

Habitat requirements of northern pike (*Esox lucius*)¹

John M. Casselman and Cheryl A. Lewis

Abstract: Over the past half century, habitat changes have significantly affected production of northern pike (*Esox lucius*), especially in the Great Lakes Basin. Loss of wetlands, reduction of shoreline cover and structure, cultural eutrophication, and siltation have negatively affected water transparency, abundance of macrophyte habitat, and even body condition. We review recent habitat restoration programs conducted in the Great Lakes Basin to reverse this trend. However, assessment has usually been inadequate to evaluate their success. Spawning and nursery requirements (first year of life) are examined, using a system for classifying and ranking major physical characteristics and requirements. Depth of nursery habitat is directly correlated with fish size and age. Spawning habitat is usually less critical or limiting but more easily manipulated and restored than nursery or juvenile-adult habitats. Year-class strength over 22 yr in eastern Lake Ontario was correlated positively with midsummer temperature and negatively with late summer–early fall water elevation; also, the largest year-class appeared immediately after catastrophic winterkill of a predator, white perch (*Morone americana*). Both implicate nursery rather than spawning associations. Adult abundance is related to the extent of macrophyte cover, which is optimal from 35 to 80% but inversely related to body size.

Résumé : Depuis un demi-siècle, les modifications de l'habitat ont nettement affecté la production de grand brochet (*Esox lucius*), particulièrement dans le bassin des Grands Lacs. La disparition des milieux humides, la réduction du couvert et de la structure des littoraux, l'eutrophisation due à l'agriculture et la sédimentation ont eu des effets négatifs sur la transparence de l'eau, l'abondance de l'habitat des macrophytes, et même la condition corporelle des poissons. Nous examinons des programmes de restauration des habitats qui ont été récemment mis en oeuvre dans le bassin des Grands Lacs pour renverser cette tendance. Les moyens d'évaluation n'ont toutefois pas permis de mesurer le succès de ces programmes. Nous examinons les besoins en frayères et en nourriceries (première année de la vie) à l'aide d'un système de catégorisation et de classement des principales caractéristiques et exigences physiques. La profondeur de l'habitat de nourricerie est directement corrélée à la taille et à l'âge des poissons. L'habitat de fraye est généralement moins critique ou moins limitant, mais plus facile à manipuler et à restaurer que l'habitat de nourricerie ou celui des juvéniles et des adultes. Sur une période de 22 ans, dans l'est du lac Ontario, l'effectif des classes annuelles étaient corrélé positivement à la température au milieu de l'été et négativement à la montée des eaux à la fin de l'été et au début de l'automne; de plus, la classe annuelle la plus nombreuse est apparue après une mortalité catastrophique d'un prédateur, le baret (*Morone americana*). Dans les deux cas, l'association se situerait au niveau des nourriceries plutôt que des frayères. L'abondance des adultes est en rapport avec l'étendue du couvert des macrophytes, qui est optimale dans une proportion de 35 à 80 %, mais en relation inverse avec la taille corporelle.

[Traduit par la Rédaction]

Introduction

Cultural eutrophication and habitat loss over the past half century have significantly affected northern pike (*Esox lucius*) production in North America and especially in the Great Lakes. Northern pike are large keystone piscivores that are

important in “top-down” predatory regulation of the fish community. They can tolerate a wide range of environmental conditions but are primarily mesothermal, or cool-water, fish best adapted to shallow (< 12 m), productive, mesotrophic-eutrophic environments. They are a common and abundant species, found in 45% of the total freshwater area of North America (Carlander et al. 1978).

Commercial harvest of northern pike from the Great Lakes declined from a high of 1.6 million kg just after the turn of the century to < 0.05 million kg in the late 1960s (Baldwin et al. 1979). This decline, which was greatest in Lake Erie, followed by Lakes Ontario, Huron, Michigan, and Superior (Fig. 1), was directly proportional across the lakes to the original abundance of the species and the extent of European settlement and associated shoreline alteration. Throughout the period of decline, fish communities were transforming, exacerbated by changes in water levels, temperature, shoreline development, watershed alterations, siltation, aquatic macrophyte cover, commercial and sport fishing, and other factors (Whillans 1979). Changes to nearshore habitats had a particularly impor-

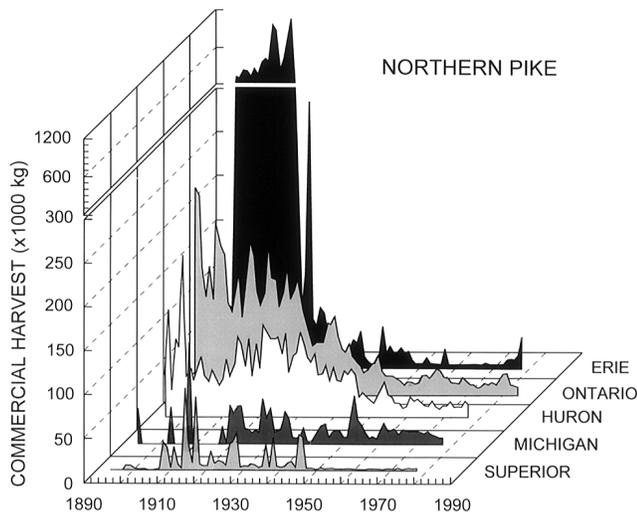
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J.M. Casselman. Ontario Ministry of Natural Resources, Research, Science, and Technology Branch, Aquatic Ecosystems Research Section, Glenora Fisheries Station, RR 4, Picton, ON K0K 2T0, Canada.

C.A. Lewis. Ontario Ministry of Natural Resources, Aquatic Ecosystems Branch, Aquatic Ecology Section, Peterborough, ON K9J 8N1, Canada.

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Fig. 1. Commercial harvest of northern pike from the five North American Great Lakes from the early 1900s to the 1970s. Harvest estimates are for the Canadian waters of lakes Ontario, Erie, Huron, and Superior. Data are from Baldwin et al. (1979).



tant negative effect on pike production and have been important in contributing to the decline of the species, reflected in the decrease in commercial harvest (Fig. 1). These changes were most obvious in the more eutrophic lower Great Lakes.

Since settlement on the Canadian shoreline of Lake Ontario, there have been substantial losses of marshes that would have contained spawning and nursery (young-of-the-year) habitat for northern pike. Whillans (1982) concluded that 50% of 62 marshes had been completely lost by the late 1970s. He noted that where populations were densest around the Great Lakes, baseline wetland had been reduced by 75–100%. Most remaining shoreline wetlands on the Great Lakes are degraded and altered by siltation and turbidity and are dominated by silt- and turbidity-tolerant fish species (Jude and Pappas 1992). Dodge and Kavetsky (1994), in their review of aquatic habitat and wetlands of the Great Lakes, concluded that the loss of inshore and nearshore habitat used by northern pike was moderate to low in Lakes Superior and Huron, moderate in Lake Michigan, high in Lake Ontario, and high to very high in Lake Erie. This habitat reduction is directly related to the decrease in commercial harvest of the species throughout the Great Lakes since the turn of the century (Fig. 1). Many recent habitat restoration programs across the Great Lakes explicitly identify the restoration of northern pike habitat as part of the fish community and habitat goals, objectives, and targets (Hartig 1993).

