so it may miss spawning in deeper water; maximum depth for visual observation during spotlight surveys is generally 1.0–2.0 m (Zorn et al. 1998; Crane et al. 2014; Nohner and Diana 2015). Implanting mini transmitters in oviducts of mature females, then locating transmitters once they are expelled during spawning, is another technique to identify spawning habitat of both species (Pierce et al. 2007; Battige 2011). This method should be coupled with collection of fertilized eggs to confirm that the transmitter was expelled during the spawning process. Although expulsion of mini transmitters can be used to detect spawning in deeper waters than spotlight surveys, validation of spawning may require extensive scuba surveys if transmitters are deposited in water deeper than what can be sampled with traditional techniques, such as standardized egg sweeps with a D-frame net (Forney 1968; Crane et al. 2014). The use of egg traps has successfully identified specific spawning sites for both species, including deeper habitats (Farrell et al. 1996; Farrell 2001), but should only be used in areas with minimal current because collection of eggs in fluvial environments may reflect device trapping and retention properties rather than the habitat being sampled (i.e., egg traps may collect drifting eggs more effectively than the habitat, resulting in inflated egg density estimates).

Both Muskellunge and Northern Pike are broadcast spawners and provide no parental care (Scott and Crossman 1973). Muskellunge in inland lakes have most commonly been observed spawning in shallow bays <1 m in depth with detritus, vegetation, woody debris, and gravel, sand, silt, or muck substrates (Zorn et al. 1998; Rust et al. 2002; Nohner and Diana 2015). However, one population of Muskellunge in an inland lake preferred deeper water (i.e., 1–2 m) with marl substrates covered by *Chara* spp. (Strand 1986). Studies of Great Lakes

Muskellunge (e.g., Lake St. Clair to the St. Lawrence River) have documented spawning at depths from <1 to 3 m at sites with vegetation coverage ranging from 0–100% and substrates consisting of gravel, sand, and silt (Haas 1978; Farrell 2001; Crane et al. 2014). Macro-habitats used by spawning Great Lakes Muskellunge have included vegetated marshes, open water and main river channel shoals, and shallow backwaters along river margins. Since Muskellunge eggs settle onto substrates, they are often exposed to anoxic conditions at the sediment-water interface. Human alterations of shoreline habitat and removal of woody debris have been linked to low oxygen conditions in sediments and reproductive failure in inland lakes, but Muskellunge often successfully reproduce in some Great Lakes waters and connecting channels, despite having highly modified shorelines (e.g., Lake St. Clair and Detroit and Niagara rivers). Possible explanations for recruitment success of these populations include deeper offshore spawning and rearing habitat and continual flushing of oxygenated water through these systems.

Although Muskellunge spawning habitats have been successfully described in a variety of waters, using information from these studies to more effectively manage spawning habitats on a broad scale has proved challenging. As the number of habitat selection studies has increased, it has become apparent that Muskellunge will spawn on a variety of shallow water habitats, depending on habitat availability in a particular lake or river. Additionally, experiments attempting to quantify habitat-related differences in egg survival have been hampered by high mortality rates (Dombeck et al. 1984; Zorn et al. 1998). This is a particular problem for Muskellunge because protection and restoration of these areas is essential to maintaining and restoring populations in response to anthropogenic influences on their habitat.

Northern Pike commonly migrate at ice-out to shallow wetlands and littoral zones in lakes and river systems to spawn, often in waters <0.5 m deep (Clark 1950; Casselman and

Lewis 1996), but spawning in water >3 m has also been documented (Farrell 2001). Since spawning occurs so early in the year, Northern Pike often disperse eggs over decaying vegetation from the previous summer. Northern Pike have adhesive eggs, and larvae have an adhesive gland on their head (Cooper et al. 2008), which maintains their location in the water column when attached to vegetation, thus avoiding anoxic substrates that are common in wetlands (Scott and Crossman 1973; Bry 1996). Seasonally-flooded terrestrial vegetation, such as grasses and sedges (*Carex* spp.), are believed to provide the highest-quality incubation habitat (Casselman and Lewis 1996). Seasonal flooding of these habitats releases terrestrial nutrients, creating a productive environment with ample food sources for recently-hatched larvae (Casselman and Lewis 1996). Aeration of seasonally-flooded habitats may also prevent micro-stratification and low dissolved oxygen levels at the substrate-water interface. Permanently submerged habitats dominated by macroalgae and vegetation, such as *Chara* spp., *Potamogeton* spp., and *Myriophyllum* spp., are also used but probably provide poorer-quality habitat compared with flooded terrestrial vegetation (Casselman and Lewis 1996). Spawning Northern Pike often avoid dense stands of emergent cattail *Typha* spp. (Casselman and Lewis 1996), as the rigid stem structure and high stem densities likely inhibit their movement and spawning activity. Northern Pike population declines in some regions of the Great Lakes have been partially attributed to the transition of sedge and grass meadows to monotypic stands of invasive hybrid cattail (*Typha x glauca*), following anthropogenic land conversion and water-level regulation (Cooper et al. 2008). Farrell (2001) found that Northern Pike in the St. Lawrence River system spawned in deeper habitats than had been observed in other waters and associated this behavior with long-term regulation of water levels and invasion of hybrid cattail.

