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COMPARATIVE LIFE HISTORIES OF THE NORTH AMERICAN AND EUROPEAN WALLEYES

By Manojlo Jovanovic

TAXONOMY

The walleye, Stizostedion vitreum vitreum (Mitchill), in North America and European walleye (or sander), Lucioperca lucioperca (Linnaeus), on the Eurasian continent, are the largest members of the perch family, Percidae. Besides these two species, the subfamily Luciopercinae is represented by four more species: the blue pikeperch, Stizostedion vitreum glaucum Hubbs, and the sauger, Stizostedion canadense (Smith) in North America, and the Volga pikeperch, Lucioperca volgensis (Gmelin) and sea pikeperch, Lucioperca marina Cuvier in Eurasia (Berg, 1949).

Collette (1963), in a review of the Percidae, reassigned all Eurasian species to the genus Stizostedion and so considered North American and Eurasian forms to be congeneric. He supported his reclassification on the basis of morphological evidence. Russian workers Svetovidov and Dorofeeva (1963) concurred with Collette's findings but stated that the two groups are distinguished by rather marked ethological differences. They suggested that all existing species of the genus Stizostedion originated in Europe and that the ancestors of American Stizostedion species evolved from a form similar to that of Stizostedion marina. The latter is restricted to brackish waters of the Black and Caspian seas and the authors postulated that the fish could have found its way along the edge of a hypothetical land or island bridge across the North Atlantic, sometime between the Oligocene and Pleistocene periods.

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A morphological and anatomical description of the North American walleye, Stizostedion vitreum vitreum, has been given by Hubbs and Lagler (1949), and Berg (1949) has described the Eurasian walleye, Lucioperca lucioperca. According to both keys, the two species are very similar, diverging only in a few aspects, i.e., Stizostedion vitreum vitreum has three pyloric caeca and Lucioperca lucioperca four to nine. (In this character L. lucioperca resembles the sauger, Stizostedion canadense, which has five to eight pyloric caeca more than Stizostedion vitreum vitreum.) Some differences in coloration and mottlings of the body and fins of two species also exist. Distinctive colorations for Stizostedion v. vitreum are a large black blotch at the end of the spinous dorsal fin and a white tip on the lower lobe of the caudal fin. Rows of dark spots on the interradial membranes of dorsal and caudal fins are characteristics for Lucioperca lucioperca.

Berg (1949) describes the Volga pikeperch, Lucioperca volgensis, as a species with canine teeth absent in adults and weakly developed in the young (canine teeth are well developed in L. lucioperca). The sea pikeperch, Lucioperca marina, is similar to the American species in that the anal spines are usually weak and closely adhering to the soft portion of the fin.

Since most of European authors refer to the single species Lucioperca lucioperca (Linnaeus), the common name in further description will be European walleye. The same simplification will be applied to Stizostedion vitreum vitreum (Mitchill) as American walleye.

RANGE

Both species have a very wide distribution.

For the American walleye this range is as follows (Hubbs and Lagler, 1947): "From Great Slave Lake, the Saskatchewan River System and the Hudson Bay region to Labrador; southward on the Atlantic slope to North Carolina, and west of the mountains, to the Alabama River System of Georgia to the Tennessee River drainage of Alabama and to northern Arkansas and Nebraska. Common through the Great Lakes and many of the inland lakes and rivers of the basin; in Lake Erie chiefly to the westward."

The European walleye has the following range (Berg, 1949): "Elbe River. Basins of Baltic, Black, Azov, Caspian (Ural, Volga, Terek, Kura, Sefid-rud, Atrek), and Aral Sea (delta of the Anu-Darya; lower and middle Syr-Darya; lower Sary-Su; possibly, also in the Chu) Maritsa River, falling into the Aegean Sea. Present everywhere in the Neva Basin including Lakes Ladoga, Il'men' and Onega. In Finland as far north as 64° N. lat. and further, sporadically, to the Arctic Circle (but only in the Baltic Sea Basin). Present in the North Caucasus and Transcaucasia (both East and West). Found also in brackish waters: in the Gulf of Finland, in the Sea of Azov (including Kerch Strait and even Anapa and the Bay of Novorossiisk of the Black Sea."

HABITAT

Both the American and European walleye inhabit large lakes and rivers. The American walleye thrives in moderately fertile waters, but they occur in all types of lakes from the darkly stained dystrophic or bog lake, to the oligotrophic or clear, soft-water lake, to the eutrophic or fertile hardwater lakes--lakes which combine the necessary spawning grounds and feeding areas (Niemuth et al., 1959). Walleyes prefer waters of intermediate turbidity (Ryder, 1969). In several lakes classed as "good walleye lakes," turbidity was found to be 1.2 to 2.6 ppm (Jackson turbidity units). In Lake Gogebic, which is considered a good walleye lake, the water is soft with a methyl-orange alkalinity of 18 to 34 ppm, and pH neutral to slightly alkaline varying from 7.0 to 7.8 (Eschmeyer, 1950). In Ontario lakes, inhabited by walleyes, total alkalinity ranged from 22 to 60 ppm, and total dissolved solids from 47 to 83 ppm (Ryder et al., 1969). Moyle (1954) found that walleye waters in Minnesota have a considerable amount of total dissolved solids with carbonates predominating. The other chemical characteristics found were: total phosphorus, 0.04 ppm; total nitrogen, 0.4 ppm; chloride ion, 1.0 ppm; and sulphate ion, 2.1 ppm. Rawson (1946) refers to the successful introduction of walleye population in a Saskatchewan lake with total dissolved solids of about 15,000 ppm; mostly sodium and magnesium sulphates.

The walleye is a eurythermic animal which prefers temperatures of 70-72 F (21-22 C) in summer (Ferguson, 1958). However, Payne (1964) observed that older or larger walleyes in

Lake Ontario migrate during the summer into depths of 80 to 90 feet where temperatures probably range in the low 50's (10 C). Some authors suggested that the midsummer movement offshore and into deep water may be to avoid the high temperatures which develop in shallow water at this time. After studying the effect of temperature on walleyes in the Lac la Ronge, Rawson (1956) found that there was no evidence that the walleyes selected, or moved into, water of any particular temperature but tolerated and were active in the range from 59 to 64.5 F (15 to 18 C).

The northern-most known population of walleyes in North America inhabits Great Bear Lake where temperature rises to only about 57 F (14 C) in the summer. Some resident populations in Illinois rivers tolerate water temperatures as high as the mid-80's (30's C).[1] In southern California reservoirs, the reproduction of introduced walleyes is not successful, probably due to high temperatures. Reservoirs reach their lowest water temperatures of about 50 F (10 C) in midwinter. By spring, surface temperatures are near 65 F (18 C) (Kimsey, 1958; La Faunce et al., 1964).

The European walleye predominantly inhabits large slow moving rivers but it is commonly found in lakes and brackish waters of river deltas and continental seas. In Sweden, according to Svardson and Molin (1968), the walleye has a geographical distribution which indicates a preferred habitat of warm, eutrophic lakes with a high

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[1] Personal communication from L. L. Rock to Regier (1969).

turbidity. Koblickaya (1957) stated that channels inhabited by walleyes on the Volga delta have a velocity of 0.4 to 1.0 m/sec.

Lake Vänern, a walleye lake in Sweden, has the following hydrographic description (Puke, 1951): transparency, 0.12 to 0.46 m; pH, 6.9 to 7.3; carbonates, 24 mg/l; conductivity x 18° n. 10^{-6}, 103 to 105; electrolite content, 74-79 mg/l; oxygen content at the depths of 0 to 1.7 m, from 11.11 to 10.54 mg/l at temperatures of 61 to 63 F (15.8 to 16.8 C). Kuznecova (1955) found on the Volga River delta, an oxygen content of 4.5 mg/l appeared to be lethal for walleye embryos and fry but for older fish it was the lower limit of the optimal zone. The temperature of brackish waters of the North Caspian Sea in summer is 76 to 78 F (24.5 to 25.0 C) (Tanasiychuck, 1955). Salinity of the Caspian Sea ranges from 0.2% to 1.5%. Young-of-the-year walleye (Lucioperca lucioperca) were found in waters with salinity as high as 1.3% (Tanasiychuck and Vonokov, 1955).

Tagging experiments showed that walleyes living in brackish bays of the Baltic Sea migrate to the mouths of the bays where the salinity may be as high as 0.6% (Neuhaus, 1934). Walleyes living in the Dutch inland water system incidentally wander into the brackish Waddensea where salinities range from 1.2% to 2.9%, but they invariably die there (Deelder and Willemsen, 1964).

COMPANION FISH

The species of fish commonly found in the same habitat as the American walleye are: yellow perch, Perca flavescens; smallmouth bass, Micropterus dolomieui; largemouth bass, Micropterus salmoides; rock bass, Ambloplites rupestris; black crappie, Pomoxis nigromaculatus; nearly all members of subfamily Coregoninae (family Salmonidae); lake trout, Salvelinus namaycush; salmon species (genus Oncorhynchus--Great Lakes introduced forms); smelt, Osmerus mordax; northern pike, Esox lucius; muskellunge, Esox masquinongy; various Great Lakes Clupeidae; burbot, Lota lota; fresh water Serranidae; lake sturgeon, Acipenser fulvescens; and Great Lakes Cottidae. A number of members of the families Catostomidae and Cyprinidae and the yellow perch are important forage for the walleye.

