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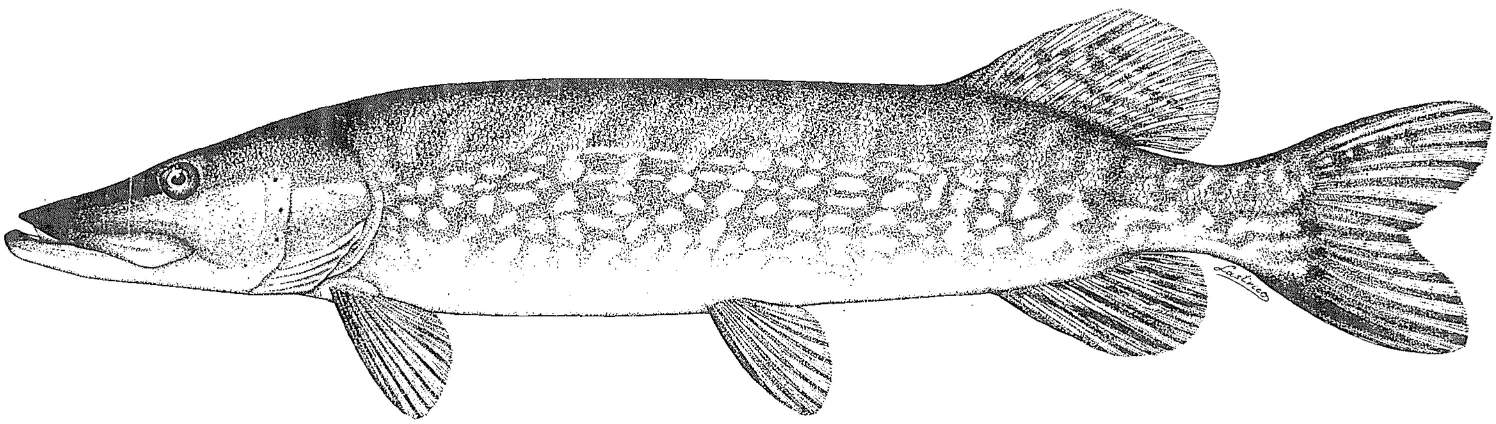
SYNOPSIS OF BIOLOGICAL DATA ON THE NORTHERN PIKE *Esox lucius* Linnaeus, 1758



FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

SYNOPSIS OF BIOLOGICAL DATA ON THE NORTHERN PIKE

Esox lucius Linnaeus, 1758

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PREPARATION OF THIS SYNOPSIS

This report was prepared as a follow-up to the offer of the Netherlands delegation to the eleventh session of EIFAC in Stavanger (FAO, 1981), to update the FAO Fisheries Synopsis of biological data on the northern pike, Esox lucius Linnaeus, 1758. In view of the enormous amount of data published on this important species since the last revision of the document (Toner and Lawler, 1969), it was necessary to rewrite it entirely.

The present report is based on an extensive literature study. Sources for the literature search included the Aquatic Science Fisheries Abstracts (ASFA), the Sport Fisheries Abstracts (SFA) and the Landwirtschaftliche Zeitschrift (LWZ). Furthermore, the reference lists of the consulted publications proved to be useful tools in the collection of published and unpublished material on the species. The synopsis summarizes data on pike gathered in many countries by a large number of biologists during the last three decades, up to 1st January 1985. Its reference list only includes studies quoted in the synopsis. These papers were consulted in autopsy unless otherwise stated in the reference list.

The author gratefully acknowledges the help he received from the numerous persons who have supplied him with data. It is impossible to quote all of them here, but special thanks are due to: Dr E.J. Crossman, Royal Ontario Museum, Toronto, Canada, who reviewed the chapters on taxonomy and distribution and furnished additional data on pike for North America; Dr J.D. Reist, Freshwater Institute, Winnipeg, Canada, who provided important information on the taxonomic status of the species from his unpublished Ph.D. dissertation; Dr J. Scott Campbell, Research, Branch Fisheries and Oceans, Moncton, Canada, who supplied unpublished data on the Heming Lake pike from Dr G.H. Lawler's files; Dr J.S. Diana, University of Michigan and Dr E.A. Huisman, Agricultural University, Wagening, Netherlands, who reviewed the chapters on metabolism; Dr L. Johnson, Freshwater Institute, Winnipeg, Canada, who supplied data from his Ph.D. dissertation on Windermere pike; Dr J. Willemsen, Ijmuiden, Netherlands, who reviewed parts of the manuscript dealing with his work on growth, culture and metabolism; Dr R.H.K. Mann, Freshwater Biological Association, East Stoke, England, who reviewed the chapters on the biology of the species. Further comments on earlier drafts of the synopsis were received from Dr H. Löffler, Langenargen, Federal Republic of Germany, Dr H. Lehtonen, Helsinki, Finland, and from the author's Dutch colleagues Dr J. Klein Breteler and Mr J. Quak. Mrs M.H.M. van Densen translated the Russian article by Shamardina (1957) on the early development of northern pike.

The author has the pleasure of acknowledging the help and support of Dr M.P. Grimm of the Research Department of the Organization for Improvement of Inland Fisheries, Nieuwegein, Netherlands. His many published and unpublished data on northern pike and his invaluable knowledge and experience with freshwater fisheries have been an important source of inspiration for the author during the writing of this study.

Part of the data collection was carried out by Mr J. Kampen (particularly the data on parasites) and Mr A. van Beusekon collected the data on growth. Mrs I.H. Willemsen-Vörös was extremely helpful in tracing down many publications and thus improving the bibliography of this report.

Research on the biology and culture of northern pike was greatly stimulated in the Netherlands since the fifties by Mr D.E. van Drimmelen, former chairman of EIFAC and of the Organization for Improvement of Inland Fisheries. The present synopsis is therefore one of the results of his inspiring activities in the field of freshwater fisheries.

Final editing of the synopsis was achieved by Ms Martina Schneider, Fishery Resources Officer, FAO Fishery Resources and Environment Division. Final revision and editing of the bibliography was carried out by Ms Gloria Soave, Research Information Unit.

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ABSTRACT

This synopsis consolidates all the available published data on the biology, growth, migration and population dynamics of a freshwater fish species which has been exploited and cultured for food since many years in European and North American waters.

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1. TAXONOMY AND DISTRIBUTION

1.1 Nomenclature

1.1.1 Valid name

Esox lucius Linnaeus, 1758

Reference: Caroli Linnaei, *Systema Naturae per Regna tria naturae* ... Tomus I. Editio Decima, Reformata. Holmiae, Laurentii Salvii, 1758, p. 314. (See Figure 1)

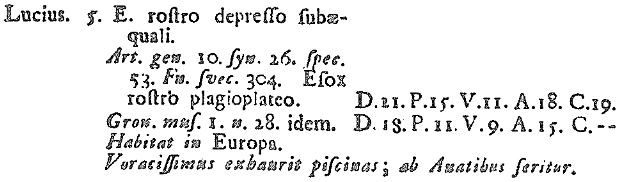

Lucius. 5. E. rostro depresso subæquali.
Art. gen. 10. *syn.* 26. *spec.* 53. *Fn. svec.* 304. Esox rostro plagioplateo. D.21. P.15. V.11. A.18. C.19.
Gron. mus. 1. *n.* 28. idem. D.18. P.11. V.9. A.15. C.--
Habitat in Europa.
Voracissimus exhaurit piscinas; ab Anatibus feritur.

Figure 1 Description of *Esox lucius* in Linnaeus *Systema Naturae* (1758)

1.1.2 Objective synonymy

Esox estor LeSueur, 1818, Lake Erie
Esox boreus Aggasiz, 1850, Lake Superior (referred to as *E. arboreus* by Toner and Lawler, 1969)
Esox lucioides Aggasiz and Girard, 1850
Esox reicherti var. *baicalensis* Dybowski, 1874, Baikal
Esox lucius var. *estor* Jordan, 1876
Lucius lucius Jordan and Everman, 1896-1900
Esox lucius var. *atrox* Anikin, 1908, Ob River
Esox lucius bergi Kaganowskii, 1933, Anadyr River
Esox lucius baicalensis Menshikov, 1948, Siberian pike from Ob River to Anadyr River
Esox lucius lucius Sorokin and Sorokina, 1948, Baikal

After Berg (1962; 1965), McPhail and Lindsey (1970), Scott and Crossman (1973), and Sorokin and Sorokina (1979).

1.1.3 Etymology

Pierre Belon in his *La Nature et diversité des poissons* (Paris, Charles Estienne, 1553), already rejected the Latin word lupus (wolf) as root for the specific name *lucius*. Hegemann (1964), however, gives the Greek ykos = lykos, and the Latin meaning of lucius = he who gives light, as possible roots for the word *lucius*. The generic name *Esox* possibly originates, according to Hegemann (1964), from the Latin esurire = to hunger.

1.1.4 Standard common names, vernacular names

Table I summarizes the standard common names and vernacular names of northern pike in various countries. John Murray, in volume VII of the *New English Dictionary on Historical Principles* (Oxford University Press, 1909), mentions several older forms of the word pike: pik, pyk, pyke, pycke, and pick. The word pike is apparently the short form for pike-fish, from the word pike in reference to its pointed beak.

1.2 Identity

1.2.1 Taxonomic status

1.2.1.1 General overview

The species is well established on the basis of morphological data (see Table II and Casselman *et al.*, 1986). According to Davisson (1972), the karyotypic similarity of the species of the esocid family is consistent with the fact that these species hybridize readily (Crossman and Buss, 1965; Buss and Miller, 1967; Buss, Meade and Graff, 1978), (see Section 1.4.1.1). Though the range of some of the North American species overlaps, the species remain separate, suggesting that physical, behavioural and ecological barriers are differentiated in the evolution of the species. A review of the natural barriers to hybridization within the esocid family is given by Buss, Meade and Graff (1978), who discussed in that context distribution, immunological barriers and similarities, spawning time, spawning sites and spawning behaviour.

Wright (In Buss, Meade and Graff, 1978), on the basis of preliminary investigations of electrophoretic patterns of certain enzymes and other proteins in esocids showed that northern pike and Amur pike (*Esox reicherti* Dybowski) are probably identical for those traits. These results, together with those of Davisson (1972), have led Wright to postulate that the two fishes are of the same species, or at most subspecies. Amur pike might be an isolate of northern pike which has developed differences in appearance through gene mutations. The muskellunge (*Esox masquinongy* Mitchell) was very similar, if not practically identical to the Amur pike and northern pike. The small pikes (pickerels) were quite different from the three larger esocids. In general, studies on electrophoretic patterns of enzymes and other problems of northern pike show little genetic variation (Healy and Mulcahy, 1980; Seeb *et al.*, 1987), (see also Sections 1.2.4 and 1.3.5).

Harrison and Hadley (1978) studied sympatric populations of northern pike and muskellunge in the Niagara River. It was shown that although the two species inhabited the same watershed, they were actually segregated throughout much of their life cycles. Northern pike preferred the shallower lentic parts of the river, muskellunge inhabited the deeper lotic parts of the water. Schiavone (1984) used radiotelemetry techniques to evaluate muskellunge movements in the Saint Lawrence River and found that muskellunge generally inhabited depths greater than 10 m during winter and summer. During spring and fall they appeared to utilize shallow water for spawning and foraging purposes.

Table I

Standard common names, vernacular names (modified after Toner and Lawler, 1969)

Country	Standard common names	Vernacular names
Austria	Hecht	-
Canada	Northern pike	Channel pickerel, Canada pike, common northern pike, slinker, shovelnose pike, short pickerel, marsh pickerel, jackfish, jack, great northern pike, hammer handle (young pike), snake
Czechoslovakia	Stika	-
Debnmark	Gedda	-
Finland	Hauki, Jänkäkoira	Jänkäkoira (Finnish Lapland)
France	Brochet, brocheton	Lance, lanceron[a/], becquet
Germany	Hecht	Heckt, Hengste, Höcht, Schneckhecht, Schnock, Schnöck, Schnöcker, Schnuck, Schnück, Snook, Wasserwolf, Snück, Häck, Höch, Bunthecht, Grashecht, Butterblumenhecht
Hungary	Csuka	-
Ireland	Pike, jack (small pike)	Lius (loose), gailliasc (golleesc), giosan, luis, grosan, gedas
Italy	Luccio	-
Luxembourg	Hiecht	Strếckel (small pike)
Netherlands	Snoek	-
Norway	Gjedde	-
Poland	Szczupzak	-
Spain	Lucio	-
Sweden	Gädda	-
Switzerland	Brochet, Hecht, Luccio	-
United Kingdom	Pike	Hacod, penhwyaden, gedd or gade Morris (very large pike), frie (very young pike), picche, pod
USA	Northern pike	Pike, grass pike, jackpike, jackfish, jack snake, common pike, pickerel, keno-shay, wistro, grass pickerel, silver pike, shovelnose, lake and spotted pike, laker, great pike, Great Lakes pike, great northern pickerel, lake pike
USSR	Shtchuka	In the Dictionary of the names of freshwater fishes of the USSR (Lindberg and Heard, 1972) about 100 names of *Esox lucius* in the languages of the peoples of the USSR and European countries are given

a/ "Le brochet est poisson industrieux en prênat sa pasture: car se tenant contre courant de l'eau, lors qu-il aduise quelque grenoiulle, ou autre chose se remuer le ans, il se darde de roideur sur sa proye. C'est de la que les pouruoyeurs et cuisinier de la cour le nomment lanceron." (Pierre Belon, 1553)

Table II

Meristic characters of esocids
(After Scott and Crossman, 1973; Berg, 1962; Merrilees and Crossman, 1974; Crossman and Meade, 1977)

Name	Submandibular pores (on each side)	Branchio-stegals (on one side): anterohyal/ posterohyal	Dorsal rays	Anal rays	Pelvic rays	Pectoral rays	Scales in lateral line (pored scales)	Vertebrae
Esox a. americanus Redfin pickerel	(3) 4 (5)	12 or 13: 5-6/7-8	15-18	13-17	8-9	14-15	102-116 (25-42)	49 or 50
Esox a. vermiculatus Grass pickerel	(3) 4 (5)	10-14: 5/7	14-17	13-15	9-10	14-15	97-118 (31-45)	42-47
Esox niger Chain pickerel	4 (5)	14-17: 6/9	14-15	11-13	9-10	12-15	117-135 (33-51)	52-54
Esox masquinongy Muskellunge	(5) 6-9 (10)	16-20: 8-10	15-19	14-16	11-12	14-19	132-167 (55-77)	64-66
Esox reicherti Amur pike	5	11-15: 5-6/8-9	6-7/14	4-5/12-14	-	-	130-165 (48-62)	60-67
Esox lucius Northern pike	(4) 5 (6)	13-16: 6-7/8	3-9/13-17	3-8/13-17	1-2/9-10	13-16	105-148 (42-56)	56-65

Data on hybridization are summarized in Section 1.4.1. Section 1.2.1.2 deals with competitive interaction between pike and muskellunge.

1.2.1.2 Interactions between pike and muskellunge

The northern pike are considered as a major competitor with muskellunge, Esox masquinongy, when the two species occur together (Threinen et al., 1966; Scott and Crossman, 1973). Northern pike are generally considered as superior to muskellunge. Harrison and Hadley (1978) and Porter (1977) summarized the reasons postulated for this superiority:

(i) earlier spawning of northern pike on common spawning grounds and subsequent predation by northern pike larvae on newly hatched muskellunge (Threinen and Oehmcke, 1950);

(ii) less size-selectiveness for food items and superior food conversion by northern pike (Scott and Crossman, 1973);

(iii) northern pike grow faster in the first year than muskellunge;

(iv) northern pike spawn two years sooner than the same year-class of muskellunge; the male gonads of northern pike are more developed (Gammon, 1986);

(v) northern pike tend to establish stable populations at higher densities than do muskellunge.

Because of unsound management practices and water-body modifications, northern pike have gained access to some waters containing native populations of muskellunge (Threinen and Oehmcke, 1950). These introductions have been detrimental to the muskellunge populations. Harrison and Hadley (1978) cited literature containing data that demonstrated an inverse relationship between the abundance of a native muskellunge population and that of an expanding, introduced northern pike population.

Analysis of changes in angler catches in Big Pine Lake, Wisconsin, also showed a trend toward substitution of northern pike for muskellunge (Inskip and Magnuson, 1983). Northern pike were first recorded in the lake in 1946, apparently having entered after an outlet dam washed out in 1944. The establishment of northern pike was accompanied by a drop in the relative abundance of small muskellunge in the angler catch. No young muskellunge were caught in the spring 1978 fyke nets. Nearly half of the muskellunge belonged to year-classes that had been augmented by stocking. Inskip and Magnuson (1983) stated that the muskellunge fishery appeared to have changed from one supported entirely by natural reproduction to one dependent on periodic stockings.

Similar trends were reported by Johnson (1981) from Lac Court Oreilles, Wisconsin. The invasion and subsequent establishment of large populations of northern pike appeared to be related to the observed decline in the muskellunge population which was strongly dependent on stocking. In Sand Lake, Wisconson, where the muskellunge population maintained itself by natural reproduction, the recent invasion of northern pike has not shown a decrease of the muskellunge population.

Inskip (1984, 1986) considered the circumstantial evidence of a negative interaction between the two species persuasive and not to be discarded. The author remarked, however, that a negative association in relative abundance might arise even in the absence of any direct species interaction. Cultural development more often results in the conversion of lotic habitat to lentic habitat than vice versa. Sequelae of human settlement, such as accelerated eutrophication, increased turbidity, siltation and accumulation of organic sediments, might be expected to have more severe impact on a species adapted for life in flowing water than on one living in still-water habitats.

Large lakes, such as Lake of the Woods and Eagle Lake in Ontario and Leech Lake in Minnesota, have harboured coexisting populations of both northern pike and muskellunge for a long time (Porter, 1977). This could be explained by the great variety of spawning grounds in these large lakes, with each species preferring slightly different, geographically separate areas. Similar conclusions were obtained by Dombeck, Menzel and Hinz (1984) in a statistical analysis of ecological factors associated with estimated muskellunge reproduction in 117 midwestern lakes. The analysis indicated that northern pike abundance accounted for 41% of the variability in muskellunge reproduction. The analysis further suggested that the coexistence of both species is favoured in drainage lakes of large area, while both species are marginal in smaller seepage lakes. Additionally, the status of populations in lakes of intermediate size may depend on local micro-habitat factors, such as edaphic factors and cultural influences.

1.2.2 Morphology

For the descriptions of the external morphology of spawn, embryos, larvae, adolescents and adults see Sections 2.1.7, 2.2, 2.3, 2.4.2-2.4.5, 2.5.3). Specific morphological differences between northern pike, muskellunge and their hybrid, tiger muskellunge, were described by Casselman et al. (1986).

1.2.2.1 Skin, slime layer, skin patterns

The thickness of the slime layer of the northern pike is, according to Fedak, Koval and Prokopenko (1973), 40-44 µm. Komarova (1969) reported that proteins are the most important components of the skin slime of the northern pike. Apparently, the proteins are bound to polysaccharides. The skin slime also contains a small, changing amount of nucleids. Kobec, Zavjalova and Komarova (1969) reported that mucous from the skin of northern pike decreased the fluid friction in experiments by 60%. According to Pjateckij and Savcenko (1969), the dragging friction is reduced by 20-25%.

Nonnotte (1981) studied cutaneous respiration of northern pike. The author concluded that the integument does not serve as an oxygen exchanger for the benefit of other organs. Czelzuga (1978) analysed extracts of northern pike by column and thin layer chromatography. Carotenoids were identified in all parts of the body. The dominant carotenoid was astaxanthin (48.5-94.7% of all carotenoids).

Casselman *et al.* (1986) and Scott and Crossman (1973) gave information on body coloration and colour patterns. Fickling (1982) described markings of northern pike of 50 cm and larger. Three basic types were noted, all typical of mature pike (small pike tend to have transverse bar markings, which disappear with increasing growth): (i) oval spots, (ii) round or stellate spots, and (iii) longitudinal bars. It is uncommon for pike to display more than one pattern type in one particular environment. Markings were found to be specific to individual fish. Subsequent recapture of pike after two years of growth, indicated that the markings could be used for the positive identification of specific pike.

According to Berg (1962), three forms of pike are distinguished in the Chud basin (USSR):

(i) large form, weight not less than 4 kg, dark-coloured, enters the Embach River under ice, spawns in March;

(ii) medium size, bluish-grey, spawning in April, this form is dominant;

(iii) "flower form" (Blumenhecht), with large yellow spots, short, robust, weighing not less than 4 kg, spawning from the middle of May till the middle of June.

In the Dnieper delta, the light-coloured migratory estuarine pike are distinguished from the dark-coloured lacustrine pike. Kulemin, Makkoveyeva and Solopova (1971) gave information obtained from fishermen, that in the 1920s three forms of pike were distinguished in Lake Pleshcheyevo (USSR):

(i) one, long and regular in shape;

(ii) one, with a terminally broadened snout;

(iii) one, with steeply rising forehead, greenish in colour.

The authors distinguished two forms of pike in the lake: one type has an elegant light-coloured trunk; the other form has a thicker shortened trunk and a dark skin.

The authors concluded that the reported differences in forms were related to the life of individual populations in different biotopes of the lake.

Crossman (personal communication) observed that in some populations of northern pike in North America, which live in highly silted (clay) waters, individuals are so pale that the yellow spots are almost invisible, particularly after death. The individuals seemed not to have the characteristic green-to-brown undercoat and looked white. In contrast, the blue or silver form (see Section 1.4.4) has a distinctive and prominent colour.

Crossman (personal communication) also reported that pike in England regularly have spots more whitish than pike in North America. The horizontal length of the spots of English pike is often equal to that of two spots of pike in North America.

The pigmentation pattern of northern pike is influenced by light stimuli (Mayerhofer, 1909). Absolute darkness resulted in fish with normal vision in an extreme contraction of the chromatophores. Blind fish did not show this reaction. In light, the pigmentation dispersed in a characteristic manner over the ventral part of the body of northern pike, which is normally uncoloured. In darkness, this process stopped and Mayerhofer (1909) reported the reduction of the pigments.

1.2.3 Cytomorphology

Svärdson and Wickson (1939) mentioned a somatic number of 18 chromosomes in *Esox lucius*. This number is so much lower than all subsequent reports that Davisson (1972) discounted the study. Prakken, Bekendam and Pieters (1955) counted a number of 48 or occasionally 49 rod-shaped chromosomes. Davisson (1972) suggested that the 2n of 49 resulted from the interpretative problems inherent in the application of the sectioning technique to chromosomal studies. According to Lieder (1956) the chromosome number of northern pike is 2n=46. In a letter of Dr Lieder to Mr C. Bungenberg de Jong (OVB), the author wrote that he was in doubt whether the chromosome number was 2n=46 or 2n=48. Davisson (1972), referring to Lieder (1956), suggests that it may be that some European pike populations exhibited intraspecific polymorphism for Robertsonian translocations.

Beamish, Merrilees and Crossman (1971), referring to Nygren *et al.* (1968), concluded that 2n=18 is probably in error, while the determination ranging from 46 to 50 might be the result of real chromosome variation among tissues or among specimens from different habitats. They made counts of chromosomes in 37 cells from the gills of five specimen and obtained 2n=50 acrocentric chromosomes. Estimated absolute DNA/mg/cell was 2.72×10^{-9} in *Esox lucius*. The authors considered polyploid mitotic cells not as an important factor.

Davisson (1972) found that representatives of all five surviving species in the esocid family and two interspecific hybrids had karyotypes consisting of 50 acrocentric chromosomes. The karyotypic similarity suggested a cytological basis for the ease of hybridization, observed among most members of the family, and showed that speciation can occur without karyotypic change (see also Section 1.2.4).

1.2.4 Protein specificity

Uthe et al. (1966) found that starch gel electrophorograms of muscle myogens and blood hemoglobins from northern pike and muskellunge showed considerable variation. At least 13 components were revealed in blood hemoglobin of northern pike. Plasma proteins of northern pike from different locations in Canada showed considerable variation between the specimens.

Eckroat (1974) compared eye lens proteins of six taxa of the genus Esox by acrylamide gel electrophoresis and by starch gel electrophoresis. The acrylamide gel electrophoresis patterns differed in that the eye lenses of pike and muskellunge had an extra band in the cathodal region when compared with the pickerel electrophorograms. No intraspecific lens protein polymorphism was found. Analysis of starch gel electrophoretic patterns revealed differences between pike, muskellunge and pickerels. By means of electrophoresis of lens proteins, differences in the genus Esox can be illustrated. However, differences between species in the genus cannot be distinguished.

According to Crossman (1978), comparisons of proteins of northern pike from the Volga River with proteins of North American specimens of Esox lucius indicated no differences which might reflect genetic difference.

Healy and Mulcahy (1979, 1980) studied genetic variation, as identified by starch gel electrophoresis and enzyme staining, in seven populations of northern pike. Samples were derived from populations in northern USA, Canada, Swedish fresh water, Swedish Baltic waters, the Netherlands, England and Ireland. The samples were analysed for variation at between 10 and 26 enzyme coding loci. Low variability, relative to reported data for other fish species, was found. Mean heterozygosity over all seven samples was estimated to be 0.019. Seeb et al. (1987) found identical results in their study of the products from up to 65 loci in muscle, liver, eye and heart tissue of pike from eight populations in north America. The average heterozygosity (H=0.001) and the proportion of polymorphic loci (P=0.01) were very low compared to values reported from other teleosts.

Healy and Mulcahy (1979, 1980) suggested that the differences between the three population samples from continental Europe on the one hand, and those from North America, England and Ireland on the other hand in the Sod-1 locus (superoxide dismutase), could be explained by colonization of relative small numbers. The absence of the Sod-1 variation from four of the populations sampled suggested, according to the authors, that ancestral stocks may have inhabited continental Europe and that colonization of new habitats by relative small numbers of individuals (founders) resulted in loss of heterozygosity. Their suggestion was accompanied by some general considerations on genetical consequences of founder effects with reference to colonization history of northern pike in England and Ireland.

Wünsche and Steffens (1968) examined contents of essential amino-acids in the protein of the total fish and in the muscles. Three male pikes (260-420 g), caught after the spawning time, were used in the analysis. The authors reported that the differences in amino-acid contents between pike and common carp (Cyprinus carpio), rainbow trout (Salmo gairdneri), cisco or whitefish (Coregonus albula) and European eel (Anguilla anguilla) were very similar.

Speckert et al. (1983) examined the primary structure of the basic nuclear protein in the sperm of pike. This protamine, 32 residues long, behaved as a single component during ion-exchange chromatography and gel electrophoresis. Amino-acid analysis gave close to molar ratios for the eight different residues with no evidence of microheterogeneity. The reciprocal nature of the substitutions resulted in glycine and serine contents which were close to a 4:2 ratio. Pike protamines are homologous to those of trout, but show less sequence variation between components.

1.2.5 Blood

Ligny and Verboom (1968), using agglutination tests, detected nine different blood groups in northern pike. Within the studied population, pike from Dutch waters, one group - AA - was detected, which represented 3% of the total. Growth and development of northern pike belonging to this blood group was comparable with pike of other blood groups. The authors suggested to use blood group characteristics as marks in population research.

Habekovic (1979) studied hematological properties of the northern pike in the period of sexual maturity. Sexually mature females had less hemoglobin and erythrocytes, while the rate of sedimentation of erythrocytes was substantially greater than in males. Sex had no effect on the number of leucocytes and thrombocytes, nor did it affect the qualitative erythrocyte and leucocyte blood picture. According to Korzhuev and Glazova (1968), northern pike belongs to the fishes (eel, tench, hagfish) with highest oxygen affinity of blood hemoglobins. It seems that the magnitude of oxygen affinity was not determined by its phylogenetic position but by its ecological peculiarities. The activity and localization of various enzymes were studied by means of cytochemical methods in blood cells of northern pike by Hoffmann, Pfeil-Putzien and Vogt (1978).

Molnár and Tamássy (1970) investigated erythocyte counts and hemoglobin content of blood of seven fish species, northern pike included (erythocyte 10^{-6}: 1.45±0.14, s.d. 0.57; hemoglobin/g %: 5.2±0.30, s.d. 1.17). Analysis of the results with use of the M index that relates to the hemoglobin content of one single red blood cell, showed that in predatory fish the hemoglobin content of erythocytes is lower than in either herbivorous or omnivorous fish. The authors suggested that oxygen demand and ability to transport oxygen can be expected to be different in fish with different food habits.

The ontogenesis of blood and blood-forming tissues was described by Bielek (1976). Bielek (1974) also described the development of the excretory system of northern pike.

1.3 Taxonomy

1.3.1 Suprageneric affinities

Kingdom Animalia
 Phylum Chordata
  Subphylum Vertebrata
   Superclass Gnathostomata
    Class Osteichthyes
     Subclass Actinopterygii
      Division Teleosti

Berg (1947, 1962), who was followed by Lindberg (1974), considered the northern pike to belong to the order Clupeiformes:

Order Clupeiformes
 Suborder Esocoidei
  Superfamily Esocoidea
   Family Esocidae

The Esocoidei are one of the 15 suborders of the Clupeiformes. Other suborders distinguished by Lindberg (1974) include the Clupeoidei and Salmonoidei (the latter with the families Salmonidae and Osmeridae). Nikolski (1957) considered the Esociformes as a separate order. According to this author, the esocids are doubtlessly related to fish of the order Clupeiformes, probably originating from fishes related to the Osmeridae, in accordance with Berg's (1947) concept. In Nikolski's classification the Clupeiformes are constituted by nine suborders which include Clupeoidei and Salmonoidei (with the families Salmonidae and Osmeridae). According to Soin (1980), the Osmeridae have a type of ontogenetic development which has very little in common with the types of development of salmonid fishes. Consequently, these fish should rather be classified in the suborder Osmeroidei. The development of the Esocidae has nothing in common with that of the Osmeridae. It is also radically different from the type of development of the salmoniform fishes as a whole. Therefore, the inclusion of the esocids in the orders Clupeiformes or Salmoniformes is considered by Soin (1980) as incorrect.

Rosen (1974) presented an analysis of the phylogeny and zoogeography of the Salmoniformes and classified esocoids as the primitive sister of a group including argentinoids, alepocephaloids, salmonoids (with Galaxiidae and Salmonidae) and osmeroids. Galaxiids are classified by Lindberg (1974) and Nikolski (1957) in a separate order (Galaxiiformes).

Nikolski (1957) gave a phylogenetic description of the taxa within the suborder Esocoidei, in which the extinct Paleoesocidae were placed in ancestral line to the Esocidae. The author distinguished three recent families: Umbridae, Dalliidae and Esocidae.

The relationships among the esocoid genera have been the subject of considerable debate in the last twenty years. Palaeoesox fritzschei †, long thought to be in direct ancestral line to Esox, is nowadays classified closer to the Umbridae than to the Esocidae (Cavender, 1969; Nelson, 1972; Merrilees and Crossman, 1974).

Reist (1983a) examined the hypotheses of interrelationships of the four genera (Esox, Umbra, Novumbra, Dallia) within the Esocoidei. The esocoid fishes are relatively primitive teleosts. Numerous characters have been advanced as putative autapomorphies for the group, but most of them are either present mosaically within the group, present also in taxa outside the group, or are primitive for fishes generally. Reist (1983a) therefore explicitly stated that he assumed the Esocoidei to be a monophyletic taxon.

Cavender (1969) noted the apparent monophyly of Umbra, Dallia and Novumbra based upon general body form, size, few vertebrae (33-42) relative to Esox (44-68), elongate and anteriorly constricted vertebral centra, four to nine branchiostegal rays, lack of a lateral line, short snout and jaws, small parietals, a well developed but uncovered post-temporal fossa, incomplete infraorbital series of bones, no supraorbital bone, and incomplete dentition.

Nelson (1972) suggested monophyly of the umbrids as a lineage distinct from Esox based on cephalic sensory canals and pitlines. Beamish, Merrilees and Crossman (1971), in examining the karyotypes of esocoids, presented information which implied that the monophyly of the umbrids was questionable. Wilson and Veilleux (1982), in their comparative osteological analysis of the five living umbrid species, concluded that umbrids represent a distinct esocoid lineage which differs from the esocids.

Reist (1983a), summarizing his own studies and former studies on the external and internal body morphometry of esocoid fishes, accepted a taxon consisting of Umbra and Novumbra. Dallia was provisionally accepted as the sister group of this taxon. Esox was accepted as the sister group of all of these. According to the author, the extreme phenetic and cladistic divergence of Dallia from all other esocoid taxa, and the association of Dallia with Esox (albeit based on data of lower reliability), do not warrant a firm commitment as to the relationships at this time. The author supported the following classification (based on Rosen, 1974):

Order Salmoniformes
  Infraorder Esocae
   Suborder Esocoidei
    Family Esocidae
     Genus Esox
    Family Umbridae
      Subfamily Dalliinae
       Genus Dallia
      Subfamily Umbrinae
       Genus Umbra
       Genus Novumbra

Rosen (1974) suggested in his study of the relationships within the Salmoniformes that the tiny, western Australian Lepidogalaxias, placed in the family Galaxiidae by Mees (1961), is more related to esocoids than to galaxiids. The characters uniting Lepidogalaxias and esocoids are few in number, and therefore a close relationship of this genus to esocoid fishes is most improbable (Crossman, 1978) or tentative only (Reist, personal communication).

In the ecological classification of Balon (1975), the northern pike is grouped in the section Non guarders, subsection Open substratum spawners, guild Phytophils.

1.3.2 Generic affinities

Esox Linnaeus, 1758 (type E. lucius)

Reference: Caroli Linnaei, Systema Naturae per regna tria naturae... Tomus I. Editio Decima, Reformata. Holmiae, Laurentii Salvii, 1758, p. 313 (See Figure 2)

154. ESOX. *Caput* ſupra planiuſculum: Mandibula ſuperiore plana breviore: inferiore punctata. *Dentes* in maxillis, lingua.
Membr. branch. radiis VIII-XIII.
Corpus elongatum.

Figure 2 Description of the genus Esox in Linnaeus' Systema Naturae (1758)

Synonyms (After Berg, 1962)

Lucius Rafinesque, 1810 (type implied L. lucius);
Trematina Trautschold, 1884 (type T. faveolata = E. lucius).

The five currently recognized species of the family Esocidae are united by the following putative synapomorphic characters (Reist, 1983a):

(i) the anterior pitline is rudimentary or absent (Nelson, 1972);

(ii) an elongate and flattened snout is characteristic (Berg, 1947) which results from the elongation of the preorbital portions of the relevant skeletal elements (Jollie, 1975);

(iii) all species have large numbers of vertebrae (44-68), especially in the the precaudal series (Cavender, 1969);

(iv) an uncinate process is present on a simple, cylindrical, fourth epibranchial (Rosen, 1974).

In addition to these, esocids share numerous primitive characters.

The following generic diagnosis was mainly taken from the family concept of the Esocidae as given by Scott and Crossman (1973) and Berg (1962).

"... Body elongate, laterally compressed. Tail forked. Dorsal and anal fins far back, equal to subequal in size and situated opposite one another. Head large, snout elongate, flat and somewhat like a duck's bill. Mouth very large, occupying one half of the head. Lower jaw prominent, mandibular joint behind posterior margin of the eye. Teeth on jaws large and prominent. Large patches of cardiform teeth on vomer, palatines, and tongue. Inframandibular present in contrast to mudminnows (Umbridae). Branchiostegal membranes not coalescing, free from isthmus. Gill rakers reduced to patches of sharp denticles (tuberculiform). Pectoral fins inserted low. Pelvic fins abdominal behind pectorals. Mesocoracoid absent from pectoral girdle (the so called simple shoulder characteristic, previously used to classify pikes and mudminnows in the order Haplomi). Head naked or scaled dorsally. Cheeks and opercular bones more or less fully or partly scaled. The pikes are physostomous, but there is no known ability to breathe atmospheric oxygen."

Within the genus, there are two readily recognizable groups (Nelson, 1972; Crossman, 1978), the pikes and the pickerels, with obvious morphological, biochemical and genetical differences (Eckroat, 1974; Beamish, Merrilees and Crossman, 1971; Davisson, 1972; Merrilees and Crossman, 1974). There is, however, incomplete reproductive isolation between members of the two groups. Natural hybrids between certain species occur, and others can readily be produced artificially (see Section 1.4.1).

For the associations within the Esocidae, the majority of evidence supported the following classification of Reist (1983a):

Family Esocidae
- Genus Esox
  - Subgenus Esox
    - Infragenus Lucius
      - Esox lucius
      - Esox reicherti
    - Infragenus Mascalongus
      - Esox masquinongy
  - Subgenus Kenoza
    - Esox niger
    - Esox americanus americanus
    - Esox americanus vermiculatus

1.3.3 Diagnosis of the species

The original diagnosis of Esox lucius by Linnaeus (1758) reads: "E. rostro depresso subaequali. Voracissimus exhaurit piscinas; ab Anatibus seritur". Linnaeus gives Europe as locality of the species. His diagnosis is based on descriptions of northern pike made by earlier authors like Petrus Artedi, Gronovius and Linnaeus himself in his Fauna Suecica (1752).

The description of northern pike given by Scott and Crossman (1973) reads as follows:

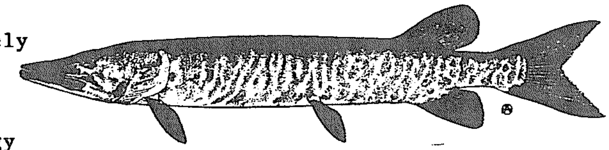
> "... Body very long, laterally compressed, only moderately deep, greatest body depth between paired fins 11.0-16.7% of total length, adults not so deep bodied as muskellunge, body cross-section a deep oval, more or less flat on top behind head; caudal peduncle moderately long, 10.1-15.0% of total length, but not deep, 4.5-6.0% of total length; individuals are usually 18-30 inches (457-762 mm) in length. Head long, 5.2-30.4% of total length, flat and naked on top, very broad, interorbital width 18.6-25.1% of head length, cheeks usually fully scaled, operculum usually scaled on top half only but variable; eyes large, high and at centre of head, eye diameter 10.7-20.6% of head length; snout long, 42.5-46.8% of head length, but longer than postorbital head length, snout moderately broad and rounded on top; mouth large, horizontal, maxillary usually reaching at least to midpupil; short, sharp, recurved, cardiform teeth along the premaxillary and in patches on tongue, basibranchials, last two pharyngobranchials, vomer, and palatines, large, strong canines on head of vomer, inner edge of palatine tooth patches and on dentaries, those on dentaries flattened with sharp edges as well as points, other canines pointed but round and peglike; lower jaw often extends slightly beyond snout, undersurface of lower jaw usually pierced by 5 pores on each side (rarely 3, 4, or 6 on one side only). Gill rakers reduced to patches of sharp, radiating denticles on one or both sides of the arches. Branchiostegal rays usually 14 or 15 on each side, usually 7 on anterohyal and 8 on epihyal. Fins: dorsal 1, soft rayed, far back, nape to dorsal origin 38.1-46.0% of total length, base shorter than height and about equal to snout length, upper edge rounded, 15-19 principal rays; caudal long, moderately forked, tips more rounded than the muskellunge; anal origin slightly behind that of dorsal fin, length of base less than height, less than base of dorsal fin, tip rounded, 12-15 principal rays; pelvics abdominal, low, and at middle of body, long, tips rounded and paddle-like, 10 or 11 rays; pectorals low, arising under edge of opercular flap, rounded and paddle-like, 14-17 rays. Scales cycloid and moderately small, 105-148 in the lateral series; lateral line complete, more or less straight, lateral line scales notched not tubed or pierced, very few notched, scales elsewhere although golden fleck on exposed edge of most scales make them appear so; intestine long and undifferentiated, no pyloric caeca. Physostomous. Vertebrae 57-65."

1.3.4 Key to esocids of the world (Crossman, 1978)[1/]

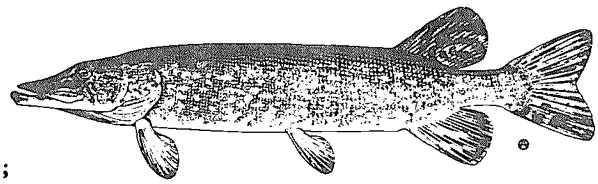
1a Submandibular pores usually 5 or more on each side, rarely 4 on one side only (in North America, in England and in western Europe 4 pores are much more common); lateral line scales as many as 176; one or both of cheeks and opercula non fully scaled; subgenus Esox 2

1b Submandibular pores usually 4 on each side, rarely 3 or 5 on one side only; lateral line scales rarely exceed 135; both cheeks and opercles more or less fully scaled; subgenus Kenoza 4

2a Submandibular pores usually 6-9 on each side, rarely 5 or 10 on one side only; branchiostegal rays 16-19 on each side, usually 8+10 (anterohyal + posterohyal) neither cheeks nor opercula completely scaled...............Muskellunge, Esox masquinongy (Mitchell, 1824)

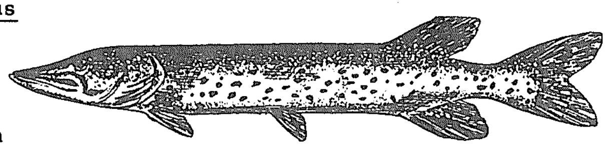

Esox masquinongy

2b Submandibular pores usually 5 on each side, rarely 4 or 6 on one side only; branchiostegal rays 11-16 on each side; cheeks more or less fully scaled, opercula approximately half-scaled 3

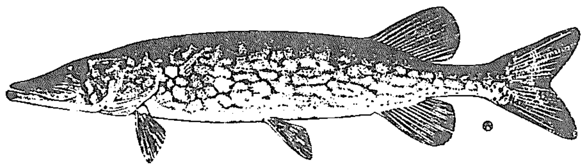

Esox lucius

3a Branchiostegal rays 13-16 on each side, usually 7+8; vertebrae 57-64; colour pattern with dark ground colour and light bars (in young) or horizontal rows of oval yellow to white spots ... Northern pike, Esox lucius (Linnaeus, 1798)

3b Branchiostegal rays 11-15 on each side but usually 5+8 or 6+7; vertebrae 63-67; colour pattern with silvery background and dark brown to black bars (in young) or large oval spots .... Amur Pike, Esox reicherti (Dybowski, 1869)

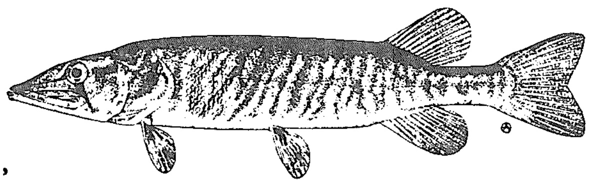

Esox reicherti

4a Branchiostegal rays 14-17 on each side, usually 6+9 .... Chain pickerel, Esox niger (Lesueur, 1818)

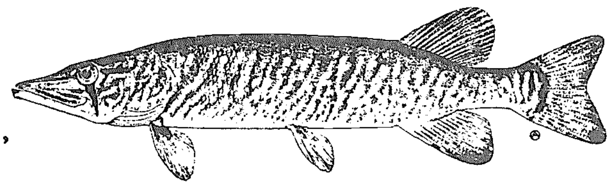

Esox niger

4b Branchiostegal rays 11-13 on each side 5

5a Branchiostegal rays usually 5+7 or 5+8 on each side, snout short and convex in profile; more than 5 cardioid scales in triangle between pelvic fins, as well as in an oblique line, from origin of anal fin to mid-dorsal line .... Redfin pickerel, Esox a. americanus (Gmelin, 1788)


Esox americanus americanus

5b Branchiostegal rays usually 4+7 or 4+8 on each side, snout longer and concave in profile; fewer than 5 cardioid scales in triangle between pelvic fins, and fewer than 5 in oblique line from origin of anal fin to mid dorsal line .... Grass pickerel, Esox americanus vermiculatus (Le Sueur, 1846)


Esox americanus vermiculatus

1/ Figures taken from Scott and Crossman (1973) and Berg (1962) (E. reicherti)

1.3.5 Subspecies

According to Crossman (1978) in his review of the esocid family, differences in meristic characters exist (see Table III), but these seem to be clinal, and those found in Canadian populations probably result from Pleistocene isolations of different stocks in separate refugia (McPhail and Lindsey, 1970). A study of pike in the fenlands of England (unpublished results in Crossman, 1978) suggested that some of the other superficial differences are basically phenotypic. According to Crossman (1978) we are probably dealing simply with a single, widely distributed and highly variable species.

Reist (1983a), however, concluded in his comparative study of the external body morphometry of northern pike from various locations of its distribution range, that four groups of pike could be distinguished. The differences between the groups were genetic and were ascribed to isolation. According to the author, they are of a sufficient magnitude for taxonomic recognition at a racial level, and may be furthermore valid for subspecific recognition. The formalization of named taxa is deferred pending a more extensive study.

Morrow (1964), who compared meristic characters of 31 pike from Tanana and upper Yukon River drainages in Alaska with 52 pike from the Cornell University collection (northeastern American pike), concluded that the differences were about what might be expected from two widely separated populations of the same form. McPhail and Lindsey (1970) demonstrated similar differences between pike found in the Yukon system and other Bering Sea drainages, as well as those along the Arctic slope of Alaska (60-64 vertebral counts), and pike in the MacKenzie system and the river systems to the east and south of northwestern Canada (57-62 vertebral counts). The differences were attributed to Pleistocene isolation in widely separated glacial refuges.

According to Reist (1983a), within North America a northern group consisting of fish from the Yukon and Northwest Territories, and a southern group consisting of fish from mid-west Canada, mid-west USA and Ontario were both consistently present. Grouped by some analyses, fish from the Yukon and Northwest Territories were quite different from each other and thus may represent a separate entitity. The results support, but a choice cannot be made between, either extensive gene flow between the Yukon and the Northwest Territories (Beringian and Mississippian origin respectively), or repopulation of the Northwest Territories almost entirely from the Beringian source.

Within Europe, two groups were apparent in the analyses of body morphometry: (i) a central group consisting of fish from Sweden, British Isles and Central Europe, with fish from western Europe associated peripherally; (ii) northern pike from Finland invariably formed a second group within Europe.

Genetic differences between northern pike from Europe and North America were also found by Healy and Mulcahy (1979, 1980) and Seeb *et al.* (1987) (see also Section 1.2.4).

With regard to the Siberian populations of northern pike, Sorokin and Sorokina (1979) presented morphometric details. The authors compared the Baikal pike with pike from other locations in the USSR. They concluded that the northern pike populations from the Ob, Irtysh, Kama and Vilyuy rivers and Lake Baikal were similar to each other and may be classified as the subspecies *Esox lucius lucius*. Earlier descriptions of the Baikal pike as a form of the Amur pike, *Esox reicherti* var. *baicalensis* Dybowski, or the segregation of the Siberian pike into the subspecies *Esox lucius baicalensis* were, according to the authors, not clearly borne out by morphological characters.

According to Wright (see Section 1.2.4.1), there are immunological and karyological arguments to consider *Esox reicherti* as a subspecies of *Esox lucius*.

1.4 Hybrids and Mutants

1.4.1 Hybridization

1.4.1.1 General overview

Reviews of esocid hybrids were given by Crossman and Buss (1965) and Buss, Meade and Graff (1978). According to these authors it would be possible for northern pike with regard to its distribution pattern (see Figure 3) to hybridize with muskellunge, *Esox masquinongy*, chain pickerel, *E. niger*, and grass pickerel, *E. americanus vermiculatus* in the southern part of its range, and with redfin pickerel, *E. a. americanus*, in the Saint Laurence River basin. The areas of overlap are limited, however, while also behavioural and immunological barriers exist between the species. The Amur pike, *E. reicherti*, is geographically isolated in the Amur River basin, south of 60°N latitude in the USSR and China. It does not overlap the range of the northern pike.

Crossman and Buss (1965) established that total sterility did not exist among esocid hybrids since one or the other reciprocal cross produced progeny. Buss and Miller (1967) found that no reproduction occurred of F_1 progeny of the northern pike x muskellunge cross or of crosses between large pike and small pickerels. Crossman and Meade (1977) established that the F_1 progeny of northern pike x Amur pike was fertile. The hybrids of northern pike with species other than muskellunge have light markings on a dark background. Buss, Meade and Graff (1978) presented photographs of the F_1 generation of various hybrid crosses of esocids. Table IV 4 summarizing the results of crossing esocid species is taken from these authors.

Table III

Meristic characters of northern pike, *Esox lucius*, from different locations
(For reference see column one)

Location		Submandibular pores (on each side)	Branchio-stegals	Pectoral rays	Pelvic rays	Dorsal rays	Anal rays	Scales in lateral line (pored scales)	Vertebrae
Irtysh[a/]	Males (n=31)	-	-	-	-/9.74±0.08	7.29±0.11/ 15.65±0.12	6.06±0.09/ 13.10±0.10	138.0±0.85 (49.7±0.60)	61.29±0.17
	Females (n=29)	-	-	-	-/9.38±0.09	6.72±0.14/ 15.41±0.14	5.45±0.17/ 13.10±0.12	134.8±1.02 (48.0±0.17	61.17±0.12
Irtysh[b/]		-	13-15	-	1-2/9-10	6-8(9)/14-17	4-7/12-14(15)	121-144(145,147)	(59)60-62(63)
Irtysh[c/]		-	-	-	-	(7)8-9/14-16	6-8/(11)12-13	-	-
Volga delta[d/]		-	-	-	-	-	-	-	(56)57-64(65)
Kama[e/]	(n=106)	-	-	14.59±0.06	9.97±0.04	22.5±0.10	19.18±0.08	126.48±0.54	60.92±0.14
Ob[f/]	(n=112)	-	-	14.87±0.06	9.85±0.04	23.42±0.07	19.7±0.06	135.56±0.82	61.29±0.17
Vilyuy River[g/]	Males (n=106)	-	-	-	-	-/14.72±0.16	-/14.72±0.16	134.86±1.0 (53.86±0.78)	59.8±0.14
	Females	-	-	-	-	-/14.88±0.12	-/14.88±0.12	134.0±0.59 (52.86±0.52)	59.91±0.13
Northern Baikal[h/]		-	-	13-15	8-10	3-8/13-17	3-7/10-15	124-136 (46-61)	56-62
Lake Illmen[i/]	(n=45)	-	13-16	-	-	-	-	-	(59)60-62
Muinak-Urga region[d/] Aral Sea		-	-	-	-	5-8/13-17	3-5/11-14	114-126 (43-50)	58-60
Tanaka, upper Yukon River, Alaska[j/]		(4)5(6)	13-16	14-16	10-11	17-22	(14)15-18	121-136	60-64
Northeastern North America[j/]		(4)5(6)	14-17	13-16	10-11	(18)19-22	16-18(19)	111-136	56-62

a/ Sorokin and Sorokina (1979) after Yefimova
b/ Berg (1962) after Efremova
c/ Berg (1962) after Menshikov
d/ Berg (1962)
e/ Sorokin and Sorokina (1979) after Menshikov
f/ Sorokin and Sorokina (1979) after Menshikov: *Esox lucius baicalensis*
h/ Sorokin and Sorokina (1979)
i/ Berg (1962) after Tyurin
j/ Morrow (1964) and McPhail and Lindsey (1970)

Table IV

Results of crossing esocid species and the fertility of F_1 generation (Buss, Meade and Graff, 1978)

	Northern pike	Muskel-lunge	Amur pike	Chain pickerel	Redfin pickerel	Grass pickerel
Northern pike	XX F	XX S	XX F	-	-	X ?
Muskellunge	XX S	XX F	XX ?	X S	X S	XX *
Amur pike	XX ?	XX ?	XX F	-	-	-
Chain pickerel	X S	X S	X ?	XX F	XX F	XX F
Redfin pickerel	X S	X *	0 ?	XX F	XX F	XX F
Grass pickerel	XX S	XX ?	X ?	XX F	XX F	XX F

Key: Hybridizing

XX = Good hatch and fry survival
X = Some survivors but poor egg fertility or fry survival
- = Unsuccessful cross
0 = Cross not made
* = Fry hatched and died

F_1 fertility

S = Hybrid sterile
F = Hybrid fertile
? = Hybrid fertility not determined

1.4.1.2 Muskellunge x northern pike (tiger muskellunge, tiger musky)

This hybrid is also referred to as norlunge, a name promoted by New York State. Tiger muskellunge is a very descriptive name, but it introduces confusion because the western populations of Esox masquinongy in Minnesota and Wisconsin are called like this in the early literature (Crossman, personal communication).

Threinen and Oemcke (1950) mentioned that muskellunge x northern pike crosses have occasionally occurred in nature. Harrison and Hadley (1978) in their study of sympatric populations of muskellunge and northern pike in the Niagara River, found a profound segregation between the species. The authors did not mention the occurrence of hybrids. These hybrids are rarer in moving water situations and are more apparent in waters like the Great Lakes, where the two species have cohabited for longer periods of time (possibly 9 000 years). The hybrids of northern pike and muskellunge are more frequent in smaller water bodies, especially lakes where separate spawning grounds are less frequent. The numbers of hybrids reported recently, since anglers have become more aware of how to recognize them, suggest either that they are more abundant now than in the past, or that they were always abundant but unrecognized (Crossman, personal communication).

Early records of crosses between the species are given by Eddy (1940) and Black and Williamson (1947). The cross was created by mistake in early days in Minnesota when sperm of "silver muskellunge", now known to be silver pike, the mutant of northern pike (see Section 1.4.2), was used to fertilize Esox masquinongy eggs when no muskellunge sperm was available (Crossman, personal communication). The hybrids are more easily cultured and have fewer disease problems, and eat dry feed better than muskellunge (Pecor, 1978; Hesser, 1978). The F_1 has an excellent growth rate in the hatchery. Consequently larger fish may be stocked with a better chance of survival in most cases. Tiger muskellunge have higher survival rates than northern pike or muskellunge (Weithman, 1975). According to Scott (1964) there appears to be some hybrid vigor in F_1 hybrids of northern pike and muskellunge. The hybrids tend to be more resistant to thermal stress at the average acclimatization and test temperatures. Greater physiological differences between hybrids and parents occurred at lower test temperatures.

Meade, Krise and Ort (1983) reared juvenile tiger muskellunge at a constant temperature range of 14°-28°C. For fish of 3-4 cm length, growth, production and feed conversion efficiency were highest at 20°-22°C. For fish of 12-13 cm length, feed conversion efficiency and mean individual growth were highest at 23°C. Bevelhimer, Stein and Carline (1985) found similar results for tiger musky. At 15°C, the hybrid had better growth than either of the parent species; hybrid growth was also fastest at 20° and 22.5°C, but not significantly so. At 25°C, the growth rate of the hybrid had drastically decreased and was significantly slower than that of the parents at temperatres between 25° and 27.5°C.

The faster growth is generally related to increased feeding activity which in turn means more predation. Gillen, Stein and Carline (1981) described differential predation by pellet-reared tiger muskellunge and those reared on minnows (Pimephalus promelus) and bluegills (Lepomis macrochirus) in aquaria and experimental ponds. The results are in agreement with field studies in Wisconsin lakes (Johnson, 1978), which showed that survival of hybrids reared on fish in hatcheries was much higher than that of hybrids reared on pellets.

The hybrids are sterile and therefore can be introduced into watersheds where a spread of large piscivorous fishes is not desired. The results of stocking tiger muskies and the implications on their management in Pennsylvania are reported by Hesser (1978). The hybrid increases in importance yearly in North America. It is being artificially cultured in many State hatcheries in the USA. The fish is introduced widely as a sport fish in areas marginal to that of Esox masquinongy, or where that species occurred but does no longer (Crossman, personal communication). The hybrids are less vulnerable to angling than northern pike (Beyerle, 1973; Weithman, 1975).

1.4.1.3 Northern pike x Amur pike

The cross of northern pike male x Amur pike female produces viable, hardy progeny. It is established that the progeny is fertile (Crossman and Meade, 1977), but it is not known if it will reproduce in the wild (Hesser, 1978). The hybrid is potentially a stream inhabitant and thus of value where a coolwater predator may be required. A small number of hybrids were stocked in two Pennsylvania waters primarily on experimental basis (Hesser, 1978). No significant fishery has been identified as having resulted from these introductions. A few hybrids, apparently escaped from the Pennsylvania Fish Commission hatchery, have been taken by anglers. One of these fishes had a total length of 119.7 cm and weighed 11.9 kg.

In 1968, young Amur pike, hatched in the Pennsylvania State hatchery from eggs imported from the USSR, were stocked in Glendale Lake (650 ha) (Crossman and Meade, 1977). Hybrids of Amur pike and northern pike were reported from there resulting from natural reproduction. In 1979, a hybrid weighing 12 kg and measuring 118 cm was caught (Eggers, 1984).

1.4.1.4 Northern pike x grass pickerel

McCarraher (1960) presented evidence of natural hybridization between northern pike and grass pickerel (Esox americanus vermiculatus) in shallow sandhill lakes in Nebraska. Natural hybrids of northern pike and grass pickerel have also been reported from Michigan and Wisconsin (Buss, Meade and Graff, 1978). Serns and McKnight (1977) reported natural hybrids of northern pike and grass pickerel from Rice Creek, Vilas County, Wisconsin. The population of grass pickerel and the hybrids represent the northernmost known distribution of species and hybrids. The population of grass pickerel in Rice Creek appeared to be isolated and may be due to an accidental introduction in the early 1940s. Schwartz (1962) described the morphological characteristics of the hybrid of the artificial cross between grass pickerel females and northern pike males which was made at a Pennsylvania hatchery. The author compared the hybrid with fish described by McCarraher (1960). Progeny hatch and survive well. It is a sterile hybrid with potential for stream utilization.

1.4.1.5 Chain pickerel x Northern pike

Crossman and Buss (1965) listed all the reports of natural hybrids of Esox lucius to that date. The authors found evidence that northern pike and chain pickerel (Esox niger) hybrids were identified in New York State.

Development of impoundments has led to an expansion of the range to the west of North America in Atlantic coast states. Hereby the area in which northern pike and chain pickerel are sympatric, will be greatly extended. They have overlapped recently only to a limited extent in Quebec, New York, and Pennsylvania. The two species hybridize readily, and in certain habitats northern pike may overrun chain pickerel (Crossman, 1978). According to Buss, Meade and Graff (1978) these hybrids have no apparent value over parental species. Armbruster (1966) described propagation, growth and scale development of hybrids of chain pickerel and northern pike. Underhill (1939) artificially produced this hybrid.

1.4.1.6 Perca fluviatilis x northern pike

A most improbable cross between perch females and northern pike males is reported by Nikolyukin (1935).

1.4.2 Mutants

Crossman (1978) reports that over the whole of at least the northern portion of the distribution of the northern pike in the USA and Canada, a mutant form occurs irregularly. This form, usually called "silver pike", is distinguished from ordinary northern pike by its silvery blue or silvery green colour, while it also lacks the white-to-yellow spots characteristic of the species. It is different in apparently being more tenacious than ordinary northern pike (Lawler, 1960, 1964). The mutant was at one time thought to be a form of muskellunge.

Lawler (1960, 1964) described the morphology of the silver pike. In Heming Lake, Manitoba, 0.2% of the pike population is comprised of silver pike. The fish had the morphological characters of northern pike except that the silver pike are somewhat smaller and narrower than normal pike. There is some evidence that mandible and maxillary are both shorter in silver pike. Records of silver pike come from:

- Heming Lake, Manitoba;

- two small lakes adjacent to Heming Lake;

- Mississippi Lake, near Ottawa, eastern Ontario;

- Ontario (few scattered reports);

- Beaverlodge Lake, east of the Great Bear Lake, Mackenzie (northernmost record of oc currence);

- Lake Belletaine, Minnesota (Eddy and Surber, 1947);

- various lakes in northern Minnesota, Wisconsin;

- Sweden (Runnström, 1949, 1952; Lawler, 1960);

- Alaska, three specimen taken at the mouth of Kandik River, on the Yukon (first record from west of the Rocky Mountains) (Bartholomew, Divall and Morrow, 1962);

- Stuttgart (Federal Republic of Germany), in the natural history collection where white specimen of northern pike is preserved (Hegemann, 1964);

- Poland, oral reports about two white northern pike in a fish shop in Kraków in 1959 (Hegemann, 1964)

- Grote Vliet (Andijk), Netherlands (Eggers, personal communication);

- a photograph of a blue specimen of northern pike, published on the front page of La pisciculture française 51 (1985). The blue pike or Brochet-Gremlin was captured in lake Lindre (France). It was the second capture of a blue specimen from that lake within 15 years.

Svärdson (Runnström, 1949) found in 1948 an abnormal, silver-coloured mature pike, the spawn of which was fertilized with milt from a one-year-old male. An F_1 generation was thus created consisting of about 50 fishes that were reared in aquaria and ponds of the Drottningholm Institute of Freshwater Research. In 1951 the colour mutants gave rise to a new generation (Runnström, 1952). A total of 19 one-summer-old fingerlings were collected from the ponds in autumn. They were just like their parents. Therefore, a definite proof has been found that the variation in colour was genetically based.

Runnström (1949) reported that Lindroth found 40 abnormally light yellow-coloured pike fry at Fuse (Sweden). "By special efforts with enormous feeding of plankton, roach fry, etc., these pike have been raised to unusually big yearlings, 26 of which are still alive. The still visible colour deviation is probably due to a mutant gene...".

1.4.3 Hardiness

Northern pike can tolerate a wide range of environmental conditions, but they are mesothermal or "coolwater" fish and are best adapted to the mesotrophic-eutrophic environment (Casselman, 1975).

Lawler (1960, 1964) recorded examples of extreme hardiness of the "silver" pike - a mutant of the northern pike (see Section 1.4.2). With reluctance we report about a gillnet captured "silver" pike that was replaced in fresh water and revived. A day later it was weighed and measured. The small intestine was removed through a 4-cm long cut in the abdominal wall. The fish was left lying on a wet table for about 20 min and, as it still showed signs of life, was put in an aquarium where it began to swim. The incision was then sutured and the fish continued to live for a total of 30 days from the time the intestines were removed and apparently took no food at all during that time. Lawler (1964) suggests that "silver" pike are superior in hardiness to normal northern pike.

Heuschmann (1957) gives a photograph of a pike whose dorsal and anal fins are transformed into a pseudotail fin as a result of loss of the tail part of the body.

1.4.4 Abnormalities

Lawler (1964, 1966) described mutant northern pike with accessory fins attached to the ventral surface of the head and the ventral surface of the body between the pectoral and pelvic fins, respectively. The author suggested that the accessory fin possibly arose from an unusual development of the muscle buds during early embryonic period.

Lawler (1966a), in examining about 10 000 northern pike from Heming Lake, Manitoba, found three pike showing pugheadedness. This abnormality resulted from an uprising of the median portion of the cranium. Both environmental and genetic factors may be responsible for the defect - mechanical damage was ruled out as an important factor.

A snub-nosed northern pike was caught in 1979 in Lake Tyrifjorden, Norway. Age determination from the cleithrum showed that the pike was 9 years old. The fish was 83 cm long and the weight was 4.5 kg. Veterinary analyses showed no reason for the malformation (Skurdal, 1981).

Piwernetz (1968) studied regeneration of dorsal fin and tail fin. Fins were extirpated from a pike four days after hatching. According to the author, the young pike had no more possibility of regeneration than adult pike. Removed parts of the chorda and of the embryonal seams of the fins did not regenerate. If there are removed parts of the fin which show no regeneration, the neighbouring tissue will form compensation tissue structures. After damaging a tail fin of pike the surrounding tissue formed a "mini tail fin".

Heuschmann (1957) (see Section 1.4.3) and Wunder (1982) gave examples of regeneration in northern pike after mechanical damage.

A curious abnormality was reported by Hegemann (1964), who referred to literature in which a northern pike with two heads is mentioned.

Wunder (1960) reported growth abnormalities in the jaws and fins of young northern pike in a German pond. The causative agent must have been external because pike from the same parents in other ponds showed no irregularities.

1.5 Distribution

1.5.1 Origin and fossil records

Esocids are without doubt of freshwater origin (Nikolski, 1957). In spite of the rather extensive fossil history of esocid fishes, or possibly as a result of it, there is conflicting information about their place of origin and routes of dispersal (Crossman, 1978).

Wilson (1980) described fossil esocids from Paleocene formations in Alberta and Saskatchewan. The discovery of Paleocene esocids was unexpected because the oldest previously recorded esocids were Oligocene species in Eurasia (Hegemann, 1964; Nelson, 1972; Crossman and Harington, 1970; Sytchevskaya, 1976). The Paleocene Esox tiemani is an elongate, narrow-snouted pike with 59 vertebrae, more similar to E. lucius than to European Tertiary Esox. This indicates that E. lucius is not a derived species and that the body form and vertebral number is primitive for the other recent esocid species.

The existence of a well-differentiated and distinct Esox in the North American Paleocene suggests that all esocids are much older than previous work implied. Reist (personal communication) speculated that a late Cretaceous or early Tertiary origin of Esox in freshwater environments of the Holarctic was most likely. The geologically much older pike species from North America calls into question the view that the origin of the family was southern Europe. It also negates the speculation that Esox invaded North America from Europe during the Oligocene and later during the Pleistocene (Merrilees and Crossman, 1974). The much older fossils show that recent access to North America from Asia via the Bering land connection, as commonly inferred for both pike and cyprinoids, should not automatically be preferred over such alternatives as North American origins or immigration from Europe via the deGeer route, which was not finally broken until Eocene times (Wilson, 1980).

Pike fossils are among the most common teleost remains in the Paleocene assemblages of western Canada (Wilson, 1980). They are about twice as old as early Oligocene pike in Europe. Fossil pike from the Tertiary period are found in great numbers in Europe. Esox papyraceus has been found as far back as the early Oligocene. E. waltschanus was discovered in early Miocene layers (Hegemann, 1964). Sytchevskaya (1976) pointed out, however, that E. waltschanus is not an esocid but rather a cyprinid. E. robustus and E. lepidotus were found in upper Miocene layers. Very perfect specimens of the last species have been found in Oeningen (Baden Württemberg). It differs from the recent esocids in its much larger scales and in the greater approximation of the ventral and anal fins, two characteristics in which it approaches Umbra (Harmer and Shipley, 1910). E. lepidotus has 60 vertebrae and is according to Nelson (1972) closely related to, or may be a member of the subgenus Esox.

The relationships of the small fossil esocids in Eurasia with recent esocids is obscure. The vertebral number of E. papyraceus, E. robustus and the Siberian fossil pike (Sytchevskaya, 1976) is between 48 and 51. Compared with these fossils and with recent North American E. niger and E. americanus, E. lucius has more vertebrae, a narrower and longer snout, a longer mandible with smaller "articular angle", and a more elongate opercle, considered advanced features by Sytchevskaya (1976), together with more branchiostegals, considered a primitive feature (Wilson, 1980). However, the much older North American species is more similar to E. lucius than are Tertiary species of Esox from Eurasia. E. tiemani combines the possession of many vertebrae and few branchiostegals with an elongated snout, lower jaw and opercle. This suggests, according to Wilson (1980), that some or all of these characteristics previously considered advanced, are in fact primitive for at least some modern and fossil pike species. The Paleocene Esox discovery thus tends to support interpretations of pike phylogeny involving an E. lucius-like ancestry for species of living pike, rather than an interpretation of E. lucius as one of the most derived of living pike species (Wilson, 1980).

Although the Tertiary fossil record of Esox in North America is far from well understood (Wilson, 1980), the presence of Esox in North America in Paleocene times, before the separation of North America and Eurasia, does suggest that modern Esox species in North America represent survivors of an ancient fauna (Wilson, 1980). The speculation that the recent pickerels diverged at some point of time between the origin of E. papyraceus and E. waltschanus after an Oligocene invasion of Esox from Europe (Merrilees and Crossman, 1974), seems implausible.

A problem in the reconstruction of esocid evolutionary history is the lack of strong divergence in recent Eurasian and North American E. lucius. This can be explained by contact and gene flow between fish from various refugia during Tertiary and Pleistocene glaciations. Such gene flow was unlikely, however, for all other recent species and most fossil species, since they occupy or occupied only a single glacial refugium (Reist, personal communication).