Figure 1. A pair of Muskellunge observed during a spotlight spawning survey in Northern Wisconsin. (Photo credit: J. Nohner)

Recently, models have been developed to identify important spawning habitat characteristics and habitat availability (based on habitat use or habitat suitability indices) to spawning Muskellunge and Northern Pike within a body of water (Mingelbier et al. 2008; Crane et al. 2014; Nohner and Diana 2015). These models can guide restoration and conservation of spawning habitat. However, the Mingelbier et al. (2008) and Crane et al. (2014) spawning habitat models were developed for specific waters, potentially limiting broad applications. Nohner and Diana (2015) predicted relative probability of Muskellunge spawning based on habitat characteristics in 28 self-sustaining populations in northern Wisconsin lakes, making it applicable to a broader geographic area, but variability in spawning habitat availability and selection among lakes limited the model's predictive performance. Predictive models of Muskellunge and Northern Pike habitat use (i.e., occurrence), particularly for early life stages, are useful and should continue to be developed. To account for among-system variability in spawning habitat use and to develop broader models, future studies should develop predictive models of habitat use and quality based on multiple waters within a specific class of lakes or rivers across a broad geographic range.

Although spawning habitat models developed by Mingelbier et al. (2008), Crane et al. (2014), and Nohner and Diana (2015) were based on habitat use by self-sustaining populations of both species, they did not account for differences in survival of eggs and larvae among habitat types. Developing a better understanding of the relationship between micro-habitat characteristics and survival of Muskellunge and Northern Pike during early life stages is also essential for effective habitat management. Management strategies based solely on spawning habitat characteristics, without knowledge of successful reproduction at the micro-habitat scale, may lead to conservation or restoration of habitats that are ecological sinks. Genetic tools, such as parentage analysis, may aid in quantifying relationships between survival and habitat characteristics. For example, experiments planting large numbers of eggs (with genetically unique markers) in a variety of natural or manipulated spawning habitats may be useful for estimating survival based on habitat characteristics. However, predator and prey dynamics are likely correlated with spawning habitat characteristics and should be considered in any such experiment (Grimm 1989; Murry and Farrell 2007; Kapuscinski and Farrell 2014). Future studies of Muskellunge and Northern Pike spawning habitat should also focus on comparing healthy populations in relatively undisturbed ecosystems to depressed populations in order to elucidate limiting factors and mechanisms that inhibit natural reproduction. Finally, investigations on the reproductive ecology of Muskellunge in small to medium-sized rivers would also prove beneficial due to the paucity of information on these populations, despite their importance as fishery resources.

HABITAT AND POPULATION RESTORATION

Loss and degradation of spawning and rearing habitats have been hypothesized as major factors contributing to population declines of Muskellunge and Northern Pike (Trautman 1981; Axon and Kornman 1986; Casselman and Lewis 1996; Rust et al. 2002; Farrell et al. 2006; Kapuscinski et al. 2007; Cooper et al. 2008). Although both species are sensitive to habitat degradation, Muskellunge are generally more vulnerable than Northern Pike because (1) Muskellunge spawn later in spring, increasing the likelihood of anoxic conditions and (2) Northern Pike demonstrate greater reproductive plasticity. Nearly 30 years ago, Hanson et al. (1986) recognized a need to identify and protect high-quality Muskellunge habitats, particularly for early life stages, given the loss of self-sustaining populations throughout the 19th and 20th centuries. Conservation of high-quality habitats should remain a top priority in waters that support self-sustaining Muskellunge populations, but habitat restoration may be necessary where populations have been significantly depleted or extirpated. Based on studies of inland Muskellunge populations, Dombeck (1986) recommended removal or sealing of substrates with high biological oxygen demand and adding sand, gravel, and coarse woody debris to improve spawning site conditions. However, Zorn et al. (1998) cautioned that dredging of sediments and placing sand and gravel is costly and may have unintended negative effects. Zorn et al. (1998) suggested that placement of coarse woody debris is more feasible and may increase natural reproduction by suspending eggs above sediments with low dissolved oxygen levels. Crane et al. (2014) recommended that Muskellunge spawning habitat restoration efforts in the Niagara River should (1) incorporate aquatic vegetation that emerges early in the growing season and is beneficial to multiple life stages of Muskellunge and their associated prey, (2) create shoals with low to moderate density emergent vegetation that maximize edge habitat, and (3) develop conditions with low to moderate water velocities that sustain muddy-sand to sand-sized class substrates in water depths of 1–2 m. The conservation and restoration of riparian buffers adjacent to Muskellunge spawning and rearing sites has also been deemed a priority because riparian habitat quality affects littoral habitat quality (Craig and Black 1986; Zorn et al. 1998; Murry and Farrell 2007).

