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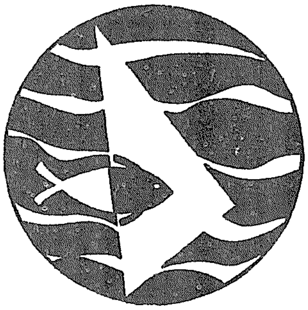

SYNOPSIS OF BIOLOGICAL DATA ON THE WALLEYE
Stizostedion v. vitreum (Mitchill 1818)

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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FIR/S119	Synopsis of biological data on the walleye, **Stizostedion v. vitreum** – P. COLBY, R.E. MCNICOL and R.A. RYDER	March 1979

SYNOPSIS OF BIOLOGICAL DATA ON THE WALLEYE

Stizostedion v. vitreum (Mitchill 1818)[1]

Prepared by

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CONTENTS

1 IDENTITY

1.1 Nomenclature

1.1.1 Valid name

Stizostedion vitreum (Mitchill 1818); Fig. 1

1.1.2 Objective synonymy (= primary synonymy)

Perca vitrea Mitchill 1818
Perca salmonea Rafinesque 1818
Lucioperca americana Cuvier and Valenciennes 1828
After Jordan, Evermann and Clark (1930) and Collette (1963)

1.2 Taxonomy

1.2.1 Affinities

- Suprageneric

Kingdom Animalia
Phylum Chordata
Subphylum Vertebrata
Superclass Gnathostomata
Class Osteichthyes
Subclass Actinopterygii
Division Teleostei
Cohort Acanthopterygii
Order Perciformes
Suborder Percoidei
Family Percidae
Subfamily Luciopercinae
Tribe Luciopercini (Collette, 1976 pers. comm.)

- Generic

Stizostedion Rafinesque 1820 (type-species by original designation *Perca salmonea* Rafinesque 1820 = *Perca vitrea* Mitchill 1818).

Genotype: *Stizostedion lucioperca* (L. 1758)

The following concept of the tribe Luciopercini will serve also as a generic concept of *Stizostedion* which is the only genus included in the Luciopercini: "Luciopercinae reaching large size; nasal flap slightly developed on anterior nostril, absent on posterior; maxillary free posteriorly; well-developed canine teeth present except in *S. volgense*; swim-bladder well developed; auxiliary interneural bone present, supraoccipital crest well developed; body slightly compressed; breeding tubercles absent; vertebrae 42-50. One genus, *Stizostedion* Rafinesque with five species" (Collette, 1963).

- Specific

Stizostedion vitreum (Mitchill)

- Type: *Perca vitrea* Mitchill 1818. Amer. Month.Mag.Crit.Rev. 1817-1818, 2:241-8; 321-8
- Type Locality: Cayuga Lake, N.Y., U.S.A.

Diagnosis: dorsum compressed; dorsal fins with obscure dusky mottlings; a large dark blotch at the end of the spinous dorsal fin; no large prominent dark spot at the base of each pectoral fin; pyloric caecae 3; D, XII-XVI, D, I-II, 18-22, A, II-III, 10-14, lateral line scales 83-104 (Svetovidov and Dorofeeva, 1963; Scott and Crossman, 1973).

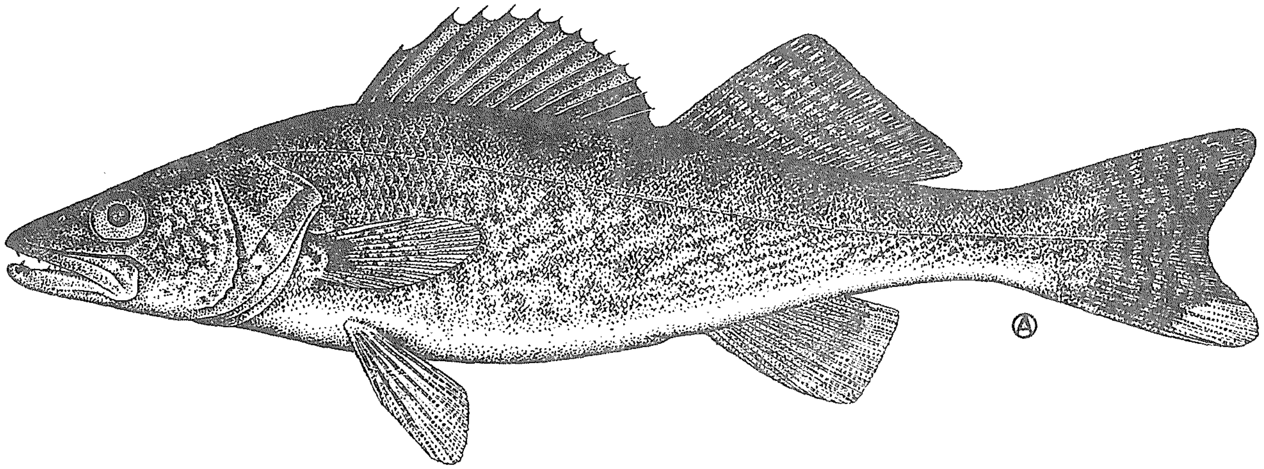

Fig. 1 Walleye *Stizostedion vitreum vitreum*; from "Freshwater Fishes of Canada" by W.B. Scott and E.J. Crossman, 1973 (Courtesy of the Royal Ontario Museum)

- Subjective synonymy

Perca Fluviatilis Pennant 1792
Perca fluviatilis L. Richardson 1823
Lucio-perca Americana (Cuvier) Richardson 1836
Lucioperca Canadensis Forelle 1857
Lucioperca grisea Forelle 1857
Lucioperca Americana Forelle 1857
Stizostedion glaucum Hubbs 1926

(After Scott and Crossman, 1973)

1.2.2 Taxonomic status

This species is well established on the basis of morphological data (Bailey and Gosline, 1955; Svetovidov and Dorofeeva, 1963; Collette, 1963); biochemical, genetic information and breeding experiments (Uthe and Ryder, 1970; Clayton, Tretiak and Kooyman, 1971; Clayton, Harris and Tretiak, 1973).

This species may be considered as polytypic with two subspecies.

1.2.3 Subspecies

Two subspecies are recognized (Bailey et al., 1970). The blue pike (*Stizostedion vitreum glaucum* Hubbs 1926: type locality - Lake Erie off Ashtabula, Ohio) intergrades commonly with the walleye (*Stizostedion vitreum vitreum* Mitchill 1818) according to Trautman (1957). The blue pike possessed several behavioural, ecological, morphological and physiological characteristics not found in the walleye. It had an extremely restricted distribution (Trautman, 1957) and is currently believed to be either extinct (McAllister, 1970) or absorbed into the gene pool of *S. vitreum vitreum* through the process of introgressive hybridization (Regier, Applegate and Ryder, 1969). Further discussion will deal only with the walleye, *S. vitreum vitreum* unless reference is specifically made to *S. vitreum glaucum*.

1.2.4 Standard common names

Walleye, yellow walleye, pickerel, yellow pickerel, pikeperch, yellow pikeperch, walleye pike, pike, yellow pike.

Vernacular Names

Doré, doré jaune (Quebec), Okow, Okanz (Algonquian), Susquehanna salmon (Eastern U.S.A.), perch pike, glasseye, green pike, grass pike, jack, jack salmon, white salmon, dory, picarel, blowfish and hornfish.

1.3 Morphology

1.3.1 External morphology (for description of spawn, larvae, and adolescents see 3.1.7; 3.2.2; 3.2.3)

In addition to the descriptions and diagnosis given under section 1.2, Table I provides a listing of values for some meristic and morphometric characteristics showing geographic variation within the known range.

Attempts to define subpopulations on the basis of morphology alone in general have been unsuccessful.

All major external morphological changes occur during the first growing season and will be described in the section dealing with larvae and adolescents.

1.3.2 Cytomorphology

No information available to authors.

1.3.3 Protein specificity

Starch gel electropherograms of muscle myogens showed a polymorphism involving three patterns: A, B and AB (Uthe et al., 1966). The distribution of these patterns were consistent with the two glacial refugia postulated for this species (Radforth, 1944) with a possible intermixing of the two subpopulations in the Great Lakes and their tributary waters (Uthe and Ryder, 1970). The plasma proteins were variable but within the limits of species specificity. Subsequent studies on electrophoresis of white skeletal muscle revealed a total of six phenotypes of malate dehydrogenase isozymes. The heritabilities of the six phenotypes were tested in a breeding experiment and provided evidence for the existence of three nondominant alleles at one malate dehydrogenase locus. The allele frequency varied in fish from four Canadian locations (Clayton, Tretiak and Kooyman, 1971). Identification of supernatant and mitochondrial isozymes of malate dehydrogenase on electropherograms were also used to separate *S. vitreum* from *S. canadense* and their suspected interspecific hybrids (Clayton, Harris and Tretiak, 1973).

2 DISTRIBUTION

2.1 Total area

The original distribution (Fig. 2) is limited to the fresh waters of Canada and the

TABLE I

Meristic counts and morphometric proportions for selected North American walleye populations

Region	Canada[a]	N.W. Canada[b]	Central U.S.A.[c]	Central U.S.A.[d]	Great Lakes[e]	Southern U.S.A.[f]
1st Dorsal Spines	12-16	12-16	13-14	12-15	12-14		11-15
2nd Dorsal Spines	1	1		1-2			
2nd Dorsal Rays	18-22	17-22	19-22	19-21	19-22		17-21
Anal Spines	2	2	2	2	2		2
Anal Rays	11-14	12-14	12-13	12-14	12-14		13
Pectoral Rays	13-16	15-16	15-16				14
Lateral Line Scales	83-104	93-108	80	83-95	80-132		88
Branchiostegals	7,7 or 7,8	6-8+7-8			7		
Gill Rakers		4-5+12-15					
Pelvic Spines	1	1	1				1
Pelvic Rays	5	5	5				5
Interneural bones						18-21	
Interhaemal bones						13-15	
Vertebrae	44-48					45-47	
Orbit/interorbital width						1.0-1.8	
S.L./head length						3.0-3.5	
Interpelvic/pelvic width						0.8-1.6	
Upperjaw length/gape						1.2-2.0	

[a] Scott and Crossman (1973)
[b] McPhail and Lindsey (1970)
[c] Cross (1967); Svetovidov and Dorofeeva (1963)
[d] Beckman (1952)
[e] Uthe and Ryder (1970) and unpublished
[f] Cook (1959)

Fig. 2 Natural distribution of the walleye in North America. Eastern limit of the walleye does not include rivers folowing into the Atlantic in which the species may have been introduced. Western limit does not include rivers, lakes and reservoirs in such states as Texas, Oklahoma, Colorado, Washington, Utah and California in which this species has been introduced (Modified from Regier, Applegate and Ryder, 1969)

United States with rare occurrences in brackish water (Scott and Crossman, 1973). Its northward penetration in Canada approximates the 13°C mean July isotherm. It ranges from near the Arctic coast in the MacKenzie River southeastward through Quebec to the St. Lawrence River and southward to the Gulf Coast in Alabama. Much of its distribution is restricted to east of the foothills of the Western Cordillera and west of the Appalachian Mountains, although there is a residual stock, apparently native along the Atlantic coast from Pennsylvania to North Carolina. The walleye has been widely introduced outside of its natural range, particularly in western reservoirs (Goodson, 1966), and along the Atlantic sea-board and elsewhere in North America (Whitworth, Berrien and Keller, 1968). Only one introduction outside continental North America is known. It was apparently introduced into the United Kingdom in 1925 but extant stocks are not known to exist (Wheeler and Maitland, 1973).

The range of the walleye in North America follows closely the distributional patterns of the northern boreal forests and the central and southern hardwood forests. It occurs as well in the larger lakes and rivers of the prairie region. This species shows a preference for large, semi-turbid waters over much of its range. Suitable lakes are generally well in excess of 400 ha in area although smaller waters may contain natural populations particularly if they form part of a larger contiguous system. Clear-water lakes, if sufficiently large and deep, may also be inhabited by the walleye. The walleye is truly a eurybiont and is capable of tolerating a great range of physical and chemical variability with the possible exception of illumination levels. Its post-glacial dispersal likely originated from two glacial refugia (Radforth, 1944; McPhail and Lindsey, 1970; Collette, pers. comm.), one on the Atlantic seaboard and a second in the Mississippi Valley.

2.2 Differential distribution

2.2.1 Spawn, larvae and juveniles

Walleye eggs are deposited in relatively shallow waters, generally varying in depth from a few centimetres to several metres (see section 3.1.6.4). Upon hatching, the fry appear to leave the spawning beds within a few hours and are carried by currents into limnetic waters. At a length of approximately 25-30 mm, the fry become benthic and move back inshore. As the summer progresses all age groups move to deeper waters. Adults and sub-adults were observed to move back inshore in the early autumn (Johnson, 1969; Kelso, 1976). Most authors have observed that by late autumn, and on through winter, all age groups have moved into deeper waters, although a few authors found them only in shallow waters at this time (Rawson, 1957; Niemuth, 1957); see section 3.5.1.

2.2.2 Adults

Adult walleyes generally occur in moderately shallow waters near boulder shoals or rock outcrops during the daytime. Diurnal feeding migrations occur in the morning and evening into shoal areas or toward the surface as light intensity reaches relatively low levels of illumination. A large part of daylight hours may be spent in contact with the substrate or concealed under boulders, log piles or brush shelters (Ryder, 1977). They are usually found above the thermocline in thermally stratified lakes although the hypolimnion may be penetrated for feeding forays or to seek shelter in extremely clear lakes. Shallow boulder reefs in lakes or rapids and waterfalls in streams are frequented following ice break-up in springtime where spawning takes place. Walleyes tend to occupy a wider depth range during winter months although fast currents and turbulent areas are avoided. Seasonal distributions occur as mentioned in section 2.2.1.

2.3 Determinants of distribution changes

Ecological

Temperature - A range of water temperature from 0-30°C is tolerated although the preferred temperature is about 20-23°C (Ferguson, 1958). Spawning occurs at about 8°C (Eschmeyer, 1950). Early life stages of the walleve are adapted to rising temperature regimes (Hokanson, 1977). Thermal requirements for growth and survival of juvenile walleye appear to be higher in outdoor experimental channels (Wrenn and Forsythe, 1978) than in laboratory studies (Smith and Koenst, 1975). Limited walleye growth was possible above 30°C in the presence of abundant forage and total population mortality occurred when minimum temperatures exceeded 33-34°C. These data suggest fewer differences in thermal requirements among percids than indicated by Hokanson (1977); Hokanson (pers. comm.).

Light - This is probably the primary factor affecting the diurnal distribution. Because of the presence of a *Tapitum lucidum* in the retina of the eye (Moore, 1944) the adult walleye is negatively phototactic (Scherer, 1976) and crepuscular or nocturnal in its feeding habits (Ali and Anctil, 1968; Ryder, 1977). However, where dissolved oxygen levels are too low to satisfy respiratory requirements the reaction to light levels diminishes (Scherer, 1971).

Turbidity - Tolerant of a wide range of turbidity; they tend to be more active in the daytime in extremely turbid lakes (Ryder, 1977).

Water colour - Frequently occurs in humic acid-stained lakes where the dark colour facilitates daytime activity. Apparently tolerates a broad range of true water colour.

Depth - Normally found in moderately shallow waters where sufficient shelter, turbidity or colour occurs to shield eyes from ambient daytime light intensities. Usually found in 1-15 m depths. May occur at depths as great as 27 m (Regier, Applegate and Ryder, 1969).

Oxygen - May tolerate dissolved oxygen concentrations in the laboratory as low as 2 mg/l. Oxygen levels at 1.0-1.5 mg/l cause walleyes to rise to the surface and at 0.6 mg/l a loss of coordination and equilibrium occurs (Scherer, 1971). Walleyes in natural conditions generally achieve their greatest levels of abundance at dissolved oxygen concentrations greater than 3 mg/l (Dendy, 1948).

Carbon Dioxide - Increases in CO_2 tension between 3 and 10 mm Hg caused walleyes to move upward into surface waters (Scherer, 1971).

pH - A pH range between 6 and 9 probably has no significant effect (Scherer, 1971). Anthony and Jorgensen (1977) noted that walleye ceased to spawn in Duchesney Creek, Lake Nipissing, Ontario, when the pH dropped below 4 but returned when the pH rose to 7.

Dissolved Solids - Tolerates a wide range up to 15 000 mg/l (Rawson, 1946). Optimum range about 40-80 mg/l (Regier, Applegate and Ryder, 1969).

Organic Compounds - Tolerant of relatively large amounts of suspended and dissolved organic compounds providing they do not create an oxygen deficit below the preferred levels.

Pollution - Reasonably tolerant of moderate levels of domestic pollution subject to the above conditions. Generally intolerant of industrial effluents releasing toxic ions or creating sedimentation on the substrate. Wastes from Kraft mills (sulphate) may inhibit spawning, alter migration routes or prove otherwise deleterious (Smith and Kramer, 1963; Smith, Kramer and MacLeod, 1965; Smith, Kramer and Oseid, 1966; Colby and Smith, 1967; Ryder, 1968).

Substratum - Preference shown for a clean, hard substratum where daylight hours are spent with the walleyes resting in contact with the bottom. Deep, organic substrata are usually avoided.

Vegetation - Tendency to avoid dense submergent vegetation. Sparse vegetation offers favourable feeding or resting areas. *Isoetes*, a small submergent plant forming dense bottom growths 1-5 cm in height, forms suitable resting areas.

Shelter - Large boulder shoals, sunken trees, or brush shelters are often sought for daytime shelter from high light intensities. Resting walleyes tend to obscure themselves from ambient illumination levels in the daytime by seeking shelter (Ryder, 1977). Dense aquatic vegetation is used only occasionally for the same purpose.

Ice - Not a limiting factor unless winterkill conditions created. Walleyes thrive in lakes at the northern end of their range with over 2 m ice depths.

Fauna - Lakes lacking suitable forage fishes usually maintain only low stocks of walleyes. Highest standing stocks usually occur in lakes with abundant small percids, cyprinids, osmerids, percopsids or coregonines.

Behaviouristic

Spawning - Spawning is generally restricted to clean, hard substrata, especially coarse gravel or small boulders. Submergent vegetation is rarely used for spawning.

Feeding - Restricted by ambient light conditions. Most active feeding periods occur during greatest percentage changes in subsurface illumination, usually at dusk and dawn or prior to rainstorms. Nocturnal feeding is common, particularly in clear-water lakes.

Adaptability

This species is truly eurybiont and is especially tolerant of a wide range of natural abiotic and biotic conditions with the exception of its extreme light sensitivity which limits most of its active period to dim-light conditions.

2.4 Hybridization

2.4.1 Hybrids; frequency of hybridization; species with which hybridization occurs; methods of hybridization

Norris Reservoir, Tennessee (Stroud, 1948), Lake Erie (Trautman, 1957) and some Missouri River (Nelson and Walburg, 1977) impoundments (e.g., Lewis and Clark Lake, South Dakota-Nebraska) are some of the few inland waters in which natural walleye hybrids have been identified. These hybrids resulted from a walleye and sauger cross. Overlap in both spawning seasons and spawning grounds may account for hybridization in these areas. Nelson and Walburg (1977) reported that approximately

10 percent of the walleyes and saugers collected by gill-nets in Louis and Clark Lake resembled hybrids. Viable offspring from artificial reciprocal crossings between these two species have also been made in laboratories and hatcheries (Nelson, Hines and Beckman, 1965; Nelson, 1968). Intergrades between walleye and blue pike were common in Lake Erie in the past (Scott and Crossman, 1973).

2.4.2 Influence of natural hybridization in ecology and morphology

Nelson (1968) describes the morphology of the reciprocal hybrids of walleyes and saugers from the embryo stage on through larval development. Embryos of the reciprocal hybrids are characteristic of the female parent for egg size, development and pigmentation. Larval development is generally intermediate to that of the parents but more closely allied to the female parent. Up to a length of 100 mm, it is not possible to distinguish hybrids from the female parent. At lengths greater than 100 mm, hybrids can be distinguished by their colouration pattern. Reciprocal hybrids have two rows of indistinct blotches on the spiny dorsal fin membrane, a small faint black spot on its posterior tip, and a distinct black spot at the base of the pectoral fins. The ventral two rays of the caudal fin are white. Walleye (female) X sauger (male) hybrids averaged 6 (range 4 to 7) dark saddles across the back while sauger (female) X walleye (male) hybrids averaged 4 saddles (range 3 to 5). Stroud (1948) described adult hybrids as having a walleye-like head and a sauger-like body with pigmentations of fins being intermediate between the two. The growth rate of these hybrids was found to be intermediate between that of the walleye and sauger.

Regier, Applegate and Ryder (1969) suggested that introgression among *Stizostedion* species could, at least to some extent, explain the disappearance of the blue pike and sauger in Lake Erie. The destruction of spatial isolation between blue pike and walleye populations would facilitate such introgression and may have resulted from two events. They are the large increase in numbers of walleyes in the Central and Eastern Basins during the 1950s (Davies, 1960) and the inferred stress of increasingly large areas of anoxic waters in the Central Basin, which presumably forced the blue pike into shallower water (Regier, Applegate and Ryder, 1969 after Carr, 1962). Both probably caused an overlap in ranges. Introgression may also have been one of the causes of the disappearance of the sauger from Lake Erie, although this is highly speculative (Regier, Applegate and Ryder, 1969).

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

Identification of sex of adult walleyes without dissection can be very difficult unless they can be stripped during spawning (Eschmeyer (1950) citing Deason (1933), Carlander (1945), Kennedy (1949), and Eddy and Surber (1947)). However, Adams and Hankinson (1928) reported that females in Scriba Creek, New York, could be distinguished readily by the indistinctness of the white on the tip of the lower lobe of the caudal fin and Bean (1913) reported that females can be distinguished during spawning by their larger size and when accompanied by several males. Eschmeyer (1950) found no external characteristics by which the sex of walleyes could be determined throughout the year. However, by dissection they can be distinguished with reasonable facility, especially by experienced workers, and if both sexes are present in a given collection. Microscopic examination of the gonads may be necessary at certain times of the year, however, or in immature individuals.

Walleyes are heterosexual; however Dence (1938) reported on a hermaphroditic walleye, 356 mm long, caught in Chittenango Creek at Bridgeport, New York, in April 1933. Also Halnon (1963) suspected sex reversal in walleyes from tagging studies in Lake Champlain, New York. At least 9.3 percent of tag returns were identified as being opposite in sex to what they apparently were when marked.

3.1.2 Maturity

Age and size of walleyes at maturity vary with the water temperature (climate) and probably food availability (lake fertility) within a given lake.

Male walleyes mature at an earlier age than do females. Scott and Crossman (1973) reported that male walleyes generally mature at 2-4 years of age, over 279 mm in length, and females at 3-6 years of age at 356-432 mm. However in Canton Reservoir, Oklahoma, where first year growth for walleye is exceptionally great, nine age I males were found to be sexually mature along with 6.2 percent of the age II females (Grinstead, 1971).

A trend toward an earlier maturity among the more rapidly growing fish, both males and females, has been reported in Oneida Lake, New York (Forney, 1965). A similar trend has been observed for heavily exploited walleye stocks in Saginaw Bay, Lake Huron (Hile, 1954), the western basin of Lake Erie (Wolfert, 1969), and Dexter

TABLE II

Relationship between life span and age of maturity of walleyes

Location and Reference	Observed life span	Age at which majority of age-class are sexually mature ♂	♀
El Capitan Reservoir, California (Miller, 1967)	III+	II	III
Lake Meredith, Texas (Kraai and Prentice, 1974)	VII+	II	III
Canton Resevoir, Oklahoma (Grinstead, 1971)	VII+	II	III
Center Hill Reservoir, Tennessee (Muench, 1966)	VIII+	II	III
Pike Lake, Wisconsin (Mraz, 1968)	X+	III	IV
Lake Erie (Wolfert, 1966)	XI+	II	III
Current River, Missouri (Fleener, 1966)	XI+	III	-
Deer Lake, Ontario (Armstrong, 1961)	XII+	VI	VIII
Lac la Ronge, Saskatchewan (Rawson, 1957)	XIII+	VII	VII
Lake of the Woods, Minnesota (Carlander, 1945)	XIV+	IV	VI
Big Trout Lake, Ontario (Armstrong, 1961)	XVIII+	IV	VI
Dexter Lake, Ontario (Moenig, 1975)	XVI+	IV	V

Lake, Ontario (Moenig, 1975). A wide range in percentage of mature fish has been reported for walleyes ages I to VIII. Late maturity in walleyes is usually associated with colder waters and there is a tendency for late maturing walleyes to have a longer life span than early maturers (Table II). Deason (1933) and Carlander (1945) have also reported that some older female walleye may be sterile or fail to spawn annually. Summer body growth during the gonad refractory period may determine the proportion of females that mature. Forney (1965) observed that the proportion of non-ripening female walleyes was highest (16 percent) in the year of poorest growth in Oneida Lake, New York.

3.1.3 Mating

Courtship of walleyes in a stream compound has been described by Ellis and Giles (1965). They explained that overt courtship began by either males or females approaching another of either sex from behind or laterally and pushing sideways against the fish, or drifting back, circling around and pushing the approached fish backward. The first dorsal fin was alternately erected and flattened during these approaches, while the approached fish would either hold position or withdraw. This behaviour appeared to constitute the preliminary essentials of courtship and was promiscuous with no continued relationship between any particular pair of fish. As activity increased in frequency and intensity, individuals began to make preliminary darts forward and upward until one or more females and one or more males came closely together and the compact group rushed upward. At the surface the group swam vigorously around the compound until the milt and eggs were emitted; swimming then stopped and the females frequently turned or were pushed violently onto their sides. This movement by the females was taken by the authors as an indicator of spawning even when no eggs or milt were seen. On one occasion during the emission of milt a male was clearly seen to have the first dorsal fin fully erect. Ellis and Giles (1965) reported spawning groups to consist of one female with one or two males, but larger groups occurred occasionally with maxima of two females and six males.

Individual females tended to spawn in bouts (one female spawned up to three times in one minute) with occasional spawnings outside the main bout for each female. The upward spawning rush by a group and emission of sexual products takes only a few seconds (of the order of 5 sec) to complete, although courtship behaviour may occasionally last 1-2 min before consummation or cessation. Baker (1967b) observed spawning walleyes in Lake Erie and noted that in one instance the entire spawning act, i.e., the time involved in swimming to the surface, emitting eggs and presumably milt, and swimming back to the bottom, lasted about 5 sec. Approximately 200-300 eggs were released at this time. Ellis and Giles (1965) summarized spawning, based on clear sightings of simultaneously released eggs and milt, as consisting of a series of synchronized acts by promiscuous groups of fish. Each act was preceded by a simple short courtship consisting of approaches and bodily contacts between individuals. There was no indication of territorial defence, which agrees with Eschmeyer's (1950) observations, even though some fish maintained this position for hours.

Eschmeyer (1950) observed and described several apparent spawning acts in Lake Gogebic. The behaviour consisted first of a grouping of walleyes, then a movement of the female followed by approaches by males. This led to group movement over the shoals, in water usually less than 0.9 m deep, with vigorous splashing and milling about. The dorsal fins and backs frequently protruded from the shallow water. After 15-20 sec of such activity, the fish became quiet and continued swimming leisurely as before. Although a considerable amount of splashing could sometimes be heard at many places along the shoreline, particularly on quiet nights, little or no splashing was heard on other nights, even during the peak of the spawning season. Chance observations at night suggested that there was a considerable variation in spawning behaviour. Eschmeyer observed two fish lying parallel facing out toward the lake about 2.5 cm apart and with barely perceptible fin movement. Suddenly and simultaneously, each fish tilted slightly, so that their vents were closely adjacent. Fanning with the caudal fins became more vigorous, and slight quivering of the abdomen of one fish was observed. The action lasted for only a few seconds, after which the fish resumed their original position, became alarmed, and fled to deeper water. During extensive spawning on another evening, three separate groups of fish (between 10 and 12 fish/group) were observed, milling about in a circle (0.9-1.8 m in diameter) next to the shore or beside a large boulder. Movement within the groups was vigorous and accompanied by much splashing. These closely grouped, milling fish were undisturbed by the light for several seconds and were undoubtedly spawning.

Eschmeyer noted that except when specific spawning acts were in progress, the majority of fish were close to shore, on or near the bottom, in water less than 0.6 m deep. Although most of the activity was confined to water less than 0.9 m, a few eggs were in 1.2 m of water. Most fish seen in Lake Gogebic showed little activity, either moving slowly or laying motionless, in pairs or singly, or in loosely aggregated groups of 3-15 or more individuals. Eschmeyer counted the number of walleyes in 40 groups of fish and obtained a mean of 6.7 fish per group with seven being the number most commonly observed. Such groups were more readily identifiable early and late in the spawning season than near the peak when uniformly large numbers of fish were present over considerable areas.

Eschmeyer (1950) citing Miles (1915) describes still another manner of mating in which the female walleye swam through the grass emitting spawn as she passed. She was followed at a distance of 1.5-6.1 m by one or two males who delivered the milt and fertilized the eggs.

3.1.4 Fertilization

Fertilization is external with sperm and ova shed freely into the water.

3.1.5 Gonads

The development of the reproductive organs in walleyes has been described by Eschmeyer (1950). He described the gonads as lying close to the ventral wall of the swim bladder often extending forward to about its anterior end. The right and left members are free for most of their length but unite posteriorly, just anterior to the genital aperture.

In young females 51-76 mm long, the ovaries are small, little developed, and usually heavily pigmented throughout their length. Their location (in preserved specimens) is revealed by the presence of a double row of large melanophores lying along the ventral surface of the swim bladder. At 127 mm the ovaries are much larger, and the melanophores are either scattered over much of the surface of the organs, or more frequently, are confined to a rather narrow band along each side of the mesovarium. In adult females the pigment is usually confined to a few scattered melanophores located anteriorly and dorsally on the organs. Larger immature females have translucent ovaries (opaque when preserved), which are quite cylindrical, with transverse blood vessels throughout their length that become increasingly conspicuous as the fish grows. The anterior end of the ovary is broadly rounded or comes to a blunt point.

The ovaries of spent females consist of a pair of elongate thin-walled sacs, bluish-red in colour, with transverse blood vessels clearly evident. Small round yellowish-white spots (residual eggs) are often scattered irregularly about the ovary lying against the inside wall. Others' eggs occur in the lumen, or are buried in the fleshy interior and are easily exposed by a longitudinal dissection of the ovary. Some of the residual eggs are spherical, turgid, and translucent, while others (being resorbed) are white, often soft, and no longer spherical. Some eggs (often those lying free in the lumen) may persist in the organs for months.

In male walleyes 51-76 mm long the testes appear as fine threads with little or no pigmentation and are markedly smaller in cross-section than the ovaries of fish of similar size. When melanophores occur they are few and usually restricted to the anterior-dorsal portion of the gonad. Testes of larger immature males are elongated, lacking the bluntly tapered anterior end typical of ovaries, and unlike ovaries the transverse blood vessels are scarcely evident. Testes of immature males are about equal in diameter throughout their length and much smaller in cross-section than are ovaries of females of similar size.

The testes of spent males are also smaller than are ovaries of spent females of the same size. They are greyish-white (not greatly different in colour from mesenteric fat) having a smooth, glossy appearance and are sharply tapered anteriorly. Eschmeyer found little change in appearance of the testes in July and August at Lake Gogebic (northern Michigan), but by mid-October they were large, milky-white, flossy, soft in texture, and had attained a size and weight about equal to that of the ovaries of females. The testes later became firmer and during the spawning season pressure on the abdomen caused milt to exude or spurt from the genital aperture. The milt of some males was nearly exhausted during the spawning season. However, Eschmeyer reported that all males handled at Lake Gogebic between 29 April and 27 May 1947 released milt in quantity, although it appeared to be more viscous later in the period.

Eschmeyer found that the location of the longitudinal blood vessel in the gonads is of some help in recognizing the sex of mature fish. The vessel occurs at the surface of ovaries but lies in a dorsal groove in testes. The groove is shallow in spent males, but becomes increasingly deep with approaching maturity. By October (at Lake Gogebic) the blood vessel comes to lie at the bottom of a groove which sometimes extends almost to the centre of the testes.

One ovary is usually longer than the other. Of 60 females (immature and mature) examined at random, Eschmeyer reported the right ovary was longer in 39, the left in 9, and the ovaries of 12 were of approximately equal length. Conversely, testes were more frequently of equal length.

Eschmeyer described the development of the reproductive organs with the progress of the season showing the proportion of the total body weight of walleyes contributed by the ovaries or the testes. The proportions were in slight error because Eschmeyer found that fully developed ovaries averaged 5.1 percent heavier in the field than after fixation in 10 percent formalin. Ovaries of immature females averaged 0.3 percent of the weight of the fish (May-October). In mature females from Lake Gogebic this percentage was 0.7, 4.7 and 16.3 in August, October and just before spawning in May, respectively. In larger fish from other waters the ovaries averaged 24.1 percent (Muskegon River, Michigan) and 27.8 percent (Saginaw Bay, Lake Huron), indicating an apparent positive correlation between relative size of ovary and size of fish. In spent fish from Lake Gogebic taken in May, immediately after spawning, the ovaries averaged 1.4 percent of the body weight. This decreased to an average of 0.7 by early July or about the same percentage as that observed in August.

The relative weights of reproductive organs of males varies from 0.1 percent (average of two immature fish taken from Lake Gogebic in October) and 0.2 percent (for 15 males collected in August) to 4.3 percent (20 males taken in October). Eschmeyer believed the testes showed little weight increment after this time. Three males taken before and during the spawning season at Lake Gogebic averaged 3.0 percent of body weight, by late June 0.4 percent and by July this proportion was 0.2 percent.

Values from Ioganseṇ's (1955) modification of Severtsov's (1941) formula for specific fecundity, $SF=(x.r)^{\frac{1}{2}pj}$, (p = period between two successive spawnings; x = number of spawnings during lifetime; r = number of eggs produced per spawning; j = age onset of maturity) range from 15 for Lake of the Woods walleyes (data from Carlander, 1945) to 144 for walleyes in the western basin of Lake Erie (data from Walfert, 1969). The number of eggs produced by a female during a single spawning may vary considerably. A 1.6 kg female may produce from 72 000 to 110 000 eggs (MacKay, 1963). Average egg production in various waters (Table III) ranges from 29 700 eggs/kg in Norris Reservoir, Tennessee (Smith, 1941) to 82 700 eggs/kg in

TABLE III

Fecundity of walleyes from some North American waters

Location and Reference	Number of eggs/kg of fish Range	Average
Lake of the Woods, Minnesota (Carlander, 1945)		50 000
Wisconsin Waters (Niemuth, Churchill and Wirth, 1966)	28 600 - 99 000	
Lake Winnebago, Wisconsin (Priegel, 1970)	63 441 - 96 116	
Lake Gogebic, Michigan (Eschmeyer, 1950)	57 922 - 67 797	61 846
Little Cutfoot Sioux Lake, Minnesota (Johnson, 1971b)	48 840 - 73 700	65 239
Muskegon River, Michigan (Eschmeyer, 1950)	65 778 - 95 955	
Lake Erie (western basin) (Wolfert, 1969)	56 314 - 123 249	82 700
Lake Erie (eastern basin) (Wolfert, 1969)	41 191 - 96 914	61 149
Utah Lake, Utah (Arnold, 1960)	27 900 - 52 562	47 410
Mississippi River (Nord, 1967)	50 600 - 110 100	
Center Hill Reservoir, Tennessee (Muench, 1966)	37 954 - 143 827	64 715
Norris Reservoir, Tennessee (Smith, 1941)	28 415 - 32 727	29 700
Lake Meredith, Texas (Kraai and Prentice, 1974)	36 500 - 72 200	52 000

the western basin of Lake Erie (Wolfert, 1969). Fecundity of walleyes increases with age. There appears to be a curvilinear relationship between the number of eggs produced and the total length of the walleye (Fig. 3) while the relation between weight and the number of eggs produced (Fig. 4) is almost linear (Johnson, 1971b; Wolfert, 1969).

3.1.6 Spawning

3.1.6.1 Season

Spawning has been reported as early as January or February, and as late as June depending on water temperature. Cook (1959) reported that walleye moved up the Pearl River, Mississippi and into the tributaries to spawn in January and February. She reported that a commercial fisherman caught two females heavy with roe in the Pearl River, 4 February 1948. However, observations of actual spawning in

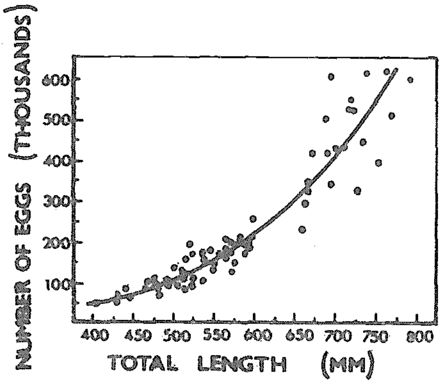

Fig. 3 Relation between number of eggs and length in 78 walleyes from the western basin of Lake Erie in March and April, 1966 (Redrawn from Wolfert, 1969)

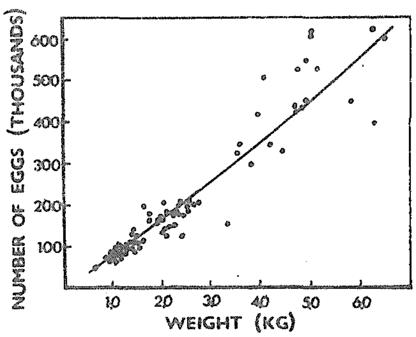

Fig. 4 Relation between number of eggs and weight in 78 walleyes taken from the western basin of Lake Erie in March and April 1966 (Redrawn from Wolfert, 1969)

areas at the southern limits of their distribution have not been reported to the knowledge of the authors. Further north, spawning occurs from March to late May. Spawning occurs as early as March in Kentucky (Clay, 1962) and Utah (Arnold, 1960); begins in April and ends in May in Michigan (Eschmeyer, 1950) and Wisconsin (Churchill, 1962); and may occur near the end of June or later in northern Canada (Scott and Crossman, 1973). Northern populations do not spawn some years, when temperatures are not favourable (Scott and Crossman, 1973).

The first day of spawning activity at a given location may vary up to four weeks on a year to year basis, depending on yearly variations in the arrival of spring. Examples are as follows: 5 April to 2 May, Red Lakes, Minnesota (Smith and Pycha, 1960); 5 April (1946) to 7 May (1950), Escanaba Lake, Wisconsin (Anon., 1957). Duration of the spawning season may range from 4 to 34 days with peak periods ranging from 1 to 10 days (Table IV).

3.1.6.2 Temperatures

A review of the Canadian literature by Scott and Crossman (1973) indicates that spawning normally begins shortly after ice breaks up in a lake, at water temperatures of 6.7-8.9°C but has been known to take place over a range of 5.6-11.1°C. A review of U.S. literature (Cobb, 1923; Eddy and Surber, 1947; Herman, 1947; Eschmeyer, 1950; Arnold, 1960; Clay, 1962; Mraz, 1962; Baker, 1964-1969) indicates that spawning temperatures are very similar to those in Canada, especially those in the northern U.S.A., Cobb (1923) reported taking eggs at a water temperature as high as 17.2°C but commented that eggs taken at the higher temperatures are "poor" as a rule.

In Alabama, walleye spawning begins at water temperatures of about 8.9-10°C. Spent and ripe females have been collected from streams at water temperatures of 12.8-14.5°C where, once spawning begins, water temperatures may increase rapidly during a one-week period (Barry W. Smith, Alabama Dept.of Cons. and Nat. Resour., pers. comm.).

Spawning temperature appears to be a function of the thermal history and maturation state of the stock. In Lac la Ronge, Saskatchewan, walleye spawning runs commenced at higher temperatures (7.2-11.1°C) in years when this event occurred sooner (30 April-7 May) and at lower temperatures (3.3-7.2°C) in years when spawning was delayed by cold weather (17-21 May) (Rawson, 1957).

The upper temperatures limiting successful spawning and egg viability and how this may vary between races is of much concern (Edsall and Yocom, 1972). A chill temperature hypothesis has been suggested whereby females may require cool water temperatures during maturation for producing viable eggs. Walleyes that have been planted in El Capitan Reservoir, San Diego County, California, where winter water temperatures rarely drop below 10°C, have excellent growth but do not reproduce naturally (Miller, 1967). However, walleye are present in natural reproducing populations as far south as Mobile, Alabama, where the water temperature in these streams rarely drops below 10°C, even for a short period of time (Barry W. Smith, pers. comm.). Thus, if a cooling period is necessary for high walleye egg viability, the requirements may vary greatly between races.

Scott and Crossman (1973) explain that prespawning behaviour (courtship) may begin much earlier than spawning when the water temperature is 1.1°C. Cobb (1923), Rawson (1957) and Priegel (1970) found walleye to run up streams in which the water comes to suitable temperatures for spawning before the ice is out of the lakes. Walleye spawning runs from Oneida Lake into Scriba Creek were blocked when creek temperatures were colder than lake temperatures (Forney, 1967). In the Lake Winnebago system in Wisconsin, the walleye spawning run commenced sooner in the warmer tributary river marshes (2.2-15.6°C) than in the larger, colder main lake (4-11°C). Eschmeyer (1950), citing Jan Metzelaar (unpubl.), reported that during the first week in April a commercial fisherman, Lee Lounsbery, observed walleyes spawning under the ice in shallow water in Saginaw Bay, Lake Huron.

3.1.6.3 Behaviour

A summary of walleye behaviour during the spawning season, excluding previously described courtship behaviour (3.1.3 Mating), follows:

TABLE IV

Duration of spawning season for walleyes from various North American lakes

Location and Reference	Year	Length of spawning season			Peak
		Start	Finish	Number of days	
Lake Winnibigoshish, Minnesota					
(Stoudt, 1939)	1937		1 June		
(Stoudt, 1939)	1938	28 March	1 May	34	
Red Lakes, Minnesota (Smith and Pycha, 1960)	1941-1957	5 April-2 May		10-28	
Wolf River (Lake Winnebago) Wisconsin					
(Kmiotek, 1952a)	1949			14	
(Kmiotek, 1952a)	1951	12 April	27 April	16	
Lac la Ronge, Saskatchewan					
(Rawson, 1957)					
Montreal River	1951	28 April	11 May	13	30 April-5 May
Montreal River	1952	17 April	8 May	21	1-7 May
Potato Lake	1953	2 May	13 May	11	5-9 May
Potato Lake	1955	30 April	15 May	15	7-12 May
Highway Creek	1954	4 May	25 May	21	17-21 May
Highway Creek	1956	6 May	22 May	16	12-18 May
Mille Lacs Lake, Minnesota		2nd week April	2nd week May		
(Maloney and Johnson, 1957)					
Pearl River, Mississippi		January-February			
(Cook, 1959)					
Bobcageon Region, Kawartha Lakes, Ontario					
(Bradshaw and Muir, 1960)	1960	25 April	29 April	4	
Provo River (Utah Lake), Utah					
(Arnold, 1960)		25 March	2 April	8	25-27 March
Lake Erie					
(Baker and Scholl, 1971)	1960	31 March			
Escanaba Lake, Wisconsin					
(Churchill, 1962)	1961	29 April	22 May	23	
Wolf River (Lake Winnebago), Wisconsin					
(Priegel, 1962a)	1961	8 April	18 April	10	12 April
Kentucky					4th week March
(Clay, 1962)		March			
Wolf River (Lake Winnebago), Wisconsin					
(Priegel, 1963)	1962	12 April	19 April	7	16 April
Wolf River (Lake Winnebago), Wisconsin					
(Priegel, 1964a)	1963	13 April	18 April	5	15 April
Lake Winnebago					
(Priegel, 1966a)	1964	11 April	24 April	13	16-18 April
Fox River (Lake Winnebago)					
(Priegel, 1965a)	1965	8 April	14 April	6	10-11 April
Lake Winnebago					
(Priegel, 1966a)	1965	20 April	4 May	14	21-22 April
Fox River (Lake Winnebago)					
(Priegel, 1967b)	1966	30 March	10 April	11	3-4 April
Lake Winnebago					
(Priegel, 1967b)	1966	7 April	29 April	22	13-14 April
Center Hill Reservoir, Tennessee		2nd week March	2nd week April		1st week April
(Muench, 1966)					
Fox River (Lake Winnebago)					
(Priegel, 1968)	1967	31 March	9 April	9	3-4 April
Lake Winnebago					
(Priegel, 1968)	1967	8 April	16 April	8	12-13 April
Lake Erie					
(Baker and Scholl, 1969)	1969				11-21 April
Lake Erie					
(Baker and Scholl, 1971)	1970	19 April			
Canton Reservoir, Oklahoma					
(Grinstead, 1971)					10-20 March

Males precede the arrival of female walleye to the spawning grounds and remain for a number of days after the females have left (Eddy and Surber, 1947; Eschmeyer, 1950; Rawson, 1957; Johnson and Johnson, 1971).