More recent fossil findings of esocids from Europe are reported by Thienemann (1950) from the Diluvium: E. lucius and E. otto. Frey (1964) summarized Quarternary findings of E. lucius from Europe. Tsepkin (1986) gave a brief review of the quarternary ichthyofauna in the Asian part of the USSR. Late Pleistocene-Holocene remains of Esox lucius were reported from the Amudar'ya basin, the upper Ob, the middle course of the Irtysh, the middle lower course of the Lena, from the Vilyuy basin, the middle Aldan, the Selenga basin and in the upper and middle course of Angara. The first definite Tertiary records of esocids from North America were described by Crossman and Harington (1970). The authors described fish dentaries from Pleistocene deposits in the Old Crow Area, Yukon Territory. The finding suggests that northern pike probably had crossed the fresh waters of the Bering land bridge into North America by the Illinoian glaciation. The Yukon fossils tend to confirm the idea that the species was present in the Beringian refugium during the Wisconsin glaciation. Although no older records of pike are known from northwest North America, it is not impossible that the Yukon fossils are survivors of an ancient fauna. Gene flow between fish from the Yukon Territory and fish in mid-west Canada and USA, however, must have been restricted. Morrow (1964), McPhail and Lindsey (1970) and Reist (1983a) demonstrated differences in meristic characters and body form between pike from those locations (see Section 1.3.5).

Bland and Bardack (1973) described fossil pike, referable to Esox lucius, from a site at the southern end of Lake Michigan. The age of the fossil, late Pleistocene (Lake Chippendale stage), and the locality demonstrated the occurrence of northern pike during postglacial times within the present range of the species in North America. Teller and Bardack (1975) described fossil northern pike materials, which occurred in lacustrine, postglacial clays on the shoreline of Lake Michigan, near Michigan City, Indiana. The fossils occur in the beds more than 5 500 but less than 6 300 years old.

Bailey and Smith (1981), in their review of the origin and geography of the fish fauna of the Laurentian Great Lakes basin, give indications that northern pike gained access to the Mississippi drainage after the ice had disappeared. The pike probably colonized the drainage after the muskellunge (E. masquinongy). The authors do not exclude the hypothesis that pike colonized the Great Lakes from the northwest during deglaciation. Seeb et al. (1987), however, found data suggesting that northern pike repopulated northern America from more than one southern refuge.

Wheeler (1977) discussed the origin and distribution of freshwater fishes of the British Isles and concluded that primary freshwater fishes like northern pike, loaches (Cobitis taenia and Noemacheilus barbatulus), perch (Perca fluviatilis) and bullhead (Cottus gobio), appear to be native only to the English river catchments of the North Sea and some to the eastern English Channel rivers. They must owe their occurrence in England to former connections between English and continental European rivers during the period of post-glacial sea-level depression (see also Thienemann, 1950). Their restricted natural distribution can be explained with the sparcity of opportunities to disperse in the relative short space of time between the period of the existence of the Flandrian land bridge and the present day. Crossman (1971) noted about the Pleistocene fossils of Esox lucius from the freshwater beds of West Runton, Norfolk, in the British Museum natural History collection, that the bones seem more massive than those of today's northern pike. Crossman (1971) remarks that this may reflect the process of fossilization.

The present wide distribution of northern pike over Britain and Ireland can be attributed to human activities (see Section 1.5.2).

1.5.2 Present distribution

The northern pike is the only circumpolar species and the only species in the esocid family with a broad geographical and environmental range (see Figure 3). The esocids are restricted to the cold and temperate parts of the northern hemisphere, holarctic in distribution including most of the north temperate zone above 40^{o} latitude and penetrating into the Arctic zone; from Alaska and Siberia, south to Missouri, the Ohio River and New York in the USA, and to Italy, Greece and Turkey in Europe. Thienemann (1950) describes the northern pike as a holarctic species that is distributed in Europe with the exception of the drainage area to the White Sea, Norway, north of 60° latitude, the Iberean Peninsula, South Italy, Dalmatia, Wardar and the Crimean Isle. In Asia it is found from Siberia to Kamtchatka eastward and to Lake Baikal southward, the Caspian area and Russian Turkestan. The species is not found on the Faröer Islands, Iceland or Greenland.

McCarraher (1961) described the extension of the range of northern pike in the USA and Canada. Reports of pike introductions in North Carolina, Maryland, Colorado and Montana are shortly discussed by this author. Northern pike are abundant throughout the MacKenzie River watershed including Great Bear and Great Slave Lakes, and from all the rivers emptying into the west coast of of Hudson Bay south of the Maguse River. Northern pike, however, have not yet occupied all of the northeastern Barren Grounds. In Alaska, pike are found in Alsek and Taku systems. They failed to ascend the Peace River above Peace Canyon and will probably not be found upstream of the Portage Mountain dam at Hudson Hope (McPhail and Lindsey, 1970).

The absence of northern pike today, and almost certainly in the past, from the eastern Arctic coast of Canada, from part of Labrador, and from Cape Breton and the maritime provinces is probably due to a combination of unsuitable

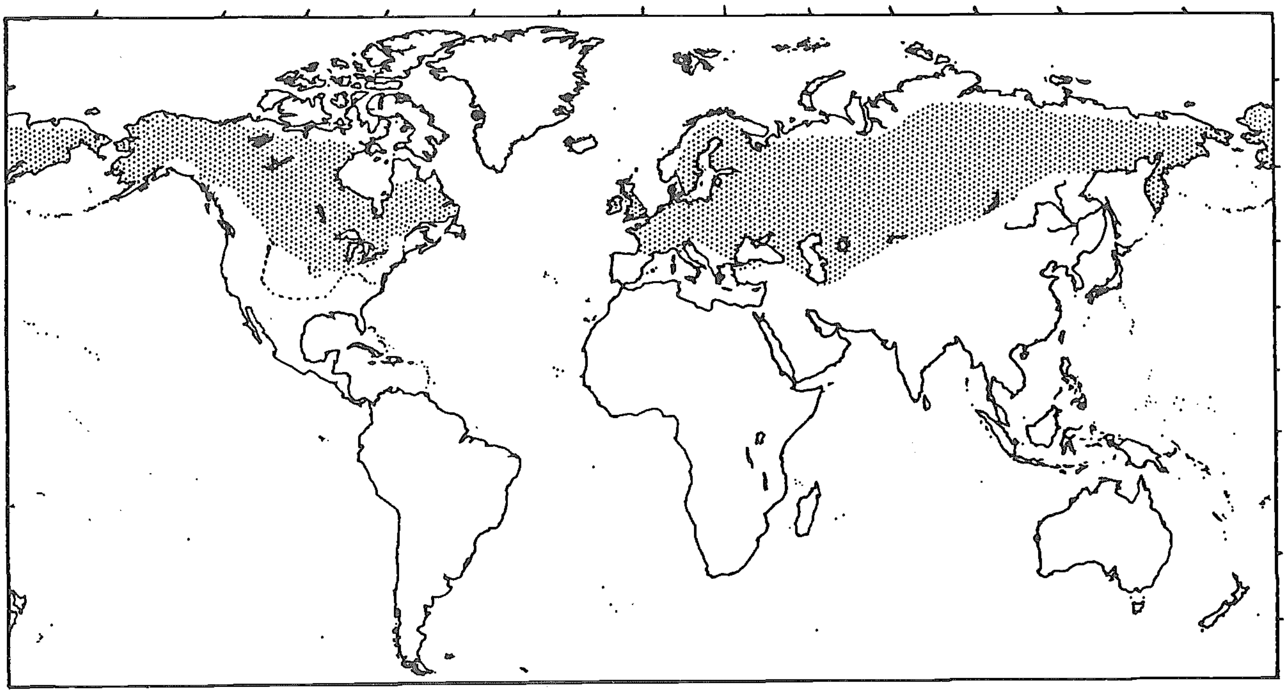


Figure 3 Geographical distribution of northern pike

habitat and a failure to colonize the area (Crossman, 1978).

Carlander, Campbell and Muncy (1978) reported, on the basis of a questionnaire research in the USA and Canada, that the area of total freshwater in North America occupied by northern pike was 54%. From California, Missouri and Georgia unsuccessful or unsatisfactory results from stocking are reported.

Although generally considered to constitute a single species over the whole of its holarctic distribution, the Eurasian and North American populations of northern pike have been isolated at least since the late Pliocene (see Section 1.5.1). In addition, there are certain morphological differences and other circumstantial distinctions (i.e., body proportions, usual maximum size, utilization of brackish water) used at times to suggest separation, at least at the subspecies level (Crossman, 1978) (see Section 1.3.5).

Introduction of the species is reported from Ireland between the 12th and 16th centuries (Went, 1957, 1965). Since that time the pike have distributed widely in Irish waters (Bord Failte Eireann, 1978). Welcomme (1979) reports introductions of northern pike for cultivation purposes in Spain, Madagascar and Uganda. Almaça (1965) reported the species from the Guadiana River (Portugal). Preudhomme (1975) describes problems encountered in breeding of introduced northern pike in Morocco. The species was introduced there in 1935 and stocked into impoundments in the Atlas Mountains (Crossman, 1978).

Heuschmann (1957) gives some data about the vertical distribution of northern pike. Naturally reproducing populations of pike are reported from 1 400 m in the Alps. Northern pike were found in lakes as high as 1 621 m (Seewenalpsee). Obviously, the pike were stocked in those alpine waters.

1.5.3 Differential distribution

1.5.3.1 Spawn and larvae

Numerous authors (see Section 2.1.6) reported that pike eggs are well scattered on dense vegetation (Fabricius and Gustafson, 1958), flooded marsh vegetation (Franklin and Smith, 1963; Forney, 1968), shallow littoral zones protected from the wind (Frost and Kipling, 1967), freshly inundated meadow vegetation (Drimmelen, 1969) and shallows with reed beds of higher aquatic plants (Koz'min, 1980). The eggs and larvae can tolerate fluctuations in oxygen conditions that occur in vegetated areas (Drimmelen, 1969)(see also Section 2.2.3).

Emigration of larvae from spawning grounds takes place when the northern pike attains a length of about 20 mm (see Section 2.3.6). Emigration of the larvae is directed to sparser vegetation compared to the dense vegetation where the eggs developed (Toner and Lawler, 1969). Data about the distribution of young pike over the vegetation cover are summarized in Section 2.7.4. Grimm (personal communication) found indications in shallow waters in the Netherlands, that pike up to 15 cm length occupied zones of vegetation that were physically inpenetrable for larger pike.

1.5.3.2 Juveniles and adults

Typically, adult northern pike live in clear lakes and streams with weedy bottoms and margins, but they also occur in turbid waters

(Toner and Lawler, 1969). Pike are found in shallow waters in spring and summer with a gradual return to deeper parts of the water as winter approaches. According to Eddy and Surber (1947), northern pike prefers sluggish streams and seems to be fond of the warm, muddy waters of shallow, weedy lakes, but is equally abundant in most of the cold, clear waters of the deep, rocky waters of the north. Threinen et al. (1966) described pike as inhabitant of the shallow waters of lakes. The pike is most abundant in shallow lakes with numerous extensive weed beds. Large marshes with rivers flowing through them can be described as northern pike factories according to these authors.

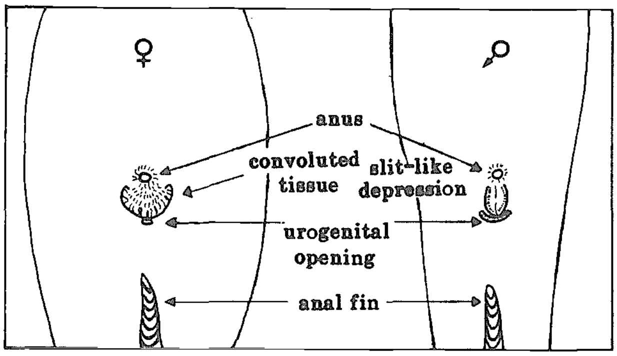


Figure 4 External differences in the urogenital zone of northern pike males and females (Redrawn after photographs in Casselman, 1974a)

2. BIONOMICS AND LIFE HISTORY

2.1 Reproduction

2.1.1 Sexuality

2.1.1.1 Hermaphroditism, heterosexuality

June (1977) examined 1 936 ovaries of northern pike from Lake Oahe (North and South Dakota), a Missouri River reservoir, and found two hermaphrodites. Both male and female portions of the gonads were maturing or apparently had reached maturity simultaneously. In both cases the gonads consisted of an ovotestis and an ovary.

The northern pike is heterosexual in its behaviour. Fabricius and Gustafson (1958), however, reported incidental occurrence of homosexual behaviour of males during spawning.

2.1.1.2 Sexual dimorphism

There are no obvious external differences between the sexes. Casselman (1974a) examined 5 199 northern pike from 1961 to 1969 and concluded that spontaneous passage of reproductive products from the urogenital pore is the most accurate indicator of sex. However, it can be used to differentiate only a small percentage of individuals annually. A technique of sexing mature and immature pike by external appearance of the urogenital region is described. Accuracy of the technique was tested throughout the year with success (see Figure 4).

According to Demchenko (1963, cited by Casselman, 1974a, who used the original Russian article as source and not the misleading abstract in Biological Abstracts 43(4):16910) the urogenital-anal region offered the most reliable sexing characteristics. The author emphasized the width of the urogenital opening relative to the anal opening. He suggested that in females the urogenital opening is as wide or wider than the anal opening, whereas in males the urogenital opening is narrower than the anal opening.

Casselman (1974a) considered that Demchenko's (1963) sexing technique, because of variation on seasonal basis, better be ascribed to immature than to mature northern pike.

2.1.2 Maturity

The age and size at maturity varies with the geographical latitude in which northern pike are found, the environment and possibly the fertility of the water (Toner and Lawler, 1969). According to Nikolski (1957) northern pike is usually sexually mature in its fourth year of life. Diana (1983) suggested, in analysing the growth of pike in three Michigan lakes, that increased fishing mortality resulted in an earlier age at first maturation and increased total allocation of energy to gonads in females.

Many authors report that one-year-old northern pike can be sexually mature. Hopke (1934) reported progeny from one-year-old northern pike in fish-culture ponds in Germany. Frost and Kipling (1967) concluded from an analysis of age and size at first spawning that it is size rather than age which determines when a pike will first spawn, the growth rate determining the age in which this size is reached. Heuschmann (1957) concluded that favourable feeding conditions and maturity of one-year-old pike were related. Willemsen (personal communication) recorded at the end of March mature male and female northern pike in a pond that was stocked with northern pike larvae one year before. From this observation in the pond situated in Holland, Willemsen concluded that pike of one year can mature at lengths of 19 cm (male) and about 30 cm (female). The weight of the ovaries amounted to about 4% of the body weight. Grimm (personal communication) made comparable observations in ponds at the same location. He also observed fertilized eggs and fry resulting from spawning activities of one-year-old pike. Grimm suggests that the absence of larger and older pike in the rearing ponds, together with favourable feeding conditions, probably resulted in the early maturity of the northern pike. Clark (in Toner and Lawler, 1969) also reported mature one-year-old hatchery pike. He recorded that out of 93 one-year-old hatchery pike, 12 showed signs of maturity. Only one of these was a female from which the eggs flowed on handling.

Frost and Kipling (1967) examined 52 males of the pike from Lake Windermere and found that 46 were aged two years when they spawned for the first time. One fish was aged one year and 5 fish were aged three years at first spawninsg. Examination of 42 females revealed that 39 were aged two years, 1 fish was aged one year and 2 were aged three years when they first spawned. The one-year-old spawning male and female were 24.7 cm and 27.0 cm, respectively. Munro (1957) reported from the Scottish Loch Choin that in the 2^+ group 40% of the males and 37% of the females were mature. The smallest maturing male and female were 26.3 cm and 25.7 cm, respectively. No fish in the 0^+ and 1^+ groups were ripe.

In Ireland, Healy (1956) found that in Barnagrow Lake, where the rate of growth was slow, only 2% of the males were mature 12 months from hatching and only 11% of the females were mature 24 months from hatching. In Lough Clore, where the growth rate was more rapid, she found that 74% of the males were mature 12 months from hatching, while 70% of the females were ripe 24 months from hatching. Kennedy and Fitzmaurice (1969) reported from the Irish limestone lakes that the majority of the male pike spawn when only a year old; the majority of the females when two years old. Mature one-year-old pike are also reported from Spanish waters (Calderon-Andreu, 1955) and from the Italian Trasimeno Lake (Calderoni, 1967).

Goedmakers and Verboom (1974) found a correlation between vitellin content of the blood of the northern pike and their maturation stage. Further study of the vitellin cycle may possibly reveal a tool for fertilization experiments with northern pike.

Data on the age of northern pike at first spawning are summarized in Table V.

2.1.3 Mating

Zawisza (in Toner and Lawler, 1969) reported that each female is accompanied by a few males onto the spawning grounds (for sex ratio see Section 3.1.3). Rawson (1932) reports that males and females were about equal in number in spawning runs, but Clark (1950) says that while males predominated in the early spawning movements, females were more numerous later on.

Unripe females adopt the threat posture on the approach of a courting male, or show the male off by a sudden sideward bending of the head. Ripe females respond to the approach of the male by a slow forward swimming which initiates the courtship swimming of the couple. The males seem to prefer females which are larger than themselves (Fabricius and Gustafson, 1958).

Mating can be described as polygamous and promiscuous.

2.1.4 Fertilization

According to Lindroth (1946) fertilization is external and the micropyle closes after about 0.5 to 1 minute; at 20°C closure is reached after 45 seconds.

Fertilization is not influenced by oxygen content of the water, salinity or light. The micropyle remains open for the longest time at pH 7; at other pH values, the fertilization time becomes shorter (Elster and Mann, 1950). The influence of water and other factors on the opening and closure of the micropyle is described by Lindroth (1946) and Sorenson, Buss and Bradford (1966).

Huisman, Koeman and Wolff (1972) analysed rates of fertilization in pike eggs from different locations in the Netherlands. A negative relationship was indicated between fertilizability of eggs and DDT residue in eggs.

2.1.5 Gonads

2.1.5.1 Testes and sperm

Hoffmann, Wondrak and Groth (1980) described the morphological structure and seasonal changes in the testes of the northern pike. They are confined to both sides of the swim bladder. The lengths of the testes increase in relation to the swim bladder, while the proportion of body weight to testicle weight depends on the season and changes in gonadal diameter.

The histological appearance of the germinal tissue is also influenced by the season, which agrees with the macroscopic changes. Four stages in the development cycle of the testes can be distinguished:

Stage I: June to August - stage of rest: epithelium of the tubules consists of a single layer of spermatogonia;

Stage II: September to November - stage of development: diameter of tubules increases, intensive spermatogenesis takes place;

Stage III: December to March/April - stage of maturity: largest tubule diameter 82.87± 21.81 μm is reached. No spermiogenetic activity;

Stage IV: March/April to May - post-spawning stage: after spawning the diameter of the tubules decreases to 54.81±13.32 μm

The male gonads, when fully built up, form 2-4% of the total body weight of the fish (Hoffmann, Wondrak and Groth, 1980; Frost and Kipling, 1967; Steffens, 1976; Mann, 1980; Billard, Mackay and Marcel, 1983).

Montalembert, Marcel and Billard (1980) studied the quantitative and qualitative evolution of sperm release during the spermiation period. The authors used pike kept in captivity in a 400-m² pond.

The quantity of sperm collected every week over a period of two months was very small and showed strong individual variation. It

Table V

Age of northern pike at first spawning
(Modified after Frost and Kipling, 1957)

Location	Age and length at which the majority of the age-class is sexually mature				Remarks	References
	Males		Females			
	Age (years)	Length (cm)	Age (years)	Length (cm)		
Lake Windermere (UK)	2	38	2	42	-	Frost and Kipling (1967)
Loch Choin (Scotland)	3	30	3	31	-	Munro (1957)
Lough Glore (Ireland)	2	-	2	-	-	Healy (1956)
Lough Barnagrow (Ireland)	3	-	3	-	-	Healy (1956)
Irish limestone lakes	1	-	1	-	-	Kennedy and Fitzmaurice (1969)
Greifswalder Bodden (GDR)	1	-	2	-	Brackish water, Baltic coast	Hegemann (1958), Permitin (1959)
Rybinsk Reservoir (USSR)	2-3	40-44	3-4	40-44	-	
Lake Lacha (USSR)	4	37	5	44	-	Koz'min (1980)
Wisconsin lakes	2	38-46	2-3	51	-	Scott (1954)
Gilbert Lake (Wisconsin)	2	34-43	2	40-57	-	Priegel and Krohn (1975)
Escabana Lake (Wisconsin)	1	33.5	2	49	Before size limit	Kempinger and Carline (1978)
Escabana Lake (Wisconson)	3	42	4	-	After size limit	Kempinger and Carline (1978)
Bleury Stream (Canada)	2	30-35	2	35-40	-	Fortin et al. (1982)
Waskesiu Lake (Canada)	4	-	3	38	-	Rawson (1932)
Great Bear Lake (Canada)	5	39-45	6	39-45	-	Miller and Kennedy (1948)
Lake Oahe (North Dakota)	2-3	32-40	3-4	42-63	-	June (1971)
Murray Lake (Michigan)	1 (71%)	-	1 (17%)	-	Earliest age at maturation	Diana (1983)
	2 (80%)	-	2 (67%)	-	occurred in the lake with	
	3(100%)	-	3(100%)	-	highest mortality rate,	
Houghton Lake (Michigan)	1(100%)	-	1 (80%)	-	whereas the latest age at	Diana (1983)
		-	2(100%)	-	maturation coincided with	
Lac Vieux Desert (Michigan)	1 (80%)	-	1 (31%)	-	lowest mortality rate	Diana (1983)
	2 (94%)	-	2(100%)			
	3(100%)	-				

gradually increased until the fifth week and then decreased again. The quality of the sperm, estimated by activity and duration of motility, followed a similar evolution to that of total quantity of sperm gathered. (First ovulation in females was noticed six weeks after the beginning of the experiment when spermiation had already declined. The difference in time between the occurrence of spermiation and ovulation period is, according to the authors, probably caused by the stressing experimental conditions).

Lindroth (1946) gives a short description of the sperm of northern pike which is built like most of the sperm of vertebrates. The head of the sperm is about 1.5 µm in diameter, and together with the tail the sperm measures 20-25 µm. Sperm concentration in undilluted circumstances is in the range of $18\text{-}30 \times 10^9$.

2.1.5.2 Ovaries and ova

Ovaries of northern pike consist of two elongate sacs, pear-shaped and orange-coloured, lying parallel to the swim bladder and individually suspended over most of their length by the mesovarium. They narrow posteriorly and join to form a short, broad oviduct that opens behind the anus and in front of the urinary pore. The bulk of the ovary consists of a complex series of transverse ovigerous lamellae. At maturity, ova are discharged from the follicles into the parovarial canal, which runs the entire length of each sac (June 1971).

The ovaries contain ova of varying size which are evenly distributed over the organs (Kipling and Frost, 1969) and mature uniformly (June, 1971). Smísek (1967), however, found differences in fertilizability between eggs in different parts of the ovary. Spawn from the cranial part had lowest fertilizability; spawn from the medial part highest.

Three distinct developmental stages were recognized by June (1971). The following description is mainly adapted from this author, who studied pike from Lake Oahe.

Stage I: Ovaries with immature eggs - both the primitive ova found in all ovaries throughout the year and those that have begun differentiation for the spawning season can be distinguished. Ovaries of sexually immature females contain only the primitive ova that are spherical or irregularly shaped and range to about 0.18 mm in diameter. Ovaries containing only primitive ova are thin, ribbonlike and transparent. Ovaries containing immature eggs that started differentiation for the seasonal spawning are slender and whitish to pinkish. The ovarium is in this stage (a) after complete evacuation of ova, or (b) when ova are not fully evacuated, or (c) ova are undergoing resorption (June, 1970). Period: June - mid August/mid October.

Stage II: Ovaries with maturing ova - which are yellow and opaque. Yolk spherules form a dense mass. Ova vary widely in size and measure from about 0.49 to 3.23 mm. Ovaries are yellowish to orange and turgid; the ovarian artery and its lateral branches are prominent. From mid August to mid October is the onset of this stage of rapid growth of immature ova. The growth continues uninterruptedly during the winter.

Stage III: Ovaries with mature ova - ovaries are turged and yellowish. Some ovulated ova may lie loosely within the ovarian canal, and slight pressure forces most ova from the follicles. The ova have undergone distinct morphological changes. Yolk spherules and globules disappear, yolk is confined to thin granular surface layer. Mature ova are spherical translucent pale yellow and range from 1.83 to 3.29 mm. Within this stage, that is reached in the active spawning season, ovaries and fish may be further classified as:

(a) running ripe, if ova flow freely from the oviduct when the fish is handled;

(b) partially spent, if the ovaries contain some unovulated mature ova with freshly ovulated residual mature ova from an earlier spawning;

(c) recently spent, if a few freshly ovulated residual mature ova lie scattered among the transverse folds or within the ovarian canal.

Frost and Kipling (1967) show that in Lake Windermere the growth of ovaries starts in late summer. The development continues steadily from October to the end of December. At the end of February the ovaries comprise about 15% of the total body weight. When northern pike are in the running ripe stage the ovaries form 18-20% of the total body weight of the fish.

The yearly growth cycle of ovaries and the development of ova of northern pike is also described by Carbine (1943) from Houghton Lake, Michigan, by Shikhshabekov (1978) from waters in Russian Dagestan, and by Mann (1976) from River Stour, Dorset, England.

Diameter measurements of eggs provide a rather precise assessment of the stage of maturation of the ovum. The technique, however, is time consuming and tedious. June (1971, 1977) therefore proposed to use the so-called "ovary index" in the study of maturity stages in northern pike. This index can be calculated with the use of:

$$\text{Ovary index} = \frac{W}{L^3} \cdot 10^4$$

where W = weight of both ovaries in grams and L = length of the fish in centimetres, millimetres or inches. The ovary index gave an acceptable relation with the maturity stage of the ova (see Figures 5 and 6).

Jalabert (1976) studied the endocrine processes which control the oocyte maturation (structural and biochemical modifications which

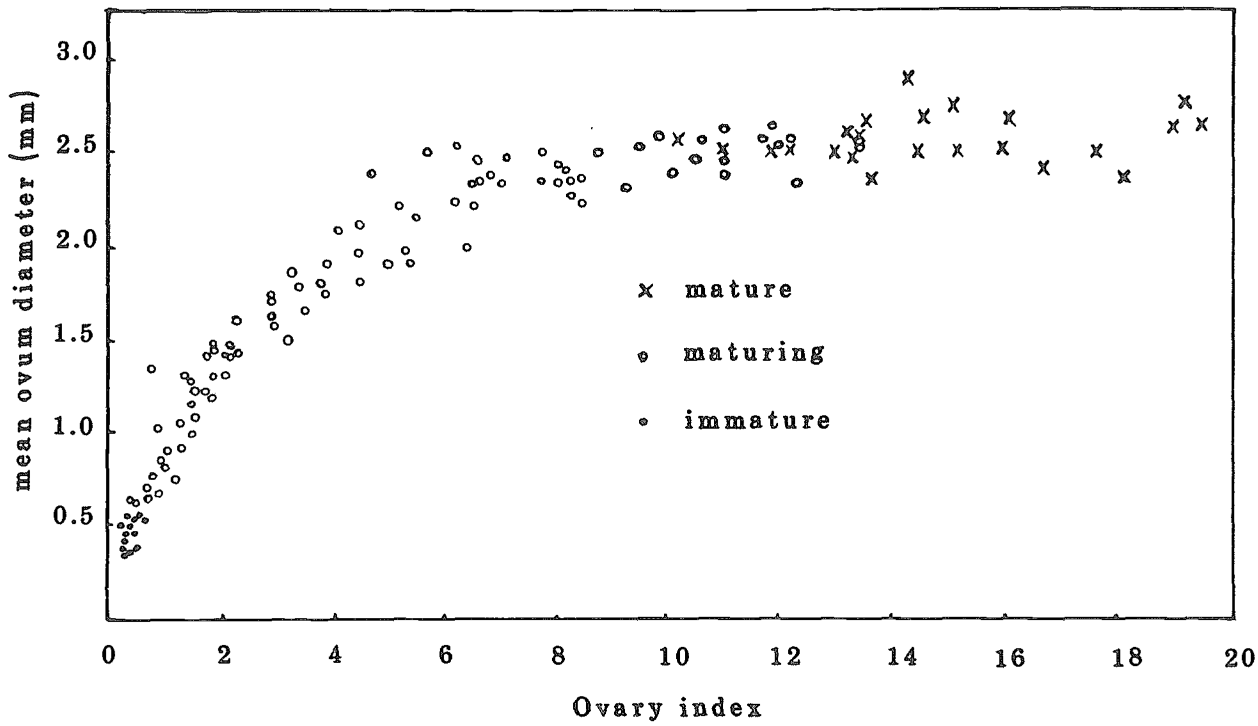


Figure 5 Relation between the ovary index and the mean diameter of the most mature group of ovarian ova of 125 northern pike from Lake Oahe examined in 1964 and 1965 (Redrawn after June, 1971)

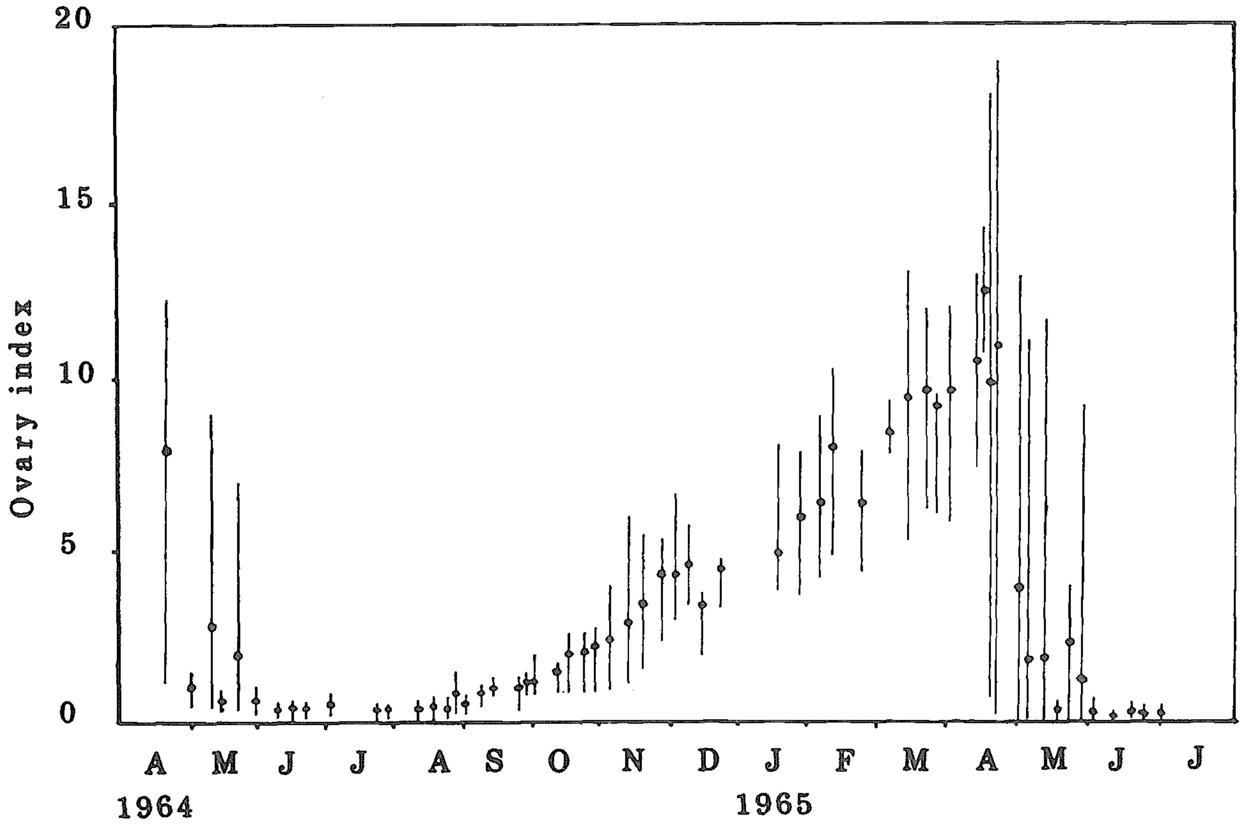


Figure 6 Seasonal maturation cycle of northern pike, based on the range (vertical lines) and mean (dots) of the ovary indices of 621 females from Lake Oahe, examined in 1964 and 1965 (Redrawn after June, 1971)

develop simultaneously with resumption of meiosis) and ovulation (emission of the denuded oocyte from the follicle) in vitro. Follicular maturation is ultimately under control of a pituitary gonadotropin, which induces the follicle to synthesize specific steroids. These steroids act in turn directly on the oocyte to promote maturation.

The ovulatory process has been experimentally dissociated from oocyte maturation. The author proposed the hypothesis that the relay between maturation and ovulation could be the sympathetic nervous system receiving an end-of-maturation signal and then inducing stimulation of α-adrenergic receptor sites of the ovary and follicle. These would then trigger and/or release prostaglandin acting on the contraction of follicular envelopes.

Montalambert, Bry and Billard (1978) also tested the effect of retention of ova on fertility. Ageing of ova is a rapid phenomenon. The drop in fertility occurred in vivo experiments within two days after ovulation had taken place, induced by hormonal stimulation (see Section 5.2.2).

2.1.5.3 Fecundity

The dynamics of fecundity of northern pike are determined by physiological features, ecological factors, spawning conditions and prey fish availability (Spanovskaya and Soloninova, 1983).

According to Bagenal (1970), the annual variations in fish egg number related to fish of the same length were 23% in northern pike. Kipling and Frost (1969) suggested that changes in the number of eggs per gramme of total fish weight could be a density dependent population regulating mechanism in Lake Windermere. The authors postulated that stress caused by overcrowding results in the effect that pike produce fewer eggs for the next spawning season. Fecundity, however, is considered as only one of several factors which determine how many viable eggs will be laid in any particular year. Biomass of all female mature pike and efficiency of fertilization are considered as other determining factors.

Craig and Kipling (1983) described the potential for variation in reproduction by northern pike populations in Lake Windermere. The relative fecundity of pike has responded to changes in adult biomass. There is a highly significant inverse relationship between numbers of egg per gramme of pike and stock biomass two years before spawning. In 1950 and 1961 mean values of relative fecundity (No./g) were 19.3 and 19.6. Since 1964 a general trend upward was observed from 27.3 to the maximum observed, 39.3 in 1981. This increase in relative fecundity occurred with the decline in population numbers and biomass. A peak value in population numbers of pike was reached in 1961, followed by a sharp decline. Then, after a few years with little change, the general trend has been downward. Estimates for 1980 and 1981 were the lowest ever found in Windermere (Kipling, 1983a).

The number of eggs rapidly increases with increase in body length and is roughly proportional to weight (Carbine, 1943). Relative fecundity partly decreases with increasing weight (Steffens, 1976). Sukhanova (1979), however, reported from Vilyuy reservoir (USSR) that the relative fecundity of pike increases with the increase of body weight, while with age it increases only slightly.

Marked differences in fecundity were reported between pike of the middle Volga River and those of the lower Volga and the north Caspian Sea (Nikolski, 1969). The same author and Berg (1962) reported differences in fecundity between pike from the Ob River and Aral region and pike from the lower Volga River.

According to Schäperclaus (1940), large northern pike have larger eggs than small pike. Nikolski (1969) did not find any change in egg size with advancing age. Random variation in egg size was found. The author suggests that decrease in size occurs in the group that is most numerous in the population. The fecundity could be affected as a response to lower food intake that results from competition between individuals of the same age or size.

June (1970, 1977) reported about a factor that can have considerable influence on the amount of viable eggs that will be deposited in a particular year. The author found that in Lake Oahe and Lake Sharpe, two large Missouri River impoundments in South Dakota, between 71% and 74% of the running ripe females of the northern pike examined in 1966 and 1968, contained atretic mature ova; 27% to 63% of these pike had 50% or more atretic mature eggs. The occurrence of atresia was associated with fluctuations in water temperature and water level that apparently interrupted spawning. Atresia may lead to considerable error in estimates of the reproductive potential of northern pike populations. Kennedy (1969) examined unspawned northern pike that were caught in June in Lough Derravarragh, Ireland. A drop in the level of the Lough in the course of a drainage scheme prevented the pike from getting into their normal spawning sites. The eggs in the ovaries were being resorbed. Bruyenko (1976) observed in the Kremenchug reservoir (USSR) that in 1972, when the spawning grounds were not flooded, approximately 80% of the female pike did not spawn and had resorbed eggs.

Sycheva (1965) and Poddubny (1976) found that modified environment in the Kakhovskoe reservoir (fluctuating water level, irregular temperature of the water, etc.) produced disruptions in the timing of gonadal maturing stages and the ensuing decrease in fertility. Partial deposition of roe was noted despite the lack of favourable spawning grounds where favourable temperatures prevailed. Roe retained in ovaries was subject to complex and prolonged resorption processes. Losses of eggs laid on non-typical substratum up to 70-100% were reported. This delayed the development of new ovocytes and, in consequence, caused disruptions in the timing of individual developmental stages. Asynchronization of oocyte development during vitellogenesis occurred. Gonads in some females did not attain maturity in spring due to resorption, as noted above. Such females failed to spawn, their immature oocytes maturing in some cases by fall and then being resorbed. Testes were not subject to noticeable changes. In Table VI the data on fecundity of northern pike are summarized.

2.1.6 Spawning

2.1.6.1 Spawning migration

In spring, some individuals may migrate from lakes into tributary streams, ditches or marshes to spawn, while those that remain in the lake move extensively during this time (Miller, 1948; Diana, Mackay and Ehrmann, 1977). Increasing day length and increasing water temperatures may release migration activities in pike. Migration distances travelled can be considerable, as is shown by Carbine and Applegate (1946) in Houghton Lake, Michigan (between 2 and 76 km). One marked pike was reported to have travelled 16 km in 22 hours.

Dubé and Gravel (1980) reported that the gloom within irrigation pipes can impair the movements of fish. The authors demonstrated that the gloom can function as an impediment to the utilization of draining pipes by northern pike during a spawning run. The construction of small bridges as a solution to the problem of maintaining favourable conditions for the migratory movements of fish is recommended, although this method remains a compromise to the ideal solution which would preserve the integrity of the natural environment.

The individual spawner may arrive on the breeding ground considerable time before it actually spawns, the males arriving several days - sometimes several weeks - earlier on the spawning grounds or the surroundings than the females (Fortin et al., 1982; Frost and Kipling, 1967). The males generally remain longer on the breeding grounds, although northern pike does not guard its spawn. Svärdson (1947) found that in Lake Malar (Sweden), an individual fish may stay a month on the spawning ground, the minimum for a female being 10 days, for a male 14 days. In Windermere, evidence from the recapture of tagged fish suggests that a male can remain 38 days in the spawning area and the mean length of stay of 32 males recaptured on the spawning ground was 14 days. The maximum time for recapture of a female was 27 days; the mean length of stay was 10 days (Frost and Kipling, 1967; see also Fabricius and Gustafson, 1958).

Richard (1979) hypothesised that adult northern pike returns to its spawning grounds in the period between February and April because it recognizes the spawning ground by the smell of decayed organic material. The hypothesis that pike remembers its birthground, which is based on observations on spawning behaviour of northern pike in River Marne (France), is supported by observations from other places. Frost and Kipling (1967) report that pike in Lake Windermere use the same spawning grounds every year. Bregazzi and Kennedy (1980) found evidence that pike in Slapton Ley (England) may return each year to the same area to spawn. According to Franklin and Smith (1963), pike in Lake George, Minnesota, exhibited no homing tendency for particular spawning grounds.

Forney (1968) reported that northern pike started spawning migration from Oneida Lake, New York, to adjacent marshes when the lake was still covered with ice. Shikhshabekov (1978) reports from Dagestan waters (USSR) that spring spawning migration begins at the time of ice melt. In the Dniepr delta the spring run of pike begins under the ice (Berg, 1962). Franklin and Smith (1963) and Priegel and Krohn (1975) made similar observations in lakes in Minnesota and Wisconsin. Migration to spawning areas in these studies took place within a period of 5 to 15 days, at water temperatures between 1° and 4°C. Clark (1950) recorded runs of northern pike at 0°C in Ohio waters. Vostradovsky (1981) reported that the activity of northern pike increases in direct dependance of water temperature. At the inflow region of the Czech Zelivka reservoir, the capture rate of pike by electrofishing culminated at a temperature of about 6°C. At temperatures above 10°C, the capture rate rapidly decreased and the fish returned from the spawning grounds to their scattered original residences in the reservoir.

Johnson and Müller (1978) and Müller (1982) report for northern pike in the coastal area of the Bothnian Sea that the fish is in many cases anadromous. At the time of spawning, pike ascend the coastal rivers up to 6 km from the estuaries. There the fish can intermingle with pike that are more stationary in lakes. In 1977 and 1978, the upstream migration started on 17 and 5 May, respectively, with a maximum of ascending fishes a week later. After spawning in the second part of May, most of the adult pike leave the stream again for the sea. The 0^+ pike develop in the stream and migrate in the course of the summer to the sea. According to Kaukoranta and Lind (1975), brackishwater populations of northern pike in Finnish waters used the same spawning grounds in fresh water every year.

2.1.6.2 Spawning grounds and spawning time

Berg (1965) reports that pike in the delta of the Volga River spawn in the early spring. The local non-migratory pike spawn from the middle of April, before the pike come from the sea. Spawning females of the latter may occasionally be found in the lower and middle sections of the delta till 25 May. Between 6 and 9 May 1941, all the pike in the floodlands had liquid roe; the water temperature was 21°C.

Spawning usually takes place at temperatures ranging from 6° to 14°C (see Table VIII).

Table VI

Fecundity of northern pike

Locality	Length (in cm)	Weight (in kg)	Absolute fecundity (in No.x10^3)	Relative fecundity (mean No./g weight)	References
Lake Siljan	50-110	0.6-7	3.7-71	4-29	Lindroth (1946)
Waters in Ireland	-	-	-	20-42	Healy (1956a)
Loch Lomond, Scotland	43-100	-	-	29	Shafi and Maitland (1971)
Windermere	50-59	-	-	26-31	Kipling and Frost (1969)
	60-69	-	-	27-32	
	70-79	-	-	25-32	
	80-89	-	-	26-33	
	90-99	-	-	23-29	
	100-109	-	-	21-27	
	110-119	-	-	24	
Windermere	-	-	-	19.3 (1950)	Kipling (1983a)
	-	-	-	19.6 (1961)	
	-	-	-	27.3 -> 39.3	
	-	-	-	(1964 -> 1981)	
Waters in German Dem. Rep	-	0.3-2	8.8-72.9	-	Anwand (In Steffens, 1976)
Province of South Holland	44-72	0.1-3	8-120	-	Goedmakers and Verboom (1974)
Waters in Czechoslovakia	-	0.5-4.5	7.7-61	15-21	Smísek (In Steffens, 1976)
Lipno reservoir, Czechoslovakia	-	0.4-2.8	7.4-63.6	-	Vostradovsky (1983)
Rheinniederung and Starnberger Sea	31-35	0.2-0.35	9.4-16	38-46	Mast (In Steffens, 1976)
Waters in Poland	-	0.4-5.1	14-141.5	20-29	Terlecki (In Steffens, 1976)
	-	9.1	192	21	
	-	-	-	27	Zawisza (Toner and Lawler, 1969)
Muinak (southern coast of Aral)	36-40	-	8.3	-	Berg (1962)
	41-45	-	13.2	-	
	46-50	-	24.6	-	
	51-55	-	26.7	-	
	56-60	-	43.0	-	
Volga delta	36-40	-	16.6	-	Berg (1962)
	41-45	-	31.2	-	
	46-50	-	43.7	-	
	51-55	-	59.9	-	
	56-60	-	79.7	-	
Dnieper delta	33	-	7.1	-	Berg (1962)
	85	-	182.2	-	
Tsimlyansk reservoir	30-90	-	9.2-149.2	-	Domanevski (In Sukhanova, 1979)
Rybinsk reservoir	30-100	-	6.4-233.8	-	Zakharova (In Sukhanova, 1979)
Vilyuy reservoir	60-95	2.4-8.8	29-121	11-14	Sukhanova (1979)
Houghton Lake, Michigan	-	-	7.7-99.3	-	Carbine (1943)
Waters in Minnesota	34-64	-	-	20-30	Carlander (1958)
Lake Oahe, Lake Sharpe, South Dakota	45-95	-	15-198	-	June (1971)
Bleury Stream, Quebec	-	-	-	30	Fortin et al. (1982)

Table VII

Regressions for the number of eggs (E) versus the length (L)/weight (W) of the female from various locations

Location	Regression formula	Total/ fork-length	Unit	References
Pleasant Lake Marsh (Wisconsin)	$10^{-3}.E = 4.417\ L\ 62.556$	TL	inch	Fago (1977)
Gilbert Lake (Wisconsin)	$10^{-3}.E = 4.980\ L - 74.885$ $\log E = 3.161 \log L - 7.227$	TL TL	inch cm	Priegel and Krohn (1975)
Houghton Lake (Michigan)	$10^{-3}.E = 3.798\ L - 57.256$	TL	inch	Carbine (1943)
Lake George (Minnesota)	$10^{-3}.E = 4.401\ L - 66.245$	TL	inch	Franklin and Smith (1963)
Lake Oahe (South Dakota)	$\log E = 3.128 \log L - 3.999$	FL	cm	June (1971)
Marsh near Lake Oneida (New York)	$10^{-3}.E = 4.417\ L - 65.555$	TL	inch	Forney (1968)
Bleury Stream (Canada)	$\log E = 3.522 \log L - 5.269$	FL	mm	Fortin *et al.* (1982)
Water in South Holland (Netherlands)	$10^{-3}.E = 3.200\ L - 129.740$ $10^{-3}.E = 40n\ W - 6.590$	TL	cm	Goedmakers and Verboom (1974)
Slapton Ley (SW England)	$\log E = 3.4861 \log L - 5.045$	FL	mm	Bregazzi and Kennedy (1980)
River Stour (England)	$\log E = 3.56 \log L - 5.40$	FL	mm	Mann (1976)

Fabricius (1950) demonstrated with field observations that a rise in water temperature releases spawning activity, but at the same time the right kind of spawning substratum (one of vegetation) must be present to effect this release. Experiments on the effect of temperature, which Fabricius and Gustafson (1958) carried out in tanks, show that warming up of water (to between 12.5° and 18.5°C) stimulated spawning and that cooling suppressed it. Clark (1950) observed spawning groups as early as 6 a.m. and as late as 6.30 p.m. in tributaries to Lake Erie. Cool nights seemed to delay spawning activities the next morning. No spawning activities were noted until water temperature reached 9°C. Decrease in water temperature resulted in retarded or no spawning activity (Fabricius, 1950; Sycheva, 1965; Fortin *et al.*, 1982; Kennedy, 1969). No spawning activity was noted in the field during the night (Clark, 1950; Kennedy, 1969).

Frost and Kipling (1967) report that the kind of place where pike spawn in Lake Windermere is a relatively sheltered part of the shore, usually backed by a stand of *Phragmites*. The substratum is essentially silt and gritty sand rather than stony, although stones are occasionally present. The vegetation consists of *Elodea*, *Myriophyllum* and *Nitella* in stands of mixed or single species, and in some places there are patches of *Littorella*. The plants are in 2 to 3.5 m of water. Sometimes breeding pike have been seen in water which was only 15 to 30 m deep.

In most other places, spawning activity of northern pike is reported from areas with emergent vegetation like *Phragmites*, *Carex* or *Equisetum* (Fabricius, 1950). Kennedy (1969) reports that spawning in several Irish limestone lakes took place in shallow water over grass or sedges. Eggs were deposited on *Fontinalis* sp. or *Agrostis stolonifera*, *Juncus bulbosus*, some *Apium inundatum* amd *Mentha aquatica*. Spawning was associated with high or rising lake levels. Koz'min (1980) reports from Lake Lacha (USSR) that pike spawns during the period of rise in temperature and water level. The end of the spawning coincides with the peak of the spring flood. Batches of eggs were found at depths to 50 cm on the stems of reeds and on freshly inundated meadow vegetation. The main spawning grounds were located in parts of the lake rich in shallows with reed beds of higher aquatic plants.

Franklin and Smith (1963) observed at Lake George, Minnesota, that pike spawning never occurred in cattail areas (*Typha*), but that all other vegetation types were utilized in marshy locations of the lake. The same is reported by

Table VIII

Spawning season and spawning temperatures recorded in various locations

Locat on	Year	Length of spawning season		Temperature in Celsius	References
		Beginning	End		
FINLAND					Kaukoranta and Lind (1975)
Small lakes and ponds near Lammi	1900–15	April 21	May 27	1–11	
Lake Lappajärvi	–	Early May	Late June	–	
Lake Oulujärvi	–	Late May	Early June	–	
Mouth of Oulujoki River	1971	May 17	May 28	4.5–6	
Mouth of Oulujoki River	1972	May 19	May 26	7.5–9.5	
SWEDEN					Fabricius (1950)
Lake Vojmsjä (two sites)	1949	May 13	May 29	–	
	1949	May 20	June 2	–	
Lake Mälar	1945	March 27	May 17	–	Svärdson (1947)
Lake Mälar	1946	April 4	May 25	–	
DENMARK					Larsen (In Toner and Lawler, (1969)
Fresh water	–	April	April	–	
Brackish water	–	Late May	Early June	–	
UNITED KINGDOM					
Lake Windermere	–	Early April	Early May	> 6	Frost and Kipling (1967)
Slapton Ley	–	February	Late April	–	Bregazzi and Kennedy (1980)
IRELAND					
Three Irish Loughs	–	February	April	–	Healy (1956)
Lough Corrib	1965	March 30	Mid April	> 9/10	Kennedy (1969)
Lough Corrib	1966	February 14	–	> 9/10	
GERMAN DEMOCRATIC REPUBLIC					
Greifswalder Bodden (Brackish water, Baltic coast)	1955	April 16	May 18	–	Hegemann (1958)
POLAND					Zawisza (In Toner and Lawler, 1969)
–	1957	March 26	–	> 2–4	
–	1958	April 28	–	> 2–4	
NETHERLANDS					Author (based on internal OVB reports, periods in which eggs were obtained for northern pike culture)
Westeinderplas	1968	March 19	April 16	–	
(Province of South Holland)	1969	March 25	April 29	3.5–10	
	1970	March 24	April 27	min. 6	
USSR					
Vilyuy reservoir	1976	May 20 (male)	Mid June	> 4	Sukhanova (1979)
		May 26 (female)	Mid June	> 4	
Ukraine		February 20	April 20	> 4	Fedin (In Toner and Lawler, 1969)
River Lena, middle reaches	–	Early June	–	5–7	Sokolov (1971)
Rybinsk reservoir	–	April 17	May 6	10–18	Poddubny (1976)
Currents of Rybinsk reservoir	–	April 15	April 25	2–10	
Lake Lacha	–	End April	Through May	4.8–7	Koz'min (1980)
Waters in Dagestan	1972	March 14	Begin. April	6–7	Shikhshabekov (1978)
Waters in Dagestan	1975	March 12	Begin. April	–	
USA					
Oneide Lake, New York	1964	April 7	–	1–14	Forney (1968)
	1965	April 7	–	1–10	
	1966	March 31	–	4–14	
Lake Conesus, New York	1979	March 15	March 31	5.5–12.5	Alldridge and White (1980)
Nettle Lake, Ohio	1947–49	March 28	April 18	> 5	Clark (1950)
Houghton Lake, Michigan		April 2	April 25		Carbine (1942)
Ball Club Lake, Minnesota		April 7	May 7		Johnson (1956)
Lake George, Minnesota	1955–57	April 1	April 19	11–17	Franklin and Smith (1963)
Lake Gilbert, Minnesota	1968	March 25	Begin. April	10–18	Priegel and Krohn (1975)
Lake Oahe, South Dakota	1964–70	March 28	June 5	8.4 (seasonal peak spawning)	June (1971, 1977)
CANADA					
Bleury Stream, Quebec	1975	April 22	End April	± 6	Fortin *et al.* (1982)
	1977	March 30	About April 19	± 8	
	1978	April 16	–	± 8	
Saskatchewan Lakes	–	May 1	May 15	13	Rawson (1932)
Waters in Manitoba	–	Late April	Mid May	–	Lawler (In Toner and Lawler, (1969)

Alldridge and White (1980) from an area in Conesus Lake, New York. Heavy and thick types of vegetation (cattail, buttonbrush, brush), were avoided by pike. More than 140 observations of spawning indicated that preferences were correlated with depth, not with vegetation type, and that as depths changed in the marsh, substrates utilized shifted accordingly. The authors suggest that spawning occurs in open water areas over any available vegetation as long as depths are within the range of 25-100 cm and cattail, brush or brushes are absent. Spawning occurred consistently at temperatures above 5.5°C.

Forney (1968) found in a spawning marsh adjacent to the Oneida Lake, New York, that pike eggs were distributed throughout the marsh where the bottom had been covered with vegetation and flooded to a depth of 25 cm or more. Neither density nor type of vegetation seemed closely related with egg deposition. McCarraher and Thomas (1972) collected information from six Nebraska sandhill lakes to evaluate northern pike-spawning success based on the type of aquatic vegetation preferred by the pike for spawning. Areas of vegetated and non-vegetated shoreline were sampled for northern pike eggs. Greatest egg densities were found on flooded native prairie grasses. In the absence of such flooded grasses, similar numbers of eggs were found on mowed hay and broken hay bales left on the grounds and inundated during the March-April spawning period. Although some lakes had extensive emergent vegetation, such plants were seldom utilized as spawning sites.

Fortin *et al.* (1982) found that pike in Bleury Stream, Quebec, preferred spawning in areas of depths less than 60 cm, covered with bottom vegetation.

Clark (1950) reported that all spawning groups observed in tributaries of Lake Erie, Ohio, started to spawn near the open lake and gradually worked back into the more shallow waters of the area. The type of bottom over which spawning took place varied greatly, but a soft silt filled with decaying vegetation predominated. From Poland, Zawisza (*In* Toner and Lawler, 1969) reports that inshore spawning occurred in shallow littoral zones protected from the wind. Spawning also occurred in flat meadows covered by spring floods. Later the deeper spawning takes place on *Elodea canadensis*.

In the Baltic Sea, pike mostly spawn in small rivers or estuaries, but also on vegetation in shallow inlets or bays. In southwestern Finland, spawning takes place also over a substrate of marine type. Pike usually choose bladderwrack (*Fucus vesiculosus*) at a depth of about 0.5-2 m (Lehtonen and Toivonen, 1981).

2.1.6.3 Spawning behaviour

Frost and Kipling (1967) believe that adult Windermere pike spawn annually. Svärdson (1947) and Nikolski (1969), however, report from other localities that northern pike do not spawn every year. Egg resorption in female spawners resulting from unfavourable water temperature and water level conditions is reported by several authors (June, 1970, 1971, 1977; Chimits, 1951; Kennedy, 1969; Sycheva, 1965). Makowecki (1973) reports from Seibert Lake, Alberta (Canada), that some females (aged 4 and 5) remained ripe until late May and early June. Four fish were recovered in this state, while virtually 100% of the other pike had finished spawning by 5 May.

Northern pike do not exhibit territorial behaviour nor do they have special spawning colours. Although no spawning territories are maintained, aggressive behaviour often occurs when individuals meet within the spawning grounds. This aggressiveness is limited to a threat posture with the branchiostegal membranes lowered and the back arched. The paired fins are extended to a maximum and the mouth is slightly opened.

During the courtship, the fish swim slowly side by side, orienting themselves so that the eye region of the male is at level with the eye region of the female. As a result of this orientation and of the different size of the partners, the genital opening of the male is usually slightly ahead of the female. Just prior to spawning, the pair slackens speed and the male moves into position. When the male is lined up with the genital pore of the female, he flips his tail fin under the female's body and mixes the eggs and the sperm as they are extruded. The spawning consists of a long series of mating acts, repeated at short intervals. The mating occurs at an average of 1.5 to 2.6 acts per minute (Fabricius and Gustafson, 1958).

Clark (1950) made comparable observations. The spawning act according to this author was completed with a splash. Each male curved the caudal position of its body outward and brought it against the female with a slap. All fish would then dart forward from the spawning site. Observations on the spawning of pike are also reported by Wilonska and Zuromska (1967).

The spawning act has a total duration of 0.5 to 0.8 seconds (Fabricius and Gustafson, 1958). Clark (1950) observed on several groups of spawning pike that spawning took place every 3 to 5 minutes. One group of 3 males and 1 female was observed to spawn on an average of every 5 minutes for nearly 2 hours. One female was seen spawning on 3 consecutive days, accompanied by 3 small males. No spawning was heard or seen by night.

The study of the olfactory organ of northern pike brought Devitsina and Malyukina (1977) to the suggestion that this species can make active use of odour signals in the spawning period. According to the authors, the occurrence of dense aggregations of spawners, splashing and stirring of the water and poor conditions of visual orientation on the spawning grounds suggest that lateral line and visual stimuli may not always play a key role in spawning.

2.1.7 Spawn

The diameter of mature ova from running ripe northern pike from Lake Oahe is presented in Table IX.

Bregazzi and Kennedy (1980) found egg diameters in the range of 2.26 to 2.56 mm just prior to spawning in the Slapton Ley (England) pike population. Carbine (1944) gives the egg size in Houghton Lake as 2.3 to 3.4 mm, and Franklin and Smith (1963) report 2.4 to 3.0 mm as egg diameters in Lake George. In Irish investigations (Kennedy, 1969) eggs of northern pike were both collected in the field and stripped artificially. Fertilized eggs were golden-to-honey coloured, translucent with moderate perivitelline space containing large numbers of oil globules distributed in numerous minute clusters. Eggs artificially fertilized in Lough Sheelin in March 1959 were 3.0 mm in diameter; in Lough Mask 2.8 to 3.0 mm, and in Lough Owel in April 1964 the diameter was 2.75 mm. Eggs in the field gave corresponding measurements.

Goedmakers and Verboom (1974) found that the mean largest diameter of eggs was between 2.91 and 4.24 mm; the values for the mean smallest diameter varied between 2.68 and 4.00 mm. The eggs were boiled and stored in formaline, however, and kept one night in tap water before measurement. An attempt to measure fresh eggs gave, according to the authors, principally the same results, but these data are less reliable.

Lindroth (1946) described the changes occurring in the egg after shedding into water:

- swelling: 25-40% increase in volume within 1 hour; the yolk sac does not take part in this swelling;

- changes in the egg capsule: hardening of the egg shell (Schäperclaus, 1940);

- within 3 minutes after shedding, the egg becomes sticky, a process completed after an hour;

- closure of the micropyle;

- rotation: movements of cytoplasma and yolk sac in the egg.

Gottwald and Winnicki (1966) described malformation of egg shells. Innerphysiological changes are supposed to have caused these malformations. The causative agent is unknown, but it is suggested that deterioration of water quality results in pathological changes. A case of swelling of eggs from older females is described. The authors refer to Russian research indicating that malfunction of the enzyme that hardens the egg shell results in osmotic swelling of the eggs.

Water exchange in the eggs of northern pike was studied by Loeffler (1971), who used isotopes. A rapid initial exchange of the fluid-filled perivitelline compartment was found, followed by a prolonged fluid exchange of the egg proper. This exchange type is characteristic of a diffusion process in the presence of a surface restriction to the waterflow.

Gajdûsek and Rubcov (1983) used a scanning microscope to examine the microstructure of the two egg membranes of pike and their changes during embryonic development. The membranes of the pike eggs from different locations exhibited an identical basic structure. They possess a complex microstructure which is subject to changes during embryogenesis. In a non-fertilized egg the canals of the inner membrane are open. After the perivitelline space has formed, lamellae that develop in the canals gradually fill their lumen. The outer membrane's canal-like openings reach into the depth of the membrane. Gajdûsek and Rubcov (1983) suggested that the openings are the former trophic ways of metabolism

Table IX

Seasonal mean and range of mean diameters of mature ova from running ripe northern pike from Lake Oahe, 1965-70 (June, 1971)

Year	Number of females	Seasonal mean (mm)	Standard error	Range of means (mm)
1965	30	2.51	0.0104	2.34-2.59
1966	14	2.61	0.026	2.43-2.79
1967	15	2.50	0.041	2.14-2.70
1968	63	2.53	0.009	2.39-2.71
1969	117	2.46	0.009	2.20-2.64
1970	44	2.55	0.009	2.42-2.72

between the maternal organism and the oocyte during the late steps of oocyte development. During embryogenesis, the thickness of the outer membrane decreased.

2.2 Embryonic Period

2.2.1 General aspects

In the following description of the development of northern pike from egg to adult until death, the terminology of intervals of fish development of Balon (1975, 1979) is used.

The embryonic period begins with the fertilization and is characterized by an exclusively endogenous nutrition from the yolk of the ovum.

The embryonic period can be divided into three phases:

(i) cleavage phase: encompasses the first interval of development within the egg membranes from the time development commences until organogenesis begins;

(ii) embryonic phase: encompasses the interval of intense organogenesis within the egg and continues until hatching is completed;

(iii) eleutheroembryonic phase: commences with hatching and lasts until most or all of the yolk is digested and the fish begin to feed externally.

Figure 7 shows the development of the egg of northern pike.

2.2.2 Cleavage phase

Kotlyarevskaya (1969) distinguished, on the basis of direct observations and data from Gihr (1957, 1958) and other authors, the following steps in this phase of northern pike development:

Step 1: From fertilization to commencement of division. Formation of the blastodisc. Lindroth (1946) gives illustrations of the fertilized egg in this step of development.

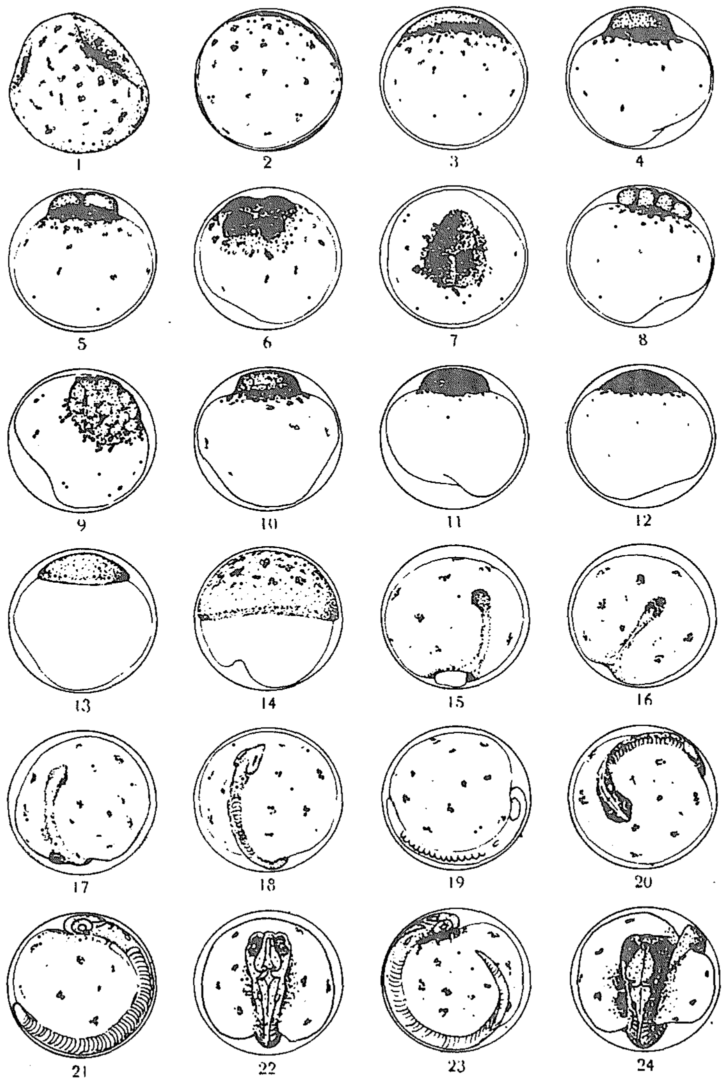


Figure 7 Development of the egg of northern pike (From Lindroth, 1946)

Step 2: Division. Blastula formation. Kennedy (1969) observed that artificially fertilized eggs were in the 2-cell stage after 5 hours. Lindroth (1946) reported that the cell divisions till the 16-cell stage occurred regularly. Blastula formation was generally completed after one day.

Step 3: Gastrulation. During this step in the development the embryo is outlined. The germ cap grows over the yolk sac and the beginning of segmentation becomes visible (Lindroth, 1946). During steps 2 and 3, the rotation of the yolk sac continually takes place. As a result of the growth of the embryo, however, the rotation of the yolk sac experiences more friction. Kennedy (1969) reported eggs to be in this step of development three days after fertilization.

2.2.3 Embryonic phase

According to Kotlyarevskaya (1969), the following steps of development can be distinguished in this phase (see Figure 8):

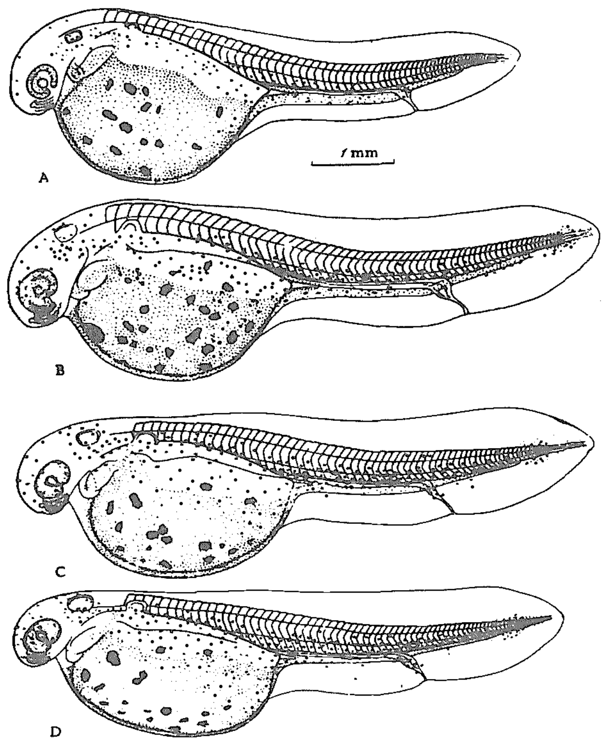
Step 4: Further segmentation of the body of the embryo into 30-40 myotomes takes place. The rudiments of a number of organs (eyes, auditory and olfactory placodes, lateral line) are in process of formation. The cerebral vesicles are being formed. Oscillatory lateral movements take place. Rudiments of hatching glands appear. Lindroth (1946) reports that growth in length during this step is unimportant.

Step 5: Development of neuromuscular movement. Increase of body segmentation to 55 myotomes. Formation of unpaired fin fold. Appearance of rudiments of pectoral fins. Heart begins to beat. Secretory granules in the hatching glands become visible (Schoofs, Opstelten and Denucé, 1982). According to Georges (1964), no cell-differentiation for the adhesive organ can be distinguished up to this step. Lindroth (1946) observed that muscle movements commence.

Step 6: Initiation and development of circulation. Development of the inferior intestinal vein as the main embryonic organ of respiration. Completion of the body segmentation. Body S-shaped. Accumulation of enzyme in the hatching glands. According to Schoofs, Opstelten and Denucé (1982) the number of hatching gland cells in the 66-somite stage is about 1 200, containing about 30 granules each. During this step, formation of the adhesive organ takes place (Georges, 1964).

Step 7: Development of ability to swim. Straightening of the body. Reduction in size of the yolk sac. Secretion of hatching enzyme. Hatching.

Till developmental step 6, all morpho-physiological features of the pike embryo, and particularly the development of the blood-vessel network on the yolk-sac and embryo movements, which perform respiratory functions, are related to their presence within the egg membrane. The embryo is not yet in a position to free itself



A - Embryo in step 6: 2.5 days before hatching, able to swim when liberated from the membrane, commencing secretion of hatching enzyme.

B - Embryo in step 7: shortly before hatching, able to swim when liberated from the membrane, commencing secretion of hatching enzyme.

C - Embryo in early step 8: early hatching, able to swim, but does not move upward. (for description of step 8 see section 2.2.5)

D - Embryo in late step 8: late hatching, moves upward and attaches itself to underwater objects.

Figure 8 Developmental steps 6, 7 and 8 in the embryonic period of the northern pike (From Kotlyarevskaya, 1969) from the membrane or to exist outside of it, as hatching enzyme is not yet being secreted. It is not yet able to swim and the adhesive organ is not functioning.

