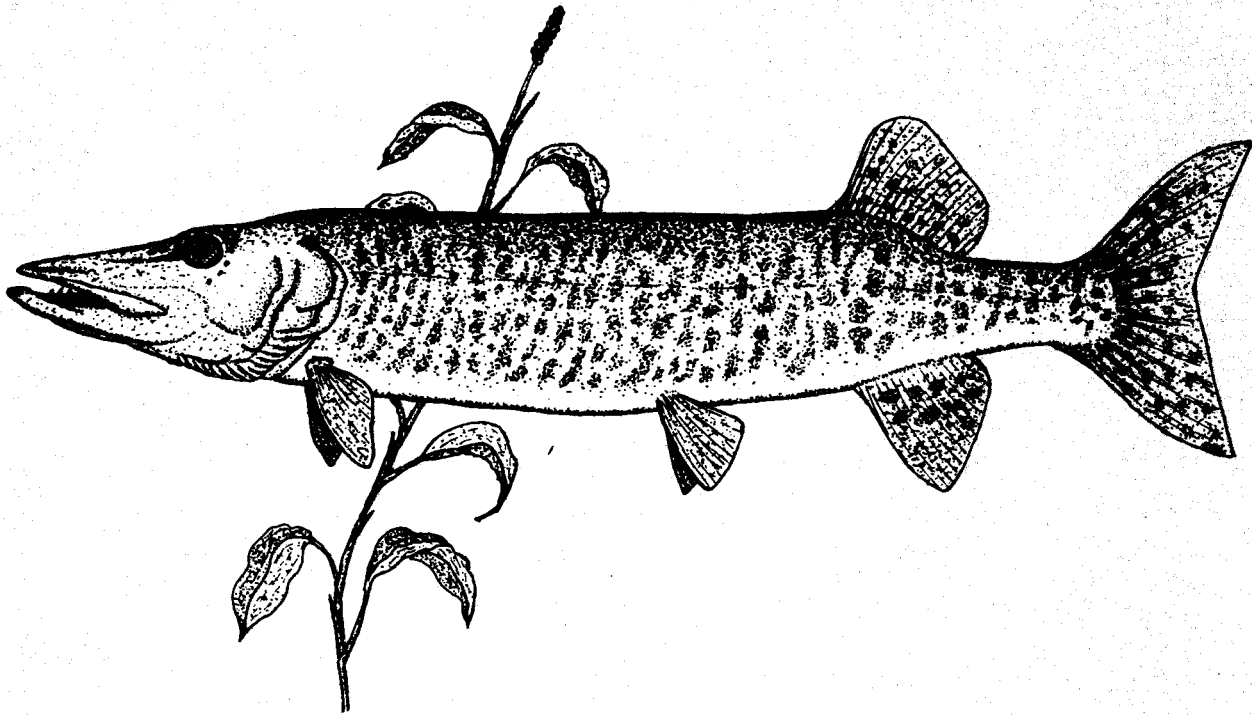


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HABITAT SUITABILITY INDEX MODELS: MUSKELLUNGE



Fish and Wildlife Service

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HABITAT SUITABILITY INDEX MODELS: MUSKELLUNGE

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PREFACE

This document is part of the Habitat Suitability Index (HSI) model series [Biological Report 82(10)], which provides habitat information useful for impact assessment and habitat management. Several types of habitat information are provided. The Habitat Use Information section is largely constrained to those data that can be used to derive quantitative relationships between key environmental variables and habitat suitability. This information provides the foundation for the HSI model and may be useful in the development of other models more appropriate to specific assessment or evaluation needs.

The HSI Model section documents the habitat model and includes information pertinent to its application. The model synthesizes the habitat use information into a framework appropriate for field application and is scaled to produce an index value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). The HSI Model section includes information about the geographic range and seasonal application of the model, its current verification status, and a list of the model variables with recommended measurement techniques for each variable.

The model is a formalized synthesis of biological and habitat information published in the scientific literature and may include unpublished information reflecting the opinions of identified experts. Habitat information about wildlife species frequently is represented by scattered data sets collected during different seasons and years and from different sites throughout the range of a species. The model presents this broad data base in a formal, logical, and simplified manner. The assumptions necessary for organizing and synthesizing the species-habitat information into the model are discussed. The model should be regarded as a hypothesis of species-habitat relationships and not as a statement of proven cause and effect relationships. The model may have merit in planning wildlife habitat research studies about a species, as well as in providing an estimate of the relative suitability of habitat for that species. User feedback concerning model improvements and other suggestions that may increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning are encouraged. Please send suggestions to:

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MUSKELLUNGE (Esox masquinongy Mitchell)

HABITAT USE INFORMATION

General

The native range of the muskellunge (Esox masquinongy) was restricted to the fresh waters of eastern North America. Its range extends south from Quebec through western Vermont, south to Tennessee but west of the Appalachian mountains. From Tennessee, the range extends north into the Great Lakes States and extreme southeastern Manitoba, excluding the main stem of the Mississippi River (Scott and Crossman 1973; Crossman 1978). Muskellunge have been introduced in recent years into many States, including North and South Dakota, Nebraska, Texas, and California.

The muskellunge was recognized as a distinct species relatively late, and its nomenclature is varied and confused (Crossman 1986). Currently, only one species of muskellunge (E. masquinongy) is recognized, with a variety of strains (Crossman 1986; Koppelman and Philipp 1986). Until recently, it was thought that there were three subspecies of muskellunge found across its native range (Scott and Crossman 1973; Eddy and Underhill 1976; Smith 1979). These three subspecies were thought to be separated geographically by major drainages (Trautman 1981) and, to some degree, by color pattern. The subspecies were thought to be separated as follows: E. masquinongy masquinongy in the Great Lakes drainage, with a spotted color pattern; E. masquinongy ohioensis in the Ohio River drainage, frequently with a barred or diffuse spot and blotched pattern; E. masquinongy immaculatus (the northern muskellunge) in Minnesota, Wisconsin, and northwestern Ontario, often without prominent bars or spotted patterns. Although three subspecies were recognized, Seaborne (1937) reported that all three patterns could be found in the same habitat.

Muskellunge were once plentiful enough to be commercially fished in the late 1800's and early 1900's (Porter 1977; Crossman 1986). By the late 1800's, the muskellunge was becoming a prized trophy fish (Crossman 1986). Muskellunge are treasured for their fighting ability and large size, which may be in excess of 31 kg (Crossman and Goodchild 1978). Anglers that pursue this fish are often purists and will fish for days and even years to catch one fish (Eddy and Underhill 1976).

Native populations of muskellunge are seldom abundant in any of the lakes in which they occur (Eddy and Underhill 1976). Throughout the species' range, native populations of muskellunge are declining (Dombeck 1986; Hanson et al. 1986a). Many of these lakes, such as Lac Court Oreilles, Wisconsin, are being

supplementally stocked with muskellunge to maintain higher standing crops (Johnson 1981). Populations in Tennessee have declined in abundance due to pollution, destruction of habitat, and introductions of other highly competitive species (Riddle 1976). Poor reproductive success and loss of reproductive habitat also are suspected in the decrease of muskellunge populations (Craig and Black 1986; Dombeck 1986; Hanson et al. 1986a). Northern pike introductions also are suspected of reducing native muskellunge populations (Dombeck et al. 1986; Inskip 1986). Overharvest and habitat alteration may cause declines in muskellunge populations (Bimber and Nicholson 1981).

Age, Growth, and Food

The age of the muskellunge is often difficult to determine using scales (Johnson 1971; Hess and Heartwell 1978). In addition, for old or slow-growing muskellunge the aging of scales may be invalid (Casselman 1983). The cleithrum (a pectoral girdle bone) is the best hard part for aging large esocids (Casselman 1974, 1979; Casselman and Crossman 1986). Muskellunge are a long-lived species; individuals frequently live to an age of 15 years, with the oldest individuals living up to 30 years (Casselman and Crossman 1986).