We examine habitat requirements of northern pike throughout its life history by considering spawning, nursery, and juvenile-adult habitat in relation to vegetative cover and substrate, water temperature, oxygen, transparency, and turbidity. Specifically, we (i) review the literature, (ii) present a system for classifying and ranking habitat associated with spawning and nursery grounds, (iii) analyze new data concerning nursery habitat, considering depth distribution and year-class strength for the Bay of Quinte and eastern Lake Ontario for a 22-yr period (1971–1992), and (iv) review and evaluate some recent restoration projects.

Habitat requirements of northern pike

Spawning habitat

There are many thorough and practical studies, reviews, and bibliographies of the spawning habitat and requirements of northern pike (e.g., Clark 1950; Johnson 1957; Franklin and Smith 1963; Forney 1968; Coble 1972; McCarragher and Thomas 1972; Alldridge and White 1980; Crossman and Casselman 1987; Raat 1988; Masse et al. 1993). Habitat suitability index models have been developed (Inskip 1982), and those aspects associated with spawning and nursery habitat have been refined and improved (Anderson 1993). Documentation of the loss of spawning habitat is historic and extensive (Brynildson 1958; Threinen et al. 1966, 1969; Reid 1990).

Quite generally, northern pike spawn in shallow water over vegetation in spring shortly after ice-out, when these shallows have warmed to 8–12°C. The fish tend to migrate up tributaries to flooded marshes and wetlands or shallow shoreline inundations. Optimal spawning substrate is flooded vegetation in a shallow, sheltered area. Grasses and sedges are preferred, but other vegetation may be used. The vegetative hummocks and mats should be adequate to entrap the eggs and suspend them above the substrate, where anoxic conditions can develop.

We devised a system for classifying, ranking, and weighting the physical requirements of habitat used by spawning northern pike (Table 1) that uses criteria gleaned from published literature, court evidence (J.M. Casselman, unpublished data), and extensive field observations of spawning northern pike in 18 marshes and wetlands. The system emphasizes the importance of vegetative type, water level, the exposure of a site, its proximity to connecting waterways, and to a lesser extent, substrate type and water exchange (Table 1). We use a simple single-digit ranking system to compare among and within these important habitat variables. Although other attributes could be considered, these physical conditions are of primary importance and are usually readily apparent on site inspection. These criteria apply to spawning time; however, some can be reasonably evaluated at other times of the year (e.g., vegetative type and density). The system can be used to build a matrix to numerically rank and compare and contrast the extent and quality of various habitats.

Spawning success has been linked to water-level changes (see review by Inskip 1982). High water levels at time of spawning with stable levels after the incubation period are associated with large year-classes of northern pike (Johnson 1957). High water levels increase nutrient concentrations and primary and secondary production in inundated areas, increasing the amount of available prey for the larval fish, make more spawning habitat accessible, expand the amount of cover, and reduce the potential for predation and cannibalism. This is obvious when new impoundments are flooded and previously unflooded terrestrial vegetation is inundated. Production of young-of-the-year can be 4–10 times greater the first year after impoundment than in subsequent years (Bodaly and Lysack 1984). Widely fluctuating water levels can inhibit the development of nearshore vegetation; as well, very consistent annual levels are less productive, with low levels being least productive (e.g., Inskip 1982; Gravel and Dubé 1980).

Other environmental conditions can be critical for early life

Table 1. Criteria for classifying and ranking physical characteristics of spawning and nursery habitat of northern pike using a subjective numerical ranking system that ranges from 1 (lowest, poorest) to 9 (highest, best) and can be used to document and quantitatively describe the relative importance of various habitat characteristics.

Habitat variable	Rank of relative importance	General habitat description	
		Best (highest rank 9)	Poorest (lowest rank 1)
Spawning habitat			
Vegetation			
Type	9	Hummocks of grasses and sedges (e.g., <i>Carex</i> spp.) meadowgrass <i>Calamagrostis canadensis</i>	Cattails, bog laurel, Potamogeton spp., floating aquatic plants
Density	8	Moderately dense, 2–4 hummocks per m ²	Sparser or denser
Water level			
Depth ^a	9	10–70 cm, averaging 20–40 cm (high water associated with strong year-classes)	Deeper or shallower
Fluctuation	7	Gradually increasing prior to spawning; stable until fry start to move from spawning grounds, approximately 6–8 weeks, then gradually decreasing	Fluctuating or not increasing prior to spawning; decreasing abruptly immediately after spawning
Exposure of the site	6	Sheltered, warming rapidly in early spring; receiving direct sunlight from south or west	Warming very slowly in early spring; exposed to north or east
Connecting waterways	4	Rivulets that permit easy movement of spawners into more sheltered spawning areas of the marsh and allow fry to move out with receding water	Few or no deeper connecting channels for drainage or access, or very deep channels congregating predators
Substrate type	3	Well-oxygenated vegetative detritus; good rooting medium for inundated grasses and sedges	Decomposing organic debris or any type of relatively infertile organic or inorganic substrate
Water exchange	2	Moderate; during high water some exposure to wind and wave action	Little or no wind exposure or water movement, or extreme water movement or wave action
Nursery habitat^b			
Proximity to spawning habitat	9	Contiguous	More distant or separated from the spawning ground by various obstructions or restrictions, docks, etc.
Vegetation			
Submergent and emergent	8	Dense submergent and emergent aquatic plants (40–90% cover)	Sparser or denser
Extent	6	Extensive; >10 times size of adjacent spawning habitat	Limited; equal in size to adjacent spawning habitat

Note: For simplicity, we defined only extremes. Nursery habitat applies to young northern pike that are older than yolk-sac fry and younger than 1 yr old (young-of-the-year). Depth of nursery habitat is detailed in Figs. 2 and 3. A guideline for determining nursery habitat is that the water is approximately 10 cm deep for every 10 mm of body length (more precisely 12) or for every week after peak spawning.

^aThis criterion describes North American populations because in Lake Windermere, England, pike spawn in 2.0–3.5 m of water over *Elodea*, *Myriophyllum*, and *Nitella* (Frost and Kipling 1967).

^bThe general rule of thumb for locating and determining nursery habitat, detailed above, can be used as a habitat variable. If so, its rank of relative importance is 8, and poorer conditions would involve either much shallower or deeper water.

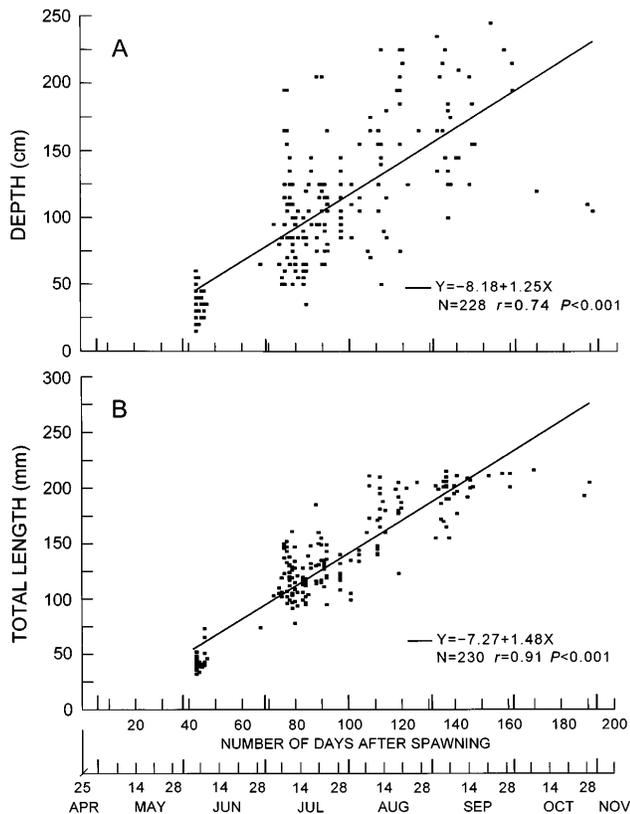
stages. When oxygen concentration falls below 30–35% air saturation, hatch of northern pike eggs and survival of embryos and larvae are greatly reduced (Siefert et al. 1973). Hydrogen sulphide increases when dissolved oxygen concentrations decrease. Hydrogen sulphide concentrations > 4–6 µg·L⁻¹ decrease growth and survival of sac fry (Adelman and Smith 1970). Hummocks and vegetative mats are optimal spawning substrate because they help keep the eggs suspended in better oxygenated water, away from anoxic conditions and elevated hydrogen sulphide in the organic sediments.

