Hydrobiologia (2008) 601:41–53
DOI 10.1007/s10750-007-9265-0

INTERNATIONAL PIKE SYMPOSIUM

Potential effects of spawning habitat changes on the segregation of northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) in the Upper St. Lawrence River

John E. Cooper · Jerry V. Mead · John M. Farrell · Robert G. Werner

Abstract Changes in spawning habitat of northern pike (*Esox lucius*) may affect their segregation from and coexistence with the closely related muskellunge (*E. masquinongy*). We estimated the areal coverage of robust and shallow emergent vegetation in three shared-spawning bays in the Upper St. Lawrence River from aerial photographs taken from 1948 to 2003. Robust emergent vegetation (e.g., cattail) increased in coverage by 155–241% while shallow emergents (sedges) decreased by 46–96%. The loss of sedges, an important northern pike-spawning habitat, may facilitate greater spawning overlap in offshore-submersed aquatic vegetation within bay habitats used by muskellunge. Development rates and characteristics of northern pike and muskellunge eggs and larvae were compared to better understand the implications of greater spawning overlap. Northern pike eggs developed faster than muskellunge eggs at temperatures of 4.7–19°C, and adhesive eggs and the presence of adhesive papillae were present in both species. Equations were used to predict degree-day requirements for hatching and swim-up in three habitats (shallow emergents, bay, and offshore shoal) along a temperature gradient. Northern pike required more estimated degree days to reach hatching in bay and offshore shoal habitat relative to shallow emergent habitat due to cooler temperatures. Significant spawning overlap is known to occur within bay habitats, but poor success of northern pike in deep bay habitats and overall reductions in abundance are hypothesized to currently buffer muskellunge from potential negative interactions between these species.

Keywords Adhesive papillae · Development · Cattail · Segregation · Water level regulation

Guest editors: J. M. Farrell, C. Skov, M. Mingelbier, T. Margenau & J. E. Cooper
International Pike Symposium: Merging Knowledge of Ecology, Biology, and Management for a Circumpolar Species

J. E. Cooper · J. V. Mead · J. M. Farrell · R. G. Werner
Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA

J. E. Cooper (✉)
Cooper Environmental Research, 1444 County Route 23, Constantia, NY 13044, USA
e-mail: cooperesearch@localnet.com

Present Address:
J. V. Mead
Department of Earth and Environmental Science, University of Pennsylvania, 162 Hayden Hall, 240 South 33rd Street, Philadelphia, PA 19104-6319, USA

Introduction

Segregation of spawning and nursery habitat of northern pike and muskellunge is hypothesized to be an important characteristic of their successful coexistence (Inskip, 1986). Northern pike are believed to have competitive superiority over muskellunge during

the first year of life and native muskellunge populations declined in lakes following the introduction of northern pike. Spawning segregation has been reported in large lakes of Wisconsin (Dombeck et al., 1986), the Niagara River, NY (Harrison & Hadley, 1978), Presque Isle Bay, Lake Erie, PA (Buss & Larsen, 1961), and Leech Lake, MN (Strand, 1986). Intensive studies in the upper St. Lawrence River, however, showed significant overlap between the species in spawning (Farrell, 1991; Farrell et al., 1996; Farrell, 2001) and nursery bays (LaPan, 1985; Farrell & Werner, 1999). The occurrence of natural northern pike X muskellunge hybrids in the upper St. Lawrence River supports the idea of overlap of spawning times and habitat. Similar findings that northern pike spawn in the same habitat as muskellunge were documented in bays on the Ottawa River, Quebec (Monfette et al., 1996).

Northern pike spawning in the upper St. Lawrence River is initiated in seasonally flooded areas of tributaries, and shallow (≤30 cm), littoral areas of coastal bays following ice-out in late April and early May but shifts to deeper, off-shore bay habitats (≤6 m) during mid to late May (Farrell et al., 2006) and several populations have been shown to be genetically different even in close proximity (Bosworth & Farrell, 2006). Muskellunge do not use tributaries for spawning in the region, but do overlap with pike in the coastal bay habitats (Farrell et al., 2007). Vegetation is critical to the life cycle of northern pike (McCarraher & Thomas, 1972; Bry, 1996). A conversion of high quality spawning habitats composed of sedges (*Carex* sp.) and grasses (Graminae) to dominance by robust emergent cattail (*Typha* spp.) was hypothesized to have altered the relative spawning distributions of the esocids and promoted a greater degree of overlap in spawning and nursery within bay habitats (Farrell, 2001).

Spawning northern pike exhibits low use of cattail dominated habitats (Franklin & Smith, 1963; Casselman & Lewis, 1996; Farrell, 2001). High density of cattail may also prevent access of northern pike to preferred seasonally flooded habitats. Nearly all emergent habitats in tributaries and coastal bays in the St. Lawrence River are currently dominated by the robust emergent cattail, but patches of submersed aquatic vegetation in bays remaining from the previous growing season are targeted for spawning and represent areas where species overlap is most pronounced (Farrell et al., 1996; Farrell, 2001). There is a need to quantify emergent habitat change for coastal bays of the St. Lawrence River to help understand its potential effects on spawning distributions and its influence on northern pike and muskellunge segregation during early life.

Information on the relative development rates of northern pike and muskellunge given ambient thermal conditions and larvae adaptations would be of value in assessing the ability of these species to reach critical developmental stages under conditions of overlap. Models of developmental rates for eggs and larvae are needed to make these comparisons. Spawning in shallow habitats early in spring requires that eggs be resistant to colder water temperature and low dissolved oxygen, particularly at night. The more northerly distribution of northern pike (Crossman, 1978) implies that northern pike eggs would be tolerant of colder water, and northern pike eggs have an adhesive coating that allows the eggs to become attached to vegetation above low oxygen areas. Northern pike larvae utilize adhesive papillae on their heads to attach to the vegetation soon after swim-up. Dombeck et al. (1984, 1986) have attributed superior reproductive success in northern pike over muskellunge to the presence of adhesive eggs, papillae, and the associated attachment behavior which they state is lacking in muskellunge. However, in contrast, several authors have noted the existence of adhesive eggs (Sorenson et al., 1966; Cooper, 1983) and papillae (Leslie & Gorrie, 1985) in muskellunge, and the attachment behavior of muskellunge larvae (Sorenson et al., 1966; Colesante, 1977). The conflicting reports require further examination for the presence of adhesive eggs and papillae in muskellunge.