Muskellunge densities throughout the species' range are composed of very few fish per hectare. In Kentucky streams, the standing crop of all muskellunge was 2.5 fish/ha (Brewer 1960). A slow-growing population of muskellunge in Nogies Creek, Ontario, was found to support 10-12.5 fish/ha (Crossman 1956; Muir 1963). Kempinger (1971) reported the standing crop of muskellunge in Escanaba Lake, Wisconsin, to be 0.75 fish/ha. Standing crop of age 2 and older muskellunge for Escanaba Lake, Wisconsin, from 1956-1981, averaged 0.5 fish/ha (Hoff and Serns 1986). Hanson (1986) examined eight northern Wisconsin lakes and found legal-sized muskellunge to have a mean density of 0.83 fish/ha; the range was 0.23-1.53 fish/ha.

Growth of muskellunge is highly variable from one location to another and appears to be controlled by the availability of prey fishes (Crossman 1956; Scott and Crossman 1973). Muskellunge growth will range from 180-460 mm in the first year of life (Oehmcke et al. 1965); however, under optimum conditions in rearing ponds they may reach a length of 300 mm in only 4 months (Eddy and Underhill 1976). Under natural conditions, muskellunge are approximately 153 mm at 10 weeks of age and 254-305 mm by November of the first year (Scott and Crossman 1973). Schloemer (1936), however, reported muskellunge in Wisconsin to be only 178-mm SL (standard length) at the end of their first year of growth.

Many States and Provinces have set a 762-mm (30-inch) TL (total length) minimum size limit as the legal size for the creel (Ragan et al. 1986). The number of years required for a muskellunge to reach this size varies greatly with location, sex, and forage. Muskellunge attained legal size (762 mm) at an estimated age of 5+ in northern Wisconsin lakes, but this varied greatly among lakes (Hanson 1986). In Wisconsin, Johnson (1967b) reported that muskellunge reached 762 mm in 4-5 years, whereas Oehmcke (1969) reported growth to legal size in 3-5 years. Johnson (1971) reported that there are some populations in Wisconsin that might take 8-9 years to reach legal size.

Canadian muskellunge usually reach legal size in 5 years, but this may vary from 4-7 years (Hess and Heartwell 1978). Muir (1960) found that wild muskellunge required 7 years to reach 762 mm, whereas stocked muskellunge required 9 years in Nogies Creek Sanctuary, Ontario. Generally, growth is slower and the muskellunge lives longer in the northern part of its range than in the extreme southern part of its range. Muskellunge exhibit sexual dimorphism in their growth; females grow faster, are usually larger at any given age, and live longer (Hourston 1952; Scott and Crossman 1973; Hanson 1986).

The age at which muskellunge become sexually mature probably depends on their growth rate, as described for northern pike by Inskip (1982). In northern Wisconsin, male muskellunge have been found to sexually mature before females (Hanson 1986). Males first matured at ages 3-4 (the majority at ages 5-6), whereas some females matured at ages 4-5 (the majority at ages 6-8). Muskellunge have been reported to mature at age 3-4, at a length of 610-711 mm (Karvelis 1965). Scott and Crossman (1973) reported that sexual maturity is reached between ages 3-5.

Newly hatched muskellunge will begin feeding on zooplankton soon after the yolk sac is absorbed and the fry swim up. This diet of zooplankton continues for 1-3 weeks (Scott and Crossman 1973). After reaching a length of about 40 mm, the muskellunge will switch to a piscivorous diet. This switch may occur at about 30 mm in some individuals; in a hatchery, catostomid fry were consumed by 30-mm muskellunge (R. Ramsell, Minnesota Department of Natural Resources, St. Paul, pers. comm.).

There appears to be a direct relationship between the size of the muskellunge and the size of the food selected (Hess and Heartwell 1978). Growth and survival of the muskellunge may be impaired if food of an adequate size is not available, in spite of the vast number of smaller fishes (Scott and Crossman 1973). However, two studies found that muskellunge were not significantly selective about prey selection by species and appeared to be midwater feeders (Buss 1960; Engstrom-Heg et al. 1986). Muskellunge have been reported to consume catostomids, percids, coregonids, cyprinids, centrarchids, clupeids, and ictalurids. Brewer (1969) observed that Kentucky stream muskellunge fed on Notropis sp. and catostomids. Oehmcke (1969) reported that muskellunge in Wisconsin fed on catostomids and coregonids. Common carp (Cyprinus carpio) and gizzard shad (Dorosoma cepedianum) were the only items identified in the stomachs of the muskellunge in Cave Run Lake, Kentucky (Axon 1978). Hess and Heartwell (1978), in a review of the literature, concluded that the gizzard shad is probably the best forage fish for esocids, but shad rarely occur in the muskellunge's native range.

The muskellunge has a reputation for being a voracious predator. It appears to be more of a lurking (lie and wait) than a stalking predator, and rarely pursues prey after a miss (Engstrom-Heg et al. 1986).

Reproduction

The muskellunge spawns in spring when water temperature reaches 9.4-15.0 °C; optimum temperature is 12.8 °C (Scott and Crossman 1973). Dombeck (1979) found that muskellunge moved on to the spawning grounds when water temperature reached 8-10 °C and remained there for 5-10 days until water temperature reached about 14 °C. In Nogies Creek, Ontario, muskellunge moved to the spawning grounds when water temperature was between 8.0-10.5 °C; spawning occurred at water temperatures of 10.5-15.5 °C; and males abandoned the spawning grounds when water temperature reached 16.0 °C (Minor and Crossman 1978). Muskellunge in Leech Lake, Minnesota, began movement to the spawning grounds shortly after ice-out, when water temperature was 8.3-11.6 °C (Strand 1986). Movements to the spawning grounds (up to 21 km) were direct and frequently included crossing large expanses of open water. Males were the first fish on the spawning grounds and remained there longer than females. Strand (1986) concluded that spawning occurred 15-35 days after ice-out at water temperatures of 11.6-14.0 °C. Both sexes (especially females) were sensitive to drops in water temperature on the spawning grounds. A cooling of water temperature caused females to move into deeper water.

In Leech Lake, the spawning areas chosen were in open-water areas with depths of 1-2 m, over a soft calcareous substrate, with Chara spp. as the dominant vegetation (Strand 1986). There was no microstratification of DO (dissolved oxygen) at the substrate-water interface during the time of egg incubation, and temperature was uniform throughout the water column. Haas (1978) found that muskellunge in Lake St. Clair, Michigan, also spawned in deep, open water (>9 m) with little or no vegetation.

Muskellunge also have been known to spawn in tributary streams and shallow lake channels (Eddy and Underhill 1976). Dombeck (1979) reported that radio-tagged muskellunge in Wisconsin spawned in water generally <1 m, on a substrate of muck or muck and sand covered with much debris or dead vegetation. Three of four spawning areas identified by Dombeck (1979) were in bays with influent streams. Minor and Crossman (1978) found spawning substrate to consist of matted vegetation and tree leaves that had fallen the previous fall, in areas <1 m deep (mean depth = 0.65 m) upstream of Nogies Creek, Ontario. Schrouder (1973) found one strain of muskellunge spawned at the edge of channels over detritus, whereas another strain of muskellunge spawned in shallow bays in Michigan. Spawning habitat in rivers is usually associated with low-gradient pools (Brewer 1969).

There is some evidence that the eggs of female muskellunge develop and are deposited in two distinct periods (Lebeau et al. 1986). There is a maximum ovarian volume in esocids, and a bimodal development pattern of oocytes is considered to be an adaptation that allows an individual to carry and deposit a greater number of eggs. This, however, would classify the muskellunge as a multiple spawner (Lebeau et al. 1986).

The following discussion on muskellunge spawning behavior is taken from Scott and Crossman (1973:366):

During the spawning period the fish pair off, usually a larger female is accompanied by one, or at times two smaller males. They swim about over the vegetation during the day, and at intervals the fish roll so the anus of the male and female are approximated; a small number of eggs and sperm are shed simultaneously during rapid vibrations of the bodies; the lashing of the tails spreads the fertilized eggs and the pair swim on. The spawning act is carried out many times at irregular intervals over several days. No nest is built, the semidemersal, apparently nonadhesive eggs are scattered at random and drop into the vegetation. Spawning usually lasts no more than a week. The number of eggs increases with the size of the female and ranges from about 6,000-265,000 with the usual number about 120,000. Fertilized eggs are 2.5-3.5 mm in diameter, clear, and amber colored.

On hatching, the young are 9.5-10.3 mm in length and may, in nature, remain dormant in the vegetation for about 10 days or until the yolk sac is consumed, at which time they become active and begin feeding.