Northern pike embryos are sensitive to heavy siltation resulting from movement of organic sediment caused by excessive wave action and currents. Siltation of 1.0 m·day⁻¹ was associated with mortality exceeding 97% (Hassler 1970).

Nursery habitat

As is true for many species, nursery (young-of-the-year) requirements for northern pike are much less thoroughly studied than spawning habitat requirements. This is partly because young-of-the-year are often solitary, difficult to catch, require specialized sampling techniques or gear (e.g., electrofishing

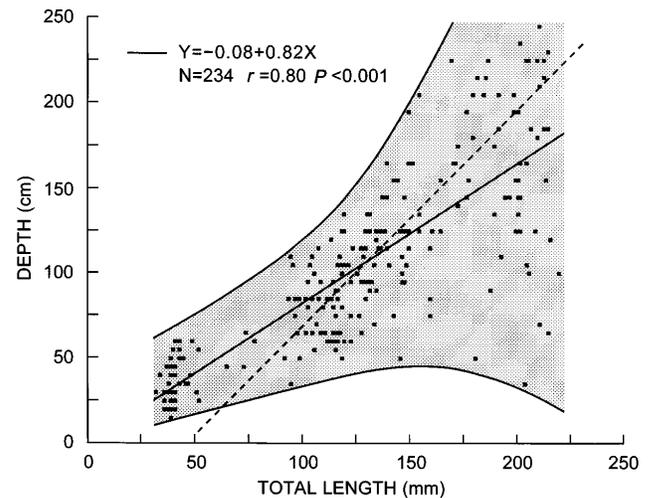
Fig. 2. Relations between depth at time of capture and total length and age of young-of-the-year northern pike. Relations between (A) depth and (B) total length are plotted on number of days and date after peak spawning, which during the study period occurred during the last week in April. Northern pike were caught in 1968 to 1971 in two shallow lakes (<3 m), Wickett and Smoky Hollow. Regressions, correlation coefficients, and probability levels are provided.



gear or Plexiglas traps; Casselman and Harvey 1973), and either are caught in low numbers or, if congregating, catches are much more variable when compared with older, larger life stages; this all affects predictability. Activities in the deeper, more extensive nursery habitats are less easily observed than those associated with spawning. It is difficult to study small fish in the natural environment, especially when they are not easily caught or handled. This lack of knowledge has led to the misconception that nursery habitat and requirements are probably less limiting and important than spawning habitat requirements.

Because young fish in the nursery environment grow rapidly and increase in size and activity, their physical habitat needs expand. As they disperse into deeper water, they are usually found in moderately dense vegetation. Presumably, this increased activity makes them more vulnerable to predation, so dense vegetative cover is important in providing them shelter, enhancing survival. Although woody debris and other structures can afford cover and are sometimes important, young northern pike prefer submerged vegetation with some emergent and floating vegetation interspersed. Such cover is especially critical. Johnson (1960) found that growth in tanks

Fig. 3. Relation between depth at which young-of-the-year northern pike were captured throughout the year by electrofishing and Plexiglas traps (Casselman and Harvey 1973) and total length. Regression equation (solid line), correlation coefficient, and probability level are provided. Broken line illustrates the predictive regression of body length on depth. Northern pike were caught from 1968 to 1971 in two shallow (<3 m) lakes, Wickett and Smoky Hollow. Shaded area and lighter curved lines of best fit delineate the extremes.

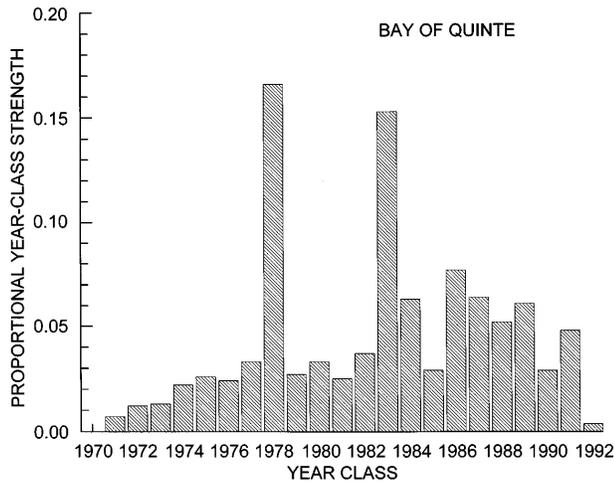


devoid of vegetation was erratic and considerably less than when northern pike were reared with vegetation.

The relationships between depth of the habitat, length, and age of young-of-the-year northern pike were examined with electrofishing and Plexiglas trap catches from 1968 to 1971 in two shallow lakes (< 2 m deep) on Manitoulin Island. Sampling effort was distributed uniformly over all depths throughout the open-water period. Depth and age (of young-of-the-year) were highly correlated (Fig. 2A). Since the fish grew during the period, length was linearly correlated with age over the size range studied (Fig. 2B). Hence, the relationship between water depth and size of northern pike during the first year was highly correlated (Fig. 3). This quantified the association between habitat depth and size and age of young northern pike, confirming that as fish grow, their preferred depth range increases. This relationship appears to be less significant in larger, older young-of-the-year; in late summer and early fall, large individuals appear to use a wider range of depths (Fig. 3). These quantitative results make it possible to devise practical criteria for describing depth of young-of-the-year nursery habitat, based on age and date. A general guideline for describing the habitat frequented by young northern pike during the first year is that the water is approximately 10 cm deep for every 10 mm of body length (more precisely 12) or for every week after peak spawning, at least until they reach 150 mm in length.

Anderson (1993) used field surveys and laboratory preference experiments to develop suitability indices for water depth, vegetation type, and density for young northern pike in their nursery habitat. He concluded that intermediate densities of vegetative cover were optimal and that young-of-the-year preferred a combination of submerged and emergent vegetation with densities ranging from 20 to 50%. Predator feeding

Fig. 4. Proportional year-class strength of northern pike from the Bay of Quinte and eastern Lake Ontario for a 22-yr period from 1971 to 1992.



efficiency is reduced in areas of dense cover (Cooper and Crowder 1979) and in habitat of increased complexity (Savino and Stein 1982). Anderson (1993) observed that young northern pike preferred *Myriophyllum* and *Potamogeton* over *Scirpus* and *Vallisneria*. Optimal predator efficiency and productivity occurred with intermediate plant densities, where preferred prey could be easily caught but prey populations were not decimated. This was also important for muskellunge (*Esox masquinongy*) (Craig and Black 1986).