The objectives of this study were to (1) estimate the conversion of shallow emergents (preferred northern pike spawning habitat) to robust emergents in selected bays that have known northern pike and muskellunge reproduction, (2) determine, and compare between species, the time required to reach selected egg and larvae development characters, and larvae survival, at different temperature regimes, and compare the presence of adhesive eggs and adhesive papillae, and (3) develop a predictive model to determine the timing of hatching and swim-up of larvae in shallow emergent, bay, and offshore shoal habitats based on in situ temperature measurements.

Methods and materials

Estimation of changes in spawning habitats

Vegetation coverage was estimated from aerial photographs in three bays in the Thousand Islands region of the upper St. Lawrence River (Fig. 1) from 1948 to 2003. Buck and Flynn bays were located on the southwest end of Grindstone Island (river kilometer 1,088) and Cobb Shoal Bay was located in the American Narrows section (river kilometer 1,075). The surface area of Cobb Shoal was 10.6 ha, Buck Bay was 18.3 ha, and Flynn Bay was 69 ha.

Aerial photographs were available from several sources taken at different times of year and at varying scales (Table 1). Two vegetation categories (simplified from Geis & Kee, 1977) were used for photointerpretation: shallow emergents (SE: meadows, broad- and narrow-leaved emergents, and floating vegetation); and robust emergents (RE) dominated by *Typha*. Northern pike spawning habitat was considered to be that area bounded by upland plants out to a water depth of ≤ 1 m and thus included SE, RE, and open water. Open water area within the northern pike spawning habitat was estimated separately. Muskellunge spawning habitat was estimated as the area of each bay between the 2.5 m depth contour and RE. SE delineated in this study were bounded by the upland plant community and by RE. Boundaries of the upland plant community and the vegetation categories were ground-verified in 1995 in Buck and Flynn bays and in 2003 in Cobb Shoal. Scales of distance were determined from measuring man-made structures in each bay (e.g., barns, boat docks, and bridge supports) and comparing the distances to those calculated from aerial photographs.

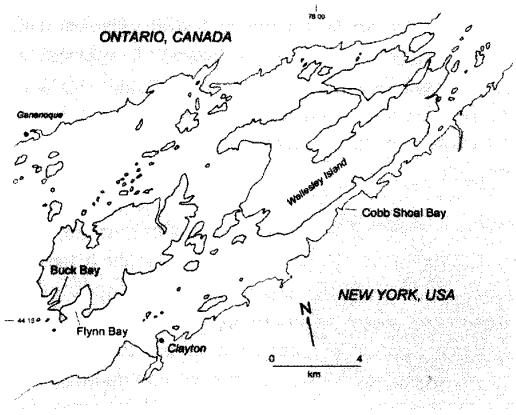

Fig. 1 Location of Buck, Flynn, and Cobb Shoal bays in the Thousand Islands region of the Upper St. Lawrence River

Profiles of the bays were estimated from hypsographic curves derived from digital elevation models based on field surveys and existing bathymetric and elevation data. All elevation data were projected in meters (International Great Lakes Datum 1985). Underwater elevations were estimated by measuring water depth using a sonar system linked to a Global Positioning System (GPS). Water depth was converted to elevation using water level recorded at a gauge on the survey date. The shoreline was estimated using an infrared-based electronic distance measuring device geo-referenced to control points (accuracy to <7 cm) established using a Leica rover and base station GPS. A raster surface image was created from a triangulated irregular network resulting in 10-m resolution grid cell surfaces. The

Table 1 Aerial photographs, and their sources, used to delineate the vegetation categories in Buck, Flynn, and Cobb Shoal bays from 1948 to 2003

Year	Month	Photograph description and scale	Bays	Photograph source
1948	Sept.	Vertical, rectified, panchromatic, 1:24,000	All bays	NYS Conservation Dept.
1970	Sept.	Vertical, rectified, panchromatic, 1:14,000	Cobb Shoal	US Air Force
1972	May	Vertical, rectified, panchromatic, 1:12,000	Buck, Flynn	Dickerson, Czerwinski, Warneck, surveyors
1973	April	Vertical, rectified, color infrared, 1:121,000	Cobb Shoal	US Geological Survey
1974	Oct.	Vertical, unrectified, color, 1:2,400	Flynn	J. Geis, SUNY
1994	May	Vertical, rectified, color infrared, 1:40,000	All bays	US Geological Survey
1995	July	Oblique, unrectified, color, 1:8,500	All bays	J. Farrell, SUNY
2003	April	Vertical, rectified, color infrared, 1:14,400	All bays	New York State Dept. Environ. Conservation

boundary of the RE from the aerial photographs was overlayed and rectified on the bay model using latitude and longitude coordinates of structures common to all aerial photographs used.

Egg and larvae development time at different temperature regimes

Adult northern pike and muskellunge were trapnetted in local bays in spring of 1998. Northern pike (maximum weight 1.4 kg) were artificially spawned in the field using the dry method (Sorenson et al., 1966; Klingbeil, 1986). The milt from two or more male northern pike were used to fertilize the eggs of a single female resulting in multiple families of eggs that were pooled. Fertilized northern pike eggs were placed into coolers, allowed to water harden, and returned to the laboratory. Muskellunge were trapnetted as spawning pairs (one male, one female) and, due to their large size (9–23 kg), were transported back to the laboratory for spawning (dry method; single family) where additional personnel were available. This was done to avoid injury to the fish and the potential loss of eggs. All fish were released at the place of capture.

Eggs and larvae of northern pike and muskellunge were raised in the laboratory under controlled temperature conditions. Water temperature was regulated by an immersion circulator in a single tank for each target temperature. The temperatures used represented those at which northern pike and muskellunge eggs would develop in the wild. Treatments were not replicated. Temperature was measured every hour with an automatic recorder. Eggs were held at ambient water temperature only until they had been counted for their respective treatments. One hundred recently fertilized northern pike and muskellunge eggs chosen randomly were incubated at target temperatures of 6, 9, 12, 15, and 18°C and an additional 100 muskellunge eggs were incubated at 21°C. Northern pike were not raised at 21°C because survival at this temperature has been found to be low (Hokanson et al., 1973) and this temperature is not typically reached during the egg development period (Cooper, 2000). Counted eggs were placed in 0.9 l ice-cube storage bins in which the sides and bottom were replaced with 1.5 mm mesh netting. Paired ice-cube bins (one containing northern pike eggs, one containing muskellunge eggs) were suspended in a 95 l tank for each target temperature. Five eggs chosen randomly out of the original 100 eggs were placed in a floating plastic cup with a screened bottom suspended in each ice-cube bin. Each cup was placed in a petri dish with water from the appropriate bin for observations of development under a stereo microscope. Observations for development and presence of adhesive papillae and attachment behavior began at 25 h for northern pike eggs and at 42 h for muskellunge eggs. The difference in time of first observations was due to the ongoing trapnetting efforts, but was not critical since observations occurred prior to the time of the first development character. Observations of development were made at least twice per day for: formation of somites, placodes (olfactory, optic, and auditory), heart, tail-free condition, heartbeat, eye pigment, red blood, hatching, and swim-up of larvae. Dead eggs in the observation cups were replaced with eggs from the ice-cube bins but dead larvae were not replaced.