A study that examined a variety of information on watershed characteristics, water chemistry, hydrology, fish communities, and cultural perturbations found that nine variables (out of 94) accounted for 57% of the variability in muskellunge reproduction (Dombeck et al. 1986). Conditions in these lakes that were identified as most strongly promoting natural reproduction were limited northern pike abundance, rising spring time water level, high alkalinity, a high shoreline development factor, and drainage lake systems that increase lake area and allow rising spring water levels.

Specific Habitat Requirements

Muskellunge are found in a variety of river and lake types throughout their native range. Muskellunge are often associated with aquatic vegetation or submerged structures (e.g., rock reefs, fallen trees).

Muskellunge in lacustrine and riverine habitats have defined home ranges that vary from a 300-800-m reach in a stream to a 300-m (diameter) circle in a lake (Crossman 1977). Dombeck (1979) reported the home range in lacustrine habitats to vary from 0.2-27.7 ha in Black Lake (52 ha) and Moose Lake (676 ha), Wisconsin. The home ranges of these muskellunge were smaller during winter, intermediate during summer, and larger in May, September, and October (Dombeck 1979). In Nogies Creek (35 ha) and Stony Lake (3,725 ha), muskellunge had home ranges that varied from 1.1-7.2 ha (Minor and Crossman 1978). These fish established both winter and summer home ranges, but the size of the home range was correlated with the size of the muskellunge (Minor and Crossman 1978). In West Okoboji Lake (1,540 ha), Iowa, muskellunge had home ranges that averaged 146 ha (range 39-443 ha, Miller and Menzel 1986). In this

study, eight muskellunge used the same home range in consecutive summers. The home ranges of the muskellunge in West Okoboji Lake were broadly overlapping, and, occasionally, two or more fish were found in close proximity to each other. Therefore, Miller and Menzel (1986) concluded that the muskellunge in West Okoboji Lake were not territorial. In Leech Lake (45,134 ha), Minnesota, Strand (1986) found that home range size depended on the basin of Leech Lake in which the muskellunge were located. During summer, the Leech Lake fish had large home ranges when compared to other studies, ranging from 200-3,390 ha; winter home ranges (range 50-1,840 ha) were smaller than summer home ranges. Muskellunge found in the larger areas of the lake tended to have separate winter and summer home ranges, whereas those in a smaller bay had winter home ranges that were contained in the summer home ranges. Based on these studies, it appears that lake size, season, and size of the muskellunge all affect the location and size of the home range selected by individual muskellunge.

As muskellunge grow, they exhibit a broad range of tolerances and requirements for different habitat types. The different stages of growth of the muskellunge are defined as follows:

1. Embryo/larva. Includes requirements for the developing embryo through hatching, and the larval stages (from hatching to the swim-up or feeding stage).
2. Fingerling. From the onset of feeding until they assume adult proportions, approximately 75 mm (Buynak and Mohr 1979).
3. Juvenile. From 75 mm to the onset of sexual maturity (beginning of gonadal maturation).
4. Adult. From sexual maturity until death.

Embryo/larva. Some strains of muskellunge will spawn in <1 m of water on flooded vegetation, detritus, and woody debris (Scott and Crossman 1973; Minor and Crossman 1978; Dombeck 1979; Dombeck et al. 1984). Other muskellunge will spawn in deeper water (>1.5 m) on beds of Chara spp. or areas of little vegetation (Hass 1978; Strand 1986). It appears that no type of vegetation, depth, or substrate is critical to reproduction, but that muskellunge spawning habitat varies from location to location (Dombeck et al. 1984). High DO levels are critical for the developing embryos and larvae (Dombeck et al. 1984). If the muskellunge spawn on vegetation, it should provide enough structure to keep the eggs off the bottom yet allow for the circulation of water, as with the northern pike (Inskip 1982). Dombeck (1979) reported that eggs may be covered by detritus and silt, which could cause anoxic conditions. Some spawning habitats may have a high biochemical oxygen demand (BOD), which may cause microstratification in the DO at the bottom-water interface, resulting in anoxic conditions around the developing eggs (Dombeck et al. 1984). Depletion of DO near the bottom will limit the success of muskellunge reproduction. Microstratification may also allow toxic substances such as hydrogen sulfide (H₂S) to increase to toxic levels, causing mortality in the developing embryos (Adelman and Smith 1970).

Low water levels during spawning will negatively impact the muskellunge and produce poor year classes (J.M. Casselman, Ontario Ministry of Natural Resources, Maple; letter dated January 1986). Rising spring water levels have been positively correlated with muskellunge reproductive success (Dombeck et al. 1986). Therefore, one would expect that receding water levels would reduce reproductive success.

Hatching occurs in 8-14 days at water temperatures of 12.2-16.7 °C (Oehmcke et al. 1965). Often, only 34% of the eggs spawned are fertilized, whereas fertility of eggs reared in a hatchery is as high as 95% (Scott and Crossman 1973). Gammon (1986) reported naturally spawned eggs were 21.0% and 34.7% viable in Trout Lake, Wisconsin.

Upon hatching, the larval muskellunge remain quiescent for the first few days of life, while the yolk-sac is absorbed. Therefore, the same limitations on embryo survival also apply to larvae for approximately 7-14 days, depending on water temperatures (Ramsell, pers. comm.). Muskellunge have cephalic adhesive glands (Leslie and Gorrie 1985), but do not use them as do northern pike, which use the glands to stay suspended above the bottom to avoid hypoxic conditions (Inskip 1982). Therefore, microstratification of DO and toxic substances such as H₂S may cause mortality in the larvae. Adelman and Smith (1970) found that exposure to concentrations as low as 0.004-0.006 ppm H₂S will decrease survival and growth of sac fry northern pike.

Newly hatched muskellunge are eaten by predacious diving beetles (Dytiscidae), giant water bugs (Belastomatidae), and other predacious insect larvae (Elson 1941; Johnson 1958). Young muskellunge lie just under the water surface waiting for forage to pass nearby. At this stage, they are subject to predation by fish and birds.

Fingerling. Aquatic vegetation in nursery areas provides cover for fingerling muskellunge. Typical nursery habitat in Southern Georgia Bay, Lake Huron, for 50-mm (range 16-98 mm) muskellunge was composed of eight families of emergent and floating vegetation and nine species of submergent vegetation (Craig and Black 1986). Sedge (Cyperaceae) was the most abundant emergent family, while bushy pondweed (Najas flexilis), Chara spp., and variable pondweed (Potamogeton gramineus) were the predominant submergent species. Emergent and floating vegetation were most common near shore and decreased in density as mean depth increased; submerged vegetation increased in density off-shore. These nursery areas were 1 m deep, and substrate consisted of sand, muck, and a silt-detritus mixture. Nineteen other fish species were found in the nursery areas, with largemouth bass (Micropterus salmoides), yellow perch (Perca flavescens), and pumpkinseed (Lepomis gibbosus) being the most common. The mean water temperature was 24 °C in the nursery habitats.

Juvenile. Habitat use and environmental requirements of juvenile muskellunge are not well documented for self-sustaining populations. Hanson (1983, 1984) documented the movements and habitat selection of stocked muskellunge that averaged about 300 mm in length. Movements of stocked muskellunge across large expanses of open water were rare, and mean daily movements averaged about 100 m. In Whitefish Lake, Wisconsin, these fish

tended to establish small home ranges, and they preferred areas with bulrush (*Scirpus* spp.) and pondweed *Potamogeton* spp. or areas with well-developed structures, such as sand bars or rocky points (Hanson 1983). In Trego Lake, Wisconsin, the stocked fish used areas near fallen trees, boat docks, and an offshore shoal on which watermilfoil *Myriophyllum spicatum* and wild celery *Vallisneria americana* were the dominant submerged vegetation. Juvenile muskellunge are able to withstand water temperature as high as 32.2 °C.

Adult. The optimum temperature for muskellunge is 25.6 °C (Scott and Crossman 1973). Water temperature affects growth rates; muskellunge in the southern part of their range grow faster than those in the northern part.