As developmental step 7 is reached hatching enzyme secretion begins. It is possible that the secretion of the adhesive cell glands in the epidermis, which begins about the same time, protects the embryo tissues from the action of the hatching enzyme.

New structural and behavioural features develop in step 7, the most characteristic being development of the ability to swim, whereby the newly hatched pike can move away from places where oxygen conditions are unfavourable. Another important feature is the functioning of the epidermal mucous glands: the adhesive organ is beginning to function (Kotlyarevskaya, 1969).

2.2.3.1 Effect of temperature

The egg development of northern pike tolerates a temperature range that varies between 4° and 23°C (Willemsen, 1959). The velocity of development is dependent on temperature. Incubation time is prolonged at low temperatures and accelerated by high temperatures.

Lindroth (1946) described the relationship between temperature and development of northern pike from fertilization to hatching as:

$$E = 4 + 1.26^{19-t}$$

where E = duration of development from fertilization to hatching in days, and t = water temperature (constant during the experiment). Braum (1964) found that at a mean temperature of 12.2°C hatching of pike eggs took 9 days, which is in agreement with Lindroth's (1946) formula. Swift (1965) also found data roughly in accordance with Lindroth's function.

Lillelund (1967) gave the following formula for the relationship between development of northern pike from fertilization to hatching and temperature:

$$T = 602.6\ t^{-0.681}$$

where T = duration of development from fertilization to hatching in day degrees, and t = water temperature (constant during the experiment). This empirical formula only agrees with Lindroth's (1946) formula in the temperature range of 10°-14°C. Above these temperatures Lindroth's formula results in too many day degrees, which can be explained by oxygen shortage in the Lindroth experiments, that retarded hatching at higher water temperatures (Lillelund, 1967) (see Figure 9).

According to Lillelund (1967), the optimal temperature for the egg development is between 9° and 15°C, which agrees with Heuschmann (1940). Willemsen (1959) gave a somewhat broader range: 7°-16°C (see Figure 10). Hiner (1961) found the range between 9° and 11°C optimal for the development of northern pike in North America. Lillelund (1967) suggests that the North American populations of Esox lucius have a lower optimal temperature for development compared to European populations. Hassler (1982), however, reports from South Dakota that optimum hatching range was 6.2°-20.9°C and maximum hatch occurred at 9° to 15°C.

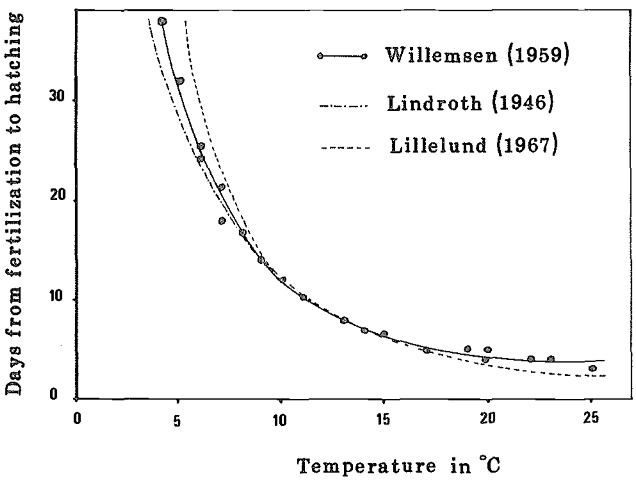


Figure 9 Relationship between duration of development from fertilization of pike eggs to hatching and temperature (Redrawn after Willemsen, 1959)

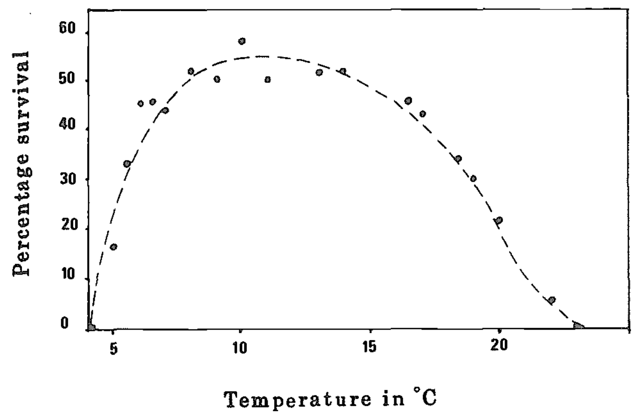


Figure 10 Influence of temperature on the survival percentage of fertilized eggs to hatching (Redrawn after Willemsen, 1959)

Two factors are of importance in the research about the influence of high or low temperatures on the egg development of pike: stage of development of the pike and duration of the temperature influence. Willemsen (1959) found that eggs can survive without damage several hours' exposure to 2°C. The sensitivity to low temperatures is not limited to certain steps in the embryonic period. Although some hatching occurred at the lower lethal temperature of 3°C, larvae did not survive at 3°C (Hassler, 1982).

Hokanson, McCormick and Jones (1973) observed that larvae that hatched at 3.7°C were all abnormal. Lillelund (1967) indicated that all larvae died soon after hatching at 3.7°C. Larvae hatched at 5.8°C developed normally when they were brought to higher temperatures soon after hatching. If they were kept at the breeding temperature of 5°-8°C after hatching, most of them died the next day. Surviving larvae did not swim up. Therefore, for normal hatching and survival of larvae, water temperature should be 6°C and over. Under field conditions, 5°C approached the lower tolerance limit of artificially fertilized pike eggs (Hassler, 1970).

Within the optimal temperature range, mortality rates of eggs between fertilization and hatching fluctuated from 60% to 80% (range of 6° to 16°C, Swift, 1965), and from 40% to 55% (range of 7° to 16°C, Willemsen, 1959).

At higher temperatures there is a close relationship between temperature tolerance and step in the embryonic development.

The first stages are the most sensitive toward high temperatures (Lillelund, 1967); this results in increased mortality rates even after short exposure to such conditions. Embryos were most sensitive (indicated by low hatching success) to temperature change and handling within the first 5 hours of development (Hassler, 1982). Hassler (1970), using artificially fertilized pike eggs which were incubated on the spawning ground, found that:

- mortalities were higher when the drop of water temperature occurred during the first 3 to 5 days of incubation and not later;

- pike eggs incubated at higher, less variable temperatures later in the spawning season had a higher percentage of hatch.

Swift (1965) found 100% mortality at temperatures of incubation above 20°C. Lillelund (1967) found that at constant rearing temperatures of 18°C 7-29% died, at 21°C 66-81% died. Experimental oscillations of temperature in daily rhythms between 15° and 20°C decreased the rates of hatching to 12%, although the upper limit of temperature during the first day of incubation had been exceeded only by 5 hours.

Franklin and Smith (1963) in their investigation of the production of northern pike in the slough of Lake George, Minnesota, noted that in 1956, when survival of eggs to hatching was estimated 89.6%, the greatest rate of temperature change was 0.7°C/hour. In 1957, when survival of eggs was estimated 67.4%, maximum rate of change was 1.7°C/hour.

Fortin et al. (1982) found that survival of eggs to the hatching stage was probably related with variations in water temperature. Eggs incubated in a period when water temperature was near freezing hatched in 15-19 days, of which 8-14% survived. Eggs incubated after the freezing period hatched in 11 days with a survival rate of 48%.

2.2.3.2 Effect of oxygen

Gulidov (1969) investigated embryonic development of artificially fertilized eggs in water of varying oxygen content. The number of eggs that hatched generally increased with increasing oxygen content. Lindroth (1946) refers to older literature in which reduced development is reported under anaerobic conditions. According to this author, eggs of northern pike tolerate oxygen deficiencies without damage for future development.

Gulidov (1969) reports that at oxygen concentrations higher than 36.4 mg O_2/litre the hatching rate was lower than at natural oxygen levels. When oxygen level was at 42.2 mg O_2/litre and above, the hatching rate was 0%. Mortality of embryos hatching at lower than normal oxygen contents comprised body defects, yolk shortage, bleeding of the pericardial cavity, blood defects and hemorrhage. At oxygen saturation up to 36.4 mg O_2/litre, lethal body, blood and yolk defects were observed. At oxygen contents above 42.2 mg O_2/litre, lethal blood and muscle deficiencies and non-response to stimulation were noted. The number of hatching embryos showing no deformities was always highest at normal oxygen contents.

The same author found that hatching under conditions of oxygen deficit occurred in an earlier stage of step-7 development than after incubation under normal oxygen conditions. When the water was oxygen-saturated, hatching took place in a much later phase of step-7 development.

Kipling and Frost (1970) found in aquarium experiments that pike eggs, if sufficiently aerated, can survive on silty substrata and so no vegetation is strictly necessary for their life. Franklin and Smith (1963) attributed egg mortality in the slough of Lake George, Minnesota in 1955, to low levels of oxygen on the bottom. Lindroth (1946), referring to data obtained by Brundin, reports that eggs in boxes on mud, sand and on reed beds gave hatching percentages from 9 to 63%. Hassler (1970) found in Lake Sharpe, South Dakota, survival of embryos depending on water temperature (see Section 2.2.3.1) and silt deposition. Silt deposition of 1.0 mm per day was associated with mortalities of 97% and above.

Siefert, Spoor and Syrett (1973) studied the effect of continuous dissolved oxygen concentrations of 50-12.5% saturation on the survival and development of northern pike from fertilization to the moment that the hatched pike began to feed. A dissolved oxygen saturation of 50% appears to be sufficient for survival and development to the first few days of feeding. Saturations as low as 33% could be survived provided that other environmental conditions were favourable, but survival would not be ensured once feeding had started.

2.2.3.3 Effect of other factors

Lillelund (1967) found that light influenced the rate of hatching in experiments at constant temperatures between 15° and 24°C. For pike eggs light was of no influence on hatching rate or temperature tolerance. Other authors found that light stimulated hatching (see Section 2.2.4.1).

Adelman and Smith (1970) and Smith and Oseid (1970) studied the effects of hydrogen sulfide on northern pike eggs at various oxygen levels. Eggs were less sensitive to hydrogen sulfide than hatched larvae. Lowered oxygen levels increased the toxicity of H_2S. Eggs subjected to hydrogen sulfide resulted in an increased number of anatomically malformed larvae. According to the authors, the highest possible safe level of H_2S for eggs is between 0.014 and 0.018 ppm and for hatched larvae between 0.004 and 0.006 ppm for 96 hours' exposure.

Helder (1980) studied the effect of TCDD (Section 2.3.7.8 - tetrachlorodibenzo-p-dioxin) on freshly fertilized pike eggs. Egg development was retarded and growth of fry was also retarded for a long period after exposure. A dose-related mortality was also recorded. Death was preceded by development of severe generalized edemas.

Fago (1977) found high mortalities (> 99%) of artificially fertilized eggs placed on nylon mats or in petri dishes in Pleasant Lake Marsh, Wisconson. The cause of the mortality could not be determined, but high siltation on the eggs and resulting blockage of dissolved oxygen were probably influential. Other possible causes for mortality include toxicity of the materials used to hold the eggs, insufficient flow of water through the dishes, injury due to handling and low water temperatures. Survival of eggs naturally deposited in the marsh must have been relatively high in view of the large number of young northern pike that were produced.

According to Muntyan (1978), maturation of sexual products, spawning and development of embryos of northern pike were not affected in waters in which radioactivity had become an element in the environment (strontium-90: 2.10^{-7} curie/litre; cesium-137: $2.5\ 10^{-8}$ curie/litre.

2.2.4 Hatching

2.2.4.1 Description

According to Braum (1964), northern pike hatches in a relatively early developmental phase. The head is still bent over the yolk sac which works as respiratory epithelium.

Kotlyarevskaya (1969) published a detailed description of the hatching process (see also Figure 8). Referring to the work of Nuesch (1958) on the formation of pigmented epithelium and the beginning of the differentiation of the retina in the eyes of the northern pike shortly before hatching, the author suggested that activation of pike embryos in the light shortly before hatching is a form of visual reaction. Lyubitskaya (1961) found evidence that darkness suppressed the activity of the hatching gland in northern pike. Lindroth (1946) also found that light stimulated hatching.

Without visible movements the larvae break through the egg scale. Head and yolk sac emerge passively from the egg. Gradually, by means of vibrating movements of the tail, the pike larvae free themselves from the egg membrane (Braum, 1964). The actual process of escape took from several seconds to 8 minutes in 15 cases observed by Kotlyarevskaya (1969). At hatching the blood supply on the yolk sac has reached its maximal development. The yolk sac is large when compared with hatching coregones (Braum, 1964). Newly hatched pike measure 8.41 ± 0.03 mm (Kotlyarevskaya, 1969). Length variations from 6.5 to 8.0 mm were observed (Franklin and Smith, 1960). The heart, in lateral view, appears to project partly into the yolk sac. The head is inclined over the front of the yolk sac (Kennedy, 1969). Soon after hatching the embryo straightens.

According to Kotlyarevskaya (1969) hatching in nature was seen to occur in an early stage of step 7. The pike larvae swam a little and then lay on their side. The adhesive organs secreted mucus. Newly hatched pike larvae could be seen in the water lying horizontally on plant leaves and being attached to them. Older pike larvae, which were more pigmented (an adaptation to life amongst vegetation rather than in open water (Kennedy, 1969), could be seen hanging from their point of attachment. Swimming in the water, the pike larvae travelled over open space very rapidly and hid among the vegetation or (less developed individuals) swam with difficulty falling from side to side as if trying to find shelter. Girsa (1969) and Shamardina (1957) reported that newly hatched pike showed no reactions to light. Conversely, Kotlyarevskaya (1969) observed that pike, when startled, move from the light areas into the shade.

Hatching of pike eggs is stimulated by temperature. A rise of temperature increases motility of embryos (Drimmelen, 1969). Eggs incubated at low temperatures hatch in a later stage of step 7 development (Lillelund, 1967).

2.2.4.2 Hatching gland cells, hatching enzyme

Schoofs and Denucé (1981) isolated a proteolytic enzyme from the hatching medium of northern pike embryos. The molecular mass is approximately 24 000 dalton. The experiments further lead to the conclusion that the hatching enzyme is a zinc-metalloprotease. The purified hatching enzyme (HE) was used by Schoofs, Opstelten and Denucé (1982) to examine aspects of the presence of the enzyme in the ontogeny of teleostean fishes. Immunofluorescence microscopy by means of anti-HE -bodies demonstrated that HE is localized in hatching gland cells. They are oval to round in shape, and measure 10-15 μm.

Ultrastructural changes in the hatching gland cells and evidence for their degeneration by apoptosis is presented by Schoofs, Evertse and Denucé (1982). Hatching gland cells are interspersed as single cells between periderm and presumptive epidermis. Release of hatching enzyme takes place in an exocytotic secretory process. The cell death in posthatching steps is characterized by condensation of the cell, formation of surface protuberances and splitting up into globular cell fragments. These fragments are eventually ingested into epidermal cells and digested. Schoofs et al. (1982) found evidence that the digestion of the zona radiata interna by enzymatic activity is incomplete in northern pike. In vivo the layer is probably also affected by microbal digestion.

2.2.5 Eleutheroembryonic phase

2.2.5.1 General description

By definition, the eleutheroembryonic phase refers to the interval during which young fish exist beyond the confines of the egg membranes while still feeding mainly on yolk.

During this phase the pike are inactive and connected to the substratum by means of their adhesive gland (Montén, 1948; Georges, 1964). The adhesive gland or cementum gland has not been recorded in the literature for any other species of esocid. Its presence in other esocids seems doubtful (Crossman, personal communication).

The pike show the tendency to hang vertically in the water and the dark camouflage stripes are adaptations to clinging to vegetation in spawning shallows (Kennedy, 1969). The eleutheroembryos show no phototaxis (Braum, 1964; Shamardina, 1957). Attraction to light was first observed a week after development at aquarium temperatures of 13°-15°C (Girsa, 1969).

The eleutheroembryonic phase can be characterized in three steps of development (Shamardina, 1957). The following description of the developing eleutheroembryo is taken from several authors (Shamardina, 1957; Kotlyarevskaya, 1969; Girsa, 1969; Braum, 1964); Franklin and Smith, 1960; Kennedy, 1969; Lindroth, 1946; Gihr,1957), (see also Figure 8):

Step 8: Finfold not divided. Pectoral fins in development. No mouth opening and gills. Respiratory epithelium on surface of yolk sac serves as basic oxygen supply. Size of animals 7.5-10 mm, weight 9-11 mg. Duration of the step 2-3 days (11°-12.5°C) or 1-2 days (19°C).

Three types of behaviour of newly hatched pike are described. Kotlyarevskaya (1969) suggested that this represented different stages in step 8 development:

- although actually able to move about, the newly hatched pike remain more or less motionless and do not swim upward (observed in natural and under artificial conditions (Girsa, 1969; Shamardina, 1957));
- shortly after hatching, the pike move upward (development under artificial conditions at high incubation temperatures);
- the newly hatched pike swim upward, attach themselves to objects such as plant leaves by means of their adhesive glands (observed under artificial conditions (Tschörtner, 1956; Chimits, 1951; Braum, 1964).

Step 9: Pectoral fins vibrating, mouth opening formed. Gill covers open, commencement of gill respiration, importance of yolk sac as respiratory organ decreases. Heart clear of yolk sac. Paired fins noticable. Size 10-11.5 mm, weight 11-12 mg. Duration of the step 4-5 days (11°-14°C).

Step 10: Swim bladder filled with air. Adhesive glands reduced in size. Free swimming, not chasing for food. Size 11.5-13 mm, weight 12-13 mg. Duration of the step 2-3 days (11°-13°C).

2.2.5.2 Effect of environment

Geiger, Meng and Ruhlé (1975) studied the effects of periodic water level fluctuations on newly hatched pike in aquaria. Daily fluctuations of 10 cm caused a significant increase in the daily mortality rate. Waves reduced the detrimental effect of water level fluctuations at least during the adhesive phase of the pike development.

Johansson and Kihlstrom (1975) reared newly hatched pike from artificially fertilized eggs in water solutions with different pH values. The pike at pH 4.2 showed a less rapid development than those reared at pH 5.2 and 6.8. A less marked pigmentation, smaller size and a bigger yolk sac were the most obvious differences among the developing pike. After 8 days the mortality at pH 6.8, 5.2 and 4.2 was 17%, 26% and 97%, respectively. The authors suggested the possibility that the most pH-sensitive step in the development is passed before hatching. The authors expressed their doubts on the validity of Finnish data in EIFAC (1968) (see Section 2.7.7) about the possibility for pike to breed within the pH range of 4.0-4.5.

Hokanson, McCormick and Jones (1973) studied temperature requirements for hatched pike. Newly hatched pike were more sensitive than the more developed individuals during the swimming stage to 7-day exposures to high temperatures, irrelevent of their acclimatization temperature (6°-18°C). Growth of the pike was highest at 26°C and negligible below 7°C. The high larval growth at 26°C was offset by an increased mortality rate during the first two weeks of life. Consequently the net biomass change was highest at 21°C.

Montén (1948) estimated the mortality from the moment of fertilization to the pterygolarval phase as 99.4%. He also calculated the mortality at various stages in the first year. Thus the mortality in the period from hatching eggs to larvae of 9.0-13.0 mm was 99.1%, while that of larvae of 9.0-13.0 mm was 78.1%. This represents the mortality during the first days of development of hatched pike when the fish is feeding on the yolk sac. Predation and unfavourable conditions on the silt bottom are supposed to be the causes of this high mortality. Hassler (1970), however, found that silt deposition had no influence on the survival of hatched pike during the first 15 days of their development.

Adelman and Smith (1970) and Smith and Oseid (1970) showed that eleutheroembryos were more sensitive to hydrogen sulfide than pike in earlier developmental phases. The highest possible level of H_2S for the eleutheroembryos is between 0.004 and 0.006 ppm for 96-hours' exposure.

Vuorinen and Axell (1980) studied the effect of the water-soluble fraction of crude oil on young pike of about 20-mm length in brackish water. The authors found after 96 hours the LC 50 value to be 43 mg/litre, while the corresponding LC 90 value was 64 mg/litre. Growth of young pike was poorer in high oil concentrations than in the controls. In the gills of the pike exposed to oil, the secondary lamellae were bent and changes were observed in the epithelium of the lamellae. The epithelium of the intestine was also damaged.

2.3 Larval and Juvenile period

2.3.1 General aspects

The larval period commences when the transition to exogenous nutrition takes place. the end of this phase is marked by the formation or ossification of the axial skeleton and the differentiation of the embryonic median fin fold. Figure 11, taken from the comprehensive study of the development of northern pike by Shamardina (1957), illustrates the various steps of the development in the larval period.

The juvenile period begins when the fins are fully differentiated and most of the temporary organs are replaced by definite organs. The period lasts until the fish have reached maturity (after Balon, 1975a).

Two phases can be distinguished in the development of the northern pike larvae.

2.3.2 Protopterygiolarval phase

This phase encompasses the interval between the transition to exogenous feeding and the commencement of differentiation of the median fin fold (Balon, 1975a). Shamardina (1957) characterized two steps in this developmental phase:

Step 1: Differentiation in the fin fold. Between the body lengths of 12 and 25 mm the tail shifts gradually from the heterocercal to the homocercal condition (Franklin and Smith, 1960). Development of sense organs on the sides of the head. Free-swimming in a horizontal position.

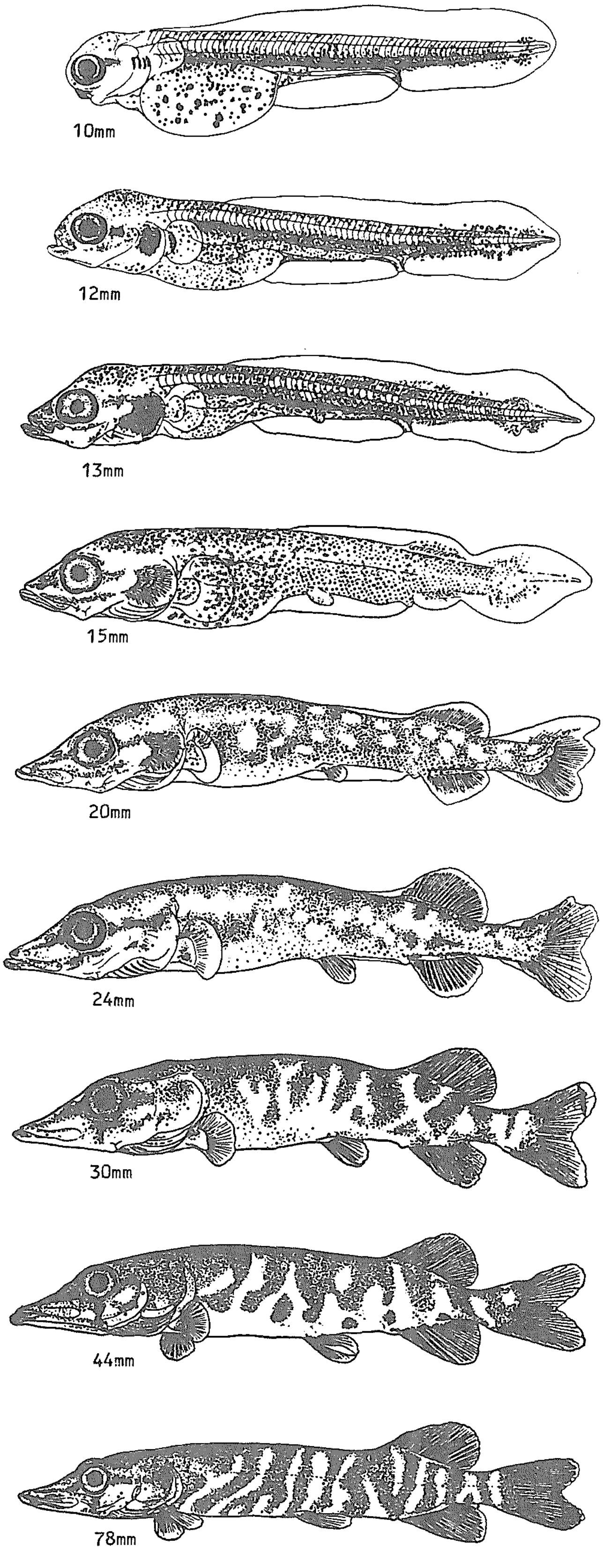


Figure 11 Development of northern pike during the larval period (From Shamardina, 1957)

Distributed in open water. Snapping at copepods. Yolk sac absorbed. Snout becomes wedge-shaped instead of rounded, not yet pike-like (Kennedy, 1969). Maxillary and pharyngeal teeth appear, making it easy to catch and hold the prey (Ivanova and Lopatko, 1983). Size 13-14.5 mm, weight 13-17 mg. Duration of the step 4-5 days (13°C).

Step 2: Fin fold decreasing, dorsal and anal fins formed. Appearance of mesenchymatic buds of lepidotrichia. Stomach formed, S-bend in alimentary canal. Almost vertical position in water, caused by increase in size of swim bladder. Distributed in open water. Size 14.5-18 mm, weight 17-30 mg. Duration of step 7 days (14°C).

2.3.3 Pterygiolarval phase

This phase lasts from the beginning of the differentiation of the unpaired fins until the embryonic median fin fold is entirely differentiated and no longer apparent (Balon, 1975a). Shamardina (1957) described 5 steps in this developmental phase:

Step 3: Caudal fin consists of three lobes. Sense organs on sides of the head become embedded in furrows. Relative size of the eye decreases. Movements in horizontal position. Nocturnal feeding on chironomids and small crustacea. Distributed in open water. Size 18-22 mm, weight 30-55 mg. Duration of step 7-10 days (16°C).

Step 4: Caudal fin has two lobes with branched fin rays. Rays and mesenchym buds in ventral and pectoral fins. Feeding on larger plankton. Distributed in open water. Size 22-28 mm, weight 55-100 mg. Duration of step 10-13 days (16°C).

Step 5: Median fin fold reduced. Pectoral fins with rays. Branched rays in anal and dorsal fins. Development of scales. Sense organs on side of the head in canal buds. Distributed in open water and in shore vegetation. Size 28-40 mm, weight 100-500 mg. Duration of step 14 days (17°C).

Step 6: Whole body covered with scales. Branched rays in all fins. Development of secondary neuromasts on body and tail. Distributed in deeper parts of vegetated zone. Size 40-55 mm, weight 500-1 000 mg. Duration of step 30 days (18°C).

Step 7: Caudal and pectoral fins increased in size. Further development of sense organs on the head and body. Distributed in the vegetated zone in deeper water layers (0.5-1 m). Size larger than 50 mm.

Franklin and Smith (1960a) and Wydallis (1960) provided information on the development of scale patterns in northern pike. Fish less than 30.5 mm had not started to form scales. Fish between 32.0 and 35.0 mm had formed one-half to one and one-half rows of scales. The first scales form all along the lateral line in the area below the anterior half of the dorsal fin and develop more rapidly anteriorly and ventrally than posteriorly and dorsally. The fish in the 40.0 to 45.0-mm range had formed from 6 to 10-scale rows and only the dorsal and ventral midlines were not scaled at 60.0-63.0 mm. Complete scalation was noted in fish as short as 66.5 mm. (See also Figure 12).

Jollie (1975) described a 90-mm pike with fully developed body scalation, but the cheek was still completely bare (no evidence of developing scales). Partly developed, but distinct scales were present on the cheeks of a pike of 106 mm.

Wydallis (1960) concluded that length seems to be more the determining factor than age in scale development. The author suggests that for this reason scales for age determination should be taken from the part of the body where they grow first.

Franklin and Smith (1960) and Shamardina (1957) analysed allometric growth of northern pike. Their studies revealed that the growth of the head, jaw, eye and tail was much more rapid than that of the body up to a length of about 65 mm (see also Figures 13 and 14). After that length was attained, growth in all regions of the body and head was relatively constant. The fish have assumed the general form of the adult pike and could be considered as juveniles.

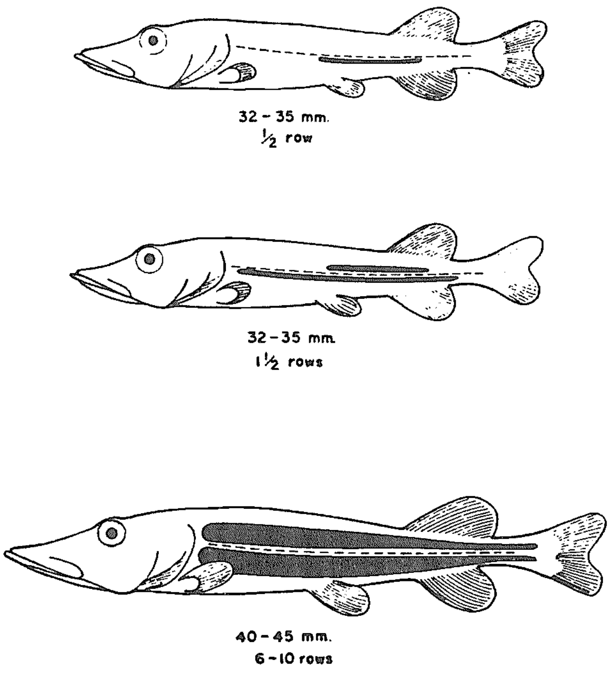


Figure 12 Location of first scales and approximate advance in scaled area with increasing length (From Franklin and Smith, 1960a)

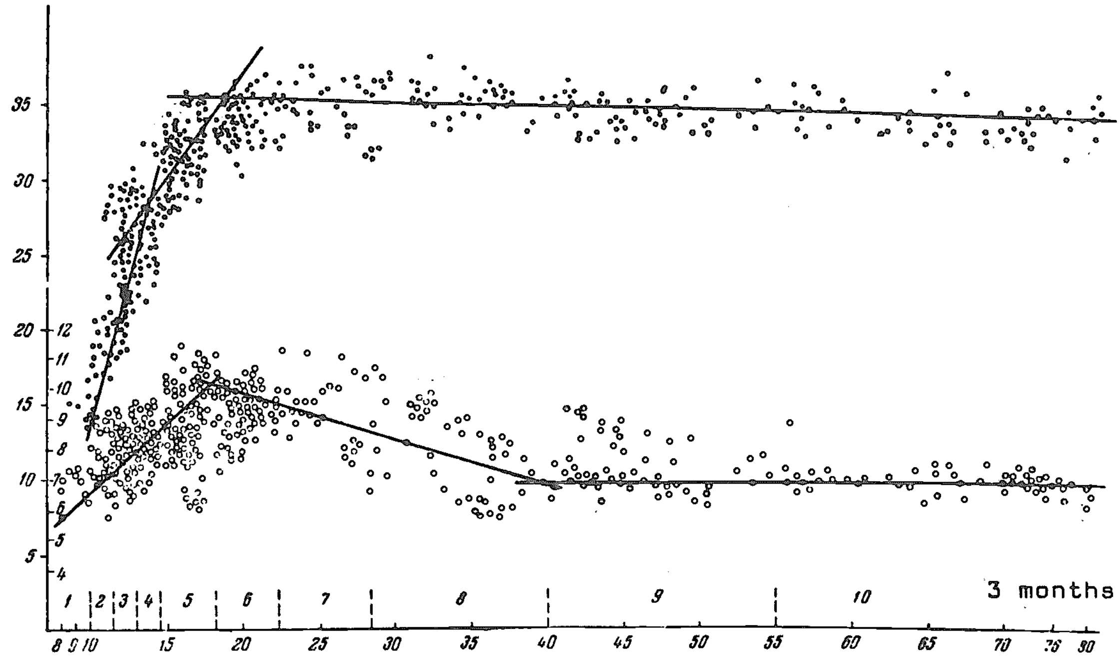


Figure 13 Variation of relative head lengths (•) and horizontal eye diameter (o) as percentage of body length during the development of northern pike (After Shamardina, 1957)

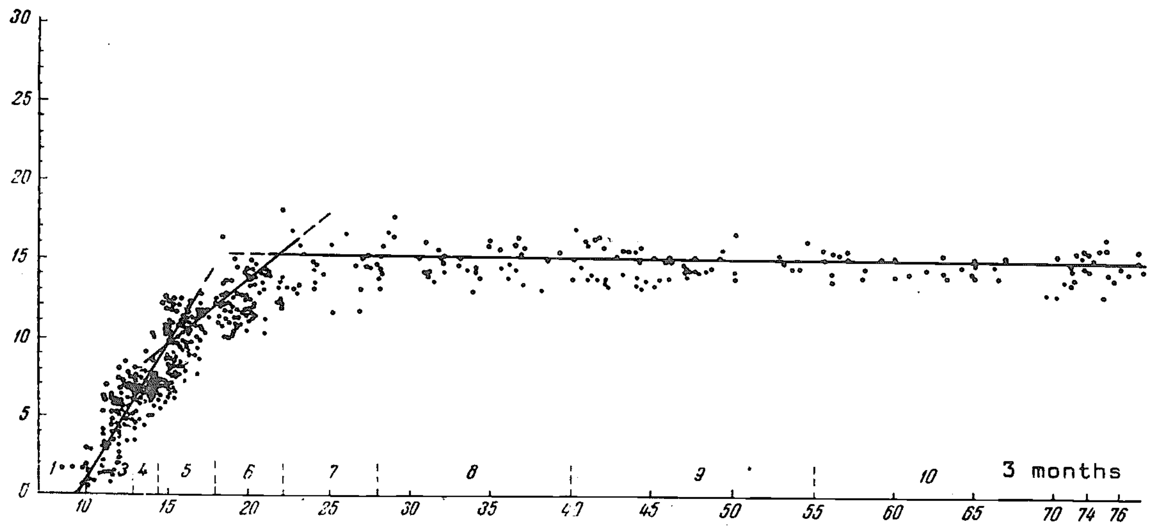


Figure 14 Change of relative snout length as percentage of body length during the development of northern pike (After Shamardina, 1957)

2.3.4 Feeding and feeding behaviour

2.3.4.1 Development of organs and feeding

Active feeding starts before the resorption of the yolk sac is completed at lengths between 11 and 12 mm (Frost, 1954; Hunt and Carbine, 1951). Kostomarova (1959, 1961) found that lack of external food in the stage of yolk resorption (12.5-13 mm) retards growth and development and provokes pathological changes in the digestive tract. In the absence of external food all pike perished from hunger in the course of 3 days following resorption of the yolk sac. The author suggested that additional feeding of artificially bred pike should start 48 hours before the pike become mobile. Kennedy (1969) showed in laboratory studies that starvation during the early feeding stage was a major cause of mortality. Cannibalism occurs as soon as there is sufficient difference in size between individual fish.

The result of histological and histochemical studies by Szlaminska (1980) indicated that amylolytic, trypsin-like and pepsin-like activities were present in the digestive system of protopterygiolarvae. The faeces of these larvae consisted of intact, undigested crustaceans and, to a lesser extent, their empty skins and shells (Ivanova and Lopatko, 1983). After stomach formation the food was digested to a greater extent than earlier. The shells of large Cladocera were found in the faeces 8-10 days after the beginning of external feeding, whereas Copepoda were digested completely. During the eleutheroembryonal development phase the alimentary canal develops from a straight tube to the S-bend form of the adult (Shamardina, 1957; see also Figure 15). The development is completed when the pike is about 17.5 mm long (Frost, 1954).

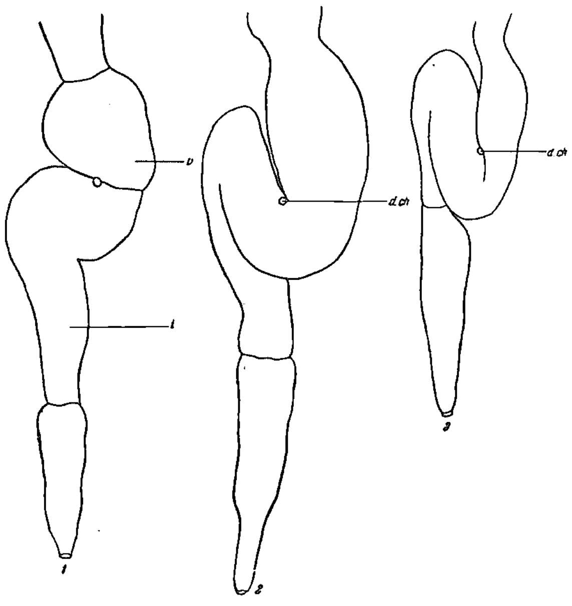


Figure 15 Development of alimentary canal from straight tube to S-bend form (Shamardina, 1957)

Disler (1967) and Shamardina (1957) observed that rapid differentiation of the sense organs took place in the eleutheroembryonic phase when the embryo's mobility increased. Sensitivity to current direction, as well as to tactile stimuli arose. With transition to the larval period of development, endogenic feeding is replaced by external feeding, the larvae start moving in search of food and rearrangement of sensory organs commences. The eyes become mobile and binocular vision appears. Girsa (1969) first observed attraction to light one week after hatching at aquarium temperatures of 13°-15°C. At this stage of development the differentiation of primary neuromasts is completed.

Dabrowski (1982) studied first feeding of northern pike larvae in laboratory experiments in relation to light intensity and spectral composition of the light. First-feeding larvae had light tresholds which were lowest in green light (500-600 nm). Light thresholds in red light (600-750 nm) and blue light (480-500 nm) were respectively 3.4 and 4.9 times higher than the light threshold in green light. The green-sensitive retina is best suited to finding dark bits of food silhouetted against the predominantly green vertical space light in the pike habitat (Levine and MacNichol, 1982).

According to Disler (1967) the lateral-line organs are not used in hunting for food in the early stages of the larval period. They are adapted mainly to perception of signals and serve as protection against the approach of danger. During the larval period the neuromasts remain exposed. With transition to the juvenile period of development, part of the neuromasts located on the head become modified to sensory canal buds. Those that remain exposed become embedded in the epidermis and change into pit organs. The fish start to frequent weeds under conditions of lower illumination. Their eyes become relatively smaller, and larvae of other fishes acquire greater importance in the diet. Girsa (1969) reported that pike of about 45 mm no longer showed positive phototropic reactions. Vision begins to play a relatively less important role in the orientation of the juvenile pike among the dense growth of underwater vegetation. Disler (1967) reports that numerous secondary neuromasts arise on body and tail. In contrast to other fishes, these are distributed not transversely but longitudinally with respect to the body axis.

The foregoing observations on the development of feeding behaviour and organs in northern pike agree with the findings of Johnson (1960). This author found in experiments with pike that had no previous experience of feeding, that the primary stimuli that elicit the feeding response are entirely visual.

From the developmental step in which the young pike feed on plankton to the step when fish-feeding commences, Johnson (1960) found a change in the pike's interpretation of external stimuli. A much more complex releasing situation had been built up. Initially, mechanical stimuli were very likely received by the young pike, however, little use could be made of these stimuli during this step of development. Later on, the mechanical stimuli became a component of the releasing mechanism. Johnson (1960) found, however, that visual stimuli were still adequate to elicit the full feeding response, as was shown by the readiness of pike to attack food fish when kept behind a glass partition. The author concluded that the mechanical stimulus can replace, to a certain extent, the original movement stimuli. Such a situation would be of great advantage to a fish living in waters with low visibility, a condition that must arise frequently in a species inhabiting shallow, vegetated waters.

2.3.4.2 Feeding behaviour

Braum (1963, 1964) gave a detailed description of the movements and prey capture of northern pike at the beginning of its exogenous feeding. The following observations were made (see also Figure 16):

- filling of the swim bladder: movements oriented towards the water surface, overcoming the surface tension and swallowing air. Gravity is overcome by locomotion only;

- change in locomotion movements: the rowing movements of the body are changed into vibrations of the tail and pectoral fins;

- noticing of pray: the young pike notice movements of the prey that are transverse to the longitudinal axis of their own body. Their posture, before pushing forward is related to the direction of the prey's movements;

- the prey capture: eye movements, nearing the prey, correcting movements, push forward movements from an S-shaped position of the body, and snapping at prey by sucking it.

While pushing forward, the head of the pike necessarily deviates to one side which is determined by the starting-posture chosen. The deviation corresponds to the movement direction of the prey.

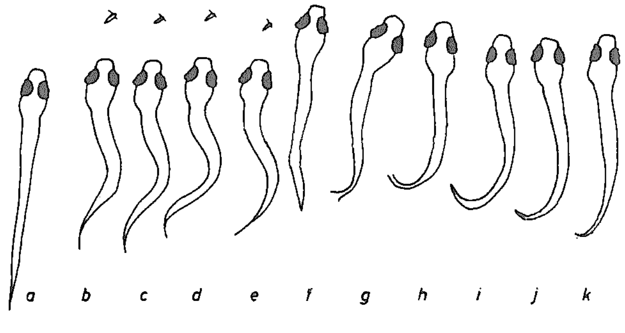


Figure 16 Fixation and snapping of prey by young northern pike, seen from above (From moving pictures, Braum, 1964)

The horizontal visual field of pike is 150° and binocular vision is 80° when fixation of the prey occurs. Long fixation periods imply snapping success with more probability than short fixation periods. The percentage of successful preying is initially about 30%, but it increases with experience. Snapping success at 12°C is higher than at 5°C.

Frost and Kipling (1967) also studied the technique of prey capture of young northern pike. The pike "marks down" the prey which it stalks stealthily to within a certain distance and then, before striking, flexes its body. This gives the impetus for the lightning dart forward and strike. The prey is grasped crossways in the mouth and firmly held by the backwardly projecting teeth. Then it is swallowed head first.

Usually, pike in the aquarium did not seek their food but waited until it came near to them (Frost and Kipling, 1967).

The prey capture reactions of young pike are innate (Braum, 1963), but the ability of individual larvae to catch and hold prey differ within the progeny of a single female (Ivanova and Lopatko, 1983). The changeover to exogeneous feeding was not uniform in individual larvae. Some individuals started catching food successfully within the first few hours after the food was given, and made on an average two strikes to catch a single crustacean. Such larvae performed few strikes only, 8-15 per hour. On the other hand, other larvae hunted almost continuously and less successfully, making up to 115 strikes per hour. Most of the larvae under observation (8 out of 11) on the third day after change over to external feeding learned to catch food almost without failure, making an average of 1-3 strikes to get the prey.

The actual attack of prey by northern pike larvae, lasting 5-20 ms, was observed by Drost (1987) with the help of high-speed cinematography. The progressive catch success during ontogeny was caused by an increase in the ratio mouth radius/aiming accuracy.

The ability to catch large prey appeared in pike very early. Pike measuring 19 to 20 mm caught conspecifics measuring 12-17 mm when food was in short supply and pike density was high. The young pike mainly injured the smaller members in the population, cutting their caudal fin before breaking the backbone, since they could not swallow an entire prey of more than 70% of their own body length. The ability to catch and hold large prey organisms first manifested itself in a small number of larvae. At the start of the pterygiolarval phase only 8 of 300 pike became cannibals. Gradually, the proportion of pike consuming conspecifics increased and was about 40% at the end of the larval phase. Other larvae, under similar conditions, continued to feed only on zooplankton till the juvenile period.

2.3.4.3 Phases in nutrition

Chodorowska and Chodorowski (1975) distinguished three nutritional phases in the larval and juvenile development of northern pike: plankton-, insect- and fish-feeding. During these phases more than 50% of the stomach volume was found to contain plankton (1-6 cm), insect larvae (6-10 cm) or fish (larger than 30 cm), respectively. The composition of the diet depended on the availability of prey organisms. The optimal nutriment assuring the highest growth rate was often replaced by more available substitute food. The authors found in ponds that the availability of prey was dependent on the presence or absence of vegetation.

Food for young pike was studied in detail by Hunt and Carbine (1951) and Frost (1954) whose data are, in general, in accordance with Chodorowska and Chodorowski (1975). Conversely, Hunt and Carbine (1951) and Frost (1954) found that the insectivorous and pisciphageous phases in the nutrition occurred in an earlier step of development. Entomostraca were the only food found in fish of 17.5 mm and less in Windermere, and continued to be important up to a length of 50 mm. Insect larvae occurred in the diet when fish were 25 mm long, but never became of primary importance. This was in contrast with the feeding of fish in Peterson's Ditch in Michigan (Hunt and Carbine, 1951), where insects were of major importance as food item between 26 and 50 mm. Fish appeared in the stomach of Windermere pike when these were 35 mm long. In Peterson's Ditch, fish other than pike did not appear in the stomach contents of pike smaller than 51 mm but formed an increasingly large part of the food of larger specimens. The difference in importance of insect larvae in the two waters may be associated with their relative abundance in these places and the availability of prey fish. Munro (1957), Makowecki (1973) and Vostradovsky (1981) gave evidence that the importance of food items other than fish in the pike diet was related with the availability of prey fish.

Other studies on food of young pike are from Minnesota (Franklin and Smith, 1963), Wisconsin (Priegel and Krohn, 1975; Fago, 1977) and Nebraska (McCarraher, 1957). All of them illustrated that the food items consumed by growing pike follow the sequence microcrustacea, insects and vertebrates (chiefly fish and tadpoles). Local differences occurred and were related to the relative availability of food items (Franklin and Smith, 1963).

Most authors reported Entomostraca (Cladocera, Copepoda) as important food items for pike up to about 60 mm long. Nikolski (1963) suggested that when in young pike the amount of energy expended on the capture of crustaceans started to exceed their caloric value, the pike started to feed on young fish. When pike were kept on a diet of planktonic crustaceans, they gradually ceased to grow, and eventually died. Clark (In Toner and Lawler, 1969) reported that at Saint Mary's Fish Farm, Ohio, northern pike up to at least 12.7 cm long would feed on small crayfish (Orconectus). Clark considered that by eliminating fish from the diet and forcing the pike to feed solely on the young crayfish a greatly increased pond production would be obtained. He also reported that when very young pike were fed with Daphnia magna, these crustaceans would get stuck in their throats and kill them. Ivanova (1970) found that when the pike becomes piscivorous the surface of the intestine increases prominently.

Franklin and Smith (1963) reported from the Lake George slough that the incidence of fish in the food of young pike was not great. The principle food items taken by pike were Cladocera and insects. Cladocera were important for pike up to a length of 120 mm or more. Kennedy (1969) reported from Irish limestone trout lakes that fish are less important as food than invertebrates until the pike are well into their second year.

Balvay (1983) presented a review on feeding of northern pike larvae and concluded that management of extensive rearing ponds should stimulate the production of natural food adapted to the needs of the larvae in order to reduce the effects of cannibalism.

Figures 17-20 illustrate the changes in the stomach contents of northern pike larvae during development.

2.3.4.4 Digestion and periodicity of feeding

Feeding experiments with northern pike fry between 21 and 31 mm in length were executed by Lillelund (1957) in order to establish the duration of digestion of prey. It was found that passage of Eurytemora affinis, a copepod, and of cyclopids through the digestive tract of pike was dependent on whether the stomach was filled or not. Passage time through pike with empty stomachs was 2 hours. Passage time through pike with filled stomachs was about 4-5 hours at temperatures of 17°C.

Smísek (1968) carried out experiments with pike ranging in total length between 71 and 76 mm on the intensity of food acceptance during the day. It was found that average food consumption in the course of 24 hours amounted to 36.3% of the total body weight of the larvae. In daylight, the pike accepted predominantly small organisms (plankton), while at twilight and at dawn coarser organisms, such as fry of other fish, were taken. At high light intensity intake of food is low. The experiments were done at the beginning of June at water temperatures varying between 13° and 15°C.

Luquet and Luquet (1983) did not notice any feeding activity in northern pike larvae during darkness in their experiments with artificial food. The intestines of 16.6 mm larvae were full after 4 hours and those of 28.0 mm larvae, after 6 hours. The initial rates of food intake corresponded to 0.9% and 0.4% of the live weight per hour, which is in reasonable agreement with the results of Smísek (1968) in his feeding experiments with natural food.

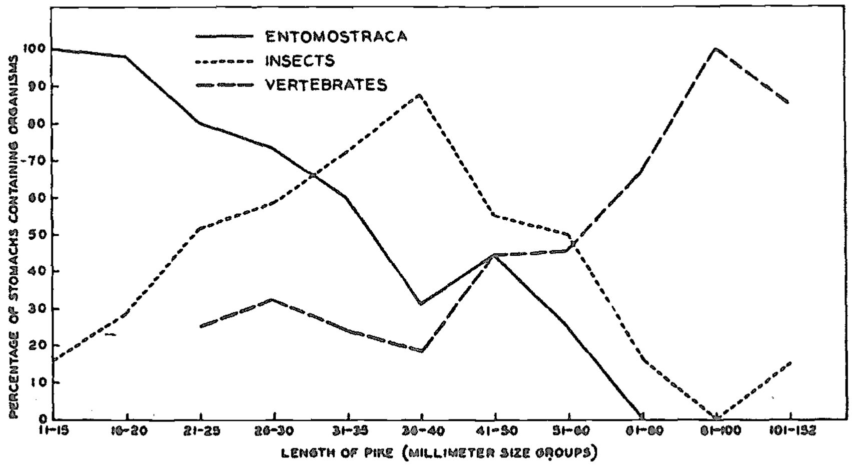


Figure 17 Frequency of occurrence of major groups of food organisms in pike stomachs collected in 1939. Houghton Lake, Michigan (Hunt and Carbine, 1951)

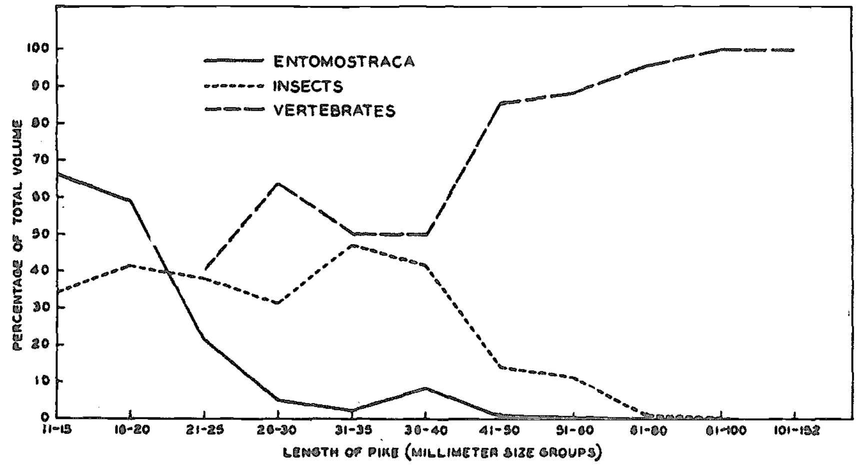


Figure 18 Percentage of major groups of food organisms in total food volume in pike stomachs collected in 1939. Houghton Lake, Michigan (Hunt and Carbine, 1951)

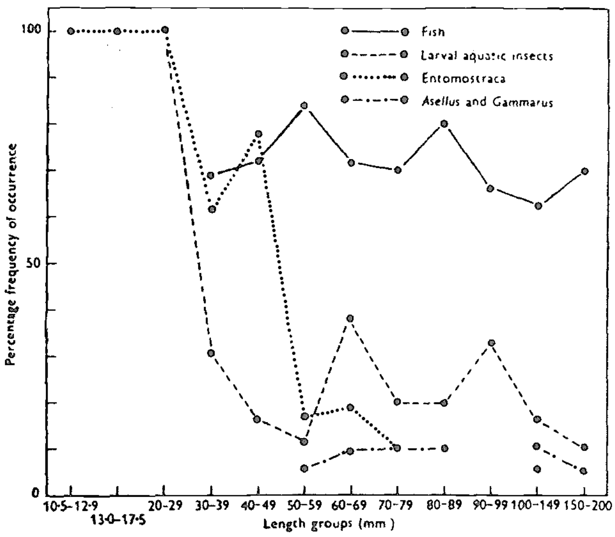


Figure 19 Frequency of occurrence (in percentage) of each of the four major groups of food organisms in pike of different length groups. Lake Windermere (Frost, 1954)

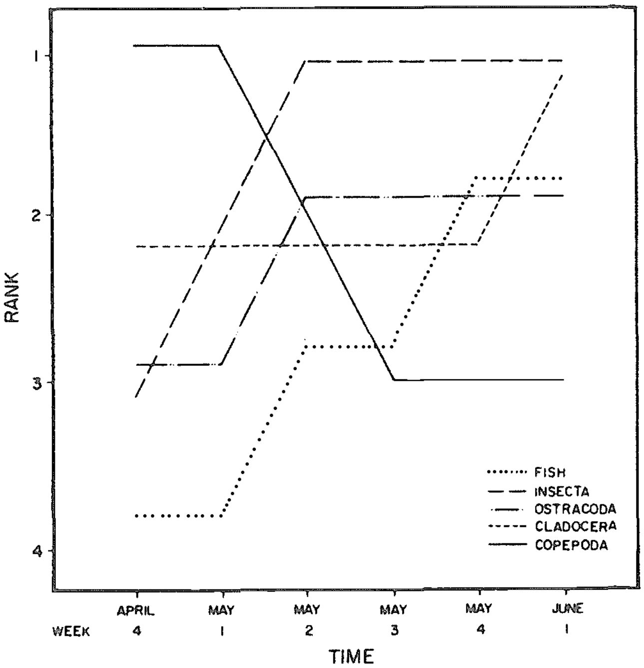


Figure 20 Average change in northern pike stomach contents at the Pleasant Lake Marsh, Wisconsin, 1969 and 1971-73 (Fago, 1977)

2.3.4.5 Cannibalism among larvae

Braum (1964) reported that the feeding of young pike is non-selective, as no special food items from the offered plankton are preferred. In the first two days, pike needed 52 planktonic crustacea in 10 hours (14°C). A minimal light intensity of 0.1 lux is necessary for feeding. The author observed cannibalism in cases of short hunger periods already 17 days after the young pike had started feeding. Frost and Kipling (1967) recorded only a few instances of aggression among three pike that lived in a glass tank for four months during which they grew from 2.5 to 10.0 cm.

Johnson (1960) who found that vibrating particles released a feeding response in pike larvae, stated (personal communication) that the initial clue to the vibratory stimulus came from observing young pike prior to feeding. A pike would line up directly behind one of its confreres in a tank and then make attacks on the vibrating tail of the other. Fago (1977) reports field observations of pike trying to capture and eat one another. Attempts were many times unsuccessful, leaving the prey injured and possibly dying without being of nutrient value to the surviving fish. In a tank holding many small pike (less than 3.0 cm length), tail nipping, repeated chasing and cannibalism were common, even though their food, zooplankton, was plentiful (Frost and Kipling, 1967). This suggests that crowding of pike might lead to cannibalism. In this context, Kipling and Frost (1970) quote Montén (1950) who found in ponds that an ideal population density of pike was sustained in later developmental stages by cannibalism under conditions of increasing population density.

Giles, Wright and Nord (1986) studied cannibalism of pike larvae in 12 tanks. They found that cannibals exhibited fast growth during a period when the teeth had stopped growing (at 22 mm) and the larvae were just maintaining condition on a zooplankton diet. Three weeks after hatching no social agression (biting, chasing, posturing) was observed. At 21 days differences in feeding success among the larvae became apparent. At 25-35 days cannibalism occurred independently in all 12 tanks. Cannibals became more active, patrolling the tank, frequently fixating smaller larvae and orienting toward them. The smaller larvae remained immobile during most of the time. Sudden movements made by larvae within the viewal range of a cannibal often started an attack.

Bry (1980) stocked 3-months-old pike in three densities in different ponds. The numbers of pike after nine months were about the same in all ponds. The net pike biomass yielded was inversely related to initial population density. Density-dependent mortality of 7-week-old pike larvae due to cannibalism was also found in tank experiments (Giles, Wright and Nord, 1986). No crowding effects were observed before cannibalism started. Wright and Giles (1987) reported identical observations in pond experiments. Cannibalism occurred despite the abundance of other suitable food. Ivanova and Lopatko (1983) suggested that this could be due to individual differences in catching skill among larvae. Cannibalism among young pike can therefore be an important population-regulating mechanism (Kipling and Frost, 1970).

According to Bry and Gillet (1980, 1980a), survival of pike larvae cultured for 50 days in ponds was 20 to 33% lower when full-sib families were mixed than when full-sib families were cultured separately. This difference is ascribed by the authors to a higher rate of cannibalism in mixed lots due to a more heterogeneous growth.

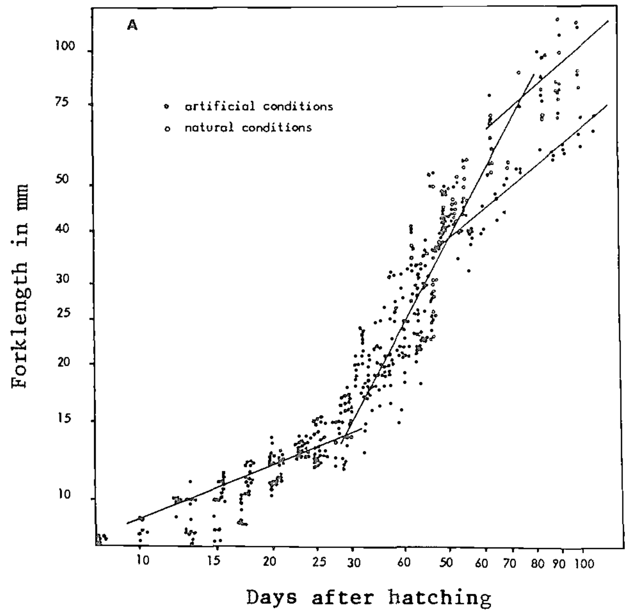
Cannibalism is considered by Carbine (1945) as the chief cause of pike mortality in experimental ponds and in ditches adjacent to Houghton Lake, Michigan (Hunt and Carbine, 1951). In Pleasant Lake Marsh, Wisconsin, cannibalism occurred in pike as small as 38 mm (Fago, 1977). The same author found also that six weeks after hatching northern pike was, in terms of biomass, one of the most important food items in the diet of other fingerlings. Franklin and Smith (1963), however, reported from the Lake George slough, Minnesota, that young pike preferred insects to other pike or tadpoles. Chodorowski (1975) observed in ponds that cannibalism has an influence on the population structure of young northern pike. Analysis of six-weeks-old pike populations sometimes revealed the presence of much larger individuals (2-5% of the population) are exclusively cannibalistic in their feeding behaviour. These animals showed a very rapid growth as they were the first to profit from the available prey fish.

Carbine (1944) observed in rearing ponds differences in growth within the 0^+ population. In autumn the distribution emerged as two groups, one with a range of 83-105 mm and an average of about 100 mm. The other group showed a range of 225-325 mm and an average of 280 mm. Kipling and Frost (1970) suggested as the most acceptable explanation for this observation the fact that stunted fish were those 0^+ pike which had never learned to switch over from smaller (invertebrate) to larger (fish) food organisms as they increased in age. The authors reported from Windermere that 0^+ pike resolved themselves in November in two distinct length groups, and it is suggested that mortality among the smaller 0^+ pike was extraordinarily high. Therefore few or no survivors of the smaller group up to the adult period existed. This is in accordance with the high mortality of small pike found by Carbine (1944) and with the fact that it was rare to find an adult pike less than 20 cm long at the end of its first year in Windermere.

The phenomenon of bimodality within the first year class can also be explained by differential distribution patterns of pike belonging to this class. Differences in the availability of food for growth between different habitats can result in differential growth. In this respect it is interesting to note that Grimm (personal communication) found data indicating that pike up to 15 cm occupy parts of the vegetated zones that are physically impenetrable for larger pike. The diet of these small pike may be restricted to invertebrates.

2.3.5 Growth of larvae

Data on the growth of northern pike during its first growth season are scarce. Carbine (1942), Franklin and Smith (1963), Shamardina (1957) and Forney (1968) report on the first months of growth of northern pike in spawning marshes (see Figures 21-23). Growth rates of pike in Houghton Lake, Michigan, in 1939 (Carbine, 1942) and in Linwood Lake (southeastern Minnesota) in 1954 (Lux, 1960) were higher than in Lake George slough, Minnesota (Franklin and Smith, 1963) and in the marsh at Oneida



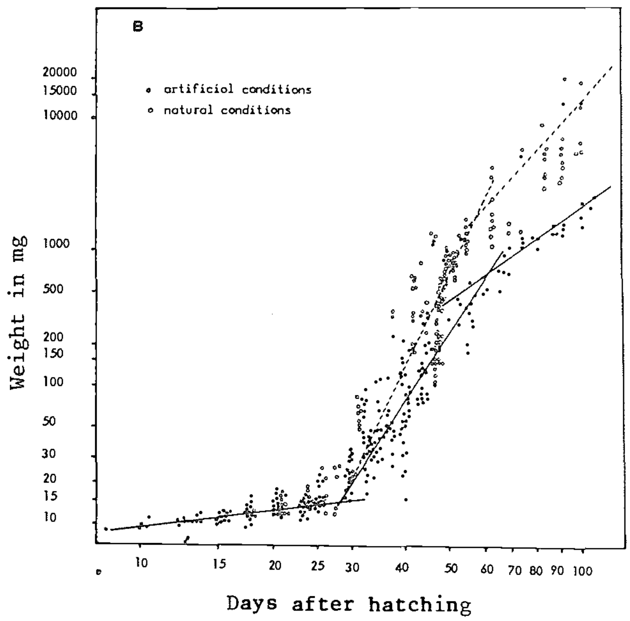


Figure 21

Growth in length (A) and in weight (B) of northern pike under artificial conditions (•) and natural conditions (○)
(After Shamardina, 1957)

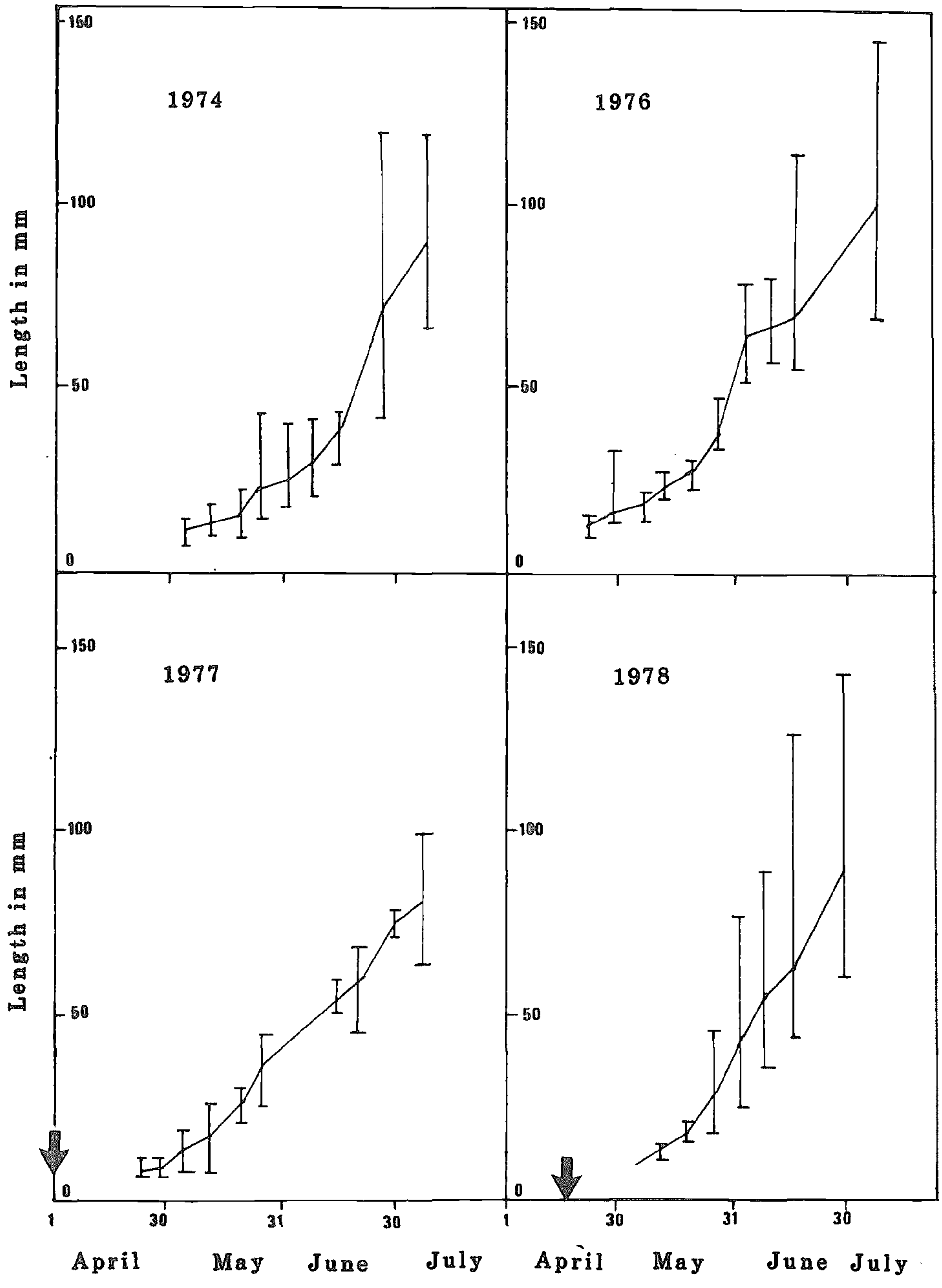


Figure 22 Average growth and range of 0^+ pike in Bleury Stream, Quebec, during the first months of development. Arrows indicate dates of first spawning activity
(After Fortin et al., 1982)

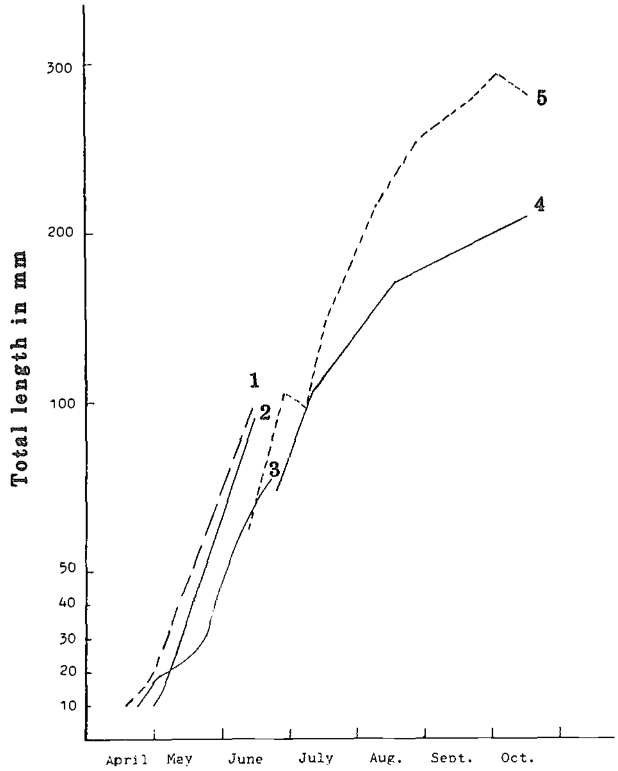


Figure 23 Growth of northern pike in Shackleton Point, New York: 1 (1964), 2 (1965), 3 (1966); Houghton Lake, Wisconsin, 4; Linwood Lake, Minnesota, 5. (After Forney (1968), Carbine (1942) and Lux (1960)

Lake, New York (Forney, 1968). Fortin et al. (1982) published field data about growth of northern pike in Bleury Stream, Quebec. These data revealed slightly lower growth rates than in Oneida Lake and Lake George.

All authors found that the growth of young pike is strongly influenced by temperature. The growth data obtained by Fortin et al. (1982) make it possible to compare two year classes of pike resulting from early spawning by end March/ early April (1976 and 1977), with two year classes of pike resulting from later spawning activity, by mid-April (1974 and 1978). It is shown that the length range of pike in the first week of July is not dependent on the period of spawning. Better growth of the 1976 year class as compared to the 1977 year class resulted from higher temperatures from June to July. The growth of the 1978 year class was better than that of the 1974 year class because temperatures in May were higher, while in June the temperatures were comparable.

According to Hakkari and Bagge (1985), the length of young pike in the Finnish Lake Saimaa in June seemed to be positively correlated to the mean temperature of the surface water. In addition, high water levels may have had a positive effect on growth. The authors reported higher densities of larvae in sheltered bays among vegetation than on more open sandy or stony shores.

Holland and Huston (1984) determined whether distribution of young pike was associated with specific plant communities in backwater areas of the upper Mississippi River. In spring, average catches of 0^+ pike from areas with submerged vegetation exceeded by nearly three times those from areas with emergent vegetation and more than 10 times those from an area devoid of vegetation. This pattern prevailed until late summer, when the number of young increased in the better oxygenated and less heavily vegetated waters.