The common fish species accompanying walleyes in European waters are: European perch, Perca fluviatilis; pope (ruff), Acerina cernua; zingel, Aspro zingel; streber, Aspro streber; striped ruff, Acerina schraetser; pike, Esox lucius; wels, Silurus glanis; a number of Coregoninae; rarely huchen, Hucho hucho; and brown trout, Salmo trutta; burbot, Lota lota; anadromous Acipenseridae; all salt water fishes of the Caspian and Aral seas; a number of Cobitidae (loach family); and many cyprinids including the genera Rutilus, Leuciscus, Phoxinus, Scardinius, Aspius, Leucaspius, Gobio, Barbus, Alburnus, Abramis, Blicca, Idus, Caspialosa, Carassius and Cyprinus. In some south European waters of the Danube basin, walleyes are found in community with such fish as the tench, *Tinca tinca*, which inhabits extremely stagnant and weedy waters.

SPAWNING GROUNDS

Spawning grounds have been a point of interest for a number of workers concerned with walleye life history, both in North America and in Europe.

For the American walleye, many spawning areas are reported by various workers: mouths of rivers and creeks (Smith, 1892); sandy bars in shallow water (Bean, 1903); near shore on gravel bottom (Everman and Latimer, 1910); flats at the edge of deep water (Miles, 1915); on sticks and stones in running water (Bensley, 1915); over broken rocks at the point where waves break (Cobb, 1923); in streams or in shallow sandy bays (Dymond, 1926); small creeks and rivers or in shallow bays near shore (Bajkov, 1930); on hard bottoms usually in moving water (Hinks, 1943); in riffles of tributary streams or on gravel reefs in shallow waters of the lake (Eddy and Surber, 1947); in a tributary stream over a stony bottom (Derback, 1947); over rock, rubble, or gravel in streams, shallow offshore reefs, or along shorelines of lakes (Eschmeyer, 1950); in tributary streams or in the lake (Rawson, 1956); in flowing water in streams or along lake shores where wave action keeps the water in motion and where the substrate is usually broken rocks or gravel, but spawning may occur on sand (Niemuth et al., 1959).

From all of these reports the conclusion is that the American walleye spawns in either streams or lakes, depending upon local conditions. The spawning substrate is hard material--gravel, rubble, or boulders. Sand is used occasionally. Spawning may occur in the flowing water of streams or in lake shallows close to the shoreline or on gravel bars where wave action scours the bottom and aerates the water. Usually, walleyes inhabiting lakes spawn in tributary rivers with moderate current velocity. Eschmeyer (1950) stated that spawning runs are not known in creeks and other smaller inlet streams.

Only a few deviations from this general pattern have been reported for the North American walleye. Niemuth et al. (1959) mentioned a population of walleyes spawning over the flooded marsh vegetation of the Wolf River bottoms and over tangled root masses of bog vegetation in Tumas Lake, Wisconsin. Spawning over vegetation in flooded areas has also been reported by Nevin (1900). Still, the absence of suitable spawning areas seems to be a major factor preventing walleyes from establishing themselves in some eutrophic lakes (Moyle, 1954).

The distribution of the European walleye does not seem to be as restricted by spawning grounds. It successfully inhabits some oligotrophic soft waters in northern Europe (Finland and Sweden) which have substrates of bed rock, boulder, and gravel as well as highly eutrophic, or dystrophic waters such as dead meanders of the Danube, Tisa and other rivers in the Panonic Flat of Hungary and Yugoslavia. The bottoms of these meanders usually consist of hard clay covered with a layer of silt and decaying organic material and overgrown with aquatic weeds. However, walleyes inhabiting flowing waters of the same rivers tend to concentrate in spawning season over harder substrate consisting of hard clay (thoroughly washed by current), sand, and fine gravel. Between these two extreme environments there are many intermediate conditions throughout Europe and Asia. It seems that the walleye thrives most successfully in mesotrophic waters.

The spawning grounds of the European walleye are described by many authors. Sabaneev (1911) found that Lucioperca lucioperca spawned in the brackish waters of sea bays. Berg (1949) stated that the Kuban walleye oviposits among thickets of cattails (Typha) and bulrushes (Phragmites), on the submerged portions of the plants, as well as offshore, in the middle of the bays and in the flooded coastal plains overgrown with vegetation. Some walleyes spawn in the brackish bays in the coastal zone of the Sea of Azov.

On the delta of the Volga River, spawning took place on the roots and stems of dead vegetation along the flooded banks (Alexandrov, 1915). However, Tanasiychuck (1955) stated that Volga River walleye spawn on the river bed but never on flooded brushy areas. Similar findings, that spawning of the Volga River walleye is not directly dependent on water level and flooding, were reported by Koblickaya (1957). Tanasiychuck (1955) describes the spawning grounds in the lower Volga delta as follows: "At the places where spawning nests were found the prevailing depth was 1.5 m. In the middle of the stream there was a pretty wide ditch with a depth of 2.5 m. Substrate was hard, sandy and partially covered with clay. In April and May the current in the middle of the stream was 0.04-0.12 m/sec. Banks were overgrown with reed and grass. High willows grow on the edge of the water and their roots extended into the water. These roots were mostly used as a substratum for spawning." Shcherbukha (1968) in a description of the spawning grounds of the South Bug River, stated: "The feature of these spawning grounds is the absence of dense vegetation. There are scanty growths of reeds (Scirpus and sometimes Phragmites) and, on the bottom, many water-lily roots (Nymphaea, Nuphar); the entire water surface being covered by their leaves; occasional growths of pondweed (Potamogeton) were seen. The bottom was fairly solid in these areas, the top layer being one of grey sands, sometimes with a small admixture of silt or crustacean shell and living Dreissena."

For the walleyes in the Don River, Konstantinov (1949) found that spawning is performed in the shallows close to the banks which are overgrown with reeds. Walleyes of the Ural River spawn on clay substrate close to the bank at a depth of no more than 0.5 m (Kuzmina, no date).

Schumann (1964) found that some populations of walleyes spawn over vegetation in flooded areas. According to Ristic (1968), and Bocharnikova (1952), walleyes never spawn over live vegetation but usually over remains of dead particles from the previous year.

For the walleyes in Lake Vänern (southern Sweden), Puke (1951) reported spawning conditions in Detter Bay as follows: "The water in this area is most markedly mixed with clay. Here the bottom consists of firm clay in which stones and gravel are inbedded, here and there overgrown with Litorella. The bottom of the central part is soft and consists mainly of clay mud, which scarcely provides a suitable ground for spawning."

In still water spawning places are not limited to a given depth. They are often situated in rather shallow water, but eggs have been found in deep water by Willemsen (1958) at a depth of 4 m; Tesch (1959) at 6.5 m; Woynarovich (1963) down to 11 m; and Belyi (1962), in a deep lake, even to 17 m. Belyi also observed that eggs laid in deep water developed just as well as those in shallow water.

SPAWNING BEHAVIOR

Generally, North American walleyes begin to arrive at the spawning grounds immediately after breakup of the ice in the spring. The number of walleyes increases rapidly as the water warms. Males appear first and tend to remain on the spawning area longer than females.

Spawning occurs almost exclusively at night. Prospective spawners lie off a spawning grounds in the daytime and come in to spawn at night. Detailed observations of the spawning act were nearly always prevented because walleyes were disturbed by artificial light and swam to deep water. The negative phototropism of this species and possibility of dazzlement is evident.

Eschmeyer (1950) described spawning activities of walleyes in Lake Gogebic, Michigan, as follows: "A group of 35 to 40 walleyes was observed. The fish were spread out along an area of shoreline about 25 feet in length, and they were within 10 feet from shore in water less than 8 inches deep. There was little activity when the fish were first seen, since they were either motionless or were swimming very slowly. Within a few minutes one of their number (presumably a female) made a sudden forward movement. Immediately 4 of the others (presumably males) approached the first and the group swam about over the shoals with great vigor, milling about and splashing, with dorsal fins and backs frequently protruding from the shallow water. After 15 to 20 seconds of such activity, they became quiet again."

More frequently walleyes will run from the lake into tributary streams for spawning. Spawning runs of walleyes from Great Lakes into their tributaries are well known and have been studied (Eschmeyer, 1950; Ryder, 1968).

Probably the most striking characteristic in the spawning behavior of the European walleye, which distinguishes it from the American walleye, is the building of a spawning nest. Almost all European workers observed and described this behavioral characteristic.

Martushev (1958) described the walleye nest and nesting behavior. Natural spawning is in nests. These nests, or pits, have a regular, circular shape and are bounded by a low mound of sediments which were excavated from the depression. Diameter of the nests is 35 to 55 cm. Walleyes use their caudal fin for digging the nest. A pair of walleyes (male and female) dig only one nest per spawning season. At the bottom of the nests there are roots and small branches of willows.

Nikolskiy (1957) stated that eggs are deposited in special hole-like nests, circular in shape, about 0.5 m in diameter, and 5 to 6 cm deep. Roots of reeds, exposed by the digging efforts of the fish, serve as substrate for the sticky eggs.