Adult muskellunge locations were correlated with physical structure such as weed beds, rock reefs, and changes in the bottom contour in Leech Lake, Minnesota (Miller and Menzel 1986; Strand 1986). Miller and Menzel (1986) reported that muskellunge adjusted their basic foraging patterns to maintain an optimal feeding strategy in response to seasonally changing environmental factors. After the spawning period and through midsummer, the fish behaved as searching predators as evidenced by relatively high levels of activity, extensive movements, utilization of a variety of water depths and habitat types, and pronounced crepuscular (twilight) activity. By late summer the fish exhibited behavioral characteristics of a sedentary ambush predator; reduced activity, strong allegiance to activity centers associated with vegetation, and little diel variation. In streams, muskellunge are associated with pools, sections of river with low gradients, and fallen trees (Kornman 1983; Axon and Kornman 1986).

Habitat Alterations and Perturbations

Habitat loss and alterations are considered to be the major cause of the decline of self-reproducing native muskellunge populations (Trautman 1981; Dombeck 1986). Knowledge of specific habitat requirements of the muskellunge during all life stages is limited and incomplete (Dombeck 1986). However, loss of critical habitat will probably result in the reduction or elimination of a self-reproducing muskellunge population. Habitat changes and perturbations most often cited as impacting muskellunge populations are presented in Table 1.

Dombeck (1986) presents guidelines for preserving and improving muskellunge habitat, and these guidelines are directed toward enhancing natural reproduction. Dombeck's (1986) recommendations include the location of spawning habitat and the placement of spawning structure, the control of northern pike population, and watershed management.

Table 1. A summary of habitat perturbations/modifications impacting muskellunge (after Dombeck 1986).

Perturbation/modification	Life stage	References
Stream impoundment		
Blocks spawning migration	spawning-embryo	Trautman (1981)
Eliminates riverine habitat	adult	Axon and Kornman (1986) Brewer (1980)
Draining wetlands, filling marshes	spawning-embryo	Bimber (1978)
Eliminates spawning areas		Trautman (1981)
Channelization	spawning-adult	
Eliminates habitat		Trautman (1981)
Decreasing springtime water level		
Strands spawners and young and exposes eggs	all	Scott and Crossman (1973)
Eutrophication		
Excessive weed growth and buildup of organic substrates	spawning-embryo	Dombeck et al. (1984)
Low winter dissolved oxygen	adult	Dombeck (1979)
Sediments		
Loss of spawning habitat	spawning-embryo	Muncy et al. (1979) Axon and Kornman (1986)
Suspended solids		
Impairs sight feeding	fry-adult	Farnworth et al. (1979) Muncy et al. (1979)
Elimination of vegetation		
Elimination of habitat	fry-adult	Bimber and Nicholson (1981) Trautman (1981)
	fry	Craig and Black (1986)
Loss of woody cover	fry-adult	Axon and Kornman (1986)
Acid mine drainage	all	Axon and Kornman (1986)
Brine drainage from oil wells	all	Axon and Kornman (1986)
Gravel dredging	all	Axon and Kornman (1986)
Shoreline modification		
Clearing trees in riparian zone for recreational use	all spawning-fry	Axon and Kornman (1986) Craig and Black (1986)

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area. This model may be applied to lacustrine habitats (lakes and reservoirs) anywhere in the 48 contiguous United States and Canada.

Season. The model provides several variables that account for seasonal changes in habitat requirements. Thus, this model may be used to evaluate the lacustrine environment of the muskellunge on a year-round basis.

Cover types. This model applies to all lacustrine cover types (e.g., lakes, ponds, and reservoirs) with a mean depth >1 m during midsummer.

Water quality. The model does not take into consideration heavily polluted waters or waters that are being actively perturbed over the majority of the lake (e.g., dredging, mechanical vegetation removal).

Minimum habitat area. Minimum habitat area is defined as the minimum area of contiguous suitable habitat that is required for a species to live and reproduce. Minimum habitat for successful reproduction, growth, and survival of the muskellunge for the purpose of this model has been set at 20 ha.

Verification level. This model has been constructed from a review of the literature and has not been field tested. This model is the authors' interpretation of how the muskellunge is affected by natural environmental factors.

Earlier drafts of this model were reviewed by the following individuals:

Dr. J.M. Casselman, Ontario Ministry of Natural Resources, Maple, Ontario
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Model Description

This model attempts to quantify the habitat of the muskellunge with a numerical index from 0 (unsuitable habitat) to 1 (best habitat). A positive relationship is assumed between the HSI and long-term potential carrying capacity (U.S. Fish and Wildlife Service 1981). The model is designed to determine the highest HSI's for lacustrine systems capable of producing muskellunge biomass on a sustained basis or systems supported by stocking, regardless of how that biomass is apportioned among individual fish.

The muskellunge HSI model consists of four life requisite components (Figure 1): food (C_F), water quality (C_{WQ}), cover and reproduction (C_{CR}), and other variables affecting the muskellunge (C_O). Each component contains variables that are thought to measure (directly or indirectly) the habitat's ability to meet the requirements for the appropriate life requisite. The structure of the HSI model for the muskellunge is graphically presented in Figure 1. Not every variable that affects muskellunge populations has been included in the model (e.g., cultural eutrophication or development, ambient pH levels, harvest rates). Modifications to this model (i.e., adding variables) may be necessary in some situations.

Food component. Mean Secchi disk water transparency (V_1) was included in the food component because the muskellunge is a sight feeder, and extremely turbid waters would limit foraging efficiency. In most cases, the SI value for mean Secchi disk transparency will not be a limiting factor.

Relative abundance of forage fish (<12 cm) during spring and summer (V_2) and size diversity of forage fish (V_3) are assumed to be direct measures of the quality and availability of food for the muskellunge. We feel that both of these variables are of equal importance to the quality of the forage base. Therefore, they were combined by a multiplication and square root formula. When they are combined in this manner, an extremely low SI value of one variable will cause the overall forage suitability SI to be low as well.

Water quality component. Based on a review of existing literature, winter dissolved oxygen levels (V_4) and maximum water temperature in the epilimnion (V_5) are the only water quality variables that obviously limit adult muskellunge populations. Since these two variables induce stress in different seasons, the lowest SI value should be used to determine the water quality component SI value.

Cover and reproduction. Cover for the muskellunge is expressed in terms of the percent of midsummer area with emergent or submergent aquatic vegetation and terrestrial plants (V_6). The cover variable was included with the reproductive variables because it is at the early life stages when cover is most important. Three variables measure the quality of the reproductive habitat: minimum dissolved oxygen content in nursery and spawning areas (spring) (V_7), drop in water levels during embryo and early larval stages (V_8), and the ratio of spawning habitat to summer habitat (V_9). Low Suitability Index (SI) values for any of the previous four variables can eliminate a successful breeding season, therefore, the lowest SI value should be used for the cover/reproduction component SI value.

