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NOTES

Egg Distribution and Spawning Habitat of Northern Pike and Muskellunge in a St. Lawrence River Marsh, New York

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Abstract.—Coexistence of northern pike *Esox lucius* and muskellunge *Esox masquinongy* in the Niagara and St. Lawrence rivers has been hypothesized to depend on segregation during spawning. However, large overlap in the use of spawning areas by these two species occurs in the Thousand Islands section of the upper St. Lawrence River. In this study, egg collections in Point Marguerite Marsh in the upper river revealed a partial temporal and spatial overlap in egg deposition by northern pike and muskellunge. Northern pike began spawning earlier but overlapped with muskellunge spawning for 2 weeks, May 13–27. Northern pike eggs were collected over a larger area than muskellunge eggs and at all locations where muskellunge eggs were collected. Both species deposited eggs over three dominant genera of vegetation: pondweeds *Potamogeton*, duckweeds *Lemna*, and stonewort *Chara*. Northern pike spawned over a wider range of water depths (0.5–2.6 m) than muskellunge (0.8–1.5 m) and selected habitats with denser, taller vegetative cover. The temporal and spatial overlap of northern pike and muskellunge egg deposition suggests that mechanisms other than spawning segregation permit these two species to coexist in the St. Lawrence River.

Northern pike *Esox lucius* are hypothesized to cause declines in populations of muskellunge *Esox masquinongy* where both species are native and occur sympatrically (Inskip 1986). Negative interactions between northern pike and muskellunge have been proposed to explain their inability to coexist and include interference by adults on the spawning grounds, predation by age-0 northern

pike on muskellunge, interspecific competition in nursery areas, and a differential ability to withstand environmental change (Inskip 1986). However, both species have probably coexisted in the St. Lawrence and Niagara rivers for at least 600 years (Crossman 1978, 1986). Successful coexistence of northern pike and muskellunge in these systems has been attributed to temporal and spatial segregation during spawning (Buss and Larsen 1961; Harrison and Hadley 1978; Osterberg 1985).

Northern pike are known to spawn earlier than muskellunge (Scott and Crossman 1973), but the reported temperature range during the spawning periods overlaps considerably. Northern pike spawn at 4.4–17.2°C and muskellunge at 7.5–15°C (Clark 1950; Franklin and Smith 1963; Scott and Crossman 1973; Gammon 1986). The hypothesis of spatial segregation during spawning is based primarily on observations of adults during the spawning period. Harrison and Hadley (1978) reported that Niagara River northern pike spawn in backwater habitats with little current, whereas muskellunge spawn on shoals in the main river. A similar inshore-offshore segregation of spawning was reported by Buss and Larsen (1961) in Presque Isle Bay, Lake Erie. Osterberg (1985) observed northern pike during the spawning period in the St. Lawrence River in areas less than 1 m deep with negligible current; he also observed muskellunge pairs in water deeper than 1 m, where the water velocity was greater than 0.1 m/s. Osterberg (1985) interpreted these differences as evidence of spatial segregation. However, trap-net surveys of adult northern pike and muskellunge during the

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spawning season and seine surveys for fingerlings during the nursery period in the Thousand Islands section of the St. Lawrence River showed that both species were present in 29 of 36 embayments (R. G. Werner, unpublished data). In the present study, we tested the spawning segregation hypothesis by comparing the timing, distribution, and habitats of egg deposition of northern pike and muskellunge at a shared spawning site in the upper St. Lawrence River.

Methods

Egg collection.—Northern pike and muskellunge eggs were collected in traps set in Point Marguerite Marsh near Alexandria Bay, New York, from 19 April to 12 June 1989 (Figure 1). Traps were constructed of steel rings, 56 cm in diameter and 3.8 cm tall, with a base of 1.6-mm-mesh nylon netting, and a top of 6.4-mm-mesh hardware cloth. Traps were set on the marsh bottom in strings. A string consisted of three or five traps spaced 1 m apart on a rope. Twenty-two strings of five traps each were deployed from 19 to 28 April, and 64 strings of three traps each were deployed from 29 April to 12 June. Traps were set within 16 (61-m²) stations. Five stations were in water 1.5–2.6 m deep, and 11 stations were in water shallower than 1.5 m. Trap strings were retrieved, and traps were emptied and reset on 24 occasions during the 8-week period. The eggs collected in all traps of a string were pooled for statistical analysis.