The sex ratio among walleyes during spawning runs and on the spawning grounds usually favours males which mature earlier. The preponderance of males over females has been reported by Adams and Hankinson (1928), Schneberger (1938, 1939 and 1940), Derback (1947), Eddy and Surber (1947), Eschmeyer (1950), Harlan and Speaker (1956) and Kmiotek (1952b). Individual observations varied from 51 to 99 percent males depending on time of sighting and its coincidence with time of peak spawning. Eschmeyer (1950) found the maximum proportion of females on the spawning grounds to coincide fairly well with the peak of the spawning season as determined by counts on the spawning beds. He found females constituted 58 and 72 percent of the spawning run in 1947 and 1948 respectively in the Muskegon River, Michigan. He did not explain the wide difference in sex ratio compared with other observations, but suggested that dip nets used to collect the fish may have been selective for females burdened with eggs (about one quarter their body weight). Eschmeyer also suggests that females come to the vicinity of the spawning grounds before they are ready to spawn. He speculated that the increase in proportion of spent females with the season meant that some females remain near the spawning grounds after spawning, thus becoming more numerous as a group as the season progresses.

Courtship (see 3.1.3) and spawning behaviour have been described in a lake and stream by Eschmeyer (1950) and Ellis and Giles (1965) respectively. They found that walleye are essentially nocturnal spawners and usually vacate their shallow water spawning grounds during the day. This behaviour pattern, according to Ellis and Giles (1965), implies either that the fish usually complete spawning in one night and are replaced by others later, or if spawning takes more than one night to complete, there must be a diel behavioural cycle. Rare occurrences of diurnal (between 13.00 and 16.30 h) spawning behaviour have been reported by Adams and Hankinson (1928), Eschmeyer (1950), Priegel (1970) and MacCrimmon and Skobe (1970), although emission of sex products was not observed.

Ellis and Giles (1965) observed a diel behavioural cycle by walleyes on natural spawning grounds, in experimental tanks and in a stream compound. The cycle consisted of low activity in daytime, expressed mainly by position-holding, and an increase of activity in the evening (expressed in courtship behaviour) when illumination fell below 0.172 lux.

It appeared to Ellis and Giles (1965) that females can spawn out completely in one night whereas males have the potential for spawning over a longer period. Priegel (1970) provided evidence that tagged "green" female walleyes that were released, would ripen, spawn and leave the spawning grounds within one day. Ellis and Giles also believed the suggestion by Niemuth, Churchill and Wirth (1966) that isolated pairs spawn less actively than grouped fish, implying that the activity of grouped fish is a product of mutual stimulation, not actually necessary to successful fertilization, but perhaps facilitating it. However, Regier, Applegate and Ryder (1969) have viewed group spawning as a behavioural adaptation that increases the chance of fertilization success in light of the low viability of either the sperm or egg.

Homing behaviour (tendency to return to the same spawning area in successive years) has been reported by Smith, Krefting and Butler (1952), Eschmeyer and Crowe (1955), Rawson (1957), Crowe (1962), Olson and Scidmore (1962), Forney (1961a, 1962b), Payne (1963), Ryder (1968), Johnson and Johnson (1971), and Spangler, Payne and Winterton (1977).

The walleye is usually regarded as a relatively far ranging species (Eschmeyer and Crowe, 1955) with simple spawning habits; there are no redds and they broadcast their eggs with no parental care for incubating eggs (Johnson, 1961) or newly hatched fry (Crowe, 1962).

3.1.6.4 Spawning grounds

Walleye spawn in relatively shallow water, varying usually from a few centimetres to several metres. Some reported spawning depths are as follows: as shallow as 10.1 cm and usually less than 0.9 m in Lake Gogebic, Michigan (Eschmeyer, 1950); in 0.6 m of water in the Provo River, Utah (Arnold, 1960); 5.1-12.2 cm but mostly between 30 and 76 cm in Lake Winnibigoshish and connecting water, Minnesota (Johnson, 1961); 0.61-1.52 m in Kentucky waters (Clay, 1962); 1.83-4.57 m in Lake Erie (Keller and Manz, 1963; Baker, 1964); and 0.2-0.9 m in Talbot River, Ontario (MacCrimmon and Skobe, 1970).

The literature indicates that walleye spawn over various bottom types in streams and lakes where sediments and sufficient exchanges or movement of water permit an adequate supply of oxygen to the developing embryo.

Eschmeyer (1950) reviewed spawning ground descriptions by various workers and summarized them as follows: "Mouths of rivers and creeks (Smith, 1892); sandy bars in shallow water (Bean, 1902 and 1903); along the entire shoreline, near shore, on gravel bottom (Evermann and Latimer, 1910); shallow bars or "flats" at the edge of deep water (Miles, 1915); on sticks and stones in running water at the foot of waterfalls (Bensley, 1915); on sand and gravel, in shallow water (Henshall, 1919); in lakes (over broken rocks, at the point where waves break) if prevented by weather or other causes from entering streams (Cobb, 1923); in streams or in some cases in shallow sandy bays (Dymond, 1926); anywhere near the mouths of streams where depth and other conditions are suitable, or in lakes if prevented by weather or other causes from entering streams (Adams and Hankinson, 1928); small creeks and rivers or in shallow bays near shore (Bajkov, 1930); in streams, on sandy bars in shallow water (Fish, 1932); in tributary streams or in the lake (Stoudt, 1939); on hard bottoms, usually in moving water (Hinks, 1943); up tributary streams in riffles or on gravel reefs in shallow waters of the lake (Eddy and Surber, 1947); in a tributary stream, over a stony bottom (Derback, 1947); and on gravel shoals and bars in a lake, or gravel bottoms in a stream with a good flow of water (Kingsbury, 1948)." Some populations spawn over vegetation in flooded marshy areas (Schumann, 1964; Priegel, 1970).

In spite of the diversity of spawning habitat, the absence of suitable spawning areas seems a significant factor preventing them from establishing themselves in certain eutrophic lakes (Moyle, 1954). Colby and Smith (1967) found that oxygen concentrations drop to low levels very near the mud-water interface and that hydrogen sulphide concentrations are high over wood-fibre sludge deposits and are inimical to walleye eggs. It is very likely that similar conditions occur in eutrophic lakes. Both Eschmeyer (1950) and Johnson (1961) found that in lakes walleyes avoided sandy shorelines and utilized isolated patches of gravel and rubble; some areas used being less than a metre in diameter. They also noted that unused areas generally had steeper depth gradients and were less often wave-washed. Where rock or gravel is not available walleyes spawn over sand or silt bottoms. However, fine substrates may hinder egg survival which is suspected for Missouri River main stem reservoir populations (Benson, 1968).

Walleye eggs are adhesive for some hours after spawning (Nevin, 1887; Reighard, 1890; Leach, 1927; Raney, 1959; Nelson, Hines and Beckman, 1965). If deposited on rocky bottoms they may adhere to the rocks for a short time, but ultimately drop into the cracks and crevices where they may be protected from predators. If these openings fill with mud or organic material, however, they do not provide this protection and in addition the eggs may actually be destroyed by decomposition products, since walleyes provide no parental protection for the eggs. In contrast the European pikeperch (see Appendix 3) male ventilates the eggs - which may partially account for their competitive advantage in lakes to a later stage of eutrophy (Rundberg, 1977).

Johnson (1961) observed walleye eggs on several bottom types in Lake Winnibigoshish, Minnesota, and found survival poorest on the soft muck detritus bottom, intermediate on fine sand bottom, and best on gravel rubble bottom (Table V).

Johnson (1961) believed that eggs on clean firm gravel-rubble substrates were subject to less entanglement in debris and presumably less scouring from waves than on the other bottom types. Probably current velocity or wave action is also important. Daykin (1965), applying the mass transfer theory to the problem of respiration of fish eggs, suggested that the observed limiting or critical levels of ambient oxygen are velocity-dependent. Thus in areas of slow current velocity, flocculent material settles on the bottom and this may interfere with gas transfer in two ways: first, if there is an oxygen demand by the bottom material, the current velocity may not be sufficient to supply ambient oxygen to the eggs and second, coating of the egg case with debris may also interfere with gas exchange through the egg membrane. However, this hypothesis needs to be confirmed with critical laboratory studies before any definitive cause-effect statements can be made.

3.1.7 Spawn

Walleye eggs are spherical, translucent and pale yellow in colour (authors' pers. observ.). Derback (1947) described their colour as being slightly pinkish. They have a mean diameter range of 1.5-2.0 mm (Scott and Crossman, 1973) but the means in some areas have been reported to be as small as 1.37 mm (Schultz, 1971) and as large as 2.12 mm (Miles, 1915). Whitaker (1890) described the yolk of an unfertilized egg as being spherical and 1.44 mm in diameter. Within this yolk, near the surface, is one spherical oil-drop 0.8 mm in diameter. This oil drop is always at the top of the egg where it displaces the germinal disc (which covers about one third of the area of the yolk) to one side (Reighard, 1890). Johnson (1961) states that early in development, the eggs are hyaline and turgid but often become flaccid during the eyed stage, especially just before hatching.

When first laid walleye eggs are considered to be heavy; they are quite adhesive and remain so for about 1 h (Niemuth, Churchill and Wirth, 1966) until water-hardened.

3.2 Pre-adult phase

3.2.1 Embryonic phase

The various steps in embryonic development are listed in Table VI.

TABLE V

Percentage survival of walleye eggs (egg to fry) during incubation on various bottom types in Lake Winnibigoshish, Minnesota (Data from Johnson, 1961)

Bottom Type	1956	1957	1958	1959	$\bar{x}$
Muck-detritus	0.6	4.5	3.6	1.2	2.5
Fine sand	[2.7][a]	(9.9)	13.2	-	8.6
Gravel sand	-	17.4	-	-	17.4
Gravel-rubble	17.5, 34.3	17.9	5.2, (35.7)	(25.9)	25.0

[a] Observations in 1956 and 1957 indicated that egg survival was best on natural gravel bottoms. These observations were tested experimentally in 1958-59. The natural sand bottom area (survival given in brackets) was covered with gravel and rubble in the autumn of 1957. Nineteen cubic metres of pit-run gravel screenings containing rocks from 2.5 to 15.2 cm in diameter were spread over the sand (water depth 27.9-66 cm) to form a layer approximately 15.2 cm thick. The respective survival (in parentheses, Table V) on this artificial spawning area was greatly enhanced from 2.7 to 9.9 percent in 1956-57 to 35.7-25.9 percent in 1958-59.

TABLE VI

Embryonic development of the walleye (after Reighard, 1890)

Embryonic stage		Water temperature (°C)	Elapsed time after hatching (h; days in parentheses)
Number	Description		
1	First cleavage	7.2	4.0
2	Second cleavage	7.2	4.8
3	Third and fourth cleavage	7.2	5.8
4	End of segmentation	7.2	48
5	Early gastrulation (epiboly)	8.9	56
6	End of gastrulation	8.9	70
7	Embryo appears and blastoderm nearly covers yolk	8.9	70-80
8	Embryo lengthens so that it reaches half way around yolk - optic vescicles appear	9.4	100-144
9	Heart forms and begins to beat	9.4	(8)
10	Tail becoms free of yolk	9.4	(11-25)
11	Embryo ready to hatch - yolk reduced to half original volume	9.4	(25)

Cleavage occurs about 4 h after fertilization and segmentation is completed by 48 h at 7.2°C (Reighard, 1890). Olson (1966) did not observe cleavage to begin until after 6 h at the same temperature; it began in all eggs within 8 h. The embryo first appears at approximately 70 h at 8.9°C and is ready to hatch at 25 days (Reighard, 1890). The walleye has the lowest temperature tolerance for embryos of all percids showing a median tolerance limit (TL 50) ranging from less than 6.0 to 19.2°C (Hokanson, 1977). Just before hatching, the embryo has well developed eyes and numerous chromatophores on the yolk sac and along the ventral line from the anus to the caudal peduncle (Nelson, 1968). Unfertilized eggs often divide parthenogenetically but usually only to the 4 cell stage. Such division is usually erratic and easily distinguished from bisexual cleavage. For further differences see Olson (1966).

The rate of development varies directly with the mean incubation temperature (Reighard, 1890; Johnson, 1961; Anon., 1967; Oseid and Smith, 1971). Hatchery-incubated eggs reached the eyed stage in 7 days at 12.8°C but in only 3 days at 23.9°C (Table VII). As the development rate increases with temperature, the incubation period decreases (Fig. 5). Incubation periods ranging from 4 days at 23.9°C to 33 days at 4.5°C have been reported (Table VII). W.L. Hartman (unpubl.), combining data from four different studies (Fig. 6), found a straight line relationship ($Y = 5.481 + 1.062X$) between 100/days (Y) to mid-hatching and the average incubation temperature (X). The length of the hatching period is also affected by oxygen concentrations. Oseid and Smith (1971) found for a given constant temperature, at oxygen concentrations between 2 and 7 mgl^{-1} and at flow rates of 200 and 300 ml/min, that eggs held at a lower oxygen concentration required 1-4 days longer to reach 100 percent hatch (Fig. 7).

The percentage viability of walleye eggs at spawning may vary widely. Values as high as 100 percent (Johnson, 1961) and as low as 3.4 percent (Baker and Scholl, 1969) have been recorded (see section 4.3.1). Most egg mortality seems to occur within the first 5 days of fertilization (Kramer and Smith, 1966; Kleinert and Degurse, 1968). Johnson (1961) also observed that most egg mortality occurred early in development. However Hurley (1972) recorded mortalities of 5 and 3 percent during the fertilization to the eyed stage among hatchery-reared eggs, but 23 and 44 percent during the eyed to hatching stage. Allbaugh and Manz (1964) found that temperature fluctuations (4 h rise to 4.4°C above base temperature, held 4 h, then gradually decreased to base within the next 4 h) during cleavage, differentiation, and organogenesis, did not cause egg mortality. They suggested that the predominance of river-spawning populations among walleyes tends to indicate that the eggs and fry are tolerant of rapid temperature fluctuations. Experiments at the Genoa, Wisconsin hatchery indicated that at constant incubation temperatures, the optimum range for survival of walleye eggs is 17.8-19.5°C (Table VII). However, it was found that optimum temperatures were 6-12°C for fertilization (Fig. 8) and 9-15°C for incubation (test range 6-21°C) (Smith and Koenst, 1975; Koenst and Smith, 1976). Hubbs (1971) suggested that there may be racial differences in maximum developmental temperature tolerances. Eggs from Lake Meridith, Texas (introduced from Iowa) developed at 20°C whereas eggs from the Thames River, Ontario had trouble developing at 16.5°C. Kramer and Smith (1966) found no significant difference in mortality rates between eggs incubated in water at 33 percent oxygen saturation and those incubated at 100 percent saturation (flow rate-400 ml/min; temperature, 12°C). Oseid and Smith (1971) also failed to show a clear relation between oxygen concentrations (2-7 mgl^{-1}) and survival at flow rates of 200 and 300 ml/min. However, under natural conditions, extremely low oxygen levels may be encountered when eggs are deposited on such substrates as mud and detritus which, through oxidation, reduce oxygen levels and increase mortality (Priegel, 1970).

Other abiotic factors, especially water levels and velocity, may affect the mortality of walleye eggs. Eggs spawned in shallow marshes often are left stranded above the water level

TABLE VII

Relation of constant incubation temperature to days to eyed stage, days to hatch and percentage hatch in walleye eggs (Anon., 1967)

Temperature °C	Days to eyed stage	Days to hatch	Percent hatch
12.8	7	10	50
14.4	6	10	50
16.1	5	8	51
17.8	4	8.5	65
19.4	3.5	6	60
21.7	3	5	<10
23.9	3	4	<10

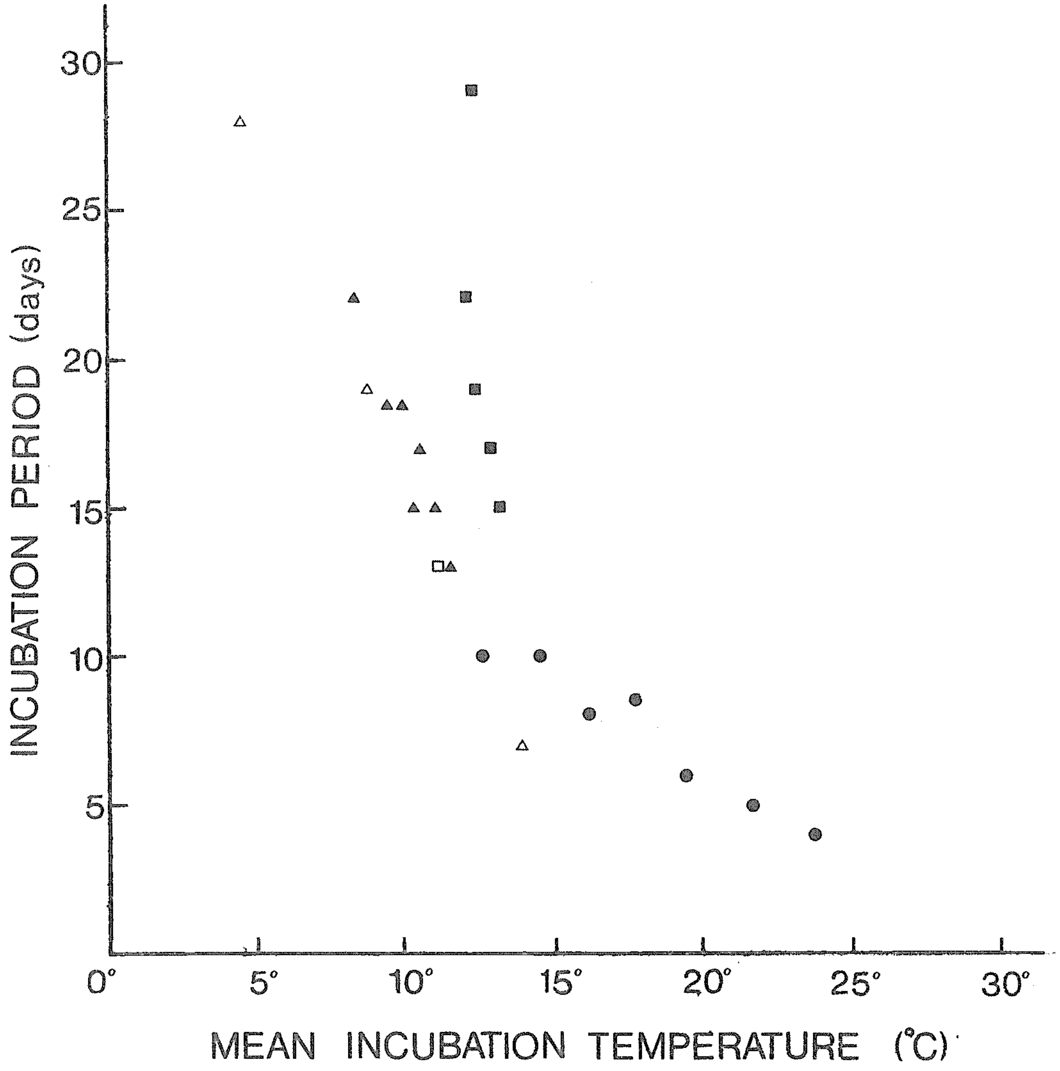

Fig. 5 The relationship between incubation temperature and incubation period: △, Hatchery (U.S.C.F.F., 1903); □, Hatchery (Nelson, Hines and Beckman, 1965); ▲, Lake Winnibigoshish (Johnson, 1961); ●, Hatchery (Anon., 1967) and ■, Oseid and Smith's (1971) hatchery sample, dissolved oxygen (4.0 mgl^{-1})

during times of low water (Priegel, 1970). In such areas current velocity is probably important for oxygen transfer and distribution of fry to suitable nursery areas. High winds have also been known to blow significant numbers of eggs on to shore (Priegel, 1970) or on to poorer substrates (mud, detritus) where survival is reduced (Johnson, 1961; Busch, Scholl and Hartman, 1975). Eggs placed on pulp mill sludge deposits suffered large mortalities when exposed to the high hydrogen sulphide, low oxygen, and high carbon dioxide levels at the sludge-water interface (Colby and Smith, 1967).

A number of species of fish, including carp, yellow perch, bluegills, white suckers, bullheads, spottail shiners, stonecats, and yellow bass (Appendix 3 - Scientific Nomenclature), prey upon walleye eggs (Goode, 1903; Bean, 1912; Cobb, 1923; Adams and Hankinson, 1928; Kraai and Prentice, 1974; Wolfert, Busch and Baker, 1975). Hydra have been observed to cause high egg mortality in hatcheries (Erickson and Stevenson, 1967b). Newburg (1975) observed significant predation of walleye eggs by the planarian, *Dugesia tigrina*, in laboratory experiments. Strand (1973) noted a high mortality of eggs covered by a heavy green carpet-like growth of filamentous algae in the Mississippi River near Bemidji, Minnesota. Parasites may also be an important factor contributing to egg mortality. *Saprolegnia* fungus may cause up to 100 percent egg mortality (Erickson and Stevenson, 1967b) while the stalked, colonial ciliate *Carchesium*

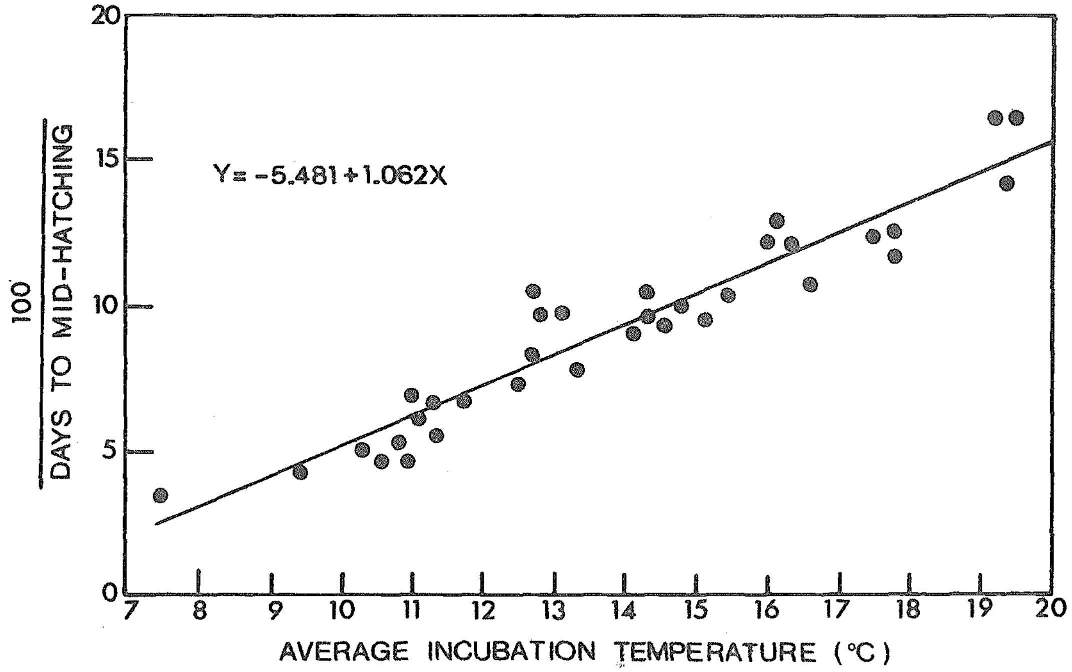

Fig. 6 Relationship between incubation temperature and the number of days to mid-hatching (Redrawn from W.L. Hartman, unpubl.)

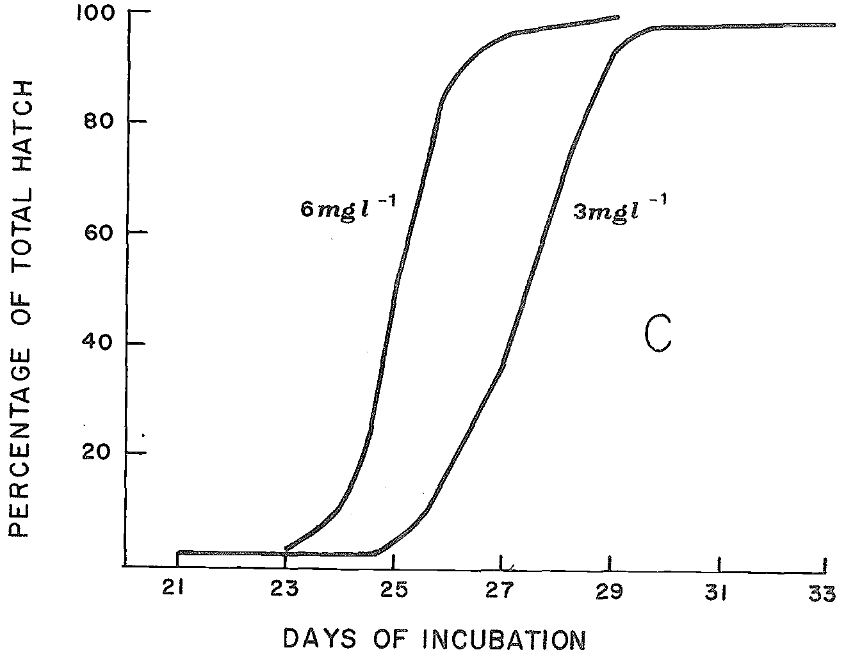

Fig. 7 Influence of dissolved oxygen on rate of hatch of walleye eggs in 1967; Lot III; 4-5°C for first 21 days, 12.3°C thereafter; flow rate - 300 ml/min (Modified from Oseid and Smith, 1971)

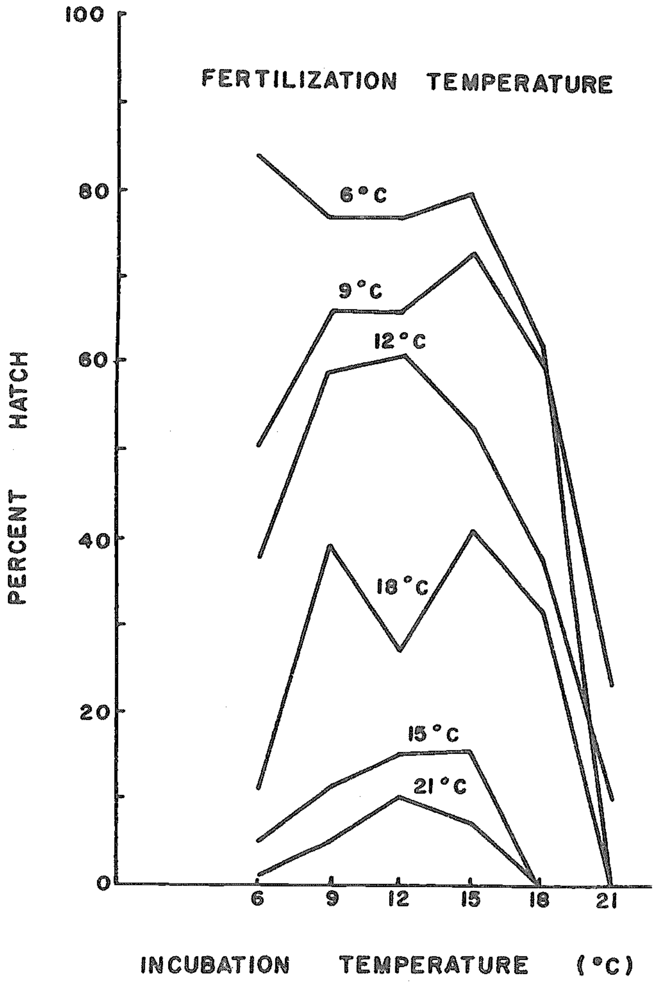

Fig. 8 The combined effect of fertilization temperature and incubation temperatures on the hatchability of walleye eggs. Each line represents the percentage hatch of eggs fertilized at one of six temperatures and incubated at six temperatures, 6, 9, 12, 15, 18 and 21°C (Redrawn from Smith and Koenst, 1975)

has been reported to cause a 20 percent increase in mortality among hatchery-reared eggs (Anon., 1941). *Sphaerotilus natans*, a slime bacterium, often abundant in rivers receiving pulp mill effluents, grows on the surface of eggs and entangles the emerging fry at hatching time (Smith, 1963; Smith and Kramer, 1963). For further information on factors affecting egg mortality, see section 4.4.2.

Reighard (1890) described the mode of hatching as follows: "The rupture of the membranes seems to be brought about by the attempts of the embryo to straighten the body and tail. In this way the tail is brought violently against the membranes and finally ruptures them so that it protrudes. The embryo then often swims about with the head still enveloped in the egg membrane, but usually it manages to free itself entirely from the egg membranes by a few vigorous movements of the body and tail".

3.2.2 Larval phase

Newly hatched prolarvae are from 6.0 to 8.6 mm long (Scott and Crossman, 1973). The stage in development as well as morphometric and meristic measurements of the prolarva are given in Tables VIII and IX. Reighard (1890) observed the yolk sac to disappear after 38 days from fertilization when the larvae were kept at 9.4°C. Hurley (1972) found the yolk to be completely absorbed on the 36th day at the temperature regime tested by him (Table IX). The prolarval stage is complete at the absorption of the oil globule, which has been observed to occur 44 days after fertilization at 9.4°C (Reighard, 1890) and at a total length of about 10 mm (Nelson, 1968).

During the post-larval stage, the larvae become much more heavily pigmented and begin to take on many adult characteristics (Table VIII).

This stage was considered by Nelson (1968) to be completed when the larvae had developed the adult complement of pyloric caeca (3) which he found to occur at a total length of about 19 mm.

Mortality rates at this stage are not well known. Forney and Houde (1964) determined the percentage mortality to be 67-75 percent among Oneida Lake, New York, young-of-the-year (YOY) between July and October. Certain environmental factors can affect fry development and survival. Laboratory studies indicate early larval development is retarded at low oxygen concentrations. Below certain levels, larval size at hatching (Fig. 9) is reduced (Oseid and Smith, 1971; Siefert and Spoor, 1974). Siefert and Spoor found this to occur at saturation levels of 35 percent (3.4 mg/l) or less (flow rate 60 ml/min). Furthermore, larvae raised at 25 (2.4 mg/l) and 20 (1.9 mg/l) percent saturation were

TABLE VIII

Development of larval walleyes (data from Nelson, 1968)

Stage	Total length (mm)	Description
Early prolarval	approximately 7	notochord straight; finfolds complete; pectoral finbuds present; single oil globule at anterior end of yolk sac; dorsal finfold extended forward from 2nd to 5th preanal myomere; few faint, small chromatophores on yolk sac
Late prolarval	approximately 9	distinct and profuse chromatophores on yolk sac and ventral line from anus to caudal fin; by end of stage, ventral line of chromatophores enlarged and form continuous chain of interlocking, stellate chromatophores; 1-5 small chromatophores scattered over notochord: oil globule completely absorbed by end of stage
Early postlarval	approximately 11	fin ray ossification begins at 10-11 mm; anal, soft dorsal and pectoral rays at 13 mm
Mid postlarval	approximately 15	spiny dorsal ray ossification begins at 14 mm, pelvic rays at 16.5 mm
Late postlarval	approximately 18	spiny dorsal ray ossification completed by 18 mm; complete number of pyloric caeca (3) present at 19 mm

noticeably weak swimmers. Similarly, lower incubation temperatures produce larger fry at hatch (Smith and Koenst, 1975). Busch, Scholl and Hartman (1975) observed that in years of good to excellent year-class success in Lake Erie, the rate of water warming during the spawning and incubation periods was steady and rapid (>0.28°C per day) while in years of poorest year-class success, the rates of water warming were low. From laboratory studies, Smith and Koenst (1975) found the optimum temperature range for fry survival to be 15-21°C (test range 6-21°C) while optimum oxygen concentrations occur at 50 percent (4.8 mg/l at 17°C) saturation (flow rate 60 ml/min) or more (Siefert and Spoor, 1974). There is also some evidence to suggest a positive correlation between *Daphnia* abundance and fry survival (Mraz and Kleinert, 1965; Kleinert and Mraz, 1966). Priegel (1967b) believed that a scarcity of zooplankton was responsible for the poor 1966 year-class on the Wolf River, Wisconsin.

A number of fish species feed on walleye fry. These include yellow perch, white bass, yellow bass, smallmouth bass, rainbow smelt, saugers, bullheads, burbot and probably most importantly, northern pike (see Appendix 3 for scientific names). Other predators include fish-eating birds, predacious insects and hydra. However, cannibalism may be the most important source of fry mortality especially when food is scarce (see sections 3.4.2 and 4.4.2). Walleye fry may have to compete with other planktivorous fishes, such as they do with fry of fresh water drum for such microcrustaceans as *Cyclops* and *Leptodora* on Lake Winnebago (Priegel, 1965b). Alewife (Schneider and Leach, 1977) and rainbow smelt (Regier, Applegate and Ryder, 1969) have been implicated as serious competitors with walleye fry for food items in Lake Michigan and Lake Erie. Johnson (1969) believed that competition for food, as a factor limiting survival in Lake Winnibigoshish and Cutfoot Sioux Lake, occurs mostly during the first 60 days of life, when the young walleyes are feeding largely on plankton and insects or when they are making the transition to a predominantly fish diet.

No information is available on parasitic infections at this stage of development.

Reighard (1890), observing fry in aquaria, noted that they did not begin feeding until just after the yolk sac was absorbed (about 30 days after fertilization at 9.4°C). In laboratory studies, initiation of feeding behaviour by fry was observed at temperatures in excess of those optimal for egg incubation (Smith and Koenst, 1975). However, food studies conducted by Hohn (1966) on Lake Erie larvae suggested that some larvae feed on diatoms before their yolk sacs are absorbed. Bulkley, Spykermann and Inmon (1976) observed that walleye fry stocked in Clear Lake, Iowa, first contained food at a length of 9 mm even though many still retained small amounts of yolk material at this body length. Hurley (1972) noted cannibalism amongst walleye larvae near the end of yolk absorption. While observing fry during their first feeding,

TABLE IX

Record of thermal data and egg and fry development (Hurley, 1972)

Date	Days after fertilization[a]	Temperature (°C)		
		Maximum	Minimum	Mean
April				
19	0	-	-	5.6
20	1	-	-	5.6
21	2	6.7	6.7	6.7
22	3	6.7	6.7	6.7
23	4	8.9	6.7	7.8
24	5	7.8	6.7	7.2
25	6	7.8	7.2	7.5
26	7	8.9	8.3	8.6
27	8	10.0	6.7	8.3
28	9	10.0	7.8	8.9
29	10	10.0	9.4	9.7
30	11	10.0	8.9	9.4
May				
1	12	10.0	7.8	8.9
2	13	10.0	10.0	10.0
3	14	10.0	8.9	9.4
4	15	10.0	8.9	9.4
5	16	10.0	7.8	8.9
6	17	9.4	7.8	8.6
7	18	9.4	8.3	8.9
8	19	9.4	8.3	8.9
9	20	10.0	8.9	9.4
10	21	10.0	9.4	9.7
11	22	11.1	8.9	10.0
12	23	10.6	8.9	9.7
13	24	10.0	7.8	8.9
14	25	8.9	7.8	8.3
15	25			13.9
16	26			12.2
17	27			12.2
18	28			11.6
19	29			12.2
20	30			12.2
21	31			13.9
22	32			13.9
23	33			15.3
24	34			15.6
25	35			16.1
26	36			13.9

[a] Days after fertilization on which successive events occurred: 15-eggs eyed; 23-a few eggs hatched; 25-main hatch began, eggs transplanted to aquariums; 27-hatch ended; 36-yolk disappeared

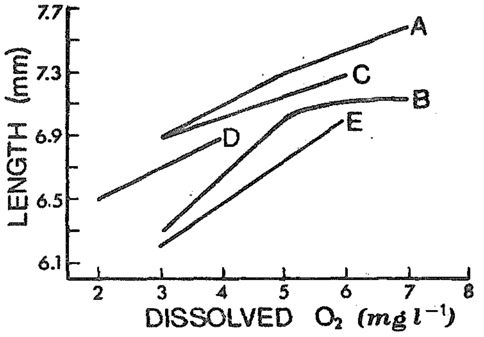

Fig. 9 Mean length of walleye fry at hatch after incubation at various levels of dissolved oxygen (ppm or mgl^{-1}); flowrate ($mg\ min^{-1}$) in parentheses: (A) Lot II, 1966 (300); (B) Lot I, 1966 (300); (C) Lot I, 1967 (200); (D) Lot II, 1967 (300); and (E) Lot III, 1967 (200); From Oseid and Smith, 1971

Reighard (1890) noted that when one of the tiny fish saw a small piece of liver floating down through the water column, it poised itself with its tail bent. As the food passed by, the fish suddenly straightened its tail, and with mouth open, quickly darted forward to engulf the particle.

3.2.3 Adolescent phase

Walleye young-of-the-year do not develop adult colouration until they reach a total length of about 35 mm (Nelson, 1968). Scale development (Fig. 10) begins at a total length of about 24 mm but is not completed until about 45 mm (Priegel, 1964b).

Temperatures during the first year of life are important in determining the rate of growth and length at the end of the first growing season.

Smith and Pycha (1960) found that in seasons of very late or very early hatching, total length at the end of the season is less and greater, respectively, than average in the Red Lakes, Minnesota. Surges in growth rate have been observed to occur in mid-summer during some years of poor early growth, so that total lengths by the end of these seasons were near average (Smith and Pycha, 1960; P.J. Colby, unpubl.). P.J. Colby (unpubl.) observed this surge in growth to occur immediately after a period of above-average water temperatures. Poor growth during the first season of life may result in increased predation and a consequent reduction in year class strength. The optimum temperature for growth of juveniles (65.0-86.5 mm long) apparently is 22.0°C (Fig. 11), but the range can be extended to include 19-25°C (Smith and Koenst, 1975; Koenst and Smith, 1976; Huh, Calbert and Stuiber, 1976). Pond culturing of walleyes has shown that first year growth is inversely related to population density (Dobie, 1956; 1969). Whether natural populations of young-of-the-year ever reach a size where density-dependent factors are significant is unknown (see section 3.4.3).

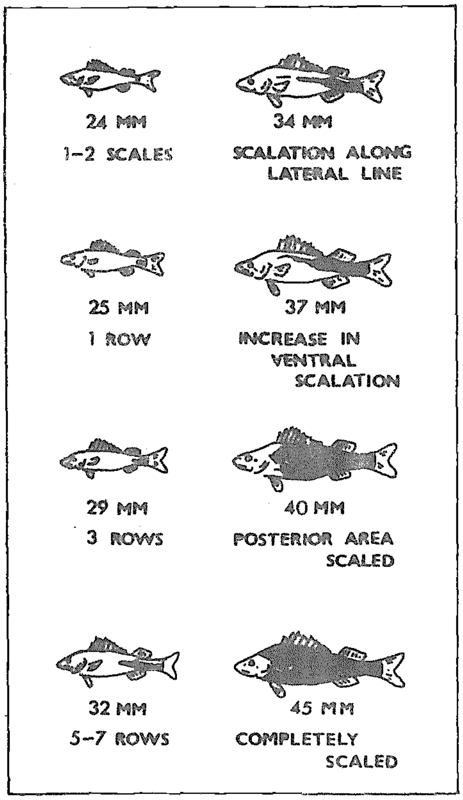

Fig. 10 Location of first scales and advancement of scale pattern with increasing length (Redrawn from Priegel, 1964b)

Parasites and diseases infecting adults are probably also found among adolescents. However, infections of lymphocystis, dermal sarcoma and epidermal hyperplasia among immature walleyes have not been recorded. The same animals that are predacious on adults are also predacious on adolescents. However, sea lamprey predation on small walleyes is probably rare.

During early adolescence, walleyes change from a predominantly insect-crustacean diet to one consisting mainly of fishes (unless these fish are scarce). During this period, diet and feeding habits are essentially the same as those of adults (see sections 3.4.1 and 3.4.2).

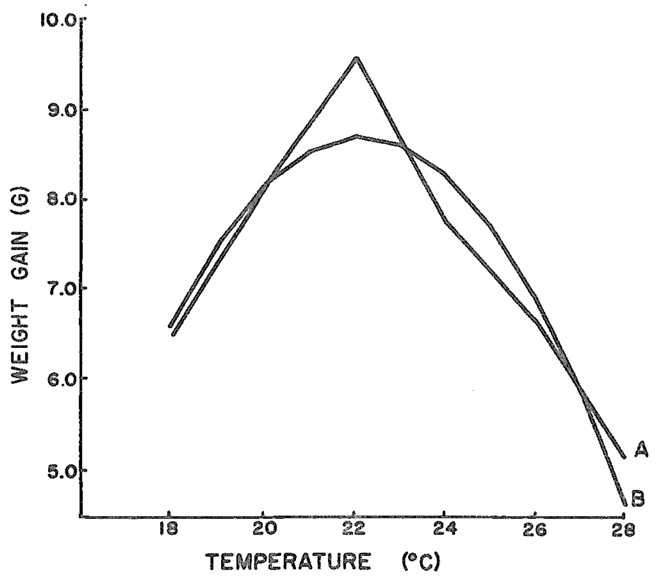

Fig. 11 Growth of juvenile walleyes exposed to temperatures ranging from 18 to 28°C. Line A represents the actual data points. Line B represents the predicted points calculated from the equation, $Y = -50.917 + 5.374\ OX -.1211X$ (Redrawn from Smith and Koenst, 1975)

3.3 Adult phase

3.3.1 Longevity

The average life-expectancy of the walleye varies with latitude, from about 12 to 15 years near the extreme northern limits of its range to about 5 to 7 years near the extreme southern limits (see section 3.4.3 and Appendix 1). In general, where walleyes grow fast and mature early, their life span is shortened. The maximum age reported for a walleye is 20 years (Scott and Crossman, 1973). However, on the basis of estimated ages from their lengths at tagging and the known period of liberty, three male walleyes jaw-tagged in 1947 in Lake Gogebic, Michigan, and recaptured 16, 17 and 18 years later were estimated to be 26, 23 and 23 years old, respectively (Schneider, Eschmeyer and Crowe, 1977).

3.3.2 Hardiness

Walleyes are tolerant of a wide range of environmental conditions. They may tolerate dissolved oxygen concentrations in the laboratory as low as 2 ppm, temperatures between 0 and 30°C, up to 15 000 ppm dissolved solids, and a wide range of turbidity. However, they avoid high levels of illumination (see section 2.3).

Hoff and Chittenden (1969) conducted experiments on the effects of oxygen drawdown on 30 adult walleye. First signs of distress were noted when dissolved oxygen approached 1.9 mgl^{-1} after 145 min of drawdown. Mortalities occurred below 1.6 mgl^{-1}; between 160 to 250 min after oxygen drawdown had begun (Fig. 12). However, Scherer (1971) observed walleye in aquaria to be able to survive oxygen drawdown to 1 mgl^{-1} (occurring 150-200 min after drawdown) without mortality. Loss of coordination and equilibrium first occurred at 0.6 mgl^{-1}. Oxygen concentrations below 5 mgl^{-1} appear to result in poor survival of stocked walleye fry in Lake Traverse, Minnesota (Moyle and Clothier, 1959).

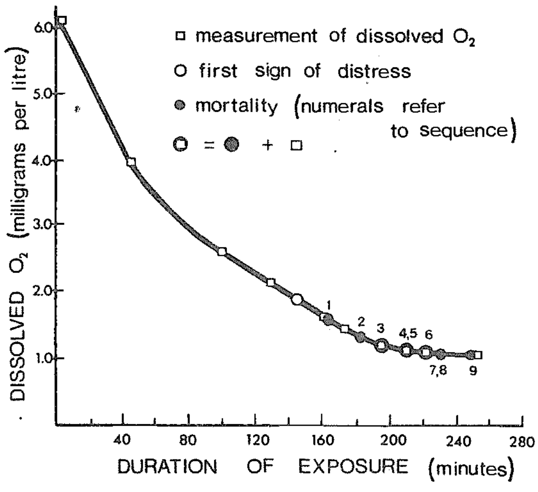

Fig. 12 Curve showing response of adult walleyes (T.L. = 437-724 mm) to reduced levels of dissolved oxygen at 24°C (Redrawn from Hoff and Chittenden, 1969)

Walleye tolerance of certain pollutants, to which it is often subjected, has also been studied. Smith, Kramer and Oseid (1966) concluded that conifer-groundwood fibre at concentrations from 50 to 150 mgl^{-1} acts as a loading and limiting stress and reduced the scope for activity of walleye fingerlings. Under added environmental stresses, such as high temperature or low dissolved oxygen, these results suggest that suspended fibre loads may decrease survival rates or reduce fish production in natural habitats. Smith and Oseid (1970), who measured the tolerance of juvenile walleyes to hydrogen sulphide, a common decomposition product particularly in anoxic water, determined a 96-h median tolerance limit to be 0.018-0.020 mgl^{-1} H_2S.

Diurnal vertical migrations of fish at dawn and dusk reflect periods of optimum illumination levels for feeding. Above and below these levels, feeding is reduced or non-existent (see sections 3.4.1 and 3.4.2).

Little information relating to the hardiness of walleye in aquaria is available. D. Zumwalt (pers. comm.) kept juveniles and adults (up to 406 mm long) in 2x271-l tanks (10-15 adults/tank) at 10-23.9°C for periods of 3-4 years at the John G. Shedd Aquarium in Chicago, Illinois. Diseases, such as fungus and *Ichthyophthiris*, sometimes developed but usually were treated successfully.