Franklin and Smith (1963) observed that the curve of growth in length is sigmoid. The authors, however, could not associate the changes in the rate of growth deceleration with changes in the diet of the pike, as was suggested by Hunt and Carbine (1951).

Growth of pike after one season is variable. Bimodality in growth is reported by several authors. Grimm (1981, 1981a) argued, on the basis of field data and data obtained in drainable ponds, that 0^+ pike biomasses are tied to a maximum in a population of a given composition and density. The author found biomasses of 0^+ pike not influenced by water temperature. Average growth of pike could not be related with temperature or biomass of larger pike (see Table X).

Kuznetzov (1972) compared growth characteristics of young pike in the Kuybyshev reservoir with those of bream (Abramis brama), perch (Perca fluviatilis), pike-perch (Stizostedion lucioperca) and roach (Rutilus rutilus). The characteristics of these species are slightly different from those of pike. In correspondence with the larger eggs, the eleutheroembryos are comparatively large and grow more intensively. At the time of transition to exogenous food intake they are already capable of consuming large food. Pike are able to change early to predatory feeding.

Table X

Average length and range of lengths of 0^+ pike stocked as fingerlings (4-6 cm) and captured after one growing season by electrofishing and seining in four waters in the Netherlands (After Grimm, 1983 and unpublished data)

Location	Year (Oct.-Nov.)	Average length (cm (FL))	Range of lengths (cm (FL))	Number captured a/	Average air temp. (°C) May-Sept.	Estimated biomass of larger pike in kg/ha of aquatic vegetation	
Fortgracht (3.5 ha)	1974	22	18-31	19 (59)	15.0	121.1	
	1975	23	16-32	22 (70)	15.9	129.3	– 0^+ > pike $\geq$ 54 cm
	1976	22	17-27	20 (80)	16.9	114.2	
Jan Verhoefgracht (4.5 ha)	1974	27	15-43	56 (80)	14.6	96.0	
	1976	28	16-35	87 (84)	17.2	70.9	– 0^+ > pike $\geq$ 54 cm
	1979	16	11-25	48 (6)	14.5	55.7	
Kleine Wielen (40 ha)	1975	19	12-25	53 (16)	15.1	61.4	
	1976	23	15-31	210 (46)	16.1	57.0	
	1977	19	14-25	41 (28)	14.0	67.0	– 0^+ > pike $\geq$ 41 cm
	1978	22	18-26	66 (31)	13.7	45.0	
	1979	23	14-29	228 (66)	14.0	55.2	
Parkeerter-reinsloot (0.3 ha)	1975	19	14-29	73 (59)	15.1	99.4	
	1976	19	16-23	23 (38)	16.1	143.0	
	1977	17	13-20	30 (71)	14.0	92.8	– all pike > 0^+
	1978	16	11-25	53 (77)	13.7	71.8	
	1979	13	11-15	36 (26)	14.0	167.8	

a/ In parentheses are the frequencies of occurrence (%) of the stocked 0^+ pike in the estimated 0^+ population

2.3.6 Emigration of larvae

Emigration of young pike from spawning marshes is reported by several authors. Franklin and Smith (1963) stated that emigration to Lake George (Minnesota) began 16 to 20 days after hatching. The average length at the onset of migration was between 17 and 19 mm. Hunt and Carbine (1951), Carbine (1942) and Forney (1968) reported the starting downstream movements when the pike had attained lengths in the range from 15 to 22 mm. It seems probable that emigration of larvae does not start before the pike have reached the pterygiolarval phase of development.

Hunt and Carbine (1951) stated that the chief factor causing actual emigration appeared to be the light intensity. Franklin and Smith (1963) concluded that the stimuli starting the emigration of young pike have not yet been clearly determined. It appears that this complex of factors consists largely of physiological forces which become effective at a length of about 20 mm.

Once the fish are ready to emigrate, light intensity is one of the most important factors influencing their movements. Periods of low illumination may delay the emigration for several days, but factors other than illumination probably control the number of young ready to migrate on a particular day. Length composition of emigrating young pike and duration of the migration from the marshes varies between locations and between years as it is shown in Table XI. Forney (1968) suggests that competition for food or other population stresses may possibly induce the fish to emigrate soon after attaining a length of 20 mm if the initial population density is high. The same author did not find that an increase of the volume of water flowing over the spilway of the marsh stimulated the migration. Royer (1971), who reported peak periods of escapement from the Kenosee Lake marsh (Saskatchewan) during the night, suggests that pike at that location are reacting more to the effect of rapidly decreasing water levels than to light intensity. Migration to brackish water of adult and juvenile pike in Swedish coastal areas revealed a diurnal rhythm that excludes the possibility of a passive outdrift of the fish (Johnson and Müller, 1978).

Behaviour of the small pike during movement to the lake was described by Franklin and Smith (1963) and Forney (1968). According to the first authors, this behaviour appears to reduce predation. Young pike came over the heads of

Table XI

Length composition of young pike emigrating from spawning marches

Location and authority	Year	Duration of emigration (in days)	Estimated number of emigrants	Length composition (mm)	Length composition (%)	Survival (estimated by author) from egg deposition (%)
Lake George Slough, Minnesota (Franklin and Smith, 1963)	1956	80	93 000	17-35 35-100	95.0 5.0	4.62
	1957	71	4 400	19-35 35-120	25.0 75.0	0.30
	1958	-	750	35	100.0	0.08
Shackelton Point on Oneida Lake, New York (Forney, 1968)	1964	51	45 121	17-24 25-49 50-74 75	29.0 57.0 10.0 4.0	4.10
	1965	65	40 543	17-24 25-49 50-74 75	11.0 86.5 2.0 0.5	3.16
	1966	76	18 666	17-24 25-49 50-74 75	33.0 20.0 40.0 7.0	2.79

predatory blunngills, *Lepomis macrochirus*, most of them looking like pieces of debris, since forward movement was provided by the current, and direction was attained by very rapid but almost imperceptible flutters of the tail.

Forney (1968) reported that young northern pike seemed to locate the outlet by swimming parallel to the shore until they detected the outlet current. As the fish approached within a few feet of the outlet, some swam or drifted toward it, while others swam vigorously against the outlet current and continued to move parallel to shore, but away from the outlet.

Although it is difficult to calculate survival of eggs in the field during the first two phases of development, several authors give estimates. The problems encountered are (i) estimation of the number of fertilized eggs deposited on the spawning ground, and (ii) estimation of losses of eggs from predation and decomposition. Survival values of young northern pike reported from spawning marshes are generally low. Based on the potential egg deposition by adults compared with the number of young that from a spawning marsh at Houghton Lake, Michigan, during three seasons, Carbine (1941, 1943) estimated survival at 0.07-0.44%.

Estimates of survival from egg to lakeward migrant at Lake George, Minnesota, were variable, ranging from 0.08 to 4.62% between 1956 and 1958 (Franklin and Smith, 1963). These authors based their estimates on the ratio live/dead eggs collected during incubation in the marsh. Forney (1968) estimated at 83% the loss of the young between hatching and emigration from an experimental marsh at Shackelton Point on Oneida Lake, New York, in 1965 and 1966. This calculation was based on the potential egg deposition and the estimated number of eleutheroembryos. Royer (1971) reported from a marsh at Kenosee Lake (Saskatchewan) that 60 days after stocking of northern pike spawners, the calculated survival of potential egg production was 0.98% and 0.40% in 1964 and 1968, respectively. Mann (1980) approximated to 0.035% the mean percentage survival of fry from the rivers Frome and Stour, England, when the size of pike was 55 mm and 1.0 g. Kipling and Frost (1970) quoted survival rates from Sweden (Lake Malar: 25-76%; Lake Strakan: 4%) and Poland (up to 96%).

Table XII, taken from Fago (1977), summarized data on northern pike production from managed spawning and rearing marshes in the USA.

Table XII

Northern pike fry and fingerling production from managed spawning and rearing marshes in six states of the United States
(Taken from Fago, 1977)

Location	Marsh size (acres)	Year	Eggs deposited Acre (x 1 000)	Fingerlings: Number per acre	Fingerlings: Average length (mm)	Fingerlings: Size range (mm) Min.	Fingerlings: Size range (mm) Max.	Fingerlings: Survival (%)	Reference
New York									
Oneida Lake	7.3	1964	151	6 181	≈36	18		4.1	Forney (1968)
(Snackelton Point)		1965	171	5 554	≈36	18		3.2	
		1966	92	2 557	≈46	18		2.8	
Michigan									
Houghton Lake	≈4	1939	1 006	1 810				0.18	Carbine (1941)
(Peterson's Ditches)		1940	523	374				0.07	
		1942	451	≈2 000				0.44	
Townline Lake (Lower)	4.2	1958	60	3.976	66	48	99	6.6	Williams (1963)
		1959	21	425	51	33	79	2.0	
		1960	490	196	30	18	46	0.04	
		1961		6 262	30				
Ostego Lake	31.0	1959	72	43	69	36	132	0.06	
		1960	28	1 242	58	41	112	4.4	
		1961	84	3 027	58	23	114	3.6	
		1962	470	470	79	33	142	0.1	
		1963	162	1 459	43	25	84	0.8	
Rose Lake	2.0	1961		2 067	48				Di Angelo (1961)
Halls Lake	10.0	1961		1 983	43				
Crooked Lake (Lower)	1.9	1961		1 132	56				
Bertha Lake	0.5	1961		237	56				
Schoolsection Lake	3.2	1961		2 329	41				
Townline Lake (Upper)	8.0	1961		1 059	38				
Eagle Lake	7.0	1961		553	46				
Minnesota									
I.W.L.A. Pond #1	20.0	1962	180	6 679	51			3.71	Jarvenpa (1962, 1963)
		1963	5 957	2 740		25	51	0.046	
Mission Lake Pond #1	20.0	1962	100	29 205	51			29.25	
		1963	998	4 293		25	76	0.043	
St. Croix Park Pond	5.0	1962	209	3 400	76			1.63	
		1963	10 213	9 600				0.094	
St. Paul Pond #4	0.5	1963	14 286	2 000				0.014	
Sabre Lake	5.0	1962	297	1 100	51			0.37	
		1963	25 000	25	38			0.0001	
Waterville Pond #2	9.0	1962	407	2 567	64			0.63	
		1963	17 600	352	51			0.002	
Rose Lake	2.0	1963	14 286	1 000		38	51	0.007	
Whitehead	4.5	1963	4 010	3 689		51	102	0.092	
Hutchenson Pond	11.9	1963	981	1 079	89			0.11	
Shetek Pond #1	10.2	1962	120	24	76			0.02	
		1963	8 333	5		32	44	0.00006	
Shetek Pond #2	7.4	1962	171	24	89			0.014	
Jacobs Pond	2.0	1962	107	630	51			0.59	
		1963	8 685	1 737	56			0.020	
Cannon R. (I.W.L.A.)	1.0	1962	258	103	76			0.04	
		1963	52 250	1 045	38			0.002	
Pine Island Lake	2.0	1963	8 250	495	86			0.006	
Lattimer Lake Pond	2.0	1962	1 883	3 578		25	38	0.19	
		1963	8 750	350	89			0.004	
Ann Lake	1.0	1963	12 763	5 616	46			0.044	
Wilkoske Pond	2.0	1962	1 129	10 500	64			0.93	
Harriet Lake	17.0	1962	63	2 056	64			3.25	
Fox Lake	4.5	1962	67	447	127			0.67	
Kiester Pond	30.9	1962	24	184	127			0.76	
Lieuna Lake	10.0	1962	124	21				0.017	
Miss. River (Brainerd)	20.0	1962	55	11	102			0.02	
Coyote Creek	20.0	1962	75	3				0.004	
Phalen Pond	2.9	1965	375	≈3 000				0.8	Bryan (1967)
Lake Ge	9.0	1955		≈377					Franklin and Smith (1963)
		1956	234	≈10 327				4.62	
		1957	152	455				0.30	
Nebraska									
Valentine Pond A	2.6	1955	57	1 885	43			3.3	McCarraher (1957)
Valentine Pond B	1.0	1955	58	1 946	58			3.3	
Valentine Pond C	1.0	1956	330	1 700	66	38	79	0.5	
Valentine Pond D	1.5	1956	160	3 367	38			2.1	
Bluestem	325.0	1971		45		51	104		Morris (1974)
		1972		88		38	117		
		1973		261	-	38	91		
Wisconsin									
Lake Ripley	10.0	1964	174	70	53			0.4	Kleinert (1970)
		1966	533	52	48			0.1	
Pleasant Lake	3.7	1969	151	1 009	91	41	137	0.67	Fago (1977)
		1970	216	324	81	38	124	0.15	
		1971	136	541	99	41	155	0.40	
		1972	121	3 243	71	53	132	2.69	
		1973	104	2 473	79	48	130	2.39	
Pabst Marsh	18.5	1971	133	681	97	48	173	0.51	Fago (1977)
		1972	126	1 052	109	38	152	0.83	
South Dakota									
North Dimock	0.5	1957		3 260	43				Boussu (1958)
South Dimock	0.4	1957		2 285	43				
Hanson	0.3	1957		22 600	43				
Clear	4.1	1957		292	91				
French	1.6	1957		No est.	69				

A multiple regression was run with the number of fingerlings per acre as the dependent variable and the average length of the fingerlings at the time of draining and the number of eggs deposited per acre as the independent variables, using 60 marsh-years of managed spawning marsh data from a combination of work done in six states in the USA. This regression had a multiple correlation coefficient of only 0.313. The analysis suggested that many other factors may also have affected production. It must be remembered when drawing conclusions from this analysis, that the regression is subject to any bias in the techniques of estimating the number of eggs, in counting or estimating the number of fingerlings produced and in estimating the average length of the fingerlings. Thus it is possible that one or both of the independent variables may be highly influential in determining the numbers of fingerlings produced, but masked by one or more of the errors and biases mentioned.

Larsen (1966) obtained indications that the recruitment of northern pike in Danish trout streams did not result from spawning in the rivers. Analysis of samples taken from streams by electrofishing from April to September suggested that the 0^+ pike from spawning places in bogs and lakes migrate downstream to biotopes in the streams. According to the author, cannibalism is more common in northern pike in streams than in lakes. Both the spatial restriction of the pike biotopes and the "flow" of small pike offer increased opportunities for the pike to encounter and to prey upon another.

2.3.7 Adult period and senescent period

The adult period commences with the first maturation of the gametes. The senescent period is old age, occurring when growth has been extremely slowed down. Data on the life history of adult and senescent pike are given in the following chapters.

2.4 Feeding and Food of Adult Northern Pike

2.4.1 Introduction

The approach of a prey is guided by visual stimuli. The dash to a prey is released by a combination of visual and mechanical stimuli. Odour stimuli probably do not play a role in feeding of northern pike. In the following summary of data about feeding of northern pike short descriptions are included of the eye, the olfactory organ and the lateral system. Furthermore, an anatomical and histological description is given of the alimentary tract of northern pike. The section concludes with a description of feeding behaviour and food of northern pike.

2.4.2 Eye and vision

The cornea of the eye of northern pike is yellow and acts as a light filter. Braekevelt (1974) described the microscopic retinal structure of adult northern pike. The pigment epithelium is composed of a single layer of large cells containing many mitochondria. Bruch's membrane is composed of three layers. The innermost is the basal lamina of the pigment epithelium. The outermost layer is the basal lamina of the choriocapillaris endothelium. The endothelial wall of the choriocapillaris bordering Bruch's membrane is typically very thin but non-fenestrated. This region of the pike eye differs morphologically from that described for most other vertebrates.

Braekevelt (1975) studied the morphology of retinal photoreceptors in adult northern pike. Three types of photoreceptors are seen: rods, single cones and twin cones. The proportion of rods to cones is 1 to 9 (Walls, 1942). Rods are elongate cells basically similar to other vertebrate rod cells described. Twin cones are the more numerous of the two cone types present and are formed by two cone cells lying in close apposition along their inner segments with a membrane specialization where the two cells are apposed. Each member of the twin cone is morphologically similar to the other and to the single cone. The cone photoreceptors are arranged in a well defined, repeating mosaic pattern. The author presumes that the regular mosaic pattern of cones facilitates the retina's gathering of visual stimuli.

According to Wunder (1936), the composition and structure of the retinal photoreceptors of northern pike is typical for a fish with good vision in clear light. Compared to the horned pout, Ictalurus nebulosus (a bottom fish looking for food especially in the evening and by night), the northern pike has big and few rods. The cones are relatively big compared to those of bottom feeders.

Adaptation to darkness results in contraction of the cells of the pigment layer in the retina and exposition of the rods to the light. Adaptation to light results in contraction of the rods, and exposition of cones. The rods are protected against the light by the cells of the black pigment layer and the cones.

The great mobility of the eyeball of the northern pike allows it to see in almost any direction (Polyak, 1957) and to follow fast-moving prey. Northern pike are especially adapted to judge distance and depth with veritable sighting groves on their snouts in front of their eyes (Lagler, Bardach and Miller, 1962).

Scroczynski (1976) found that focal length of the crystalline lens was an important parameter of the dioptrical system of northern pike. The distances inside the eye chamber, refraction for front range of vision and size of iris are strictly dependent on the focal length. The direction of trophic locomotion of pike coincides with the direction of highest myopy and highest stability of the relative distance from the crystalline lens to the retina.

Basical distance of the binocular vision, i.e., the distance between centres of lenses in both eyes, increases during ontogenesis proportionally to body length, and exceeds the growth of focal length of the lens.

A remarkable Russian publication about 2 fish scales as organs of vision (Sokolov, 1962) was only consulted in abstract. The anterior portions of scales, situated in scale pouches of pike, were studied. The chromatophores in fish scales were investigated under the microscope. The author found similar images (entire fish, their heads, etc.) on the pigmented cells of the scales, and concludes that the fish exibit bipartition of the organ of vision, which is characteristic of many invertebrates.

Falcon (1979, 1979a) and Falcon and Moquard (1979) described the light microscopic and electron-microscopic structure of the pineal organ of northern pike. The photosensory function of the organ was studied and found to be mainly developed in the proximal than the distal regions and regressed (or lost) in the middle pineal. The pineal organ possibly plays a role as a receptor of photoperiodic stimuli.

2.4.3 Lateral line and reactions to mechanical stimuli

The development of the lateral line sense organs is described by Disler (1967) (see Section 2.3.4.1). . Wunder (1927, 1936) reported experiments and gave a discussion on the role of lateral sense organs in feeding behaviour of northern pike.

According to Wunder, blinded pike could capture living prey fish in aquaria and tanks, while dead prey was not captured. Blind pike reacted strongly on mechanical stimuli near the head region. The distance to the head of a 25-cm long pike had to be in the range of 5-10 cm; at greater distances no reaction followed. In comparison to pike with normal vision, blinded pike seemed to capture prey fish faster.

Field observations supported the concept that blind pike can be viable. Grimm (personal communication) reported that during three successive years of sampling in the Dutch Kleine Wielen (see Grimm, 1981), a blind pike, that could be recognized by a deformation of the back, was captured on the same location.

Destruction of the lateral sense organs on the head of northern pike resulted in the absence of reactions to mechanical stimuli. Blind fish without functioning lateral sense organs could not feed themselves (Wunder, 1927; 1936). The sense organs are more developed on the head of the pike than on the rest of the body. This indicates that the lateral sense organ is of primary importance in prey capture behaviour of the pike.

2.4.4 Olfactory organ and reactions to chemical stimuli

Northern pike can be considered as a micromatic fish having small olfactory sacs that are broadly open to the environment and an olfactory rosette consisting of several weakly developed folds. Water flows through the olfactory sac only when fish is moving (Devitsina and Malyukina, 1977). Malyukina *et al.* (1977) reviewed literature on the significance of olfaction in feeding behaviour and reported that pike are totally devoid of the capacity to respond to the smell of food (Wunder, 1927). Devitsina and Malyukina (1977) found that pike has a very limited range of active olfactory stimuli. The odour of its sexual products is a stimulus for the olfactory organ of pike. The authors suggest that northern pike make active use of odour signals in the spawning period.

Devitsina and Belousova (1978) found that the trigeminal system of northern pike reacts to stimulation of the olfactory lining. The authors concluded that trigeminal and olfactory systems have close functional relationships.

Morphology and anatomy of the olfactory organ is described by several authors (Bakhtin, 1976; Hara, 1971; Malyukina *et al.*, 1977). Bakhtin (1976) gives an attempted interpretation of the function of cell types constituting the organ in order to arrive at an understanding of the mechanism of olfactory reception and the role of the organ in behavioural reactions.

Kreutzberg and Gross (1977) described the general morphology and axonal ultrastructure of the olfactory nerve. It represents the extreme in high density axonal packing and is therefore exceptionally well suited for biochemical, biophysical and physiological investigations. Gross and Kreutzberg (1978) and Weiss *et al.* (1978) established rapid axoplasmatic transport parameters for proteins and aminoacids in the olfactory nerve of pike.

2.4.5 Alimentary tract

2.4.5.1 Mouth and dentition

The pike has long, wide jaws which open to a considerable width. The large ankylosed teeth are situated around the upper and lower jaw bone. Tongue and vomer are covered by hinged teeth which point backward. The openings of the gill arches are seen on the bottom of the lower jaw behind the tongue, leading into the oesophagus. Histologically, the epithelium of the tract starts at the lips with a thin layer of stratified squamous epithelium interspaced with goblet cells. Toward the eosophagus the epithelium becomes thicker, more goblet cells and occasional taste buds are seen in the gill-arch region and hinged teeth become more numerous. The tongue is immobile and covered with hyaline substance, with a pseudostratified epithelium, mainly composed of goblet cells, plus a few taste buds. Hinged teeth are also seen (Bucke, 1971).

The anatomy of the mouth of northern pike is typical for a predatory carnivore (Heuschmann, 1957; Bucke, 1971). The shovel-like snout, large-jawed mouth and arrangement of the teeth are adapted for seizing and holding the prey.

Tereshenkov (1972) described the replacement of teeth in the jaws of northern pike. The number of functioning canine teeth is not dependent on season, age or sex. It showed to be comparatively constant on jaws of pike from different lakes and does not exceed 11-12 on average over a year. Replacement of teeth is a natural process which takes place continuously and irregularly (Heuschmann, 1957). It does not affect the feeding rate. This is also concluded by Zadul'skaya (1960) in her study of pike in the Rybinsk reservoir (USSR). The shedding of teeth and the pathological occurrences associated with it exert a slight influence on the feeding of pike.

Herold (1971) described the development and the mature structure of dentine in the pike which was analysed by microradiography. Furthermore, he investigated by electronmicroscopy the role of the dental epithelial cells in the formation of the teeth (Herold, 1974).

2.4.5.2 Oesophagus and stomach

The prey is swallowed head first down the short oesophagus into the pouch-like stomach. There is no clear outer demarcation between both parts. The stomach narrows at the pyloric end to enter the intestine. In the oesophagus the pseudostratified squamous epithelium contains many goblet cells. The lamina propria consists of loose connective tissue, interspersed with blood vessels and lymphocytes. The inner circular smooth muscle layer is separated anteriorly from longitudinal muscle by the nerve plexus of Auerbach. At the gastero-oesophageal junction there is a definite change in the epithelium of the mucosa. The mucosa is thrown up into large rounded folds and its cells are mainly columnar, tall and surmounted by a top-plate. Goblet cells are not found in the stomach. The lamina propria is made up of loose connective tissue and the fibres are more easily distinguished than in the oesophagus. Numerous blood vessels and a few smooth muscle fibres are present. The muscle layers consist of smooth muscle fibres, with the longitudinal muscle layer thicker than in the oesophageal region (Bucke, 1971).

Linns and Geyer (1968) provided an electronmicroscopic study of the structure of the oesophagus.

Fish have no salivary glands but mucin is excreted into the buccal cavity and oesophagus by goblet cells. The mucin serves as a means of mechanical protection of the alimentary canal from hard or spiny pieces in the food. The columnar epithelial cells have digestive and absorptive functions. The mucin of these cells is secreted in the stomach and the first part of the intestine and emulsifies the food into a chyme (Bucke, 1971).

Molnár and Tölg (1963) studied the mechanical functioning of the stomach using X-ray photographs. Food was not moved in the stomach, but pressed into the intestines. Remorov (1965) recorded stomach activity by the balloon method and found "hunger" movements in the form of regular tonic contractions. The movements of the stomach arise shortly after the pike has ceased to be fed and continue for up to 40-70 hours. Most often each contraction lasts 3 minutes after which a pause of 5 to 7 minutes follows. Transection of the nervus vagus leads to a fall in stomach tonus and terminates stomach movements. However, from the second day on the tonus begins to re-establish and on the 4th or 5th day weak stomach contractions reappear.

2.4.5.3 Intestine

The intestine convolutes up to two-thirds of the stomach length, while the remaining longer part runs straight to the anus (Bucke, 1971). The development of the S-bend form of the alimentary canal is completed early in the larval period (Frost, 1954; Shamardina, 1957) (see Figure 15).

The anterior intestine has a long filiform mucosa with many goblet cells. There is a thick banding of connective tissue in the lamina propria, and the circular muscle layer is very prominent, consisting of loosely packed muscle fibres with blood vessels and nerves running between them. The longitudinal layer consists of tightly packed muscle fibres.

The posterior intestine does not greatly differ from the anterior, but folds in the mucosa are much longer. The lamina propria is narrower and there are prominent connective bands. The muscle layers are narrower.

The liver has a single elongated lobe, linear at the anterior pole, rounded posteriorly. Fat was demonstrated in the hepatic cells. The pike, as a carnivore, uses its liver as a storage organ for oil (Boldyreff, 1935). The gall bladder lies ventral to the liver, the bile duct running straight along the ventral surface of the liver to enter the intestine (Bucke, 1971).

The pancreas of the northern pike is a well defined and compact gland located on the small intestine (Boldyreff, 1935). The hepatic end is formed by two lobes lying just below the gall bladder and encircling the bile duct. The body of the gland is attached to the gut and extends from the liver to the pyloric valve where it terminates at the spleen. It has a uniform structure, is of considerable size, and composed mainly of secretory acini.

2.4.6 Feeding behaviour

2.4.6.1 Behaviour of northern pike

A. General aspects

Prey capture by pike larvae is described by Frost and Kipling (1967) and Braum (1964) (see Section 2.3.4.2). Behaviour of young pike toward its prey is not essentially different from the prey-capture behaviour of adult northern pike.

Adults are almost entirely fish eaters and they catch prey mainly by sight during day hours (see Section 2.7.9). Observations indicated that northern pike are usually located in some type of concealment from which they attack their unsuspecting prey (Threinen, 1969). When hungry, they also make feeding forays, slowly moving about looking for schools of fish. Such behaviour can be inferred from angling observations and from studies on the migratory patterns of northern pike (see Section 2.7.1).

Hoogland, Morris and Tinbergen (1957) summarized the prey-catching behaviour of pike as a sequence of the following activities:

(1) eye movements toward the prey;
(2) turning toward the prey;
(3) stalking;
(4) leaping;
(5) snapping;
(6) turning the prey head-forward;
(7) swallowing.

B. Strike tactics

Kashin, Malinin and Orlovskij (1976) who studied the behaviour of pike as a predator of bream, *Abramis brama*, and roach, *Rutilus rutilus* in aquaria, observed that pike wait till the prey is at a distance of about half its body length. Hoogland, Morris and Tinbergen (1957) described the reaction of pike to a passing fish initially as visual. Usually, the prey is first seen with one eye. The pike turns its eyes to the prey, followed by a slow turning of the body which comes to a stop when the prey is exactly in front of the pike's head. The predatory movements primarily consist of an orientation of the body axis toward the prey followed by a stealthy approach ("axial tracking" (Nursall, 1973)). At about 5 cm from the prey this stalking motion stops.

Webb and Skadsen (1980) analysed the strike tactics of the tiger musky (*E. lucius* female x *E. masquinongy* male). Their analysis is also applicable to northern pike behaviour. Two aspects are therefore the most important:

(a) What is the best target on the prey?

(b) How is the target likely to move so that adaptation of strike behaviour can minimize the probability of prey escape?

The authors concluded from their analysis of the locomotory kinematics of predator and prey that optimal strike tactics for a leaping predator could be summarized as follows:

(1) strike at the prey's centre of mass;
(2) strike the prey from the side;
(3) utilize S-start kinematics;
(4) strike at maximum acceleration, utilizing a pre-strike S-posture, when possible.

The tiger musky strike tactics were consistent with the expectations. Strike tactics of northern pike were, in general, in agreement with the analysis of Webb and Skadsen (1980). Hoogland, Morris and Tinbergen (1957) and Neill and Cullen (1974), observed that before northern pike stroke it curved its body in an S-shape.

During stage 1 of an S-start, the body of the fish quickly bends from a straight stretched position into an S-shape. During the propulsive stroke of an S-start, the body of the fish bends from this S-shape into an opposite S-shape (stage 2) followed by continued propulsion or braking (Rand and Lauder, 1981).

S-starts may be divided into two distinct types. Webb and Skadsen (1980) described "pattern A" starts or strikes as the characteristic S-start, beginning from a streight body posture and progressing through stages 1 and 2. In a second type of S-start the preliminary stroke is deleted and the fast start begins at stage 2 after the fish assumes a full S-posture ("pattern B").

Under normal conditions the final curving and subsequent stretching of the tail takes place so quickly that the eye can scarcely follow the movement. Kashin, Malinin and Orlovskij (1976) observed that during the swift forward movement the speed was non-uniform, increasing at the beginning of the charge and decreasing sharply as the predator caught its prey.

C. Strike tactics and body morphology

Webb (1984) observed that, of the four principal tactical components of the predator behaviour of northern pike (target, strike angle, closure rate and manoeuvre), target and strike angle need not depend on locomotory-morphology, while speed and manoeuvrability are dependent. The elongated cylindrical body shape - minimizing body surface area and adding body volume for maximum muscle mass - (Webb, 1978, 1978a) and the mucous skin surface (Kobec, Zavjalova and Komarova, 1969; Pjateckij and Savcenko, 1969), add mass drag during acceleration and minimize friction. According to Webb (1982) the body form of *Esox* is sub-optimal for acceleration because it lacks an anterior median fin. Therefore, energy is wasted as lateral recoil of the anterior of the body or by its control using muscles. According to Webb (1984), the high rate of acceleration results in frequent overshooting of the prey and possibly reduces the success of lunges. The ventro-lateral position of the paired fins prevents effective braking. Therefore the S-start strike tactic is actually optimal only for the initial stage of an attack and must be considered sub-optimal if an extended interaction is likely. Hence, the important corolary of the lunge tactic is that prey should normally be intercepted before escape manoeuvres can develop and hence is effected only if prey response thresholds are low (Webb, 1982).

In the evolutionary history of esocids the sub-optimal body form did not result in essential morphological changes or adaptations. Reist

(1983a) in his study of the external body morphometry of esocoid fishes concluded that changes in the vertebral number during evolution of esocids appear to have been confined to the precaudal region (also Cavender, 1969). The differences in the morphometry of the tail and head regions of recent esocids were small. The discovery of a paleocene pike in western Canada (Wilson, 1980) showed that the basic pike body form and feeding mechanism have persisted largely unchanged for at least 60 million years.

D. Capture of prey

In the final leap to the prey the mouth is kept closed until just before the target is reached. Then it opens with force so that the prey is sucked into the mouth. Leeuwen and Muller (1983) recorded buccal and opercular pressure during the movement of pike to its prey. A high pressure on the opercle reflected the accelerated swimming of the fish to its prey. The pressure inside the mouth was according to the authors built up of velocity and acceleration components due to mouth expansion and forward motion. The hydrodynamic events during suction feeding of pike could be described with a model (Muller, Osse and Verhagen, 1982).

Rand and Lander (1981) correlated patterns of jaw-bone movement of Esox niger with the locomotory categories defined by Webb and Skadsen (1980). Pattern B strikes were initiated at shorter distances from the prey, had higher acceleration rates, and the velocity of mouth opening and suspensorial abduction was greater than for pattern A strikes. In general, pattern B strikes were more successful (Webb and Skadsen, 1980). Rand and Lander (1981) found no difference in the excursion amplitudes of jaw movements between pattern A and pattern B strikes. Significant differences were found between midwater and corner strikes in the amplitude of mouth opening and hyoid depression: both were smaller in corner attacks and suction velocity was higher. Both velocity and amplitude of each mechanical unit in the head can be varied depending on the locomotor pattern and position of the prey.

Once the prey is in the mouth, it is practically impossible for it to escape, mainly because of the long sharp teeth that are directed backward. A small prey is swallowed without any difficulty; a large one is first turned by short jerky shaking movements of the head until it can be swallowed head first. Swalling is effected by movements which resemble exaggerated breathing (Hoogland, Morris and Tinbergen, 1957).

For diurnal periodicity and activity of northern pike and influence of light on feeding behaviour and growth see Section 2.7.9.

2.4.6.2 Predator-prey interactions

Kashin, Malinin and Orlovskij (1976) reported that usually after two to four successful attacks the charging speed and the frequency of charges of northern pike decreased, which resulted in a higher rate of escape of the prey fish.

Neill and Cullen (1974) measured the effect of prey group size (Cyprinidae) on the hunting success of northern pike. The authors found that the attack success per encounter decreased with increasing prey density. Northern pike is an ambush predator and increasing prey numbers reduces its hunting by success causing frequent performance of acts not related directly to hunting. Interruption of hunting caused by these acts was responsible for the lower capture rate with increasing prey numbers.

The reactions of cyprinid fish to predation are possibly influenced by the release of an alarm substance after a predatory attack of pike. Verheijen and Reuter (1969) observed an alarm reaction in blinded minnows (Phoxinus laevis) after contact with water in which a pike had swallowed a small roach (Rutilus rutilus). However, they did not react to water in which a large minnow had swallowed a small roach. The authors concluded that the amount of alarm substance, if any, which is liberated when a large cyprinid swallowed a small one, was smaller than when a pike with its pointed teeth damaged the skin of a cyprinid prey.

Schooling behaviour of prey fish can be considered as a defence reaction against predation of northern pike. Andörfer (1980), who investigated schooling behaviour of Leucaspius delineatus in relation to the presence of northern pike in aquarium experiments, found that the presence of northern pike increased the school concentration. School concentration was observed to be highest at low-water level and low quantities of water. Dobler (1977) found in aquarium experiments that at low light intensities (less than 1 lux) the school of Leucaspius gradually dispersed. He concluded that by and large, the pike captures Leucaspius at illumination levels at which the school of the prey fish is no longer completely unified.

When a school of prey fish is attacked by the predator, the fish usually disperse ("local flash expansion", Nursall, 1973), which disorients the predators (Nikolsky, 1963). Shortly after an attack, the school is formed again.

Nursall (1973), studying behavioural interactions of spottail shiners (Notropis hudsonis) and northern pike, stated that peripheral members of schools of shiners, or abnormal outliers of the school, are probably most subject to attack. The author also put forward that the abundance of prey more than compensates for apparent limited effectiveness of the predator.

Moody, Helland and Stein (1983) analysed escape tactics used by bluegills and fathead minnows to avoid predation by the esocid predator tiger muskellunge (E. lucius x E. masquinongy), and found results in agreement with the findings of Beyerle and Williams (1968), and Mauck and Coble (1971). Bluegills in tank experiments required more following, longer pursuit and more strikes per capture than fathead minnows, and as such were less vulnerable to predation. The authors suggested that antipredatory behavioural patterns and the morphology of the two prey species appeared to combine to account for their differential susceptibility to the esocid predator.

The result of the analysis of predator-avoidance behaviour of fathead minnow (Pimephales promelas) suggested (Webb, 1982) that configuration differences between predators are important contributors to the stimulus initiating avoidance reactions. Webb (1982) suggested that the rounded body cross-section of esocids was associated with lower response thresholds than the elliptical and lenticular cross-sections of trout (Salmo gairdneri), smallmouth bass (Micropterus dolomieu) and rock bass (Ambloplites rupestris).

Coble (1973) studied in laboratory experiments the influence of appearance of prey and satiation of pike on food selection of pike. The results indicated that differences in form of the tail, brightness and colour of the prey fish are not important to northern pike. He also found that food deprivation did not affect prey selection of northern pike; the behaviour of the prey is more important than physical appearance in influencing the predator. A comparable conclusion was drawn by Hoogland, Morris and Tinbergen (1957) who found that their aquarium observations were in contrast with the observations of stomach contents made by Frost (1954) in Lake Windermere. Although minnows are much more abundant than sticklebacks (Gasterosteus) in Windermere, the percentage of Gasterosteus in pike stomachs rises above that of minnows. Hoogland, Morris and Tinbergen (1957) conclude that minnows may have anti-predator adaptations which work even better than spines, at least compared with large pike.

Reist (1980, 1983) studied northern pike predation on pelvic skeletal phenotypes in a population of Culea inconstans in laboratory experiments and by analysing the food of pike in Wakomao Lake, Alberta (Canada). The author found that individuals possessing a pelvis and pelvic spines have a selective advantage over individuals lacking these parts. The latter seem to compensate behaviourally for their morphological disadvantage.

Jacobson and Järvi (1976) studied anti-predator behaviour of 30 2-year-old hatchery-reared smolts of Atlantic salmon in a stream tank that also contained four pike and burbots (Lota lota). During the period of observation the pike never hunted - this in contrast with the burbots that tried to catch the prey in free water. When the predators were inactive, the smolts formed one or two schools. If a pike approached the school, it tightened, even when the pike moved tail-first toward the school. The smolts tried to keep a respectful distance of 1-1.5 m from the pike and 0.1-0-2 m from the burbots. When pike came within a respectful distance from the smolts they showed escape reactions. Predator-inexperienced smolts reacted instinctively on specific stimuli of pike; no similar reactions were seen among burbots.

Bartmann (1973) reported a case of cleaning symbiosis between stickleback (Gasterosteus aculeatus) and northern pike from an aquarium. No distinct signal movement or signal position to invite cleaning existed. The normal resting posture of the pike seemed to elicit cleaning responses in sticklebacks. Compared with the specialized cleaning symbiosis of some marine fishes, the symbiosis between stickleback and pike is at a primitive stage.

2.4.7 Food selection

2.4.7.1 Species selection

Ivlev (1961) studied several aspects of food selection by northern pike in experimental situations. His study furnishes a theoretical basis for the analysis and interpretation of feeding and food relations of fish. Selection of food is determined both by the vulnerability of available prey and preference of the predator. Preference could be affected by innate inclination, satiation and conditioning of the predator, and vulnerability and availability of the prey fish by appearance, behaviour, abundance, relative abundance, size distribution and armament (Ivlev, 1961; Mauck and Coble, 1971). Both aspects of selection of food by northern pike were studied in laboratory and field experiments.

In general, pike have been known to feed non-selectively. Frost (1954) concluded from her investigations on the food of pike in Windermere that there was no evidence of positive selection by pike for any of the prey species present. Rather, external factors such as relative abundance and seasonal availability determine the species of prey, even though the size of the individuals eaten is selected by the pike.

Various studies of northern pike diet, including Banks (1965) in Chesire waters, Lawler (1965) in Homing Lake, Manitoba, Willemsen (1965; 1967; 1967a) in polder waters in the Netherlands, Vostradovsky (1981) in Czech reservoirs and Lux and Smith (1960) in a small Minnesota lake, reported findings generally in agreement with the conclusion on food selection presented by Frost (1954).

Wolfert and Miller (1978) reported that northern pike in Eastern Lake, Ontario, positively selected alewife (Alose pseudoharengus). Compared with the relative abundance of fish in gillnet captures, white perch (Morone americana) and yellow perch (Perca flavescens) were less prominent in the pike diet than alewife. Wagner (1972) showed that the large numbers of spawning alewife in Little Bay de Noe, Lake Michigan, made them a readily available food supply for northern pike and other piscivores in the Bay.

The analysis indicated that the large number of alewifes buffered the predation on the abundant perch population.

Armament of prey fish was shown to decrease vulnerability of the fish against predation of northern pike. Hoogland, Morris and Tinbergen (1957) observed in laboratory experiments that pike (10-25 cm) reject and avoid the 10-spined stickleback (Pygosteus pungilius) more than minnows or other non-spined fishes. The rejection of sticklebacks is based on two distinct processes: a non-conditional response to the strong mechanical stimuli caused by the spines, and a learned response to visual stimuli which cause the pike to avoid sticklebacks before they have even touched them.

Northern pike (10-35 cm) prefer soft-rayed fish over spiny-rayed fish, as was shown by Beyerle and Williams (1968) and Mauck and Coble (1971). The most vulnerable species in laboratory experiments, in decreasing order were: gizzard shad (Dorosoma cepedianum), common carp (Cyprinus carpio), bigmouth buffalo (Ictiobus cyprinellus), fathead minnow (Pimephales promelas), and smallmouth bass (Micropterus dolomieui). White sucker (Catostomus commersoni), green sunfish (Lepomis cyanellus), pumpkin seeds (Lepomis gibbosus), largemouth bass (Micropterus salmoides), golden shiner (Notemigonus chrysoleucas) and yellow perch (Perca flavescens) showed intermediate vulnerability. Channel catfish (Ictalurus punctatus), northern pike, bluegill (Lepomis macrochirus) and black bullhead (Ictalurus melas) were least vulnerable. Beyerle (1971, 1973, 1978) found that age II northern pike in ponds fed largely on insect larvae, crayfish and tadpoles, despite an abundance of edible-sized bluegills. Tomcko, Stein and Carline (1984) came to comparable conclusions in pond experiments with tiger muskellunge and bluegills.

In experiments in small ponds, Doxtater (1967) compared northern pike, chain pickerel (Esox niger), grass pickerel (Esox americanus vermiculatus), walleye (Stizostedion vitreum vitreum) and channel catfish (Ictalurus punctatus) as predators of bluegills. Northern pike was found to be the most successful.

Solman (1945) reported from the Saskatchewan River delta that about 1% of the examined pike stomachs contained young waterfowl. Predation of pike on young waterfowl was reported from 44% of the areas scattered over the Canadian Prairie Provinces by 207 observers. The author found in laboratory experiments that young duckling is much slower digested by pike than fish food. Pike responsible for the predation on the ducklings were between 48 and 76 cm. The author estimated that pike in the Saskatchewan River delta destroyed four waterfowl per hectar per season. Lagler (1956) estimated much lower predation pressure of pike on waterfowl in the flooded portions of the lowlands at the Seney National Wildlife refuge.

Larsen (1966), in his study of pike in streams in Denmark, reported from the stomach of a 4-kg pike from a peat pit in South-Seeland a young coot (Fulica atra) as well as a water-vole.

Differences in vulnerability to northern pike predation are reported among salmonids. Kamyshnaya and Tsepkin (1973) found, by analysing stomach contents of adult pike in the Umba River (USSR), that juvenile Atlantic salmon (Salmo salar) reared in hatcheries were more vulnerable to predation than juveniles of hatchery-reared pink salmon (Oncorhynchus gorbuscha). Hunt (1965) analysed food in stomachs of northern pike captured in a trout-inhabited creek in Wisconsin. Rainbow trout (Salmo gairdneri) were eaten more often than brown trout (Salmo trutta). Higher vulnerability of rainbow trout to northern pike predation was also indicated in a tabulation of electrofished trout that had been scarred by pike. In a sample of 305 brown trout, 9% had scars, while a sample of 43 rainbow trout contained 37% of trout with scars.

Mann (1982) noted in the River Frome (England) that young pike (1+) ate migrating Salmo salar smolts in April, while larger pike (age 2+ and older) preyed on Salmo trutta returning from the sea to the river spawning grounds in August. Frost (1954) also observed a vulnerability of trout to pike predation during their pre-spawning migration. Stein and Enzler (1983) concluded from experiments in raceways that pike selected trouts from stocks that also contained rudd (Scardinius erythrophtalmus). When confronted with trout from hatcheries and wild trout, the pike preferred the fish from the hatcheries as food.

2.4.7.2 Size selection

Frost (1954), Lawler (1965), Willemsen (1965) and Mann (1982) found a positive relationship between size (or weight) of the pike and size (or weight) of the prey. Frost (1954) also found that for northern pike in the range of 20-105 cm, increase in size meant a change of the fish species eaten. Willemsen (1965) found that the range of sizes of food-fish taken by northern pike was variable for all sizes of pike examined.

Nursall's (1973) data suggest that about one-quarter of the pike's length is the optimal prey size. Popova (1967) showed a relative decrease in size of prey with increase in size of pike. Zadul'skaya (1960) found that the diet of pike in the Rybinsk reservoir (USSR) ranged from 3 to 15 cm; fish longer than 15 cm were seldom eaten. Larger pike consumed slightly larger fish; in fall and winter, pike took somewhat smaller fish than in spring and summer.

Mann (1982) reported from his observations in River Frome that the stomachs of individual pike in age group 1 and older contained about the same number of prey fish. None of the pike in the oldest age group contained more than two fish.

Hart and Connellan (1984) interpreted from experiments in an artificial tank environment that as prey (Phoxinus phoxinus) weight increased, the number of prey consumed by pike (50-149 g) decreased. The pursuit time did not vary with prey weight under the experimental conditions that offered predator and prey no shelter. The manipulation time, the period between capture and swallowing increased somewhat with increasing (0 to 5 g) prey weight. Based on a regression function, the authors suggested that the growth rate of pike was a positive function of the size of the food ration and a negative function of the amount of time spent in capturing each prey. The authors discussed their results with reference to the optimal foraging theory.

2.4.7.3 Seasonal food

Ivanova and Lopatko (1979) concluded from their study on diet determination of predator fish in the Rybinsk reservoir (USSR) that, on quantitative evaluation of food of predatory fish, based on specimens collected with passive gear, leads to considerable underestimation of the value of food rations. Frost (1954) compared seine net catches and gillnet catches and found that seined fish were smaller than gillnetted fish and remarked that catching methods could influence food utilization studies of pike. Lawler (1969) reported differences in catch rhythm between deep water and inshore locations of gillnets. These differences were related to pike activity and are therefore of influence on the result of food studies. A review of the literature on stomach analyses is given by Hyslop (1980). Mann and Beaumont (1980) and Crossman and Casselman (1969) described methods to identify well digested remains of fish prey from pike stomachs.

Diana (1979a) measured the daily food ration of pike in Lac Sainte Anne (Canada). He found that daily food rations were highest in June, while food rations (expressed in kcal/kg day^{-1}) were high from May to August. Frost (1954) deduced from the proportion of feeding fish in her monthly samples that the highest percentage of feeding fish in Windermere is found in May, while the lowest percentage is found from January to April. Lowest figures in March-April are probably indicative of a fast, associated with spawning time. Seaburg and Moyle (1964) and Lawler (1965) found in waters in Minnesota and Manitoba that spring and fall are the periods of heaviest feeding. Lawler (1965) and Clark (In Toner and Lawler, 1969) related the high frequency of empty stomachs during the summer months to high-water temperatures. The authors suggest that when temperatures rise above the optimum, pike activity is restricted and feeding practically stops. However, increased digestion rates at higher temperatures can also result in larger frequency of empty stomachs. Diana (1979a) found gastric evacuation time of northern pike to be two days at 16°C and 12 days at 2°C. At higher temperatures shorter evacuation times can be expected. Moreover, Zadul'skaya (1960) correlated variations in frequencies of empty stomachs of pike in the Rybinsk reservoir (USSR) to the changes in availability of prey fishes and to changes in size of prey fish. Her results indicated that larger prey fish catch fewer times. Also, Diana (1979a) found a decline in pike's diet over mid-summer even when water temperatures remained fairly constant.

Ivanova (1969) reported that in the Rybinsk reservoir the highest feeding activity of northern pike was observed immediately after spawning. The author found differences in the feeding of males and females; males remained longer on the spawning grounds than females. Ivanova (1969) based her analyses on estimates of food consumption. Zadul'skaya (1960) related feeding intensity to frequency of empty stomachs. The author found that all size groups of pike did not simultaneously intensify feeding immediately after spawning in the Rybinsk reservoir. This could not be explained merely by the extended spawning period, but by additional factors including water level of the reservoir that influenced the availability of prey fish.

Willemsen (1965, 1967a) found that during spawning time, pike in Dutch polder waters have the highest frequency of empty stomachs. Bruyenko (1976) found that male and female pike continued to feed during spawning in the Kremenchug reservoir (USSR), although feeding rate and number of species consumed decreased. Diana (1979a) (see Table XIII) found that pike from Lac Sainte Ann underwent a spawning fast which resulted in a depletion of body reserves (Diana and Mackay, 1979) (see Section 2.6.3). The rate of feeding increased to a maximum immediately after this depletion, and high rations continued during the major period of body growth (May to August). Winter rations were extremely low, and winter metabolism must be very low to allow growth to occur (see Section 2.6.3). Female rations were greater than male levels during summer and winter. From May to March, female production was twice as high as that of males, although both sexes produced similar amounts of somatic tissue annually. Immature pike in their first year grew extremely fast, putting all energy into somatic growth (Diana and Mackay, 1979).

Frost (1954) and Lawler (1965) found that seasonal changes in the diet of the pike appeared to be related to the availability of the fish food. Different species composition in different waters results in diverging pike diets. Lawler (1965) reports that the most important food types eaten in each of several periods during the year in Haming Lake are: May and June - trout-perch (Percopsis omiscomaycus); July - spottail shiner (Notropsis hudsonius); August to September - yellow perch (Perca flavescens); October to March - sticklebacks (Pungitius pungitius and Eucalia inconstans). In Windermere (Frost, 1954), perch (Perca fluviatilis) occur in the pike diet at all times, but predominate from May to October. Char (Salvelinus willughbii) are eaten only in November and December, brown trout (Salmo trutta) to a greater extent from October to February. Sticklebacks (Gasterosteus aculeatus) and minnows (Phoxinus phoxinus) are taken in spring and summer. Such seasonal variations are associated with the changes in habits of the food species.

Table XIII

Daily ration of northern pike for various time-periods sampled during 1976-78 in Lac Sainte Anne (Diana, 1979a)

Time period	Sex	Meal size (kcal/kg)	Time between meals (days)	Daily ration (kcal/kg day^{-1})
May	Male	30.4	3.1	9.6
	Female	32.4	2.3	14.0
June	Male	35.0	1.9	18.1
	Female	66.5	2.2	30.9
July	Male	36.5	2.1	11.5
	Female	54.1	2.8	19.2
August	Male	23.1	3.8	6.0
	Female	25.4	2.6	9.8
September	Male	22.5	3.5	6.4
	Female	31.4	4.2	7.5
October	Male	17.4	2.2	7.9
	Female	16.5	1.9	8.6
January	Male	9.8	34.0	0.3
	Female	22.0	23.0	1.0
March	Male	10.9	22.0	0.5
	Female	21.6	26.0	0.8
April	Male	14.8	59.0	0.3
	Female	14.8	59.0	0.3
Winter	Male	10.6	25.0	0.4
	Female	21.8	25.0	0.9
Summer	Male	30.8	2.8	11.4
	Female	47.0	2.7	17.4

2.4.8 Cannibalism

By producing an offspring capable of utilizing a food source smaller than the adults can handle efficiently, pike are adding a connecting link between themselves and a lower, otherwise inaccessible level in the food chain (after Nikolsky, 1963 and Helfman, 1978). In low-diversity communities, small conspecifics may even be the main source of food for adults (Munro, 1957).

In general, food shortage results in higher occurrence of northern pike in pike stomachs. Hegemann (1964) suggested that this was the reason for the high percentage (10%) of pike in the stomachs of pike in the Greifswalder Bodden (German Democratic Republic). Vostradovsky (1981) reported from the Czech Hubenov reservoir, where perch (Perca fluviatilis) and roach (Rutilus rutilus) were absent after the construction of the impoundment, that pike fed on caddis fly (Anabolia sorror) which could not provide sufficient energy, so the bigger pike resorted to cannibalism. Munro (1957) examined 418 stomachs of northern pike recovered after rotenone reclamation of the Scottish Loch Choin. The water was devoid of other fish and pike continued to feed very largely on invertebrates (Gammarus). This was the major food type of pike up to a length of 50 cm, measured by the frequency of occurrence in their stomachs. With the increase in size, frogs and smaller pike became more and more important in the diet. Analysis of pike stomachs indicated that in the size range 30-100 cm frogs and pike were of equal importance as prey.

Munro (1957), Lawler (1965) and Lagler (1956) observed that examination of stomach contents of pike after rotenone poisoning resulted in biased data on their feeding behaviour. Immediately after poisoning, small fish showed distress and pike were observed to feed actively on these weakened, erratically moving individuals. Examination of stomach contents of these pike showed them to be gorged with small fish. Munro (1957) therefore excluded freshly consumed pike in pike stomachs from his data on cannibalism in Loch Choin.

In situations where other food items are available, the incidence of pike in pike stomachs is reduced. Frost (1954) reported from Windermere that out of 2 783 northern pike (20-105 cm), caught between 1940 and 1953, stomach analysis revealed that only 33 (1.2%) had eaten pike. This percentage is somewhat higher when corrected by excluding the pike with empty stomachs (2.28%). Stomach analysis of 29 477 pike from Heming Lake, Manitoba, from 1950 to 1962 (Lawler, 1965), revealed that

169 pike had eaten conspecifics (0.57%; 1.15% when corrected by excluding pike with empty stomachs).

Larsen (1966) analysed stomach contents of 895 pike from 18 Danish trout streams and found that the frequency of cannibalism was about 1.5%. Pike were not recorded in stomachs of pike smaller than 20 cm. Toner (1960) examined pike from three Irish loughs and found the remains of northern pike in 87 (3.9%) of the 2 215 individuals with filled stomachs. Willemsen (1967) supplied data for stomach contents of 576 pike from six water bodies in the Netherlands and found 13 individuals with pike in their stomachs. Other authors detected no cannibalism in their studies of food habits of northern pike (Wolfert and Miller, 1978), or did not report or recognize pike as separate food item in the northern pike's diet.

The data are inconclusive as to seasonal trends in cannibalism. Lawler (1965) marked an increase in the number of pike eaten in October when all monthly data of 12 years of food analysis from Heming Lake were added. The frequency of pike in pike's stomachs was highest in the small December sample (7%). From the analyses of data collected throughout 13 years, Frost (1954) reported highest frequencies of northern pike in stomachs in May and July. Bruyemko (1976) studied stomach contents of 630 pike caught in gillnets during the spawning period (April and May, 1970-73) in the Kremenchug reservoir (USSR). The author found a high incidence of pike in pike stomachs (10-20% numerical frequency in filled stomachs), which was related to the small number of prey fish present in the shallow waters, from where pike samples for the investigation were taken. Pike of all size groups (30-80 cm) consumed their young. The stomachs of spent females often contained male pike with running milt.

Mann (1982) found the highest weight percentage of pike in the stomachs of northern pike in the River Frome in August, when they consumed the largest biomass of prey fish. Consumption of pike in other months was negligible or absent.

Cannibalism mainly focusses on individuals in the length range of 5-25 cm (Lawler, 1965; Larsen, 1966). These authors, as well as Munro (1957), Vostradovsky (1981), Bruyenko (1976) and Mann (1982), found that the percentage of pike in the diet increased with increasing size or age of the predator. Lawler (1965) gives data, summarized in Table XIV for 12 years of stomach analyses. It is noteworthy that in the years 1958, 1959 and 1960, when gillnet activity in Heming Lake was most intensive and affected the population structure of northern pike (population mainly formed by individuals smaller than 46 cm). The incidence of cannibalism remained low (see Table XV). There is a statistically significant negative correlation between the frequency of stomachs containing pike as a food item and the average length or weight of pike in the index nets.

Mann (1982) found that in the River Frome pike of the age groups 4 years and more had the highest amount of pike in their stomachs (7.65 kg/ha/year; 55 individuals had eaten 30 pike). As a food item, pike made up 13% of the annual weight of the prey-fish eaten by this age group.

2.5 Growth of Northern Pike

2.5.1 Correlated factors

Data on the first year growth are presented in Section 2.3.5. Figures 24-28 and the Appendix summarize the growth data of northern pike from different locations.

Casselman (1978) studied the growth of the species under laboratory conditions and found the growth rate to be dependent on oxygen conditions, temperature and the light/dark cycle (see Sections 2.7.5, 2.7.8, 2.7.9). Temperature conditions of the water are also reported to have an influence on the growth of pike in field conditions. Lawler (1965) and Williams (1955) related high water temperatures to growth inhibition. Food consumption of pike at high water temperatures is also reported to be inhibited (Clark, In Toner and Lawler, 1969; Seaburg and Moyle, 1964). According to Miller and Kennedy (1948), northern pike showed better

Table XIV

Incidence of cannibalism in relation to size of northern pike in Heming Lake, Manitoba (1950-62) (Lawler, 1965)

Length range (in cm)	Pike with pike in stomaches		Total number of pike with other food in stomachs
	No. of indiv.	Percentage	
15-30	16	0.2	8 000
30-45	94	1.9	4 959
45-60	57	6.6	860
>60	2	4.2	48

Table XV

Data on gillnet fishery in Heming Lake, Manitoba (1945-66) and frequencies of pike in pike stomachs
(Data taken from Lawler, 1961, 1965 and Campbell, 1982)

Year	Fishing effort a/	Number removed		Harvest (kg/ha)	Pike > 46 cm		Length-weight composition in index nets b/		Cannibalism	
		Total	Index nets b/		Number	Percent	Mean length/cm	Mean weight/g	% total stomachs analysed	% stomachs with food
1945	-	563	-	2.47	462	82.0	-	-	-	-
1946	-	571	-	2.02	331	58.0	-	-	-	-
1947	-	931	-	2.58	447	48.0	-	-	-	-
1948	-	705	-	2.13	515	73.0	-	-	-	-
1949	-	490	-	1.34	289	59.0	-	-	-	-
1950	-	1 071	-	2.58	417	39.0	-	-	2.5	3.8
1951	-	1 026	-	3.03	482	47.0	-	-	2.9	4.3
1952	685	1 468	214	3.60	601	40.9	42.8	572	1.0	1.9
1953	618	1 376	143	4.34	660	48.0	44.1	711	1.2	2.8
1954	605	1 394	211	3.36	613	44.0	38.4	516	1.3	2.4
1955	900	1 948	435	4.33	720	37.0	39.4	493	1.7	4.0
1956	1 618	2 257	210	4.47	361	16.0	38.1	444	1.5	3.3
1957	3 453	3 700	137	4.87	333	9.0	37.4	419	1.4	2.2
1958	4 769	7 175	181	4.17	65	0.91	25.1	124	0.3	0.6
1959	4 963	2 378	75	2.33	121	5.1	35.3	423	0.6	1.1
1960	5 528	7 336	182	3.83	73	1.0	25.0	136	0.1	0.2
1961	162	201	171	0.02	-	-	34.8	373	-	-
1962	162	539	397	1.21	-	-	41.1	596	0.4	0.9
1963	162	858	548	1.98	-	-	40.3	609	-	-
1964	162	743	542	1.63	-	-	39.7	578	-	-
1965	162	656	361	1.47	-	-	40.4	590	-	-
1966	162	881	624	1.70	-	-	-	-	-	-

a/ Unit of effort = one 50-yard gillnet set for 24 h

b/ Index nets = 2 gangs of three gillnets of 1½, 2¼, 3½ inches stretch mesh set in the same localities for the same time period each year 1952-66

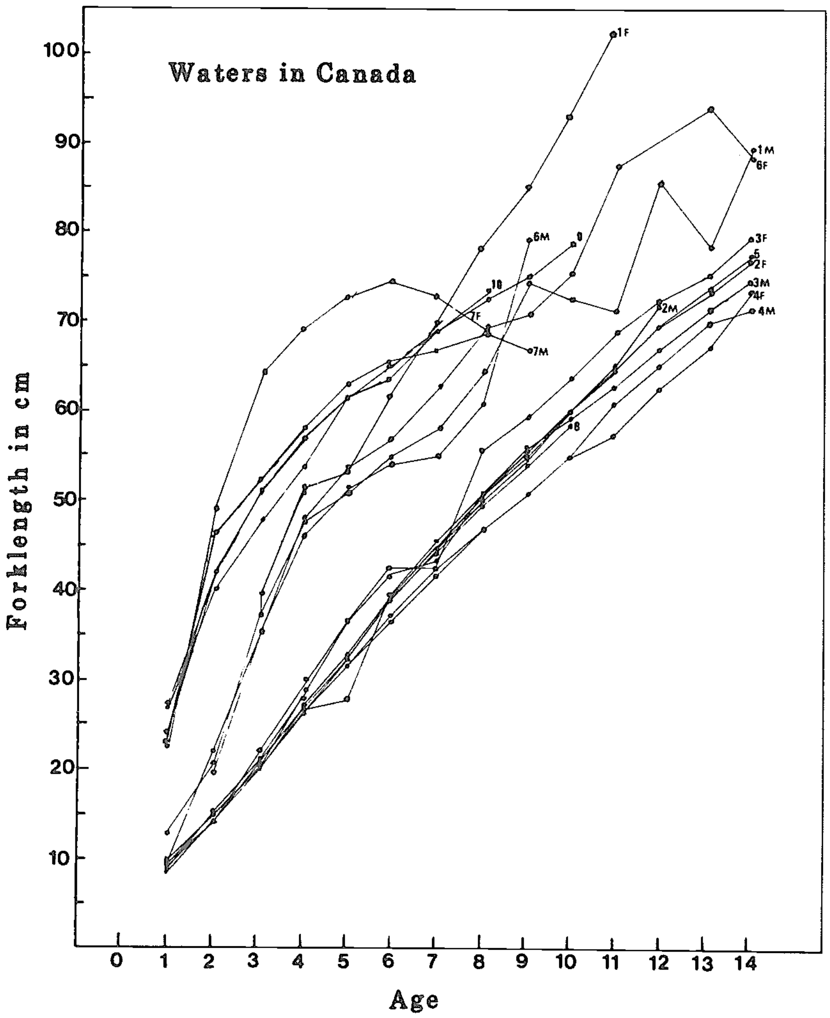


Figure 24 Growth of northern pike in Canadian waters. Growth data of females (F) are presented apart from growth data of males (M). Length of pike transformed to forklength with use of: Forklength (cm)=Total length (cm) x 0.940924 - 0.107946 Standard length (cm)=Forklength (cm) x 0.934034 - 0.093271. The numbers of the growth curves refer to the following localities:

No.	Locality	Season	Year(s)	Method	Reference
1	Seibert Lake	May/June	1971-1973	Scales	Makowecki (1973)
2	Lesser Slave Lake	-	-	-	Miller and Kennedy (1948)
3	Great Bear Lake	-	-	-	
4	Great Slave Lake	-	-	-	
5	Lake Athabaska	-	-	-	
6	Saskatchewan River Delta	summer	1940-1941	Scales	Solman (1948)
7	Eastern Lake	summer	1972-1973	Scales	Wolfert and Miller (1978)
8	Northern Canadian	-	-	-	Miller and Kennedy (1948)
9	Lake Erie	-	-	-	Clark and Steinbach (1959)
10	Lake Ontario	-	-	-	Greeley (1940)

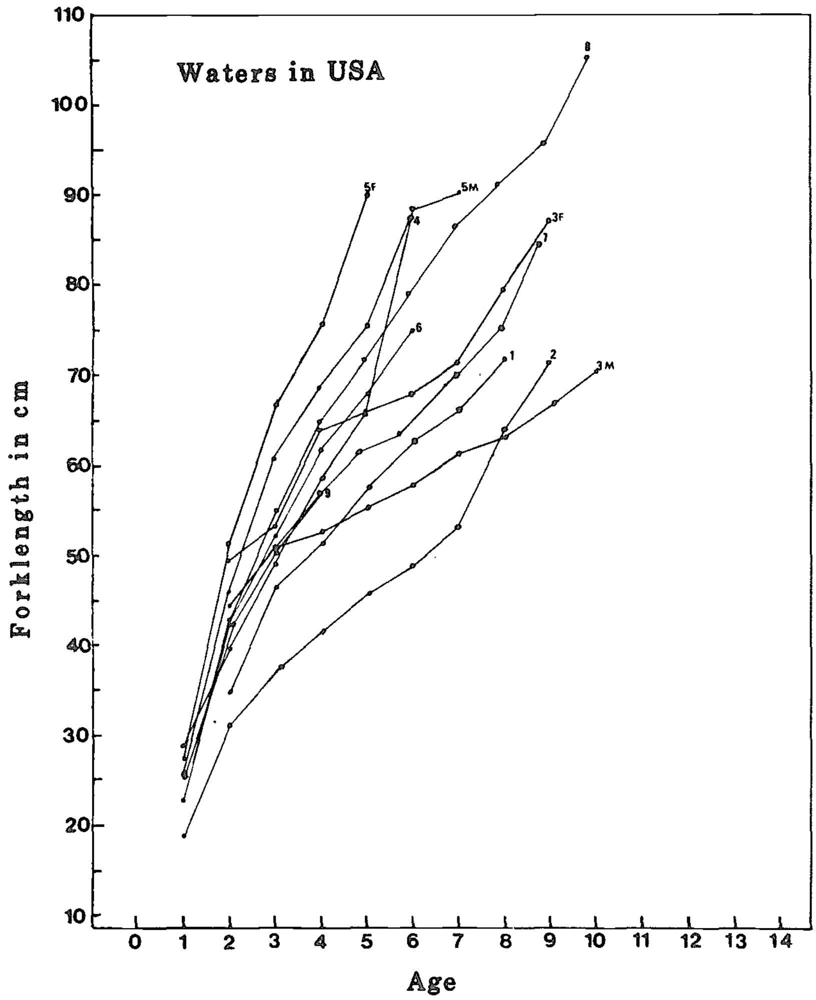


Figure 25 Growth of northern pike in waters in the USA. Growth of males (M) and females (F) presented separately. Length of pike transformed to forklength (see legend figure 24). The numbers of the growth curves refer to the following localities:

No.	Locality	Season	Year(s)	Method	Reference
1	Escabana Lake	spring	1961-1963	Scales	Kempinger and Carline (1978a)
2	Bucks Lake	spring	1961-1969	Scales	Snow and Beard (1972)
3	Big Cedar and Gilbert Lakes	spring	1968-1969	Scales	Priegel and Krohn (1975)
4	Clear Lake	summer	1941-1955	Scales	Ridenhour (1957)
5	Lake Oahe	whole year	1965-1964	Scales	Nelson (1974)
6	Wisconsin Lakes	-	-	-	Nikolski (1957)
7	Minnesota Lakes	-	-	-	Kuehn (1949)
8	Illinois Lakes	-	-	-	Van Engel (1940)
9	Wisconsin Lakes	-	-	-	Van Engel (1940)

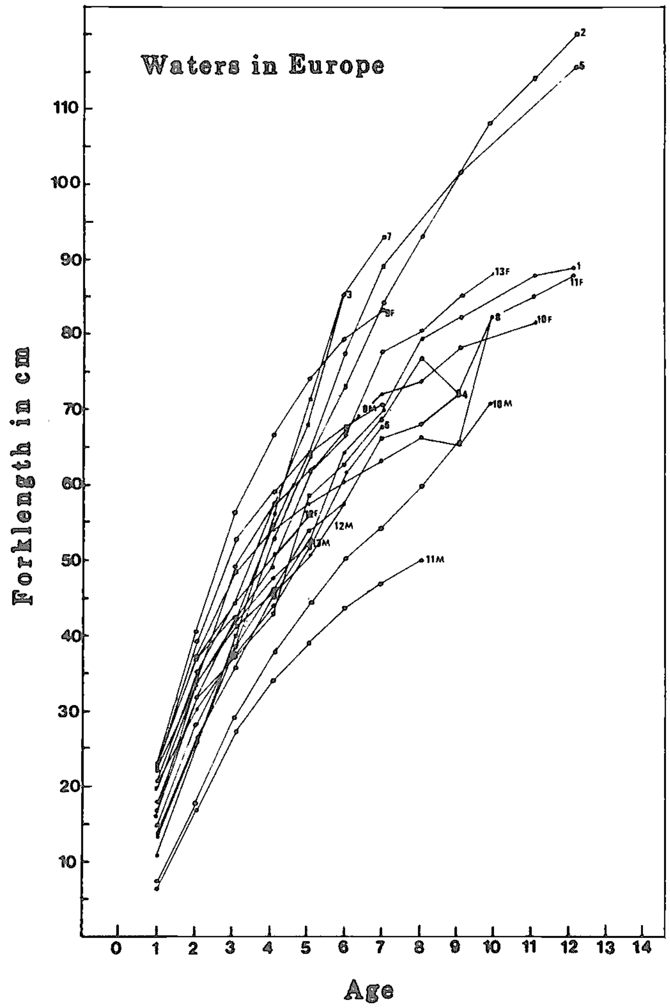


Figure 26 Growth of northern pike in waters in Europe. Growth of males (M) and females (F) presented separately. Length of pike transformed to forklength (see legend figure 24). The numbers of the growth curves refer to the following localities:

No.	Locality	Season	Year(s)	Method	Reference
1	15 North German Lakes	-	-	-	Hegemann (1964)
2	Bodensee	-	-	-	Hegemann (1964)
3	Hohenwarthetalsperre	-	-	-	Hegemann (1964)
4	Grosse Jasmunder Bodden (river mouth)	-	-	-	Hegemann (1964)
5	Greifswalder Bodden like 4 brackish	-	-	-	Hegemann (1964)
6	Berounka	whole year	1969-1977	-	Johal (1980)
7	Waters in Central	-	-	Scales	Poupe (1974)
8	Lake Warniak	whole year	1966-1969	Scales Marking	Ciepielewski (1973)
9	Windermere	winter	1939-1959	Opercula	Frost and Kipling (1967)
10	Slapton Ley	whole year	1975-1977	Scales Opercula	Bregazzi and Kennedy (1980)
11	Loch Choin	winter	1955	Scales	Munro (1957)
12	Västra Sjö	whole year	-	Scales	Otto (1979)
13	Orava Stausee	-	1960-1962	Scales	Balon (1965)
14	Lough Corrib	-	1954	-	Bracken and Champ (1971)
15	Lough Sillan	-	1966	-	

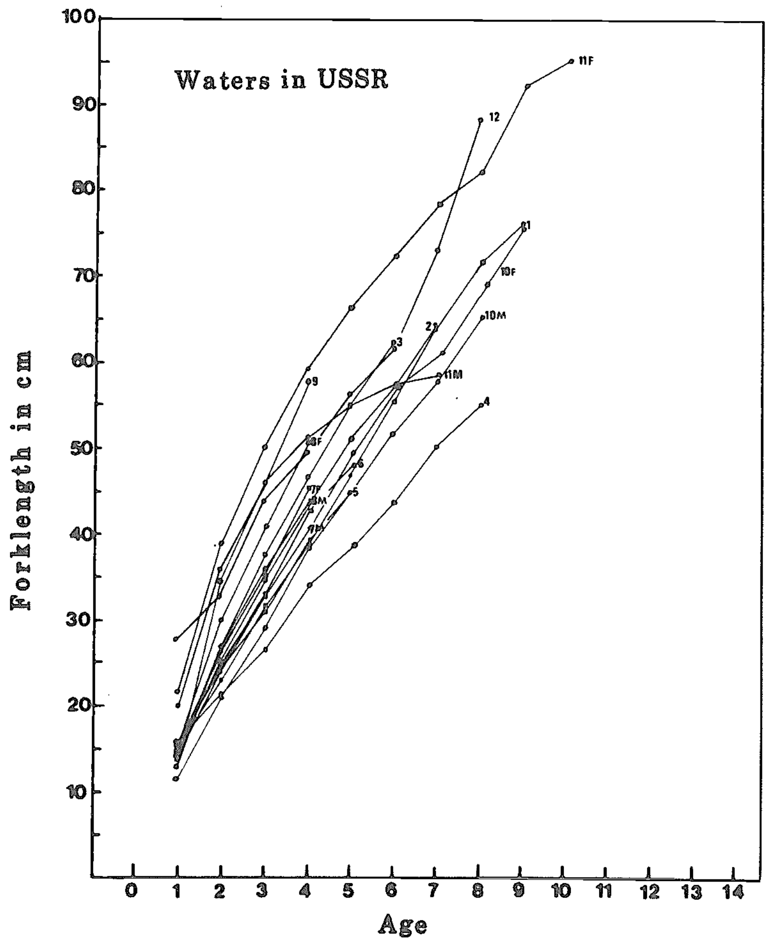


Figure 27 Growth of northern pike in waters in the USSR. Growth of males (M) and females (F) presented separately. Length of pike transformed to forklength (see legend figure 24). The numbers of the growth curves refer to the following localities:

No.	Locality	Season	Year(s)	Method	Reference
1	Rybinsk Basin	-	1959	-	Kulemin, Makkoveyeva and Solopova (1971)
2	Lake Nero	-	1934	-	
3	Lake Galichskoya	-	1934	-	
4	Lake Glubokoye	-	1968	-	
5	Upper Volga	-	1944	-	
6	Aral Lake	-	-	-	Nikolski (1957)
7	Tschany Lake	-	-	-	
8	Peipus Lake	-	-	-	
9	Lake Ilmen	-	-	-	
10	Pleshcheyevo Lake	-	-	-	Kulemin, Makkoveyeva and Solopova (1971)
11	Bukhtarma Reservoir	-	1961-1973	Scales	Soloninova (1976)
12	Kremenchug Reservoir	-	-	-	

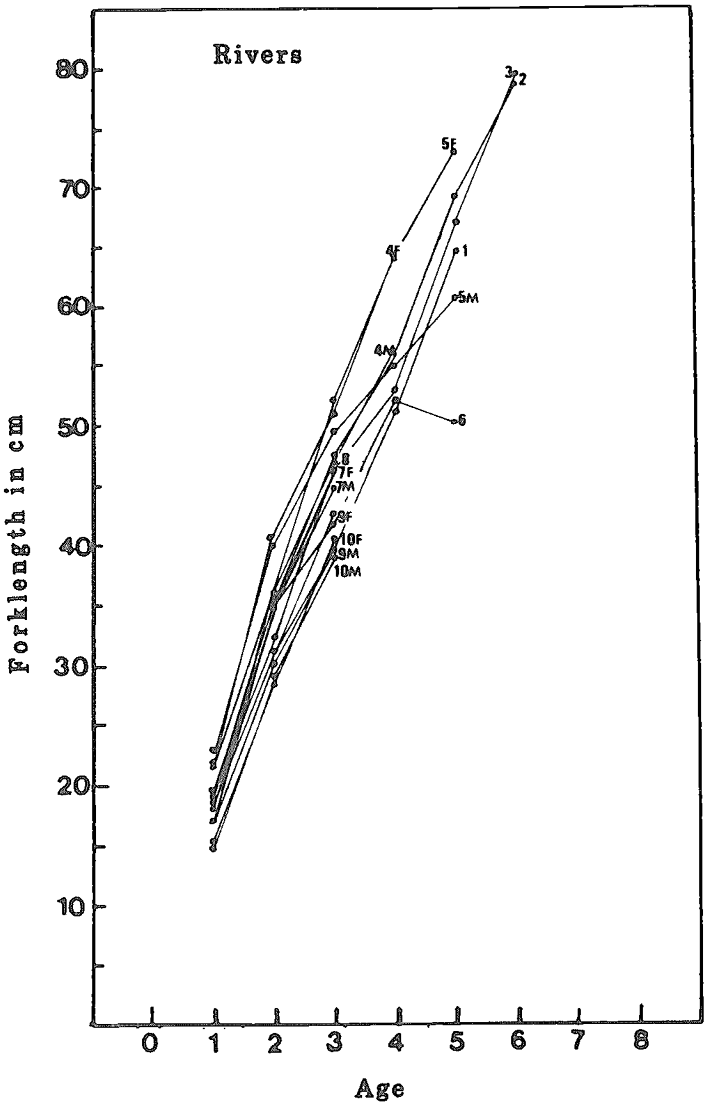


Figure 28 Growth of northern pike in several European ditches and rivers. Growth of males (M) and females (F) presented separately. Length of pike transformed to forklength (see legend figure 24). The numbers of the growth curves refer to the following localities:

No.	Locality	Season	Year(s)	Method	Reference
1	Poltruba (ditch)	-	-	-	Johal (1980)
2	Procházkova (ditch)	-	-	-	
3	Waters Czechoslovakia	-	-	-	
4/5	Dutch polder waters	winter	1964-1968	Scales	Willemsen (1978)
6	River Nene	autumn	1969	Scales	Hart and Pitcher (1973)
7	Robe River	summer	1967-1969	Scales	Bracken (1973)
8	Little Brosna River	summer	1967-1969	Scales	
9	Brosna River	summer	1967-1969	Scales	
10	Camlin River	summer	1967-1969	Scales	

growth in southern than in more northern latitudes, but better growth was also associated with a decrease in life span.