Estimation of development time in different habitats

Estimates of the time required for northern pike development in SE, bay, and offshore shoal habitats were made using the results of the previous experiment and field temperature. The estimates for northern pike were compared to the time required for muskellunge development in bay habitat. The time required to reach development characters was converted to degree days using a threshold development temperature of 1°C for northern pike and 2°C for muskellunge. The threshold value represents the lowest temperature at which development will occur regardless of the incubation time (Craig Snyder, USGS, personal communication). The estimated cumulative degree days for development were plotted against hourly water temperature values from 1998 (converted to cumulative degree days) taken from an automatic recorder in Flynn Bay to represent bay habitat (from 18 April–10 June, $N = 1{,}296$), hourly data from the National Oceanic and Atmospheric Administration recording buoy at Alexandria Bay, New York, to represent offshore shoal habitat (18 April–10 June, $N = 1{,}272$, data for 6 May missing), and from field observations (12 April–27 May,

$N = 10$) in SE in Flynn Bay. The field observations were reconstructed to cover missing daily values ($N = 36$) by linear regression: SE temperature = 0.19 × calendar day − 7.09, $R^2 = 0.97$.

Northern pike spawning dates were determined by presence of eggs in 1998: 12 April in SE and 18 April in bay habitat. Northern pike spawning in offshore shoal habitat was set as the same date as the bay habitat to simulate conditions of no access to SE and lack of vegetation in bay habitat due to ice-scouring. Muskellunge spawning date was set as 23 May in bay habitat when the first eggs were collected in 1998. Predictive equations of degree days required for hatching and swim-up by larvae were calculated from the controlled temperature development series. Temperature means used in the predictive equations for northern pike were derived from water temperature: 12 April to 27 May in SE, 18 April to 31 May in the bay, and 18 April to 10 June in offshore shoal, and 23 May to 30 June for muskellunge in the bay. Differences in hourly temperatures from bay and offshore shoal habitats were compared using ANOVA (SAS, 2002) for the period of 18 April–10 June. Temperature from SE habitat was not compared statistically to that in other habitats since only daytime values were used.

Results

Changes in spawning habitat

Scales of distance from aerial photographs were 1.9–5% (mean = 3.1, SD = 1.3) greater than ground measurements, thus the vegetation estimates could be as much as 5.5% greater than what was present. A general pattern of expanding RE coverage, and thereby a loss of northern pike spawning habitat, was evident from 1948 to 2003 in each bay. An example of these changes is shown for Flynn Bay (Fig. 2), where northern pike spawning habitat was reduced by 72% in the NE area and by 96% in the SW area (Table 2). Decline of northern pike spawning habitat ranged from 46–62% in the other bays. Robust emergent vegetation colonized the northern pike spawning habitat at elevations from 74.6 to

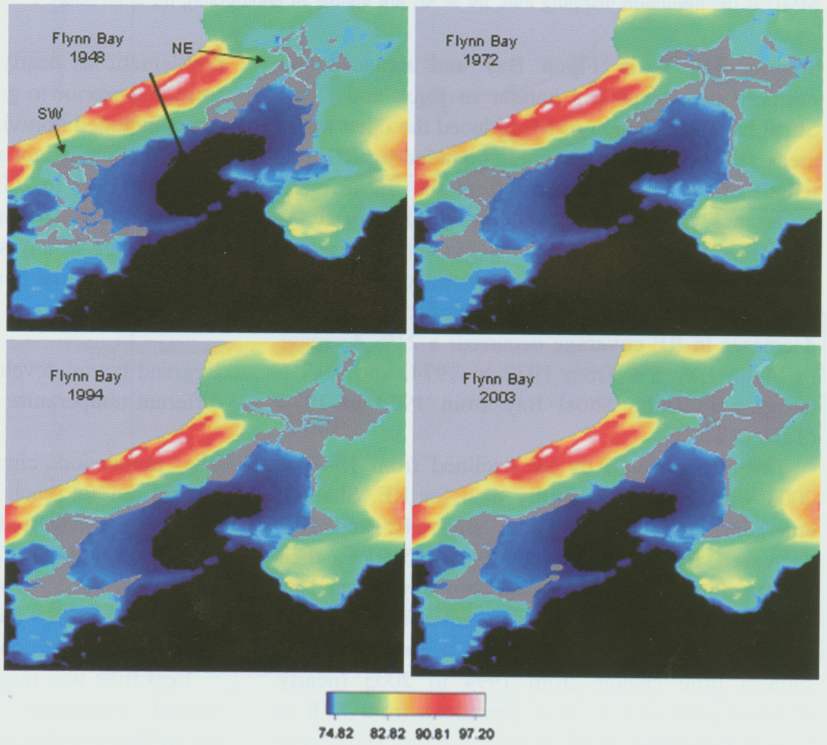

Fig. 2 Elevation of Flynn Bay (International Great Lakes Datum 1985 in meters) for 1948, 1972, 1994, and 2003. Flynn bay was divided into two regions, SW and NE, shown by a solid black line. Polygons shown in gray represent robust emergents. Light blue color represents the elevation corresponding to the northern pike spawning habitat. Muskellunge prefer to spawn in the area represented by dark blue and black. Depth of water increases from light blue to black. Terrestrial vegetation is represented by green, yellow, red, and white, in increasing elevation

Table 2 Estimated hectares of northern pike habitat, robust emergent (RE), shallow emergent (SE) vegetation, and open water (OW) at water depth of ≤1 m in Buck, Flynn, and Cobb Shoal bays from 1948 to 2003, and in parentheses, RE as percent of northern pike habitat