Treatment of eggs.—Eggs removed from the traps were counted and evaluated in the field for viability. Opaque eggs were considered dead and transparent ones unfertilized (Galat 1973). Eggs were reexamined for viability in the laboratory under a dissecting microscope, measured with an ocular micrometer, and provisionally identified to species based on egg diameter. Egg diameters are reported to vary between 2.5 and 3.0 mm for northern pike and 2.5 to 3.5 mm for muskellunge (Scott and Crossman 1973). Potential overlap in egg diameters and the lack of other discriminating characteristics between northern pike and muskellunge eggs required their hatching for a positive identification of the species. Live eggs were incubated individually in petri dishes in a recirculating-water system until they hatched. The newly hatched free embryos were identified to species based on yolk sac pigmentation. Northern pike have numerous melanophores on the yolk sac, whereas muskellunge yolk sacs are unpigmented (Auer 1982).

Characterization of habitats.—Water depth,

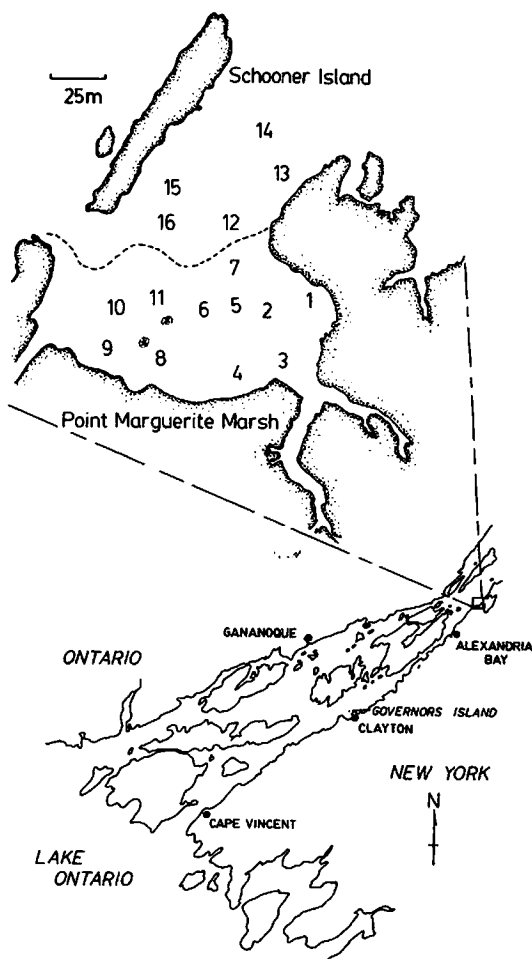


FIGURE 1.—The Thousand Islands section of the upper St. Lawrence River, Cape Vincent to Alexandria Bay, New York, and sampling stations (numbers) in Point Marguerite Marsh. The dashed line represents the 1.5-m water depth contour; asterisks represent rock piles.

dominant submergent vegetation, percent vegetative cover, and vegetation height were estimated where each trap string was set. Water depth was measured to the nearest 0.1 m. Dominance of vegetation genera was estimated from the water surface with the aid of a diving mask. Vegetation coverage was estimated in a 1-m² space between adjacent egg traps on each string and scored according to a logarithmic scale: 0 = bare to 5%, 1 = 5–15%, 2 = 15–25%, 3 = 25–50%, 4 = 50–75%, and 5 = 75–100% (Causton 1988). Vegetation height was estimated and recorded as 0–15 or 15–30 cm. Water temperature was continuously monitored to the nearest 0.2°C from 29 April to 16 June with two Peabody–Ryan® submersible thermographs.

