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and P. flavescens – 1,70(14)002,02

FAO Fisheries Synopsis No. 113

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Perca fluviatilis Linnaeus, 1758
and
Perca flavescens Mitchill, 1814

Prepared by

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CONTENTS

1 IDENTITY

1.1 *Nomenclature*

1.1.1 Valid names

Perca fluviatilis Linnaeus 1758 Ref: Systema naturae, ed. X, p. 289 and *Perca flavescens* Mitchill 1814 Ref: Report in part of Samuel L. Mitchill M.D. on the fishes of New York.

1.1.2 Objective synonymy

a) *P. fluviatilis*

Earlier names:

Perca major Schonevelde 1624
Perca fluviatilis major Aldrovandus 1638
Abbor suecorum Artedi 1738

Junior synonyms:

Perca vulgaris Schaeffer 1759
Perca helvetica Gronovius 1763
Perca italica Cuvier and Valenciennes 1828
Perca fluviatilis intermedius Svetovidov and Dorofeeva 1963

b) *P. flavescens*

Junior synonyms:

Perca americana Schrank 1792 (name preoccupied in *Morone*)
Centropomus luteus Rafinesque 1814
Perca notata Rafinesque 1818
Perca serro-granulata Cuvier and Valenciennes 1828
Perca granulata Cuvier and Valenciennes 1828
Perca acuta Cuvier and Valenciennes 1828
Perca gracilis Cuvier and Valenciennes 1828

1.2 *Taxonomy*

1.2.1 Affinities

– Suprageneric

Kingdom Animalia
 Phylum Chordata
  Subphylum Vertebrata
   Superclass Gnathostomata
    Class Osteichthyes
     Subclass Actinopterygii
      Division Teleostei
       Cohort Acanthopterygii
        Order Perciformes
         Suborder Percoidei
          Family Percidae
           Subfamily Percinae
            Tribe Percini

– Generic

Genus: *Perca* Linnaeus 1758

Ref: Systema naturae, ed. X, p. 289 (based on Artedi's description of 1738)

Diagnostic characters:

Refs: Berg, L.S. (1965): Freshwater fishes of the USSR and adjacent countries. Isr. Progr Sci Transl Jerusalem. Collette and Benarescu (1977): J. Fish. Res. Board Can. 34.

Body laterally compressed, ovate, covered with small scales. Cheeks scaled entirely. Opercular bone with a single flat spine; preopercular serrated posteriorly, with uncinate spikes below. Premaxillaries protractile. Setiform teeth set in multiserial bands on the jaws, vomer, palatines, and ectopterygoids. No canines. Branchiostegal membranes not grown together. Branchiostegal rays 7. Anterior most interhaemal bone greatly enlarged. Two dorsal fins, meeting or set slightly apart with XII-XVII, I-III 12-16 rays. Anal fin short with II 7-10 rays: anal spines large and well developed. Caudal fin emarginate. Pectorals almost symmetrical, with 11-17 rays. Ventrals behind the pectoral base, set close together with a distinct spine. Lateral line not continued on the caudal fin. Pseudobranchiae present. Sensory canal cavities on the head developed slightly. Swimbladder well developed. Breeding tubercles absent. Vertebrae 36-43.

– Specific

Artificial key to the identification of all species of *Perca*:

1(2) First dorsal fin markedly higher than the second. Not less than 54 scales in the lateral line. A dark spot at the posterior of the dorsal fin. 3.

2(1) First dorsal fin usually not higher than the second sometimes slightly higher. Not more than 55 scales in the lateral line. No dark spot at the posterior end of the dorsal fin.

D1 XII-XIII D2 II-III/12-13; A II/(7)8-9. Lateral line scales 41-54; Vertebrae 36-40. Asiatic highlands of eastern Kazakh S.S.R.: Balkhash and Alakul Lake systems.

P. schrenki Kessler

3(4) Base of dorsal fin in front of base of pectoral fins, above, or rarely behind them. Cranium wide. Supraoccipital crest usually low, its upper edge directed upward, and rear edge as a rule not projected backward to the end

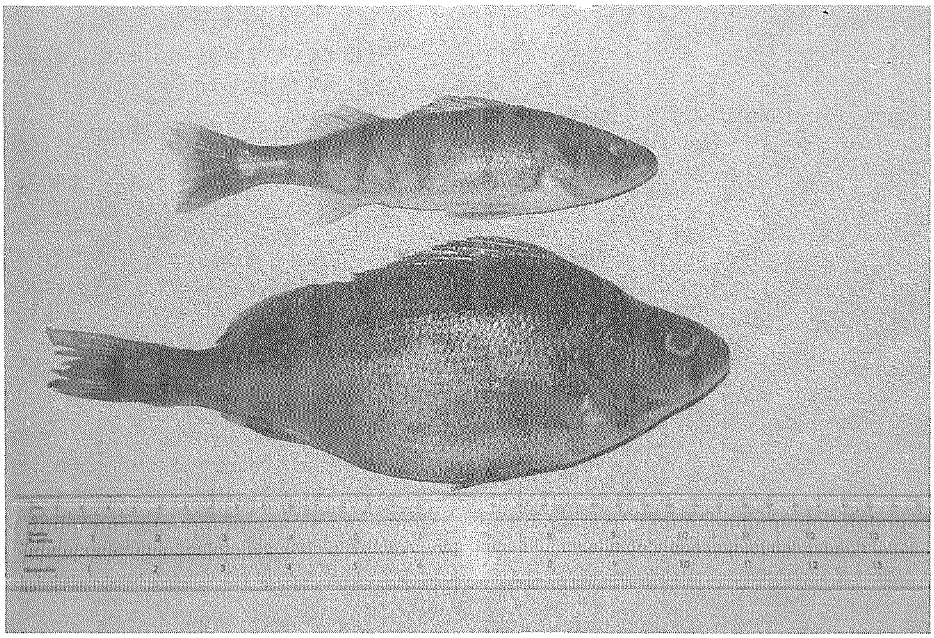
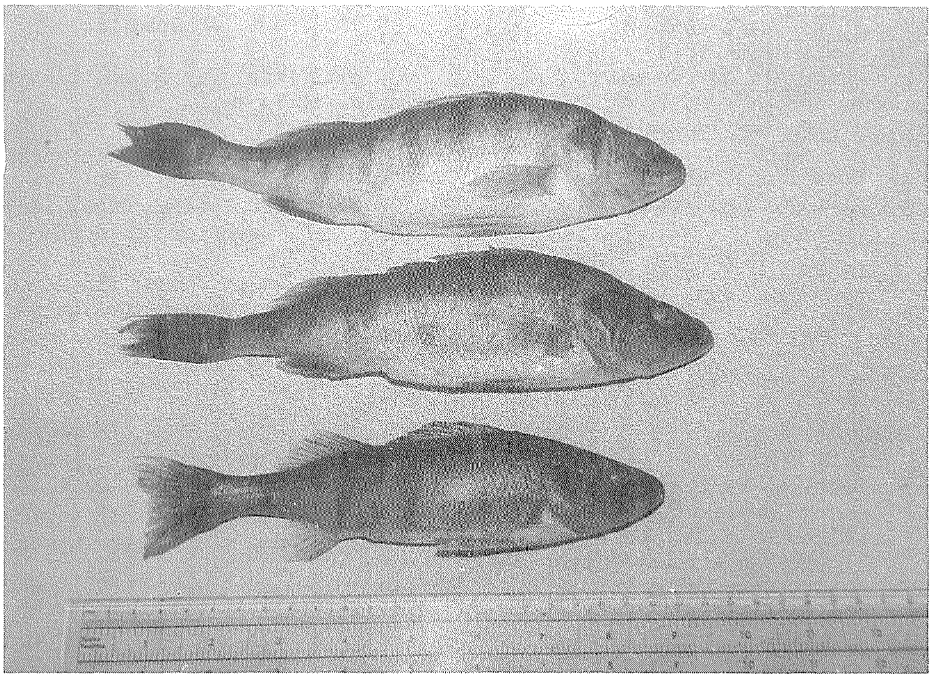


Fig. 1 a. top: P. flavescens from Lake Tadenac, Ontario
bottom: P. fluviatilis from Loch Leven, Scotland



b. P. flavescens from Lake Tadenac, Ontario

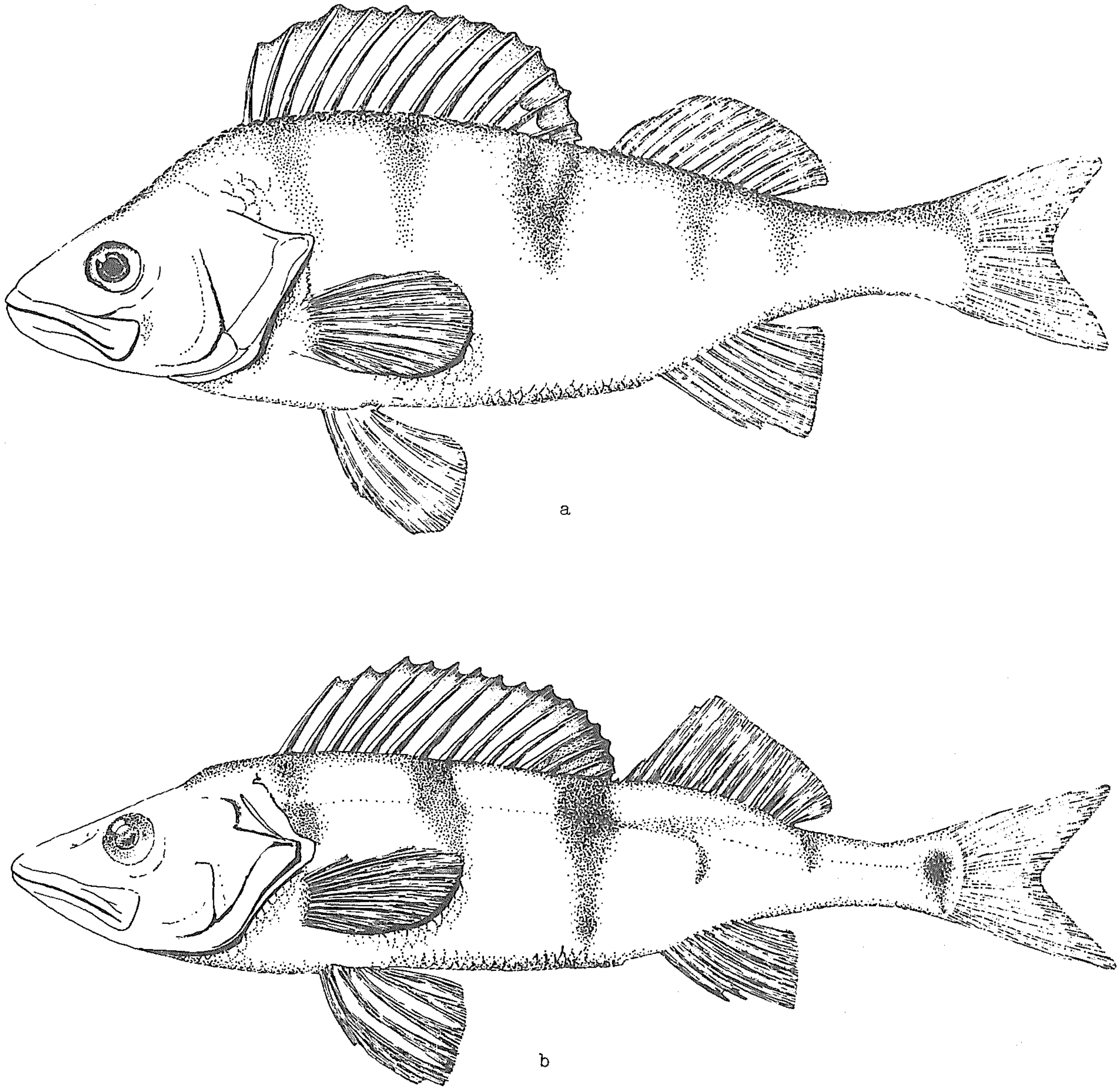


Fig. 2 a. *Perca fluviatilis vulgaris* from Lake Syabersk (after Pokrovskii, 1951)

b. *Perca fluviatilis gracilis* from Lake Lyubivo of the basioccipital. Interocular width 20.6–29.0% of head length. First spine of dorsal fin 37–94% of length of second, and 33–149% of length of first anal. Predorsal bone extends anterior to the first neural spine; pterygiophore supporting the first dorsal spine extends between the first and second neural spines.

D1 XII–XVIII, D2 I–III/13–15; A II/(7)8–9(10). Lateral line scales 56–77; Vertebrae 18–22 and 19–23, total (39, 40) 41–42 (43, 44). Europe, Siberia east to Kolyma basin.

P. fluviatilis L.

4(3) Base of dorsal fin behind base of pectorals or rarely above them. Cranium narrow. Supraoccipital crest low, upper edge in straight line with top of skull, near edge projected beyond end of basioccipital. Interocular width 17.9–24.6% of head length. First spine of dorsal fin 35–69% of length of second, and 36–83% of length of first anal. Predorsal bone extends between the first and second neural spines; pterygiophore supporting the first dorsal spine extends between the second and third neural spines.

D1 XIII–XV, D2 II/12–15; A II/7–8; Lateral line scales 54–62; Vertebrae (18) 19 (20) and (20) 21–22, total 40–41. Canada, U.S.A., east of Rocky Mountains.

P. flavescens Mitchill

1.2.2 Taxonomic status

A morpho species, not established by breeding data. Fast-growing and slow-growing morpha are recognized occurring within the same population. Small morpha may occupy shore areas, are gregarious, and feed on invertebrates; large morpha occupy open water, are solitary and feed on fish. Examples, and a list of references to Russian populations is given in Berg (1965).

1.2.3 Subspecies

Taxonomists have disagreed on the status of the Eurosian perch (*P. fluviatilis* L) and the American perch (*P. flavescens* Mitchill) as valid separate species. Svetovidov and Dorofeeva (1963) argued from comparisons of morphological characteristics that intraspecific variation in *P. fluviatilis* showed a continuous directional trend from Europe eastward to the Kolyma area of Siberia, and that *P. flavescens* was the easternmost expression of this range of variation. Bailey *et al.* (1970), however, recommended that *P. flavescens* Mitchill should be retained as a good species, on the grounds that Svetovidov and Dorofeeva's data was inconclusive, distribution was discontinuous, and there were differences in growth-rate and colour. No definitive genetic experiments have been undertaken to test the separate identity of these fish. Thorpe (1977a) has compared biological characteristics of the two forms, and as the range of expression of these in *P. flavescens* falls wholly within the range of *P. fluviatilis*, including growth-rates, he concluded that the two species are biologically equivalent. However, Collette and Banarescu (1977) have discovered that the predorsal bone extends between the first and second neural spines in *P. flavescens* but is anterior to the first neural spine in *P. fluviatilis*. This osteological character separates the two species definitively.

Pokrovskii (1951) reviewed data on intraspecific variation in perch, and, defining a type-form from Lake Onega, he supported the subspecific status of *P. f. vulgaris* Schaeffer 1759 (Fig. 2a), a faster-growing deep-bodied form of relatively high fecundity from lakes with a good food base. Similarly, he supported subspecific status for the contrasting *P. f. gracilis* Cuvier and Valenciennes 1828 (Fig. 2b), a slower-growing slender form from poorer lakes. He also suggested that the forms described by Smitt (1893) as *P. f. var. maculata* and by Grimm (1899) as *P. f. var. macrophthalma*, should be considered to belong to the subspecies *gracilis*. Further, Dianov (1955) described the form *P. f. zaissanica* from Lake Zaisan, and Karaman (1924) the form *P. f. macedonica* from Lake Dojran. However, these variants are now considered to be growth forms only (Collette, pers. comm.) and not subspecies.

1.2.4 Standard common names, vernacular names

Standard common names:

Australia	Redfin, English perch
Austria	Barsch, Flussbarsch
Belgium	Perche commun, Baar
Bulgaria	Kostur
Canada	Yellow perch
Czechoslovakia	Okoun říční, Ostriez
Denmark	Aborre
Estonia	Ahvena
Finland	Ahven
France	Perche fluviatile
Germany	Barsch
Greece	Perca
Hungary	Sügér, Csapó Sügér
Ireland	Perch
Italy	Pesce persico
Latvia	Asers
Lithuania	Eszerýs
Luxembourg	Pîsch
Netherlands	Baars
Norway	Abbor
Poland	Okón

Portugal	Perca
Romania	Biban
Spain	Perca
Sweden	Abborre
Switzerland	Barsch, Perche, Perca
Turkey	Tatlisulevreği baliği
United Kingdom	Perch
U.S.A.	Yellow perch
U.S.S.R.	Okun
Yugoslavia	Gregeč, Ostriž, Perkija

The name perki (περκη) was first used by Aristotle (Seeley 1886), a word signifying the dusky colour of ripening grapes, and is thought to refer to the banded marking of this fish. The name has been introduced to many European languages, sometimes via the Latin form perca.

Vernacular names:

Abbor	Norway
Abborre	Sweden
Aborre	Denmark
Ahon	Finland
Ah-sah-waince	U.S.A. (Chippewa)
Ahun	Estonia
Ahven	Finland
Ahvena	Estonia
Alabuga	Kazakhstan
Alygar	Yakut
American perch	Canada, U.S.A.
Anbeiss	Netherlands
Asers	Latvia
Asprisor	Romania
Baars)	Netherlands,
Baas)	Belgium
Baboi	Romania
Baes	Belgium
Bandar	Yugoslavia
Bandirolo	Switzerland, Italy
Bars	Germany
Barsch	Austria, France, Germany, Switzerland
Bärsch	Germany
Bärschling	Austria, Germany
Barse	England
Barster	Germany
Base	England
Beerschke	Germany
Bersh	U.S.S.R.
Bersich	Germany
Bersig	Switzerland
Bersing	Germany
Berster	Austria, Germany
Berton	Switzerland, Italy
Bertonscello	Switzerland
Bertsch	Germany
Bertuscell	Italy
Biban	Romania, Bulgaria
Bibanul	Romania
Boillat	Switzerland
Bors	Germany
Börs	Germany
Bules	Germany
Buljesh	Yugoslavia
Burschig	Germany
Bürschling	Germany
Bürstel	Switzerland
Bürstla	Austria
Butz	Switzerland
Butzen	Switzerland
Centin	Switzerland
Cent-in-bocca	Switzerland
Chretzer	Switzerland
Cocassette	Switzerland
Cochonnet	France
Common perch	U.S.A.
Costes	Romania
Costras	Romania
Costrasul	Romania
Costrus	Romania
Creagag	Ireland
Crutchet	England
Csapó sügér	Hungary
Draenog	Wales
Dübér	Hungary
Egli	Austria, Germany, Switzerland
Egling	England
English perch	Australia
Eszerýs	Lithuania
Ferskvandsaborre	Denmark
Flussbarsch	Austria, Germany
Gheub	Switzerland
Ghibanul	Romania
Grgeč	Yugoslavia
Grundaborre	Denmark
Guelb	Italy
Hurlin	France
Hurling	England
Hürling	France, Switzerland
Jôlerie	France
Khakhynai	Yakut
Kostresh	Yugoslavia
Kostriz	Poland
Kostur	Bulgaria
Krabegli	Switzerland
Krätzer	Austria, Germany, Switzerland
Lake perch	Canada, U.S.A.
Lutz	Switzerland
Méché	Bulgaria
Méscé	Bulgaria
Meshé	Bulgaria
Milcanton	Switzerland
Okon	Poland
Okoun říční	Czechoslovakia
Okun	U.S.S.R., Poland
Ostresh	Yugoslavia
Ostriez	Czechoslovakia
Ostrizh	Yugoslavia

Paidleach	Ireland
Pasghen	Italy
Pas perseg	Italy
Pèirse	Ireland
Perc	Wales
Perca	France, Greece, Portugal, Spain, Switzerland
Perch	Canada, U.K., Ireland
Perchat	France, Italy
Perchaude	France, Canada
Perche	France, Switzerland
Perche commune	Belgium
Perche de rivière	France
Perche fluviatile	France
Perchette	France
Perchia	Italy
Perchiné	Ireland
Percho	France
Perchot	France
Percig	France
Perco	France, Belgium
Percot	France
Perdrix de rivière	France
Pergo	France
Perki	Greece
Perkija	Yugoslavia
Persch	Germany
Perschke	Germany
Persec	Italy
Persegein	Italy
Persego	Italy
Persic	Italy
Persich	Italy
Persico reale	Italy
Persighin	Switzerland
Persing	Italy
Pes pasi	Italy
Pes persach	Italy
Pes persec	Italy
Pes persegh	Italy
Pes persich	Italy
Pes persog	Italy
Pes persogh	Italy
Pesc persi	Italy
Pesce persico	Italy
Pesce perso	Italy
Pess persech	Italy
Pess persigg	Switzerland
Pess perssi	Italy
Pesse persego	Italy
Piche	Belgium, France
Pichette	Belgium
Pierche	France
Pirsholz	Switzerland
Pisch	Germany
Pîsch	Luxembourg
Pisci persicu	Italy
Precchia di sciumni	Italy
Raccoon perch	U.S.A.
Raspar	Romania
Rattel	Switzerland
Raubfisch	Switzerland
Rechling	Switzerland
Redfin	Australia
Red perch	U.S.A.
Rehling	Austria
Rerlig	Switzerland
Rerling	Germany
Ring perch	U.S.A.
Ringed perch	U.S.A.
River perch	U.S.A.
Rødaborre	Denmark
Rode baars	Netherlands
Rohrbarsch	Austria
Salmerino	Italy
Schratz	Austria, Germany
Schrazen	Germany
Seebarsch	Austria
Seidthar	Ireland
Sildingjager	Denmark
Singer	Hungary
Slipak	Poland
Steargan	Ireland
Stichling	England
Strandaborre	Denmark
Streifbarsch	Germany
Striped perch	U.S.A.
Sügér	Hungary
Sürger	Germany
Tatlisuleyreği baliği	Turkey
Trasling	England
Trauling	England
Tryte	Norway
Tusindbrødre	Denmark
Warschieger	Austria
Warschinger	Germany
Yellow Ned	U.S.A.
Yellow Perch	Canada, U.S.A.
Zängel	Germany
Zboras	Romania
Zebra	Ireland

1.3 Morphology

1.3.1 External morphology

Some morphological data are shown in Table I.

Gaschott (1928) distinguished colour variants of perch in Europe, those from rivers and lakes of North Germany being brightly coloured with red pectoral, ventral and anal fins, and those from subalpine and alpine lakes being generally pale. He acknowledged Schneider's observations (1908, 1923) that fin colouration is related to diet, those fish feeding on crustaceans (especially Astacus fluviatilis) having the reddest fins. Schiemenz (1909) distinguished three ecological groups which he called weed-perch, deepwater-perch, and predatory perch: These three types were progressively less strikingly coloured from brassy with deep red fins to generally pale and no red pigment.

TABLE I

Meristic data for Perca fluviatilis

COUNTS								
D1	D2	P	V	A	C	L L Scales	Vertebrae	Author
XIV-XV	1-11/13-14	14	1/5	11/8-9	18	55-60	41-42	Day (1880)(Europe)
XIII-XIV	1-11/13-15	-	-	11/6-7	-	55-70	-	Day (1880)(America)
XIII-XVI	1-11/13-15	14-17	1/5-6	11/8-9	17	54-72	-	Seeley (1886)
XIII-XV	1/13-14	14	1/5	11/8-9	17	60-68	-	Kammerer (1907)
XIII-XVI	1/13-15	-	1/5	11/8-9	-	58-67	-	Smolian (1920)
XIII-XVI	1-11/13-16	14-16	1/5	11/7-10	17	53-74	-	Chevey (1925)
XIII-XVII	11/13-15	14	1/5	11/8-10	17	58-67	-	Gaschott (1928)
XIII-XV	1-111/13-15	-	-	11/8-9	-	57-77	-	Staff (1950)
-	-	-	-	-	-	-	39-42	Bailey and Gosline (1955)
XIII-XVII	1-11/13-15	14	1/5	11/8-10	17	58-68	-	Schindler (1957)
XIV-XV	11-111/12-15	-	-	11/7-9	-	60-66	40-42	Serov (1959)
XV	11/14	-	-	11/9	-	63-65	41	Shilenkova (1959)
XIII-XVI (XVII)	1-11/13-16	14-16 (17)	1/5(6)	11/(7)8-9(10)	17	(53)60-70(74)	41-43	Spillman (1961)
XII-XVII	1/14-15	-	1/4-5	11/8-9	-	57-72	-	Suskiewicz (1961)
-	-	-	-	-	-	-	38-43	Collette (1963)
XII-XIV	11-111/12-13	-	-	11/7-8	-	57-62	-	Herman *et al.*(1964)
XIII-XVII	1-111/13-15	11-17	-	11/(7)8-9(10)	-	57-77	39-42	Berg (1965)
XIII-XV	11-111/13-15	13-15	1/4-5	11/7-8	-	55-60	40-41	McPhail and Lindsey (1970)
XIII-XV	1-11/12-15	13-15	1/5	11/6-8	-	51-61	38-41	Scott and Crossman (1973)
XIII-XV	1-111/14-15	12-15	1/5	11/8-10	16-18	56-68	38-43	Thorpe (unpublished)

Crossman (1962) describes a single specimen from Lake Erie which was bright orange in ground colour and lacked dark vertical bars. The cheek and lower operculum were a brilliant metallic silver. In all other respects, this fish was normal and was therefore regarded as a colour mutant. Completely black perch are sometimes found in Lake Ladoga (Vologdin, In Berg1965), but the normal colouring of perch is usually very stable. Dymond (1932) reported a blue perch from Lake Erie. When fresh, this fish was otherwise typical except for a lack of yellow colouration. Dymond regarded this as a physiological variation. Hubbs (In Dymond 1932) also reported blue perch from Saginaw Bay, Michigan.

Driver and Garside (1966) investigated the effects of salinites of up to 10 300 ppm in Manitoba lakes on meristic characteristics and concluded that perch were structurally rather stable; the slight differences of vertebral counts and anal fin-ray counts between lakes were not related to salinity differences.

During development, many body proportions alter, and Repa (1973 a) has shown that the relative size of several skull bones especially the frontal bone is related to body length and the changes continue gradually throughout life. Repa (1973 a) also showed that the number of rakers on the anterior and posterior edges of the first gill arch increased as the fish grew from 70 to 90 mm in length: The definitive number of rakers was higher in reservoir fishes than elsewhere, and he attributed this to differences in nutrition.

1.3.2 Cytomorphology

Nygren et al. (1968) showed that in perch gonadal tissues, there were 48 small acrocentric chromosomes, but that there was some variability in chromosome numberin somatic tissues. Such constancy in gonadal tissue and variability in somatic tissue is typical of teleosts examined (Post 1965). Lieder (1963) found in 4 male perch a satellite attached to a rod-shaped chromosome. This satellite was absent in 5 female perch examined, and Lieder suggested tentatively that this was a definitive sex chromosome (Y). By comparison with similar bodies in eels (Anguilla anguilla L) and ruff (Gymnocephalus cernua L), he suggested that sex-determination should be considered as of the YO type, the Y element not requiring a distinctive homologue.

Ohno and Atkins (1966) found that the DNA content of the nucleus in Percidae was 30-35% that of the mammalian nucleus as compared with 20% in Cyprinodontidae, 40% in Clupeidae, 50% in Cyprinidae and 80% in Salmonidae. Hinegardner (1968) showed that highly specialized fishes tend to have less DNA per cell than more generalized ones of the same phyletic grouping, and Hinegardner and Rosen (1972) found perch to have 1.2 picograms haploid DNA content. This was more than the average of 1.1 for generalized species of the Percoidei.

1.3.3 Protein specificity

Nikkila and Linko (1955) analysed proteins from the skeletal muscle of perch by paper-electrophoresis and found characteristic patterns distinguishing the fish from 9 other species (see Fig. 3).

An exploratory study of serum proteins of a range of poikilotherms by Deutsch and McShan (1949) included samples from 25 yellow perch. The relatively complex eletrophoretic pattern included 12 component proteins, and was quite distinct from that of walleye (Stizostedion vitreum) (Fig. 3).

Nyman (1965, 1965 a) compared electropherograms of serum proteins and esterases, and liver proteins and esterases between perch and 5 other freshwater fish. He reproduced only drawings from his data so that there is no real means of assessing its validity but what is shown is as follows:

Serum proteins:	polymorphic variations in 2 band systems. Clearly distinct from pike (Esox lucius L.).
Serum esterases:	variable pattern but species specific and distinct.
Liver proteins:	not species specific.
Liver esterases:	species specific; stable patterns with little variation.

2 DISTRIBUTION

2.1 Total area

(See map, Fig. 4.) Perch are found throughout Europe except the Iberian Peninsula, southern Italy and the western part of the Balkan Peninsula (Berg 1965); they occur in Turkey, in the Istanbul area and in lakes close to the Black Sea coast of northern and north western Anatolia (Kosswig 1952); throughout the U.S.S.R. eastward as far as the Kolyma River except for the Caspian Sea and the river basins of the Crimea, Turkmenia, Balkhash and Tarim, the Pacific Ocean basin, Anadyr, Kamchatka, Amur, Sakhalin and rivers south of the Amur (Berg 1965); in North America from Nova Scotia (except the Cape Breton Islands) south along the Atlantic coast as far as Florida, Alabama, to the west of the Appalachian mountains from Pennsylvania to Missouri, Kansas to Montana, northward to Great Slave Lake and thence south-east to James Bay, Quebec and New Brunswick (Scott

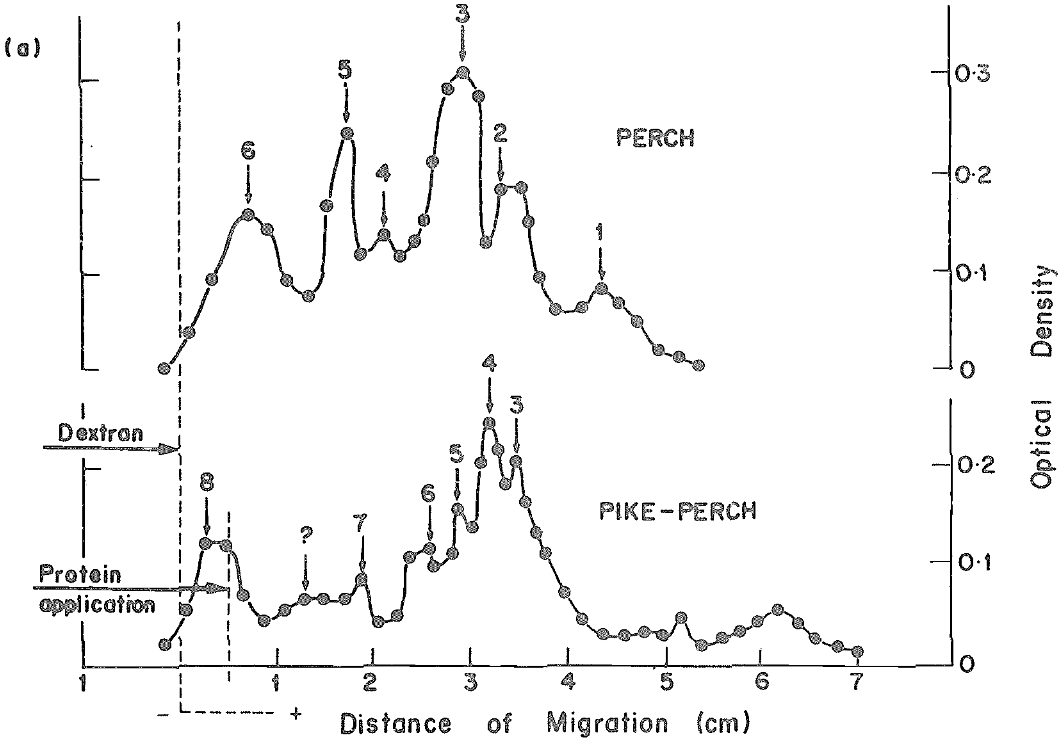
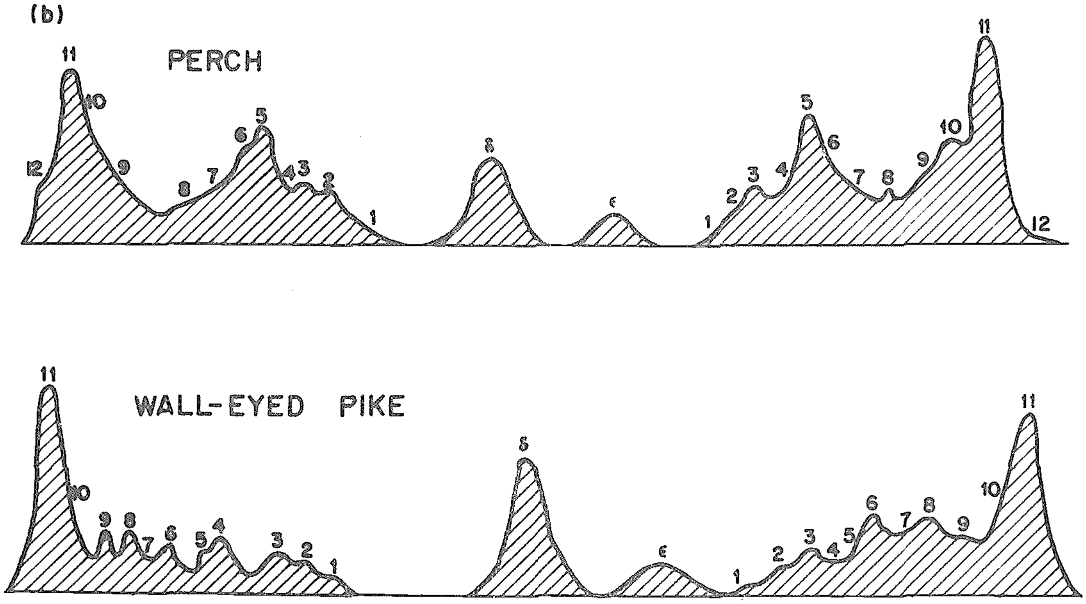


Fig. 3 a. Paper-electrophoretic diagrams of extracts of fish skeletal muscle in sodium phosphate buffer, at I = 0.05, pH 7.55. The dextran line represents the starting-point after allowing for electroendosmosis and the solid line the point of protein application (from Nikkila and Linko (1955))



b. Electrophoretic diagrams of blood serum proteins of perch (above) and walleye (Stizostedion vitreum) (from Deutsch and McShan, 1949)

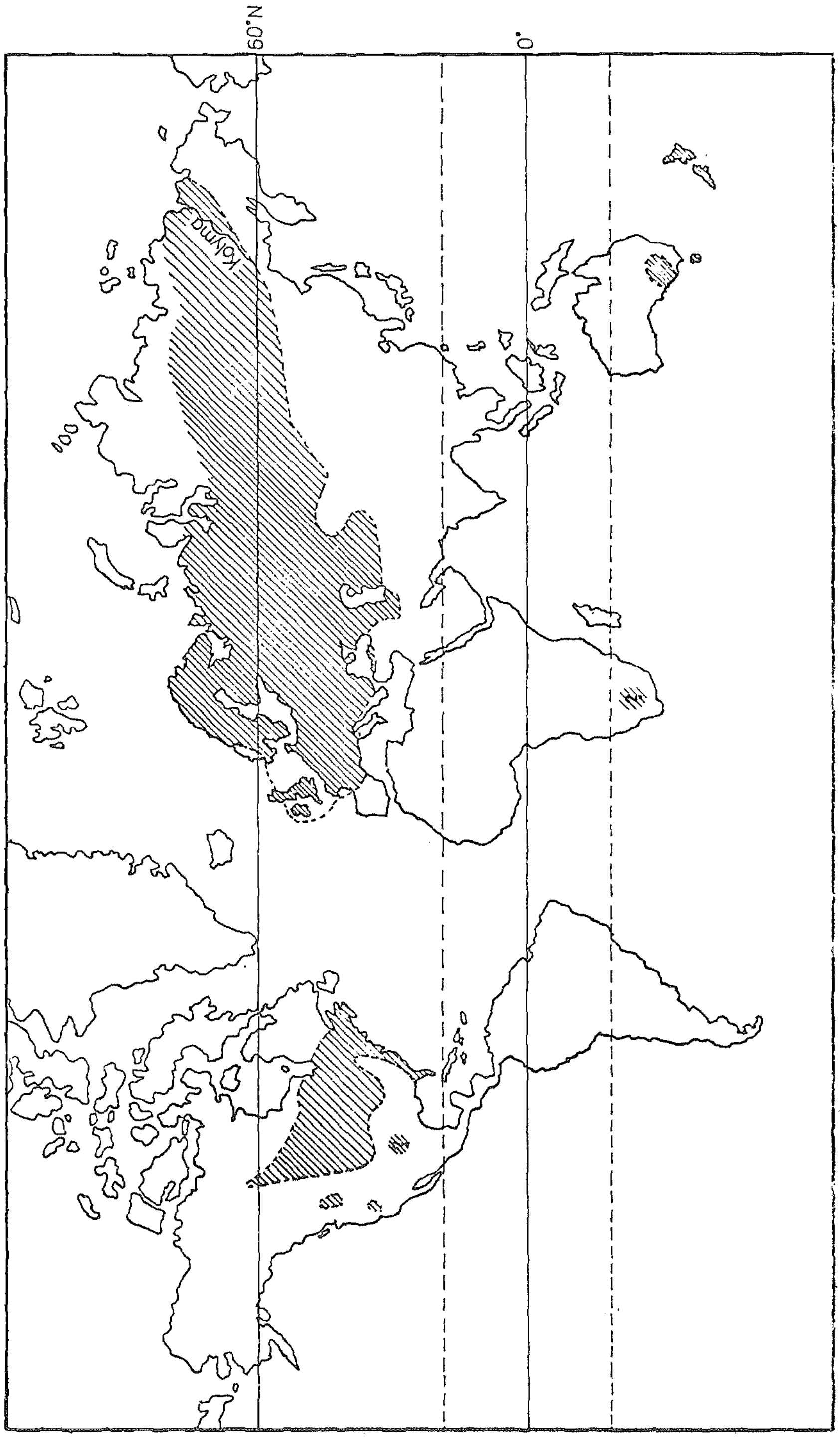


Fig. 4 Distribution of *P. fluviatilis* (from Thorpe in press a)

and Crossman 1973). They range from altitudes of over 1 000 m to sea-level and enter brackish water in the Baltic Sea (Ehrenbaum 1905-09), the Arctic Ocean (Chevey 1925, Dryagin 1948) and the Atlantic seaboard of North America (Muncy 1962, Keup and Bayless 1964 and McKenzie 1959).

From the fossil record *P. fluviatilis* is known from Miocene deposits in the Zaysan basin of Kazakhstan (Lebedev 1959), the middle Irtysh area of western Siberia (*P. f. lepidoma* Yakovlev 1960) and also possibly from the far east and from Olkhon Island in Lake Baikal (Svetovidov and Dorofeeva 1963). In Mio-pliocene, middle and upper Piocene, it occurs in the Altai (Sychevskaya and Devyatkin 1960) and has been found in pliocene remains in Austria (*P. edlaueri*, Weinfurter 1950) and Belgium (Newton 1908). In the Pleistocene deposits, it has occurred at Willershausen, Germany (Weiler 1933), at Billstedt, Hamburg (Gripp and Beyle 1937), at Chaunsk Bay on the Kyrchak peninsula (Svetovidov and Dorofeeva 1963). These later fossils lend support to Yakovlev's (1961) hypothesis that perch entered North America in Late Tertiary times via a land bridge in the Bering area. Banarescu (1960, 1973), however, maintains that the route was via a North Atlantic land bridge, a view which Svetovidov and Dorofeeva (1963) reject on the grounds that a long narrow isthmus of this type does not constitute a suitable dispersal route for freshwater fishes (of Panama).

Spillman (1961) states that perch probably arrived in northern France in Tertiary times after the elevation of the Pyrenees but before that of the Alps as the fish is found naturally in the basin of the Po in Italy. It has spread into southern France in recent times probably entering the Garonne basin in the early nineteenth century and that of the Hérault by means of the Canal du Midi about 1850 (Moreau 1881 in Chevey 1925).

In North America, Metcalf (1966), arguing from fossil evidence, claims that perch were distributed well to the south in the Great Plains in Illinoian time (c 300 000 BP) later disappearing from the western part probably due to periods of extreme aridity. McPhail and Lindsey (1970) classify perch with 17 other species which spread into north-western Canada from the Mississippi refuge after the Wisconsin glaciation (c 10 000 BP), and Bailey and Allum (1962) suggest that perch moved westward into the middle Missouri basin from this same refuge. The present day distribution of perch in North America is influenced by introductions into many western and southern states from which it has extended locally. Its occurrence in British Columbia, for example, is probably by dispersal from plantings in Washington State (Scott and Crossman 1973).

The distribution in the southern hemisphere in South Africa, Australia and New Zealand is entirely due to introductions, (see section 6.5.2).

Throughout its range, the perch occurs in lakes and the slower reaches of rivers, and by virtue of its relatively high fecundity and unspecialized spawning requirements, populates new reservoirs, impoundments and canals very rapidly.

2.2 Differential distribution

2.2.1 Spawn, larvae and juveniles

(See sections 3.1.6, 3.2.2 and 3.2.3.)

2.2.2 Adults

(See section 3.5.1.)

2.3 Determinants of distribution changes

2.3.1 Temperature

Weatherley (1963) discussed the temperature tolerances of perch and concluded from his own experiments (1963 a) and those of Hart (1952) that the fish could not survive for more than a few hours at an upper limit of 31°C. Weatherley (1963) showed that the natural range of perch extended southward in North America to a boundary corresponding closely with the summer 31°C isotherm and that in introduced populations in Australia, the limit of colonization also corresponded closely with the same isotherm. However, Lake (1967) has suggested by analogy with native Australian species that high minimum temperatures during the pre-spawning period may damage the oocytes and thus be an effective limiting factor controlling perch distribution there. Weatherley had found no perch in the Darling River north of Wilcannia where summer temperatures were 31°C, but Lake found them at Narrandera on the Murrumbidgee River at similar summer temperatures. At Wilcannia, the minimum winter temperatures were 12°C; at Narrandera, perch spawned at 11.5°C. Thus the winter minimum at Wilcannia was above the spawning temperature for perch, however, see section 3.1.6).

McPhail and Lindsey (1970) suggest that northerly distribution is limited by low temperatures since only one population has been found north of the 60°F July isotherm in Ontario, and the most northerly population in Canada lives in the Rae Arm of Great Slave Lake at 63°N.

Alabaster and Downing (1966) found 1 000 - minute lethal temperatures for perch of 26°C and 29.5°C at acclimation temperatures of 15°C and 25°C respectively (see also section 3.3.2). Horoszewicz (1973) found that lethal temperature (L) was correlated with acclimation temperature (a) ($r = 0.98$) and that the relationship could be expressed by the linear formula; $L = 26.16 + 0.358a$. In the field, he found no correlation between lethal temperature and maximum lake temperature during the previous 24 h suggesting that young perch did not stay in the regions of the highest temperature (in this case 31°C). 'Disturbing' temperature at which fish first showed accelerated respiratory movement occurred between 30.5°C and 32°C after acclimation temperatures of 19.8–27.8°C. At the disturbing levels, the fish died within 100 h. When given the choice, perch avoided water at temperatures above 28°C and did not acclimate to these.

Ferguson (1958) found that in Lake Nipissing, perch preferred temperatures of 19–21°C, whereas, in his laboratory experiments, they preferred 21–24°C. As young perch were found in warmer water than adults, he concluded that the discrepancy between field and laboratory data was due to the age of the fish studied. Herman *et al.* (1964) found that perch aggregated at a temperature stratum of 21°C in summer and Neuman (1974 a) recorded the highest catches in gillnets on the Swedish Baltic coast at 18–21°C (see also section 3.3.2).

2.3.2 Currents

Weatherley (1963) concluded that mountain ranges prevented the natural extension of perch westward in North America and southward in Europe since the fish was unable to live in streams with a rapid flow. Kreitmann (1932) established that the limiting water-velocity (V) that the perch could resist was 10–15 times the square root of its length (L) in his case $V \ngtr 45$–60 cm/sec, but he noted that perch flourished in the Danube at places where velocities were greater than 60 cm/sec. Ohlmer and Schwartzkopff (1959)found $V/\sqrt{L}$ values of c 24 for individual undisturbed wild perch swimming through a measured section of the outflow of the Seeburger See, Germany. Hergenrader and Hasler (1967) using sonar in Lake Mendota found that swimming speeds increased linearly with temperature, the maximum sustained level being 54 cm/sec at 20–25°C. Fish size is not stated, but Bardach (1951) gave mean length of Mendota perch as 24.3 cm in 1948: Using this value, $V/\sqrt{L}$ is about 11, corresponding closely with Kreitmann's values. Ohlmer and Schwartzkopff's value probably represents a burst speed rather than a sustained value or else small fish. Houde (1969) found that perch larvae of 8.5 mm could sustain swimming against 2.5 cm/sec current speeds: this is equivalent to a $V/\sqrt{L}$ value of about 85. Holčik (1966) found perch present in tributaries of the Orava River, Czechoslovakia, at slopes ranging from 0.2–1.2%, but absent in streams whose lowest slope was $>0.4\%$. Gee *et al.* (1974) have shown experimentally that perch are capable of small adjustments to flow changes, being just negatively buoyant in still water (mean flotation pressure 0.977 ml/g), but reducing buoyancy to 0.500 ml/g at 40 cm/sec flow.

In extreme cases, waterfalls present barriers to distribution as at Harpefoss (Norway) and Gäddedefors (Sweden) (Ekman 1922).

2.3.3 Waves

In some shallow lakes, perch appear to avoid lee shores during stormy conditions: At Loch Leven, Scotland, Thorpe (unpubl.) found carcasses of healthy perch along lee shores after rough weather during the spawning season, but not at other times of the year.

2.3.4 Depth

In general, perch occupy deep water in lakes during winter and move inshore to spawn in spring remaining in the littoral or epilimnetic waters until the autumn before returning to deep water (cf. Ferguson 1958, Carr 1962). In Wisconsin, Lakes Hile and Juday (1941) found no simple relation between depth distribution, temperature and dissolved oxygen and found depth distribution differed between lakes being predominantly 3–5 m in Nebish and Trout Lakes, and 5–7 m in Silver and Muskellunge Lakes. In Clear Lake, 5 perch were caught between 19.5 m and 24.5 m in the hypolimnion indicating that they occasionally penetrate deep deoxygenated waters. Scott and Crossman (1973) state that perch are not normally found below 9.2 m, but Ferguson (1958) recorded them down to 45.7 m in May and Stone (1944) recorded them from 28 m in August and 56 m in November in Lake Ontario. In Finland, Lind *et al.* (1971) found perch in depths to the thermocline at 6 m and none below it. Herman *et al.* (1964) reported perch normally at <27 (45) m fathoms in Lake Michigan and young fish occupying shallower water than adults. Carr (1962) found a similar distribution in Saginaw Bay and Lake Huron with fry only in very shallow (<1 m) water until October when they too moved offshore to the 2–7.5 m zone. In Australia, Tunbridge (1972) reported perch commonly to 9 m. In the Baltic, Neuman (1974 a) found perch prefer shallow warm sheltered areas, but move out to open deeper areas in August. Peak catches were made at 2–5 m, but fish were caught to 25 m depth. Hergenrader and Hasler (1967) recorded shoals at all depths from near the surface to close to the bottom (26 m) of Lake Mendota in all months from January to June but, with stratification in early July, the perch were found mostly in the thermocline at 10–12 m.

Hasler and Wisby (1958) state that the older the animal, the more likely it is to be found in deep spots in a lake.

2.3.5 Light

Perch have 25 rods and 9 cones to 80 µ of retinal surface (Wunder 1926) and thus were classified by Wunder as "bright-light" fish.