Year	Vegetation category Pike habitat	Buck Bay 1.44	Flynn Bay SW 7.87	Flynn Bay NE 17.29	Cobb Shoal 4.39	MMU (m^2)
1948	RE	0.39 (27.1)	2.24 (28.5)	5.49 (31.7)	1.55 (35.3)	15
	SE, OW	0.26, 0.79	3.94, 1.69	4.39, 7.41	2.71, 0.36	
1970	RE	nd	nd	nd	2.48 (56.5)	9
	SE, OW	nd	nd	nd	nv, 3.14	
1972	RE	0.65 (45.1)	3.60 (45.7)	8.40 (48.6)	nd	7.5
	SE, OW	<0.01, 0.78	0.43, 3.84	2.40, 6.49	nd	
1973	RE	nd	nd	nd	3.73 (85.0)	76
	SE, OW	nd	nd	nd	nv, 1.89	
1974	RE	nd	2.84 (36.1)	11.07 (64)	3.97 (90.4)	1.5
	SE, OW	nd	1.42, 3.61	5.81, 0.41	1.28, 0.37	
1994	RE	0.61 (42.4)	6.92 (87.9)	13.27 (76.7)	2.91 (66.3)	25
	SE, OW	0.04, 0.75	0.77, 0.18	2.99, 1.03	0.64, 2.07	
1995	RE	0.68 (47.2)	7.04 (89.4)	14.33 (82.9)	3.65 (83.1)	5
	SE, OW	<0.01, 0.78	0.27, 0.93	2.66, 0.3	0.32, 1.65	
2003	RE	1.04 (72.2)	7.63 (96.9)	14.03 (81.1)	3.96 (89.5)	9
	SE, OW	<0.01, 0.39	0.23, 0.01	1.5, 1.76	nv, 1.66	
Percent change	RE	+166	+241	+155	+155	
	SE + OW	−96	−96	−72	−46	

MMU is the minimum mapping unit, nv = SE not visible in photograph, nd = no data

76.5 m (Fig. 3) in Flynn Bay and replaced the northern pike spawning habitat in Buck and Cobb Shoal bays. Expansion of RE reduced the open water areas seen in 1948 to channels bounded by RE: the length of the center channel from the SE to open water in Flynn Bay northeast increased from about 200 m in 1948 to 570 m in 2003 (Fig. 2). Open water within the northern pike habitat declined in all study areas primarily due to consolidation of RE. Two large decreases in RE coverage occurred: a 21% decrease in Flynn Bay SW from 1972 to 1974, and 16.7% decrease in Cobb Shoal Bay from 1973 to 1974 (Table 2).

The area covered by SE declined from 1948 to 2003 with greater variability than for RE. Shallow emergent coverage in Flynn Bay NE and SW decreased from 1948 to 1972 by 55–91%, then increased in 1974 by 230% in Flynn Bay SW and by 142% in Flynn Bay NE; both areas decreased in coverage from 1974 to 2003. Conversion of SE to RE showed little change from 1994 to 2003 (nearly identical plots in Fig. 3) at elevations from 74.6 to 76.0 m. Estimation of SE changes in Cobb Shoal were problematic as nearly half of the photographs used were taken prior to growth of SE. Estimates of open water included non-visible SE in these photographs.

Muskellunge habitat changed less than 3% in each bay from 1948 to 2003. There was greater coverage of muskellunge spawning habitat by RE in Flynn Bay in 1948 than in any subsequent year (Fig. 2) due to formation of large islands.

Egg and larvae development and survival at different temperature regimes

The immersion circulators used for temperature control did not reach stabilization until one day after the experiment started resulting in a wide temperature range and high SD. The circulator set at the target temperature of 18°C was less accurate than the others and allowed the water to warm 1.5°C about every three days before cooling.

Less time was required to reach selected developmental characters in northern pike than in muskellunge within each temperature regime (Fig. 4).

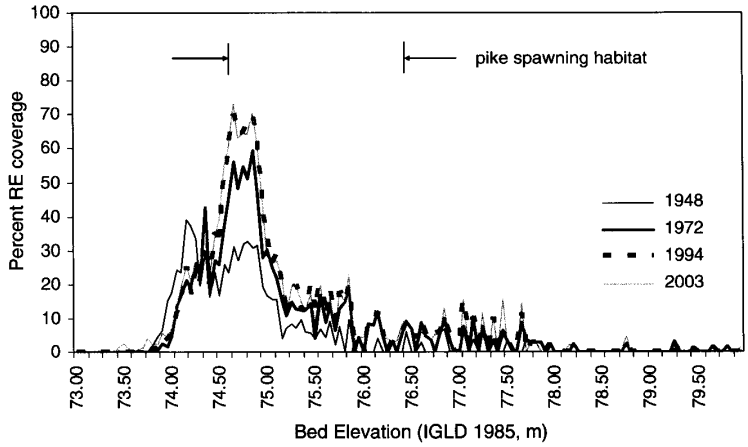

Fig. 3 Percent robust emergent coverage in relation to bed elevation for Flynn Bay in 1948, 1972, 1994, and 2003. Lines representing 1994 and 2003 are nearly identical. The greatest increase occurred within the elevations that correspond to northern pike spawning habitat