Results and Discussion

Egg Collection, Species Identification, and Egg Viability

We collected 205 eggs and provisionally identified 123 as northern pike and 82 as muskellunge. The identities of 65 of the northern pike and 33 of the muskellunge eggs were confirmed by positive identification of hatched larvae. Although a complete overlap in egg diameters of northern pike by muskellunge was reported by Scott and Crossman (1973), eggs collected at Point Marguerite Marsh overlapped only by 0.1 mm. A one-tailed *t*-test showed that northern pike egg diameters (2.8–3.1 mm; mean = 2.96 mm; SD = 0.008 mm; *N* = 62) were significantly smaller ($P = 0.0001$) than muskellunge egg diameters (3.1–3.4 mm; mean = 3.32 mm; SD = 0.016; *N* = 33). Overlap occurred at 3.1 mm in five eggs. Three of the eggs were hatched; two were identified as northern pike and one as a muskellunge. The two remaining unhatched eggs were assumed to be northern pike based on their early collection date. In all, 107 unhatched eggs were identified to species from their diameters; 58 were northern pike and 49 were muskellunge.

The egg viability rate was 75% for northern pike and 67% for muskellunge. Gammon (1986) reported lower potential sperm production for muskellunge than for northern pike, as indicated by lower testes weights and reduced sperm densities, but was unable to correlate this with natural egg fertility rates in several Wisconsin lakes. He reported northern pike egg viability of 47.2–70.6% and muskellunge egg viability of 30.8–88.4%. The muskellunge egg viability at Point Marguerite Marsh, although lower than that of northern pike, was not statistically different ($\chi^2 = 1.601$; *df* = 2; $P = 0.26$).

Egg Distribution

The first northern pike eggs were collected on 25 April, and egg deposition continued for 33 d until 27 May. Northern pike spawning peaked on 13–16 May when 24 of 48 trap strings contained eggs (Figure 2B). Muskellunge spawning began on 13 May, peaked on 23 May, and lasted for at least 31 d until 12 June when the last trap strings were pulled from the marsh. Water temperatures were 5–13°C during northern pike egg deposition, and 7–12°C at peak deposition. Muskellunge eggs were deposited at 7–17°C, and deposition peaked at 10–13°C.

Reproductive periods for northern pike and mus-

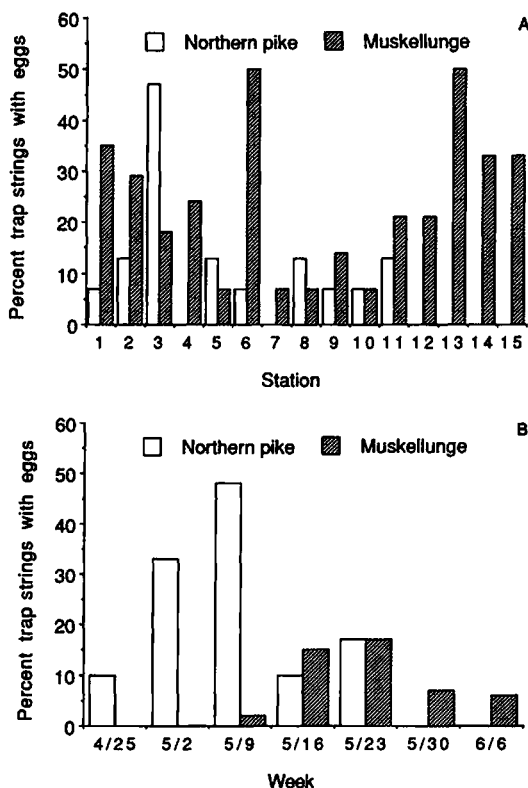


FIGURE 2.—(A) Spatial and (B) temporal distribution of northern pike and muskellunge eggs in Point Marguerite Marsh in the St. Lawrence River near Alexandria Bay, New York, 19 April–12 June 1989. Blocks 1–11 were in water less than 1.5 m deep and blocks 12–16 were in water 1.5–2.6 m deep. No eggs were taken at station 16.

kellunge overlapped by 15 d, and spawning for both species peaked during the overlap. Temporal segregation occurred only between early-spawning northern pike and late-spawning muskellunge. Northern pike spawning began more than 2 weeks before the onset of muskellunge egg deposition and peaked more than a week before muskellunge spawning peaked. Earlier spawning by the northern pike may enhance survival by providing a longer growing season and larger size during the first growing season (Scott and Crossman 1973).