Hergenrader and Hasler (1966, 1967, 1968) recorded the periodicity of movement of perch in Lake Mendota and found that they remained inactive on the bottom at night and formed shoals in the morning twilight moving out into open water.

The general activity patterns are discussed in section 3.5, but it is clear that perch are day-active in all localities and inactive at night on the bottom.

2.3.6 Turbidity

Muncy (1962) suggested that increased turbidity reduced spawning success among Severn River perch, Maryland, but did not distinguish the effects of this from those of increased salinity. Scott and Crossman (1973) state that the numbers of perch decrease as turbidity increases which is consistent with a mode of life dependent primarily although not wholly on sight (Wunder 1926) (see below, section 2.3.8).

2.3.7 Substratum

Scott and Crossman (1973) note that perch are most abundant in lakes with a muddy, sandy or gravel bottom. However, they are very adaptable and their nonspecific requirements in this respect are of advantage to them, as for example, in populating new waters such as the Kličava reservoir Czechoslovakia where the sides were steep and composed of scree material (Holčik 1970).

2.3.8 Shelter

Hartmann (MS. 1974) suggests that in the Bodensee high plankton density, since eutrophication, has provided shelter for perch fry and contributed to their success in this lake in recent years. Vashkyavichyute (1963) noted that perch fry in the Kurskiy Zaliv, Lithuania occur in water of 0.2–0.3 m near the shore but at wind strengths of force 3–4 move out to depths of 0.6–0.8 m. Also in the Baltic, Neuman compared the catches of surface and bottom gillnets inshore and at 0.5 km offshore: 96% of the surface catch and 97% of the bottom catch was from inshore.

2.3.9 Ice

Petrosky and Magnuson (1973) subjected perch 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 depths until they were nosing at the ice. Such behaviour brought them into the water layers at which oxygen tension was highest. As noted above (Depth), Hergenrader and Hasler (1966) found perch at all depths in Lake Mendota in winter.

2.3.10 Dissolved gases

Meadows (1970) found that perch returned to a polluted area of the River Lee, England, when the oxygen level rose to 1 ppm. The concentration for perch survival is given by Jones (1964) as 1.1–1.3 ppm at 16°C and he also quotes values of 0.4–0.9 at 15.5°C and 2.25 ppm at 20–26°C from other workers. He points out that critical levels below which activity is restricted are more meaningful. Fry (1957) determined this level as 7 ppm at 20°C and Wunder (1936) gave values of 7–10 ppm. Andreasson and Stake (1970) found perch distributed in Lake Tullingesjön, Sweden, down to depths at which the oxygen concentration was just above 7 ppm at the beginning of July (15°C) and at 7 ppm at the end of July (19°C). At these depths, caged fish survived, but at 1 m deeper, all fish died at oxygen concentrations only just below 7 ppm. In Petrosky and Magnuson's experiments (1973) (see section 2.3.9, above), lethal oxygen concentrations at temperatures of 2.5–4°C were shown to be less than 0.25 ppm, but increased gill-ventilation rate began when oxygen tension fell from 4 to 1 ppm. Besides increased ventilation rate, Petit (1973) found that at oxygen levels below 6 ppm, the amplitude of opercular movement also increased. General activity decreased as the lethal concentration was approached and bleaching, cessation of feeding and loss of equilibrium occurred. At 22°C, he found that the lethal oxygen concentration for perch fry was 1 ppm.

Black <u>et al.</u> (1954) recorded that the CO_2 tension at which perch can utilize half the available oxygen is about 80 mm Hg and that at which no oxygen is available is 110 mm Hg.

2.3.11 Dissolved (inorganic) solids

Chevey (1925) described perch as occurring in weakly saline areas of the North Sea and Arctic Ocean. Dryagin (1948) recorded perch in the Obskaya Guba area of northern Siberia and large populations of perch feed in summer in the Baltic Sea (Berzins 1949, Subklew 1955, Henking 1923, Neuman 1974 and 1974 a) in areas where salinities range from 0–8‰. Hildebrand and Schroeder (1928) reported perch from Chesapeake Bay in salinities up to 13‰; Muncy (1962) also from Chesapeake Bay at 5–7‰; and Keup and Bayless (1964) from the Neuse River, North Carolina at 12.2‰, but preferring 1.8–3.5‰. Inland, perch are absent from the Caspian Sea (Berg 1965) although present in the inflowing rivers, but occur in the Aral Sea (Letichevskii 1946). The Caspian and Aral Seas have salinities of 12‰ and 10‰ respectively (Zenkevitch 1957). Driver and Garside (1966) found perch in a range of prairie lakes in Manitoba having salinities ranging up to 10.3‰. Lutz (1972) showed experimentally that perch were able to survive in one-third strength seawater approximately isosmotic with perch plasma, but in one-half strength seawater symptoms of muscular paralysis appeared within 24 h and the fish died soon afterwards in a dehydrated state with total body chloride rising by 73% and body sodium by 25%.

Privolnev (1970) measured the depression of freezing point of perch plasma (Δ°) for fish of 25–150 g kept at 0, 5, 10, 12 and 15‰ salinity for 24 h. This rose from 0.51 at zero salinity to 0.72 at 15‰. At 10‰, the blood and environment were approximately isotonic. Salts entered the blood rather slowly, 6 h being required to reach equilibrium in water at 10‰. At this salinity, the fish were maintained satisfactorily for the three-week experiment with no abnormal behaviour, but did not tolerate concentrations above this level.

2.3.12 Pollutants

Härdtk (1934) found the limiting concentration of phenol for perch is about 20 ppm, and Wuhrmann and Woker (1950) established a relationship between survival time in minutes (t) and concentration in mg/l (C) as follows:

$$(C - 12)^{1.202} (t - 3) = 344$$

Wuhrmann (1952) found the threshold concentration for toxicity of cyanide to be 0.13 ppm at 15°C with a reaction time of 4 min.

Christie (1974) has suggested that the recent dominance of Lake Erie by perch and smelt (*Osmerus*) may reflect pollution resitance by these species. The egg-strands of perch may be protected from deoxygenation by attachment to plants (Regier *et al.* 1969).

2.3.13 Vegetation

Herman *et al.* (1964) found perch most numerous in lakes with abundant open water and modest amounts of vegetation. Larval perch are pelagic until reaching a length of c 2 cm (Faber 1967), at which stage they move inshore to littoral and take up a diet of benthic invertebrates (see below section 3.2.2).

2.3.14 Fauna

Breder and Rosen (1966) noted that perch in the New York Aquarium were the least influenced of all fishes kept in crowded conditions and were apparently uninfluenced by the presence of other species. However, in the wild, Lind and Turunen (1971) found that perch less than 25 g weight were segregated from minnows (*Phoxinus phoxinus* L) in a 2 ha pond in Finland.

Many authors have recorded that perch fry form mixed shoals with other fry of spring-spawning fish (e.g. Vashkyavichyute 1963, Scott and Crossman 1973).

The shoals formed by the adults in summer often appear to be predominantly of one sex and they may be occupying different habitats as Hartmann (MS. 1974) has noted that in spring, almost three times as many males as females are severely infected with *Diplostomum* trematodes.

2.4 Hybridization

Natural hybridization has been thought to occur between perch and ruffe (*Gymnocephalus cernua* L) in the Danube near Vienna (Kammerer 1907). Forty one specimens of an unusual percid were found and Kammerer established by hybridization experiments that these were crosses with ruffe. Among the hybrids, the males showed no interest in the females at spawning and no milt could be obtained from the males by stripping. Successful crosses were made between the female hybrids and the males of each parental type. The hybrids were intermediate in appearance between the parental species, but usually more similar to the female parent. In general, the hybrids were less active than the pure-bred fish, grew faster and were more resistant to temperature extremes, pollutants and periods of starvation. Kammerer attempted to produce hybrids as follows:

P. fluviatilis x *Gymnocephalus schraetzer*
(Embryos developed but did not hatch.)

P. fluviatilis x *Lucioperca lucioperca*
(Larvae died just after hatching.)

Balon (1956) repeated this last cross using Danube fish from Czechoslovakia, but with less success: In those eggs which developed at all, development was abnormal. Segmentation was irregular beginning at the tail which developed doubled-back over the body. The heart was tube or droplet-shaped, weak and incapable of pumping blood through the vessels: only a lymphatic fluid circulated within the heart itself. With circulatory failure, the individual organs gradually degenerated. The organism was incapable of any movement and the last embryo died 9 days after fertilization.

Schwartz (1972) lists a further 5 types of hybrid as follows:

Perca x *Lina* (Nikolyukin 1958)

P. flavescens x *Lucioperca* (Day 1886)

P. fluviatilis ♀ x *Abramis brama* ♂ (Nikolyukin 1935)

P. fluviatilis ♀ x *Esox lucius* ♂ (Nikolyukin 1935)

P. fluviatilis x *Rutilus rutilus* (Kryzanovskii 1947, 1968)

And Kryzhanovskii (1953) also records:

ø *P. fluviatilis* ♂ x *Leuciscus danilcivskii* ♀

Schwartz does not give details of the success of these crosses, but in those carried out by Kryzhanovskii (1953), only perch x ruffe was successful.

Recently, some doubt has been expressed about the identity of the wild fish reported by Kammerer as Holčik and Hensel (1974) have described a new species, *Gymnocephalus baloni*, also from the

Danube, which possesses transverse dark bands very similar to those of *P. fluviatilis*. It is possible that Kammerer had found this fish, but did not recognize its specific identity. However, he did nevertheless succeed in producing viable hybrids artificially.

An extensive series of hybridization experiments was carried out by Hubbs (1971) to evaluate the relationships between the tribes of North American Percidae. Crosses and reciprocal crosses were carried out between *P. flavescens* and the following species:

Stizostedion vitreum
Percina sciera
Etheostoma spectabile
E. blennioides
E. caeruleum
E. tetrazonum
E. zonale)
Lepomis macrochirus)
L. cyanellus) x ♀ *P. flavescens* only
L. punctatus)
Chanenobryttus coronarius)
Cichlasoma cyanoguttatum)

In all cases, the progeny either failed to develop or died before feeding. As hybrids of *S. vitreum* and the darters (*Etheostomatini*) were more successful, Hubbs suggested that the walleyes should be separated from the perch and included with darters in the Etheostomatinae.

BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

- Hermaphroditism,
  heterosexuality,
  intersexuality

Chevey (1922) records the occurrence of a protandrous perch which fertilized the eggs of one female and several weeks later developed an ovary itself. It elicited courting behaviour in a true male, but the spawning was not successful. On dissection of this specimen, no trace of testicular tissue was found. Chevey reviews four previous reports of hermaphrodite perch, all from dissected material in which either testicular tissue was present on one side and ovarian tissue on the other or else a single gonad was formed partly of testicular and partly of ovarian tissue. Turner (1927) also reported a hermaphrodite specimen from America which had a 52 mm ovary to which was attached an abnormally shaped testis anteriorly. Both gonads were histologically normal with a sharp boundary between them and no transition zone. Perch with an ovotestis was also reported by Brunelli and Rizzo (1928).

- Sexual dimorphism

The males at spawning are generally brighter in colour than the females (Wunder 1936, Breder and Rosen 1966). Vladykov (1931) found that the paired fins were longer in the male. Adult females are generally larger than adult males of the same age and gravid females in spring are distinct due to their swollen appearance and slight protrusion of the genital orifice.

3.1.2 Maturity

(See Table II.) Tesch (1955) noted that sexual maturity was first achieved by males during their second summer and by females 1–2 years later. Thus, for most populations, spawning occurred first at AG I for males and AG II or III for females. However, Healy (1954) reported 5–9% of females of AG I spawning in Lough Barnagrow, Ireland; Shilenkova (1959) noted mature females of AG I in Kazakhstan lakes; and Lake (1959) also gave AG I as the age of first maturity among stunted perch in Australia. In all populations studied, most females of AG III at spawning time are mature and all at AG IV.

Among males, the size at first maturity is usually quite small (5–12 cm), but Laskar (1943) reported 16.0 cm for perch in the Grosser Plöner (see AG II). Among females, spawning occurs first at a larger size, usually 12–18 cm, but Thorpe (1974) found no ripe females at less than 24.0 cm in the fast growing population in Loch Leven. Weight at first maturity ranges from 10–60 g in males and 20–240 g in females.

Alm (1953, 1959) concluded from the study of experimental populations of perch in ponds at Kälarne, Sweden, that within a year-class maturity was reached earlier by larger fish, that is, growth rate influenced maturation. Between year-classes and populations, the age at first maturity was influenced by genetic factors and tended to be higher in faster-growing forms than in slower-growing ones. Krasikova (1958) reported an example of this from the Yenisei system where the river perch matured at AG III–IV at 12 cm and 80 g whereas those of Lake Munduyisk matured at AG III at only 7 cm and 13 g. Similarly, Dryagin (1948) quoted Tyurin and Sviderskaya concerning two growth-rate groups of perch in the Ob-Irtysh basin where the smaller form matures at AG III–IV and the larger at AG IV–V. First maturation may also be determined by a size threshold and thus by growth-rate affecting differentiation as well as somatic growth. Environmental conditions, especially temperature, influence maturation age which tends to be lower at higher temperatures.

Eutrophication, leading to increased growth-rate, has been suggested as the cause of the reduction in age of first maturity in recent years in the Bodensee (Hartman MS. 1974).

TABLE II

First maturation

Locality	Males			Females			Authority
	AG	Length (cm)	Weight (g)	AG	Length (cm)	Weight (g)	
East Anglia	I	5.7	-	II	8.6	-	Hartley 1947
Barnagrow Lake	I	10.4	-	I	10.4	-	Healy 1954
Ponds in Sweden	I	7.0	-	II	14.0	-	Alm 1946
Kličava Resr.	I	8.5	-	II	12.5	-	Stehlik 1968
Lake Dojran	I	9.5	-	II	15.0	-	Petrovski 1960
Loch Leven	I	10.0	-	III	24.0	-	Thorpe 1974
Lake Kiutajärvi	-	12.0	15	-	19.0	80	Lind et al. 1973
Ponds in Finland	I	-	10	II	-	20-30	Lind et al. 1971
Green Bay	I	12.7	-	III	18.5	-	Hile and Jobes 1941
Lake Manitoba	II	12.7	-	III	> 12.7	-	Kennedy 1949
Gr. Plöner See	III	16.0	-	III	18-22	-	Laskar 1943

3.1.3 Mating

At mating, the female perch sheds all her eggs at once in a continuous connected strand and is attended by a 'queue' of males which all take part in fertilizing them (Fabricius 1956, Fabricius and Gustafson 1959, Harrington 1947, Hergenrader 1969) (see section 3.1.6). Lindroth (1947) showed that perch sperm is viable for only a few minutes after shedding.

3.1.4 Fertilization

Fertilization is external, the cloud of milt being shed by the males close to the egg-strand. Kothbauer and Schenkel-Brunner (1974) have shown an anti-Hb activity of extracts of the female gonad which is inhibited by extracts of the male gonad: They suggest that the function of this mechanism is to stick the sperm to the eggs at the start of fertilization. Natural fertilization rates are high - about 95% in Belgian waters (Huet, pers. comm.) and 78-91% in Lake Dojran (Petrovski 1960).

3.1.5 Gonads

Le Cren (1951) described the seasonal pattern of the growth of gonad tissue and recorded an increase from September to October of 1 to 7-8% of body weight in males at which maximum the proportion was maintained until the spawning season in April. Lind et al. (1973) found that in Finland, the male gonad increased from 0.5% body weight in August to a maximum of 4.8% in September, remained constant until April and then declined to 3.4% at spawning in June. Turner (1919) described a similar seasonal pattern for male perch in North America. The female perch possesses a single ovary. Le Cren (1951) recorded that ovaries of immature fish remain at a constant value of about 0.5% body weight but a maturing fish shows a steady increase in ovary weight from about 1% in July to about 23% body weight in April immediately before spawning. Lind et al. (1973) found a similar steady increase from 1.0% body weight in July to 16.3% at spawning in the following June. The lower maximum sizes for gonads in Finnish fish are attributed by Lind to the shorter "resting period" for gonads (males: 1 month, females: 2 months in Finland as opposed to 3 and 4 months respectively in England) and the shorter growth season both under climatic influence. Dryagin (1948) gives values of 15.7-20.0% for females and 0.9-6.28% for males from Ob-Irtysh basin. Lagler, Bardach and Miller (1962) give proportions for the gonads of American perch similar to those of Le Cren's with maxima at about 20% for females and 8% for males. Female perch at

TABLE III

Coefficient of maturity: $100 \times \frac{\text{gonad weight}}{\text{body weight}}$

Locality	Males Length range (cm)	 Coefficient (%)	Females Length range (cm)	 Coefficient (%)	Authority
Windermere	10–45	8.0	12–44	23.0	Le Cren 1951
L. Kiutajärvi	10–26	4.8	11–32	16.3	Lind *et al.* 1973
L. Vortsjärv	8–10	4.19	12–14	27.8	Pihu 1964
	10–12	3.82	14–16	25.3	
	12–14	4.69	16–18	25.0	
	14–16	5.05	18–20	26.5	
	16–18	6.69	20–22	28.3	
	18–20	6.84	22–24	29.0	
	20–22	9.68	24–26	29.2	
	22–24	8.35	26–28	29.6	
	–	–	28–30	27.0	
	–	–	30–32	28.4	
	–	–	32–34	27.0	
L. Dojran	–	–	15–18.5 (AG I)	20.6	Petrovski 1960
	–	–	17–23 (AG II)	18.7	
	–	–	19.5–28.5 (AG III)	19.6	
	–	–	26.5–29.5 (AG IV)	22.6	
	–	–	28–33 (AG V)	22.8	
	10.5–23.5	5.9	15–33 (AG I–V)	20.0	
Ob–Irtysh	21 (mean)	0.9–6.28	21 (mean)	15.7–20.0	Dryagin 1948
North America	–	>8.0	–	>20.0	Lagler, Bardach and Miller 1962
Oneida Lake	–	–	23 (March 1968)	18.41	Hutchinson 1974
	–	–	23 (March 1971)	20.18	
	–	–	25 (March 1968)	20.73	
	–	–	25 (March 1971)	20.90	
	–	–	25 (April 1971)	29.53	
	–	–	28 (March 1968)	24.20	
	–	–	28 (March 1971)	21.99	
	–	–	29 (April 1971)	30.98	

Oneida Lake, New York, showed a similar increase during winter up to 31% of body weight at spawning (Hutchinson 1974): however, there are differences between years and larger females have relatively larger ovaries.

Pihu (1964) tabulated maturity coefficients (defined as weight of gonad: weight of fish minus viscera) for perch from Lake Vortsjärv, Estonia (Table III). For males, his values were 3.66–9.80% (mean 5.91), and females 15.5–39.1% (mean 27.3%). By this method, Le Cren's values would be at least 10% for males and at least 30% for females.

In all accounts, the gonads are reduced to about 1% of body weight after spawning.

TABLE IV

Fecundity of perch

Locality	Perch Length L cm	Absolute fecundity	Relative fecundity eggs/g	Egg No = bl^a exponent a	Authority
L. Zagli-Nur	9-19	950-9 100	30	2.60	Evtyukhova-Rekstin 1962
Baltic Sea, Askö	19-36	6 500-85 000	50-156	3.18	Aneer and Grahn (pers. comm.)
Slaptonley	10-28	1 000-30 500	52-188	2.62-2.79	Craig 1974
Baikal; Posolsk (slow)	11-32	2 360-82 440	59-127	2.79-3.02	Evtyukhova-Rekstin 1962
Mjösa	23-47	10 000-210 000	60-120	-	Huitfeldt-Kaas 1916
Baikal; Mukhor	18-28	5 140-37 030	62-90	2.62	Evtyukhova-Rekstin 1962
L. Dojran	15-33	4 370-81 801	70-202	3.95	Petrovski 1960
Cutfoot Sioux L.	17-29	7 353-28 944	73-125	2.34	Smith (pers. comm.)
L. Dzalangash	10-22	1 263-19 749	74-128	-	Shilenkova 1959
L. Ontario	13-26 (fork)	3 035-61 465	79-223	2.73	Sheri and Power 1969
Loch Leven	23-31	26 200-61 300	80-156	1.89	Thorpe (unpubl.)
Patuxent R.	17-29 (fork)	5 266-75 715	82-184	3.72	Tsai and Gibson (1971)
Oneida Lake	19-36	6 500-85 000	90-156	3.86	Hutchinson (pers. comm.)
R. Yenisei	18-35	14 918-93 145	90-163	2.71	Krasikova 1958
Kličava Reservoir	12-33	6 710-144 000	91-317	2.48	Stehlik 1968
Rybinsk Reservoir	19-30	16 400-69 300	95-183	2.52	Sergeev et al. 1955
Rybinsk Reservoir	13-36	111 800	-	2.69	Zakharova 1955
Baikal; N. Bay	18-27	11 650-48 340	104	2.72	Evtyukhova-Rekstin 1962
R. Ob	22-30	28 190-74 600	111	-	Dryagin 1948
Yakhromsk Reservoir	22-33	19 200-64 000	114-178	2.55	Konovalova 1955
L. Vortsjärv	12-34	6 380-93 500	118-397	2.71	Pihu 1964
Starnbergersee	12-26	3 700-30 500	121-218	2.99	Mast 1916
Volga Delta	6-35	3 100-127 700	121-281	-	Popova 1965
Ponds, U.S.S.R	17-25	11 600-32 600	130-240	2.18	Konovalova 1955
R. Rhine	15-(?)	6 100-134 000	142-300	-	Mast 1919
Dnieper Delta	19-43	12 000-199 000	147	-	Syrovatskaya 1927
Baikal; Peschanaya	15-31	7 230-110 620	310	3.61	Evtyukhova-Rekstin 1962
Baikal; Posolsk (fast)	23-43	25 750-196 710	368-419	-	Evtyukhova-Rekstin 1962
Severn River Md.	17-36	4 600-109 000	-	4.00	Muncy 1962
W. Lake Erie	18-33	8 618-78 742	-	2.79	Nepszy (pers. comm.)
E. Lake Erie	-	-	-	3.18	Nepszy (pers. comm.)
Wisconsin Lakes	-	5 899-11 272	-	-	Pearse 1925
Minnesota Lakes	-	10 000-48 000	-	-	Eddy and Surber 1960
Cassidy Lake	10-30	-	-	3.42	Schneider 1972
Whole Range	6-47	950-210 000	30-419	1.89-4.00	

– Coefficient of fecundity

Fecundity relationships for perch have been calculated by several authors or can be derived from their data. Some examples are given in Table IV.

Grahn and Aneer (1975: pers. comm.) have established relationships for Baltic perch from the Trosa area of Sweden as follows:

(F = egg number)

$\log F = 0.061 + 3.182 \log L$ (body length in cm)

$F = 491.31 + 115.43\ W$ (body weight in g)

$F = 5\ 764.9 + 434.54\ G$ (gonad weight g)

$F = 25\ 031 + 8\ 434.4\ A$ (age in years)

Fecundity-length relationships vary widely between localities and also within localities. Letichevskii (1946) noted that perch from the southern part of the Aral Sea were relatively infertile compared with those from the Volga Delta and attributed this to poorer feeding conditions in the Aral Sea. In Lake Baikal, Evtyukhova- Rekstin (1962) showed differences in fecundity between populations from separate habitats and within single habitats differences between fast and slow growth-rate groups (see Table IV for data). She analysed this further using comparisons between individuals of one size or one age or both between years at the same locality. Her conclusions were, that like many other fish species (see Nikolsky 1953), fecundity like growth rate depends on food supply so that when feeding conditions are secure and stable fecundity is high whereas it is low if food supply is poor. Conditions for reproduction may also affect fecundity, as for example, in the Mukhor Zaliv of Lake Baikal where growth rates and feeding for the parent perch were good but fecundity was rather low at 90 eggs per g of female. This locality is well protected from the prevailing southerly winds and allows very good conditions for the subsequent growth and development of fry. In Peschanaya Bay where feeding for the adults is good, reproductive conditions are bad since it is exposed to the full force of south and southeast winds at the spawning time and much spawn is washed ashore and lost. Here fecundity is high at 310 eggs per g of female.

The relationships between rate of increase of length, weight and fecundity with age were investigated and are shown in Fig. 5. Fecundity increase with age is very similar to that of weight increase in all the stocks she studied.

Tsai and Gibson (1971) showed that for Chesapeake Bay perch, absolute fecundity increased with length, weight and age, and that in this particular case, the high exponent in the fecundity-length relationship was probably due to favourable feeding conditions and the large visceral space available for gonad development. They showed significant differences between the fecundity-length relationships among their population from Patuxent River and those from Lake Ontario (Sheri and Power 1969) and the Severn River Maryland (Muncy 1962).

– Number of eggs per individual

(See Table IV.) Perch spawn only once per year, but it is not known with certainty that they spawn every year after reaching maturity. As individuals are known to have survived in the wild to at least 18 years (Vostradovsky 1962) and in ponds to 27 years (Alm 1952), it is likely that the range of lifetime egg-production extends from a few thousand to 500 000. However, Evtyukhova-Rekstin (1962) noted a decrease in fecundity of Baikal perch after AG VIII.

– Variation in fecundity with health or condition

As noted above, high fecundity values are associated with good feeding conditions as evidenced from data of Letichevskii (1946), Evtyukhova-Rekstin (1962), and Tsai and Gibson (1971).

– Correlation between number of eggs and nature of environment

Zakharova (1955) suggested that fecundity of perch was lower in the more northerly waters. In Fig. 6, the scatter of median values of relative fecundity derived from data of Table IV relative to latitude, shows that this relationship is not a clear one. The correlation coefficient $r = 0.10$ gives no evidence of a significant relationship. As noted above, Evtyukhova-Rekstin (1962) indicated dependence of fecundity on ultimate reproductive success such that in conditions of equally good feeding for the progeny localities with high exposure were linked with higher fecundity than protected localities.

3.1.6 Spawning. Number of spawnings per year: one only

– Spawning seasons

The spawning season occurs between February and July in the northern hemisphere, and August and October in the southern. Thorpe (in press a) has reviewed the timing of the spawning seasons of perch and the following conclusions were drawn: the fish spawn in the spring during a period of accelerating temperature increase, the first females spawning at an earlier date the lower the latitude of the locality, but at a lower temperature the higher the latitude. As the date of first spawning varies between years at one locality and although photoperiod will affect maturation, temperature is probably the master factor governing spawning. Since temperature at spawning

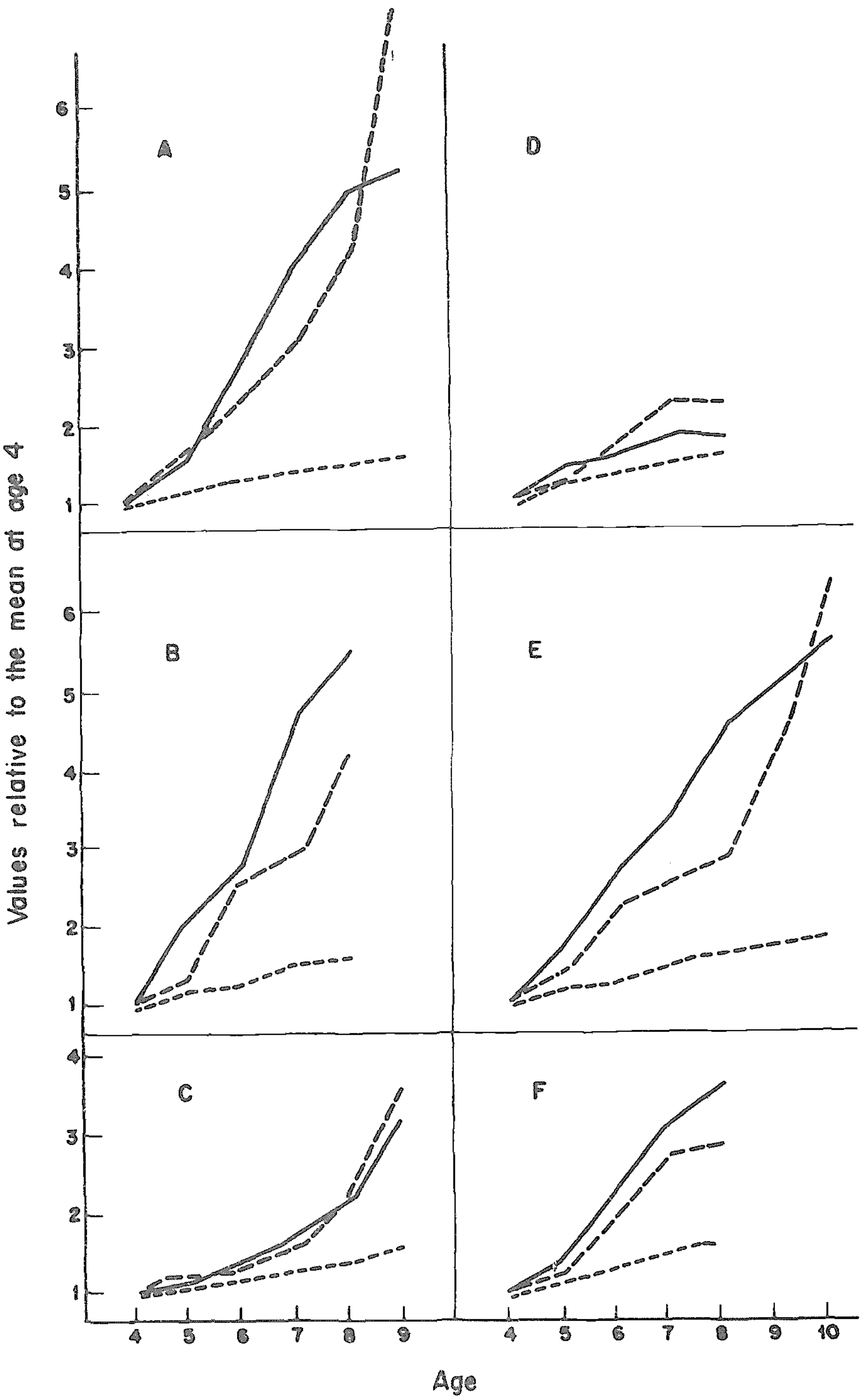


Fig. 5 Relationships between increase of length, weight and fecundity of Lake Baikal perch with age. (Mean values for first mature age group taken as unity)

A:	Posolsk Bay	1955	1: length increase	- - - - -
B:	Posolsk Bay	1957	2: weight increase	———
C:	Posolsk Bay	1959	3: fecundity increase	— — —
D:	Lake Zagli-Nur	1957		
E:	Peschanaya Bay	1957		
F:	Mukhor Bay	1958		

(From Evtyukhova-Rekstin 1962)

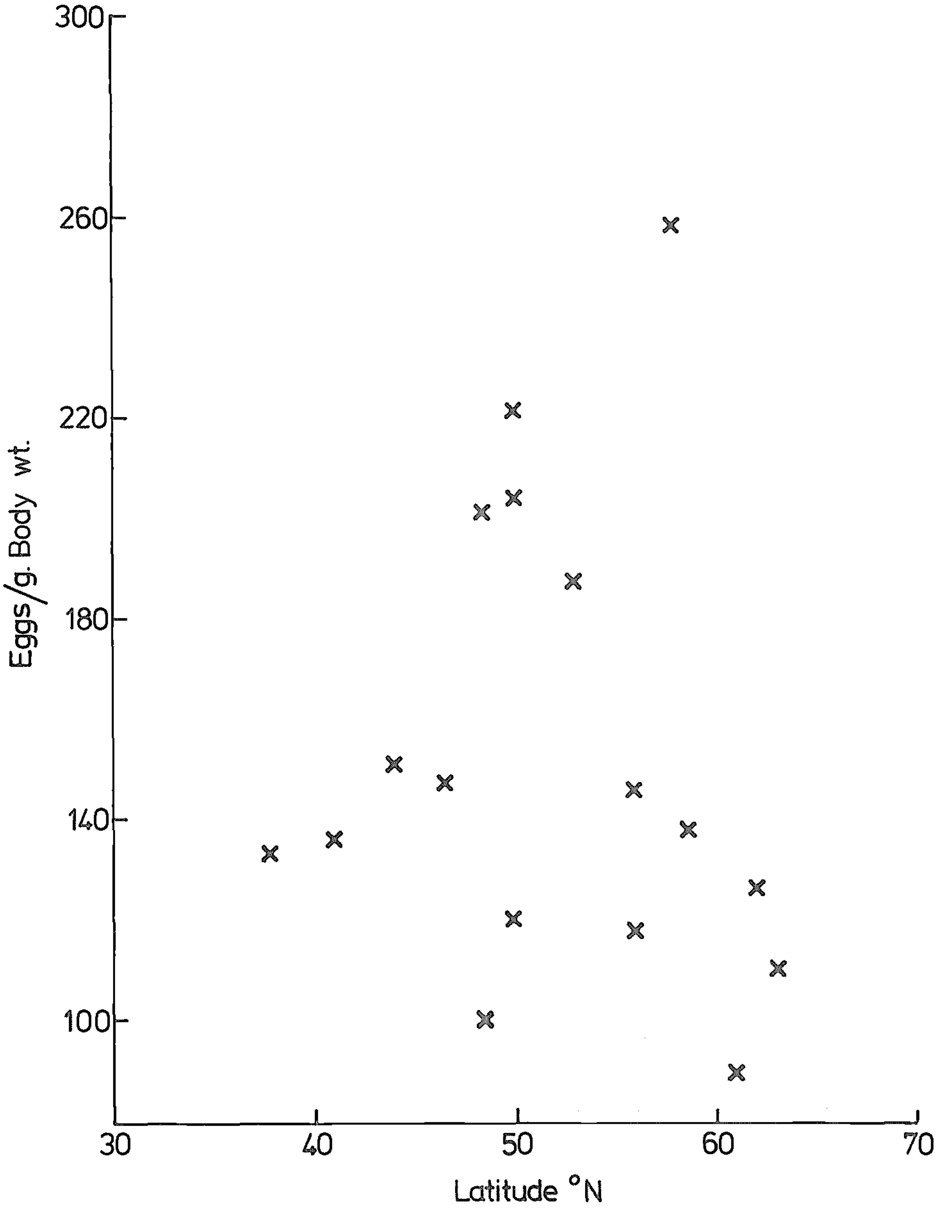


Fig. 6 Relative fecundity and latitude

differs between localities, other local factors must influence the timing of this event and a major example is the occurrence of spring floods which enable the perch to use the inundation zones of large rivers (e.g. the Danube before regulation (Balon 1963), the Volga (Popova 1965) and others). Lake (1967) noted that the onset of spawning in several native Australian fishes followed the first rains after periods of drought. He postulated that the leading of aromatic substances from the parched ground (e.g. Petrochor) acted as the releaser of spawning activity. Introduced perch could be induced to spawn when such flood-water was piped into their ponds, but he regarded temperature as the main stimulus to spawning. Selection will ensure that reproduction is timed such that the ensuing larvae enter an environment with adequate food resources for their arrival. Thus no one environmental factor is likely to assert total control over hatching and even the dominant one, temperature, ranges from c 4°C in the Aral Sea (where the perch spawn under ice (Filatov and Duplakov 1926) to c 14°C in Thompson Lake, Montana (Echo 1955).

The duration of the spawning period varies also, the males arriving on the spawning grounds days or weeks in advance of the females and remaining behind afterwards. Kukko et al. (1972) observed males on the spawning grounds at Hildenlampi Finland from 24 May to 14 June while females were only present from 2-9 June. Individual males remained on the grounds from 2-18 days (average 8.4 ± 0.47 days) and individual females only 1-4 days (average 1.2 ± 0.08 days). Tsai and Gibson (1971) record spawning at Patuxent River, Maryland lasting 3 days only, 23-25 March 1969. Dryagin and Muratova (1948) noted that in 1940, the perch in the Cheboksar area of the River Volga spawned from 8-10 May. Zakharova (1955) stated that spawning lasted not more than 2 weeks at Rybinsk Reservoir, the duration depending on temperature fluctuations and water-level. In 1951, spawning was completed between 27-29 April with an early spring warm-up and high water levels: in 1952, it lasted from 4-13 May when the spring warm-up was later and the water-level rose more slowly.

Nikitinsky (1928) found ripe males 15-18 days before the females appeared and 7-10 days before spawning 90% of the males but only 5-10% of the females were ripe. Spawning itself lasted only 2-3 days.

In other populations, the spawning period may be much extended. At Loch Leven, Scotland, Thorpe (in preparation) found that ripe males were present over a 7-week interval from mid-April to early June and that the average duration for individuals was less than 16 days. The peaks of occurrence of successive age-groups from AG I upward followed each other through the season such that although all age-groups were represented all the time, the AG I group dominated at the beginning and the AG IV-VIII at the end. The sequence of spawning among females was not observed. In Kličava Reservoir, Czechoslovakia, Holčik (1969) noted the same sequence of young males predominating at the beginning and old males at the end, but also observed that the reverse was true for females. In American populations, Herman et al. (1964) noted that the males arrive first and stay longer than the females. Tsai and Gibson (1971) recorded dominance of males at the beginning and end of the run with 1:1 sex ratio at the peak of spawning. The latter authors state that there was no size or age sequence in spawning. Hartman (MS. 1974) considers that the postponement of the spawning beyond mid-May in the Bodensee since eutrophication is due to a reduction in age of spawners, thus implying that young females spawn last.

- Time of day for spawning

The time of spawning is variously reported as at night (Kammerer 1907, Eddy and Surber 1960, Breder and Rosen 1966, Lake 1967, Scott and Crossman 1973) and by day (Chevey 1925, Hergenrader 1969).

Kammerer (1907) expressed the view that intensification of colour in perch at spawning must serve an aggregating function preparatory to the act rather than a signal function at the time of egg-laying which he maintained occurred at night. Lind et al. (1972) published data on trap catches during spawning and showed that these were greatest between 21.00 and 24.00 h at a time when the light intensity was only 800 lx (as compared with 51 000 lx between 09.00 12.00 h). They state that the occurrence of spawn on the traps was also maximal at this time. However, although this may be evidence of spawning at night, it is not evidence of absence of spawning by day when the fish could have been avoiding the traps.

- Time of breeding related to that of other associated species

Konovalova (1955) observes that the early spawning season for perch ensures favourable food resources for its fry and makes it an unpopular species with fishermen as it is thus a successful competitor with other more valuable spring spawners. In many localities, spawning follows closely that of pike (Esox lucius L.) for whose fry the perch fry will form an important food. In North America, Herman et al. (1964) observed that perch spawning follows closely that of walleyes (Stizostedion vitreum) with which the subsequent perch fry are related as prey to predator. Herman also noted that perch spawning coincides with that of suckers (Catostomus spp.).

- Location and type of spawning ground

Perch spawn mostly at depths of 0.5–3 m in natural lakes (e.g. in the Karelian Lakes – see Belyaeva (1959), Zakharova (1955), Pokrovski and Novikov (1959) and in Oneida Lake – Forney (1971), but may also spawn at depths to 8 m in large lakes and reservoirs (e.g. L. Onega (Iyudina 1951), L. Ladoga (Virolyainen 1940), Pyalovsk and Yakhromsk Reservoirs (Mikheev 1953)). Tunbridge (1972) found that they chose weedy shores in Australia while Lake (1959) stated that they would spawn anywhere away from fast currents attaching their eggs to plants or logs. Scott and Crossman (1973) add to this fallen trees, submerged brush, and over sand and gravel. Ereshchenko (1959) noted that they would also use floating debris. By experiment, Echo (1955) found that they preferred submerged fir branches. This general unspecialized requirement for spawning substrata allows the fish to utilize a wide variety of habitats, for example, Zakharova (1955) recorded spawning in "high-water years" at Rybinsk Reservoir on submerged vegetation in flooded meadows: in "low-water years" spawning took place in the beds of tributary rivers and on trees in their inundation zones. Thus the fish has the chance to be successful at whatever the water level.

In Kličava Reservoir, the perch can spawn quite satisfactorily where there are steep scree slopes (Holčik 1970). Sebentsov et al. (1940) also noted that conditions for perch spawning were particularly good in the Ivankovsk Reservoir. In the Gulf of Riga, Baltic Sea, Berzins (1949) recorded regular spawning on stony substrates where algal growth (Fucus spp.) was plentiful but that after hard winters such areas were abandoned in favour of sandy shallows where the water temperature was 5–8°C higher.

- Ratio and distribution of sexes on spawning grounds

Kukko et al. (1972) found 2–3 males to every female at the beginning and end of spawning and 5–10 at the peak period: Holčik (1969) found male:female ratios were 55.8:44.2 at the beginning and 69:31 at the peak, and 56.2:43.8 at the end. It is likely that all such ratios are biased by differential vulnerability of the sexes to capture at this time (see above, Spawning seasons).

- Nature of mating act

Fabricius (1956) described the spawning of perch from tank observations. The gravid female was followed closely by several males which became particularly excited as the female swam repeatedly through groups of dead tree branches on the bottom of the aquarium. Finally, the female swam in tight circuits round a barren willow branch flexing herself in a U-shape and expelling her egg-strand. All the males attempted to bring their anal openings close to hers and the female then darted through the branches to the surface and back again until the whole strand was shed and festooned the branches. The males followed her throughout this performance shedding milt close to her anal opening, but showed little interest in the eggs. After the spawning act was complete (c 5 sec), the female attacked and drove the males away from the eggs which she then patrolled for 5 h. She threatened by opening the mouth and spreading the gill-covers, arching the back and depressing the first dorsal fin. The black stripes on the flanks faded and the body became dark below the lateral line. Harrington (1947) described spawning aggregations in which the female was followed by queues of 15–25 males, the closest prodding her belly with its snout. Hergenrader (1969) also recorded the approach of males to the female's vent and noted that they rushed to her if she made any quick movement and then they seemed to contest for position closest to her vent. The egg-strand was completely expelled in a series of rapid movements accompanied by almost simultaneous release of milt by the males as a cloud in the water close to the eggs. The sequence lasted about 5 sec after which the female did not protect her eggs. Her sides appeared compressed and swimming was inhibited, but when it stopped, the tail tilted toward the water surface. Disturbance of equilibrium lasted about 1 h. Fabricius and Gustafson (1959) also noted this phenomenon. Kammerer (1907) recorded that the males swam with outspread fins and convulsive, interrupted twitches of the whole body as they released milt. Loss of equilibrium probably affects both sexes as Kammerer also reported head-down postures in the males. Chevey (1925) also noted that during the pursuit activity prior to spawning, the transverse dark bands sometimes disappeared, leaving the fish uniformly greyish-green. Parker (1942) claimed that the spawn is released from the female by the rupture of a papilla which forms between the urinary and anal openings.

3.1.7 Spawn

- External morphology

Chevey (1925) described perch spawn as a hollow cylinder whose walls are formed by the eggs enclosed in a network of tissue, the thick shells connected to each other in parts at plane surfaces so that they form polyhedra rather than spheres. Worth (1892) figured a section of the egg-strand demonstrating that it was "accordion-folded". Mansueti (1964) described the strand as c 3.8 cm thick, slightly heavier than water and floating in the current until entangled in debris and fallen branches in shallow water. The cylinder itself may be up to 3.75 m long and 8 cm wide (Chevey 1925). Konovalova (1955) noted that the strand is already formed in the ovary and its durability is due to the individual connexions between the eggs and the thick mucilaginous sheath which protects it against mechanical damage, infection by Saprolegnia and predation by invertebrates (perch eggs are not eaten by fish – even starving ones). The strand is resistant to desiccation and to "a range of spring temperatures". Aeration of the strand is accomplished by water circulating through spaces between the eggs (which are not completely bound to one another at all parts of their surfaces) between the central canal and the outside (Scott and Crossman 1973). Through these same holes, the milt must pass into the centre of the strand to fertilize the eggs (Fabricius and Gustafson 1959) whose micropyles face inward toward the cylinder cavity (Ranson 1855, in Chevey 1925). Lagler et al. (1962) pointed out that the advantage of the egg-rope was that the eggs were not scattered and could not fall into the mud.

The egg is a clear pale amber colour with a thick membrane consisting of an outer adhesive layer, a wide middle area composed of fine radially arranged fibres or striae and an innermost layer considered the zona radiata by Ryder (1887) (in Mansueti 1964). Laskar (1943) noted the radially arranged "needles" to which he attributed the sticky texture of the egg mass and noted that this texture is lost toward hatching as the whole mass becomes slippery and the eggs separate easily. The membrane is very strong and elastic until just before hatching. Before fertilization, there are 500-1 000 eggs to the gramme: after fertilization, 170-180 eggs per g (Sergeev et al. 1955).

Before hardening, the fertilized egg had a diameter of 1.6-2.1 mm (Mansueti 1964) or 1.0-1.6 mm (Lake 1967, Schneider pers. comm. 1975). Within about 3 min after fertilization, the membrane swelled and after hardening lost its adhesive qualities. The mean diameter after hardening was 1.9-2.8 mm (Lake 1.9-2.4 mm) and was almost entirely due to a thickening of the egg membrane which came to occupy one third to one fourth of the egg diameter.

Before hardening, the mean yolk diameter was 1.3 mm (Lake 1.2 mm) and the single oil globule 0.6 mm (Lake 0.5 mm). Schneider (pers. comm. 1975) found yolk diameters ranging from 1.0-1.5 mm and oil globules from 0.4-0.5 mm.

3.2 Pre-adult phase

3.2.1 Embryonic phase

Fourteen minutes after fertilization, the oil droplet has become drawn from the centre of the yolk mass to one side and bulges out pulling yolk with it (Mansueti 1964). In about 30 min, clear colourless blastodemal tissue thickens over the oil droplet. At about 5 h, the first cleavage occurs. At about 21 h, the blastula shows a peripheral germ ring and a blastocoel, and by 29 h, the gastrula stage has been reached with a thick germ ring one third of the way round the yolk. At 3-6 days, the embryo develops slightly off-centre of the yolk, the head proximal to the oil droplet and the tip of the tail free from the yolk which itself becomes elongate by the sixth day. From 6-11 days, the pectoral buds, auditory vesicles, caudal finfold and some body melanophores appear with some stellate melanophores over the yolk near the embryo. From 14-16 days, pigment appears in the posterior and anterior quadrant of the eyes, the pectorals are now well-developed, the myotomes are nearly complete, melanophores cover most of the yolk and the vent is visible at the junction of the tail and the yolk. The mouth is wide and gaping, and primitive gill-structures are present. The internal structure of the heart and the auditory vesicles is plainly visible and the tail is extended in a curve over the head except in large eggs where the thin walls and large perivitelline space allow the tail to remain not curled back. At about 24 days, the egg case begins to soften and appears ragged. Hatching occurs at 25-27 days after incubation at 8.5-12°C.

Mansueti noted that this incubation time was long for estuarine fishes (the description was made from Chesapeake Bay material). It is also unusually long for perch elsewhere as incubation time in other localities usually ranges from 120-200 degree days (see Table V) and normally takes 8-10 days in North America (Scott and Crossman 1973). Consequently, the timing of the developmental events does not correspond with other accounts such as that of Laskar (1943) who noted that 2 days after fertilization, 15 segments were formed; by 3 days, the eyes and auditory capsules were evident, the heart was pulsating and the tail is free from the yolk but does not reach the head. At 4 days, pigment has appeared on the yolk-sac and at the lower edges of the myomeres of the hind-body, there are 5 melanophores. The gut and notochord are differentiated, the vent appears just beyond the body midpoint, the pectoral buds appear and the embryo begins to move inside the shell. At this stage, the embryo is 3.6 mm in length. On the fifth day, pigmentation increases and the embryo becomes browner. On the sixth day, pigment is visible macroscopically on the yolk-sac and the eyes, and the vitelline circulation is evident. Otoliths appear shiny and refract the light. The "needles" in the gelatinous membrane of the shell disappear and individual larvae start to hatch through long splits in the shells. Most larvae hatch on the seventh day at a mean length of 5.6 mm with a maximum yolk diameter of 0.9 mm and an oil globule of 0.5 mm.