3.3.3 Competition

Interspecific competition for food can be important in some adult walleye populations. Walleye are known to compete with such piscivorous fish as northern pike, yellow perch, sauger, and smallmouth bass, of which northern pike is probably the most important (Scott and Crossman, 1973). In Maple Lake, Minnesota, Seaburg and Moyle (1964) noted that walleyes also compete with largemouth bass for yellow perch. Muskellunge can probably be added to this list also. Johnson and Hale (1977) found that interspecific competition for food between walleyes and smallmouth bass in four Minnesota lakes of low productivity was probably not an important determinant in the abundance of both species. Walleyes fed predominantly on fish and ephemerids, whereas the bass fed mainly on crayfish and odonata. Earlier studies by these authors (Johnson and Hale, 1963) indicate that after smallmouth bass were introduced into some northeastern Minnesota walleye lakes, bass generally became the dominant species (over walleyes) in the boulder/rubble-lined lakes with high shoreline development factors and low populations of minnows and small fish. However, in lakes with little shoreline irregularity, moderate to extensive shoreline, shoal areas of gravel, sand and muck, and sizeable populations of small forage fish, walleyes remained dominant. In Falcon Lake, Manitoba, little competition occurred between these two species (Fedoruk, 1966). In a number of lakes, where forage fish are scarce and walleye are forced to feed on aquatic insects, they may compete with a variety of insectivorous species, such as black crappie (Seaburg and Moyle, 1964), bluegill (Scidmore and Woods, 1960), lake whitefish (Bajkov, 1930), fresh water drum (Scidmore and Woods, 1960; Priegel, 1965b), and suckers (Burrows, 1969; Johnson, 1977). Such competition may involve complex interactions with other species of fish (Johnson, 1977).

In Wilson Lake, Minnesota, Johnson (1977) demonstrated that the walleye standing crop of a relatively simple fish community could be increased by as much as one third by white sucker removal, white suckers being the primary competitors with walleyes and the important prey species (yellow perch, minnows and darters). During a seven-year post-removal study, yellow perch abundance increased as a result of decreased white sucker competition, thereby benefiting the adult walleye population in providing a more abundant and desirable food source than the previously utilized minnow and darter populations. The feeding shift to yellow perch by adults probably alleviated the predator pressure on minnows and darters, which subsequently became forage for yound walleyes. Furthermore, young walleyes benefited directly from the sucker removal, inasmuch as the competition pressure on benthic organisms was reduced.

Although walleyes in some lakes and streams share their spawning grounds with suckers or northern pike, which spawn more or less concurrently, no serious competition for spawning grounds has been reported in the literature. However, Priegel (1970) observed that considerable walleye egg mortality can result when carp in the Fox River (Lake Winnebago), Wisconsin, move into the walleye spawning marshes to spawn immediately after completion of the walleye run. In the process of spawning they roil up the bottom and dislodge walleye eggs from the vegetative mats, causing them to settle on the silt bottom where they quickly die from lack of oxygen. Muench (1966) felt that competition was severe for spawning space among walleyes, white bass, suckers, and gizzard shad in Center Hill Reservoir, Tennessee.

3.3.4 Predators

Being a large carnivore, the adult walleye is not usually preyed upon by other fish species. Northern pike is probably the most important predator on adult walleye over much of its range while muskellunge also prey on walleye in more restricted areas (Scott and Crossman, 1973). It is generally believed that sea lamprey predation on adult walleyes is of little importance in most waters. Lamprey scars have been observed on less than 1 percent in Lake Michigan (Shetter, 1949), Lake Superior (Ryder, 1968), Lake Huron (Winterton, 1975b), and up to 3 percent in the Lamoille River, Vermont (Anderson, 1969). On the other hand, Scriba (1910) observed a large mortality of walleyes in Oneida Lake, New York caused by lamprey predation. Adult walleye have been found in stomachs of the double-crested cormorant, *Phalacrocorax auritus* (Munro, 1927) and the common loon, *Gavia immer* (Olson and Marshall, 1952). However, predation by these fish-eating birds is probably not important.

3.3.5 Parasites, diseases, injuries and abnormalities

Virtually 100 percent of all walleyes examined from various populations have been parasitized (Reighard, 1894; Fischthal, 1945; 1950; 1952; 1953; Dechtiar, 1972a; 1972b). A list of known walleye parasites, along with information on the intensity of individual and population infections, is given in Table X.

Little information is available regarding the influence of these various parasites on the physiology of adult walleyes. Miller (1945) found that the gut wall of walleyes infected with *Triaenophorus stizostedionis* increased in thickness. What effect this has on the health of the fish was not determined.

Lymphocystis is a viral disease (Yamamoto et al., 1976) commonly found in walleye populations. It produces wart-like protuberances, usually in regions subject to damage by abrasion such as fins, jaws and opercula. Walker (1962) described these warts as being composed of enormously hypertrophied connective tissue cells up to 1 mm in diameter and with the nucleus proportionally enlarged. These cells are heavily encapsulated, but after a growth period of several months they slough off, presumably releasing virus particles. The free virus in the water probably attacks connective tissue when the skin surface has been abraded or broken (Walker, 1958). Only mature walleyes have been observed to be infected, although fingerlings are easily infected in aquaria (R. Walker, pers. comm.). Infection seems to be severe during and near the spawning season (Ryder, 1961; Walker, 1969). Infected fish tagged in the spring in Nipigon Bay, Lake Superior, showed no traces of the disease in the summer and autumn (Ryder, 1961). However infected specimens have been collected from Oneida Lake from August through December for two years (R. Walker, pers. comm.). Evidence suggests that handling and tagging procedures tend to increase the spread of the disease (Halnon, 1963; 1967; Moenig, 1975). Walker (1958) stated that the incidence of the disease among Oneida Lake, New York walleyes varies from 1 to 5 percent during the spawning season. The percentage infection was 11 in the spawning population on the Lamoille River, Vermont (Anderson, 1969) and the incidence increased from 17.5 to 30.4 percent during the spawning season in the Nipigon River, Ontario (Ryder, 1961). Hile (1954) found that in Lake Erie, infected walleyes weighed 5.5-6.5 percent less than uninfected walleyes of the same length. Nevertheless, mortality due to the disease is probably low (Ryder, 1961; Johnson, 1971b). According to Moenig (1975), neither Olson (1958) nor Ryder (1961) found a differential mortality for infected and uninfected walleye. The incubation period of this disease is not known, but R. Walker (pers. comm.) suspected that the heavy load of lymphocystis warts observed at the Constantia Hatchery one April may have been related to the rough handling and crowding of these fish at the hatchery in the previous April; if so, the virus was still viable after one year. Moenig (1975) has suggested, based on walleye recapture data from Dexter Lake, that the disease runs its course after about two years. In addition, Zimmerman (1966b) suggests that some individuals in a population become immune as a result of previous infection.

Two other diseases associated with virus have been identified in walleye: dermal sarcoma and epidermal hyperplasia. Walker (1947) first described dermal sarcoma among walleyes in Oneida Lake, New York. Since then, it has been identified on walleyes from Lakes Champlain, Huron, and Erie (Walker, 1969), Crean Lake, Alberta (Yamamoto et al., 1976), as well as on fish from Savanne Lake, Ontario (M.W. Lankester, pers. comm.), and Saratoga Lake, New York (R. Walker, pers. comm.). Yamamoto et al. (1976) described the close association of this disease with lymphocystis amongst small spawning walleye in Prince Albert National Park. The two diseases were observed to coexist on the same fish at the same time, and even in the same mass of tissue. Dermal sarcoma has probably been mistaken for lymphocystis in other waters, because it produces warts similar to those of lymphocystis. However, the sarcotomous warts show no giant cells, are generally more smoothly hemispheric than lymphocystis warts, and fine textured and variable in vascularization from pink to white, and appear on the body more often than on the fins (Walker, 1969). Microscopically, the texture ranges from highly cellular, often chaotically arranged sarcoma, to densely fibrous. tightly whorled, hard fibroma (Walker, 1969). Only mature walleyes have been observed to be infected. This disease is also virally induced (Yamamoto et al., 1976), but as yet no adequate experimental or epidemiological evidence for the time course of the disease has been produced, nor is the mode of infection known. Walker (1969) observed the disease to infect up to 5 percent of mature Oneida Lake walleyes during the spawning runs. No information is available on the effect of this disease on the physiology of walleyes or on mortality rates. Epidermal hyperplasia is another disease associated with a virus which has so far been identified only in Oneida Lake walleyes. Walker (1969) described the greyish lesions as broad, flat, sharply delimited plaques of thickened epidermis up to several centimetres in diameter. As with lymphocystis and dermal sarcoma only mature specimens were observed to be infected. Up to 5 percent of the population on the spawning

TABLE X

Parasites of adult walleye (from Hoffman, 1967, unless otherwise indicated)

Parasite	Stage[a/]	Location in host	Degree of infestation[b/]	Percentage occurrence (locality[c/] in parentheses)
Protozoans				
Ichthyophthirius multifiliis (Stiles, 1894)	A	Beneath epithelium		
Myxobilatus asymmetricus	A	Urinary bladder		
Myxobolus sp.				
Trichodina sp.	A	Gills		
Platyhelminthes				
Trematodes				
Allocreadium lobatum (Fischthal, 1952)	A			
Apophallus americanus	L			
A. venustus	L			
Azygia acuminuta	A			
A. augusticauda	A	Intestines	L(LW)	14(LW)
A. bulbosa	A			
Bucephaloides pusilla	A			10(LH)
Bunodera sacculata	A	Intestines	L(LW)	21(LW)
Centrovarium lobotes	A			
Cleidodiscus aculeatus	A	Gills	L to H(LW)	100(LED); 100(LEB)
Clinostomum marginatum	L	Encysted in musculature		
Cotylurus communis	L (as *Tetracotyle*)	Pericardial cavity Mesentaries	L(LW)	48(LW)
Crassiphiala bulboglossa	L (as *Neascus*)	Black cysts in skin		
Crepidostomum sp.	A			
Diplostomulum scheuringi	L	Black cysts in skin, eyes, bronchial arches, and myotomes	L(LW)	14(LW)
Diplostomulum sp.	L			
Neascus sp.	L			
Phyllodistomum superbum	A	Ureters	L(LW)	34(LW)
Posthodistomum minimum	L (as *Neascus*)	.		
Sanguinicola occidentalis	A	Blood		>90(LEB)
Uvulifer ambloplitis	L (as *Neascus*)	Black cysts in skin		19(LED)
Cestoda				
Abothrium crassum (Cross, 1938)	I and A	Intestines		
Bothriocephalus cuspidatus	A	Intestines	L to H(LW)	100(LW); 51(LH); 47(HL); 58(LC)
Dibothriocephalus latus (Lawler and Watson, 1958)				

TABLE X continued

Parasite	Stage[a/]	Location in host	Degree of infestation[b/] (locality[c/]	Percentage occurrence in parentheses)
Diphyllobothrium latum	L		L(NC)	
Proteocephalus ambloplitis	L	Ovaries Mesentaries, liver		
P. luciopercae	A	Pyloric caecae		
P. macrocephalus	A			
P. pearseli	I			
P. stizostethi	I and A	Intestines	L(LW)	28(LW); 24(LH)
Proteocephalus sp.	A			
Triaenophorus nodulosus	L	Encysted in liver and mesentaries		
T. stizostedionis	I and A	Intestines	L(LW)	21(LW); 5(LH)
Nematoda				
Camallanus oxycephalus	A	Intestines		
Capillaria catenata	A	Intestines		
Contracaecum brachyurum	A	Intestines	L(LW)	55(LW); 2 (LH)
Contracaecum sp.	A	Encysted in mesentaries		
Dactinitoides cotylophora	A			10(LH)
Eustongylides sp. (Dechtiar, 1972a)	L	Encysted in muscle	L(LW)	7(LW)
Oxyuroidea (accidental?)	A			
Philometra cylindracea	A			
Spinitectus carolini	A			
S. gracilis	A			
Spinitectus sp.	A			2(LH)
Acanthocephala				
Leptorhynchoides thecatus	A	Pyloric caecae		27(LH)
Metechinorhynchus salmonis (Dechtiar, 1972a)	A	Intestines	L(LW)	41(LW)
Neoechinorhychus cylindatus	A	Intestines		35(LH)
N. tenellus	A	Intestines	L(LW)	79(LW); 7(LED)
Pomphorhynchus bulbocolli	A			
Annelida				
Hirudinea				
Cystobrunchus verrilli	A			
Illinobdella moorei	A	Fins	L(LW)	62(LW); 19(LED)
Piscicola punctata (Oliver, 1960)	A	Gills, fins, tail		
P. geometra (Rawson, 1957)	A			

TABLE X continued

Parasite	Stage[a]	Location in host	Degree of infestation[b] (locality[c])	Percentage occurrence in parentheses)
Arthropoda				
Crustacea				
Argulus biramous	A			
A. appendiculosus	A			
A. stixostethi	A			
A. versicolor (Dechtiar, 1972a)	A	Fins	L(LW)	17(LW)
A. canadensis (Dechtiar, 1972b)	A	Fins	L(LW)	24(LW)
Ergasilus caeruleus	A	Gills	L to H(LW)	100(LW); 24(LH)
E. centrachidarum	A	Gills		
E. confusus	A	Gills		
E. luciopercarum	A	Gills		
Mollusca				
Glochidia (various species)	L	Gills	L(LW)	21(LW); 7(LH)

[a] L = larva; I = immature adult; A = mature adult

[b] L = light (1 to 10 parasites per host); M = medium (10 to 50); H = heavy (>50)

[c] LW = Lake of the Woods (Dechtiar, 1972a);
LH = Lake Huron (Bangham, 1955)
LEB = Lake Erie (Bangham and Hunter, 1939)
LED = Lake Erie (Dechtiar, 1972b)
HL = Houghton Lake, Michigan (Schneider and Kelly, 1973)
LC = Lake Cadillac, Michigan (Schneider and Kelly, 1973)
NC = Northern Canadian lakes (Vergeer, 1929)

grounds were infected and double infection i.e., in combination with either lymphocystis or sarcoma, was common (Walker, 1969). No information is available on the method of transmission (though it is probably viral), the incubation period of the disease, or its effect on the physiology or mortality of the walleye.

Recently, a form of skeletal muscle degeneration (named myofibrogranuloma) was found to occur among adult walleyes in a number of Minnesota lakes (Economon, 1975). This affliction is characterized by swollen, heavy, coarsely fibrous, lipogranuliform muscle lesions of an opaque, to semi-translucent yellowish-brown colour. Such lesions are often more severe in the general musculature surrounding the spinal column and in the deeper strata of the large dorsal muscles. The author states that histopathological similarities of the myopathy in walleye specimens as compared with those of muscular dystrophy in man and hereditary dystrophy-like myopathies in other animals, suggests that this anomaly might also have a hereditary connexion. Myofibrogranuloma does not appear to cause serious morbidity nor measurable mortality.

Injuries incurred as a result of gillnetting are common and have been observed to occur in up to 1 percent of the population in the Missiquoi River, Vermont (Anderson, 1969). Such injuries probably made these walleyes susceptible to the fungus infections (probably *Saprolegnia*) found on 1 percent of this population. Bleeding and flesh damage have been observed as a result of tagging (Roseborough, 1958).

Regeneration of clipped fins is common; however, the regenerated fin is distorted to some degree depending on how closely the clip was made to the base of the fin.

3.4 Nutrition and growth

3.4.1 Feeding

Walleyes feed to the greatest extent from the evening to early morning (Bailey and Harrison, 1945; Reed, 1962; Swenson and Smith, 1973). Both in the laboratory and in the field, Swenson and Smith (1973) observed that walleye feeding activity was uniformly distributed throughout the night and day during periods of low food consumption. With increased consumption, feeding activity was greatest during the night and early morning hours. These periods of heaviest feeding are apparently related to light and the necessity for optimum light intensities to initiate feeding. Both wind action on shallow reefs and the approach of storms have been observed to decrease light intensities and to stimulate daytime feeding activity of walleye (T. Mosindy, pers. comm.).

This relationship between light and feeding is further evidenced by the fact that walleyes have been observed to feed throughout the day in very turbid lakes (Arnold, 1960; Ryder, 1977). Ryder (1977) determined that on Shebandowan Lake, Ontario, this optimum occurs when a surface intensity of 1 500 lux is reached. He also found that winter feeding under ice and snow cover occurs at the same surface light intensities but at substantially lower subsurface intensities. Consequently, he concluded that the rate of change of illumination is the factor that stimulates the initiation of feeding, once suitably low levels of illumination are reached. Furthermore, adaptation to the lower winter light regime may occur and the optimum level of illumination required for efficient feeding may be an order of magnitude or more lower than during ice-free periods.

Feeding usually occurs near or at the bottom. During feeding periods walleyes may move into shallower waters to feed (Bailey and Harrison, 1945). Walleyes, as members of the tribe Luciopercini, rely primarily upon vision as opposed to tactile modes in obtaining food (Disler and Smirnov, 1977). Also, the role of the lateral line canal systems of this tribe is not as significant as that of other members of Percidae (Disler and Smirnov, 1977). However, because much of the walleye's feeding is done during the night, other senses such as hearing, taste and smell must be involved at least to a small extent (Regier, Applegate and Ryder, 1969). Underwater observations of adults have revealed that walleye tend to seize their prey (fish) from the side and then move it around in the mouth until it can be swallowed head first (Ryder, pers. observ.). Titcomb (1921) and Reighard (1890) noticed that when hatchery fry preyed on other fry, they attempted to swallow them tail first. These cannibalistic fry apparently did not always die from such attempts; the swallowed portions were sometimes digested and the head and attached tissues finally rejected (U.S. Commission of Fish and Fisheries, 1903).

Most feeding occurs during the summer and autumn and is reduced during the winter, perhaps due to non-availability of forage species in areas frequented by walleyes during this time (Galligan, 1960; Swenson, 1972). Careful observations have provided evidence that walleyes do feed during the spawning season but not during the spawning act itself (authors' pers. observ.). Laboratory studies indicate that walleye fry feed infrequently at water temperatures below 15°C (Smith and Koenst, 1975). In similar studies on adult walleye, fish held at temperatures below 12°C fed only at maintenance levels (Kelso, 1972). Swenson and Smith (1976) found consumption rates for adult walleyes to increase from June through August and then taper off in the autumn. Food consumption rates of a walleye population in

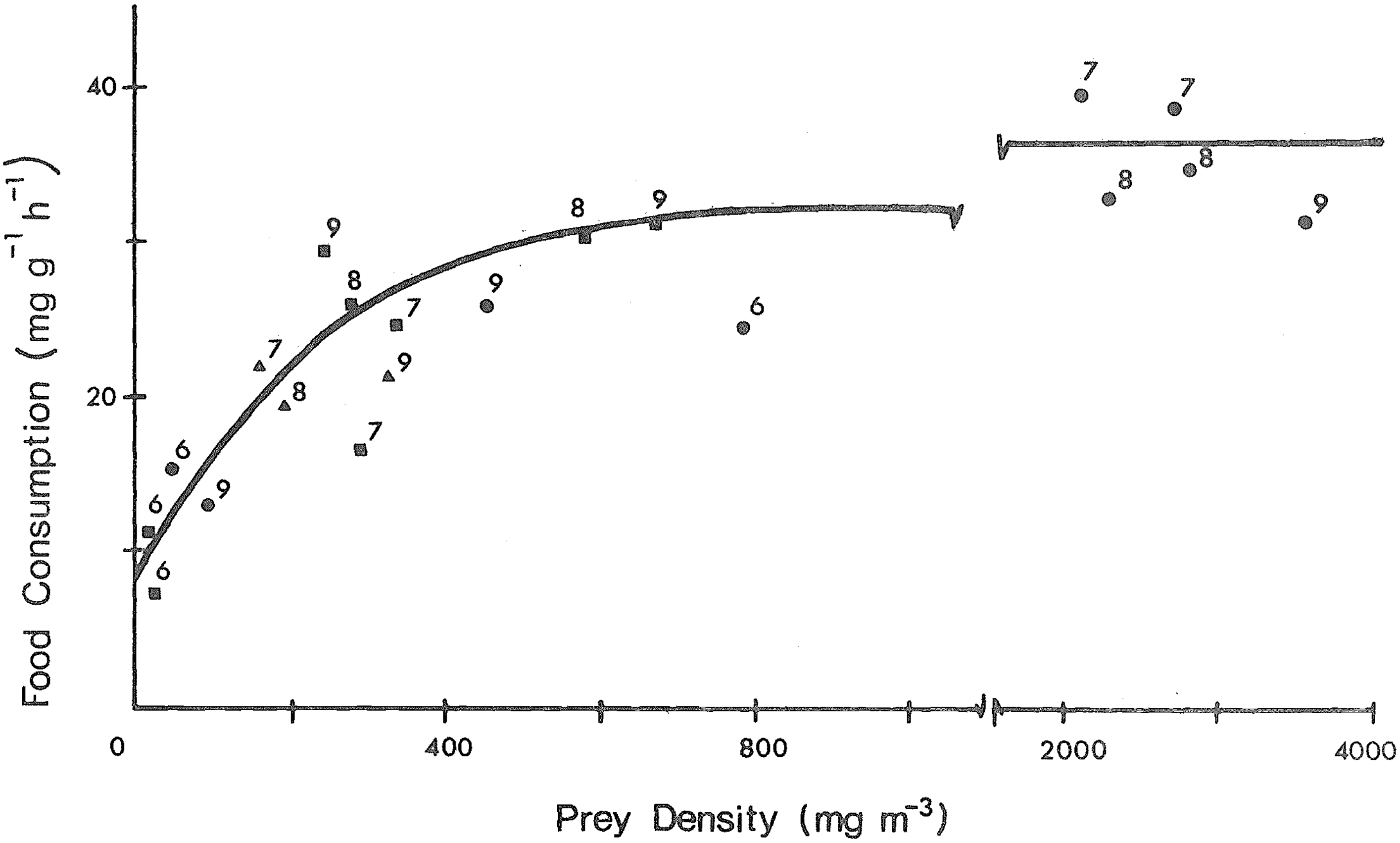

Fig. 13 Relationship between daily food consumption rates of Shagawa Lake walleyes (●), Lake of the Woods walleyes (■), Western Lake Superior walleyes (▲) and prey density. Numbers indicate calendar month (Redrawn from Swenson, 1977)

Lake of the Woods, Minnesota was found to be 1 percent of body weight in June, 2 percent during July, and 3 percent during August and September (Swenson and Smith, 1973). Forage density is the primary factor limiting food consumption. Swenson and Smith (1976) found that as the forage density increased, food consumption also increased until it stabilized at a rate of 30 mg/g/day at a forage density of 400 mg/m^3 (Fig. 13). Food consumption was seen to increase at a slower rate to 4 percent body weight at prey densities from 400-3 500 mg/m^3 (Swenson, 1977).

3.4.2 Food

Adult and juvenile walleyes are largely piscivorous, feeding on a great variety of prey fishes. In many lakes invertebrates form a large part of the diet in late spring and early summer. The most important of these, in many waters, are mayfly nymphs and amphipods (Eddy, 1942; Eschmeyer, 1950; Rawson, 1960; Chambers and Macins, 1966; Swenson, 1972; and Kelso, 1972). Invertebrate food is gradually displaced by a diet consisting mainly of fish later in the summer when, presumably, most of the immature insect forms have metamorphosed and YOY prey fish are pelagic and readily available (Eddy, 1942; Eschmeyer, 1950; Chambers and Macins, 1966; Dobie, 1966a; Fedoruk, 1966; Johnson, 1969; Swenson, 1972). In many lakes in the northern and central regions of walleye distribution, YOY yellow perch, when available (Appendix 2), seem to be the predominant prey fish (Hankinson, 1908; Eddy, 1942; Raney and Lachner, 1942; Eschmeyer, 1950; McCrimmon, 1956; Maloney and Johnson, 1957; Rawson, 1960; Seaburg and Moyle, 1964; Dobie, 1966a; Fedoruk, 1966; Forney, 1966; Glenn and Ward, 1968; Johnson, 1969; Moenig, 1975; Swenson and Smith, 1976).

When yellow perch are not available or abundant, other species become more important, e.g., lake emerald shiners (Doan, 1942; Galligan, 1960), trout-perch (Priegel, 1967a), nine-spine sticklebacks (Rawson, 1957; Micklus, 1961), suckers (Rawson, 1951), cyprinids (Scidmore, Elsey and Caldwell, 1961), white perch (Forney, 1977; Hurley and Christie, 1977), alewives (Payne, 1965), rainbow smelts (Payne, 1963; Wagner, 1972; Spangler, Payne and Winterton, 1977), lake herring (Rawson, 1957; Micklus, 1961), and centrarchids (Eschmeyer, 1950). In lakes near the central and southern limits of walleye distribution, gizzard shad (Dendy, 1946; Kutkuhn, 1958; Muench, 1966; Henderson, 1967; Kraai and Prentice, 1974), threadfin shad (Fitz and Holbrook, pers. comm.) and centrarchids (Rosebery, 1951) are the most important forage fish for walleyes. In waters where forage fishes are scarce or absent, adults feed on a variety of invertebrates (Bajkov, 1930; Scidmore and Woods, 1960; Priegel, 1962a; Koshinsky, 1965; Burrows, 1969). These consist mainly of immature mayflies and chironomids as well as amphipods and leeches.

Parsons (1971) determined that YOY and yearling walleyes in Lake Erie exhibit a size preference for forage fishes consumed. As walleyes increase in length, the mean and range in length preference of forage species increases (Fig. 14). Wagner (1972) and Davis (1975) observed a similar phenomenon in Lake Michigan and Belle Lake, Minnesota, respectively. If several forage species are available at preferred lengths, walleyes tend to feed on the most abundant species. Thus perhaps yellow perch are often the primary food of walleyes because the perch stay within the preferred forage size range, <45 percent of the walleye length (Swenson, pers. comm.), for a longer period than do such fast growing forage fishes as fresh water drum, gizzard shad and white bass which are available as food for only short periods. Yellow perch then may not be a preferred food but only one which is abundant and of suitable size for a longer time than most others. However, in the event of a delayed walleye hatch, young walleye may be disproportionately small and therefore unable to utilize the young-of-the-year perch as forage (Schupp and Macins, pers. comm.).

Arnold (1960) found yellow perch to be the preferred forage species in Utah Lake, Utah, when other forage species of similar size (Utah chub, European carp) were more numerous. Similarly, Priegel (1962a, 1962c), in Lake Winnebago, found lake emerald shiners to be preferred over a more numerous forage species (fresh water drum). Nevertheless these findings may again be related to size preference. Olson (1963) found that the walleyes of Many Point Lake strictly avoided common white suckers even though they were numerous in the lake. Wagner (1972) found that Lake Michigan walleyes fed mainly on alewives and rainbow smelt even though yellow perch were abundant and available. Similarly, the stomachs of YOY walleyes in western Lake Erie contained no trout-perch during the summer of 1959 even though they were relatively abundant and fit all of Parson's (1971) criteria for preferred forage.

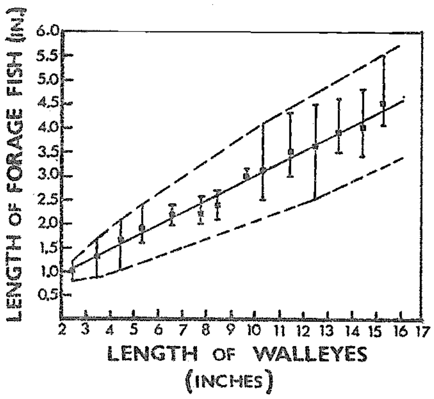

Fig. 14 Sizes of forage fish eaten by walleyes of different lengths in 1959-1960; average lengths (dots), ranges of lengths (vertical lines through dots), calculated average length (solid line), and estimated maximum and minimum lengths (broken lines) (Redrawn from Parsons, 1971)

Young-of-the-year walleyes follow a seasonal feeding pattern similar to that of adults, i.e., progressing from a predominantly invertebrate to a predominantly fish diet (see Appendix 2). Nonetheless their food preferences appear to be related entirely to their size. Few observations have been made on first feeding of walleye fry. Up to a length of about 7 to 8 mm, YOY walleyes in Lake Erie appeared to feed exclusively on phytoplankton, of which diatoms made up the greatest bulk and blue-green algae made up the remainder (Hohn, 1966; Paulus, 1972).

Walleyes 5-9 mm long, in rearing ponds, fed largely on rotifers, *Keratella cochlearis*, *Brachionus* spp., *Asplanchna* sp., *Euchlanis* sp., and *Synchaeta* sp.; copepod nauplii and adults, *Cyclops* and *Diaptomus*; and small cladocerans, *Chydorus* and *Bosmina* (Smith and Moyle, 1945). As the fry grew, copepods (now including *Epischura*) and cladocerans, including larger genera such as *Daphnia* and *Leptodora*, became the predominant food. Insects (predominantly mayfly nymphs) and fish soon become more important as the fry grow larger, until eventually fish become the predominant food (Kidd, 1927; Smith and Moyle, 1945; Smith and Pycha, 1960; Forney and Houde, 1965; Dobie, 1966a). Bulkley, Spykermann and Inmon, (1976) observed walleye fry in Clear Lake, Iowa, to feed initially upon larger zooplankters, especially the cladoceran *Daphnia*, even though rotifers and copepod nauplii were fairly abundant. Dobie (1966a) reported that when young walleyes had reached a length of 30 mm, they shifted to feeding on fish. YOY yellow perch are the forage fish most often consumed by walleye fry (Eschmeyer, 1950; Maloney and Johnson, 1957; Dobie, 1966a; Johnson, Thomasson and Caldwell, 1966; Wolfert, 1966), although when abundant, other species have been important, especially fresh water drum and trout-perch (Priegel, 1960; 1963; 1969b), johnny darters (Raney and Lachner, 1942), spottail shiners (Smith and Pycha, 1960), and black crappies (Johnson, Thomasson and Caldwell, 1966). In Little Cutfoot Sioux Lake, Minnesota, where yellow perch are relatively unavailable because of their rapid growth rate, YOY walleyes continue feeding on invertebrates, mainly aquatic insects (Johnson, 1969).

Walleye fry appear to consume forage fish selectively by size. Yellow perch consumed by walleye fry tend to be smaller than the mean length of yellow perch fry at any given time (Forney, 1965; Hofmann, 1969, 1972; Morsell, 1970). YOY walleye at the extreme western end of Lake Erie displayed their size preference by consuming alewives and gizzard shad during the summer and changing to rainbow smelt in the autumn, when the alewives and shad had become too large (Wolfert, 1966).

Cannibalism among walleyes has been observed in a number of lakes (Eschmeyer, 1950; Dobie, 1956; Rawson, 1957; Smith and Pycha, 1960; Fedoruk, 1966; Forney, 1968; Johnson, 1969). Titcomb (1921) observed cannibalism among hatchery reared fry as small as 13 mm long. Chevalier (1973) and Forney (1976) found cannibalism by adults on the YOY in Oneida Lake, New York to be a decisive factor in the formation of eight year-classes which were followed from egg through age I. The duration of such cannibalism was influenced by the growth rate of young walleyes. Forney (1974) found that in Oneida Lake, cannibalism involving YOY walleyes decreased in years when YOY yellow perch were abundant but increased in years when YOY yellow perch were scarce. Incidence of cannibalism was seen to increase in the autumn as available perch abundance decreased. Thus, YOY yellow perch tended to act as a buffer in controlling cannibalism, and indirectly regulating walleye population size. Walleye predation regulated year class strength of yellow perch (Forney, 1971) and it is the primary source of perch mortality in communities dominated by both species (Swenson, pers. comm.). Adult walleyes have also been observed to feed occasionally on juvenile walleyes (Ryder, 1977).

Winter foods consist mainly of fish (Doan, 1942; Galligan, 1960; Priegel, 1962a, 1962b) but when the availability of forage fish is limited, invertebrates become important (Eschmeyer, 1950; Priegel, 1962a).

3.4.3 Growth

Priegel (1964b) found that scale development begins when the walleye fry are about 24 mm long. Development begins at the base of the caudal peduncle and proceeds anteriorly until the fish is completely scaled, usually at a length of about 45 mm (section 3.2.3, Fig. 10).

In most waters annulus formation on walleye scales occurs from mid-May to mid-June (Carlander, 1945; Cleary, 1949; Schmulbach, 1959; Parsons, 1972). However, some authors have observed extreme variability in the time of annulus formation from one year to another and between individuals in the same year (Beckman, 1943; Smith and Pycha, 1961). Smith and Pycha (1961) found that in the Red Lakes, Minnesota, younger walleyes tended to form annuli earlier in the season than older walleyes. In a year of good growth annulus formation among age III fish occurred largely by the last week of June, whereas age VII walleyes did not form annuli until the last week of July. In a year of poor growth, no annuli were formed by the last week of June and only 88 percent of age VII walleyes had formed annuli by the end of the third week of August. The authors thus concluded that late annulus formation takes place during years of poor early summer feeding while early annulus formation is related to good early feeding and ample summer feeding. Forney (1965) noticed that in years of poor growth some older specimens may not form annuli. Beckman (1943) found completion of annulus formation to range from 2 June (1940) to 21 October (1939) in North Manistique Lake (Michigan) and from 24 July (1940) to 15 September (1939) in Bass Lake (Michigan). Smith and Pycha (1961) claimed that the time of annulus formation is not related to water temperatures.

The body-scale relationship for walleyes in most lakes is almost linear (Fig. 15) - see, e.g., Schmulbach (1959); Arnold (1960); Carlander and Whitney (1961); Forney and Eipper (1963); Forney (1965); Mraz (1968); Priegel (1969a) - but is slightly sigmoid in others (Fig. 16) - e.g., Carlander (1945); Eschmeyer (1950); Smith and Pycha (1961). Walleyes in Scriba Creek, New York, had an irregular body-scale relationship which was linear up to a body length of 330 mm but had a slight upward inflection beyond this length (Forney, 1962a).

Length-measurement relationships between standard length (SL), fork length (FL) and total length (TL) have been calculated for a number of lakes (Table XI). For those lakes in which these ratios were determined for different length groups, all ratios - FL/SL, TL/SL and TL/FL - decrease with increasing size. Although the TL/SL and TL/FL ratio decreases are probably due at least in part to a wearing down of the caudal fin with age, a decrease in the FL/SL ratio with age seems to indicate that allometric growth occurs to some extent.

A common growth pattern seems to exist for walleyes from most lakes observed during their first year of life (Fig. 17). It has been observed that YOY growth rates gradually increase during spring and early summer (Forney and Eipper, 1963; Baker, 1966a; Grinstead, 1971). During

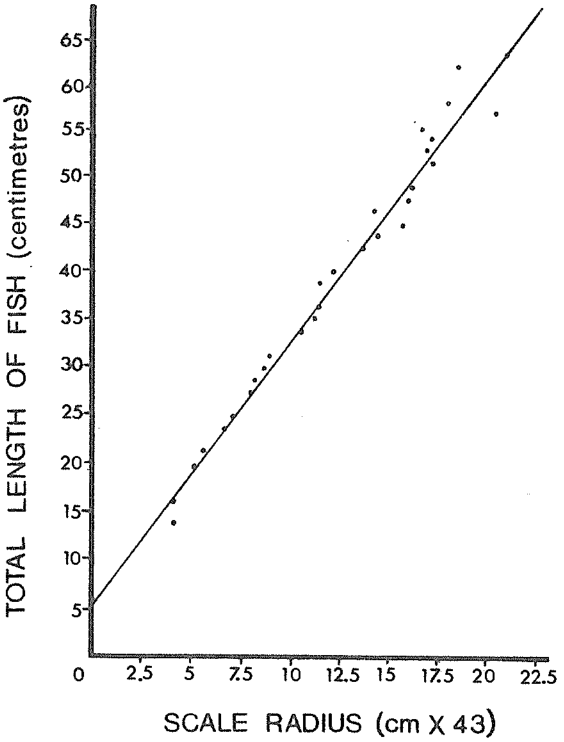

Fig. 15 Linear relationship between body length and scale radius of Pike Lake, Wisconsin walleyes (Modified from Mraz, 1968)

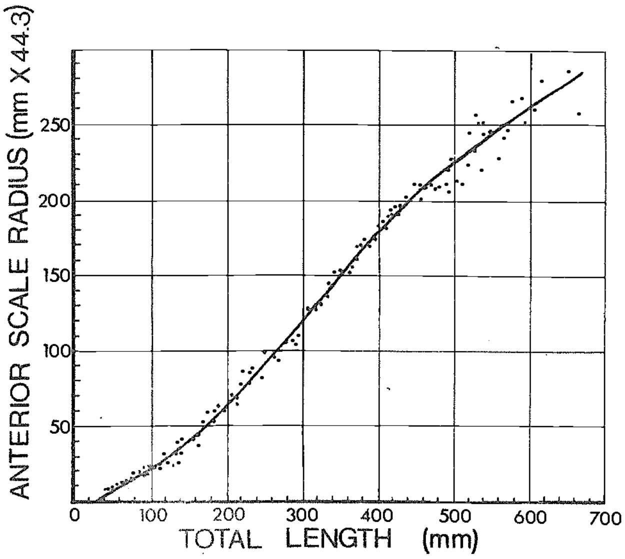

Fig. 16 Sigmoid relationship between body length and scale radius of Lake Gogebic walleyes (Redrawn from Eschmeyer, 1950)

early and mid-summer, these rates are nearly constant until late summer or early autumn, when the rates begin to decrease (Eschmeyer, 1950; Maloney and Johnson, 1957; Weber, 1961; Forney and Eipper, 1963; Grinstead, 1971).

Absolute growth rates of adult walleyes vary rather markedly from one body of water to another; even among those in proximity. In general, the growth rate of walleyes is fastest in the more southern regions of their range and slower in the more northern regions (Appendix 1, Fig. 18). Average total length at the end of the first year has been observed to range between 64 mm (Killens Reservoir, Montana) and 383 mm (Lake Meredith, Texas, Kraai and Prentice, 1974). Recently, however, higher lengths have been documented for Texas reservoirs, i.e., 460 mm sexes combined, Belton Reservoir, Prentice, 1977). Ranges for average total lengths at other ages are listed in Appendix 1. The largest walleye recorded in Ontario, 106.68 cm FL and weighing 10.71 kg, was taken in the Moon River, Ontario (Scott and Crossman, 1973). The present angling record is for a walleye taken in Old Hickory Lake, Tennessee, in 1960, which weighed 11.36 kg and measured 104.1 cm in length, 737 mm in girth (Scott and Crossman, 1973).

Huh (1976) found the total mean value of the coefficient of condition to be 1.8 for YOY walleyes raised under control conditions on a formulated diet. Specific growth rates during the 296 day study period averaged approximately 1.0 percent of weight per day. Growth rates of males and females diverge in most lakes after a certain age, depending on the lake or region: female growth rates are significantly greater than those of males (Fig. 19) after the first year in some waters (Stroud, 1949a; Kmiotek, 1952a; Lewis et al., 1964; Fleener, 1966; Muench, 1966; Seward, 1967; Ragan, 1972; Kraai and Prentice, 1974), after the second year in others (Arnold, 1960; Carlander and Whitney, 1961; Niemuth, Churchill and Wirth, 1966, Mraz, 1968; Lewis, 1970), and after the third year in still others (Carlander, 1945; Forney, 1962a; Niemuth, Churchill and Wirth, 1966; Vasey, 1967). However, this difference is sometimes not observed until after 7 (Rawson, 1957; Armstrong, 1961), 8 (Armstrong, 1961), 9 (Armstrong, 1961; Lewis et al., 1964), or even 11 years (Hile, 1954, Priegel, 1969a). On the other hand male walleyes in Sandy Lake, Ontario grew faster than females after their sixth year (Lewis et al., 1964). Similarly, Ragan (1972) observed male walleyes in Jamestown Reservoir, North Dakota, to grow faster than females for the first two years, but growth of females then exceeded that of the males after four years. Other authors have noticed no significant difference in growth rates between the sexes at any age (Kennedy, 1949; Baker, 1969a). Relative growth of walleyes is very great by the end of the first year, ranging from 6 471 percent in Belton Reservoir, Texas (Sexes combined) to 814 percent in Killens

TABLE XI

Length measurement relationships of walleyes in North American waters
(FL = fork length; SL = standard length; TL = total length)

Location and source	Length (mm)	$\frac{FL}{SL}$	$\frac{TL}{SL}$	$\frac{TL}{FL}$
Lac la Ronge, Saskatchewan (Rawson, 1957)	-			1.05
Lake of the Woods, Minnesota (Carlander, 1945)	-	1.104	1.159	1.050
Red Lakes, Minnesota (Carlander and Smith, 1945)	260-360 (SL)	1.132	1.205	1.095
	360-430 (SL)	1.126	1.196	1.062
Minnesota (Carlander and Smith, 1945)	0-199 (SL)	1.101	1.168	1.061
	200-299 (SL)	1.093	1.160	1.061
	300-399 (SL)	1.093	1.153	1.055
	400-499 (SL)	1.088	1.153	1.06
	500 (SL)	1.088	1.142	1.05
Trout Lake, Wisconsin (Schloemer and Lorch, 1942)	-		1.184	
Clear Lake, Iowa (Cleary, 1949)	-	1.127	1.198	1.065
Lake Erie (Hile, 1954)	<225 (SL)		1.179	
	225-447 (SL)		1.159	
	>447 (SL)		1.137	
Oneida Lake, New York (Raney and Lachner, 1942)	-		1.181	
Spirit Lake, Iowa (Rose, 1951)	-		1.185	
Des Moines River, Iowa (Schmulbach, 1959)	203-254 (SL)		1.227	
	254-625 (SL)		1.192	
Lake Vermilion, Minnesota (Carlander and Hiner, 1943) in Carlander, 1950)	<200 (SL)	1.106	1.169	1.057
	200-399 (SL)	1.097	1.159	1.057
	>400 (SL)	1.088	1.154	1.061
Utah Lake, Utah (Arnold, 1960)	110-575 (SL)	1.1330	1.1995	1.059
Norris Reservoir, Tennessee (Stroud, 1949a)	100-119 (SL)		1.248	
	320-339 (SL)		1.189	
	660-679 (SL)		1.162	
	Average		1.184	

Reservoir, Montana (calculated from Appendix 1, using 7 mm as the standard hatching length). Growth decreases sharply in the second year and continually decreases at a lesser rate until, on average, the fifth or sixth year. After this age, growth patterns usually are irregular (Fig. 20). In some lakes, however, the relative growth decreases each year to the last observed age class (Carlander, 1942; Eschmeyer, 1950) whereas in some (Fig. 20) the pattern is irregular after only the second year (Armstrong, 1961).

In Wunnummin Lake, Ontario, no growth increase was observed between the eighth and ninth years (Lewis *et al.*, 1964), and in Frenchman Reservoir, Montana, the average length decreased by 2.2 percent between the fourth and fifth years (Peters, 1964). Similarly, in Big Trout Lake, Ontario, decreases of 10.6 percent between the tenth and eleventh years and 3.0 percent between the thirteenth and fourteenth years (Armstrong, 1961).