Habitat restoration has been more widely implemented for Northern Pike than Muskellunge; however, rigorous scientific evaluation of Northern Pike restoration projects is rare. Franklin and Smith (1963) recommended that managed spawning marshes be designed with intermediate slopes because shallow slopes may result in large areas of air exposure following small changes in water levels, and steep slopes may result in permanent pooling of water, formation of undesirable vegetation communities, and limit total spawning area. Studies of Northern Pike spawning habitat suggest that restoration efforts should focus on encouraging sedge and native grass meadows that flood seasonally during the spring freshet (Casselman and Lewis 1996). Recent excavations of channels through dense *Typha* spp. stands in a St. Lawrence River spawning marsh have allowed Northern Pike to access and successfully spawn in previously unavailable sedge meadows (J. M. Farrell, State University of New York, College of Environmental Science and Forestry, unpublished data). Grimm (1989) recommended a reduction in external nutrient loading to shallow European lakes to facilitate the return of native aquatic vegetation, which provide essential rearing habitat for age-0 Northern Pike. Grimm (1989) also stressed that submerged aquatic vegetation should not be cut during June or July because its loss may result in substantial mortality of age-0 Northern Pike. Similarly, emergent vegetation should be conserved because it provides permanent cover for age-0 Northern Pike during late fall through early spring, when submerged vegetation is limited or absent (Grimm 1989).

Water level management has been identified as a factor affecting Muskellunge and Northern Pike spawning and recruitment (Casselman and Lewis 1996; Farrell 2001; Rust et al. 2002). Alteration of hydrologic regimes can affect Muskellunge and Northern Pike reproduction by controlling access to spawning habitats and facilitating changes in nearshore and wetland vegetation communities, water and sediment chemistry, and prey availability. In addition to hydrologic changes caused by dam construction and operation, Muskellunge and Northern Pike reproduction can also be affected by changes in hydrologic regimes associated with land use development. Oele et al. (University of Wisconsin–Madison, unpublished data) observed desiccation of age-0 Northern Pike spawned in hydrologically-flashy drainage ditches in the Green Bay, Lake Michigan watershed. Therefore, habitat restoration efforts should incorporate the principles of the natural flow regime (see Poff et al. 1997; Mingelbier et al. 2008). For example, in several coastal wetlands of the Great Lakes, water level control structures are used to mimic natural hydrologic regimes within Northern Pike spawning marshes because water levels fluctuate unnaturally at the basin level. Unfortunately, water level control structures require a substantial amount of maintenance and are prone to failure if not monitored regularly.

Reintroduction of Muskellunge and Northern Pike to areas where they were previously extirpated is an important part of the restoration process if they cannot recolonize the restored area naturally. In North America, reintroductions have been more common for Muskellunge than Northern Pike, and recent Muskellunge reintroductions in the Great Lakes region include

Lake Simcoe, Ontario; the Spanish River and Severn Sound of Lake Huron; Green Bay, Lake Michigan; and most recently, drowned river mouths along the eastern shore of Lake Michigan. It is clear that a comprehensive restoration approach addressing all aspects of Muskellunge and Northern Pike life history and its interface with the physical, chemical, and biological characteristics of a functioning habitat are necessary for success. For example, in Green Bay, Wisconsin, a trophy Muskellunge fishery has been created, but continued monitoring has revealed limited natural reproduction (Kapuscinski et al. 2007; Battige 2011), and the fishery is dependent on stocking. Kapuscinski et al. (2007) suggested that natural reproduction was limited due to a paucity of high-quality habitat in areas where most Muskellunge were historically stocked (e.g., Fox and Menominee rivers). Battige (2011) also hypothesized that inadequate habitat was limiting natural reproduction and fish community dynamics may be contributing to reproductive failure of Muskellunge in southern Green Bay. We propose a conceptual model where natural recruitment of Muskellunge and Northern Pike is sustained by interactions and dynamics of not only the spawning stock but also predator and prey populations in nursery areas, habitat viability, and genetic resources in accordance with known perturbations (Figure 2).