Schneider (pers. comm. 1975) found hatching at lengths of 4.1-5.5 mm in Michigan (Lake 1967), 4.8-5.5 mm in Australia and (Mansueti 1964) 5.5-6.0 mm in Chesapeake Bay. Konstantinov (1957) gave a range of hatching sizes encompassing all of these from 4.07-6.6 mm.

- Predators

As noted above (section 3.1.7), spawn is not normally eaten by other fish as also noted by Sumari (1971) in Finland. Day (1880) reported that it was eaten by swans (Cygnus olor L.) in the River Thames, England.

TABLE V

Incubation

Locality	Duration (days)	Temperature (°C)	Degree-days	Authority
Yakhromsk Reservoir	8-11	11-12	96-121	Mikheev 1953
Grosser Plöner See	7-8	14	98-112	Laskar 1943
Rybinsk Reservoir	10-12	12.5	125-150	Zakharova 1955
Canada	21	7.5	158	Scott 1954
New South Wales	18	10.0	180	Lake 1959
France	14-18	13.5-14	196-243	Chevey 1925
Eastern U.S.A.	27	8.3	224	Leach 1928
Chesapeake Bay	25-27	8.5-12	230-300	Mansueti 1964
Australia	7.5-8.5	14.5-20.5	120-175	Lake 1967
North America	8-10	(spawn at 8.9-12.2)		Scott and Crossman 1973
Northern Europe	18	10-12	180-216	Ehrenbaum 1905

- Mortality

There may be losses of spawn due to exposure when floods subside as noted by Dryagin and Muratova (1948) in the Volga River. Scott and Crossman (1973) also reported that egg masses may be cast ashore by wind, waves or currents and then lost. Also Clady and Hutchinson (1975) found "windrows" of millions of perch eggs washed up on beaches of Oneida Lake after severe storms and noted that there may also have been losses due to dislodgement of egg masses and transfer of these to deep unsuitable substrates. Tesch (1955) referred to destruction of spawn on shallows exposed to storm winds at the Schweriner Aussensee, and Evtyukhova-Rekstin (1962) to similar occurrences at Peschanaya Bay, Lake Baikal.

Swift (1965) exposed perch eggs to a range of incubation temperatures and found that hatching ranged from after 3 days at 22°C to after 33 days at 6°C: optimal temperatures were around 12°C above and below which mortality was high (see Table VI).

Kokurewicz (1969) and Hokansen and Kleiner (1975) each confirmed Swift's findings and showed that at constant temperatures, survival was optimal between 10-16°C. The latter authors also found optimal survival, shorter time to hatching and lower incidence of abnormalities when incubation temperatures increased by 0.5-1.0°C per day.

3.2.2 Larval phase

In Hokansen and Kleiner's (1975) experiments, larval swim-up occurred within 2 days of hatching (within 1 day at temperatures 13°C) and they survived unfed for 9 days at 19.8°C or 21 days at 10.5°C. These authors and Kokurewicz (1969) found that the hatching larvae were largest at the optimal incubation temperatures (5.6-6.3 mm) and that at temperatures below 7°C, hatching was morphogenetically premature.

Konstantinov (1957) defined four prolarval stages corresponding to total lengths of 3.7-4.7 mm, 4.7-6.0 mm, 6.0-7.0 mm and 7.0-9.0 mm. The first three of these correspond to the last 9-11 days of embryonic development in Mansueti's (1964) description and only the last is comparable as a true prolarval (i.e. post-hatching) stage.

Mansueti described the prolarva as having an undifferentiated finfold, pigmented eyes and 15-20 pigment spots along the ventral surface of the tail. The mouth is fully developed and feeding starts while the vestiges of yolk remain (at c 7.0 mm). Laskar (1943) noted traces of food in the hind-gut of larvae at 6.75 mm at 18 days after fertilization when the yolk-sac was almost completely resorbed and the oil-globule only 0.1 mm in diameter.

At hatching, Laskar noted that the pectorals were formed and beat, and the mouth was below the head. The gill arches and opercula were formed by the twelfth day (5 days after hatching), the

TABLE VI

Effect of temperature on mortality, and rate of development of perch eggs (from Swift 1965)

22°C		20°C		18°C		16°C		14°C		12°C		10°C		8°C		6°C	
Day	No. hatched	Day	No. hatched	Day	No. hatched	Day	No. hatched	Day	No. hatched	Day	No. hatched	Day	No. hatched	Day	No. hatched	Day	No. hatched
3	22	5	1	7	24	7	5	All dead		14	54	16	1	24	1	33	93
		6	36	8	97	8	130			15	78	17	5	29	2	Alive not hatched	
		7	51			9	52					19	12	30	3		
												20	5	33	55		
												21	5	33			
												22	8	Alive not hatched	84		
												23	8				
												24	8				
Average no. days to hatch: 3		6.3		7.8		8.3		-		14.6		20.9		32.8		33	

Temp. °C	24	22	20	18	16	14	12	10	8	6
% Mortality	100	97.7	65.8	63.9	49.2	100	38.0	54.0	44.4	70.4

mouth was nearly terminal and the swimbladder was visible as a small oval shape covered above with pigment. By the seventeenth day, the blood was coloured and vessels in the head and gill region were clearly visible. The nasal cavities were recognizable. On the eighteenth day, the pectorals were 0.8 mm long with pigment cells at the base.

Lake (1967) stated that the pectorals were formed at 6½ days and the eyes partly pigmented. Hatching occurred 1–2 days later and the larva swam straight away. At 10 days at a length of 7 mm, it fed for the first time; at 20 days was 10 mm long; and at 60 days at 15–17 mm, the fin complement was complete. In this post-larval stage, Mansueti (1964) states that pigmentation increases over the body, the head elongates and flattens, and a few teeth protrude from the maxillary. Fin formation starts at about 11 mm total length with differentiation of the base of the caudal. Thereafter, the sequence of fin development is anal; second dorsal: some spines of first dorsal, pelvics; and finally the remaining spines of the first dorsal. All fins are formed by 14 mm, but not complete with all rays until 21–27 mm. When the first soft ray of the anal fin becomes a spine, body bands begin to appear at 20 mm. The mytome number is 35–40, most commonly 36–37; 18–21 preanal (usually 19) and 16–19 postanal (usually 18), which distinguishes perch from other fry. At 49 mm, fin formation is complete and the fry is fully scaled. Ehrenbaum (1905–9) reported body bands appearing at 12–13 mm (1 month old) and fully formed by 25 mm. At this length, the swim bladder extends almost to the anus. The sequence of scale formation was studied by Pycha and Smith (1955) whose illustration is reproduced here as Fig. 7. Pockets of scales first appear on the caudal peduncle at c 20 mm total length and scalation proceeds along the lateral line and at the same time dorsoventrally. The first scales are fully imbricated in the region ventral to the 12–14 lateral line scales by 24 mm and the fish fully scaled at 36–37 mm. The nape and the anterior part of the belly are the last areas to be scaled. Size rather than age determines scalation. Segerstråle (1933) reported the first scales formed on perch in Scandinavia at 2.0–2.5 cm total length.

– Growth of fry

Tesch (1955) plotted the length growth of fry from the Müggelsee throughout their first growing season and compared his results with data from several other localities (Fig. 8).

Pycha and Smith (1955) noted that length growth was approximately linear from mid-June until late August as the fry grew from 19–60 mm, but that as growth was not correlated with that of older year-classes in the same year, it depended on different factors. Since the habitat for the fry and their food differs from that of other year-classes, this is not surprising. The weight-length relationship among these fry was:

$W = (0.6198 \times 10^{-5})\ L^{3.1251}$ (g and mm). No correlation could be shown between growth and year-class strength of fry. Ward and Robinson (1974) found that from 1 July to 31 August, perch fry tripled their length and increased their weight by a factor of 9. Growth equations were derived as follows:

(t in days)

$$\mathrm{Log}_e L_t = \mathrm{Log}_e L_o + 0.022\ t$$

$$\mathrm{Log}_e W_t = \mathrm{Log}_e W_o + 0.074\ t$$

$$\mathrm{Log}_e W = 3.4\ \mathrm{Log}_e L - 2.6$$

In experimental ponds in Michigan, Schneider (1973 a) demonstrated inverse density dependence of growth during the first 6 months of life over a range of autumn densities of 4–32400 per ac (10–82 300 per ha). At densities below 2 000 per ac (5 080 per ha), fry growth (at 11.2 cm and 15 g) became influenced by the presence of one-year-old perch with which they were probably competing. In the absence of any older perch, growth of fry reached a maximum level at densities $\leqslant$500 per ac (1 270 per ha) at 15–20 cm and mean weight of 57 g.

– Survival

Noble (1972 b) found that predation on fry by older perch and walleye (Stizostedion vitreum) seldom occurred before the perch fry were 1.8 cm long. However, Menshutkin et al. (1968) found fry in the stomachs of 2% of adults in Lake Razdelnyy, Karelia, on 24 May, 6% of adults on 30 May, 24% on 3 June and none on 6 June. This period corresponded to the first two weeks after hatching. Despite this evident cannibalism, the authors argue that the catastrophic decline in numbers of survivors from 13.4×10^6 on 30 May to 2.3×10^6 on 6 June can be accounted for by food-shortage alone. They base their conclusions on plankton density measurements which indicate a sharp decline in available nauplii for the perch fry over this same two-week interval. Cerny and Pivnicka (1973) also found high daily mortality rates at this stage (10.7% per day). Tarby (1974) also claimed that predation was insufficiently intense to account for high fry mortality rates in Oneida Lake where he reported 25% of the June population of fry were eaten by adult perch in the period June–October. However, as his estimates of evacuation rate were made from force-feeding experiments, it is likely that his estimates of food-turnover are too small (see Thorpe 1974 and in press b). Hence, cannibalism could account substantially for the high fry mortality.

Holčik (1969) found that in Kličava Reservoir in 1960, the survival of perch fry in the absence of adult perch was very high. Thorpe (1974) found that adult perch of Loch Leven consumed 88.6% of their own wet weight of perch fry between June and September.

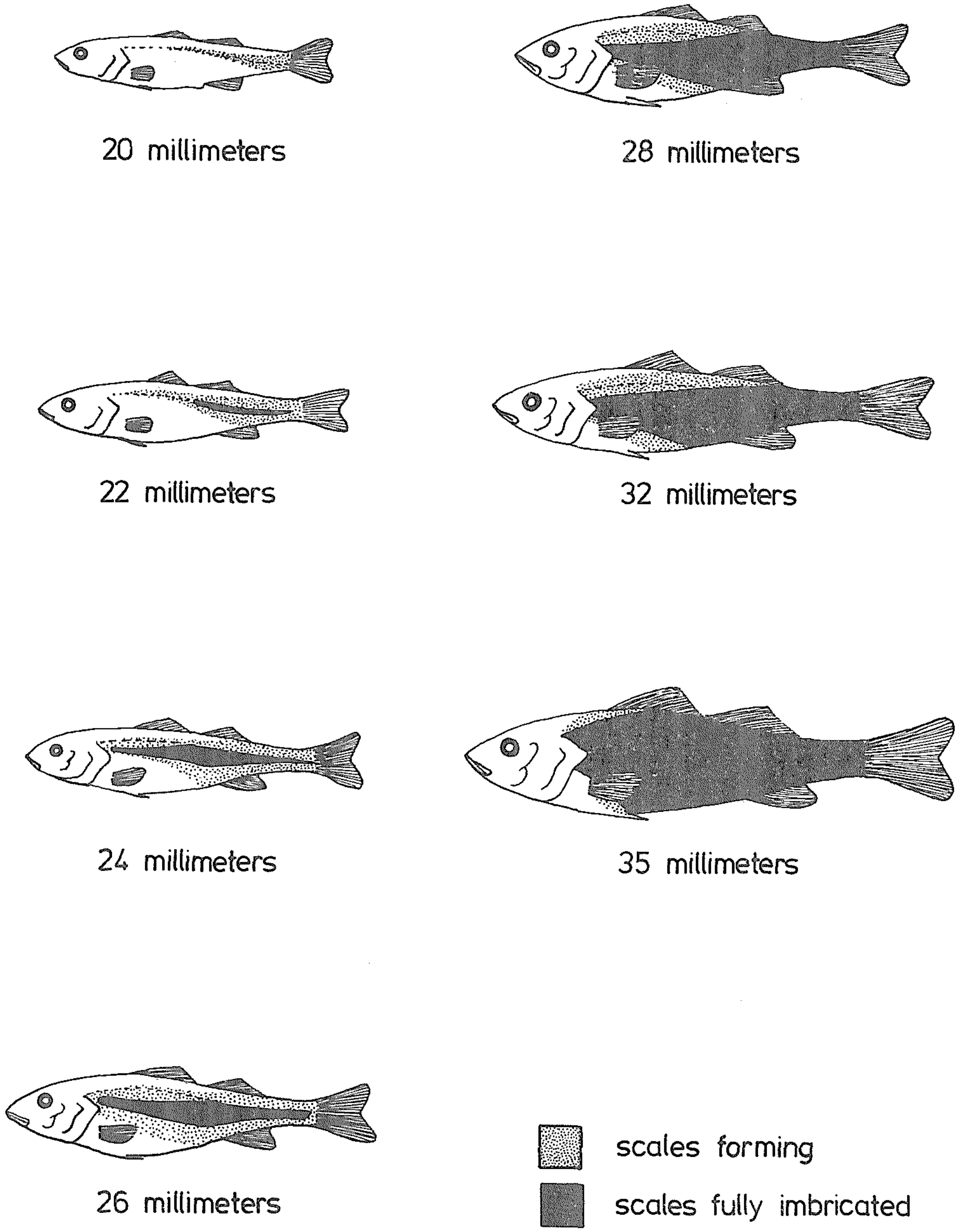


Fig. 7 Scale formation in 0-group yellow perch
(From Pycha and Smith 1955)

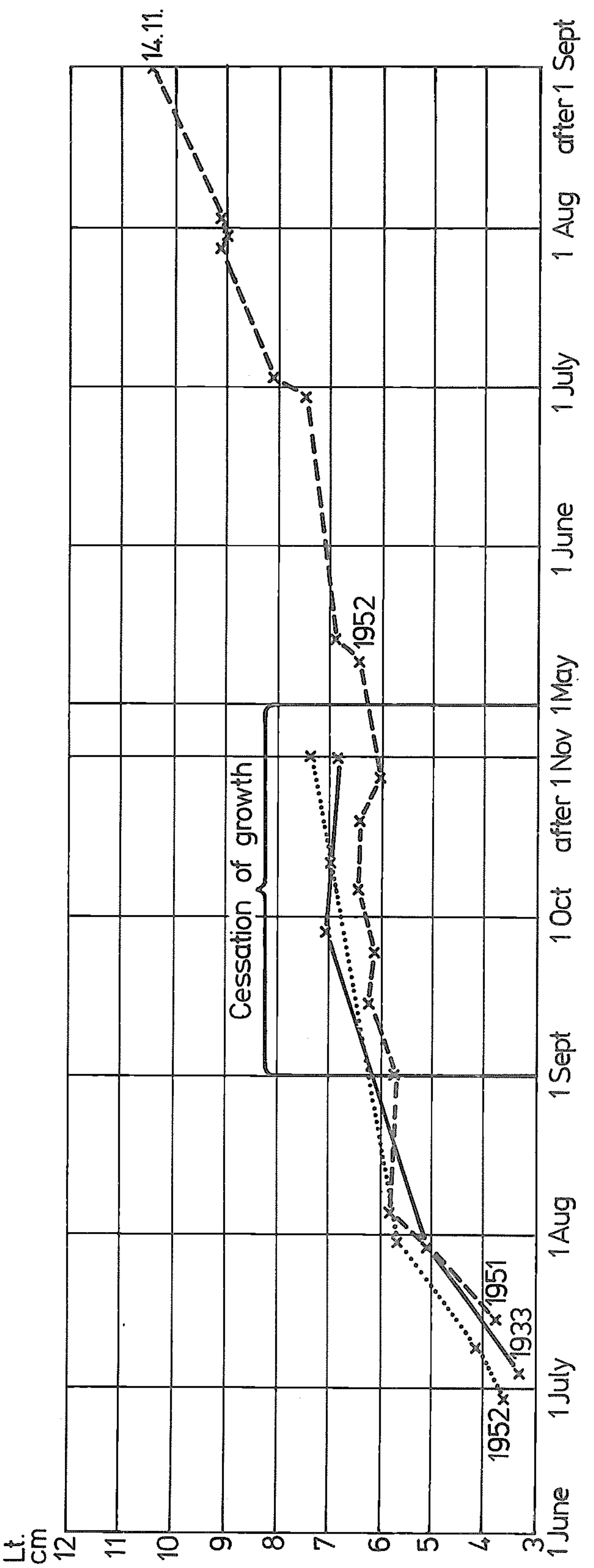


Fig. 8 Growth of young perch in Müggelsee (after Tesch 1955)

Houde (1967) found that walleyes of 9 mm total length were feeding on 0+ perch and that these perch became more important as a food item as the walleyes reached 19 mm in length.

Parsons (1971) found that 0+ walleyes fed primarily on 0+ perch in Lake Erie until July when the surviving perch grew out of the length range of fry preferred by the walleyes. In June, they made up to 93% of the identifiable food in walleye stomachs. By September or October, they were reaching the size preferred by 1+ walleye (see Fig. 9). Smith and Pycha (1960) noted that 0+ perch were the major food of post-pelagic 0+ walleyes and Eschmeyer (1950) estimated that 68% of the 0+ walleye diet in Lake Gogebic consisted of 0+ perch. Many authors report movement of post-larval perch offshore to the epilimnion for the first part of the summer (e.g. Schneider 1908, Alm 1922, Chirkova 1955, Konovalova 1958, Forney 1971, Ward and Robinson 1974). The fry mingle with those of other spring-spawning species in open waters where there are fewer predators than in the vegetated zone (e.g. Zakhromsk Reservoir, Konovalova 1958). Steinmann (1950) found perch fry to be epilimnetic until they reached a total length of 2 cm and during this phase, they were the favoured food of Blaufelchen (*Coregonus*) in Swiss lakes. Frey (*in* Tesch 1955) noted that coregonids in such lakes were full of young perch in July, one fish containing 47 fry of 3-4 cm length.

In the case of the central basin of Lake Erie, Regier *et al.* (1969) have suggested that together with smelt (*Osmerus mordax*), the perch fry are probably protected from walleye predation due to hypolimnial oxygen depletion which excludes the walleye from their foraging base. Ward and Robinson (1974) also note heavy predation of perch fry by walleyes in West Blue Lake, Manitoba, in midsummer. Parallel fluctuations in year-class strengths of perch and walleye have been recorded in many American lakes (e.g. Heyerdahl and Smith 1971, Forney 1965, Hartman 1972) and Forney (1965) showed that density of young perch fluctuated in the same sense as growth increments of walleye - thus the latter depended on the former. In Rybinsk Reservoir, Romanova (1955) found that perch fry from 1.7-8.3 cm (75% of these were 4.1-4.7 cm) formed the major food of pike-perch, *Lucioperca lucioperca*, almost all being eaten between June and September with a maximum in July. Chirkova (1955) had found these fry on the littoral just after hatching in early June and then distributed mainly pelagically until October when they were again found in the shallows. At all times, spatial distribution of fry was clustered and not uniform.

Allison *et al.* (1974) found perch fry in the stomachs of goosanders (*Mergus merganser*) during the winter months on Loch Leven, Scotland. Forney (1971) calculated instantaneous daily mortality rates of fry in Lake Oneida at 0.30-0.56.

Le Cren (1955) suggested that survival of perch fry was influenced by weather conditions. Such factors probably operate through their influence on the abundance of zooplankton (cf. Menshutkin *et al.* 1968). In experimental ponds, Schneider (1973 a) showed that survival rates were higher in ponds rich in plankton than in those with extensive stands of *Typha latifolia* which were less turbid, independent of the density of fingerling perch present in the ponds. However, although fry survival was reduced only at fingerling densities <800 per ac (1 975 per ha) in the Typha ponds, it was reduced at densities <500 per ac (1 234 per ha) in the plankton-rich ponds. In these experimental ponds, survival from egg to October of the first year of life was 4.7-32.4%. In the wild, Schneider (1972) has found much lower values from 0.02-12.4%.

- Type of feeding

Kammerer (1907) found that perch larvae of 7 mm started to feed on infusoria and diatoms. Chevey (1925) recorded Ostracoda and Cladocera taken on the first day of feeding and Nikitinsky (1929) stated that the first foods of perch (1+ and older) in Zarizino Lake near Moscow were Rotatoria and Copepoda. Rogowski and Tesch (1960) from a comparative study of the first feeding of fish fry also found Rotatoria and Copepoda taken by perch from 6 mm total length. Teodorescu (1943) reported rotifers as the first food. Siefert (1972) showed that *Polyarthra* was selected by fry from 5.4-9 mm total length and cyclopoid copepods from about 6 mm onward (see Fig. 10). He noted that the fry had small mouths and were weak swimmers and therefore the food had to be small enough to be ingested and slow enough to be caught. Chevey (1925) divided a group of freshly hatched alevins into two offering one group Cladocera and the others nothing. After 5 h both groups had completed yolk absorption, but the group offered food still had an oil globule of 10 µ in diameter. The group without food had an oil globule of 4-5 µ diameter and at this stage attempts to feed them failed and they died. He described the method of food capture as follows: the prey is stalked by swimming in which only the pectorals are used for propulsion and the tail held still; when the prey is within 1-2 cm, the body is slowly curved at right-angles and suddenly straightened, the animal flicking forward in the process and grabbing the prey. This method is used until 2-2½ months old, the fish gradually taking larger and larger particles up to larval Diptera.

Pycha and Smith (1955) found that the main food of post-larvae was small entomostraca, the fish utilizing larger forms as available by the time they reach 30 mm total length and then beginning to take benthic invertebrates. Wong and Ward (1972) showed that the gape of perch fry less than 1.8 cm total length was too small to take *Daphnia* with a body-depth greater than 0.7 mm, but

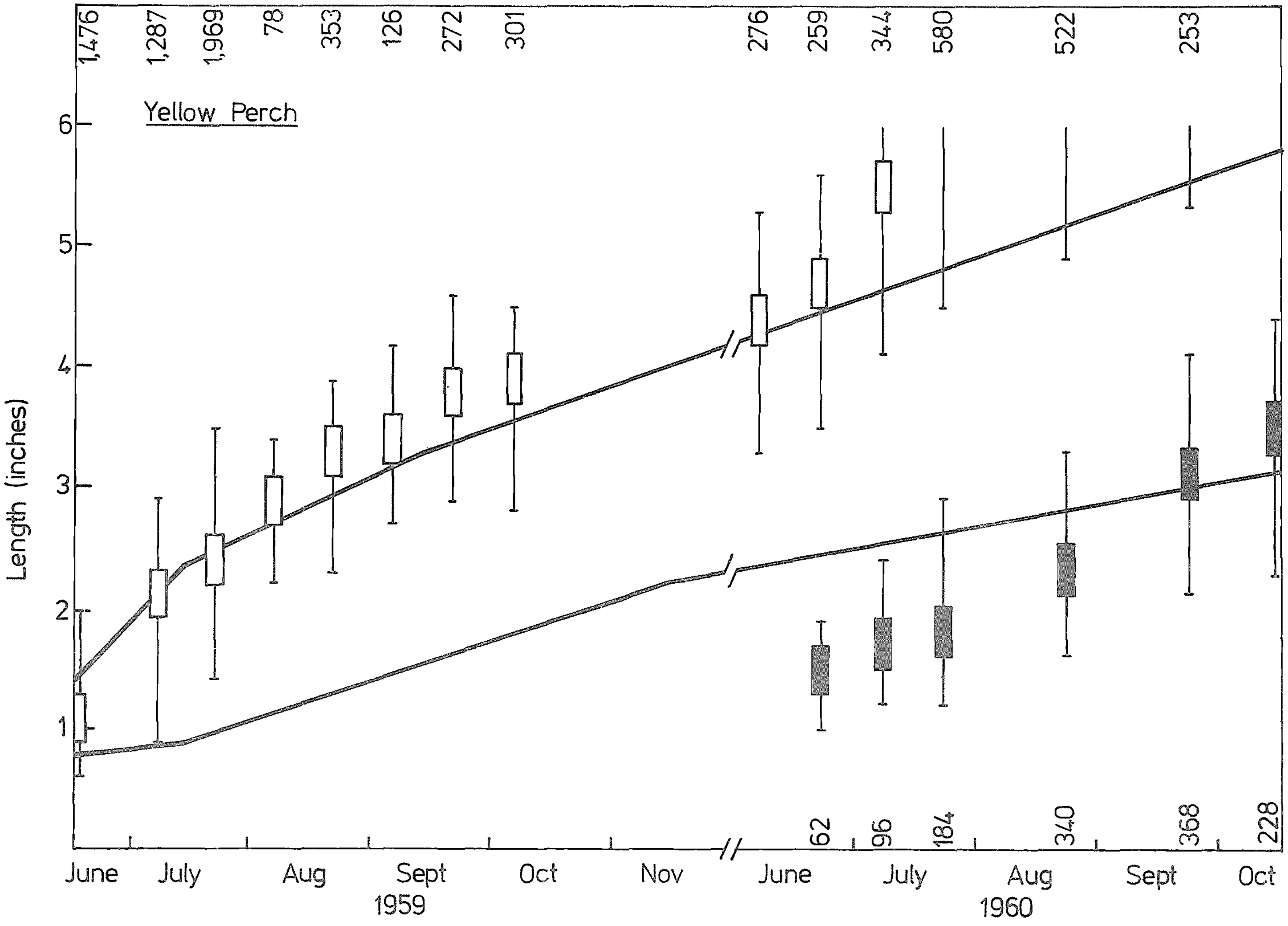


Fig. 9 Selective size preference of yellow perch as prey by walleyes. Length distribution (vertical lines) and modal groups (vertical bars: unshaded for 1959 year classes, shaded for 1960 year classes) of yellow perch and (solid running lines) maximum and minimum preferred lengths of yellow perch by monthly or semi-monthly periods, 1929-60; the numbers of fish of the 1959 year class that were measured are given along the upper border and those of the 1960 year are given along the lower border (from Parsons, 1971)

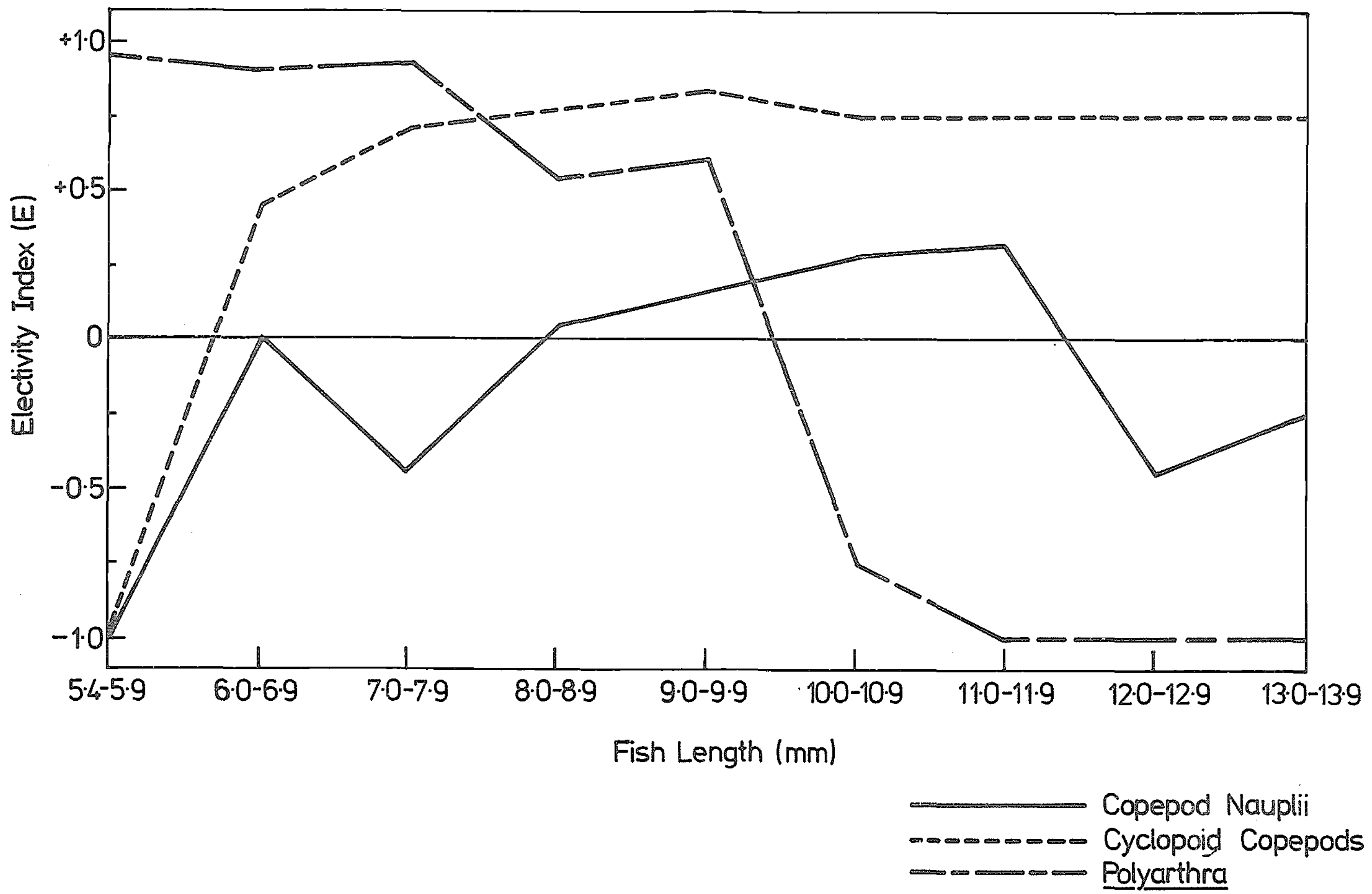


Fig. 10 Electivity indices (E) for major food organisms of larval yellow perch of different size, Greenwood Lake Minnesota (from Siefert, 1972)

as jaw growth was differentially greater than total length growth, the fry were able to utilize the Daphnia quickly. Even at this early stage, the perch is an opportunist feeder as Ilina (1973) showed experimentally. The progeny of individual pairs of perch occupied three separate food niches in ponds during their first summer such that three ecological groups formed feeding on plankton, benthos and fish respectively.

Cannibalism in perch seems to be universal and also starts very early. Smyly (1952) found 2.1 cm fry eating their own kind in Windermere and Clemens et al. (1924) 2.5 cm fry as cannibals in Lake Nipigon. Pekav (pers. comm. 1970) found that in experimental ponds in Czechoslovakia, fry which hatched early started to feed on their late-hatching fellows very quickly.

Lane and Jackson (1969) estimated the rate of passage of a single meal through perch fry of 3.5–4.8 cm as 36–60 h at 12°C. However, Noble (1973) fed perch, hatched in the laboratory with Daphnia and estimated rates of passage by staining the plankton periodically to act as an indicator. In single meal experiments, perch of 60 mm evacuated a meal of 170 Daphnids in just less than 12 h at 15°C: if the meal was 150–250 Daphnids followed immediately by excess food, the evacuation was completed in 6.1 h. Similarly, a single meal of 10 daphnids fed to 30–40 mm perch fry at 22°C was evacuated in 6.5 h whereas if excess food was fed immediately after the experimental meal, the passage time was only 1.5 h. As Noble (1972) noted that perch fry fed continuously during daylight hours under natural conditions, therefore the higher evacuation rates are more realistic.

In a range of experiments using perch of 5.2–23.7 g at temperatures from 9.4–30.6°C, Schneider (1973 b) found that maintenance ration, appetite and growth were optimal at about 23°C. These small perch grew best on a diet of fish (Pimephales promelas) and required such a meal equal to 2% of their body weight per day for maintenance. When fed "to excess", they consumed a daily ration of 7.6% of their body weight of fish or 6.6% of redworms (Helodrilus foetidus). On the former diet, they grew at a rate of 1.95% body weight per day, but on the latter not at all. The highest conversion rate, 26%, occurred at 22.9°C, but a level of 13–18% was found at other temperatures. Thus, the qualitative composition of the diet affects growth very markedly and food conversion efficiency is low compared to other warm-water fish of comparable size.

3.2.3 Adolescent phase

– General development

The young perch begin to resemble the adults toward the end of their first summer when pigmentation is complete and the dark spot at the posterior end of the first dorsal fin has appeared.

3.3 Adult phase (mature fish)

3.3.1 Longevity

Herman (1964) considered that perch in North America were relatively short-lived, seldom exceeding 7 years and in Lake Mendota, few lived beyond 5 years. Further north, the life-span was longer. For Canadian populations, Scott and Crossman gave 9–10 years as the normal span, but one of 11+ had been taken from Lake Erie. Muncy (1962) figured examples of up to 12 years old from Chesapeake Bay. Eurasian populations show a wider age range. Backiel (1971) found perch up to 13 years old in the Vistula River and Vostradovsky (1962) reported one of 18+ (1.43 kg, 38 cm) from Mseno Reservoir. Neuman (1974) found perch up to 18+ in populations on the Baltic coast of Sweden. Alm (1952) recorded perch of 27–28 years from pond populations in Sweden. In dystrophic lakes, he noted that rich year-classes could dominate the slow-growing populations for up to 15 years, implying a maximum age greater than 15 years: in oligotrophic and eutrophic lakes, rich year-classes dominated the better growing populations for a much shorter period and life-span was shorter.

Nevertheless, he found no correlation between life-span and growth since rapidly-growing fish in ponds lived to a great age. He concluded that long life-span in stunted populations was related to low predation pressure. In a later paper, Alm (1959) recorded 1:1 sex ratios in pond populations of 9-year-old perch and suggested that the observed longer life of females (e.g. Eschmeyer 1937, 1938; Hile and Jobes 1942; Carlander 1950) in the wild was a consequence of higher activity in the males exposing them to greater risk of predation. There was no evidence of physiological mortality being higher in males.

3.3.2 Hardiness

(See also section 2.3.)

Alabaster and Downing (1966) investigated the possible effects of heated effluents on fish in rivers in which temperature changes could occur rapidly. Tests included perch (mean length 8.4 cm) which were acclimatized in groups at a range of temperatures. The test temperatures at which 50% of the fish survived for 100 and 1 000 min were as follows:

		Acclimatization Temperature °C			
		6	15	20	25
Temperature at which 50% of perch survived	1 000 min	24.0	28.0	29.7	31.4
	100 min	24.8	28.2	30.5	32.8

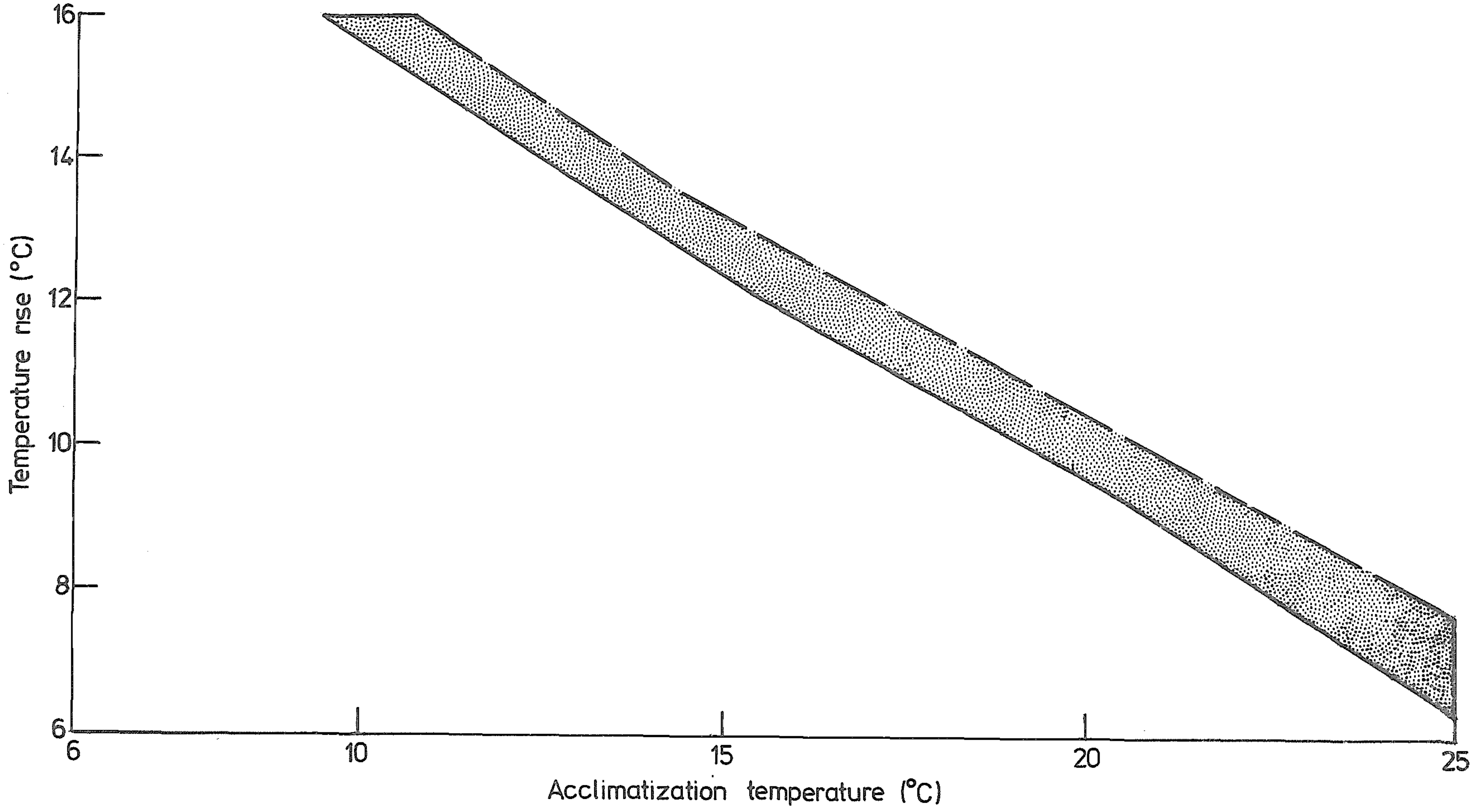


Fig. 11 Comparison of increases in temperature lethal to perch and acclimatization temperature. The stippled areas indicate lethal temperatures; the broken boundary lines indicate the 100-minute temperature and the solid boundary lines the 1 000-minute (from Alabaster and Downing 1966)

From this, it is clear that perch are tolerant of sudden temperature increases of up to 8°C for short periods even when the normal environmental temperature is 25°C. However, such an increase would be lethal if maintained for 16–17 h when the normal environmental temperature was 22°C. Fig. 11 shows the actual increases observed at seven generating stations and the 100 and 1 000-minute lethal values for perch obtained from the tank experiments, assuming the acclimatization temperatures are the same as normal mean river temperature.

Perch were also subjected to fluctuating temperatures and were observed to begin to move when the temperature had risen to a few degrees above their acclimatization value. Thereafter, they tended to remain in that area of the gradient, continually avoiding further temperature change (no temperature values were given). When tested under constantly rising temperatures to establish at what point the avoidance started, the perch which selected 15.6°C as their preferred temperature initially responded to a steadily increasing temperature of 1.7 or 4.7°C per h only after a change of 5–7°C (average 6.4°C) and then selected a new level at 17.9°C. Neill and Magnuson (1974) commented that "it matters little whether in the laboratory yellow perch... can grow at 30°C or can survive 33°C for 1 000 min if yellow perch never occur in an outfall area where temperatures exceed 29°C. The more important question is whether yellow perch given a choice will invade waters of a particular temperature, and if so, for how long and for what reasons, ecologically prudent or otherwise". (For data on tolerance to current speed, turbidity, dissolved gases, dissolved solids and pollutants, see section 2.3.)

Lake (1959) regarded perch as "reasonably hardy and not as prone as native Australian species to fungal infections." Andre (pers. comm.) has found that transporting perch for stocking purposes can only be done satisfactorily in the winter months at low temperatures when the fish are relatively inactive: at other times, high losses occur. Breder and Rosen (1966) found that of all North American freshwater fish kept in the New York Aquarium, perch were the most apt to spawn in a crowded aquarium and the presence of many fish seemed to have little inhibitory influence on them.

3.3.3 Competitors

Perch have no competitors for spawning area since, as pointed out in section 3.1.6, their site requirements are not restricted and more or less any submerged object will suffice for the attachment of the egg-strand.

For food, perch may compete with any or all other predatory fishes present in the same water. Scott and Crossman (1973) include among these potential competitors brook trout (*Salvelinus fontinalis*), ciscoes (*Coregonus* spp.), lake whitefish (*Coregonus clupeaformis* Mitchill), basses (*Morone* spp., *Micropterus* spp.), crappies (*Pomoxis* spp.) and bluegill (*Lepomis macrochirus* Rafinesque). They also noted that intraspecific competition may lead to stunting (see section 3.4.3). Potential competitors in the Bodensee (Hartmann, MS. 1974) are roach (*Rutilus rutilus* L) and *Coregonus lavaretus* since both these fish feed on the same spectrum of planktonic organisms as does the perch there. However, open and effective competition is avoided through spatial segregation vertically and seasonally, and hence the similarity of food preferences has no apparent effect on growth. In 1971, for example, perch and its competitors showed very good growth. In June–October, perch dominate in the bottom areas of the sublitoral while *C. lavaretus* is concentrated in the upper water layers. Ivanova (1969) found that the larger perch of Rybinsk Reservoir shared the same principal diet components with pike (*Esox lucius* L), pike-perch (*Lucioperca lucioperca* L) and burbot (*Lota lota* L) namely, roach, small perch, ruff (*Gymnocephalus cernua* L.) and smelt (*Osmerus eperlanus*). However, she claims that competition is not evident since the periods of intense feeding are separated, that is, seasonal segregation of feeding as Hartmann suggests for the Bodensee fish. In Loch Leven, Thorpe (1974) found that the spectrum of organisms in the diet of perch >20 cm fell almost completely within that of adult trout, the food-turnover of the two species being estimated simultaneously. However in this instance, concentration of predation by the two potential competitors on a single prey species occurred at different times of day so that a diurnal rather than seasonal segregation of predatory activity took place.

Regier *et al.* (1969) reported an increase in the perch stocks of Lake Erie after the collapse of the blue pike (*Stizostedion vitreum glaucum*) and they regarded this as a response to increased food resources freed by the decline of blue pike. Similarly, Christie (1973) suggested that the increase of perch in the eastern outlet of Lake Ontario was due to improved littoral food resources after the collapse of whitefish stocks. However, in a subsequent paper, Christie (1974) also noted that perch had increased in Lake Ontario around the dense beds of *Cladophora* which had appeared with eutrophication at the same time as whitefish had disappeared. Thus the improvement for perch may have been due to the creation of new habitats for food organisms in the weed beds rather than the removal of competition. Muncy (1962) also quoted *Roccus saxatilis* Walbaum, *Roccus americanus* Gmelin and *Esox niger* Le Sueur as competitors for invertebrates in the shallow water areas of the Severn River estuary, Chesapeake Bay.

Sumari (1971) found that among 32 ponds in Finland, the biomass of perch was usually very small when there was a reproducing roach population present which utilized the food supply of the perch and also preyed on the perch fry. The average biomass of perch in ponds without roach was 14.3 kg/ha (Range 3.8–41.3 kg/ha): in ponds with roach, it was 11.9 kg/ha (Range 1.8–23.4 kg/ha), a difference which was significantly less (t = 2.39, df = 30).

Rudenko (1967) listed roach, ruffe (*Gymnocephalus cernua* L), rudd (*Scardinius erythrophthalmus* L), tench (*Tinca tinca* L), crucian carp (*Carassius carassius* L) and pond loach (*Misgurnus fossilis* L) as competitors of benthophage perch in Lake Somino.

3.3.4 Predators

As Scott and Crossman (1973) pointed out for North American perch, almost all warm to cold water predatory fish will eat perch. They listed the following as predators: basses (*Morone*, *Micropterus* sp.), sunfish (*Lepomis* spp.), crappies (*Pomoxis* spp.), walleye (*Stizostedion vitreum*), sauger (*Stizostedion canadense*), perch pike (*Esox lucius*), muskellunge (*E. masquinongy*) and lake trout (*Salvelinus namaycush*). To this list should be added pike perch (*Lucioperca lucioperca*) and burbot (*Lota lota*) (e.g. Ivanova 1969) and brown trout (*Salmo trutta*) (e.g. Thorpe 1974). Perch were one of the main foods of burbot in the river months of Lake Simcoe (MacCrimmon and Devitt 1954) and Clemens (1957) noted that burbot of over 30 cm length ate much perch of marketable size.

In Heming Lake, Manitoba, Lawler (1963) found perch in about every fourth stomach of burbot sampled, and it was the second most frequent prey species from a sample of almost 30 000 pike (Lawler 1965). Allen (1939) and Frost (1954) found perch to be the most important prey of pike in Windermere. Holčik (1968) found that pike preferred perch as prey rather than roach. Ward and Robinson (1974) found perch to be an important food for walleyes in West Blue Lake, Manitoba. Ivanova (1969) calculated the consumption of perch by the four main predatory fish in Rybinsk Reservoir and her findings are reproduced in Table VII. Consumption was estimated by Fortunatova's method (Fortunatova 1940, 1961) and the differences between the two years are attributed to the water regime: in 1960 (and winter 1960–61) the water level was low while in 1961 (and winter 1961–62), it was high. The mechanism of influence of the water regime on predator food consumption was not defined, but changes in foraging conditions with changes in level were implied. In Chesapeake Bay, Maryland, Muncy (1962) included *Roccus saxatilis*, *R. americanus* and *Esox niger* as predators of perch.

Zadulskaya (1960) also gives consumption of perch by fish predators in Rybinsk Reservoir as follows:

	Percentage of annual diet consisting of perch
pike	17.2%
pike-perch	10.0%
burbot	44.9%

The reasons for the discrepancies with Ivanova's data are not clear. Among the 32 Finnish ponds studied by Sumari (1971), it was possible to distinguish the effects of predation on perch in one pair which were very similar in all environmental respects except that Koukkulampi I contained 3.6 kg/ha of burbot and 10 kg/ha of perch whereas Koukkulampi II contained 26 kg/ha of perch only.

Herman *et al.* (1964) commented that perch were not readily available to shore birds and mammals, but that herring gulls and mergansers would take them. Coots (1956) also mentions mergansers as predators of perch on the Klamath River, California. Salyer and Lager (1949) reported kingfishers (*Megaceryle alcyon alcyon* Linnaeus) eating perch from streams and lakes, and to this list of birds, Scott and Crossman (1973) added loons. Allison (1972) reported perch of 24.9 cm mean length from the stomachs of 14 cormorants (*Phalacrocorax carbo*) shot on Loch Leven, Scotland and the remains of several perch were found at the nest of a Tawny Owl, *Strix aluco* near Tring, England (Glue 1969).

In Finnish lakes, Lind (1974) calculated average annual production of perch as 5.6 kg/ha of which 1.3 kg was taken by fishermen and 4.3 kg eaten by predators, the most important being pike and other perch.

– Defence reactions

Lake (1959) observed that the dark transverse bars disappear from the flanks and the general colour fades giving the fish a "negative" appearance when frightened. Lagler *et al.* (1962) stated that there was a concomitant slight increase of body temperature. Kammerer (1907) described threat postures in which the back was arched slightly, all fins and the opercula were spread out, the latter at right-angles to the body revealing the bright red gills and projecting the opercular spines outward.