Great variation in growth rates may occur between year classes (Smith and Pycha, 1961; Forney, 1962a; Fleener, 1966) and even among individuals of the same year class (Eddy and Carlander, 1939; Schloemer and Lorch, 1942; Stroud, 1949a; Eschmeyer, 1950; Schmulbach,

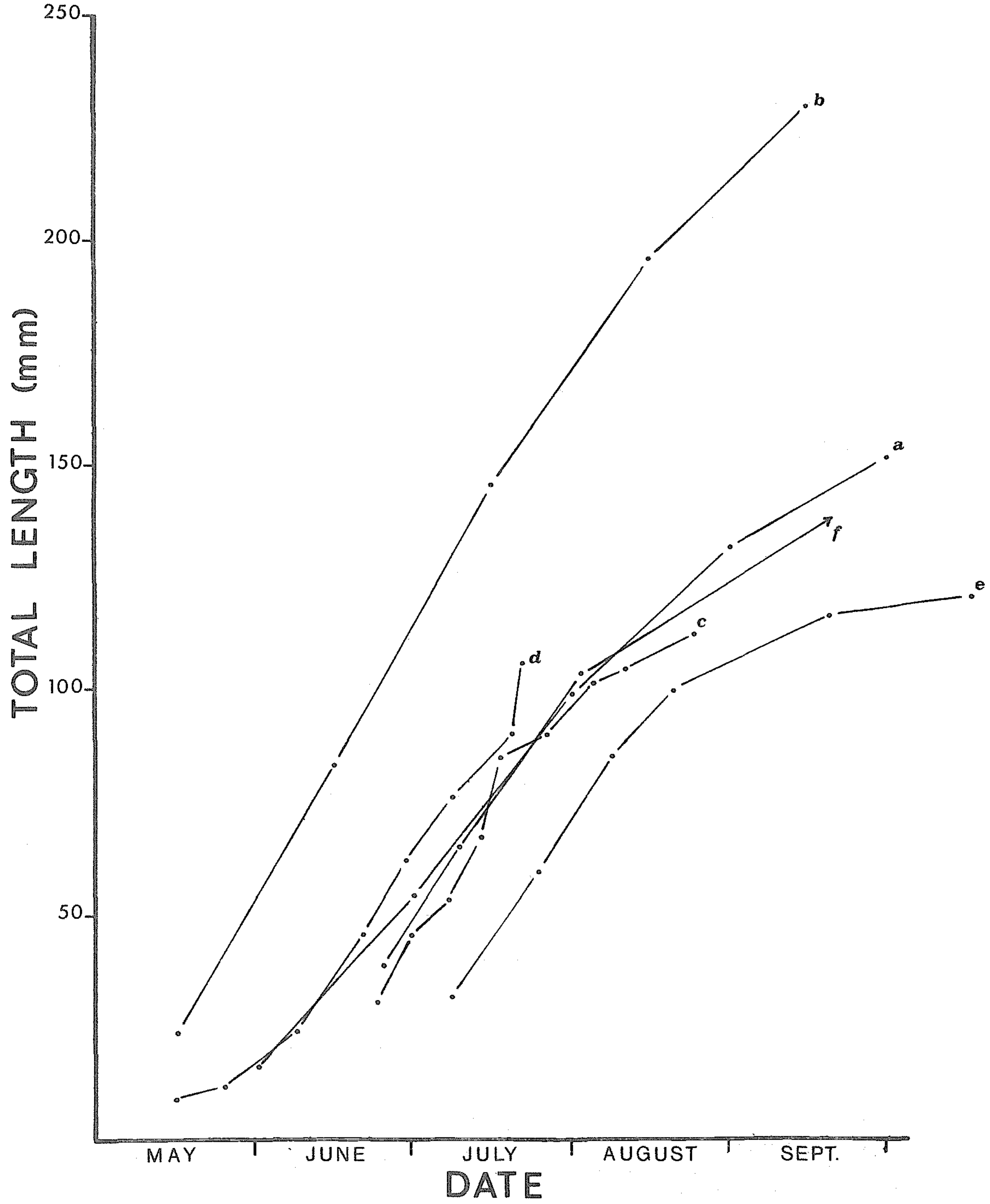

Fig. 17 Growth rates of young-of-the-year walleye from selected waters: (a) Oneida Lake, New York. The data points represent an average of the growth rates for 1959, 1961 and 1962, interpreted at month end from Fig. 2, Forney and Eipper, 1963; (b) Canton Reservoir, Oklahoma (Grinstead, 1971). The data points plotted at mid-month represent Grinstead's monthly combined averages; (c) Lake Winnibigoshish, Minnesota. Data points represent the mean rate of growth derived from Fig. 2, Maloney and Johnson, 1957; (d) Lake Erie (Baker, 1966a). Data points represent average growth rates for young-of-the-year walleye, Western Lake Erie trawl samples, 1965; (e) and (f) Lake Gogebic, Michigan for 1947 and 1941, respectively (Eschmeyer, 1950)

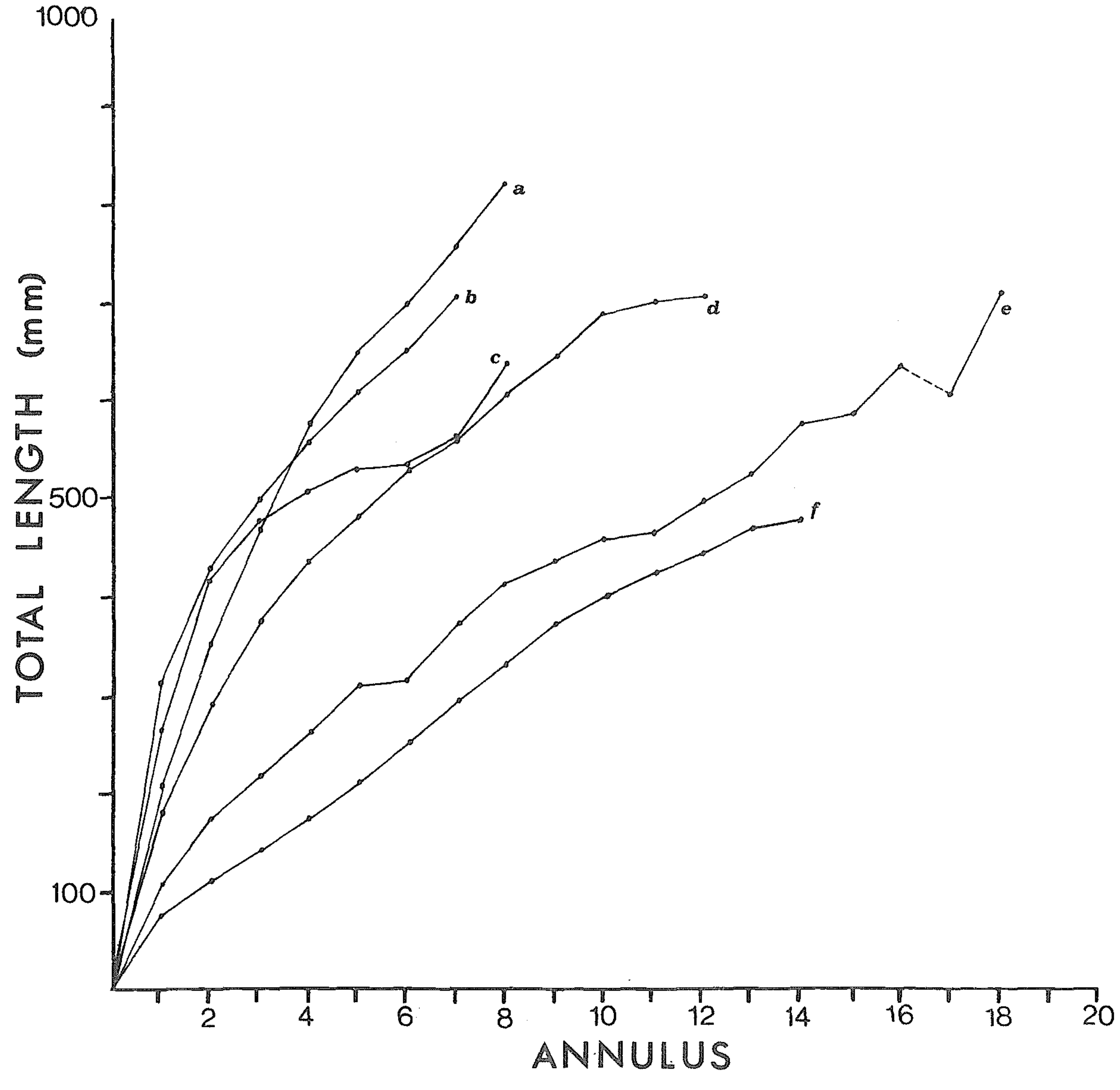

Fig. 18 Average absolute growth rates of walleye from selected waters showing differences between southern and northern populations: (a) Claytor Reservoir, Virginia (Rosebery, 1951); (b) Canton Reservoir, Oklahoma (Lewis, 1970); (c) Norris Reservoir, Tennessee (Stroud, 1949); (d) Clear Lake, Iowa (Carlander and Whitney, 1961); (e) North Caribou Lake, Ontario (Armstrong, 1961); and (f) Great Slave Lake, Northwest Territories (derived from Fig. 13, Rawson, 1951)

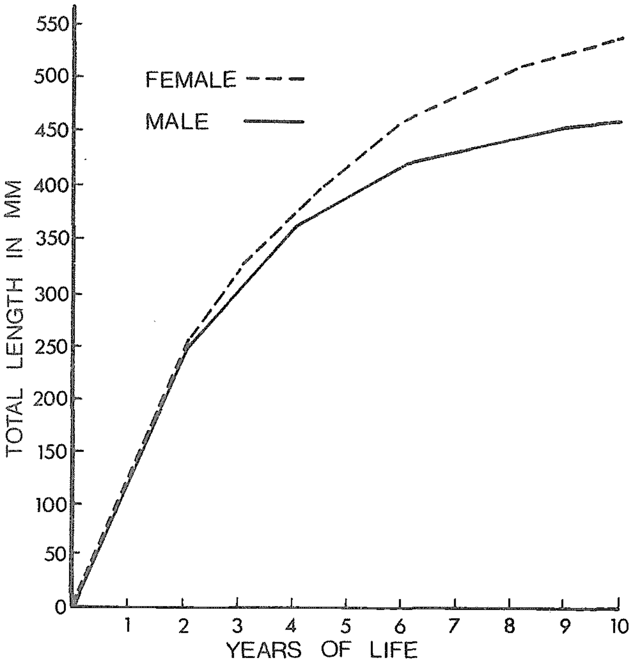

Fig. 19 Growth curves for male and female walleyes from Lake Gogebic, Michigan (Eschmeyer, 1950)

1959; Muench, 1966). This variation is probably due in part to the difficulty often encountered in distinguishing the different annuli on walleye scales and recognizing false annuli. This is especially true for older specimens which, as mentioned earlier, may not form annuli during years of slow growth (Forney, 1965). Carlander (1961) found that when 671 walleye scales were read three times by the same person, 31 percent of the second readings did not agree with the first reading, and 23 percent of the third readings did not agree with either the first or second readings. For growth studies, it has been recommended that scales be taken from the second to fifth row below the lateral line where the end of the pectoral fin touches (Smith, 1949).

Limited investigations of a few lakes have revealed that most growth of adult walleyes occurs in the late spring and late summer (Stroud, 1949a; Schmulbach, 1959). Little growth in length was observed from May to mid-July for walleye in Dexter Lake, Ontario (Moenig, 1975). This pattern was confirmed by Kelso and Ward (1972) who estimated that 90 percent of walleye growth occurred from July to October in West Blue Lake, Manitoba. In Lake of the Woods, growth of three year olds was fastest during August and September (Swenson, 1972). In Norris Reservoir, Tennessee, early spring growth was rapid for all age groups (Stroud, 1949a), then slowed during early and mid-summer but increased again during late summer and finally tapered off during the autumn. He suggested that, although forage species are abundant in the reservoir, they may not be readily available at all times in the strata of water occupied by walleyes. Walleyes in this reservoir tended to more into deeper, cooler water at about the same time that summer growth rates become reduced. Little or no growth appeared to occur during the winter (Stroud, 1949a; Kelso and Ward, 1972). This absence of winter growth appeared to be due to low temperature, and not to lack of food in Norris Reservoir, where forage fish suitable for walleyes were abundant throughout the winter (Stroud, 1949a).

Female walleyes appear to live longer than males. In general, walleyes have a longer life span in the more northern regions of their distribution (Carlander, 1948; Carlander and Whitney, 1961; Smith and Pycha, 1961) than those in the southern regions (Appendix 1). Walleyes 18 years old have been aged in Big Trout and North Caribou Lake, Ontario (Armstrong, 1961) while walleyes in lakes in the most southerly regions rarely live longer than 8 years (see section 3.3.1):

Maloney and Johnson (1957) found coefficient of condition values for YOY walleye in Lake Winnibigoshish, Minnesota, to remain nearly constant during their first year of life with an average "k" value (wt = g; L = SL, mm) of about 0.88. However, Dobie (1969), in Minnesota rearing ponds and Smith and Pycha (1960) in the Red Lakes, Minnesota noticed that walleye fry had a higher condition factor as fry than they did near the end of their first year (Fig. 21).

The average condition factor (k) for adult walleyes (Tables XII and XIII) ranged from 1.26 (Mud Lake, Iowa) to 1.855 (Utah Lake, Utah). Some authors found no significant differences in conditions with increasing length (Schloemer and Lorch, 1942; Cleary, 1949; Rawson, 1951; Hile, 1954; Smith and Pycha, 1961; Lewis, 1970), whereas others noticed a slight tendency for the coefficient to increase with increasing length (Stroud, 1949a; Slastenenko, 1956; Van Oosten and Deason, 1957; Schmulbach, 1959; Seward, 1967). In Lake Winnebago, Wisconsin, condition factors of walleyes increased markedly with age (Priegel, 1969a). These "k" values (wt = g; L = TL, mm) increased from 0.64 for age class I to 0.89 for age class VIII.

No significant differences in conditions occurred between the sexes in most lakes. However female walleyes in the Iowa region of the

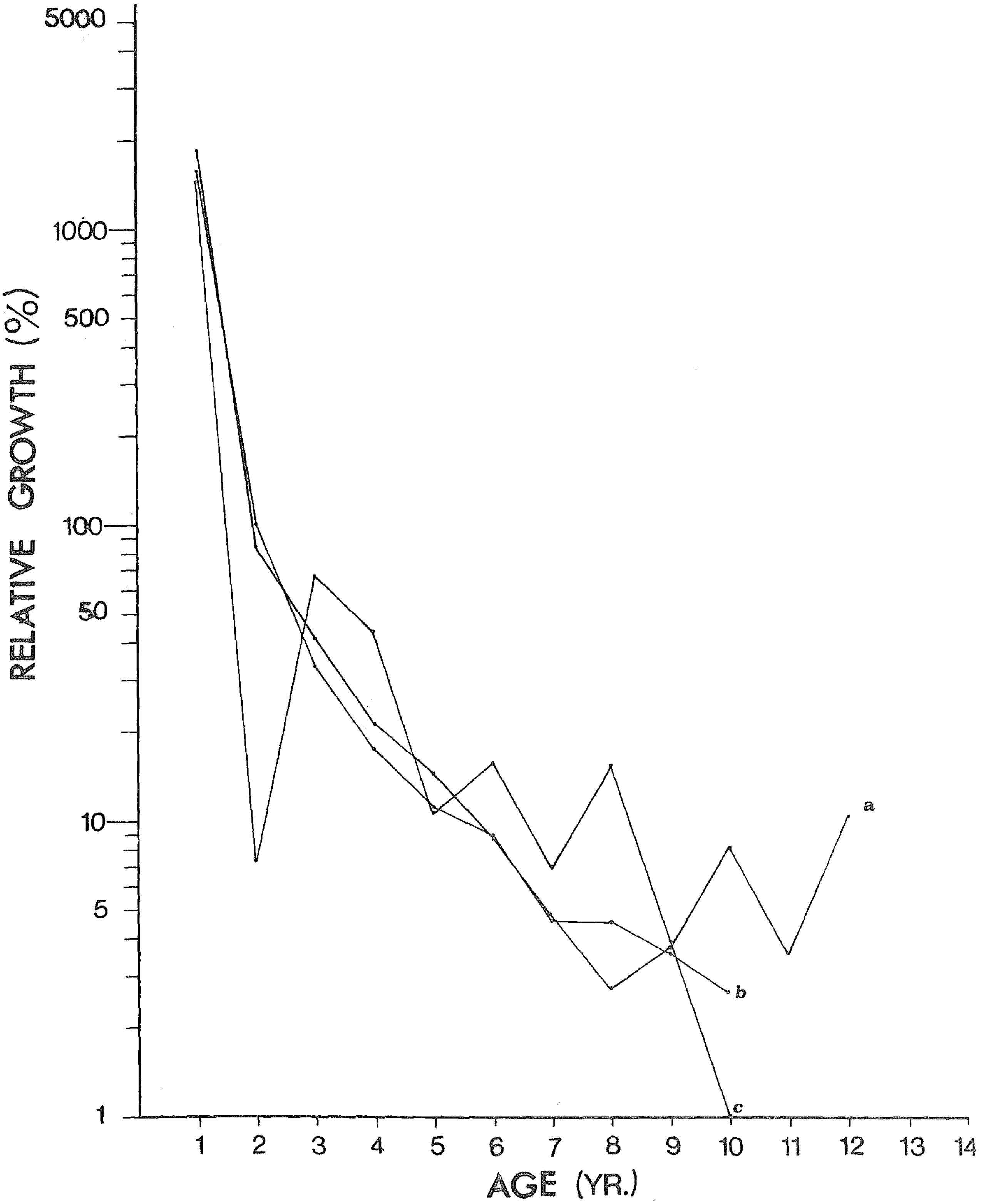

Fig. 20 The percent relative growth at each annulus for three walleye populations: (a) Deer Lake, Ontario (Armstrong, 1961); (b) Lake Gogebic, Michigan (Eschmeyer, 1950); (c) Trout Lake, Wisconsin (Schloemer and Lorch, 1942)

TABLE XII

Coefficient of condition $\frac{(W \times 10^5)}{L^3}$ for walleyes from various waters and size groups

(Units-weight in g and SL in mm; ranges, where known, in parentheses)

Location	Condition factor (sexes combined)	Source
Utah Lake, Utah	1.85[a]	Arnold (1960)
Lake of the Woods, Minnesota	1.47	Carlander (1945)
West Okoboji Lake, Iowa	1.37	Carlander (1948)
Spirit Lake, Iowa	1.71	Carlander (1948)
Spirit Lake, Iowa	1.63	Rose (1951)
Diamond Lake, Iowa	1.84	Carlander (1948)
Mud Lake, Iowa	1.26	Carlander (1948)
Welsh Lake, Iowa	1.52	Carlander (1948)
East Okoboji Lake, Iowa	1.66	Carlander (1948)
Clear Lake, Iowa	1.49 (1.05-1.73)	Cleary (1949)
Lake Gogebic, Michigan	1.66	Eschmeyer and Crowe (1955)
Great Slave Lake, N.W.T.	1.44	Rawson (1951)
Trout Lake, Wisconsin	1.45 (1.35-1.65)	Schloemer and Lorch (1942)
Three Mile Lake, Ontario	1.38 (1.09-1.53)	Slastenenko (1956)
Hiwassee Reservoir, Tennessee	1.29	Stroud (1949b)
Norris Reservoir, Tennessee	YOY-1.38	Stroud (1949a)
Norris Reservoir, Tennessee	Older-1.51	Stroud (1949a)
Red Lakes, Minnesota	1.57 and 1.59	Smith, Krefting and Butler (1952)
Red Lakes, Minnesota	1.48 (0.90-1.60)	Van Oosten and Deason (1957)
Lake Huron (Saginaw Bay)	1.28	Hile (1954)
Des Moines River (Iowa)	1.58	Schmulbach (1959)

a/ males, 1.88; females, 1.83

TABLE XIII

Coefficient of condition $\frac{(W \times 10^5)}{L^3}$ for walleyes from various waters and size groups

(Units-weight in g and TL in mm; ranges, where known, in parentheses)

Location	Condition factor[a]		Combined	Source
	♂	♀		
Red Lakes, Minnesota			0.89 (0.86-0.91)	Smith and Pycha (1961)
Lake Winnebago, Wisconsin	0.80	0.82	0.81	Priegel (1969a)[b]
Canton Reservoir, Oklahoma			1.03	Lewis (1970)
Mississippi River (Iowa)	1.02	1.16	1.11	Van Oosten and Deason (1957)
Lake Erie (Sandusky Bay)	1.08	1.07	1.10 (0.98-1.23)	Seward (1967)

a/ Excellent >1.02; average 0.89-0.97; and poor <0.83 (Carlander, 1944 in Carlander, 1950)
b/ Calculated from average lengths and weights at each annulus

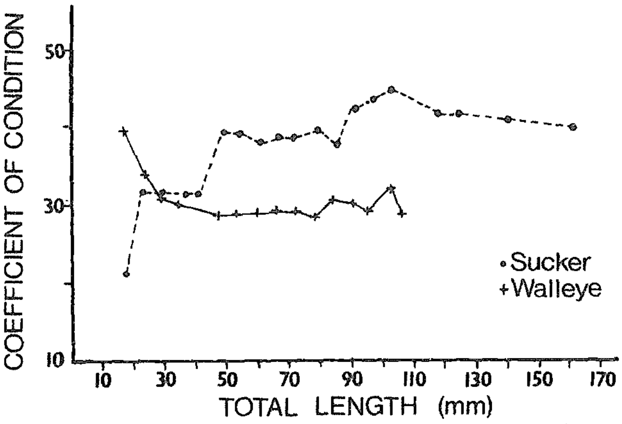

Fig. 21 Coefficient of condition for walleye and white sucker fingerlings in Minnesota rearing ponds (Modified from Dobie, 1969)

Mississippi River had an average "k" value of 1.16, whereas that of the males was only 1.02 (Vasey, 1967). Significant differences did not occur, however, until after the walleyes had attained a length greater than 481 mm. Food availability appears to be the main factor governing the condition of adults. Condition factors tend to be low in areas where forage is scarce (Stroud, 1949b; Slastenenko, 1956) and high in areas where forage is abundant (Rose, 1951; Arnold, 1960).

Length-weight relationship equations for various walleye populations are listed in Table XIV. As with condition factors, no significant difference was found between the length-weight relationship of males and females in various waters studied (Van Oosten and Deason, 1957; Priegel, 1969a; Lewis, 1970) except for the Mississippi River in Iowa (Vasey, 1967) and Center Hill Reservoir, Tennessee (Muench, 1966).

The growth rate of adult walleyes seems to be affected by two factors - temperature and amount of food consumed (forage abundance and population density). Growth rates tend to increase with decreasing latitude (Appendix 1), probably because of the longer growing season and more productive waters encountered in the southern part of the walleye's range. If temperatures are too high during the summer, however, growth may be inhibited. Eschmeyer and Jones (1941) noted that in Norris Reservoir, Tennessee, only 16 percent of the season's growth occurred between late July and early October, when water temperatures were highest.

The effects of forage abundance and population density are usually interrelated. Low walleye density usually means adequate food for all members of the population whereas a high density usually results in a scarcity of forage. Excellent forage abundance has been cited as a chief reason for good growth in a number of lakes (Stroud, 1949a,b; Rose, 1951; Forney, 1965; Miller, 1967; Hofmann, 1972). This factor not only influences adult growth but is seen to directly affect recruitment. Forney (1977) has observed the production of strong year classes of walleyes in years when growth of older walleyes was rapid.

An inverse relationship between walleye population density and growth has been documented by a number of authors - e.g., Carlander (1948), Carlander and Whitney (1961), Koshinsky (1965), and Beeton (1966). Growth records in reservoirs show this relationship very well. Growth was rapid in the first year after stocking in Canton Reservoir then declined in later years until a stable rate developed, presumably reflecting the stabilization of a growing walleye population (Lewis, 1970) Stroud, (1949a) concluded that a reduction in the rapid growth rate of walleyes, after 9 years of impoundment of Norris Reservoir, was probably due to a decreased food supply, accompanied by an increased population density. Rapid growth rates have been observed in walleye stocks undergoing heavy exploitation and a resulting severe decline in abundance. The growth rates of female walleyes in Lake Erie from 1927-1933 (18 cm at age II; Deason, 1933) were considerably slower than during the period 1964-1966 (37 cm at age II; Parsons, 1971). Moenig (1975) observed a similar increase in growth for an experimentally exploited walleye population in Dexter Lake, Ontario. Interspecific competition has been cited as a factor contributing to a reduced growth rate of Lake Winnebago, Wisconsin walleyes, which must compete with burbot, sauger, and yellow perch for a limited number of forage fishes (Priegel, 1969a). In Oneida Lake, if a high proportion of the annual prey production is consumed during a short interval, weight gain is restricted to a short period of the potential growing season resulting in a slow annual growth rate and small adult size (Forney, 1977).

Carlander (1948) observed that among some Iowa lakes growth was slowest in the deepest lake studied and fastest in the shallowest. This observation may indicate that walleye growth rates are directly related to the productivity of a body of water.

Growth rates of YOY walleyes are also closely related to water temperature. Late springs result in later-than-normal reproduction and hatching, whereas early springs have the opposite effect (Smith and Pycha, 1960; Keller, 1964a; P.J. Colby, unpubl.). Smith and Pycha (1960) found that total length at the end of the season is below average in seasons of very late hatching and above average in seasons of very early hatching.

TABLE XIV

Length-weight relationships for walleye from various waters

Equations	Location	Authority
Units: wt = g; SL = mm		
$\text{Log } W = -5.0996 + 3.099 \text{ Log } L$	Lake of the Woods, Minnesota	Carlander (1945)
$\text{Log } W = -4.8613315 + 2.988737 \text{ Log } L$	Lake Huron (Saginaw Bay), Michigan	Hile (1954)
$\text{Log } W = -5.9408 + 3.0445 \text{ Log } L$	Clear Lake, Iowa	Cleary (1949)
$\text{Log } W = -5.01127 + 3.09036 \text{ Log } L$	Spirit Lake, Iowa	Rose (1951)
$\text{Log } W = -4.79031 + 3.02554 \text{ Log } L$	Utah Lake, Utah	Arnold (1960)
$\text{Log } W = -5.06917 + 3.097 \text{ Log } L$	Norris Reservoir, Tennessee	Stroud (1949a)
Units: wt = lb; TL = in		
$\text{Log } W = -3.1443 + 2.7499 \text{ Log } L$	Attawapiskat Lake, Ontario	Lewis et al. (1964)
$\text{Log } W = -2.9550 + 2.5658 \text{ Log } L$	Lake St. Joseph, Ontario	Lewis et al. (1964)
$\text{Log } W = -3.5433 + 3.0513 \text{ Log } L$	Winnummin Lake, Ontario	Lewis et al. (1964)
$\text{Log } W = -3.4781 + 2.9932 \text{ Log } L$	Sandy Lake, Ontario	Lewis et al. (1964)
$\text{Log } W = -3.36303 + 3.1103 \text{ Log } L$	Deer Lake, Ontario	Lewis et al. (1964)
$\text{Log } W = -3.3684 + 2.9141 \text{ Log } L$	North Caribou Lake, Ontario	Lewis et al. (1964)
$\text{Log } W = -3.55502 + 3.04957 \text{ Log } L$	Red Lakes, Minnesota	Smith and Pycha (1961)
$\text{Log } W = -5.3596 + 3.2162 \text{ Log } L$	Lake Winnebago, Wisconsin	Priegel (1969a)
$\text{Log } W = -2.7514 + 3.2618 \text{ Log } L$	(♂) Mississippi River, Iowa	Vasey (1967)
$\text{Log } W = -2.8991 + 3.3959 \text{ Log } L$	(♀) Mississippi River, Iowa	Vasey (1967)
$\text{Log } W = -3.4030 + 2.9721 \text{ Log } L$	Canton Reservoir, Oklahoma	Lewis (1970)
Units: wt = oz; TL = in		
$\text{Log } W = -2.1701 + 2.8930 \text{ Log } L$	Makoop Lake, Ontario	Armstrong (1965)
$\text{Log } W = -2.422 + 3.140 \text{ Log } L$	Des Moines River, Iowa	Schmulbach (1959)
Units: wt = g; TL = in		
$\text{Log } W = -1.00949 + 3.15399 \text{ Log } L$	Pike Lake, Wisconsin	Mraz (1968)
Units: wt = g; TL = mm		
$\text{Log } W = -0.02770 + 3.03 \text{ Log } L$	(♂) Center Hill Reservoir, Tennessee	Muench (1966)
$\text{Log } W = -0.03119 + 2.99 \text{ Log } L$	(♀) Center Hill Reservoir, Tennessee	Muench (1966)
$\text{Log } W = -0.01719 + 3.16 \text{ Log } L$	(Comb.) Center Hill Reservoir, Tennessee	Muench (1966)
$\text{Log } W = -4.92519 + 2.96224 \text{ Log } L$	Savanne Lake, Ontario	P.J. Colby (unpubl.)
$\text{Log } W = -4.584 + 2.845 \text{ Log } L$	(♂) Lake Meredith, Texas	Kraai and Prentice (1974)
$\text{Log } W = -5.099 + 3.040 \text{ Log } L$	(♀) Lake Meredith, Texas	Kraai and Prentice (1974)
$\text{Log } W = -5.80964 + 3.20447 \text{ Log } L$	Lake Sakakawea, North Dakota	Wahtola, Miller and Owen (1972)
$\text{Log } W = -5.39540 + 3.18672 \text{ Log } L + 0.0106Y$ where Y = year of capture (0, 1, 2)	Dexter Lake, Ontario	Moenig (1975)

However, they observed that during some years of late hatching, a period of above normal growth rate occurred during late summer (mid-August) which reduced total lengths at the end of the growing season (Fig. 22) between fish from late and early season hatches (Smith and Pycha, 1960; P.J. Colby, unpubl.). This surge in growth rate appears to be due to an abnormal water temperature increase just before the observed increase in growth. P.J. Colby (unpubl.) found that in Savanne Lake, Ontario, in a year with a late spring, growth was slow initially, but increased sharply during the first two weeks of August after a period of water temperatures 2-3°C higher than normal during the last two weeks of July. By the end of the season the total lengths were similar to those of YOY walleyes hatched during a year with an early spring and more nearly normal summer temperatures. During a year with a late spring and normal summer temperatures, the growth rate was slow and steady, and final total lengths were significantly less than normal. Forney and Eipper (1963) observed a significant positive correlation between water temperatures in Oneida Lake, New York, and YOY growth, especially during May and June. During one season in the same lake, the greatest rate of growth occurred during the first half of August which followed the period of highest summer temperatures which occurred during the last two weeks of July (Raney and Lachner, 1942). Smith and Koenst (1975) and Huh (1976) have shown that the temperature range for optimum growth of juvenile walleyes (84.2-86.5 mm long) is 19 to 25°C.

Pond culturing of YOY walleyes (Fig. 23) has shown that growth is inversely related to population density (Dobie, 1956; 1969). Dobie (1969) concluded that density alone was the cause, because food availability was not considered a limiting factor. Keller (1964a) attributed the increase in first year growth in Lake Erie walleyes, between 1920 and 1962, to a reduction in population density. Smith and Pycha (1960), on the other hand, observed that at the population levels in the Red Lakes, Minnesota, variation in brood size had no significant effect on first year growth.

Size and type of forage species appears to have some effect on YOY walleye growth. Morsell (1970) found that growth of walleye fingerlings in Escanaba Lake, Wisconsin depended on the size of perch fry, the dominant prey. Walleye growth was highest when they were more than twice as long as perch fry. However, the abundance of yellow perch and growth of YOY walleye appears to be unrelated (Smith and Pycha, 1960; Forney and Eipper, 1963). The relationship between the growth rate of YOY yellow perch and that of YOY walleyes is in question. Smith and Pycha (1960) found a negative correlation between the two in the Red Lake, Minnesota, whereas Forney and Eipper (1963) noticed a positive relationship between the two in Oneida Lake, New York. Similar conflicting results have been recorded for the relationship between types of food consumed and growth. Growth rates of YOY walleyes tended to be greater when fish formed the major portion of the diet than when the diet consisted mainly of invertebrates (Forney, 1966; Priegel, 1969b). However Smith and Pycha (1960) discerned that there is no relationship between type of food consumed and growth rates.

The only marking method that appears to affect the growth rate of walleye is jaw-tagging. In every instance where the rates between jaw-tagged and untagged fish were compared, growth rates of jaw-tagged walleyes were slower compared to those of untagged fish (Smith, Krefting and Butler, 1952; Patterson, 1953; Eschmeyer and Crowe, 1955; Mraz, 1968). Neither Petersen tags (Rawson, 1957) nor excision of one (Kempinger, 1963) or two fins (Mraz, 1968) retarded growth among adults. Among YOY, neither dart-type tagging (Wolfert, 1963) nor excision of both pectorals or pelvics (Churchill, 1963) affected growth rates.

3.4.4 Metabolism

Digestion rate does not appear to differ among different populations of walleye (Swenson and Smith, 1973). Hofmann (1969) determined that the digestion rate increased logarithmically with temperature (Fig. 24). On the other hand, as meal size increases or particle size increases, the digestive rate (Table XV) decreases (Swenson and Smith, 1973). Although a large meal reduces the digestive rate, more food is processed by the digestive system in a given period.

Kelso (1972) determined the maintenance ration for adult walleyes to be 36.5-38.2 mg emerald shiner/g body wt/day (temperature, 4-12°C). Maintenance rations appear to be similar for various size ranges of walleye (Hofmann, 1969; Kelso, 1972) and increase logarithmically (Fig. 25) with temperature (Kelso, 1972).

Laboratory studies indicate that gross conversion (total growth/total food consumed) for walleyes is rather low - ranging from 0.106 to 0.142 between temperatures of 12 and 20°C (Kelso, 1972); averaging 0.20 for walleyes sampled between June and September (Swenson and Smith, 1973). Kelso determined gross conversion to be independent of temperature at any one meal size but inversely related to walleye weight. Gross conversion is only slightly less than net conversion (total growth/assimilated food) due to the efficient assimilations by walleye (95 percent or higher for emerald shiner) of an ingested meal (Kelso, 1972).

Kelso (1972) determined that assimilation efficiencies (wt of food assimilated/wt of food

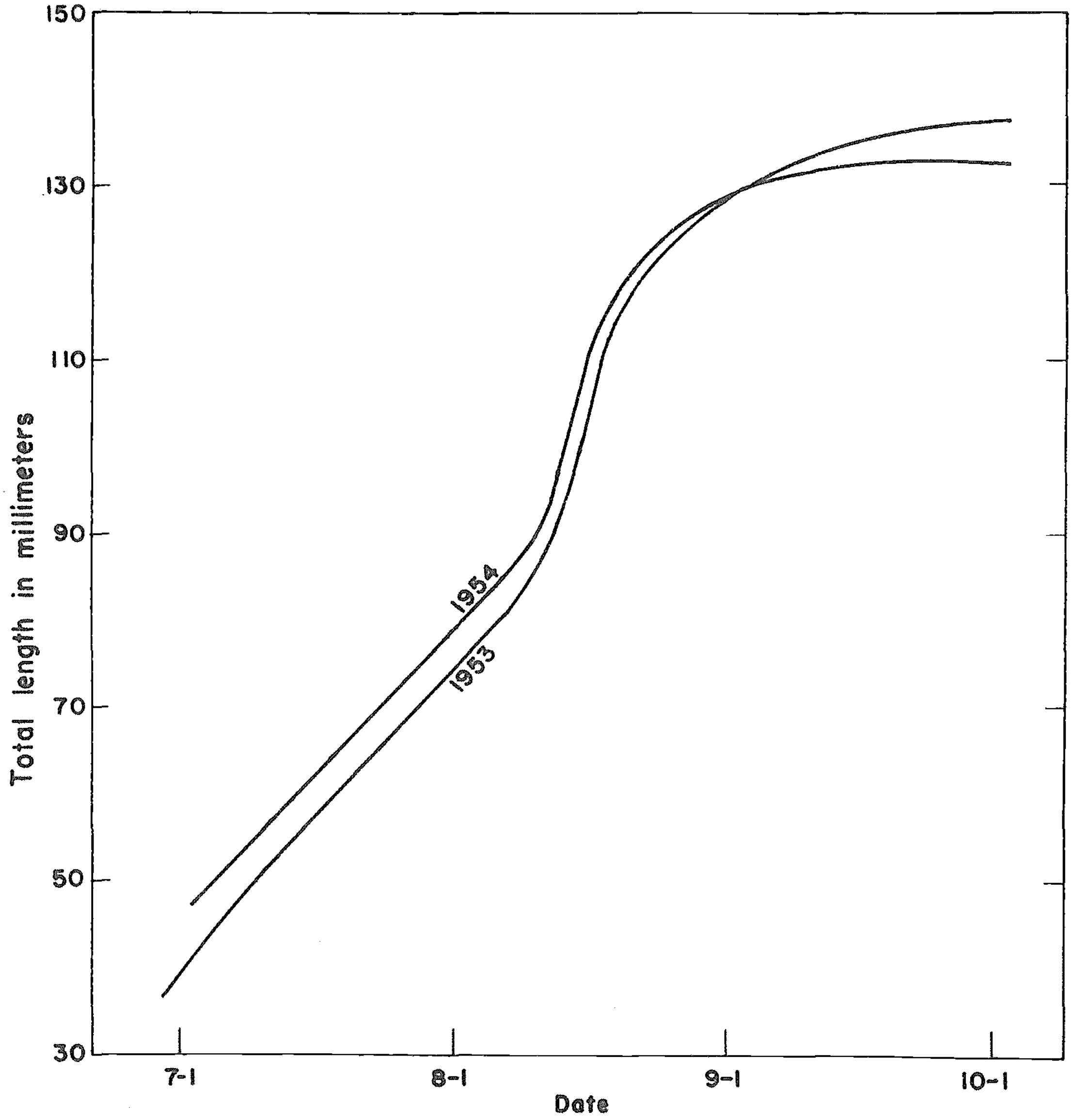

Fig. 22 Growth of YOY walleyes in 1953 and 1954 (years of poor early growth) showing growth compensation in mid-season (Redrawn from Smith and Pycha, 1960)

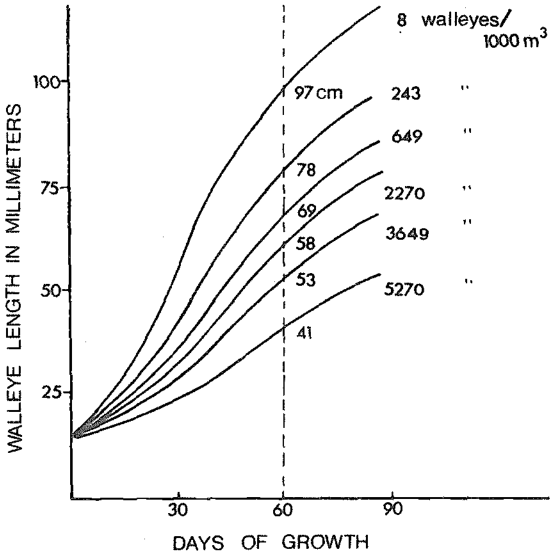

Fig. 23 Relationship between population density of walleyes in ponds and average total length of fish in millimetres (Modified from Dobie, 1956)

ingested) varied with diet type. It was highest for fish (96.9 percent for YOY yellow perch and 97.0 percent for emerald shiners) and least for invertebrates (82.1 percent for amphipods and 83.5 percent for crayfish). Assimilation efficiency decreased with increasing walleye size (Fig. 26).

Kelso (1973) determined that energy content of walleye (entire body) increases from May through October (Fig. 27). This increase occurred regardless of age and was probably due to a buildup of fat deposits.

3.5 Behaviour

(For feeding behaviour, see 3.4.1; for reproductive behaviour see 3.1.3, 3.1.6.3.)

3.5.1 Migrations and local movements

Mature members of all self-propagating walleye populations, whether stream-spawning or lake-spawning, migrate from their overwintering grounds to their spawning grounds in spring and continue to their summer feeding grounds shortly after spawning. In a number of areas, walleyes have been observed to disperse throughout available habitat shortly after spawning. This behaviour is common to walleyes of the Moon River (Spangler, Payne and Winterton, 1977); Oneida Lake (Forney, 1963) and Lake Winnebago,

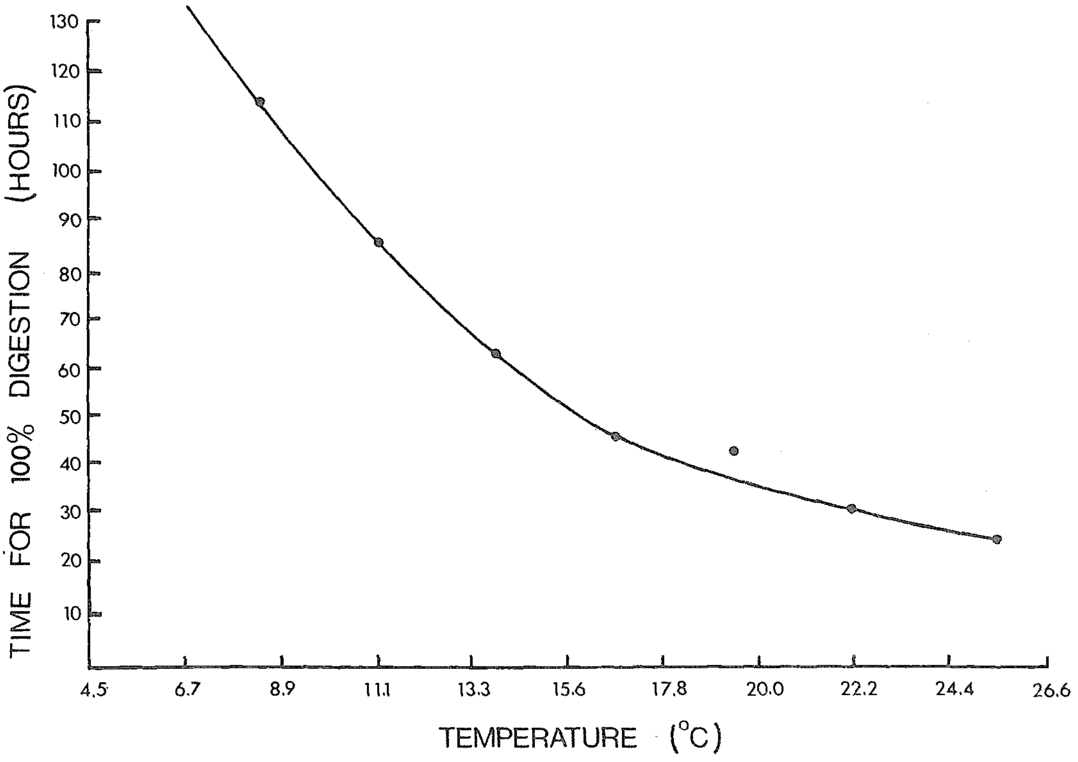

Fig. 24 Change in rate of digestion at various temperatures. Line fitted by inspection (Modified from Hofmann, 1969)

TABLE XV

Mean percentage digestion of three sizes of minnows by walleyes after voluntary feeding. Number of observations is in parentheses (Swenson and Smith, 1973)

Food size, temperature and duration (h)	Meal size (mg food/g fish)		
	0.1-10	10-20	20+
0.8 g (20°C)			
4	50.4 (7)	47.1 (3)	32.2 (6)
8	88.2 (8)	74.2 (4)	62.2 (10)
12	96.9 (4)	95.8 (8)	90.0 (16)
1.1-1.9 g (14.5°C)			
4	36.0 (13)	32.9 (15)	28.0 (9)
8	60.1 (7)	54.9 (12)	44.2 (13)
12	84.3 (7)	75.0 (13)	60.8 (6)
16	97.3 (1)	96.0 (1)	77.8 (8)
3.1-5.0 g (14.5°C)			
4	8.5 (2)	13.3 (5)	12.0 (14)
8	46.2 (1)	29.8 (7)	27.9 (12)
12	-	58.5 (1)	40.0 (15)
16	-	-	67.2 (9)
20	87.3 (4)	-	84.8 (15)
24	96.1 (2)	91.2 (1)	94.4 (12)

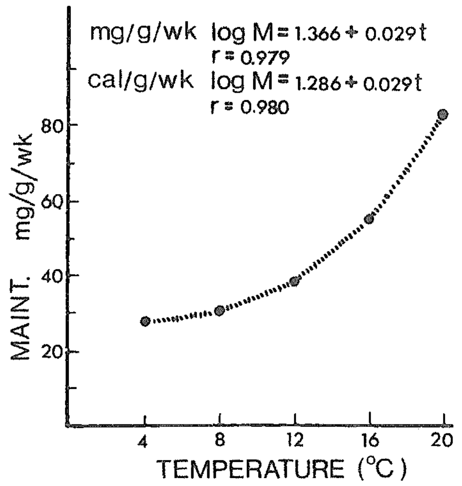

Fig. 25 Relation between maintenance requirements and temperature for walleye (Redrawn from Kelso, 1972)

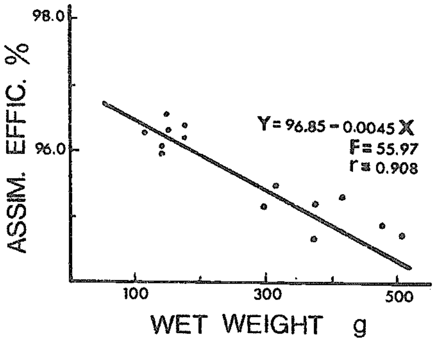

Fig. 26 Effect of walleye size (g wet weight) on assimilation efficiency at 16°C (Redrawn from Kelso, 1972)

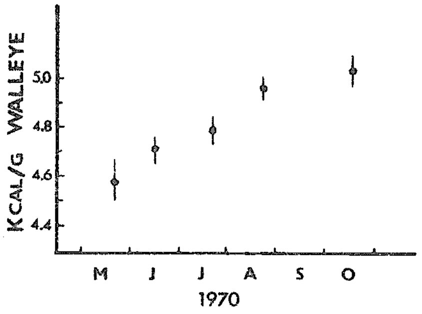

Fig. 27 Change in energy content of whole walleyes in West Blue Lake during 1970 (Redrawn from Kelso, 1973)

Wisconsin (Priegel, 1968). During the spring, stream-spawning walleyes move into their spawning streams and up to their spawning grounds while lake-spawning stocks move inshore to the spawning shoals. After spawning the fish return, generally by the same route, with males usually remaining longer on the spawning beds than females (see section 3.1.6.3). Recoveries from spring tagging operations on spawning grounds indicate that the majority of a spawning population, in most waters, migrates less than 16 km from its spawning grounds (Carbine and Applegate, 1946; Rawson, 1946; Bonde, Elsey and Caldwell, 1961; Priegel, 1966b; Baker, 1967a). Even in such large bodies of water as Lake Superior (Kmiotek and Daly, 1957) and Georgian Bay (Zimmerman, 1966a), a large majority of the spawners move no further than 5 km from their spawning grounds. Distances moved are largely related to environmental suitability of the lake. Lake Superior waters, in general, provide an ecological barrier to walleye movement. However, walleyes moved extensively in Nipigon Bay and contiguous inland waters (Ryder, 1968; Table IV). As an example, of 202 first-year tag returns, a mean distance of 20.5 km from the spawning grounds was recorded or 11 to 58 km (range). It is not uncommon for some individuals to be recaptured at much greater distances from their point of release. Twenty-one percent of the adults tagged in Lake Winnebago, Wisconsin, were recovered from 40 to 156 km from their point of release (Priegel, 1968). Recaptures at distances of 211 km (Carbine and Applegate, 1946), 282 km (Desrochers, 1953; Ferguson and Derksen, 1971) and 380 km (Wolfert, 1963) have also been reported. Recaptures of walleyes tagged on Lake Champlain spawning grounds (north end) indicate that more than 60 percent of the spawning fish migrate distances greater than 48 km down river toward and into the St. Lawrence River (Desrochers, 1953).

