Morphological, Physiological, and Ethological Differences Between Walleye (*Stizostedion vitreum vitreum*) and Pikeperch (*S. lucioperca*)[1,2]

T. R. MARSHALL

Ontario Ministry of Natural Resources, Fish and Wildlife Research Branch, Thunder Bay, Ont.

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A review of the literature indicated that pikeperch (*Stizostedion lucioperca*) are generally more tolerant than walleye (*S. vitreum vitreum*) of a wide range of environmental sources of stress, such as organic pollution, sedimentation, and fluctuating water levels. This advantage presumably arose from numerous morphological and physiological specializations which are expressed through appropriate behavioral patterns. Of prime importance is the ritualistic redd building and guarding behavior developed by the pikeperch which contributes to a consistently successful rate of fertilization and lowered mortality of their eggs and larvae. In addition, pikeperch have a much higher fecundity and require a less specific set of spawning conditions than do walleye. These attributes allow the pikeperch much greater reproductive success under stressful conditions and thus more flexibility in their range.

Key words: behavior, cultural eutrophication, environmental stress, morphology, physiology, pikeperch, reproductive potential, reservoirs, *Stizostedion*, walleye

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Une revue de la littérature indique que le sandre (*Stizostedion lucioperca*) est généralement plus tolérant que le doré jaune (*S. vitreum vitreum*) à une gamme étendue de sources ambiantes de stress, telles que la pollution organique, la sédimentation et les fluctuations du niveau de l'eau. Cet avantage résulte probablement de nombreuses spécialisations morphologiques et physiologiques qui s'expriment par des modalités appropriées de comportement. La construction rituelle de sillons de fraie et le comportement de garde développés par le sandre ont une importance capitale: ils contribuent à assurer un taux de fécondation uniformément élevé et une diminution de la mortalité des œufs et des larves. En outre, le sandre est beaucoup plus fécond et a besoin d'un ensemble de conditions de fraie beaucoup moins spécifiques que le doré jaune. Grâce à ces attributs, le sandre a un succès de reproduction beaucoup plus grand dans des conditions difficiles et, partant, plus de flexibilité dans sa distribution géographique.

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A review of the literature was undertaken to establish the major morphological, physiological, and ethological differences between walleye (*Stizostedion vitreum vitreum*) and pikeperch (*S. lucioperca*). This paper describes some of these characteristics and attempts to relate them to the present day distribution and success of the taxa. Special emphasis is given those attributes which have proven instrumental in the pikeperch's survival in culturally advanced trophic systems and reservoirs.

It has been proposed that all contemporary members of the genus *Stizostedion* originated in Eurasia, where the ancestors of the three North American species radiated via a land bridge or archipelago across the North Atlantic, between the Oligocene and Pleistocene periods (Svetovidov and Dorofeeva 1963). Accordingly, walleye and pikeperch have evolved over the past several million years as spatially discrete taxa.

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Humid continental and west-coast marine climates (moderated by the Gulf Stream) prevail over most of the pikeperch's range in Europe and contribute to a generally warmer and seasonally less variable climate than that found at equivalent latitudes of North America. There, much of the walleye range is influenced by a high-latitude continental climate (Bradley 1950), with seasonal extremes in temperature. In addition, lakes and rivers of Europe have been subjected to large organic inputs from a denser human population and over a much longer period of time than in comparable situations in North America, resulting in the cultural eutrophication of many European water systems. Pikeperch possess a number of unique characteristics which enable them to flourish in these advanced trophic conditions, which would probably inhibit walleye reproduction or perhaps even prove lethal.

Morphology

Pikeperch and walleye have nearly identical meristic counts (Table 1) and are superficially similar in appearance due to the commonality of a number of generic traits. Close examination, however, reveals many small structural differences. Pikeperch are slightly terete in cross-section with a proportionately smaller, more streamlined head and a deeper, more robust caudal peduncle than the walleye (R. A. Ryder unpublished data). The maximum body depth in relation to body length is consistently greater for the pikeperch, as is the ratio of the base of the pelvic fin to the interpelvic width (Shcherbukha 1968; Scott and Crossman 1973). In this way the pikeperch appears morphologically closer than does the walleye to the genus prototype which resembles the contemporary genus *Perca*.