Young northern pike in the upper Mississippi River were 10 times more abundant in emergent vegetation and 3 times more abundant in submergent vegetation than in areas that were unvegetated (Holland and Huston 1984). The authors concluded that this preference was related to cover and not to food. Young fish that are associated with deeper and less restrictive habitats grow more rapidly because they are more piscivorous than fish living at confined depths in channels (Mann and Beaumont 1990). In confined marshes and backwaters, the migration of young fish in fall is associated with decreased water temperature and, in some cases, reductions in dissolved oxygen concentration (Holland and Huston 1984; Derksen 1989).

We extended the system for classifying and ranking the physical requirements for spawning habitat to young-of-the-year nurseries (Table 1). We used field observations of young-of-the-year nursery habitats in 12 different lakes in Ontario and data from Anderson (1993). These emphasize the importance of the proximity of quality nursery habitat to spawning habitat and the extent and type of vegetative type and cover, which we estimate to be optimally 40–80%. These physical habitat conditions are most obvious on site inspection; they apply to the summer period, but proximity of habitats can be evaluated at other times of the year.

Optimum temperature for linear body growth of young-of-the-year northern pike was higher (22–23°C) (J.M. Casselman, unpublished data) than that of age 1 and older (19°C) (Casselman 1978) when the same fish were studied. Bevelhimer et al. (1985) observed that maximum growth of young northern pike in Ohio (24–25°C) was higher than that reported by Cassel-

Table 2. Correlation between mean monthly water temperature of the Bay of Quinte for the open-water period (March–December) and the logarithm of the proportional size of the year-class of northern pike from the Bay of Quinte and eastern Lake Ontario from 1971 to 1992.

Month	Temperature		<i>r</i>	<i>P</i>
	Mean	95% CI		
March	1.5	0.34	0.391	ns
April	6.7	0.89	0.226	ns
May	14.7	0.61	0.141	ns
June	20.4	0.48	0.255	ns
July	23.5	0.41	0.569	0.006
August	23.2	0.49	0.540	0.010
September	19.1	0.38	0.182	ns
October	12.2	0.52	0.219	ns
November	5.8	0.54	0.152	ns
December	1.4	0.26	0.497	0.019
March–December	12.8	0.29	0.483	0.023

Note: Daily water temperatures were from the Belleville, Ont., domestic water filtration plant. Probability values are provided. ns, not significant.

man. They attributed this apparent difference to adaptation resulting from 25 yr of selection in warm Ohio hatchery ponds; however, Bevelhimer et al. studied younger, smaller fish (young-of-the-year, total length (TL) range 125–210 mm, total weight (TW) mean 19.3 g) than did Casselman, who used much older, larger fish (second and third calendar years of life, TL range 281–466 mm, TW mean 340 g). So the results published for these two studies were not exactly comparable. When fish of the same age are compared (young-of-the-year), unpublished results reported above are more similar to those of Bevelhimer et al. (1985) (22–23 vs. 24–25°C); however, a difference exists, although slight, that may be attributed to high temperature adaptation. Fry have an optimum temperature for growth that is even higher (25.6°C; Hokanson et al. 1973). It is apparent that the optimum temperature for growth of northern pike decreases with age.

Small northern pike are more tolerant of oxygen depression than are larger individuals, and critical values are lower (Casselman and Harvey 1975). Casselman (1978) has reported summer mortalities of young-of-the-year resulting from oxygen depression because of prolonged respiration of dense vegetation on dull, calm days.

We examined 22 yr of data on relative year-class strength of 489 northern pike from the Bay of Quinte and eastern Lake Ontario to determine what environmental factors affect recruitment or survival. Fish were collected over a 14-yr period from 1980 to 1994 (fork length (FL) = 66.5 ± 0.9 cm, TW = 2.20 ± 0.10 kg, mean \pm 95% CI) in a routine indexing program conducted by Research and Assessment, Ontario Ministry of Natural Resources. Fish were captured in multimesh experimental gill nets and bottom trawls. Similar effort was used each year. Cleithra were used to assess age. Proportional strength of each of the 22 year-classes was measured by calculating the relative abundance of each year-class in each year of sampling, estimating their proportion by age, and averaging this proportion over the ages vulnerable to the sampling gear. The correlations between the mean monthly water temperature

Fig. 5. Relation between the logarithm of the proportional size of the year-class of northern pike and mean midsummer (July–August) water temperature in the Bay of Quinte and eastern Lake Ontario from 1971 to 1992. The polynomial equation, correlation coefficient, and probability level are provided. Years are indicated. Mean daily water temperature was measured in the Bay of Quinte at the Belleville, Ont., water filtration plant.

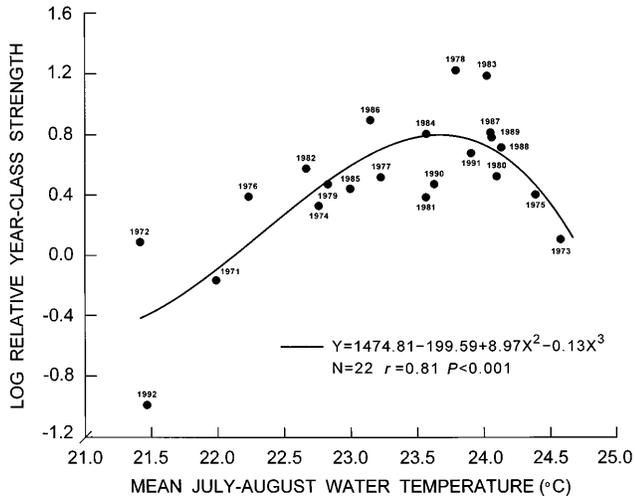
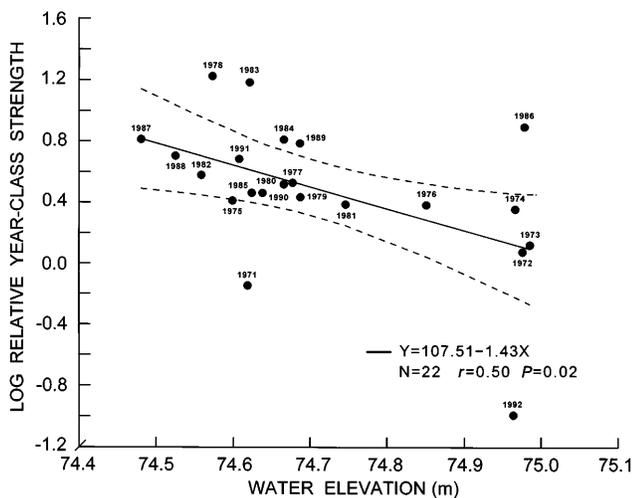


Fig. 6. Relation between the logarithm of the proportional size of the year-class of northern pike and mean late summer - early autumn (August–October) water elevation in the Bay of Quinte and eastern Lake Ontario from 1971 to 1992. Regression equation, correlation coefficient, and probability level are provided. The years are indicated, and the dashed curves delineate the 95% confidence limits. Water elevation was measured in eastern Lake Ontario at Oswego, N.Y.



and water elevation for the open-water period, March–December, were examined.

Two year-classes, 1978 and 1983, dominated during this period (Fig. 4). The 1978 year class appeared after a substantial winter mortality during two successive winters, 1976–1977 and 1977–1978, affected the fish community. There is evidence that the extreme strength of this year class

Table 3. Correlation between mean monthly change in water elevation (m) in eastern Lake Ontario and logarithm of the proportional size of the year-class of northern pike from the Bay of Quinte and eastern Lake Ontario for the open-water period (March–December) from 1971 to 1992.