The emerging discipline of restoration ecology along with traditional fisheries management approaches should be used to guide restoration of sustainable Muskellunge and Northern Pike populations. Applying the general principles of restoration to esocid population recovery can provide a starting point for a framework (see Inset). An adaptive approach for restoration is recommended where assessment plays a key role in evaluating actions relative to population restoration and sustainability goals.

Inset – Core Principles of Restoration for Muskellunge and Northern Pike Population Sustainability (U.S. Environmental Protection Agency 2000)

- *Address ongoing causes of degradation*
- *Restore ecological integrity*
- *Work within the watershed and broader landscape context*
- *Develop clear, achievable, and measurable goals*
- *Use a reference site to guide habitat restoration and assess outcomes*
- *Anticipate future changes*
- *Involve stakeholders throughout the restoration process*
- *Involve the skills and insights of a multi-disciplinary team*
- *Design for self-sustainability*
- *Use passive restoration, when appropriate*
- *Use native genetic strains, when possible*
- *Monitor and adapt where changes are necessary.*

Directed well-designed evaluations of efforts to restore Muskellunge and Northern Pike populations are limited yet necessary to further our ability to restore populations. For example, before/after-control/impact studies of restoration projects, based on current knowledge of Muskellunge and Northern Pike habitat use, would provide better guidance for future projects and could address questions about both habitat quality and quantity, because understanding how both interact is essential. Muskellunge and Northern Pike reintroduction efforts would benefit from a forum in which restoration practitioners, resource managers, and scientists can share experiences to facilitate learning from past successes and failures and prevent individual restoration programs from being overly insular.

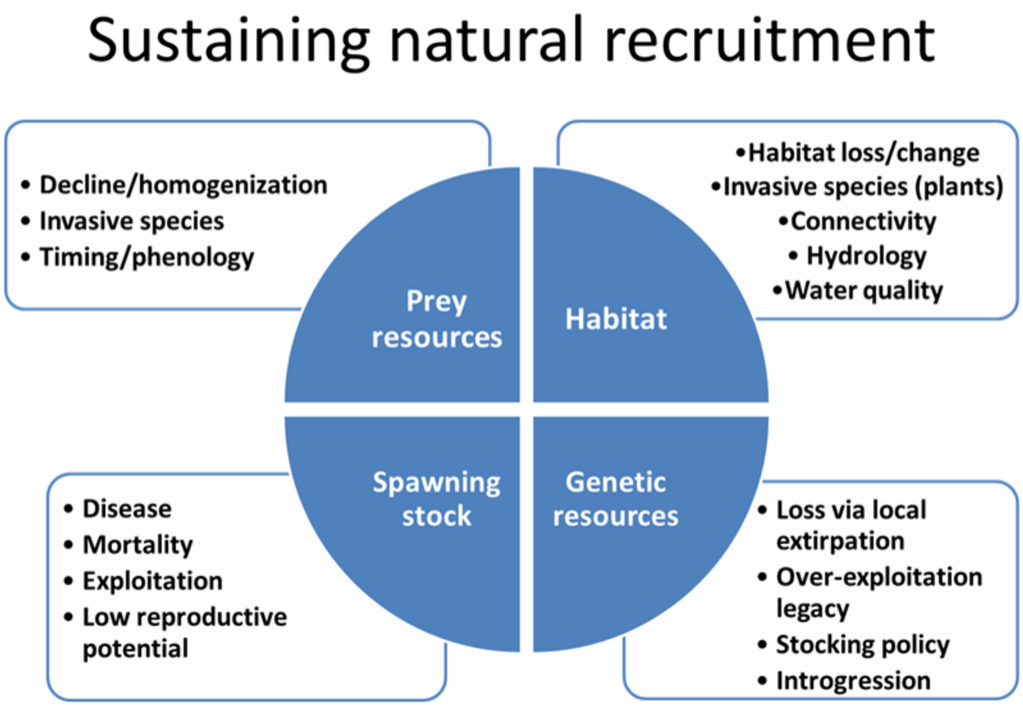

Figure 2. During the Muskellunge and Northern Pike Symposium at the American Fisheries Society Annual Meeting in Little Rock, Arkansas, author, John Farrell proposed a conceptual model of sustaining natural recruitment of Muskellunge in context of known perturbations that could be used in consideration of conservation and restoration efforts.