Though both species have a subretinal tapetum lucidum consisting of a light-reflecting pigment, its effective area is relatively smaller in the pikeperch (Wunder 1930; Moore 1944; Ali and Anctil 1968). In addition, the ratio of eye diameter to head length is much smaller for the pikeperch than for the walleye (Shcherbukha 1968; Scott and Crossman 1973).

The gill rakers of the two species are unique. In walleye, the inner edge of the gill arch supports a series of stublike "knobs" adorned with short, tooth-bearing processes. Similar processes extend laterally on a series of elongated rakers supported by the outer edge of the arch. Approximately the same number of rakers are present in pikeperch, but they are all of one variety, that is, stubby, tooth-bearing nodules similar to those found along the inner gill arch of walleye.

Slight to substantial color differences exist between the two species, and subpopulations of each vary with the turbidity of the water that they inhabit. The back and sides of pikeperch (Schindler 1957) are greenish to blue-grey, with the underside silvery white or bluish. The dorsal fins have longitudinal rows of black spots, whereas the caudal fin is spotted in transverse rows. Other fins are yellowish grey. Background colors of the walleye (Scott and Crossman 1973) range from olive-brown through golden brown to yellow, with the dorsal surface somewhat darker than the sides and the ventral surface milk-white or yellow-white. The second dorsal and caudal fins have regular rows of tiny spots, whereas the first dorsal fin is unmarked except for a black blotch present at its posterior-basal border. The lower tip of the caudal and tip of the anal fin are milk-white.

Color can be used to distinguish the sexes in pikeperch, the male often exhibiting a dark pigment on its ventral surface whereas the female is lightly colored or immaculate. The genital papilla, which protrudes in the female, is another distinguishing characteristic (Gaschott 1928). Superficial sexual dimorphism is not apparent in the walleye.

The pikeperch has four to six pyloric caeca, whereas three are usually present in the walleye (Gaschott 1928; Scott and Crossman 1973). R. A. Ryder (unpublished data) observed that pikeperch have a proportionately smaller liver than that of walleye, and that the abdominal musculature of pikeperch appears to be of greater diameter than that of walleye.

The egg diameter of pikeperch ranges from 0.8 to 1.5 mm (Deelder and Willemsen 1964); in contrast, walleye eggs range from 1.4 to 2.1 mm (Miles 1915; Schultz 1971). Consequently, the ratio of surface area to volume is much greater for the pikeperch's egg, averaging 2.9 mm^2/mm^3 as compared with 1.8 mm^2/mm^3 for walleye.

Pikeperch produce a large quantity of these comparatively small eggs, accounting for their greater fecundity than that of walleye. The number of eggs per gram of body weight ranges from 110 to 260 for the pikeperch (J. Willemsen personal communication), and from 20 to 65 for the walleye (Colby et al. 1977).

Physiology

Both species can tolerate a rather great temperature range; however, pikeperch can withstand, and generally prefer, warmer water than do walleye. Temperatures allowing optimum growth range from 28 to 30°C for pikeperch, approximately 5.5 deg. C greater than for wall-

TABLE 1. Selected morphological, physiological, and behavioral characteristics of the walleye and pikeperch, on basis of literature.