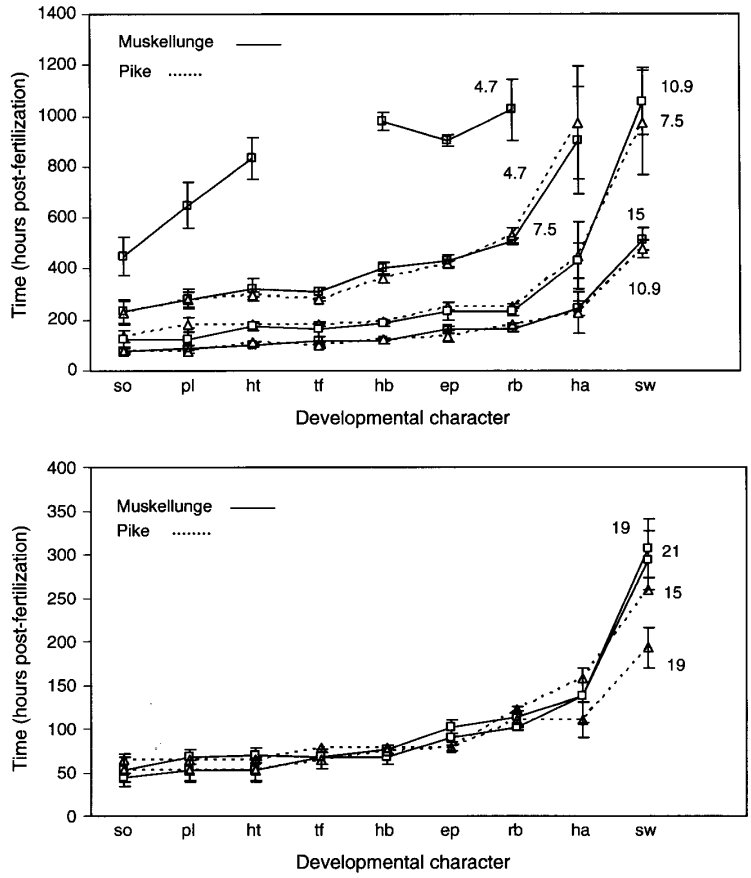

Fig. 4 Time required for northern pike and muskellunge embryos to reach specific developmental characters when incubated at mean temperatures of 4.7, 7.5, 10.9, 15, 19, and 21°C. Bars represent the range in hours. Muskellunge embryos did not achieve the tail-free condition at 4.7°C. Key to characters: so—somites, pl—placodes (olfactory, auditory, optic), ht—heart, tf—tail-free, hb—heartbeat, ep—eye pigment, rb—red blood, ha—hatching, and sw—swim-up by larvae

Development time of muskellunge was similar to that of northern pike but at a differential of 3–4°C: for example, muskellunge development time at 7.5°C was similar to northern pike development time at 4.7°C. Muskellunge development time was similar at 19 and 21°C. Northern pike did not develop to the swim-up condition at 4.7°C nor did muskellunge at 4.7 and 7.5°C: these northern pike and muskellunge embryos were incubated for an additional 23–25 days but their developmental condition did not advance. Muskellunge embryos failed to achieve the tail-free condition at 4.7°C although gross development of other characters appeared to be normal. Muskellunge embryos required 99% (at 7.5°C) and 34% (at 19°C) more hours for 50% to hatch compared to northern pike embryos (Fig. 5), and 134% (at 10.9°C) and 69% (at 19°C) more hours to reach swim-up. Embryo survival was similar at 10.9–19.2°C in both species (Table 3). Fewer survivors of both species occurred at colder temperatures and fewer muskellunge embryos survived at 21°C than at 19°C.

Adhesive eggs and papillae

Eggs of northern pike and muskellunge were adhesive prior to water hardening but lost the adhesive property shortly after water hardening. Adhesive papillae were present in front of the eyes in northern pike up to 12 mm TL and in muskellunge up to 14 mm TL. Papillae remained visible for 6–17 days after hatching but were reduced in size and area after the gas bladder was filled. Attachment behavior was exhibited by northern pike at temperatures of 4.7, 7.5, and 15°C, and by muskellunge at temperatures of 15, 19, and 21°C.

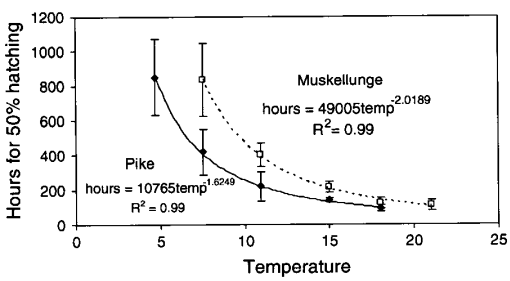

Fig. 5 Hours required for 50% of northern pike and muskellunge embryos to hatch under controlled temperatures. Bars represent the range in hours

Development time in different habitats

The mean water temperature (16.2°C, SD = 2.97) of SE habitat was greater than the mean water temperature in bay habitat (13.2°C, SD = 3.15) or that in offshore shoal habitat (10.0°C, SD = 3.06). Mean water temperature of bay habitat was significantly greater than that in offshore shoal habitat ($F_{1,2494} = 594.2$, $P < 0.0001$). Predictive equations relating degree days to mean water temperature for 50% of northern pike and muskellunge eggs and larvae to reach hatching and swim-up were:

$$\text{Northern pike hatching: DD} = 297.09T^{-0.445}, \quad R^2 = 0.99,\ N = 5$$

$$\text{Northern pike swim-up: DD} = 1081.6T^{-0.71}, \quad R^2 = 0.96,\ N = 4$$

$$\text{Muskellunge hatching: DD} = 799.08T^{-0.674}, \quad R^2 = 0.92,\ N = 5$$

$$\text{Muskellunge swim-up: DD} = 3215.4T^{-0.894}, \quad R^2 = 0.92,\ N = 4,$$

where DD is degree days, and T is the mean temperature for the habitat. N is the number of DD–temperature combinations in the equation. Northern pike required an estimated additional 9 DD (10 calendar days) and 20 DD (18 calendar days) to reach hatching in bay and offshore shoal habitat compared to northern pike in SE habitat (Fig. 6). Swim-up required an estimated additional 27 DD (14 calendar days) and 60 DD (25 calendar days) for northern pike in bay and offshore shoal habitat compared to SE habitat. Muskellunge required about the same estimated number of DD to reach hatching and 8% more estimated DD to reach swim-up in bay habitat as did northern pike in the offshore shoal habitat.

Discussion

A conversion of preferred sedge dominated northern pike spawning habitat to dense stands of cattail was

Table 3 Percent survival to selected developmental characters of northern pike and muskellunge incubated at a range of temperatures

Temperature (°C)				Northern pike Percent survival to			Muskellunge Percent survival to		
Target	Mean	Range	SD	Embryonic shield	Normal hatching	Swim-up	Embryonic shield	Normal hatching	Swim-up
6	4.7	3.4–6.1	0.66	86	68	0[a]	37	0	0[b]
9	7.5	5.7–9.1	0.89	96	85	76	89	82	0[c]
12	10.9	9.6–16.7	0.54	96	79	78	92	85	76
15	15.2	10.1–16.3	0.84	96	81	81	91	80	77
18	19.2	14.3–22.7	1.3	98	73	67	82	80	69
21	21.4	19.9–24.2	0.8	–	–	–	77	50	37

Target is the intended temperature and mean is the realized temperature. The experiment was terminated when larvae achieved swim-up or died