3.3.5 Parasites, diseases, injuries and abnormalities

A checklist of parasites recorded from perch is given in Table VIII. Where parasites have been recorded from both Eurasia and North America, two authorities are quoted. It is thus clear that the majority of parasite species are not found in perch of both areas, the widespread ones being:

Trypanosoma percae
Bunodera luciopercae
Crepidostomum farionis
Diplostomum spathaceum
Cyathocephalus truncatus
Diphyllobothrium latum
Triaenophorus nodulosus
Neoechinorhynchus rutili

TABLE VII

Ivanova (1969) Predation on perch in Rybinsk Reservoir
(Measured using Fortunatova's Method (1940, 1961))
(Table extr. from data in paper)

PREDATOR				PERCH IN DIET = %			Perch consumed in multiples of predator body weight
Species	AG	Size	Season	Fry	Juv.	Total	
Pike	0+	<100 mm	Jun–Sep	46.1	–	46.1	2.4
		38 g					
	1+	<200 mm	May–Sep 1960	21.2	36.3	57.5	2.4
		60 g					
		64 g	May–Sep 1961	14.6	29.2	43.8	1.5
		<400 mm					
	2–3+	236 g	May–Sep 1960	31.7	10.0	41.7	0.9
		264 g	May–Sep 1961	4.5	22.2	26.7	0.5
		>400 mm					
	3+	1 056 g	1960	9.8	11.8	21.6	1.0
		1 158 g	1961	1.9	18.2	20.1	0.7
Pike Perch	2–4+	>440 mm					
		376 g	1960	17.6	–	17.6	0.2
		424 g	1961	25.0	11.5	36.5	0.6
	AD>4+	>440 mm					
		1 041 g	1960	11.0	–	11.0	0.08
		981 g	1961	6.5	19.2	25.7	0.5
Perch	Juv.	61 g	1960	1.5	42.3	43.8	0.5
		109 g	1961	58.7	–	58.7	0.8
	Ad	256 g	1960	5.1	23.2	28.3	0.8
		210 g	1961	17.1	24.4	41.5	0.7
Burbot	Juv.	358 g	Dec 1960 – Mar 1961			12.4	0.2
		287 g	Dec 1961 – Mar 1962			19.2	0.3
	Ad	786 g	Oct 1960 – May 1961			36.5	1.3
		650 g	Sep 1961 – May 1962			34.5	1.1

Period 1960 (including winter 1960–61) was one of low water level in Rybinsk: 1961 (including winter 1961–62) was high water.

TABLE VIII

Checklist of parasites recorded from perch

Phylum	Species	Authority
Protozoa	Apiosoma sp.	6
	Balantidium sp.	5
	Dermocystidium percae	1
	Eimeria laureleus	7
	Eimeria percae	1
	Glossatella campanulata	1
	Glossatella sp.	2
	Henneguya doori	5
	Henneguya percae	5
	Henneguya psorospermica	1
	Henneguya wisconsinensis	5
	Henneguya zschokkei	1
	Henneguya sp.	6
	Ichthyophthirius multifiliis	5
	Myxidium percae	5
	Myxobolus dispar	1
	Myxobolus ellipsoides	1
	Myxobolus minutus	1
	Myxobolus mülleri	6
	Myxobolus percae	5
	Myxobolus phyriformis	5
	Myxobolus wegeneri	1
	Myxobolus sp.	5
	Myxosoma anurus	1
	Myxosoma neurophila	5
	Myxosoma scleroperca	5
	Spironucleus sp.	7
	Thelohanellus piriformis	5
	Trichodina domerguei	1
	Trichodina meridionalis	1
	Trichodina nigra	1
	Trichodina urinaria	1
	Trichodina sp.	5
	Trichodinella epizootica	1
	Trichophyra intermedia	1
	Trichophyra piscium	5
	Trypanosoma percae	1, 5
Trematoda	Allocreadium isoporum	1
	Ancyrocephalus paradoxus	1
	Ancyrocephalus sp.	5
	Apophallus americanus	5
	Apophallus brevis	11
	Apophallus itascensis	5
	Apophallus mühlingi	1
	Apophallus venustas	5
	Apophallus sp.	5
	Ascocotyle coleostoma	1
	Aspidogaster limacoides	1
	Asymphylodora sp.	5
	Azygia acuminata	5
	Azygia angusticauda	5
	Azygia longa	5
	Azygia lucii	1
	Azygia sebago	5
	Azygia sp.	5
	Bolboforus confusus	1
	Bucephalopsis pusillum	5
	Bucephalus elegans	5
	Bucephalus polymorphus	1
	Bunocotyle cingulata	1
	Bunodera luciopercae	15
	Bunodera nodulosum	5
	Bunodera sacoulata	5
	Centrovarium lobotes	5
	Cleidodiscus sp.	5
	Clinostomum complanatum	1
	Clinostomum margiatum	5
	Cotylurus pileatus	1
	Crassiphiala bulboglossa	5
	Crepidostomum cooperi	5
	Crepidostomum farionis	5, 6
	Crepidostomum laureatum	5
	Crepidostomum solidum	5
	Crowcrocoecum skrjabini	1
	Cryptogonimus chyli	5
	Cyrodactylus longiradix	1
	Dactylogyrus tenuis	1
	Diplostomulum clavatum	1
	Diplostomulum huronense	5
	Diplostomulum scheuringi	5
	Diplostomulum sp.	5
	Diplostomum spathaceum	1, 7
	Diplostomum volvens	4
	Diplostomum sp.	6
	Distomum nodulosum	5
	Echinochasmus donaldsoni	5
	Euclinostomum heterostomum	1
	Euparyphium melis	5
	Gyrodactylus sp.	5, 6
	Hemiurus appendiculatus	1
	Hysteromorpha triloba	1
	Ichthyocotylurus cucullus	6
	Ichthyocotylurus sp.	6
	Leuceruthrus sp.	5
	Maritrema medium	5
	Metagonimus yokogawai	1
	Microphallus medius	5
	Microphallus opacus	5
	Neascus brevicaudatus	1
	Neascus ellipticus	5
	Neascus longicollis	5
	Neascus oneidensis	5
	Neascus pyriformis	5
	Neascus sp.	5
	Paracoenogonimus ovatus	1
	Petasiger nitidus	5
	Phyllodistomum americanum	5
	Phyllodistomum angulatum	1
	Phyllodistomum folium	1
	Phyllodistomum pseudofolium	1
	Phyllodistomum superbum	5

Phylum	Species	Authority
Trematoda	Posthodiplostomum outicola	1
	Posthodiplostomum minimum	5
	Ptychogonimus fontanis	5
	Rhipidoootyle illense	6
	Rossiootrema donicum	1
	Sanguinicola oooidentalis	5
	Sphaerostoma bramae	1
	Stephanophiala farionis	5
	Tetracotyle diminuta	5
	Tetracotyle echinata	1
	Tetracotyle percafluviatilis	1
	Tetracotyle variegatus	6
	Tetracotyle sp.	5, 6
	Tylodelphys clavata	6
	Tylodelphys podicipina	6
	Urocleidus adspectus	5
	Uvulifer ambloplitis	5
Cestoda	Bothriocephalus cuspidatus	5
	Bothriocephalus sp.	6
	Corallobothrium sp.	7
	Cyathocephalus truncatus	1, 3
	Cysticercus Gryporhynchus oheilancristrotus	1
	Diphyllobothrium latum	1, 5
	Diphyllobothrium sp.	6
	Eubothrium crassum	1
	Eubothrium sp.	6
	Ligula intestinalis	5
	Proteocephalus ambloplitis	5
	Proteocephalus cernuae	1
	Proteocephalus dubius	1
	Proteocephalus pearsei	5
	Proteocephalus percae	1
	Proteocephalus pinguis	5
	Proteocephalus sp.	6
	Schistocephalus solidus	7
	Triaenophorus nodulosus	1, 5
	Triaenophorus tricuspidatus	5
Nematoda	Camallanus lacustris	1
	Camallanus oxycephalus	5
	Camallanus truncatus	1
	Camallanus sp.	5
	Capillaria catenata	5
	Capillaria salvelina	6
	Contracaecum aduncum	1
	Contracaecum brachyurum	5
	Contracaecum spiculigerum	5
	Contracaecum squalii	1
	Contracaecum sp.	5
	Cucullanus truttae	6
	Daonitoides cotylophora	5
	Desmidocercella sp.	1
	Diohelyne sp.	10
	Eustrongylides excisus	1
	Eustrongylides mergorum	1
	Eustrongylides sp.	5, 6
	Gnathostoma sp.	1
	Ichthyobronema gnedini	1
	Philometra cylindracea	5
	Porrocaecum reticulatum	1
	Raphidascaris acus	1
	Raphidascaris cristata	6
	Rhabdochona ovifilamenta	5
	Rhabdochona sp.	5
	Spinitectus carolini	5
	Spinitectus gracilis	5
	Spinitectus sp.	5
	Spiroxis contortus	7
	Spiroxis sp.	5
Acanthocephala	Acanthocephalus anguillae	1
	Acanthocephalus clavula	6
	Acanthocephalus jacksoni	5
	Acanthocephalus lucii	1
	Corynosoma semerme	1
	Corynosoma strumosum	1
	Echinorhynchus coregoni	5
	Echinorhynchus lateralis	5
	Echinorhynchus salmonis	5
	Echinorhynchus salvelini	5
	Echinorhynchus truttae	2
	Echinorhynchus sp.	6
	Leptorhynchoides thecatus	5
	Metechinorhynchus salmonis	1
	Neoechinorhynchus cylindratus	5
	Neoechinorhynchus rutili	1, 10
	Pomporhynchus bulbocolli	5
	Pomporhynchus laevis	6
	Pseudoechinorhynchus clavula	1
Hirudinea	Actinobdella sp.	5
	Hemiclepsis marginata	1
	Illinobdella alba	5
	Illinobdella moorei	5
	Illinobdella sp.	5
	Piscicola geometra	1
	Piscicolaria sp.	5
	Placobdella picta	5
Mollusca	Anodonta anatina	2
	Anodonta sp.	9
	Elliptio complanatus	9
	Lampsilis radiata	8
	Glochidia	5
	(Unionidae)	1
Crustacea	Achtheres lacae	5
	Achtheres percarum	1
	Argulus appendiculosus	5
	Argulus biramosus	5
	Argulus catostomi	5
	Argulus foliaceus	1
	Argulus stizostethi	5
	Argulus versicolor	5
	Caligus lacustris	1
	Ergasilus briani	1
	Ergasilus caeruleus	5
	Ergasilus confusus	5, 9
	Ergasilus sieboldi	1

Phylum	Species	Authority
Crustacea	Lernaea cyprinacea	1
	Lernaea esocina	1
	Thersitina gasterostei	1
Arachnida	(Hydrachnellae)	1

Authorities

1. Bykhovskaya-Pavlovskaya et al. (1964)
2. Campbell (1974)
3. Dechtiar & Loftus (1965)
4. Deufel (1961)
5. Hoffman (1967)
6. Kennedy (1974)
7. Molnar & Fernando (1974)
8. Tedla & Fernando (1969b)
9. Tedla & Fernando (1969a)
10. Bangham (1955)
11. Noble (1970)

Where perch were recent entrants in the Klamath River, California, Coots (1956) found that they were without parasites.

In other areas, the intensity of infestation has been examined for a number of parasite species as follows:

Eimeria laureleus: Molnar and Fernando (1974) found high infestation in the intestine of 70% of perch in Laurel Creek, Ontario.

Henneguya doori: Sixteen out of 44 perch in March and May from northern Green Bay, Lake Michigan, had this parasite incysted in the gill filaments (Guildford 1963). The parasite was not present in 29 fish in August nor in fish from the summer or autumn in southern Green Bay.

Myxobolus sp.: This sporozoan was thought to be the cause of high annual summer mortalities of perch in Lake Mendota, Wisconsin (Herman et al. 1964).

Myxosoma neurophila: Eighteen out of 40 perch 5-25 cm in length from southern Green Bay, Lake Michigan, were infected while 29 perch from northern Green Bay were unaffected. The myxosporidian occurred in the optic tectum (Guildford 1963).

Myxosoma scleroperca: The parasite develops throughout the summer, large inflammatory cysts being evident in the eyes of 12 out of 107 perch from southern Green Bay in October. No cysts were apparent among 167 other perch examined from the same areas in spring and summer. Infections were restricted to fish over 10 cm long (Guildford 1963).

Spironucleus sp.: In Laurel Creek perch, high infestation in the intestines of 20% (Molnar and Fernando 1974).

Trichodina sp. i: High infestation on gills and fins of 85%.

Trichodina sp. ii: High infestation in urinary ducts of 75% of Laurel Creek perch (Molnar and Fernando 1974).

Azygia angusticauda: One in the stomach of each of 20% of perch at Laurel Creek (Molnar and Fernando 1974). In Lake Huron, Bangham (1955) found only 2% incidence and in Algonquin Park, Bangham and Venard (1946) found only 1% infected.

Bucephalus elegans: Less than 2% of Lake Huron fish were infected (Bangham 1955).

Bunodera luciopercae: Campbell (1974) found a regular cycle of incidence, this trematode being common in the guts of all Loch Leven perch during autumn and spring with a rapid decrease of incidence in early summer. The variation of intensity of infestation was similar. Year to year variability ranged over a factor of 10. Such regularity of annual cycles was also reported by Dogiel et al. (1961), Rizvi (1964), Kozicka (1969), Cannon (1971) and Wootten (1973). Cannon (1973) found that the numbers of this parasite increase with fish size in the female perch only at Lake Opeongo, Ontario. Wootten (1973) found the mean intensity of infestation of perch at Hanningfield Reservoir to be maximal at a length range of 15-19.9 cm. He also found infestations positively correlated with those of Proteocephalus percae.

Intensity of infestation of adult perch with B. luciopercae is probably increased through cannibalism: such infestation was low at Loch Leven in 1969-70 when perch fry were scarce (Campbell 1974).

Bunodera sacculata: Cannon (1973) found a seasonality of infestation similar to that of B. lucioperca. In Lake Huron, 22% were infected (Bangham 1955) and 24% in Algonquin Park (Bangham and Venard 1946).

Clinostomum marginatum: The "yellow grub" as the "black spot" (Neascus) makes the fish unsightly and leads the angler to discard infected individuals (Scott and Crossman 1973). Herman et al. (1964) found them commonly among Wisconsin fish, and Molnar and Fernando (1974) found one in the skin and musculature of each of 15% of perch at Laurel Creek. Ten percent were infected in Lake Huron (Bangham 1955) and 4% in Algonquin Park (Bangham and Venard 1946). Elliott and Russert (1949) found that numbers increased directly with the size and age of the host, but were not correlated with the condition of the fish. They suggested that older fish with a heavier burden of metacercariae may be more susceptible to oxygen deficiency than younger fish.

Cotylurus sp.: Campbell (1974) found metacercariae encysted on the swim-bladder of almost every Loch Leven perch examined including 0+ fish in the autumn. Cysts were also found less frequently on the heart wall and the pericardium.

Crepidostomum cooperi: The highest infestations occurred at Lake Opeongo during the summer and the numbers present increased with host size (Cannon 1973). Forty-two percent of Lake Huron perch were infected (Bangham 1955) and 23% in Algonquin Park (Bangham and Venard 1946).

Diplostomulum scheuringi: All Laurel Creek perch were infected with numbers ranging from 1-34 worms (average 9) in the vitreous chamber of the eye (Molnar and Fernando 1974).

Diplostomulum spp.: Campbell (1974) reported two forms from Loch Leven perch; one from the lens and the other from the vitreous body. The former parasite decreased in intensity gradually over a period of 4 years while the latter showed an increase over the same interval. Bangham (1955) found 68% incidence of *Diplostomulum* spp. in Lake Huron perch.

Diplostomum spathaceum: Molnar and Fernando (1974) found 1-9 worms (average 6) in the lenses of 15% of Laurel Creek perch. Herman *et al.* (1964) reported *Diplostomum* sp. as common in the eyes of Wisconsin perch.

Diplostomum volvens: Mass deaths of perch in the Bodensee were thought to be due to infestation by this trematode (Deufel 1961). In 1972, three times as many males as females of age Group III and older died with *Diplostomum* infestations (Hartmann MS. 1974).

Gyrodactylus spp.: Herman *et al.* (1964) reported this parasite commonly from the fins, gills and scales of Wisconsin perch, and Campbell (1974), from the fins of two individual perch of less than 10 cm total length from Loch Leven, Scotland. Forty-nine percent of Lake Huron perch carried Gyrodactyloid parasites (Bangham 1955).

Neascus pyriformis: The "black spot" parasite is common in Wisconsin fish (Herman *et al.* 1964), and Molnar and Fernando (1974) found 6-50 individuals on the fins or the skin of 30% of Laurel Creek perch. Twenty-one percent were infected in Lake Huron (Bangham 1955) and 56% with *Neascus* sp. in Algonquin Park (Bangham and Venard 1946).

Posthodiplostomum minimum: A single larval trematode was present in the liver of 5% of Laurel Creek perch (Molnar and Fernando 1974) and 5% were infected in Algonquin Park (Bangham and Venard 1946), and 7 perch out of 201 were infected in Lake Huron (Bangham 1955).

Urocleidus adspectus: 1-24 (average 7) worms on the gills of 65% of Laurel Creek perch (Molnar and Fernando 1974).

Uvulifer ambloplitis: 1-80 (average 16) worms on the fins, skin and gills of 70% of Laurel Creek perch (Molnar and Fernando 1974).

Bothriocephalus sp.: No seasonality could be identified in the incidence of this cestode at Lake Opeongo, but like *Bunodera luciopercae*, intensity increased with size among female perch only (Cannon 1973). Fourteen percent of perch in Lake Huron were infected (Bangham 1955) and 5% in Algonquin Park (Bangham and Venard 1946).

Corallobothrium sp.: 5-30 (average 14) worms were present attached to the intestinal serosa of 65% of perch at Laurel Creek (Molnar and Fernando 1974).

Cyathocephalus truncatus: Twenty-seven perch from Lake Huron were found to be infected with mature *Cyathocephalus* in the pyloric caeca. The intermediate host of this cestode is *Pontoporeia affinis* on which the perch feed in winter (Dechtiar and Loftus 1965). In Loch Leven, Scotland, Campbell (1974) found no *Cyathocephalus* in perch although it was present in trout particularly those which had recently entered from the inflowing streams.

Diphyllobothrium latum: Ghittino (1963) quoted Scolari (1955) as reporting 88% of perch in the Varese lakes, Italy, infested with D. latum, such occurrences being legally notifiable in Italy due to the importance of this cestode as a human parasite. Ojala (1963) reported that the plerocercoids showed little effect on the perch host, but that 25% of Finland's human population were infested through the habit of eating raw lightly salted fish.

Eubothrium crassum: Plerocercoids occurred occasionally in the lumen of the guts of Loch Leven perch (Campbell 1974) and from August-October 1971, 135 were recovered from 98 fish sampled. A seasonal cycle of the cestode in trout (*Salmo trutta*) was suspected and this increase in the autumn corresponds to that in trout.

Ligula intestinalis: Four percent of Algonquin Park lakes perch were infected (Bangham and Venard 1946).

Proteocephalus ambloplitis: Seven percent of Lake Huron perch were infected with this cestode (Bangham 1955) and 19% in Algonquin Park (Bangham and Venard 1946).

Proteocephalus pearsei: Seasonality was demonstrable for this helminth in Lake Opeongo perch (Cannon 1973) where the lowest levels of infestation occurred during the summer. The parasite was more

TABLE IX

Effect of *Triaenophorus nodulosus* on size and blood counts of perch fry (Data from Kuperman 1973)

Sample group	Length (mm)	Weight (mg)	Erythrocytes (1 000/mm^3)	Leucocytes (1 000/mm^3)
1 Uninfected	54.5 ± 0.5	1 335 ± 51	2 500 ± 53	76.0 ± 2.2
Infected: Parasite/Liver 5–20%	54.8 ± 1.3	1 400 ± 113	2 520 ± 15	60.0 ± 9.0
Infected 20–60%	51.2 ± 0.8	1 060 ± 49	2 660 ± 130	104.0 ± 15.0
2 Uninfected	62.2 ± 0.2	2 288 ± 101	2 730 ± 46	87.2 ± 3.0
Infected: Parasite/Liver 5–20%	61.5 ± 0.7	2 116 ± 68	2 537 ± 38	74.0 ± 10
Infected 20–60%	59.8 ± 1.3	2 160 ± 74	2 460	116

common in female perch. It was also common in Wisconsin fish (Herman *et al.* 1964). Thirty-three percent were infected in Lake Huron (Bangham 1955) and Algonquin Park (Bangham and Venard 1946).

Schistocephalus solidus: A single record for this parasite exists as single worms from the abdominal cavity of 5% of perch at Laurel Creek (Molnar *et al.* 1974).

Triaenophorus nodulosus: Larval and adult forms are found in perch, plerocercoids in the liver and adults in the gut usually with loss of condition in the fish (Ojala 1963). Matthey (1963) reported mass mortalities of perch in the Lac de Zoug, Switzerland, in May 1957 and January 1958 associated with heavy infestations with *T. nodulosus*. Herman *et al.* (1964) found it to be common in Wisconsin perch and Lawler (1969) investigated its biology in Heming Lake, Manitoba.

Markevich (1943) reported a mass infection of perch with *T. nodulosus* in Lake Kandry-Kul. Kuperman (1973) noted that the apparent effect of this cestode on perch was less pronounced than in trout and suggested that this indicated an equilibrium in a long-established host-parasite system which originated through prolonged mutual evolution. Experiments were carried out on 0+ perch from Rybinsk Reservoir to test the assumption that the effect of *T. nodulosus* on perch fry would be severe since the young fish appeared to be less resistant to the damaging influence of the tapeworm. Infection occurred first among 8-day-old fry through eating infected *Cyclops*, and the parasite then became located in parenchymatous tissue which would later become the liver. Incidence increased during the summer months to 70% and intensity was from 1-6 plerocercoids. In Rybinsk Reservoir, most infection takes place from late May to early July. The effects of infestation were studied during August and September using the ratio of parasite weight to liver weight as an index of degree of infection. From experimental ponds, two samples were taken and the infected fish divided into two groups having parasite/liver weight ratios of 5-20% and 20-60% respectively. The lengths, weights and blood cell counts of these groups are shown in Table IX. Length and weight showed a significant reduction in only those fish having 20-60% infection in the first sample: otherwise, size differences were not evident. Red cell counts only showed a real decrease in the heavily infected group of the second sample, but white cell counts increased notably in both heavily infected samples. This increase is due to monocytes which increase from 9.7% in uninfected fish to 21% in infected ones.

Although little or no visible effect was caused by the parasite, there might still have been relative weakening and therefore greater risk of predation among infected fish. To test this, 2 000 fry were placed in a winter pond with predaceous perch, pike-perch and pike. Seven months later, the incidence of infection was 23.2%, the same value as at the start of the predation experiment. In another experiment, the fry were held over winter without food: again the level of incidence of *T. nodulosus* in the survivors in the spring was unchanged. Thus the presence of the parasite did not appear to put the host at any obvious disadvantage.

However, Strazhnik and Davydov (1971) have shown that *Triaenophorus nodulosus* had a high vitamin B_1 content when in the liver of its host, and that liver from infected perch contained only 0.27 µg B_1 per g as compared with 2.23 µg in uninfected fish.

Lien (1970) found that the plerocercoids can remain infectious for 2-3 years in perch and if transferred to pike in the spring, the parasite can remain alive for up to 4 years before its life-cycle is completed. In this case, perch plays a role as intermediate host.

Capillaria salvelini: A single specimen of this nematode common in trout (*Salmo trutta*) was found in a Loch Leven perch in June (Campbell 1974).

Dacnitoides cotylophora: The highest incidence occurred in summer in Lake Opeongo perch (Cannon 1973).

Eustrongylides sp.: Present as single individuals in the abdominal cavity of 5% of Laurel Creek perch (Molnar and Fernando 1974).

Philometra cylindracea: Twenty percent of Laurel Creek perch contained 1-3 individuals (average 2) in the abdominal cavity or the swimbladder (Molnar and Fernando 1974). Only 1% of Lake Huron fish were infected (Bangham 1955).

Raphidascaris acus: The highest incidence occurred in the summer months, varying from 2.5-4.5 worms per fish for mean maximal intensity (Campbell 1974). This peak occurred at times of lowest incidence of *Bunodera luciopercae* suggesting an antagonistic relationship between the parasites. In large perch, *Raphidascaris* infestations were probably acquired by eating small perch which have ingested *R. acus* eggs (Moravec 1970) as during June-September, adult Loch Leven perch consumed their own weight in perch fry (Thorpe 1974).

Rhabdochona sp.: Six percent of Lake Huron perch were infected (Bangham 1955).

Spinitectus gracilis: No seasonal differences in incidence were recognizable for this nematode in Lake Opeongo perch (Cannon 1973). Infestation increased with increasing fish size in females only. Four percent of Lake Huron perch were infected (Bangham 1955). Ten percent of Algonquin Park perch were infected (Bangham and Venard 1946).

Spiroxys contortus: Single worms occurred in the intestinal serosa of 5% of Laurel Creek perch (Molnar and Fernando 1974). Only 1 out of 201 fish from Lake Huron carried this parasite (Bangham 1955).

Echinorhynchus truttae: Forty percent of Loch Leven perch contained this acanthocephalan in July 1967 and 10% in December 1967, but at no other time in the period 1967-73 (Campbell 1974). From the parallel decrease in intensity of infestation in trout, it appears that this parasite belonged mainly to the inflow stream system rather than the lacustrine one.

Leptorhynchoides thecatus: As with *Spinitectus*, there was no clear seasonal pattern of incidence in perch from Lake Opeongo (Cannon 1973), and this parasite was commoner in female perch than in males, increasing in intensity in the former with size. Ten percent were infected in Lake Huron (Bangham 1955) but only 2% in Algonquin Park lakes (Bangham and Venard 1946).

Neoechinorhynchus cylindratus: Three percent of Lake Huron perch were infected (Bangham 1955).

Neoechinorhynchus rutili: Ten to 20 percent of perch of over 25 cm total length were infected with this acanthocephalan at Loch Leven (Campbell 1974) on odd occasions in the winter November 1969, February and April 1970, and January 1971. None were found at other seasons over a 7-year period. In Lake Huron, Bangham (1955) found 11 perch infected out of 201.

Illinobdella moorei: Three percent of Lake Huron perch were infected with this leech (Bangham 1955).

Pomphorhynchus bulbocolli: Less than 2% of Lake Huron fish were infected (Bangham 1955).

Anodonta anatina: Glochidia from this freshwater mussel occurred seasonally from November to June with peak numbers in May on the gills and fins of Loch Leven perch (Campbell 1974).

Elliptio complanatus: Matteson (1948) found that perch experimentally infected with glochidia carried them for 18 days at 18°C.

Lampsilis radiata: Glochidia were found on the gills of perch in Lake Ontario from May to October, the numbers per fish increasing rapidly to 60 in late May and then steadily to a maximum of 90 in late July. The decrease was more rapid to 4 in early September. Incidence was 100% in midsummer (Tedla and Fernando 1969 a). They state that infestations of more 200 glochidia per fish are rare. Infestation and fish size are negatively correlated (r = 0.7578). In experimental infestations, the parasite was carried for 40-50 days after exposure of the perch in May or up to 98 days after exposure in August, the experimental temperatures being 15°C in each case.

Ergasilus confusus: The occurrence of three *Ergasilus* species on percid fish in Lake Ontario was investigated by Tedla and Fernando (1969) who found that among 118 perch examined, 91.5% were infected with *E. confusus* with a mean intensity of 3.2 parasites per fish. None were found to carry *E. caeruleus* although the parasite was present in 66% of pumpkin seeds (*Lepomis gibbosus*).

TABLE X

Sporozoan infection in Lake Mendota perch, winter 1946-47
(Data from Bardach 1951)

Age (years)	Number caught	% infected
2	7	0
3	44	4.5
4	177	22.6
5	46	52.0
6	3	66.6
Total	277	24.6

Diseases: Epidemics among perch have been recorded from several localities. For example, Lassleben (1953) wrote of the "Krätzersterben" which accounted for the deaths of millions of young perch in the Bodensee in many years in late summer and autumn. He doubted the pathogenic origin of these mass deaths attributing them to radiation. Matthey (1963) listed mass mortalities among perch fry in Lac Léman on 6 occasions between 1867 and 1946, and in Lac de Neuchâtel in 1959/60 and 1962. The causative organisms were not identified.

In 1867, Forel called the outbreak "Typhus de la Perche" (Day 1880) on account of bacteria found in the blood of infected fish. In the Neuchâtel outbreaks, no such bacteria were present. These perch had gill anaemia, pale whitish livers with haemorrhagic spots and pronounced kidney anaemia: their intestines were normal. In the 1960 outbreaks, many other fish were affected including trout (Salmo trutta) coregonids, roach (Rutilus rutilus) and pike (Esox lucius): in 1962, only perch and roach were affected. On account of its high fecundity, the loss of fry did not appear to affect the adult stock noticeably. Jensen (pers. comm.) noted epidemics in some Norwegian lakes in 1952 and a widespread "perch disease" appeared in England in 1970 (Bucke: pers. comm.) but its causative agents were not identified. Mass mortalities of AG I perch (12-19 cm), first maturation spawners, occurred in Lago Maggiore in March and April 1962 and 1967 (Grimaldi 1967). There were no obvious pathogens. Grimaldi commented that such extensive mortality (>600 000 in 1962: c 60 000 in 1967) must have affected the age structure of the population as loss to the 1967 population was about 8% of the annual commercial catch and the potential loss of eggs about 200 x 10^6 (in 1962, the corresponding quantities would have been 20 000 kg of fish and 2 x 10^9 eggs). Mass mortalities in spring are now characteristic in the Bodensee (Hartmann MS. 1974) and those summer outbreaks recorded by Nümann (1939) have not occurred in recent years.

Ojala (1963) reported a "spot disease" probably of pseudomonad origin affecting perch in Finland. This consisted of septicaemia with haemorrhagic enteritis and subcutaneous abscesses followed by deep skin ulceration. In milder forms, there were superficially inflamed areas of skin with some loss of condition.

Nordstrom et al. (1960) reported a large kill of perch in May 1959 in Dailey Lake, Montana. Associated with this catastrophe was a gram-negative pleomorphic bacillus (probably related to Pseudomonas) on the exterior, in the muscles, kidney and liver. In experimental infections, similarities were seen between this disease and that of the nineteenth century outbreaks in Switzerland.

In Lake Mendota, Wisconsin, over 200 t of dead fish, mostly perch, had to be removed in 1884 (Bardach 1951). No causative organism for the mass deaths was found. In 1939, an infectious outbreak occurred among perch in the summer characterized by red sores and open lesions, and attributed to a Myxobolus species. Many thousands died from it every summer from 1940-1946, the most serious outbreaks coinciding with the onset of hot weather in mid-July. From subsequent gillnet samples, the incidence of infection was greater amongst older fish (see Table X).

Bardach considered that these epizootics were the most important single influence accounting for the decreased numbers and increased growth-rate of Mendota perch.

Red sores and open lesions on the flanks of adult perch have also been noted in the early summer at Loch Leven (Thorpe, unpubl.) where incidence rose from 0.6% at the end of April to 5.0% over the next three weeks. The effect on the population is not known, but later in the year, individual perch with regenerated scales on the flanks were frequent in net catches.

The bacterium Aeromonas salmonicida, the causative organism of furunculosis in Salmonidae, has also been recorded as affecting perch in Europe (Vibert and Lagler 1961).

With regard to injuries and abnormalities, Pokrovskii (1951) published a figure of a perch from the Yenisei River described as monstrositas exocoetoides with elongate fins such that the caudal was approximately 50% of the length of the remainder of the fish and the pectoral, pelvic, anal and second dorsal fins were all approximately equal to the length from the snout to the opercular spine.

A blue variety having the typical vertical black bars but lacking all yellow colouration was caught in Lake Erie (Dymond 1932) and the captor claimed to have seen 6 during 50 years fishing there. Similar blue perch have been noted from Saginaw Bay, Lake Michigan (Hubbs In Dymond 1932). A bright orange form lacking vertical dark bars was reported by Crossman (1962) also from Lake Erie. The back sides and top of the head were a solid, bright, transparent orange; the lower sides and ventral surface were milky white. The orange areas were speckled with black pigment which from the occiput to the first dorsal was condensed into a black line. The cheek and lower operculum were metallic silver and mirror-like. The upper operculum was orange. The pupil of the eye was black and the upper crescent section of the white-of-the-eye was orange speckled with black.

In other respects, these blue and orange forms appeared to be typical perch. Structural abnormalities were reported by Linnaeus from Fahlun, Sweden (Day 1880) where a hunchback form occurred, locally called Rudaborre (meaning a hybrid between perch and crucian carp, Carassius carassius). Similar forms were also reported from Wales and from England (Day 1880). Smitt (1893) published illustrations of these fish and Reichenbach-Klinke (1956) quoted Wahlgren as attributing their shortened spinal column to osteomalacia caused by a sporozoan parasite. Svob et al. (1974) illustrate a perch fry with a shortened upper jaw, a malformation which they attribute to lack of oxygen during embryonic development. Pugheadedness has been reported several times most recently by Lawler (1966) from perch in Heming Lake, Manitoba.

Schäferna (1934) reported elongated fins in perch probably resulting from a pituitary disturbance similar to that giving rise to acromegaly in man.

3.4 Nutrition and growth

3.4.1 Feeding

- Time of day

Wunder (1926) described the retinal structure of the perch eye as having 25 rods and 8 cones per 80 µ of retinal surface, and designated the animal as a "bright light" fish. In a later paper (1927), he demonstrated the olfactory function of the nostrils, but the degree to which this was used in prey detection and capture varied widely between individuals. Physiologically, therefore, perch appears to be adapted to daylight feeding. Lagler et al. (1962) refer to the limnodromous movement of perch: onshore with coming darkness and offshore at dawn. This activity appears to be connected with feeding as the principal feeding periods reported are in the morning and evening (Scott and Crossman 1973). Scott (1955) recorded daily migration at sunrise from Rondeau Bay out into Lake Erie where the 2-3 year old (mean length 13.5 cm) perch fed on Daphnia returning just before sunset and remaining inactive at night. Keast and Welsh (1968) found that in Lake Opinicon, perch of 9-13 cm (1-2 years old) showed peaks of stomach fullness at mid-morning and dusk in June: the timing of this index could only be approximate as some of the materials used were taken from gillnets where the fish could have been entangled for up to 2½ h. However, the general pattern agrees with that found by Manteifel et al. (1965) for planktivorous perch in Rybinsk Reservoir in July. Adult Loch Leven perch (>20 cm total length) showed a similar pattern of early morning and evening peaks of food consumption (Thorpe in press a) (Fig. 12) in June and July but consumption became concentrated into the middle of the day in September. Manteifel et al. (1965) reported that benthophage perch filled their stomachs rapidly from 03.00-08.00 h and then maintained full stomachs until 18.00 h after which the quantity decreased to zero by 02.00 h. Piscivorous perch in Rybinsk Reservoir showed a much more variable feeding rhythm possibly dependent on the irregular availability of perch or cyprinid fry. At West Blue Lake, Manitoba, Ward and Robinson (1974) found that perch fed in the morning and evening only during June to September.

- Place

General area: As noted above, limnodromous movements take perch offshore during the day so that feeding occurs in the open water and on the sublittoral. Klemetsen (1973) found fish in Gjökvatn, Finnmark, Norway in July feeding both pelagically on plankton and fish fry, and benthically on insect larvae and molluscs. In Loch Leven, adult perch were feeding heavily in shallow littoral areas (<5 m depth) all summer from June-September, but as evening catches tended to be much greater than midday ones, the bulk of the population was probably feeding in open water or on the sublittoral areas (Thorpe in press a). Hartmann (MS. 1974) found that in the Bodensee since eutrophication, perch move on to the sublittoral (at a depth of c 10 m) and into the pelagial regions where they eat Cladocera in summer. Prior to eutrophication, the adults had been restricted to the littoral areas in summer. Neill and Magnuson (1974) established experimentally that perch, given a choice of preferred temperature conditions (23°C) without food and extreme

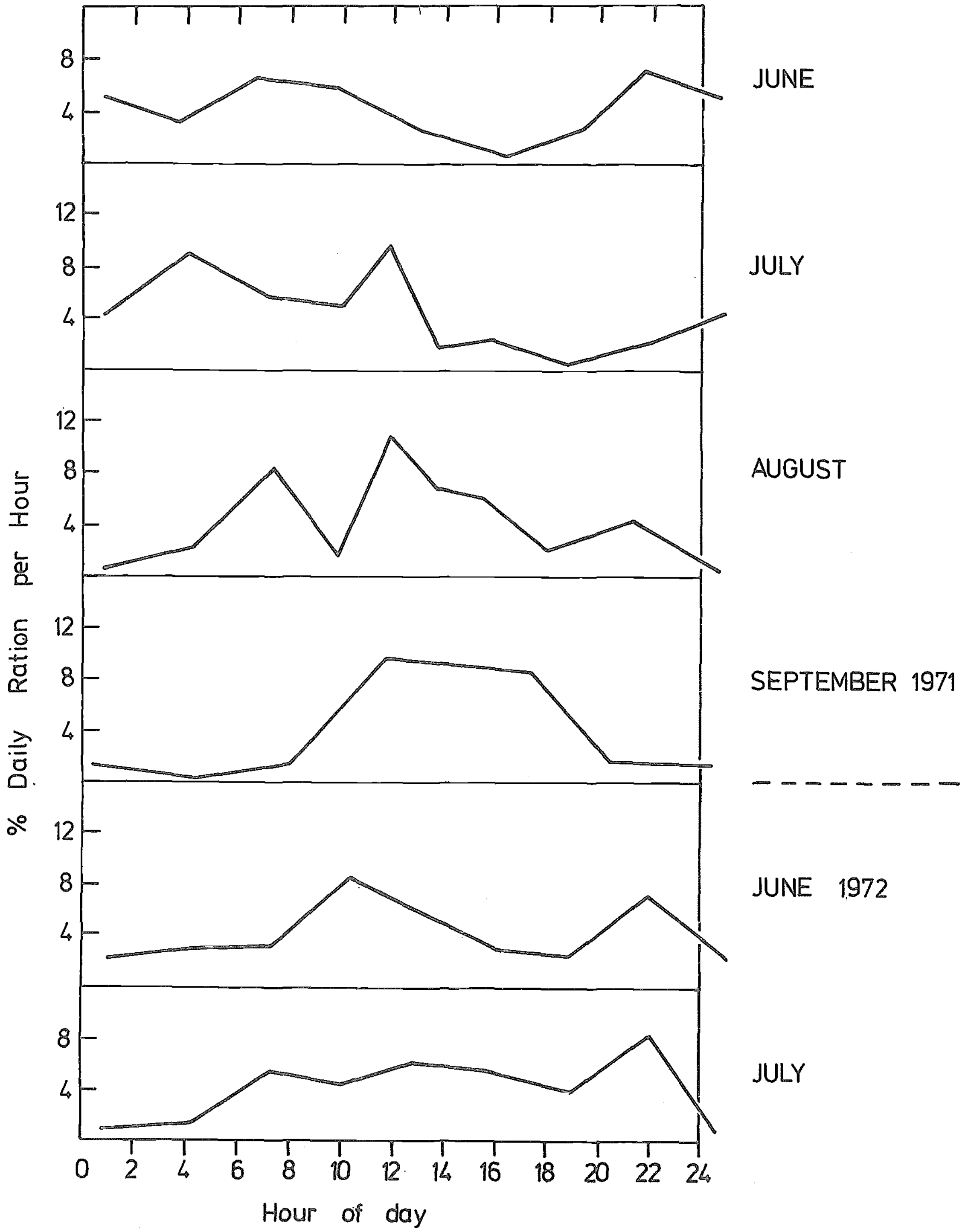


Fig. 12 Food consumption by Loch Leven perch
(From Thorpe in press b)

temperatures (29°C) with food, chose to live in the part of the tank at the preferred temperature and make forays out for food. Neither laboratory nor field results at Lake Monona, where fish distribution was studied in the area affected by the heated outfall from a power plant suggested that thermoregulatory behaviour was overridden by feeding behaviour even though zooplankton was more abundant in the outfall area than in unheated parts of the littoral.

Neuman (1974 a) found that perch on the Baltic coast of Sweden moved out into open water as the temperature rose in summer, but in this case, temperatures did not exceed the thermal optimum for the species of about 21-24°C (see sections 2.3 and 3.3.2).

In winter, perch tend to occur in deep water (Hergenrader and Hasler 1966) and although the food turnover may not be high, a low level of feeding occurs probably chiefly on benthic animals. Craig (pers. comm. 1975) has found Gammarus taken by Windermere perch in winter in deep water.

Perch appear to be reluctant to enter vegetated areas to feed and depend chiefly on open water (see next section).

- Manner

Methods of capture, selection: Deelder (1951) described the feeding behaviour of a shoal of perch held in the Amsterdam aquarium. Prey was first searched for visually and moving objects attract interest while stationary ones do not. Small roach (Rutilus rutilus L) of 1.5-10 cm were used as prey animals. When swimming, the roach were vulnerable and excited responses from perch several metres away. A predatory perch darting toward its prey attracted the attention of other perch, but as rather inefficient in capturing the prey fish. Characteristically, the perch attempts to approach the prey and seize it head-first so that a hunting fish has to pass its quarry and turn sharply to capture it. As healthy roach were at least as agile as perch, they escaped the initial attack frequently, but as other perch were present all around, turning away from one implied turning toward another. Thus, cooperative hunting in shoals ensured feeding success. In trials with individual perch in tanks with roach as prey, none succeeded in capturing a roach in the open water but only at the edges from which the roach could not escape. Hunting in shoals would have success in open water where the perch can keep its prey in sight, but when small clusters of floating plants were introduced to the tank, the roach moved into them and the perch did not follow but remained at the periphery of the cluster. Deelder concluded that for satisfactory growth, perch required a prey fish which remained available in open water and considered the smelt (Osmerus eperlanus L) fulfilled this role. Absence of this fish from some Dutch waters was not compensated for by the abundance of roach because vegetation prevented the use of roach as an alternative forage resource.

Boulet (1958) examined the responses of perch to moving objects experimentally. The speed of the object on its trajectory, the form of the trajectory, the size and shape were all important in releasing responses and receptivity to the objects increased when fish were tested in groups (see section 3.5.3 for details).

Deelder (1951) also noted that in the absence of fish fry as prey, the perch searched plants growing in the observation tank and ate small animals between and attached to these plants.

Boulet (1958) had observed that white plastic balls smaller than 2 mm in diameter elicited little or no response from perch in the test apparatus. However, Daphnia-like movements were particularly attractive to the fish. Galbraith (1967) found that Daphnia were not utilized as food in a lake by perch of 7-25 cm total length unless the individuals were larger than 1.3 mm, and Klemetsen (1973) found that Daphnia galeata eaten by perch in Gjökvatn had a carapace length of 1.2-2.2 mm whereas those caught in plankton nets ranged from 0.8-1.7 mm. Copepods were abundant in the plankton but hardly touched by perch.

In Oneida Lake, the rate of decline of Daphnia in summer was linked causally with perch food consumption (Hall 1971) and the fish selected the larger Cladocerans. In D. galeata and D. retrocurva, the body size was reduced after June and in D. pulex, the species disappeared in midsummer.

- Frequency

Feeding frequency of individual adult perch appears to be unknown, but in a population, some individuals appear to be feeding at all times during daylight hours. Thorpe (in press a) published data on the consumption of separate taxa of food items by adult Loch Leven perch, and although concentration on particular foods was restricted to short periods of the day, at no period was nothing being eaten.

- Variation of feeding habits with availability, season, age, size, sex and physiological condition

Perch are adapted to a diet of small live animals. Backward-slanting teeth line their jaws and the inner edges of the gills are lined with comb-like rakers. They will take whatever small animals are most available (Herman et al. 1964). Since feeding appears to depend primarily on availability of prey, seasonal changes in food eaten reflect seasonal changes in availability of foods. For example, data in Thorpe (in press a) indicate monthly differences in the intake of Daphnia, Bythotrephes, perch fry, Chironomidae and

TABLE XI

Daily food consumption by adult perch in Loch Leven. (from Thorpe in press a)

Food	June (^{o}/000)		July (^{o}/000)	August (^{o}/000)		September (^{o}/000)	Total Consumption June-September 1971	
	1971	1972	1971	1971	1972	1971	(^{o}/000)	%
Asellus	208	214	233	239	176	45	22 222	33.8
Daphnia	22	5	93	136	5	62	9 619	14.6
Perch fry	111	5	52	46	4	83	8 858	13.5
Chironomidae	142	132	100	31	191	11	8 651	13.1
Hirudinae	115	76	156	7	6	-	8 503	12.9
Gammarus	10	26	9	3	34	111	4 002	6.1
Bythotrephes	-	-	3	53	1	2	1 796	2.7
Miscellaneous	43	7	23	1	12	4	2 154	3.3
Total	651	465	669	516	429	319	65 805	100.0

TABLE XII

Comparison of food consumption by adult perch in Loch Leven: 1971 and 1972 (from Thorpe in press a) (Data in ^{o}/000 by freshweight)

Food type	Month			
	June		August	
	1971	1972	1971	1972
Benthic				
Crustacea	218	240	242	210
Annelida	115	81	7	6
Chironomidae	142	132	31	191
Planktonic				
Cladocera	111	5	46	4
Perch fry	22	5	189	15

leeches (Table XI). Between-year differences also occur (Table XII); in the case of Loch Leven fish, this was particularly true of planktonic prey where Anabaena blooms appeared to affect the availability of Cladocera and a poor brood year the availability of fry.

Hartmann (MS. 1974) records a change from plankton feeding in summer to benthos feeding in winter in the Bodensee. However, Brofeldt (1922) found the qualitative composition of food in stomachs of perch caught in the Müggelsee, Germany in November, January and April to be the same as that in summer, but the quantity present in the digestive tract was less.

Scott and Crossman (1973) note that in America the perch feed actively through the winter.

It was suggested on the basis of data from Windermere that perch graduated from a diet of plankton to one of benthos at a length of c 14 cm and then to one of fish at a length of 18 cm (Allen 1935). The implication was that successful growth of larger fish depended on the intake of larger food particles. However, although this may be the case in some oligotrophic waters or in lakes where the total food supply is limiting, the provision of a predominantly fish diet is not essential for perch over 18 cm as is evident from Table XI and from Klemetsen's (1973) data on plankton eating perch which changed to a predominantly benthic diet at c 25 cm, and if there was a change to piscivory, it was at a length of >40 cm.

Nümann (1939) described characteristic changes of diet from plankton to benthos to fish for Bodensee perch with size of fish, but by 1973, Hartmann (MS. 1974) found that fish >26 cm fed partly and those 17–25 cm wholly on plankton in summer, and all size-classes eat benthos in winter. In experimental ponds, Ilina (1973) found that the progeny of a single pair of perch formed three separate ecological groups during their first summer, feeding on plankton, benthos and fish fry respectively. Thus the differences are primarily a response to availability, perch making use of any prey of a size appropriate to its gape.

In the Bodensee, Hartmann (MS. 1974) found that female perch of 17–25 cm ate more fish in summer than did males of the same length-range. This probably reflects a separate distribution of males and females at this time.

- Abstention from feeding

Although feeding during the winter has been shown to occur, the frequency of empty stomachs in samples does increase in some populations. Pearse (1919) (in Keast 1968) claimed that perch do not feed at spawning. In samples from Little Cataraqui Creek, Ontario, Keast showed that feeding began immediately after spawning. On 14 April at a water temperature of 6.5°C, all perch caught had empty stomachs; apart from 2 fish which had food in them on 16 April, the first feeding perch were 30% of the sample on 30 April at a temperature of 10.5°C. By 2 May, all fish were feeding at 11.5°C. Nikitinsky (1929), however, found that at Lake Zarizino, Moscow, feeding began actively before spawning such that from no feeding fish in the population 41 days before spawning, 12% were feeding 11 days before, 61% 4 days before and 78% 4 days after. Shilenkova (1959), however, found that in Lake Dzhalangash, 92% of spawning fish had empty stomachs and only 2% had well-filled ones: at the same time, 64% on non-spawning perch had food in the guts, 41% being well-filled. Hartmann (MS. 1974) recorded 9% of stomachs empty among Bodensee perch from June to October, 55% empty December to January and 29% empty February to April. The increase in empty stomachs in December was attributed to a change from one diet to another. No increase in empty stomach percentage occurred during spawning.