Quality of the pike habitat and food conditions during the year can be considered as factors influencing the growth of this species (Poupe, 1974). Diana (1979) observed that the inclusion of large, rare prey items in the diet of northern pike may have a significant effect on growth. This would lead to a faster growth rate for the individuals able to feed regularly on higher rations. Since sizes and availability of prey vary between habitats, the author expects pike food ration and growth to be equally variable.

Vostradovsky (1981) studied the growth of pike in their first years of age in three Czechoslovakian reservoirs. Growth was more rapid in the period immediately following the filling of the reservoirs. Females grew, on the average, faster than males. Higher growth rates were recorded in those reservoirs where prey fish had lived since the first year of operation of the reservoir. In reservoirs initially devoid of prey fish, the pike ate sedge fly larvae, and larger individuals resorted to cannibalism. As the reservoir became older, the growth rate did not increase, the reverse often being the case.

Individual tagging experiments proved that in the more active fish, the increase in length and weight was up to twice as high as in passive specimens. These differences are more pronounced in females than in males.

Kulemin, Makkoveyeva and Solopova (1971) reported that the rate of increase in length of pike in Lake Pleshcheyeva (Yaroslav Province, USSR) rose sharply after they had reached the age of 5 years (about 60 cm). The authors explain this as a result of an improvement in the pike's diet caused by the movement of the fish from the shallow-water inshore zone into the open areas of the lake. According to the authors, the relatively slow growth of younger pike is influenced by the poor development of the littoral zone of the lake and the relatively high transparency of the water. A sharp weight increase in larger sized northern pike, interpreted as the result of the transition from smaller to larger food items, is also reported from the Rybinsk reservoir (USSR) by Permitin (1959).

According to Holcik (1968), poor growth of northern pike was associated with high population densities. In this respect, it is interesting to note that Kennedy and Fitzmaurice (1969) reported considerable growth increments of the surviving 0^+ pike in Irish lakes treated with the pesticide rotenone. Mann (1985) concluded from his studies on pike in Dorset rivers that density dependent effects on growth of 0^+ pike were much stronger than temperature effects.

2.5.2 Longevity

Figures 24-28 summarize data on growth and age of northern pike from different locations. Most of the pike populations consist of individuals younger than 5 to 6 years of age.

Life expectancy varies with location. Miller and Kennedy (1948) reported that pike could reach 25 years of age in the upper Saskatchewan River. Frost and Kipling (1967) reported a female pike aged 17 years from Windermere, while two 16-year-old male pike were reported from the same location. Mann (1975) concluded from his study of northern pike in the River Frome (Dorset, England) that male and female pike appeared to have the same growth rate. However, females live longer (12 to 13 years maximum) than males (5 to 6 years maximum). Lehtonen (personal communication), referring to data in Finnish literature, stated that the oldest pike caught in Finland were about 30 years old.

2.5.3 Scales and ageing

(For scale development see Section 2.3.3).

Several reports exist on the ageing technique of northern pike by scale reading. Runnström (1954, after Svärdson) reports that age estimates of northern pike would have been higher if scale samples of fish of unknown age had been used. The reason for this is the formation of false growth rings. Grimm (personal communication) reported similar findings for 0^+ pike aged 1^+ judged to be older from scale samples. A thesis on age determination from scales of northern pike with detailed descriptions of growth ring characteristics and formation was published by Williams (1955). Frost and Kipling (1959) published a comprehensive study on the determination of age and growth of northern pike from scales and opercular bones. They found that age can be determined from the growth rings on both the anterior and posterior parts of the scale, but careful identification and discarding of false rings is required. Correction for allometry was found to be necessary for back-calculation of growth from growth rings for the anterior, but not for the posterior part of the scale. Growth of the opercular bone is isometric and no correction is needed for length data of fish once the bone has been formed. The authors conclude that the opercular bone provides a valid method for determining the age and growth (but not the age without growth) of northern pike.

Anwand (1969) studied growth ring development on scales of tagged northern pike kept in lakes, aquaria and basins. A narrow space between the striae and furthermore incomplete striae, are characteristic for true growth rings. In contrast to false rings, they are arranged concentrically on the entire scale. Growth ring development takes place during spring.

Also, other calcified tissue is used for ageing purposes. Hederström [1759](1959), in his remarkable article in the Transactions of the Royal Swedish Academy of Sciences, published the first account of age determination by counting the rings on the vertebrae of northern pike. Casselman (1974) studied calcified tissue growth of northern pike by means of macro- and micro-analysis with a microprobe X-ray analyser, using the cleithrum, a flat bone from the pectoral girdle. The author found a relationship between protein metabolism and matrix production in calcified tissue. Any condition affecting the general body metabolism may be reflected in a change of the protein metabolism. Casselman (1978a) published a thesis on calcified tissue and body growth which was not consulted during the preparation of this synopsis.

The chemical composition of the scales is summarized in Table XVI.

Table XVI

Chemical composition of scales by weight (%)

Ash in dry matter:	40.44	$Ca_3(PO_4 2$:	52.25
$Mg(PO_4)2$:	5.01	$CaCO_3$:	41.73
CaO:	21.93	MgO:	0.51
P_2O_5:	18.00	CO_2:	2.30

Analysis of length-frequency data with the aid of modern computer techniques was refined by Mac Donald and Pitcher (1979) and Schnute and Fournier (1980). They successfully structured the data on pike of Heming Lake, Manitoba, in age classes. Raat (unpublished results) applied the methods on pike data from De Kleine Wielen (Netherlands), given by Grimm (1981, 1983), and reconstructed growth and yearclass composition.

2.5.4 Greatest size

Buller (1979) presented an impressive documented account of record captures of northern pike, made on the British Isles, in Continental Europe and in the USA. According to this author, V.H. Maxwell in Wild Sports of the West (1832), reported that around 1815, a pike of 41.7 kg was lifted out of the River Shannon, Ireland. Two other records of pike of over 40 kg in weight were also reported from Ireland. One pike, caught by trailing (1862) and another found dead (1927) measured 173 and 175 cm, respectively.

An earlier record list of northern pike captures was published by Buller (1971). The author presents an interesting discussion on possible errors in the record list.

Berg (1962) reported a record capture of northern pike from the Russian Lake Illman, caught in January 1930 and weighing 34.8 kg.

A recent record capture of northern pike from Continental Europe was reported in the German Sport Fishing Magazine "Blinker" (1978). In January 1978, a pike of 135 cm long that weighed 26.8 kg, was caught by plug fishing in a lake near Hamburg. The record pike reported from the USA in Buller (1979) measured 138 cm and had a girth of 63.5 cm. It weighed 20.9 kg and was caught by fly-fishing in the Sacandaga reservoir in September 1940.

Blok (1968) analysed the size distribution of northern pike captures recorded in a Dutch national angling competition. He found a regular distribution of pike in the size range from 75 to 95 cm. Pike larger than 95 cm were not regularly distributed according to size. Only occasional records of these pike were received.

2.6 Metabolism

2.6.1 Food conversion

The metabolism of northern pike has been studied in fish, kept under laboratory conditions and in pike, captured in the field. Food consumption experiments were conducted in tanks, aquaria and respirometers in which the fish were kept under controlled conditions. Other methods used stomach contents to estimate food consumption (Diana, 1979a; Backiel, 1971). In tanks and aquaria food intake, excretion and weight increase of pike can be monitored (Scholz, 1932; Willemsen, 1965; Weithman and Anderson, 1977; Johnson, 1966; Mann, 1982; Diana, 1982). In respirometers, oxygen consumption of fish can be followed as a function of the metabolic processes that take place (Dolinin, 1973, 1975, 1975a; Diana, 1982). Energy deposition in the body was also studied by sampling northern pike of known ages at regular intervals. Yearly cycles of production and depletion could be investigated by means of this method, and differences could be made between gonads and somatic tissue (Medford and Mackay, 1978; Diana and Mackay, 1979; Diana, 1983).

Data on consumption of food are expressed in weight or energy values. Gross efficiency of food consumption (g/kcal grown per g/kcal eaten) was determined by several authors. Scholz (1932) quoted 19 papers with estimates of the food coefficient in pike; gross efficiency rates ranged from 0.33 to 0.022. The author's experiments with 0^+ and 1^+ pike resulted in an average estimate of 0.33. Willemsen (1965) studied during several months weight increment of northern pike fed with roach (Rutilus rutilus) and bream (Abramis brama). Weight increase and food consumed were compared. The author found gross efficiency values of food conversion for 13 individuals (lengths between 20 and 60 cm) ranging from 0.33 to 0.18. Weithman and Anderson (1977) conducted a study on growth and food of pike in concrete tanks, using age 1 individuals. Average efficiency in food consumption was found to be 0.29. The experiments were performed at high summer temperatures.

Johnson (1966) studied food consumption of immature pike kept in small still-water tanks and found that growth followed consumption very closely. Gross conversion of food was found to be 0.29. Bialokoz and Krzywosz (1978) found that gross conversion efficiency for pike in Polish Lake Dgal Wielki ranged from 0.28 for 10 g of fish to 0.20 for 8.6 g of fish. Mann (1982) found that mean values for gross conversion efficiency in northern pike from River Frome, Dorset, England, was 0.15. Caloric food efficiency in Polish River Vistula was calculated to be 0.15 (Backiel, 1971). Diana (1982), in his study of metabolism of northern pike from Lac Sainte Anne, found gross conversion efficiency (caloric) in young of the year pike to be 0.277 in summer and 0.246 in winter. According to Ivanova (1968) in her study of stomach contents of northern pike in Rybinsk reservoir, food conversion changed considerably with age. Food conversion efficiency was 0.4 in pike aged 1^+ to 3^+ (40 cm), while it was 0.10 in larger individuals. Similar conclusions were reached on the basis of theoretical considerations.

Johnson (1966), who used voluntary feeding methods in his study, found that maintenance requirements of northern pike over a full-year period are not a constant factor due to changes in temperature. The author found in his experiments with pike (weight range 21.3 to 107 g) that a significant change in metabolism took place during the late spring when actual maintenance requirements nearly doubled. The average support feeding level calculated from the annual maintenance coefficient was 3.79 g/kg/day. Peak support requirements were reached in late June, followed by a decline through August and September, and subsequently by a fairly stable period from October to April, when the gradual rise toward the June peak was initiated. Maintenance levels calculated from weekly values were 6.43 g/kg/day in June and 3.57 g/kg/day in October. Weithman and Anderson (1977) estimated maintenance feeding levels of 1^+ pike in summer (T>29°C) to be 8.21 g/kg/day (calculated from values corresponding to a 28-day period). Mann (1982) found maintenance levels for 624 to 1 010 g pike from the River Frome to be 60% of Johnson's (1966) levels: 2.23 g/kg/day (calculated from the annual maintenance coefficient). This lower value was observed despite the larger volumes of water flowing through the Frome channels (c 5.3 - 7 m^3), compared with Johnson's (1966) tanks with stagnant waters (0.47 m^3), which require the pike to spend more energy in the search for and capture of prey.

Dolinin (1973) measured oxygen consumption of northern pike (average weight about 1 kg) using mask respirometers. The data on oxygen consumption found by the author can be used to calculate standard metabolic activity. By converting his data from hours to days and from oxygen consumption to calories using the factor 3.2 cal per milligramme oxygen consumed (protein as energy source), this can be accomplished.

Table XVII

Data on oxygen consumption of northern pike at various temperatures from USSR (Dolinin, 1973), Canada (Diana, 1982) and Ohio (Bevilhimer, Stein and Carline, 1985)

Temperature (in °C)	Oxygen consumption (in mg/kh/hour)		
	USSR	Canada	USA (Ohio)
5	19.5	15	43
10	39.8	33	56
15	69.7	73	74
20	107.3	163	97
25	-	363	128

Diana (1982) and Bevilhimer, Stein and Carline (1985) obtained similar results (see Table XVII) and suggested that maintenance requirements of northern pike could be best estimated from oxygen consumption measurements. The differences in the data of Table XVII might be due to different geographical locations and the thermal history of separate populations. The oxygen consumption could be described by the equations:

$$R_{met} = 27.5\ W^{0.82} \text{ at } 14°C, \text{ and}$$

$$R_{met} = 1.6\ W^{0.97} \text{ at } 2°C$$

where R_{met} is metabolic activity in cal/day and W is weight of the pike in grammes.

Adelman and Smith (1970) found in laboratory experiments with young pike (about 10 cm long), that conversion efficiency depended on oxygen conditions. The mean conversion efficiency was 0.42 and decreased to 0.34 when the dissolved oxygen concentration was lower than 3 ppm.

Yield efficiency conversion (g/kcal grown per g/kcal remaining after maintenance costs are removed) was found by Johnson (1966) to be 0.437. Diana (1982) found summer values of 0.513 and winter values of 0.353 for yield conversion. He also determined that the efficiency of food absorption was 0.870, a value that showed no variations from winter to summer.

2.6.2 Energy deposition

Diana (1983) studied growth and early maturation of northern pike in three Michigan lakes. The fish were caught in October, March and May with gillnets operating outside the vegetation cover. Somatic and gonad caloric growth equivalents were determined. Total growth (in kcal) of a fish over several years includes body growth (which is accumulated over that time) and gonad growth (which is built up and then mostly lost seasonally). The author estimated for both sexes the total energy production by individual northern pike over the first three years of life by adding the mean somatic energy for age-3 fish in March and the mean gonad energy for age-1, age-2 and age-3 fish in March (see Figure 29). Females deposited 6 to 18 times more energy in ovaries than males did in testes.

Diana and Mackay (1979) and Billard, Mackay and Marcel (1983) studied the energy deposition in body, liver and gonads of northern pike from the Canadian Lac Sainte Anne, Alberta.

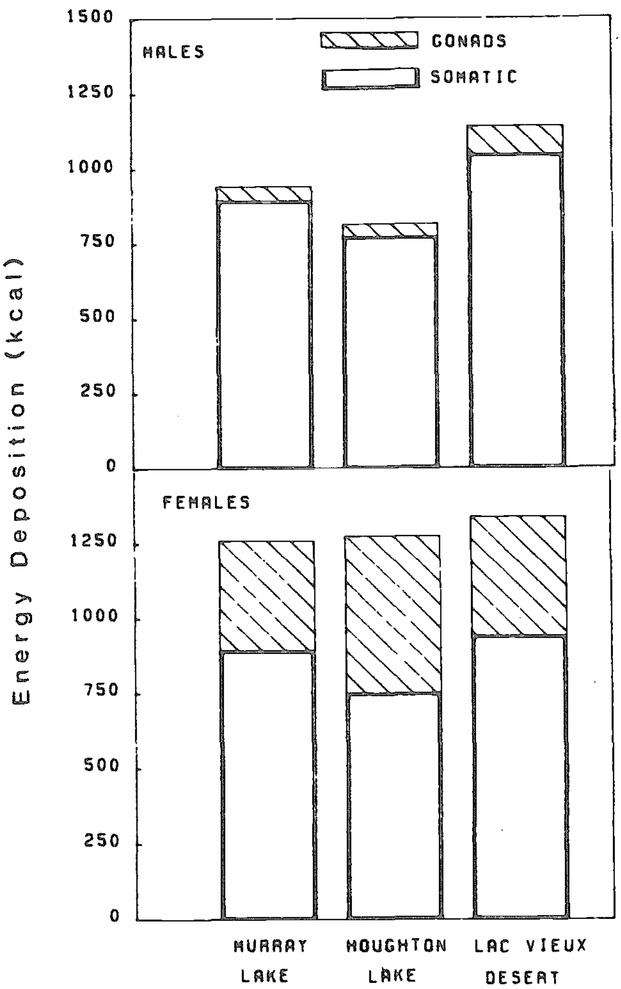


Figure 29 Total individual energy allocation over 3 years for Northern pike from three Michigan lakes. Body energy = energy content at end of 3rd year of life. Gonad energy = sum of average annual gonad energy contents for years 1-3. (From Diana, 1983)

The yearly cycle of energy production and depletion was determined for individual 3-year-old fish. Body growth in length was similar for both sexes and occurred during summer. Total energy accumulation occurred in both sexes during winter and summer. Somatic caloric growth was completed in females during the summer, while in males it continued throughout the winter. Testicular growth was completed by September, while ovarian growth began in August and continued mainly during winter. There was no loss of somatic energy during ovarian growth. Energy requirements for testicular growth appeared to come from liver stores, while the energy required for ovarian growth must have resulted from food intake. Both sexes lost considerable somatic energy between March and May during the spawning period. This loss appeared to be due to spawning activity and not to late gonad growth.

Loss of condition after spawning was also reported by Mann (1976) who analysed mean monthly values of relative condition of northern pike from River Stour, England. In mature pike, minimum relative condition values were reached in midsummer (July); after that, the values increased sharply, attaining their maximum during winter. Immature pike reached their maximum condition in May and declined to a minimum during the winter months.

Assuming that there was no size-selective mortality in the populations sampled by Medford and Mackay (1978), by Diana and Mackay (1979) in Lac Sainte Anne, Alberta, and by Diana (1983) in Michigan, it can be concluded that winter growth of pike occurred in Alberta and three lakes in Michigan, near the southern geographical boundary of the species. Winter contribution to the annual somatic growth of males in Lac Sainte Anne (35%) was similar to the average value for males in three Michigan lakes. Female pike in Lac Sainte Anne showed no somatic growth in winter, whereas approximately 35% of the female somatic growth in three Michigan lakes did occur in winter. Relative ovarian growth during winter in Lac Sainte Anne and in the Michigan lakes was similar (80%). Weight increase of northern pike during winter was also reported from the Polish Pilica River (Penczak, Zalewski and Molinski, 1976). The data, however, may be biased by size selective mortality during winter, small sample sizes and selective capture by the fishing gear. These data should therefore be interpreted with caution.

Grimm (1983) found small pike to be vulnerable to intraspecific predation by larger pike, which is especially relevant during the winter season when the vegetation cover diminishes in size and quality. Casselman (1978) reported from laboratory studies that at low temperatures, the rates of length and weight increases were very low. Johnson (1966) found no growth in northern pike at winter temperatures in tank experiments. Furthermore, food consumption estimates for pike in Lac Sainte Anne during winter (Diana, 1979a) (males

0.4 kcal/kg/day, females 0.9 kcal/kg/day) are lower than standard metabolic rates measured by Diana (1982) for fish from Lac Sainte Anne (pike 1-2 kg/day) and Dolinin (1973) (pike about 1 kg at 5°C 1.5 kcal/kg/day). Consequently, data on somatic growth of northern pike during winter are conflicting. Data on the relative growth of ovaries of female northern pike during autumn and winter are less contradictory, and most authors agree that ovarian growth takes place during that period.

2.6.3 Energy sources

Ince and Thorpe (1976) found that pike did not decrease their rate of weight loss during 1 or 3 months of starvation. Their results are in agreement with Diana (1982) who concluded that pike were unable to reduce their metabolic rate in response to starvation.

Ince and Thorpe (1976) showed that starvation resulted in reduction of liver and muscle glycogen and of liver lipid; blood glucose concentration and hematocrite values were reduced, total plasma cholesterol levels were increased, while the levels of plasma-free fatty acids, amino-acid nitrogen and proteins remained unaltered. No significant changes were observed in either muscle protein, muscle water or in the response to amino-acid loading during the starvation period. The results indicate that pike are well adapted for periods of prolonged starvation and that hepatic and extra-hepatic lipid and glycogen stores serve for metabolic needs during food shortage, while body protein is conserved.

Timoshina (1970) studied free and combined amino-acids in the muscles of pike by means of paper chromatography. After starvation of the fish connected with overwintering, the set of amino-acids and the proportions of amino-acids in the muscle proteins did not show significant changes. Twenty two free amino-acids were found in the muscles; after winter starvation, the quantity of amino-acids was reduced with the exception of threonine; acid amino-acids showed the least variation. This suggests an important contribution of free muscle amino-acids either to protein synthesis or to the pool of carbon substrates.

Medford and Mackay (1978) and Diana and Mackay (1979) found that specific constituents, which alter caloric equivalents, were preferentially stored in the liver, which showed significant changes in caloric equivalents during the year. Energy for testicular growth probably comes from liver stores; the testicular growth was completed in September. The ovarian growth continued until March and probably received the required energy from food intake. Depletion of somatic energy stores occurred in both sexes during spawning and resulted from spawning activities and fasting. The depletion appeared to be due to catabolism of the whole tissue rather than to catabolism of specific constituents. This discrepancy with the results of Ince and Thorpe (1976) is explained by Diana and Mackay (1979) by different methods of analysis, the effects of much longer starvation and possible differences between North American and European pike. Based on laboratory experiments, Diana (1982) agrees with the conclusion derived from the field population studies of Medford and Mackay (1978) and Diana and Mackay (1979). Food ration experiments showed that pike growth concurred with significant protein accumulation, while depletion resulted in the use of protein as energy source.

Ince and Thorpe (1976a) studied the effect of insulin on the glucose and glycine metabolism in northern pike. Their results suggest that the metabolic role of insulin in pike is similar to that observed in mammals. The same authors published in 1978 data in support of the hypothesis that insulin plays a major role in the regulation of the protein metabolism of northern pike. Ince (1979) provided results indicating that partial pancreatomy does not lead to the development of a diabetic state in northern pike over a period of one month.

Schwalme and Mackay (1985) noted a large accumulation of lactate anion in the blood after exercise-handling in laboratory experiments. This result conflicts with reports on the related muskellunge (E. masquinongy) in which blood lactate increase following exercise was low.

In pike caught by angling and allowed to recover in captivity, the blood glucose level remained elevated even after 4 days. The authors found indications that the increase of the plasma glucose after exercise is not simply the result of lactate removal by conversion into glucose, most likely caused by a hormone-induced breakdown of liver glycogen.

Oikari and Soivio (1977) reported slightly increased concentrations of blood lactate and glucose in pike captured in polluted water as compared with specimens from unpolluted water. Stress-induced hyperglycemia was also described in tiger muskellunge (see Section 1.4.1.2) due to stocking stressors such as handling, temperature increases and confinement at high densities (Mather, Stein and Carline, 1986).

2.7 The Species in Relation to its Environment

2.7.1 Migration and local movements

Carbine and Applegate (1946) observed in Houghton Lake (Michigan), that a number of adult northern pike returned each year after spawning to the same areas of the lake. They concluded that their data indicated the sedentary nature of certain aggregations of the species during the summer months in large lakes with dispersed summer habitats for pike. Carbine (1944) found in a pond experiment that young northern pike could be found throughout the summer in definite spots about the pond, which indicated that young pike occupied definite home ranges of limited extent.

Makowecki (1973) found very little displacement of large northern pike which had been tagged in the shallow Seibert Lake (Alberta) and recaptured there a year later. Malinin (1970, 1972) cited evidence that pike were sedentary and lived in an area approximately 100 m in diameter for a long time. In his studies of pike movements in the tributaries of the Rybinsk reservoir (USSR), Malinin (1970, 1972) found that pike moved within a very limited area (500 to 1 500 m^2) toward the end of the fattening period. The pike stayed within home ranges in areas where the bottom was flat. In areas of an old riverbed the fish moved along the bed for up to 500 m.

An interesting observation on the behaviour of pike was made by Poddubny (1976) in the Rybinsk reservoir. After reduction of the distribution area of pike, caused by water level fluctuations, the concentration of adult pike increased on the slopes of the bottom depressions of the sublittoral and bathyal layers not yet affected by silt depositions. The large pike moving along the slopes of old riverbeds, moved much farther away into the lake-part of the reservoir.

Vostradovsky (1975, 1983) studied the recaptures of tagged northern pike in the Czech Lipno reservoir (4 650 ha) and found 84% of the recaptured pike in almost the same places as the sites of release (within 3 km). Only in spring several individuals moved away for a distance greater than 10 km, but always less than 20 km. Northern pike moving to a distance greater than 3 km showed higher daily gains in weight than resident pike, which was ascribed to a greater opportunity of contact with prey.

Bregazzi and Kennedy (1980) reported from Slapton Ley (England) that most pike seemed prone to wander; most migrations were found in shallow water regions. These authors suggested that the distribution of pike is dictated by that of prey fishes.

Diana, Mackay and Ehrmann (1977) studied movements and habitat preferences of northern pike in the Canadian Lac Sainte Anne and concluded that these fish did not have a well defined home range, but rather appeared to move at random throughout a relatively narrow zone around the edge of the lake. Diana (1980) presented a similar conclusion. Langford (1979) reported that pike marked with ultrasonic tags rarely exceeded 1.0 km in daily journeys in the River Thames. The author concluded that the evidence for homing was somewhat contradictory to his date.

The distances covered by pike in Lac Sainte Anne (Diana, Mackay and Ehrmann, 1977) were within the range of 160 to 1 600 m per day as found by Moen and Henegar (1971) in a tag and recapture study of pike in Lake Oahe, North and South Dakota for time intervals of 2 to 3 months.

Chapman and Mackay (1984) in their study of habitat selection of large pike (2.6-6.8 kg females) in Seibert Lake, Alberta, used radio location and ultrasonic telemetry data. They found that the pike were versatile in their behaviour, making long distance displacements from one area to another in a period of a few hours. The pike preferred shallow vegetated areas of the lake. On windy days pike chose habitats which were further offshore but not deeper than those occupied on calm days. On sunny days pike moved into habitats that were close to shore and relatively shallow. Habitat selection of pike was not significantly influenced by rain.

In Finland, the recaptures of tagged pike have been studied since the year 1915 mainly in the Baltic coast, but also in lakes (Lehtonen, personal communication, based on Finnish literature data). The results showed that pike are stationary fish which are usually recaptured at almost the same place as the site of release. When moved to another place, they usually return to their original home areas, but if the distance is very long (hundreds of kilometres), they migrate farther than normally, although not necessarily to their original home areas.

Kaukoranta and Lind (1975) reported on the basis of recoveries of tagged northern pike from brackish waters around the Åland Islands and off Porvoo (Finland) that most fish were recaptured within 0.5 km of their tagging place. The longest range of migration was about 5 km. Stocked pike have the tendency to move, and return to their site of capture when transferred for a distance of several kilometres. Material from the Oulujoki River (Finland) estuary (also brackish water) showed that 84.8% of the recaptured pike had not moved more than 1 km away from their tagging place, the longest migration being about 16 km.

On the basis of available evidence on activity patterns of northern pike, Diana (1980) concluded that during most of the year, activity is not an important part of a pike's energy budget except in the spawning period.

Northern pike do not exhibit schooling behaviour. However, they can be found in small areas. Larsen (1966) noted in Danish trout streams that up to four pike of the same size could exist in one and the same rather limited biotope (30-40 m^2), while two or more pike of different sizes were never caught at the same time in the same locality.

2.7.1.1 Tagging and marking

Kendle and Morris (1965, 1972) described a device for holding objects in the stomachs of fish and developed an experimental gastric battery in this harness. Diana, Mackay and Ehrmann (1977), Diana (1979), Cunningham, Craig and Mackay (1983), and Mackay and Craig (1983) described several systems for radio and ultrasonic tagging and tracking of northern pike. Ross and Kleiner (1982) described a technique for surgically implanting radio frequency transmitters with whip antennas in northern pike and other fish, which enables the study of the distribution of fish in aquatic vegetation. Margenau (1987) described angling captures from under ice of three radiotagged pike (48-58 cm), 85 days after implantation of radio transmitters. He concluded that the tagging method is efficient for localization of northern pike.

Koshinsky (1972) evaluated in a 4-year study at Lac La Ronge (Canada) barb-anchored spaghetti dart tags and monofilament-attached preopercular disc tags. Losses after 2 years were 13% and 92%, respectively. Tagging mortality tended to be higher among dart-tagged individuals, but was only 12% after 2 years. The physical condition of the fish tended to be depressed by both tags. Growth increments were smaller for disc-tagged than for dart-tagged individuals of the same sex. Disc-tagged pike dispersed more widely and were more vulnerable to angling.

Kipling and Frost (1970) and Kipling and Le Cren (1984) described pike-tagging experiments in Windermere. The tags were loops of monel metal and were punched with a 6-figure number for individual identification. In the years from 1949 to 1952, the tags were attached through a hole punched in the opercular bone, but it became apparent from the many fish recaptured with damaged opercular bones that a large portion of the tags had been torn out. Therefore in 1953, half of the tags were attached as before, and the other half were fastened to the upper jaw. The jaw tags proved more satisfactory, and from 1954 onward tagging has been done on the jaw.

Grimm (1980, 1981, 1983a) anaesthetized (chlorobutanol about 750 ppm) pike before marking. He used several marks: clipping of parts of a fin, perforation of finrays, Alcian-blue injected in finrays using a jet inoculator (Hart and Pitcher, 1969). Young pike (4-6 cm) were marked by means of a finpulling technique (Patrick and Haas, 1971), which had no effect on mortality or growth in pond experiments (Grimm, unpublished results). Koshinsky (1972) demonstrated that small northern pike completely regenerated partially clipped fins over a 2-year period.

McNeil and Crossman (1979) studied in laboratory and field experiments the effects of fin clips and total removal of one or two fins on short-term (3 months) and long-term (10 months) survival and growth of hatchery muskellunge (Esox masquinongy). The results of their study are applicable for northern pike (Grimm, unpublished results).

2.7.2 Competitors of northern pike

Intraspecific competition for food can be important and eventually leads to predatory activities within the species (see also Sections 3.2.1.3 and 3.2.2.4). A special case is reported from Murphy Flowage, Wisconsin, by Snow (1974). Heavy stocking of pike in that impoundment resulted in competition between stocked and native pike, which may have forced the stocked pike to move out of the impoundment (see Section 4.2.3).

Several fish species are reported as competitors for food with northern pike. Seaburg and Moyle (1964) reported that northern pike, walleye (Stizostedion V. vitreum) and largemouth bass (Micropterus salmoides), fed mostly on yellow perch, (Perca flavescens), even when minnows and small centrarchid fishes were common in several Minnesota warm waters. In Heming Lake, Manitoba (Lawler, 1965), competitive predatory species include burbot (Lota lota) and walleye. Burbot, however, was never abundant in Heming Lake and therefore probably never was a major competitor of the pike for yellow perch. Besides that, the distribution patterns of the fish are different. The preferred habitat of burbot is deep water, while northern pike feed in the more shallow parts of the water. Lawler (1965) considered the walleye as the most important direct competitor of the pike, particularly during early spring and fall when walleye is found inshore.

Forney (1977) related enhanced walleye reproduction in Oneida Lake, New York, to reduced competition for food with esocids in the lake. Kempinger and Carline (1977) reported from Escabana Lake, Wisconsin, that the walleye population was not affected by the rapid development of a northern pike population in that lake. As northern pike numbers increased, densities of adult prey declined and remained low. Walleye and northern pike responded differently to the changes in the community structure. Walleye growth rates did not change despite large variations in densities of adult prey. Initially, pike grew rapidly when the population was building up (Kempinger and Carline, 1978, 1978a). As its density increased, growth rates began a steady decline. The authors suggested that walleye were better able to exploit alternate food resources than were northern pike.

Although pike and smallmouth bass (Micropterus dolomieui) occupied the same stream segment of Plover River, Wisconsin, Paragamian (1976) provided data indicating that abundance of smallmouth bass was not influenced by abundance of pike. The same is reported for largemouth bass (Micropterus salmoides) in Italian waters (Alessio, 1984). The ecology of largemouth bass revealed no niche-overlap with pike and, because of relatively different food preferences and feeding strategies, largemouth bass and pike did not seem to compete.

In Windermere (Frost, 1954), the relationship between pike and other fish was determined to some extent by competition for food. This may be a factor during the first year of life when the diet of pike (Entomostraca and bottom-living insects) is similar to that of other fishes in the lake. Competition during this period of development was, however, believed to be negligible. It is considered unlikely that perch (Perca fluviatilis) over 18 cm, and trout (Salmo trutta) 40-60 cm long are serious competitors of northern pike because these fish make up only a very small portion of the population in Windermere and food fish are apparently abundant.

Popova (1966), in her study on the ecology of pike and perch in the Volga delta, prior to and during the first years of damming of the river, reported similar results. Despite the fact that pike and perch occupy the same areas, no competition for food and breeding grounds has developed. The author explained this by the morphological specificity of these species which occupy different ecological niches.

Larsen (1966) concluded that northern pike is a food competitor of trout and eel (Anguilla anguilla) in Danish trout streams.

Perch (Perca fluviatilis), pike-perch (Stizostedion lucioperca) and pike are the fish predators in the fish communities of many eutrophic Swedish warm lakes (Svärdson, 1976). All three species are spawning at the shore, but shift over to a more pelagic habitat in different phases in their lives: the pike as adult fish, the perch in schools hunting collectively for prey, and the pike-perch in their early life as a permanent roaming predator. These differences in habitat requirements and behavioural patterns cause a well differentiated utilization of the aquatic food resources. Direct or indirect competition for food and intra- and interspecific predation are regulating mechanisms within the predator fish communities. According to Svärdson (1976), the pike-perch dominates the pike and perch populations under suitable habitat conditions (turbid, well oxygenated water with firm bottom).

Svärdson and Molin (1973) analysed catches of the three predator species from lake Erken before and after introduction of pike-perch and found that a decrease in pike and perch captures continued after the introduction of pike-perch. According to Svärdson (1976), the introduced pike-perch reduced the pike and perch populations in the lake. The increase in perch and pike catches after some years was related to lower predatory pressure of pike on perch and to failure of the pike-perch to reproduce in Lake Erken.

The more favourable the habitat is for pike-perch, the more this species dominates the pike population (Svärdson, 1976). Progress in eutrophication contributes to a change in the community structure. In this context, the changes in the fish community structure in the Netherlands Veluwemeer (Hartmann, 1977; Willemsen, 1980), in the Berlin Grosse Müggelsee (Barthelmes and Waldow, 1978), Finnish lakes (Lehtonen, personal communication), and in Lake Constance (German-Austrian-Swiss border, Nümann, 1973, 1975) are illustrative. In all these lakes, water transparency decreased and macrophytic aquatic vegetation declined drastically. As a result of these changes in vegetation structure and abundance, northern pike populations declined and pike-perch populations increased (see also Section 3.2.1.2).

2.7.3 Predators of northern pike

Kipling and Frost (1970), quoting Swedish research work by Montén (1948), reported that the larvae of the water beetle Dytiscus prey heavily on pike larvae in ponds. On the other hand, Franklin and Smith (1963) considered predation by dytiscid larvae as not significant. They observed that in view of the fact that insect larvae were incapable of holding fish which were too small, predation actually occurred only over a particular range of sizes. Le Conseil supérieur de la pêche (1972) reported that the larvae of Dytiscus marginalis are the most redoubtable predators of northern pike embryos and larvae in the ponds of Vivier du Grès (Oise, France).

Kennedy (1969) reported from Ireland that no pike eggs were found in stomachs of eels (Anguilla anguilla), while bream eggs (Abramis brama), perch larvae (Perca fluviatilis) and larvae of the stickleback (Gasterosteus) and the stoneloach (Noemacheilus barbatulus) were found in stomach analyses. Hunt and Carbine (1951) reported that in ditches adjacent to Houghton Lake (Michigan), yellow perch (Perca flavescens) and other fish consumed many young northern pike. Other animals, such as birds, dragonfly and damselfly nymphs, beetle larvae and water bugs (Belostomatidae) were observed to capture and eat young pike. Furthermore, pike in the size range of 21-30 mm made up 25 to 32.2% of the vertebrate food of pike. Franklin and Smith (1963) considered predation by Umbra limi as not important in the spawning marshes where developing pike were monitored.

Hubley (1961) reported scars caused by lampreys (Ichthyomyzon unicuspis and I. castaneus) on pike in the upper Mississippi River. In Alaska, inconnu (Stenodus leucichthys) feed on pike, even though to a lesser extent than they do on salmon or broad whitefish (Alt, 1965).

Erlinge (1968, 1969) and Erlinge and Jensen (1981) described the otter (Lutra lutra) and the mink (Mustela vison) as predators of northern pike. In a trout water in southern Sweden, the trout population suffered less mortality than fishes more easily available to predation, viz. Lota lota, cyprinids, northern pike and perch.

According to Nikolsky (1963), the pike make up 6.1% of the food of cormorants in the Volga delta. Dobben (1952) found that the share of pike in the food of the cormorant (Phalacrocorax carbo sinensis) in the Netherlands was as a rule less than 1%. Only in the early spring this share was somewhat higher. The majority of the captured pike were large specimens. Stomach analyses made in March, April and May 1939 produced 6 pikes between 13 and 21 cm, and 19 between 28 and 42 cm long. Doornbos (1979) reported that northern pike was sometimes found in stomachs and gullets of smew (Mergus albellus), shot in winter at different places along the south coast of Lake IJssel (Netherlands). Toner and Lawler (1969) further mention the prey heron (Ardea cinerea), the grebe (Podiceps lath) and the diver (Colymbus) as bird predators of northern pike. The osprey (Pandion haliaëtus) is a common predator of pike in Sweden, Norway, Finland and the northern parts of the USSR, Canada and USA. Dunstan and Harper (1975) reported northern pike remains from the bald eagle (Haliaëtus leucocephalus) nests in Minnesota.

2.7.4 Vegetation

In lake environments the northern pike prefers the weedy bottom of bays, estuaries and shoals as spring and summer habitat. Carbine and Applegate (1946), who reported virtually all recoveries of tagged pike by anglers from localized areas in Houghton Lake, Michigan, found that all of them were offshore weedbeds. Vegetation was both submergent and emergent in combination, or submergent only. Dominant types were wild rice (Zizania), bulrush (Scirpus) and pondweeds (Potamogeton). In the Baltic Sea, pike lives mainly in areas where bladder-wrack (Fucus vesiculosus) or Phragmites communis occur (Lehtonen, personal communication).

Using telemetry data, Diana, Mackay and Ehrmann (1977) and Diana (1979) found that pike preferred vegetated zones in the Canadian lac Sainte Anne during summer. They were seldom found in water over 4 m deep during that season, and 78% of their locations were within 300 m off shore. Pike abundance was found to be inversely proportional to bareness (Makowecki, 1973). Various authors emphasized the importance of vegetation for the maintenance and quality of northern pike populations (Grimm, 1981, 1983a; Threinen, 1969). According to Grimm (1981), the success of hunting depends on the chance to stay unnoticed. Cover is of major importance and can be found in vegetated areas or on broken bottoms. The eutrophication-induced decline of northern pike populations in Oneida Lake, New York (Forney, 1977) and in the Grosse Müggelsee, near Berlin (Barthelmes and Waldow, 1978), stresses the importance of aquatic vegetation for this species (see also Section 3.2.1.2).

Obstacles and broken bottoms are, according to Grimm (1983, 1983a) of importance in non-vegetated waters. This type of cover was accepted by pike of 41-54 cm, especially in the vicinity of vegetated zones. Within the available space, not all areas are accessible to pike of every size (Grimm, 1983, 1983a). The depth of the water column and the width of vegetation belts are, below a certain limit, physical barriers for pike of a given length. Dense stands of emersed vegetation might prove impenetrable. Grimm (1983, 1983a) reported that distribution patterns of pike smaller than 30 cm were dependent on the biomass of pike larger than 41 cm. When the biomass of larger pike was low, the small pike were found within emersed/submersed, ingrowing and occasionally floating vegetation. In the period when the biomass of large pike was high, pike smaller than 30 cm were caught only within emersed/submersed vegetation.

Bregazzi and Kennedy (1980) reported from Slapton Ley (England) that small pike remained closely associated with fringe vegetation and dense weedbeds.

Makowecki (1973) found in Seibert Lake, Alberta, that vegetation types, such as Nuphar variegatum, Potamogeton praelongus and Potamogeton natans were positively correlated with pike abundance. The large pike were distributed only in the prime habitat areas where vegetation diversity was greatest. This is in contrast with Grimm's (1983) results, who found pike larger than 54 cm to be less dependent on vegetation. However, forage fish for pike in Seibert Lake (mainly Coregonus clupeaformis) were found to be concentrated in the vegetated zones. In the shallow meso-eutrophic waters, forage-fish for large pike (Cyprinids) were distributed also in non-vegetated areas. In this respect it is interesting to note that Kulemin, Makkoveyeva and Solopova (1971) related a sharp rise in the growth rate of pike of 5 years (about 50 cm) in Lake Pleshcheyeva (5 000 ha, Yaroslavl Province, USSR), to its movement from the shallow-water inshore zone into the open-water zone of the lake where larger prey fish were available.

Malley and Brown (1983) observed in Lough Erne (northern Ireland) that the location of pike caught by electrofishing was closely associated with the emergent vegetation and hence with the shore length. Pike under 25 cm in length showed even closer association with the vegetation. The authors found that 66% of pike captured with electrofishing gear were associated with bulrushes (Scirpus lacustris), reeds (Phragmites communis) and waterlilies (mostly Nuphar lutea and some Nymphea alba). Within the group smaller than 25 cm, horsetails (Equisetum fluviatilis) were found to house significantly larger pike than other plants do, while mixed vegetation - providing closer cover - had significantly smaller pike.

In an estimate of pike's preference for each of the main vegetation types in Lough Erne, it was found that larger fish (over 25 cm) were found in greatest densities in bulrush and waterlilies. Horsetails had the lowest density of larger individuals. Waterlilies had the highest densities of small pike, with reeds and bulrushes both having higher than average densities. Both reedmace (Typha latifolia) and horsetails had very low densities of small pike.

Chapman and Mackay (1984) concluded from diving observations in Twin Lakes, Alberta, that an ecological segregation existed between pike larger than 25 cm and pike smaller than 25 cm. Large individuals were found in deep, non-vegetated waters more often than small ones. The authors suggested that the segregation was due to different trophic relationships and different predator avoidance strategies used by the two size classes.

Threinen (1969) emphasized the significance of aquatic vegetation diversity in the maintenance of water temperature. Besides this thermoregulatory advantage which allows the fish to hover in the shade of the vegetation, such sites facilitate its perception of approaching objects, allowing it at the same time to remain more or less hidden (Helfman, 1979, 1981). Makowecki (1973) suggested that a well vegetated area will adequately house pike of small size, but there must be a certain minimum amount of vegetation to house a large pike. A well protected area will allow a pike to expend less energy in activities other than feeding. A pike in a well vegetated area is possibly much more successful in its feeding ventures when it is able to wait in a well hidden spot and thus let the food come to it. In a habitat of lesser quality, the pike may expend more energy in seeking protection from other pike and will therefore be less effective in capturing prey. The poorer the vegetative habitat, the greater must be spatial requirements of each individual.

According to Grimm (1981), the habitus of individual pike is tuned to the hunting behaviour of the species and to the habitat occupied. Smaller pike (less than 41 cm), which are restricted to vegetated areas, have a dorsolaterally striped pigmentation pattern. Their dominant colour consists of shades of green. Pike larger than 41 cm, also to be found outside the vegetation belts, vary in external appearance; besides a striped pattern, a spotted pigmentation occurs with dominance among pike larger than 54 cm. These pike were found to be coloured darker (brown) in four shallow-water bodies in the Netherlands (Grimm, 1981). The skin patterns are associated with light-shadow effects in vegetated and non-vegetated areas (see Section 1.2.2). They protect the fish against predators (northern pike, birds) and offer them better hunting facilities (Heuschmann, 1957).

2.7.5 Temperature

The thermoadaptive properties of fish change during ontogeny (Lapkin, Poddubnyy and Svirskiy, 1983). The embryonic development of northern pike is characterized by a temperature tolerance range of 4° to 23°C (Willemsen, 1959). During the phase of organ development, the tolerance zone expands and reaches its maximum level in the juvenile period. The physiological optimum temperature for larval fish was 26°C (Hokanson, McCormick and Jones, 1973). The zone of temperature tolerance narrows up to the initiation of sexual maturation. Casselman (1978) studied the influence of temperature on the growth of young northern pike and found that their physiological optimum was between 19° and 21°C. This temperature range is intermediate between the optimum temperatures for the growth of cold- (14°C) and warm-water (27°C) fishes. Pike therefore can be truly classified as a cool-water fish. Values for optimal growth temperatures are derived from fish fed maximum rations, whereas fish populations in nature probably do not very often achieve maximum consumption rates. Brett (1979) showed that the optimal growth temperature decreases as the food ration decreases.

Bevelhimer, Stein and Carline (1985) found maximum growth of northern pike in Ohio at 25°C. Their data suggest that local stocks might have adapted to the warm temperature regimes in the 25 years of maintenance in Ohio hatchery ponds.

The final preferendum temperature for northern pike was slightly higher than the optimum temperature for growth. It was determined in the range between 23° and 24°C (McCauley and Casselman, 1981). The final temperature preferendum is defined as the water temperature to which a fish will eventually gravitate regardless of its previous acclimation history. The similarity between optimal growth temperature and final preferendum temperature suggests that these parameters are probably useful indices of water temperatures at which biomass accumulation and potential yield would be maximized under natural conditions (Schlesinger and Regier, 1983). From the standpoint of thermodynamics and theory of automatic regulation, the final preferred temperature can be considered as the one where the condition of the fish is stable and stationary (Lapkin, Poddubnyy and Svirskiy, 1983).

The effect of seasonal conditions on the thermoresistance of northern pike was not studied, so there are no data on the seasonal dynamics of lethal temperatures.

The upper incipient lethal temperature of subadult pike in laboratory studies was 29.4°C (Casselman, 1978). Cvancara, Stieber and Cvancara (1977) determined temperature tolerance of the young of the year pike from Mississippi River during periods of high summer temperature. The LD-50 value was determined as 30.8°C. Ridenhour (1957) reported northern pike mortality from Clear Lake, Iowa, resulting from high temperatures (over 30°C) and low oxygen contents of the water.

The lower incipient lethal temperature is more difficult to determine. Northern pike can tolerate water temperatures very close to freezing. They show no apparent stress when subjected to a temperature of 0.1°C for extended periods of time prior to the freeze-up in the shallow lakes on Manitoulin Island (Casselman, 1978).

Mortalities resulting from "cold shock" have been reported when northern pike that had been congregated in a thermal discharge channel and acclimatized to a temperature of 21.8°C were exposed to a temperature of 4.9°C after the heated effluent was shut off (Ash, Chymko and Gallup, 1974).

Henley and Applegate (1982), while studying seasonal distribution of two northern pike (52 and 95 cm) marked with radio tags, found indications, based on pike localizations during the year, that fish were seasonally distributed in areas where temperatures appeared to be most favourable for their survival and growth.

2.7.6 Ice

Petrosky and Magnuson (1973) subjected northern pike to simulated winter conditions in aquaria and noted that as the dissolved oxygen levels fell from 4.0 to 0.25 ppm, the fish rose from the lower middle depth until they were nosing at the ice. Ventilation movements increased with lower oxygen tensions. Magnuson and Karlen (1970) observed pike beneath the ice in a net enclosure during the winter in a winterkill lake. The pike were immediately under the ice; oxygen tension of the water was very low. During the last week of their existence, the pike rested with head slightly higher than tail and snout almost touching the ice. The opercular movements and the pectoral fin movements apparently created a weak but steady flow of water that melted a dome under the ice. The two fish in the dome often slowly moved pectoral and caudal fins to retain stability. The dorsal fin and the top of caudal fin often touched the ice. Usually, both fish were in the dome with their snouts almost touching its top and their caudal fins apart - their bodies forming a V. The combination of reduced locomotory movement and a position immediately beneath the ice apparently favoured the longer survival of pike in the lake when compared with yellow perch, Perca flavescens and bluegill, Lepomis macrochirus.

Casselman and Harvey (1975) and Grimm (1983, 1983a) reported selective fish mortality due to low winter oxygen among northern pike. Individuals longer than 40 cm suffered severely while the younger fish survived. Significantly more males than females survived the winterkill. The authors suggested that their findings could be explained with physiological arguments. It is also possible that differences in distribution patterns within the population have contributed to the selective mortality.

Poddubny, Malinin and Gaiduk (1970) followed the path of a tagged pike (5 kg) which was let out under ice into the mouth of a former stream in Rybinsk reservoir. The fish entered the bed of the stream and moved slowly along the slope. A day after being released it moved actively to the old bed of the Mologa River. It swam against the current (20 cm/sec) at an average speed of 3.3 m/min, strictly following the 10-m isobaths.

2.7.7 pH

McCarraher (1962) reported that northern pike is moderately euryionic and has survived in Nebraska waters having average pH values of 9.5. A permissible range of 9.5-9.8 has been recorded for periods up to four months. Embryos and larvae appeared to be more sensitive to extremes of pH, bicarbonate and monocarbonate than adults. McCarraher (1971) obtained similar data when he tested 14 species of freshwater fish in cages in one or more of 13 alkaline lakes and ponds in Nebraska (more than 300 mg/litre Na_2CO_3 and KCO_3). Northern pike was among the most tolerant species.

EIFAC (1968) and Alabaster and Lloyd (1980) reviewed Swedish literature on observations of roach (Rutilus rutilus), perch (Perca fluviatilis), bream (Abramis brama) and northern pike in Lake Sladen which has a pH value of 3.7 to 3.8 and an iron content of 0.3 to 1.2 ppm Fe. From Lake Sysmajärvi (Finland), with pH values in the range of 3.5 to 4.6, bream, roach, perch and northern pike were reported. Pike was able to breed in the large zone where the pH values were between 4.2 and 4.4.

Milbrink and Johansson (1975) made acidification tests of pike roe in a series of pH intervals between 7.5 and 4.0, which gave a very modest decline in hatching success - only about 30% between the extremes. However, all the embryos below pH 4.5 were seriously malformed. They could not possibly be given any chance of survival. At pH 5.1, about 10% of the embryos were already malformed.

2.7.8 Oxygen

The effect of critically low oxygen concentration on the survival of northern pike has been widely studied. The relation between critical oxygen concentration and temperature is highly significantly, curvi-linearly related (Casselman, 1978; see Figure 30). Dolinin (1975a) concluded that the process of gas exchange regulation at oxygen concentrations exceeding critical values was accomplished through simultaneous changes of the volume of ventilation and the surface of the gills participating in the extraction of oxygen.

The lower incipient lethal oxygen concentration is frequently encountered at low temperature in association with winterkill. Northern pike can readily survive in oxygen concentrations of 0.3 mg/litre. Doudoroff and Shummway (1970) gave 0.2-0.5 mg oxygen/litre as critical dissolved oxygen value for northern

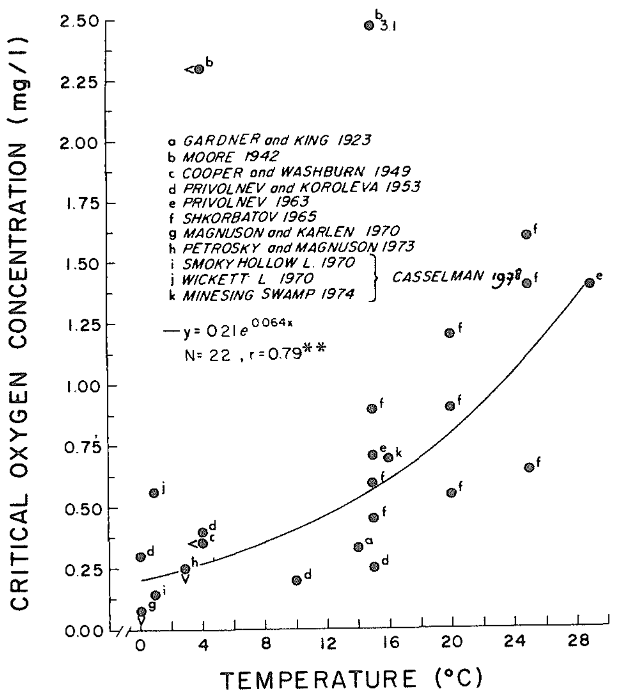


Figure 30 Relation between lower incipient lethal oxygen concentration for northern pike and temperature. The symbol "<" indicates "less than" and applies to the variable in the direction opposite to which it points. Regression includes the results of Moore (1942). (From Casselman, 1978)

pike. Magnuson and Karlen (1970) observed over some weeks northern pike beneath the ice in water with dissolved oxygen concentrations lower than 0.1 mg/litre.

According to Casselman (1978), the ability of northern pike to withstand critically low winter oxygen is probably also genetic, since an experimental determination of critically low oxygen concentration conducted under field conditions was higher for northern pike from Wickett Lake (0.55 mg/litre) than for fish from Smoke Hollow Lake (0.15 mg/litre). In this lake, minimum winter oxygen concentrations are consistently lower and partial winterkills occur more frequently than in Wickett Lake.

Diurnal patterns of respiratory activity were measured by Dolinin (1973). Under conditions of constant illumination (natural light during the day and electric light at night), and constant water temperature of 13.5°C, using mask respirometers, the author determined oxygen consumption for 17 northern pike (weight around 1 kg). Highest rates of respiratory exchange were found between 19 and 23 h after initiation of the experiments. Respiratory activity was lowest from 12 to 18 h. The author considered the alteration in motor activity, connected with the daily feeding rhythm, as the cause of the observed fluctuations.

2.7.9 Light and dark; day and night

Day length has a demonstrable effect on the growth of northern pike (Casselman, 1978). Maximum growth rate in the natural environment occurs during long day periods. Although natural prolonged day length appeared to stimulate growth, continuous light caused a significant decrease in weight and a slight decrease in length. Abnormally short day length produced inconclusive trend. Northern pike, reared under permanent light, were extremely active, appeared to swim almost continually, and were hyperactive when disturbed.

Dobler (1977) found in laboratory experiments that northern pike (23-25 cm) eat prey fish (Leucaspius delineatus) predominantly when there is little light (50-70% of the prey was taken at less than 1 lux). The author supposed that northern pike is optically superior to its prey at low illumination levels and profits from this advantage when catching it. Also, Volkova (1973) found in aquarium experiments highest consumption of prey fish at twilight illumination (0.1-0.01 lux). According to the author, the well developed vision and lateral line make it possible for pike to feed at night (see also Section 2.4).

Telemetry and gillnet data from Lac Sainte Anne (Canada) indicate the trend of diurnal activity and nocturnal inactivity (Diana, 1980). Lawler (1969) reported similar observations based on the catches of pike in gillnets in shallow and deep water from May to August in Heming Lake, Manitoba. The cpue was used as an index of fish activity. In shallow water, the catch of pike was highest during the hours of darkness. After sunrise, the catch declined sharply and a peak was reached soon after sunset. In deeper water, the catch rose sharply just after sunrise, declined until late afternoon and then increased slightly with approaching darkness. Diana (1980) suggested that these data may be the result of net avoidance during periods of high light intensity.

Mackay and Craig (1983), using telemetric data, found pike to be inactive for substantial periods of time, particularly at night. The fish showed more periods of activity at dawn and dusk than during the day. Malinin (1970) and Poddubnyi, Malinin and Gaiduk (1970) reported similar results from summer and winter observations of tagged pike in the Rybinsk reservoir; maximum activity was recorded in the morning (6 to 8 am) and in the evening (5 to 7 pm); during the day and at night pike hardly moved.

According to Casselman (1978), data from angling studies conducted during the open-water period indicate that northern pike feed more actively on cloudy, overcast days than on bright sunny ones. On days with high light intensity they feed more actively during the evening and to a lesser extent in morning twilight when light intensity is low.

Lind (1974) and Kaukoranta and Lind (1975) noted a phase shift in the activity pattern of northern pike. The pike in Finnish waters was day-active in winter, whereas activity in June and July was non-synchronized, with a weak peak in the middle of the night. The activity pattern in August and September showed two peaks, one in the morning and one in the evening. Towards autumn, these peaks fused at noon-timed, which they became the principal period of activity. The observed activity patterns are related to the location of the fish in northern latitudes of Finnish waters.

Bakshtanskij and Nesterov (1976) studied hunting behaviour of pike in relation to light intensity and time of day under natural conditions. Their observations were evidently made during the summer at a northern location in the USSR. During 113 h of observation 42 attacks were recorded: 25 x from 6 pm to midnight (light intensity decreasing from 15 000 to 350 lux); 16 from midnight to 5 am (350-7 000 lux); 1 x at 12 (50 000 lux). Attacks were seen most often between 10 and 11 pm.

2.7.10 Currents

Harrison and Hadley (1978), in their study of sympatric populations of northern pike and muskellunge in the Niagara River, New York, found that the segregation between the species was most pronounced during spawning and appeared to result from adaptation of muskellunge to a nearly exclusive use of the riverine environment. Northern pike appeared to be intolerant to the lotic characteristics of the river, and their distribution was restricted to lentic habitats in the river watershed.

According to Paragamian (1976), northern pike occupied the same stream segments of Plover River, Wisconsin, as smallmouth bass, Micropterus dolomieui. Pike were usually captured in regions where current velocity was low, aquatic vegetation present and bank cover available. Smallmouth bass were usually found in pools of moderate current velocity with rock and rubble substrate.

Jones, Kiceniuk and Banford (1974) found, on the basis of laboratory experiments, a relationship between fork length of northern pike and the inability to move 100 m in 10 min against water velocities of up to 80 cm/sec. The fish showed a tendency to swim slowly at lower temperatures. In comparison to other species tested, northern pike showed a low ability to move in currents for longer times. Critical velocity (maximum sustainable velocity) for 10 min would be 44 cm/sec, and the highest maintained speed (for 100 min) was about 60% of the critical velocity or 26 cm/sec. Both values are close to the maximum and mean speeds of pike observed for free swimming fish by Diana (1980). This author reports that calculated swimming velocities of pike were significantly slower in winter than in summer.

2.7.11 Salinity

Northern pike is a common fish species in the Bothnian Sea from the southern part of the Åland Islands (salinity 5-6 ^{o}/oo) to the northern Bothnian Bay into the mouth of the River Torneälv (salinity 0.5-1 ^{o}/oo)(Johnson and Müller, 1978; Alm, 1957; and Müller, 1982). Northern pike is also reported (Hegemann, 1958) from the lagoons and in the bays of the Baltic Sea in the German Democratic Republic (Greifswalder Bodden) and from Finnish Coastal waters (Lind and Kaukoranta, 1975; Kaukoranta and Lind, 1975), at salinities varying between 3 and 7 ^{o}/oo. Marshall and Johnson (1971) mentioned local reports of pike occurring in the Quill Lakes (Saskatchewan) in 1929 when salinities were 11 to 15.5 ^{o}/oo. Other sources consulted by these authors reported that the highest salinity at which pike was found to occur was 3.5 ^{o}/oo. Pike in Lake Leonore (Saskatchewan) perished at a salinity of 6 ^{o}/oo.

In connection with the sharp fluctuations of salinity in brackish waters, Shlyumpberger (1966) made an investigation into the sale tolerance of adult and immature northern pike. The fish were placed in a solution containing the isotope Na^{22}, and after that in water with varying salinity values. The periods of absorption and excretion of Na^{22} were measured. The rate of excretion was found to rise with increased salinity. At 11.33-12.4 ^{o}/oo salinity, impairment of mobility and sideward inclination of the body were observed. In fresh water, up to 65% of the total Na^{22} content was excreted from the fish perivisceral fluid. After they were transferred from fresh water to salt water, the Na^{22} excretion rate increased within 5 to 15 h. On transfer from salt to fresh water, the Na^{22} excretion rate fell off within 10 h.

Ionic and osmotic balance of northern pike was also studied by Oikari (1975, 1975a, 1978), who also collected data on the hydromineral balance of the fish in relation to temperature. The hydromineral balance was found to be well regulated at near-zero-winter temperatures.

2.7.12 Pressure

Einsele (1964) reported on the reactions of fish to explosives tested during World War II in several Austrian and German lakes. The author noted that northern pike is highly sensitive to pressure changes in the water resulting from explosions. This is related to its anatomy, particularly to the fact that the ventral side in the fish is not protected by muscle layers. Destruction of swimbladder and damage to kidneys are reported as a result of explosions. The author also observed that northern pike (mostly smaller individuals) survived repeated heavy explosions in the vegetated zones along the shore. The strength of pressure waves in shallow water with plants is less than in deeper parts devoid of vegetation.