[a] Northern pike were incubated for 611 h after hatching but did not swim-up

[b] Muskellunge were incubated for 600 h after the red blood character but did not hatch

[c] Muskellunge were incubated for 552 h after hatching but did not swim-up

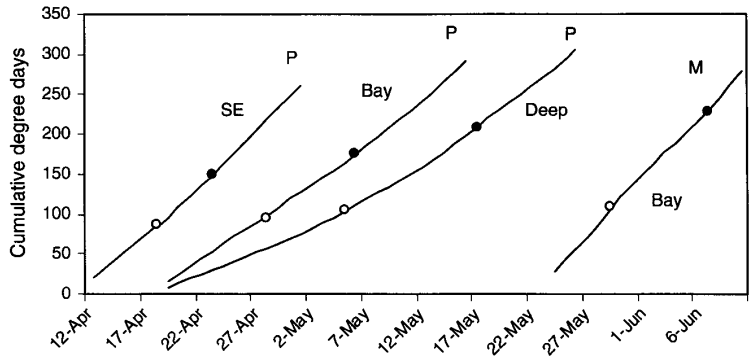

Fig. 6 Prediction of cumulative degree days (lines) for northern pike (P) and muskellunge (M) from observed spawning in SE and bay habitat (simulated for offshore shoal habitat) from the equations derived for development time (degree days) under controlled temperatures. Open circles represent hatching and closed circles represent swim-up

clearly evident in the three bays studied. Spawning by northern pike in deeper water may be a direct response to elimination of quality habitat and water-level regulation that prevents access to SE, as suggested in previous studies. Monfette et al. (1996) and Farrell (2001) described northern pike spawning in deeper water when low spring water levels prevented the flooding of the lowland sedge and grass dominated habitat. Under these conditions spatial segregation of spawning northern pike and muskellunge in bays and spawning periods was reduced (Farrell et al., 1996; Monfette et al., 1996).

Robust emergents generally exist at shallower water depths (<60 cm; Hudon, 1997) and muskellunge spawning has been shown to occur primarily within new growth of submersed vegetation not present during earlier northern pike spawning (Farrell et al., 1996; Farrell, 2001). RE colonization, therefore, is believed to affect northern pike spawning to a greater extent than for muskellunge, because the preferred northern pike habitat (SE) has been reduced or eliminated.

A documented historical change in vegetation in a St. Lawrence River marsh from pollen analysis of a peat core also indicated diverse sedge meadow communities converted to dominance by cattail (Beland, 2003). Logging and land conversion to agriculture of the St. Lawrence River watershed, and associated nutrient and sediment run-off were hypothesized to cause vegetation change. Water level regulation of the upper St. Lawrence River, through the Moses–Saunders Dam, is also thought to have

promoted the continued dominance of cattails through the elimination of low water levels that encourage a more diverse wetland community (Wilcox & Meeker, 1992). Vegetation changes have been facilitated by water level regulation of Lake Ontario and the St. Lawrence River with the completion of the St. Lawrence Seaway and Power Project in 1959. The regulation of water levels has eliminated the extremes in low levels and reduced the extremes in high levels which has benefited the production of robust emergents, such as *Typha* spp. (Keddy & Reznicek, 1986).

Our results also indicate that, under conditions of overlap, northern pike would be expected to develop and grow faster than would muskellunge. No other studies have compared a complete development series for northern pike and muskellunge eggs over a range of controlled temperatures. Experimental units were not replicated, but the time required to reach specific developmental characters was in agreement with specific developmental characters in previous studies (Table 4). A few differences with other studies are noted, including the number of hours to northern pike hatching (Leslie & Gorrie, 1985) and the formation of heartbeat and eye pigment in muskellunge (Galat, 1973), all of which were greater than our estimates. The assertion that northern pike eggs develop faster than muskellunge eggs is supported by the results of our study, although the difference declined as temperatures increased.

Northern pike are generally larger than muskellunge at the end of the first season because northern pike are spawned earlier and exhibit faster development relative to muskellunge (LaPan, 1985; Farrell, 1998). Faster development and, therefore, larger size of northern pike would be expected to give northern pike the advantage over muskellunge when spawning occurs in SE or bay habitats. Interaction between northern pike and muskellunge would favor northern pike as they would be larger and more advanced in development, have greater prey resource availability, and have the ability to prey on muskellunge (Inskip, 1986). Water column segregation in bay habitat (muskellunge near the surface, northern pike at lower

Table 4 Comparison of hours required to reach specific events in northern pike and muskellunge development at controlled temperatures

Northern pike
Hours to hatching

Source Temperature	Swift (1965) Hours	Leslie & Gorrie (1985) Hours	Temperature	Present study Hours
6	552–696		4.7	614–1,054
8	360–456		7.5	372–639
12	192–288		10.9	182–348
15		240–288	15	147–171
16	96–144			
18	96–120		19	88–134

Muskellunge

Source Developmental state	Galat (1973) at 13°C Hours	Hassan & Spotila (1975) Hours	Present study at 15°C Hours
Placodes	93		80–101
Tail-free	144		101–138
Heartbeat	204		101–120
Eye pigment	216		140–170
Hatching	312–360		198–262
Hours from hatching to swim-up at 15°C		192–288	198–308

depth; Osterberg, 1985) may have evolved to reduce potential conflicts.

Adhesive eggs, temporary adhesive papillae, and the behavior associated with the papillae have also been cited as advantages in northern pike reproductive strategy (Dombeck et al., 1984; Zorn et al., 1998) over that of muskellunge. The assertion that adhesive properties were lacking in muskellunge eggs and larvae was contrary to the findings of Sorenson et al. (1966), Cooper (1983), Leslie & Gorrie (1985), and the present study. Adhesiveness in eggs was lost after water hardening (Sorenson et al., 1966), thus observations made after water hardening would conclude that muskellunge eggs were not adhesive. Contradictory observations for muskellunge eggs in US Fish and Fisheries Commission (1897: 182, nonadhesive; 247, table, slightly adhesive) may be the result of timing of observations. Naturally spawned eggs of both species have been found unattached to a substrate (Williamson, 1942; Farrell et al., 1996; Farrell, 2001) and raises the question of the adaptive significance of early adhesiveness.