Month	Elevation relative to open water mean (m)		r	P
	Mean	95% CI		
March	-0.11	0.09	0.114	ns
April	+0.10	0.09	0.105	ns
May	+0.25	0.09	-0.071	ns
June	+0.28	0.10	-0.118	ns
July	+0.21	0.09	-0.226	ns
August	+0.09	0.09	-0.423	0.050
September	-0.04	0.07	-0.534	0.011
October	-0.18	0.07	-0.453	0.034
November	-0.30	0.06	0.235	ns
December	-0.31	0.06	0.323	ns
March–December	0.00	0.06	-0.155	ns

Note: Water elevations were measured at Oswego, N.Y. Probability values are provided. ns, not significant.

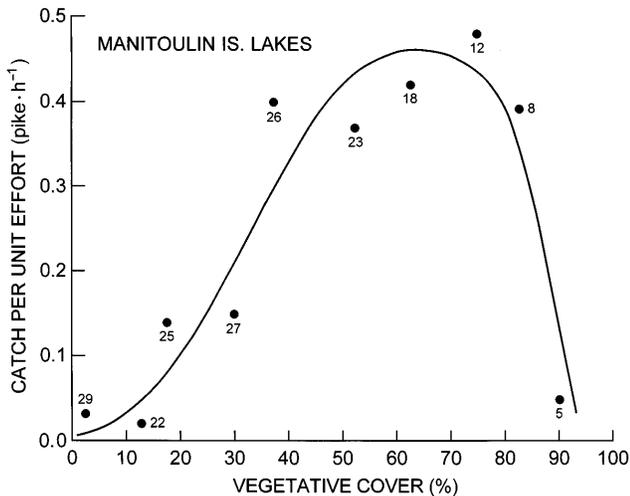
was related to the substantial reduction in the white perch (*Morone americana*) population (Minns and Hurley 1986). White perch are major predators on small and young fish. If there was predation by this species on northern pike, it would no doubt have occurred on young-of-the-year in the nursery habitat.

Relationships between year-class strength and water temperature were examined, using mean monthly temperature (Table 2). Overall, year-class strength was positively correlated with mean temperature of the open-water period ($P = 0.023$). The proportional size of the year-class was highly significantly correlated with the warmest months of the summer, July and August, when mean water temperature exceeded 23°C. The mean temperatures for these 2 months were averaged to illustrate the significance and the trend of the relationship ($P < 0.001$) (Fig. 5). The data were best fit by a curvilinear relationship that peaks between 23 and 24°C. The two strongest year classes, 1978 and 1983, were stronger than would be expected, given midsummer water temperatures in those years (Fig. 5). Since this relationship no doubt involves the first year of life, this temperature response coincides well with the growth of young-of-the-year northern pike. Maximum growth of young-of-the-year occurs at 22–23°C, whereas maximum recruitment occurs at a temperature that is only slightly higher (23–24°C).

An unexpected positive correlation was also obtained with December water temperatures (Table 2). The correlations with midsummer temperatures appear to implicate nursery rather than spawning conditions, because spring spawning time was not involved. This correlation may be related to increased growth and associated survival of young fish. The direct effect of temperature during the first year of life appears to be rather universally important (Le Cren 1987; Fortin et al. 1982). Increased summer temperature could also affect survival by increasing vegetative growth and cover.

Year-class strength and mean annual water elevation during

Fig. 7. Relation between catch of northern pike per unit of gill-net effort and percent vegetative cover in Manitoulin Island lakes Wickett and Smoky Hollow, in midsummer 1968–1971. Catch is expressed as the number of northern pike caught per hour in a 50-m experimental green multifilament multimesh gill net set for 24 h in various densities of vegetative cover in the two shallow (<3 m) lakes. The number of gill-net sets ($N = 195$) is indicated with each data point. Relation fitted by running averages. Vegetative cover was measured at two randomly chosen locations within 50 m of the gill net and was averaged.



the open-water period were not correlated (Table 3). Year-class strength was, however, negatively correlated with elevation for those open-water months when water levels were decreasing (August–October) from late summer to early autumn ($P = 0.02$) (Fig. 6). It is apparent that recruitment was not related to spring water elevations at spawning time. Correlations with late summer and autumn implicate effects on young northern pike in the nursery habitat. It is not readily apparent how low water elevations in late summer would influence year-class strength of northern pike, especially when the relationship was negative. These correlations are not spurious, because they are strong and show a gradually changing monthly trend (Table 3). Lower water levels in late summer and early autumn could force young fish to move offshore earlier, reducing the possibility of fall and early winter entrapment in degraded shallow backwaters (Derksen 1989). Lower water levels in late summer and early fall could increase the amount of cover present per volume of habitat, decreasing susceptibility of the fish to fall predation by other species. Decreasing water levels could also concentrate small prey species, improving growth and survival.

Juvenile and adult habitat

Adult northern pike are found in relatively shallow water in summer, usually < 4 m but sometimes as deep as 12 m, that is relatively clear, cool, and well oxygenated ($> 3 \text{ mg} \cdot \text{L}^{-1}$) with some vegetative cover. Habitat and environmental requirements of juvenile (yearling to maturity) and adult northern pike are relatively well known (see review, Inskip 1982); however, their association with vegetative habitat needs to be better quantified.

To better understand the association between vegetative

cover and northern pike, we analyze data from multiple experimental multimesh gill nets set in midsummer during 1968–1971 in two shallow (< 3 m) lakes, Smoky Hollow and Wickett, on Manitoulin Island. Throughout the open-water period in the two lakes, there was a range of densities of aquatic macrophytes. Plants were primarily species of *Potamogeton*, including *P. crispus*, *Ceratophyllum demersum*, and *Elodea canadensis*. The catches of juvenile and adult northern pike were low at low macrophyte densities, highest at intermediate densities (35–80%) and low in very dense, virtually continuous vegetative mats (Fig. 7). The larger pike were caught at low vegetation densities, and the smallest were taken in the densest vegetation. Randall et al. (1996) conducted littoral-zone electrofishing surveys in the lower Great Lakes and concluded from general categories that northern pike were most abundant when vegetation was moderately dense (31–70%), results that are similar to the peak abundance reported here. These independent results are similar to those of Grimm and Backx (1990, Table 5), who measured vegetative cover and biomass in six different water bodies in the Netherlands. Our quantitative results support Grimm and Backx's (1990) observation that northern pike populations require at least 30% vegetative cover.

As northern pike mature, their vegetative associations change from emergent for fry to emergent, floating, and submergent for young to submergent for adult. Northern pike are visual predators and are primarily active during the day but usually feed crepuscularly. Their "ambush" predation style requires cover, and aquatic macrophytes are preferred. Vegetation provides a refuge from predation for the young and cover to conceal feeding fish of all sizes (Inskip 1982).

Northern pike generally prefer shallow vegetated areas (Diana et al. 1977; Inskip 1982; Chapman and Mackay 1984a; Cook and Bergersen 1988). For a large piscivore such as northern pike, however, there is likely an advantage to exhibiting some versatility in habitat selection, depending on availability of prey and other factors. Chapman and Mackay (1984b) demonstrated that northern pike distribution in a moderate-sized lake in Alberta was not necessarily strongly tied to shallow vegetated areas. Although fish were associated with macrophytes more often than would be predicted if they were choosing habitats randomly, northern pike were versatile in habitat selection.