GENETICS

Muskellunge and Northern Pike genetics research has focused primarily on describing patterns of genetic diversity within and among populations to identify genetic management units and guide broodstock management and stocking (e.g., Jennings et al. 2010). Northern Pike populations are often characterized by low genetic diversity, which has been ascribed to glacial bottlenecks or postglacial founder effects and small population sizes typical of a top predator that are compounded by lower effective population sizes (Miller and Senanan 2003). These characteristics also logically apply to Muskellunge, but Kapuscinski et al. (2013) argued that additional data do not support uncharacteristically low diversity within Muskellunge populations. A lack of common genetic markers applied to numerous populations across the ranges of these species precludes strong conclusions. It is possible that many Muskellunge and Northern Pike populations lack diversity, but low diversity does not characterize all populations and genomic regions.

Genetic data indicate that major lineages of Northern Pike are associated with multiple glacial refugia in North America and Europe (Senanan and Kapuscinski 2000; Launey et al. 2006). Avoiding stock transfer among major lineages will conserve high levels of genetic divergence, but genetic differences are also commonly found among populations within lineages, even on small geographic scales because of physical isolation, limited movement, or reproductive site fidelity within waters (Bosworth and Farrell 2006). Geographic groupings of genetically similar populations, which could provide the basis for management units, may be weakly supported for Northern Pike because of recent differentiation, low resolving power of genetic markers, or stocking effects (Senanan and Kapuscinski 2000; Launey et al. 2006). Muskellunge populations reportedly derived from a single glacial refuge (Crossman 1986), but allozyme data supported the existence of three major Muskellunge stocks in the drainages of the upper Mississippi River, the Great Lakes, and the Ohio River (Koppelman and Philipp 1986). In the Great Lakes, Kapuscinski et al. (2013) found numerous genetically distinct groups of Muskellunge, sometimes among nearby locations (e.g., Georgian Bay, Lake Huron) but hypothesized that geographic proximity and low habitat complexity facilitated genetic similarity in other areas (e.g., Niagara River).

Stocking can be a substantial anthropogenic influence on esocid genetic diversity. Miller et al. (2012) showed that ancestry derived from stocked Muskellunge in Minnesota varied by lake and source population but did not relate to the amount of stocking (Figure 3). Miller et al. (2009) also showed that ancestry from a slow-growing population likely limited the size attained by descendants in stocked lakes. Launey et al. (2006) showed that stocking Northern Pike likely contributed to poorly-defined genetic structure among populations in France, whereas Larsen et al. (2005) found no effects in a Denmark population, which they attributed to freshwater source populations being poorly adapted to brackish water stocking locations.

To build on existing knowledge, four key areas of genetics research are needed to advance management and conservation of Muskellunge and Northern Pike: range-wide genetic structure, effects of stocking on genetic structure, adaptive genetic variation, and evolutionary response to exploitation.

Increased sampling in underrepresented regions is necessary to understand range-wide genetic structure of Muskellunge and Northern Pike. For Northern Pike, this includes several regions where populations likely derived from different refugial origins (Alaska, Eastern Europe, and Russia). For Muskellunge, only the Great Lakes populations are well represented in the primary literature. Studies using a common set of markers and comprehensive sampling would provide a full picture of the distribution of genetic variation across the ranges of these species. Range-wide assessments should explicitly incorporate stocked populations. Retrospective analyses of past stocking can provide information on where native genomes persist and may be conserved or where stocking makes the greatest contribution, which can guide source selection if stocking is required for restoration. Furthermore, cases where supplementary stocking has made no apparent genetic contribution to native populations may provide insights on the risks of outbreeding depression. The genome of stocked fish may have been poorly adapted or had negative interactions with the genome of the resident population, leading to negative fitness consequences as populations "purged" non-native genes.