Rudakovskiy et al. (1970) studied the effect of weak explosion impulses on the fish fauna, a subject which is considered of great interest for the development of methods controlling fish behaviour. They found indications that northern pike may possibly be frightened by the effects of pneumatic emitters and gas detonators in water.

Tsvetkov (1969) studied the sensitivity of northern pike (70-95 mm) to rapid pressure changes. When the hydrostatic equilibrium was disturbed, the compensatory activity of the fins was intensified as a result of which the body returns to a position of neutral buoyancy. The author found that the minimum required to alter the buoyancy of the pike was a pressure change of 1-2 mm H_2O and that a sharp rise of 5-6 mm H_2O immediately altered the functional rhythm of the fins. The experiments further showed that the perception of pressure changes was the same at different depths. The data indicate that the swimbladder may be an organ of perception of pressure changes.

2.7.13 Pollution

Northern pike kept in tanks retained an average of 19% (range 6-31%) of the methyl-mercury which they ingested during consumption of young-of-the-year carp (Cyprinus carpio), collected from a pond (Phillips and Gregory, 1979). The total amount of mercury in pike increased with time, but the concentration in the tissue decreased due to growth dillution.

Lockhart et al. (1972) found half-life times of 2 years for elimination of methyl-mercury contaminating northern pike tissue. This is in agreement with data from laboratory studies (Jarvenpaa, Tillander and Miettinen, 1970). These authors suggested that intestinal reabsorption of bile methyl-mercury occurs in pike and contributes to its long half-life time. Obvious physical signs of methyl-mercury poisoning were not found in histological examination of liver, kidney, spleen and gill tissues. There is some evidence that fat storage in the liver was reduced by methyl-mercury. Biochemical measurements indicated internal differences between pike captured in a lake, polluted with methyl-mercury and pike caught in a lake free of mercury. Data obtained from experiments with transplanted fish suggest that biochemical differences can be induced by environmental changes.

Scott (1974), studying large samples of northern pike from areas of Clay Lake (Ontario) - a highly mercury-contaminated lake - found that the larger the fish, the greater was the white muscle mercury concentration. Armstrong and Scott (1979) found a decrease in white muscle mercury concentrations of pike in Ball Lake (Ontario) after mercury discharges in the lake were controlled. The authors supposed that the decrease was associated with the decrease of mercury in suspension. The sediment mercury levels were probably not affected by control of the mercury discharge.

Turner and Swick (1983) studied the interaction between selenium and mercury in young northern pike caged in the mercury-contaminated Clay Lake (Ontario). Pike were held in water containing traces (<0.2µg Se/l) or elevated concentrations (4.5-6.4µg Se/l) of selenium and were able to accumulate ^{203}Hg and ^{75}Se either from food (yellow perch) only, water only, or from food and water. Control pike acccumulated as much as 20 times more ^{75}Se from food than from water, assimilating about 30% of selenium present in food. With increased levels of selenium in the water (around 5µg Se/l), food and water were of similar importance as sources. Waterborne selenium did not alter either the amount of ^{203}Hg accumulated from water or its subsequent partitioning among the pike tissues sampled. When highly concentrated in food, selenium decreased both the body burden of ^{203}Hg in pike and the proportion in muscle tissue. It is inferred by Turner and Swick (1983) that selenium, when added to aquatic ecosystems and subsequently incorporated in the food web, would interfere with biomagnification of mercury. Furthermore, future studies of selenium toxicity in fish should emphasize its accumulation from food.

Olsson and Jensen (1975) found high levels of mercury, DDT and PCB substances in pike from one of two island lakes in the prevailing wind direction of Stockholm, which indicates airborne fallout. Lower levels were recorded in a neighbouring lake. This difference in pollution levels in pike from the same region was explained by the authors as the result of greater biomass and more rapid water exchange in the lake housing pike with lower contamination levels of the polluting substance.

Moilanen et al. (1982) reported that PCB and DDT components in northern pike in the Turku Archipelago (northern Baltic Sea, Finland) were decreasing in the period 1971-82. The decrease in DDT and PCB levels in pike is related to the ban of the use of these substances in Finland and Sweden. During the same period, an increase in chlordane concentrations in fish was measured.

McFarlane and Franzin (1980) examined concentrations of cadmium, copper and mercury in livers of northern pike from five lakes in the vicinity of, and receiving metal fallout from a base metal smelter complex at Flin Flon (Manitoba). Concentrations of these heavy metals increased with age. Liver metal concentrations were not relative to the degree of contamination in the five lakes. The authors suggest that a poorly understood mechanism is at work which involves competition between heavy metals and calcium for cellular binding sites or an accidental active uptake by a calcium-regulatory mechanism.

Il'yenko (1970) studied the uptake of artificial radio-isotopes in the fish body under natural circumstances. The bulk of the isotopes entered the fish via the food and not from the environment. In northern pike the concentration of both strontium-90 and ceasium-137 in the muscles and skeleton reflected the feeding level of the tested individuals.

2.8 Parasites, Diseases

2.8.1 Introduction

Dorson, Kinkelin and Michel (1983) and Graff (1978) stated that the pathology of the northern pike had not been studied as well as that of salmonids, probably due to the fact that pike have not been used very much in aquaculture (only for a short period during the reproductive cycle). While little is known about the pathology of pike in the wild, young pike raised in fish farms are potential targets for many types of pathogens, including uni- and multi-cellular parasites, bacteria and viruses. Parasitical problems are exacerbated by the fact that invertebrates in the plankton, the obligatory food of pike embryos and larvae, are the intermediate hosts of some parasites. The bacterial pathology of pike in natural waters is practically limited to septicemic diseases accompanied by ulcers and haemorrhages due to Aeromonas hydrophila and strains of Aeromonas salmonicida. Pike in natural waters also have a high number of lymphosarcomas induced by an oncornavirus.

Rhabdovirus disease causes haemorrhagic septicemias in pike larvae raised in aquaculture. Due to this disease, there is a high mortality rate in larvae until they reach 4-5 cm in length. The haemorrhagic form of trout rhabdovirus disease may also result in a mortality rate of nearly 100% in pike larvae. It can be predicted that the number of such accidents will increase with the extension of pike farming. The vertical transmission of these rhabdovirus diseases (to other age classes) can be stopped by disinfecting the eggs, but there are also other methods such as the use of attenuated viral strains which vaccinate against the disease. The role of temperature in the development of these rhabdovirus diseases should also be studied.

2.8.2 Viral diseases

2.8.2.1 Pike fry rhabdovirus disease

Bootsma (1971) described symptoms, pathology and till then unknown etiology of the "red disease" in pike larvae. The disease is an acute infection of the circulatory system of eleutheroembryos or larvae up to a length of about 6 cm. It caused severe losses in Dutch pike culture and was also reported from Germany (Schäperclaus, 1979). Electron microscopical examination of pike fry (Bootsma and Vorstenbosch, 1973) revealed the presence of bullet-shaped virus particules in kidney tissue.

Kinkelin, Galimard and Bootsma (1973) isolated and identified the causative agent of the disease as a rhabdovirus that is transmitted through the water to the larvae. It seems likely that the pike virus is carried by adult fishes, spread into the water, and during spawning onto the surface of the eggs, inducing propagation of the disease very early after hatching. Bootsma, Kinkelin and Le Berre (1975) performed transmission experiments with pike-fry rhabdovirus (PFR) and showed that infection of fertilized eggs with the virus caused 100% mortality. The experiments indicated that red disease and hydrocephalus internus are different manifestations of the same disease. Experimental egg transmission of the PFR could be interrupted by disinfecting the eggs with Wescodyne solution.

Clerx (1978) characterized PFR physico-chemically and antigenetically. Immunological investigations of serum from spawners did not provide indications that these animals were carriers of the virus or had regular contact with it. Also, no indications were obtained that spawners played a part in the transmission of the virus to the offspring.

Purification of the immunoglobuli from pike serum and its physicochemical characterization have been described. It has been proven that pike eggs contain antibody-like substances. Their quantity increases in larvae shortly after the young pike can move freely. In the serum of the smallest fish from which blood could be collected, immunoglobulin is already present. However, the serum of small pike (smaller than 8 cm) contains only 1-2% of the amount of immunoglobuli found in the serum of adults.

2.8.2.2 Egtved disease

This disease (Haemorrhagic septicemia of rainbow trout VHS) is generally known as a virus disease of rainbow trout (Salmo gairdneri). It also occurs in Salmo trutta and can be transmitted experimentally to salmon (Salmo salar), gold fish (Carassius auratus) and brook trout (Salvelinus fontinalis)(Schäperclaus, 1979).

Meier and Jørgenson (1979) described the characteristics of a viral strain related to the Egtved virus, isolated from pike larvae in a hatchery on the Hallwillersee, Switzerland. The fry originated in the lake and had been kept on plankton diet for 3 weeks in filtered water when the first signs of the disease occurred. During a 7-day period, the hatchery lost a total of 120 000 pike larvae - close to 100% of the population.

Ahne (1980) described the sensitivity of pike embryos and larvae to Egtved virus originating in salmonids. Infection occurred between 3 and 10 days after transmission and caused pathological and anatomical changes. The pike embryos and larvae can be infected by the virus via water, food and by injection. The author concluded that pike populations can be considered as potential Egtved reservoirs causing distribution of the virus. Meier and Jørgenson (1980) state that it is still unknown whether pike in later developmental stages can be attacked by the disease or become carriers of the virus.

2.8.2.3 Lymphocystis disease

Amin (1979) reported the first record of this highly infectious viral disease in northern pike from Wisconsin. Schäperclaus (1979) gave a comprehensive review of the disease, its dispersal prophylaxis and therapy. He describes it as a mild-tumour disease.

2.8.2.4 Lymphosarcoma

Sonstegard and Hnath (1978) and Sonstegard and Chen (1986) summarized the biology, geographic distribution and control of the disease, a malignant blood cancer, which infects northern pike and muskellunge. It is geographically widespread and has been diagnosed histopathologically in northern pike from Alaska, the Northwest Territories, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, New York and Michigan. Mulcahy (1976) reports pike with lymphosarcomas from all major areas in Ireland, although their incidence is sporadic, varying from 0% to 12%. Thompson (1982) described an epizootic of lymphoma in northern pike occurring in the Åland Islands in Finnish waters of the Baltic Sea. Macro- and microscopic inspection showed that this lymphoma is similar to those previously reported in esocid fishes. The skin tumours of the pike population along the Swedish baltic coast were described by Ljungberg and Lange (1968).

Mulcahy and O'Leary (1970) transmitted lymphosarcomas to northern pike by using a cell-free homogenate of tumour tissue. These results suggest that a virus or mycoplasma may be involved. Winquist, Ljungberg and Hellstroem (1968) observed by electron microscopy viral particles in epidermal proliferations of northern pike from the Baltic coast. These particles resemble mammalian tumour viruses. Mulcahy (1970) injected pike with ultrafiltered homogenate of tumours and studied the resulting histological effects in the thymus gland. The author concluded that the thymus is not always the primary site of the lymphosarcoma, but that thymic malfunction may be a prerequisite of lymphosarcoma development, perhaps by reducing the natural resistance of the fish to the etiological influences which may include viral infection (see also Wolf, 1972).

Sonstegard and Hnath (1978) consider the lymphosarcomas highly infectious. The authors hypothesized that the elevated water temperatures in summer are non-permissive for virus expression and may be the reason for spontaneous regression of the tumours. Although a virus has been found to be associated with the tumours, a viral etiology has not been confirmed.

Haematological aspects of the disease were studied by Mulcahy (1975).

2.8.3 Bacterial diseases

Harvey (1986) reviewed the case histories of disease incidence at the Pennsylvania Fish Commission hatcheries for a five-year period from 1978 to 1982. Bacterial columnaris, bacterial haemorrhagic septicemia, gill fungus, bacterial gill disease, and others caused by external protozoans and monogenetic trematodes were the most prevalent disease agents diagnosed in conjunction with excessive fish mortalities. The author discussed various treatments used in controlling esocid diseases, recommending that the culturists respect the following rules:

(1) to keep the level of dissolved oxygen in rearing units as close to saturation as possible;

(2) to maintain tank hygiene in intensive culture;

(3) to avoid supersaturated gas levels, but to keep the levels as close to saturation as possible;

(4) to maintain and monitor optimal water temperature;

(5) to treat prophylactically for gill diseases on a regular basis;

(6) to feed healthy forage fish or high-quality dry diet;

(7) to observe the fish as often as possible for the purpose of detecting abnormal or changing signs.

2.8.3.1 Red sore disease

The disease is described from Central and northern Europe and Canada (Ontario and Quebec Provinces). According to Schäperclaus (1979), morbidity and mortality are high to very high. Symptoms of the disease include necrosis of the epidermis, loss of scales and red colouring of the infected zones. On the head the necrosis can grow deeper and seriously affect muscle and jaw tissue. Infections and tumours can develop on the basis of the fins. According to Scott and Crossman (1973), the disease is caused by the bacterium Pseudomonas hydrophilia, which is also responsible for the so-called "red legs" in frogs. According to Schäperclaus (1979), the causative agent of the disease is Aeromonas punctata. The author draws attention to publications in which the primary agent of the disease is considered to be a virus. Results of bacteriological research are not uniform and according to Schäperclaus (1979), this supports the assumption of a primary virus-etiology.

2.8.3.2 Black-spot disease

Harrison and Hadley (1982, 1983) found that 22% of 623 examined northern pike from Niagara River had black-spot infection. Their data suggest that this disease is related to retarded growth and increased mortality, but the cause-effect relation is still unclear. An attempt to identify the causative digenic trematode was unsuccessful.

2.8.3.3 Furunculosis

The disease is described for brook trout (Salvelinus fontinalis), brown trout (Salmo trutta), rainbow trout (Salmo gairdneri) and tench (Tinca tinca) (Schäperclaus, 1979). Economon (1960) isolated the bacterium Aeromonas salmonicida, the causative agent of the disease in salmonid fishes, from an intramuscular abscess and from the posterior portion of the kidney of two northern pike that were found dead in a spawning pond at Waterville, Minnesota, in May 1959.

Schäperclaus (1979) reported that Aeromonas salmonicida can cause skin infections and skin tumours in pike. Bleeding in the mouth and internal organs can also be caused by A. salmonicida.

2.8.3.4 Mycobacteriosis

Otte (1969) isolated from pike a Mycobacterium believed to be related to M. fortuitum. This tuberculosis bacterium can hardly be considered pathogenic to warm-blooded organisms. Local skin reactions in human beings are reported from tropical regions. Mycobacteriosis can occur in stagnant waters with high fish densities.

2.8.4 Parasites of northern pike

Table XVIII summarizes the data on parasites.

3. POPULATION

3.1 Population Structure

3.1.1 Introduction

Several aspects of the dynamics of northern pike populations are presented in this section. A short note on the methodological problems of population research introduces the available data and their interpretation.

Population parameters are generalized characteristics of groups of fish mostly based on estimates, inferences from observations of individual fish or extrapolations in space and time of data pertaining to small groups of fish. A wide range of literature exists on factors influencing static parameters such as abundance, density and yearclass structure of populations and factors affecting dynamic parameters, e.g., growth, reproduction, recruitment, exploitation, migration and mortality. For the parameterization of fish populations it is essential to include factors that affect simultaneously the various processes in the fish.

Direct observations on the role of population interactions and on the influence of environmental factors on the population's dynamic system are scarce and not feasible methodologically in many field situations. Hence, the data are generally based on estimates. The evidence available on the forces governing the population in time and in a continuously changing habitat is therefore indirect and subject to interpretation, bias and error. This procedure is common in biological research and its application is dependent on knowledge and assumptions on the dynamics of the population, the biology of the species and the estimation techniques. In general, however, many of the assumptions underlying the interpretation of dynamic processes remain implicit. This may result in diverging interpretations, and even in confusion about the validity of the basic data. It is therefore essential to consider any conclusion on the population dynamics of a species within the framework of explicit and implicit assumptions and possible errors derived from the basic data available.

Most interpretations of data resulting from population research are not definite in the sense that they do not represent "biological laws". They are intended to indicate trends and processes which are, at the present state of our knowledge, the best available materials for building up general concepts of the population dynamics of a species.

3.1.2 The population in the community and the ecosystem

The role of northern pike in relation to its environment is treated in various sections (2.1.6, 2.2.3, 2.2.5, 2.3.4, 2.4.6, 2.7). Generally, pike are top predators in the food chain consuming fish while predatorial pressure on individual pike is low. The species is moderately tolerant to changes in its environment caused by physical, chemical or biological agents.

According to Maclean and Magnuson (1977), in their review of species interaction in percid communities, Stizostedion seems to have a greater effect on the percid community than other predators, such as northern pike. According to Svärdson (1976), the pike-perch (Stizostedion lucioperca) is, under suitable habitat conditions, a dominant predator (see Section 2.7.2).

Johnson *et al.* (1977), in their analysis of data from the lake survey files of the Fisheries Branch of the Ontario Ministry of Natural Resources, screened the records of about 2 500

Table XVIII

Parasites of *Esox lucius*

Parasites	Stage of parasite	Geographic location[a]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b]
PROTOZOA						
Brachyspira epizootica	-	E	-	-	-	1
Chilodonella cyprini	-	E	Gills	-	-	6
Chloromyxum sp.	-	R	Gall bladder	-	6.6+	13
Chloromyxum esocinum	-	R	Gall bladder	-	-	1, 2, 6, 31, 37
Corynebacterium sp.	-	A	-	-	-	6
Cryptobia guerneyorum	-	E,R	-	-	-	1, 31, 37
Cryptognimum chyli	-	A	-	-	-	1
Dermocystidium vejdovski	-	E,R	-	-	-	31, 37
Eimeria esoci	-	R	-	-	-	1, 31, 37
Glossatella sp.	-	E	-	-	-	1
Haemogregarina esoci	-	R	-	-	-	1, 31, 37
Henneguya creplini	-	E	Gills	-	-	7
Henneguya lobosa	-	E,R	Gills	-	-	1, 4, 6, 31, 37
Henneguya periintestinalis	-	R	Gills	-	0-5	8
Henneguya psorospermica	-	E,R	Gills	-	0-93	1, 3, 6, 8, 9, 10, 11, 31, 37
Henneguya oviperda	-	E,R	Gills, ovary	21-96	6-93	3, 6, 8, 9, 10
Henneguya schizura	-	A,E	-	-	-	1, 31, 37
Henneguya zschokkei	-	R	-	-	0-20	1, 6, 8, 10, 31, 37
Hepatozoon esoci	-	R	-	-	-	1, 31, 37
Ichthyophthirius multifiliis	-	E,R	Head	-	6.6+	3, 4
Myxidium lieberkühni	-	E,R	Urethra, vesica, urinary bladder, kidneys	Many	0-100	1, 2, 3, 5, 6, 8, 10, 11, 12, 31, 37
Myxobolus sp.	-	A	-	-	-	17
Myxobolus mülleri	-	R	Gills	-	-	6
Myxosoma anurus	-	R	-	-	-	1, 31, 37
Myxosoma dujardini	-	R	Gills	0-96	33-66	3, 5, 8, 10, 11
Myxosporida sp.	-	R	-	20	-	12
Nephrocystidium pickii	-	E	-	-	-	1
Ophistoreis felineus	-	E	-	-	-	6
Scyphidia sp.	-	A	-	-	-	1

Table XVIII (continued)

Parasites	Stage of parasite	Geografic location[a]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b]
PROTOZOA (continued)						
Trichodina sp.	-	A	Gills	-	-	6, 29
Trichodina epizootica	-	A,E	Gills	-	-	1, 6
Trichodina domerguei	-	E,R	Gills, skin	1	0-62	1, 4, 6, 8, 10, 31, 37
Trichodina pediculus	-	E	-	-	-	1
Trichodinella epizootica	-	R	-	-	-	1, 31, 37
Trypanosoma remaki	-	E,R	-	-	0-62	1, 8, 12, 31, 37
TREMATODA						
Monogenea						
Ancyrocephalus monenteron	-	E	-	-	-	1
Dactylogyrus anchoratus?	-	R	-	-	-	31, 37
Dactylogyrus crufifer?	-	R	-	-	-	31, 37
Dactylogyrus intermedius?	-	R	-	-	-	31, 37
Dactylogyrus tuba?	-	R	-	-	-	31. 37
Dactylogyrus vastator?	-	E,R	-	-	-	1, 31, 37
Diplozoon paradoxum	-	E,R	-	-	-	1, 31, 37
Eucephalus polymorphus	-	E	Intestine	-	-	1
Gyrodactylus elegans	-	E	-	-	-	1
Gyrodactylus lucii	-	R	-	-	-	31, 37
Gyrodactylus wagneri lucii	-	E	-	-	-	1
Neodactylogyrus megastoma	-	E	-	-	-	1
Tetraonchus sp.	-	Mongolia	-	-	-	16
Tetraonchus monenteron	-	E,R	Gills	1-235	0-93	1, 2, 3, 4, 5, 6, 8, 10, 11, 12, 13, 14, 15, 31, 33, 36, 37
Digenea						
Allocreadium isoporum	-	A,R	Intestine	-	-	1, 2, 6, 31, 37
Apophallus venustus	Metacercaria	A	-	-	-	1
Asocotyle coleostoma	Metacercaria	R	-	-	-	1, 31, 37
Azygia angusticauda	-	A	Intestine, stomach	-	-	1, 6, 33
Azygia longa	-	A	Intestine, stomach	-	-	1, 33
Azygia lucii	-	E,R	Intestine, stomach	1-19	27-100	1, 3, 5, 6, 8, 10, 11, 18, 19, 20, 31, 37

Table XVIII (continued)

Parasites	Stage of parasite	Geografic location[a]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b]
TREMATODA (continued)						
Digenea (continued)						
Azygia robusta	-	R	-	-	-	1, 31, 37
Azygia tereticolle	-	A	-	-	-	1
Bolbophorus confusus	Metacercaria	E	-	-	-	1, 31, 37
Bucephalopsis pusilla	-	A	-	-	-	1
Bucephalus markowitschi	-	R	Intestine	3-985	0-47.3	3
Bucephalus papillosus	-	A	-	-	-	1
Bucephalus polymorphus	-	R	Intestine	0-985	0-92	1, 3, 5, 8, 10, 11, 12, 31, 37
Bunodera luciopercae	-	E,R	Intestine	1-20	0-65.7	1, 2, 11, 20, 14, 31, 36, 37
Centrovarium lobotes	Metacercaria	A	-	12.9+	-	1, 13
Clinostomum complanatum	Metacercaria	R	-	-	-	1, 6, 31, 37
Clinostomum marginatum	Metacercaria	A	Muscle, mesenteries	-	-	1, 33
Contracaecum bidentatum	-	R	-	-	-	31, 37
Cotylurus pilaetus	Metacercaria	A,R	-	-	-	1, 31, 37
Crassiphiala bulboglossa	Metacercaria	A	-	-	-	1
Crepidostomum cooperi	-	A	-	-	-	1, 6
Crepidostomum farionis	-	A	-	1.86+	-	13
Crepidostomum metoecus	-	A	Intestine	-	-	2
Crodactylcidae	-	A	-	-	-	1, 31, 37
Crowcrocoecum skrjabini	-	R	-	-	-	1, 31, 37
Cryptogonimus chyli	Metacercaria	A	-	-	-	1
Diplostomulum sp.	Metacercaria	R,A	Eyes, muscles	-	0-25	1, 3, 6, 32, 33
Diplostomulum clavatum	Metacercaria	R	Eyes	1-329	0-73	3, 5, 6, 8, 10, 31, 37
Diplostomulum cuticola	Metacercaria	E	-	-	-	1
Diplostomulum hughesi	Metacercaria	R	Muscles	Seldom	75	11
Diplostomulum scheuringi	Metacercaria	A	-	-	-	1
Diplostomulum spathaceum	Metacercaria	A,E,R	Lens of eye	2-16	0-30	1, 3, 4, 5, 6, 10, 12, 20
Hysteromorpha triloba	Metacercaria	R	-	-	-	1, 31, 37
Macroderoides flavus	-	A	-	-	-	1, 16
Mesostephanus appendiculatus	Metacercaria	E	-	-	-	6
Neascus sp.	Metacercaria	A	-	-	-	1, 6, 30

Table XVIII (continued)

Parasites	Stage of parasite	Geografic location[a]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b]
TREMATODA (continued)						
Digenea (continued)						
Neascus oneidensis	Metacercaria	A	-	-	-	1
Paracoenogonimus ovatus	Metacercaria	A,E,R	-	-	-	1, 6, 31, 37
Paracoenogonimus viviparae	Metacercaria	E	Muscle	-	-	6
Phyllodistomum sp.	-	A	-	-	-	1
Phyllodistomum americanum	-	A	-	-	-	1
Phyllodistomum folium	-	E,R	Ureters, urinary bladder, vesicles	6-13	0 28.5	1, 5, 6, 8, 11, 20, 31
Phyllodistomum superbum	-	A	-	-	-	1
Plagiocirrus primus	-	A	-	-	-	1
Posthodiplostomum minimum	Immature	A	Liver, mesenteries	-	-	33
Rhipidocotyle illense	Metacercaria	R	Urethra, vesicle	-	-	1, 6, 31, 37
Sanguinicola inermis	-	R	-	-	-	1, 31, 37
Sanguinicola volgensis	-	R	-	-	-	1, 31, 37
Sphaerostoma bramae	-	E,R	Intestine	-	-	1, 6, 31, 37
Tetracotyle sp.	Metacercaria	R,A	Kidney, heart, mesenteries	1-27	0-33	3, 5, 33
Tetracotyle ovata	Metacercaria	R	-	-	0-6.6	8
Tetracotyle percae-fluviatilis	Metacercaria	R	-	-	-	1, 31, 37
Tylodelphys clavata	Metacercaria	A	Humor of eye	1-150	25.7	1, 20, 36
Uvulifer amblopitis	Metacercaria	A	Skin	-	-	1, 33
CESTODA						
Acanthocephalus lucii	-	R,E	Intestine	0-9	0-20	3, 34
Bothriocephalus cuspidatus	-	R	-	-	-	1
Cucullanus truttae	-	E	-	-	-	6
Cyathocephalus truncatus	-	R	-	5	-	1, 13, 31, 37
Diphyllobothrium latum	Larval	R,A	Liver, gonads	1-238	70-100	1, 3, 5, 6, 8, 10, 31, 32, 37
Diphyllobothrium sp.	Larval	A	-	-	-	13, 35
Glaridacris catostomi	-	A	-	5	0	13
Paraclon sp.	-	A	-	-	-	6
Proteocephalus sp.	-	E,R	Intestine	0-16	0-13	3, 6, 10, 30
Proteocephalus amblophlites	-	A	-	-	-	6

Table XVIII (continued)

Parasites	Stage of parasite	Geografic location[a]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b]
CESTODA (continued)						
Proteocephalus carnuae	-	R	-	-	-	1, 6, 31, 37
Proteocephalus esocis	-	R	-	-	0-6.6	1, 6, 8, 31, 37
Proteocephalus nematosoma	-	A	-	-	-	1
Proteocephalus percae	-	E,R	-	-	0-20	1, 8, 20, 31, 37
Proteocephalus pinguis	-	A	Intestine	70, 38+	-	1, 6, 13, 14, 30, 33
Proteocephalus stizostethi	-	A	-	-	-	1, 6
Proteocephalus tumidocollus	Immature	A	Intestine	-	-	2
Triaenophorus crassus	-	A,R	Intestine	4-15+	0-60	1, 2, 6, 8, 10, 13, 21, 31, 33, 37
Triaenophorus nodulosus	Plerocercoid, larvae, imago	A,E,R	Intestine	1-86	0-100	1, 2, 3, 4, 5, 6, 8, 10, 11, 13, 20, 21, 28, 32, 33, 36, 37
Triaenophorus robustus	-	A	-	-	-	1
Triaenophorus tricuspidatus	-	A	-	-	-	1
Triaenophorus lucii	Plerocercoid, (immature larvae)	E	Ova	-	-	26, 31
NEMATODA						
Anisakis mucron	Larval	E	-	-	-	1
Ascaris lucii	-	A	-	-	-	1
Cammallanus sp.	-	A	-	-	-	14
Cammallanus lacustris	-	E,R	Intestine	1-24	0-75	1, 3, 5, 6, 8, 20, 31, 35, 37
Cammallanus oxycephalus	-	A	-	-	-	1
Cammallanus truncatus	-	R	-	-	-	1, 31, 37
Contracaecum bidentatum	-	R	-	-	-	1, 31
Contracaecum brachyurum	-	A	Intestine	15, 96+	-	1, 6, 13, 33
Contracaecum cayugensis	-	A	-	-	-	1
Contracaecum osculatum baencalensis	-	Iran	Body cavity	-	36	22
Contracaecum spiculigerum	Adult/larval	A	-	-	-	1
Cucullanus truttae	-	E	Gut	-	-	35
Cystidicoloides tenuissima	-	E	Mocus of stomach	-	-	35
Esocinema bohemicum	-	E	Under serosa of air bladder	Rare	-	25
Eustrongylides sp.	Larval	R	Intestine	-	0-13.3	3
Eustrongylides excisus	Larval	R	-	-	-	1, 31, 37

Table XVIII (continued)

Parasites	Stage of parasite	Geografic location[a]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b]
NEMATODA (continued)						
Eustrongylides mergorum	Larval	R	-	-	-	1, 31, 37
Haplonema sp.	Adult/larval	A	-	-	-	1
Hedrurus tiara	-	A	-	-	-	1
Philometra obturans	Gravid/subgravid	E,R	Blood system, vitreous body	-	0-38	1, 6, 8, 20, 31, 37
Porrocaecum capsularia	Larval	R	-	-	-	1, 31, 37
Raphidascaris sp.	-	A	-	10, 89+	-	13, 14
Raphidascaris acus	-	A,E,R, Iran	Intestine, alimentary tract	-	16-63	1, 6, 8, 10, 20, 22, 31, 37
Raphidascaris canadensis	-	A,E	-	-	-	1, 6, 30
Raphidascaris denudata	-	R	-	-	-	1
Raphidochona denudata	-	E,R	-	-	-	31, 37
Spinitectus carolini	-	A	-	-	-	1, 6
Spinitectus gracilis	Adult/larval	A	-	1	-	1, 6, 13
Spiruridae	Larval	A	-	-	-	1
ACANTHOCEPHALA						
Acanthocephalus anguillae	-	R	-	-	-	1, 31, 37
Acanthocephalus lateralis	-	A	-	-	-	14
Acanthocephalus lucii	-	E,R	Intestine	0-53	3.3-63.5	1, 5, 6, 8, 10, 11, 24, 31, 33
Corynosomum sp.	Larval	E	-	-	-	1
Corynosomum semerme	Larval	R	-	8+	-	1, 10, 31, 37
Corynosomum strumosum	Larval	R	-	4+	0-13.3	1, 6, 8, 10, 31, 37
Echinorhynchus clavula	-	E,R	-	-	0-10	1, 6, 8, 35
Echinorhynchus gadi	-	E,R	-	-	-	1, 31, 37
Echinorhynchus salmonis	-	A	-	-	-	1
Echinorhynchus truttae	-	E	-	-	-	6
Leptorhynchoides thacatus	-	A	Intestine	-	-	1, 6, 33
Metechinorhynchus salmonis	-	R,A	Intestine	-	-	1, 31, 33, 37
Metechinorhynchus truttae	-	R	-	-	-	1, 31, 37
Neochinorhynchus cylindratus	-	A	-	-	-	1
Neochinorhynchus rutili	-	A,E,R	Intestine	Occasionally	0-15	1, 2, 6, 8, 20, 31, 37
Neochinorhynchus tenellus	-	A	Intestine	-	-	1, 6, 33

Table XVIII (continued)

Parasites	Stage of parasite	Geografic location[a/]	Location of infection in host	Number of parasites in host	Degree of infection of population	References[b/]
ACANTHOCEPHALA (continued)						
Neochinorhynchus tumidus	-	A	Intestine	-	-	2
Pomphorhynchus bulbocolli	-	A	-	-	-	1
Pomphorhynchus laevis	-	R,E	-	-	-	1, 31, 35, 37
Pophorhynchus proteus	-	E	-	-	-	1
Pseudoechinorhynchus clavula	-	R	-	-	-	1, 31, 37
CRUSTACEA						
Achtheres percarum	-	E	-	-	-	1
Argulus biramosus	-	A	-	-	-	1
Argulus canadensis	-	A	-	1^+	-	13
Argulus coregoni	-	R	-	-	-	1, 31, 37
Argulus foliaceus	-	A,R,E	-	0-1	0-13	1, 3, 6, 8, 12, 31, 35, 37
Argulus versicolor	-	A	-	-	-	1
Caligus lacustris	-	R	-	-	-	1, 31, 37
Ergasilus briani	-	R	-	-	-	1, 31, 37
Ergasilus folaceus	-	E	-	-	-	4
Ergasilus luciopercarum	-	A	-	1.0^+	-	13
Ergasilus sieboldi	-	E,R	Gills	1-305	0-100	1, 3, 4, 5, 6, 8, 10, 11, 12, 31, 37
Lernaea cyprinacea	-	A,R	-	-	-	1, 31, 37
Lernaea esocina	-	E,R	Gills, skin	-	-	1, 6, 31, 32, 37
Salmincola extensus	-	A	-	$1, 0^+$	-	13
HIRUDINEA						
Hemiclepsis marginata	-	R	-	-	-	1, 31, 37
Piscicola geometra	-	E,R	-	-	-	1, 4, 31, 34, 35, 37
Piscicola milneri	-	A	Fins, external body surface	1^+	-	2, 13
Illinobdella sp.	-	A	Fins	-	-	1. 6. 33
Illinobdella moorei	-	A	-	-	-	1
MOLLUSCA						
Anodonta cygnea	Glochidia	A,R,E	-	25^+	-	1, 8, 13, 35
Unionidae gen. sp.	-	R	-	-	13	1, 10, 31, 37

Table XVIII (continued)

Parasites	Stage of parasite	Geographic location a/	Location of infection in host	Number of parasites in host	Degree of infection of population	References b/
FUNGHI						
Dermocystidium vejdovskyi	-	E	Gills	-	-	1
Saprolegnia sp.	-	E	Eggs	-	-	27

a/ A: North America, E: Europe, R: USSR
+ Average number of parasites in the host

b/ Underlined numbers refer to publications that contain quantitative data about number of parasites in host and degree of infection in population. The numbers refer to the following authors and localities where the parasites were detected

No.	Author	Locality
1	Hoffman (1967)	Waters in North America, Europe and Russia
2	Arthur, Margolis and Arai (1976)	Lakes in Yukon Territory, Canada
3	Kogteva (1961)	Pskov-Chud reservoir, USSR
4	Ergens (1966)	Lipno reservoir, Czechoslovakia
5	Shlyapnikova (1961)	Lake Vyrts'Yaro, USSR
6	Toner and Lawler (1969)	Waters in North America, Europe and Russia
7	Hegemann (1958a)	Greifswald Bodden, German Dem. Rep.
8	Nagibina (1961)	Vygozero, water in Karelia, USSR
9	Davies (1967)	River Lugg, Herefordshire, England
10	Barysheva and Bauer (1961)	Ladoga Lake, USSR
11	Akhmerov and Bogdanova (1961)	Mouth of Eruslan River, USSR
12	Kosheva (1961)	Kutuluk Basin, USSR
13	Watson and Dick (1980)	Southern Indian Lake, Manitoba, Canada
14	Threlfall and Hanek (1970)	Rivers in Labrador, USA
15	Kearn (1966)	River Yare, Norwich, England
16	Ergens (1971)	Mongolia
17	Snow (1974)	Murphy Flowage, Wisconsin, USA
18	Odening and Bockhardt (1976)	Waters in German Dem. Rep.
19	Halvorsen (1968)	Bogsted Lake, Norway
20	Moravec (1979)	Ponds in North Bohemia, Czechoslovakia
21	Lawler (1959, 1960, 1961, 1965)	Heming Lake, Manitoba, Canada
22	Eslami, Anwar and Khatiby (1972)	Caspian Sea, northern Iran
23	Engashev (1964)	Lake Makpaikul (Amu Darya River delta), USSR
24	Mishra (1978)	Shropshire Union Canal, Cheshire, England
25	Moravec (1977)	Waters in Czechoslovakia
26	Aisa (1976)	Italy
27	Bootsma (1973)	Pike hatchery, the Netherlands
28	Chubb (1963)	Llyn Tagid, England
29	Goddard and Redmond (1978)	Stockton Lake, Missouri, USA
30	Woods (1971)	Forrest River, North Dakota, USA
31	Reichenbach-Klinke (1966)	Waters in North America, Europe and Russia
32	Hegemann (1964)	Waters in Germany
33	Dechtiar (1972)	Lake of the Woods, Ontario, Canada
34	Alessio (1983)	Rivers Po, Sesia and Ticino, northern Italy
35	Conneely and McCarthy (1984)	Catchment area, Corrib, western Ireland
36	Üzcelik (1978)	Bodensee (Lake Constance)
37	Bykhovskaya-Pavlovskaya (1964)	Waters in USSR

lakes and found that the most common combinations of fish species were walleye/pike (22%), pike "only" (19%), lake trout "only" (16%) and smallmouth bass "only" (10%). Lake depth and area were variables of greatest significance in distinguishing lake types by discriminant analysis. Lake area was the only gross feature that shed some light on the question why some lakes do not house walleye but only pike.

Tonn, Magnuson and Forbes (1983) used techniques of multi-variate community analysis to reveal distinct patterns among fish assemblages and relate them to the lake's habitat characteristics. Application of this approach to fish assemblages in small lakes in northern Wisconsin resulted in the identification of two assemblage types. Centrarchid-*Esox* assemblages occurred in lakes with high winter oxygen concentrations and in lakes with low winter oxygen where access to a refuge was provided by an inlet or outlet stream or a connecting lake. Low-winter-oxygen lakes without refuges lacked piscivorous fishes, but contained *Umbra*-cyprinid assemblages.

Le Cren, Kipling and McCormack (1977) concluded that in Windermere, numbers and biomass of perch (*Perca fluviatilis*) had been affected by many factors, including climatic conditions and predation of northern pike and merganser (*Mergus serrator*). The main factor producing the changes in the population structure of perch was the intensive trap fishery operated in the lake. Its consequences were long-lasting and have remained apparent for 30 years. They were enhanced and modified by the concurrent fishery for larger pike. In Heming Lake (Manitoba), Lawler (1965) found that the density of yellow perch (*Perca flavescens*) increased when the northern pike population was reduced by netting pike of all sizes.

Kipling and Frost (1972) and Kipling (1984), in their study of the charr (*Salvelinus alpinus*) and pike population of Windermere from the 1940s to the 1970s suggested that the continued removal of large pike has enabled the charr population to increase. Only the mature charr come to the shallow water to spawn in autumn, and it is then that they are captured by northern pike (Frost, 1954). Only the larger pike are able to eat these charr, so the removal of many large old pike has had an effect on the rise in numbers of charr after 1944, the year in which the pike fishery was started.

A definite trend upward in the catches of a net set annually on a charr autumn spawning ground in the lake was evident since pike netting began. Fishermen confirmed this observation (Kipling and Frost, 1972).

Larsen (1966) in his study on food of northern pike in Danish trout streams, concluded that where trout (*Salmo trutta*) and northern pike live in the same stream, predation inevitably causes losses of trout which, according to estimates, is rather severe. The author also found a definite food competition between trout and pike. In Ireland, the numbers of northern pike in trout lakes (Healy, 1956a; Kennedy, 1969) and in rivers (Bracken, 1973) are reduced in order to maintain trout stocks.

Koz'min (1980) mentioned the role of pike as a "biological improver", which reduces the abundance of fish of little economical value. According to the author, pike proves to be of significance for bream (*Abramis brama*) waters in raising the abundance of this species. He considered pike to be important for the removal of sick and injured fish.

According to Hessen (1983) the introduction of small northern pike in a small pond in Norway, stocked with larvae of planktivorous smelt (*Osmerus eperlanus*) resulted in a strong reduction of the smelt larvae. This had effect on the cladocera population, which grew fast, thus affecting the algal biomass. The algae started originally to increase in number in early summer but were then reduced as the cladocera increased.

3.1.3 Sex ratio

The true sex ratio of a northern pike population differs considerably from that of pike caught by different fishing gear (Kipling and Frost, 1970). Moreover, sex ratios of samples of northern pike populations show seasonal trends which indicate varying susceptibility of the sexes to fishing gear during the year (Casselman, 1975).

Males are often reported to be predominant on the spawning grounds (see Table XIX). However, large differences in sex ratio of pike caught in the spawning season are noted by many authors. They can be attributed to differential migration of the sexes to the spawning grounds. Priegel and Krohn (1975) reported from Gilbert Lake, Wisconsin, that relative to their number in the run, males tended to move into and out of the spawning area faster than females. Males may also run in greater numbers and at younger ages (see Section 2.1.6.1) than females. Sukhanova (1979) reported from Vilyuy reservoir (USSR) that during the pre-spawning foraging periods, males predominated slightly over females. The same author reported that males predominated over females (65.4%) on the spawning grounds in Vilyuy reservoir, which is in accordance with data from the Ob river basin. However, reports from the more southern Rybinsk reservoir and the Tsimlyansk reservoir do not follow up with these results.

Seidlitz (1979) observed that after prohibition of the commercial pike fishery with gillnets and other gear in the Edertal reservoir (Federal Republic of Germany), male pike became less dominant in the spring catches than females. The size of the male spawners was also larger than before the fishery had been forbidden.

Table XIX

Sex ratios of northern pike populations

Location	Ratio male/female	Remarks	References
Vilyuy reservoir, USSR	1.89/1	Spawning time	Sukhanova (1979)
Lake Lacha, USSR	6/1-3/1	Varying during spawning season	Koz'min (1980)
Oulujoki River, Finland	5.1/1-3.6/1	Fish tagged in early run to spawning grounds	Lind and Kaukoranta (1975)
Åland (Bothnian Sea, Finland)	1977-82;0.77/1	714 pike samples	Lehtonen (unpublished data)
Lake Warniak, Poland	0.97/1	1^+ to 7^+ caught in seine nets in autumn	Ciepielewski (1981)
Loch Choin, Scotland	1.10/1	Loch treated with rotenone in October; average of total population caught 2^+ to 9^+	Munro (1957)
Slapton Ley, England	0.85/1	Overall sex ratio of pike caught during the year with gillnets, seine nets and electrofishing	Bregazzi and Kennedy (1980)
Windermere, England	0.96/1-1.78/1	Sex ratios obtained from estimates of population numbers of pike 2 years and older from 1944 to 1963	Kipling and Frost (1970)
River Stour, England	1/1: males dominated in age classes < 5 years; 70% of pike older than 5 years were females	Electrofishing (76%), gillnets (6%) and traps (18%)	Mann (1976)
Lough Arrow, Ireland	1.56/1	Northern pike of 1964 yearclass taken by rotenone spraying in May/June 1965	Bracken and Champ (1971)
Lough Arrow, Ireland	1.98/1	Northern pike of 1964 yearclass caught with perch traps in March and April 1965	Bracken and Champ (1971)
Lough Arrow, Ireland	2.66/1; 3.08/1 and 1.24/1	Northern pike of the 1965 yearclass taken in perch traps in September, October and November 1965	
Waters in Ireland	0.86/1	Overall sex ratio 1961-63	Toner (*In* Toner and Lawler, 1969)
Saskatchewan River delta, Canada	1.17/1	Age groups 3 to 7 taken during the summer 1940, 1941	Solman (1945)
Bleury Stream, Quebec	1975: 3.84/1 1978: 8.33/1	Spawning grounds, April	Fortin *et al.* (1982)

Table XIX (continued)

Location	Ratio male/female	Remarks	References
Tributaries to Lake Erie	1/1-3/1	Males were smaller than females	Clark (1950)
Heming Lake, Manitoba	About 0.5/1 but increasing with continued fishing		Lawler (In Casselman, 1975)
Three Ontario populations	Summer: 0.69/1 Winter: 0.79/1 Spring: 0.96/1 Autumn: 1.02/1	Sex ratios for northern pike captured by nets, electrofishing and angling	Casselman (1975)
Upper St Lawrence River	Winter: 0.4/1	Sex ratio of pike caught by angling	Pearce (1961)
Niagara River watershed	1975-76: 3.56/1	191 pike sampled with several catch techniques. Sex ratio biased toward males	Harrison and Hadley (1983)
Murphy Flowage, Wisconsin	0.82/1	Northern pike angled mainly during the summer	Johnson (1969)
Murphy Flowage, Wisconsin	1958-68: 1.27/1 1950-68: 0.78/1	4 498 pike sampled during spring fyke netting 4 225 angler-caught fish (without size limits)	Snow (1982)
Pleasant Lake marsh, Wisconsin	2.8/1-4.0/1 Average 3.2/1	Northern pike netted at the spawning grounds	Fago (1977)
Gilbert Lake, Wisconsin	1968: 2.3/1 1969: 2.0/1	Northern pike netted at the spawning grounds	Priegel and Krohn (1975)
Lake George, Minnesota	1957: 2.15/1 1958: 1.91/1	Northern pike netted at migration to spawning grounds	Franklin and Smith (1963)
Lake Oahe, South Dakota (Reservoir upper Missouri River)	1965: 1.5/1 1966: 1.4/1 1967: 1.7/1 1968: 2.8/1 1969: 1.3/1 1970: 2.4/1	Sex ratios of northern pike taken in standardized trap and gillnets on the spawning grounds	June (1971)
Houghton Lake, Michigan	1939: 2.24/1 1940: 1.25/1 1942: 1.25/1	Northern pike caught at Peterson's ditches, spawning ground of pike in Houghton Lake	Carbine (1943)

Healy (1956) found in samples from three Irish loughs, and Rudenko (1971) in samples from Lake Demenets (USSR) that males were generally more numerous than females in the lower age groups, while females predominated over males in higher age groups. In the Scottish Loch Choin and in Irish waters, males were found to be predominant in catches of 0^+ and 1^+ pike (Munro, 1957; Bracken and Champ, 1971). Kipling and Frost (1970) found equal numbers of males and females in gillnet catches of northern pike in Windermere and concluded that, in view of the higher death rate of males and the selective action of the gillnet, there must have been more males in the youngest age groups.

Ciepielewski (1981) reported from Lake Warniak (Poland) a sex ratio of 1/1 for age groups 1^+, 2^+ and 3^+. In older age groups, however, there was a predominance of females (Snow, 1982). However, June (1971) found that in Lake Oahe, males of age groups 5 and 6 contributed substantially to the spawning stock. The data on overall sex ratio, which are summarized in Table XIX, indicate that females slightly dominate over males at higher ages. In this context it is interesting to note that Lawler (In Casselman, 1975) found that initial gillnetting in Heming Lake, Manitoba, produced sex ratio of nearly two females for every male and that with continued fishing the proportion of females decreased. Kipling and Frost (1970), however, did not obtain comparable results from the analysis of intensive gillnetting activity in Windermere. Initially, males and females were caught in equal numbers, but subsequently (1944-45) females dominated the catches (till 1963-64). It is suggested that the production of three strong year classes in 1957, 1958 and 1959, together with good growth rates, resulted in higher fishing mortality of female pike older than 3 years. Therefore gillnet catches in 1963-64 and 1964-65 were dominated by males.

Casselman (1975) presented sex ratios for about 4 800 pike captured by nets, electrofishing and angling from three Ontario populations. Anglers captured more females than males (1.24/1) than fishermen using other methods (1.14/1). Regardless of method or region of capture, sex ratios showed similar seasonal trends. Males were relatively more abundant during spring and autumn when sex ratios were approximately equal. Often 1.5 to 2.0 times more females than males were present during summer and winter in anglers' catches and net samples. Johnson (1969) reported similar trends in angler catches from Murphy Flowage (Wisconsin). Priegel and Krohn (1975) found in Big Cedar Lake (Wisconsin) that females were consistently more susceptible to angling than males.

Casselman (1975) concluded from the consistency of the trends, indicated by his data, that the frequency of occurrence in the catches reflects intrinsic seasonal activity patterns of the sexes which may be related to growth cycles.

3.1.4 Age and size composition

Anwand (1972) compared commercial catches of northern pike from 11 lakes in the German Democratic Republic and found that age and length composition of the captured pike were correlated with the size of the lakes.

3.1.5 Average abundance and density

Table XX summarizes the data available on abundance and density of northern pike populations from different locations.

Estimation of the abundance of northern pike populations is usually based on the use of the Petersen mark and recapture technique (Ricker, 1975). The application of this technique is tied to conditions concerning mortality, vulnerability to fishing gear, mark losses, distribution patterns, recruitment to the catchable population, and fishing effort. Many authors implicitly assume that these conditions are met in their experiments. Unfortunately, however, it is often questionable whether these assumptions are justified, in view of the selectivity of the fishing gear used, the distribution patterns of marked and unmarked fish, the differential behaviour of marked and unmarked fish toward the fishing gear and the rate of retention of fish marks.

Reliable estimates of density and abundance of 0^+ populations in natural waters are scarce. Most authors report estimates of northern pike in the second yearclass and older, and assumed that the strength of these yearclasses is indicative of the number of fish in 0^+ class. Survival and growth is assumed to be comparable, after the first growth season, for pike belonging to different yearclasses. Grimm (1981, 1983) obtained reliable estimates of 0^+ populations with the Petersen technique, using catch data obtained in intensive fisheries with various types of gear (electrofishing, seine, trawl).

Turner and Mackay (1985) used a stratified systematic sampling regime of detailed under-water observations for estimating the population size in Lake Roi (8 ha, Alberta, Canada). The pike concentrated in depths of less than 1 m and their distribution pattern remained constant throughout the summer months, thus justifying the stratified methodology utilized in the population estimate.

Pollock and Mann (1983) published an age-dependent generalization of the Jolly-Seber mark-recapture model for fish populations based on birth rates, death rates and migration. The model was illustrated using data from studies of northern pike populations in Dorset (Mann, 1980, 1982).

Kipling and Frost (1970) estimated population numbers of pike in Windermere from 1944 to 1963, based on yearclass strength between 1941 and 1961 and on catch data from

Table XX

Data on the standing stock of northern pike from different locations

Location	Area (ha)	Year/ ages/ length	Standing stock Number/ha (range)	Standing stock kg/ha (range)	Comments	References
Lake Demenets (USSR)	6.6	-	45.6	13.3	-	Rudenko (1971), Gulin and Rudenko (1973)
Klicava reservoir (Czechoslovakia)	67.0	1957/>age 1 1964	7.9 2.6	6.9 2.3	- -	Holcík (1968)
Lake Warniak (Poland)	38.4	1969 2-9 years	33.0	22.3	Estimates based on DeLury method, biased by sampling errors	Ciepielewski (1973)
Lake Warniak (Poland)	38.4	1969-76 2-7 years	20.8-79.6	10.0-40.6	Estimates based on virtual population	Ciepielewski (1981)
Lake Windermere (England)	14 800 stock related to 550 ha with depth less than 10 m	1944 1944-59 1960-68 1969-78 age 2 years and older	4.2 2.5-6.2 3.5-8.0 2.4-4.4	10.2 4.5-8.5 3.8-9.8 3.3-6.3	May estimates, north and south basin and males and females together. Paloheimo method	Kipling and Frost (1970), Kipling (1983a)
Slapton Ley, Devon (England)	90.6	> 45 cm	10.1 (5.3-13.9)	22.6 (11.9-31.3)	Biased estimate in view of tag loss and long marking period	Bregazzi and Kennedy (1980)
Loch Choin (Scotland)	26.3	> 20 cm	79.0	5.4	Recoveries after rotenone reclamation	Munro (1957)
Dubh Lochan (Scotland)	10.0	Adults, 1967 1968		7.8 3.9	Estimates based on mark-recapture. Schnabel estimates	Shafi and Maitland (1971)

Table XX (continued)

Location	Area (ha)	Year/ ages/ length	Standing stock Number/ha (range)	Standing stock kg/ha (range)	Comments	References
Northern part of the Archipelago Sea (SW Finland)	166 800	1978/2 1979/2 1980/2	1.5 1.4 1.1	1.3 1.3 1.2	Estimates based on virtual population analysis	Lehtonen (data from Finnish research)
Four mesoeutrophic water bodies in the Netherlands:						Grimm (1981); 1903; 1983a)
Jan Verhoefgracht (1974-81)	4.5	0^+ 0^+-54 cm $\geq$ 54 cm	- - -	5.8-33.0 101.0-136.6 54.1-115.2	Standing stock is related to the vegetation	
Fortgracht (1974-79)	3.5	0^+ 0^+-54 cm $\geq$ 54 cm	- - -	5.7-28.9 89.2-118.0 71.4-255.4		
Kleine Wielen (1975-81)	40.0	0^+ 0^+-54 cm $\geq$ 54 cm	- - -	0.8-48.0 120.3-170.0 27.8-73.7		
Parkeerterreinsloot (1975-79) (small ditch)	0.3	0^+ $> 0^+$	- -	8.1-43.0 100.9-180.8		
Lakes in Illinois and Minnesota	-	-	-	9.2 (0.01-24.4)		Carlander (1955)
Two lakes in Minnesota	-	> 35.5 cm	29.4 46.0	- -		Seaburg and Moyle (1964)
Murphy Flowage (Wisconsin)	73.0	1955-63 > 25 cm	5.9-33.9	5.0-19.8	Standing stock before stocking pike (see Section 4.2.3)	Snow (1974)
Escabana Lake (Wisconsin)	119.0	1959-77 > 25 cm	6.9 (2.1-10.1)	5.5 (1.9-9.9)		Kempinger and Carline (1978, 1978a)

Table XX (continued)

Location	Area (ha)	Year/ ages/ length	Standing stock		Comments	References
			Number/ha (range)	kg/ha (range)		
Bucks Lake (Wisconsin)	34.0	> 25 cm	67.5 (30.6–121.8)	27.3 (14.9–41.2)	Spring estimates	Snow and Beard (1972)
Bucks Lake (Wisconsin)	34.0	> 25 cm	89.2 (66.5–125.0)	37.0 (32.5–47.6)	Fall estimates	
Daggett Lake (Michigan)	5.0	0^+ (35.1 cm) 1^+ (47.8 cm) 2^+ (48.8 cm) 3^+ and older (70.4 cm)	2.0 3.6 59.6 2.6	0.7 2.5 40.6 5.4 Total 49.2	Lake stocked 3 successive years with 135 fingerlings (about 8 cm)/ha. Water covered with 50% *Elodea*; bluegills as prey fish	Beyerle (1971)
Daggett Lake (Michigan)	5.6	0^+ (22.0 cm) (natural) 0^+ (31.2 cm) (stocked) 1^+ (44.7 cm) 2^+ (51.3 cm)	135.9 19.5 42.9 65.9	7.2 2.5 17.8 41.4 Total 68.9	Lake stocked 3 successive years with 120.5 fingerlings (about 8 cm)/ha. Water covered with 50% or more *Elodea* and other water plants; minnows as prey fish	Beyerle (1973)
Emerald Lake (Michigan)	2.3	0^+ (27.2 cm) 1^+ (40.1 cm) 2^+ (45.7 cm)	10.0 0.9 27.0	1.0 0.3 38.0 Total 39.3	Lake stocked 3 successive years with 109 fingerlings (about 8 cm)/ha. No aquatic vegetation; bluegills as prey fish	Beyerle (1971)
Emerald Lake (Michigan)	2.3	0^+ (25.9 cm) 1^+ (47.8 cm) 2^+ (57.9 cm)	4.8 12.2 34.3	0.6 7.2 46.3 Total 54.1	Lake stocked 3 successive years with 109 fingerlings (about 8 cm)/ha. Aquatic vegetation "essentially non-existent". Prey fish minnows, in 1971 coho salmon	Beyerle (1973)

Table XX (continued)

Location	Area (ha)	Year/ ages/ length	Standing stock		Comments	References
			Number/ha (range)	kg/ha (range)		
Wisconsin lakes			6.2-7.4	-	-	Priegel and Krohn (1975)
River Pilica (Poland)		age 0-5	26.0	9.3	-	Penczak, Zalewski and Molinski (1976)
River Pilica (Poland)	2.5	age 0-3	11-12	1.2	-	Mann and Penczak (1984)
River Vistula (Poland)		age 1-9	-	1.8-2.4	-	Backiel (1971)
Oulujoki River (Finland)		> age 2	4.5	7.2	-	Lind and Kaukoranta (1975)
River Nene (England)		age 1-6	200.0	115.0	-	Hart and Pitcher (1973)
River Stour (England)		age 1-10	61.0 (21-127)	45.8 (15.9-95.6)	June estimates	Mann (1980)
River Frome (England)		age 0-10	159.0 (127-227)	68.6 (55.4-94.3)	June estimates	
Plover River (Wisconsin)		-	-	28.9	-	Paragamian (1976)
Saskatchewan River delta (Canada)		-	66.7	-	-	Solman (1945)

gillnets between 1944 and 1965. The authors used the Paloheimo (1958) method which implies estimation of average mortalities for the population. In view of the selectivity of the gillnets, calculations were made for males aged 6 years and older and for females of 5 years and over. Gillnet mortality for younger pike was assumed to be higher than for older fish. Kipling and Frost (1970) also determined the virtual population number of pike in Windermere. This provided absolute minimum figures of the number of pike which had been alive in the lake. Kipling (1983a) used both the Paloheimo (1958) method and the determination of the virtual population in her analysis of the abundance, density and structure of the population of northern pike in Windermere from 1944 to 1980.

From the analysis of 2 952 pike caught by gillnets in Windermere in the period from 1961 to 1971, Bagenal (1972) concluded that many settings of gillnets were required to obtain a reliable mean catch. This implies that trends in the catch patterns of pike do not necessarily reflect trends in population numbers. Therefore, interpretations of population processes based on catch data must be considered with caution.

The population estimates of pike in Windermere, based on tag recapture (metal loops in the jaw - Kipling and Le Cren, 1984), were biased by variation in growth from year to year, as in some years certain age groups were included and in other years not. Therefore, the estimates were not consistent. Without background knowledge of growth and gillnet selection such results can be misleading.

3.2 Population Dynamics

3.2.1 Population abundance and density

3.2.1.1 Effects of fishing

Sumari and Westman (1969), Donetz (1982) and Svärdson (1964) observed that fishing generally increases the density of pike populations and decreases the average size of northern pike. In cases where adequate spawning grounds are available, it is impossible to remove all pike from a water body by fishing. Similar conditions were reported from Ireland; the annual report of the Irish Inland Fisheries Trust Inc. (1977) stated that large-scale removal of northern pike from Irish waters did not result in the disappearance of the species. In Ireland, the numbers of pike in trout lakes are reduced in order to maintain trout stocks (Fitzmaurice, 1978; Kennedy, 1969). It was found that in small lakes only complete, virtually complete eradication of pike by means of rotenone enabled trout to survive. In the big Irish limestone lakes, however, it is possible to reduce pike stocks sufficiently by using gillnets, longlines and wire traps. Treatment with rotenone has proved to be a method for reducing the numbers of a few-weeks-old pike. According to Bracken (1973), electrofishing reduces pike numbers in Irish rivers.

Mills (1964) reported a decrease in average weight of pike caught by gillnetting in River Bran (Scotland). The length frequency data of pike caught in several years suggested that the decline of the 0^+ age group was the effect of fishing with the gillnets.

Frost and Kipling (1967), Kipling and Frost (1970, 1972), Kipling (1983, 1983a) and Bagenal (1977) described the effects of fishing on the northern pike population in Windermere, where each year about one third of the population of fish over 55 cm was captured with gillnets, and a further 9% were accounted for by anglers or found dead. The effect of fishing in Windermere on the pike population was that in most years, young pike aged under 4 years, were relatively more abundant than previously. The quantitative changes in the pike population in Windermere from 1944 to 1981 were described by Kipling (1983a) as responses to temperature conditions during the summer months, predation pressure during the first year of life (see Section 2.3.4.3) and availability of perch as food fish.

Otto (1979) studied size structure of northern pike caught during 7 years in intensive fishery with gillnets and bownets in a small Swedish lake. The average size of pike in the catches was reduced in the years of the study. The proportion of large individuals in the catch decreased in the early years of the fishery, while the relative numbers of smaller individuals increased in the later years. The study showed that a fishery can have an effect on the size structure of northern pike populations. The effects on density and abundance of pike populations, however, cannot be assessed from the catches because data on the selectivity of fishing gear are not available. Data on the efficiency and intensity of the fishing effort in the years of the study are also lacking. Furthermore, it is doubtful whether catch data can be used for accurate stock assessment purposes (Bagenal, 1972, 1979; Kipling, 1975).

Lawler (1959, 1960, 1961, 1965) and Campbell (1982) described the effects of intensive fishing in Heming Lake (Manitoba) on the catch composition of northern pike. Data on this fishery are summarized in Table XVI. They show that the frequency of pike larger than 46 cm in the catch decreased sharply in the years of very high fishing effort (1956-60). In these years, the average size and weight of pike caught in index nets decreased, as is also shown in Figure 31. When intensive fishing was stopped in Heming Lake (1961), the average size and weight of pike caught in index nets increased. These variations in size composition of the catches are indicative of changes in the structure of the northern pike population as a result of fishing.

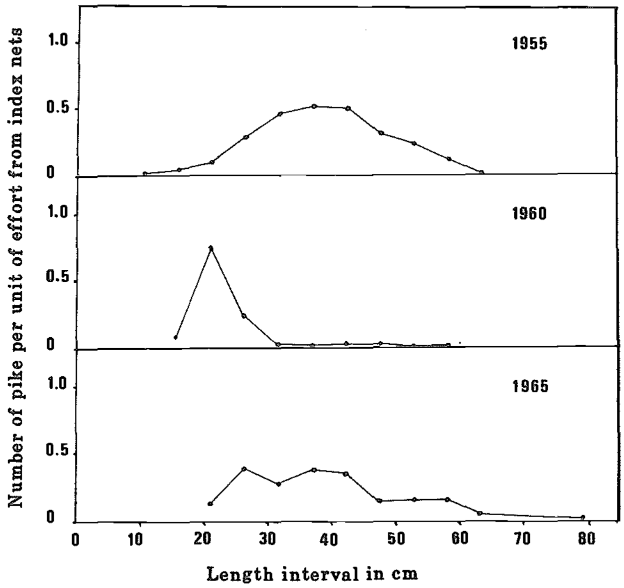


Figure 31 Gillnet catches from Heming Lake, Manitoba, from index nets, 1955, 1960 and 1965. (After data furnished by Campbell, 1982)

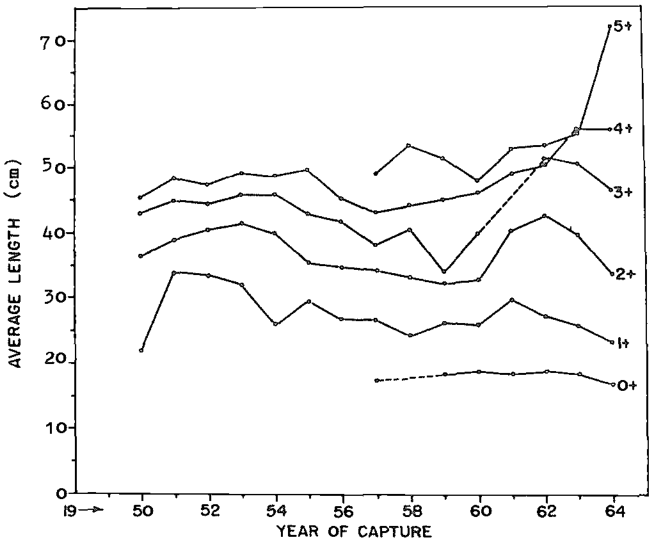


Figure 32 Annual average length of Pike of various ages during the period 1950-64 in Heming Lake, Manitoba. (After data furnished by Campbell, 1982)

The catch results from Heming Lake do not furnish reliable data on changes in density of northern pike populations as a response to intensive fishing. If catch per unit effort can be taken as an index of the density of the pike population, the data show a decrease in numbers, owing to intensive fishing in 1956-60. After intensive fishing effort was stopped, the catch per unit effort increased sharply, indicating increased density of the northern pike population in the lake. However, catch per unit effort data are biased by the fishing effort and therefore the results obtained in years of intensive fishery do not furnish a reliable measure of the population density.

The decline in the proportion of large pike in the Heming Lake population in the years of intensive fishing possibly induced increased growth activity of the remaining larger pike (see Figure 32). Soon after the intensive fishing pressure on the pike population was reduced, average growth of the larger pike resumed its former lower level.

The effect of the commercial fishery in Lough Erne (northern Ireland), a 15 300-ha eutrophic lake with an outstanding fishery, was studied by Malley and Brown (1983). Sampling by electrofishing over nine miles of shoreline showed that the relative density of 0^+ pike in an area where the commercial fishery took place was reduced by 75% when compared with the relative density in an area where commercial fishing was not permitted. The numbers of pike larger than 25 cm, caught per 100 m^2 by netting and electrofishing from July to September, were much lower in the commercial area than in the sanctuary of Lough Erne.

Lebedev (1962) analysed fish fossils from archeological finds which permitted a determination of the character of the fish fauna before intensive fishery affected its composition. Maximum size and age of the fish were approximately the same as for present-day fish. However, the average sizes of the pike, white bream (Blicca bjoerkna), bream (Abramis brama), perch (Perca fluviatilis) and pike perch (Stizostedion lucioperca) were larger in the early settlements than they are at present.

3.2.1.2 Effects of vegetation and eutrophication

Vegetation is a factor of major importance for the distribution of the species (Section 2.7.4). The spatial structure and the species composition of the aquatic vegetation determine the quality of the vegetation as northern pike habitat. The density, abundance and structure of northern pike populations are influenced by the quality of the vegetation (Makowecki, 1973) and by the seasonal changes that take place in the spatial structure of the aquatic plants.

Threinen (1969) concluded in a literature survey that the extension of adequate habitat is proportional to the strength of the pike population.

Decline of northern pike populations related to decreases in aquatic vegetation are reported from various locations. Barthelmes and Waldow (1978) described the changes in the catch composition that took place in the Grosse Müggelsee, near Berlin, as a result of eutrophication. Drastic decreases of reed along the border of the lake, and almost complete disappearance of pike and tench (Tinca tinca) from the catches, were related. The contribution of pike perch (Stizostedion lucioperca) to the catches increased from 0.4 kg/ha per year to 10 kg/ha per year. Decline of northern pike populations owing to eutrophication is also reported from Slapton Ley (Bregazzi and Kennedy, 1980), from the Veluwemeer in the Netherlands (Hartmann, 1977; Willemsen, 1980), and from Hsälmaren in Sweden (Svärdson and Molin, 1981).

In Lake Constance, development of eutrophication since the 1940s resulted in a ten-fold increase of the phytoplankton production. The phosphorus content of the water changed from less than 1 mg/m^3 in 1935 to 70 mg/m^3 in 1974 (Deufel, 1975). Charaphytes that were found in the 1930s until depths of 25 m, had practically disappeared. Along the lake shore, the area with Potamogeton vegetation vastly increased, especially P. pectinalis. The large-leaved Potamogeton species, however, decreased from 435 ha (1967) to 160 ha (1978) (Löffler, personal communication). The reed belt along the lake shore declined in quantity and quality by the effects of eutrophication and by the development of the shore for recreational and industrial activities (Deufel, 1978). The data on fishery in Lake Constance (Nümann, 1973, 1975) indicated that the changes in aquatic vegetation, together with the changes in the fishery (decline in number of commercial fishermen, higher fishing intensity due to the use of better netting material, increase in sportfishermen), were responsible for the declining catches of northern pike. However, the reliability of catch statistics from Lake Constance is also questionable because since the last years only part of the catches has been registered.

Hurley and Christie (1977) suggested that the collapse of northern pike catches in the Bay of Quinte (northeast margin Lake Ontario) was caused by fishing pressure combined with low water levels of the Bay in the mid 1930s. Cultural eutrophication at that time was not serious. The macrophyte beds decreased in density due to eutrophication in the late 1950s. Therefore, reduction in aquatic plants was considered to be responsible for the fact that the northern pike contribution to the catch remained low.

In Oneida Lake (New York), dense stands of emergent vegetation that occupied much of the shoreline as late as 1927, disappeared. According to Forney (1977), emergents were sparse in 1946 and by the 1950s only remnants of the once vast beds remained. The lake can be characterized between meso- and eutrophic. According to Forney (1977), the northern pike population remained low in the lake after the winter 1945-46, which implies that stocking of pike, which were reproduced in spawning marshes (Forney, 1968), did not substantially increase the pike population in Oneida Lake.