Habitat variables

Life requisites

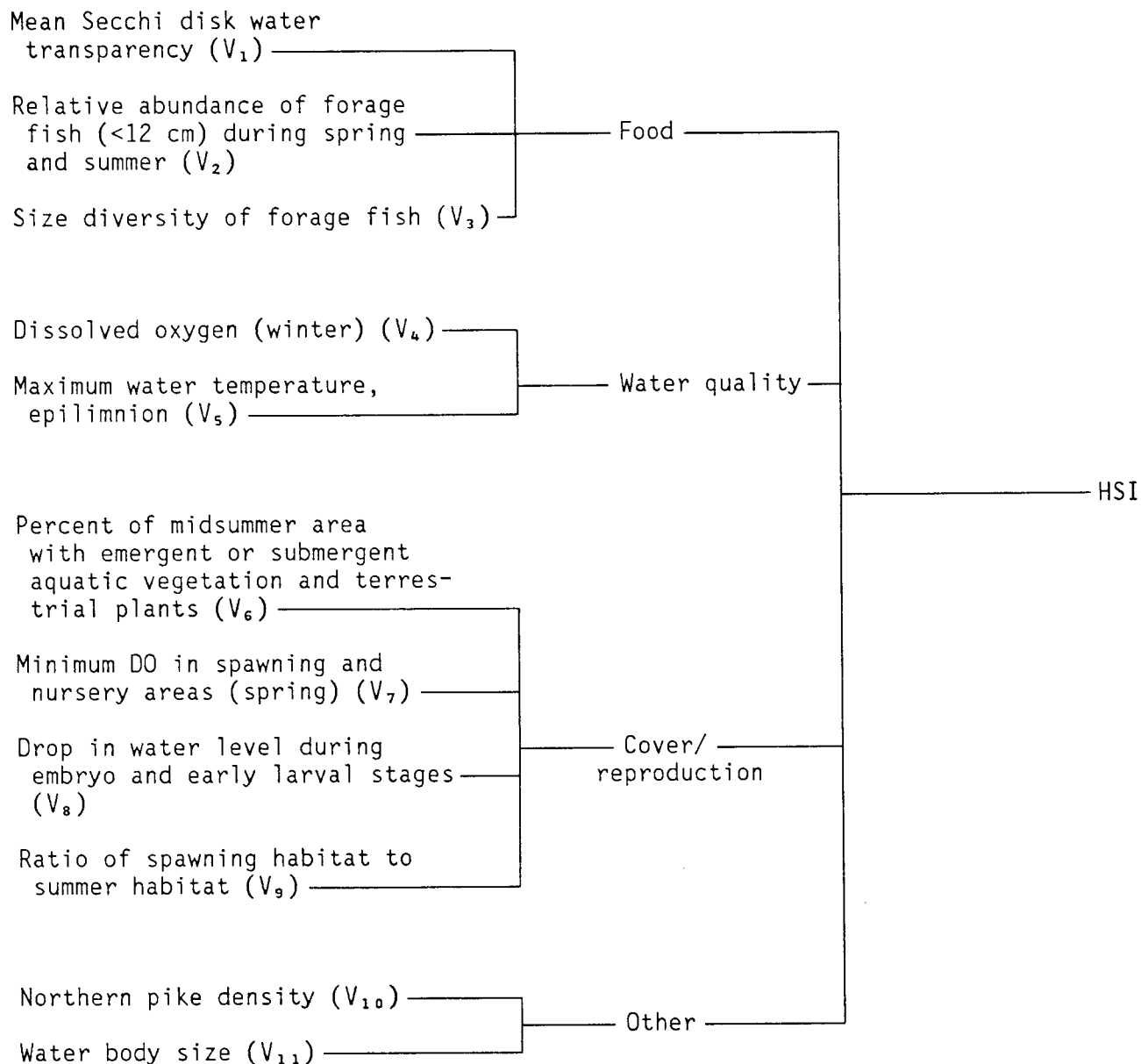


Figure 1. Tree diagram illustrating relationships between model variables, model components (life requisites), and HSI for the muskellunge in lacustrine environments.

If this model is to be used in systems where a population of muskellunge is supported by stocking, then this component can be deleted. This component may be used to estimate the possibility that a stocked population will reproduce.

Other. Two other variables that affect muskellunge but do not conveniently fit in the other life requisite components are northern pike density (V_{10}) and water body size (V_{11}). High densities of northern pike may reduce or eliminate muskellunge populations. This interaction between the species seems to be less severe in larger lakes. Therefore, the SI values for both variables are factored together for a final SI value.

HSI Calculations

This model examines each of the life requisites separately and consists of four components: food, water quality, cover/reproduction, and other.

Food (C_F).

$$C_F = \text{the lowest of } V_1 \text{ or } (V_2 \times V_3)^{1/2}$$

Water quality (C_{WQ}).

$$C_{WQ} = \text{the lowest of } V_4 \text{ or } V_5$$

Cover/reproduction (C_{CR}).

$$C_{CR} = \text{the lowest of } V_6, V_7, V_8, \text{ or } V_9$$

Other (C_0).

$$C_0 = (V_{10} \times V_{11})^{1/2}$$

HSI determination.

$$\text{HSI} = \text{the lowest of } C_F, C_{WQ}, C_{CR}, \text{ or } C_O$$

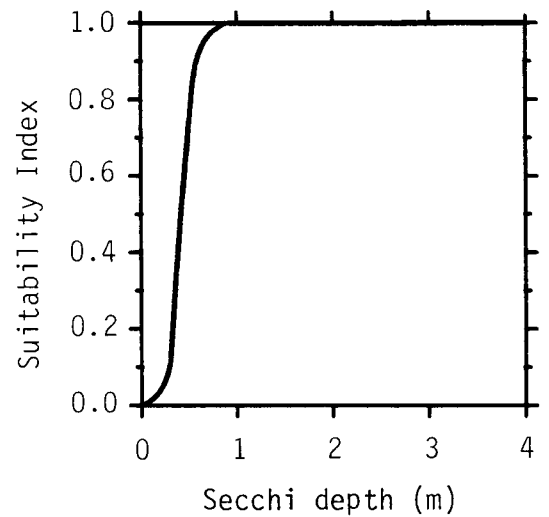
Suitability Index (SI) Graphs for Model Variables

The suitability index for each variable and how it changes with the habitat is graphically shown in this section. Suitability indices can be computed from the following set of curves.

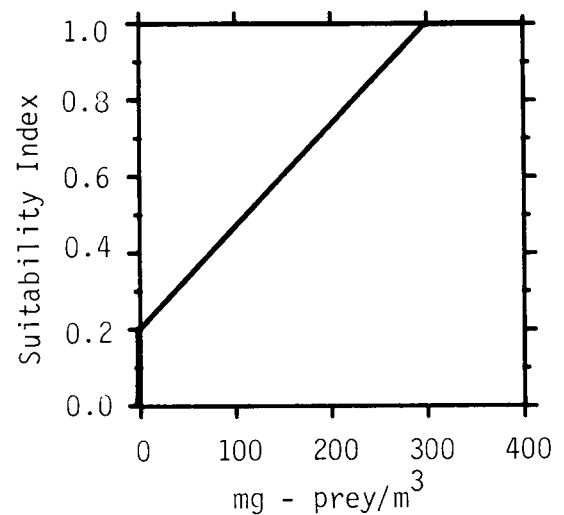
Variable

V_1 Mean Secchi disk water transparency.

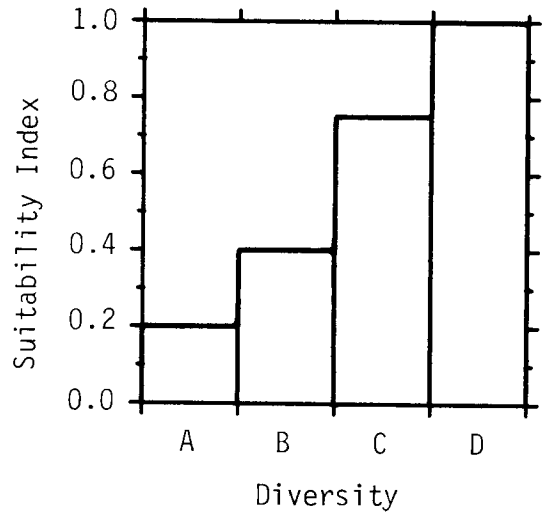
Suitability graph



V_2 Relative abundance of forage fish (<12 cm) during spring and summer.



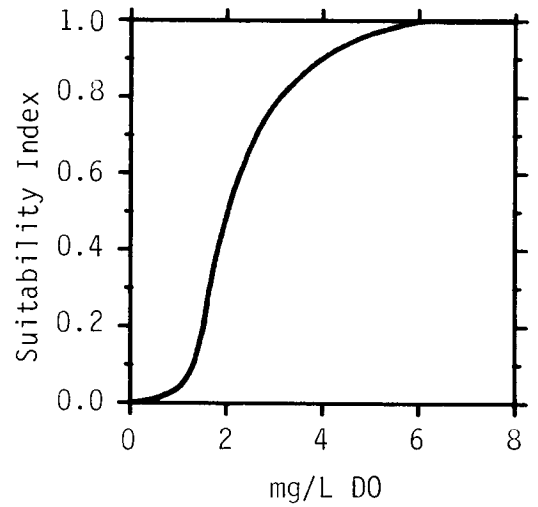
V₃ Size diversity of forage fish.