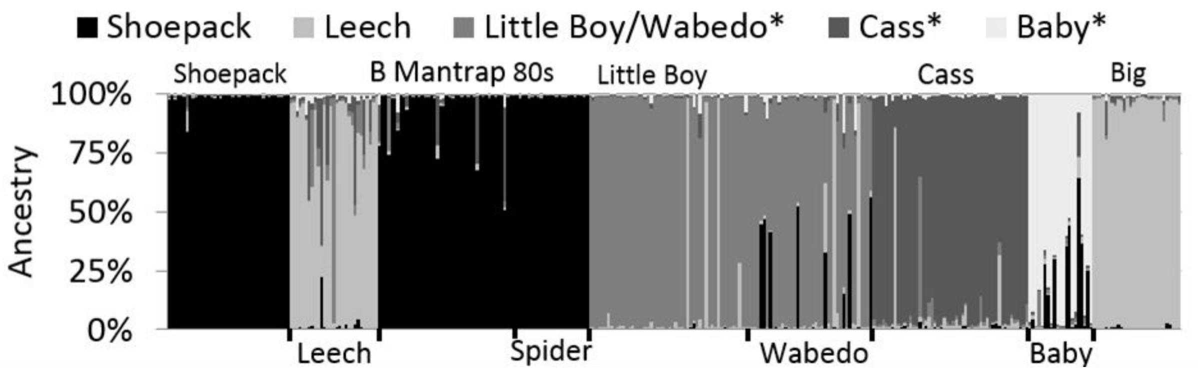

Figure 3. Ancestry estimated by a Bayesian analysis for individuals in seven lakes stocked with one or both of the Shoepack or Leech strains of Muskellunge (strain and lake samples indicated immediately above and below the figure). Each vertical line represents an individual fish with its ancestral composition indicated by the different colors. The legend indicates ancestry corresponding to the two stocked strains or three distinct native ancestries (indicated by asterisks). Adapted from Miller et al. (2012).

Researchers have yet to apply the power of genomics to studies of Muskellunge and Northern Pike. Previous studies have mostly used mitochondrial DNA or microsatellites. These markers are limited in number and generally reflect neutral genetic variation shaped by mutation, population size, and isolation. Genomic approaches allow for rapid development of many more markers (single nucleotide polymorphisms) and identification of those under selection (adaptive markers). Funk et al. (2012) argued for using a combination of neutral and adaptive markers to better delineate management units. Identifying adaptive differentiation can be used to prioritize which populations should be conserved to maintain adaptive variation within the species and to determine source populations for supplementation or translocations. Genomic approaches also will increase understanding of the genetic basis for adaptation, which will further inform researchers and managers about issues including risk of outbreeding depression and ability to persist in changing environments.

Harvest is another direct way by which humans affect esocid genetics. Northern Pike have been featured in evaluations of evolutionary change due to selective harvest (Matsumura et al. 2011). Muskellunge and Northern Pike are both model species for such evaluations and as populations of concern about selective change because of their often intensive and trophy-based fisheries. An exciting research direction will be elucidating relationships between genomic data derived from molecular techniques and phenotypic data used in selective harvest models (e.g., growth rates and age-at-maturity) to understand the genetic basis of responses to human-induced selection.

SELECTIVE MORTALITY AND EXPLOITATION

Muskellunge and Northern Pike are heavily utilized, supporting important trophy, recreational, commercial, and subsistence fisheries, and in general prior to the 1980s most received no special management. Both fishing and natural mortality greatly alter fish populations and are important in assessing and managing fisheries. Exploitation and even management can produce both intentional and unintentional selective harvest and mortality. Selective mortality can result from many factors, including environmental change (Casselman and Harvey 1975), seasonal activity patterns (Casselman 1975, 1978), differential growth, and epizootics (Casselman 2011), and can greatly alter population size, structure, and dynamics. Also behavioral diversity in esocid populations (Kobler et al. 2009) can result in differences in activity that would cause selective vulnerability and mortality.

To meet current and future challenges and produce high-quality, sustainable Muskellunge and Northern Pike fisheries, selective exploitation and mortality should be taken into consideration. Provided here are some examples of how selective mortality can be assessed and affect Muskellunge and Northern Pike populations and fisheries. By example, they draw on former science but, by perspective and application, are new. Differential mortality involving the sexes should be taken into consideration through appropriate assessment and management. Special attention should be made to reduce selective harvest of larger individuals in Northern Pike populations because their role as keystone predators is particularly important in maintaining stable and productive prey-fish communities. Northern Pike populations can contain more than just "hammer handles" and can be managed to provide sustainable, high-quality recreational fisheries; where commercial fisheries exist, they should be certified as sustainable. We encourage those who assess and manage esocid populations to be watchful for selective mortality and exploitation; we find them to be more prevalent and have a greater effect on population structure, productivity, and fisheries than heretofore thought.

Seasonal growth cycles, both somatic and reproductive, inherently affect between-sex activity patterns, which differ. Females are faster-growing than males, showing sexually dimorphic growth. In mature Northern Pike of both sexes, gonad development commences in early fall but is completed much more quickly in males; for females, gonadal development continues into mid to late winter. Feeding and activity associated with differences in seasonal growth affect vulnerability to assessment gears and angling. Examination of seasonal sex ratios of captured Northern Pike confirms this. Regardless of fishing technique, more female than male Northern Pike are caught during the summer period (2.0 F : 1.1 M), with disproportionately more females caught during winter (6.0 F : 1.5 M) (Casselman 1975). The former relates to feeding associated with somatic growth and the latter to reproductive growth. Muskellunge and Northern Pike fisheries can be particularly selective in late fall and early winter, when disproportionately more mature females are harvested (Casselman 1975). Increased fishing pressure during gonad development can result in selective removal of maturing females, greatly reducing reproductive potential of the population.