3.4.2 Food

- Types eaten and their relative importance in the diet

As mentioned above (section 3.4.1), perch will eat whatever small animals are most available. Almost every ecological study of perch populations has included a list of animals in the diet, but almost as many have based their statements on static samples, that is, on data from stomachs collected irrespective of time of day and therefore reflecting neither rate of evacuation nor diurnal rhythm of feeding. Therefore, data on relative importance in the diet from such samples is meaningless and only represents the relative numbers or weights present at that instant. Among adult fish, only one attempt to estimate relative importance of specific items in the diet has been made (Thorpe 1974, in press a) allowing for diurnal variation in intake and evacuation rate of different food items (Table XI). This showed that in Loch Leven, Asellus was the most important food component by weight during the summer feeding period and that benthic crustacea accounted for about 40% of the diet. Planktonic crustacea, chiefly Daphnia, account for a further 17% and most of the remaining diet is made up approximately equally at 13% for each of perch fry, Chironomidae and leeches.

- Volume of food eaten during a given feeding period

Table XI shows that the estimated daily ration for adult Loch Leven perch was about 6.5% wet body weight per day in mid-summer, falling to 3.2% per day in early autumn. As pointed out by Thorpe (in press a), these values were minimal estimates, but since the calculated values of daily energy requirements of perch of this size and at these temperature intervals derived from respirometry data of Morgan (1974) were in close agreement with the food consumption estimates, they must be realistic values (Table XIII).

TABLE XIII

Food intake compared with metabolic requirements for Loch Leven perch 1971
(From Thorpe 1974)

Period	Food intake kj.kg^{-1}day^{-1}	Total metabolic requirement* kj.kg^{-1}day^{-1}	Growth rate % wet body weight day^{-1}
June-July	223.8	162.0	0.19
July-Aug	186.5	174.8	0.19
Aug-Sept.	128.6	154.0	0.10

* Calculated from data of Morgan (1974)

It therefore seems unlikely that Keast and Welsh's (1968) estimates of 2% body weight per day as the ration for Lake Opinicon fish would be adequate to maintain them, let alone for them to grow, and likewise the older estimate of 2% per day for 1+ fish of Hathaway (1927) (quoted in Belyy 1937). Keast and Welsh took diurnal periodicity into account but did not attempt to estimate evacuation rates. Similarly, Ivanova's (1969) estimates of food turnover among predatory perch at Rybinsk Reservoir using Fortunatova's method for calculating rate of passage of food, but not apparently allowing for diurnal feeding rhythms, are probably too low, namely, total annual consumption of 1.7-2.8 times mean body weight. She comments that feeding intensity is lower than among perch in the Volga Delta (Ivanova 1956) where 50-150 cm perch eat twice their own body weight in June to July. However, these values also are probably underestimates.

3.4.3 Growth rate

- Relative and absolute growth patterns and rates

The growth in length and weight of perch has been recorded from many habitats throughout its range. Numerous data on the growth of perch in North American waters can be found in papers by: Carlander (1950), Eschmeyer (1937, 1938), Hile and Jobes (1941, 1942) and Muncy (1962); in European waters in the works of Alm (1946), Chevey (1925), Deelder (1951), Hartley (1947), Holčik (1969), Le Cren (1958), Tesch (1955) and Vostradovsky (1961); and in Russian waters in Berg (1965), Ereshchenko (1959), Serov (1959), Shilenkova (1959) and others.

Fig. 13 shows a selection of data to illustrate the variability in growth rate over a range of localities and Fig. 14-15 (from Neuman 1974) show the spread of size by age and sex in a Baltic population.

Le Cren (1958) noted that there was no sex difference in growth during the first 2 years of life among Windermere perch, but that subsequently, females grew slightly faster than males (see Fig. 16). This sex difference has been reported from all parts of the range of distribution of the fish, as for example, by Alm (1946), Herman et al. (1964), Tesch (1955) and Berg (1965), and Fig. 17. Scott and Crossman (1973) quote data from several American sources showing that here females grow faster from the first year and achieve larger ultimate size. Once adult in their third or fourth year, the fish of each year-class in Windermere had a constant annual increment in weight regardless of age. Such a growth pattern implied that growth could not be described by a formula of the Von Bertalanffy type where growth rate declines as the fish approaches its maximum size (see Fig. 18). However, such a growth pattern is not true of all localities. Craig (1974 a) arrived at L∞ values of 22.0 cm for males and 25.0 cm for females at Slapton Ley using Ford-Walford plots which imply a regularly decreasing length increment in successive years. Similarly, Heyerdahl and Smith (1971) showed steadily decreasing length increments with age among perch at Red Lakes, Minnesota (see Fig. 19). A model of length-growth of perch at Loch Leven, Scotland, based on data from 1968 to 1973 is shown in Fig. 20: it is clear that annual increments are decreasing each year after the second and an L∞ value of 32.2 cm was calculated from data of 1968 to 1969.

In the Bodensee, Hartmann (1974) described within-season length growth as sigmoid falling into three phases (see Fig. 21). In the early and late phases, the rate was 0.01-0.06 mm per day while it was 0.26-0.45 mm per day during the main phase. At this latter time, weight growth was: males 26 g per month, females 34 g per month.

In 1972, males and fish with relatively small growth began their main growth phase 3-4 weeks later than the females and the young fish,

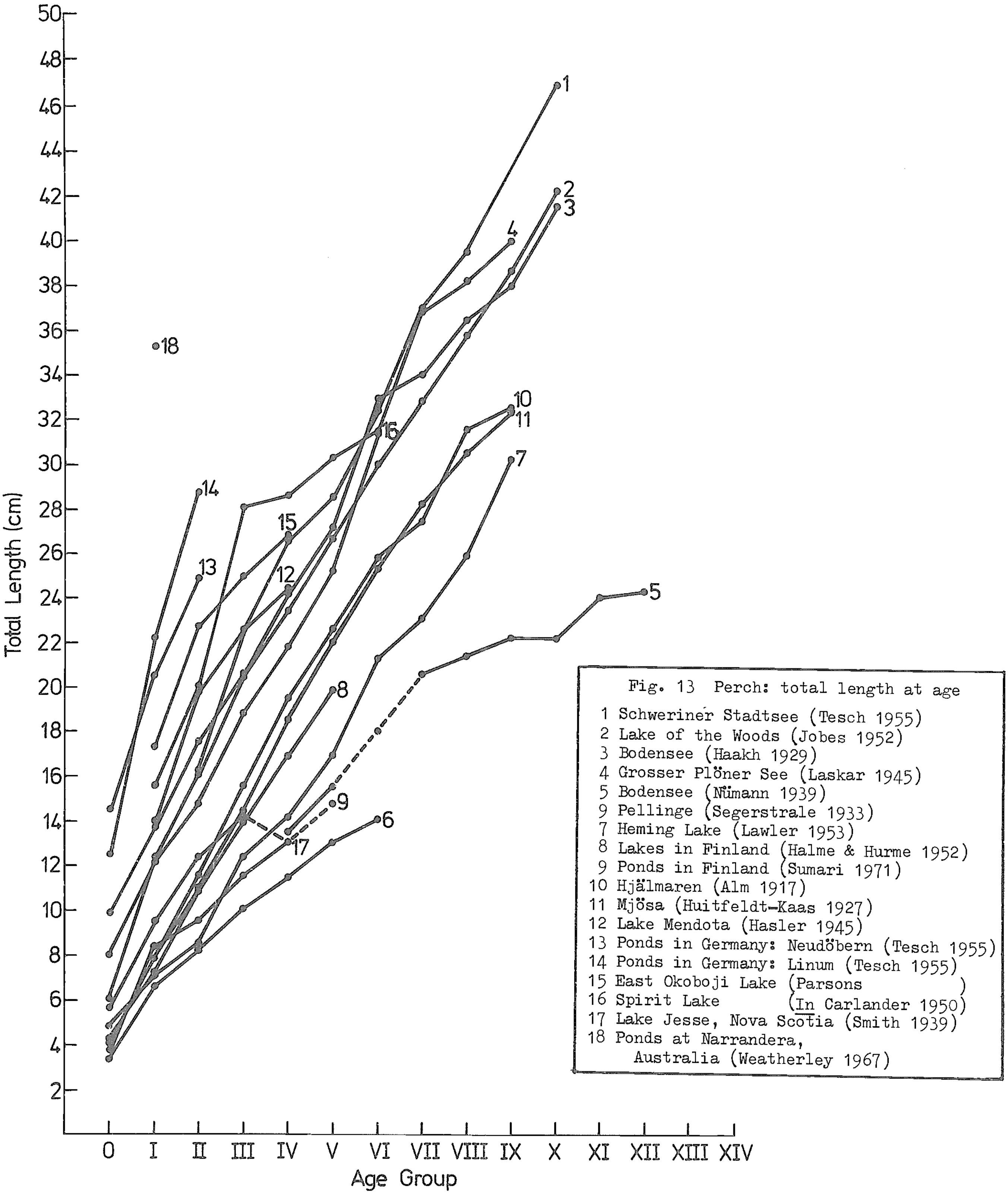


Fig. 13 Perch: total length at age

1 Schweriner Stadtsee (Tesch 1955)
2 Lake of the Woods (Jobes 1952)
3 Bodensee (Haakh 1929)
4 Grosser Plöner See (Laskar 1945)
5 Bodensee (Nümann 1939)
9 Pellinge (Segerstrale 1933)
7 Heming Lake (Lawler 1953)
8 Lakes in Finland (Halme & Hurme 1952)
9 Ponds in Finland (Sumari 1971)
10 Hjälmaren (Alm 1917)
11 Mjösa (Huitfeldt-Kaas 1927)
12 Lake Mendota (Hasler 1945)
13 Ponds in Germany: Neudöbern (Tesch 1955)
14 Ponds in Germany: Linum (Tesch 1955)
15 East Okoboji Lake (Parsons)
16 Spirit Lake (In Carlander 1950)
17 Lake Jesse, Nova Scotia (Smith 1939)
18 Ponds at Narrandera,
Australia (Weatherley 1967)

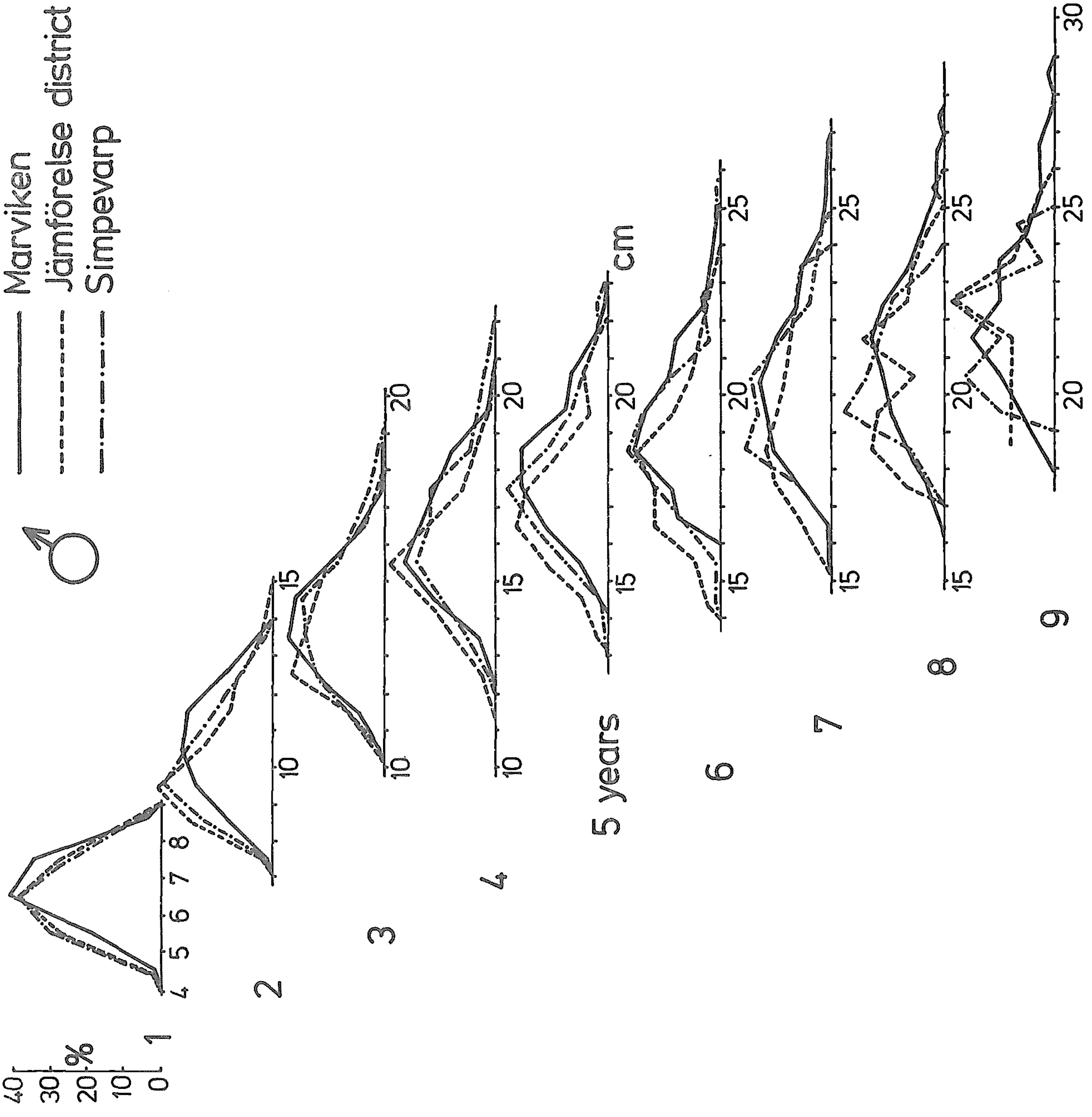


Fig. 14 Length distribution of males by age-groups
(From Neuman 1974 a)

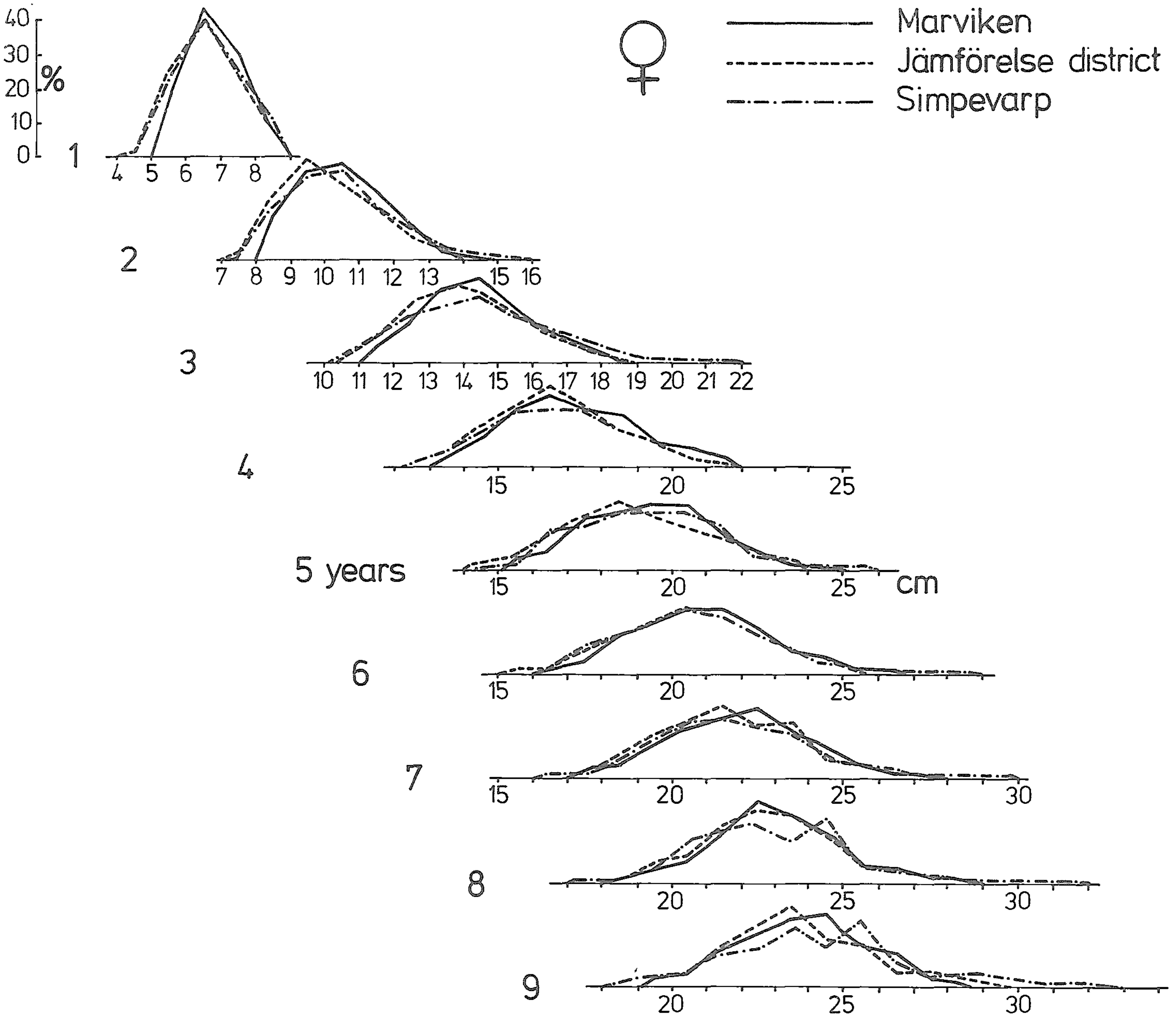


Fig. 15 Length distribution of females by age-groups
(From Neuman 1974 a)

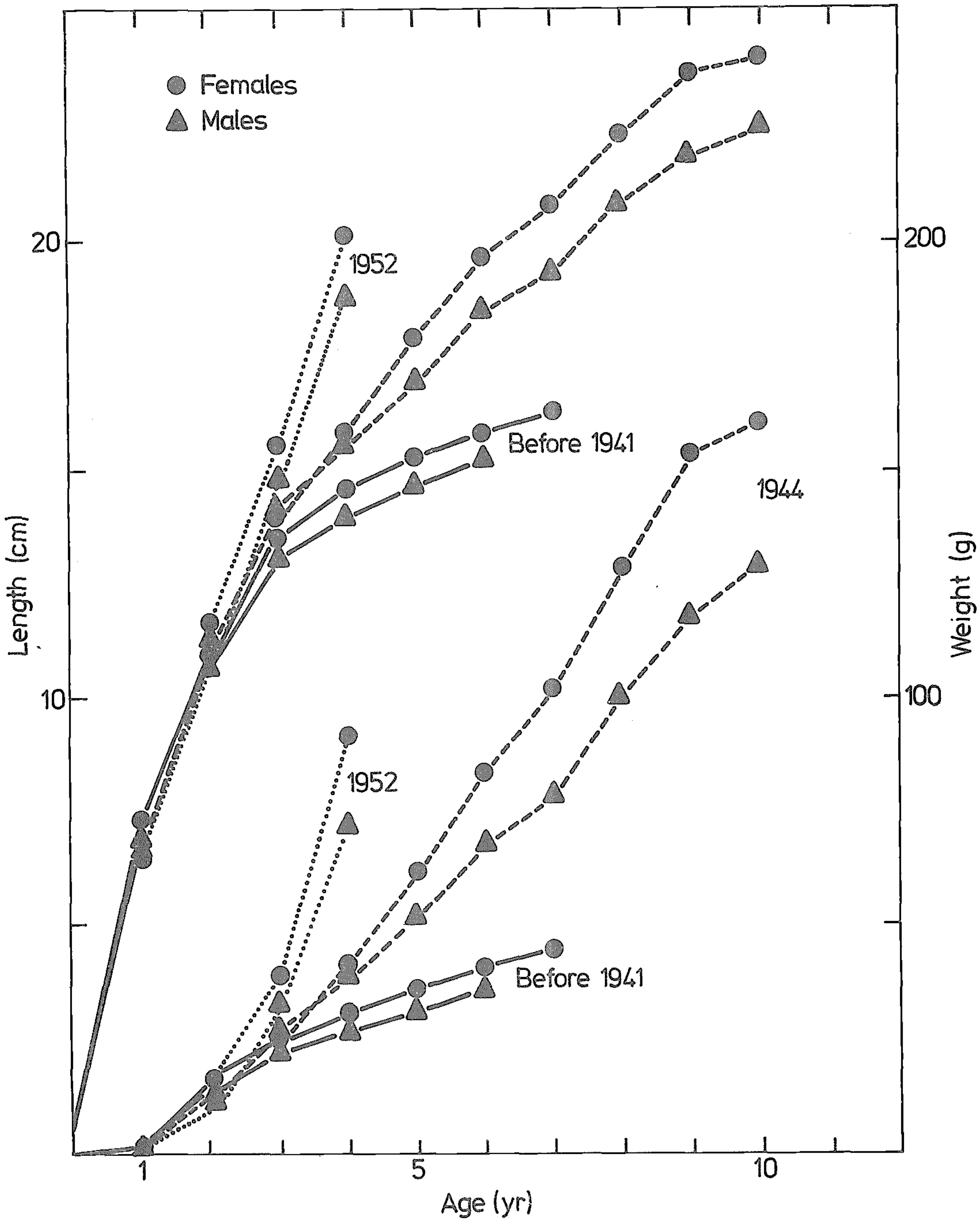


Fig. 16 Length-for-age and weight-for-age growth-curves for male and female fish of the combined year-classes before 1941, and the 1944 and 1952 year-classes. The data have been adjusted for year-to-year temperature variations (Lake Windermere). (From Le Cren 1958)

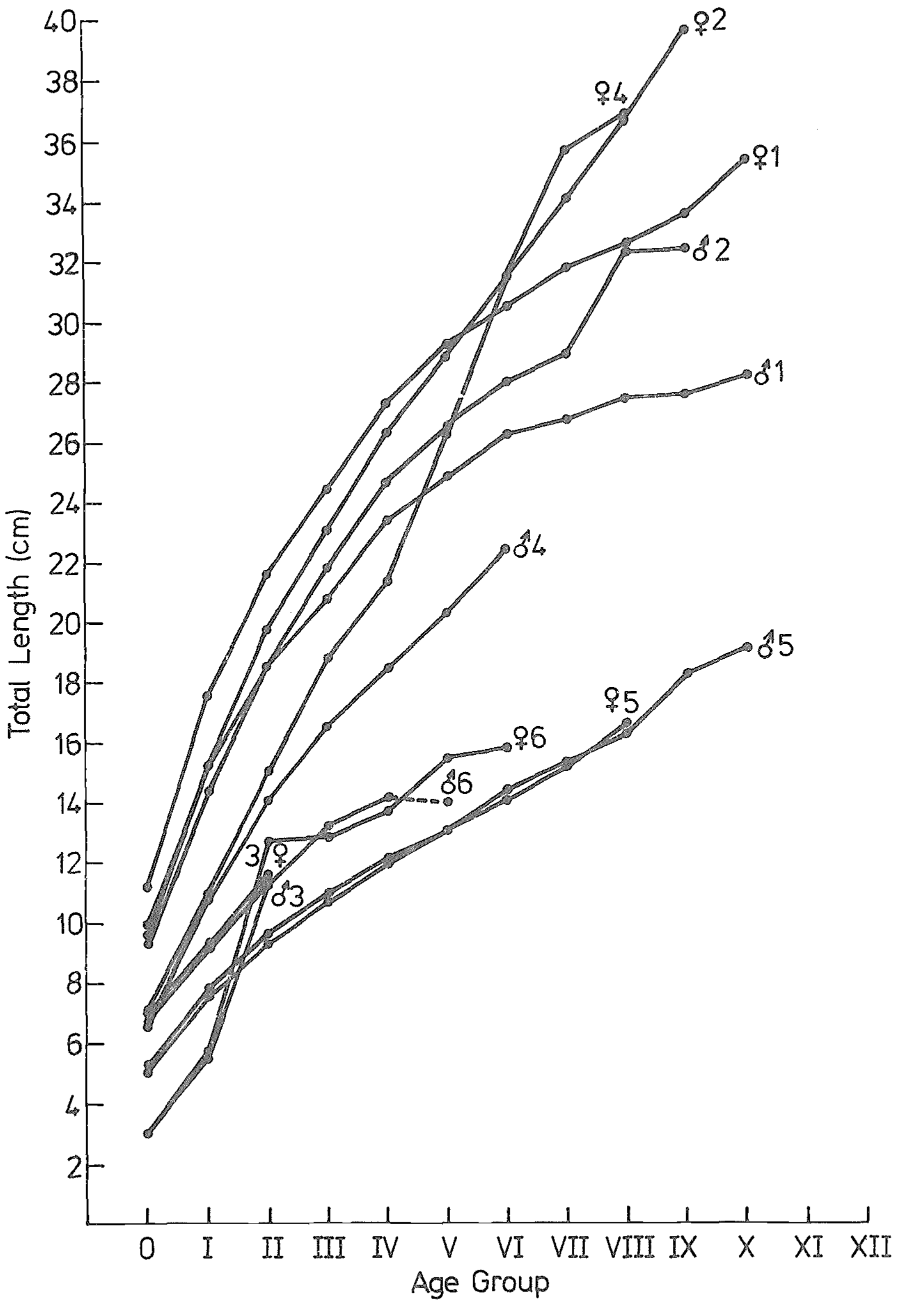


Fig. 17 Comparison of length-growth of males and females

1	Severn River, Maryland	(Muncy 1962)
2	Lake Chany (fast)	(Tyurin 1935)
3	Lake Chany (slow)	(Tyurin 1935)
4	Saginaw Bay	(El-Zarka 1959)
5	Dubh Lochan, Loch Lomond	(Shafi & Maitland 1971)
6	Yxtasg̈n	(Alm 1922)

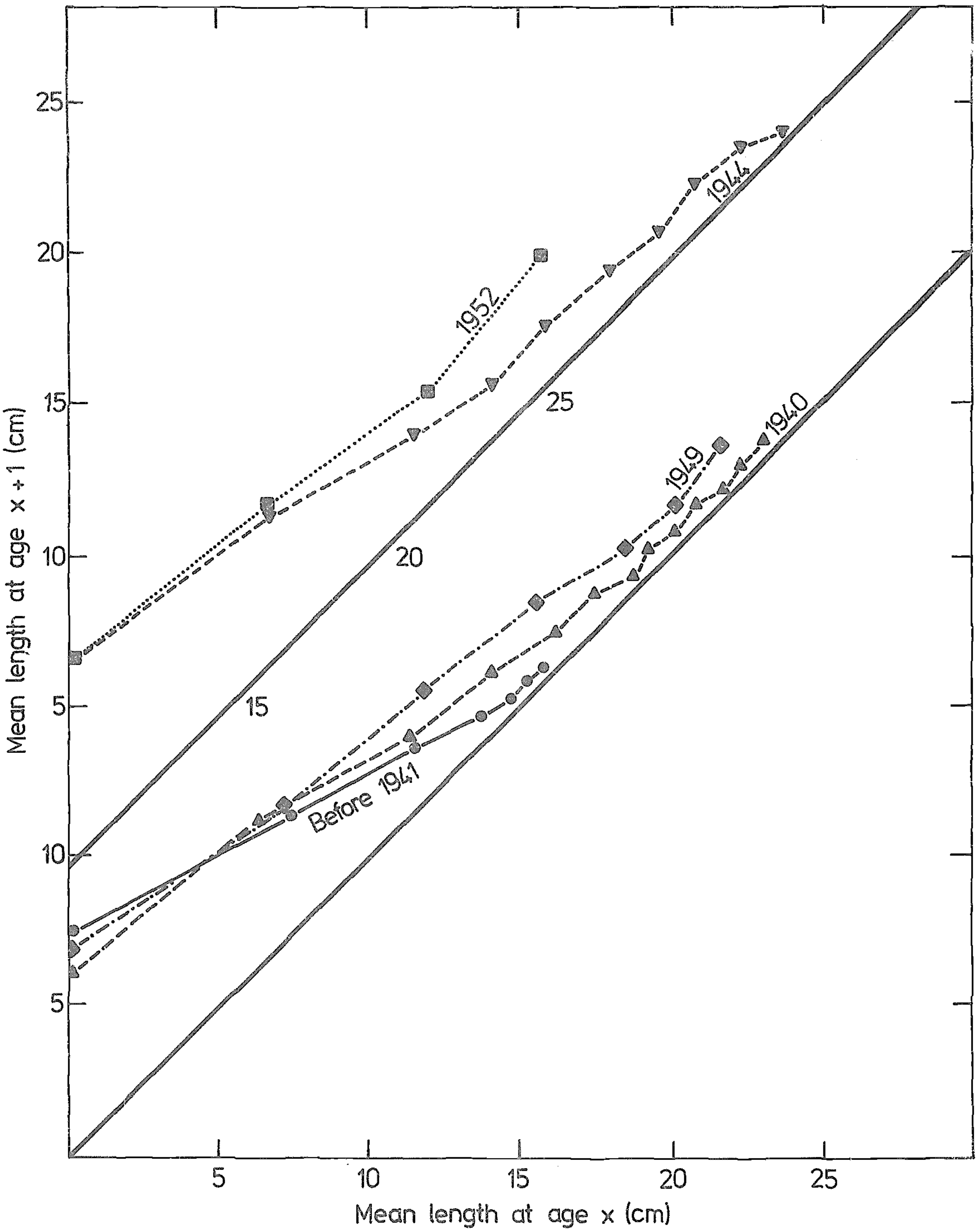


Fig. 18 Ford-Walford plots of the mean length at age (x + 1) against the mean length at age x: female fish of the combined year-classes before 1941, and the 1940, 1944, 1949 and 1952 year class from Lake Windermere. (From Le Cren 1958)

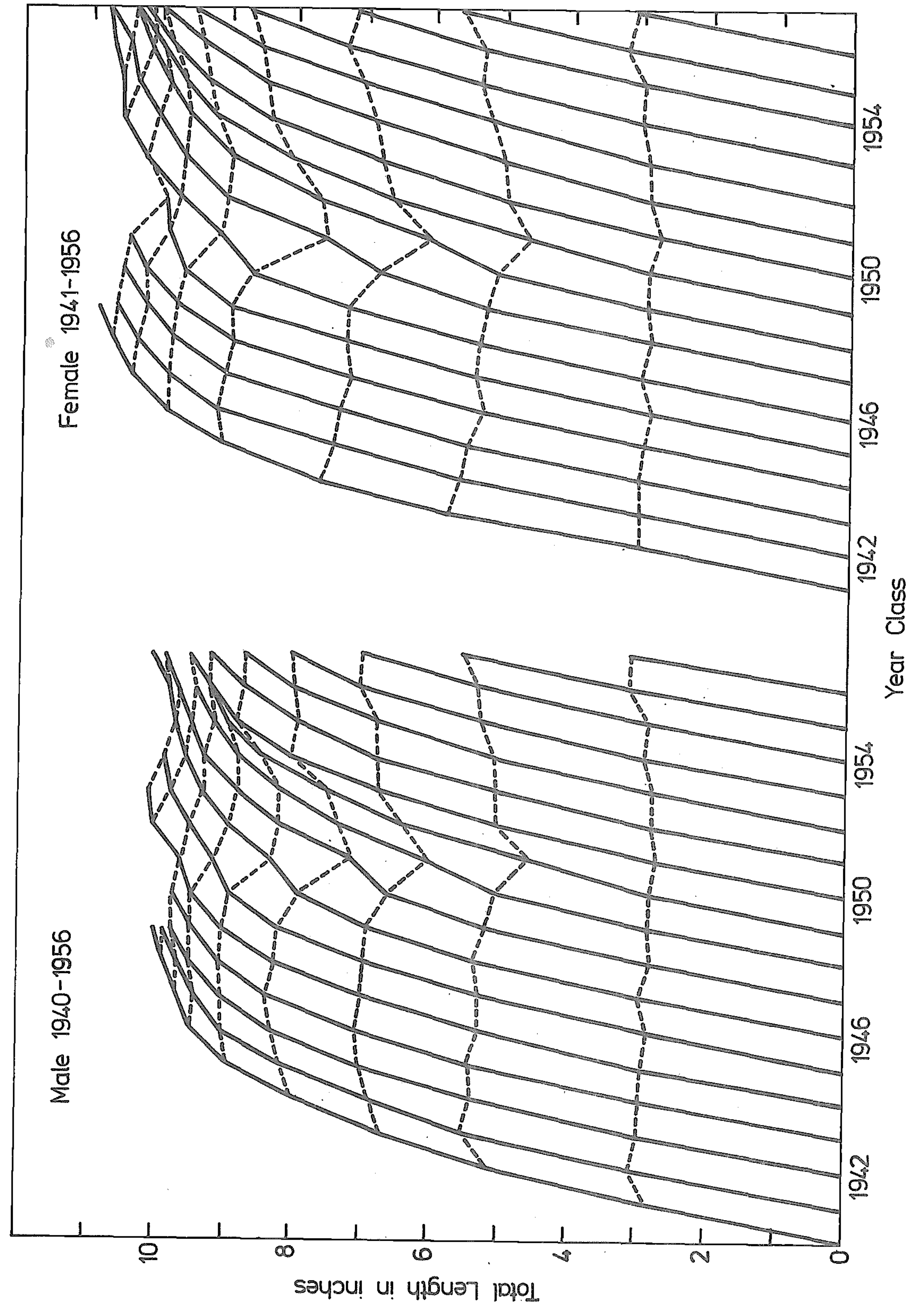


Fig. 19 Growth of male and female perch of the 1940 to 1956 year-classes in Red Lakes, Minnesota (From Heyerdahl and Smith 1971)

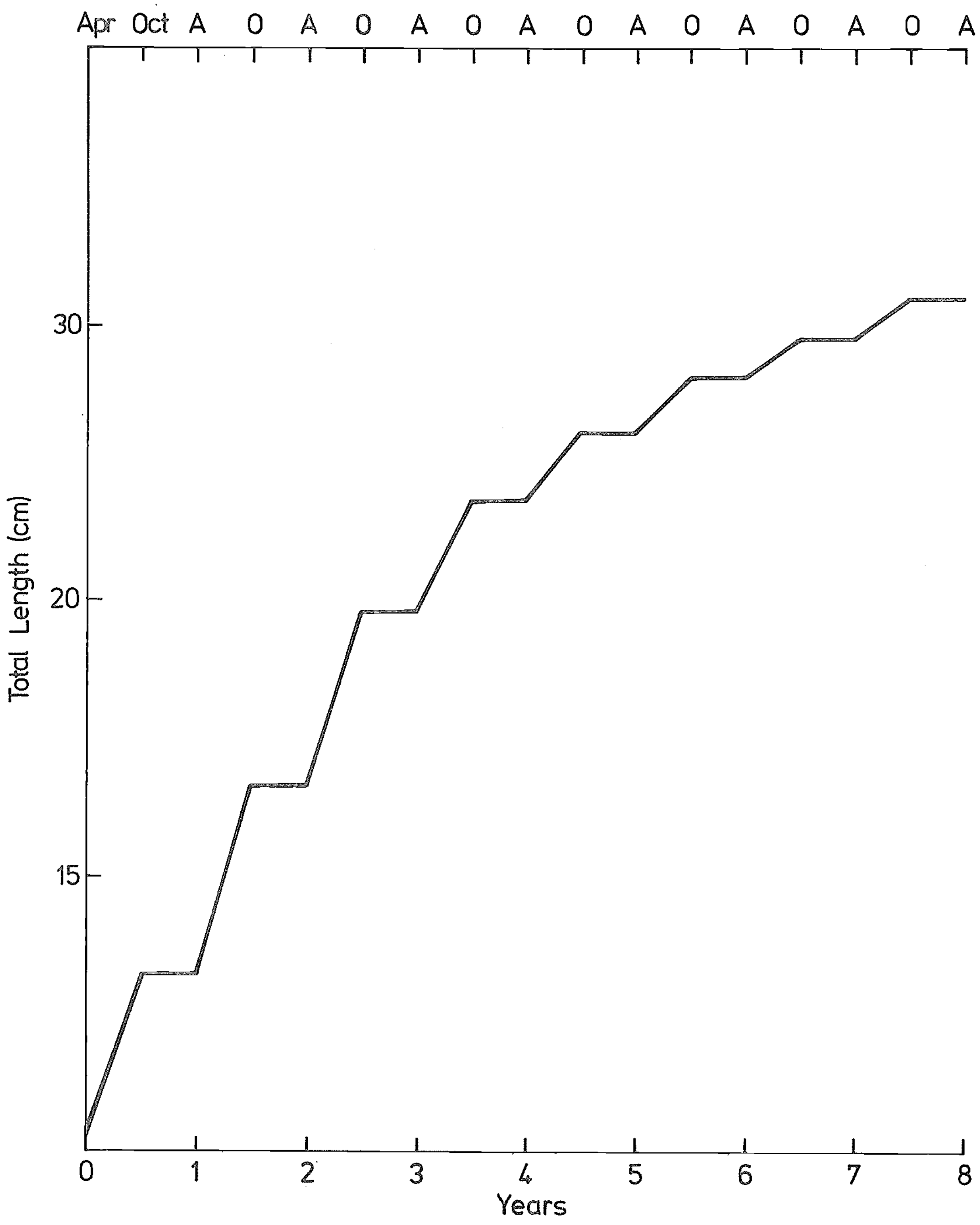


Fig. 20 Model of length-growth of perch in Loch Leven

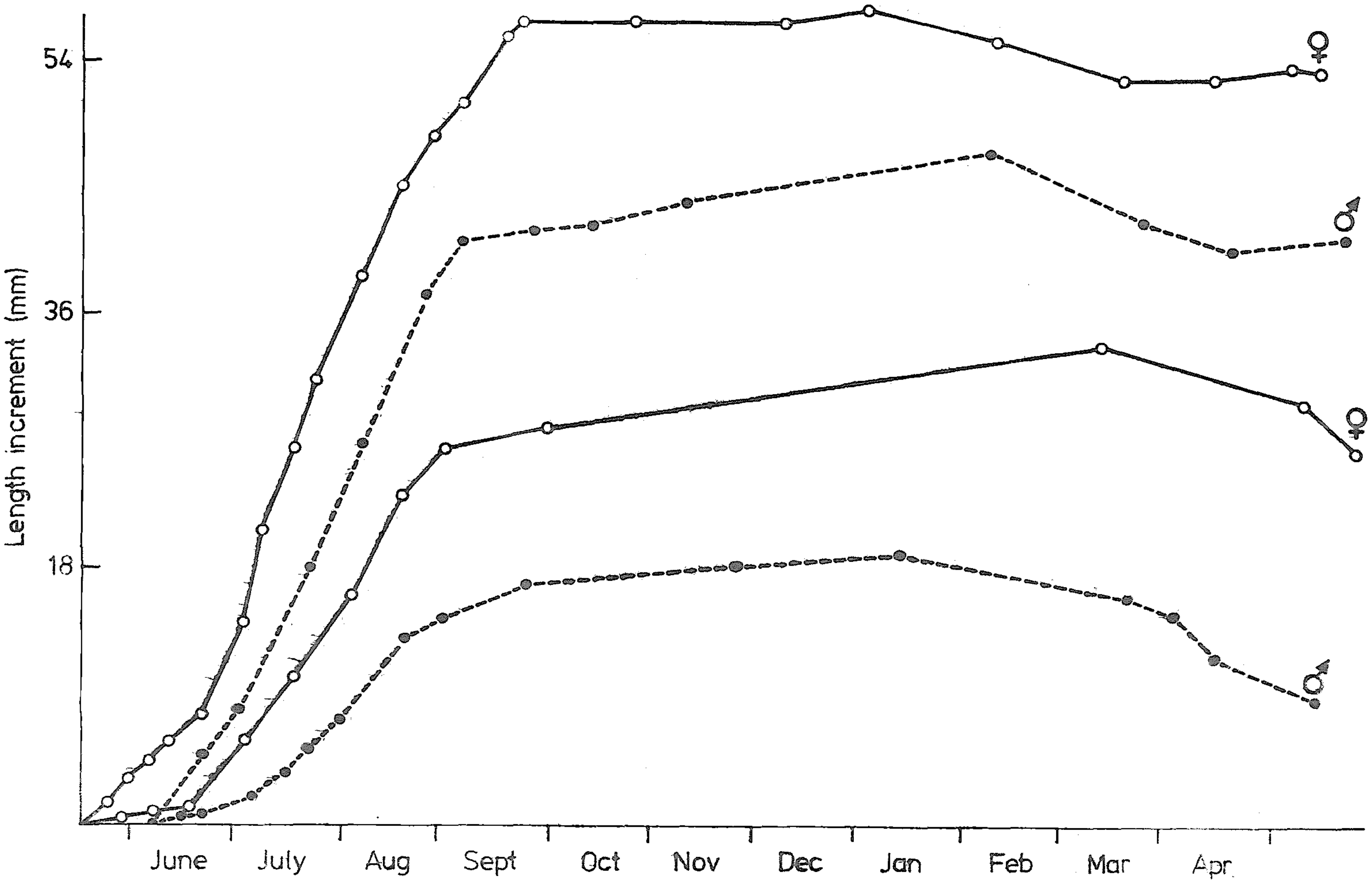


Fig. 21 Within season length growth of perch in Bodensee, 1972-73
Upper curves AG II; lower curves AG IV and V
(From Hartmann 1974 MS.)

TABLE XIV

Slow and fast growth among perch of the Yenisei River area
(From Krasikova 1958)

Lake	Growth Rate	Variable	Age of Fish				
			5+	6+	7+	8+	9+
Makovsk	Fast	Length cm	24.9	26.2	28.5	-	-
	Slow	Length cm	21.8	22.3	22.8	-	-
	Fast	Weight g	284	370	455	-	-
	Slow	Weight g	175	195	208	-	-
Karasinsk	Fast	Length cm	24.5	-	28.0	29.3	30.0
	Slow	Length cm	18.6	19.5	22.7	24.6	26.5
	Fast	Weight g	247	-	405	480	530
	Slow	Weight g	108	23	214	263	323
Munduyisk	Fast	Length cm	-	27.0	-	-	-
	Slow	Length cm	-	23.0	-	-	-
	Fast	Weight g	-	460	-	-	-
	Slow	Weight g	-	215	-	-	-

and ended 2-4 weeks earlier with their maximum growth rate also slower. With older perch, the main phase began and ended less abruptly (Fig. 21).

Many authors have noted the occurrence of separate growth-rate groups within the same water-body, for example, Schneider (1908), Schiemenz (1919) and Röper (1936) all describe three forms of perch, "Krautbarsch" which have higher backs than "Jägebarsch" and "Tiefenbarsch". The first group live close to the weed-beds, the second are open-water piscivorous forms and the latter deep-water fish. Dryagin (1948) referred to a large form from perch-roach lakes of the Ob-Irtysh basin in western Siberia which usually reach a weight of 1.0-1.2 kg and exceptionally 2.5 kg. Krasikova (1958) described two types from the Yenisei River region with slow and fast growths respectively: some data taken from her paper are shown in Table XIV.

Other data from Russian and Czechoslovak waters are shown in Fig. 22.

The existence of separate growth groups is probably a reflection of the perch's ability to occupy more than one ecological niche as evidenced from Ilina's (1973) data above (section 3.4.1). Those fish which became specialist piscivores at an early age may form the high growth-rate group whereas the slower group may have utilized the wider range of invertebrate fodder (cf. Shentyakova 1959). Experimental and field data are lacking on this topic.

The growth season is generally fairly short, lasting from May to October over most of the geographical range but being longer in warmer waters and shorter in colder. Thus the perch of Lake Dojran, Yugoslavia, grow actively for 8 months each year (Petrovski 1960) while those of some northern lakes in Finland grow for only 3-4 months (Lind et al. 1973). Swift and Pickford (1965) noted that the perch pituitary was adapted to a short growing season and unable to support a prolonged period of growth.

The most rapid growth of perch on record appears to be that achieved in ponds at Narrandera, Australia, where the fish reached a maximum length of 35.3 cm in 22 months without artificial feeding (Weatherley 1967).