Muskellunge larvae exhibited attachment behavior in the present study in 50% of the laboratory temperatures (15, 18, and 21°C), and papillae remained visible for 17 days after hatching. Leslie and Gorrie (1985) noted the presence of adhesive glands in muskellunge larvae, as in the present study. Sorenson et al. (1966) and Colesante (1977) noted that muskellunge larvae would cling to the sides of the rearing tank, implying that adhesive papillae were present. The presence of adhesive eggs and papillae in northern pike and muskellunge would not confer an advantage of one species over the other, but would allow for successful reproduction of both species in habitats that have the potential for low dissolved oxygen. Although larvae of both species possess the ability to attach, general observations seem to suggest northern pike may have a greater affinity for the behavior. There is a need to examine this process for both species in greater detail in natural conditions.

The simulation of northern pike spawning in offshore shoal habitat in this study showed that northern pike eggs required about the same number of degree days to reach hatching and swim-up as did muskellunge in bay habitat despite having spawned 36 days earlier. The slower development of northern pike in offshore shoal habitat, and subsequent delayed feeding on lower zooplankton density, could result in recruitment failure for northern pike due to low survival of larvae (Farrell et al., 2006).

Although significant overlap of the esocids exists in bay habitats, recent trends in northern pike abundance may buffer muskellunge from significant negative interaction. Interestingly, in an intensive study of young-of-year muskellunge habitat in the Upper St. Lawrence River, positive correlations were found among abundances of muskellunge and other esocids, including northern pike that suggested a shared habitat affinity (Murry & Farrell, 2007). Northern pike YOY abundance, however, was very low relative to muskellunge in these nursery bays. In a study of stocked and native YOY muskellunge in the same sites, a negative correlation was found between abundance of northern pike and muskellunge in a shared bay (Farrell, 2001). A site with high pike abundance also exhibited poor muskellunge fry stocking success over multiple years (Farrell & Werner, 1999). It is likely that the abundance of YOY northern pike may regulate the degree of interaction between these species. Recent declines in northern pike abundance may alleviate potential predation and competitive effects with muskellunge associated with conditions of overlap.

Northern pike indexed with gillnets by the New York State Department of Environmental Conservation indicate relative abundance has declined from a mean of 4.4 (CPUE, 1982–1991) to 2.5 (CPUE, 1992–2005) per set (McCullough & Hart, 2005). The yearly index has been less than 2 from 2003 to 2005 and there has not been a strong year class since 1991. Abundance by age has also declined for all age classes, but particularly for ages 1 and 2. Mean length at age decreased about 10% from the 1970s to the 1990s and northern pike required an additional year of growth to recruit to the fishery at 56 cm in the late 1990s (Smith, 2000). An analysis of the factors contributing to year-class formation of Upper St. Lawrence River northern pike indicated habitat loss, water levels management, declines in nutrient loading, and increased predation by double-crested cormorants have a role in the decline (Smith et al., 2007).

Results were consistent with the hypothesis that the spawning by northern pike on the offshore shoals may be a result of the loss of SE habitat. The loss of SE habitat is believed to create a greater degree of overlap within the bay habitat, but vegetation in the bay habitat exists primarily in the deeper areas, due to

ice-scouring. Simulations indicated slow development and poor success for northern pike spawning in these areas (Farrell et al., 2006). Segregation would be increased between northern pike and muskellunge in those years when submersed aquatic vegetation is present in the bay habitat (less scouring), and access to SE is prevented by low water. That scenario would result in greater interaction, with northern pike having the advantage, due to faster development. However, the decline in abundance of northern pike, due to recruitment failure, would suggest that there is a release from the interaction between northern pike and muskellunge due to low population size. Those years when northern pike spawn in what remains of the SE habitat, or in the bay habitat (but not the offshore shoal habitat), would comprise the total recruitment to each year class. Currently, segregation of the two species during spawning does not appear to be a strong driving force regulating coexistence in this system.

Acknowledgments This research was partially funded by the New York State Department of Environmental Conservation (Federal Aid in Sport Fish Restoration grant FA-5-R), Wildlife Forever, Inc., and the Wilford A. Dence Memorial Fellowship (to JEC). We also thank Richard T. Colesante, Rodger Klindt, and Steven LaPan of NYSDEC, and Brian Smith, Ducks Unlimited. Kim Farrell provided a critical review of the work. This research is a contribution of the Thousand Islands Biological Station.

References

Beland, M., 2003. Holocene vegetation dynamics of an Upper St. Lawrence River coastal wetland and surrounding uplands: effects of climate change and anthropogenic disturbance. Master's Thesis, SUNY College of Environmental Science and Forestry, Syracuse, NY.

Bosworth, A. & J. M. Farrell, 2006. Genetic divergence among northern pike from spawning locations in the Upper St. Lawrence River. North American Journal of Fisheries Management 26: 676–684.

Bry, C., 1996. Role of vegetation in the life cycle of northern pike. In Craig, J. F. (ed.), Northern Pike: Biology and Exploitation. Chapman and Hall, Fish and Fisheries Series 19, London: 45–67.

Buss, K. & A. Larsen, 1961. The northern pike of Presque Isle Bay, Lake Erie. Pennsylvania Angler 30: 4–6.

Casselman, J. M. & C. A. Lewis, 1996. Habitat requirements of northern pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 161–174.

Colesante, R. T., 1977. Behavior of muskellunge fry during yolk absorption and swim-up. New York Fish and Game Journal 24: 94.

Cooper, E. L., 1983. Fishes of Pennsylvania and the Northeastern United States. Pennsylvania State University Press, University Park, Pennsylvania.

Cooper, J. E., 2000. Comparative development and ecology of northern pike *Esox lucius* and muskellunge *E. masquinongy* eggs and larvae in the Upper St. Lawrence River and the implications of changes in historical spawning habitat. PhD thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Crossman, E. J., 1978. Taxonomy and distribution of North American esocids. American Fisheries Society Special Publication 11: 13–26.

Dombeck, M. P., B. W. Menzel & P. N. Hinz, 1984. Muskellunge spawning habitat and reproductive success. Transactions of the American Fisheries Society 113: 205–216.

Dombeck, M. P., B. W. Menzel & P. N. Hinz, 1986. Natural muskellunge reproduction in midwestern lakes. American Fisheries Society Special Publication 15: 122–134.

Farrell, J. M., 1991. Spawning ecology of sympatric northern pike and muskellunge in the St. Lawrence River. Master's thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Farrell, J. M., 1998. Population ecology of sympatric age-0 northern pike and muskellunge in the St. Lawrence River. PhD thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Farrell, J. M., 2001. Reproductive success of sympatric northern pike and muskellunge in an Upper St. Lawrence River bay. Transactions of the American Fisheries Society 130: 796–808.