The selection and use of vegetated areas depends on the size of fish. Chapman and Mackay (1984a) found that large northern pike were often observed at the macrophyte - open-water interface, while small ones were rarely seen there. Grimm (1981, in Chapman and Mackay 1984b) found that large northern pike used open-water and vegetated areas, while smaller northern pike were restricted to more heavily vegetated areas. Chapman and Mackay (1984a) found that large (> 25 cm) and small (< 25 cm) northern pike differed significantly in their selection of depth but not in their selection of vegetation type. Large fish were found in deep, unvegetated waters more frequently than were small fish. Cook and Bergersen (1988) found that female northern pike occupied deeper habitats than did males of the same size.

Very dense vegetative cover appears to be suboptimal, especially for larger northern pike (Fig. 7). The boundary zone between stands of aquatic vegetation and open water may pro-

Table 4. Examples of recent northern pike habitat restoration projects in the Great Lakes Basin.

Lake	Site	Diagnosis	Objectives	Remediation	Evaluation	References
Ontario	Bay of Quinte Pine Point	Overmature <i>Typha</i> marsh	Improved spawning and nursery for northern pike	Dredged a complex of 480 m of channels 1.2–2.5 m deep, 10–15 m wide (1993)	No assessment of northern pike spawning (1993); YOY northern pike found in summer (1993)	1,2,3
	Sawguin Creek	Overmature <i>Typha</i> marsh	Improved spawning and nursery habitat	Dredged a complex of 380 m of channels, removing the entire root mass, ensuring 1-m depth; channel edge slope 1.5:1 (1992)	No assessment of northern pike spawning (1993); YOY northern pike found in summer in 1994, YOY northern pike found in dredged but not in natural channels; channel depth inadequate to maintain DO and temperature requirements	1,2,3
	Toronto Shoreline Mimico Creek	Loss of wetlands	Wetland creation	Planted species of emergent vegetation using triangular log cribs, fibre pots, and individual plantings; installed fencing to exclude carp and minimize disturbance	Slow to establish due to continuing hydrological effects on sediment	4,5,6
	Bluffers Park	Loss of wetlands	Wetland creation	As above	Washed out due to wave action from lake; failed to address stormwater flow and wave action effects	4,5,6
	Toronto Islands	Loss of wetlands	Create northern pike spawning	Three cuts in barrier berm to allow fish passage; hummocks created and seeded with soft-stem vegetation (1992)	Northern pike observed in 1994; no YOY documented; YOY likely dispersed rapidly to lagoon system as temperature and DO became suboptimal	4,7,8
	Hamilton Harbour	Declines in water levels limit recruitment; lack of vegetation	Maintain water levels until fry dispersed; reestablish vegetation	Installed water control structures and excluded carp from some ponds (1994)	Where carp excluded, transparency increased and rooted vegetation established; 6-yr monitoring program planned	9
Superior	Thunder Bay Neebing– McIntyre Floodway	Habitat destroyed by filling	Recreate spawning, nursery, adult habitat	Excavated four 20-m embayments into sides of floodway; planted banks with willow (1991)	More fish in channels than in floodway; not known if actual increase in production or only attraction of fish (1992, 1993)	10
	McVicar Creek	Wetland lost; failed to reestablish due to wave action	Create shelter from wave action	Created 175-m rock island (1992)	Newly established vegetation at most sample sites; no northern pike documented in 1993	10

Table 4 (concluded).

Lake	Site	Diagnosis	Objectives	Remediation	Evaluation	References
	McKellar River	Wetland lost	Reestablish wetland	Created two 1-ha lagoons by excavating the riverbank; planted trees, shoreline cover and macrophytes (1994)	Extensive use by northern pike in 1995	10
Inland	Wilcox Lake	Wetland loss and physical exclusion of spawners; recruitment failure	Create new wetland in senescent marsh	Dredged a 50 × 40 m grid of channels 2–4 m wide; dredging spoils used to elevate a grid of similar mounds; seeded (1986)	Used by spawning fish; egg deposition and juvenile production estimated; after 2–3 yr natural succession, slumping channel banks and sedimentation from wave action had reduced available habitat	11, 6
	Creek between Butterfly and Minnitaki lakes	Altered nursery habitat with dredging spoils from channelizing length of waterway	Reduce nursery habitat alteration and stabilize clay spoil spit	Cut spoil spit and create spawning hummocks	Hummocks were built and aerially seeded, reducing erosion; northern pike use was not assessed	12

Note: The reasons for the restoration program, the specific objectives, the remedial action, and evaluation of the outcome are provided. The references for the table are numeric and are as follows: (1) Anonymous 1993a; (2) K. Hartley, Moira River Conservation Authority, R.R. 2, Belleville, Ont., personal communication; (3) L. Cope, OMNR, 1 Richmond Boulevard, Napanee, Ont., personal communication; (4) Anonymous 1993b; (5) Anonymous 1993c; (6) I. Buccanan, OMNR, 10401 Dufferin Street, Maple, Ont., personal communication; (7) Anonymous 1992; (8) R. Strus, Metropolitan Toronto Region Conservation Authority, c/o OMNR, 10401 Dufferin Street, Maple, Ont., personal communication; (9) K. Minns, Department of Fisheries and Oceans, P.O. Box 5050, Burlington, Ont., personal communication; (10) E. Iwachewski, OMNR, P.O. Box 5000, Thunder Bay, Ont., personal communication; (11) Reid 1990; (12) F. Cole, OMNR, P.O. Box 309, Sioux Lookout, Ont., personal communication.

vide important edge, affording ambush hunting sites (Reighard 1915, in Inskip 1982; Chapman and Mackay 1984a).

Changes to the amount of vegetation affect distribution. Cook and Bergersen (1988) found that northern pike abundance varies in response to changes in macrophyte density and distribution. In a year when macrophyte growth increased near shore, fish frequented those areas more than in the previous year. Cook and Bergersen noted that with an increase in macrophyte growth, fish remained in shallower water, closer to shore. However, Holland and Huston (1984) found that juvenile northern pike avoided very dense macrophyte beds, and they speculated that low oxygen levels associated with these vegetative mats may have caused that behaviour. In winter, northern pike tend to occupy deeper habitats as ice cover and die-back of vegetation change the inshore habitat and oxygen depletion commences (Casselmann 1978; Cook and Bergersen 1988; Derksen 1989).

Macrophyte density influences the size structure of northern pike populations. Since large fish require more open water and vegetation – open-water interface, lakes with dense vegetation are usually dominated by smaller northern pike (Grimm and Backx 1990).

Northern pike exhibit a preference for type and density of vegetation. In Eleven Mile Reservoir, Colorado, Cook and Bergersen (1988) found the most abundant and widespread species to be *Ceratophyllum demersum*, *Elodea canadensis*, *Potamogeton* spp., and *Chara* spp. Males preferred areas of

Potamogeton spp. in combination with other macrophytes, while females preferred stands of *Potamogeton* spp., *Elodea canadensis*, or *Ceratophyllum demersum*.

Temperature is an important environmental factor affecting this cool-water fish (Casselmann 1978). The physiological growth optimum for yearlings to adults fed ad libitum was 19°C for biomass and 21°C for length. When fish 2 and 3 yr old from the laboratory and from studies in the natural environment were compared, the optimum temperature for linear growth for laboratory fish was 20.9 ± 0.1°C and under natural conditions, 19.8 ± 0.6°C (Casselmann 1978). This slight difference was attributed to available food and feeding rate, which directly affect optimum temperature for growth.