Item	Walleye	Pikeperch
Morphology		
Meristic counts		
Vertebrae	44–48[a]	45–48[ll]
Lateral line scales	83–104[a]	75–150[ll]
1st dorsal spines	XII–XVI[a]	XII–XVII[ll]
2nd dorsal spines/rays	I/18–22[a]	I–III/19–25[ll]
External		
Head length/body length	.261[a]	< .250[mm]
Body depth/body length	.159[a]	.220[nn]
Snout length/head length	.253–.335[a]	.221–.222[nn]
Interobital width/head length	.157–.215[a]	.133–.141[nn]
Eye diameter/head length	.161–.267[a]	.152–.154[nn]
Base of pelvic fin/interpelvic width	.582–.746[a]	1.165–1.397[b]
Body shape in cross section	subterete[b]	strongly subterete[b]
Head shape	relatively blunt[b]	moderately streamlined[b]
Caudal peduncle	relatively slender[b]	deep, robust[b]
Teeth	numerous[b]	less numerous[b]
Tapetum lucidum	great effective area[c]	relatively smaller effective area[c]
Preopercles	posterior edge strongly serrate[b]	posterior edge less serrate[b]
Caudal fin	tips terminate in rounded lobes[b]	tips terminate at sharper angles[b]
Sexual dimorphism	not obvious[a]	ventral surface of female much lighter colored than that of male; genital papilla protrudes in female[mm]
Gill rakers	slender and elongate on outer edge of gill arch, compressed on inner edge[b]	short and robust on both edges of gill arch[b]
Color differences	trunk olive brown, golden brown, or yellow with a darker dorsal surface and white ventral surface; black blotch at posterior-basal portion of 1st dorsal (no spots), lower tip of caudal and tip of anal fin milk white[a]	back and sides greenish to blue-grey, ventral surface white or bluish; black spots on longitudinal rows on dorsal fins, caudal fin spotted in transverse rows, other fins yellowish-grey[oo]
Internal		
Pyloric caeca	3[a]	4–8[mm]
Physiology		
Water temperature		
Preferred	21–23°C[d]	24°C[d]
Upper incipient lethal	31.6°C[d]	34.3–35.0°C[d]
O_2		
Lower limits	loss of coordination and equilibrium at 0.6 mg/litre[e]	4.5 mg/litre lethal limit for embryos and fry, and lower limit of optimal zone for adults[pp]
Turbidity		
Preferred	intermediate levels[f]	high levels[jj]
Light		
Ambient daylight illumination levels	larvae positively phototactic, adults and subadults negatively phototactic[b,g,h,i]	
Reproduction		
Maturity		
Initial age	♂2–4 yr ♀3–6 yr[a]	♂2–6 yr ♀3–6 yr[mm]
Size	♂28 cm ♀36–43 cm[a]	♂32 cm ♀42–44 cm[mm]
Fecundity		
Egg no./g body wt	30–65[j]	110–260[mm]
Coefficient of fecundity	10–144[k]	12–144[qq]
Spawning		
Seasons	usually April-May with extremes from late March to late June[h]	usually April-May with extremes from late February to late July[mm,rr]