Drastic decreases of submerged vegetation and increased transparency of the water, the result of intense stocking of phytophageous fish and carp, was probably the main cause of the catastrophic reduction of the northern pike population in the pond-like-type Lake Warniak, Poland (Ciepielewski, 1981). Young yearclasses deprived of vegetation in the shallow litoral, found adverse living conditions and thus were subject to greater pressure by predators. The exploitation of northern pike in the lake accelerated the decline of the population. A similar situation was found in Murphy Flowage (Wisconsin). Elimination of aquatic vegetation by winter drawdown of the water level (Beard, 1973), resulted in reduction of the population of small pike (Snow, 1974, 1978).

3.2.1.3 Effect of availability of prey

Snow and Beard (1972) found no relationship between the variation in abundance of northern pike in Bucks Lake (Wisconsin) and increases and decreases in food fish from year to year. In Murphy Flowage (Wisconsin), Snow (1978) found a significant relationship between estimated abundances of northern pike and of its main prey (bluegill, Lepomis macrochirus) three years later. The author considered that, except when northern pike densities were artificially high (stocking), availability of suitable forage was the most important determinant of population density in Murphy Flowage.

According to Grimm (1983), differences in prey fish abundance in four water bodies in the Netherlands were not reflected in the standing stocks of pike smaller than 54 cm, which indicates, according to the author, that the abundance of prey fish did not influence the density of the pike populations. The author, however, suggested that the changes in availability of prey fish to northern pike during the summer influences competitive and predatory interactions between pike belonging to different size classes.

Pitcher (1980), in comparing the density of pike in Windermere (Kipling and Frost, 1970) with that in the River Nene, suggested that pike density may be limited by visibility of both prey schools and other pike. The density of pike in Windermere, with much less turbidity than the enriched Nene water, was much lower than that estimated for the Nene. Comparison of density data is difficult however, in absence of a reliable estimate of the pike habitat in both waters.

3.2.1.4 Effect of winterkill

Mortality of pike under ice as a result of low oxygen conditions (see Section 2.7.6) can result in changes in the population structure. High mortality among pike during the winter is counterbalanced by the high fertility of the surviving spawners. Data supplied by Grimm (1983) illustrate the effects of winterkill on the population structure of northern pike in a small shallow water in the Netherlands (see

Figure 33). According to Casselman (In Smith, 1986) winter oxygen depletion in a small lake on Manitoulin Island, Ontario, resulted in losses of 81% of pike longer than 20 cm. Only few specimens spawned during spring after the winterkill, so that the northern pike population remained low for at least one year.

3.2.2 Natality and recruitment

3.2.2.1 Reproduction rates

Various sections of chapters (2.1 and 2.2) in this synopsis deal with factors influencing the development and survival of fertilized eggs of northern pike under natural conditions. Although they do have effects on the population structure, most studies only furnish circumstantial evidence because methodical and interpretative difficulties prevent quantitative assesment of the effects of the various factors on population level.

3.2.2.2 Factors affecting reproduction

The availability of spawning grounds is reported to be a factor of influence on the success of spawning. From reservoirs, lakes and rivers, it is reported that high and stable water levels in spawning time and for at least one month after spawning, have a positive influence on the reproduction of northern pike populations (see Section 2.1.6 and Johnson, 1956; Hassler, 1970; Nelson, 1978; Rundberg, 1977; Threinen, 1969; Groen and Schroecker, 1978; Fortin et al., 1982; Gaboury and Patalas, 1984; Gravel and Dubé, 1980). Holcík (1968) found in the Czech Klícava reservoir that the age composition of the northern pike population showed the influence of water level during the spawning period as well as the spawning condition in different years. New reservoirs typically produce strong yearclasses of pike only when spring and early summer water levels are high enough to flood terrestrial vegetation. This condition usually exists during the filling phase of reservoirs (Sumari and Westman, 1969; Backiel, 1985; Holcík, 1968; Holcík and Pivnicka, 1972; Hassler , 1969, 1970; Beckman and Elrod, 1971).

Kuznetsov (1972) reported that the spawning of pike under the conditions of the Kuybyshev reservoir (USSR) is effective only in the years when the water level in spring is high, and shallows bearing the vegetation of the previous year or growing vegetation are inundated. Kuznetsov (1980) and Poddubny (1976) concluded that the first years of the existence of the

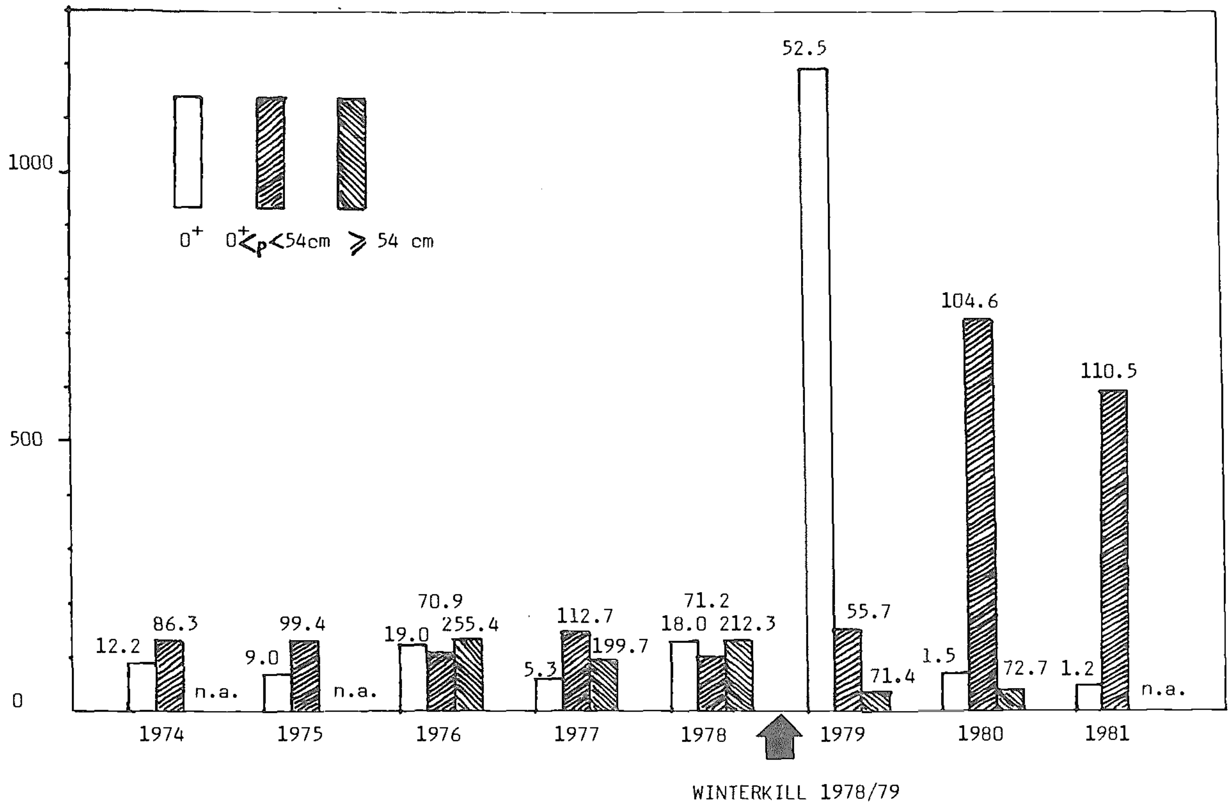


Figure 33 The structure of the northern pike population in the 4 ha shallow water Jan Verhoeffgracht, Maarsseveen, Netherlands, at the end of the growing season, from 1974 to 1981. The histogram shows estimated biomass of distinguished pike classes per hectare aquatic vegetation expressed in numbers. (Data from Grimm, 1983a)

reservoir were favourable for production and growth of pike. The reproductive conditions deteriorated strongly as a result of sharp reductions in water level during the spawning period. The authors observed that as a reaction, the population tended toward prolongation of the spawning time and laying eggs under different temperature conditions.

An increase in productivity at all trophic levels has been frequently observed in new reservoirs. Pike growth rates generally are highest in the early years of a reservoir because of increases of water nutrients and forage fish (Hassler, 1969; Nelson, 1974; Holcík and Pivnicka, 1972; Svärdson, 1976; Backiel, 1985). The duration of the trophic surge for pike varies among reservoirs.

Bodaly and Lesack (1984), in their study of the effects of impoundment in Wupaw Bay, Southern Indian Lake, Manitoba, found no evident changes in the northern pike population. Wupaw Bay increased in area by only 9% as a result of impoundment, one of the smallest increases in surface areas for basins of Southern Indian Lake. Moreover, the influx of nutrients and the effects on flooded terrestrial vegetation were much smaller than is commonly observed in newly created reservoirs.

Popova (1966) and Orlova and Popova (1976) concluded that the sharp fall in the level of the Caspian Sea during 30 years and the regulation of the Volga flow, which began in 1956, have led to substantial changes in the ecological conditions in the Volga delta. The living conditions for young pike and tench (Tinca tinca) became impoverished, as did the conditions for their spawning and early development. Heavy shoaling in the pre-estuarine region and utilization of this new habitat have led to a significant improvement in the biological indices of adult predators in that region compared with the lower zone and to a sharp increaser in the numbers of predators throughout the entire delta.

Poddubny (1976) described the development of the ichthyo-fauna since the formation of the Rybinsk reservoir (USSR) in the early 1940s (see Figure 34). The reservoir fills up from April to June and has a decreasing water level during the rest of the year. The coastal areas in general do not succeed in growing surface vegetation. In the very first year of water impoundment, catches of pike increased sharply relative to the catches of other species. This was explained by the mass migration of fishes from the reservoir in the zone of flooding to the river reaches and to the coastal zone of the lake. Simultaneously, a high yield of 0^+ pike was obtained. In 1947, pike covered the entire coastal belt of the littoral zone in the lake reach of the reservoir: the low-lying depressions of the reaches and the estuaries. The largest accumulation of different-aged individuals was recorded in the estuarian part of the shallow waters beyond the protective flooded forest wall. The distribution of pike at that time was greater than at any other period in the history of the reservoir.

Until 1953-54, the distribution area of the pike was markedly reduced, which is explained by the reduction of protected coasts. The catches nevertheless remained fairly high. Young pike were found in comparatively large quantities in nearly all parts of the protected coasts in which a vegetation zone was preserved. The reproductive rate of pike was on the whole much lower than in the initial years of water impoundment.

The spawning of pike is generally successful in the Rybinsk reservoir, and eggs develop normally even under significant temperature fluctuations. The increase in population density of pike was therefore attributed to the drying up of parts of the reservoir where young pike were distributed.

After the decomposition of the flooded forests and the levelling of the bottom of the coastal zone that dried up with decreasing water level, a sharp reduction in the spawning area of pike and the feeding places of young pike occurred. In 1967, only the river reaches and the small creeks in the lake part of the reservoir, which are protected from the influence of waves, were used by pike as primary habitats. The distribution of young pike shows that effective spawning is very limited in the reservoir.

An analysis of the reproductive potential of the northern pike population in Windermere (Craig and Kipling, 1983) indicated a population response to decreasing density and abundance of pike. Although the authors concluded that there was a relationship between relative fecundity of pike and stock biomass two years before spawning, they found no relationship between estimated number of eggs laid by fish and number of fish recruited at age 2 years resulting from these eggs. The authors concluded that responses of the pike population by changes in fecundity, mortality or growth cannot prevent wide fluctuations in recruitment caused by abiotic factors, although they could modify them. Domanevskii (1963) came to similar conclusions for the pike population in the Tsimlyan reservoir (USSR).

3.2.2.3 Effect of vegetation on recruitment

Fortin et al. (1982) suggested that the temperature-influenced development of aquatic vegetation can be a factor influencing the strength of a yearclass. The retarded development of vegetation in a sector of the Canadian Haut Richelieu River in 1977 and the subsequent development of a weak yearclass were arguments for the hypothesis that cannibalism may have a strong influence on yearclass strength.

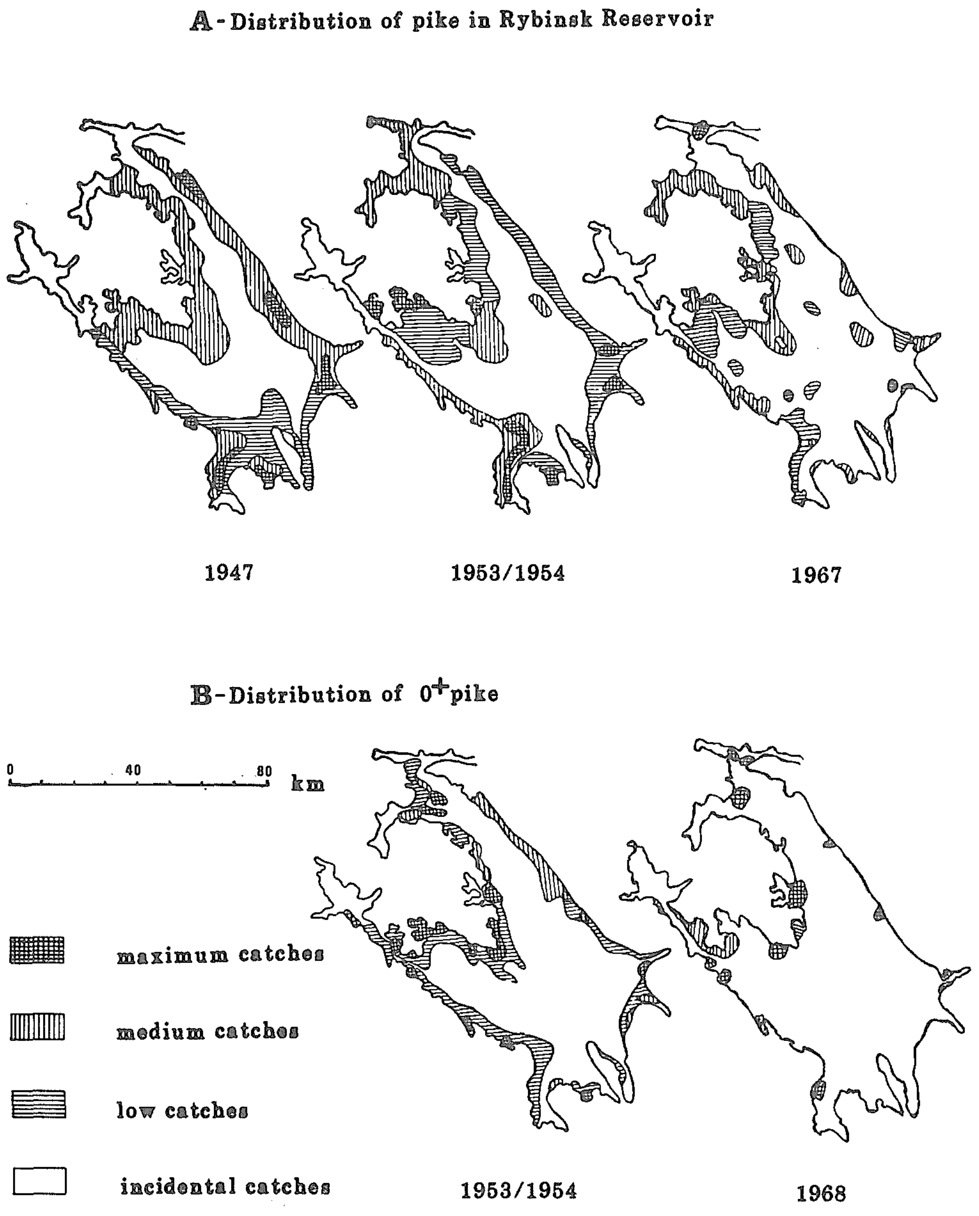


Figure 34 Distribution of pike in Rybinsk Reservoir (USSR) since impoundment in the early 1940's. (Redrawn after Poddubny, 1976)

High densities of northern pike populations in the English River Frome and the River Stour (Dorset) were related by Mann (1980) to abundance of several species of forage fish, and extensive growth of aquatic plants which provide shelter for young pike.

Experiments with pike of single size classes stocked in drainable ponds suggested that vegetated shore length was a factor governing the abundance of the 0^+ pike (Grimm and Riemens, 1976).

Grimm (1981, 1983, 1983a) investigated the structure of northern pike populations during several years at the end of the growth season in four meso-eutrophic waters in the Netherlands. The author related pike numbers and biomass to the area with aquatic vegetation at the onset of the sampling period. From the results it was concluded that the carrying capacity of northern pike in the length range 0-54 cm (forklength) per hectare of aquatic vegetation was between 80 and 150 kg. The strength of the 0^+ yearclass (in biomass) was found to be governed by the carrying capacity of the pike habitat and the biomass composition of the size classes of larger pike, distributed in the same habitat.

3.2.2.4 Effect of interactions among pike on recruitment

Generally, the first steps of development of northern pike take place in shallow waters with dense vegetation, i.e., difficult to access for large pike and spatially separated from the areas where large pike are foraging. In these areas, predatory pressure of larger pike remains low. Availability of food and the need for space may be factors influencing the control of density of the developing northern pike population on the spawning grounds.

From the data available on cannibalism among 0^+ pike which are summarized in Section 2.3.4.3, it can be concluded that the small pike themselves are responsible in a large measure for the reduction in numbers observed during the first months of development. When pike reach a length of 4 to 6 cm, their food habits become mainly piscivorous. These pike forage in the same habitat as larger pike with which they share increasingly the same food resource. Therefore they become more vulnerable to interactions with larger pike.

Depending on the age composition of the population, even very low cannibalism rate can cause significant mortality (Fox, 1975). To illustrate this fact, Le Cren (1965) used Frost's (1954) data for estimating the consequences of cannibalism on 2-year old pike in Windermere. By taking into account the age distribution (1.5 2-year-olds; 1.0 4-year-olds) and the fact that smaller pike made up about 1% of the diet of large pike, and by assuming that a 4-year-old pike ate 50 fish of all species in a year, he calculated that cannibalism could account for the total mortality in the younger yearclasses of pike.

Beyerle's (1971, 1973, 1978) experiments in Michigan showed the importance of the structure of pike populations for the strength in numbers of the 0^+ class. The author showed that survival of northern pike fingerlings (about 8 cm), stocked for three consecutive years in two small lakes that were treated with rotenone before the experiments started, was highest for the pike stocked in the first year of the experiment and lowest for the pike stocked in the third year. Survival of pike stocked in the second year was relatively low (see Table XX).

The pike in the experiments in the two lakes used both bluegills (Lepomis macrochirus) and minnows (Pimephales promelas and Notemigonus crysoleucas) as prey fish. The results indicated that the survival of northern pike fingerlings was also influenced by the availability of prey fish. The data from Beyerle's (1971, 1973) experiments also suggest that in absence of aquatic vegetation (Emerald Lake), the total standing stock of the pike population is lower and survival of all age groups is relatively lower, compared with stock density and survival in the lake with vegetative cover (Daggett Lake).

Fortin et al. (1982), Mann (1982), Kipling (1983, 1983a) and Grimm (1983, 1983a) concluded that the 0^+ population is strongly influenced by predatory pressure of larger pike. Availability of food to pike in the first year of life is, according to Kipling (1983a), a factor that can influence the predation pressure. She stated that from 1969 to 1978 the main food item of pike in Windermere, perch, Perca fluviatilis (Frost, 1954; Allen, 1939), was only scarcely available. Fast growth of perch and almost complete elimination of the perch population by a disease deprived the young pike of prey of a critical size. Under these circumstances cannibalism became a major factor in the survival of the pike population. Before 1969, yearclass strength of pike was dominantly influenced by temperature in the first summer after hatching (Kipling, 1983a; and Craig and Kipling, 1983).

The studies of stomach contents of northern pike also furnish evidence that cannibalism may be a factor in the regulation of pike numbers (see Sections 2.3.4.5 and 2.4.8). Incidence of cannibalism and availability of food fish are related. The studies are inconclusive as to seasonal trends in cannibalism, and they also furnish no data on the relative importance of intraspecific predation as a factor influencing the structure, density and abundance of northern pike populations.

Fortin et al. (1982) found a relationship between indices of yearclass strength, indicating that the strength of any yearclass was negatively related to that of the preceding year. The authors interpreted this relationship as an effect of cannibalism which takes place in early summer and when the young pike leave the spawning grounds to congregate in the summer habitat of the pike in the main course of the Haut Richelieu River. Yearclass strength was assessed by the method of Johnson (1956). The relative contributions of fish of a yearclass (ages 2-5) to the gillnet catches were added over successive years. In the above-given interpretation the authors therefore assumed that survival of pike during its early development was similar to the successive yearclasses.

Yearclass strengths of 2-year-old pike observed in Lake Windermere over 34 years (Kipling, 1983a) were not related to each other. The same results were obtained when numbers or biomasses of 0^+ in four Dutch waters (Grimm, 1983, 1983a) over successive years were related with one another.

Grimm (1981, 1983, 1983a) concluded from negative relationships between the biomasses of size classes at the end of the growth season that the structure of northern pike populations was the result of interactions between pike of different size classes. The biomass composition of size classes at the end of the growth season is, according to Grimm (1983, 1983a), the result of an autoregulation of the species. The author considers that the biomass of small pike smaller than 41 cm (0^+ pike) is determined by the biomass of the larger pike in the vegetated areas.

3.2.2.5 Forecasting yearclass strength

Franklin and Smith (1963) and Forney (1968) suggested that the strength of a yearclass depended on the production of large juvenile pike migrating from the nursery areas. Franklin and Smith (1963) found that the abundance of 1-year-old pike caught with a seine net in the period from June to November in Lake George (Minnesota), was related to the number of pike that were 3.5 cm and larger, and had migrated the year before from the spawning marsh. Forney (1968) based his finding on the high incidence of pike that originated from larger migrants (over 6.5 cm) from a spawning marsh in the recaptures in Oneida Lake (New York). The sampling methods used, however, are not reliable enough to obtain representative measurements for determining the strength of a yearclass. It is also doubtful whether the relative contribution of the different sizes of migrating 0^+ fish to the yearclass was adequately assessed. Pike from the managed marsh in Oneida Lake (1964-66) at least did not contribute to a recovery of the population in the lake. Forney (1977) reported that pike remained scarce after the decline of the population in the winter 1945-46. This decline can be related to increased eutrophication of the lake.

According to Mills and Mann (1985) pike yearclass strengths in Dorset rivers showed less variation than those of cyprinid populations. The extremes represented only a 2.8 fold variation. The two best yearclasses were those resulting from years in which 0^+ pike reached the largest overwinter size, but no overall significant correlation was found. The three coolest summers produced the poorest yearclasses. The strongest yearclass occurred in the year of average temperature. Mann (1985) concluded that there was no relationship between the size of the adult population and subsequent yearclass strength. Environmental conditions, especially water temperature and river flow were the most influential factors in recruitment.

Kipling and Frost (1970) found, from an analysis of the catches of northern pike made over 20 years in Windermere, that yearclass strength (estimated at age 2 years) was highly correlated with temperature conditions in the first six months of that yearclass. The determining factor in most years appeared to have been the growth during the first six months of life, which was closely associated with temperature conditions in the lake. In her analysis of catches made over nearly 40 years in Windermere, Kipling (1983, 1983a) concluded that availability of food and cannibalism were also factors of determining influence on the strength of a yearclass. When food supply for northern pike was low, its growth did not respond to temperature conditions.

Kipling (1983) drew a more general conclusion from her study of northern pike populations in Windermere in the form of a warning to those studying natural ecosystems. "Having studied the growth of pike for 20 years from the 1940s, we might have been tempted to assume we could predict what was reasonably likely to happen in the future. The results given in this paper clearly refute any such assumption."

3.2.3 Mortality and morbidity

3.2.3.1 Mortality rates

The estimation of mortality rates is subject to biases in techniques of estimating yearclass strength from catch curves or from estimates of population numbers. Errors in ageing pike, selectivity of catching gear, variations in susceptibility of pike to fishing tools per season, age, sex or lengthclass and fluctuations in yearclass strengths, can result in erroneous estimates of population structure over successive years. Therefore, mortality rates must be interpreted with caution, and implicit and explicit assumptions underlying the estimates must be taken into account when the data summarized in Table XXI are considered.

Most authors report strong fluctuations in mortality rates. Snow (1974, 1978) analysed mortality rates of northern pike aged 2 years and older from 1955 to 1969 in Murphy Flowage (Wisconsin). He found that total annual mortality did not depend on the (estimated) density of northern pike (age 2 years and older). Snow and Beard (1972) also failed to find a significant relationship between estimated population density of northern pike (age 1 year and older) and estimates of total annual mortality. They considered that mortality was dependent on food availability and not directly on population density. This investigation dealt with the northern pike population in Bucks Lake (Wisconsin) from 1961 to 1969. The results suggest that total annual mortality decreases with increasing population numbers. This is also suggested when virtual numbers of pike in the Windermere southern basin (1954-63, Kipling, 1983a) are related with the total annual mortality rates determined for tagged pike (Kipling and Frost, 1970): $r = -0.594$, $n = 10$, N.S.). The relationship between the conditional annual mortality percentage by angling and by natural causes and the virtual population in Windermere was found to be significant: $r = 0.794$, $n = 10$, $p<0.025$. However, netting activity in Windermere was reduced in three years of the 10-year period and the mortality data available refer mostly to

Table XXI

Data on mortality rates of northern pike

Location	Age groups	Mortality rates (symbols as in Ricker, 1975)	Remarks	References
Pilica River (Poland)	Age 1 and older	A = 62%	Based on yearclass strength in electro-fished catch	Penczak, Zalewski and Molinski (1976)
Lake Warniak (Poland, pond-type)	Age 3-4 Age 5-6 Age > 6	A = 56% A = 75% A = 45%	Estimates based on catch curves (not corrected for selectivity of the seine net)	Ciepielewski (1973)
Lake Warniak (Poland, pond-type)	Age 4 Age 5 Age 6	A = 77% A = 86% A = 81%	Estimates based on minimal numbers of year-classes over successive years	Ciepielewski (1981)
Klicava reservoir (Czechoslovakia)	Age 2 and older	A = 46%	Annual percentage of mortality is very fluctuating	Holcik (1968)
Helsinki (Gulf of Finland)	Age 4 and older	A = 57% Z = 0.85 F = 0.22 M = 0.74	Estimates from recaptures of tagged pike	Lehtonen (In Lind and Kaukoranta, 1975)
Oulujoki River (Finland)	Mature fish	A = 52-56% Z = 0.75 F = 0.42 M = 0.33	-	Lind and Kaukoranta (1975)
Northern part of Archipelago Sea (Finland)	Age 5 and older	Z = 0.8	Estimated from year-class strength	Lehtonen (data based on several Finnish research publications)
Estuary of the Kyrönjoki River (Western Gulf of Finland)	Age 5 and older	Z = 0.9	Same	
	Same	Z = 0.5-0.8	Same	
Lake Konnevesi (Finland)	Age 4 and older	Z = 1.05 Z = 1.04	Same Estimated from recaptures of tagged pike	
River Frome and River Stour (England)	> age 0	A = 54% A (males) = 58% A (females) = 37%	Catch curve estimate	Mann (1976, 1980)
Rivers in England	Age 1 Age 2 and older	A = 66% A = 50%	Based on Jolly-Seber method estimates	Pollock and Mann (1983)
Lake Windermere (England)	Age 2 and older	A (males) = 32-49% A (females) = 29-44%	Prior to netting in lake, estimates based on age frequencies in 1944-45 catch	Kipling and Frost (1970)
	Age 4 and older (males) Age 5 and older (females)	A = 56% A = 59%	Mortality since netting (1944) in lake. Estimates based on age frequencies in gillnet catch	

Table XXI (continued)

Location	Age groups	Mortality rates (symbols as in Ricker, 1975)	Remarks	References
Lake Windermere (England) (continued)	Age 3,4,5 (1954-64)	A = 40-54% n = 18-36% m = 16-30%	Estimates from tagged recaptured pike	
	Age 2, 3	A = 40%	Estimate based on tagged recaptured pike	
Slapton Ley (England, eutrophic lake)	Age 1 and older	A = 41% A (males) = 55% A (females) = 38%	Estimated from year-class strength	Bregazzi and Kennedy (1980)
Mill Lake (Michigan)	-	v = 56%	-	Schneider (In Latta, 1972)
Grebe Lake (Michigan)	-	v = 43%	-	Patriarche (In Latta, 1972)
Murphy Flowage (Wisconsin)	Age 2 and older (1955-69)	A = 66% (47-90%) A = 54-60% (in absence of angling) v = 40% (9-86%) u = 26% (3-50%)	Estimated from catch curves	Snow (1978)
Wisconsin waters	-	u = 50%	-	Threinen et al. (1966)
Escabana Lake (Wisconsin)	Age 2-5 (1957-58) Age 4-7 (1962-66)	A = 60% u = 44% (27-64%) A = 82% (69-91%) u = 6% (after 1964)	(1) Population in process of building up; (2) size limit 56 cm implemented in 1964. Estimates based on catch curves (fyke catches)	Kempinger and Carline (1978, 1978a)
Plover River Wisconsin)	Age 1-5	A = 62%	Catch curve estimate	Paragamian (1976)
Bucks Lake (Wisconsin)	Age 1 and older (1961-69)	A = 64% (35-84%) v = 37% (33-41%) u = 9% (2-15%)	Catch curve estimates	Snow and Beard (1972)
Lake George (Minnesota)	Age 2-5 (1957-60)	A = 65% v = 51% u = 14%	Based on catches in traps and gillnets	Groebner (1964)
Lake Nokay (Minnesota)	-	A = 71%	-	
Lake Grove (Minnesota)	-	A = 73-88% u = 32-49%	-	
Lake Francis (Minnesota)	-	A = 77%	-	
Ball Club Lake (Minnesota)	-	A = 60% v = 37% u = 23%	-	Johnson and Peterson (In Latta, 1972)
Grace Lake (Minnesota)	-	u = 22-28%	-	Wesloh and Olson (1962)
Niagara River watershed	Age 4 and older (1975-76)	A = 75% (males) A = 64% (females)	-	Harrison and Hadley (1983)

younger pike (aged 3, 4 and 5 years). Therefore both virtual population numbers and mortality rates are only indicative and subject to error as indices of population parameters.

Kempinger and Carline (1978, 1978a) investigated the northern pike population in Escabana Lake (Wisconsin) in the period from 1958 to 1976. In that lake a pike population had been established by natural reproduction since 1956. Trends in the mortality rates indicate an increase in natural mortality in the process of building up the population.

Snow (1974) showed in Murphy Flowage that losses of northern pike from disease and emigration were density-dependent and positively correlated in the first 3 to 5 years after stocking northern pike.

3.2.3.2 Effects of fishing

Kipling and Frost (1970), by comparing mortality estimates from the two basins of Windermere, concluded that the differences in mortality could be explained by changes in levels of exploitation. They also assumed that the changes in age and size structure of the pike population since the netting activity in the lake started (1944) did not necessarily have much effect on the natural mortality of adult pike, particularly in regard to cannibalism.

Groebner (1964) concluded from estimated mortality data of northern pike in Lake George (Minnesota), that there was little relationship between total fishing pressure and total mortality. The greatest natural mortality (78%) in the lake occurred in the year when the estimate of the population number was highest.

Snow (1978) analysed mortality rates of pike (2 years and older) in Murphy Flowage (Wisconsin) from 1955 to 1969. The author concluded that, except for the period 1964-66, when high natural mortality occurred after stocking of 8 000 pike (26-56 cm), natural mortality and exploitation by angling were linearly and negatively correlated.

Kempinger and Carline (1978, 1978a) investigated the effect of implementation of a size limit of 56 cm on the northern pike population of Escabana Lake (Wisconsin). Mortality estimates were based on fyke-net catches and were not corrected for selectivity of the fishing gear. Moreover, the pike population in the lake was in the process of building up. Therefore, the conclusion that natural mortality compensated for the decrease in fishing mortality after implementation of the size limit is only indicative.

Snow and Beard (1972) found that the implementation of a size limit of 45 cm had no effect on the mortality rate of the northern pike population in Bucks Lake (Wisconsin). The authors interpreted their results as indicating that the decrease in fishing intensity after implementation of the size limit can be compensated by an increase in natural mortality. However, estimates of total mortality fluctuated strongly; after an initial decrease at the introduction of the size limit, total mortality increased sharply despite the low exploitation level of the northern pike population. Moreover, an interpretation is difficult in view of unknown effects that the applied estimation method may have on the mortality estimates.

Riemens (1977, 1978) studied the effect of hooking on mortality of pike in drainable ponds. In his experiments, two types of baits (roach (Rutilus rutilus) and spinner) and two types of hooks (single and treble) were used. As a result of angling, 98% of the 62 spinner-caught pike and 83% of the 152 roach-caught pike were not deeply hooked and the hook could be removed. Six months after hooking the mortality was 2% for the not deeply hooked pike captured with the spinner. The mortality of roach-captured pike that were not deeply hooked was 6%. In both cases there was no difference in mortality between pike caught with single hooks and pike captured with treble hooks.

In another angling experiment based on 200 pike, 40 of the 63 individuals caught with a single hook, and 37 of the 87 pike caught with a treble hook were deeply hooked. The hooks that had been swallowed were not removed, but the line was cut as deeply as possible to the hook. Six months after hooking the mortality of deeply hooked pike was 13%. The mortality of pike hooked in the mouth was 2%. In both cases there was no difference in mortality between pike caught with single hooks and with treble hooks. The pike that had no hook experience suffered no mortality. Four months after the pike were restocked, no further mortality was recorded. Dissection showed the disappearance of nearly 60% of the swallowed hooks (treble hooks 54%; single hooks 62%). It was found that pike that had swallowed hooks showed the same growth as the other pike in the ponds.

Wydoski (1977) summarized data on hooking mortality from fisheries in Manitoba and Missouri. Mortality of pike caught and played with artificial lures with barbed treble hooks was found to vary between 1.7% and 5.3%. Hooking mortality for pike caught on lures with barbless hooks was reported to be 10.5%. Weithman and Anderson (1976) in their study of angling vulnerability of esocids in ponds found that hooking mortality was insignificant.

3.2.3.3 Factors affecting morbidity

Ergens (1966) investigated the effect of parasites on the health of northern pike in the Czech Lipno reservoir. The identified parasites included Ichthyophthirius multifiliis, Tetraonchus monenteron, Diplostomulum spathaceum, Triaenophorus nodulosus, Ergasilus sieboldi and Ergasilus foliaceus, which are highly pathogenic and may be directly or indirectly responsible for the death of fish, especially of the younger ones. T. nodulosus appears to be the most dangerous parasite in the reservoir, causing severe intestinal inflammation followed by inadequate digestion and regardation of growth.

Harrison and Hadley (1982) concluded that black-spot infection of pike in the Niagara River was related to retarded growth and increased mortality.

Snow (1974) reported from Murphy Flowage (Wisconsin) northern pike mortality caused by the parasite Myxobolus. The parasite was believed to have been introduced at the time of stocking of 8 534 (3 290 kg) northern pike (length range 26-58 cm) in Murphy Flowage (73 ha). Larger native pike were found dead in greater numbers than smaller native pike. Although parasitic infection was the factor which actually caused the mortality observed, high pike density, especially during the first year after stocking, was believed to have increased the susceptibility of the fish infection, and this resulted in higher mortality than would have occurred at lower pike densities.

Goddard and Redmond (1978) reported a chronical die-off of northern pike in the reservoir Stockton-Lake (Missouri). The authors suggest that the pike were weakened by high summer temperatures (32°C) and infections from the protozoan parasite Trichodina sp., which was found in large numbers in the gills and over the bodies of the examined fish. The weakened pike were secondarily infected by Aeromonas liquifaciens.

3.2.3.4 Mathematical models

Several mathematical models have been developed to predict yields from different combinations of fishing intensity and ages of recruits to fishery. Accuracy of predicted yields under a given set of conditions depends upon how well inherent assumptions of the model are met (Kempinger and Carline, 1978).

Kempinger and Carline (1978, 1978a) applied the Ricker (1975) equilibrium yield model to the northern pike fishery in Escabana Lake (Wisconsin). Basic assumptions of the model are that growth rate, recruitment and natural mortality do not change with variations of fishing mortality and age of recruits at first harvest. The authors found that the equilibrium yield model suggested that yield could be increased by 34% with a 56-cm size limit, when in fact the observed yield declined by 73%. Reduced growth rates of pike appeared to be responsible for the difference between theoretical and observed yields.

Latta (1972) and Dunning, Gross and Gladden (1982) used simulation models of pike populations which were based on the same assumptions as the Ricker (1975) equilibrium model.

Latta (1972) investigated the effect of winter exploitation of northern pike by ice fishing (spearing) in Wisconsin. In the model it was assumed that 80% of the growth and natural mortality occurred between April and October. Natural mortality was taken as constant and age specific mortality rates were not simulated. Growth rate was decreased with increased age in the model. Yearly production of pike was taken as constant. Exploitation rates were varied in the model to investigate the results of exploitation on the yield of pike in biomass and numbers. The model was not applied to an actual fishery but served as a feasability study for effects of management measures on winter exploitation of pike.

Dunning, Gross and Gladden (1982) analysed the imposition of a minimum size limit using a matrix model of northern pike populations. Matrix parameters were estimated. Natural mortality of age classes was assumed to be constant across ages and years. Fishing mortality was also taken as constant.

Models as those described above are statical, as the parameters do not react to population changes. Moreover, predator-food relationships are not taken into account in the models. Therefore, the application of these models in analysis of localized fisheries is restricted by the lack of flexibility in the parameters.

Hart and Connellan (1979) developed a computer model to describe the relationships between a pike population, a prey population and fishermen who exploit both. The central concepts of the model were derived from Beverton and Holt (1957). The authors summarized the information required, before the influence of pike predation on a fished prey population can be assessed as follows:

(1) numerical abundance of the pike population;

(2) numerical abundance of the prey population;

(3) size distribution in the pike population;

(4) size distribution in the prey population;

(5) habitat area within which the pike population can always be found;

(6) habitat area within which the prey population can always be found;

(7) seasonal movements of pike and prey within these habitats;

(8) the sizes of prey eaten by each size of pike;

(9) for a given pike size, the prey size and its frequency;

(10) the effects of reduced prey abundance on growth rates;

(11) the size ranges of prey caught by fishermen;

(12) for a given sized hook, the frequency with which each prey size is captured;

(13) the mortality rate caused by the capture of a prey individual.

The model is considered by the authors as a prototype and was not applied to an existing fishery (Hart, personal communication).

4. EXPLOITATION AND MANAGEMENT

4.1 Exploitation

4.1.1 Fishing equipment

4.1.1.1 Gears and boats

Several types of fishing gear are used in northern pike fisheries. Electrofishing is used for sampling small northern pike in vegetated areas (Grimm, 1981, 1983; Vostradovsky, 1981; Beyerle and Williams, 1973; Bracken, 1973; Mann, 1976, 1982). Larger pike are caught in seines, trawls and traps (Grimm, 1981; Frost and Kipling, 1967; Ciepielewski, 1981). According to Le Cren, Bagenal and Kipling (1975), seining in Windermere gave poor catches, required too many people and could be done at only a few favourable sites. In Poland, however, seine fisheries contribute significantly to the yearly commercial catch of northern pike (Leopold et al., 1975).

Gillnets are used by many scientists and commercial fishermen for sampling and catching pike (e.g., Lawler, 1965; Frost and Kipling, 1967; Leopold et al., 1975b; Broughton and Fisher, 1981; Otto, 1979). Le Cren, Bagenal and Kipling (1975) reported from Windermere that longlining was also successful, but very time-consuming. Craig, Sharma and Smiley (1986) analysed the variability of catches by multi-mesh gillnets taken in three Canadian lakes. They concluded that in sampling programmes more than six nets must be used for ensuring confidence limits below half or more than twice the geometric mean (see also Bagenal, 1972).

Fyke nets and trapnets are used for the collection of spawners in the Netherlands and in Pennsylvania (Drimmelen, 1969; Sorensen, Buss and Bradford, 1966).

Peterson, Taylor and Hanson (1980) reported the removal of an adult pike population from a 288-ha lake by means of double-throated frame nets with 1.2 x 9.2 m leads and 16 mm bar mesh throughout. The nets were placed at random around the shore line. A total catch of 6 104 pike was obtained by fishing during 9 days from end of March to early April 1978 with 10 to 15 nets (129 days of netting).

Collection of northern pike by using the piscicide rotenone is reported by several authors (e.g., Munro, 1957; Kennedy, 1969).

Northern pike are caught by sportfishermen by angling. In winter, northern pike in Michigan and Minnesota are sometimes caught under ice by spearing (Latta, 1972; Groebner, 1964; Weslow and Olson, 1962).

Boats do not need any special requirement for northern pike fishing.

4.1.2 Fishing areas

4.1.2.1 General geographic distribution

Northern pike are prized sport fish and make up an important contribution to the commercial catch over their geographic range (see also Section 1.5.2).

Commercial northern pike fisheries exist in Canada in the provinces Manitoba, Saskatchewan and Ontario (Carlander, Campbell and Muncy, 1978). In Western Europe, Scandinavia, Eastern Europe and the USSR important commercial northern pike fisheries exist in lakes, reservoirs and river deltas. Northern pike are commercially fished in brackish waters of the Baltic Sea coast (Sweden: Alm, 1957; Finland: Kaukoranta and Lind, 1975; Lind and Kaukoranta, 1975).

Northern pike sport fisheries are widespread throughout the geographic distribution range of the species in North America, Europe and the USSR.

4.1.2.2 Geographic ranges

Regression equations for predicting potential fish yields from freshwater lakes and reservoirs have become common in fisheries literature. Total fish yields have been correlated with environmental parameters as surface area, mean depth, total dissolved solids, total and biologically available phosphorus, morphoedaphic index, primary production, benthic standing crop and fishing effort (Schlesinger and Regier, 1983; Ryder et al., 1974; Jenkins, 1968, 1982; Jenkins and Morais, 1971 (see also Section 1.5.2).

Although most correlations relate total fish yield with environmental factors, some studies give equations for the prediction of potential yield of northern pike. Jenkins (1982) concluded on the basis of data from 35 reservoirs (larger than 200 ha) in the United States that the best two-variable predictor of yield of northern pike included mean depth and growth season. Both are negatively related to northern pike yield in United States reservoirs. Schlesinger and Regier (1983) fitted a curvilinear relationship between "long-term mean annual temperature" (TEMP) and sustained yield of northern pike, using data from 23 intensively fishing lakes in Canada and the northern United States. Optimum TEMP value for sustained yield of northern pike was approximately 1.5°C.

4.1.2.3 Depth ranges

Northern pike are usually caught in water less than 10 m in depth.

4.1.2.4 Conditions of the grounds

The determinants of distributional changes are summarized in Section 2.7 of this synopsis.

4.1.3 Fishing season

Latta (1972) summarized the information available on harvest percentages during winter and summer by spearing and angling. In Minnesota lakes, 86% of the northern pike were taken during summer. On the other hand, Threinen et al. (1966) estimated that 50% of the Wisconsin pike harvest occurred during summer. In Bucks Lake (Wisconsin), Snow and Beard (1972) estimated northern pike captures before and after implementation of a size limit of 46 cm. In the fishing season 1965-66, 28% of the total pike harvest of 797 individuals was taken in the ice-fishing season. After implementation of the size limit, the yearly catches of northern pike decreased to 90 individuals. In the two ice-fishing seasons 1966-67 and 1967-68, captures of northern pike represented respectively 80% and 56% of the yearly pike harvest by anglers.

According to Latta (1972), pike harvest in Michigan lakes by summer angling varied from 36% to 86% with a mean of 58%. The remaining catch was obtained by winter spearing and winter angling. Detailed catch data of the fishery in Long Lake (Michigan) from summer 1974 to summer 1978 (Beyerle, 1980) showed that 89% of the northern pike were caught in summer. The proportion of northern pike in the angler's harvest was 1.1% in winter and 4.9% in summer. The catch of pike per hour was on the average higher in summer (0.05; range 0.035-0.077) than in winter (0.036; range 0.016-0.045).

According to Lux and Smith (1960), angler success for pike was best when the percentage of stomachs containing food was lowest. In May, when the pike catch in Linwood Lake (a small water body in Minnesota) was relatively high, nearly half the stomachs of the pike were empty. Later in the season, when the catch was low, the proportion of empty stomachs dropped. No food other than fishes was found in the stomachs. According to the authors, physical and chemical factors had little or no measurable influence upon angler success during the summer season in Linwood Lake. Clark (In Toner and Lawler, 1969) found that net and sport catches in Ohio were negligible during the summer months when water temperatures of 24° to 27°C prevailed. The same was found in a pond fishery experiment by Weithman and Anderson (1976).

Broughton and Fisher (1981) reported from Grafham, Cambridgeshire, that the best results with pike angling were obtained before the first frosts. The catches of northern pike declined from mid-November onwards. The most productive angling locations were usually in deeper water near underwater features, e.g., sharp depth variations and deeper channels.

Seasonal differences in catch results are also reported from fisheries with commercial gears. Leopold et al. (1975) reported from Polish lakes that seine catches in lakes smaller than 80 ha were highest in October. In larger lakes no such maximum in northern pike captures was found; the catches remained at a level close to the annual average in all months.

Leopold et al. (1975b) reported for the same lakes that the catches of northern pike with gillnets were at a maximum in February. This is evidently related with the location of the gillnets near the shore and the migration of spawners to the spawning grounds. Gillnets that were set in somewhat deeper water showed an increase in northern pike catches in November, December and January. The catches of northern pike with trammel nets in Polish waters were maximal in April; a second maximum was recorded in November-December (Leopold et al., 1975a). Fyke and wing nets obtained maximum daily catches in March and April in Poland (Leopold et al., 1975). Both types of fishing gear also showed a slight increase in daily pike catches in autumn.

Table XXII summarizes the data on the exploitation of northern pike that were communicated to the present author.

4.1.4 Fishing operations and results

4.1.4.1 Effort and intensity

The data on northern pike fishery with various types of gear in Polish lakes are summarized in Table XXIII. The effect of intensive gillnet fishing on the northern pike population in Heming Lake (Manitoba) is discussed in Section 3.2.1.1. The data on the fishery in that lake are presented in Table XIV. The household and sportfishery in Finland were described in detail in the studies of Lehtonen and Salojärvi (1978, 1983) and Salojärvi and Lehtonen (1980). The most common types of gear used were gillnets, different kinds of rods and wire traps. Pike were caught by 76% of the non-professional fishermen in 1978. The subsistence and recreational fishery is responsible for the major part of the northern pike captures in waters in Finland. Table XXIV summarizes the results of the non-professional fishery on northern pike with different types of gear.

Latta (1972) reported from Shaw Lake (Michigan) that two anglers caught 28% of the northern pike population in 11 hours fishing (less than 6 hours angling/hectare). The northern pike population of that lake had not been fished before. Beyerle (1978) found that angling vulnerability of pike was higher than that of walleye (Stizostedion vitreum). In Emerald Lake (2.3 ha), 10.6% of 153 age-1 and age-2 pike were captured in 11 hours of angling, while 30 hours were required to take only 5.0% of the catchable walleyes. In Daggett Lake (6.1 ha), 28% of the catchable northern pike,

Table XXII

Data on the exploitation of northern pike in several countries
(Based on personal communications to the author)

Country/ Province	Exploitation	Fishing season	Fishing gears	Catch data	Source
CANADA					
- Alberta	Both for sport and commercial fisheries	Generally all year, except some spring closures on spawning streams	Pike taken as secondary species in commercial lake whitefish nets	Sport: Number caught in 1975 -1 499 190; in 1980 - 2 807 999 Commercial: In 1975 - 158 410 kg; in 1980 - 316 455 kg	K.A. Zelt
- British Columbia	Mainly for sport	All year	Rod and reel	Estimated 50 000 pike/year	L.A. Sunde
- Manitoba	Both for sport and commercial fisheries	Sport: Northern Manitoba open all year; north Manitoba open from mid-May to 31 March Commercial: Summer, winter and fall	Sport: Spinning bait casting spoons, spinners, plugs. Commercial: Gillnets	Sport: About 4 million/year Commercial: About 2.5 million kg/year	G. Nelson
- Ontario	Both for sport and commercial fisheries	Great Lakes: all year except few months. Inland waters mid-May to March	Trolling with large spoons, plugs, bucktail spinners, large bait fishes or worm harness - best mid-summer	Commercial: In 1982 - 321 338 kg	A. Wainio
- Saskatchewan	Both sport and commercial fisheries	Sport: Early May to 15 April. Commercial: both in open water and under ice	Sport: Rod and line, underwater spear guns. Commercial: gillnets	Sport: 1 923 million fish weighing 2.69 million kg Commercial: 0.77 million kg (1980 data)	R.P. Johnson
FINLAND	Both sport and commercial fisheries	Whole year, catch concentrated to spawning season	See Table XXIV	See Table XXIV	J. Jurvelius and M. Lehtonen

Table XXII (continued)

Country/ Province	Exploitation	Fishing season	Fishing gears	Catch data	Source
GERMANY (FED. REP. OF)					
- Baden Württemberg	Both commercial (Lake Constance, parts R. Rhine) and sport	Lake Constance: 31.05-31.03; rest of county 01.05-14.02	Hook and line, gillnets, fykes, trap nets	Lake Constance: catch decrease from about 40 t in 1940s and 1950s, to about 10 t in 1970s	H. Löffler and R. Berg
- Bavaria	Mainly sport	Depending on area 16.04 or 01.05-31.01 or 14.02	Hook and line, gillnets, fykes	20 t	M. von Lukowicz
- Berlin (West)	Both sport and commercial fishery	Whole year open	Seines, trawls, angling 12 months; gillnets from February to May and from October to December; fykes March to December	<u>Sport</u>: 2 t/year; <u>Commercial</u>: 3 t/year	U.A. Grosch
IRELAND	Only sport	No closed season	Rod and line with artificial lures. Use of live bait is prohibited	-	J. O'Connell
LUXEMBOURG	Only sport	15.06-31.12	Spinning with small artificial lure or dead fish;float-fishing with living fish	-	Administration des Eaux et Forêts, Service de la Pêche
NORWAY	Mainly sport and household fishing	Whole year open	Spinners and spoons of all kinds as well as nets of different kinds in ice-covered waters; jiggors and baited hooks	-	K. Jensen
SWITZERLAND	Both sport and commercial fishery	01.06-31.03	Gilnets, trap nets	<u>Sport</u>: 10 t/year; <u>Commercial</u>: 50 t/year	E. Staub

Table XXIII

Northern pike fishery with various gears in Polish lakes
(Data from Leopold et al., 1975, 1975a, 1975b, 1975c, Leopold and Dabrowski, 1975)

Gear	Fishing season	Size classes of lakes	Northern pike as % of total catch/day	Average catch of pike/day (in kg)	Total number of lakes (total surface area)	Fishing intensity in gear days (total)
Summer seine: Length 90-180 m depth 5-6 m, wings mesh size 28-40 mm, bag 28 mm, conical bag terminates in cod-end with 25-mm mesh size	July-December	Up to 80 ha 80-500 ha 500 ha and larger	15.52 ± 10 12.8 12.8[a/]	24.44 ± 20 32.29 26.65[a/]	- - - 206 (35 762 ha)	- - - 4 000
Winter seine: Length 120-270 m, depth 6-22 m, wings mesh size 28-42 mm, bag mesh size 28 mm, cod-end with 22-26 mm mesh size	December-April operated under ice	Up to 100 ha 100-500 ha 500 ha and larger	10.99 3.17 5.47 5.63[a/]	26.97 10.24 27.39 22.02[a/]	- - - 108 (24 430 ha)	- - - 2 000
Gillnets						
- Bream nets: 40-50 m, depth 2.5-3.5 m, mesh size 60-90 mm;	Early spring to late autumn	-	16.2	-	10	-
- Perch/roach nets: 35-40 m, depth 1.3-3.3 m mesh size 30-40 mm;		-	13.1	-	10	-
- Vendace nets: 45-50 m, depth 7.5 m, mesh size 28 mm;		-	13.1	-	10	-
Trammel nets: Length up to 45 m, depth between 1 and 2 m, mesh size of two outer sheets in the range of 110-250 mm, inner sheet in the range of 20-90 mm	During almost all year	Up to 100 ha 100-500 ha 500 ha and larger	20.7 40.2 55.7 36.7[a/]	2.71 5.74 4.45 4.03[a/]	- - - 176 (41 726 ha)	- - - -
Fyke nets Type 1: Length range 1.3-2.2 m, diameter of first hoop 35-90 cm, mesh size 25-35 mm, wings leaders 4-5 m, mesh size 28-30 mm	March-October	Up to 100 ha 100-500 ha 500 ha and larger	31.43 27.83 23.98 26.13[a/]	0.43 0.49 0.36 0.40[a/]	- - - 105 (23 100 ha)	- - - 100 057
Fyke nets Type 2: Like Type 1 nets plus additional portion stretched on a semicircular hoop which increases fishing intensity	March-October		44.2a/	0.77a	44 (15 042 ha)	54 042

Table XXIII (continued)

Gear	Fishing season	Size classes of lakes	Northern pike as % of total catch/day	Average catch of pike/day (in kg)	Total number of lakes (total surface area)	Fishing intensity in gear days (total)
Wing nets: Three or four hoop nets connected by wints and leaders, mesh size between 25 and 40 mm	All periods with open water		13.0[a/]	0.33[a/]	140	-
Combined pound nets: Fyke nets wing nets combined with trap opening at top, usually the main elements	Spring to autumn		<10[a/]	-	7 (about 20 000 ha)	-

a/ Average

than 55 cm fork-length. Smaller fish were only infrequently taken and these were usually held because the jaw or teeth had become entangled in a strand of the net. As the fish length increased from 55 to about 65 cm, the chances of capture increased and fish over 65 cm had a very small chance of escape having once come into contact with the net (see Figure 37).

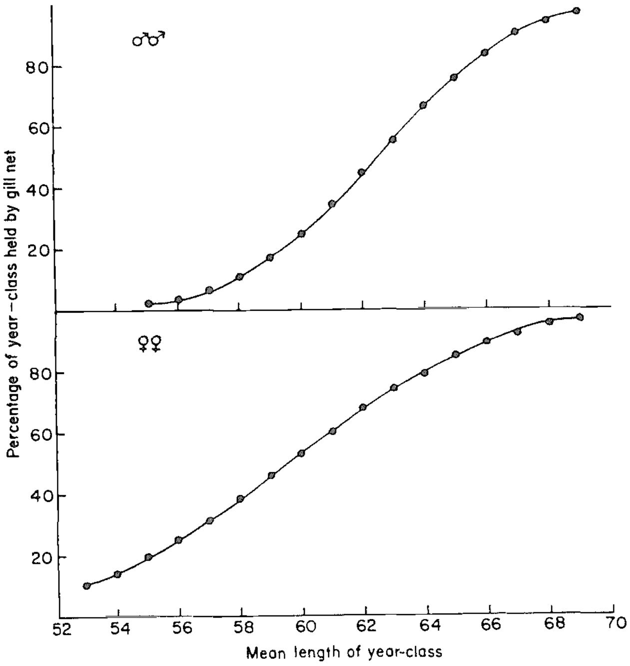


Figure 37 Selection of northern pike by 13.6 cm stretched mesh size gillnets in Windermere, mean length in centimetres forklength. (After Frost and Kipling, 1967)

Kipling (1975) described a model which was used to provide information on the effects of gillnet selection on a population of pike in Windermere. The results of the calculations agree in general with observed results from gillnettings in Windermere during more than 20 years. The model shows that great care is needed in using catches from gillnets as a basis for stock assessment (see also Bagenal, 1972).

Bracken and Champ (1971) gave the results of a large-scale mesh experiment carried out with gillnets in Lough Ennell (Ireland) by the Inland Fisheries Trust Inc. Mesh sizes used in the experiment were smaller than those in Windermere. The results are presented in Figure 38. The 6.35 and 7.62-cm stretched nylon mesh sizes showed a much different result compared to nets with larger mesh sizes. The 6.35 and 7.62-cm mesh-sized nets mainly captured 2-year old pike. In the 8.89-cm mesh nets, the numbers of 2-year old pike dropped substantially, but larger and older pike were retained. This trend continued with the 10.16 and 11.43 cm mesh nets. Returns from ulstron gillnets were very low and it was concluded that these nets were not as efficient in northern pike fishing as nylon nets. The same experiment was carried out in Lough Sheelin (Ireland) and the results were very similar to those from Lough Ennell.

Broughton and Fisher (1981) used gillnets made up of 11 cm stretched nylon mesh in Grafham Water, a storage reservoir in West Cambridgeshire. The catch initially was considerable, but declined with time. The authors suggested that pike may have learned to avoid a net set in a particular area.

Beukema (1970) studied the catchability of tagged pike in drainable ponds by hook and line fishing, using either an artificial lure (spinner) or a small live fish as bait. All captured pike were immediately returned to the pond and mortality was low. The catchability of pike by the spinner decreased to very low levels after about half of the population had been caught. The catchability of pike by live baits remained unaffected both by intensive spinner and by live-bait fishing. It was difficult to capture pike more than once by spinning. In live-bait fishing, the number of recaptures closely matched those expected, provided that catchability remained unaffected by earlier captures.

4.1.4.3 Catches

The data on northern pike catches from the FAO Yearbooks of Fisheries Statistics for 1980, 1982 and 1984 are summarized in Tables XXV and XXVI.

The catches of northern pike from the Baltic Sea coast of Sweden from 1944 to 1955 are presented by Alm (1957). Carlander, Campbell and Muncy (1978) reviewed catches of northern pike in North America. In the period 1955-76, the marketed catch in Canada averaged 3 500 mt. In 1976, the total commercial catch in Manitoba amounted to almost 60% of the total Canadian catch for that year. Substantial percentages of the remainder were taken in Saskatchewan and Ontario. Although northern pike was not identified in the US freshwater fisheries, the total in 1973 would have been 59 mt.

The catch data of northern pike in Finland between 1974 and 1981 are summarized in Table XXVII. Next to the Baltic herring (*Clupea harengus*), the pike is economically the most important fish in Finland (Sumari and Westman, 1969).

Berka (1980) presented a production data analysis of marked-sized and young northern pike, produced both in natural waters and by cultural methods. Chronological statistical data are given for German Democratic Republic, Yugoslavia, the Netherlands, Finland, Poland, Switzerland, Turkey, the USSR and Czechoslovakia.

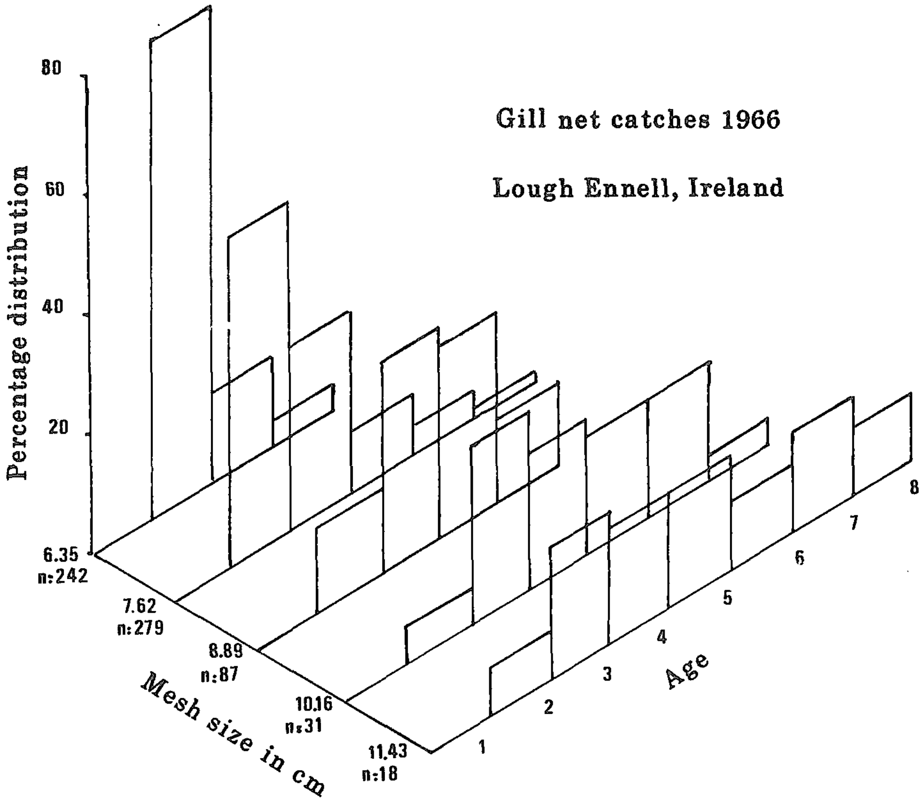


Figure 38 Gillnet catches in Lough Ennell, Ireland. (Redrawn after data Bracken and Champ, 1971)

4.2 Management and Conservation

4.2.1 Introduction

The ontogenetic development of northern pike is not only characterized by changes in time. During its life history, the pike also changes its utilization of the habitat, its feeding and its behaviour. The influence of the environment and environmental changes in reproduction, growth, activity and mortality is thus dependent on the development stage of the individual pike. Management measures often reflect ideas that are based on the analysis of the life history of a species at the organismic level. However, in order to assess the effects of regulatory measures, the relationship with the environment and the effects of direct manipulations of fish populations must also be studied at a population and community level. This provides information on factors influencing population abundance and structure in time and space.

The analysis of the life history of northern pike results in detailed information on habitat utilization and habitat requirements. This is of great importance for the management and conservation of species because it furnishes information and criteria on the environmental requirements for its reproduction and persistence. The Habitat Suitability Index Model for northern pike (Inskip, 1982) is based on the analysis of the species' life history. On the basis of a comprehensive literature survey, Inskip (1982) distinguished several evaluation criteria to judge the suitability of the habitat for northern pike in lacustrine and riverine environments. He considered the following habitat variables for pike in lacustrine habitats:

- ratio of spawning habitat to summer habitat (area that is less than 1 m deep and vegetated (in spring), divided by total midsummer area). When the ratio is less than 0.2, the habitat is not optimally suitable for pike. The suitability of the habitat is also considered to be dependent on the density of vegetation or plant debris within the area included as spawning habitat. Areas covered with filamentous algae, living or dead, are not considered as suitable spawning habitat;

- drop in water level during the embryonal and larval periods. Declining water levels can strand the embryos, larvae and even adults on the spawning grounds. Embryos are particularly vulnerable because of their immobility;

Table XXV

Nominal catches of pike by major fishing areas and countries (in mt)
(After FAO, 1980, 1982, 1984)
The data exclude catches taken in recreational fishing

Country	Statistical area	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
Canada	02	3 336	3 365	3 300	3 888	3 920	4 162	4 200	3 742	4 666	3 352	3 200
Turkey	04	440 F	410 F	384	188	188	395	635	796	667	463	642
Finland	05	3 649	6 018	6 018 F	4 608	5 304	5 219	5 439	5 923	5 987	6 062	6 048
German Dem. Rep.	05	329	329 F	329 F	233	228	222	211	261	316	283	...
Netherlands	05	0	0	0	-	-	-	1	1	0	0	1
Poland	05	467	475	363	358	254	324	271	287	408	413	551
Romania	05	a/	a/	a/	a/	a/	a/	a/	680	266	115	116
Sweden	05	0	0	0	...	...	...	...	a/	a/	a/	a/
Switzerland	05	75	78	79	80	75	74	70	74	77	76	74
USSR	07	15 800	16 101	12 925	13 120	10 357	12 968	13 594	11 866	11 361	9 540	10 047
Denmark	27	a/	a/	a/	a/	a/	a/	a/	9	10	5	6
Finland	27	1 921	1 868	2 021	2 048	1 743	1 604	1 657	1 700	1 683	1 620	1 649
German Dem. Rep.	27	155	159	199	188	158	159	130	145	211	203	219
Poland	27	-	34	16	12	34	8	-	1	-	10	9
Sweden	27	288	374	286	305	283	278	248	249	284	324	401
USSR	27	400	458	-	-	-	438	593	218	198	167	185

Table XXV (continued)

Country	Statistical area	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
USSR	37	300	405	368	-	-	-	32	25	11	15	18
USSR	61	100	148	81	a/	a/	a/	a/	a/	a/	a/	a/
Total	S	27 261 F	30 222 F	26 369 F	25 028	22 544	25 851	27 081	25 977	26 145	22 648	23 166

02 = North America, inland waters
04 = Asia, inland waters
05 = Europe, inland waters
07 = USSR, inland waters
27 = NE Atlantic, coastal area Baltic Sea
37 = Mediterranean Sea and coastal area of Black Sea (estuaries, large rivers)
\- = None, magnitude nil or zero
0 = More than zero but less than 0.5 mt (1974-76)

a/ Data not available

Table XXVI

Northern pike as a percentage by weight of the total catch of freshwater fish
(After FAO, 1980, 1982, 1984)

Area	Statistical area	1974	1975	1976	1977	1978	1979
North America Total/mt	02	2.2 153 963	2.4 145 321	2.2 139 200	2.8 140 800	2.6 153 400	2.7 153 000
Europe (inland waters) Total/mt	05	1.7 266 421	2.4 F 281 697	2.3 F 293 800	1.7 312 100	1.9 304 500	1.9 365 800
Europe (Baltic)[a/] Total/mt	27	22.6 11 689 070	40.6 12 014 689	43.5 13 163 100	0.02 12 575 100	0.02 11 677 200	0.02 11 719 600
USSR Total/mt	07	2.0 772 900	1.7 943 970	1.7 770 310	1.7 772 600	1.9 726 800	1.9 805 500

Table XXVI (continued)

Area	Statistical area	1980	1981	1982	1983	1984
North America Total/mt	02	2.5 173 500	2.5 226 800	2.9 261 200	1.4 243 300	1.2 258 500
Europe (inland waters) Total/mt	05	1.6 365 800	2.0 366 400	1.8 395 200	1.8 393 100	1.7 398 500
Europe (Baltic)[a/] Total/mt	27	0.02 11 798 000	3.8 11 648 400	5.3 10 719 200	3.3 11 170 900	3.3 11 268 100
USSR (inland waters) Total/mt	07	1.8 753 100	1.5 808 400	1.4 803 600	1.2 796 500	1.1 881 500

a/ Expressed as percentage of catch of freshwater fish from the Baltic

Table XXVII

Catch data of northern pike from fisheries in fresh water and sea water in Finland 1974-81
(Data taken from Suomen Kalatalous 48 (1976), 48(1977), 48 (1978), 49 (1980), 50 (1983))

Year	Sea fisheries: Number of fishermen/Catch of pike in tons				Freshwater fisheries: Number of fishermen/Catch of pike in tons				Grand total of fisheries in Finland
	Professional fishermen	Semi-professional fishermen	Non-professional fishermen	Total sea fisheries	Professional fishermen	Semi-professional fishermen	Non-professional fishermen	Total freshwater fisheries	
1974	1 989/ 430	3 079/ 431	3 079/ 1 060	-/ 1 921	407/ 63	4 848/ 371	-/ 3 215	5 255/ 3 649	449 200/ 5 570
1975	1 888/ 338	2 940/ 360	107 845/ 1 376	112 673/ 2 074	450/ 63	4 758/ 335	338 209/ 4 336	343 417/ 4 734	456 090/ 6 808
1976	1 879/ 348	3 070 297	109 971/ 1 435	114 920/ 2 080	380/ 41	3 439/ 198	346 448/ 4 522	350 267/ 4 761	465 187/ 6 841
1977	1 793/ 345	2 939/ 315	108 816/ 1 388	113 548/ 2 048	328/ 32	2 576/ 192	342 203/ 4 384	345 107/ 4 608	458 655/ 6 656
1978	1 703/ 252	3 064/ 308	191 678/ 1 183	196 445/ 1 743	337/ 38	2 552/ 133	652 469/ 5 133	655 358/ 5 304	851 803/ 7 047
1979	1 793/ 236	2 935/ 308	188 803/ 1 060	193 531/ 1 604	307/ 33	2 534/ 130	642 682/ 5 056	645 523/ 5 219	839 054/ 6 823
1980	1 783/ 231	2 942/ 348	192 013/ 1 125	196 738/ 1 704	343/ 31	2 410/ 137	653 608/ 5 143	656 361/ 5 311	853 099/ 7 015
1981	1 800/ 222	2 742/ 306	210 983/ 1 172	215 525/ 1 700	331/ 54	2 182/ 142	826 442/ 5 727	828 955/ 5 923	1 044 480/ 7 623

- percentage of midsummer area with emergent and/or submerged aquatic vegetation or remains of terrestrial plants (bottom debris excluded). Inskip (1982) considered habitats with 25 to 75% midsummer vegetation cover as optimally suitable for northern pike;

- TDS levels (Total dissolved solids concentration) in surface waters (1 to 2 m deep) during midsummer. Habitat suitability is assumed to remain constant for TDS levels between 80 and 800 ppm and to decrease at higher levels with zero suitability for TDS values higher than 3 500 ppm;

- least-suitable pH in spawning habitat during the embryonal and larval periods. There is no evidence of any adverse effects over the pH range of 6.0 to 9.0;

- average length of the frost-free season. A period between 120 and 220 days is considered suitable for northern pike. The length of the frost-free season correlates with the length of the growth season for northern pike; however, if the cold season is too short, normal gonadal development may be impaired;

- maximal weekly average temperature of surface water (1 to 2 m deep). Maximal suitability is assumed for average weekly peak temperatures of 20° to 25°C.