Spatial overlap of northern pike and muskellunge egg deposition in Point Marguerite Marsh was common, with northern pike spawning at all sampling stations used by muskellunge. Northern pike spawned at 15 of 16 stations in both shallow (<1.5 m) and deep (1.5–2.6 m) zones of the marsh, whereas muskellunge eggs were taken only at 9 stations in the shallow zone (Figure 2A). Spawning

overlapped temporally and spatially on six occasions, when eggs of both species were collected in the same trap string. The water depths where muskellunge eggs were collected (mean = 1.1 m) were significantly less than depths where eggs were not present (mean = 1.4 m; $P = 0.003$). Northern pike spawned over a broader range of depths (0.5–2.6 m), and egg distribution was independent of water depth sampled ($P = 0.26$).

The distribution of northern pike and muskellunge eggs in Point Marguerite Marsh differs from the apparent distribution of northern pike and muskellunge spawning at Presque Isle Bay, Lake Erie (Buss and Larsen 1961), and the Niagara River (Harrison and Hadley 1978) and from the distribution of muskellunge spawning in Lake St. Clair (Haas 1978). In Presque Isle Bay and the Niagara River, northern pike are thought to spawn inshore and muskellunge are believed to spawn offshore. Larger water bodies including Lake St. Clair (>3 m deep) (Haas 1978) and Leech Lake (1.57 m deep) (Dombeck et al. 1984; Strand 1986) are reported to have deeper-spawning muskellunge populations. However, shallow-water spawning by muskellunge, consistent with observations at Point Marguerite Marsh, has been documented by Scott and Crossman (1973) and Oehmcke et al. (1974).

Point Marguerite Marsh is the first site where deepwater spawning by northern pike has been reported. Use of deep water by northern pike spawning in Point Marguerite Marsh may be related to the availability of vegetation. Northern pike typically spawn in shallow, vegetated habitats, often in recently flooded areas (Clark 1950; Franklin and Smith 1963; Forney 1968; McCarragher and Thomas 1972; Scott and Crossman 1973; Dumont et al. 1978; Kozmin 1981). However, at Point Marguerite Marsh, wind and ice scour removed much of the vegetation from inshore areas, leaving large bare areas and patchy inshore vegetation. Northern pike spawning was focused on submersed aquatic vegetation in the deeper areas unaffected by scouring.

Three aquatic vegetation types—pondweeds *Potamogeton*, duckweed *Lemna*, and stonewort *Chara*—were dominant in Marguerite Marsh during northern pike and muskellunge spawning periods. *Lemna trisulca* was often found mixed in association with two types of filamentous algae, *Cladophora* and *Spirogyra*. More northern pike eggs were collected in areas where the percent vegetative cover was greater ($\chi^2 = 12.953$; $df = 1$; $P = 0.0003$) and vegetation was taller ($\chi^2 = 4.04$; $df = 1$; $P = 0.04$). Muskellunge egg distri-

bution had no apparent relation with plant cover ($\chi^2 = 0.524$; $df = 1$; $P = 0.46$) or height ($\chi^2 = 0.771$; $df = 1$; $P = 0.38$); however, their spawning sites did not differ statistically from those of northern pike in terms of vegetative cover ($\chi^2 = 1.378$; $df = 1$; $P = 0.24$) or vegetation height ($\chi^2 = 1.70$; $df = 1$; $P = 0.19$).

The selection by northern pike for habitat features may be an adaptation to increase survival of spawned eggs. Dombeck et al. (1984) suggested that the adhesiveness of northern pike eggs allows them to stick to vegetation, suspending them above the substrate–water interface in an area where oxygen levels are greater. After water hardening, however, the eggs lose their adhesiveness (Williamson 1942); all of those collected at Point Marguerite Marsh were nonadhesive. Spawning over dense vegetation may prevent contact of nonadhesive eggs with the sediments, stop eggs from being displaced by currents, and provide greater surface area exposure to enhance water hardening of eggs.

This study shows that the temporal and spatial segregation of spawning by northern pike and muskellunge was incomplete and occurred only among northern pike spawning early or in deepwater and muskellunge spawning late. We conclude that other mechanisms regulate the ability of northern pike and muskellunge to coexist during their early life history.

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