TABLE 1. *Continued.*

Item	Walleye	Pikeperch
Time of day	throughout night[a]	dawn[mm]
Temperature	normally 8°C range 4.4–14.4°C[l,m]	normally 12°C range 6–18°C[h,mm]
Depth	less than 5 m[n]	as deep as 17 m[ss]
Substrate	sand, gravel, boulders and occasionally vegetation[o]	plant roots or submerged trees on organic, sandy or stony bottom[mm]
Duration	no evidence of protracted spawning[b]	often spawn intermittently over a number of days[tt,uu]
Spawning behavior		
Mating	polygomous, broadcasts eggs[a]	monogamous, redd builder[h,mm,vv]
Postspawning	no protection of eggs[h]	fans eggs, guards nest[h]
Egg		
Egg diameter	1.4–2.1 mm[p,q]	0.8–1.5 mm[mm]
Oil globule diameter	0.8 mm[r]	0.4–0.5 mm[mm]
Surface area/volume	1.8 mm^2/mm^3[s]	2.9 mm^2/mm^3[qq]
Adhesive qualities	agglutinative until water hardened[a]	highly agglutinative until end of incubation[mm]
Resorption of eggs	observed after cold front disrupted spawning activities or during protracted cold spawning period[t,u,v]	
Fertilization		
Success	3–100%[w,x]	63–100%[mm,ww]
By artificial means	practical[y]	difficult and seldom successful[h]
	Embryonic Development	
Incubation period		
At low temp. (6–12°C)	15–34 days[z]	13–26.5 days[mm]
At high temp. (12–24°C)	4–15 days[aa]	4–13 days[mm]
Egg mortality		
Mortality rates	4–82%[o,bb]	5–10%[mm]
Temperature allowing greatest % hatch	9–15°C[z]	12–20°C[mm]
	Larval Development	
First feeding		
Initial diet	diatoms, nauplii, rotifers[cc,dd]	mostly nauplii, some rotifers[mm]
Rate of development		
Length at hatch	6.0–8.6 mm[a]	4.0–5.0 mm[mm]
Length when oil globule and yolk sac resorbed	10.0 mm[ee]	5.8–7.0 mm[mm]
Temperature of optimal growth	20–25°C[d]	28–30°C[d]
Food of postlarvae and juveniles		
Transition diet	progress from diatom-rotifers diet, to microcrustaceans (cladocerans and copepods), then to mixture of microcrustaceans and insect larvae, and finally to fish (yellow perch)[j]	progress from diet of nauplii and copepodites to copepods, then to *Neomysis*, and finally to fish (smelt)[mm]
Behavior of fry		
Schooling behavior	continue to school when piscivorous and through adult stage[o,ff]	school when plankton-feeding but become increasingly solitary when piscivorous[xx]
Factors affecting year-class strength		
Rapid spring temperature increases	positive correlation[v,w,gg,hh,ii,jj]	
	Adult Phase	
Food and feeding		
Feeding habits	opportunistic feeder, cannibalistic[j]	opportunistic feeder, seldom cannibalistic[mm]
Preferred food species	yellow perch (*Perca flavescens*) and cisço (*Coregonus artedii*)[j]	smelt (*Osmerus eperlanus*) and ruffe (*Gymnocephalus cernua*)[mm]
Swallowing of prey	usually head first[b]	often tail first[mm]
Growth		
Growth rates	the two species appear to grow at similar rates in equivalent environmental conditions[h]	

TABLE 1. *Concluded.*

Item	Walleye	Pikeperch
Behavior		
Spawning migrations	often long range; occur throughout the walleye's range[j]	usually short range; occur in isolated areas only[yy,zz]
Daily movements	related primarily to levels of subsurface illumination[b,kk]	
Daytime habitat	under submersed shelter (weed beds, submerged trees, boulders) in clear water; shielded by water column in turbid water[a,kk]	normally shielded by column of turbid waters[b,vv]

[a] Scott and Crossman (1973); [b] Ryder (unpublished data); [c] Moore (1944); [d] Hokanson (1977); [e] Scherer (1971); [f] Ryder (1968); [g] Ali and Anctil (1968); [h] Jovanovic (1970); [i] Toivonen (1966); [j] Colby et al. (1977); [k] calculated from published data, Colby et al. (1977); [l] Herman (1947); [m] Rawson (1957); [n] Baker (1964); [o] Eschmeyer (1950); [p] Schultz (1971); [q] Miles (1915); [r] Whitaker (1890); [s] calculated from published data, Schultz (1971), Miles (1915); [t] Derback (1947); [u] Kukuradze (1968b); [v] Nagiéc (1977); [w] Baker and Scholl (1969); [x] Johnson (1961); [y] Olson (1971); [z] Smith and Koenst (1975); [aa] Anonymous (1967); [bb] Smith and Kramer (1963); [cc] Smith and Moyle (1945); [dd] Hohn (1966); [ee] Nelson (1968); [ff] Hughson and Sheppard (1962); [gg] Baker (1966); [hh] Rudolph and Scholl (1970); [ii] Busch et al. (1975); [jj] Svärdson and Molin (1968); [kk] Ryder (1977); [ll] Gaschott (1928); [mm] Deelder and Willemsen (1964); [nn] Shcherbukha (1968); [oo] Schindler (1957); [pp] Kuznetzova (1955); [qq] calculated from published data, Deelder and Willemsen (1964); [rr] Svärdson and Molin (1973); [ss] Belyy (1962); [tt] Kukuradze (1968a); [uu] Kuznetsov (1970); [vv] Pollet (1959); [ww] Bastl (1969); [xx] Woynarovich (1960); [yy] Neuhaus (1934); [zz] Wiktor (1954).