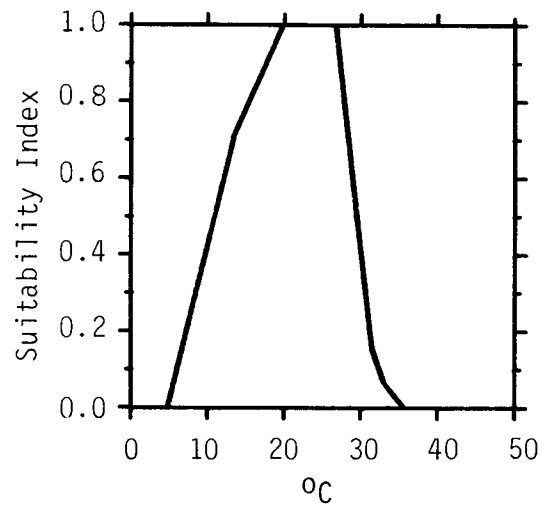
The four levels of this suitability index are separated by a qualitative judgment on the size classes of forage fish. With one or more size classes missing, muskellunge growth can be impaired. All forage species may be considered together and one SI computed. An alternative and preferred method is to compute an SI for each of the prey species separately, and then average the SI's for a final value. For the purpose of this variable, prey may be classed into the following groups: small (0-150 mm), medium (151-300 mm), and large (>300 mm).

- A. No diversity in size classes, most forage fish are large with few small or medium.
- B. No diversity in size classes, most forage fish are small with few medium or large.
- C. Two size classes are present in large numbers but the third size class is scarce.
- D. All three size classes are found in large numbers.

V₄ Dissolved oxygen (winter).

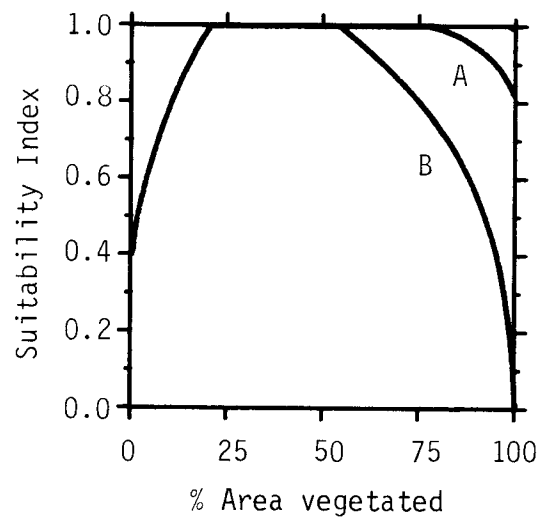


V₅ Maximum water temperature, epilimnion.

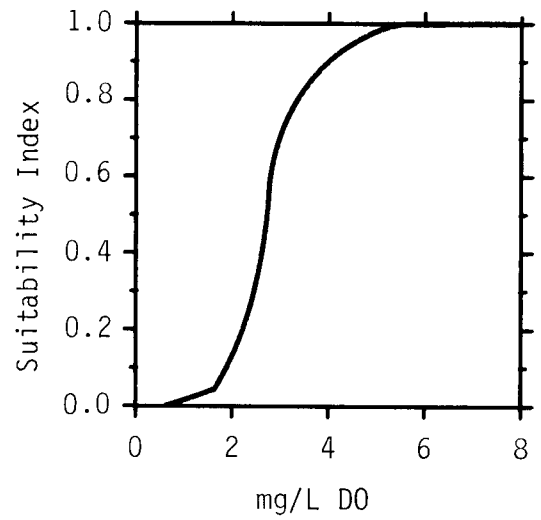


V₆ Percent of midsummer area with emergent or submergent aquatic vegetation and terrestrial plants.

- A. Large lakes with no winter kill problems.
- B. Small lakes likely to winter kill.



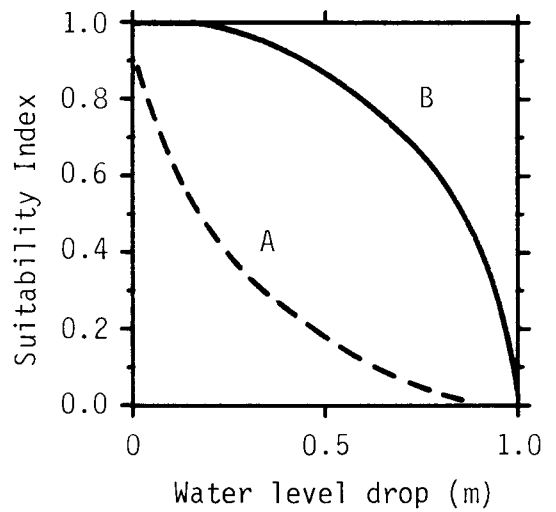
V₇ Minimum dissolved oxygen level in spawning and nursery areas (spring).



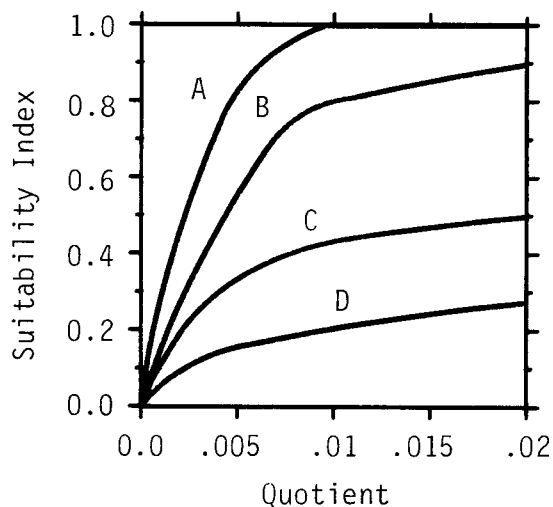
V₈ Drop in water level during embryo and early larval stages.

- A. Embryo and early larval stages (until yolk sac absorbed).
- B. Larval stage, after yolk sac absorbed.

SI for V₈ = A or B, whichever is lowest.



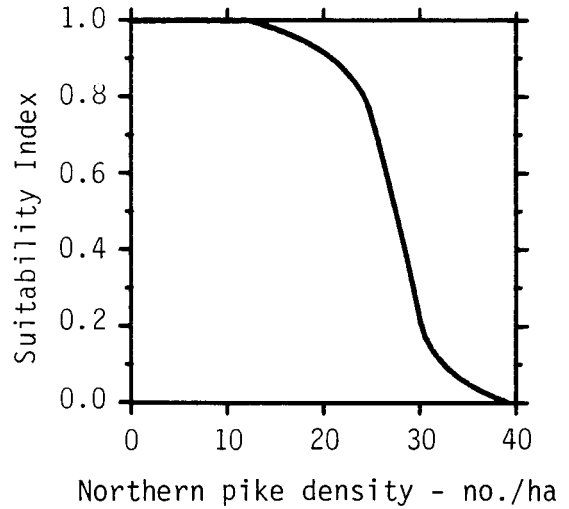
V₉ Ratio of spawning habitat to summer habitat.



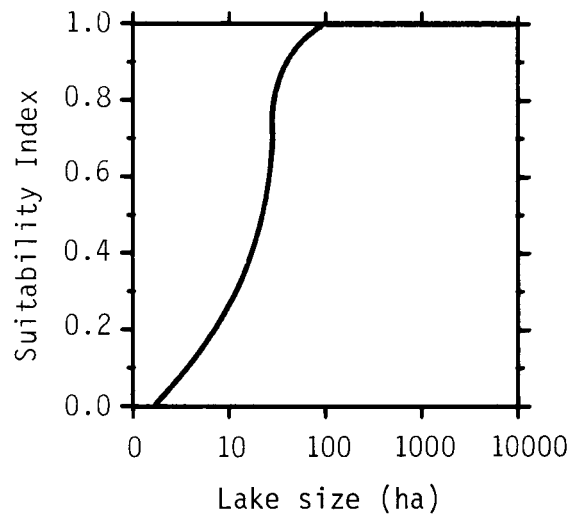
The appropriate curve should be selected according to the type of vegetation or plant debris that is found in the spawning area(s). Filamentous algae is never included as suitable spawning habitat.