Konstantinov (1949), in his investigations of the walleyes of the Don River, stated: "Walleyes spawn in a number of river arms where banks are overgrown with reed. Males appear first on the spawning grounds and at this time they are still without signs of sperm secretion. Each of them prepares a nest, employing pectoral fins for cleaning silt. Particles of reed 0.5 cm in diameter and 4 to 5 cm long are carefully arranged at the bottom. Later, the sticky eggs are attached to them."

Shcherbukha (1968) described walleye nests in the Bug River as follows: "Pikeperch eggs were often found in large quantities on water-lily roots and, to a lesser extent, on reed roots. The roots were washed carefully where the nest was to be. The bottom around the nest was cleared of silt, as the scraper bag contained only clean sand with shell and roots of the plants mentioned." Building of nests has been mentioned also in the works of Syrovatskiy (1936), Tanasiychuck et al. (1956), Kuznecova (1955), Bilii (1958), Koblickaya (1957), Lavrovskiy (1964), and Poltavchuk (1965).

The spawning act of walleyes in rearing ponds was observed by Ristic (1968). Spawning began at 7:45 A.M. and continued until 10:30 A.M. Observation of spawning was made on two nests. Immediately before the spawning act the male and female swam rapidly around and above the nest fanning their caudal and pectoral fins vigorously. Periodically, the female discharged her eggs above the nest and the male fertilized them. This sequence was repeated six times at 10-minute intervals, until the female was spent.

Bocharnikova (1952) describes egg deposition as follows: "The female stays right over the nest and the male rapidly circles her at a distance of about one meter. Occasionally the male assumes a vertical position. All this preliminary behavior lasts approximately 20-25 minutes. After that, both fishes swim around energetically, thus making the water very turbid. During this 10-15 minute period the eggs are laid."

Many studies have shown that the European walleye spawns in the daytime. Bocharnikova (1952) stated that Kuban River walleyes start spawning at 5 or 6 o'clock in the morning. Djordjevich (1961) found that walleyes in the rearing ponds at Ecka (vicinity of Danube River, Yugoslavia) start spawning about 9 o'clock in the morning.

He also stated that more spawning activity occurred on bright, sunny and calm days. According to Tesch (1959), spawning seems to be stimulated by the approach of a meteorological depression. No record was found of the European walleye spawning at night nor of it taking place more than once a year.

SPAWNING SEASON

The spawning migration of walleyes begins soon after the ice goes out, coincident with the first warm weather, when water temperatures are 38 to 44 F (3 to 7 C). Onset of spawning depends on geographic location and climatic conditions. Reports by many workers in various localities show that the spawning season extends from late March to early June but always includes a portion of April or May.

Spawning seasons for American walleyes have been reported as follows: late March to late May (U.S. Commission of Fisheries, 1903); late March and April in Oneida Lake, New York (Raney and Lachner, 1942); April in Lake Ontario and in lakes of Manitoba (Smith, 1892; Hinks, 1943); April and May in Lake of the Woods and its tributaries (Everman and Latimer, 1910); April, May and June in the prairie provinces (Bajkov, 1930); and May and June in Lake Nipigon (Dymond, 1926).

Water temperature appears to control the spawning run. Little movement was observed at water temperatures below 38 F (3.3 C) (Rawson, 1956). At Lake Gogebic, Eschmeyer (1950) recorded spawning temperatures of 38 to 50 F (3 to 10 C). Niemuth et al. (1959) found that spawning of walleyes in Wisconsin ordinarily reaches a peak when the water temperatures are 48 to 50 F (9 to 10 C). Rawson (1956) recorded that active spawning in tributary streams of Lac la Ronge was usually between 45 and 50 F (7.7 - 10 C).

Regier (1969) stated that fluctuating temperatures would tend to disrupt spawning in the sense that the fish might spawn intermittently over a period of weeks instead of over a much shorter interval. Schumann (1964) reported that during a cold spring, which began with a warm initial burst, many walleyes failed to spawn and that many eggs spawned late in the season were sterile, apparently because they were physiologically too old.

The spawning season and spawning temperature of the European walleye are similar to those of the American walleye.

For the European walleye, spawning times are as follows: March and April in the Aral Sea basin (Berg, 1949); late April in the Don River (Berg, 1949; Nikolskiy, 1954); late April and early May in the Volga River (Tanasiychuck et al., 1954; Koblickaya, 1957); late April to mid-May in the Dnieper delta (Syrovatskiy, 1929); late March through the end of May in the Danube River (Ristic, 1968); end of April and May in Lake Vänern (Puke, 1951); and first half of June in Lake Onega (Berg, 1949).

In the rivers of southern Russia, in addition to the resident walleye which permanently lives in the rivers, there is also a migratory walleye (Lucioperca lucioperca) which ascends the rivers from the estuarine areas and the brackish regions of the sea. The resident freshwater walleye is small and spawns in the second half of April; the migratory walleye is large and spawns in May, about 2 weeks later.

Considering the beginning of walleye spawning season in different European regions, Djordjevich (1961) found that spawning in the Danube River takes place a month or more earlier than in northern Russia (Lake Ill'man and Neva Bay). Regional differences in the spawning season are, no doubt, related to differences in temperature, and to some extent, latitude.

European authors recorded water temperatures in the walleye spawning season as follows: 6-8 C in the Volga River (Tanasiychuck et al., 1954); 6-11 C on the Volga River delta (Koblickaya, 1957); and 9-11 C in the Dnieper River (Belyi, 1958). For rearing ponds, spawning temperatures are somewhat higher: 9-13 C in the Don basin (Syrovatskaya, 1953); 9-18 C in the Danube basin, Yugoslavia (Ristic, 1968); and 12-15 C in ponds of the Danube River (Martishev, 1958).

SEX RATIO ON THE SPAWNING GROUNDS

Sex ratio of walleyes on the spawning grounds has been reported by many authors. Often, disagreement in their findings is partially due to the fact that the number of fish as well as the sex ratios vary during the spawning season.

In Lake Gogebic, Eschmeyer (1950) found that males were the first to arrive on the spawning grounds in numbers. The number of females increased in the next few days until a maximum of 28% of the total was reached, then declined sharply. Males remained on the area for a number of days after the females had left. Sex ratios reported by other authors are as follows: four times as many males as females near Scriba Creek, Oneida Lake (Adams and Hankinson, 1928); 93% males in the spawning run up the Wolf River, Wisconsin (Schneberger, 1938); two males to one female during the course of a season's run at the Bemidji, Minnesota, station (Eddy and Surber, 1947).

Sex ratio of walleyes caught in the Muskegon River, were greatly different from that at Lake Gogebic (Eschmeyer, 1950). Females constituted 58% and 78% of the sample in 1947 and 1948, respectively. Three explanations for the unusually high percentage were suggested by the author. First, the dip nets may be selective (i.e., heavier females were unable to escape the net as it was lifted); second, the barrier (Newaygo Dam) may affect the sexes differently in that some males may return downstream after encountering the barrier whereas females may remain at the dam; and third, the sex ratio may, indeed, be different in this population.

For the European walleye, it has also been reported that males are the first to arrive on the spawning grounds. Their activity at this time is limited to preparing nests for spawning (Konstantinov, 1949).

Sharonov (1963) found that the sex composition of spawning walleyes in the Kuibyshev Reservoir (upper Volga River) was characterized by a slight predominance of females over males in all age groups. This was also noted by Zaryanova (1960) for a school of walleyes in the lower Volga.

Analysis of the age composition of spawning fish in the Bug River Shcherbukha, 1968) showed that more males than females were mature at 2 and 3 years of age. Young males begin spawning migrations in larger numbers and earlier than the females and they also leave the spawning grounds later. The author stated that females are not exposed to commercial fishing as much as the males because their spawning migrations occur within the period in the spring when fishing is prohibited. Sex ratio was not constant during the spawning migration; the proportion of females in April of 1962 and 1963 was only 30.8% and 54.3%, respectively; in May of 1962 and 1963, females predominated (59.0% and 80.8%, respectively).

In summary, the sex ratio of the American and European walleye varies greatly during the spawning run because of the tendency for males to mature at an earlier age and remain on the spawning grounds longer. There is no reason to believe that the sex ratio of either species is consistently other than 1:1 (Filuk, 1962; Alm, 1959).

MOVEMENT DURING AND AFTER THE SPAWNING SEASON

During the spawning season walleyes concentrate in large numbers and are easily taken in nets. In order to study the movement of walleyes during and after spawning season, investigators use the method of tagging and releasing the fish at the point of capture. Recovery of tagged fish has provided much data about the movement of walleyes. Knowledge of walleye movement has practical importance as well as intrinsic biological interest.

Spawning migrations of the American walleye have been thoroughly studied throughout its range. A number of tagging experiments demonstrated that walleyes can move considerable distances. Doan (1942) reported the recovery of a walleye that had moved 200 miles in Lake Erie. Eddy and Surber (1947) stated that in Minnesota, tagged walleyes were caught within a few months after release at distances of 70-100 miles from the place of tagging. Kingsbury (1948) reported that a female walleye tagged in Lake Champlain, New York, was caught 100 miles distant 30 days later. Tagged walleyes released in Chambly Reservoir, Quebec, traveled distances of 100 to 175 miles (Desroches, 1953). In Spirit Lake, Iowa, Rose (1949) found that some walleyes moved 5 miles in 8 hours. After spawning in the Muskegon River, Michigan, some fish moved a distance of 115 miles within 39 days at an average rate of 3 miles per day (Eschmeyer, 1950).