Presumably a migration of similar magnitude must be undertaken to return to the spawning grounds the following spring, since evidence strongly suggests that mature walleyes tend to return to the same spawning grounds year after year (see section 3.1.6.3). Cross (1964) supports repetitive migration, but he has found that considerable intermingling can occur in areas where several spawning sites exist in close proximity. In studying movement of walleyes transferred to upstream impoundments, Eschmeyer and Crowe (1955) observed that walleyes exhibited a marked tendency to move downstream past dams to their original habitat. Olson, Schupp and Macins (1978) state that homing is probably an adult-learned behaviour influenced by physical characteristics of the environment and strengthened by repeated migrations. Also, they suggest that dispersal of walleye eggs and fry from the site of egg deposition by wind and river currents precludes natal behaviour.

The rate of migration of individuals (measured by tag recoveries) has rarely been reported to be greater than about 3 km/day. Ryder (1968) indicated an average rate of about 0.8 km/day for walleyes of the Nipigon Bay region of Lake Superior. However, Ferguson and Derksen (1971) recovered one walleye, tagged in the Thames River, Ontario, which had travelled 280 km to Saginaw Bay, Lake Huron in 31 days (9.1 km/day).

Differences in migration patterns for different age groups have been observed among some Great Lakes stocks. Tagging studies conducted by Ferguson and Derksen (1971) indicated that adults and juveniles (age II) from the Thames River (Lake St. Clair) stock moved in opposite directions during periods of migration. Through late spring and summer, adults moved north from their spawning grounds on the Thames River into the St. Clair River and southern Lake Huron, while juveniles move south through the Detroit River and into the western basin of Lake Erie. Through the autumn, winter and early spring, these migrations were reversed (Fig. 28). These authors observed similar migration patterns in Lake Erie.

Upon hatching, walleye fry disperse from their spawning grounds. When first hatched the fry are unable to swim far because of their heavy yolk sacs. In aquaria, the fry remain on the bottom except for occasional excursions to the surface, after which they immediately sink back to the bottom (Houde, 1968; Houde and Forney, 1970). This behaviour persists for about 5 days, at which time the yolk reserve is completely exhausted (Houde, 1968) at a length of approximately 9.5 mm (Houde and Forney, 1970). The fry then swim continuously at the surface (Houde and Forney, 1970). Studies by Houde and Forney (1970) on Oneida Lake showed that newly hatched fry drifted passively and that currents moving over the spawning grounds probably carried them into the limnetic zone. Although currents are important in early dispersal from the spawning grounds, these studies indicated that young walleyes were capable of regulating their distribution within 1 to 2 weeks after hatching. Active immigration inshore seems unlikely, since sustained swimming ability at this stage is not enough to counteract the surface currents at most times. Possibly fry can regulate their distribution at this stage by coordinated vertical migrations and active swimming, although the ability of walleye fry to orient to currents while pelagic has not been demonstrated. Eschmeyer (1950) found evidence to suggest that fry in Lake Gogebic, Michigan, lead a pelagic life shortly after hatching until they reach a length of about 25 mm, at which time they move inshore (late June-early July). Bulkley, Spykerman and Inmon (1976) reported that walleye fry in Clear Lake, Iowa were moving inshore to

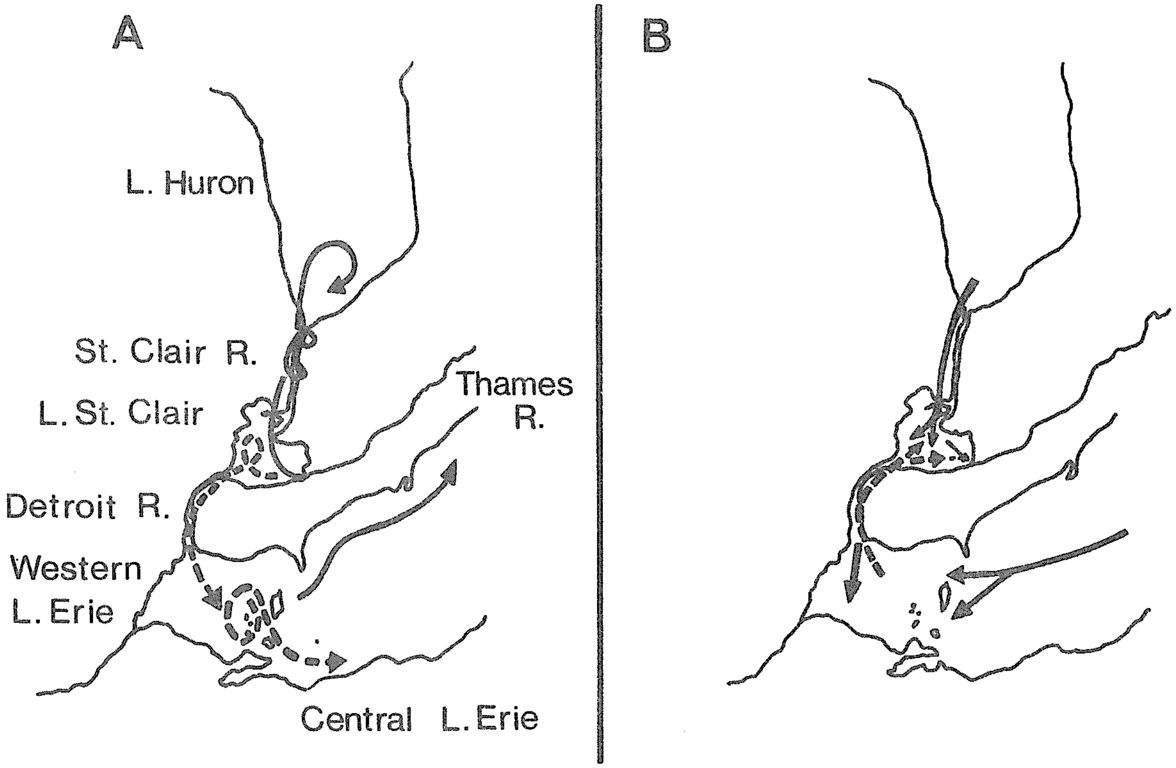

Fig. 28 Walleye migration patterns of Thames River stock. (A) Spring postspawning and summer migrations of adults (solid lines) and immature (broken lines) fish. Whorls suggest milling areas. (B) Autumn to early spring (prespawning) migrations. Broken lines here indicate maturing fish that have not spawned previously (after Ferguson and Derksen, 1971)

feed as early as 31 May. Forney (1976) observed a transition from a pelagic to an inshore, demersal mode by fry upon attaining a mean length of 35 mm. Ryder (1977) stated that walleye fry at lengths of 25-30 mm become benthic and move toward shore into shallow, sheltered bays. Johnson (1969) observed newly-hatched fry in Little Cutfoot Sioux Lake, Minnesota, to move from the vicinity of the spawning beds a few hours after reaching the swim-up stage. After reaching a length of 24 mm, these fry were observed close to shore in 0.3-1.2 m of water. However Priegel (1970) observed that YOY walleye in Lake Winnebago, Wisconsin, do not frequent nearshore areas at any time during their first year of life.

Local movements during summer, autumn and winter occur among walleyes of all ages. Late summer movement by adults into deeper waters has been observed by a number of authors (Kennedy, 1935; Niemuth, 1957; Rawson, 1957; Arnold, 1960; Hughson and Sheppard, 1962; MacCrimmon and Skobe, 1970). Spangler, Payne and Winterton (1977) observed the movement of walleye from large tributaries into Lake Huron during periods at high water temperature in late summer. Johnson (1969) observed adults (>II) in Little Cutfoot Sioux Lake, Minnesota, to move from depths of 1.2-3.0 m to 3.7-4.3 m during mid-August. However, juveniles (I and II) moved little during this time, suggesting a differential movement by size or age class. Young-of-the-year have also been observed to move from shore into deeper waters during mid-summer to early autumn (Raney and Lachner, 1942; Forney, 1966; Johnson, 1969; Grinstead, 1971). These summer movements appear to be an avoidance reaction in response to rising water temperatures (Kennedy, 1935; Johnson, 1969). Walleyes in Norris Reservoir, Tennessee exhibit an aversion to temperatures above 24°C, even to the point of utilizing relatively deoxygenated water (1-2 mg/l) below the thermocline (Fitz and Holbrook, 1978). The critical temperature at which this response is initiated seems to be higher for smaller (or younger) walleyes (Kennedy, 1935; Johnson, 1969). However, Ryder (1977) suggested that such movement, in the case of fry, may be in response to a continuing adaptation to progressively decreasing light intensities or conversely, a shunning of high daytime intensities. Because surface water temperatures during the summer on Lac la Ronge, Saskatchewan, rarely exceed 19°C, Rawson (1957) suggested that the movement of adults into deeper waters (to 20 m) in the late summer is not a response to high temperatures but perhaps reflects a pursuit of ciscoes and young whitefish (important food items) which also move deeper at this time.

Johnson (1969) observed adult walleye to move back inshore during early September in Little Cutfoot Sioux Lake but by 21 October, all age classes had moved into deeper waters. Elsey and Thomson (1977) found that the autumn (September and October) commercial trap net catch for Lac des Mille Lacs, Ontario, consisted of older walleye than the summer (July) catches conducted by the Ontario Ministry of Natural Resources, using similar gear (B. Hamilton, pers. comm.). YOY walleyes in Canton Reservoir, Oklahoma, also moved into deeper waters during the autumn and winter (Grinstead, 1971). Johnson (1969) suggested that walleyes may have a minimum water temperature preference, and seek deeper waters in late autumn and early winter because water temperatures remain higher there than on the shoals. However Niemuth (1957) and Rawson (1957) observed walleyes to move into shallower water in the autumn and remain there on into the winter. In late September, Kelso (1976) observed the movements of walleyes in West Blue Lake, Manitoba to be restricted to the homothermous epilimnion, above 10 m and usually within 100 m of shore.

3.5.2 Schooling

Yearlings, sub-adults and adults are usually closely associated with respect to movement and schooling. Johnson (1969) observed yearling and older walleyes in Cutfoot Sioux Lake, Minnesota, to follow the same depth distribution patterns throughout most of the year. Ryder (1977) often observed all three of these age groups schooling together. Underwater observations have revealed that the size of these schools may range from 3 to 4 to several hundred or more fish (Ryder, 1977). Hughson and Sheppard (1962) observed one school of 45 individuals (ranging from 0.34 to 2.0 kg in weight) to have a diameter of about 6 m. White suckers often orient themselves in walleye schools and behave as integral members (Scott and Crossman, 1973).

Young-of-the-year walleyes seem to show stronger schooling tendencies and are often associated with schools of YOY yellow perch (Eschmeyer, 1950; Maloney and Johnson, 1957; Johnson, 1969). Eschmeyer (1950) observed a school of 14 YOY walleyes in close association with a mixed school of YOY yellow perch and walleye. Maloney and Johnson (1957) observed that YOY walleye seen mixing with schools of YOY yellow perch in Mille Lacs Lake, Minnesota, were always larger than the perch and suggested that this association facilitated predation by the walleyes.

In many of the larger lakes there may be more than one spawning stock, each of which spawn in a distinctly different area with little straying of individuals from one ground to another. These include, among others, Lake Superior (Ryder, 1968); Lake Huron (Regier, Applegate and Ryder, 1969; Spangler, Payne and Winterton, 1977), Lake Winnibigoshish (Johnson and Johnson, 1971), Lac la Ronge, Saskatchewan (Rawson, 1957) and Lake Champlain, Vermont (Halnon, 1960). Most often these stock are homogeneous during the summer, autumn and winter and separate only during the spring when they migrate to their separate spawning areas (Rawson, 1957; Forney, 1961a; Crowe, Karvelis and Joeris, 1963; Regier, Applegate and Ryder, 1969; Johnson and Johnson, 1971; Spangler, Payne and Winterton, 1977). However some closely associated populations remain spatially distinct throughout the year (Halnon, 1960; Ryder, 1968; Regier, Applegate and Ryder, 1969). Spangler, Payne and Winterton (1977) noted evidence of discrete populations of walleye associated with larger tributaries in Lake Huron. These were observed to remain within 10 km of the river mouths.

In most waters walleyes exhibit a diurnal vertical migration that is associated with changing light intensities. Carlander and Cleary (1949) observed that walleyes in Lake of the Woods, Minnesota, and Clear Lake, Iowa, came into shallow waters at night to feed and suggested that this movement was effected by diminishing light intensities. Bardach (1955) observed a similar movement in Lake West Okoboji, Iowa. Because of the walleye's light-sensitive eyes, such movements into shoal areas and pelagic waters are necessary for this fish to reach optimum illumination levels for feeding (Ryder, 1977; see section 3.5.3). Net catches (Carlander and Cleary, 1949; Sieh and Parsons, 1950; Lawler, 1969) and angling success (Zimmerman, 1966a); Cheshire, 1968; Anderson, 1971; Ryder, 1977) have also been observed to be greatest at dawn and dusk, indicating that these are periods of greatest movement and feeding activity. Ultrasonic tracking studies on West Blue Lake, Manitoba have corroborated these conclusions (Kelso, 1976). In a similar study employing radio-biotelemetry to monitor walleye movement in Lake Bemidji, Minnesota, Holt et al. (1977) found no diel pattern of onshore-offshore movement. Instead, it was found that test walleyes moved chiefly parallel to the shore at depths ranging from 1.6 to 5.0 m. This study also suggested that the distance of mean daily movement is related to the season; with greatest daily movements occurring in the spring and autumn and least daily movements during the summer season. Test walleye appeared to inhabit particular areas of the lake and their movements within these areas seemed to be restricted by the lake bottom morphometry.

3.5.3 Responses to stimuli

During laboratory studies Houde (1969) observed that an increasing percentage of walleye fry exhibited positive rheotaxis as their size increased from 7.0 to 16.5 mm. Furthermore, swimming ability increased sharply between the lengths of 7.5 and 9.5 mm, the growth interval during which time the heavy yolk sac is being absorbed. At lengths between 9.5 and 15.5 mm, swimming ability reaches an asymptotic value of 3.0 to 3.25 body lengths/sec at 13°C (Fig. 29). Through underwater observations Ryder (1977) noted adult walleye in currents were always headed upstream unless disturbed, whereupon they turned downstream and swam away. Most eventually worked their way back to their former position in the current or eddy.

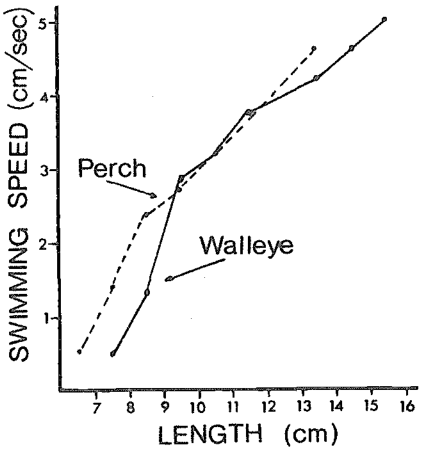

Fig. 29 Relation of swimming speed in cm/sec to fish length for walleye and yellow perch larvae. (Swimming speed is the calculated current velocity that is sustained for 1 h by 50 percent of the fish (1 h FV_{50}).) (Redrawn from Houde, 1969)

Jones, Kiceniuk and Bamford (1974) formulated a critical velocity equation of $V = 13.07\ L^{0.51}$ where V is the critical velocity (maximum velocity in cm/sec that can be maintained for 10 min) and L is the fork length (cm). As an example, the critical velocity of a 12 and 62 cm walleye would be 46.4 and 107.2 cm/sec, respectively. Walleyes appear to avoid currents during the winter (Scott and Crossman, 1973).

In laboratory studies Mount (1961) observed that adult walleyes are rather inactive at an oxygen concentration of 6 ppm; as levels are reduced, they become more active and begin to come to the surface. Below 3 mgl^{-1}, the ventilation rate and amplitude increases rapidly, activity decreases, normal colours fade, feeding ceases, and the fish become less responsive to stimuli (Fig. 30 and 31). At 0.6 mgl^{-1}, equilibrium and coordination are lost (Scherer, 1971).

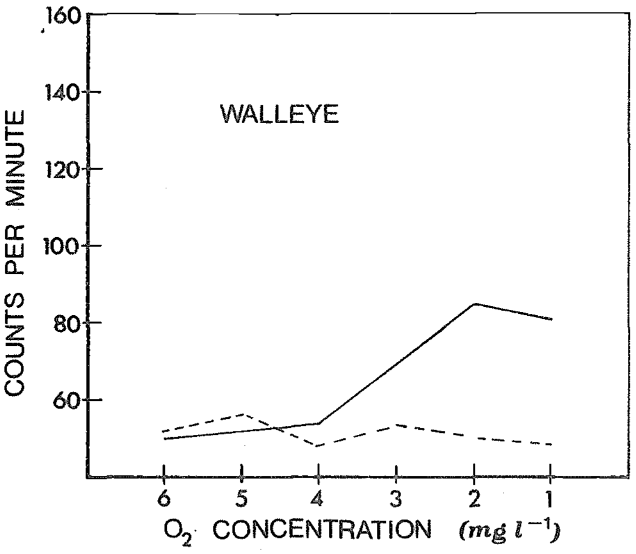

Fig. 30 Average ventilation rates at various oxygen concentrations. Broken line indicates control fish at oxygen concentrations between 6 and 7 mgl^{-1} (Redrawn from Mount, 1961)

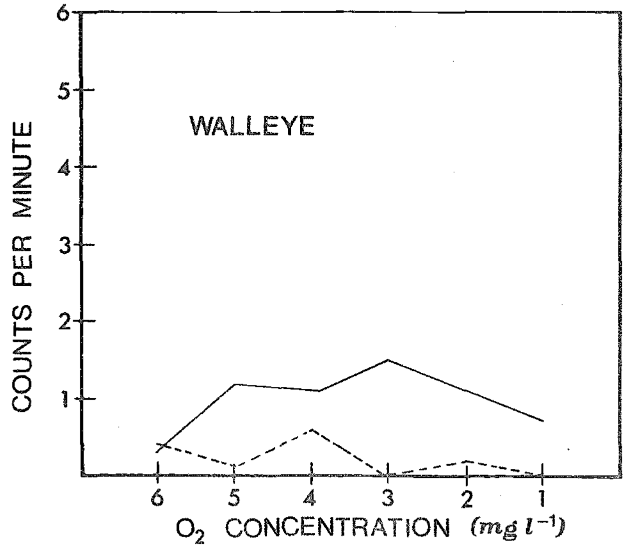

Fig. 31 Average activity index counts at various oxygen concentrations. Index counts represent the number of times a minute that a fish's eye crossed a grid line. Broken line indicates control fish at oxygen concentrations between 6 and 7 mgl^{-1} (Redrawn from Mount, 1961)

Net catches were greatest at depths where temperature ranged from 13 to 18°C in Lac la Ronge, Saskatchewan (Rawson, 1957), and at 20.6°C in Wisconsin (Scott and Crossman, 1973). Dendy (1948) stated that in Tennessee reservoirs, walleyes are found at water temperatures of about 25°C during July. Movement into deeper waters during late summer and again in autumn and winter has been attributed to water temperature influences (see section 3.5.1). However, seasonal differences in "preferred" temperature, as well as differences in "preferred" temperatures between lakes, may be due to the walleyes making use of the differential in turbidity levels to screen out the light (Ryder, 1977).

Light is probably the most important and overriding environmental stimulus affecting walleye behaviour. Because of the retinal structure (Moore, 1944; Ali and Anctil, 1968; Zyznar and Ali, 1975; Ali, Ryder and Anctil, 1977) and the large amount of the light reflecting pigment 7,8 - dihydroxanthopterin in the tapetum lucidum of the eye (Zyznar and Ali, 1975), the walleye is light-sensitive and its behaviour is correspondingly affected.

Walleye larvae are positively phototaxic from the time of hatching through the postlarval stage (Houde and Forney, 1970). At precisely what time they become negatively phototaxic is not known. Vertical position of juvenile walleye in a laboratory tank was inversely related to overhead light intensity (Scherer, 1976). Ryder (1977) suggested that this transition may occur at the time the pelagic fry become benthic (25-30 mm long). However, it is known that by at least age I, walleyes are negatively phototaxic (Scherer, 1971; Ryder, 1977).

As mentioned in section 3.5.2 walleyes undergo diurnal vertical migrations at dawn and dusk in response to changing light intensities. Such movements facilitate feeding (see section 3.4.1). On sunny days in the shallow waters of clear-water lakes, dazzlement may be possible (Moore, 1944). This situation is usually avoided by walleyes remaining in shallow water and using some form of physical shelter, such as boulders, weed beds, sunken trees, and cribs (Krueger, 1969; Scott and Crossman, 1973; Ryder, 1971, 1977). Evidence suggests that light is a stronger directive factor than such factors as temperature and oxygen. Walleyes have been observed to remain at a depth where the temperature is above that usually selected but where there is better shelter from light (Scott and Crossman, 1973). Walleyes in Norris Reservoir appear to stay close to the thermocline during intense summer stratification, occupying water with an oxygen concentration of 1-2 mg/l (Fitz and Holbrook, 1978). This type of displacement distribution may be induced by increased illumination and/or temperature in the epilimnion. Scherer (1971) observed walleyes held in aquaria under a constant light intensity (ranging from 700 lux at the bottom to 2 400 lux at the top) which were subject to a gradual oxygen reduction or gradual CO_2 increase. It was not until oxygen levels as low as 1.5-1.0 ppm or CO_2 levels greater than 5-6 ppm were reached that the walleyes began to overcome their negative phototaxic tendencies and leave their shelters to move to the surface. However, walleyes in aquaria, kept in rooms illuminated only by natural light, showed the same movements toward the surface when oxygen levels were reduced from 6 ppm to only 5 ppm (Mount, 1961).

Newberg (1973) found that a pulsed D.C. shocker was highly effective in attracting adults, but much less so for collecting smaller walleyes (76-203 mm long). When the current is applied, movement is toward the anode. A direct D.C. shocker was ineffective in attracting walleyes.

4 POPULATION (stock)

4.1 Structure

4.1.1 Sex ratio

A number of investigations have revealed that the percentage of females in commercial catches increases with age after approximately the fourth or fifth year (Carlander, 1945; Hile, 1954; Van Oosten and Deason, 1957; Armstrong, 1961). The percentage of females in Lake Erie catches was 46.1 percent between ages II and V, 60 percent between ages VI and VII and 83.9 percent between ages VIII and XV (Hile, 1954). Such an increase has been attributed to the apparent greater longevity of females and to the higher vulnerability to exploitation during spawning migrations of the more active and earlier maturing males. Smith and Pycha (1961) found the opposite situation in the commercially-fished Red Lakes, Minnesota. Experimental gill-netting in July and August (1955 to 1957) revealed that the proportion of females in the catch decreased with increasing age after age VI, until at age X only 23.5 percent of the catch consisted of females. This was attributed to the fact that females grow at a faster rate than males and consequently would become more vulnerable to the fishery at an earlier age.

During the spawning run males predominate with individual observations varying from 51 to 99 percent males depending on the time of sighting and its coincidence with the time of peak spawning (3.1.6.3).

4.1.2 Age composition

The number of age groups in a particular population increases with the longevity of the fish in that population. Data collected on the age composition of walleye populations has been accomplished by experimental gill-netting, trap-netting, trawling or shocking. The percentage composition of the population has then been calculated either directly from the catch or population estimates derived from the catch. Because of selectivity of all types of gear used toward large size groups, few walleyes less than two years old are captured (Fig. 32). Age groups III and IV constitute the majority of the adult population vulnerable to sampling gear in most lakes. In such cases the combined percentages of these two age groups range from 41.5 percent (39 Minnesota walleye lakes; Johnson, 1971a) to 85.3 percent (Escanaba Lake, Wisconsin; Kempinger, 1963). The percentage composition of the estimated population (or catch) or age groups greater than IV generally tends to decrease with each subsequent age group. Some populations were sampled on the spawning runs while others were sampled in the open lake. The age composition of trap-net catches on the spawning runs in Oneida Lake, New York, was not significantly different from samples obtained from the open lake during the summer and autumn by experimental gill-nets, trawling, shocking and angling (Forney, 1961c). Trap-net samples taken in the autumn and winter ice-fishing results, however, did show highly significant differences favouring older age groups in the population. Thus, in Oneida Lake, the age structure of the spawning population appeared to be similar to the adult population in the open lake.

There is a tendency for the proportion of younger to older fish in the catch to increase as the season progresses due to recruitment (Smith and Pycha, 1961; Kelso and Ward, 1972). The age composition of a population can also change from year to year as exceptionally large or small year classes are produced and move through the various age groups (Churchill, 1961). As well, years of exceptionally good or poor growth will probably tend to alter somewhat the age composition of the catch.

Male walleyes mature at anywhere from II to VI years while females mature at from III to VIII years (see section 3.1.2). Females tend to have a greater longevity than males. Walleyes over XX years of age have been reported (Scott and Crossman, 1973; Schneider, Eschmeyer and Crowe, 1977); see section 3.4.3.

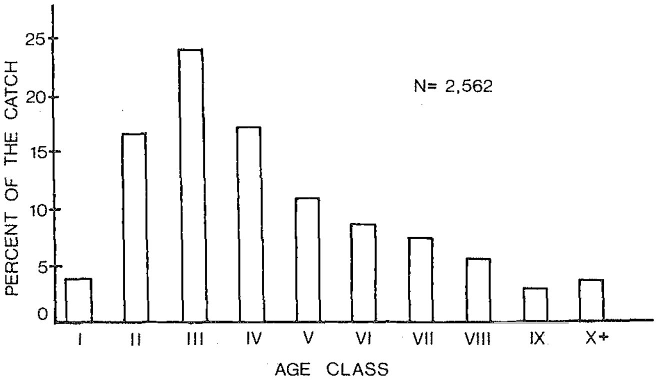

Fig. 32 A composite of walleye age-distributions in experimental gill net catches from 38 northern Minnesota walleye lakes illustrating the typical catch curve for this gear (Redrawn from Johnson, 1971a). The experimental gill nets were 76.2 m long and contained five 15.24 m sections each of 1.91, 2.54, 3.18 and 5.08 cm bar mesh

Kempinger and Churchill (1972) determined the density of the various age groups in Escanaba Lake, Wisconsin (Table XVI). Fingerling densities ranged from 37.1/ha to 266.8/ha over a 12-year period. By age V the densities had dwindled to a range of 2.1/ha to 8.4/ha. Williamson (1965) reported a fingerling population of 1 914/ha in Little John Lake, Wisconsin (area 67.2 ha), in 1964.

TABLE XVI

Density of age groups (no./ha) in Escanaba Lake, Wisconsin from 1958 to 1959 (Kempinger and Churchill, 1972)

Age groups	1958	1959	1962	1963	1964	1965	1966	1967	1968	1969
0 (autumn)	37.1	219.8	123.5	111.2	266.8	88.9	187.7	74.1	71.6	160.6
I (spring)	16.0	106.2								
(autumn)					85.9					
III	5.1	27.0	15.2	11.0	37.1	12.6	16.9			
IV	3.4	7.6	8.4	6.7	15.2	6.7				
V		3.4	3.4	2.1	8.4					

4.1.3 Size composition

As mentioned in section 4.1.2, most collecting gear has a tendency to capture samples biased toward the larger members of the population. As well, the size composition of adults on the spawning grounds appears to be different from that on the open lake at other times of the year inasmuch as only the mature (and hence larger) members of the younger adult age classes travel to the spawning grounds. In general, the majority of the males on spawning runs tend to range in size from 375 mm to 464 mm while the females tend to range in size from 421 mm to 518 mm (Table XVII). Together, the majority of the spawning adult population consists of walleyes 382 mm to 477 mm. Whitney (1958), however, found evidence to suggest that experimental gill-net samples from spawning runs may be proportional to the adult population greater than 406 mm.

Male walleyes generally mature at lengths over 279 mm while females generally mature at lengths between 356 mm and 432 mm (see section 3.1.2). The longest walleye on record is a 1 067 mm fork length specimen (see 3.4.3).

4.2 Abundance and density of population

4.2.1 Average abundance

The size of a population will vary from one body of water to another.

4.2.2 Changes in abundance

Changes in abundance may result from changes in turbidity, predation, competition, variations in year-class strength, overfishing and pollution.

When walleye and sauger occur sympatrically, an increase in turbidity may change the relative proportion of these two species in favour of the sauger (Ryder, 1977). This is due in part to the sauger's eye structure which is better adapted to dim-light conditions. However, walleyes are not likely to be at a disadvantage in extremely turbid waters unless competing with the more efficient sauger, and usually thrive in this type of environment (Ryder, 1977).

Predation on walleye eggs and larvae by other species of fish may be important in limiting the abundance of walleyes in some waters (see section 4.4.2). As well, cannibalism may be important in reducing fry abundance especially when forage abundance is low (Chevalier, 1973).

Competition for food is undoubtedly an important factor in controlling walleye numbers. In Wilson Lake, Minnesota, walleyes appear to compete with white suckers for invertebrates but do not feed on the suckers themselves (Burrows, 1969). An intensive sucker removal programme on this lake resulted in a marked increase in walleye yield and a higher C.U.E. only one year later (Johnson, 1977), implying that an increase in numbers of walleyes had resulted. Such removal programmes may also reduce indirect competition. Sucker removal in Trout Lake, Minnesota, resulted in a remarkable increase in the abundance of yellow perch (Burrows, 1969), an important food for walleyes.

Introduction of exotic forage fishes (e.g., alewife, rainbow smelt and gizzard shad) into the upper Great Lakes resulted in initial increases in walleye populations in a number of areas (Schneider and Leach, 1977).

Years of good or poor year classes probably result in an increase or decrease, respectively, in the size of a population. Kelso and Ward (1977) noted that walleye abundance in unexploited West Blue Lake, Manitoba was dependent upon spawning success and autumn-winter mortality. In the Red Lakes, Minnesota, it is evident that the general level of abundance of walleyes is strongly influenced by the strength of the individual year classes (Smith and Krefting, 1954; Smith and Pycha, 1961). Population size was found to be significantly related to brood stock abundance five years earlier in heavily exploited Rainy Lake (Chevalier, 1977).

Depletion of walleye populations in a number of lakes has been due to overfishing. Overfishing by commercial fisheries has been implicated, at least in part, in the decline of stocks in Lake Erie (Regier, Applegate and Ryder, 1969), Lake of the Woods (Carlander, 1945; Schupp and Macins, 1977), Black Bay, Ontario (Ryder, 1968), and Rainy Lake (Chevalier, 1977). Intensive sport fisheries are also known to reduce population size.

4.2.3 Average density

From shoreline seining studies, estimates of YOY walleye densities have been determined on a number of lakes. On Mille Lacs Lake and Lake Winnibigoshish, Minnesota, peak densities of 2 979 YOY/shoreline ha (26 July) and 1 964 YOY/shoreline ha (13 July), respectively, were recorded (Maloney and Johnson, 1957). YOY densities computed over the whole lake area, based on shoreline seining and electrofishing, have also been determined: 37-267 YOY/ha in Escanaba Lake, Wisconsin (Kempinger and Churchill, 1972); 44-64 YOY/ha in Wilson Lake, Minnesota (Johnson, 1974); and 13-24 YOY/ha in Pike Lake, Wisconsin (Mraz, 1968). Densities of separate age classes in Escanaba Lake, Wisconsin, for 1964 (Table XVI) have been determined as follows: 267 YOY/ha, 86 age I/ha, 37 age III/ha, 15 age IV/ha and 8 age V/ha (figures derived from data from Kempinger and Churchill, 1972). Densities of mature populations in other bodies of water are listed in Table XVIII.

TABLE XVII

Size ranges (total length) in which majority of adult walleyes are found on spawning grounds and in open lakes

Location and source	Comments	♂	♀	Combined
Samples from spawning runs				
Golden Lake, Wisconsin (Kleinert and Mraz, 1966)	From fyke netting in 1965	457-533 mm	508-584 mm	457-533 mm
Spirit Lake, Iowa (Rose, 1949)	Experimental gill-netting in 1947			370-460 mm
Red Lakes, Minnesota (Smith and Pycha, 1961)	Experimental gill-netting during 1949-1958	345-384 mm	386-434 mm	345-394 mm
Oneida Lake, New York (Forney, 1965)	Trap-netting during 1951-1958	356-406 mm	381-483 mm	368-432 mm
Little Cutfoot Sioux Lake, Minnesota (Johnson, 1971b)	Weir-type trapping during 1951, 1957-58, 1959	356-457 mm	457-584 mm	381-533 mm
Hoover Reservoir, Ohio (Erickson and Stevenson, 1967a)	Fyke netting during 1967	325-475 mm	350-400 mm	350-425 mm
Lake Gogebic, Michigan (Eschmeyer, 1950)	Samples - 1947	381-483 mm	406-533 mm	381-483 mm
Clear Lake, Iowa (Whitney, 1958)	Experimental gill-netting 1952	406-508 mm	457-610 mm	406-559 mm
Average		375-464 mm	421-518 mm	382-477 mm
Samples from open lakes				
Pike Lake, Wisconsin (Mraz, 1960)	From spring fyke netting and autumn shocking - 1959			152-226 mm
Pike Lake, Wisconsin (Mraz, 1961)	From spring fyke netting and autumn shocking - 1960			152-201 mm and 279-328 mm
Clear Lake, Iowa (Whitney, 1958)	Experimental gill-netting 1952 June-September			254-356 mm

Standing crops of walleyes in natural waters have been estimated to be as high as 37.1 kg/ha in Storm Lake, Iowa (Rose, 1949) and 61.2 kg/ha in a southern Minnesota game-fish lake (Moyle, Kuehn and Burrows, 1950). Standing crop estimates from other waters are listed in Table XVIII.

Only a few annual production estimates (annual increase of fish flesh) exist for walleye populations. Kelso and Ward (1972) calculated the annual production (1969-70) of walleye in West Blue Lake, Manitoba to be 2.1 kg/ha from a population with a mean annual standing crop of 6.1 kg/ha. Carlander and Payne (1977) estimated annual production in Clear Lake, Iowa to fluctuate from 1.23 to 9.71 kg/ha with standing crops ranging from 2.63 kg/ha in 1963 to 16.53 kg/ha in 1954 (Carlander and Payne, 1977). Moenig (1975) calculated summer production (1967) of walleye, ages III-XIII in Dexter Lake, Ontario to be 1.78 kg/ha from a population with a biomass of 7.20 kg/ha.

4.2.4 Changes in density

Forney (1961b) has suggested that efforts to obtain a density index of young-of-the-year may be seriously hampered by the yearly changes in distribution of population. Shoreline densities of YOY walleyes change as the summer progresses, as first they become pelagic then move inshore and finally, in the autumn gradually move into deeper waters (see section 2.2.1). Densities of juveniles and adults will also change as a result of seasonal movements as well as spawning migrations (see section 2.2.2).

TABLE XVIII

Standing stock of walleye in various waters

Location and authority	Area (ha)	Standing stock (Number of walleye/ha)	(kg/ha)	Comments
Storm Lake, Iowa (Rose, 1949)	1 239	53.2	37.1	Based on angler recapture data
Big Sand Lake, Wisconsin (Niemuth and Klingbiel, 1962)	398	62.1	19.8-20	Age ≥I
Many Point Lake, Minnesota (Olson, 1958)	695	16.6-26.2		Age ≤III
Oneida Lake, New York (Forney, 1967)	20 648	23.8-44.5	18.5-30.6	Age ≤III
Burnt Camp Lake, Minnesota (Maloney, 1956)	3.6	8.9	2.8	Lake poisoned out
Lake Sallie, Minnesota (Olson, 1955)	511	168		Age ≤III
Spirit Lake, Iowa (Rose, 1949)	2 301	13.3		Size ≤297 mm
Escanaba Lake, Wisconsin (Kempinger *et al.*, 1975)	117	14.8-88.9	6.7-29.2	Age ≤II
Escanaba Lake, Wisconsin (Kempinger and Churchill, 1972)	117	364 and 413		All ages except age II
Hoover Reservoir, Ohio (Erickson, 1970)	1 336	7.3-31.6		Adult
Clear Lake, Iowa (Whitney, 1958)	1 475	9.5		Size ≤305 mm
Mississippi River (upper) (Christenson, 1960)			0.7-6.9	
Minnesota Game-Fish Lakes (25) (Moyle, Kuehn and Burrows, 1950)			9.1	From seining of littoral areas
Minnesota Rough-Fish Lakes (14) (Moyle, Kuehn and Burrows, 1950)			7.9	From seining of littoral areas
Long Lake, Wisconsin (O'Donnell, 1943)	11	162.5	4.2	Lake netted and poisoned
East Twin Lake, Wisconsin (O'Donnell, 1943)	5.3		2.4	Lake netted and poisoned
Savanne Lake, Ontario (P.J. Colby, unpubl.)	364	18	11.2±1.8	Age ≥III
Grebe Lake, Michigan (Schneider, 1973)	29		35.9	
East Twin Lake, Michigan (Schneider, 1973)	336		13.5	
Lake Wingra, Wisconsin (Juday, 1938)	81		8.4	Lake completely netted
Butternut Lake, Wisconsin (Bever and Lealos, 1975)	407	32	11.3	Size ≥178 mm (spring)
West Blue Lake, Manitoba (Kelso and Ward, 1972)	162	23	6.7	All ages
Spauldings Pond, Wisconsin (Threinen and Helm, 1952)	11		33.6	
West Twin Lake, Wisconsin (O'Donnell, 1943)	5		2.3	
Cadillac Lake, Michigan (Schneider, 1973)	465		8.2	
Dexter Lake, Ontario (Moenig, 1975)	368.5	10.8	4.9	Age ≥IV

4.3 Natality and recruitment

4.3.1 Reproduction rates

The number of eggs produced by a female during a single spawning may vary considerably from one body of water to another. Average egg production (see section 3.1.5) has been observed to range from 29 736 eggs/kg body wt (Smith, 1941) to 65 317 eggs/kg body wt (Johnson, 1961). Total egg production in Oneida Lake, New York ranged from 12 to 18 billion per year (580 000/ha to 870 000/ha) between 1966 and 1973 (Forney, 1976).

The percentage of viable eggs among spawn collected from spawning grounds may also vary quite markedly. Eschmeyer (1950) reported that 34 and 55 percent of eggs gathered from two different areas on Lake Gogebic, Michigan, were viable while on Cisco and Big Portage Lakes, 17 and 72 percent, respectively, were viable. The normal range of viable egg percentages for Lake Erie was 20 to 35 percent between 1961 and 1968 (Baker and Scholl, 1969).

From fertilization to hatching, Smith and Kramer (1963) determined the mortality rates to range from 50 to 82 percent in the Rainy River, Minnesota, while Eschmeyer (1950) determined the rate to be only 4 percent for viable eggs obtained from spawning beds and hatched in the laboratory (see sections 3.1.6.4 and 4.4.1).

4.3.2 Factors affecting reproduction

Spring water temperatures before, during and after spawning as well as egg and larval survival, are important in governing reproductive success and both ultimately affect year class strength.

Cold fronts occurring just prior to or shortly after the onset of the spawning season may delay, interrupt or prevent spawning. A cold front, occurring shortly after the onset of spawning in Heming Lake, Manitoba, stopped spawning activities such that some females captured in June were found to be resorbing their eggs (Derback, 1947). Ova resorption is known to interfere with the development of the next generation of oocytes in walleyes, leading to the omission of the following spawning period (W.B. Horning II, pers. comm.). This agrees with the findings of Kukuradze (1968) for European pikeperch. Studies by Olson (1971) on Lake Sallie, Minnesota, indicated that a delay in spawning due to a cold front had no great effect on the percentage of fertilization among eggs deposited thereafter. Downstream from a reservoir, deep-water discharge from a dam might delay or even prevent reproduction (Pfitzer, 1967). Payne (1964b) found evidence that stronger year classes of walleyes developed during warmer-than-average spawning seasons. It also appears that the more rapidly the water temperature rises during the incubation period (and hence, the shorter the incubation period) the higher is survival of the eggs (Johnson, 1961; Busch, Scholl and Hartman, 1975). A positive correlation between rapid spring temperature increases during spawning and incubation and the number of walleye eggs collected per sampling operation has been observed (Baker, 1966b; Baker and Scholl, 1969; Rudolf and Scholl, 1970; Busch, Scholl and Hartman, 1975), and also the abundance of YOY walleye (Fig. 33, Busch, Scholl and Hartman, 1975). It has been suggested that the shortened incubation period would minimize egg exposure to such possible stresses as smothering by inorganic sediments, low oxygen tensions from organic sedimentation, disturbances by storm generated wave and current action, and predation and disease (Busch, Scholl and Hartman, 1975). However, it may be that early hatches coincide more closely with spring plankton pulses than do late hatches and hence there is a better food supply and greater growth and subsequent survival potential. As well, feeding activity may be enhanced by higher temperatures. Smith and Koenst (1975) found that laboratory-reared fry fed poorly at temperatures below 15°C but fed well at 21°C.

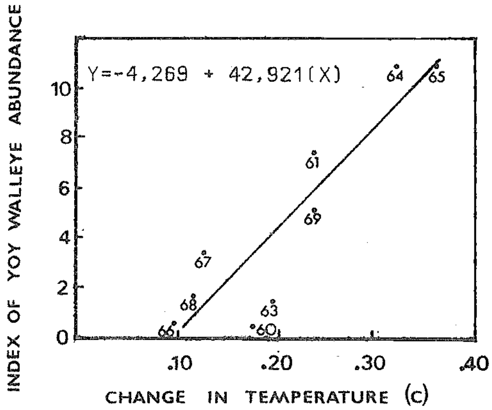

Fig. 33 Relation between index of abundance of young-of-the-year and mean daily temperature (C) increase during spawning and incubation each year, 1960-70 (r = +0.896). Values for 1962 and 1970, when exceptional year classes were produced, are omitted (Redrawn from Busch, Scholl and Hartman, 1975)

Wind-induced waves and currents are probably important in determining survival of both eggs and fry. Wave action may cause considerable egg mortality by washing viable eggs up on shore (Eschmeyer, 1950; Maloney and Johnson, 1957; Priegel, 1970; Newburg, 1975) or by moving them onto poor substrates where survival is reduced (Johnson, 1961; Busch, Scholl and Hartman, 1975). Nevertheless wind is important in generating adequate circulation of oxygenated waters in and around incubating eggs. Wind induced currents in Oneida Lake, New York, have been shown to disperse walleye fry quite extensively (Houde and Forney, 1970) and may be important in governing fry survival, although evidence to suggest either favourable or unfavourable effects has not been produced. River current velocities appear to be important when fry emerge from upriver spawning grounds and must reach the open lake (where food supplies are more abundant) before their food reserves are completely exhausted. Studies by Priegel (1970) indicate that fry hatching up the Wolf River must reach Lake Winnebago, Wisconsin, in 3-5 days or they will perish.

Rainfall may be a critical survival factor in lakes where spawning beds are in very shallow water or in shallow marshes. In such instances eggs may be left dry when water levels recede (Niemuth, Churchill and Wirth, 1966; Priegel, 1970), or stagnation of the water may result in reducing the oxygen exchange rates to critical levels (Priegel, 1970). Population size was found to be significantly related to spring water levels five years earlier in Rainy Lake (Chevalier, 1977). Carlander and Payne (1977) observed a strong correlation between walleye year class strength and water levels in Clear Lake, Iowa. Similarly, a significant positive correlation has been observed between year class strength of river-spawning walleye populations and spring discharge rates in Granville Lake, Manitoba (Swain, 1974); Moon River, Ontario (Winterton, 1975a) and the Missouri main stream reservoirs (Nelson and Walberg, 1977). A sudden reduction in flow rate (through a control dam) was observed to disrupt walleye spawning activities in the riffle areas of the Talbot River, Ontario (MacCrimmon and Skobe, 1970) and low water levels may also reduce emergent vegetation and provide less shelter for forage.

Once the fry have grown to a size where they begin to feed on fish, abundance of this forage becomes important for their survival during the first year of life. Strong year classes of walleyes have been correlated with abundant year classes of yellow perch (Maloney and Johnson, 1957; Smith and Krefting, 1954; Forney, 1977). The abundance of forage YOY fish appears to govern the extent of cannibalism among YOY walleyes. High yellow perch abundance in Oneida Lake, New York, resulted in little cannibalism while during years of low perch abundance a substantial increase in cannibalism was observed (Forney, 1974). As well, Chevalier (1973) suggests that the low density of young perch observed in this lake in 1969 may have accounted for the simultaneous observations of a high incidence of cannibalism by adult walleyes.