eye. In addition, the upper incipient lethal temperature is 35°C for pikeperch and only 31.6°C for walleye (Hokanson 1977). The normal spawning temperature is approximately 12°C for pikeperch, with a range from 6 to 18°C (Jovanovic 1970). Walleye generally spawn at cooler temperatures, normally 6.7–8.9°C (Scott and Crossman 1973); however, a range of 4.4–14.4°C has been recorded (Herman 1947; Rawson 1957). Temperatures of 12–20°C allow optimum egg development for pikeperch (Deelder and Willemsen 1964). Similarly, Smith and Koenst (1975) found the greatest percentage hatch of walleye eggs to occur between 9 and 15°C.

In laboratory experiments, walleye have been known to thrive at dissolved oxygen concentrations of 1.5 mg/ℓ and to withstand levels as low as 0.6 mg/ℓ (Scherer 1971). Conversely, the oxygen requirements of pikeperch are relatively high, 4.5 mg/ℓ being recorded as the lower limit of the optimum zone for adults and as the lethal level for both embryos and fry (Kuznetzova 1955).

Both pikeperch and walleye are common in waters of various turbidities and can probably withstand very high concentrations of suspended materials (Wallen 1951). Pikeperch, however, seem to prefer somewhat more turbid conditions than do walleye (Jovanovic 1970).

Ethology

Adult walleye are negatively phototactic to ambient levels of subsurface illumination and during the daylight hours seek some form of physical shelter, such as boulders, weed beds, sunken trees, and other types of submerged debris (Ryder 1977). Pikeperch are also negatively phototactic as adults, but to a lesser degree than walleye due to a reduction in the effective area of the tapetum lucidum (Moore 1944; Toivonen 1966). There have been isolated reports of pikeperch seeking physical cover (Pollet 1959); however, it appears this species generally makes use of the differential in turbidity levels and simply descends in the water column to avoid excess illumination.

The feeding transition is similar for both species from larva to adult (Table 1), at which time they become opportunistic feeders preying mainly on fish. Data collected by W. J. Scidmore (personal communication) suggests that young-of-the-year and yearling walleye ingest their prey tail-first, however, adult walleye have been observed to always seize their prey from the side, and gradually work it around in their mouths until it can be swallowed headfirst (R. A. Ryder unpublished data). Pikeperch seize their prey in a haphazard manner, usually from the side or tail, particularly in the case of smelt (*Osmerus eperlanus*). N. P. Van Zalinge (unpublished data) reported that in the Tjeukemeer adult pikeperch ingest their prey headfirst; however, over most of their range they have been observed to swallow at least some species tailfirst (Neuhaus 1934; Steffens 1960; R. A. Ryder unpublished data). R. A. Ryder (personal communication) suggests that this phenomenon may be attributed to the absence of elongated gill rakers in pikeperch, which if present (as in adult walleye), would tend to snag on protruding fins and opercula of their prey. In addition, it is suspected that all spiny-rayed specimens must be oriented headfirst before ingestion to prevent spines or the preopercles from lodging in the pikeperch's buccal cavity and esophagus.

Cannibalism among walleye has been observed over most of their range and appears to be a principal source of mortality for walleye fry when the density of forage species is low (Chevalier 1973; Forney 1974). Occurrences of pikeperch cannibalism have been reported when young of its own kind were abundant and other prey fish were scarce (Steffens 1960; Willemsen 1977), however, pikeperch are generally less cannibalistic than walleye (R. A. Ryder unpublished data). This is clearly evident when examining the ease in which pikeperch are raised in hatchery ponds; a practice usually proving difficult for walleye due to high rates of cannibalism.