Hydroelectric dams, located on the walleye migratory routes, block spawning runs and may kill fish. The degree of difficulty in passing power dams appears to vary widely, presumably as a result of differences in height and construction.

Each year large numbers of walleyes on their spring spawning migration move up the Muskegon River in Michigan, and congregate below Newaygo Dam, an impassable barrier to upstream movement. Eschmeyer and Crowe (1955) studied movement of fish tagged and released below the dam and fish tagged and transported to upstream impoundments (operation known as the "Newaygo transfer"). Tagged walleyes released in the river below Newaygo Dam had a total recovery of 17.1%; for those transferred upstream (all impoundments combined), the total recovery was 18.3%. Walleyes transferred to upstream waters showed a marked proclivity to move downstream past the power dams toward their original habitat. Movement was accompanied by some mortality, and as suggested by Eschmeyer (1950), hazards to survival multiply with the number of dams which must be passed to reach the original habitat. Prevost, Lagendre, and Lesperance (1944) also noted that some walleyes were killed in passing through a 125-foot power dam in Quebec. Priegel (1968) reported that spawning walleyes in the Lake Winnebago area had a tendency to return to the spawning area where they had been marked in previous years. The tendency of the walleye to return to specific spawning areas in lakes and streams has been noted by several investigators: Stoudt, 1939; Eschmeyer, 1950;

Rawson, 1956; Olson and Scidmore, 1962; and Crowe et al., 1963. Crowe (1962) stated: "The return of tagged walleyes to areas where they had been in previous seasons and the scarcity of tagged walleyes from other areas provide strong evidence for homing behavior by this species."

Movements of Lucioperca lucioperca during and after the spawning season are similar to those reported for Stizostedion.

For walleyes inhabiting brackish water of the Don River delta (Sea of Azov), Berg (1949) stated that the main spawning grounds are situated 70-80 km upstream from the mouth of the river. Spawning also takes place in the delta of the Don and its estuarine area. Similar findings, that walleyes may migrate up stream and travel long distances for spawning or may spawn on river deltas, has been reported by three Russian authors: Nikolskiy (1940), for Aral Sea walleyes; and Koblickaya (1957) and Tanasiychuck et al. (1954), for Volga walleyes. It was also found that migration in rivers could be upstream or downstream, depending on the location of the spawning grounds, which are, in some cases, distributed throughout the river.

For the walleyes inhabiting the Danube River basin, Ristic (1968) reported that spawning migrations were characterized by very fast movement over long distances. Studies on the Sava, Danube and Tisa rivers (Yugoslavia), demonstrated that most walleyes migrate downstream after spawning. Some tagged fish moved a distance of 30-320 km within 8-149 days at an average rate of 2-18 km per day. A similar downstream mass movement was also noticed in winter.

Puke (1951) found extensive migrations by the walleye population of Vänern Lake, Sweden. One walleye was recaptured 48 km from the locality where marking took place. Similar to findings in certain American lakes, most walleyes return to the same spawning ground each year. Berg (1934, 1949) and some other Russians refer to and describe another migratory run which takes place in the fall. According to Petrov (1928), this run in the Ural River begins at the end of July, or in the beginning of August. The peak occurs in the second half of October, and the run terminates at the end of November. Talking about migration of the Don River walleye, Berg (1949) stated: "Unlike the Kuban' pikeperch, the pikeperch of the Don has two distinct runs in the river: in spring (for spawning) and in autumn. The autumn run in the Don is weaker; it begins in August and reaches its peak in October; in November, the pikeperch concentrates in the bottom pools of the river for the winter." Some remain in the sea during the winter.

Judging from the fishing success of stationary gear and from tagging studies, the autumn movement of walleyes occurs in some North American waters. According to Regier et al. (1969) some young-of-the-year walleyes tagged in September of 1959, off Pt. Pelee, Lake Erie, were caught the next spring on the south shore of Lake St. Clair. Young-of-the-year European walleyes migrate each fall (September to October) from the Caspian Sea to the Volga and Ural rivers (Tanasiychuck, 1955).

SIZE DISTRIBUTION

The best time to investigate the size distribution is during the spawning season, when walleyes are congregated in a small area and are easy to catch.

Eschmeyer (1950) found that, in the peak of the spawning season, at Lake Gogebic, male walleyes ranged from 12.2 to 22.1 inches in length and averaged 16.9 inches (43.1 cm); and females ranged from 15.4 to 28.8 inches, and averaged 18.8 inches (45.7 cm). Later, toward the end of the season, the average size of the males constantly increased indicating that smaller males left the spawning area before the large fish. The size distribution of walleyes from Lac la Ronge varied from year to year (Rawson, 1956). During the 5 years of the investigation, the males averaged 19.2 inches (48.8 cm) and the females 21.7 inches (55.1 cm). In Dixon Lake, Minnesota, Stoudt (1939) found males averaged 14.9 inches (37.9 cm) in standard length and females averaged 16.0 inches (40.6 cm).

European writers have also reported that the average length of female walleyes caught during the spawning season exceeds the average length of males. Shcherbukha (1968) stated that at the height of prespawning migration of walleyes in the Bug River, the males were smaller than the females. The differences were 2.3-6.5 cm in some years. The average sizes of mature individuals of both sexes were 40.8, 42.6, and 46.7 cm in three successive years, 1962, 1963, and 1964.

Berg (1949) cites a 1935 publication of A. V. Klimova indicating the average standard length of spawning males in Lake Onega was 50.8 cm and of females, 53.6 cm.

FECUNDITY

Estimates of the number of eggs produced by walleyes have been made by a number of workers. Some were based on counts of eggs in the ovaries, and others on the numbers of eggs stripped in spawn-taking operations.

Numerous investigations of the fecundity of the American walleye showed that the number of eggs may vary with locality or rate of growth: about 90,000 eggs for a fish weighing 2 pounds from Lake Erie (U.S. Commission of Fish and Fisheries, 1903); 30,000 to 40,000 per pound of fish (Miles, 1915); 28,000 eggs per pound of body weight for fish from Lake Gogebic (Eschmeyer, 1950); 388,000 eggs from a 12-pound female walleye taken in Wolf Lake, Minnesota (Eddy and Surber, 1947); 50,000 to 60,000 per fish at the Oneida Lake hatchery (Adams and Hankinson, 1928); and in Lake Winnebago, the average production per female is 66,500 eggs (Niemuth et al., 1959).

Fecundity of the European walleye seems to be markedly greater than the American walleye. A female from the Don weighing 2.1-3.0 kg has an average of 315,000 eggs while a Kuban' River female of the same size group has 487,000 eggs (Berg, 1949).

Dnieper delta walleyes from 0.9 to 4.5 kg varied from 180,000 to 900,000 eggs (Syrovatskaya, 1927). Specimens measuring 40 to 50 cm had 2,000 eggs per gram of spawn and specimens 70 to 80 cm long had about 1,250 eggs per gram.

For Bug River walleyes, Shcerbukha (1968) found that the fecundity of females measuring 36-63 cm averaged 269,900 eggs with extremes of 73,100 and 1,004,700. The number of eggs per gram of spawn ranged from 1,030 to 2,470 (average 1,753). Fecundity increased with body length.

EGGS ON THE SPAWNING GROUNDS

American walleyes usually broadcast their eggs and leave them without parental care. The eggs are adhesive for some hours after spawning (Leach, 1928; Eschmeyer, 1950; Nelson, Hines, and Beckman, 1965). If deposited on rocky or gravelly areas, they may adhere to the rocks for a short time, but ultimately drop between them. If these cracks and crevices are partly filled with mud and sand, there would be a greater likelihood of eggs being found by egg-eating fish or other organisms, or washed out onto an even less hospitable bottom (Regier et al., 1969).

A very high percentage of dead eggs has been reported by many workers. Eschmeyer (1950), in collections from Lake Gogebic, found that 58% of the eggs were dead and 34% were viable. In a sample from Cisco Lake, Michigan, 75% were dead and only 17% were viable.

The rest were egg shells. It is not certain if the eggs were infertile as they may have died from unknown causes after fertilization. It is not unusual for a high percentage of the eggs to die after having been attacked by fungi or protozoans. Baker and Manz (1967) found that between 19 and 49% of the eggs taken from reefs in western Lake Erie had live, developing embryos. Data from hatcheries in the Great Lakes region showed that about 45% of the eggs hatch (Van Oosten, 1937).

Regier et al. (1969) stated that weather conditions may be the critical factor affecting survival at this early life stage. Winds that generate strong currents or seiches would tend to sweep eggs from reefs and shores and deposit them in less suitable places.

Johnson (1961) studied walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and connecting waters. These bottom types included soft muck, sand, gravel, rubble and boulders. Initial fertility of eggs was high (96-100%), but the percentage of live eggs declined steadily during incubation. During the eyed-egg stage, however, there was an apparent increase in the percentage survival because dead eggs disappeared. Egg survival was best on gravel-rubble; both in terms of percentage survival and numbers of eggs surviving to the eyed stage. Survival of eggs on gravel-rubble bottom was as high as 35.7%, but as low as 0.6% on muck bottom.