Laboratory studies indicate that the final preferred temperature of northern pike is slightly higher (2 or 3°C) than the optimum for growth (McCauley and Casselmann 1981). Headrick and Carline (1993) used temperature-sensitive radio transmitters on adult northern pike in two southern Ohio impoundments and showed that, when water temperature exceeded 20°C, fish sought a cooler average temperature but that they sought significantly cooler temperatures only when the surface exceeded 25°C. However, once the surface temperature reached 25°C, the coolest available water with > 3 mg·L⁻¹ dissolved oxygen was 25°C. Adult fish lost weight during this period of habitat constriction.

Juvenile and adult northern pike can tolerate a broad range of temperatures. The upper incipient lethal of subadult north-

ern pike was 29.4°C in the laboratory (Casselman 1978) and over 30°C in the natural environment (Ridenhour 1957). The lower incipient lethal temperature has not been measured. Casselman (1978) observed, however, that northern pike showed no apparent stress when subjected to temperatures as low as 0.1°C prior to freeze-up in shallow lakes.

Water transparency can affect body condition of northern pike (Craig and Babaluk 1989). The authors showed that weight of a northern pike was positively related to Secchi depth. With every increase in Secchi depth of 1 m over the 3-m range, the fish's weight increased 6%. Craig and Babaluk concluded that high turbidity during the open-water period in prairie lakes in Canada reduced the ability of northern pike to feed.

Food consumption, conversion efficiency, and growth rate are maximal when oxygen saturation is 100%; any decrease in oxygen concentration directly affects growth (Adelman and Smith 1977). Feeding decreases markedly when oxygen concentration falls to approximately 2–3 mg·L⁻¹ (20–30% air saturation) and ceases below 2 mg·L⁻¹.

Under the ice, the concentration of dissolved oxygen affects activity and vertical distribution of northern pike. In shallow, eutrophic water bodies, as the oxygen is progressively depleted during winter from the substrate to the ice-water interface, the fish move increasingly higher in the water column to the bottom of the ice sheet (Casselman 1978). This behaviour has been studied in the natural environment (Magnuson and Karlen 1970) and under simulated winter conditions in the laboratory (Petrosky and Magnuson 1973). When oxygen concentration decreased to approximately 2–3 mg·L⁻¹, northern pike approach the ice-water interface. At oxygen concentrations below that level, there was a noticeable decrease in activity (Casselman 1978). In winter under the ice, northern pike stop feeding when oxygen concentration reaches approximately 2 mg·L⁻¹. When oxygen concentrations are low (< 4 mg·L⁻¹), some fish actively seek higher levels. From observations in the natural environment by Headrick and Carline (1993) on restricted summer habitat and by Casselman (1978) on restricted winter habitat, adult northern pike attempt to avoid oxygen concentrations of < 3–4 mg·L⁻¹. Johnson and Moyle (1969) observed that northern pike were attracted to an aerated discharge when oxygen concentrations under the ice were < 1 mg·L⁻¹. However, under winter conditions, northern pike were extremely inactive at oxygen concentrations below 0.7 mg·L⁻¹ (Casselman 1978). Casselman captured live northern pike in stationary gear at oxygen concentrations as low as 0.04 mg·L⁻¹ (0.3% air saturation).

Depending upon temperature, the upper range of the lower incipient lethal oxygen concentration is 0.5–1.5 mg·L⁻¹ (Casselman 1978). Winterkills of northern pike in the natural environment resulting from critically low winter oxygen levels are selective (Casselman and Harvey 1975; Grimm 1983). The fish that died were usually significantly larger, older, and faster growing than the ones that survived. As well, significantly more females than males died.

It is apparent that vegetative cover, temperature, oxygen, water transparency, and light intensity interact to affect the physiology of the fish. These must be taken into consideration when examining and restoring northern pike habitat, and many of the restoration projects that have been conducted, especially

those associated with spawning, have taken these specific requirements into consideration.

Habitat restoration in the Great Lakes Basin

Restoration of northern pike populations through habitat manipulation has usually focused on spawning habitat. The use of dikes or low-head dams in wetlands, marshlands, and swamps to control water level to create and manage northern pike spawning marshes is well established (Franklin and Smith 1963; Forney 1968; Kleinert 1970; Williams and Jacob 1971; Fago 1977). Such managed marshes can increase recruitment over that from unmanaged spawning areas and can compensate, at least in part, for historical losses of wetlands (Kleinert 1970).

In the Great Lakes Basin, recent habitat restoration projects for northern pike have focused on spawning and nursery habitat but generally have not been of the "managed marsh" type (Table 4). We summarize, describe, and evaluate some examples of recent restoration projects that have been conducted in the Great Lakes Basin (Table 4). These projects involve attempts to either improve or create existing or new habitat or wetlands where historical ones have been lost or altered. Habitat improvement has been attempted by cutting channels in senescent *Typha* marshes, controlling water levels, and excluding carp to allow reestablishment of vegetation (e.g., Bay of Quinte, Hamilton Harbour; Table 4). Habitat creation projects have involved planting emergent vegetation, using a variety of planting techniques, excluding carp from the new sites, reclaiming a trout pond by allowing access for northern pike, excavating upland channels, altering dredging spoils, and changing site hydrology (e.g., Toronto shoreline, Lake Superior, Wilcox Lake, Butterfly and Minnitaki lakes; Table 4).

Assessing the restoration of northern pike habitat

Successful habitat restoration efforts must include clear objectives, measurable criteria, and a well-planned assessment program. The latter was often lacking. For northern pike habitat restoration projects, the specific habitat requirements that are limiting must be identified and restoration must focus on meeting those requirements. Clearly, planning for such projects must take into account all factors contributing to the quality and quantity of northern pike habitat, including location and size of the habitat, water levels, site elevation, and morphology, as well as accessibility. New habitats should be constructed not only with the species' requirements in mind but also with a view to facilitating future assessment (e.g., ease of observing use and enumerating spawners and juveniles; Reid 1990).

Most of the northern pike habitat projects reviewed target both spawning and nursery habitat (Table 4). The distinction between the habitat requirements for each of those life stages has not been clearly defined in the planning nor has a rigorous attempt been made to determine factors limiting production. In most cases, the objectives and criteria for success of these projects have not been strictly defined. Similarly, most assessment efforts have not strictly matched measurement require-

ments (what to measure and at what scale) with stated objectives.

As a result, we have found it difficult to evaluate whether these projects resulted in improved habitat for northern pike and ultimately in increased production. It is surprising that habitat restoration for this species has not been more quantitatively evaluated, since habitat requirements are much better defined for this species than for most. In several instances, failure to plan for all factors influencing habitat dynamics at the site compromised the potential for success. Often this was because of factors operating at different spatial or temporal scales. For example, larger-scale hydrological effects must be addressed in advance if new patterns of sedimentation and vegetation distribution are desired. Natural changes of the site over the long term must also be considered; several projects (Table 4) suffered from deterioration of the site over time, particularly the settling of bank slopes (e.g., Bay of Quinte, Wilcox Lake), sedimentation (Mimico Creek), movement of dislocated marsh into new channels (Bay of Quinte), and excessive vegetation growth (Wilcox Lake, Bay of Quinte).