Growth rate and activity can affect vulnerability and selective harvest and mortality. Fast growing Muskellunge and Northern Pike feed more heavily, making them more vulnerable to capture. In a Northern Pike removal study involving angling and electrofishing, angled Northern Pike were significantly faster growing; the difference was greater for females (17%) than males (10%) (Figure 4). This comparison documents that angling exploitation can selectively remove faster growing Northern Pike and result in a slower growing, less productive population. Cleithral bone fractures and calluses associated with handling (Casselman 1996) indicate that in some populations about 30% of the Northern Pike have been caught and released at least once; thus, intensive exploitation can lead to selective overharvest of large individuals. In Northern Pike populations, this can result in abundance of small fish that are colloquially referred to as "hammer handles". Lysack (2004), in an extensive survey of fish populations in Manitoba, examined the occurrence of small Northern Pike and concluded, from size distributions, that 63 cm TL was an important benchmark for assessing population structure, selective exploitation, and their effects on piscivory. Lysack (2004) showed that size limits and restrictive harvest of large Northern Pike increased important cannibalism, which controlled Northern Pike numbers and effected a more appropriate Northern Pike population size structure and a better balanced fish community

Careful examination of sex ratio at age can help evaluate exploitation rates in Muskellunge and Northern Pike populations. The oldest, largest individuals are usually females, and natural mortality of males is higher. However, where this is not the case and environmental conditions are relatively stable, then selective harvest and mortality are occurring. In the 1960s to 1980s in the St. Lawrence River, the oldest Muskellunge in the population were male, underlining the selective mortality of females related to heavy exploitation. In recent years, with increased size limits and voluntary catch and release, the oldest and largest Muskellunge are now female, indicating decreased exploitation (J. M. Casselman, Queen's University, unpublished data).

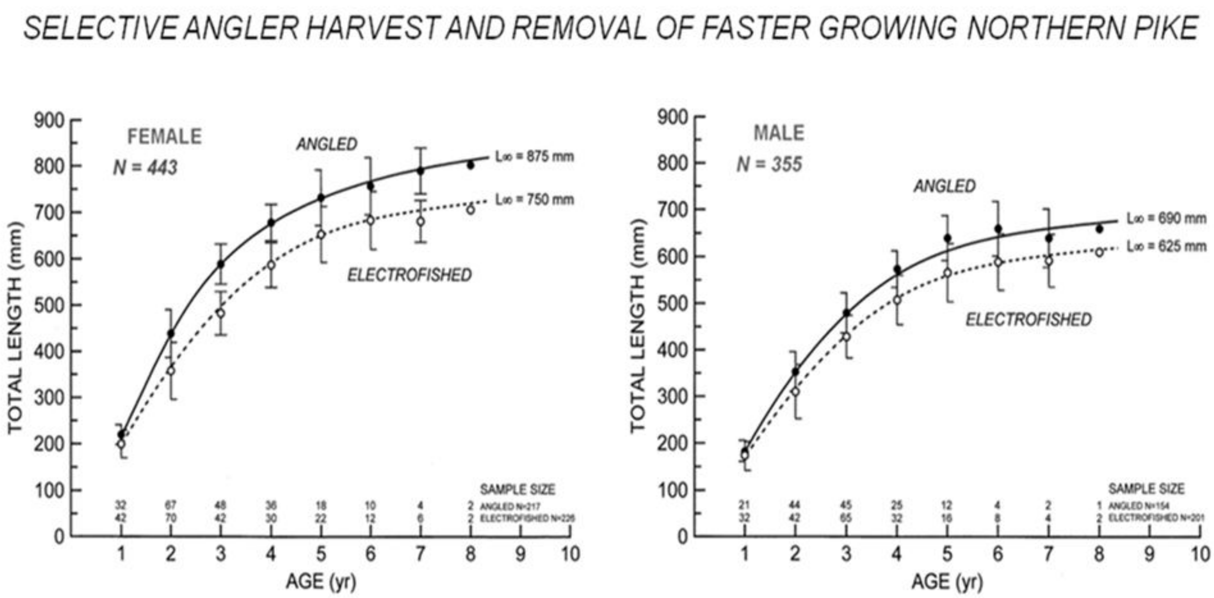

Figure 4. Mean length-at-age of angled and electrofished female (left pane) and male (right pane) Northern Pike from Wickett Lake, Ontario, 1972. Closed circles represent angled Northern Pike and open circles represent electrofished Northern Pike. Error bars represent 95% confidence intervals. L∞ represents the asymptotic length from the von Bertalanffy growth equation. Data, analyses, and figure provided by author John Casselman.