Niemuth et al. (1959) reported that eggs hatch in 26 days when the water temperature is 40 F (5 C), 21 days when 50 to 55 F (10 to 13 C), and 7 days at a mean temperature of 57 F (14 C).

Baker and Manz (1967) found no discernible relation between abundance of young-of-the-year walleyes in late summer and the relative abundance of eggs or the percentage of them viable. Payne (1964) found some evidence that stronger year classes of walleyes tend to arise during warmer-than-average spawning seasons. However, no correlation was found by Carlander (1945) or Doan (1942), and data by Baker and Manz (1967) suggest an inverse relationship.

Walleyes inhabiting central and south European waters deposit their eggs into nests prepared by males immediately before spawning. Organic material at the bottom of the nest is usually carefully cleared of silt before the adhesive eggs are deposited. On good spawning grounds the nests may be situated so close together that they almost touch each other (Konstantinov, 1957).

Unlike the American walleye, which does not exhibit any parental care, the males of the European walleye are known for their habit of guarding their nests until the eggs hatch. This characteristic has been studied and described by many European workers (Syrovatskiy, 1936; Konstantinov, 1949; Nosal, 1950; Bocharnikova, 1952; Koblitskaya, 1957; Bilii, 1958; Lavrovskiy, 1964; Poltavchuk, 1965; Ristic, 1968).

Konstantinov (1949) stated that the male is extremely devoted to his nest. On occasions when the water level is suddenly dropped, the back of the guarding male may protrude out of the water. He is often exposed to wind and wave action, but will not desert the nest. Attempts to drive him away from the nest with the hand may result in bites on the fingers.

Most authors point out the importance of nest guarding. The male maintains a constant flow of water over the nest by fanning with his fins. This prevents the deposition of silt and the build-up of metabolites and brings fresh supplies of oxygen to the eggs.

Koblickaya (1957) found walleye nests 37 to 50 cm deep in slow-moving water and 1 to 2 m deep in faster moving water where aeration was better. Nests were at a depth of 2.5 m on the Volga River delta (Tanasiychuck, 1955). Observations on artificial nest-type spawning places provided convincing evidence that the walleye can spawn at greater depths if there is a suitable substrate for the eggs (Belyi, 1962). It was found that with adequate oxygen, eggs at depths of 1.5 m or more developed just as those in shallower water, indicating that depth in itself was not an environmental factor which had any serious effect on development of walleye eggs.

Tanasiychuck et al (1954) found 229,000 to 592,000 eggs in Volga delta walleye nests. Initial fertility of eggs was very high (98 to 100%). Siltation occurred in the nests located in faster flowing water and the percentage of dead eggs was 12% (time after fertilization was not given).[2]

Development of eggs in natural conditions took 18 to 19 days when the water temperature fluctuated from 6-16 C (mean 9.6 C). Spawn from the same location was transferred to laboratory conditions while in the gastrula stage and incubated. Results are shown in Table 1.

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[2] Probably the current velocity did not exceed the critical current velocity for the transport of silt. Nest depression slowed down the current and deposition of silt and sand occurred.

Table 1. --Hatching of walleye larvae in different incubation temperatures (after Tanasiychuck et al., 1954)

Temperature range during incubation (° C)	Mean temperature (° C)	Period of hatching (days)	Hatching percentage	Condition of eggs or larvae
4.4-15.8	10.0	-	-	All eggs died.
5.8-18.5	10.4	19-25	83	Embryos hatched at late stage of development. Pigmented.
6.0-16.2	9.6	22	-	"
6.2-14.8	9.8	14-17	96	"
8.6-21.1	15.7	6-11	97	Embryos not pigmented.
9.2-19.9	14.9	7-8	100	"
9.6-22.5	15.8	5-6	100	All larvae deformed and died after hatching.

Optimal results were obtained when temperature fluctuated from 6.2 to 14.8 C, when 96% of embryos hatched in the 8th stage of development.[3] At higher temperatures, hatching time was shorter, but embryos were small, without pigment, inactive, and hatched in the 7th stage of development.

In summary, the American and European species are similar in their rate of embryonic development. The single observation on egg mortality within the nest of Lucioperca suggests it may be lower than Stizostedion. If egg mortality is, indeed, less, which is very likely because of parental care, then the European species may be better adapted to silty habitats than the American species.

Considering the ability of the European walleye to stand different environmental conditions, Belyi (1968) stated: "The biology of walleye in the different stages of its development is such that it can live under unusual, as well as its usual conditions. The extent to which the walleye can adapt itself to environmental conditions is much greater than has been thought."

Russians found that some populations of European walleye (Lucioperca lucioperca) spawn in the brackish backwaters and in the coastal zone of the sea. The ability to spawn, hatch, and live in saline waters has not been noticed for Stizostedion sp. and seems to be one notable characteristic which distinguishes the European walleye from its North American relative.

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[3] Stages of embryonic development according to Krizhanovsky (1953).

An objective of the study conducted by Tanasiychuck and Vonokov (1955) was to establish the influence of salinity on the sperm, eggs, larvae, and fry of the walleye. Natural water from the central Caspian Sea, with a salinity of 1.3% was used in their experiments. It was diluted to concentrations of 0.2, 0.5, 0.7, and 1.0% with fresh water from the Volga River.

Experiments with sperm showed that the duration of spermatozoid movement increased up to a salinity of 0.5% and decreased in waters of higher salinity (Table 2). In fresh water and in water with salinity of 0.2% all spermatozoids moved, but in water of 0.7% salinity only a small number moved. The authors concluded that water of 0.2% was best for spermatozoids.

Experiments on fertilization and incubation of eggs showed that a high percentage of embryos developed normally in salinities of 0.2% to 0.7%. In 1.0% only a small number of embryos developed and some of them were degenerated and deformed. In 1.3% the eggs died the next day, apparently unfertilized.

Table 2.--Duration of movement of walleye spermatozoids in 10 C waters of various salinity (after Tanasiychuck, 1955)

	Salinity of water					
	Fresh water	0.2%	0.5%	0.7%	1.0%	1.3%
Duration of movement in seconds	88	145	558	144	46	0

BEHAVIOR OF YOUNG

Movement of walleyes immediately after hatching and for a period thereafter was not well known until recently. Bajkov (1930) said the fry usually school in comparatively shallow places. Raney and Lachner (1942) found young walleyes in water from a few inches to 2 feet in depth during the first two weeks in July. By the first week in August, fingerlings were in weed beds in about 4 feet of water. Movement toward deeper water continued with the summer, and fish were at a depth of 10 feet during September and October.

However, other studies found that fry were pelagic. Observations at Lake Gogebic and in rearing ponds (Eschmeyer, 1950), indicated that walleyes did not remain near shore after hatching. He suggested that the fry move into the open water of the lake shortly after hatching and lead a pelagic existence until a length of nearly an inch or more is attained.

Houde (1967) stated that after absorption of the yolk sac, fry concentrate from 1 to 12 feet below the surface. Wind-inducted surface currents transport the fry and concentrate them in semi-protected bays.

Forney (1966) found that the fry rise to the surface where they remain for several weeks feeding upon plankton and being preyed upon themselves by other fish.

When compared to findings of European authors, no considerable difference can be seen between the behavior of young American and European walleyes.

Belyi (1968) observed walleye larvae immediately after hatching. After hatching, young migrate towards the surface in a series of swimming and sinking ("candle") movements. About 11 hours out of each 24 are spent in active swimming. Distances traveled could be 5,616 cm in 24 hours. Romanycheva (1966) found that the newly hatched walleye larvae in the Sea of Azov remained at the bottom for 1-3 days before migrating upwards; however, Belyi felt these may have hatched prematurely and, ordinarily, larvae will migrate soon after hatching.

Krizhanovsky (1952) and Belyi (1968) stated that positive phototropism is one of the reasons for the movement of walleye larvae upwards. Experiments in aquaria, in which one part was darkened, showed that the larvae immediately moved into the lighted part.

Tanasiychuck (1955) emphasized the importance of water current over spawning grounds in rivers. The most favorable condition for larvae is when they are drifted into flooded areas rich with food and of a temperature favorable for further development. It was observed that in early stages larvae remain close to the surface but move toward deeper water as they become older. A number of larvae, drifted by current, reach the mouths of rivers and continue their growth and development in brackish waters.

In the Volga and Ural rivers, active migration of fry to the sea takes place in June. In the beginning, fry stay in waters of low salinity (up to 0.2‰), but later, in July and August, they are spread throughout the Caspian Sea. They usually do not inhabit water of salinity exceeding 0.8%, although some were found in water of 1.3% (Tanasiychuck, 1955).

FOOD

Food habits of walleyes have been studied by many workers, both North American and European. The diet of the two species is similar. Initially, they feed on zooplankton. As they grow, insects, and eventually fish, enter the diet. By adulthood they feed almost exclusively on fish.