These problems point to three important restoration requirements. First, some sites may require a continuous process of rejuvenation to ensure suitability for northern pike and other species. More importantly, attempts to restore habitat at sites with dense, pure stands of cattail, for example, may need to be more aggressive than at first appears. The natural succession of such sites, coupled with the settling of newly disturbed sediments, may require that channels be initially constructed deeper and wider than "optimum" for northern pike.

Second, the case studies described here (Table 4) point to the need to consider all factors that might influence the site. Failure to consider and plan for the full range of natural and human factors, particularly the hydrology of the area, may jeopardize the success of any project. In this sense, project plans must examine the requirements at a variety of physical and temporal scales to understand the dynamics of the site before and after restoration.

Third, restoration projects require thorough assessment and documentation so that the contribution can be evaluated, preferably quantitatively. This is necessary not only to evaluate and document restoration success but also to document unforeseen outcomes so that future attempts and projects can benefit from the experience, regardless of the results. Long-term followup would be extremely useful to completely evaluate the extent and duration of the contribution. It is also apparent that precise and detailed knowledge now exists to evaluate habitat requirements of northern pike. It follows that precise, quantitative data must be collected when assessing habitat if interpretations and predictions are to be accurate.

When designing and implementing habitat restoration projects for northern pike, it is important to realize that habitat changes, either predicted or unpredicted, could affect, displace, or even eliminate other species.

Important habitat requirements and critical factors

Considering habitats used by northern pike, spawning has received the greatest amount of attention and is best understood. Physical habitat features have been reconstructed and altered in restoration programs with moderate success. Manipulation

of managed northern pike marshes has reached such a level that use and production can exceed those of natural conditions (Williams and Jacobs 1971). Indeed, it is possible to convert dry ground to wetlands that northern pike will use for spawning and nursery habitat (Reid 1990). Other artificial habitats have been created successfully. Gillet (1989) created artificial floating substrates that attracted spawning northern pike. Egg deposition was high, exceeding 1000-m^{-2} , on structures that were anchored away from shore. The creation of artificial habitat must be carefully evaluated because, although it may increase the presence of one life stage, this may not result in an overall increase in productivity and may also displace other ecologically important species not currently considered to be important or to have human-valued priority.

Year-class strength of northern pike over the past 22 yr in the Bay of Quinte has not been correlated with spring water elevations, as has frequently been observed for other populations (e.g., Johnson 1957; Masse et al. 1993). Even though the fluctuations were relatively extreme over this period, spawning and recruitment were less important in influencing year-class strength than were summer conditions associated with young northern pike and nursery habitat. Also, the strength of the 1978 and 1983 year-classes indicates that adequate spawning and reproductive potential existed in the northern pike population of the Bay of Quinte and eastern Lake Ontario even though numbers were at record low levels (J.M. Casselman, unpublished data).

These observations support our contention that, contrary to general belief, spawning habitat requirements are usually less critical or limiting than heretofore considered. Furthermore, these requirements are relatively well understood, and spawning habitat is more easily manipulated and restored. Minns et al. (1996) reached a similar conclusion through simulation modelling. They contended that fry and juvenile-adult habitat supplies are more limiting than spawning habitat. There is no doubt that since European settlement, the extensive loss of marshes and wetlands along the shores of the Great Lakes (Whillans 1979, 1982; Dodge and Kavetsky 1994), especially Lake Ontario, has reduced and, in some situations, virtually eliminated northern pike recruitment. If northern pike are to become abundant again in Great Lakes embayments, then this trend must be reversed. Although restoration of spawning habitat is important, we consider that it is not the major factor limiting rehabilitation of northern pike stocks in the Great Lakes but that reestablishment of macrophyte habitat and cover is more important.

Macrophyte cover is an important feature of nursery habitat that not only reduces susceptibility to predation but also provides cover for important prey species and for young pike to lie in wait for prey. We conclude that optimal vegetative densities for nursery habitat range from 40 to 90%. Turbidity and eutrophication can reduce transparency and affect feeding, but more importantly and critically, can also reduce light penetration, inhibiting macrophyte growth. This is important not only for young-of-the-year pike but also for juveniles and adults. Loss of cover can expose young northern pike to predation; our study of year-class strength provides circumstantial evidence that predators in the nursery habitat, such as white perch, can affect survival of young-of-the-year survival and yearling recruitment. Since year-class strength was correlated with temperature, especially in midsummer, temperature may

directly affect growth and enhance survival of young northern pike, by increasing vegetative cover. Nevertheless, this 22-yr case history study of year-class strength demonstrates the importance of midsummer nursery habitat conditions on northern pike production.

Catch and abundance of adult northern pike was related to the extent of macrophyte cover. Larger individuals frequent lower densities; smaller individuals, higher densities. Optimal juvenile and adult habitat requires vegetative cover that ranges from 35 to 80% (Fig. 7). This agrees with Grimm's (1989) observation that a water body must contain more than 25% submerged macrophytes for a northern pike dominated fish community to exist.

Abundance of vegetation is inversely related to turbidity, eutrophication, and algal production. In recent years, macrophyte production on the south shore of Lake Ontario has increased in one location (Makarewicz and Dilcher 1988). This coincided with a significant decrease in turbidity from the late 1970s to the early 1980s. Makarewicz and Dilcher concluded that the reestablishment of macrophytes was probably associated with phosphorus-abatement programs in Lake Ontario. Decreased turbidity allowed increased light penetration and macrophyte resurgence. With increased vegetative cover, northern pike feeding would be enhanced and their condition factor would improve. Macrophyte biomass and diversity were greater in the large bays of Lake Ontario (e.g., Bay of Quinte) prior to anthropogenic loading of phosphorus (Bristow et al. 1977; Warwick 1980). There is no doubt that cultural eutrophication in the mid-1950s caused reduced light penetration, decreasing and virtually eliminating vegetative cover, greatly reducing northern pike habitat and abundance (e.g., Bay of Quinte; Hurley and Christie 1977). Jagtman et al. (1990) demonstrated that eutrophication can cause loss of littoral-zone vegetation with the disappearance of northern pike habitat. From data from the late 1980s, Loftus et al. (1992) estimated that 34.7% of the Bay of Quinte supported submerged macrophytes and that Remedial Action Plan options (Hartig 1993) would increase average coverage by only 11%. However, from the relationship between catch and vegetative cover (Fig. 7), this change in vegetative cover could increase northern pike abundance by an additional 35%. It is apparent that if northern pike abundance is to be increased in the Great Lakes Basin, water transparency and macrophyte cover must be improved.

Climate warming could increase available nearshore habitat in the Great Lakes for cool-water fish (Meisner et al. 1987) such as northern pike but would make shallow embayments less optimal as juvenile and adult habitat, although probably more optimal as nursery habitat. If increased temperature causes increased vegetative growth and if macrophytes expand, northern pike abundance will do the same. If zebra mussel (*Dreissena polymorpha*) expansion in the inshore waters and embayments in the lower Great Lakes increases water transparency and leads to more macrophyte cover, more optimal nursery and juvenile-adult habitat will be restored and northern pike production improved. However, increased light penetration could increase water temperatures, having obvious effects on growth and production. An increase in macrophytes would probably result in increased organic degradation and associated biological oxygen demand, and in severe winters, with thickened ice cover, critical oxygen depressions could occur and become locally severe in confined embayments.

This could result in selective winter mortalities (Casselman and Harvey 1975) of northern pike and other species. Increased macrophyte cover would not only increase northern pike abundance but could also make it more variable.

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