Pikeperch exhibit schooling behavior while feeding on zooplankton, but become increasingly solitary as they reach the piscivorous stage (Woynarovich 1960). Walleye, however, continue to school as they become piscivorous (Eschmeyer 1950) and form schools even as adults (Ryder 1977).

No distinct seasonal migratory habits have been discovered that are valid for the whole range of the pikeperch's distribution (Deelder and Willemsen 1964) although isolated cases have been described throughout Eurasia: Nikol'skii (1940), for Aral Sea pikeperch; Puke (1951) and Rundberg (1977) for pikeperch in Swedish Lakes; Tanasiychuck et al. (1954), for Volga pikeperch; Toivonen (1969), for Baltic pikeperch; and Willemsen (1977), for Ijsselmeer pikeperch. On the other hand, mature members of all self-propagating walleye populations, whether stream or lake-spawning, migrate from their overwintering grounds to their spawning grounds in spring and continue to their summer feeding grounds shortly after spawning (Ryder 1968; Colby et al. 1977). J. Thorpe (personal communication), however, suggests that this may not be such an obvious difference, but instead a function of the relative scarcity of large water bodies in the pikeperch's range, limiting the distance available for travel, and thereby making any migration less noticeable.

Balon (1975) considered pikeperch and walleye to belong to divergent ecoethological guilds based on their reproductive behavior. Walleye belong to the nonguarding, open-substrate spawning lithophil guild, whose members are adapted to well-oxygenated waters and have moderately developed respiratory organs. Pikeperch are members of the guarding, nest-spawning, phytophil guild. These fish are adapted to nesting above or on a soft organic bottom with low oxygen concentrations and a high oxygen demand.

The male pikeperch build more or less elaborate redds by excavating a round pit until the roots of submerged plants become exposed (Deelder and Willemsen 1964). The eggs are then deposited above the bottom on these plant roots, or submerged trees or various other objects exposed within the redd, where they remain until the end of incubation due to their highly agglutinative qualities. In contrast, walleye simply broadcast their eggs across a large area of unguarded substrate, usually consisting of rock, rubble or gravel. This nesting behavior results in a consistently greater fertilization rate for pikeperch, ranging from 63 to 100% (Deelder and Willemsen 1964; Bastl 1969). Johnson (1961) and Baker and Scholl (1969) report the percentage of fertilized walleye eggs to be quite variable — from 3 to 100%.

The male pikeperch guards the redd up to the early fry stages, allowing little predation on the eggs. In addition, it fans the eggs with its pectoral fins, creating water currents around them. Walleye provide no parental protection whatsoever, leaving their eggs vulnerable to predation. Hence, egg survival for pikeperch is high, with losses not exceeding 5 to 10% under normal circumstances (Deelder and Willemsen 1964), whereas up to 82% mortality of fertilized walleye eggs has been recorded (Colby et al. 1977).

Pikeperch seem to require a less rigorous set of spawning conditions than walleye. Viable pikeperch eggs have been collected as deep as 17 m (Belvy 1962), whereas the maximum depth at which walleye spawn is 4.6 m (Baker 1964). Both species are spring spawners; however, in contrast to walleye, pikeperch often spawn in batches over a protracted period of time (Kukaradze 1968a; Bastl 1969; Kuznetsov 1970). This increases the likelihood of survival of at least some offspring as some eggs of an individual would probably hatch during optimum conditions.

Adaptations of Pikeperch to Culturally Advanced Trophic Systems and Reservoirs

The preferred biotope of pikeperch can be characterized as moderate to relatively warm, productive waters, stagnant or slowly running, with a high turbidity. Waters with these attributes are usually considered as advanced mesotrophic to eutrophic in nature. Walleye generally inhabit cooler, less turbid, mesotrophic waters although early eutrophy may be tolerated in special circumstances. Various adaptations have evolved which enable pikeperch to tolerate the conditions associated with enhanced productivity and compete in such an environment.