Priegel (1969) studied the food of young walleyes in Lake Winnebago. Walleyes in the 10-15 mm size class fed principally on Diaptomus sp., Leptodora sp., and chironomid larvae. Fry of white suckers, carpsuckers, trout-perch and yellow perch were eaten to a limited extent. Food organisms eaten by fingerling walleyes in the 51-75 mm size class were (in order of frequency): Leptodora sp., Diaptomus sp., Daphnia sp. and chironomid larvae. Fry of northern pike, white bass, and yellow perch were eaten sparingly. In the 76-100 mm size class, chironomid larvae were the most important food item consumed. Fish remains were found in 96.1% of the walleye stomachs.

Smith and Moyle (1945), in a study of factors influencing production of walleyes in rearing ponds in Minnesota, made a detailed analysis of feeding by walleye fry and found rotifers to be the most important food early in life. Houde (1967), however, suggested some food selectivity at an early stage of development. Although rotifers were abundant in plankton samples from Oneida Lake, walleye fry did not eat them. Hohn (1966) found that diatoms were the first food of pelagic walleye fry in western Lake Erie.

Fish constituted 99% of the food taken by 1-year-old walleyes collected at Lake Gogebic (Eschmeyer, 1950). Stomach analysis of adult walleyes showed that fish made up 89% of the total volume of food. Insects (particularly mayflies) were also important.

Matveeva (1955) found that copepoda (*Cyclops* sp.) and cladocera (*Moina* and *Bosmina*) were the principal food of *Lucioperca* fry in rearing ponds on the Volga River delta. At the end of May, zooplankton in the ponds can reach 17 g/m^3 of water. Walleyes in the 6-10 mm size class feed exclusively on copepoda and cladocera. In the 11-20 mm size class, Chironomidae were added to the diet. Fry of walleye, pike and other fish were also taken to a limited extent. In the size class 21-30 mm, invertebrates constituted only 8% of the food (by weight) and the rest was fish.

Tanasiychuck et al. (1955) stated that weather conditions after the spawning season are critical for young fish because weather largely determines whether suitable food organisms will be available when needed. The same has been reported by Tesch (1962) and Einsele (1965).

Experiments conducted by Kuznecova (1955) showed that walleye fry, in the period when they start feeding on fish, have a daily ration as high as 20% of their body weight. The daily ration of walleye was reported to be similar to pike and perch, but food conversion efficiency of the walleye was much higher. Steffens (1960) studied feeding in young pond-reared walleyes and discovered that stomach and intestinal contents can amount to 7.7% of the body weight.

Feeding intensity is greatest at about 10 o'clock in the morning. Dekker (1962) investigated stomachs of walleyes 6-7 cm long and found that the stomachs are empty at dawn, that feeding starts at about that time and that it continues until late in the afternoon. A similar conclusion could be drawn from my personal experience on the Danube River in Yugoslavia. The most successful period for angling was between 9 A.M. and 12 noon; afterwards, fishing success declined and was at a standstill by about 6 o'clock in the afternoon.

AGE AND GROWTH

The growth of walleyes, both in North America and in Europe, varies greatly among individual fish of the same age. In many cases, by late summer of the first year of life, young-of-the-year can no longer be distinguished with certainty on the basis of length alone, because some young are larger than the smallest yearlings.

Various factors may influence fluctuations in the annual growth of walleyes. At Lake of the Woods, Carlander (1945) found that summer temperatures, especially mean temperatures in July, were positively correlated with the growth of the walleyes. Forney (1965) found that annual changes in growth increment were closely correlated with yearly fluctuations in abundance of forage fish. Smith (1966) found that water pollution can slow growth.

The average size (fork length) of young-of-the-year walleyes in Lac la Ronge was (Rawson, 1956): June 30, 0.9 inch; July 31, 2.2 inches; August 31, 3.5 inches; September 30, 4.1 inches.

Forney (1966) studied first-year growth of the walleyes in Oneida Lake, New York. He found that growth in length gradually increased until walleyes reached a length of about 20 mm during early June. Weekly growth increments from mid-June to mid-August were relatively constant, and growth rate decreased rapidly in September. Mean lengths of nine successive year classes of walleyes ranged from 118 to 163 mm on October 1 of the first growing season. The author stated that the two most important factors determining differences in first-year growth were May-June air temperatures and the relative availability and density of forage fish in late summer.

Priegel (1969) stated that lack of forage fishes and competition from other fish species in Lake Winnebago are limiting the growth of the walleye. He suggested that the long spawning migration may also be a factor related to slow growth since migration must require great amounts of energy.

A marked difference between the rates of growth of male and female walleyes was noted by many authors. Stroud (1949) found that the female walleye grew faster than males throughout their life span in Norris Reservoir. Eschmeyer (1950) found females to be faster growing than males, particularly after reaching an age of 2 years. Carlander (1945), however, found only a small difference in the rates of growth of the sexes in Lake of the Woods (3% at about 15 inches long). Female walleyes in Lac la Ronge (Rawson, 1956) were about 6% longer than the males at age X.

Many authors have reported on the growth rates of walleyes in various bodies of water. The walleye population in each usually differs in growth rate from populations in other bodies of water.

Eschmeyer (1950) summarized data on growth rates from 16 characteristic waters throughout the United States and Canada and calculated an average (Table 3).

Table 3.--Average total length in inches and centimeters, at annulus formation, of 16 walleye populations (after Eschmeyer, 1950)

	Age-group									
	1	2	3	4	5	6	7	8	9	10
Inches	6.1	10.0	13.0	15.1	16.9	18.4	19.5	21.4	22.2	22.5
Centimeters	15.5	25.4	33.0	38.3	42.9	46.7	49.5	53.3	56.4	57.1

The fastest growth rates occurred in southern reservoirs, Clayton Lake, Virginia (Roseberry, 1951), and Norris Reservoir, Tennessee (Stroud, 1949), and in moderate-sized lakes in Minnesota (Eddy and Carlander, 1939), and in Iowa (Carlander, 1948).

Temperature and availability of food in earlier growing stages are among the most important factors influencing the growth of the European walleye.

Tanasiychuck (1955) found that the best growth of walleye fry in the Volga River and its delta occurred in years when water temperatures in May and June were higher than average. Willemsen (1961) stated that in the natural habitat, the temperature preference of walleye nearly 2 cm long was about 24 C. Under laboratory conditions, the preference of fish 4 cm long was about 26 C, whereas growth was fastest at a temperature of 22 C (Vonte, 1960). The food conversion index is lowest at a temperature of 19-20 C or higher (Steffens, 1961).

Another condition influencing first year growth of walleye which is often mentioned by European workers is the water level in spring and early summer. High water level (higher than average) in conjunction with higher temperatures favors development of zooplankton and forage fish. Russian authors recorded that exceptionally good first-year growth occurred in years when mean temperature in May-June was about 25 C (Tanasiychuck, 1955).

Average size of young-of-the-year walleyes from the Volga River are given as follows (Tanasiychuck, 1955): June, 29.4 mm; July, 68.6 mm; August, 117.2 mm; September, 136.3 mm; and October, 159.2 mm. Sharonov (1968) found that the greatest growth of young-of-the-year walleyes in Knibishev Reservoir occurred in the second half of June and July, and growth declined precipitously in August.

Ristic (1968) found that some tagged walleyes had grown 196 g while migrating 80 km in 4 months. This was good growth for Danube walleyes and suggests that long migrations do not cause, or are related to, poor growth.

Difference between the rates of growth of male and female walleyes was also noticed by European authors. However, there was no numerical data in the literature available.

Data on average size of different age groups of walleyes from rivers in the Azov-Black Sea basin by Shcherbukha (1968) are presented in Table 4.

Table 4.--Mean length (cm) of different age groups of walleyes from rivers in the Azov-Black Sea basin (after Shcherbukha, 1968)

	Age-group						
	1	2	3	4	5	6	7
South Bay	19.6	31.6	39.2	43.6	49.4	56.7	63.6
Dnieper	16.9	26.9	39.3	44.3	51.3	60.1	69.5
Dniester	23.8	31.7	37.6	45.3	47.6	58.2	-
Don	17.8	35.0	40.4	46.9	53.5	59.8	64.0
Kuban'	17.8	36.2	43.2	50.1	56.7	61.5	63.1

Berg (1949 reported for the Kuban' walleye a much higher growth rate than for walleye from other European basins. This fish inhabits the Sea of Azov and its brackish waters are rich in forage fish.

The growth of the Volga walleye was given by Berg (1949) (standard length in cm):

Age in years								
1+	2+	3+	4+	5+	6+	7+	8+	9+
20.6	28.0	34.3	41.2	46.8	53.0	59.1	65.2	68.0

It is interesting that Berg's data on growth of walleye which cover the period mostly between 1920 and 1940, show considerably higher growth rates than more recent data.

One of the areas with good walleye growth is Stettiner Bay, Baltic Sea. Here the average length after one summer is about 15 cm. By contrast in Toften Lake, Sweden, they are only about 7 cm. Subsequent average total lengths for these two areas and for 24 lakes in northern Germany are given in Table 5.