Growth rates and total lengths of YOY walleyes at the end of their first year of life may be indirectly related to survival. Forney's (1966) results suggest that year classes which grow rapidly during their first year should experience lower mortality over winter than slower-growing year classes. Chevalier (1973) states that the tendency for adult walleyes in Oneida Lake, New York, to prey upon smaller members of a YOY walleye cohort suggests that year classes which grow rapidly and attain a large mean length by autumn, should experience a lower mortality than slow-growing year classes. If true, then any factors affecting YOY growth such as population density (see section 3.4.3), forage growth rates (Parsons, 1971) and abundance, and temperature may indirectly affect year class strength. However, the possible effect of first-year growth on survival and the establishment of year class strength needs further study.

No correlation was found between brood stock size and year class strength in the Red Lakes, Minnesota (Smith and Krefting, 1954). Chevalier (1977) found brood stock size to be of major importance in determining walleye population sizes in Rainy Lake, Ontario. In Escanaba Lake, Wisconsin, the size of a year class appears to be independent of the size of previous year classes (Kempinger and Churchill, 1972).

Fluctuations in the success of natural reproduction are usually similar in most of the lakes in any area (Anon., 1957), suggesting the importance of climatic effects on year class abundance. The year 1959 produced dominant walleye year classes in such North American lakes as Oneida Lake, New York (Forney, 1966), Black Lake, New York (Letendre and Schneider, 1969), Pike Lake, Wisconsin (Mraz, 1968), Lake Winnebago, Wisconsin (Priegel, 1970), Escanaba Lake, Wisconsin (Kempinger and Churchill, 1972), Lake Erie (Parsons, 1971), and Lake Ontario (Christie, 1973), Lake Huron (Payne, 1964b), and the Rock River, Illinois (Rock, 1969), while in the same year, dominant European pikeperch year classes occurred in a number of Swedish lakes (Svärdson and Molin, 1973). This phenomenon may be due to the above normal 1959 summer temperatures recorded during the period of May through August in such disparate places as Duluth, Berlin and Stockholm (Svärdson and Molin, 1973).

4.3.3 Recruitment

By averaging 3 years of angler catch frequency data in Cutfoot Sioux Lake, Minnesota, Johnson (1953a) determined that at age IV, walleyes were completely vulnerable to angling. It was found that age IV walleyes recruited into the fishery comprised 52 percent of the fishable stock. Chevalier (1973), citing Forney's (1967) paper, states that an average annual recruitment of about 300 000 walleyes (14.5/ha) at age IV has been sufficient to maintain the population in Oneida Lake, New York since 1957.

In most lakes walleyes become completely vulnerable to the angling fishery at age III or IV. However, in lakes in which growth rates are slow, recruitment tends to occur at a later age, while in lakes in which growth rates are rapid, recruitment tends to occur at an earlier age. Since natural mortality tends to be reduced as exploitation increases (Ryder, 1968; Kempinger and Churchill, 1972; Moenig, 1975; Spangler, Payne and Winterton, 1977) both the absolute and relative numbers of recruits entering into a fishery would probably be greater in an exploited lake than in an unexploited lake, assuming that the populations are stable. As well, variation in annual recruitment would tend to fluctuate more widely in an exploited population as poor and good year classes, occurring more frequently in an exploited population, enter the fishery. Such variability in recruitment has been observed for walleye stocks in Lake Erie (Nepszy, 1977) and Lake of the Woods (Schupp and Macins, 1977).

Little information is available on the seasonal pattern of recruitment. The pattern of recruitment of the 1959 year class into the 1960 Ohio trapnet fishery on Lake Erie was as follows: none of the members of this year class captured were of legal length (then 330 mm) until late June; between 16 to 31 July, 5.5 percent were of legal length, and this percentage increased sharply to 56.5 percent during the last half of August and 86 percent in the first half of September; in October, nearly all fish (98.7 percent) were of legal length (Parsons, 1972).

4.4 Mortality and morbidity

4.4.1 Mortality rates

Various mortality rates during the different stages of development are presented in Table XIX. From fertilization to hatching, total annual mortality (a) has been found to range from 4 percent (Eschmeyer, 1950) to 82 percent (Smith and Kramer, 1963). Egg production and larval abundance estimates in Oneida Lake, New York, suggested a total mortality consistently greater than 99.5 percent between spawning and the time fry attained a mean length of 9-10 mm (Forney, 1976). During the first year of life, Forney and Houde (1964) observed the total annual mortality among Oneida Lake, New York, walleyes to range from 67 to 75 percent. However, the mortality rate was 95 percent over a two-week period (approximately 1-15 June) for a localized fry population in this lake (Noble, 1972). Reported mortality rates among adult populations (Table XIX) range as follows: total annual mortality from 13 percent (Forney, 1962a) to 84 percent (Olson, 1955) with common rates ranging between 40 and 55 percent; annual natural mortality from 3 percent (Forney, 1962a) to 81 percent (Olson, 1955); annual fishing mortality from 6 percent (Schneider, 1969) to 49 percent (Forney, 1962a).

The mortality during the first year of life appears to be high (Forney and Noble, 1968). Forney (1976) reported that the mortality of walleye fry and fingerlings was much more important in determining year class strength than mortality occurring during the first few weeks of life. The mortality rate decreases and remains fairly constant over the next few years of life, followed by a period of increasing rate with age. Total annual mortality rate among walleyes between ages IV and VII in Lake Winnibigoshish, Minnesota, was 30 percent, while between ages VII and XII it averages 53 percent. It was suspected that this was due to an increase in natural mortality (Johnson and Johnson, 1971). Work by Ryder (1968), Kempinger and Churchill (1972) and Moenig (1975) suggests that, with increased fishing mortality, the natural mortality rate tends to decrease.

4.4.2 Factors causing or affecting mortality

Early studies revealed that such fishes as carp, yellow perch, suckers, and minnows may feed on walleye eggs (Goode, 1903; Bean, 1912; Cobb, 1923; Adams and Hankinson, 1928). Carlander et al. (1960) recorded that bullheads and yellow bass fed extensively on walleye eggs in Clear Lake, Iowa. Christie (1973) observed high predation of walleye eggs by white perch in Bay of Quinte. Stomachs of yellow perch, spottail shiners, stonecats and white suckers were found to contain walleye eggs in Lake Erie (Wolfert, Busch and Baker, 1975). It was found that low water temperatures extended the time of predation on walleye eggs by yellow perch (Wolfert, Busch and Baker, 1975). In addition, Kraai and Prentice (1974) found walleye eggs in the stomachs of bluegills and lesser scaup, *Aythya affinis*. Hydra may also cause high egg mortality in hatcheries (Erickson and Stevenson, 1967b).

Cannibalism is one of the most important sources of predation and in some situations among fry, it may be the principal mortality factor (see section 3.4.2). Northern pike are important predators of walleye fry. Other species such as saugers (Scott and Crossman, 1973; Swenson and Smith, 1976); bullheads (Carlander et al., 1960); burbot (Clemens, 1951; Hewson, 1955; Bonde and Maloney, 1960) and yellow bass (Carlander et al., 1960) are known to feed on YOY walleyes. In addition, Regier, Applegate and Ryder (1969) have suggested yellow perch, white bass, alewives and rainbow smelt as possible predators. A variety of fish-eating birds also prey upon fry. Predaceous aquatic insects can be important predators in rearing ponds (Dobie and Moyle, 1956; Dobie, 1956; Dobie, 1957). In one instance, large numbers of hydra were believed to be responsible for the drastic decline in numbers of walleye fry in Diamond Lake, Iowa (Moen, 1951).

TABLE XIX

Mortality rates of walleye at various stages of development

Location and source	Comments (Data Year)	a	u	v	i	p	q	m	n
1. Spawning to hatching									
Hatchery (Allbaugh and Manz, 1964)		(0.61-0.72)							
Lake Winnibigoshish, Minnesota (Johnson, 1961)		(0.64-0.99)			(0.054[a]-0.233)				
Devil's Lake, Wisconsin (O'Donnell, 1942 in Kramer, 1967)		0.98							
Lake Gogebic, Michigan (Eschmeyer, 1950)		0.31							
Hatchery, Ontario (Hurley, 1972)		0.52							
2. Fertilization to hatching									
Hatchery (Smith and Kramer, 1963)		(0.23-0.63)			(0.011[a]-0.068)				
Rainy River, Minnesota (Smith and Kramer, 1963)		(0.50-0.82)			(0.014[a]-0.050)				
Lake Gogebic, Michigan (Eschmeyer, 1950)		0.04							
Hatchery, Ontario (Hurley, 1972)		0.28							
3. Hatching to age I									
Oneida Lake, New York (Forney and Houde, 1964)	July-October 1963	(0.67-0.75)			(0.011[a]-0.014)				
Oneida Lake, New York (Forney and Noble, 1968)	August-October 1967				(0.003-0.28)				
4. Adult									
Mississagi River, Ontario (Payne, 1966)	Age III-VI	0.53	0.20	0.33	0.75[b]	0.28[b]	0.47[b]	0.25[b]	0.35[b]
Sallie Lake, Minnesota (Olson, 1955)	Age VI-VIII	0.84	0.09	0.75	1.83[b]	0.20[b]	1.63[b]	0.18[b]	0.81[b]
Butternut Lake, Wisconsin (Bever and Lealos, 1975)	Size >178 mm	0.32	0.04	0.28					
Nipigon Bay, Lake Superior									
(Ryder, 1968)	>356 mm - 1955	0.55	0.07	0.48	0.80	0.10	0.70	0.10	0.50
(Ryder, 1968)	>356 mm - 1956	0.55	0.13	0.42	0.80	0.19	0.61	0.17	0.47
(Ryder, 1968)	>356 mm - 1957	0.55	0.34	0.21	0.80	0.49	0.31	0.39	0.27

Location and source	Comments (Data Year)	a	u	v	i	p	q	m	n
Oneida Lake, New York	Spawning								
(Forney, 1962a)	Population - 1957	0.20	0.14	0.06	0.22$^{b/}$	0.15$^{b/}$	0.07$^{b/}$	0.14$^{b/}$	0.07$^{b/}$
(Forney, 1962a)	- 1958	0.13	0.10	0.03	0.14$^{b/}$	0.11$^{b/}$	0.03$^{b/}$	0.10$^{b/}$	0.03$^{b/}$
(Forney, 1962a)	- 1959	0.55	0.47	0.08	0.80$^{b/}$	0.68$^{b/}$	0.12$^{b/}$	0.49$^{b/}$	0.11$^{b/}$
Many Point Lake, Minnesota (Olson, 1958)	>Age III - 1955-1958	0.31	0.27	0.04	0.37	0.32	0.05	0.27$^{b/}$	0.05$^{b/}$
Lake Winnibigoshish, Minnesota (Johnson and Johnson, 1971)	Age IV-XII	0.44						0.22	0.37
Red Lakes, Minnesota									
(Smith and Pycha, 1961)	Age VI-VII	0.51							
(Smith and Pycha, 1961)	Age III-IX	0.70							
Fife Lake, Michigan (Schneider, 1969)	Age III-IV	0.22	0.05	0.17	0.25$^{b/}$	0.06$^{b/}$	0.19$^{b/}$	0.06$^{b/}$	0.17$^{b/}$
Clear Lake, Iowa (Whitney, 1958)	Age >IV	0.35	(0.08- 0.18)	0.27 0.17	0.44$^{b/}$	(0.10-$^{b/}$ 0.23)	(0.34-$^{b/}$ 0.21)	(0.09-$^{b/}$ 0.20)	(0.29-$^{b/}$ 0.19)
Escanaba Lake, Wisconsin									
(Wirth, 1960)	- 1956		0.45						
	- 1957		0.43						
	- 1958		0.13						
	- 1959		0.17						
(Kempinger and Morsell, 1969)	- 1968		0.16						
(Kempinger and Churchill, 1972)	Age I-V	0.50							
Lake Manitoba, Manitoba (Kennedy, 1950)		0.50							
Lake of the Woods, Minnesota (Schupp, 1974)	Age IV-IX	0.55			0.80				
West Blue Lake, Manitoba (Kelso, 1977)	Greater than 25 cm								0.80

a/ Daily instantaneous mortality rate
b/ Calculated from equations in Ricker (1958) p. 25

a - annual mortality rate (annual expectation of death)
u - rate of exploitation
v - expectation of death from natural causes
m - annual fishing mortality rate
n - annual natural mortality rate
i - annual instantaneous mortality rate
p - instantaneous rate of fishing
q - instantaneous natural mortality rate

Predation by either fishes or fish-eating birds is probably not an important source of mortality among adults. Large mortalities of walleyes occurred in Oneida Lake, New York, in 1909 due to lamprey predation (Scriba, 1910).

Only limited investigations into the relationship between food availability and survival of larvae and postlarvae have been conducted. Work on Lac la Belle, Wisconsin, indicated that if *Daphnia* abundance was high at the time the fry began to feed, survival of the year class was high, while in years when the level was low, survival was poor (Mraz and Kleinert, 1963, 1964, 1965; Kleinert and Mraz, 1966). Priegel (1967b) believed low zooplankton levels in marshes of the Wolf River, Wisconsin, resulted in the poor 1966 year class. As well, Forney (1966) observed what appeared to be a high overwinter mortality rate among small YOY walleyes in Oneida Lake, New York, and suggested that year classes which grow rapidly during their first year may experience lower mortality over winter than slower growing year classes.

Certain environmental parameters may affect mortality rates. Bottom oxygen levels can be critical for egg survival. Survival is poor on detritus or muck, where oxidation of organic materials at the mud-water interface reduces oxygen concentrations drastically (Priegel, 1970). Clean rubble bottoms or elevated vegetation provide good spawning sites conducive to high egg survival. Wood-fibre sludge deposits on the Rainy River, Minnesota, have been found to cause a significant increase in egg mortality due to high hydrogen sulfide and carbon dioxide levels and low oxygen levels at the sludge-water interface (Colby and Smith, 1967). Winter-kill from oxygen depletion has been observed to cause large mortalities among adults in Red Deer Lake, Manitoba (Dickson, 1963) and Lake Koshkonong, Wisconsin (Threinen, 1952). Mortalities among walleye in the Yahara River, Wisconsin, occurred due to oxygen depletion resulting from the decomposition of huge masses of algae (*Aphanizomenon flos aquae*). At the other extreme, supersaturation of Lake Waubesa, Wisconsin, waters with oxygen (up to 32.1 mgl^{-1}) due to large concentrations of *Chlamydomonas*, was believed to have caused gas embolisms which were responsible for a number of walleye deaths (Woodbury, 1942).

An inverse relationship has been found to occur between the relative abundance of a year class (survival) and the length of the incubation period. On Lake Erie good year classes were observed during years accelerated incubation temperatures occurred after peak walleye spawning activity (Baker, 1966b; Baker and Scholl, 1969; Rudolf and Scholl, 1970; Busch, Scholl and Hartman, 1975). An increase in the population mean length between autumn and the following spring (even though scale samples revealed little growth during this period) indicated high overwintering mortality of smaller walleyes and suggested that year classes which grow rapidly during the first year should experience lower mortality over winter than slower growing year classes. This has also been observed among European pikeperch populations (Svärdson and Molin, 1973).

Water level is another environmental parameter affecting mortality. Low water levels occurring after spawning in shallow marsh areas may leave eggs high and dry (Priegel, 1970). Wave action may also cause considerable egg mortality by washing viable eggs up on shore (Maloney and Johnson, 1957; Priegel, 1970; Newburg, 1975) or by moving them onto poor substrate (mud, detritus) where survival is reduced (Johnson, 1961).

Parasites have not been reported as causing any significant mortalities among fry or adults. However, hatcheries have reported large outbreaks of *Saprolegnia* fungus among eggs, causing at times 100 percent mortality (Erickson and Stevenson, 1967b). Stalked colonial ciliates of the genus *Carchesium* were reported to have caused a 20 percent increase in mortality of eggs in one hatchery. Dirt and debris accumulated in the stalks to such an extent that respiration was thought to have been affected (Anon., 1941). *Sphaerotilus natans*, a slime bacterium which thrives on the wood sugars released from pulp and paper mills, attacks incubating eggs on the Rainy River, Minnesota. Although it does not affect the egg directly, the emerging fry cannot escape the tangle of filaments surrounding the egg and soon dies (Smith, 1963). Smith and Kramer (1963) believed this was the principal cause of walleye egg mortality on this river.

Johnson and Johnson (1971) reported an outbreak of the bacterial disease *Columnaris*, which resulted in mortality among fin-clipped walleyes in Little Cutfoot Sioux Lake, Minnesota.

Mortality may be induced by some of man's activities. Johnson (1953b) measured the mortality occurring among stocked fry from the time of removal from the hatchery to the time of release after clipping and found it to average about 7.3 percent. Tagged fish have also been observed to suffer greater mortality than untagged fish (Olson, 1955; Zimmerman, 1966a; Ryder, 1968). Hydroelectric dams may cause some mortalities through entrapment on panstocks (Lapworth, 1953) and passage through turbines (Prévost, Legendre and Lespérance, 1944) and sluice gates (Armbruster, 1962).

Due to a paucity of information, any statements made concerning the direct or indirect effects of fishing are conjectural. Van Oosten (1938a) believed that the occurrence of dead walleyes (mostly immature) found on Lake Erie beaches resulted from fishermen releasing undersized fishes from their trap-nets and gill-nets.

4.4.3 Factors affecting morbidity

Lymphocystis-infected walleyes in Lake Erie weighed 5.5-6.5 percent less than uninfected walleyes of the same length (Hile, 1954). Injuries incurred during netting leave walleyes more susceptible to fungus infections such as *Saprolegnia.* No doubt pollutants, such as those from pulp and paper mills, have some weakening effects upon walleyes (Smith, Kramer and MacLeod, 1965; Smith, Kramer and Oseid, 1966).

4.4.4 Relation of morbidity to mortality rates

Studies by Smith and Kramer (1965) demonstrate that groundwood pulp produces greater mortality among fry at lower oxygen levels than at higher levels.

4.5 Dynamics of population (as a whole)

Walleye populations have been observed to fluctuate widely in waters where they are heavily exploited - e.g., Lake Erie (Regier, Applegate and Ryder, 1969); Rainy Lake, Ontario - Minnesota (Chevalier, 1977); and Red Lakes, Minnesota (Smith and Pycha, 1961). Under heavy exploitation, density-dependent factors lessen in importance and year class success becomes more and more dependent on abiotic factors. Adult walleye abundance was significantly correlated with spring water levels and brood stock abundance five years prior in Rainy Lake (Chevalier, 1977). In Lake Erie, year class success was positively correlated with rates of water warming in spring and to some extent, brood stock abundance (Busch, Scholl and Hartman, 1975).

If long-term sustained commercial yields (all species) do not exceed theoretical yields (based on the MEI; Ryder, 1965) in northern Ontario lakes, the community structure appears to remain relatively stable. Even under varying degrees of fishing intensity, percids (mainly walleyes) consistently comprised approximately 30 percent of the catch (by weight) among certain northern Ontario lakes where theoretical yields were not exceeded. This may exist as an emergent property of predominantly percid fish communities in boreal shield lakes. However, among over-exploited lakes where actual commercial yields exceeded theoretical yields for several years and walleye yields exceeded 30 percent of total theoretical yields, walleye populations have collapsed or are beginning to collapse (Adams and Olver, 1977). In certain cases walleye angling yields may exceed commercial yields suggesting that the manner of harvest may be an important factor in determining long term sustainable yields. Kempinger and Carline (1977) reported a 9 $kg/ha^{-1}/y^{-1}$ mean angling yield for walleyes in Escanaba Lake, Wisconsin, over a period of 27 years. Yearly walleye yields varied between 3 and 26 $kg/ha^{-1}/y^{-1}$ in Escanaba Lake and the relatively high yield of walleyes was associated with significant changes in the structure of the fish community.

Kerr and Ryder (1977) have described the niche occupied by walleyes as a hypervolume of which two of the major dimensions are defined by the parameters of light intensity response and selected prey size. Ryder and Kerr (1978) further expanded the definition of walleye niche on the basis of its food habits, feeding behaviour and interspecific ethology within the percid community. The application of this model to the former Lake Erie percid community has accounted for niche separation among the four larger percids of economic value throughout their respective life cycles in that community.

4.6 The population in the community and the ecosystem

Walleyes are tolerant of a great range of environmental situations, but appear to reach greatest abundance in large, shallow, turbid lakes (Scott and Crossman, 1973). Schupp (1978) demonstrated an increase in abundance and growth for walleye populations partitioning the mesotrophic portions of a large lake of disparate environments, ranging from eutrophic to morphometric oligotrophic. As well, lakes having a lower shoreline development factor appear to support larger walleye populations than those with a higher factor (Johnson and Hale, 1963). They are at home in moderate to large rivers which provide adequate littoral and sublittoral habitats (Kitchell et al., 1977). Walleyes may exist in large oligotrophic lakes where sufficient littoral environments are more likely to exist.

Walleye populations in the more northern reaches of their distribution are usually associated with substantial populations of northern pike, yellow perch and white suckers and troutperch or troutperch populations. They are often sympatric components in a salmonid-dominated community. Other species commonly included in these fish communities are burbot, cisco, darters, and spottail shiners. Further south in the range centrarchids become more prevalent in the community and may include various species of *Lepomis*, the smallmouth bass, and black or white crappies (Ryder and Kerr, 1978). In such lakes competition for food may be more severe. In Big Sand Lake, Wisconsin, where the fish community consists of a substantial yellow perch and muskellunge population, along with smaller populations of smallmouth bass, rock bass, black crappie, bluegill and pumpkinseed, walleyes comprise just over half the standing crop (Niemuth and Klingbiel, 1962). Toward the extreme southern limits of walleye distribution, such species as gizzard shad, bullheads, freshwater drum and perichthyids become important in the community structure.

The walleye is a general predator feeding on invertebrates and fish, and thus is usually a top carnivore in the community. It seems to be well qualified as a dominant predator to help stabilize various populations of larger prey organisms in an aquatic ecosystem (Regier, Applegate and Ryder, 1969). Johnson (1949) states that if the northern pike was rated at 100 as a predator, then the walleye would rank as 50. Furthermore, if the walleye is the dominant predator it must make up 45-50 percent of the fish biomass (in Minnesota lakes) in order to control fish populations. Although the walleye is not markedly sensitive to most environmental fluctuations, changes in turbidity within a lake may produce a change in the size of the walleye population especially in lakes in which walleye and sauger occur sympatrically. An increase in turbidity would be to the advantage of the sauger which, being better adapted to dim-light conditions, would have a greater feeding advantage (Ryder, 1977 - see section 4.2.2.). Clady (1978) notes that the presence of saugers usually indicates a reduction in the normal community portions of yellow perch and walleye, and also that the diversity of species in these communities is positively correlated to the abundance of sauger and negatively to that of yellow perch.

Walleye populations are seen to persist throughout the continuum of cultural eutrophication. Progressive eutrophication is seen to first expand and then constrict optimum habitat (Chevalier, 1977; Leach et al., 1977). Cultural eutrophication has in fact increased the suitability of some post-glacial oligotrophic lakes for percids such as the walleye (Kitchell et al., 1977).

5 EXPLOITATION

5.1 Fishing equipment

5.1.1 Gears

The first European settlers on the Great Lakes used spears, brush weirs, baskets, simple seines, and hooks and lines to capture walleyes (Regier, Applegate and Ryder, 1969). However, gill nets are said to have been used by the Indians on the upper Great Lakes as early as 1781 (Van Oosten, 1938b). A hook and line commercial fishery began in eastern Lake Erie in 1795 but was replaced by seining and pound-netting (Regier, Applegate and Ryder, 1969). Pound nets were first introduced to the Great Lakes in 1836 on Lake Ontario and later on Lake Erie (1850), Lake Huron (1854), Lake Michigan (1856 and 1857) and Lake Superior (1864) (Van Oosten, 1938b). Gill nets were first used commercially on eastern Lake Erie in 1852 and were, of course, cotton twine, but by 1870 these nets were made from finer and stronger cotton or linen (Regier, Applegate and Ryder, 1969). By the 1880s fyke nets were becoming very numerous in Lake Erie (Regier, Applegate and Ryder, 1969) and around 1890, trap nets were introduced on western Lake Erie (Langlois and Langlois, 1948) and Lake Huron (Anon., 1968). During the 1940s "canned" gill nets were used by Ontario fishermen in 1948, nylon-mesh gill nets were first used experimentally on Lake Erie (Regier, Applegate and Ryder, 1969).

Presently, gill nets of between 7.6 and 11.4 cm mesh and trap nets are the most widely used commercial gear for the capture of walleyes.

5.1.2 Boats

Steam ships were first introduced into the Great Lakes fishery in 1860 on Lake Huron and later on Lake Michigan in 1869, Lake Superior in 1871 and Lake Erie in 1876. Motor boats were first used in the Great Lakes fishery in 1899 on Lake Superior (Van Oosten, 1938b).

5.2 Fishing areas

5.2.1 General geographic distribution

Walleyes, in general, are prized sport fish over their geographic range and in more northerly inland waters, they make up a considerable portion of the commercial catch (see section 5.2.2).

5.2.2 Geographic ranges

Important commercial walleye fisheries exist on inland lakes of the provinces of Ontario, Manitoba and Saskatchewan in Canada, and the state of Minnesota in the U.S.A. Among the Great Lakes, only Lakes Erie and Huron presently support substantial commercial walleye fisheries (Schneider and Leach, 1977).

Walleye sport fisheries are widespread throughout most states and provinces in which the species is found.

5.2.3 Depth ranges

Walleyes are captured in a wide range of depths depending on the time of day, transparency of the water, oxygen and temperature gradients, etc.

5.2.4 Condition of the grounds

Not applicable to this species.

5.3 Fishing seasons

5.3.1 General pattern of season

Regulations concerning closed seasons for the sport fishery vary from one province or state to another. In general, the fishery is open all year except for a period of about 1 to 3 months in the spring which allows adults to spawn unmolested. However, many states currently have an open angling season year-round for walleye in most of their walleye waters.

Commercial fishery seasons usually follow the same general pattern although wide variations may occur. For example, commercial fishing seasons in the Red Lakes, Minnesota, are normally limited to approximately four months of the year; during years of high yield, the season may be restricted to three months only (L.L. Smith, pers. comm.).

5.3.2 Dates of beginning, peak and end of season

The angling season usually extends from some time in May to some time into the following April. The commercial fisheries often have a shorter season than the angling fisheries.

5.3.3 Variations in date or duration of season

Closed seasons may be altered somewhat to accommodate changes in the timing of spawning runs in particular lakes or regions from year to year.

5.4 Fishing operations and results

5.4.1 Effort and intensity

Angling effort on a lake is usually recorded in the literature as the number of hours fished for all species per unit area (h/ha). Therefore, it is difficult to relate yield data to effort data for any one species in a lake. Summer walleye angling pressures of 25.4, 30.1 and 19.5 h/ha in 1956-1958 produced a yield of 3.6, 3.0 and 3.0 kg/ha from Caribou Lake, Minnesota (Micklus, 1959). Forney (1967) stated that in 1959, an angling effort of 62 h/ha harvested nearly half the spring standing crop of walleyes in Oneida Lake, New York (20 648 ha).

In general, angling success is greatest at dawn and dusk (Zimmerman, 1966a; Cheshire, 1968; Anderson, 1971) when optimum light conditions for feeding occur (see section 3.4.1). Furthermore, success is generally better during the first month of the season and then tapers off as the summer progresses (Lux and Smith, 1960; Wesloh, 1961; Leach, 1964; Rice, 1964; Payne, 1964a; 1965; Zimmerman, 1965; 1966a; Armstrong, 1967; Gregory and Powell, 1969; Johnson and Johnson, 1971). During the summer months when fishing is generally poorer, Eschmeyer (1937) found that milder, warm, calm and clear weather produced the best walleye fishing on Fife Lake, Michigan.

Angling catch per unit effort is usually given as the number of walleyes captured per unit time. However, the effort data used are often the number of hours fished for all species, not just for walleyes. In such cases, comparisons of walleye C.U.E. values of one lake to another may be meaningless. In Caribou Lake, Minnesota, walleye angling C.U.E. (based on the number of hours fished for walleye only) over three years was found to range from 0.18 to 0.32 (Micklus, 1959). Some Ontario C.U.E. values computed in a similar manner, are as follows: 0.14 to 0.31 over three summers for the Mississagi River (Payne, 1965) and 0.33 for Polly Lake (Ryder, 1968). On Savanne Lake, Ontario (a relatively unexploited lake since its closure to the public in 1969) during the summer of 1974, a walleye C.U.E. value (based on the number of hours fished for all species) of 1.23 was computed (P.J. Colby, unpubl.). On Lake of the Woods, Ontario, similarly computed C.U.E. values as high as 1.31 have occurred (V. Macins, pers. comm.). Hiner (1943) stated that a walleye C.U.E. (based on the number of hours fished for all species) of 0.32 was average for Minnesota lakes. In general, a good fishery exists when walleyes are caught at a rate of 0.3 walleyes per hour fished for all species (Tables XX and XXI). In addition, there appears to be an inverse relationship between walleye vulnerability to angling and the abundance of forage in a lake (Moyle, 1949; Lux and Smith, 1960; Forney, 1967; Schupp, 1972).

Commercial C.U.E. figures are usually given as the unit weight per lift (24 h set) in the case of pound, trap and fyke nets and as the unit weight per 914 m of gill net lifted (24 h set). Some C.U.E. values for commercial gear set on Lake Erie between 1948 to 1961 are listed in Table XXII. Values for all gears peaked during the period 1955-1957 when catches were at record highs. Between 1954 and 1960, commercial pound net sets in Nipigon Bay, Lake Superior, averaged over 100 kg/24 h set in all years except one and peaked at 236 kg in 1957 (Ryder, 1968). Between 1948 and 1963, Rainy Lake, Minnesota-Ontario, gill net catches ranged from 20.4 to 49.5 kg per 914 m of 10.2 cm mesh net (Bonde, Elsey and Caldwell, 1965).

5.4.2 Selectivity

Since the introduction of the nylon gill net into the Great Lakes fishery in 1948, studies have been conducted to compare the efficiency and selectivity of nylon versus cotton gill nets in capturing walleyes. In all studies, nylon was found to be more efficient than cotton (Newson, 1951; Atton, 1955; Ridenhour and DiCostanzo, 1956; Scidmore and Scheftel, 1958). Two studies revealed that nylon gill nets tend to catch approximately 1.5 times as many walleyes as cotton ones (Ridenhour and DiCostanzo, 1956; Scidmore and Scheftel, 1958). In addition, Scidmore and Scheftel (1958), demonstrated similar properties for the weight of the catch. However, Hewson (1951) found 7.6 cm mesh nylon nets captured up to 5 times the weight as cotton ones. The greater efficiency of nylon tended to decrease with increasing mesh size in Lac la Ronge and Last Mountain Lake, Saskatchewan (Atton, 1955). Nylon gill nets also appear to capture a greater proportion of larger walleyes than the cotton nets (Hewson, 1951; Atton, 1955). No significant difference was found in the ability of green versus white nylon gill nets in capturing walleyes (Bonde, 1965).

From their studies, Hamley and Regier (1973) made a number of observations concerning the selectivity of nylon gill nets (Fig. 34) which are as follows: (1) amplitudes of the selectivity curves increased with mesh size indicating that the smaller-meshed nets were less effective even toward the sizes of fish they caught best; (2) the curves appeared flat-topped or bimodal and obviously were not normal; (3) fish on the left part of each curve were mostly wedged while the larger fish on the right were mostly tangled (teeth, maxillaries, preopercles and opercles); (4) tangling contributed as much as wedging on the selectivity curves; (5) larger-mesh nets were more efficient both in wedging and in tangling walleye.

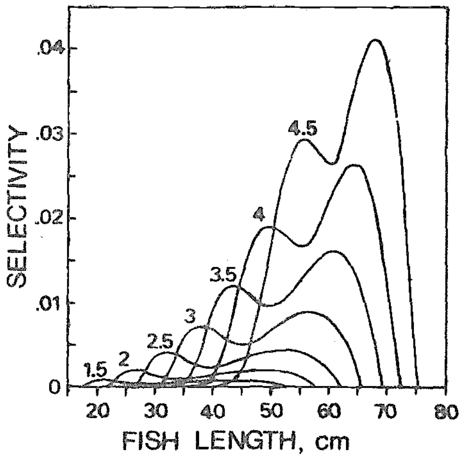

Fig. 34 Estimated selectivity curves of 3.8-11.4 cm gill nets to walleyes (Redrawn from Hamley and Regier, 1973)

5.4.3 Catches

A yield of 3.4 kg/ha^{-1}/y^{-1} was considered by Olson and Wesloh (1962) to be characteristic of walleye production in many of Minnesota's natural walleye waters. Schneider (1969) citing Groebner (1960) and Johnson (1964), stated that a "good" walleye lake should yield 2.2-4.5 kg/ha^{-1}/y^{-1}. One of the most productive waters for walleyes recorded is Little Cutfoot Sioux Lake, Minnesota. For the summers of 1952, 1957 and 1958, the estimated summer angling yield was 10.3, 9.8 and 17.7 kg/ha^{-1}/y^{-1} (Table XXIII). From 1946 to 1950, the yearly walleye angling yields from Escanaba Lake, Wisconsin, climbed to a peak of 25.7 kg/ha^{-1}/y^{-1} and then fell to a relatively constant level averaging about 5.9 kg/ha^{-1}/y^{-1} between 1958 and 1965 (Table XXIII). Yields from other waters are also listed in this table.

Adams and Olver (1977), studying long-term commercial yields from 70 northern Ontario lakes, determined that few of these lakes were capable of sustaining percid (essentially walleye) yields greater than 1.5 kg/ha/y. They further stated that a sustainable percid yield of 1.0-1.25 kg/ha/y or about one third of the total yield, is probably a reasonable expectation for many moderately to intensively fished lakes in this region, although some lakes will be able to sustain higher or lower yields, depending on their yield potentials (based on the MEI; Ryder, 1965). The average annual yield of walleyes to commercial fisheries in North American lakes ranged from 0.04 to 3.06 kg/ha (Carlander, 1977).

Total commercial production of walleyes for the Great Lakes has dropped drastically from a high of 7 803 000 kg in 1956 to 164 000 kg in 1973 (Table XXIV). Lake Erie, which previously had been the major producing lake, has shown the greatest decline in walleye production. In 1958, Lake Erie produced 90 percent of the Great Lakes walleye catch while in 1973, it contributed only 43 percent. Manitoba has been the leading province in inland walleye production, producing 1 692 000 kg in the 1973-1974 season. Manitoba is followed by Saskatchewan and Ontario as the three largest producers of walleyes from inland lakes. Yields from inland lakes have also dropped significantly since the early 1960s such that the total commercial walleye catch from all major producing states and provinces in 1973 is less than 45 percent of the 1960 catch.

Walleye angling exploitation rates tend to average between 20 and 30 percent (Table XXV) but have been reported as high as 47 percent (Forney, 1967). Kempinger et al. (1975) found a significant negative correlation between the average weight of 356 mm walleye captured in August and the rate of angling exploitation for that year in Escanaba Lake, Wisconsin (Fig. 35).

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.1.1 Limitation or reduction of total catch

Most provinces and states with a walleye sport fishery have daily catch limits. These limits generally range between six and ten walleyes per day but may be as low as five (e.g., Northwest Territories, Michigan, Iowa) or as high as 15 (e.g., Mississippi, Montana, Alabama).

Commercial walleye quota regulations vary considerably from one state or province to the next, being based on political and economic factors as well as biological ones. For the Red Lakes fishery, Minnesota, mean annual commercial yield and mean commercial C.U.E. over a 20 year period are used as a basis for setting

TABLE XX

Summer walleye angling C.U.E. (number caught/h fishing) for selected North American waters[a]

Location and source	1938	1939-1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
ONTARIO																
Savanne Lake (P.J. Colby, unpubl.)																
Lake Mindemoya (Zimmerman, 1962; 1965)																
Bright Lake (Payne, 1964a)																
Lake Temagami (Jorgensen, 1967)																
Sturgeon Lake (Armstrong, 1967)																
Mississagagon Lake (Hughson, 1966)																
Kashwakamak Lake (Cheshire, 1968)																
Plevna Lake (Cheshire, 1968)																
Big Clear Lake (Cheshire, 1968)																
Mississagi River (Cheshire, 1968)																
Lake Nipissing (Anthony and Jorgensen, 1977)																
Lake Erie (western) (Keller, 1964b)																
Pickerel Lake (Caldwell, 1961)																
Marmion Lake (Caldwell, 1961)																
Rainy Lake (Burrows, 1951; Bonde, Elsey and Caldwell, 1965)		1.10														0.52
Lake of the Woods (Burrows, 1951; Chambers and Macins, 1966; Schupp, 1974; V. Macins, pers. comm.)		1.26		1.10[e]										0.71	0.80	0.69
Basswood Lake (Burrows, 1951; Caldwell, 1961)		0.53														0.13
Jean Lake (Caldwell, 1960, 1961)																
Kawnipi Lake (Caldwell, 1960)																0.28
Quetico Lake (Caldwell, 1960; 1961)																
Beaverhouse Lake (Caldwell, 1960; 1961)																
Finlayson Lake (Caldwell, 1961)																
Lake Despair (Caldwell, 1961)																
Pipestone Lake (Caldwell, 1961)																
Burditt Lake (Caldwell, 1961)																
Polly Lake (Ryder, 1968)																
White Lake (Rice, 1964; Price, 1972)																
Lac des Mille Lacs (Drysdale, 1972; 1973)																
Whitefish Lake (Drysdale, 1974)																
Eagle Lake (Chevalier, 1975)																
MANITOBA																
Paint Lake (Schlick, 1973)																
MINNESOTA																
Lake Vermilion (Carlander and Hiner, 1943)	0.65															

1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
																	1.23
				0.38	0.39	0.37											
							0.08[g]										
									0.05								
								0.19									
							0.02	0.04	0.03	0.02							
							0.06	0.13	0.07	0.05							
							0.57[g]	0.15[g]	0.15[bg]	0.11[bg]							
								0.08[bg]	0.11[bg]	0.19[bg]							
						0.14[g]	0.15[g]	0.31[cg]	0.31[dg]								
			0.41	0.28	0.23	0.58	0.35	0.32	0.29		0.39	0.12	0.20		0.12	0.28	0.37
	0.02	<0.01	0.01														
			0.27														
			0.68														
	0.58	0.53	0.65	0.24	0.41												
1.31	0.54	0.45	0.97	0.65	0.52	0.58	0.63	0.59[df]	0.62	0.87	0.49	0.42	0.68	0.54	0.52	0.34	0.38
0.10	0.25	0.55	0.45														
0.44	0.41	0.88	0.34														
0.44	0.95	0.56															
0.64	0.29	1.34	1.64	0.34													
0.63	0.44	0.69	0.95	0.62													
				1.14													
				0.30													
				0.10													
			0.16														
			0.33[g]														
				0.64	0.48	0.58							0.31	0.4	0.3		
	0.5	0.6	0.8	0.7	0.7	0.9		0.5	1.6	0.4	0.9	0.4		0.46	0.44	0.55	
																	0.34
															0.19	0.19	
											0.61						

TABLE XX continued

Location and source	1938	1939-1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
Mille Lacs Lake (Burrows, 1951; Schupp, 1959; Johnson, 1964)	0.29															
Lake Andrew (Larson, 1961c)															0.03	
Lake Mina (Larson, 1961b)															<0.01	
Cutfoot Sioux Lake (Johnson, 1953a; Johnson and Johnson, 1971)												0.21				
Grace Lake (Wesloh and Olson, 1962)																
Lake Winnibigoshish (Burrows, 1951; Johnson and Johnson, 1971)	0.24								0.7[e]							
Pequaywan Lake (Burrows, 1951)	1.20															
Crane Lake (Burrows, 1951)	0.68															
Lake Minnewaska (Burrows, 1951)		0.15														
Kabetogami Lake (Burrows, 1951)		0.70														
Seagull Lake (Micklus, 1961)																
Toad Lake (Wesloh, 1961)															0.13	0.14
Linwood Lake (Burrows, 1951)		<0.01												<0.01	<0.01	<0.01
Lake Francis (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Johnson, 1957)														<0.01	0.02	0.02
Maple Lake (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Johnson, 1957)														0.03	0.05	0.03
Grove Lake (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Johnson, 1957)														<0.01	0.01	<0.01
Little Pine Lake (Moyle and Franklin, 1955)														0.19		
Sally Lake (Moyle and Franklin, 1955)														0.24		
Ball Club Lake (Moyle and Franklin, 1955)														0.02		
Moose Lake (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Johnson, 1957)														0.12	0.08	0.10
Gladstone Lake (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Johnson, 1957)														<0.01	<0.01	<0.01
Nokay Lake (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Johnson, 1957)														<0.01	<0.01	<0.01
Mazaska Lake (Hiner, 1943; Johnson and Kuehn, 1956; Johnson, 1957)	<0.01													0.02	0.01	
Many Point Lake (Johnson and Kuehn, 1956; Johnson, 1957; Olson and Wesloh, 1962)															0.11	0.16
Splithand Lake (Johnson and Kuehn, 1956; Johnson, 1957)															0.19	0.20
Park Lake (Johnson and Kuehn, 1956)															0.02	
Nine Mile Lake (Johnson and Kuehn, 1956)															0.13	
Pike Lake (Johnson, 1957)															0.13	

1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
	0.39			0.26	0.26												
0.20	0.31																
0.06	0.08	0.07	0.10														
0.19	0.26																
0.15																	
0.15	0.17	0.17	0.19														

TABLE XX continued

Location and source	1938	1939-1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
Caribou Lake (Johnson, 1957)																0.32[g]
Round Lake (Hiner, 1943)		0.01														
Martin Lake (Hiner, 1943)		0.01														
Bear Lake (Hiner, 1943)		<0.01														
Waconia Lake (Hiner, 1943)		<0.01														
Roosevelt Lake (Hiner, 1943)		0.01														
Big Thunder Lake (Hiner, 1943)		0.01														
Orchard Lake (Hiner, 1943)		<0.01														
Belle Taine Lake (Hiner, 1943)		0.01														
Knife Lake (Hiner, 1943)		0.01														
Grindstone Lake (Hiner, 1943)	0.03															
Gilchrest Lake (Hiner, 1943)	0.05															
Horseshoe Lake (Hiner, 1943)	0.01															
Rice Lake (Hiner, 1943)	0.05															
Cedar Lake (Hiner, 1943)	0.01															
MICHIGAN																
Fife Lake (Schneider, 1969)												<0.01[f]	<0.01[f]	<0.01[f]	<0.01[f]	<0.01[f]
Bear Lake (Schneider, 1969)												0.04[f]	0.02[f]	0.02[f]	0.02[f]	0.01[f]
WISCONSIN																
Escanaba Lake (Churchill, 1956, 1959, 1960, 1962; Anon., 1957; Kempinger, 1963, 1964, 1965, 1966; Kempinger *et al.*, 1975)						<0.01	0.01	0.43	0.11	0.16	0.10	0.14	0.15	0.13	0.11	0.19
Nebish Lake (Kempinger, 1967)						0	0	0	0	0	0	0	0	0	0	0
Fish Lake (Hiner, 1943)	0.02															
Diamond Lake (Hiner, 1943)	0.5															
Green Lake (Hiner, 1943)	0.3															
Bronson Lake (Hiner, 1943)	<0.01															
South Twin Lake (Hiner, 1943)	0.05															
Budd Lake (Hiner, 1943)	<0.01															
Amber Lake (Hiner, 1943)	0.02															
Sullivan Lake (Hiner, 1943)	0.02															
Okabena Lake (Hiner, 1943)	0.02															
Island Lake (Hiner, 1943)	0.01															
Waubesa Lake (Frey, Pedrocine and Vike, 1939)	0.04															
Kegansa Lake (Frey, Pedrocine and Vike, 1939)	0.06															
NEW YORK																
Oneida Lake (Grosslein, 1961)																

1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
0.18[g]	0.30[g]																
<0.01[f]	<0.01[f]	<0.01[f]	0[f]	<0.01[f]	<0.01[f]	0.01[f]	<0.01[f]	<0.01[g]									
0.01[f]	0.01[f]	<0.01[f]	<0.01[f]	0.01[f]	0.01[f]	0.02[f]	0.02[f]	0.02[g]									
0.15	0.04	0.04	0.11[f]	0.19	0.11	0.06	0.13	0.15	0.20[f]	0.23[f]	0.10[f]	0.09[f]					
0	0	0.01	<0.01	0.01	0.01	0.21	0.12	0.09	0.08								
0.04	0.08	0.34															

TABLE XX continued

Location and source	1938	1939-1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
IOWA																
West Okoboji Lake (Rose, 1956)													0.05[f]	0.12[f]	0.15[f]	
East Okoboji Lake (Rose, 1956)													0.02[f]	0.08[f]	0.13[f]	
Spirit Lake (Rose, 1956)													0.20[f]	0.12[f]	0.13[f]	
Clear Lake (DiCostanzo and Ridenhour, 1957)													0.01	<0.01	<0.01	<0.01
Des Moines River (Harrison, 1962)													0.03[h]	0.02[h]	<0.01[h]	<0.01[h]
Lost Island Lake (Rose and Moen, 1951)						0.01[e]	0.01[e]	0.01[e]	0.01[e]	0.05[e]						
Mississippi River (Nord, 1964)																
Pool 4																
Pool 5																
Pool 7																
Pool 11																
Pool 13																
Pool 18																
Pool 26																

a/ Values given as number of walleye caught/h fished for all species, unless otherwise stated
b/ Evening C.U.E. only
c/ Autumn data included
d/ Number of walleye retained/h fished
e/ June and July data only
f/ Data for all seasons included
g/ Number of walleye caught/h fished for walleye only
h/ All seasons included except winter