- Condition factors

In Windermere, England, the seasonal changes in weight-length relationships among perch of different age-groups were studied by Le Cren (1951). He found that the perch could be divided into six groups corresponding with age, sex and maturity, each group homogeneous within itself throughout the seasons but significantly different from the

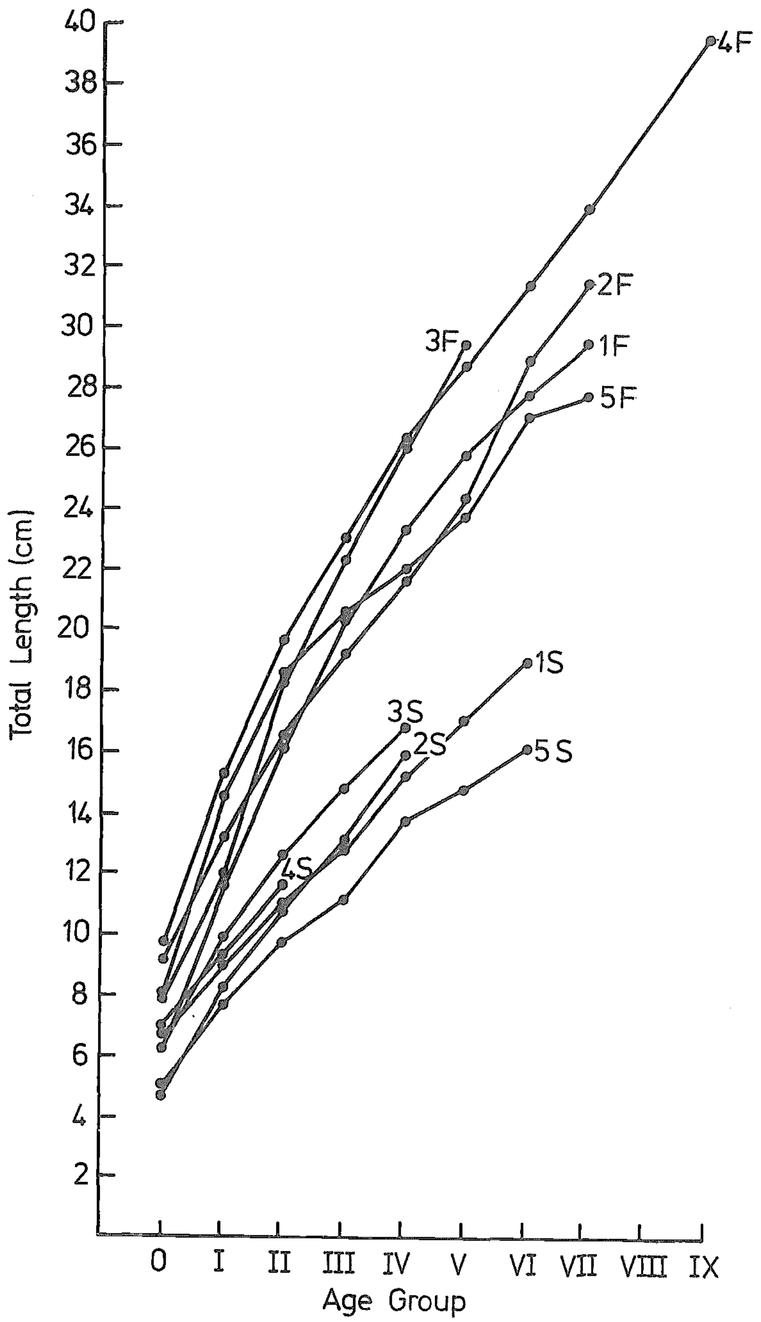


Fig. 22 Comparison of fast and slow growth groups
F = Fast S = Slow

1.	Rybinsk Reservoir	(Svetovidova 1960)
2.	L. Ubinsk	(Svetovidova 1960)
3.	L. Pereslavsk	(Svetovidova 1960)
4.	L. Chany (♀ only)	(Tyurin 1935)
5.	Orava Reservoir	(Balon 1967)

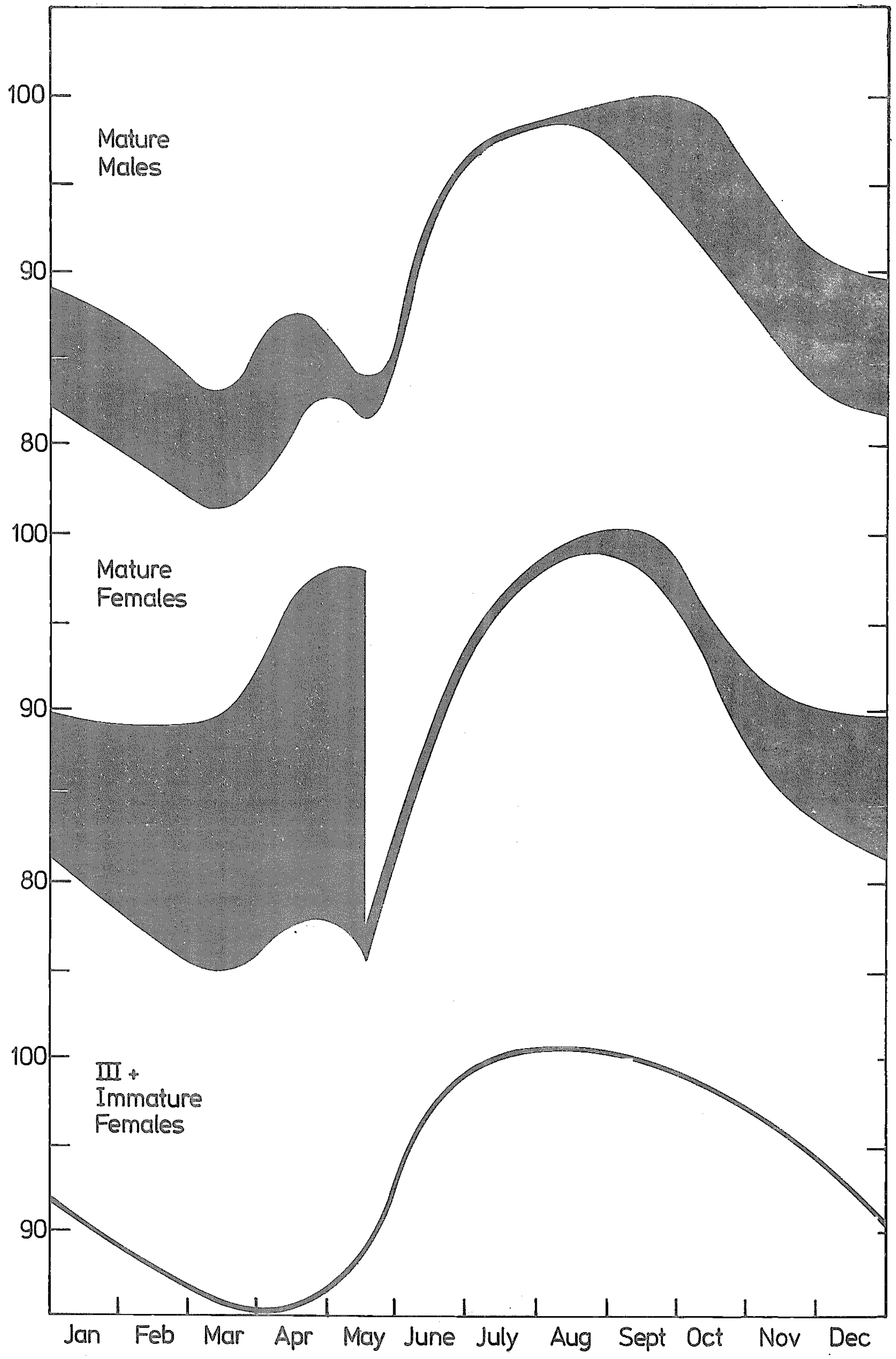


Fig. 23 Diagrammatic seasonal curves for relative condition with and without gonads. The solid black represents the gonad weight; the upper edge of the black, the condition with gonads and the lower edge, the condition-minus gonads (from Le Cren 1951)

TABLE XV

Condition factors in perch
(Data from Lind *et al.* (1973))

Fish group	Maxima		Minima	
	Q_1	Q_2	Q_1	Q_2
Small immatures	1.09	0.95	0.78	0.63
Immature females	1.12	1.03	0.86	0.74
Small mature males	1.09	0.96	0.86	0.74
Mature females	1.20	1.04	1.02	0.83
Large mature males	1.09	0.96	0.94	0.82

others. He emphasized that the condition factor $K = \frac{cW}{L^3}$ is affected by length and many environmental and genetic factors which make its interpretation difficult. The effect of length was removed by using a relative condition factor $K_n = \frac{W}{aL^n}$ derived empirically from length-weight data and not assuming a cube-law relation between the two. Expressing these values as a percentage of their maxima, the curves of Fig. 23 were obtained, indicating a seasonal cycle with high values during the summer feeding period, decreasing to minima in the spring. Among mature fish, the effect of the gonad maturation cycle on condition is very clear, the "condition-minus-gonads" falling sharply over the winter months indicating gonad development at the expense of somatic tissue.

Lind *et al.* (1973) calculated condition factors (Q) in two ways: $Q = 100\ W/L^3$, Q_1 where W was the intact weight and Q_2 where W was the weight of the fish without gonads and alimentary canal. He found maximum and minimum values in August and "winter" respectively as shown in Table XV.

Among the maxima, there were no significant differences between the groups, but the differences among the minima were statistically significant. These latter were probably due to the seasonal scarcity of plankton and benthic invertebrates under the ice (the food of the smaller fish) whilst small fish remained available as food for the large perch.

Carlander (1950) tabulated data on condition indices for perch in American populations, using the formula, $K = \frac{10^5 W}{L^3}$ where standard length was measured in millimetres and weight in grammes.

Mean values of K ranged from 1.43-2.58 increasing with length, with individual ranges at particular localities from 1.10-3.94. Without data for each population on the relation between total and standard length measurements (which vary from 1.14 -1.21), it is not possible to convert K values to Q values and vice versa. In the Klamath River, California, Coots (1956) found that K = 1.73 on average and noted that this fell low in the range quoted by Carlander. However, Coots' fish were living in a riverine environment and the majority of Carlander's data came from lake stocks. It would not be surprising that river fish should be slimmer than those occupying the quieter waters of lakes. However, Chikhova (1973) found differences among populations of perch in the Kuybyshev Reservoir, U.S.S.R. ranging from 1.43 in Usa Bay to 1.75 in the region below the dam. She notes that those from below the dam were more fusiform than those from the reservoir itself, but they nevertheless had the highest condition factor. Hutchinson (1974) found that condition of females from Oneida Lake increased directly with total length and over the sampling period from December to April (Table XVI).

Condition of spawning female perch in 1968 was significantly ($P<0.05$) higher than in 1969 or 1971. The increase in condition with season was attributed to one of the following causes:

(a) a true increase due to winter feeding;

(b) uptake of water by the ovaries;

(c) differential gear selectivity with respect to plumpness.

(Winter catches were made by gillnets, spring catches by trapnet.)

These three causes were not analysed further. On Morgan's (1974) respirometry evidence, food

TABLE XVI

Calculated values of condition factor (10^5 W/L^3)
(From Hutchinson 1974)

Total Length (mm)	Period	1968	1969	1971
230	Early March	1.64	1.50	1.65
250	Early March	1.70	1.56	1.67
280	Early March	1.79	1.65	1.70
250	End April	-	1.58	1.76
190	End April	-	1.70	1.81

intake in winter would be unlikely to allow an increase of condition during that interval.

Changes in condition with growth will be related in part to changes in body composition. Morawa (1956) measured the fat content and found muscle fat low at all seasons (1.5-2.0%): fat storage was chiefly in the visceral mass (Fig. 24 and Tables XVII-XIX). The head area appeared to be a subsidiary storage region also. Young perch were leaner than old ones and females generally contain more fat than males.

From tables XVII and XVIII, it may be calculated that fat accounts for 2.4% of total dry weight of perch in May, increasing to 4.0% in August and September. This is of the same order as found by Newsome and Leduc (1975) for mature perch in Lakes Tamaracouta and Archambault, Quebec, where mean fat composition ranged from 2.03-4.31% at the end of spawning to 4.03-7.9% in August and September. The latter authors noted that total body fat remained at an approximately constant level throughout the winter, dropped sharply during spawning and then increased equally sharply in June and July to a peak in late summer.

Using small perch (5-24 g), Schneider (1973 b) found that their mean water content was 77.6% and that starved fish contained more water than well-fed fish.

Craig (1974 a) plotted calculated weights of perch of 12.25 cm lengths on a monthly basis as a means of illustrating change in condition with season. His data are reproduced in Fig. 25.

A number of authors have considered the environmental controls on growth-rate in perch. In an exhaustive review, Tesch (1955) pointed out first that the establishment of growth-rates from wild stocks depended on accurate ageing methods. He used scales and validated his methods by marking fish, confirming Van Oosten's statement (In Beckman 1943) that, in winter, a few incomplete circuli are laid down followed by one or two complete but very closely spaced ones in spring. Recently, Holčik (1967) has shown that in the Kličava Reservoir during 1964, perch of AG I-X all formed the scale annulus between 23 April and 9 May at a temperature range between 8-11°C: thus, the timing of this scale index is quite precise. Tesch (1955) found that each population required calculation of its own body-scale relationship and he used the Dalh-Lea method for back-calculation of length-growth from scales; with a correction factor of 2.4 cm:

$$\text{Length at age A} = 2.4 + \frac{\text{Oral radius (A)}}{\text{Oral radius (t)}} (L_t - 2.4)$$

He characterized five types of length growth from his own data and from the literature as shown below:

A	Very good	AG II	fish greater than 20 cm total length
B	Good	AG III	fish greater than 20 cm total length
C	Moderate	AG III	fish greater than 16 cm total length
D	Poor	AG III	fish less than 16 cm total length
E	Very poor	All	fish less than 16 cm total length

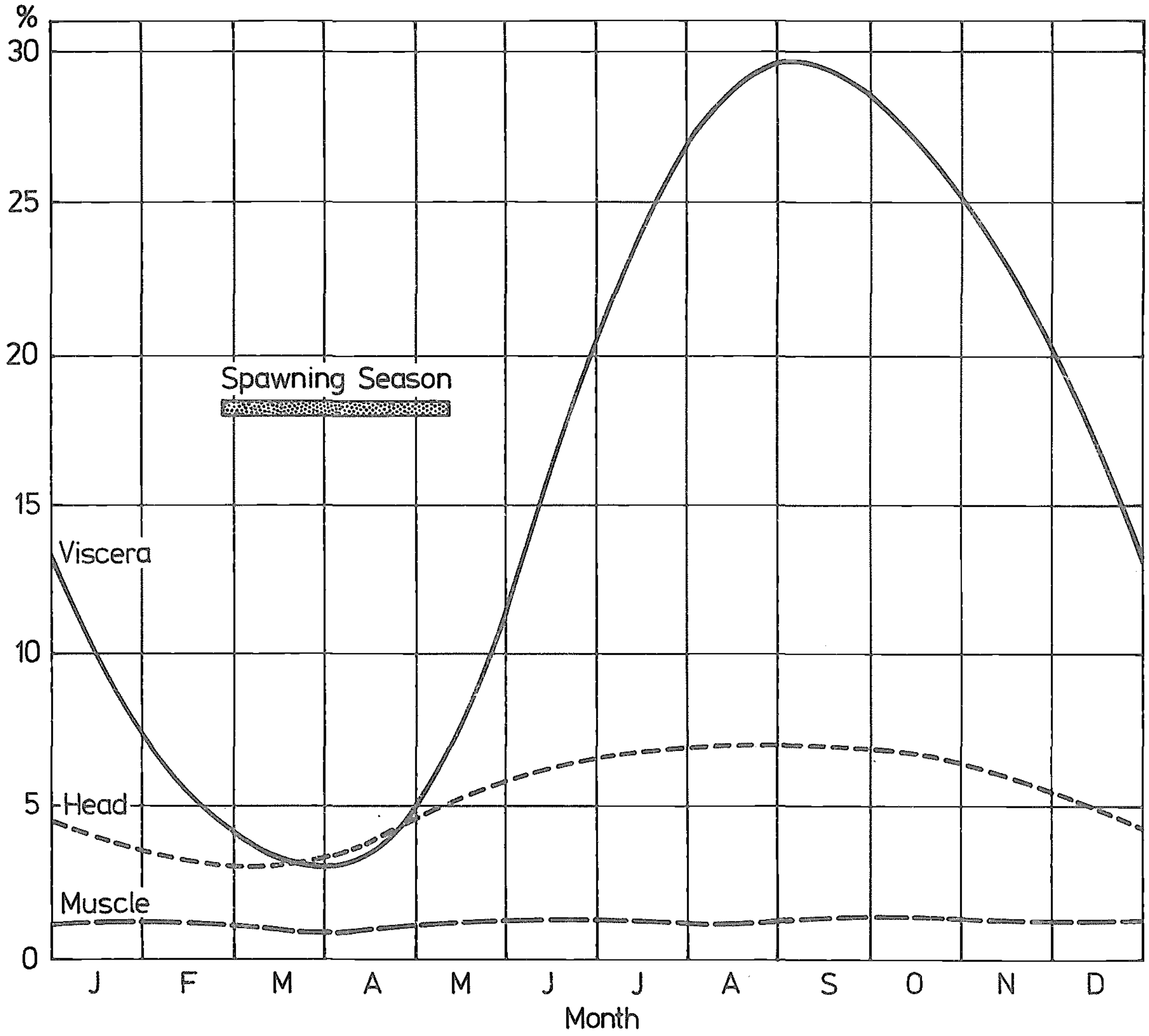


Fig. 24 Changes in fat content of 20 cm perch from Grosser Plöner See (From Morawa 1956)

TABLE XVII

Body composition (%) of perch from Grosser Plöner See
(From Morawa 1956)

Date	3 May 1955			4 August 1955			5 September 1955		
Body Part	Fat	Dry Weight Remainder	Water	Fat	Remainder	Water	Fat	Remainder	Water
Head	5.3	20.4	74.3	7.3	22.2	70.5	7.7	21.6	70.7
Flanks	1.5	22.5	76.0	1.5	23.7	74.8	1.6	22.8	75.6
Back	1.3	20.2	78.5	0.8	23.3	75.9	1.4	21.2	77.4
Tail area	1.1	22.9	76.0	0.7	24.3	75.0	1.3	23.0	75.5
Spinal column	8.8	33.9	57.3	10.3	34.9	54.8	11.4	34.8	53.8
Liver	3.0	18.6	78.4	2.6	20.1	77.3	4.7	16.9	78.4
Viscera	4.3	15.4	80.3	29.4	13.1	57.5	23.9	13.5	62.6
Fins	3.3	35.6	61.1	1.8	34.0	64.2	2.2	30.9	66.9

TABLE XVIII

% composition of total weight of perch
(From Morawa 1956)

Part	Date		
	3 May 1955	4 August 1955	2 September 1955
Head	18.6	15.5	15.9
Flesh	71.2	73.3	73.2
Spinal Column	2.3	1.8	2.0
Liver	2.3	1.5	1.3
Viscera	3.7	6.4	6.0
Fins	1.9	1.5	1.6

TABLE XIX

Fat content (%) of different sexes
(From Morawa 1956)

Date	Part	Males	Females
4. 8.55	Viscera	24.8	34.1
2.11.55	Viscera	18.0 (Range: 10.5-25.4)	30.0 (12.7-47.3)
2.11.55	Head	6.9 (6.4-7.3)	8.6 (7.3-9.9)
January	Gonads	2.7 (2.3-3.4)	2.9 (2.1-3.7)

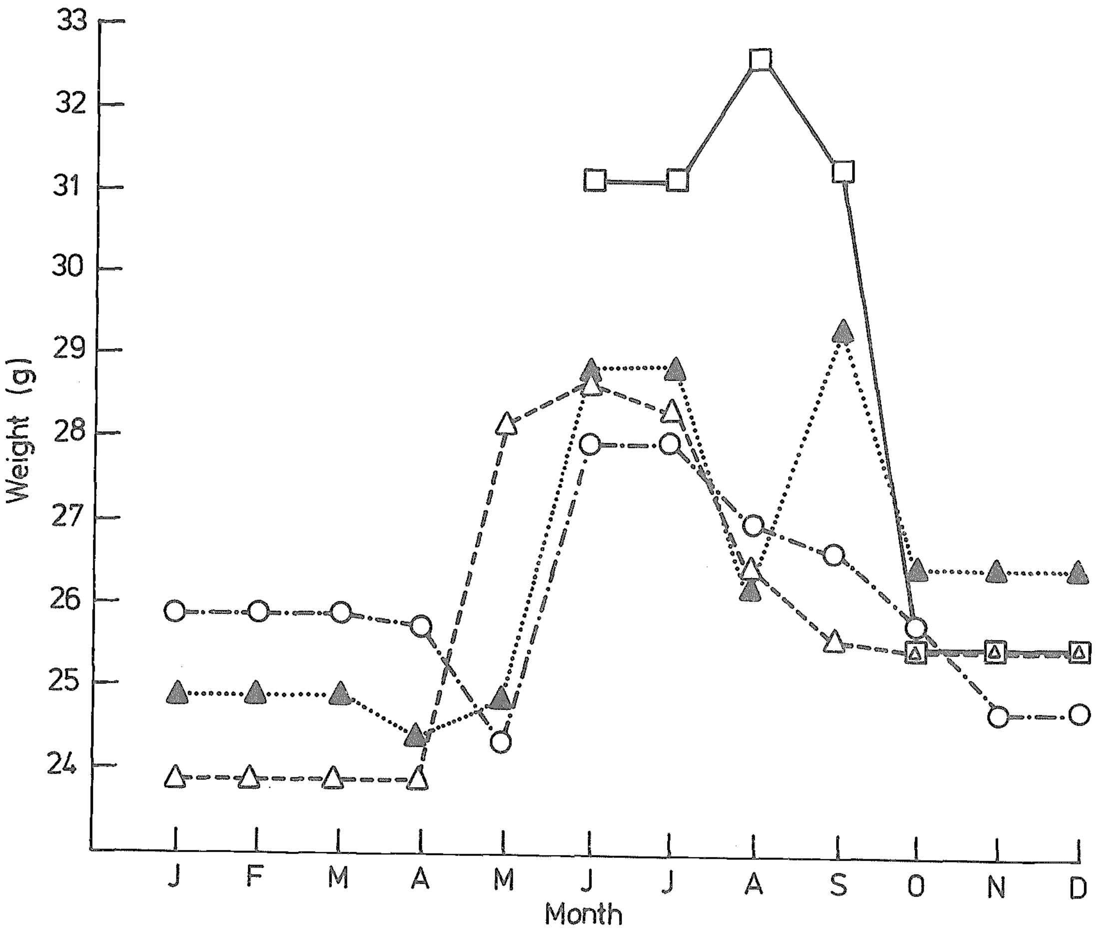


Fig. 25 Plots of monthly calculated weights for 12.25 cm fish for each maturity group as an expression of condition. The weights are based on a pooled value for 'b' (the regression coefficient) and a monthly value for 'a' calculated from monthly mean weights and lengths: □, Fry; △, immature females; O, mature females; ▲, mature males (from Craig 1974 b)

Examples of each category were cited from European and American waters. Normal length growth was concluded to be as follows (taking the Schweriner Stadtsee population as his model of standard growth):

AG	Total length (cm)
0	8.0
I	12.2
II	14.8
III	18.9
IV	21.8
V	25.2
VI	31.4
VII	36.8
VIII	39.5

He noted that the growth of large perch differed very little whatever their origin among categories A–E above.

Males grew faster than females during their first summer, but by the third summer, females were growing faster than males.

The growth categories A–E were achieved under a range of environmental conditions and Tesch exemplified these as follows:

A: (1) Pond culture: the very best growth where density was low and both benthic and fish foods were plentiful.

(2) Coastal waters: density again low due to effective predation and dispersal over an almost unrestricted area of excellent feeding conditions.

(3) Very large lakes: e.g. Bodensee where conditions apart from salinity were essentially similar to those in the Baltic (A(2) above).

B: (1) Most large non-alpine coregonid lakes and bream lakes with good food conditions, that is plentiful fodder fish and crayfish.

(2) Some more oligotrophic lakes where perch density is kept low.

C: A large group of waters:

(1) Large non-alpine coregonid lakes and bream lakes where fish yield is high.

(2) Weedy smaller lakes with low perch density.

D: (1) Lakes with moderate to poor fish yield, shallow, weedy with little open water and high perch density.

(2) Small weed-free bream lakes.

E: (1) As in 'D', but with dystrophic or oligotrophic conditions as in alpine lakes.

(2) At high perch densities and poor feeding conditions.

Optimal growth conditions he defined as: mesotrophic waters of large area, not too shallow, weed-free with a food-fish stock of smelt, roach, etc. Such conditions lead to moderate growth, but high yield.

Recently, Neuman (1974) investigated the effects of temperature on perch growth at 3 sites on the Swedish Baltic coast. At each site, the mean growth was the same and the between-year variation similar. The mean annual growth of 0+ and 1+ fish was positively correlated with water temperature in August and that of older fish (2+ – 10+) with water temperature in September. In areas affected by heated effluent from a power station, the growth season of 0+ fish extended longer into the autumn. The variation in growth between years increased strongly with age and its correlation with temperature increased likewise. Neuman suggested that as the unfavourable balance of anabolism and catabolism increased as the fish became older and the growth period became shorter so growth in older fish became more and more dependent on environmental factors.

Generalizations of this kind were based on population data but if individual dispersion of growth was considered, it was found to be apparently independent of temperature. In fact, this dispersion was so great that 10–33% of the individuals differed to the opposite extreme when mean growth was very good or very bad. This individual variation was not primarily genetic as particular fish seldom deviated from the year-class mean in the same direction for more than two years in succession. However, two successive years' deviation in the same direction was fairly frequent and usually occurred if the two years were themselves similar. Neuman suggested that if habitats favoured one individual one year and if circumstances remained the same, then they would do so again the next. Conversely, if there were a drastic temperature change, then the habitat combination might change favouring different individuals. He agreed with Le Cren (1958) that the main effect of temperature

TABLE XX

Temperature and growth of Windermere perch: correlation and regression data of weight increment on degree-days above 14°C (from Le Cren 1958)

Age Group	Range of years	r	Number of observations	Regression Coefficients			Regression as % of total variation
				a	b	b when growth%	
1st year	1939-1953	0.76	15	0.68	0.0056	0.251	58
2nd year	1935-1954	0.79	20	3.43	0.0340	0.272	63
3rd year	1936-1954	0.59	19	52.52	0.1600	0.160	34
Adults	1937-1955	0.71	189	11.84	0.3179	0.318	50

on growth was directly physiological and only effective to a lesser degree through its influence on food supply.

In Windermere, Le Cren (1958) noted that most growth took place between June and September, a period which roughly coincided with that of surface water temperatures above 14°C. He found significant correlations between annual weight increment and the number of degree-days above 14°C, and that temperature had the greatest influence on the growth of adults (3+ and older) (see Table XX). For adults, of the 50% of the variation remaining after the regression, 23% was due to year-to-year variation in growth not attributable to temperature and 27% to variation in growth of individual age-groups within any one year. Thus, temperature accounted for about two-thirds of year-to-year growth variation not attributable to chance or variation between age groups.

In Lake Huron, Coble (1966) found that annual growth increments of adult female perch were correlated with mean summer (June-October) water temperature at a depth of 20 ft (6 m).

In contrast to these findings, Grimaldi and Leduc (1973) have asserted that temperature is less important than other environmental factors in determining growth-rate in some Quebec waters.

Dymond (1926), Schneberger (1935), Eschmeyer (1937, 1938) and Alm (1946) all found that length growth was inversely related to abundance. Alm (1946) experimenting in ponds and small lakes in Sweden found that in many stunted stocks, growth was normal for the first one to two years and extremely slow thereafter, resulting in populations of 10-18 cm fish of a wide range of ages. In one 16-ha pond which had not been fished for twenty years, the mean length of adult perch was 15 cm in 1937. Twenty-five thousand fish were then removed and over the following six years, a further 17 500 in total were taken out. Spawn was carefully removed each spring to reduce recruitment. By 1943, the average length of adults was 20 cm with some fish up to 32 cm. This demonstration of inversely density-dependent growth has also been made among American populations, as for example, at Lake Mendota where Bardach (1951) reported increases in growth-rate following a severe reduction of the population by a Myxosporidian epizootic. In Duck Lake, Michigan, Beckman (1950) recorded growth-rate increases of up to 61% after a severe winterkill. However, such increases under natural conditions are usually short-lived, as Tesch (1955) found at the Sakrower See, East Germany, where, after catastrophic fish kills in 1945 due to explosions, the perch at first showed accelerated growth-rate and then this declined due to the upsurge of strong new year-classes in the absence of predators. Similarly, in attempting to test the density-dependence of growth, Parker (1958) found that after removal of perch from Flora Lake, Wisconsin, for four successive years, the growth-rate, condition factor and weight-length exponent of the population were reduced rather than increased. Unlike Alm, he had not controlled recruitment and he suggested the decreased growth-rate was due to the presence of new large year-classes.

In Holland in the weedy inland waters, Deelder (1951) reported similar poor growth of perch after they had reached a length of 13 cm. He attributed this to the lack of an available forage fish as food for the perch at this size and larger since in lakes where smelt (Osmerus eperlanus) was present, the perch grew well and in many instances where smelt have now declined or disappeared, for example, in the Zuider Zee since its isolation from saline water, the perch have become stunted. The implication that food became limiting for further growth in high-density populations was illustrated incidentally during a pest-control exercise in southern France (Chimits 1947). Stunted perch stocks were of common occurrence in the Landes area when Gambusia was introduced to control mosquito larvae. In ponds where perch had not been known to reach weights of more than 100 g for many years, the introduction of Gambusia provided a forage fish which resulted in perch growth to 250 g.

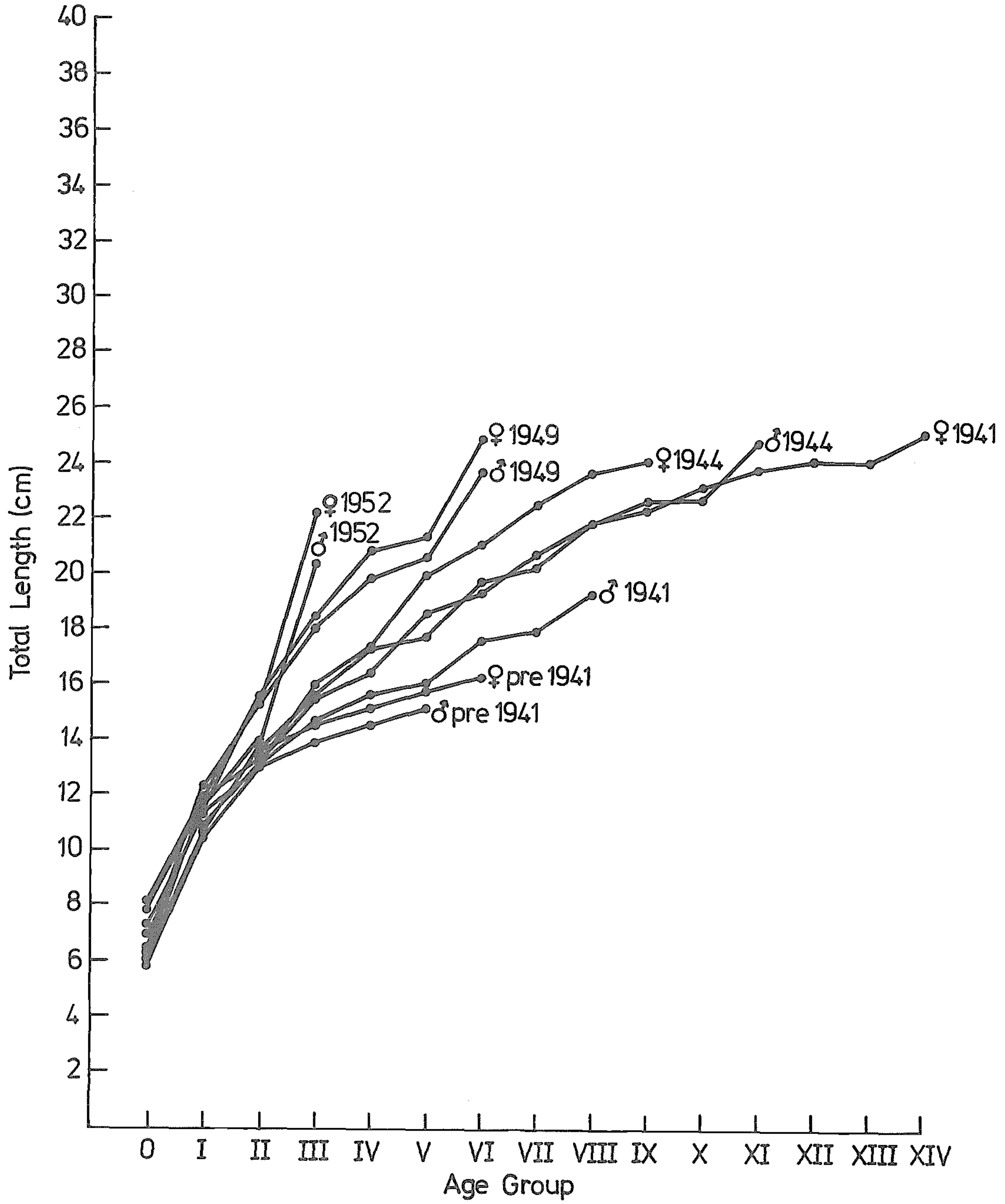


Fig. 26 Changes in growth rate in Lake Windermere (from Le Cren 1958)

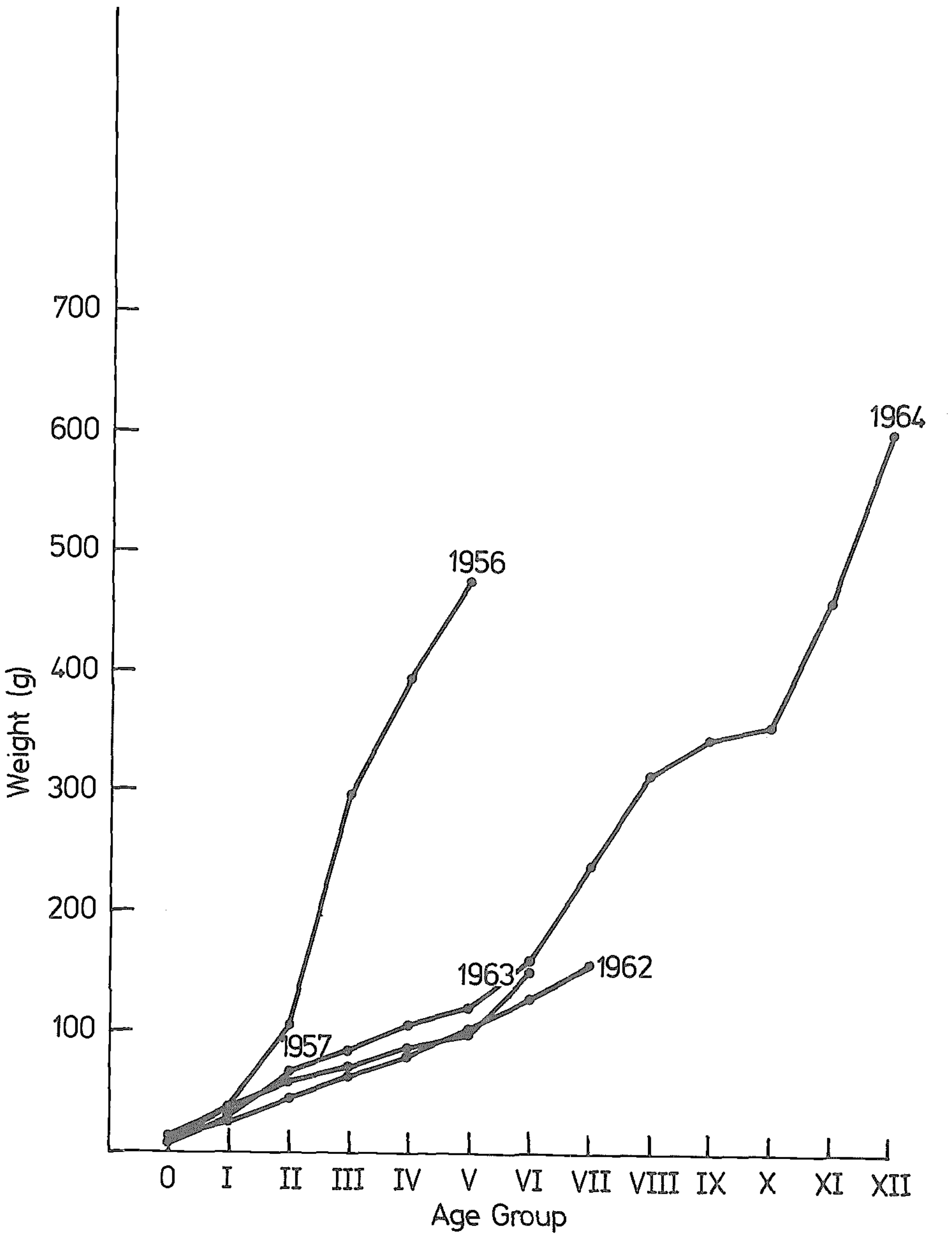


Fig. 27 Changes in weight growth of perch in Kličava Reservoir
(Data from Holčik 1970)

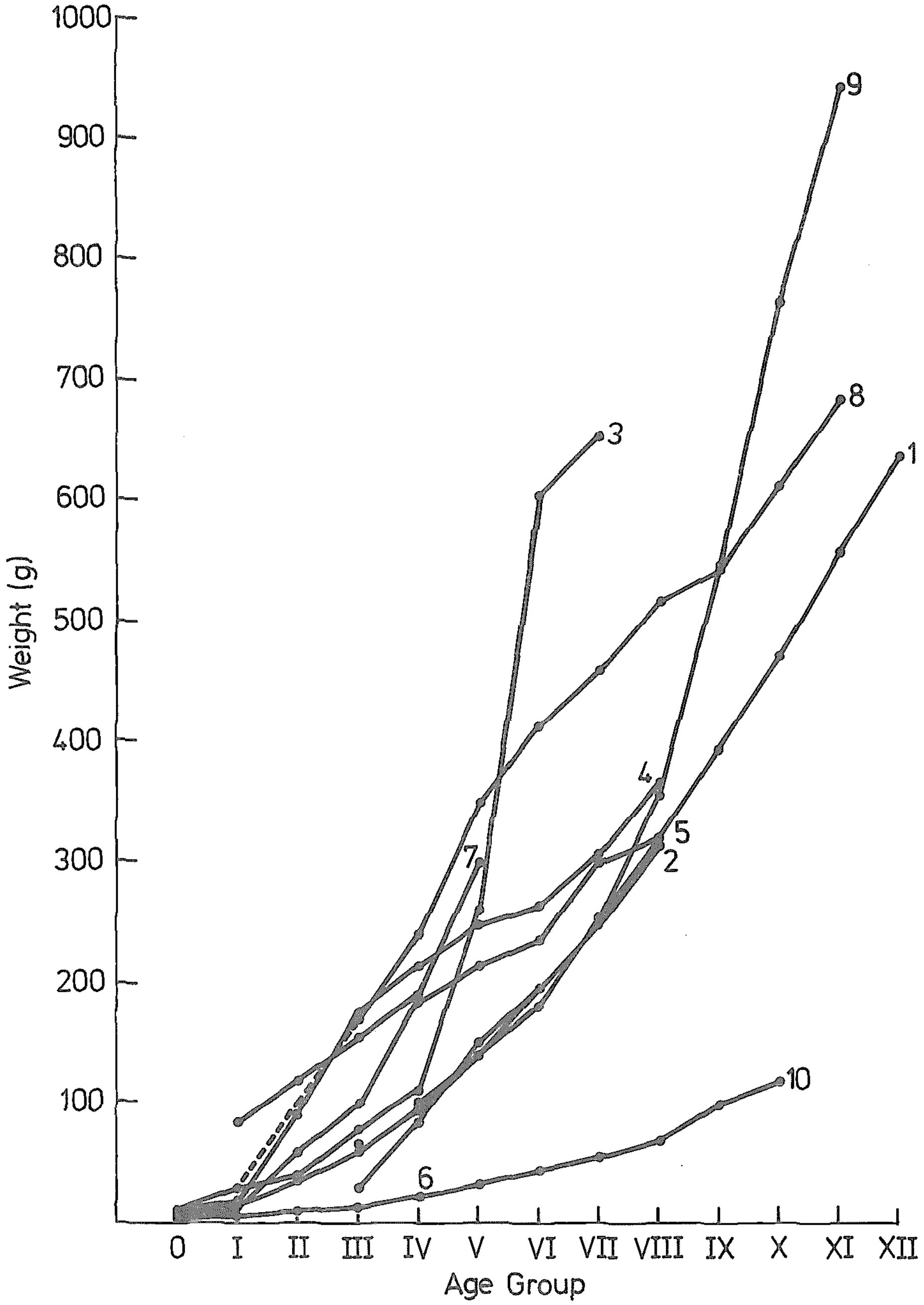


Fig. 28 Weight at age

1. Vistula River (Backiel, 1971)
2. River Ob, Krivolutsk (Dryagin, 1948)
3. Lake of the Woods (Carlander, 1950)
4. Loch Lomond (♀ only) (Shafi and Maitland, 1971)
5. Dubh Lochan (♂ only) (Shafi and Maitland, 1971)

Le Cren's (1958) analysis allowed him to adjust the observed values of growth increment to those expected for a given mean temperature and thus to examine trends in growth independent of temperature effects. The density of the perch populations of Windermere had been reduced experimentally from 1941 to 1944 at the rate of about 45% per year and then at a decreasing rate until the stock fell to a steady value of about 3% of its initial level by 1948. The partial regression coefficients between growth, population density and year since 1941 showed that there was high correlation between growth and year, and between density and year, but no significant correlation between density and growth. This conclusion that no direct relationship existed between density and growth was supported by evidence from the steady increase in growth-rate of successive year-classes in the absence of decreases in density after 1948 (see Fig. 26).

In the Bodensee, Germany, both growth rate and population density of perch have increased during the years since eutrophication (Hartmann 1974). Two-year-olds in 1973 were 5 cm longer than 2-year-olds in 1939 (data from Nümann 1939). Hartmann suggested that the increased density of invertebrate organisms provided a better food supply and hence a better growth-rate, and also a buffer for the fry against heavy predation by larger fish and hence a better survival rate and increased adult density subsequently.

In Saginaw Bay, Lake Huron, El-Zarka (1959) recorded a decrease in growth-rate since the previously available data of 1929-30. Changes in limnological conditions over the interval could not be determined and there was no evidence of major climatic changes. The lake had become polluted but he claimed that this was lessening in 1959. Larger Saginaw Bay perch eat smelt (*Osmerus mordax*) often taking fish up to 75% of their own length. These fish first appeared in Saginaw Bay in 1928, increased rapidly in the nineteen thirties until the population crashed after an epidemic in 1942, remaining scarce until 1950. Perch growth during this time has declined steadily and does not appear to be related to the abundance of smelt. The population density of perch had increased by about 10 times so that the decreased growth was attributable to crowding rather than food limitation since the fish were generally plump (weight-length exponent was 3.262 (see section 4.1.3).

Some changes in the weight growth of perch in the Kličava Reservoir were given by Holčik (1970) and are shown graphically in Fig. 27. The reservoir was completed in 1955 and by 1957, it had become overcrowded with perch which accounted for 95% by number of all fish present. The very high growth-rates evident at the time of the colonization of the reservoir by impounded perch (higher than any shown in Fig. 27) had fallen by 1962 to levels below all but the stunted stocks shown on Fig. 28. This dramatic decrease was attributed to initial overpopulation and later unsuccessful competition with roach (*Rutilus rutilus* L) and rudd (*Scardinius erythrophthalmus* L). However, after reaching a size at which the fish can exploit the abundant stocks of forage fish, growth-rate increases again as is clear from the curve for 1964 for the oldest age groups.

In experimental stocks, Schneider (1972) found 3 separate size groups, namely $<$7.6 cm, 7.6 016.5 cm and $<$16.5 cm. He claimed that these groups were not in competition with one another for food and that growth was dependent on density within the group only, being independent of densities in the other two groups. The biomass of each group that a lake could support differed, such that in Lake Cassidy, Michigan, the fry biomass in autumn could reach 35 kg per ha (7 500 fry at 8.1 cm per ha), but for growth to continue in the following year, this biomass would have to be reduced to 17 kg per ha. When perch reached 16.5 cm, growth would only continue if biomass of the large fish was not more than 11.5 kg per ha. This situation was a reflection of relatively high plankton and low benthos productivity, and a density-independent natural mortality rate after the first summer (see also section 6.4).

Some representative data on weight growth are shown in Fig. 28.

3.4.4 Metabolism

- Metabolic rate

Respiration rate of adult perch (c 20 cm) was studied by Morgan (1974) using a tunnel respirometer for active measurements and a chamber respirometer to evaluate routine levels. He determined metabolic rates in terms of oxygen consumption and ammonium nitrogen output (Table XXI), standard metabolic rate being calculated by extrapolation from the tunnel respirometer data and routine rate from the chamber respirometer readings. Active rates increased exponentially with swimming speed as shown in Fig. 29. Solomon and Brafield (1972) measured the separate components of the energy balance equation for juvenile perch growing in a continuous-flow respirometer. They showed that the energy content of *Gammarus* was assimilated with 83.5-87% efficiency, constant for different feeding levels, and that the maintenance coefficients (energy required per gramme of fish per year to maintain weight) ranged from 4.75 k cal per g per year for a fish of 18.7 g to 8.68 k cal per g per year for a fish of 7.0 g. They also showed that the oxygen consumption was correlated with food intake. Morgan (1974) considered specific dynamic action (SDA) as the component of the equation related to food utilization within the body of the fish and by analogy, with measurements on other species assumed that SDA corresponded to an increase of 50% over the routine metabolic rate. Using his measured metabolic rate data and allowing for SDA, he predicted minimal food consumption 18-22 cm perch to be 1.7%, 1.2%

TABLE XXI

Metabolic rates of adult perch
(From Morgan 1974)

a) Oxygen consumption (mg/kg.h)

Temperature (°C)	Standard metabolic rate	Routine metabolic rate (± 1 standard error)
5	12.8	39.1
10	63.5	78.2 ± 5.6
15	54.5	13.7 ± 12.4

b) NH_3-N output (mg/kg.h)

5	2.50	1.6
10	2.29	2.8 ± 0.2
15	8.29	3.3 ± 0.3

TABLE XXII

Mean swimming speed of perch in Lake Mendota
(From Hergenrader and Hasler 1967)

Water temperature (°C)	Mean speeds				Maximum speeds of shoals (cm/sec)
	Individuals		Shoals		
	(cm/sec)	Number of Observations (n)	(cm/sec)	(n)	
0-5	6.5	119	11.6	532	20
10-15	13.5	15	17.0	270	30
15-20	12.0	26	19.6	299	36
20-25	12.1	38	25.0	536	54

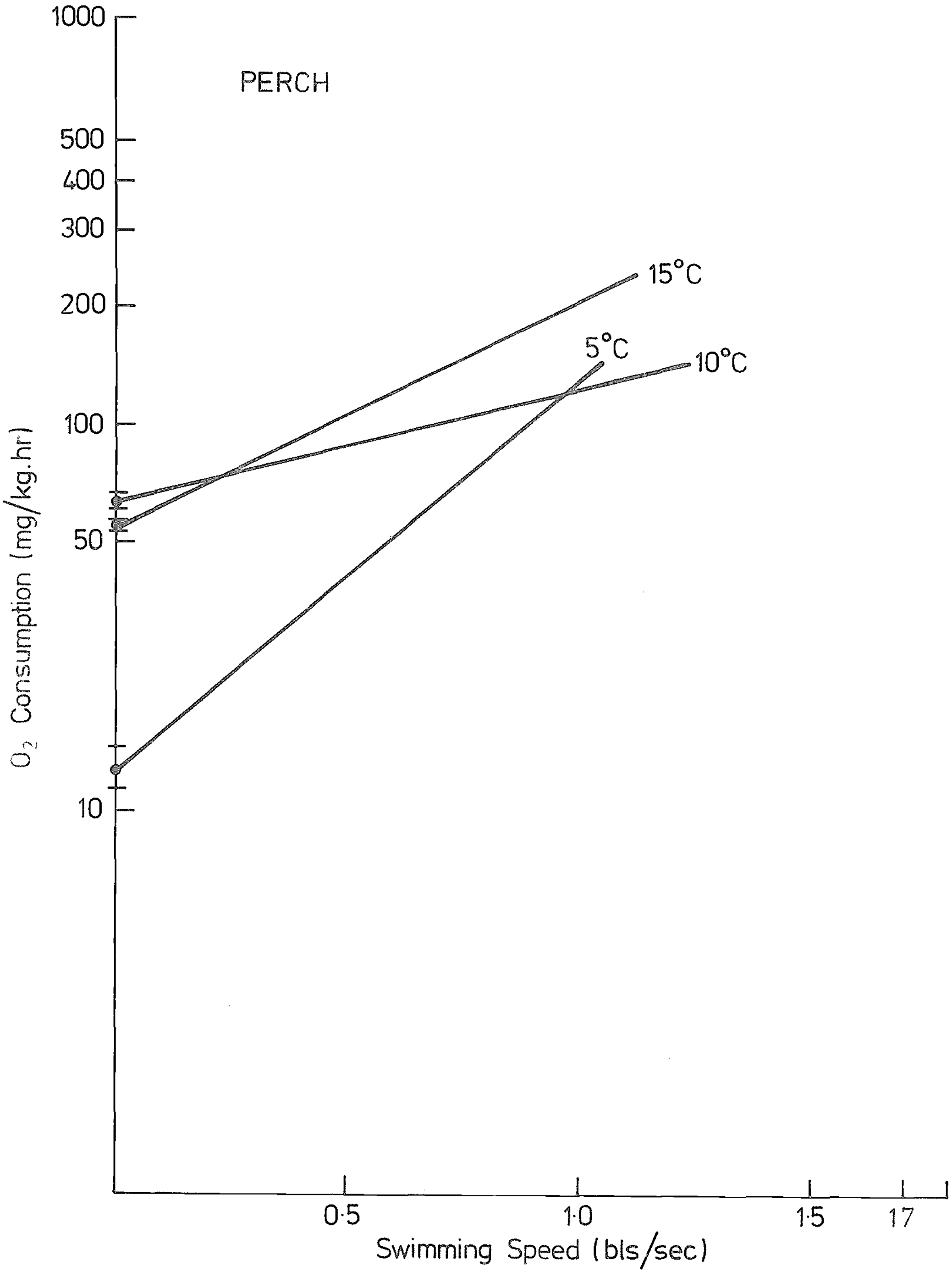


Fig. 29 Perch. Regression lines of oxygen consumption and swimming speed. Intercept on the ordinate obtained by extrapolation and is the standard rate (± 1SE). (From Morgan 1974)

and 0.5% body weight per day to maintain the fish at 15, 10 and 5°C respectively.

Birkett (1969) calculated the gross efficiency of conversion of nitrogen by small perch (100–150 g) fed live *Lumbricus* sp. in a 42-day tank experiment at 17°C in June–July. This efficiency was expressed as:

$$\xi^* = R/(A-A)$$

where

R	is rate of growth
A	is rate of absorption
A	is maintenance rate of absorption

all measured in mgN/g live-weight per day.