Table 5.--Average total lengths (cm) of European walleyes from several localities

Localities	Number of summers										Authors
	1	2	3	4	5	6	7	8	9	10	
Stettiner Bay, Baltic Sea	15	31	47	56	64	68	70	73	78	79	Neuhaus, 1934
Toften Lake, Sweden	7	15	23	29	34	39	44	48	53	58	Maar, 1947
24 German lakes	13	24	34	43	49	55	56	57	-	70	Bauch, 1953

The growth of walleyes in Swedish waters is much lower than in central Europe or rivers and seas of the Russian Plain. Growth of walleyes from Malaren Lake has been given by Svardson and Molin (1968):

	Age in years					
	1	2	3	4	5	6
Total length (cm)	9.0	19.0	30.5	36.0	43.5	46.0

Discussing growth of walleye populations in Sweden, Svardson and Molin (1968)suggested that small annual increments observed in some walleye populations are due to intensive selection by the fishery which leaves only the smallest fish of each group. For Lake Malaren, it was stated that fishing intensity is less and the annual increments of growth are apparently larger.

By comparing growth of walleyes from Swedish waters with growth of walleyes in Germany, it was found that the latter is superior, especially for populations inhabiting the brackish waters of the Baltic Sea.

It is obvious that the walleyes from Russian waters (basins of Caspian, Azov, and Black Sea) have much higher growth rates than the walleyes from Europe or North America. However, growth of walleye populations in central European waters seems to be similar to the North American average.

AGE AND MATURITY

The age of maturity of walleye differs widely throughout its range. Among the variety of factors defining the age of walleye maturity, the most important are temperature (climate), and food availability (growth).

Priegel (1969) found that male walleyes in Lake Winnebago reached sexual maturity in their third year of life (average length of 12.7 inches) and females were mature in their sixth year of life (18.9 inches). At Lake Gogebic, males mature in their third year of life and females in their fifth (Eschmeyer, 1950). At Red Lake, males mature at age 5 and females at age 6 (Smith et al., 1952). At Lac la Ronge, 50% of both sexes were mature in their seventh year of life (Rawson, 1956).

The European walleye matures at ages comparable to its North American counterpart. In Sweden, Svardson and Molin (1968) stated that maturity comes rather gradually at 3-8 years of age for the males and at 4-8 years for the females. In the Kuban' River, Russia, both sexes mature during their fourth year of life (Berg, 1949). In the Volga delta, the walleye becomes mature during the third or fourth year of life. In the South Bug, walleyes began spawning at 2 years (Shcherbukha, 1968). Sharonov (1968) stated that in the Rybinsk Reservoir, walleyes mature at age 5 to 7. For Tisa River walleyes, Ristic (1968) found that males reached sexual maturity in the third year of life and females in the fourth year of life.

Growth rate influences the age at which maturity is reached-- rapid growth leads to maturity 1-2 years earlier than when growth is slow (Alm, 1959). The higher the temperature during the winter, the greater the percentage of females of a given year class spawning for the first time following spring (Filuk, 1962).

LONGEVITY

Little specific information was found on the longevity of American and European walleyes. However, longevity may be inferred from the final age given in growth tables. These ages may be too low because walleyes often nearly stop growing when old, and they become very difficult to age from scales or other hard parts. Estimates of age from tag returns are the most reliable.

Looking at the summarized age and growth data given by Eschmeyer (1950), the longevity of walleyes in Great Lakes region, Minnesota, and Ontario, ranges from 8 to 10 years. It seems that walleyes inhabiting waters located at higher latitudes live longer than those in southern regions. Walleyes from Lac la Ronge, northern Saskatchewan (Rawson, 1956), have a longevity of 13 years, but walleyes from Norris Reservoir, Tennessee (Stroud, 1949), live only 8 years. The maximum life span known was recorded in Lake Gogebic. One tag applied in 1947 was returned by an angler in 1965. This walleye was at least 20 years old (Schneider, 1969).

Considering the longevity of the European walleye, Deelder and Willemsen (1964) stated that because of the peculiarities of the scales, it is difficult to determine the age of old specimens by counting annuli. Boiko (1936) used cuts of anal fin-rays and found that walleyes may become as old as 17 years.

According to Berg (1949) and Klimova (1935), walleyes in Lake Onega, which is located at the northern edge of the range, live 14 years. Walleyes in Lake Malaren, Sweden, may live to be 20 years, but such specimens were extremely rare (Svardson and Molin, 1968). Walleyes inhabiting southern Europe (basins of Black and Azov seas) may live 7-8 years although fossils of an ancient population were as old as 17 years (Boiko, 1963).

Thus longevity of the two species is rather similar (up to 20 years), and varies with latitude (greater in the north than in the south) and probably also growth rate (greater when growth is slower).

NATURAL MORTALITY

Natural mortality has been estimated for relatively few walleye populations either in North America or in Europe. In view of the high fecundity of walleyes, it follows that the first year mortality (eggs to yearlings) is very high. In some waters almost all of this initial mortality appears to occur at the egg and fry stage; in others considerable mortality takes place during the first winter, depending upon the relative density of adult walleyes.

For the American walleye the annual rate of natural mortality is low but variable. The following estimates have been obtained for adult walleye populations that are subject to fairly intensive sport fisheries: 4% in a Minnesota lake (Olson, 1957); 0-9% in five Wisconsin lakes (Churchill, 1961); and an average of 4.6% during a series of years at Oneida Lake, New York (Forney, 1967). Payne (1966) estimated natural mortality at 33% and Ryder (1968) reported a natural mortality rate as high as 50% and a 3-year average of 41% in Nipigon Bay, Lake Superior. Both populations are more northerly and were not exploited intensively. Niemuth et al. (1959) reported a natural mortality of 10-15% at Escanaba Lake, Wisconsin. Schneider (1969) estimated a 17% rate for walleyes between ages III and IV in Fife Lake, Michigan. Whitney (1958) found natural mortality to be 17-27% for walleyes age IV and older in Clear Lake, Iowa.

Effect of lampreys on walleye has been examined by Ryder (1968). He reported that the highest wounding rate observed in the Nipigon River was less than 1% of all examined.

Mortality of walleyes caused by wastes produced by pulp and paper industry has been reported by many workers. Smith and Kramer (1965) found that conifer groundwood was most lethal to fingerling walleyes. Groundwood fiber may be an important factor limiting the survival of young-of-the-year walleyes in natural waters below paper mills during periods of low dissolved oxygen concentrations when water temperatures are high.

Mortality of walleyes at the egg and fry stage has been studied by many European authors. Generally, mortality is highest during the first summer of life. Mortality declines considerably thereafter.

The following factors have been reported as responsible for reducing the number of eggs, larvae and juveniles of the European walleye (Deelder and Willemsen, 1964):

1. Wind may be harmful by leading to silt deposition on the eggs, or by concentrating larvae in the leeward areas, leading to food shortage (not considered as a major mortality factor in early stages of walleye life).

2. Lassleben (1953) and Perlmutter (1961) demonstrated that the early stages of different fish species may suffer from intense illumination.

According to Woynarovich (1960), light can be harmful to walleye larvae in three ways. First, sunlight may cause direct injury and death within 3-5 hours. Second, long lasting daylight for 3-8 days may cause abnormal swimming (turning around) and death before feeding starts. Third, diffuse room-light may cause disturbances in light perception and blindness which could lead to death through starvation. As soon as pigment is formed around the cerebrum, light is no longer a dangerous factor. However, Woynarovich (1957), Bocharnikova (1952), Krizhanovskiy (1952), and Belyi (1968) believe that walleye larvae are positively phototactic.

3. Kuznecova (1955) reports that an oxygen content as low as 4.5 mg/l is lethal to young walleyes. This factor may be important in stagnant waters inhabited by walleyes; rarely is so low a level reached in typical walleye habitat.

4. Temperature affects the walleye by influencing survival of eggs and by regulating the abundance of zooplankton. Normal development of eggs takes place between 9 C and 24 C. High mortality results from low and high temperature occasionally.

According to Havinga (1949), above-average May temperatures usually result in a good year class. According to Tesch (1962), water temperature in March should be held responsible for success or failure in the reproduction of walleyes. Temperature may exert a favorable influence either directly or indirectly by leading to an increase in the number of food organisms (principally zooplankton).

According to Tolg (1961), lack of food during the larval stage is mainly responsible for the low walleye yield in Lake Balaton, Hungary. Many authors emphasize the importance of food abundance for the survival of walleye larvae. Availability of zooplankton, in particular, has been found to be of primary importance to the survival of walleye larvae (Tanasiychuck, 1959; Shcherbukha, 1968; Woynarovich, 1960; Tesch, 1968). It has been shown that the survival rates of walleye larvae are highest when food organisms are present in certain densities (Logvinovich, 1955). Without adequate quantities of food organisms of suitable size, losses of young walleye begin to rise when the larvae switch to active feeding after resorption of the yolk (Poltavchuk, 1965).

The problem of food of adequate size seems to be most important when walleyes change to a fish diet. Rate of growth of forage fish such as roach, Rutilus rutilus, or common bream, Abramis brama, is very high and a large fraction of their population soon becomes unavailable for young walleyes. Many authors reported cannibalism among young-of-the-year walleyes peaked in late summer (Nikolskiy, 1957; Ristic, 1968).

Tamanskaya (1961) stated that the effects of flood waters cannot be ignored completely. In such years the quantity of suspended material is increased, and this has an adverse effect on respiration of the eggs.

Probably one of the most unusual mortalities has been reported by Tanasiychuck et al., 1959. They found that chironomid larvae may use their mandibles to injure the thin stomach walls of young walleyes (5-6 mm long) which have ingested them.