The high reproductive potential of pikeperch offsets effects of the catastrophic change in the composition of the fish community that may occur (Kerr 1977) as lakes eutrophy. Members of the family Cyprinidae, among others, become increasingly abundant, and some of these species are known to prey on pikeperch eggs and larvae as well as to compete directly with pikeperch fry for food and space. As a counter-measure pikeperch have developed a relatively great rate of reproduction, attributable to a high fecundity, consistently successful fertilization, lowered mortality of eggs and larvae, and less rigorous spawning requirements.

Several adaptations of genetic nature have transpired which allow pikeperch to cope with accumulations of silt and seston on their spawning grounds and oxygen deficiencies in the lower strata, produced through nocturnal respiration and decomposition of large algal blooms common in eutrophic systems. The relatively great ratio of surface area to volume of the pikeperch's egg allows for a more efficient gas exchange between the developing egg and the surrounding water. Behavioral adaptations include the deposition of spawn above the anoxic bottom-water interface on plant roots and other submerged objects exposed within the nest, and fanning of the eggs to remove debris and create a continuous water exchange about them. As the majority of pikeperch populations do not undergo distinct spawning migrations these responses may be sufficient to overcome abiotic variation of spawning sites from one year to the next, and may be analagous to the extensive spawning migrations of walleye, which have been termed (Harden Jones 1968) a behavioral adaptation allowing for the maintenance of a larger population by ensuring that spawning occurs only in areas with optimum conditions.

Both species have a well-developed tapetum lucidum which enhances their vision in waters of high organic turbidity, a condition common to advancing eutrophication due to dense growths of green and blue-green algae. However, the effective tapetal area is relatively larger in the walleye, indicating greater visual acuity under reduced light intensities (Moore 1944). This reduction in area may make the pikeperch a less efficient predator in the turbid waters it normally inhabits, particularly during crepuscular or nocturnal feeding forays. Conversely, however, tapetal reduction may enable this species to function at higher subsurface illumination levels and perhaps explains the pikeperch's ability to feed during daylight hours (Jovanovic 1970) while the walleye's feeding activity is generally limited to dusk or dawn (Ryder 1977).

The critical factor limiting the pikeperch's survival in eutrophic waters is apparently its high oxygen requirement, resembling that of salmonids more than the other percids (Toivonen 1966). However, this high oxygen demand may be compensated for by vertical displacement in the water column, as the more light-tolerant pikeperch are capable of inhabiting the oxygen-rich surface waters (R. A. Ryder unpublished data). Supporting this proposal, Wundsch (1963) reported that pikeperch thrive in waters which show a seasonal oxygen shortage, provided that this shortage does not occur in the topmost 4 to 6 m of water.

Pikeperch have the ability to spawn in much deeper waters and over a much wider array of bottom types than do walleye. Consequently, they are able to tolerate the frequent and wide variations in water levels common to reservoirs. This has been demonstrated in research by Bastl (1969) on the Orava Reservoir in northern Czechoslovakia and Kuznetsov (1970) on the Kuybyshev Reservoir in central Russia, where pikeperch have become an important commercial species. The wide adaptability in choice of spawning grounds has enabled pikeperch to avoid the littoral areas and make use of the open zones of reservoirs under conditions of regulated river discharge. Similarly, in the Netherlands, Willemsen (1977) reported a relatively high catch per hectare for pikeperch in the Ijsselmeer, transformed from a marine bay (Zuiderzee) to a lake in 1932, even though the lake has been reduced to one third of its original area due to the construction of polders. Walleye have become successful in reservoirs only when tributaries suitable for spawning exist, and the problem of fluctuating water levels can be avoided, or when water levels remain relatively constant (Machniak 1975).

In summary, the pikeperch, described by Toivonen (1966) as among the most important of the eutrophication-tolerant fishes, can withstand a wider range of environmental conditions and tolerate alterations of its habitat to a much greater degree than the walleye. For these reasons pikeperch may prove to be suitable species for introduction under adverse conditions not likely to be rectified and unsuitable for native species.

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