Winterkill resulting from oxygen depletion during the ice-cover period provides a good example of an extreme environmental condition that can dramatically alter Northern Pike population structure. Winterkill of Northern Pike has not been prevalent in recent decades, primarily because of global warming and decreasing ice cover; however, extreme winters can still occur (Casselman 2002). Population studies conducted in shallow lakes during winterkills in the 1960s and 1970s documented very selective mortality events (e.g., Casselman and Harvey 1975). Critically low midwinter oxygen levels in years when midwinter thaws did not occur resulted in selective mortality of the largest, oldest, and fastest-growing individuals in the population. Such selective winter mortality results in significantly slower-growing Northern Pike populations. These mortalities occurred in late winter and, given seasonal activity patterns, killed significantly more females than males (Casselman and Harvey 1975). Little can be done to manage for this type of selective mortality; however, an examination of population structure can provide retrospective insights.

Selective harvest and mortality generally produce negative effects, but there is evidence that results can be positive. For example, a 2005–2008 viral hemorrhagic septicemia outbreak in the upper St. Lawrence River resulted in about 50% mortality of the mature Muskellunge population, as estimated from anglers' diaries (Casselman 2011). Muskellunge that died were significantly older and slower growing, leaving a population that was significantly faster growing and capable of reaching a larger ultimate size. Other causes of growth changes, including density dependence, can be ruled out (Casselman 2011). The culling effect of this extreme epizootic increased the growth potential of the population and resulted in a rarely seen growth-rate change (Casselman 2011). Managing for extremes in size and associated old age can have unexpected results because extremes can be ephemeral.

Quality sustainable, recreational Muskellunge and Northern Pike fisheries require cooperative effort among fisheries professionals and anglers. Specific techniques and tools can assist this effort. For example, the cleithrum, a calcified structure, can easily be acquired by those who harvest Muskellunge and Northern Pike and used by managers to assess important population dynamics, growth, mortality, and exploitation. The Cleithrum Project, a collaborative association between anglers and professionals, has greatly assisted in the management of high-quality, sustainable Muskellunge fisheries in Ontario (Casselman et al. 1996). Anglers and taxidermists from both Canada and the United States have provided cleithra, along with data on sex and capture locations of the fish, which have been used to document harvest of an individual and provide fundamental data necessary for basic management (i.e., estimation of body size, age, growth, and mortality rates).

CONCLUSIONS

Substantial progress has been made toward understanding the biology and ecology of Muskellunge and Northern Pike, yet much more work must be done to conserve their fisheries. For example, native Muskellunge populations near the southern extent of the species' range are relatively understudied compared to northern populations, yet they may be most threatened due to climate change. Determining how climate change will affect these populations will have important implications for conservation and restoration decisions. Additional investigations that contrast the habitats and fish communities of waters that support relatively abundant, self-sustaining populations opposed to degraded ones will help identify factors that limit recruitment success and provide guidance for protecting and restoring environmental and biological conditions that are favorable for all life stages of Muskellunge and Northern Pike. To date, most research has focused on adult or age-0 Muskellunge and Northern Pike, such that our lack of knowledge about the ecology of sub-adult Muskellunge and Northern Pike may be our most substantial information gap. Similarly, most management programs have focused on protecting adult Muskellunge and Northern Pike from over-harvest and producing Muskellunge fisheries through stocking. These efforts are often not creating self-sustaining populations, indicating that a more holistic approach is needed. Such an approach should address genetic integrity, habitat and prey needs at all life stages, and incorporate the effects of human users. This is a daunting task, but recent scientific and technological advances provide exciting opportunities to meet this challenge. For example, telemetry transmitters with sufficient battery life are now small enough to be used in meaningful studies of sub-adult Muskellunge and Northern Pike and may be used to quantify movement patterns, habitat selection, and over-winter survival. Additionally, genetic tools are now available to rapidly assess diversity and spatial structure, which will be essential for conserving the evolutionary potential of these important species. Genetic analysis of archived samples and contemporary populations can also be used to determine how stocking and selective mortality have affected Muskellunge and Northern Pike populations. Novel research methods and holistic approaches to conservation and restoration are needed to meet the challenge of successfully managing native populations, especially as they face continued habitat losses and degradation, biological invasions, and climate change.

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