1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
0.01[h]	0.01[h]	0.03[h]	<0.01[h]	0.01[h]													
					0.06[h]												
					0.04[h]												
					0.04[h]												
					0.02[h]												
					<0.01[h]												
					<0.01[h]												
					<0.01[h]												

TABLE XXI

Winter walleye angling C.U.E. (number caught/h fished for all species) for selected North American waters

Location and source	1938	1939-1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
ONTARIO																
Eagle Lake (Chevalier, 1975)																
Panache Lake (Hughson, 1966)																
MINNESOTA																
Lake Vermilion (Burrows, 1951)		0.78														
Mille Lacs Lake (Burrows, 1951; Johnson, 1964)		0.12														
Grace Lake (Wesloh and Olson, 1962)																
Whitefish Lake (Burrows, 1951)		0.01														
Lake Minnewaska (Burrows, 1951)		0.16														
Kabetogama Lake (Burrows, 1951)		0.06														
Toad Lake (Wesloh, 1961)														0[a]	0[a]	0.01[a]
Lake Nipissing (Anthony and Jorgensen, 1977)																
Long Lake (Johnson and Kuehn, 1956; Kuehn and Johnson, 1956; Johnson, 1957)														0[a]	<0.01[a]	0[a]
Lake Francis (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Kuehn and Johnson, 1956; Johnson, 1957)													<0.01[a]	<0.01[a]	0.01[a]	0.01[a]
Maple Lake (Moyle and Franklin, 1955; Johnson and Kuehn, 1956; Kuehn and Johnson, 1956; Johnson, 1957)													0.02[a]	0.03[a]	0.01[a]	0.06[a]
Sally Lake (Moyle and Franklin, 1955)													0.07[a]			
Mazaska Lake (Johnson and Kuehn, 1956: Kuehn and Johnson, 1956; Johnson, 1957)														<0.01[a]	<0.01[a]	<0.01[a]
WISCONSIN																
Escanaba Lake (Anon., 1957; Churchill, 1957; 1958, 1960, 1962; Kempinger, 1963, 1964, 1965, 1966)						<0.01	0.02	0.09	0.15	0.25	0.18	0.2	0.25	0.14	0.43	0.39[a]
Nebish Lake (Kempinger, 1964)																
NEW YORK																
Oneida Lake (Grosslein, 1961)																
MISSISSIPPI RIVER (U.M.R.C.C., 1945)																
Pool 4				0.17[a]												
Pool 5				0.05[a]												
Pool 5a				<0.01[a]												
Pool 6				<0.01[a]												
Pool 7				0.03[a]												
Pool 8				0.03[a]												
Pool 9				0.01[a]												
Pool 10				0.01[a]												

[a] Figures located mid-way between two years represent walleye C.U.E. for the winter beginning in one year and ending in the next

1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
																0.22[a]	
			0.01	0.01				0.01									
		0.01[a]			0.06[a]	0.12[a]											
	0[a]	0.02[a]	0.05[a]	0.10[a]													
				0.01	0.21	0.14	0.07	0.11	0.10		0.12	0.30			0.12	0.08	
	0.29[a]	0.11		0.23[a]	0.29[a]	0.08[a]	0.1[a]	0.24[a]									
						0.02[a]											
0.11	0.53	0.52															

TABLE XXII

Effective fishing effort and catch per unit effort for gill nets, trap nets and pound nets fished in western Lake Erie (Districts O-1 and OE-1), 1948-1961 (Regier, Applegate and Ryder, 1969)

Year	Province of Ontario								State of Ohio	
	Small-mesh gill nets		Large-mesh gill nets		Pound nets		Trap nets		Trap nets	
	Millions of m lifted	C.U.E.	Millions of m lifted	C.U.E.	Lifts in thousands	C.U.E.	Lifts in thousands	C.U.E.	Lifts in thousands	C.U.E.
1948	2.7	3.8	1.5	6.2	8.4	7.5	-	-	69.7	15.9
1949	2.5	4.7	1.3	27.0	8.9	8.6	-	-	82.0	19.8
1950	6.2	7.4	1.5	29.9	6.1	8.5	0.3	13.6	68.9	20.3
1951	10	11.2	2.2	47.4	4.7	7.1	2.8	21.9	76.0	20
1952	13.6	17.0	6.2	27.8	1.9	8.5	5.9	20.2	76.7	16.0
1953	8	8.5	6.6	44.9	5.4	4.5	5.0	25.8	70.2	23.5
1954	11.5	11.1	6.5	62.3	3.2	7.4	5.9	25.2	70.7	20.7
1955	10.2	28.8	8.6	100.8	2.3	9.3	4.4	39.2	53.8	30.5
1956	9.3	56.9	10.1	152.5	3.4	4.2	6.8	25.9	50.5	30.8
1957	13.0	50.5	10.1	126.2	3.0	3.7	5.4	16.9	46.8	23.6
1958	15.9	19.3	9.1	87.3	2.4	1.5	4.5	12.2	41.5	18.7
1959	7.1	9.8	5.6	45.8	1.5	0.8	2.5	4.1	27.2	7.2
1960	13.8	9.8	2.1	35.4	1.5	3.8	4.3	2.3	26.2	8.3
1961	9.6	5.2	1.1	25.3	1.0	1.3	1.9	3.5	65.7	2

Note: No adjustment made for change in gill net mesh and methods; C.U.E. for gill nets - kg per 914 m; C.U.E. for other gear - kg per lift

TABLE XXIII

Angling yield and effort estimates from various waters

Location and source	Year	Estimated yield (kg/ha)	Estimated effort (h/ha)
ONTARIO			
Lake Nipissing	1970(s)	1.3	11.7(as)
(Anthony and Jorgensen, 1977)	1972(y)	0.9	12.9(as)
	1975(s)	0.9	12.4(as)
White Lake	1961(s)	3	-
(Price, 1972)	1970(s)	0.7	6.7(as)
	1971(s)	0.9	7.3(as)
	1972(s)	1.6	6.2(w)
Eagle Lake	1972(y)	0.8	-
(Chevalier, 1975)			
Northern Light Lake	1973(s)	0.3	1.2(w)
(Martin, 1973)			
Lac des Mille Lacs	1975(s)	4.4	14.4(as)
(Elsey and Thomson, 1977)			
MINNESOTA			
Lake Andrew	1955(s)	1.1	48.2(as)
(Larson, 1961c)			
Lake Mina	1955(s)	0.2	67 (as)
(Larson, 1961b)			
Cutfoot Sioux Lake			
(Johnson, 1953a)	1952(s)	10.3	78.6(as)
(Johnson and Johnson, 1971)	1957(s)	9.8	103 (as)
	1958(s)	17.7	112.6(as)
Grace Lake	1957(s)	2.5	41.1(as)
(Wesloh and Olson, 1962)	1958(s)	3.3	44.6(as)
	1959(s)	2.4	45.6(as)
	1960(s)	3.6	41 (as)
Lake Winnibigoshish	1957(s)	1.2	9.1(as)
(Johnson and Johnson, 1971)	1958(s)	1.7	12.1(as)
Seagull Lake	1957(s)	0.5	1.9(w)
(Micklus, 1961)			
Toad Lake	1955(s)	3.1	38.1(as)
(Wesloh, 1961)	1956(s)	2.6	30.2(as)
Linwood Lake	1956(y)	0.1	180.8(as)
(Johnson, 1957)			
Lake Francis			
(Groebner, 1960)	1952(s)	0.2	-
(Moyle and Franklin, 1955)	1954(y)	1.0	260.4(as)
(Johnson and Kuehn, 1956)	1955(y)	3.7	289.9(as)
(Johnson, 1957)	1956(y)	5.2	147.3(as)
Maple Lake	1952(s)	0.6	70.4(as)
(Larson, 1961a)	1953(s)	0.2	67.9(as)
(Moyle and Franklin, 1955)	1954(y)	1.0	85.0(as)
(Johnson and Kuehn, 1956)	1955(y)	1.7	76.4(as)
(Johnson, 1957)	1956(y)	1.6	70.6(as)
(Larson, 1961a)	1957(s)	0.6	-
Little Pine Lake	1954(y)	4.2	46.9(as)
(Moyle and Franklin, 1955)			
Sally Lake	1954(y)	13.4	88.6(as)
(Moyle and Franklin, 1955)			

continued

TABLE XXIII continued

Location and source	Year	Estimated yield (kg/ha)	Estimated effort (h/ha)
Moose Lake			
(Moyle and Franklin, 1955)	1954(y)	3.0	41.2(as)
(Johnson and Kuehn, 1956)	1955(y)	2.5	51.5(as)
(Johnson, 1957)	1956(y)	3.9	46.4(as)
Gladstone Lake	1954(s)	0.3	-
(Johnson and Kuehn, 1956)	1955(y)	0.3	111.2(as)
(Johnson, 1957)	1956(y)	<0.1	45.2(as)
Mazaska Lake			
(Johnson and Kuehn, 1956)	1955(y)	3.6	86.2(as)
(Johnson, 1957)	1956(y)	1.5	148 (as)
Many Point Lake	1955(ay)	3.1	45.4(as)
(Olson, 1958)	1956(ay)	4.3	44.1(as)
	1957(ay)	2.8	36.0(as)
(Olson and Wesloh, 1962)	1958(s)	3.5	34.5(as)
	1959(s)	3.4	39.4(as)
	1960(s)	3.1	32.9(as)
Splithand Lake			
(Johnson and Kuehn, 1956)	1955(y)	3.0	36.4(as)
(Johnson, 1957)	1956(y)	2.7	30.7(as)
Park Lake	1955(s)	0.4	-
(Johnson and Kuehn, 1956)			
Nine Mile Lake	1955(y)	1.9	27.3(as)
(Johnson and Kuehn, 1956)			
Caribou Lake			
(Johnson, 1957)	1956(y)	3.6	27.1(as)
(Micklus, 1959)	1956(s)	3.6	25.4(w)
	1957(s)	3.0	30.1(w)
	1958(s)	3.0	19.5(w)
Wilson Lake	1964(y)	3.6	23.5(as)
(Johnson, 1974)	1965(y)	2.4	18.3(as)
	1967(y)	2.0	16.3(as)
	1969(y)	2.1	16.8(as)
	1970(y)	3.5	29.9(as)
	1971(y)	4.5	34.6(as)
	1972(y)	4.9	37.8(as)
	1973(y)	6.6	43 (as)
Mille Lacs Lake	1961(s)	2.9	18.9(as)
(Johnson, 1964)	1962(s)	2.5	11.9(as)
Leech Lake	1965(s)	2.0	19.0(as)
(Schupp, 1972)	1966(s)	2.3	19.1(as)
	1967(s)	2.0	17.4(as)
Pike Lake	1956(y)	0.9	14.7(as)
(Johnson, 1957)			
MICHIGAN			
Fife Lake			
(Eschmeyer, 1935)	1934(y)		18.6(as)
(Schneider, 1969)	1964(y)		77 (as)
WISCONSIN			
Escanaba Lake	1946(y)	0.05	79.6(as)
(Churchill, 1957)	1947(y)	0.2	53.4(as)
	1948(y)	8.3	108.5(as)
	1949(y)	9.1	164.1(as)
	1950(y)	25.7	304.4(as)

continued

TABLE XXIII continued

Location and source	Year	Estimated yield (kg/ha)	Estimated effort (h/ha)
Escanaba Lake continued			
(Churchill, 1957; Kempinger, 1964)	1951(y)	10.4	185.8(as)
(Churchill, 1957; Anon., 1957)	1952(y)	16.0	218.8(as)
	1953(y)	14.3	243.4(as)
	1954(y)	6.6	151.5(as)
	1955(y)	12.8	197.4(as)
(Kempinger, 1966; Wirth, 1960)	1956(y)	10.9	205.8(as)
	1957(y)	8.9	208.9(as)
	1958(y)	4.3	222.4(as)
	1959(y)	3.9	185.3(as)
	1960(y)	8.0	187.3(as)
(Kempinger, 1966)	1961(y)	7.8	156.0(as)
	1962(y)	8.7	188.6(as)
	1963(y)	4.9	23.2(as)
(Kempinger, 1965, 1966)	1964(y)	5.1	107.7(as)
	1965(y)	4.1	84.1(as)
(Kempinger <u>et al.</u>, 1975)	1966(y)	8.7	115.7(as)
	1967(y)	10.0	121.8(as)
	1968(y)	3.6	83.4(as)
	1969(y)	3.4	94.0(as)
Waubesa Lake (Frey, Pedrocine and Vike, 1939)	1938(y)	1.5	49.0(as)
Kegonsa Lake (Frey, Pedrocine and Vike, 1939)	1938(y)	1.2	28.7(as)
Nebish Lake	1959(y)	0.3	64.7(as)
(Kempinger, 1967)	1960(y)	0.1	59.9(as)
	1961(y)	0.2	47.4(as)
	1962(y)	0.2	37.1(as)
	1963(y)	5.8	40.7(as)
	1964(y)	3.6	49.4(as)
	1965(y)	2.5	38.9(as)
	1966(y)	1.9	36.9(as)
<u>SOUTH DAKOTA</u>			
Lake Sharpe (Nelson and Walburg, 1977)	1973(ay)	1.2	7.3(as)
<u>COLORADO</u>			
Boyd Reservoir	1969(y)	1.1	102 (as)
(Weber, Powell and Imler, 1972)	1970(y)	0.8	115 (as)
	1971(y)	1.8	85 (as)

s - summer
y - combined summer and winter fishing season
ay - calendar year (or a proportion of calendar year)
as - based on the number of hours fished for all species
w - based on number of hours fished for walleye only

TABLE XXIV

Total commercial walleye catches from North American waters from 1960 to 1972

Year	Great Lakes Catch (kg x 1 000)							Inland Lakes Catch (kg x 1 000)						Total
	Erie	Ontario	Huron	Michigan	St. Clair	Superior	Total	Ontario	Manitoba	Saskatchewan	Alberta	Minnesota	Total	
1960	814	58	203	54	63	114	1 306	1 026	3 133	790	483	504	5 936	7 242
1961	488	57	157	44	107	103	956	1 028	3 190	808	381	466	5 873	6 829
1962	327	55	228	30	118	79	837	1 154	3 689	1 063	213	453	6 572	7 409
1963	1 215	32	232	28	150	76	1 733	1 052	3 355	1 105	295	320	6 127	7 860
1964	529	31	215	16	162	98	1 051	930	2 206	1 040	229	398	4 803	5 854
1965	356	23	196	12	125	132	844	888	1 727	936	161	324	4 036	4 880
1966	612	22	150	11	113	171	1 079	931	2 090	864	138	496	4 519	5 598
1967	572	12	134	7	84	125	834	790	1 300	824	103	358	3 375	4 309
1968	383	10	196	5	103	55	752	757	1 402	969	129	339	3 596	4 348
1969	216	9	150	6	149	11	541	545	1 265	1 090	89	332	3 321	3 862
1970	45	5	49	5	20	4	128	550	1 043	1 018	64	410	3 085	3 213
1971	39	3	44	5	a/	2	93	462	925	785	78	285	2 535	2 628
1972	65	2	35	3	a/	1	106	402	1 654	624	70	175	2 925	3 031
1973	70	2	89	2	a/	1	164	511	1 692	605	41	178	3 027	3 191

a/ Closed to commercial fishing

Great Lakes catch data: 1960-1968 (Baldwin and Saalfeld, 1962; Anon., 1970); 1969-1973 (U.S. Dept. of Commerce, Great Lakes Fisheries, Annual Summaries)

Inland lakes catch data: Ontario (Ont.Min.Nat.Res., Stat.Publ. - see Bibl., Anon., 1972, 1974, 1975); Manitoba (pers. comm., G. Nelson); Saskatchewan (pers. comm., Supt.Fish., R.P. Johnson); Alberta (pers. comm., Fish.Adm.Ass., D.O. Trent); and Minnesota (Heyerdahl and Smith, 1972, pers. comm., W.J. Scidmore and pers. comm., L.L. Smith, Jr.)

TABLE XXV

Exploitation rates from various waters

Location and source	Year	Rate of exploitation (%) Range	Average	Comments
Mississagi River, Ontario (Payne, 1965)	1965		14	calendar year
Nipigon River, Ontario (Ryder, 1968)	1955-57	7-34	18	calendar year
Cutfoot Sioux Lake, Minnesota (Johnson and Johnson, 1971)	1957-58	11-22	17	summer
Many Point Lake, Minnesota (Olson, 1958)	1955-57	21-33	27	angling year
Escanaba Lake, Wisconsin (Kempinger _et al._, 1975)	1953-69	13-42	27	calendar year
Oneida Lake, New York (Forney, 1967)	1957-59	10-47	23	angling year
Spirit Lake, Iowa (Rose, 1949, 1955)	1947, 1954	15-29	22	calendar year
Hoover Reservoir, Ohio (Erickson and Stevenson, 1967)	1967		29	summer

quotas on a judgemental basis. For example, if the C.U.E. at the beginning of a season exceeds the mean C.U.E. by at least 25 percent, the quota is elevated using the mean yield base increased by a proportional factor (Smith, 1977). This approach is used because variations in seasonal growth could affect yields by as much as 20 to 30 percent.

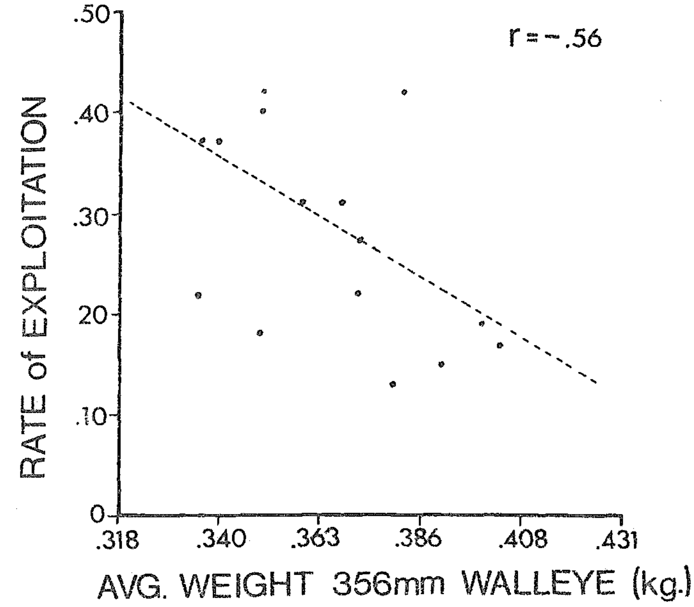

Fig. 35 Relation of rate of exploitation to condition of Escanaba Lake, Wisconsin walleye (Redrawn from Kempinger _et al._, 1975)

6.1.2 Protection of portions of the population.

Both the sport and commercial fisheries are usually closed during the spring months to protect spawning populations (see section 5.3). Restrictions on gill-netting gear usually consist of a minimum mesh size (ranging from 7 cm to 11.4 cm) and a limit on the number of metres set.

To protect immature members of a population, minimum size restrictions are often placed on angling catches, and range from 305 mm to 381 mm. Size restrictions may also be imposed on walleyes captured commercially (e.g., 381 mm for Canadian fishermen on Lake Erie). Schneider (1978) believes that the application of size limits can give the managers a certain flexibility to manage for alternative goals such as recreational values on stock sizes. However, Schneider (pers. comm.) feels that prior to the application, the walleye fishery should be assessed in terms of growth and mortality related factors. Schneider (1978) using simulation modelling, has predicted that for the average Michigan sports fishery, increasing the minimum limit (330 mm to 381 mm) will have the following effects: (1) have no significant effect on yield; (2) increase walleye egg production by 20-30 percent; (3) increase the total number of walleye caught (legal plus sub-legal) and the biomass of the population by 15-20 percent; and (4) cause a similar decrease in the numbers of legal-sized walleyes taken home. Serns (1978), reported that in a Wisconsin lake the 381 mm minimum limit effected the following changes in the fishery: (1) reduction in the yield of legal-sized fish; (2) decline in total numbers of legal fish captured with a concomitant increase in numbers of sub-legals; (3) decrease in length and conditions of legal fish; and (4) a density-dependent decline in the mortality of legal sized walleyes.

Since 1946, Escanaba Lake, Wisconsin, was set up as an experimental management lake whereby all bag and size limits were removed and sport fishing was allowed year round. Despite the lifting of regulations, anglers have been estimated to harvest only about 20 percent of the catchable walleye population annually (Klingbiel, 1953; Wirth, 1955) and up to 1969, standing crop estimates provided no evidence of stock depletion (Kempinger et al., 1975).

6.2 Control or alteration of physical features of the environment

6.2.1 Regulations of flow

In some cases where a river has been impounded, natural walleye populations have adapted well to conditions existing in the reservoir (Stroud, 1949a; R.B. Fitz and J.A. Holbrook, unpubl. data; Nelson and Walburg, 1977). Nelson and Walburg (1977) attributed the increase in walleye numbers in Missouri mainstream reservoirs to an increase in quantity and quality of spawning habitat.

Discharge flow rates from control dams may significantly influence walleye spawning in down-river areas, through fluctuations in water levels (MacCrimmon and Skobe, 1970; Bidgood, 1971; Nelson and Walburg, 1977), and decreases in water quality (Stone, 1963; Crowe, 1969).

6.2.2 Control of water levels

Klingbiel (1969) noted that in the United States most state agencies attempt to maintain stable or slightly rising water levels during spawning and incubation, although stable levels have not proved to be necessary at other times during the year. Groen and Schroeder (1978) state that in certain Kansas reservoirs, where water level management consists of a two-part cycle, walleye populations have actually been strengthened. Raising the water level in spring to improve spawning and nursery conditions, followed by a mid-summer drawdown for revegetation, has improved the forage base and water quality for walleyes. They feel that increased walleye growth, recruitment and harvest, enhanced survival of walleye fry and improved fish population structure can be attributed to water level management. Erickson (1972) observed that onstream impoundments which produced the best walleye populations were characterized by slow water level fluctuations. The manner in which water levels in impoundments are regulated has serious consequences particularly on YOY walleye. In Rainy Lake the spring water levels and brood stock abundance were significant factors in the walleye abundance five years later (Chevalier, 1977). In the case of Lewis and Clark Lake, Walburg (1971) estimated the loss of sauger and walleye fingerlings in water discharge from the control dam to be in the order of 700 000 in June, 1969 and 110 000 on 3 June 1970. The involved mortality rate was estimated to be 42 percent. High fish losses can be attributed to the fact that water was drawn from approximately 3 m below the surface. In Lake Francis Case where water was drawn from a depth of 40 m, few fish were lost (Benson, 1973).

6.2.3 Control of erosion and silting

No information available to the authors.

6.2.4 Fishways at artificial and natural obstacles

Walleyes were observed to use a modified Denil-type fishway to get by dams 4.6 m or less in height on the Des Moines River (Harrison, 1948; Harrison and Speaker, 1950).

A spiral-channelled fishway manufactured by the Aeroceanics Fishway Corporation may provide passage over dams for walleyes because no jumping is required to enter it (Biette and Odell, 1975). However, in general, fishways have been found to be an impractical means of moving walleyes past obstacles (R. Ryder, pers. comm.).

6.2.5 Fish screens

No information available to the authors.

6.2.6 Improvement of spawning grounds

Artificial spawning beds have been constructed in a number of midwestern states (at least six) and generally consist of coarse gravel and rubble deposits in shallow waters (Klingbiel, 1969; Yeager and Weber, 1972). Adults in Lonetree Reservoir, Colorado were observed to utilize two newly constructed artificial spawning beds (consisting of rock and gravel (<203 mm) covering an area of 15.2 x 30.5 m) to the same degree as the natural beds. Although these new beds increased the spawning area of the lake by only 17 percent, they resulted in a two to ten fold increase in the number of YOY walleyes (Weber and Imler, 1974). In Minnesota, marginal spawning ground improvement usually consists of placing gravel (Johnson, 1961) or rocks (golf-ball to baseball size) (Swenson, 1965; Newburg, 1975) in selected shallow areas; this has been shown to substantially increase reproduction. However Bredemus (1962) felt that because successful reproduction in Escanaba Lake, Wisconsin was dependent upon water circulation among the rocks or in flooded marsh grass, spawning ground improvement could not be easily accomplished.

6.2.7 Habitat improvement

Walleyes congregated under oak log cribs (2.4 x 2.4 x 1.5 m) constructed with galvanized wire and staples securing the corners, small poles placed across the bottom tier of logs and oak brush packed loosely inside the log framework (Krueger, 1969).

6.3 Control or alteration of chemical features of the environment

6.3.1 Water pollution control

No information available to the authors.

6.3.2 Salinity control

No information available to the authors.

6.3.3 Artificial fertilization of waters

See section 7.5.

6.4 Control or alteration of the biological features of the environment

6.4.1 Control of aquatic vegetation

No information available to the authors.

6.4.2 Introduction of fish foods

Significant increases in growth rate have been observed among fingerlings in rearing ponds following the introduction of forage fishes (see section 7.6).

6.4.3 Control of parasites and disease

No information available to the authors.

6.4.4 Control of predation and competition

Rough fish removal programmes have often been attempted in hopes of increasing walleye populations by reducing competition. Ricker and Gottschalk (1941) reported that following the removal of rough fish (carp, quillback, buffalo fish, suckers, longnose and shortnose gar pike) from Bass Lake, Indiana, gamefish populations (including walleye) showed a large increase. Seining catches of walleyes in East Okoboji Lake, Iowa, increased slightly during 12 years of rough fish (bigmouth buffalo fish, carp, fresh water drum) removal (Rose and Moen, 1953). Johnson (1977) observed competition for aquatic insects (e.g., burrowing mayflies) between suckers and other fish species inhabiting Wilson Lake, Minnesota. He found that following an intensive sucker removal programme in this lake, the walleye population increased in numbers and biomass, accompanied by an increase in angling yield and C.U.E. However, Wilson Lake contains a relatively simple fish community (walleyes and suckers comprise 90 percent of it by number) and in a more complex system, such a perturbation may not benefit the walleye population to such an extent. It should be noted that the removal of 34 percent of the adult sucker population in Many Point Lake, Minnesota, was not considered successful in reducing interspecific competition (Olson, 1963).

Similarly, 12 years of intensive fresh water drum removed on Lake Winnebago, Wisconsin, resulted only in a slight increase in walleye numbers (Priegel, 1971).

Attempts have also been made to increase walleye vulnerability to angling through species removal or introduction. Moyle (1949) reported that fishing for walleyes went from poor in 1947 to good in 1948 following yellow perch removal in three Minnesota lakes. However, the removal of 54.1 kg/ha of yellow perch from Grace Lake, Minnesota, failed to improve walleye angling success (Wesloh and Olson, 1962). On the other hand, when northern pike were stocked in this lake, possibly creating added competition for forage (perch), an apparent increase in walleye angling vulnerability occurred (Wesloh and Olson, 1962). Unfortunately, negative results from these projects are rarely analysed carefully and reported. Consequently, the literature tends to be overly optimistic (J.C. Schneider, pers. comm.).

6.4.5 Population manipulation

Walleye populations have been manipulated through exploitation, habitat modification and species introductions, but to our knowledge, no experiments have been designed to study walleye population dynamics. Johnson (1977) observed an increase of about one third in the walleye standing crop following white sucker removal (section 3.3.3). Walleyes were introduced into Escanaba Lake, Wisconsin, and their harvest monitored for 27 years (section 4.5). Ward and Clayton (1975) introduced fry possessing a distinctive biological mark into a natural population for the purpose of monitoring the interaction between native and planted walleyes.

6.5 Artificial stocking

6.5.1 Maintenance stocking

Maintenance stocking - i.e., continuous plantings of walleyes in lakes in which no natural reproduction occurs, has provided good angling returns in a number of lakes (Groebner, 1960; Schneider, 1969). More commonly, walleye fry and fingerling plantings are made to supplement naturally reproducing populations with hopes of improving the sport fishery. For most lakes which contain good reproducing populations and into which walleye have been planted, no correlation could be found between plantings and year class abundance (Hile, 1937; Carlander and Hiner, 1943 in Carlander, 1950; Carlander, 1945; Cleary and Mayhew, 1961; Mraz, 1962, 1968; Erickson and Stevenson, 1967a; Kempinger and Churchill, 1972) or angling success (Larson, 1961a; Olson and Wesloh, 1962). However, some lakes with natural reproducing populations have shown a positive correlation between stocking and year class abundance (Carlander et al., 1960; Kempinger, 1968; Ward and Clayton, 1975). Futhermore, Schneider (1969) citing Bailey and Oliver (1939), Threinen (1955), Rose (1955), Scidmore (1957), Carlander et al. (1960), Mayhew (1960) and Olson and Wesloh (1962) states that the fisheries in some lakes with natural reproducing populations can be measurably improved but only at high stocking densities (37-168 fingerlings/ha or 12 350-24 700 fry/ha). Stocking of walleyes smaller than 76 mm in waters where established populations exist has generally met with little success (Klingbiel, 1969), although introductions of newly hatched walleye fry in the spring significantly supplemented natural reproduction in West Blue Lake, Manitoba (Ward and Clayton, 1975). Supplementary stocking in lakes where natural reproduction is limited has resulted in significant increases in population size (Kleinert, 1967; Johnson, 1971a). This effect was most evident in years when at least 3 000 fry/ha were stocked (Carlander and Payne, 1977). However, in general, relatively few walleye maintenance plantings have been truly successful.

In a review of walleye stocking success, Schneider (1969) states that the survival rate of planted walleye fingerlings to catchable size appears to be about 10 percent between the stocking rates of 37 and 408 fingerlings/ha. Such success, however, can only be expected under the best of conditions (J.C. Schneider, pers. comm.). Stocking of fingerlings in Wisconsin waters suggests survival rates ranging from 0 to 14 percent (Wisc. Fish.Manage.Bur., 1968). An important factor influencing the success of fingerlings stocking is the size relationship between stocked fingerlings and other fish present in the lake (Johnson, 1971a). Not only must they often times compete with native fry but if they are stocked at a size too small to utilize forage fishes, they may have to compete with a variety of species for invertebrates upon which they would be forced to feed. It has been noted that successful year classes of walleyes resulted from stocking of walleye fry after gizzard shad, a primary prey species, had spawned (Jester, 1972; Momot, Erickson and Stevenson, 1977). Beyerle (1978) has indicated that the survival and growth of walleyes stocked as fingerlings is greater in lakes containing minnow forage than it is for those containing blue gills. Handling loss is probably also an important factor in stocking success. Johnson (1971a) states that walleye of all sizes are difficult to handle and hold when the water temperature is above 18.3°C.

Work by Mraz (1968) indicated that stocked fingerlings mixed thoroughly with native fingerlings and yearlings in Pike Lake, Wisconsin.

6.5.2 Transplantation, introduction

Walleye introductions into natural lakes have established some reproducing populations (Kempinger, 1963; Schneider, 1969). Introductions into reservoirs have met with varied success. Availability of suitable spawning sites will determine reproductive success of walleye in these sites (Machniak, 1975). Erickson and Stevenson (1967a) citing Clarence Clark (unpublished manuscript) stated that of 97 Ohio reservoirs stocked with walleyes, only 23 developed reproducing populations (e.g., Berlin Reservoir, Addis, 1966). Introductions into five California reservoirs has established small to moderate fisheries but no reproducing populations (Goodson, 1966). Illegal introduction of walleye into Roosevelt Lake, Washington has resulted in the establishment of a substantial reproducing population in that lake and the distribution of this species throughout the Columbia River below Coulee Dam and up into the Snake River system (Nielsen, 1975). Walleyes introduced into southeastern U.S. reservoirs contributed substantially to the fishery only in those reservoirs where they occurred naturally (Parsons, 1958). In Tennessee reservoirs where walleye fisheries declined, self-sustaining populations have been restored through the stocking of northern strains, although trophy fish are no longer taken (Hackney and Holbrook, 1978). Plantings in the Nee Granda Reservoir, Colorado, have established a reproducing population (Lynch, 1955) while stocking of Elk City Reservoir, Kansas, has produced a fishable population in acceptable numbers (Hartmann, 1968). Furthermore, Bailey and Allum (1962) stated that introductions into reservoirs in South Dakota have been successful (e.g., Angostura, Belle Fourche, Shadehill Reservoirs) and sometimes spectacularly so. Such success was probably due to the favourable light (high turbidity) and temperature regimes in these reservoirs. In Texas, a stocking evaluation study on 17 reservoirs elucidated three parameters responsible for the success or failure in establishing walleye populations by the introduction of fry and/or fingerlings: (1) the water temperature during their spawning time; (2) the amount of potential walleye spawning area; and (3) the standing crop of potential predators (Prentice, 1977). Furthermore, it permitted them to establish the following stocking criteria: (1) stocking density - 50 fingerlings/ha and 1 000 fry/ha; and (2) spawning habitat - ratio of spawning habitat area to surface area .001.

Introductions of walleyes into lakes with stunted panfish or perch populations in hopes of increasing the growth rate by augmenting predator pressure has also met with limited success. When 11 Wisconsin lakes, containing stunted panfish populations, were stocked with 121-637 fingerlings/ha, signigicant survival of the stocked fish occurred in only one lake (Klingbiel, 1969). Stocking of Clear Lake, Wisconsin, did not increase the growth rate of bluegills (Snow, 1968). However, introduction of walleyes into Sterling and Jackson Reservoirs, Colorado, has provided enough predation to reduce the numbers of stunted yellow perch and increase their growth rates (Taliaferro, 1959). Ten years after walleye fry were introduced into Lake Gogebic, Michigan, whose fish community was dominated by centrarchids, walleye numbers had dramatically increased while centrarchids had drastically decreased in number (Eschmeyer, 1950). With introduction of walleyes into Escanaba Lake, Wisconsin, a similar decrease in smallmouth bass numbers was noted (Kempinger <u>et al.</u>, 1975).

Three years after fry were introduced into saline (15 000 ppm) Redberry Lake, Saskatchewan, nettings revealed that survivors of the plant were thriving, although no reproduction was occurring (Rawson, 1946).

Introduction of adult walleyes into new lakes has been a fairly successful management technique in northern Ontario: 11 successful, 2 unsuccessful and 5 uncertain (C.A. Elsey and R. Hamilton, pers. comm.).

An overview of walleye stocking success can be obtained from Laarman's (1978) summary in which 125 bodies of water (inland lakes, impoundments and the Great Lakes) during the last hundred years were reviewed. He separated the lakes into three stocking categories and estimated the percent success for each: (1) 48 percent success for introductory plants where walleye were absent; (2) 32 percent success for maintenance plants where natural reproduction was absent or limited; and (3) 5 percent success for supplemental plants where efforts were made to augment natural reproducing walleye populations. Laarman stated that success or failure of walleye stocking appeared to depend more on the environmental and biological conditions of individual bodies of water than on the number and size of walleye that were stocked.

7 POND FISH CULTURE

7.1 Procurement of stocks

Spawn is usually collected from spawning walleyes trap-netted in a selected lake or river located close to the hatchery in which the eggs will be incubated. Fish culturists have recognized that the best spawn-taking temperatures for walleyes run from 7.2 to 10.0 °C (Cobb, 1923).

7.2 Genetic selection of stocks

Little research has been done in this area. Bandow (1975) selected relatively fast-growing juveniles from rearing ponds and compared the growth rates of their offspring with those of regular broodstocks over two years. In neither year did the experimental fish display an inherent capacity for rapid juvenile growth. The introduction of geographically different stocks into new waters has met with some success. Northern stocks have been used to sustain otherwise dwindling walleye populations in Tennessee Reservoirs (Hackney and Holbrook, 1978).

7.3 Spawning (artificial; induced; natural)

Fertilization of eggs is usually carried out at the time and place the broodstock is captured. The eggs are either placed in a dry, shallow tray, to which milt is added (dry method) or are placed in a tray and mixed with water before the milt is added (wet method). Experiments by Olson (1971) suggested that maximum or near maximum fertilization is attained through the latter method.

The fertilization process is often facilitated by the gentle mixing of the spawn, usually with a large feather, as walleye eggs are very delicate and rupture easily. One problem with walleye eggs is their tendency to clump together during their water-hardening period. To reduce clumping, a fine clay, starch or ground bone charcoal suspension is often added to the eggs (termed "mucking" or "mudding") which adheres to the egg membrane and reduces their adhesiveness. This process has been used fairly successfully since the late 1800s (see Nevin, 1887). Recent work on the use of tannic acid to reduce adhesiveness has revealed that not only is clumping eliminated but mortality may actually be less among treated eggs than among untreated ones. Dumas and Brand (1972) observed that when fertilized eggs were placed in a tannic acid solution (one teaspoon to 3.8 l) until water-hardened, no clumping or adhesion to the container surfaces occurred. Furthermore, mortality was no greater than among untreated eggs. Similarly, when eggs were rinsed for one to two minutes in a 130 mg/l tannic acid solution, the eggs water-hardened normally, did not clump, and actually had a higher percentage of eyed-up eggs and a higher percentage hatch than did untreated control eggs (Clark, 1974). However, Waltemyer (1975) found that spermatazoa motility was abruptly reduced when exposed to tannin solutions greater than 25 mg/l which could affect fertilization capacity. Thus he recommended that tannin solutions be added to the fertilized eggs after the first rinse to allow for proper fertilization.

The majority of the water-hardening process is completed in one to two hours; nevertheless some practitioners spread the eggs out on elongated trays covered with stretched, fine linen and leave them for 8-10 h (Huet, 1970).

After water-hardening treatment the eggs are carefully rinsed and placed in incubating jars. The jars generally used now are plastic with round bottoms which are more effective in reducing clumping than glass jars (W.J. Scidmore, pers. comm.). Because the eggs are fragile, jars are only filled one-fifth to one-quarter full with eggs, which are kept slowly moving during incubation (Huet, 1970). However, in Ontario, incubating jars are filled with eggs to about three quarters full (C.A. Armstrong, pers. comm.). Hatching success among upper American midwest hatcheries generally ranges from 55 to 70 percent (Klingbiel, 1969) while Huet (1970) gives the average range to be 75 to 80 percent for walleye hatcheries in general. From two batches of hatchery-reared eggs, Hurley (1972) observed the fertilization success to average 65 and 85 percent; the average percentage hatch from fertilized eggs ranges from 72 to 53 percent and from eyed-eggs to hatching from 77 to 56 percent. Schrader and Schrader, 1922) believed about half of the observed egg mortalities resulted from abnormalities within the eggs (observed in about 25 to 30 percent of eggs at the 29-hour stage) which lead either to malformation or death. However, Olson (1971) concluded that observed low percentage fertilization rates were due to operational procedures rather than defective eggs or sperm. Eggs from older females (>533 mm) generally demonstrated a higher fertilization rate (>50 percent) than those from young (<406 mm) females (<20 percent) taken from Berlin Reservoir, Ohio (Erickson and Stevenson, 1967b). Similarly, eggs taken from larger fish at Little Cutfoot Sioux Lake, Minnesota, tended to have a higher survival rate to the eyed stage than did eggs from smaller females (Johnson, 1960). Furthermore, eggs taken from all size-groups late in the run tended to have a higher survival rate to the eyed stage than those taken early in the run, which may be a reflection of the gradual increase in water temperatures during the run (W.J. Scidmore, pers. comm.). Forcibly stripping eggs may reduce their fertilization success (Erickson and Stevenson, 1967b).

7.4 Holding of stock

Often during spawn-taking operations near-ripe males and females will be kept in pens or holding tanks until they ripen and spawn can be taken. Schrader and Schrader (1922) felt that the practice of holding spawning stock to allow ripening may have resulted in the abnormalities which they observed among 25-30 percent of incubating eggs procured in this manner (at the 29-h stage of development). Furthermore Butler (1937) observed a 75-80 percent hatch among eggs taken from fish ready to spawn, while a somewhat lower hatch success (>50 percent) was observed among eggs taken from fish held in retainers prior to spawn-taking.

7.5 Pond management (fertilization, aquatic plant control, etc.)

After hatching, fry are usually stocked directly into open waters or placed in small rearing ponds, either natural or artificial, where they are raised to a larger size before stocking.

Although more work is needed to improve walleye pond culturing techniques, investigations to date (mainly in Minnesota rearing ponds) have established a number of pond management practices which have proven to reduce fry mortality and increase yields. Fertilization of drainable ponds (prior to filling) with such organic fertilizers as sheep and barnyard manure, alfalfa hay and soybean meal improves zooplankton production during the spring and early summer which provides the walleye fry with an abundant early food supply (Smith and Moyle, 1945; Wistrom, 1957; Martin, 1959; Dobie, 1966b; Cheshire and Steele, 1972). Such fertilizations have resulted in large increases in production. The average production of 31 unfertilized ponds in Minnesota (Smith and Moyle, 1945) was 8.4 kg/ha (751 fingerlings/ha) while that of 24 fertilized ponds (sheep and barnyard manures) was 46.7 kg/ha (6 876 fingerlings/ha). Further investigations revealed that when the rate of fertilization was based on the fertility of the water, production was spotty; but when based on soil fertility, production was observed to increase 194 percent (Dobie, 1956). Those ponds whose soil content contained less than 4 percent organic matter were generally consistent in producing few fish (Dobie, 1956; 1966b) while those ponds whose bottom soil contained 4 percent or higher organic matter generally produced enough food to satisfy normal production (Dobie, 1958, 1966b).

Cannibalism is a major source of fry loss in walleye rearing ponds (Smith and Moyle, 1945; Dobie, 1956; Cheshire and Steele, 1972). In ponds containing adequate zooplankton populations losses from cannibalism are not significant until the early summer when zooplankton levels drop and fry pursue larger food organisms. After this period fry numbers decline (often drastically) as food (usually insects) becomes scarce and larger fry are forced to feed on the smaller. Cheshire and Steele (1963a) observed this to commence when fry reached a length of 30-35 mm. Evidence that cannibalism is present often manifests itself in the development of two distinct size classes (Scott, Omand and Lawler, 1951; Cheshire and Steele, 1963a, 1967; Klingbiel, 1969; Bandow, 1975). The average lengths of the two size groups observed in Silver Lake, Ontario, were 102 and 216 mm, when harvested in early September (Scott, Omand and Lawler, 1951). Smith and Moyle (1945) stated that the two best methods of controlling cannibalism and increasing yield in Minnesota ponds are heavy fertilization and the introduction of non-predacious forage fish. Periodic cropping will also lessen cannibalism by reducing competition. Cuff (1977) found walleye less than 20 days old are more likely to cannibalize than older prolarva irrespective of the presence of alternate food. The amount of cannibalism depended on the relative abundance of starving walleyes. He concluded that to eliminate cannibalism the fish culturist apparently needs only to provide sufficient food. Klingbiel (1969) suggested an early harvest so that the smaller size groups could be restocked in different ponds to be harvested later at their optimum size.

Attempts to increase the growth rate and survival of fry in ponds through the introduction of forage fishes has largely been successful. Minnesota ponds stocked with sucker fry produced six times the yield of ponds in which no forage was introduced, while those stocked with bluntnose and fathead minnows produced 12 times as much (Smith and Moyle, 1945). Bandow (1975) also found the introduction of fathead minnows to greatly enhance the growth of walleye fingerlings. When sunfish, crayfish, and minnows were provided as forage in separate ponds, production was greatest in those ponds containing minnows, followed by crayfish and sunfish (Schneider, 1975). However, ponds containing large numbers of minnows plus small numbers of sunfish were the best producers, as food of proper size was always available. It is essential that forage fry be stocked several weeks after the introduction of walleye fry (Smith and Moyle, 1945). When sucker fry were introduced at the same time as walleye fry in some Wisconsin ponds, the suckers grew too large too quickly to be eaten by the walleye and actually competed with the walleye for food, causing a reduction in production (Wistrom, 1957).

In most areas, the cost of transporting minnows to walleye ponds, as forage, outweighs the benefits gained (Bandow, 1975). Attempts to establish minnow populations in walleye ponds containing a sizeable walleye fingerling population have failed (Bandow, 1975). It has been suggested, however, that transporting walleye fingerlings to ponds in which sizeable minnow populations have already been established may be an alternative (Bandow, 1975). Smith and Moyle (1945) observed that such attempts in some Minnesota ponds failed or resulted in low yields. Attempts to provide insect forage by introducing the eggs of the burrowing mayfly, *Hexagenia bilineata*, into rearing ponds had limited success (Bandow, 1975).

Predation on fry by aquatic insects such as dytiscids, belostomatids and notonectids can be an important source of mortality (Smith and Moyle, 1945; Dobie, 1956; Cheshire and Steele, 1963a; Campbell, 1975) and are usually controlled by the application of kerosene to the pond surface before and just after fry stocking (Dobie, 1956, 1958; Martin, 1959). Predation by an unusually large population of hydra in Diamond Lake, Iowa (a walleye nursery lake) was believed responsible for the observed drastic reduction in numbers of fry after aquarium tests revealed that fry 8 mm in length were very vulnerable to hydra nematocysts (Moen, 1951).