- A. Vegetation and debris consist of material with a high fibrous content, for example, bulrush (Scirpus), horsetail (Equisetum), rush (Juncus), stonewort (Chara), and small wood chips. Provides a support base for eggs that keeps the eggs off of the bottom substrate and allows for circulation of water around the eggs. Bottom substrate is mostly sand or a mixture of substances of a nature such that there is no depletion of dissolved oxygen at the substrate-water interface. BOD in the vicinity of the eggs is low.
- B. Vegetation and debris consist of material similar to A, but bottom is more silty or organic in nature and a moderate BOD is present.
- C. Vegetation and debris consist of material with a lower fibrous content than A or B, for example, coontail (Ceratophyllum), pondweed (Potamogeton), sedge (Carex), milfoil (Myriophyllum), and deciduous tree leaves. Provides minimal support for eggs and allows minimal circulation of water around the eggs. Bottom substrates are similar to A, and a moderate BOD is present.
- D. Vegetation and debris consist of material similar to C. Bottom substrate is silty or organic in nature with a high BOD.

V₁₀ Northern pike density.



V₁₁ Water body size.



Development of Suitability Index Graphs: Rationale and Assumptions

The preceding suitability index graphs should be regarded as tentative and subject to modification. The prospective user should understand that the curves are not products of extensive laboratory or field investigations. Rather, they reflect the authors' subjective integration of the literature, personal experience, and reviewers' comments. The following discussion documents the thought process used in constructing the curves. Some curves are better documented than others. In many cases, there is information about preferred and limiting or unsuitable conditions, but little information on which to base ratings of intermediate conditions. The model is offered as a starting point, with the hope that refinements will be made as additional information becomes available, including results of model testing.

Mean Secchi disk water transparency (V_1). All large esocids are known to be sight feeders (Scott and Crossman 1973; Eddy and Underhill 1976; Hess and Heartwell 1978). Because muskellunge rely on their sight to forage, high turbidity (i.e., low transparency) can limit feeding efficiency. Miller and Menzel (1986) found a positive association of muskellunge activity with water transparency. As water transparency decreased, so did the percentage of active muskellunge, but this relationship was confounded with other factors, such as water temperature. The density of legal-sized muskellunge in Wisconsin was positively correlated with turbidity and negatively correlated with Secchi depth (Hanson 1986). Extremely turbid waters will reduce feeding efficiency and possibly cause clogging and abrasion of the gill membranes. Mean Secchi disk water transparency will change throughout the year in most bodies of water. We recommend that the average Secchi disk reading for the six most turbid months of the year be used to compute the SI value. An average for this period will give the lowest SI value for turbidity.

Relative abundance of forage fish (<12 cm) during spring and summer (V_2). High water levels increased the production of forage fishes and as a result increased the abundance of walleyes (Groen and Schroeder 1978). Jester (1971) and Forney (1977) also reported that strong year-classes of walleyes develop when small forage fishes are both abundant and available. Oehmcke et al. (1965) reported that good populations of muskellunge are most often associated with excellent populations of suckers (*Catostomidae*), whitefish (*Coregonus* spp.), and ciscos (*Porsopium* spp.). Soft-finned forage fishes are preferred by muskellunge, and they appear to prosper where well-balanced populations of these species are abundant. The SI graph is adapted from McMahon et al. (1984).

Size diversity of forage fish (V_3). There is a tendency for muskellunge to prey upon larger fish as they grow (Hess and Heartwell 1978). This size selectivity may start at a very early age (Porter 1977). Muskellunge size and preferred prey size are related by the following equation ($r^2=0.5214$, Porter 1977):

$$\text{Muskellunge length (inches)} = 1.1513 (\text{prey length (inches)}) + 26.4173$$

This variable (V_3), therefore, assumes that if a variety of prey size classes are present, muskellunge growth will be improved. An examination of field records or a small amount of field sampling should provide information on the size classes of forage fish found in a particular body of water.

Dissolved oxygen (winter) (V_4). Muskellunge will avoid anoxic waters and concentrate in areas of higher oxygen as dissolved oxygen diminishes in a lake (Gilbertson 1986). Juveniles can survive, for short periods of time, at dissolved oxygen levels below 1 mg/L (Gilbertson 1986). Muskellunge should be able to over-winter with no adverse effects in lakes that maintain at least 3.0 mg/L dissolved oxygen during the ice-covered periods.

Maximum water temperature, epilimnion (V_5). The optimum overall temperature for muskellunge is approximately 24 °C (Ferguson 1958; Scott 1964) and the optimum temperature for growth is 23 °C (Casselman, unpubl.). The upper limit of the preferendum is 25.6 °C (Scott and Crossman 1973). Temperatures will be in the optimum range during the warming and cooling phases of a body of water if the maximum water temperature is slightly higher than the optimal temperature. Muskellunge can withstand water temperature as high as 32.2 °C, but this is at the upper end of their tolerance, so waters that warm more than this are less suitable. Larval and juvenile muskellunge have an upper lethal temperature of 36.1 °C and 32.5 °C, respectively (Hassan and Spotila 1976). It appears that adults are the most sensitive life stage to water temperature. Dombeck (1979) reported that during the summer months adult muskellunge were found in water <2 m at temperatures of 24-27 °C.

Daily variations in water temperature can be considerable. We recommend that V_5 be determined by averaging the means of daily minimum and maximum for the warmest (water temperature) week of the year (Inskip 1982). Daily maximums usually occur in midafternoon, and minimums occur around dawn on most days.

Percent of midsummer area with emergent or submergent aquatic vegetation and terrestrial plants (V_6). Vegetated cover is important to many life stages of the muskellunge. Vegetation provides the muskellunge with protective cover in the larval, fingerling, and juvenile life stages and forage cover in the adult life stage. Rooted macrophytes also add to the productivity of a body of water and presumably increase the food supply for the muskellunge.

This variable was developed for northern pike (Inskip 1982), which have been found to be associated with the macrophyte-openwater interface (Reighard 1915; Chapman and Mackay 1984; Cook and Bergersen 1985; Cook 1987). Muskellunge also are known to use this interface (Ramsell, pers. comm.); however, complete vegetative cover is probably suboptimal. A body of water that is completely vegetated would have few interfaces with open water. This would reduce the foraging positions for adult muskellunge. Furthermore, decomposing vegetation can deplete the dissolved oxygen in the winter months in shallow bodies of water. Optimal habitat would have extensive submerged or emergent aquatic vegetation interspersed with open water. At the present time, the model does not contain an interspersion variable.

This variable probably affects the early life stages of muskellunge the greatest, therefore, it was included in the reproduction life requisites. For naturally reproducing populations, if this variable has an acceptable SI value for early life stages, it will be acceptable for the adult stage as well. Therefore, in calculating this SI, the user should consider only the areas used by fingerling and juvenile muskellunge (i.e., the whole lake if it is small, or the possible nursery and juvenile habitat if the lake is large).

Minimum dissolved oxygen level in spawning and nursery areas (spring) (V_7). If low dissolved oxygen levels are present, growth and survival may be reduced, as has been demonstrated for walleye (Moyle and Clothier 1959; Siefert and Spoor 1974). Low oxygen concentrations probably will reduce the rate of development, percent normal hatch, and larval vigor of muskellunge as it does for the congeneric northern pike (Siefert et al. 1973). Dombeck (1986) suggested that habitat rehabilitation measures be taken in muskellunge spawning substrate if the dissolved oxygen concentration falls below 3.2 mg/L.

Drop in water level during embryo and early fry stages (V_8). This variable is not applicable in lakes where the majority of the spawning habitat is in deeper water (Strand 1986). The variable was designed for populations that spawn in shallow areas. Because muskellunge generally spawn in water <1 m deep, declining water levels can affect embryos, larvae, and, possibly, fingerlings and adults may be stranded. Embryos and newly hatched larvae are immobile until the yolk sac is absorbed and are perhaps the most vulnerable to a decline in water level. As muskellunge larvae grow the more likely they will be able to avoid receding water levels. The greater mobility of the older larvae is the reason for the difference between curves A and B in the suitability index graph.

Ratio of spawning habitat to summer habitat (V_9). The type of habitat chosen for spawning areas appears to vary with location. High spring water levels may create spawning habitat when terrestrial and wetland vegetation is flooded, or off-shore habitats may be used for spawning grounds. The amount of spawning habitat depends on the shoreline topography, the amount of available vegetation or detritus, and the substrate characteristics. The relative ability of spawning habitat to produce muskellunge can be estimated by the ratio of possible spawning areas to the entire surface area of the water body in the summer.

Aerial or ground surveys can be used in conjunction with water level data to estimate spawning habitat availability. In many instances, shoreline vegetation becomes spawning habitat when it is inundated by high spring water levels. Thus, its characteristics when submersed should be estimated and the area included in the SI calculations.