The above-presented habitat variables are very similar to riverine habitats. The only difference is that the riverine model contains two additional variables:

- percentage of pools and backwaters during midsummer;
- stream gradient.

Inskip (1982) assumed a direct proportional relationship between availability of standing water habitat (area of backwater pools or other standing/sluggish (less than 5 cm/sec.) water during summer as a percentage of total surface area) and habitat suitability. It is further assumed that stream reaches with gradients greater than 5 m/km (0.5%) have little or no habitat value for northern pike.

Many studies relate changes in the population structure and density of northern pike to direct or indirect influences of the habitat on the reproduction, growth, recruitment and mortality of pike. These studies emphasize the importance of various habitat variables in the Habitat Suitability Index Model of Inskip (1982), not only as indices of habitat suitability, but also as factors governing the structure and density of the species population. The most important factors mentioned in the literature are:

- availability of suitable (vegetation) areas for reproduction and persistence of the species;
- eutrophication;
- water pollution;
- availability of prey;
- intraspecific interactions;
- interspecific interactions
- fishery;
- stocking.

Various management measures have bee attempted to improve the conditions fo reproduction and persistence of the species an to manipulate its population structure. Wate level management (Groen and Schroeder, 1978) an management of spawning marshes (Forney, 1968) are reported to have improved the conditions of spawning in waters where sustained natural reproduction was insufficient or not possible.

The deteriorating effects of eutrophicatior and water pollution on the quality of the environment of northern pike is reported from many countries. The effect of measures to counteract the causes of eutrophication and water pollution has not been evaluated for northern pike populations. However, it is evident that measures which are meant to improve the water quality will have a positive effect on the living conditions of the species.

The availability of prey fish also influences northern pike populations. Increases in growth rate have been observed in rearing ponds, following the introduction of forage fish. On the other hand, the pike has effects on the abundance and structure of prey fish populations (Powell, 1972). In natural environments, pike population structure and abundance have been correlated with the availability of prey fish (Kipling, 1983a; Craig and Kipling, 1983). Regulation of prey fish populations may therefore influence pike population structure as is indicated by the effects of perch fishery in Windermere (Le Cren, Kipling and McCormack, 1977).

Fishing and stocking have a direct impact on northern pike populations. Most of the management effort concerns regulatory measures for the exploitation of the species. There is a belief that intensive fishing of spawning pike would lead to a severe diminution of the population. Sumari and Westman (1969), however, concluded that only in exceptional cases spring fishing results in excessive reduction of spawning pike. Fishing generally increases pike populations and decreases the average size of the pike. Fishing regulations can thus have effect on the size-composition of the population which, in turn, can result in changes in the fishery.

Stocking of pike embryos, larvae and larger pike is practised in many countries (Flickinger and Clark, 1978; Billard, 1983). Lelek (1980) in his report on threatened freshwater fishes of Europe, is of the opinion that present pike populations are mostly maintained by stocking. Although exceptions may occur in most cases there is no biological justification for stocking of pike embryos and larvae (Sumari and

Westman, 1969; Grimm, 1983, 1983a), nor does it result in an improvement of pike stocks or fishery.

4.2.2 Regulatory (legislative) measures

Many countries, provinces and states have adopted regulatory measures with regard to northern pike fisheries (see Table XXVIII). In many cases, the motivation steps from general concepts, such as protection of the species or its spawners. So, in many cases, management has an intuitive origin, which is an adequate justification for many situation.

Fishing can have an evident impact on the population structure and density of pike (Frost and Kipling, 1967; Lawler, 1965; and other authors referred to in Section 3.2.1.1). Therefore, catch-and-release fisheries can result in a population structure with pike of higher average weight and lower abundance than pike in populations that are being exploited.

Implementation of size limits can be justified with fishery models. Several model studies have investigated the theoretical impact of a size limit on fishery results (Latta, 1972; Dunning, Gross and Gladden, 1982). Kempinger and Carline (1978, 1978a) applied the equilibrium yield model to the northern pike fishery in Escabana Lake. The model suggested that the yield could be increased by 34% by the application of a 56-cm size limit; however, it actually decreased by 73%. Reduced growth rates of pike appeared to be responsible for this difference between theoretical and observed yields. The other two assumptions of the model that were not met were constant recruitment and natural mortality. After the size limit went into effect, recruitment more than doubled and natural mortality increased from about 14% to 76%. According to Kempinger and Carline (1978a), the effect of size limits is bound to vary with prevailing exploitation rates, growth rates and structure of the fish community. They state that it seems unreasonable to assume that a single length limit can produce desirable results over a wide range of lake types and fishing pressures.

4.2.3 Artificial stocking

Stocking of northern pike is a management measure in many countries. It is motivated by the idea that the effects of a reduction of breeding grounds and disappearance of the traditional pike habitat can be compensated by stocking pike embryos or larvae in the water (Lelek, 1980).

Flickinger and Clark (1978) evaluated stockings of pike in Colorado. Krohn (1969) gave a summary of northern pike stocking investigations in Wisconsin. Johnson (1978) discussed survival figures of stockings in Wisconsin, and Pritchard, May and Rider (1976) reviewed stockings in 26 reservoirs in nine states in the USA.

Fritsch (1984) reported that in the German Democratic Republic, an area of 36 000 km^2 is managed for 500 000 anglers. By means of intensive culture, 4 340 600 pike embryos were produced for stocking purposes in 1982. In Finland, about 20 million newly hatched pike and 1.2 million pike larvae are produced yearly for stocking purposes. In the Netherlands, the production of pike larvae (4.5 cm) for stocking in angling waters was about 1.2 million yearly till 1980. The demand for northern pike larvae decreased sharply to 400 000 in 1984 as a result of the studies on northern pike by Grimm (1981, 1981a, 1983, see Figure 39).

According to Sumari and Westman (1969), the reduction of breeding grounds cannot be compensated by stocking northern pike, because the stocked individuals are affected by the same factors that have caused the decrease of the natural population. Grimm (1983) came to the same conclusion. He found that the biomasses of length classes were related, which indicates that the species shows a self-regulation of its population density. Stocking of pike larvae (4-5 cm) did not lead to higher densities. Stocked northern pike occurred with varying frequencies in the 0^+ class. This could be explained by differences in the dates of stocking. Stocked individuals that were developmentally ahead of the naturally produced pike had better chances to survive. The same facts were demonstrated by Franklin and Smith (1963) and Forney (1968) with pike produced in managed marshes.

The results of many evaluation studies of stocked northern pike are biased by methodological problems. The use of selective capture methods and negligence of the naturally produced pike in the population analysis make it difficult to interpret these studies.

The use of beach seines by Flickinger and Clark (1978) in their evaluation of northern pike stockings (5 cm long) in small reservoirs in Colorado resulted in biased population estimates. Thus it is doubtful whether the conclusion that survival of the stocked pike was dependent upon large numbers of small forage fish is justified.

However, the positive influence of the availability of prey fish on the survival of pike stocked in ponds without predators was shown by Beyerle (1973; 1978). It was found that pike stocked in ponds with bluegills had on an average a lower survival rate than pike stocked in ponds with minnows (see Section 3.2.2.4). Survival was also influenced by the vegetative cover present in the ponds. Absence of aquatic vegetation resulted in lower survival and lower production of northern pike. The growth in ponds stocked with minnows was in general better than that in ponds stocked with bluegills (see also MacCarraher, 1959).

Beyerle and Williams (1973) estimated the survival of stocked northern pike at the end of their first growth season in Long Lake

Table XXVIII

Data on regulatory (legislative) measures with regard to northern pike fishery

Country/ Province	Limitation or reduction of catches	Size limits	Closed season	Other measures	Motivation of measures; remarks	Source
BELGIUM	-	45 cm	-	-	Pike protected by fishery law	Hofstede (1969)
CANADA - Alberta	Catch quotum 10, possession 10	None	01.04-15.05	Special catch limits and bait restrictions in "Trophy lakes"	-	K.A. Zelt
- British Columbia	Catch quotum 10, possession 16	None	None for pike but general spring closure on streams in Peace River watershed	No spear fishing	Reduction of kill of pike who are relatively easily caught by angling	L.A. Sunde
- Manitoba	Catch quotum 8, possession 8; commercial-varying poundage limits in lakes	Only one pike over 60 cm	Basically during spawning season	Translocation of pike as a result of fish kills	Protection of species	G. Nelson
- Ontario	Catch quotum 6, possession 6	None	End of March to mid-May	Conserving marshy spawning areas for pike	Maintain a healthy, naturally reproducing stock for future anglers	A. Wainio
- Saskatchewan	Sport: catch quotum 8, possession 16 in south; daily limit 11 kg, possession 22 kg in north Commercial: poundage limits set for each lake	None	15.04-first week of May	- -	General conservation	R.P. Johnson

Table XXVIII (continued)

Country/Province	Limitation or reduction of catches	Size limits	Closed season	Other measures	Motivation of measures; remarks	Source
DENMARK	-	40 cm	No closed season since 1965	-	-	Hofstede (1969)
GERMANY (FED. REP. OF)	- -	25-45 cm	01.02/01.03-15.04/30.04	Living fish as bait not permitted from 1985 on	-	Hofstede (1969)
- Baden Württemberg	-	Lake Constance 40 cm; Baden-Württemberg 50 cm	Lake Constance upper part 01.04-20.05, lower part 01.04-30.05 15.02-30.04		Size limit in Lake Constance is influenced by gillnets used for perch fishery (32 and 34 mm) Closed season to protect species during late spawning in lower part of Lake Constance	R. Berg and H. Löffler
- Bavaria	-	25-50 cm	01/15.02-15/30.04		Protection of reproduction	M. von Lukowicz
- Berlin (West)	-	32 cm	February to April on spawning grounds	-	Trophic situation; destruction of traditional spawning grounds; destruction of reeds; high fishing pressure	U.A. Grosch
FINLAND	None	40 cm	Can be locally closed in spawning season	Local gillnet mesh size regulations	-	H. Lehtonen J. Jurvelius
FRANCE	-	40 cm	During spawning season	-	-	Hofstede (1969)

Table XXVIII (continued)

Country/ Province	Limitation or reduction of catches	Size limits	Closed season	Other measures	Motivation of measures; remarks	Source
IRELAND	None	None	None	Rod and line fishing only, maximum 2 rods per angler	Conservation of pike stocks	J. O'Connell
LUXEMBOURG	Lake Upper Sûre 2 pike; other waters none	Inland waters: 45 cm; frontier waters: 40 cm	01.01-14.06	-	Conservation of the live stock	Administration des Eaux et Forêts, Service de la Pêche
NETHERLANDS	Locally	50 cm	01.03-30.06	Depending on bait, 1 or 2 rods/angler	Depending on location, regulations may vary	
NORWAY	None	In some counties	01.03-30.06	None	-	K. Jensen and Hofstede (1969)
POLAND	-	30 cm	Depending on size and use of the water locally	-	-	Hofstede (1969)
SWITZERLAND	None	50 cm	April and May	Limitation of number of nets	Conservation of species	E. Staub
USA	Locally	Locally	Locally	Locally	-	Kempinger and Carline (1978, 1978a)

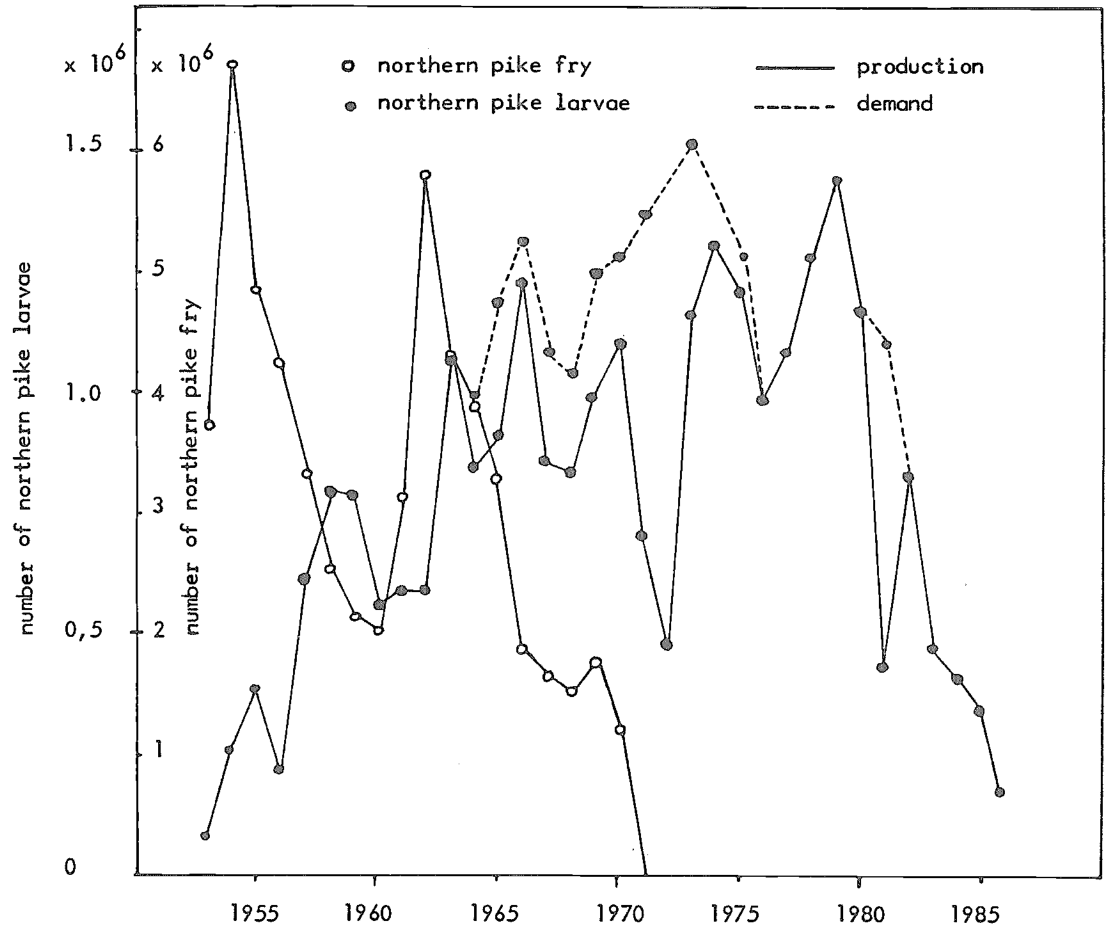


Figure 39 Production for stocking of northern pike fry (o) and larvae (●) and demand for these stocking products in the Netherlands in the period 1953-86. (Compiled from Annual Reports Netherlands Organisatie ter Verbetering van de Binnenvisserij, Nieuwegein)

(Michigan, 117 ha). The authors used a capture method of low efficiency. The estimates based on captures made in a lake area of 4 ha, were extrapolated to an area of 60 ha (depth less than 4 m). In view of the dispersal pattern of pike, this extrapolation introduced an extra bias in the estimates of the stocked northern pike. Year-to-year changes in pike habitat and differences in the speed of development of the natural population can result in strongly varying survival figures (6% to 63% in Long Lake). Beyerle and Williams (1973), however, gave no estimates of the naturally reproduced pike in the lake.

Beyerle (1980) evaluated the costs to produce marsh-reared pike in Long Lake. The survival of the stocked pike to the anglers creel varied from 15.8 to 36.6%. Marsh-reared northern pike provided 65.1% of the total harvest of northern pike. The costs to produce the marsh-reared pike were US$ 0.87 per fish or US$ 0.70 per kilogramme of pike. Goddard and Redmond (1978) reported the results of northern pike stockings during the three-stage filling of the 10 072-ha Stockton Lake (Missouri). Initially, survival and growth of the stocked embryos appeared to be good probably because of the abundance of flooded terrestrial vegetation in the three succeeding spring periods. Successful reproduction of northern pike was anticipated but never verified.

Jenkins (1973) reported that stockings of northern pike in new reservoirs in the mid-south of the USA have often resulted in excellent survival, with growth rates of 4 lb a year and maximum longevity of 6 years. Reproductive success has been limited and stockings of pike in later years of impoundment have also been relatively unsuccessful. Control of water depth in nursery areas, chemical control of undesired fishes, and planting of sedges of grasses for egg deposition are suggested as requisites to sustain northern pike production in the impoundments in the southern states of the USA.

Generally, survival figures of northern pike stockings are low (Anwand, 1968; RIVO, 1976; McCarraher, 1961; Flickinger and Clark, 1978; Le Louarn, 1983). The contribution of stocked pike to the population density shows no relationship with the length classes stocked or the moment of stocking.

Stocking of brood fish or larvae in new water bodies or in waters where the fish population has been removed or drastically reduced, are generally successful (Krohn, 1969). In a suitable pike habitat, the availability of a substantial pike population is the most important factor for the success of pike stockings. However, Beyerle (1971) concluded from stocking experiments in small ponds that it is unwise to stock young pike in waters containing pike populations. The survival of the initially stocked pike after three growth seasons was high (44-60%), whereas the survival from subsequent stockings was low (0.8-9.2%).

Generally, stocked northern pike have the tendency to move and return to their catch site, when transferred over a distance of several kilometres (Kaukoranta and Lind, 1975; Fitzmaurice, 1978; Krohn, 1969). Carlander and Ridenhour (1955) stocked 15 192 pike (26.5-40.5 cm) in Clear Lake (Iowa) (1 474 ha) and studied the dispersal of the tagged fish in the lake six months after stocking in October 1953. The results indicated that the stocked pike moved to all parts of the lake within six months even if they were stocked at one end of the lake. Although the movement was extensive and general, there was evidence that the fish stocked in some areas did not get to areas at the other end of the lake in the same abundance. This can be explained by assuming that some areas provided better habitat conditions or that a longer period of time between stocking and capture of the fish might eliminate this slight difference.

Carlander (1958) reported that when the fishing season in Clear Lake opened in mid-May 1954, the northern pike catch was unusually good. Over 20% of the fish tagged during stocking the previous fall were caught in the first six weeks of the fishing season. According to Carlander (1958), the increase of the northern pike population disturbed the predator-prey balance in Clear Lake, which was not counterbalanced by the high fishing harvest, because later in the summer a number of thin northern pike were found dead along the shore and some of the pike caught by anglers were in poor condition (Rodenhour, 1957).

Snow (1974) reported similar results from Murphy Flowage (Wisconsin) (73 ha), in which 8 500 pike (26.5-58 cm) were stocked in December 1963. Most of the movements of pike occurred within a 4-months period during the winter and early spring. The stocking totals were designed to double the number of northern pike within one year. Increasing the pike population might result in controlling the bluegill (Lepomis macrochirus) numbers. However, heavy stocking failed to increase the northern pike population, while also no discernible effect on the bluegill population was noted. Population density of stocked northern pike declined drastically. About 6% of the stocked pike were caught by anglers in the first year after stocking; 25% to 30% of the stocked northern pike went over the Murphy Flowage dam in the spring of 1965. Maximum downstream movement appeared to occur during the spawning period, involved largely stocked fish and was significantly related to population density. In addition, pike were also lost as a result of observed natural mortality, caused by a parasite, Myxobolus, believed to have been introduced at the time of stocking.

Similar events that appeared to be related to density occurred in George Lake (Minnesota) (Groebner, 1964). The greatest natural mortality (78%), and many individuals in poor condition, occurred when the population was highest.

Stocking of summer pike and winter rescue pike can result in considerable return and short-term improvement of fishing success and harvest (Krohn, 1969; Maloney and Schupp, 1977). The relative contribution to the sport fishery was, according to the authors, highest in a lake where the abundance of resident pike was low. Successful results of winter-rescue pike stockings in Grace Lake (Minnesota) are reported by Weslow and Olson (1962). The anglers caught 44.1% of the stocked pike in the course of two complete angling seasons. An additional stocking of pike in the year that followed did not result in a comparably successful angling harvest.

5. NORTHERN PIKE CULTURE

5.1 Generalities

Northern pike can be provided to the fishery manager by four general methods (Clark, 1974):

(1) salvage of trapped fish from lakes, rivers, reservoirs, irrigation systems, winterkill lakes (Johnson and Moyle, 1969; Maloney and Schupp, 1977);

(2) management of (artificial) spawning marshes, usually located adjacent to a lake, and needing additional spawners (Franklin and Smith, 1963; Forney, 1968; Williams and Jacob, 1971; Royer, 1971; Priegel and Krohn, 1973; Fago, 1977;

(3) extensive ("pond") culture (Johnson, 1958);

(4) intensive culture (Huet, 1972a; Graff, 1978).

An interesting source of information on the state of northern pike culture in Europe at the beginning of the 1940s is Heuschmann (1940). More recent studies on pike culture summarizing the experience and literature on the subject are Johnson (1958) for extensive culture; Drimmelen

(1969) for extensive and semi-intensive rearing in the Netherlands; Huet (1972, 1975) for a summary of the state of the art in the 1970s; Graff (1978) for a summary of the North American experience with intensive rearing of the species; Billard (1983) for a review of culture techniques with special attention to artificial spawning and management of stocked northern pike.

Other literature sources for the culture of northern pike are Kostomarov (1961), Koch, Bank and Jens (1976), Schäperclaus (1961) and Steffens (1976).

5.2 Terminology

In northern pike culture the terminology of the developmental phases of the fish have not been standardized. In this synopsis the terminology of Balon (1975a) is used. For a detailed description of pike development see Sections 2.2 and 2.3.

Three phases are distinguished before the pike starts active feeding. The fertilized egg passes through a cleavage phase and becomes an embryo. After hatching, the pike is called eleutheroembryo. Other terms used in practice and literature are egg and eyed egg. The words larva and fry are used for the embryo in its hanging phase.

The pike is termed larva from the moment when transition to exogenous feeding begins to the moment of complete differentiation of the median finfold and formation of the definite organs (5 to 6 cm). In the early steps of this developmental period it is called protopterygiolarva (fry in pike culture). The following steps of the larval period are part of the pterygiolarval phase. The pterygiolarvae are also called fry, larvae and fingerlings.

Juvenile pike resemble adults but have not yet reached maturity. They are usually called fingerlings and their length varies between about 6 cm and 20 cm.

5.3 Capture of Spawners

The availability of spawners depends mainly on two factors: (i) natural habitat, (ii) breeding stocks kept at the farm.

Northern pike spawners are caught in spring on the spawning grounds or on their run to the breeding grounds (Drimmelen, 1969). They are taken with hoopnets or fykes in North Dakota (Hiner, 1961). The rectangular shape of the "hoops" prevents the wind and wavec from rolling the trap. A 75-ft lead guides the fish into the mouth of the trap. In Valley City, North Dakota, the trapped adults are carried from the traps to a pontoon spawning barge in an aluminium boat which serves as a base for the actual spawning operations.

Sorenson, Buss and Bradford (1966) described the operation with a limited number of brood fish for Pennsylvania. Spawning pike were captured with trapnets. It was found that knotless nylon trapnets and dip-nets, unlike the knotted cord previously used, did not produce heavy wear on the brood fish. All captured fish were brought to a hatchery for spawning. Collection of pike in a combination carp-trap and water-control structure located on the spawning marsh side near a bridge crossing the outlet of the marsh, is described for Clear Lake, Iowa, by Moen and Lindquist (1954). Part of the collected pike was stocked in the Ventura March - which drains into the lake. The remainder of the trapped pike were checked each day to find ripe fish for hatchery use.

Drimmelen (1969) concluded on the basis of German literature that capture of spawners by means of electrofishing can be executed without damaging the fish or the gonads. Use of electrofishing in the capture of spawners is also reported by the Conseil supérieur de la pêche (1972).

In the Netherlands spawners are captured with fyke nets, bearing wings, ranging in size from 2 to 7 m. The fyke nets are placed at the mouths of or in ditches, near the reedfields (Phragmnites) (Drimmelen, 1969). High mortality of stripped spawners is reported by the author who suggests that the method of capture and stripping can be improved to decrease mortality.

5.4 Broodstock in Captivity

McCarraher (1957) described the natural propagation of northern pike in small drainable ponds in Nebraska. The ponds used in the study were winter-fallowed and had to be provided with forage fish and adult northern pike spawners in spring. The author concluded that this procedure results in a production of juvenile pike that is not as high as in hatchery-produced fish. The juveniles must be cropped when they have reached about 5 cm in length. Rearing of larger pike is possible provided that the total number of pike in the pond is greatly reduced. Stocking of about 12 females per hectare seems to be optimal. No correlation could be observed between the use of additional females and the total crop of juveniles produced.

Pecha (1983) reported that the fish hatchery of Tabor in southern Bohemia (Czechoslovakia) produces yearly 20 million embryos and as many eleutheroembryos for restocking in rivers for sport-fishery purposes. The broodstock needed for this production amounts to 5 t. These fish are held in specially prepared winter ponds which have shallow grass-grounds areas during the winter. The brood fish are captured by netting when they come to the shallows to spawn.

Horvath (1983) described the method of keeping northern pike in winter ponds together with forage fish in Hungary. In early spring, pike males and females are injected with carp pituitary extracts and eggs are stripped and fertilized.

Steffens (1976) referred to the results of East European research, which indicated that it is possible to catch northern pike in autumn and keep them in ponds during winter. The egg numbers of these pike are lower than those in pike captured during spring.

According to Montalembert, Bry and Billard (1978), ovulation does not occur spontaneously under confined conditions. Most females undergo ovarian atresia and may die after a few weeks. In small ponds, however, ripening can be attained. Natural spawning and fertilization may then also take place (Schäperclaus, 1961).

Huet (1972a, 1975) described experiments at the research station of Linkebeek (Belgium), aimed at obtaining growth and sexual maturation of brood fish in small ponds. Over a period of several consecutive years, maturation of at least 15 out of 18 females have been regularly obtained. The pike were not hypophysated.

Neveu and Bry (1983) applied the same method in France using stocking rates of 500 kg of female pike per hectare in 300-m^2 ponds and adding forage fish in quantities equivalent to 60% of the biomass of pike. The pike stayed about four months in the ponds and a high proportion of the females had ovulated by the end of February. These fish were used as spawners.

Steffens (1976) considered the method of keeping northern pike brood stocks in hatchery ponds unsuitable for increasing spawning stocks. Graff (1978) considered the maintenance of a "domestic" population of muskellunge (Esox masquinongy) as a brood stock in a hatchery as not entirely successful.

Recent experiments on managed natural spawning in small drainable (200-2 000 m^2) grassy and shallow ponds in France were described by Bry et al. (1983) and Bry, Souchon and Neveu (1984). The method is based on the introduction of one female and two males in the pond by mid-February. A comparison of the production of young pike from these ponds with the production of ponds stocked with pike embryos showed no significant differences in numerical density and biomass of the young harvested in mid-May. The average egg-to-larvae (4-5 cm) survival rate was about 4% in the case of managed natural spawning. This rate was 1.3 to 5-fold lower than the survival rate of the embryos stocked in the parallel ponds. The method of managed natural spawning limits the heterogenocity in size of young northern pike and permits the possibility of relatively homogeneous growth.

Goubier and Souchon (1982) studied the feasibility of delaying spawning of northern pike in order to improve the standing crop of pike juveniles in culture ponds. By keeping brood fish together with forage fish at a lower temperature than that of their usual environment during winter and early spring, spawning was delayed by 1 to 2 months as compared with a control lot. The experiment was executed under natural photoperiodicity conditions. Production of pike juveniles obtained from such breeders was comparable to that obtained from the control lots. Growth of the progeny of the spawning-retarded breeders was better compared with the growth of the progeny of control breeders.

5.5 Genetic Selection

Genetic selection of northern pike stocks has not been attempted. The data summarized in Section 1.2.4 do not demonstrate a high level of intraspecific genetic variability. Hybridization of esocids is treated in paragraph 1.4.1 of this synopsis.

Management programmes need to protect the genetic resources of the species by preventing the loss of genetic variability within individual populations or stocks and within the species as a whole. Therefore studies as Koppelman and Philipp (1986) on the genetic applications in muskellunge management are also important for northern pike management.

5.6 Spawning and Hatching

5.6.1 Spawning for culture purposes

5.6.1.1 Managed spawning in marshes and ponds

Several authors described the management of spawning marshes (Carbine, 1941, 1943; Royer, 1971; Forney, 1968; Franklin and Smith, 1963; McCarraher, 1957; Fago, 1977). Souchon (1983) summarized data on the reproduction of northern pike under natural conditions and in managed spawning situations.

Fago (1977) distinguished five categories of factors believed to influence northern pike production in spawning marshes:

- spawning stock,
- aquatic vegetation,
- egg survival,
- food supply,
- physical and chemical factors.

The sections dealing with reproduction and development include the data obtained in spawning marshes. Therefore, the management of spawning marshes is not further elaborated here.

The experiments on managed natural spawning in small drainable ponds in Belgium and France are described by Bry et al. (1983), Bry, Souchon and Neveu (1984) and Huet (1972, 1975).

5.6.1.2 Artificial spawning

A. Fertilization methods

Drimmelen (1969) and Huet (1975) reviewed the techniques and methods of artificial fertilization used in northern pike hatcheries. In general, three methods can be distinguished:

(1) Wet system. The sexual products are stripped simultaneously into a pan filled with water. According to Huet (1975), this method - the oldest artificial insemination method (Drimmelen, 1969) - is not used in pike culture any more.

(2) Dry system. The eggs are stripped in a dry pan. Thereupon sperm is mixed with eggs, and water is added afterwards. This method results in extended fertilization times compared with the wet system method. According to Huisman (1975), it was introduced in 1870 by the Russian, Wrassky.

(3) Superdry system. This method is based on the dry system method, but here the eggs are stripped onto a screen to remove the ovarian fluid. Under superdry conditions the fertilization time is extended.

Useful data on the fertilizing methods can be found in the study of Elster and Mann (1950), which deals with various aspects of the physiology of fertilization.

B. Spawning techniques

Sorenson, Buss and Bradford (1966) described the use of a blood pressure cuff to strip the eggs from mature female pike.

Huisman, Koeman and Wolff (1972) described an operative method to obtain sperm. The gonads were extracted from the male pike after which sperm were released by pressure. The operative method is also recommended by Sorenson, Buss and Bradford (1966).

Kennedy (1969) observed that in hand-stripped and artificially fertilized pike eggs the percentage of unfertilized eggs is very much greater than in the case of artificially fertilized salmonid eggs.

5.6.2 Hypophysation

Anwand (1963) used hypophyses extracts of bream (Abramis brama) and "Gonabion" - hormones of warmblooded animals - to induce spawning in female northern pike. Hypophysation with carp pituitary glands was described by Sorenson, Buss and Bradford (1966). Huisman, Koeman and Wolff (1972) reported a mean fertilization percentage of 12.4% for the eggs obtained from 13 pike hypophysized with carp pituitary glands. The authors also reported a decrease in fertilization when the spawners originated in DDT-polluted waters.

Montalembert, Bry and Billard (1978) induced maturation and ovulation in submature females with a single injection of partially purified salmon gonadotropin. Ovulation occurred four days after the treatment and was always over 50%. The authors also studied hormonal stimulation of sperm release.

Bry, Billard and Montalembert (1978) studied the efficiency of various hormonal treatments on oocyte maturation and ovulation in submature females of northern pike. A dose of 0.1 mg of partly purified salmon gonadotropin per kilogramme body weight, produced satisfactory ovulation (87%). Ovulation occurred four days after treatment. A dose of 0.03 mg of purified salmon gonadotropin per kilogramme body weight induced oocyte maturation but not ovulation. A review of insemination techniques developed in France was presented by Billard et al. (1976).

Pourreau et al. (1983) found that the number of ova obtained by manual stripping 50 degree-days after injection of partially purified salmon gonadotropin in March, appeared to be significantly dependent upon the oocyte stage at the time of treatment. Natural spawning resulted in a higher number of ova (15 000/kg versus 24 000/kg).

Simontacchi et al. (1983) obtained spawning in captive female northern pike by treatment with pike pituitary hormone (one gland per fish), followed by a treatment with progesteron (10 mg/kg body weight). The biosynthesis and plasma levels of ovarian steroids were studied by the authors.

Stimulation of sperm release was most effective with a dose of 100 mg progesteron per kilogramme body weight (Montalembert, Bry and Billard, 1978). The males delivered 100-150 µl of sperm at the first sampling prior to treatment. After treatment, twice as much sperm were delivered by the pike.

Billard, Marcel and Montalembert (1983) found that the number of spermatozoa produced by 1-year-old male pike varied between 400 and 888 10^9 spermatozoa per kilogramme body weight. When the pike were confined in a hatchery tank, the number of spermatozoa recovered was low. In a grassy pond, the number of spermatozoa was high, but variable among individual pike. Administration of various pituitary gonadotropin extracts considerably increased the number of spermatozoa emitted. The duration of the response was proportional to the dose and varied between 8 and 24 days.

5.6.3 Preservation of gonadal products

The activity time of spermatozoa in water at 5°C is 2 min, at 10°C 1.5 min and at 15°C 1 min (Lindroth, 1946). In water, it can be prolonged by using NaCl solutions (4^o/oo together with urea (3^o/oo) (Woynarovich, 1962). These solutions are also used for removing the sticky layer from egg shells (Huisman, 1975). After one hour, the eggs are washed in a second solutin of 85^o/oo urea. Tannic acid - although toxic for eggs - is still used to remove the sticky layer from pike eggs.

Billard (1978) reported that sperm motility times at 10°C were dependent on the diluent. In fresh water, sperm motility ranged from 0.5 to 1 min, while in physiological medium its average duration was 3-5 min. At 4°C, duration of viability of non-diluted northern pike sperm was 24 h. Lindroth (1946) and Elster and Mann (1950) reported that under extra dry conditions, sperm could be held viable for 2 days when temperatures were in the range of 2°-4°C.

Graff (1978) reported that limited amount of work had been done on storage of esocid sperm by utilizing 5% dimethyl sulphoxyde and 5% ethylene glycol as preservatives. Montalembert, Bry and Billard (1978) found considerable variability in the fertilizing capacity of sperm after cryopreservation, depending on the male donor. The authors suggest that a careful adjustment of the steps of freezing, freezing-storage and thawing procedures should allow progress toward the achievement of ideal conditions. Koldraz and Moczarski (1983) reported from Poland results of tests with freezing northern pike milt in liquid nitrogen.

Duplinsky (1982) studied the activity of sperm from northern pike at pH 3.9 to 7.9. Compared to the sperm of the chain pickerel, Esox niger, the sperm of northern pike remained motile only for short periods of time. No swimming activity was observed at pH values lower than 5.4. The results of this work also showed a strong trend toward increased time of activity with increasing pH. Esox niger sperm proved to be more acid-resistant. According to Lindroth (1946) and Elster and Mann (1950), the optimal pH for fertilization is 7. Montalembert, Bry and Billard (1978) tested the effect of ova retention on fertility. Ageing of ova is a rapid phenomenon. In "in vivo"-experiments, the drop in fertility of the eggs occurred within 2 days. According to Lindroth (1946), the micropyle of the ova closes within 2 min after contact with water.

5.6.4 Insemination diluents

Montalembert, Bry and Billard (1978) and Marcel, Montalembert and Billard (1983) developed insemination diluents for gonadal products of northern pike. According to the first authors, sperm dilution in artificial insemination should not exceed 1:1 000. The diluent used was a solution of NaCl buffered with 0.02 M Tris and 0.05 M glycine.

Marcel, Montalembert and Billard (1983) developed an insemination diluent characterized by a pH of 9 and an osmotic pressure of 250-300 mOsmol. This pH is higher than the reported optimal value for fertilization (Elster and Mann, 1950; Lindroth, 1946). Sperm fertilizing ability was satisfactory for 6 min when the spermatozoa were transferred to this diluent, while it was zero after 2 min in fresh water. In the diluent, the ova were still fertilizable after 32 min, while in fresh water their fertilizability decreased after 4 min.

5.6.5 Anaesthetization

The use of anaesthetics is described as a major contribution to an orderly spawning procedure by Graff (1978). Schoettger and Steucke (1970, 1970a) reported good results with mixtures of MS 222 and quinaldine used as an anaesthetic during transport and artificial spawning of large mature northern pike. Quinaldine and MS 222, at concentrations within the ranges of 10 to 20 ppm and 100 to 150 ppm, respectively, quickly anaesthetized northern pike. Quinaldine fails to block all reflex activity, but fish tolerate relatively long exposures. MS 222 blocks effectively the reflex activity, but the fish tolerate less exposure than those treated with quinaldine. Allen, Luhning and Harman (1972) measured residues of MS 222 in muscle tissue of pike. The traces dissipate rapidly from the muscle when fish are withdrawn from the anaesthetic and are near the background readings of the controls within 24 h.

Huisman (1975) mentions less costly chemicals as benzocaine - a local anaesthetic in human and veterinary medicine - and chlorobutanol as alternatives to MS 222. According to Huisman (1975), chlorobutanol can be used successfully for most fishes in a concentration of 1 g/litre.

According to Steffens (1976), the method to anaesthetize spawners is not used in practice in the German Democratic Republic.

5.6.6 Incubation of eggs and embryos and hatching

Hatching generally takes place about 120 degree-days after fertilization. The conditions required for the incubation of eggs and the hatching of the pike embryos were recently reviewed by Chauveheid and Billard (1983). Older descriptions, reviews and summaries of incubation methods and techniques can be found in Drimmelen (1969), Huet (1972, 1975), Huisman (1975) and Timmermans (1979).

Pecha (1983) gave a description of the methods used in the fish hatchery of Tabor in Czechoslovakia which is specialized in the production of embryos and eleutheroembryos for stocking in rivers.

In Holland, a cone-shaped jar with a top angle of 36° is used. The advantage of this jar is that dead eggs sort out at the periphery and can be siphoned off very easily (Huisman, 1975). Other types of incubators are described by Chauveheid and Billard (1983) and Huet (1972). Rahn (1978) found the quantity of water flowing through the incubator to be a factor of importance for successful rearing of pike eggs.

Treatment of eggs to prevent infections or to cure them if they occur is common in hatchery procedures. A variety of chemicals, such as Malachite green, methylene blue, formalin, acriflavine, Wescodine, are available for this purpose (Sharp, Bennnett and Saeugling, 1952; Bootsma, 1973).

Hatching normally takes place in the incubator. It can be accelerated by increasing the temperature (Willemsen, 1959; Drimmelen, 1969). In Holland, the hatching procedure, described by Sorenson, Buss and Bradford (1966), is applied. One litre of fully-developed pike embryos are placed in a pan filled with 8-9 litres of water and placed in a heated room, so that over a period of one or two hours the temperature rises to about 17°C (normal incubation temperature is 10°-12°C). The oxygen content drops from about 50% to 25%. With this procedure the embryos hatch within 60 to 120 min, whereas normally they hatch after more than 6 h (Huisman, 1975).

5.6.7 Rearing of eleutheroembryos

After hatching, most eleutheroembryos prefer to attach themselves to materials such as wood, textiles or plants to absorb the yolk. During the development phase, it is easy to siphon off dead eggs and egg shells from the bottom of the incubation basin, tray or trough. Huisman (1975) considered the use of a screen with mesh of a size that allows the eleutheroembryos to pass through but arrests the dead eggs as the easiest and most successful method to obtain clean larvae. Chauveheid and Billard (1983) give a detailed description of the separation of dead eggs from eleutheroembryos.

Huisman (1975) considered inadequate the use of aquatic plants such as Stratiotes aloides as hanging substrate because of the disadvantage of pollution. In the Netherlands, pike are kept in a clear environment during the eleutheroembryo phase, which usually lasts for about 8 days in pike culture at temperatures of about 12°C. After hatching, the pike are transferred to inset trays of a Californian trough to pass this phase. According to Johnson (1958), eleutheroembryos of E. masquinongy are kept in the same jar in which they were incubated. Hiner (1961) described the same method for northern pike and thus showed that hanging is not strictly necessary for the eleutheroembryos.

5.7 Rearing of Larvae and Juveniles

5.7.1 Rearing of larvae

The production of pike larvae is decribed in detail by Huet (1972, 1975). The author distinguished three principal methods of rearing the larvae:

(1) extensive rearing in drainable ponds or inundated grasslands;

(2) semi-extensive rearing in plankton-enriched ponds;

(3) intensive rearing in tanks.

Timmermans (1979) used the same classification in his paper that updated the extensive compilation of data on this subject by Huet (1975; partly based on Drimmelen, 1969).

5.7.1.1 Pond culture

This type of pike culture is based on natural feeding in ponds. It is the oldest form of larval rearing. The ponds are in the range between 0.5 to 5 ha and rarely over 0.5 m deep. Later in the season, most ponds are used for carp production.

The stocking density and the production period may both vary considerably. Fertilization of the ponds is recommended by most authors.

Graff (1978) described the extensive culture of northern pike as the succession of techniques for the capture of wild brood stock, spawning, incubation of eggs, and stocking of eleutheroembryos in nursery ponds where optimum conditions for survival have been established. When the zooplankton-feeding larvae in the nursery ponds attain 3.8 to 4.5 cm in length, they are transferred to growth ponds where minnows (or cyprinid and/or percid fry) are abundant. There are variations in the procedure, but the principle is the same; it consists of putting the esocids in a quasi-natural environment and in ensuring that food is always available. A valuable source of practical information on extensive pike culture is Johnson (1958). The Conseil supérieur de la pêche (1972) described the foundation of an experimental pike-culture plant based on the principle of extensive culture techniques in Vivier du Grès (Oise, France).

The stocking density and the production period may vary considerably (2 to 80 fish/m^2 and 2 to 7 weeks, respectively), this depending primarily on the productivity of the water and the pike size required at harvest time (Timmermans, 1979). The survival rate varies from 50 to 5% or less. There is a negative correlation between the survival rate on the one side and the pond size stocking density and length of the production period on the other.

According to Howard and Thomas (1970), the production of ponds stocked with eleuthero-embryos can be increased when the ponds are also stocked with eyed embryos. This method requires the presence of flooded vegetation in the pond.

Souchon (1980) studied the stocking of eleutheroembryos in three similar 400-m^2 ponds with different densities: 2.25 fish/m^2, 3.75 fish/m^2 and 5 fish/m^2. The survival rates of the larvae were identical in the three ponds after 45 days (23%); the average length of the fish was the same (9.5 cm); the total biomass of juveniles was a direct function of the initial number of pike stocked.

Bry and Souchon (1982) compared the production of pike juveniles in ponds by means of stocking adult spawners and by means of stocking eleutheroembryos. They concluded that the production was comparable. Royer (1971) also studied this problem, but his experiments did not lead to valid conclusions because the hatchery-reared eleutheroembryos suffered high post-stocking mortality.

In accordance with Bry and Gillet (1980), Bry and Souchon (1982) reported that siblings generally give higher yields than mixed contemporary families. The removal of post-spawning adults does not appear to be strictly necessary, provided that a minimum amount of adequate forage-fish is supplied.

A different method of extensive culture is practised in managed spawning ponds. It is occasionally used in the USA (Fago, 1977; McCarraher, 1957), Belgium (Huet, 1972a) and France (Bry et al., 1983; Bry, Souchon and Neveu, 1984).

The use of inundated grasslands for rearing northern pike was formerly common in the Netherlands (Huet, 1975). The survival of pike with this method was variable (Drimmelen, 1969).

Steffens (1976) cited an experiment in which pike juveniles were produced in brackish water with a salt content of 3 to 4°/oo.

Dexter and McCarraher (1967) reported that Cyzicus mexicanus constituted a pest in northern pike rearing ponds in Nebraska; fish production dropped, while labour in handling fish increased. The authors considered the prevention of the shrimp eggs to dry up and the addition of 1 ounce of liquid parathion/ 10 000 gal of pond water (10 mg/litre), effective measures for controlling the pest.

5.7.1.2 Semi-extensive rearing

In this type of culture, the pike are reared in small ponds with a surface area under 0.2 ha, to which plankton is provided daily. The plankton is obtained from carp production ponds or from ponds that are reserved and specially fertilized for this purpose. The method was formerly used in the Netherlands, but the survival of young pike was variable and generally low. The production per unit of surface area is higher as compared to the extensive culture methods, but the same disadvantages pertain, albeit, to a lesser extent. However, an additional risk of pollution and development of filamentous algae is introduced when excess plankton is administered (Timmermans, 1979; Huet, 1975).

5.7.1.3 Intensive culture

Graff (1978) described the development of esocid culture techniques from pond culture to intensive culture. According to the author, the foundation for intensive culture of pike was laid by Sorenson, Buss and Bradford (1966). The art was influenced by the discovery that esocids could be reared on artificial and dry diets (Graff and Sorenson, 1970). According to Timmermans (1979), intensive culture was first used by Einsele (1949) in Austria. Anwand (1967) reviewed techniques used in intensive culture of pike larvae in Austria and Sweden. Huisman (1975) gave a review of the intensive culture techniques used in the Netherlands. Huet (1975) and Timmermans (1979) gave detailed reviews of the state of the art of intensive culture of northern pike.

The culture of pike larvae is carried out in tanks with intensive plankton feeding (Huisman, 1975), in cages of fine mesh (Lukowicz, 1983; Jäger, Dauster and Kiwus, 1980), or in 500-litre silos (Ziebarth, 1983).

Rectangular or round tanks are used, mostly made of fiberglass. This enables easy and rapid cleaning, which is very important in this hygiene-sensitive culture.

The stocking rates vary from 500 to 30 000 fish per square metre, but it is recommended not to exceed stocking densities of 9 000 fish per square metre. In practice, 3 000 fish per square metre is usually used. The production period may vary from 2.5 to 5 weeks to obtain pike larvae of 3 to 5 cm. Survival is on the average 75% and varies between 50% and 90%.

The water flow allows for one renewal every 8 h, with or without additional aeration at the point of entry into the tanks. The discharge water should still contain at least 5 mg of oxygen per litre (Steffens, 1976). The water temperature should be between 15° and 20°C.

5.7.2 Raising juvenile northern pike

Raising one summer of 1-year-old juvenile pike in ponds usually represents a supplementary production, because the carnivorous pike cannot be packed together after reaching the age of 2 months (Huet, 1972). It is possible to raise pike up to one summer or one year in ponds in which they are not a risk for the principal fish species being raised. In ponds stocked with carp of 3 years, a secondary production can be obtained and, at the same time, the pike represents a means ("Polizeifisch") of controlling unwanted fry, such as perch (Drimmelen, 1969; Kostomarov, 1961).

Klupp (1978) described the production possibilities of raising pike juveniles raised in carp ponds. According to the author, pike could be produced in sufficient quantities to meet the demand for this species by angler associations without disturbing the carp production.

Anwand and Grohmann (1967) stocked northern pike eleutheroembryos in carp ponds. According to these authors, densities varying from 1 200 to 2 500 S_0 per hectare are used in the German Democratic Republic for this purpose. The authors found, however, that northern pike production could not be increased by stocking densities above 550 to 1 000 S_0 per hectare. Anwand and Grohmann (1967) advised stocking densities up to 1 000 S_0 per hectare to obtain productions of pike varying from 50 to 150 S_1 per hectare (3 to 13 kg/ha) with an average weight of about 100 g.

Demchenko (1959) found that simultaneous breeding of 2-year-old carp and commercial pike juveniles in drainable fattening ponds permits food resources of ponds to be utilized more fully. Moreover, it gives an additional yield of 40-60 kg per hectare of northern pike. The number of food competitors for carp is reduced and this increases the yield of carp by 9% to 10%. According to Anwand and Grohmann (1967), Demchenko (1959) used stocking densities of 100 to 400 S_0 per hectare to realize this very high northern pike production in carp ponds (Drimmelen, 1969).

Martyshev (1983) used pike larvae as additional stocking material in carp ponds. The larvae (2 to 3 cm) are not planted in the ponds before the 9th to 10th day from the moment of their changeover to active feeding, and not later than the 18th to 19th day after hatching. The author reported that the rate of additional stocking of juvenile northern pike in carp ponds in the USSR is usually taken as 70 to 100 fish per hectare (without supplying forage fish) or 200 to 250 fish per hectare (with special rearing of forage fish). In the latter case, the stocking is made with sexually mature Crusian carp (Carassius carassius) which produce progeny in the ponds. The rearing of forage fish ensures normal growth of pike and gives a survival rate of 50% to 55% of the total stocked material.

In general, adult stocking procedures are not often used in ponds, because of various difficulties (cannibalism and competition) that adults pose when they are in the same pond as their offspring (Clark, 1974).

5.7.3 Food, feeding

When yolk resorption is almost complete and exogeneous feeding commences (see Section 2.3.4), hatchery-propagated pike larvae are stocked in ponds, inundated grass lands, aquaria, tanks or cages.

The production of natural food in extensive culture was described, together with the preparation and management of rearing ponds, by Johnson (1958) for the culture of Esox masquinongy in Wisconsin. Graff (1978) considered this description as the standard reference on extensive culture of esocids.

The basic food for pike in extensive culture is provided by zooplankton culture. In Wisconsin, Daphnia pulex was selected primarily because if feeds on organic detritus (Johnson, 1958). Torula candida, a wood yeast, was used directly as food for the Daphnia, thus circumventing many steps in the food chain. Daphnia is produced in ponds as well as in artificial culture.

Plankton for the culture of pike in tanks or aquaria in hatcheries, or for pike culture in plankton-enriched rearing ponds, is collected either in big carp ponds with a plankton net mounted on a boat (Timmermans, 1979; Huisman, 1975: Netherlands) or in small ponds that are reserved and specially fertilized for plankton production (Lukowicz, 1983; Balvay, 1983; Johnson, 1958: Federal Republic of Germany, France, USA). In Austria and Switzerland, plankton for pike culture is collected from natural waters (Huet, 1975). Kriegsmann (1970) described the automatic provision of plankton from ponds and natural waters in the culture of pike, grayling (Thymallus thymallus) coregones and trout. Anwand (1967) described the "Kriegsman system" from the German Democratic Republic.

In cage culture of pike (Lukowicz, 1983; Jäger, Dauster and Kiwus, 1980), the zooplankton needed to feed the larvae is attracted to the cage by a lamp (100 W, 24 V) fixed in the middle of the 2x2x2-cm cage.

At 4 to 8 cm length, pike become piscivorous and hence fish forage must be supplied in pike culture. In Wisconsin, forage fish is provided by the propagation of suckers (Catostomus commersoni) (Johnson, 1958) and other fish species. Fathead minnows (Pimephales promelas) are trapped during the winter months in freeze-out waters and stocked in outlying ponds to provide a natural brood stock of forage fishes. For the production of summer pike, minnows are hauled to supply forage for hatchery ponds that have a low supply of forage fish.

Artificial diets, developed for other fishes (catfish and trout), were not satisfactory for esocids. Early efforts at intensive culture of esocids utilizing dry diets were plagued with problems, some due to nutritional deficiencies and poor acceptance of the diet, others to lack of knowledge about feeding methods (Graff, 1978).

Smisek (1968) fed pike larvae with mixtures of natural (plankton) and supplementary (spleen) feeds in the phase of transition from endo- to exogenous feeding. The mixture was willingly accepted by the young larvae. Graff (1968) reported successful feeding of pike larvae with a diet of trout starter only. Later in the development, a trout crumble was given. One lot of pike fed actively for 33 days. The author also reported successful conversions to dry diets of pike that had been fed Daphnia or graded Daphnia.

Graff and Sorenson (1970) raised pike larvae to a size of 12.7 cm on a dry diet. The authors found that a diet suitable for trout may not meet the nutritional needs of northern pike;

some fish had undershot or dropped jaws. Conversion of pike reared on a dry diet to natural food did not appear to present a problem.

Kaushik, Dabrowski and Luquet (1985) raised pike embryos and larvae with a high protein dry diet (protein: 60% dry mather (DM), fat: 18% DM, ash: 7.6% DM and energy: 23.07 kJ/g DM). Information on raising technique and mortality was not reported by these authors. After 40 days of rearing with the artificial diet a group of juveniles was separated and fed on live carp larvae. It was found that the specific growth rate of fishes reared on artificial diet was higher than that of the piscivorous fish.

Huisman (1975) reported from the Netherlands that a very small number of pike larvae were raised to a length of about 25 cm with a dry diet consisting of pellets. The author reported that it had been impossible to start feeding the pike with very small pellets.

Timmermans (1979) summarized French research on the development of artificial feeds suitable for the production of juvenile pike and drew the following conclusions:

- theoretically it was possible to feed pike larvae to the juvenile phase with artificial feed, but mortality was considerable especially during the first 10 days;

- when larvae were fed with live zooplankton during the first 10 days, conversion to a diet of frozen plankton and later artificial feeds took place without difficulty;

- up to the age of about a month, the young pike only took moving objects in their direct proximity. Later on the larvae actively went after the feed when it was administered;

- larvae of about 4 cm that had been adapted to artificial feeds did not show cannibalistic tendencies, provided the density did not exceed 1 fish/2 litres. However, these pike resorted back to their predatory instincts as soon as the artificial feeding was suspended.

Nutritional requirements and feeding of northern pike were reviewed on the basis of literature and unpblished data by Ketola (1978). According to this author, the success of raising pike larvae with formulated feeds resulted in moderate success and survival. Graff (1978) and Orme (1978) reported from tests of feeding formulated feeds to esocids that:

- most attempts to start pike on dry feeds in the latest steps of embryonal development resulted in failure;

- the greatest success with dry feeds was achieved when pike was in the larval phase of development;

- the tiger muskellunge (pike x muskellunge) was the most adaptable to formulated feeds, which are now offered to the hybrids on a production scale.

Contrary to Graff (1978), Timmermans (1979) concluded that in pike culture we are still far from a completely artificial feeding as is practised in the rearing of salmonids.

5.7.4 Harvest

Lemaire (1974) described a draining equipment that facilitates the recovery of small pike from fish ponds. It involves the excavation of a large sump in which the inlet of a suction pump is placed. The bed of the sump is 0.8 m below the bottom of the pond. Water enters a sack made of knotless netting which is located inside the sump. Water current from the pond to the sump is controlled.

5.7.5 Transport

Huet (1975) indicates that the development of transport techniques for northern pike embryos and larvae or juveniles in double polyethylene bags can be considered as an important improvement. Transport can take place under oxygen after use of tranquilizer and under low temperatures. According to Anwand (1967), one can transport 20 000 embryos or 2 500 larvae of 3 cm length during 2 to 4 h in a sack of 30 litres containing 15 litres of water.

6. REFERENCES

Introduction

In the bibliography all references are cited according to the FAO rules. Titles of publications in languages other than English, French or German are given in English. English titles not provided in the original publication appear in brackets. The language of the original publication other than English, French or German and that of any summaries provided, is indicated at the end of the bibliographic details.

When the publication was not consulted in the original, the source for the reference is given after the bibliographic details. The abbreviations to serial reference sources in the bibliography are:

ASFA - Aquatic Science Fisheries Abstracts (FAO, Cambridge Scientific Abstracts)
SFA - Sport Fishery Abstracts (Department of the Interior, U.S. Fish and Wildlife Service, since 1986 Fisheries Review)
LWZ III - Landwirtschaftliches Zentralblatt, Abteilung III, Tierzucht, Tierernährung, Fischerei (VEB Landwirtschaftsverlag, Berlin, GDR)

For the literature survey the Zoological Record and the Biological Abstracts were also consulted. The systematic literature survey was concluded on 31 December 1984. Additional references were included when writing the manuscript.

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APPENDIX

Table with data on growth of northern pike in various waters

Location	Water type	Season	Year(s)	Male/ Female	Length at age in cm										**	*	Reference
					1 11	2 12	3 13	4 14	5 15	6 16	7 17	8 18	9 19	10 20			
Seibert Lake (Canada)		May	'71-'73	M	13,2	20,9	37,3	47,7	50,9	55,0	58,2	64,5	74,5	72,7	FL	S	Makowecki
	Lake	June			71,4	85,9	78,6	89,5	95,0								(1973)
				F	13,2	20,9	39,5	51,4	53,2	61,8	70,0	78,2	85,0	93,2			
					101,8												
Escabana Lake (USA)	Lake	Spring	'61-'63	M + F		36,7	48,7	53,9	60,7	66,0	69,6	75,9			TL	S	Kempinger and Carline (1978)
Bucks Lake (USA)	Lake	Spring	'61-'69	M + F	20,8	32,8	39,1	43,9	48,3	52,6	55,9	68,3	75,2		TL	S	Snow and Beard (1972)
Big Cedar and Gibert				M		47,0	53,8	55,4	58,2	61,0	64,5	66,5	70,6	74,2	TL	S	Priegel and
Lakes (USA)	Lake	Spring	'68-'69	F		52,3	56,1	67,6	69,6	71,6	75,2	83,8	92,2				Krohn (1975)
Lesser Slave Lake	Lake	Summer		M	9,6	15,1	21,4	28,8	29,7	41,9	48,1	53,7	58,8	63,3	TL		Miller and
(Canada)					68,8	76,0											Kennedy
				F	10,1	15,0	21,6	28,1	34,5	41,2	47,4	52,9	58,0	63,3			(1948)
					68,2	73,5	77,6	81,3	84,2	87,8	91,6	96,0	97,7	103,5			
Great Bear Lake	Lake			M	9,3	15,3	23,6	31,8	38,8	44,3	45,8	54,0	58,9	62,6	TL		
(Canada)					66,5	70,8	75,7	79,0	84,0	90,0	93,0	95,0					
				F	9,4	16,0	22,7	30,8	38,7	45,2	45,2	57,9	62,7	67,4			
					73,0	76,5	79,5	84,0	84,0	89,0	93,0						
Great Slave Lake	Lake			M	10,3	16,0	21,7	28,1	33,6	38,8	44,2	49,6	54,0	58,0	TL		
(Canada)					64,4	69,0	74,0	76,0									
				F	10,5	16,0	22,0	28,2	33,6	39,6	44,9	49,7	54,1	57,9			
					60,8	66,3	71,0	78,0	85,0	89,0	92,0						
Lake Athabaska	Lake			M + F	10,0	14,4	22,2	29,0	35,0	41,5	47,6	53,4	58,3	63,3	TL		
(Canada)					68,3	73,5	77,6	81,3	84,2	87,8	91,6	95,7	98,0	104,3			
Murphy Flowage	Reser-	Spring	'64-'68	M	38,1	41,1	51,1	47,8	51,3	stocked					TL	S	Snow (1974)
(USA)	voir			F	41,7	47,2	57,2	62,2	69,1								
				M	28,7	36,1	45,5	51,8	57,7	resident							
				F		39,4	51,3	63,0	67,8								
Clear Lake	Lake	Summer	'41-'55	M + F	30,7	42,2	51,8	61,7	69,3	92,2					TL	S	Ridenhour
Venture Marsh (USA)	Lake		'53-'55	M	29,7	41,7											(1957)
				F	31,2	49,8											
Saskatchewan	River	Summer	'40-'41	M	10,2		37,6	48,8	54,3	57,3	58,3	64,4	83,8		TL	S	Solman
River Delta (Canada)	delta			F		21,0	37,9	50,9	56,8	60,2	66,6	73,2	75,0	79,9			(1945)
					92,4	90,2	99,1	94,0									
Horseshoe Lake	Lake	Autumn	'71-'72			52,1	62,7	stocked							TL	S	Maloney and
(USA)			'74-'75			49,3	61,5										Schupp
			'71-'72			53,8	63,0	resident									(1977)
			'74-'75			54,4	57,9										
White Sand Lake	Lake		'71-'72			49,0	54,4	stocked									
(USA)						49,3	55,6	resident									
						51,8	57,7	stocked									
Edward Lake	Lake		'71-'72			49,5	55,8	resident									
(USA)																	
Lake Oahe (USA)	Lake	Whole	'65-'67	M	27,4	48,6	64,3	72,4	79,3	92,9	94,8				TL	S	Nelson (1974)
		year		F	28,7	54,1	70,1	79,7	90,7	94,8							
Eastern Lake Ontario	Lake	Summer	'72-'73	M	24,6	49,3	61,2	66,5	69,3	70,5	72,6	70,7			TL	S	source: Wolfert
Northern Canadian L.	Lake			F	24,0	51,5	67,3	73,0	76,7	78,6	77,1	72,9			TL		and Miller(1978):
Minnesota Lakes	Lake			M + F	10,0	15,6	22,3	29,6	24,2	41,6	46,9	52,4	57,0	61,1			Kennedy (1948)
Illinois Lakes	Lake				19,8	33,6	45,0	53,6	61,5	68,1	73,7	79,0	84,1	82,2			v.Engel (1940)
Wisconsin Lakes	Lake				25,2	44,5	53,4	60,0				96,5					v.Engel (1940)
Lake Erie	Lake				25,4	45,7	58,4	68,6	76,5	83,8	91,4	76,5	101,6	111,8			Clark and
Lake Ontario	Lake				29,0	44,7	53,9	60,0	64,8	67,1	72,7	77,5	79,2	83,3			Steinbach(1940)
					28,6	42,4	50,5	56,8	65,0								Greeley (1940)
Aral Lake (USSR)	Lake			M + F	13,8	26,2	35,6	45,5	51,0								Nikolski (1957)
Tschany (USSR)	Lake			M	15,1	25,6	34,9	43,1							TL		Nikolski (1957)
Peipus Lake (USSR)	Lake			F	16,1	28,1	37,5	47,5									
Ilmen Lake (USSR)	Lake			M	14,5	29,0	38,1	46,0									
				F	16,2	31,8	43,5	54,0									
				M + F	24,5	36,6	48,8	61,0									
Lake Pleshcheyevo	Lake			M	16,8	25,9	34,3	41,7	47,7	54,5	61,0	69,0			TL	S	Kulemin, Makko-
(USSR)				F	16,9	26,6	35,1	43,0	52,3	60,5	64,4	72,8	80,0				veyeva, Solo pova (1971)

** SL = Standard length, TL = Total length, FL = Fork length

* Age determination : S = Scale reading; O = Opercula reading; M = Marked fish

APPENDIX (Continued)

Location	Water type	Season	Year (s)	Male/ Female	1 11	2 12	3 13	4 14	5 15	6 16	7 17	8 18	9 19	10 20	**	*	Reference
					Length at age in cm												
USSR																	
Rybinsk Basin	Reservoir		1959	M + F	16,0	24,6	33,6	41,1	49,6	58,6	67,4	75,5	80,3		TL	?	Permitin*
Lake Nero	Lake		1934	M + F	15,4	27,1	36,8	46,1	54,1	60,2	67,2				TL	?	Kulemin*
Lake Galichskoye	Lake		1934	M + F	14,7	28,7	39,9	49,3	57,8	65,7					TL	?	Kulemin*
Lake Glubokoye	Lake		1968	M + F	16,8	23,0	28,5	36,1	41,0	46,1	53,0	58,1			TL	?	Shamardina*
Upper Volga	River		1944	M + F	12,5	22,5	31,0	40,6	47,5						TL	?	Kulemin* *) in Kulemin, Makkoveyeva and Solopova (1971)
Europe																	
15 North German Lakes	Lakes	Summer		M + F	15	28	38	48	56	68	74	84	87		TL	S	Bauch*
					93	94											
Boden Lake	Lake			M + F	12	28	42	56	68	77	89	98	107	114	TL	S	Bauch*
					120	127											
Hohenwarthetalsperre	Reservoir			M + F		39	47	61	72	90					TL	S	Bauch*
Große Jasmunder Bodden	brack water river mouth			M + F	16	30	41	49	57	61	70	72	76		TL	S	Bauch*
Greifswalder Bodden	brack water river mouth			M + F	18	34	45	58	68	82	94		107		TL	S	Hegemann*
						122											*) in Hegemann (1958)
Basins (German)		Spring	'65-'66	M + F	29,7										TL		Anwand (1969)
		Summer				35,3											
Poltruba	Ditch				19,8	33	42	54	68						TL	S	Johal (1980)
Procházkova	Ditch				20,9	37	50	59	73	83					TL	S	
River Berounka	River	Whole year	'69 and '75-'77		19,5	28,2	35,4	41,3	48,5	58,0	63,0				SL	S	
Some locations (Czechoslovakia)	Ditch				20,5	34,2	49,0	56,0	70,5	83,0					TL	S	
Orava Stausee (Czechoslovakia)	Reservoir		'67-'69	F	23,1	33,7	42,6	49,0	61,8	66,4	77,6	80,4	85,2	87,9	FL	S	Balon (1965)
				M	23,3	34,1	41,9	47,8	52,4								
Central Bohemian inundation area of the river Labe		Whole year			14,7	28,6	42,5	59,6	75,3	90,0	98,0				TL	S	Poupé (1974)
Two Dutch polders	Ditch	Winter	'64-'67	M	18	38	50	59							TL	S	Willemsen(1978)
				F	18	38	55	68									
			'64-'68	M	24	42	52	58	64								
				F	23	43	55	68	77								
Lake Warniak (Poland)			'66-'69	M + F	19,4	33,8	39,4	45,6	61,9	66,3	71,3	81,3	76,3	86,9	TL	S M	Ciepielewski (1973)
United Kingdom and Ireland																	
The river Nene	River	autumn	± '69		23	37	44	55	53						TL	S	Hart and Pitcher (1973)
Windermere	Lake		'39-'59	F	23,3	40,9	56,5	66,9	74,1	79,5	83,6				FL	O	Frost and Kipling (1967)
			'39-'58	M	23,0	39,4	53,0	59,3	64,5	68,0	70,9						
Slapton Ley + some other waters	Lake		'75-'77	M	23,4	39,8	51,3	57,4	60,8	64,1	67,1	70,4	69,3	75,1	TL	S	Bregazzi and Kennedy (1980)
				F	17,5	36,3	52,1	60,9	65,5	71,3	76,2	78,1	82,7			O	
					86,4												
The Robe river (Ireland)	River	Summer	'67-'69	M	19,2	34,7	44,8								FL	S	Bracken (1971)
				F	19,3	36,7	49,1										
The little Brosna-river (Ireland)	River	Summer	'67-'69	M	20,6	38,5	49,6								FL	S	
				F	20,0	39,7	50,0										
The Brosnariver	River	Summer	'67-'69	M	18,0	31,8	41,8								FL	S	
				F	17,8	32,8	44,9										
Camlin river (Ireland)	River	Summer	'67-'69	M	15,2	30,9	41,3								FL	S	
				F	16,4	29,9	42,8										
Lough Corris (Ireland)	Lake		1954	M	25,8	44,5	58,8	68,2	73,8	75,4							Healy (1956)
				F	25,5	48,0	63,0	76,9	85,7	93,6	102,6						
Lough Sillan (Ireland)	Lake		1966	M	25,5	38,3	49,2	57,0	62,6	68,0	72,3						Healy (1956)
				F	25,6	42,3	54,6	65,0	74,2	86,3							
Loch Choin (Scotland)	Lake	Winter	1955	M	7,0	18,4	39,1	36,3	41,6	46,4	49,9	53,2			TL	S	Munro (1957)
				F	8,6	19,3	31,1	40,3	47,4	53,6	57,4	63,4	70,0	87,0			
					90,8	93,0											
Sweden																	
Västra Sjö	Lake	Whole year		M	19,9	34,1	41,5								FL	S	Otto (1979)
				F	20,1	35,7	44,7										

** SL = Standard length, TL = Total length, FL = Fork length

* Age determination : S = Scale reading; O = Opercula reading; M = Marked fish

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