Pond production can be further enhanced by controlling the growth of aquatic vegetation (Dobie, 1956; Campbell, 1975). Algal blooms (usually the result of overfertilization) may be particularly devastating by causing summerkill (Dobie, 1956, 1966b). Such blooms are usually controlled by the application of copper sulphate (Dobie, 1956; Martin, 1959). In addition, strains of *Cyanophyta* can produce toxic substances that are capable of causing severe losses of fry (Campbell, 1975).

To summarize the effects of various management practices on Minnesota pond production, Dobie (1956) states that when nearly all occurrences of loss from starvation and cannibalism were eliminated or greatly reduced, fish production increased 127 percent by numbers. Furthermore, when losses from summerkill were nearly eliminated by controlling the algae with copper sulphate and the losses from insect predation were eliminated by killing the insects before fry stocking, production was increased another 30 percent.

7.6 Foods; feeding

In general, attempts to raise walleye fry on artificial diets have met with limited success (Cheshire, 1966; Cheshire and Steele, 1967; Nagel, 1973; Beyerle, 1974a, 1975; Trandahl, 1974; Bandow, 1975; Linkous, 1975). Diets tested include W-3, 4, 5, 6 and 7 Spearfish Diet, Oregon Moist Pellets, Pr-6 trout granules, liver slurry, pelleted Atlantic salmon diet, egg yolk, an egg yolk and Farina slurry, and ground beef-liver - the majority of which have been accepted only to some degree, at best, by walleye fry. When prepared diets were used exclusively, mortality was usually very high (>80 percent) with only a small percentage learning to accept the food and thrive. The main problem is the length of time necessary to condition the fry to accept the food. This may require a period of from 10 to 49 days (Cheshire, 1966; Cheshire and Steele, 1968; Beyerle, 1974a; Calbert, Stuiber and Huh, 1974b) during which time starvation and cannibalism drastically reduce numbers. However, the length of this conditioning period has been reduced by introducing zooplankton (usually daphnids) prior to or at the same time as the artificial diet (Beyerle, 1974a; Calbert, Stuiber ahd Huh, 1974b; Phillips, 1974).

Attempts to feed young fry in hatcheries exclusively on live zooplankton were generally unsuccessful. Varying fry density (0.7-82.6 fry/l) and rearing temperature (10-20°C) did not improve poor survival rates (Olson, 1974). Few sac-fry would feed on infusoria (*Paramecium* sp. and *Stylonychia* sp.) introduced to their aquaria while 75 percent would feed at one time or another on newly-hatched brine shrimp (Beyerle, 1974b). Linkous (1975) found that although fry fed readily on brine shrimp, it proved unsuccessful as a long-term diet.

Recent work by Calbert, Stuiber and Huh (1974a, 1974b), studying the feasibility of raising walleyes to marketable sizes, has shown some promising results. By introducing daphnia at the same time as W-3 prepared diet, walleye fry (average length 67 mm) were conditioned to accept the prepared diet within two weeks, resulting in a first year mortality rate of only 30 percent (due primarily to mechanical handling). They found the optimum conditions for most rapid growth (over a 42 week period) to include (Fig. 36) a feeding rate of 3 percent wet body weight per day (test rates of 3, 5 and 7 percent), a 16 h light period and a water temperature of 22°C (test temperatures of 18, 22 and 26°C). Huh (1976) suggested that fingerlings of 15 g or smaller should be fed at least four times a day under these conditions. Calbert, Stuiber and Huh have been successful in raising walleye to a length of 406-457 mm, weighing 0.3 kg (2 year old fish) (Stuiber, pers. comm.). These trials indicate that raising walleye for commercial production may be economically feasible (Calbert, Stuiber and Huh, 1974b; Graves, 1974).

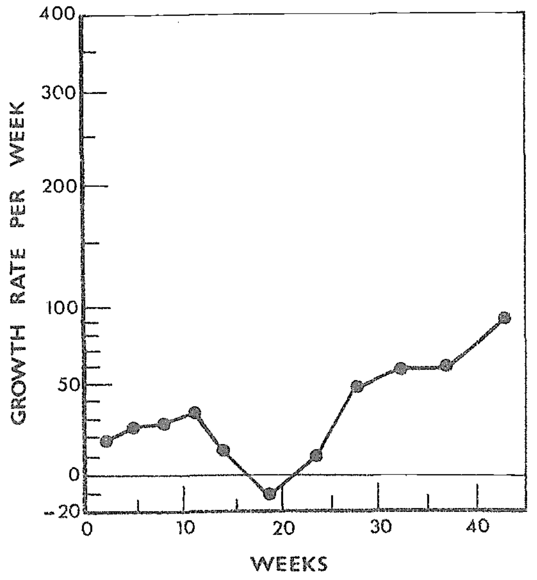

Fig. 36 Growth rate of fingerlings (as percentage weight per week) fed on an artificial diet over a 42 week period (after Calbert, Stuiber and Huh, 1974a)

Nickum (1978) reports that through intensive culture techniques, walleye fingerlings fed on W-7 dry diet have been successfully reared (survival, 60 percent) to lengths of 100-125 mm over a 10-15 week interval (water temperatures in rearing ponds fixed at 20-22°C and exchanges 2 times per hour). Post walleye fingerlings have also been reared successfully under similar (intensive) culture conditions. Reports of this nature tend to demonstrate the technical feasibility of intensive culture. However, Nickum (1978) suggests that further refinements in diet, disease control and rearing units are necessary before intensive culture can be considered economical. It is of interest to note that the intestinal tracts of these prepared-diet fish were less well-developed (thinner-walled) than those of wild fish (Calbert, Stuiber and Huh, 1974b). Also, they suggest that the stomachs of such fish can be punctured by fish spines and subsequently they may not survive if stocked directly into the wild in this condition.

During the spring and early summer, pond-reared fry feed on zooplankton (rotifers, copepods and cladocerans), gradually switching to a predominantly insect diet (Smith and Moyle, 1945; Cheshire and Steele, 1963b; Dobie, 1966b; Campbell, 1975). Rotifers were an important food for pond-reared fry 5-9 mm in length in Minnesota ponds, while copepods were consumed in quantity until the fry reached a length of 60 mm (Smith and Moyle, 1945). When fry cease to feed on zooplankton and seek insects and other larger forage, food becomes scarce. The introduction of forage fishes at this time has often been successful in alleviating this shortage and reducing cannibalism (see section 7.5). A continuous lake water inflow may also serve to supplement the invertebrate food supply in a pond (Bandow, 1975).

7.7 Disease and parasite control

Protozoan infections of *Carchesium* (Anon., 1941) and *Epistylis* (Campbell, 1975) have been reported among hatchery-reared eggs. Only *Carchesium* was observed to cause significant mortality. Fungus infections (usually *Saprolegnia*) are common and may cause high mortalities (see section 3.2.1) although outbreaks have been successfully treated (Table XXVI).

Reported infections among hatchery-reared fry and their treatments are listed in Table XXVI. Large numbers of leeches in two Minnesota rearing ponds (observed attached to many fingerlings) were believed responsible for the failure of these ponds to produce walleye fingerlings (Smith and Moyle, 1945).

7.8 Harvest

The mean and median yields of 64 Minnesota rearing ponds over a four-year period (1940-1943)

TABLE XXVI

Infections reported among hatchery-reared eggs and fry and some effective treatments

Infection	Effective treatment	Authority
1. Eggs		
Protozoan		
Carchesium		Anon. (1941)
Epistylis		Campbell (1975)
Fungal	three separate treatments of	
Saprolegnia	malachite green oxalate (2.1 g/l)	Cummins (1954)
unidentified	malachite green	Klingbiel (1969)
2. Fry and Fingerlings		
Protozoan		
Trichodina davisi; Costia	30 min flow treatment with potassium	Campbell (1975)
Schyphidia; Trichodina	permanganate solution (5 mgl^{-1})	Sanderson (1974)
Bacterial		
Columnaris	Diquat at 16 mgl^{-1}	Hnath (1975)
fin rot	acriflavine (5 mgl^{-1}) for 1 h	Hnath (1975)
bacterial gill disease	Roccal (2 mgl^{-1}) for 1 h (must be rinsed well); Hyamine 3500 (2 mgl^{-1}) active	Hnath (1975)
fin rot; bacterial gill disease	copper sulphate	Bean (1975)
unidentified	formalin (1:6 000); Roccal (2 mgl^{-1})	Nagel (1973)
unidentified	acriflavin 2 mgl^{-1}	Trandahl (1974)
Fungal		
unidentified	formalin (1:6 000); Roccal (2 mgl^{-1})	Nagel (1973)

were 54.2 and 32.8 kg/ha respectively, with the highest single yield being 262.1 kg/ha (2 470 fingerlings/ha) in one fertilized pond (Smith and Moyle, 1945). Klingbiel (1969) felt that 56.0 kg/ha was a good seasonal yield among Wisconsin ponds (Table XXVII). Because of their nature, drainable ponds can be more intensively managed and produce more consistently than natural ponds. Both survival and harvest are extremely variable in natural ponds (Klingbiel, 1969). However, Minnesota fish managers prefer to raise fingerlings in natural ponds where growth is faster due to the abundance of natural forage throughout the summer (Daley, 1975).

Fertilization of ponds prior to stocking and introduction of forage fishes afterwards are two of the most important management practices in maximizing pond production (see section 7.5). Smith and Moyle (1945) found that fertilized ponds produced nearly six times the weight of walleye as unfertilized ponds while ponds stocked with forage produced up to twelve times the weight as those in which no forage was introduced.

Time of harvest is also important in determining what weight and quantity a pond will produce. In general, a trade-off occurs between the size and numbers of fingerlings, depending on the time of harvest (Figs. 37, 38 and 39) - i.e., the longer the fingerlings remain in the ponds, the larger but fewer they become (Scott, Omand and Lawler, 1951; Smith and Moyle, 1945; Dobie, 1958; Cheshire and Steele, 1972; Campbell, 1975). By comparing the yields and time of harvest for 66 Minnesota ponds, Smith and Moyle (1945) observed that the highest yields (by weight) were obtained when fingerlings were harvested at a size of 110-174 fingerlings/kg (usually at a length of 76-89 mm). Huet (1970) states that the production goal of young fingerlings is fish 70-100 mm in length at a size of 125-143/kg.

The relationship between yield and other investigated factors is not so clear. No correlation was found between pond size and yield among 66 rearing ponds (natural and drainable) in Minnesota (Smith and Moyle, 1945). When only

TABLE XXVII

Average seasonal production (ranges in parentheses) of walleye fingerlings from selected ponds and groups of ponds

Location	Area (ha)	Comments	Number of fry stocked/ha	Size at harvest (no./kg)	Yield		Survival (%)
					kg/ha	Number of fingerlings/ha	
31 Minnesota rearing ponds[a]		four year average (1940-1943); unfertilized			8.4 (0-99.9)	743 (0-13 200)	
24 Minnesota rearing ponds[a]		four year average (1940-1943); fertilized with sheep and barnyard manures			46.7	6 876	
17 Minnesota rearing ponds[a]		four year average (1940-1943); stocked with sucker fry after walleye introduction	108 680 (4 940-1 976 000)		49.4 (2.6-195.4)	3 597 (82-8 892)	
5 Minnesota rearing ponds[a]		four year average (1940-1943); stocked with fathead and bluntnose minnows after walleye introduction			107.6 (2.2-197.6)	11 001 (143-21 711)	
8 Minnesota rearing ponds[a]		four year average (1940-1943); fertilized with sheep and barnyard manure followed by stocking with sucker fry			21.2	8 936	
4 Minnesota rearing ponds[a]		four year average (1940-1943); fertilized with sheep and barnyard manure followed by stocking with minnows			98.0	22 544	
48 drainable Minnesota rearing ponds[b]	8.6 (2-21.6)	most fertilized with commercial fertilizer, sheep manure, barnyard manure or any combination of the above; most cropped several times during season	118 903 (52 685-279 604)	818 at midsummer (264-2 860) (26-924) at autumn	44.7 (0.3-136)	23 280 (321-94 156)	19.2 (0.4-66.1)
24 drainable Minnesota rearing ponds[c]	18.7	five year average (1970-1974)	49 235	625	11.2	6 989	14.2
49 natural Minnesota state production rearing ponds[c]	39.8	five year average (1970-1974)	9 710	73	4.7	138	3.5
107 natural Minnesota cooperative rearing ponds[c]	3.6	five year average (1970-1974)	38 962	114	58.4	2 952	7.6

TABLE XXVII continued

Location	Area (ha)	Comments	Number of fry stocked/ha	Size at harvest (no./kg)	Yield		Survival (%)
					kg/ha	Number of fingerlings/ha	
34 natural Wisconsin rearing ponds[d/]		one year average (1968) cropping (by seine) began in mid-July and was completed by October			47.0		7.8
23 drainable Wisconsin rearing ponds[d/]		five year average (excluding one year of poor harvest)	185 325		129.4		83
Pond No. 29 Kentucky[e/]	0.4	one year average (1958); fertilized with hay, soybean meal and inorganic fertilizer; harvested 34 days after stocking	(109 778-197 600)	1 936 on 11 June	27.0	52 500	
Pond No. 30 Kentucky[e/]	0.4	one year average (1958) fertilized with hay, soybean meal and inorganic fertilizer; harvested 28 days after stocking	(54 889-109 778)	1 602 on 3 June	16.1	25 523	

a/ Smith and Moyle (1945)
b/ Miller (1952)
c/ Daley (1975)
d/ Klingbiel (1969)
e/ Martin (1959)

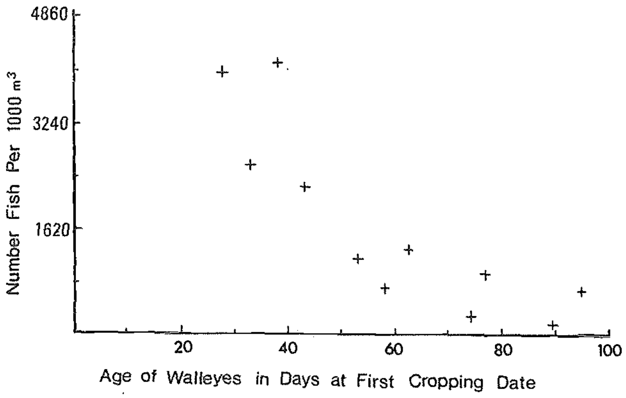

Fig. 37 Relationship between size and age of walleyes at harvest time in Minnesota drainable walleye ponds (after Dobie, 1958)

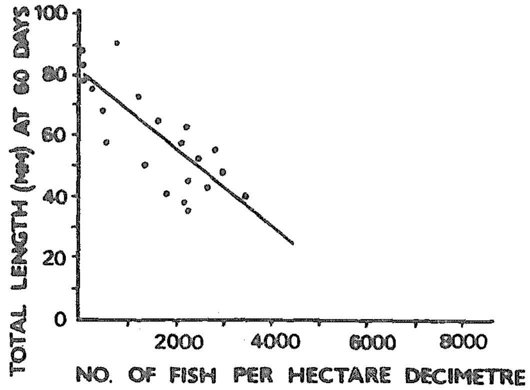

Fig. 38 Walleye fingerling growth and population size in Minnesota rearing ponds, 1953-1958 (Redrawn from Dobie, 1969)

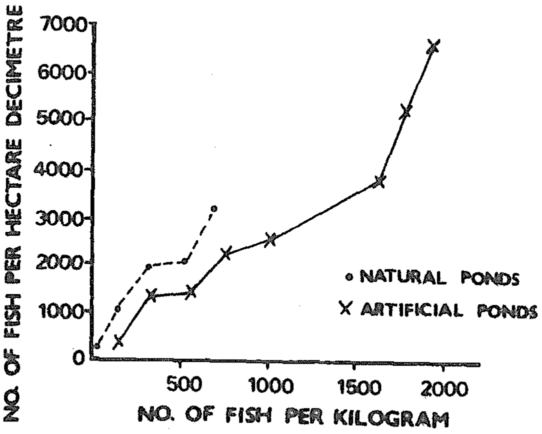

Fig. 39 Population density and size of fish in walleye rearing ponds (Redrawn from Dobie, 1969)

drainable ponds were examined, no correlation could again be found (Miller, 1952). However, yield data for Minnesota's natural rearing ponds shows that small cooperative ponds (average size 3.6 ha) consistently produced nearly five times the yield of large (average size - 39.8 ha) cooperative ponds each year from 1970 to 1974 (Daley, 1975). A stocking rate of 24 700 fry/ha (test rates - 24 700, 49 400 and 74 100/ha) may be the maximum for providing predictably satisfactory yield on an annual basis in ponds with poor invertebrate food production (Bandow, 1975). No relation between stocking rates and yield was observed in drainable Minnesota ponds within a range of 52 685 and 279 604 fry/ha (Miller, 1952). Huet (1970) states that a stocking rate of between 25 000 and 40 000 fry/ha is sufficient for acceptable pond production.

A study by Olson (1968) indicated that walleye fingerlings reared in ponds often show a preponderance of males, either due to selective sex mortality or sex reversal; but they were unable to establish a causal mechanism.

Walleye rearing ponds are usually harvested commencing in June (when zooplankton levels drop) and at regular intervals thereafter on into the autumn. This method, as opposed to a single harvest, allows for maximum (by weight) yield (Dobie, 1956; Klingbiel, 1969) by reducing competition and increasing growth rates among the remaining fry. Harvesting of both natural and drainable ponds is usually accomplished by seining. Drainable ponds are usually drained gradually as the ponds are repeatedly cropped (Klingbiel, 1969). Daley (1975) reports that in small, natural ponds in Minnesota, 6.4 or 12.7 mm mesh trap nets are used in addition to seines, while in larger natural ponds, trap nets are used almost exclusively.

7.9 Transport

Transporting walleye fry in oxygen-filled, polyethylene bags carried in cardboard boxes produced fewest mortalities and is the preferred method of conveyance (Martin, 1959; Clark, 1960; Campbell, 1975). When such containers were used to carry 100 000 fry each (in 1.9 l water), no great losses occurred even when held as long as 12 h (Campbell, 1975).

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APPENDIX 1

Absolute growth rates of the walleye in various waters

Average total length at each annulus (mm)	Big Trout Lake, Ontario Armstrong (1961)	Deer Lake, Ontario Armstrong (1961)	North Caribou Lake, Ontario Armstrong (1961)	Makoop Lake, Ontario Armstrong (1965)	Lake St. Joseph, Ontario ♂ Lewis *et al.* (1964)	Lake St. Joseph, Ontario ♀ Lewis *et al.* (1964)	Lake St. Joseph, Ontario Lewis *et al.* (1964) (comb.)	Sakwaso Lake, Ontario ♂ Lewis *et al.* (1964)	Sakwaso Lake, Ontario ♀ Lewis *et al.* (1964)	Sakwaso Lake, Ontario Lewis *et al.* (1964) (comb.)	Wunnummin Lake, Ontario ♂ Lewis *et al.* (1964)	Wunnummin Lake, Ontario ♀ Lewis *et al.* (1964)	Wunnummin Lake, Ontario Lewis *et al.* (1964) (comb.)	Lac des Mille Lacs, Ontario Elsey and Thompson (1977)	Attawapiskat Lake, Ontario Lewis *et al.* (1964)	Attawapiskat Lake, Ontario ♀ Lewis *et al.* (1964)
1	149	109	109	76	99	94	97	81	86	84	91	102	97		76	84
2	198	117	170	170	165	165	165	168	180	175	155	168	163	232	140	150
3	254	196	216	224	231	229	231	224	229	226	208	226	218	254	191	203
4	330	282	259	267	282	284	284	264	269	267	262	274	267	342	241	254
5	361	312	307	305	333	340	338	307	307	307	307	320	315	378	290	302
6	414	361	315	356	376	386	381	338	343	340	345	361	353	403	335	345
7	455	386	371	394	409	429	419	366	373	371	378	396	386	462	371	381
8	488	445	409	414	442	455	450	394	404	399	406	432	419	518	401	414
9	508	462	432	445	472	470	472	424	434	432	429	432	419	556	424	465
10	602	500	457		511	561	526	452	457	457	457	495	480		462	488
11	538	518	462		531	587	549	480	485	483	470	521	503		472	521
12	589	572	493		599		599				483	546	538			546
13	605		521								498	599	582			589
14	587		574									643	643			572
15												678	678			
16	671		582													
17	589		632													
18	673		607													

continued

APPENDIX 1 continued

Average total length at each annulus (mm)	Attawapiskat Lake, Ontario Lewis et al. (1964) (comb.)	Petownikip Lake, Ontario Lewis et al. (1964) ♂	Petownikip Lake Ontario Lewis et al. (1964) ♀	Petownikip Lake, Ontario Lewis et al. (1964) (comb.)	Sandy Lake, Ontario Lewis et al. (1964) ♂	Sandy Lake, Ontario Lewis et al. (1964) ♀	Sandy Lake, Ontario Lewis et al. (1964) (comb.)	Lac la Ronge, Saskatchewan Rawson (1957) ♂	Lac la Ronge, Saskatchewan Rawson (1957) ♀	Lac la Ronge, Saskatchewan Rawson (1957) (comb.)	Lake of the Woods, Ontario Carlander (1945)	Savanne Lake, Ontario Colby (unpubl.)	Red Lakes, Minnesota Smith and Pycha (1961) ♂	Red Lakes, Minnesota Smith and Pycha (1961) ♀	Many Point Lake, Minnesota Olson (1958)	Milk River, Montana Peters (1964)
1	81	84	84	84	91	89	91	152	152		141	119	140	142	127	130
2	145	178	183	180	185	183	185	203	203	234	203	198	213	211	218	300
3	198	251	254	251	259	262	259	259	259	282	253	267	267	267	310	429
4	249	310	315	312	315	312	315	307	307	328	295	328	310	310	376	561
5	295	356	361	358	363	358	361	355	355	378	326	386	343	345	429	615
6	340	396	399	399	404	399	401	403	401	424	366	437	363	378	470	
7	373	424	427	427	434	424	429	445	453	467	400	485	384	401	508	
8	409	447	455	452	470	457	465	480	499	508	437	523	396	424		
9	457	470	475	472	490	483	488	515	539	538	474	559	409	452		
10	475	475	500	483	518	495	513	549	581	582	498	612				
11	500		518	518				581	619	615	524					
12	546							611	651	645	532					
13	589							640	680	676	566					
14	572										580					
15																
16																
17																
18																

continued

APPENDIX 1 continued

Average total length at each annulus (mm)	Lake Huron - North Channel Payne (1965)	Lake Sakakawea, North Dakota Ragan (1972) ♂	Lake Sakakawea, North Dakota Ragan (1972) ♀	Lake Gogebic, Michigan Eschmeyer (1950) ♂	Lake Gogebic, Michigan Eschmeyer (1950) ♀	Lake Gogebic, Michigan Eschmeyer (1950) (comb.)	Jamestown Reservoir, North Dakota Ragan (1972) ♂	Jamestown Reservoir, North Dakota Ragan (1972) ♀	Spiritwood Lake, North Dakota Ragan (1972) ♂	Spiritwood Lake, North Dakota Ragan (1972) ♀	Rainbow Lake, Montana Peters (1964)	Frenchman Reservoir, Montana Peters (1964)	Hauser Lake, Montana Peters (1964)	Nelson Reservoir, Montana Peters (1964)	Killen Reservoir, Montana (1959) Peters (1964)	Killens Reservoir, Montana (1960) Peters (1964)
1		139	156	112	124	117	170	157	162	169	109	185	168	94	64	79
2	277	218	242	236	236	236	273	260	249	255	236	338	325	193	170	170
3	366	286	323	300	315	307	370	365	325	342	343	401	429	269	287	305
4	427	351	396	353	368	361	439	439	367	406	414	460	526	345	404	406
5	470	424	474	386	414	401	511	529		515	475	450		470		447
6	526	504	545	414	545	437	576	590		570	518			650		
7	564	570	604	429	480	457		661			556					
8	599		671	439	503	478										
9	627			450	518	495										
10	648			457	533	508										
11	620															
12																
13																
14																
15																
16																
17																
18																

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APPENDIX 1 continued

Average total length at each annulus (mm)	Westrope Lake, Montana Peters (1964)	North Green Bay, Lake Michigan Niemuth, Churchill and Wirth (1966) ♂	North Green Bay, Lake Michigan Niemuth, Churchill and Wirth (1966) ♀	South Green Bay, Lake Michigan Niemuth, Churchill and Wirth (1966) ♂	South Green Bay, Lake Michigan Niemuth, Churchill and Wirth (1966) ♀	Pike Lake, Wisconsin ♂ Mraz (1968)	Pike Lake, Wisconsin ♀ Mraz (1968)	Wolf River, Wisconsin ♂ Kmiotek (1952a)	Wolf River, Wisconsin ♀ Kmiotek (1952a)	Wolf River, Wisconsin Kmiotek (1952a) (comb.)	Lake Poygan, Wisconsin Kmiotek (1952a)	Lake Winnebago, Wisconsin Kmiotek (1952a)	Lake Winnebago, Wisconsin Niemuth, Churchill and Wirth (1966) ♂	Lake Winnebago, Wisconsin Niemuth, Churchill and Wirth (1966) ♀	Lake Winnebago, Wisconsin Niemuth, Churchill and Wirth (1966) (comb.)	Lake Winnebago, Wisconsin ♂ Priegel (1969a)
1	109	168	170	226	216	173	178	106	117	111	114	106			155	142
2	231	257	259	333	335	287	292	225	262	244	249	221	272	272		259
3	340	325	328	399	422	358	376	305	344	325	328	301	330	335		323
4	391	383	399	470	500	401	439	351	401	376	378	352	373	437		358
5		437	460	493	559	432	480	384	442	413	415	399				384
6		472	503		617	457	533	406	481	442	452	445				401
7		500	536		691		574	401	571	486	523	467				417
8		630	681		711		630		672	672						434
9		655	709				653									
10		681					701									
11																
12																
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APPENDIX 1 continued

Average total length at each annulus (mm)	Lake Winnebago, Wisconsin ♀ Priegel (1969a)	Lake Puckaway, Wisconsin ♂ Priegel (1966b)	Lake Puckaway, Wisconsin ♀ Priegel (1966b)	Escanaba Lake, Wisconsin Niemuth, Churchill and Wirth (1966) ♂	Escanaba Lake, Wisconsin Niemuth, Churchill and Wirth (1966) ♀	Three Mile Lake, Ontario Slastenenko (1956)	Lake Ripley, Minnesota Niemuth, Churchill and Wirth (1966) ♂	Lake Ripley, Minnesota Niemuth, Churchill and Wirth (1966) ♀	Lake Ripley, Minnesota Niemuth, Churchill and Wirth (1966) (comb.)	Trout Lake, Wisconsin Schloemer and Lorch (1942)	Black Lake, New York Letendre and Schneider (1969) ♂	Oneida Lake, New York Forney (1965) ♂	Oneida Lake, New York Forney (1965) ♀	Scriba Creek, New York Forney (1962a) ♂	Scriba Creek, New York Forney (1962a) ♀	Clear Lake, Iowa Cleary (1949)
1	152	191	198			122			170	135	173	155	160	148	156	150
2	257	323	345	267		183	328	305		246	269	234	241	228	299	277
3	338	394	439	318		236	399	417		348	328	295	307	283	300	368
4	394	432	498	358	404	292	427	460		422	363	340	358	340	365	437
5	439	460	536	386	432	315	437	495		483	389	366	394	366	400	490
6	480	480	569	411	467	366				526	411	389	424	383	426	544
7	511	498	599	434	488	381				551	424	404	447	409	454	599
8	536	516	627			500				566	439					668
9		541	648			622				587	442					686
10										592						704
11																714
12																
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APPENDIX 1 continued

Average total length at each annulus (mm)	Clear Lake, Iowa Carlander and Whitney (1961) ♂	Clear Lake, Iowa Carlander and Whitney (1961) ♀	Clear Lake, Iowa Carlander and Whitney (1961) (comb.)	Saginaw Bay, Michigan Hile (1954) ♂	Saginaw Bay, Michigan Hile (1954) ♀	Lake Erie Scholl (1965) ♂	Lake Erie Scholl (1965) ♀	Lake Erie Scholl (1965) (comb.)	Lake Erie Scholl (1966) ♂	Lake Erie Scholl (1966) ♀	Lake Erie Scholl (1966) (comb.)	Lake Erie Seward (1967) ♂	Lake Erie Seward (1967) ♀	Lake Erie Seward (1967) (comb.)	Lake Erie Seward (1968) ♂	Lake Erie Seward (1968) ♀
1	188	188	178	170	175	203	201	201	208	203	206	201	211	206	201	198
2	300	302	287	272	277	366	277	284	366	338	351	312	348	330	330	366
3	394	404	373	340	351		414	414		417	417	411	460	437	409	455
4	450	483	434	389	406		513	513					566	566		508
5	485	544	480	422	452		566	566								
6	511	572	526	447	490		632	632								
7	571	597	559	465	516											
8			605	480	533											
9			643	495	551											
10			686	516	566											
11			699	518	582											
12			706	526	597											
13				533	610											
14				541	622											
15					635											
16																
17																
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APPENDIX 1 continued

Average total length at each annulus (mm)	Lake Erie Seward (1968) (comb.)	Lake Erie Baker (1969a) ♂	Lake Erie Baker (1969a) ♀	Lake Erie Baker (1969a) (comb.)	Spirit Lake, Iowa Carlander (1948)	Spirit Lake, Iowa Rose (1951)	Mississippi River, Iowa Vasey (1967) ♂	Mississippi River, Iowa Vasey (1967) ♀	Pymatuning Lake, Pennsylvania Miller and Buss (1961)	Conneaut Lake, and French Creek, Penn. Miller and Buss (1961)	West Okoboji Lake, Iowa Carlander (1948)	East Okoboji Lake, Iowa Carlander (1948)	Welsh Lake, Iowa Carlander (1948)	Susquehanna River Dams, Pennsylvania Miller and Buss (1961)	Susquehanna River, Pennsylvania Miller and Buss (1961)	Juniata River, Pensylvania Miller and Buss (1961)
1	201	188	185	188	124	183	157	157	201	163	127	132	137	213	175	213
2	340	335	330	333	224	282	307	300	345	290	234	241	259	327	297	345
3	432	422	333	424	315	366	414	417	442	391	297	327	318	414	452	386
4	528	511	488	500	376	445	467	498	526	447	404	399		493	594	432
5		579		579	429	505	500	549	592	508	404	450		541	671	526
6					470	559		584	640	579	447	493				587
7					503	602		610	678	676	457	556				655
8					546	632		627	706	710	500	605				693
9					589	660		648	732	737						732
10					627	706		665	737							
11					658			681								
12					676											
13																
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continued

APPENDIX 1 continued

Average total length at each annulus (mm)	Allegheny River, Pennsylvania Miller and Buss (1961)	Lake Wallenpaupack, Pennsylvania Miller and Buss (1961)	Kyle Run Dam, Pennsylvania Miller and Buss (1961)	Wrighter's Lake, Pennsylvania Miller and Buss (1961)	Lake Carey, Pennsylvania Miller and Buss (1961)	Des Moines River, Iowa Schmulbach (1959)	Utah Lake, Utah Arnold (1960)	Gasconade River, Missouri Purkett (1958)	Current River, Missouri Fleener (1966) ♂	Current River, Missouri Fleener (1966) ♀	Current River, Missouri Fleener (1966) (comb.)	Claytor Reservoir, Virginia Rosebery (1951)	Cheney Reservoir, Kansas Ray and Coslett (1968)	Kirwin Reservoir, Kansas Schreyer (1967a)	Cedar Bluff Reservoir, Kansas Schreyer (1967b)	Council Grove Reservoir, Kansas Cole and Jones (1969)
1	229	173	168	157	188	213	204	157	201	216	203	206	144	259	251	221
2	366	315	290	264	333	292	353	259	320	358	316	353	324	414	389	328
3	432	447	378	356	429	366	408	386	389	429	394	467	410		472	432
4	526	505	437	429	513	422	463	406	422	508	439	574			516	
5		544		500	508	475	506		462	569	480	648				
6		546		564		516	518		460	622	526	696				
7		564				551			470	660	612	757				
8						572			470	691	648	818				
9						574				704	706					
10											752					
11											759					
12																
13																
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15																
16																
17																
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continued

APPENDIX 1 continued

Average total length at each annulus (mm)	Norris Reservoir, Tennessee Eschmeyer (1940)	Norris Reservoir Tennessee ♂ Stroud (1949a)	Norris Reservoir, Tennessee ♀ Stroud (1949a)	Norris Reservoir, Tennessee Stroud (1949a) (comb.)	Melton Hill Reservoir, Tennessee Fitz (1968)	Canton Reservoir, Oklahoma ♂ Lewis (1970)	Canton Reservoir, Oklahoma ♀ Lewis (1970)	Canton Reservoir, Oklahoma Lewis (1970) (comb.)	Hiwassea Reservoir, North Carolina Stroud (1949b)	Center Hill Reservoir, Tennessee ♂ Muench (1966)	Center Hill Reservoir, Tennessee ♀ Muench (1966)	Center Hill Reservoir, Tennessee Muench (1966) (comb.)	Tombigbee River, Mississippi Schultz (1971)	Fort Phantom Hill Reservoir, Texas ♂ Prentice (1977)	Fort Phantom Hill Reservoir, Texas ♀ Prentice (1977)	Twin Buttes Reservoir, Texas Prentice (1977) (comb.)
1	207	249	272	272	249	310	310	310	193	248	281	255	236	267	270	276
2	414	406	432	416	330	427	422	427	310	438	466	444	376	416	441	377
3	544	460	498	483	368	475	498	495	371	494	537	511	462	494	504	466
4		485	551	513		521	551	554	404	521	573	545	518			495
5		498	602	528		559	620	607	429	563	622	590	587			
6		505	610	533			650	650		608	675	666	617			
7		518	744	561			704	704			683	683				
8		564	765	632							715	715				
9																
10																
11																
12																
13																
14																
15																
16																
17																
18																

continued

APPENDIX 1 concluded

Average total length at each annulus (mm)	Canyon, Texas Prentice (1977) (comb.)	Belton Reservoir, Texas Prentice (1977) ♂	Belton Reservoir, Texas Prentice (1977) ♀	Lake Meredith, Texas Kraai and Prentice (1974) ♂	Lake Meredith, Texas Kraai and Prentice (1974) ♀	F.D. Roosevelt Lake, Washington Nielsen (1975)	Range (comb.)
1	384	454	467	343	383	217	64-460
2	415	459	511	406	464	350	117-485
3	438	464	521	438	506	440	191-544
4				456	532	532	241-574
5				466	546	579	290-671
6				475	555	617	315-696
7				481	563		371-757
8							399-818
9							419-737
10							457-752
11							462-759
12							493-706
13							521-676
14							541-643
15							678-678
16							582-671
17							589-632
18							607-673

APPENDIX 2

Food items consumed by the walleye and their relative importance[a]

Location and authority	Food	
	Vertebrates	Invertebrates
A. Juveniles and Adults		
Sulphide Lake, Saskatchewan (Koshinsky, 1965)	Fish(D)-yellow perch(D)	Insects(A)-mayfly nymphs(A), damselfly nymphs(D), dragonfly nymphs(D)
Little Deer Lake, Saskatchewan (Koshinsky, 1965)	Fish(A)-nine-spine stickleback(B), yellow perch(D), cisco(D), northern pike(D)	Insects(D)-mayfly nymphs(D)
Contact Lake, Saskatchewan (Koshinsky, 1965)	Fish(C)-lake whitefish(D), yellow perch(D), unidentified remains(C)	Insects(C)-mayfly nymphs(C), dragonfly nymphs(D), damselfly nymphs(D) Crustaceans-crayfish(D) Others-leeches(D)
Lac la Ronge, Saskatchewan (Rawson, 1957)	Fish(A)-cisco(B), nine-spine stickleback(C), yellow perch(D), lake whitefish(D), common sucker(D), spottail shiner(D), YOY walleye(D)	Insects(D)-mayfly nymphs(D), caddisfly larvae (D), stonefly larvae(D) Crustaceans-crayfish(D), amphipods(D)
Lake of the Woods, Ontario (Swenson, 1972)	Fish(1)-yellow perch(1), darters(4), trout-perch(4), cisco(4), cyprinids(4), saugers(4)	Insects(4)-ephemeroptera(4), midge larvae(4), trichoptera(4) Others(4)-leeches(4)
Lake Gogebic, Michigan (Eschmeyer, 1950)	Fish(1,A)-yellow perch(3,C), cisco(4), cyprinids(4,D), mud-minnows(4,D), Iowa darters(4), trout perch(4), northern pike(4) Others(4)-frogs(4), snapping turtle(4)	Insects(3,D)-ephemeroptera(3,D), diptera(4), neuroptera(4), hemiptera(4), coleoptera(4), odonota(4), plecoptera(4) Crustaceans(4)-cladocera(4), crayfish(4,D) Others-leeches(4), plants(4,D)
Mille Lacs Lake, Minnesota (Maloney and Johnson, 1957)	Fish(A)-yellow perch(A), johnny darters(D), spottail shiner(D), mimic shiner(D), trout perch(D), brook stickleback(D)	Insects(D)-ephemeroptera(D), midge larvae(D), odonata(D)
Cadillac Lake, Michigan (Eschmeyer, 1950)	Fish(2,B)-percids(4,C), centrarchids(4,D), cyprinids(4,D)	Insects(3,D)-mayflies(4,D), caddisflies(4,D), chironomids, zygoptera(4,D)
Androscoggin-Kennebec River System, Maine (Cooper, 1941)	Fish(A)-white perch(B), rainbow smelt(B)	
Muskegon River, Michigan (Eschmeyer, 1950)	Fish(3,C)-percids(4,D), cyprinids(4,D), centrarchids(4,D)	Insects(2,B)-ephemerids(2,C), chironomids(4,D) Crustaceans(4,C)-crayfish(4,C) Others(4,D)-gastropods(4,D), plants(4,D)
Oneida Lake, New York (Raney and Lachner, 1942)	Fish(1,A)-yellow perch(3,C), johnny darters(4,D), logperch(4,D), rock bass(4,D), cyprinids(4,D), emerald shiners(4,D)	Insects(3,D)-mayflies(4,D), caddisflies(4,D), hymenoptera(4,D) Crustaceans(4,D)-amphipods(4,D) Others(D)-snails(4,D), oligochaetes(4), plants(4,D)

continued

APPENDIX 2 continued

Location and authority	Food	
	Vertebrates	Invertebrates
Utah Lake, Utah (Arnold, 1960)	Fish(1,A)-Utah chub(4,C), carp(4,C), smallfin redsided shiner(4,D), yellow perch(4,D) white bass(4,D)	
North Twin Lake, Iowa (Kutkuhn, 1958)	Fish(A)-gizzard shad(3,C), yellow bass(4,D)	Insects(4,D)
Claytor Lake, Virginia (Rosebery, 1951)	Fish-bluegill(3), white crappies(3), smallmouth and largemouth bass(4), channel catfish(4)	Insects(4) Crustaceans(4)-crayfish(4)
Note: Other items consumed by juveniles and adults: rainbow darters, alewives, goldeyes, mooneyes, freshwater drum, black crappie, sunfish, emerald shiners, silvery minnows, topminnows, brook silverside, sculpins, brown and black bullheads, tadpole madtom, coho salmon, salamanders, homoptera, megaloptera, copepods, mysids, sea lamprey, diatoms, blue-green algae		
B. <u>Young-of-the-year</u>		
Lake of the Woods, Ontario (Swenson, 1972)	Fish(1)-yellow perch(2), cyprinids(4)	Insects(4)-midge larvae(4) Crustaceans(4)-cladocerans(4), copepods(4)
Rainy Lake, Ontario (Johnson, Thomasson and Caldwell, 1966)	Fish(1)-yellow perch(2), black crappie(3), johnny darter(4)	Insects(D)
Lake Winnibigoshish, Minnesota (Maloney and Johnson, 1957)	Fish(A)-yellow perch(B), unidentified remains(C)	Insects(D)
Lake Gogebic, Michigan (Eschmeyer, 1950)	Fish(1,A)-yellow perch(3,B), white sucker (4,D)	Insects(4,D)-ephemerids(4,D), chironomids(4,D) Crustaceans(4,D)-cladocerans(4,D)
Mille Lacs Lake, Minnesota (Maloney and Johnson, 1957)	Fish(A)-yellow perch(B)	Insects(D) Crustaceans(D)
Escanaba Lake, Wisconsin (Kempinger, 1968)	Fish(4)	Insects(2)-ephemerids(4), chironomids(2), odonata(D) Crustaceans-cladocerans(2), copepods, ostracods(4), amphipods(4)
Oneida Lake, New York (Raney and Lachner, 1942)	Fish(1,A)-yellow perch(4,D), johnny darters(4,D), log perch(4,D), largemouth bass(4,D), sunfish(4,D), spottail and emerald shiners(4,D), blacknose dace(4,D), fallfish(4,D), banded killifish(4,D), white suckers(4,D)	Insects(4,D)-chironomids(4,D), caddisflies (4,D) Crustaceans(4,D)-cladocerans(4,D), copepods (4,D), ostracods(4,D) Others(4,D)-snails(4,D)
Lake Erie (western end) mid-summer	Fish(1,A)-gizzard shad(3,C), alewives(4,C), yellow perch(4,D), spottail shiners (4,D), smelt(4,D)	Insects(4)-chironomids(4)

continued

APPENDIX 2 concluded

Location and authority	Food	
	Vertebrates	Invertebrates
Lake Erie (western end) continued autumn (Wolfert, 1966)	Fish(1,A)-emerald shiner(1,A)	
Belle Lake, Minnesota (Davis, 1975)	Fish(1,A)-Iowa darter(4,C), spottail shiner(4,D), yellow perch (4,D), sunfish(4,D), fathead minnow(4,D), johnny darter(4,D), central mudminnow (4,D)	Insects(4,D)

Note: Other food items reported consumed by YOY walleye: trout-perch, white bass, smallmouth bass, freshwater drum, northern pike, quillback, stonecat, brown bullhead, burbot, YOY walleye, fish eggs, frogs, diatoms, blue-green algae, rotifers, protozoans, coleoptera, homoptera, hemiptera, zygoptera, anisoptera, oligochaetes

a/

Percent volume of diet	Percent frequency of occurrence
A - >75	1 - >75
B - 50-75	2 - 50-75
C - 25-50	3 - 25-50
D - <25	4 - <25

APPENDIX 3

Common and scientific names of fish species mentioned in text

Family name	Scientific name	Common name
Lepisosteidae	*Lepisosteus osseus*	longnose gar
	Lepisosteus platostomus	shortnose gar
Clupeidae	*Alosa pseudoharengus*	alewife
	Dorosoma cepedianum	freshwater drum
Hiondontidae	*Hiodon alosoides*	goldeye
	Hiodon tergisus	mooneye
Salmonidae	*Coregonus artedii*	cisco
	Coregonus clupeaformis	lake whitefish
	Oncorhynchus kisutch	coho salmon
Osmeridae	*Osmerus mordax*	rainbow trout
Umbridae	*Umbra limi*	central mudminnow
Esocidae	*Esox lucius*	northern pike
	Esox masquinongy	muskellunge
Cyprinidae	*Cyprinus carpio*	carp
	Gila atraria	Utah chub
	Gila balteata	smallfin redsided shiner
	Notropis atherinoides	emerald shiner
	Notropis hudsonius	spottail shiner
	Notropis volucellus	mimic shiner
	Pimephales notatus	bluntnose minnow
	Pimephales promelas	fathead minnow
	Rhinichthys atratulus	blacknose dace
	Semotilus corporalis	fallfish
Catostomidae	*Carpiodes carpio*	quillback
	Catostomus commersoni	white sucker
	Ictiobus cyprinellus	bigmouth buffalo
Ictaluridae	*Ictalurus melas*	black bullhead
	Ictalurus nebulosus	brown bullhead
	Ictalurus punctatus	channel catfish
	Noturus flavus	stonecat
	Noturus gyrinus	tadpole madtom
Percopsidae	*Percopsis omiscomayeus*	trout-perch
Gadidae	*Lota lota*	burbot
Cyprinodontidae	*Fundulus diaphanus*	banded killifish
Atherinidae	*Labidesthes sicculus*	brook silverside
Gasterosteidae	*Culaea inconstans*	brook stickleback
	Pungitius pungitius	nine-spine stickleback
Percichthyidae	*Morone chrysops*	white bass
	Morone mississippiensis	yellow bass
Centrarchidae	*Ambloplites rupestris*	rock bass
	Lepomis gibbosus	pumpkinseed
	Lepomis macrochirus	bluegill
	Micropterus dolomieui	smallmouth bass
	Micropterus salmoides	largemouth bass
	Pomoxis annularis	white crappie
	Pomoxis nigromaculatus	black crappie

continued

APPENDIX 3 concluded

Family name	Scientific name	Common name
Percidae	*Etheostoma caeruleum*	rainbow darter
	Etheostoma exile	Iowa darter
	Etheostoma nigrum	johnny darter
	Perca flavescens	yellow perch
	Percina caprodes	logperch
	Stizostedion canadense	sauger
	Stizostedion lucioperca	European pike perch
	Stizostedion vitreum glaucum	blue pike
Sciaenidae	*Aplodinotus grunniens*	freshwater drum

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