Farrell, J. M. & R. G. Werner, 1999. Abundance, distribution, and survival of age-0 muskellunge in Upper St. Lawrence River nursery embayments. North American Journal of Fisheries Management 19: 310–321.

Farrell, J. M., R. G. Werner, S. R. LaPan & K. A. Claypoole, 1996. Egg distribution and spawning habitat of northern pike and muskellunge in a St. Lawrence River marsh, New York. Transactions of the American Fisheries Society 125: 127–131.

Farrell, J. M., J. V. Mead & B. A. Murry, 2006. Protracted spawning of St. Lawrence River northern pike (*Esox lucius*): simulated effects on survival, growth, and production. Ecology of Freshwater Fish 15: 169–179.

Farrell, J. M., R. M. Klindt, J. M. Casselman, S. R. LaPan, R. G. Werner & A. Schiavone, 2007. Development, implementation, and evaluation of an international muskellunge management strategy for the Upper St. Lawrence River. Environmental Biology of Fishes 79: 111–123.

Franklin, D. R. & L. L. Smith, 1963. Early life history of the northern pike, *Esox lucius* L., with special reference to strength of year classes. Transactions of the American Fisheries Society 92(2): 91–110.

Galat, D. L., 1973. Normal embryonic development of the muskellunge (*Esox masquinongy*). Transactions of the American Fisheries Society 102: 384–391.

Geis, J. W. & J. L. Kee, 1977. Coastal Wetlands along Lake Ontario and the St. Lawrence River in Jefferson County, New York. State University of New York, College of

Environmental Science and Forestry, Syracuse, New York.

Hassan, K. C. & J. R. Spotila, 1975. The effect of acclimation on the temperature tolerance of young muskellunge fry. In Esch, G. W. & R. W. McFarlane (eds), Thermal Ecology II. Proceedings of a Symposium Held at Augusta, Georgia, April 2–5, 1975. Energy Research and Development Administration, Oak Ridge, Tennessee: 136–140.

Harrison, E. J. & W. F. Hadley, 1978. Ecologic separation of sympatric muskellunge and northern pike. American Fisheries Society Special Publication 11: 129–134.

Hokanson, K. E. F., J. H. McCormick & B. R. Jones, 1973. Temperature requirements for embryos and larvae of the northern pike, *Esox lucius* (Linnaeaus). Transactions of the American Fisheries Society 102: 89–100.

Hudon, C., 1997. Impact of water level fluctuations on St. Lawrence River aquatic vegetation. Canadian Journal of Fisheries and Aquatic Sciences 54: 2853–2865.

Inskip, P. D., 1986. Negative associations between abundances of muskellunge and northern pike: evidence and possible explanations. American Fisheries Society Special Publication 15: 135–150.

Keddy, P. A. & A. A. Reznicek, 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12: 25–36.

Klingbeil, J., 1986. Culture of purebred muskellunge. American Fisheries Society Special Publication 15: 273–278.

LaPan, S. R., 1985. Spawning and early life history of muskellunge and northern pike in the St. Lawrence River. Master's thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Leslie, J. K. & J. F. Gorrie, 1985. Distinguishing features for separating protolarvae of three species of esocids. In Kendall, A. W. Jr. & J. B. Marliave (eds), Descriptions of Early Life History Stages of Selected Fishes: Third International Symposium on the Early Life History of Fishes, Canadian Technical Report of Fisheries and Aquatic Sciences, Number 1359: 1–20.

McCarraher, D. B. & R. E. Thomas, 1972. Ecological significance of vegetation to northern pike, *Esox lucius*, spawning. Transactions American Fisheries Society 101: 560–563.

McCullough, R. D. & J. J. Hart, 2005. Thousand Islands warmwater fish stock assessment. New York State Department of Environmental Conservation. Lake Ontario Annual Report 2005 (St. Lawrence River), Section 6: 1–14.

Monfette, R., S. Guenette, N. Dubuc, R. Fortin & H. Fournier, 1996. Northern pike and muskellunge spawning ecology and reproductive success in the lower Ottawa River. In Kerr, S. J. & C. H. Olver (eds), Managing Muskies in the 90s. Workshop Proceedings. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit WP-007, 55–66.

Murry, B. A. & J. M. Farrell, 2007. Quantification of native muskellunge nursery: influence of body size, fish community composition, and vegetation structure. Environmental Biology of Fishes 79: 37–47.

Osterberg, D. M., 1985. Habitat partitioning by muskellunge and northern pike in the International portion of the St. Lawrence River. New York Fish and Game Journal 32: 158–166.

SAS Institute Inc., 2002. Version 8. Cary, North Carolina.

Smith, B. M., 2000. Year-class formation of St. Lawrence River northern pike. Master's thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Smith, B. M., J. M. Farrell, H. B. Underwood & S. J. Smith, 2007. Year class formation of Upper St. Lawrence River northern pike. North American Journal of Fisheries Management 27: 481–491.

Strand, R. F., 1986. Identification of principal spawning areas and seasonal distributions and movements of muskellunge in Leech Lake, Minnesota. American Fisheries Society Special Publication 15: 62–73.

Sorenson, L., K. Buss & A. D. Bradford, 1966. The artificial propagation of esocid fishes in Pennsylvania. Progressive Fish-Culturist 28: 133–141.

Swift, D. R., 1965. Effect of temperature on mortality and rate of development of the eggs of the northern pike (*Esox lucius* L.) and the perch (*Perca fluviatilis* L.). Nature 206: 528.

US Fish and Fisheries Commission, 1897. Methods of the United States Commission of fish and fisheries with chapters on the cultivation of oysters and frogs. US Fish Commission Report for 1897. US Fish and Fisheries Commission, Washington, DC.

Williamson, L. O., 1942. Spawning habits of muskellunge and northern pike. Wisconsin Conservation Bulletin 7: 10–11.

Wilcox, D. A. & J. E. Meeker, 1992. Implications for faunal habitat related to altered macrophyte structure in regulated lakes in northern Minnesota. Wetlands 12(3): 192–203.

Zorn, S. A., T. L. Margenau, J. S. Diana & C. J. Edwards, 1998. The influence of spawning habitat on natural reproduction of muskellunge in Wisconsin. Transactions of the American Fisheries Society 127: 995–1005.