Inskip (1982) used fingerling production from marshes and subsequent survival through adulthood to estimate the minimum ratio of spawning to summer habitat for northern pike. We will use the same logic to develop a minimum ratio of spawning to summer habitat for muskellunge.

As Inskip (1982) indicated, the minimum ratio, below which spawning habitat limits population size, depends on the carrying capacity of summer habitat. In constructing the curves for this variable, he assumed that spawning habitat availability is positively, but asymptotically, related to the area of spawning habitat per spawning female (Inskip 1982). In other words, an increase in spawning habitat per female is more beneficial when spawning habitat is scarce than when it is plentiful. In most cases, the standing crop of muskellunge is less than two adult muskellunge per hectare (Hanson 1986; Hoff and Serns 1986); in rare cases, the standing crop may be as high as eight fish/ha (Crossman 1956). For the purpose of this variable, we chose a density of two adult muskellunge per hectare as the maximum density.

There is little known about the number of muskellunge fingerlings produced in nursery areas in the wild. Therefore, we assumed that under ideal conditions the median number of muskellunge fingerlings produced per hectare is no greater than the median number of northern pike produced per hectare (2,717 fingerlings, Inskip 1982). For the purpose of this variable, we assumed that a hectare of spawning habitat will produce 2,500 muskellunge fingerlings, under optimal conditions.

Survival of a year class of muskellunge through adulthood is highly variable. Most available mortality or survival estimates for larvae, fingerlings, or juveniles pertain to stocked fish. Survival of larvae or fingerlings is variable and usually low (Johnson 1982; Hanson et al. 1986b; Serns and Andrews 1986). Estimates of fingerling muskellunge survival through the stocking period to fall averaged 38.7% and ranged from 0-95.7% (Hanson et al. 1986b). Natural populations probably would also experience a high percentage (near the 38.7% average) of loss during the first summer. Therefore, 35% was used as the percentage of muskellunge fingerlings that survive their first summer of life. Survival after the first year of life varies with location, age, and harvest rates. Annual mortality rates range from 25% to 70% (Crossman 1956; Muir 1963; Johnson 1967a,b, 1974; Spangler 1968; Bimber 1982; Hoff and Sterns 1986). These estimates have a median value of about 45% annual mortality (55% annual survival), which we used in this variable.

Assuming 35% survival the first summer and 55% thereafter, the percentage of fingerling muskellunge from a given year class surviving to age 10+ is presented in Table 2. The number of adults produced per fingerling muskellunge is calculated by dividing the percent of surviving fingerlings by 100. Ages 5 through 10 should account for the majority of breeding stock in most locations. Assuming a stable age structure and that most mortality occurs between autumn and spring, there would be a total of 0.0384 adult fish in the population per

Table 2. The percent of a given year class of fingerlings surviving to selected ages based on a first summer survival of 35% and an annual survival rate of 55%. The adult muskellunge per fingerling produced in the spawning habitat is also calculated.

Age	Percent of fingerlings surviving	Adult fish per fingerling produced	
		Mortality occurs autumn - spring	Mortality occurs spring - autumn
0	35.0%		
1+	19.3%		
2+	10.6%		
3+	5.8%		
4+	3.2%		0.032
5+	1.8%	0.018	0.018
6+	0.97%	0.0097	0.0097
7+	0.53%	0.0053	0.0053
8+	0.29%	0.0029	0.0029
9+	0.16%	0.0016	0.0016
10+	0.09%	0.0009	0.0009
	Total	0.0384	0.0704

fingerling produced in the spawning habitat (Table 2). Conversely, if most of the mortality occurs between spring and autumn, then the age 4+ fish should be included and there would be 0.0704 adults to fingerlings produced (Table 2). The minimum ratio of spawning habitat to summer habitat can now be calculated as follows:

$$\begin{aligned}
 \frac{\text{spawning habitat area}}{\text{summer habitat area}} &= \text{max. density of adults} \times \text{spawning habitat productivity} \\
 &\quad \times \text{adults per fingerling} \\
 &= \frac{2 \text{ adults}}{\text{ha summer habitat}} \times \frac{\text{ha spawning habitat}}{2,500 \text{ fingerlings}} \times \frac{1 \text{ fingerling}}{0.0384 \text{ adults}} \\
 &= 0.02 \frac{\text{ha spawning habitat}}{\text{ha summer habitat}}
 \end{aligned}$$

If it is assumed that most of the mortality occurs between spring and autumn, then the ratio of spawning habitat to summer habitat is reduced to 0.01. The larger value of 0.02 was chosen to develop the suitability curve because the loss or lack of suitable spawning habitat is suspected in many cases as being the cause of muskellunge population declines (Dombeck et al. 1984; Dombeck 1986).

It is assumed that optimal muskellunge habitat must have at least 0.02 ha of spawning habitat for each hectare of summer habitat. The type of vegetation and substrate in the spawning areas also affects the suitability of the habitat. As the relative quality of the spawning habitat decreases, more area is required to produce the same amount of fingerlings.

Northern pike density (V_{10}). In some situations, northern pike are known to compete with muskellunge for food and habitat. Threinen and Oehmcke (1950) cite an experiment in which 25,000 northern pike swim-up fry were stocked into a pond 11 days before 25,000 muskellunge fry were stocked. One month later, the pond was drained and yielded 402 northern pike and only four muskellunge. The invasion of native muskellunge lakes by northern pike is often followed by the establishment of pike and subsequent decline of muskellunge (Dombeck et al. 1986; Inskip 1986). Predation, competition, and hybridization are all possible interaction mechanisms between the two species. There is speculation that increased angling pressure works in favor of northern pike and is detrimental to muskellunge (Ramsell, pers. comm.). Earlier spawning in the spring, shorter generation time, a more aggressive nature, and greater food conversion efficiency have been suggested as possible advantages for the northern pike (Inskip 1986). Predation by YOY northern pike on YOY muskellunge is the most attractive hypothesis (Inskip 1986). Most others agree that in lakes with viable populations of both species, there must be sufficient spawning habitat to permit spatial separation of the species.

Inskip (1986) proposes that in many cases cultural development may be responsible for northern pike out-competing muskellunge. He states that, based on zoogeographic evidence, it appears that northern pike may be favored by cooler temperatures and more-lentic habitat. Cultural development more often results in the conversion of lotic habitat to lentic habitat than vice versa. Since the muskellunge is more adapted to life in flowing waters, this phenomenon favors the more-lentic northern pike.

Water body size (V_{11}). Muskellunge are able to prosper in small lakes without much angling pressure; however, lake size >40 ha should be optimal for muskellunge. Very large lakes, such as Leech and Winnibigoshish (Minnesota) and the Great Lakes, have healthy populations of muskellunge. It appears that lack of suitable spawning habitat and other variables limit muskellunge in larger lakes, not the size of the lake per se.

Field Use of the Model

Year-to-year variation and, in some cases, yearly variation complicate the application of this model. Between-year variation can be discounted if the model is to be applied to a single year. The goal in most cases, however, will be to compare HSI's from different water bodies or for a particular body of water over a number of years. In these cases, it is best to use an average of long-term data (if it exists) to compute HSI's. If the variation is known to occur in a range where the suitability index does not change, further consideration of variability is not necessary.

Interpreting Model Outputs

The model described here is an oversimplification of the complex interactions that are occurring in a lacustrine system. The model should not be expected to discriminate between habitats to a high degree of resolution. Each variable in the model can potentially limit carrying capacity for muskellunge. The model assumes that only these variables are acting on a population of muskellunge. Species interactions and other factors not explored here may determine, to a greater degree, the carrying capacity of a lacustrine system for a population of muskellunge.

Only a few of the variables that can potentially limit a population of muskellunge are explored here. Common sense must be applied to the output of this model for best results. The following ranges are suggested as factors of poor (0.0-0.2), fair (0.3-0.5), good (0.6-0.8), and excellent (0.9-1.0) habitat. If two areas have different HSI's, the area with the higher value is assumed to have the potential to support more muskellunge biomass per hectare.

Other Models

Dombeck et al. (1986) developed a discriminant model that is useful for determining lake-stocking and habitat improvement strategies.

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