The values given were as follows:

A	0.963 x intake of food
A	0.173 mgN/g/day
ξ^*	0.413
R	0.0013–0.1504 mgN/g/day

These values of R are equivalent to daily live-weight increases of 0.01–0.56%. Such increases for perch of this size in midsummer are quite small, but the size of ration that they would accept in the tanks was also small (0.99–3.00% body weight per day) as compared with field data for daily food intake (Thorpe 1974).

Hergenrader and Hasler (1967, 1968) measured the swimming speeds of perch in Lake Mendota using sonar (Table XXII). They found that the range of speeds was narrower in winter than in summer, that is, that the "scope for activity" was greater at higher temperatures, and that the mean speeds increased linearly with temperature from winter to summer and decreased linearly as the lake cooled in the autumn.

Schlicher (1926) had noted that there was an increase in the leucocyte count of perch blood in summer and a decrease in winter, and Veldre (1959) has found maximum haemoglobin and erythrocyte values in summer in Estonian lakes. However, Smirnova (1962) reported seasonal changes in all three blood parameters in Rybinsk perch in which they were maximal in winter and minimal in early summer. Local oxygen conditions probably influenced the pattern of haemoglobin, and erythrocyte dynamics and leucocyte dynamics coincided with feeding dynamics, the Rybinsk fish apparently feeding in winter.

Lange (1919) found significantly higher erythrocyte counts and haemoglobin content in perch taken from brackish water as compared with those taken from fresh water at the same time: he concluded that the metabolic rate of brackish water perch was higher than that of freshwater perch.

– Endocrine systems and hormones

Swift and Pickford (1965) established the seasonal potency of pituitary hormones in perch as follows:

(a) Growth hormone: Maximum accumulations were evident in the hypophysis 4–6 weeks prior to the estimated natural growth peak in the summer and 100 µg of perch pituitary brei (lyophilized gland homogenized in 0.6% NaCl, 10 mg/ml) when injected into hypophysectomized male *Fundulus heteroclitus* was equivalent to 250 µg of standard beef growth hormone (N1H–GH–BI) in June. The accumulation declined in July and was near to total exhaustion of growth potency in August. During winter, the experimental fish showed that the hormone had a potency only 8–20% of its summer maximum.

(b) Gonadotrophins: Maximal at the peak of the reproductive cycle in April and severely depleted in August.

(c) Thyrotrophins: Activity cycle of these hormones was similar to but less pronounced than that of the gonadotrophic hormones; injection maintained the adrenal cortical histology near normal except in July, stimulated the restoration of melanin pigment, the proliferation of new melanocytes and the spawning reflex response.

Bibor and Leroy (1973) investigated the thyroid function of perch using the radioisotopes $Na^{125}I$ and thyroxine ^{125}I. They found a very rapid turnover of hormones with rapid incorporation of iodine into iodo-tyrosine compounds, suggesting very important biosynthetic activity. Labelled thyroxine was metabolized rapidly, confirming this view.

– Osmotic relations

It has been noted above (section 2.3) that perch occur in waters up to c 12‰ salinity during the feeding period, but normally spawn in freshwater. Natochin and Lavrova (1974) found that the K, Ca and Mg concentrations in blood serum were related to food intake and not to environmental levels, but that Na concentration depended on that of the water, as these ions were taken up directly via the gill chloride cells. Lagler *et al.* (1962) stated that perch require concentrations of more than 0.05 millimoles Cl/l before Cl ions are taken up from the water by the gills. Lutz (1972) found by experiment that perch tolerated up to one-third strength sea water, but at one-half strength, they took up ions rapidly, dehydrated and died in a few days (see Table XXIII).

TABLE XXIII

Concentration of ions in plasma and muscle of perch immersed in various salines (mM/l, mM/kg water)
(From Lutz 1972)

Bathing media	Na	K	Ca	Mg	Cl	Water (g water/g dry weight)
Plasma F.W.[1]	154.20 ± 2.06(19)	3.63 ± 0.23(16)	4.38 ± 0.46(10)	1.55 ± 0.06(16)	120.30 ± 2.69(19)	
⅛ S.W.[2]	155.62 ± 3.52(7)	3.68 ± 0.41(6)	4.83 ± 1.04(5)	1.50 ± 0.13(4)	136.50 ± 5.84*(8)	
⅓ S.W.	155.80 ± 2.87(8)	5.28 ± 0.88*(8)	3.99 ± 0.35(6)	2.72 ± 0.73*(8)	137.92 ± 6.12*(9)	
½ S.W.	210.50 ± 7.52*(7)[3]	5.96 ± 0.91*(5)	7.30 ± 0.35*(6)	7.68 ± 0.72*(6)	195.76 ± 9.79*(6)	
Muscle F.W.	19.92 ± 1.48(20)	143.0 ± 4.16(20)	2.65 ± 0.18(17)	15.17 ± 0.75(18)	10.34 ± 0.87(15)	4.24 ± 0.18(19)
⅛ S.W.	19.34 ± 2.36(6)	148.8 ± 7.0(7)	3.49 ± 0.38*(7)	16.30 ± 0.67(6)	11.47 ± 0.81(7)	3.91 ± 0.17(7)
⅓ S.W.	20.65 ± 2.40(8)	162.3 ± 4.36*(9)	3.42 ± 0.38*(8)	16.58 ± 0.55(9)	12.06 ± 0.84(9)	4.05 ± 0.12(10)
½ S.W.	47.81 ± 4.21*(6)	172.7 ± 3.18*(6)	3.75 ± 0.26*(5)	21.89 ± 0.79*(6)	32.57 ± 3.31*(6)	3.45 ± 0.02*(6)

1/ F.W. (freshwater) values from Lutz (1972). Comp.Biochem.Physiol., 48A:72-88

2/ S.W. (seawater)

3/ * Significant difference from normal (F.W.) values by Student's t-test ($P < 0.05$)

3.5 Behaviour

3.5.1 Migrations and local movements

– Extent of movements

In large unrestricted environments where tagging experiments have been conducted, perch do not travel extensively. In Lake Michigan, for example (Smith and Van Oosten 1939), 122 adult perch were marked with opercular strap-tags, and recoveries were as follows:

Miles from release point	Fish
1–10	6
11–25	2
26–50	1
51–75	1

The greatest minimum distances travelled were:

Miles	Months	Days
27	1	17
57	9	2

Among perch marked in the Stettiner Haff (Henking 1923), recoveries were made up to 50 mi along the Baltic coast near Rügen Island. In Chesapeake Bay, Maryland, perch caught in Chester River were tagged and stocked into the Severn and Magothy River estuaries, 25–30 mi away (Mansueti 1960). Recaptures of these fish showed that their movement was randomly directed to all areas of Chesapeake Bay from Susquehanna Flats to Tilghman Island, involving greatest movements of at least 50 mi by displaced fish. Resident perch in Severn River were also tagged, and recoveries showed that these dispersed downstream from the spawning area at the head of the estuary over a range of 0.5–20 mi. Muncy (1962) reported one fish recovered 40 mi away outside the Severn River system. Mraz (1952) released over 4 000 tagged perch in southern Green Bay, Lake Michigan, and recovered 108 of these. Seventy-eight of these were returned from the release area, 21 from less than 20 mi, 7 from 20–40 mi and 2 from 40–50 mi away.

In restricted water bodies, Kukko and Lind (1972) found "home ranges" of perch at spawning time in small Finnish ponds to be about 100 m. In the Mazurian Lakes, Poland, Kozikowska (1966) found that marked perch moved from lake to lake, the maximum distance being about 6 mi.

Daily movements have also been documented. Scott (1955) recorded regular movement from Rondeau Bay in the morning out into Lake Erie, the perch returning in the evening. Hasler and Villemonte (1953) noted perch active by day at 15–25 m depth in open water in Lake Mendota, followed by pre-sundown inshore movement, the fish settling to the bottom with the approach of twilight.

– Function of migration

The normal pattern of migration in perch conforms to the simple model of Harden-Jones (1968) in which during the course of life, fish move between feeding areas, wintering areas and spawning areas. Wintering migrations take perch into deep water where maximal temperatures (c 4°C) occur and spawning migrations result in the aggregation of fishes back in shallow water in spring. In the case of estuarine populations, the migrations at this time are into freshwater. Berzins (1949) recorded a gradual aggregation of perch moving in from the sea into deep waters of the lower estuary of River Lielupe, Latvia, from September to November and their emigration seaward again in February and March before the spring floods.

– Direction and mode of migratory movements

Huitfeldt-Kaas (1909) reported a mass migration of large adult perch (30–50 cm) from Lake Mälaren into the Baltic. Such apparently directed seasonal movements have not been reported frequently for perch whose seasonal migrations appear to have the character of kineses rather than taxes (see for example Berzins 1949, Neuman 1974 a). Daily movements, on the other hand, possess a directed character, as mentioned above in the case of Rondeau Bay, Lake Erie and of Lake Mendota. Eriksson (1974) found that perch were active by day at all seasons, but their level of activity depended on temperature and photoperiod. Ferguson (1958) found that they preferred a temperature of c 21–24°C; studies from the wild have shown aggregations of perch at this temperature range in summer. Privolnev (1953) found that in choice experiments, adult perch preferred darkened areas to light ones. Thus, temperature and light intensity, fluctuating daily, probably act as proximal determinants of distribution, maintaining daily migrations. The importance of temperature has been demonstrated recently by Neill and Magnusson (1974) who showed that perch avoided the heated outfall area from a power-station even though food organisms were more plentiful there than elsewhere: the fish only made occasional forays into the area, returning to a region of optimal temperature. Kelso (1976) noted that the effect of a thermal discharge from the Nanticoke generating station, Lake Erie, was to localize perch by increasing the sharpness of turns and decreasing the distance between turns. The perch were also oriented into the current, whereas those from unaffected habitats oriented in relation to the shoreline.

– Time or season of migration

Spawning migrations (see section 3.1.6) occur in spring, the male fish preceding the females on to the spawning grounds.

Feeding migrations where they are distinguishable occur immediately after spawning, as for example, in Chesapeake Bay (Muncy 1962) where the perch spawn in freshwater in late March and April, and return downstream to brackish areas of 6–10‰ salinity to feed.

Wintering migrations occur in autumn, the fish aggregating in deeper areas of lakes, or in intermediate salinities (4–8‰) in such habitats as Chesapeake Bay (Muncy 1962) or in protected waters such as the deep estuarine pools of the River Lielupe (Berzins 1949) (see above).

- Daily migrations

(See above.)

- Changes in pattern of movements with age, etc.

Eriksson (1974) noted that daily activity was quantitatively related to water temperature, but its quality also varied seasonally. In winter, perch were active on the bottom of their test tank and in summer, they were equally active at the surface and the bottom. In August, they were more active at the surface than elsewhere. Hartmann (1974) recorded that in Lake Constance before eutrophication, the adults were limited to the littoral areas in summer, but since eutrophication, they now move out into the sub-littoral and pelagial regions feeding on abundant cladoceran plankton.

Catch per unit of effort statistics for gillnets have been shown to be correlated positively with temperature by Neuman (1974 a) in the Baltic in August and September, and by Marcuson and Howse (1968) in Round Lake throughout the summer. This would imply a direct correlation between activity and temperature, assuming perch were present all the time. In Loch Leven, Scotland, Thorpe (in press a) found that peak seine catches of perch from the shore occurred in early morning and late evening in June and August 1971, but at mid-day in these months in 1972. He attributed this change between years to the occurrence during 1972 of a dense bloom of Anabaena, sufficiently thick at the surface to produce a strong shading effect below and thus to retain perch (and trout, Salmo trutta L.) in an area of low light intensity and suppress an offshore migration.

3.5.2 Shoaling

Spindle-shaped shoals of 50–200 individuals, stratified by size and age, were described from Lake Mendota by Hasler and Bardach (1949). It is likely that among adult stocks there is also stratification by sex as Hartmann (1974) noted that the diet of males and females differed and their growth periods also. Furthermore, mature females tend to grow faster than males (see Fig. 21) which would also lead to segregation of sexes if stratification of size and age was already occurring.

Even in small ponds, age classes are reported as circulating separately (Kukko and Lind 1972).

Ward and Robinson (1974) found from mark-recapture experiments that the shoals were discrete and did not intermingle in the short term. Mixing: young perch are often found in large shoals together with minnow (e.g. Notropis Hudsonius Clinton) (Scott and Crossman 1973). In Europe, they are often associated with cyprinid fry especially roach (Rutilus rutilus L) (e.g. Vashkyavichiute 1963).

Size density and behaviour of shoals: As mentioned above, the shoals are usually composed of 50–200 individuals. The shoal has been recorded by Siegmund and Wolff (1973) using underwater television as forming in the morning twilight and dispersing in the evening twilight. Hergenrader and Hasler (1966) also reported the dissolution of the shoals at night as have Ward and Robinson (1974) who found the fish resting at that time on the bottom among submerged vegetation.

Light transmission was positively correlated ($r = 0.77$) and temperature negatively correlated ($r = -0.89$) with shoal-size in perch at Lake Mendota (Hergenrader and Hasler 1968). In summer, the individual distance of perch in shoals was less than 1.5 ft, and greater than 1.5 ft in winter. The summer shoals were smaller than the winter ones, the former were c 8.5 ft from top to bottom and the latter c 22.1 ft. In the winter, Lake Mendota water was much clearer at a given depth than it was in summer due to the absence of seston and this clarity may have allowed the operation of attraction-repulsion mechanisms over a greater distance than was possible in the murky summer environment. Furthermore in winter, zooplankton was scarcer than in summer, although greater individual distance in the school allowed a greater volume of water to be searched.

Although shoals of 50–200 perch appear to be a characteristic size, larger aggregations occur at times as was clear on 5 August 1970 at Loch Leven where one sweep of a 350-ft shore seine caught 5 500 adult perch ranging in size from 18.5 to 30.5 cm (Thorpe unpubl.).

Several authors (e.g. Steinmann 1951, Neresheimer 1951) report perch shoals surrounding prey fishes and then attacking them.

3.5.3 Responses to stimuli

- Environmental stimuli

Mechanical: Although possessing no connexion between the swim bladder and labyrinth via Weberian ossicles, perch were shown by Froloff (1925) to be able to hear the ringing of a bell. Denker (1931), however, failed to elicit any response to a whistle.

(See also under optical stimuli, below.)

Chemical: (a) Smell: Pipping (1926) demonstrated the smell function of nostrils in perch which belongs to his group 4, that is, fishes in which water-flow is maintained over the olfactory epithelium both in and out of the same nostril in conjunction with respiratory currents, and an additional flow in through the anterior and out through the posterior nostril by means of ciliary movement. Wunder (1927) confirmed Pipping's findings that perch could seek food by olfactory means alone in experiments in which complementary senses were occluded.

(b) Taste: Wunder (1927) demonstrated that perch tasted food prior to swallowing it, and would reject foods made bitter with chinin. Receptors on the lips were preliminary and food "accepted" by these might yet be rejected from the mouth.

Thermal: (See section 3.3.2.)

Optical: Under (1925) categorized perch among "bright-light" fishes together with trout (Salmo trutta L) on the basis of the histology of the retina.

Herter (1929) used perch in conditioned reflex experiments to examine form discrimination and found that they could be trained to respond to the "contour-rich" letter R more easily than to the less structured letter L. He also tested (1948) patterns of vertical stripes and horizontal stripes against a uniform white card in choice experiments. The stripe pattern was postulated as part of the schema by which the fish recognized its conspecifics, but the results did not support this hypothesis.

Kettner (1948) established that 5-7 cm perch had a strong preference for yellow when offered a choice of red, yellow, green, blue or violet simultaneously as well as matched grey shades. Herter (1948) suggested that this may have been related to the colour of light in the weed-beds.

Herter (1948) trained 2 individual perch to choose:

(1) a black R on a white ground and reject a white L on black;

(2) the reverse of (1)(i.e. choose white L on black and reject black R on white).

When the signals were changed (i.e. white R on black, black L on white), the fish chose the signal whose intensity corresponded most closely with that to which they were trained. When the original signals had the same intensity values then the fish chose by the form of the symbol in the changed situation. Further, in choices between the original symbol and its inverted, mirror-image or sideways orientation, the fish chose the spatial arrangement of the original symbol. Finally, they were offered a choice between two new symbols:

(1) B and K; P and λ;

(2) L and ; and l.

Fish 1, trained to R, chose the symbol containing the upper curved portion of the letter; fish 2, trained to L, chose the symbol containing the short right-hand horizontal.

The scores for 10 trials with each pair were as follows:

Symbol:	B	K	P	λ
Fish 1:	9	1	10	0

Symbol:	L			l
Fish 2:	10	0	9	1

Perch were also trained to distinguish a positive red disc from negative white or black ones, and vice versa: they continued to choose the trained positive disc when shown an unfamiliarly coloured one, e.g. green.

Individual fish represent more complex visual symbols, but tests of ability of individuals to recognize others were made by Mobius (1875) and by Triplett (1901) who claimed that perch could recognize individual prey fishes. Gimmy (1951) held single predatory perch in aquaria with a single prey fish (guppy) enclosed behind a glass screen or in a glass container floating in the tank. The perch continued to try to snap the prey fish through the glass for 3 weeks: after such attacks had ceased for several days, the guppy was released into the tank with its predator. In 5 cases out of 6, the perch did not attempt to take its known guppy although it did take other small fish including guppies, readily.

Privolnev (1956) found that adult perch from Lake Chudskoe preferred dark areas to light ones (93% in 11 experiments on 3 successive days). Twenty-day fry moved exclusively into light and when given a choice of wavelength chose as follows:

	(%)
Daylight	66
Green light	20
Blue light	8
Red light	6
Darkness	0

Manteifel et al. (1965), using small groups of perch in aquaria in Moscow and at Rybinsk Reservoir, established that activity level was related closely to light intensity and their results are reproduced in Fig. 30. They classified perch as a "twilight-diurnal" animal, showing

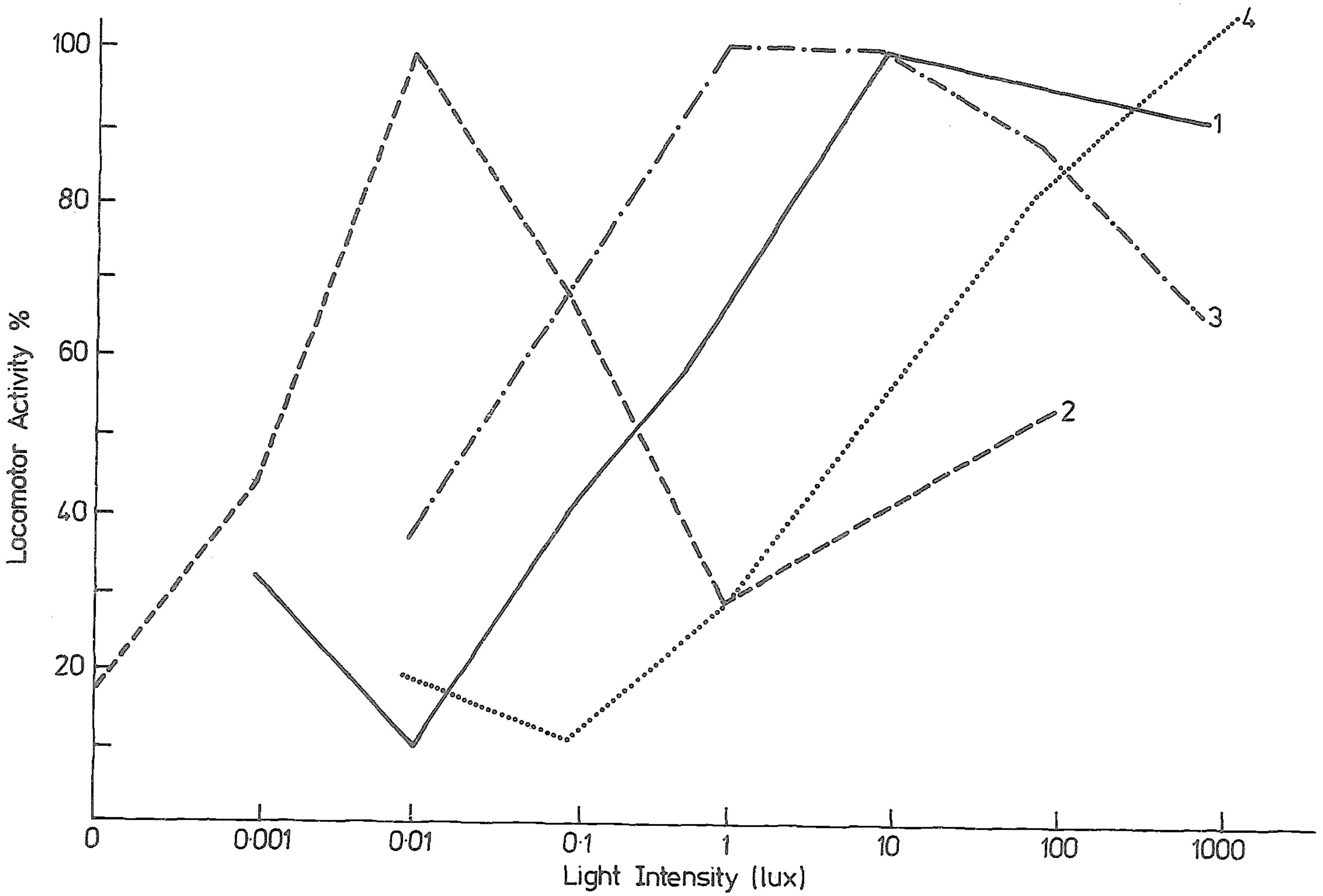


Fig. 30 Locomotor activity and light intensity

Perch at length: 1 - 35-40 cm
2 - 140-160 cm
3 - 150-160 cm
4 - 10-18 cm

(From Manteifel <u>et al.</u> 1965)

maximal locomotor and feeding activity when adult at a range of light intensity of 1-100 lx.

In another experimental study of visual perception, Boulet (1958)used 1, 2 and 3-year-old perch in an annular aquarium about which a spherical object was rotated immediately outside. Responses to the object were, chronologically: ocular movements, fin movements and general body movements. The most important characteristic of the object for releasing a response from the fish was its speed on its particular trajectory. Threshold speeds were about 2 cm per sec, but optimal speeds for reaction were up to 50 cm per sec, above which responses ceased. At lower intermediate speeds, responses were positive; at upper, negative. Horizontal movement was less stimulating than sinusoidal but the most effective was "Daphnia-like" movement. In this, the upward component of sinusoidal movement was followed by a sharp almost vertical descent. Broken horizontal movement was of little interest to the perch. Size of the object had some influence: 2 mm diameter white plastic balls were too small but 4-7 mm ones were stimulating. Twenty millimetre spheres induced flight which took the form of sinking to the bottom of the tank, depressing the fins, sheltering against the rear wall and even attempts to hide. Colour was not very important but blue, green and yellow objects provoked slight negative responses while red provoked a stronger positive reaction. Regular geometric shapes (spheres, cubes and tetrahedra) were not very stimulating, but angularity was, and a regular angular shape excited the perch as much as an artificial fish did. Background patterns of black and white stripes were not apparently important.

Perch were much more active and receptive in groups than as individuals: the larger the group (2-8 fish), the sooner pursuit reactions were elicited after the last meal.

When the test objects were allowed to circulate in the water instead of outside the tank, much more positive attack responses were released. At low to moderate speeds, optimal for purely optic stimulation, little notice was paid to the movement of an artificial fish, but this was attacked violently at 50 cm per sec, the speed at which optic stimulation had waned. The thresholds for visual and tactical stimulation therefore differed. Shock waves from the prey object stimulated a predatory response when that object was travelling too fast to elicit visual responses. Irregular movements which were of little interest optically, elicited more violent positive responses in the water than did smooth uniform or sinusoidal movements.

Chemical stimuli, such as a puree of earthworm introduced into the tank, were more stimulating than visual stimuli, as the moving bob was ignored while the source of the puree was sought.

Boulet thus concluded that the perch was "animal peu visuel".

- Artificial stimuli

Fishing gear components: von Brandt (pers. comm.) found that perch avoided light-coloured gillnets. In comparative fishing tests in north German clearwater lakes and in laboratory tests, Steinberg (1964) found that visibility of gillnets influenced their fishing success much more than softness, diameter of twine, elasticity or breaking strength. He showed that nets made of synthetic monofilaments which are transparent and give little or no contrast with the background are the type that the perch can avoid least. Using Lyon's method of observing the reactions of fish to rotating striped patterns and substituting various net materials for these patterns, he established that perch did not react to polyamide monofilament netting of diameters of ⩽0.20 mm and made only slight eye movements in response to filaments up to 0.35 mm in thickness.

Colour of net material, especially of the framing material, was shown to influence catches. Nets with green framing caught three times as many perch as those with white.

During the spawning season, mature male perch congregate rapidly and readily in cage-traps and are thus easily caught in large quantity. This feature is exploited widely where perch are of commercial interest.

- Electrical stimuli

(No information.)

4 POPULATION

4.1 Structure

4.1.1 Sex ratio

- Sex ratio of population

Data on sex ratio of natural populations of perch are widely divergent between localities. In part, this is likely to be a reflection of sample size and gear selectivity (as for example, traps appear to catch 99% males during the spawning season at Loch Leven, whereas seine-catches during the summer feeding period have shown sex-ratios of approximately 1:1 (Thorpe 1974)) and differential distribution of the sexes as implied from Hartmann's (1974) data on the growth periods and diet of perch in Lake Constance. Alm (1959) recorded sex ratios of c 1:1 under pond conditions in Sweden and these remained approximately constant over a period of nine years. He suggested that in the wild, early deaths of males due to predation, as a consequence

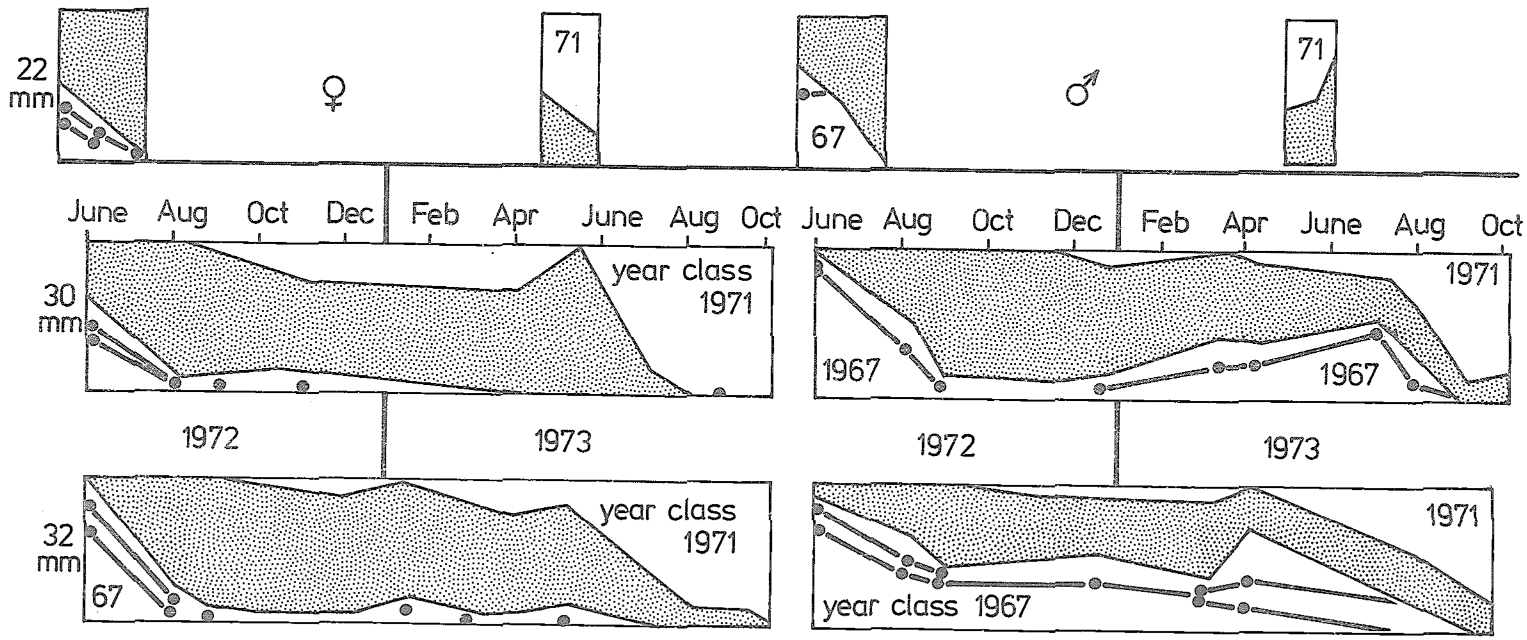


Fig. 31 Seasonal changes in the age-composition of the perch catch in Bodensee (from Hartmann MS. 1974)

top: trapnets, 22 mm mesh size
middle: gillnets, 30 mm mesh size
bottom: gillnets, 32 mm mesh size

The 1970 year-class is shaded.

of their higher activity than females may result in a preponderance of females among the older age-groups. However, such differentially greater activity has not been demonstrated experimentally although Krizenecky and Pulankova (1953) recorded a predominance of females over males appearing at AG III and increasing thereafter. In North America, Beckman (1949) noted the same phenomenon, there being 48% males in a population in Michigan at AG I, decreasing to 23% males at AG X. However, Hartmann (1974) recorded a decrease with age in the proportion of females in the catch of older year-classes in Lake Constance during the course of the year. This anomaly was linked with gear-selectivity and the increasing girth of female perch as they matured.

In populations showing divergent growth-rate groups, the sex ratios appear to differ between these groups: for example, Dryagin (1948) found that males formed only 17% of the populations of fast-growth stocks, but 58% of those of slow-growth stocks.

Konovalova (1958) suggested that in favourable ecological conditions, females flourish better than males and the rate of population increase is higher.

4.1.2 Age composition

(For data on age at maturity and maximum age, see sections 3.1.2 and 3.3.1.)

Perch exhibit strong year-to-year variation in year-class strength so that age-compositions of stocks vary widely in particular localities. Le Cren (1955) recorded such between-year variations up to a factor of 100 times the minimum year-class strength, and Heyerdahl and Smith (1971) found that relative year-class strengths at Red Lakes, Minnesota varied 26-fold over a 19-year period. Jensen (pers. comm.) noted that in many Norwegian lakes with stunted perch stocks, there were intervals of several years between successful year-classes. Consequently, statements about age-composition of perch stocks have little meaning in the absence of environmental data accounting for success or failure of reproduction or recruitment.

Furthermore (see section 3.5.2), shoals of perch have been reported from several localities stratified by age and size, further complicating sampling problems to determine age-composition accurately.

Fig. 31, reproduced from data of Hartmann (1974), shows the changing age structure of catches in standard gillnets during 1972-73.

4.1.3 Size composition

(See also sections 3.1.2, 3.3.1 and 3.4.3.)

- Length composition of populations

Figs. 32-33 illustrate examples of length frequency distributions within perch populations. As with estimation of sex-ratio and age-composition of stocks, such assessments are strongly influenced by gear selectivity and by differential distribution of sexes within populations as well as by the formation of shoals stratified by size and age (see section 3.5.2). The Loch Leven data of Fig. 32 (A-E) were obtained from the virtually nonselective seine nets which exclude only the AG 0 fish, but there are clear differences in the relative strengths of age-groups at different sites. Those from Finnish Lakes (Sumari 1971) (see Fig. 33) were obtained by rotenone poisoning and are also relatively unselected.

- Maximum size

The largest recorded perch was a specimen of c 10 kg (Lake 1959) taken in Australia. Within its natural distributional range, a fish of 1.91 kg was recorded in New Jersey in 1865 (Scott and Crossman 1973), a weight regularly exceeded in some populations of the Eurasian range. Berg (1965) noted that fish of 3.5-4.75 kg were taken exceptionally in the U.S.S.R. up to a length of 51 cm. A perch of 53 cm is recorded by McPhail and Lindsey (1970) from North America, and one of 62 cm and 2.41 kg from Poland (Leopold 1973 pers. comm.).

- Length and weight relationship

(See section 3.4.3.)

Le Cren (1951) discussed the seasonal changes in length-weight relations of Windermere perch, and some of his data are illustrated in Fig. 34. Growth stanzas (sensu Martin 1949) are clear from this figure, and at the adult stage, the maturation cycle affects the relationship seasonally which has been discussed above (section 3.4.3).

4.2 Abundance and density (of population)

4.2.1 Average abundance: estimation of population size

Incomplete understanding of the discreteness of shoals and the degree of interchange of individuals between shoals, or of the extent of movement of individual perch makes the use of indirect methods for the estimation of perch populations an unreliable approach. However, such methods have been used, and recently, Jensen (1974) compared estimates made by multiple mark-recapture experiments during the spawning period with others made later the same year by poisoning the population. His results are reproduced in Table XXIV indicating remarkably close agreement. The similarity of these results is surprising since trap fisheries at spawning tend to catch males

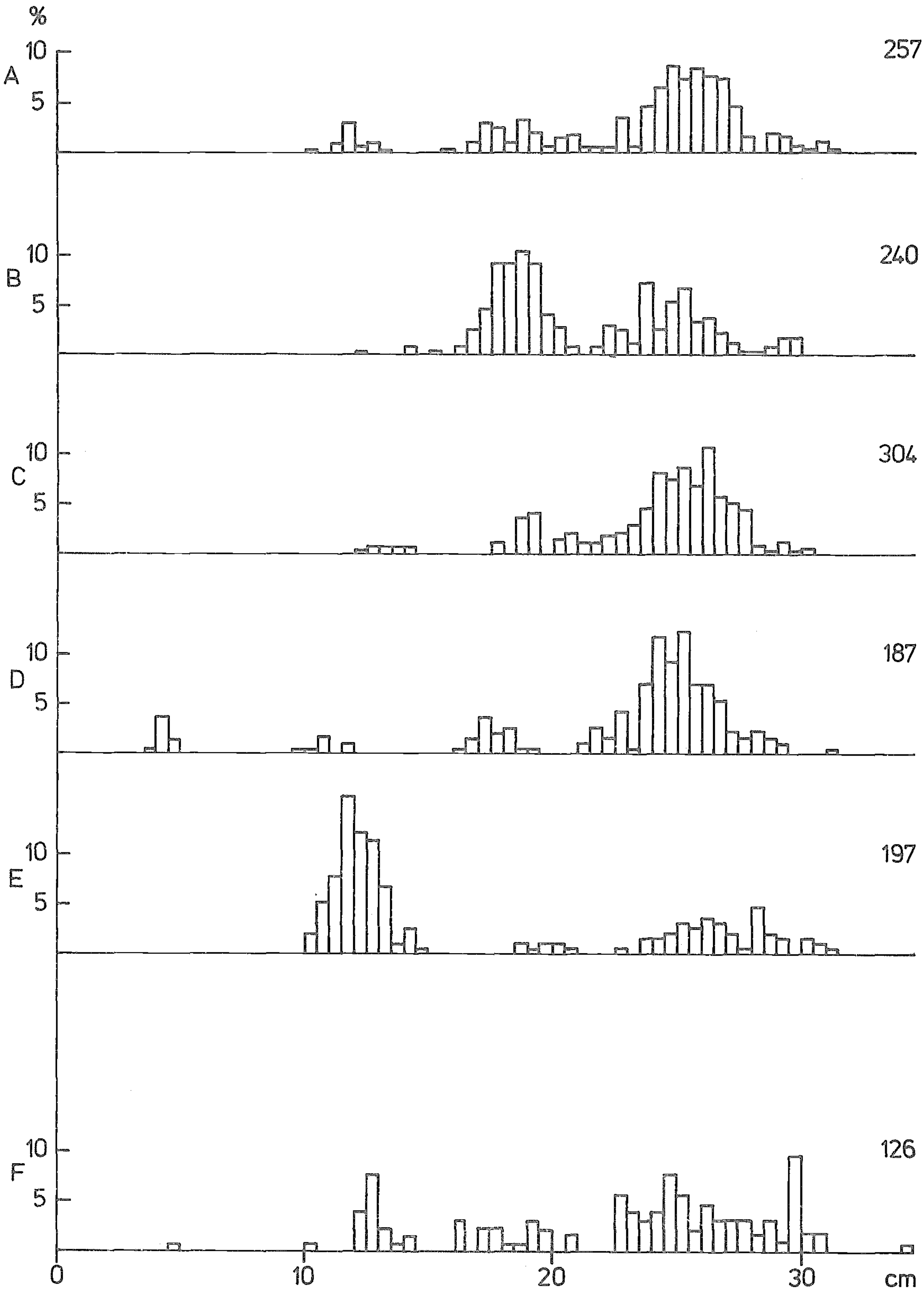


Fig. 32 Length-distribution (%) in net catches, Loch Leven, August 1968
A-D: Seine catch from 4 shore sites
E: Seine catch from shore of St. Serf's Island
F: Trawl catch from open water

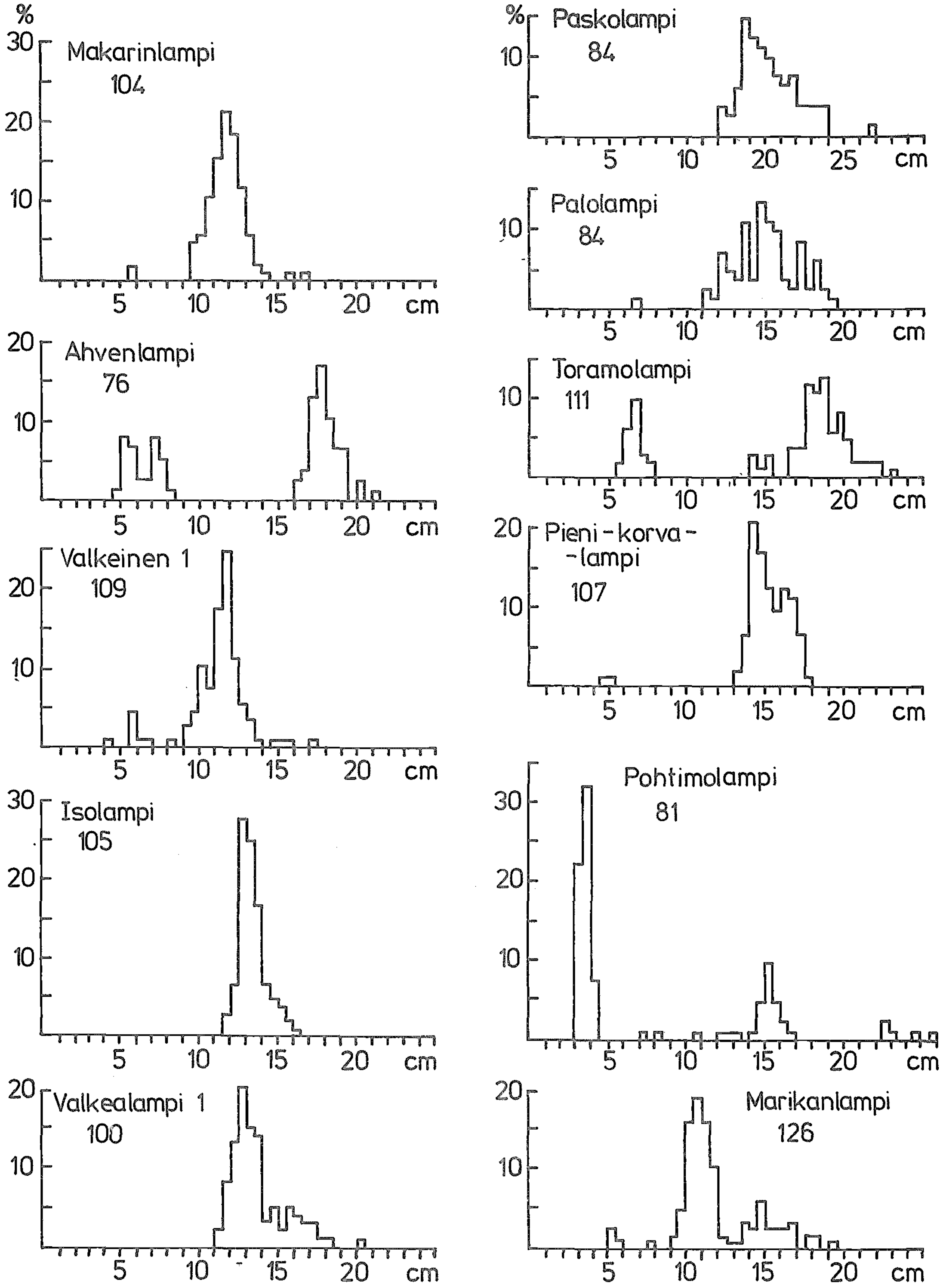


Fig. 33 Length-distribution in samples from poisoned ponds in Finland (from Sumari 1971)

Numbers of 0+ perch are not representative.
Figure below the name of the pond is the number of perch in the sample.

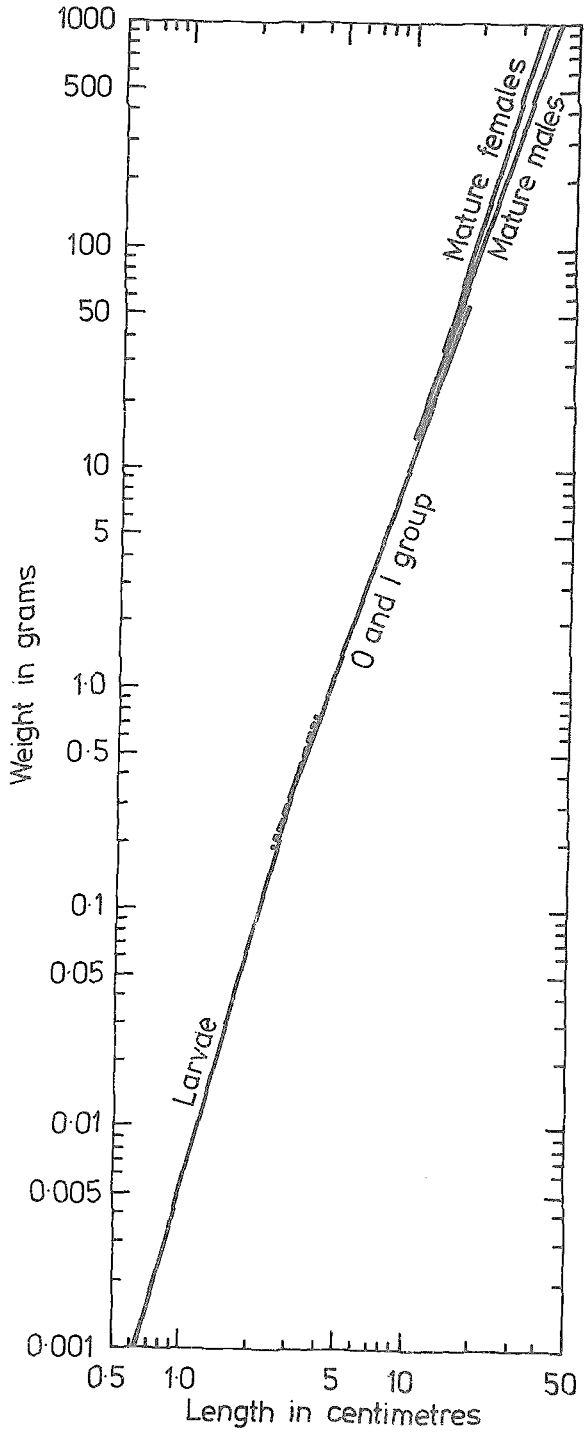


Fig. 34 The length-weight relationships of perch. The regression lines for log weight on log length are given for larvae, O and I group, mature females and mature males
(From Le Cren 1951)

TABLE XXIV

Estimates of a population of spawning perch in Norway
(From Jensen 1975)

Date	Population estimate							
	c	m	r	B	$\hat{N}s$	$\hat{N}s^*$	$\hat{N}p$	95% confidence interval
4.5 1952	29	0	0	0	-	-	-	-
5.5	365	29	2	0	5 293	5 293	-	1 500 - 43 700
6.5	320	197	5	195	14 725	14 890	-	6 300 - 45 400
7.5	70	264	10	445	9 211	9 429	-	5 000 - 19 200
8.5	405	309	19	465	11 434	11 786	-	7 300 - 19 000
9.5	590	460	31	710	15 763	16 300	-	11 400 - 24 100
10.5	170	708	32	1 040	19 032	19 662	-	13 500 - 27 800
11.5	120	757	38	1 150	18 417	18 565	-	13 400 - 26 000
13.5	389	871	48	1 150	21 639	22 465	-	16 300 - 29 300
15.5	203	966	51	1 434	24 211	25 126	-	18 700 - 32 500
17.5	75	1 013	54	1 587	24 273	25 222	-	19 000 - 32 000
15.8	1 303	1 004	97	-	-	-	15 022^{a}	13 861^{a}- 16 492^{a}

c	Number of perch caught on date shown
m	Number of marked perch present on the day shown
r	Accumulated number of marked perch recaptured
B	Accumulated number of perch killed prior to the date shown
$\hat{N}s$	Schnabel estimator
$\hat{N}s^*$	Modified Schnabel estimator (Robson and Regier 1968)
$\hat{N}p$	Petersen estimator
a	Includes 1 662 killed in May

TABLE XXV

Numbers and weight of the perch population of Lake Tyulen
(From Zhakov 1964)

Age	Mean Weight (g)	Numbers		Ichthyomass (kg)	
		Estimated from egg-strands	Actual numbers removed	Estimated	Actual
0+	1.2	540	78	0.6	0.09
1+	11.4	540	264	6.2	3.00
2+	16.9	540	467	9.1	7.9
3+	24.4	540	1 494	13.4	36.7
4+	30.4	540	528	16.4	16.0
5+	47.0	300	194	14.1	9.1
6+	65.0	60	133	3.9	8.65
7+	87.0	15	19	1.3	1.65
8+	140.0	15	4	2.1	0.56
TOTALS		3 090	3 181	67.1	83.65

selectively, and therefore the Schnabel estimator is enumerating the population of mature males. Further, the Schnabel estimator approaches an asymptotic value which represents the maximum population trappable at any given time. In this instance, that value may approximate to the whole male population as this was a stunted stock and therefore probably made up predominantly of one age-group (see section 4.1.2). But the subsequent Petersen estimate, derived from a sample of 1 303 perch recovered after the rotenone treatment of the lake, is slightly lower than the Schnabel value. As the Petersen sample should be approximately random, it would appear that the Schnabel value is an overestimate which may have arisen because of trap-shyness in newly marked fish (Lind et al. (1971) found that some perch of 30 g and over learned to avoid cage-traps).

Thorpe (1974) attempted to estimate the population of mature males in the Loch Leven population by a Petersen-type mark-recapture experiment, marking adult males from traps one spawning season, and taking the recapture ratio from similar traps during the subsequent season. This method is unsatisfactory in that there may be bias in the capture technique although there is evidence of individual rather than shoal behaviour at this time which allows the mixing element necessary for the experiment.

Kozikowska (1966) used effort data to gain minimum estimates of perch stocks in the Mazurian Lakes, Poland, as Petersen mark-recapture experiments proved unreliable due to the extensive interchange of fish between lakes.

Holčik and Pivnička (1974) used "label-models" to test the validity of estimations for perch populations in Czechoslovakia, and they concluded that multiple-sample mark-recapture methods can be used successfully provided that identical sampling methods are used and the age-structure of the samples is determined. Periods of high activity, e.g. spawning seasons, increase the chances of large samples and thus increase accuracy. However, the criticisms applicable to Jensen's results would also apply here.