Little numerical data were found in the European literature on natural mortality rates.

Boiko (1963) examined fossil remnants of walleye populations in the Azov Sea region and was able to obtain an accurate age composition of this unfished stock beyond age VI (Table 6). Mortality during the sixth year of life was 12% and increased through a maximum age of 17 years. Thus mortality rate and longevity of Lucioperca and Stizostedion are similar.

Table 6. --Age composition and natural mortality rates of an ancient walleye population in the Azov Sea region of southern Russia (after Boiko, 1963)

Age (years)	Age composition		Calculated rate of mortality (percent)
	Number	Percent	
3	4	0.7	-
4	20	3.7	-
5	75	13.8	-
6	117	21.5	-
7	103	18.9	12
8	79	14.5	23
9	58	9.8	28
10	36	6.6	32
11	25	4.6	36
12	15	2.8	39
13	11	2.0	42
14	6	1.1	45
15	-	-	50
16	-	-	65
17	-	-	100

FISHING MORTALITY

Schneider (1969) summarized literature on sport fishing for the American walleye. Exploitation rates ranged from 6 to 47% per year and depended on fishing regulations and fishing pressure. A rate of 20% is probably typical for a good fishery.

Comparable data for the European walleye were not found. Havinga and Deelder (1949) reported a fishing mortality of 80% at the Dutch Isselmen, but this figure probably refers to commercial, and perhaps also sport fishing. These authors also cite a study by Wiktor (1962), a Pole, where the fishing mortality was 58%. Again, both commercial and sport fisheries may be included in this estimate.

Like the American walleye, the commercial catch of the European walleye is greatly influenced by uneven recruitment and restrictiveness of fishing regulations. Because they are high-level predators, yields of both species are rather low. Woynarovich (1963) reported these annual yields (kg/ha) of <u>Lucioperca</u>: 2.2 for Balaton Lake, Hungary; 4.3 for Valence Lake; 6-7 for Frish-ter Bay, Baltic Sea; 7.0 in Stettiner Bay, Baltic Sea; and 7.5 in Danube, Hungary. Tesch (1959) reported a yield of 40 kg/ha from the Muggelsee, Holland.

ARTIFICIAL PROPAGATION AND STOCKING

Artificial propagation of walleyes in the United States began in the second half of the 18th century. After many years of walleye propagation there is probably not a suitable body of water in the walleye range which has not been stocked.

Presence of suitable spawning sites appears to be the limiting factor for establishing walleye populations in many waters. Schneider (1969) stated that failure to find the species in a particular lake nowadays, suggests that additional introductory plants have very little chance of establishing a self-perpetuating population. Walleye fingerlings were planted in 60 to 70 Michigan lakes between 1951 and 1963. They made a real contribution to the stock and fishery of four lakes; provided a limited amount of fishing in 20 lakes; contributed nothing to 17 lakes; results were not evaluated for the rest of the lakes. He recommended that introductory plants be made only in new impoundments or in waters in which the physical environment has been altered or the fish populations have been manipulated.

Maintenance walleye stocking programs in the United States showed that a fishery can be supplemented in some lakes, but only at high stocking densities of 15 to 68 fingerlings per acre, or 5 to 10 thousand fry per acre.

Lakes containing populations limited by inadequate reproduction may give better returns from stocked fish than lakes with large populations of walleyes or none at all. Examples are the walleye populations of Spirit and Clear lakes, Iowa, which have been increased by stocking (Rose, 1955; Carlander et al., 1960), and Bear and Fife lakes, Michigan (Schneider, 1969).

Stocking experiments showed that it is difficult to maintain a uniform age distribution by stocking. It seems that the survival of the second of two consecutive walleye plants is poorer than the initial plant (Schneider, 1969).

Plants every 4 years in some Michigan lakes reputedly maintained satisfactory fishing, and probably resulted in better survival of fingerlings than plants made in consecutive years.

Transplanting of walleyes in Europe is a very old procedure which started in the 16th century (Gaschott, 1928). During the last decades, the major reason for transplantation of eggs and larvae has been to increase the yield, because recruitment of walleyes is often insufficient.

In the transplantation of eggs, it is recommended that they be removed from the water, kept moist and at a favorable low temperature. Temperature may drop temporarily to 4-5 C without being injurious to the eggs. Silii (1959) reported that eggs in early developmental stages withstood long journeys better than eggs in later developmental stages.

In some European countries the demand for one-summer-old walleyes increases steadily. Theoretically, good results can be expected from stocking with these fish because, by far, the highest mortality occurs before this stage. Recently, however, serious doubt arose on the success of walleye planting. Alm (1961) reported planting of walleye yearlings in Sweden from which not a single one was recaptured. Rahn (1958) points to the fact that, on an average, only one adult walleye is caught out of every eight one-summer-old walleyes planted in eastern Germany. From tagging experiments in a lake and other data, Tesch (1961) concluded that probably less than 10% (maximum 16.8%) of the 2-year-old walleyes originated from fish planting, even though this planting was at a rather high density (62/ha).

Reasons for poor results of walleye planting have been listed by Deelder and Willemsen (1964):

1. Pond-cultured walleye are, as a rule, rather small compared with those grown in nature, owing to the high population density in ponds and the competition for food. When released, these walleyes grow slowly if they are too small to eat locally available prey fishes. As the difference in length between native and stocked walleyes increases, the smaller ones may fall victim to cannibals.

2. The habitat may not be suitable for walleyes. This can be due to shortage of suitable food (small fish) or to heavy predation by perch, Perca fluviatilis, pike, etc., but also to unfavorable physical conditions (temperature, turbidity, water depth, etc.).

3. Natural recruitment suffices already, which makes planting rather superfluous (Tesch, 1961). This phenomenon will, however, differ in the same water from year to year due to the remarkable variation in recruitment.

4. Transportation and subsequent handling should be carried out with great caution. If not, the young walleyes will either die within a few days, due to injuries, or be seized by predators immediately after planting, when they are still dazed (Rahn, 1958).

Tesch (1962) stated that in many waters the result of walleye planting will be far inferior to the effect of proper fishery regulations. Steffans (1960) made an interesting statement that habitat improvement is sometimes unintentionally attained, especially in densely populated countries, by increased water pollution. Many formerly clear lakes have gradually become more and more turbid, thus changing from pike habitat into one for walleye. Tesch (1961) stated that this phenomenon may be even more effective than fish planting.

Many European authors, however, slanted their studies toward walleye farming. The technical character of this subject will be reviewed here briefly. More detailed information can be found in the following publications: Martyshev (1958), Bilii (1958), Woynarovich (1960), Steffens (1960), Schäperclaus (1961), and Ristic (1968).

Artificial fertilization is seldom successful due to the stickyness of walleye eggs, and therefore of no importance in European hatcheries. Another difficulty is selecting ripe females since they are not fully ripe until they reach the spawning ground and are ready to spawn.

There are several different systems for culturing walleyes. In Hungary, artificial nests are put on the spawning grounds and inspected regularly. As soon as they are covered with spawn they are transplanted to more favorable places. The most popular materials for building nests are moss, stems of aquatic plants or cereals, hairy roots of willows and alders, and old fish nets.

Generally, the usefulness of this method seems to be dubious, for the very effective protection provided by the male is excluded. The damage caused by predators could be prevented by placing the nests in baskets, submerging them at some distance below the water surface and covering them with perforated covers.

In Hungary, the "Spray room method" is also used. Old fishnets are placed on the spawning grounds and as a nest is covered with spawn, it is taken up. In specially equipped rooms, water is sprayed over the eggs. Shortly before hatching, the nests are immersed in water where the larvae are born.

In Sweden, a wooden perforated box (120 x 120 x 70 cm) is placed in the water and the bottom covered with a layer of Juniperus branches. One ripe female and two ripe males are put together in the box.

There are several variations of a pond culture technique used in Hungary, USSR, Germany and Yugoslavia. The culture of walleye is often combined with that of carp (Cyprinus carpio). Walleyes can spawn in ponds where carp are present or they are encouraged to spawn in special small, shallow ponds with artificial nests. After spawning has occurred, the nests are distributed among other ponds stocked with carp (one nest per ha). In this way density can be controlled. Sometimes the eggs are left to hatch in the spawning pond, and young walleyes 3 to 4 cm long are transplanted into a larger pond. That is probably the best system because the high mortality period is eliminated and stocking results are more predictable. A disadvantage, on the other hand, is the necessity of handling the vulnerable walleyes at rather high temperatures. In Russia, walleye hatcheries are situated along the borders of the rivers, and young walleyes 3 to 4 cm long are liberated directly into the river.

Hatcheries often use fertilization to increase quantity of food for walleye fry in ponds. Forage fish are also raised in ponds together with walleyes and carp.

The production of walleye fry in ponds can be very high. The maximum production reported was 85,000 walleyes per hectare, 6 to 7 cm long. When cultured in carp ponds, the average production of walleyes is 14,000 per hectare. Yield of walleyes from ponds in southern Russia has been recorded to be 80 kg/ha of walleyes for each 250-300 kg/ha of carp.

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INSTITUTE FOR FISHERIES RESEARCH

Manojlo Jovanovic

Report approved by G. P. Cooper

Typed by M. McClure