Estimation of the population of mature females was made in Lake Razdelnii (5 ha) by Zhakov (1964) from counts of egg-strands at spawning. Two thousand three hundred strands were removed at the first collection, and only 58 were found at the second (2.4% of the total). In a second experiment, the second collection accounted for 4.4% of the total. Zhakov concluded that the method gave estimates accurate to within about 3% of the real value. At Lake Zhemchuzhina (68 ha), Zhakov modified this method by counting egg strands over a series of sample areas, and from these calculated a mean number of egg-strands per hectare of spawning ground. The estimate of total stock was then computed using data from sample catches on sex-ratio and age-composition, and gave values of 3 640 adult perch in the age groups 4-9+ for Lake Razdelnii. A minimal estimate of the total population was obtained by assuming that age groups 0-3+ were each numerically equal to age group 4+. The total then became 12 440 perch. The method was checked in a smaller lake, Lake Tyulen (1.8 ha), in which counts of egg-strands had led to estimates as shown in column 3 of Table XXV. Two months later, the lake was poisoned and the stock counted and weighed, giving results shown in columns 2 and 4 of Table XXV. The numerical totals are remarkably close although the age composition of the immature part of the population does not show such close agreement and in consequence, the estimated value of ichthyomass is 20% too low.

With the same qualification as applied to Jensen's (1974) methods, Zhakov's method would appearto give reasonable minimum stock estimates.

Poisoning was also used by Rudenko (1967) to remove all fish from Lake Somino, Estonia, and the total population was calculated using the counts of collections made by seining 12 sample areas of 25 m of shoreline. The stock of perch amounted to 43 353 fish of over 1-year old, but estimation of fry populations was not possible by this method. To achieve this, it was assumed, by analogy with mortality data on pike, that only 5% of 0+ perch would survive to the following year. Thus the population of 0+ fish was assumed to be 20 times the size of that of 1+, in this case giving 626 000 fry. The final total for abundance was then:

	Number	Density/ha
0+	626 000	29 252
1-9+	43 353	2 026
Total	669 353	31 278

Rudenko further calculated the ichthyomass and production of fish in Lake Somino from data on length and weight at age derived from the samples. Observed mean weights allowed calculation of individual weight increments, and calculation of annual mortality permitted the estimation of annual population increase of ichthyomass (=production). On this basis, he arrived at the following quantities:

Total biomass of perch:	835 kg
Annual biomass increment:	664 kg
Production per hectare per year:	31 kg/ha

This value compares reasonably closely with the minimum production figure of 51 kg per ha per year for perch in Loch Leven (Thorpe 1974).

4.2.2 Changes in abundance

As mentioned above, Le Cren (1955) has shown that wide year-to-year fluctuations of year-class strengths are characteristic of perch populations. In those extreme populations observed by Jensen (pers. comm.), the absence of complete year-classes could not be accounted for by cannibalism as no fry were found in the stomachs of the few dominant year-classes. Menshutkin et al. (1968) implied that success of the new broods was dependent on food availability at first feeding (see section 3.2.2). Catastrophic mass-deaths of perch have been recorded from North America (e.g. Bardach 1951) and Europe (e.g. Matthey 1963, Grimaldi 1967) due to epizootics (see section 3.3.5). Population changes due to intensive fishing have been carefully documented for Lake Windermere where an experiment designed to test the inhibitory effect of a large perch population on competitor species was begun in 1941 (Worthington 1949). Each year during the spawning period, mature fish were removed by trapping, and Le Cren (1958) estimated that the stock was reduced by 45% per annum from 1941-1944, and then at a steadily decreasing rate until the population in 1948 had reached about 3% of its original level.

Changes in abundance due to altered hydrographic conditions are seen clearly in the colonization period in new reservoirs. For example, Holčik (1966) found that in the first five years after the closing of the Orava dam, the perch population originating from the Biela and Cierna Orava rivers increased rapidly becoming one of the numerically dominant species, but then declining as roach (Rutilus rutilus L.), bleak (Alburnus alburnus L.) and ruffe (Gymnocephalus cernua L.) took over this dominant position. Similarly in the Kličava Reservoir, Holčik (1970) found that perch with unspecialized spawning requirements was able to dominate rapidly such that two years after the filling of the reservoir, they accounted for 95% by number of all fish present. Their subsequent decline was probably influenced by food competition between the fry and those of roach (R. rutilus L.). Roach fry have a wider food spectrum and are more active than perch fry. Also, as perch become fish-feeders, they tend to concentrate on their own fry, thus limiting their own populations while roach will also eat perch fry. This general sequence of initial domination by perch followed by roach has also been reported for newly built reservoirs by Ivanova (1953), Mikheev and Meisner (1954), and Wajdowicz (1959, 1961, 1964).

Bowman (1974) recorded that the abundance of yellow perch in bottom trawls of Lake Erie had shown a significant decrease over the interval 1962-66, coincident with a dramatic increase in the catch of alewives (Alosa pseudoharengus). In the Great Lakes, Christie (1974) noted an increase in the stocks of perch and attributed this to reduced food competition after the collapse of whitefish stocks in Lake Ontario, blue pike in Lake Erie, and pollution resistance by eggs and fry in Lake Erie. In Sweden, Vallin (1929) recorded a rapid decline in the perch population of Sjön Ymsen after the introduction of pike-perch (Lucioperca lucioperca L.). In 1915, the yield of perch was 1 740 kg (20.8% of the total fish catch), and at that time, pike-perch yield was about 1 420 kg. By 1927, perch yield had fallen to 87 kg (1.3% of catch) and pike-perch yield had risen to 4 680 kg.

4.2.3 Average density

Data on average density from various localities are given in Table XXVI. Sumari (1971) discussed

TABLE XXVI

Average density of various perch populations

Locality	Number of perch/ha	Ichthyomass of perch (kg/ha)	Total ichthyomass/ha	Authority	
Finland: ponds	100–1 000	7–90		Lind *et al.*	1971
Finland: ponds		11.9 (1.8–41.3)	28.7 (5.2–111.7)	Sumari	1971
Michigan: lakes		0–33		Ball	1948
Minnesota: game fish lakes		32		Moyle *et al.*	1948
rough fish lakes		8			
Wisconsin lakes	30–100			Herman *et al.*	1964
Finnish pond	300 (spawners only)	15 (spawners only)		Kukko *et al.*	(1972)
River Vistula		0.013		Backiel	1971
Lake Mikolajskie (1952-1963)		5.04		Kozikowska	1966
Lake Taltowisko		1.76		Kozikowska	1966
Lake Lisunie		0.72		Kozikowska	1966
U.S.S.R.: small lakes, perch only		40–45	40–45	Burmakin	(1960)
U.S.A.: lakes and ponds		7.27		Carlander	(1955)
Swedish ponds	2 500–3 000			Alm	(1946)
Lake Vanajavesi	681	7.5		Wikgren	(1964)
Baltic (Gulf of Finland)	242–480			Sumari	(1963)
Lake Geneva (1933–7)		2.9		Steinmann	(1948)
Lake Geneva (1938–45)		4.3		Steinmann	(1948)

the variation in biomass of perch between ponds in a group of 32 Finnish waters (0.6–64 ha). He noted that age-class variation affected biomass, and therefore biomass must be studied over several years in any one locality if true density data are to be established. For example, in "perch-only" ponds where 0+ fish accounted for more than 50% of the older fish, the biomass was 9.3 kg per ha on average: in ponds with lower proportions of 0+ fish, the average biomass was significantly greater at 16.2 kg per ha. Thus, the total biomass and the number of mature fish is smallest when a new age-class is forming in these ponds with very irregular age-class structure. He found also that biomass of perch is significantly greater in ponds without roach (14.3 kg per ha) than in those with roach (6.5 kg per ha), but did not determine whether this was a result of predation by roach on perch fry or by direct food competition. In one pair of ponds (Koukkulampi I and II), limnologically similar except for the presence of burbot (*Lota lota* L.) in I and its absence in II, there was a biomass difference. In II, perch amounted to 26 kg per ha: in I with 3 kg per ha of burbot, there were only 10 kg per ha of perch present, a reduction assumed to be a direct consequence of predation by burbot.

4.2.4 Changes in density

– Landings per unit fishing effort

It was noted above that perch catches in bottom trawls in Lake Erie declined sharply between 1962–66 (Bowman 1974) coincident with the increase of alewives. With eutrophication, perch have increased in importance in the commercial catch in various previously oligotrophic/mesotrophic salmonid waters especially in Germany, Switzerland and southeast France. For example, Hartmann (1974) (see Fig. 35) has shown an upward trend in the annual catch curve for perch in Lake Constance over the past twenty years, the period of continuing eutrophication.

In Lake Mendota, Hasler and Wisby (1958) recorded catches of 200–400 perch per day on a line with two hooks in the ice-fishery of 1920. At this time, the total stock was probably about 15 million perch: over the period 1920–56, the general decline in number and increase in size of Mendota perch was attributed to the following:

(1) disease outbreaks (see section 3.3.5);

(2) harvesting;

(3) eutrophication (agricultural and domestic pollution.

Steinmann (1948) recorded the introduction of perch into a salmonid lake, Sihlsee, in nineteen forties. From zero yield in 1942, the perch catch rose to 19.5 t by 1945, and trout yield fell from 5 000–6 000 to 1 000–1 500 kg.

– Variations with depth and season

It has already been noted (section 2.3) that there is annual movement from a winter deep-water area to a spawning and summer feeding area in shallower water in lakes. This is reflected also in the pattern of catch curves (see Fig. 36), showing peak catches in spring on the littoral areas, in summer on the sublittoral and in autumn in the pelagial, followed by a general winter decline in catch. This winter decline is related to accessibility to fishing gear as although Heyerdahl and Smith (1972) noted a fishing season from June–November in Lake of the Woods, Minnesota ceasing in November due to freeze-up, Hasler and Wisby (1958) recorded a yield of 1.5 million perch in the line-fishery through the ice of Lake Mendota in 1956.

El Zarka (1959) recorded that 75% of the annual catch of perch in Saginaw Bay, Lake Huron, was made from September–November (Table XXX).

4.3 Natality and recruitment

4.3.1 Reproduction rates

(See also section 3.1.5.)

– Annual egg production rates

For the Loch Leven (1 331 ha) population, Thorpe (1974) calculated egg-production from averages of estimated stocks of females 4 years old and older, and from fecundity-length data giving estimates of approximately 2 million eggs per ha per year. In a 2.4-ha pond in Finland, Kukko *et al.* (1972) calculated an annual egg production of 650 000 per ha.

– Survival rates

Kukko *et al.* (1972) estimated that survival of progeny to 1 year old was 0.001% in a Finnish pond. Lind *et al.* (1971) related survival to density of older perch and found values to 1 year old as 0.0001% when there were 350–500 older perch per ha or 1.1% when that density was only 100 per ha. The relation of survival to predator populations and food supply is discussed in section 3.2.2.

– Forecasting potential yields

Heyerdahl and Smith (1971) found correlations between perch year-class strength and abundance of the harvestable stock 6 and 7 years later (r = 0.615, and 0.768) at Red Lakes, Minnesota. This relationship was based on 19 years data from commercial catches, and being retrospective is not itself readily usable for predictive purposes without an independent estimate of year-class strength among prerecruits.

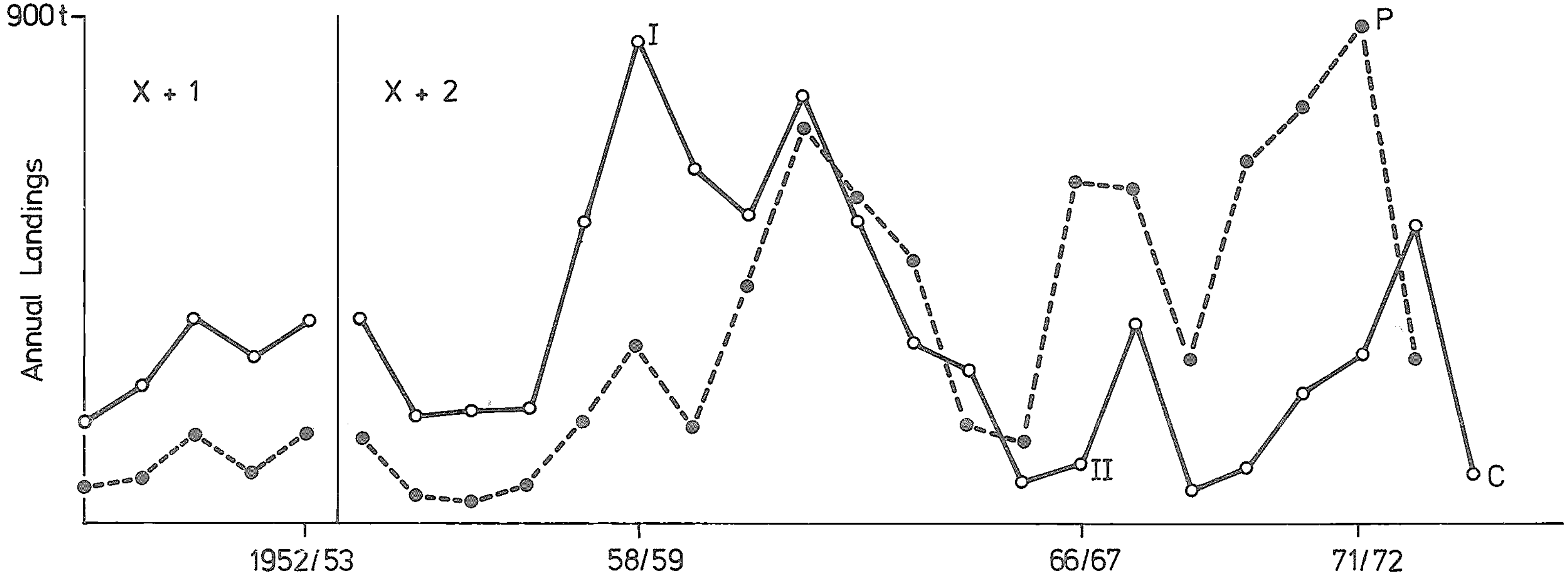


Fig. 35 Changes in importance in the fish catch of Bodensee (Obersee), of *Coregonus lavaretus* (C) and of perch (P). The *Coregonus* curve is displaced 1(x + 1) or 2(x + 2) years to the right for comparison with the undisplaced perch curve.

I: Introduction of synthetic nets

II: Fishing closed for 1 year, and mesh size increased from 40 to 44 mm

(From Hartmann MS. 1974)

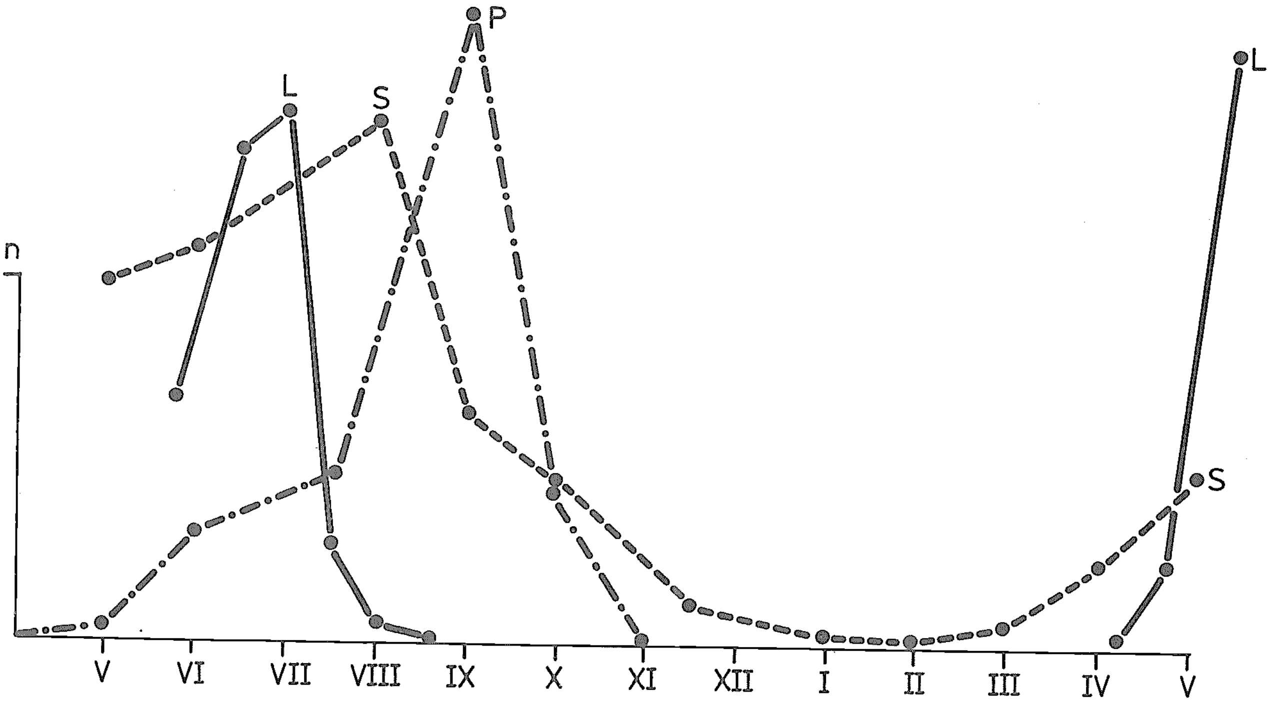


Fig. 36 Seasonal changes in catches of perch in various areas of Bodensee

Scale			
Littoral (L):	5.3	fish/day in 2 trap.nets	1972-73
Sublittoral (S):	100	fish/day in 4 gill-nets	1972-73
Pelagial (P):	20	fish/day in 6 drift-nets	1963-73

(From Hartmann MS. 1974)

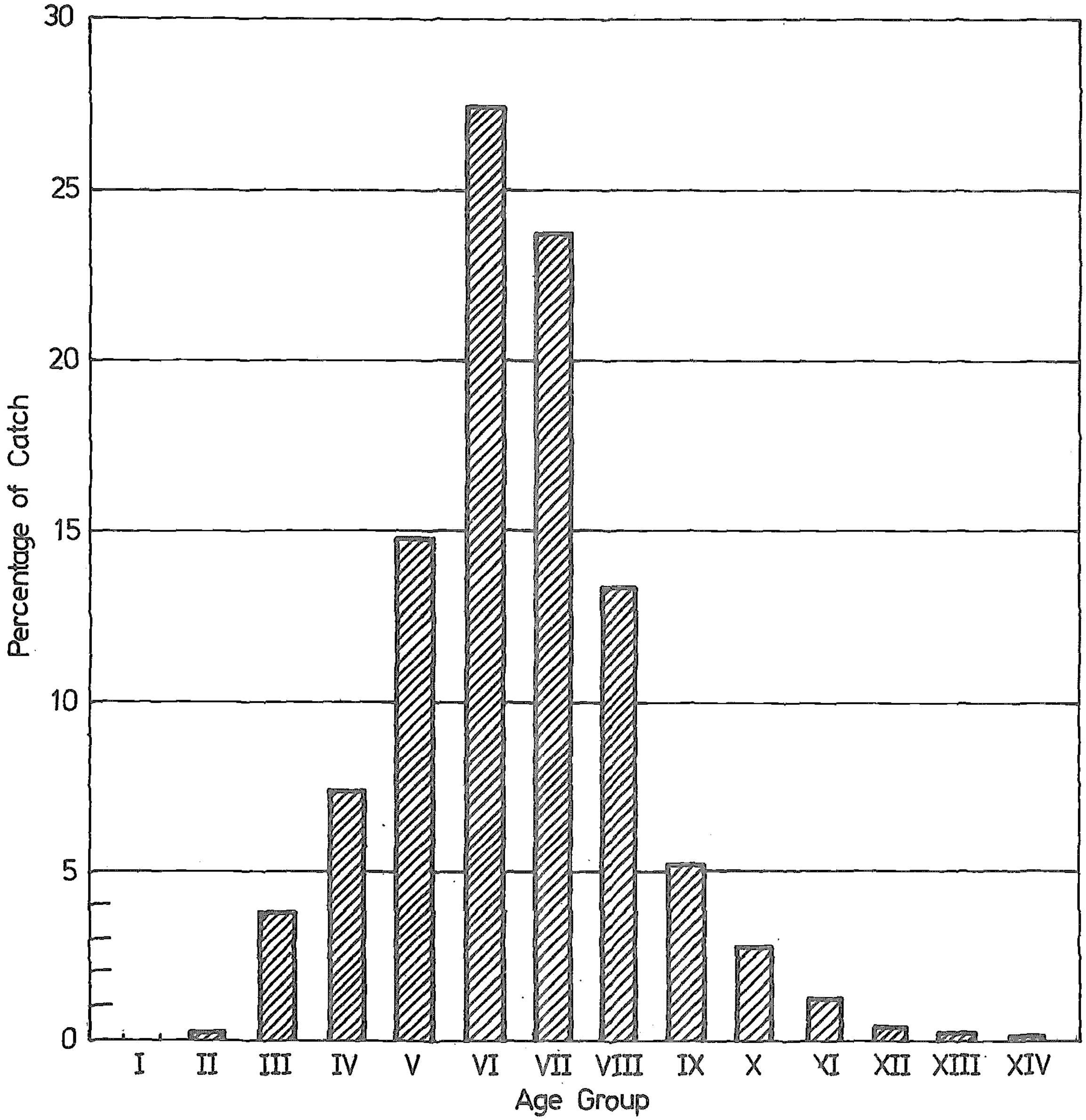


Fig. 37 Average percentage age composition of Red Lakes perch, 1949–64 (From Heyerdahl and Smith 1971)

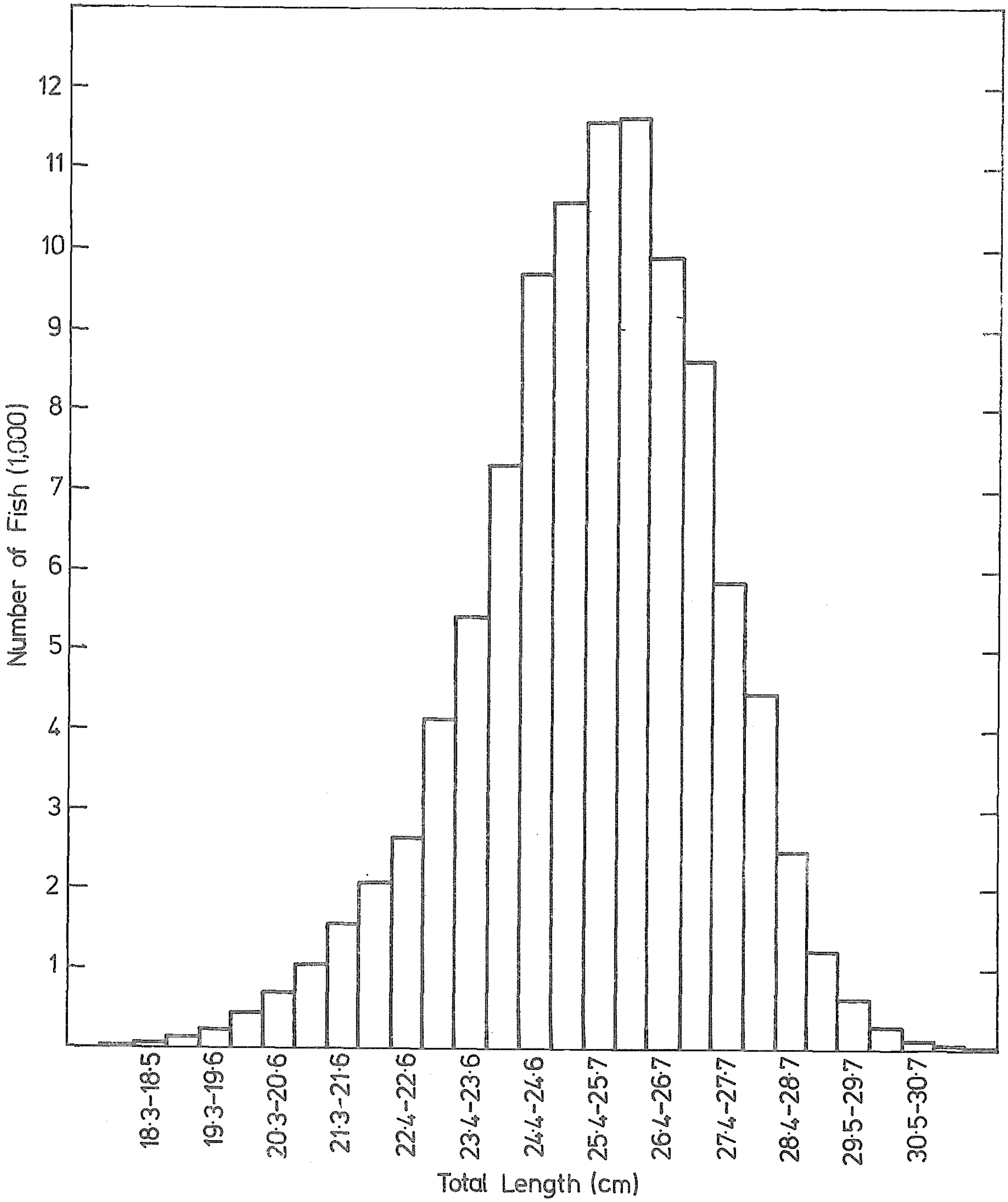


Fig. 38 Number of perch in each 0.5 cm interval per average 100 five-net lifts of commercial gear, summed for the years 1949-57 and 1959-65, Red Lakes, Minnesota (from Heyerdahl and Smith 1971)

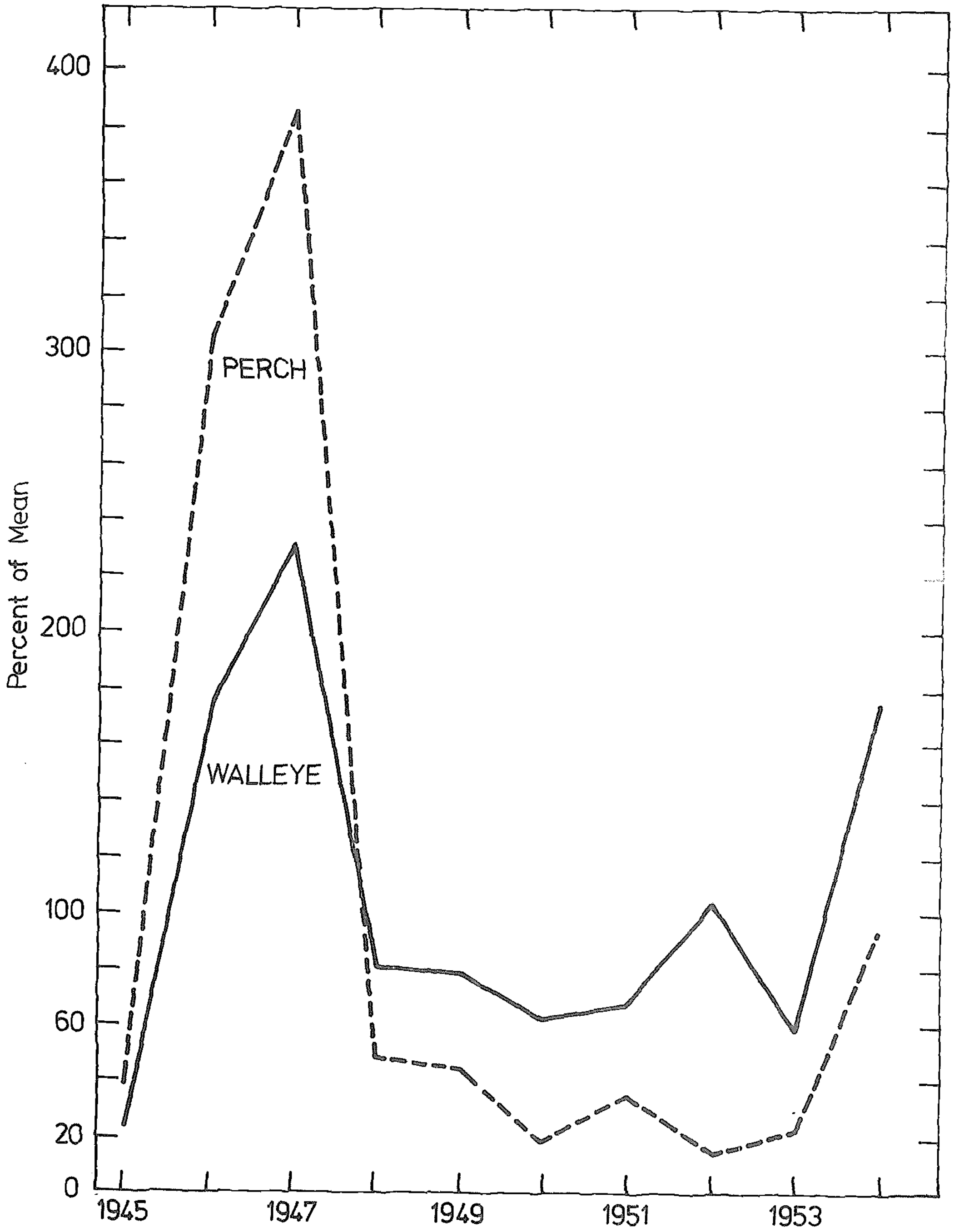


Fig. 39 Relative strength of 1945-54 year classes for walleye and perch in Red Lakes, expressed as a percentage (from Heyerdahl and Smith 1971)

TABLE XXVII

Annual mortality rates of adult perch

Locality	Total mortality (%)	Fishing mortality (%)	Natural mortality (%)	Authority
Red Lakes, Minnesota		45	20–25	Heyerdahl and Smith 1971
Windermere			28–36	Le Cren 1965
Lake Mendota	c 50			Herman *et al.* 1964
Lake Constance	c 45			Hartmann 1974
Lake Manitoba	52–60			Kennedy 1950
Ullswater	♂: 47 ♀: 30			McCormack 1965
Mill Lake	70			Schneider 1971
Cassidy and Jewett Lakes (experimental)			25 in 2nd year 41 thereafter	Schneider 1972
Cassidy Lake	80–96			Schneider 1973

4.3.2 Factors affecting reproduction

– Density dependent factors

Cannibalism, food supply, predation: (See sections 3.2.1 and 3.2.2.)

– Physical factors

(See section 3.1.6.)

4.3.3 Recruitment

Since few countries stipulate size-limits (see section 6.1) for perch and few operate fisheries specifically for this species, age and size at recruitment to the fishable stock depend largely on the characteristics of the fishery in which they are taken as a secondary or incidental catch. For example, in the River Vistula, predatory perch are first recruited to the fishable stock at AG IV in a mixed species fishery (Backiel 1971). However, in the Laurentian Great Lakes, Hile (1953) recorded that perch entered the fishable stock in their fourth year in Lake Erie and Saginaw Bay, Lake Huron, where the size limit was 21.6 cm. In Green Bay, however, with a size limit at 20.3 cm, perch were not recruited until their sixth year so that very many did not live long enough to reach legal size. Reduction of the size limit to 19 cm allowed the fishermen to retain 2½ times as many fish from their catch as before. The problem had also been vitiated by movement of larger perch out of Green Bay. Recently, perch have entered the fishable stock of the Great Lakes as 2–3 year olds (Leach and Nepszy 1975). For Red Lakes, Minnesota, Heyerdahl and Smith (1971) calculated the average percentage age- and size-composition of the commercial catch over 16 years (Figs. 37 and 38). In this particular locality, the seasonal fishery is determined primarily by the availability of walleye Stizostedion vitreum vitreum, and the high modal length (26 cm) of the netted perch is a reflection of mesh-sizes adjusted to the exploitation of walleye. Variation in annual recruitment was considerable since as noted above (section 4.1.2), year-class strengths varied by a factor of 26. Since these variations occurred in parallel with those of walleye (see Fig. 39), the authors held that a common factor governed survival of the fry of both species and they suggested that meteorological conditions controlling the availability of food were the causative agents.

In Lake Constance, Hartmann (1974) found new year-classes entering the fishery at the beginning of the period of intensive feeding in June-July; coming to dominate the fishery for one or more years.

Stock-recruitment relationships: Forney (1971) showed from Oneida Lake data that the variance between year-class strengths increased from a 2-fold range at hatching through pelagic feeding stages to benthic feeding, finally to a 70-fold range by age 1+. Year-class strength was not related to size of spawning stock. Depensatory mortality through predation by walleyes by removing an almost constant quantity of perch fry led to a much higher mortality rate when a year-class was initially low.

4.4 Mortality and morbidity

4.4.1 Mortality rates

Data from various populations are given in Table XXVII. Values of total annual mortality of adults appear to range normally between 45-70 percent. Holčik calculated mortality for each age group of perch in the Kličava Reservoir (Table XXVIII) and noted that males showed a higher mortality rate than females. He suggested that this was due to larger numbers of males, and their higher vulnerability to predators. Schneider (1971) found constant high mortality around 70% for adult perch in Mill Lake, Michigan, which was independent of density (Table XXVIII).

4.4.2 Factors causing or affecting mortality

- Predators

(See section 3.3.4.)

- Food of larvae and postlarvae

(See section 3.2.2.)

- Physical factors

In addition to data quoted in section 3.3.2, Lassleben (1953) recorded mass deaths of fry in late summer and autumn, and considered these to be caused by exceptional meteorological conditions when fry aggregated in upper strongly lighted areas where they may have been exposed to harmful radiation.

Mackenthun et al. (1948) in an experimental evaluation of the effects of decomposition of algal blooms on fish found that perch died 5 days after introduction to water deoxygenated by decomposing Aphanizomenon flos-acquae at 15.5°C.

Meadows (1973) found that perch were killed by 5 percent rotenone at an initial concentration of 0.1 mg/l, the median survival time at 10°C being about 4 h. With Salicylanilide I, a non-persistent candidate piscicide, Marking (1972) found that in the laboratory at 12°C, the LC_{50} values were as follows:

3 h	24 h	96 h
20.0	8.5	5.2 p.p.b.

with 95 percent confidence limits of

16.5-24.2	7.1-10.2	4.3-6.3 p.p.b.

In larger pools deaths of 6.6 cm perch were as follows:

	0-2 h	2-4 h	4-6 h	6-24 h
400 l pool:				
30 p.p.b.	-	-	-	100%
40 p.p.b.	-	10%	70%	100%
500 l pool:				
20 p.p.b.	-	-	10%	100%
60 p.p.b.	30%	90%	100%	-

- Fishing

(See section 4.4.1.)

4.4.3 Factors affecting morbidity

Parasites and diseases: (See section 3.3.5.)

4.5 Dynamics of population (as a whole)

Small lakes containing perch as the only fish species are often encountered particularly at high latitudes. Fluctuations of year-class strength are a prominent characteristic of such populations, and Menshutkin and Zhakov (1964) sought to account for this distinctive pattern of population dynamics largely on the basis of cannibalism. Their conceptual model of the interrelationships of the separate age group of perch in Lake Tyulen is shown in Fig. 40 where the assumptions are made that:

(a) age groups 0-5 are subject to cannibalism from age groups 1-8;

(b) age groups 0 and 4-8 suffer mortality due to starvation;

(c) age groups 6-8 suffer mortality due to old age, disease and other unspecified causes;

(d) female perch spawn every year from age 4 onward

To simplify the mathematical expression and evaluation of this model, environmental parameters were considered constant and the numerical fluctuations in the fish age groups were regarded as a function of their interactions and of their overall limitation by a maximum planktonic food supply. The model was tested in two forms, both using empirical data from the Tyulen population as starting values. In variant I, the maximal ration (R) (sensu Ivlev: that quantity of food which a fish would consume at an unrestricted prey density) was taken as 20 times the average annual increment in weight for each age group over 3+ and slightly less for the younger fish which were assumed to be less completely dependent on cannibalism. In variant II, the maximum ration was increased progressively for each age group to allow for the increasing intensity of cannibalism with age. The electivity of cannibal perch was determined partly from Ivlev's published data (Ivlev 1955) and partly from the author's own experimental data. In this way, the probability of death of any one individual due to cannibalism could be determined on the basis of the numerical strengths of the respective year-classes, and their prey and their electivity values. Similarly, the chances of death due to starvation were calculated on the basis of a planktonic food base capable of sustaining a maximum number of fry. If this fry number was exceeded, all the surplus fry would die with consequent effects on the older age groups dependent upon them. The probability of natural deaths of fish of age groups 6 and 7 was

TABLE XXVIII

Annual mortality rates of perch

a) Kličava Reservoir (Holčik 1969)

Year	Sex	Age Group											
		I	II	III	IV	V	VI	VII	VIII	I-II	I-III	III-VII	IV-VIII
1963	Both	0.64	–	0.25	0.61	0.61	0.81	–		0.55	–	0.46	–
1964		0.64	0.62	–	0.50	0.57	0.78	–		–	0.61	–	0.52
		0.42	–	–	0.32	0.52	0.53	0.94		–	0.10	–	0.43

b) Mill Lake, Michigan (Schneider 1971)

Year Class	Age Group						
	I-II	II-III	III-IV	IV-V	V-VI	VI-VII	VII-VIII
1959						0.850	1.000
1960					0.833	1.000	–
1961				0.762	0.760	0.758	0.759
1962			0.690	0.694	0.691	0.694	–
1963		0.641	0.657	0.646	0.647	–	–
1964		0.837	0.750	0.736	–	–	–
1965	0.910	–	–	–	–	–	–
Mean	0.910	0.739	0.699	0.710	0.733	0.826	0.920

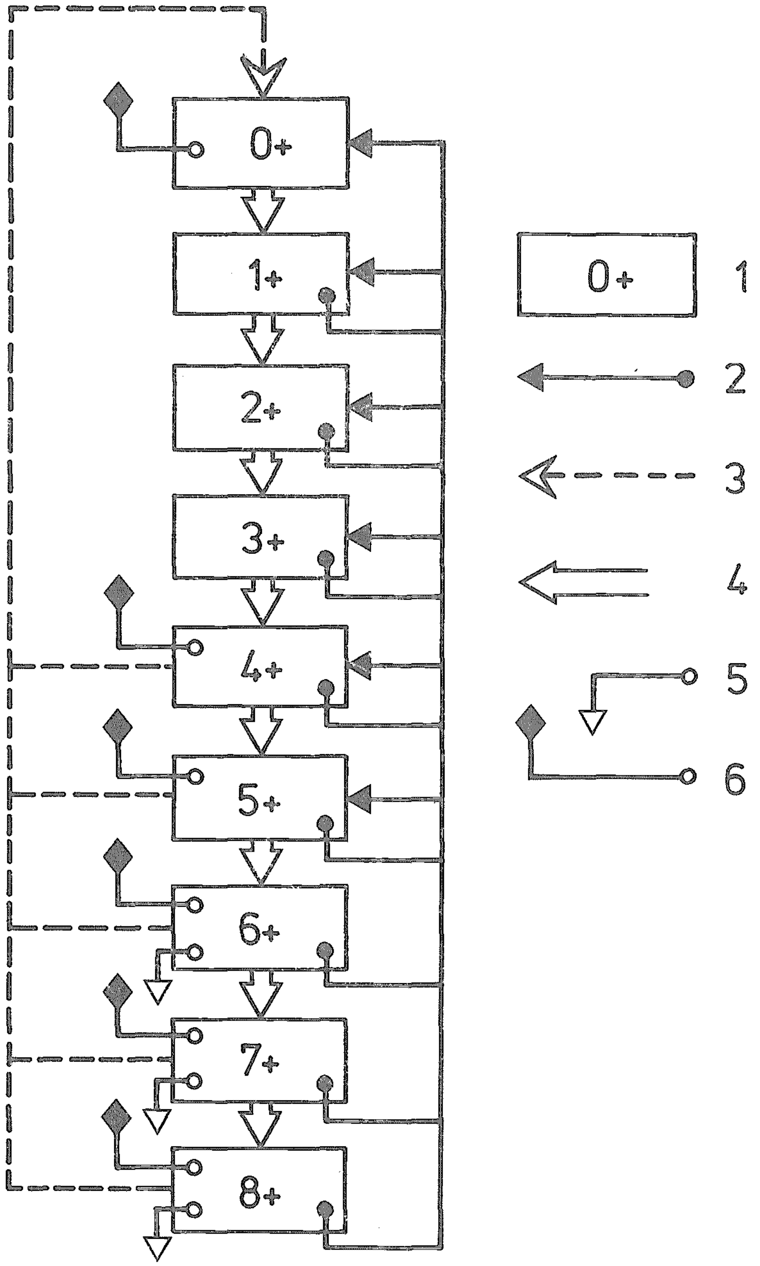


Fig. 40 Population model of perch (after Menshutkin and Zhakov 1964)

1: age groups
2: cannibalism
3: reproduction
4: growth
5: natural mortality from old age, disease and other causes
6: death from starvation

taken as 0.8 and that of age group 8 as 1.0, values which were realistic from Lake Tyulen data. Fecundity values differed between the variants; in I, a constant value of 2 400 eggs per year from age 4 onward was assumed; in II, this value started at 2 000 eggs per year at age 4 and increased by 1 000 eggs per annum thereafter. Sex ratios were taken as 1:1 throughout. From observation of the very high mortality of eggs and fry, it was assumed that only 5% of this egg production would survive to figure as the 0+ generation.

The authors gave examples worked on the basis of a series of equations, the main ones being as follows.

The number of age-class (i), N_i surviving to form age-class (i + 1) the following year was:

$$N_{i+1} = N_i(1 - \mu_i)(1 - \lambda_i)(1 - v_i)$$

where:

μ_i was probability of deaths due to cannibalism

λ_i was probability of deaths due to starvation

v_i was probability of deaths due to other natural causes

The actual number of prey of age group k(ΔN_1) available for predators was thus:

$$\Delta N_k = \mu_k \cdot N_k$$

and the number taken by each particular age group of predators was dependent on the empirically determined electivity value E and their relative density.

The relationship of actual (r) and maximal (R) ration was derived from that of Ivlev (1955) and expressed in the form:

$$r_i = \sum^{k} \mu_k \cdot N_k = \sum^{k} \frac{1}{m_k}\left(1 - e^{-\xi m_k}\right)$$

where: $m_k = \frac{N_k}{\Delta \max N_k} = \frac{1}{R_i k}$

N_k was number of prey of age

$\Delta \max N_k$ was number of these taken at maximum ration

Mortality due to starvation also depended on the relation of actual and maximal ration such that:

$$L_i = \frac{r_i}{R_i}$$

and

$$\lambda_i = 1 - L_i^n$$

(The values for the quantity v_i are the mortality constants 0.85 and 1 assumed above.)

From these relationships, the authors calculated the successive annual numerical states of their model population, and their 2 examples are illustrated. The phenomena of wide year-class fluctuations and dominance by an individual year-class over several years are well reproduced (Figs. 41 and 43), and the system is shown to have long-term stability (Fig. 42). Further, the absolute strengths of year-classes and the proportionate composition of the population by age-classes are reproduced in a realistic form in the model.

4.6 <u>The population in the community and the ecosystem</u>

4.6.1 Physical features of the biotope of the community

In rivers, the perch is found characteristically in the slower flowing parts of the barbel zone (Huet 1954) and in the bream zone. In lakes, it occurs predominantly under mesotrophic conditions but is found plentifully in some oligotrophic salmonid waters, dystrophic woodland lakes (as in Scandinavia, see e.g. Sumari (1971)) and in the full range of bream lakes categorized by Bauch (1963). Within these systems, the perch occupies the area at the open-water edge of weed beds during the summer feeding period and ranges down to the region of the thermocline. In more turbid eutrophic conditions, it appears to be replaced by <u>Lucioperca</u> or <u>Stizostedion</u> spp. Tesch (1955) suggested a developmental series in open waters characterized from coregonids → perch → roach → smelt → pike-perch correspondingly from oligotrophy → mesotrophy → eutrophy.

4.6.2 Species composition of the community

The perch occurs together with a wide range of other freshwater fishes in the Old World and with an equally varied range of cold-warm water fishes in the New. In many European waters, the fate of roach and perch is parallel (Tesch 1955), the yield of each species increasing and decreasing together. However, Sumari (1971) showed that in Finnish lakes without roach, perch yield was higher than in lakes with roach present. Bardach (1951) recorded improved growth of perch in Lake Mendota when <u>Leucichthys</u> <u>artedi</u> decreased in numbers and while he attributed this to reduced competition,

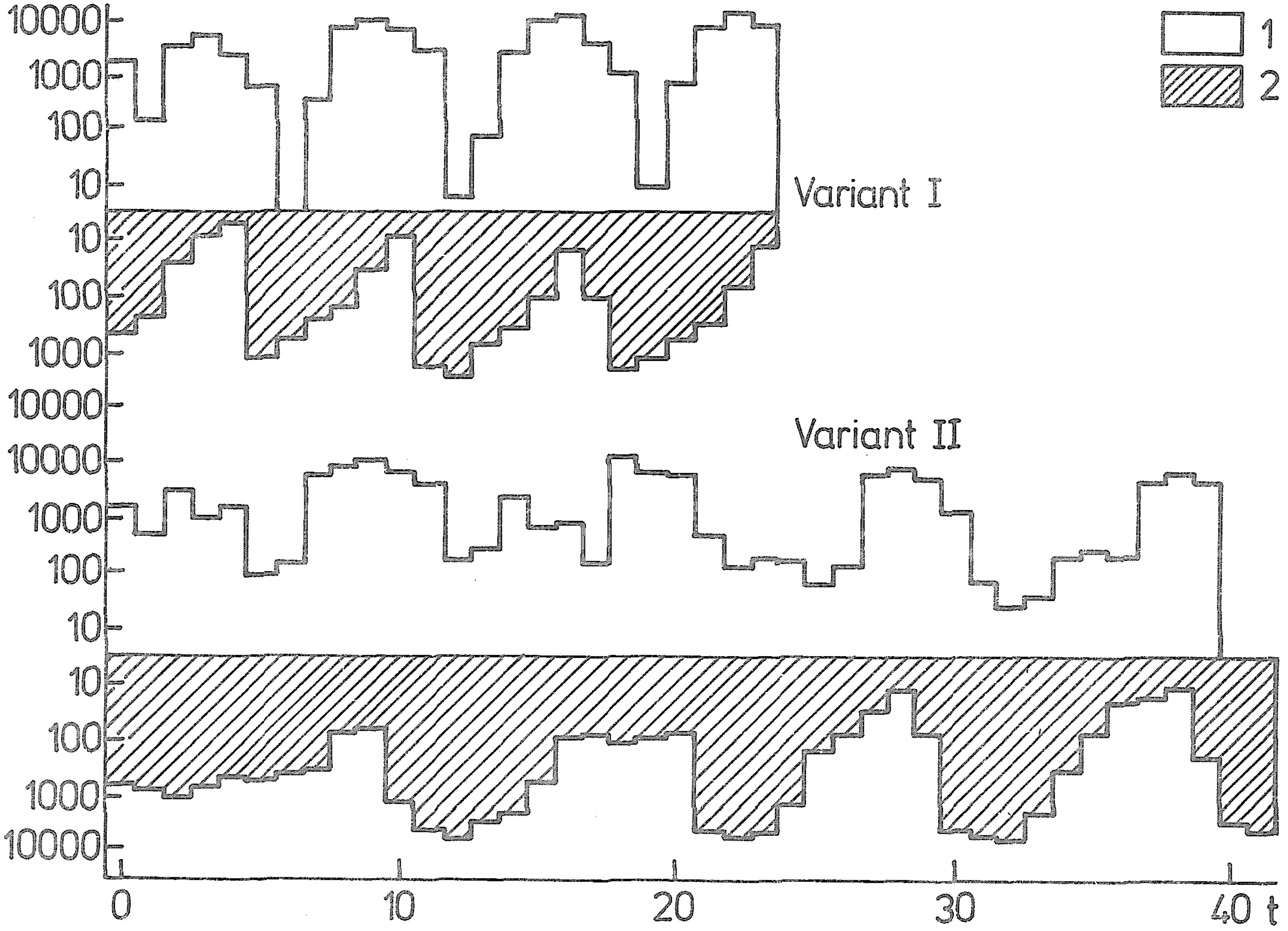


Fig. 41 Numbers of mature and immature perch (excluding fry) predicted from Menshutkin and Zhakov's model

1: Immature stock
2: Mature stock

(After Menshutkin and Zhakov 1964)

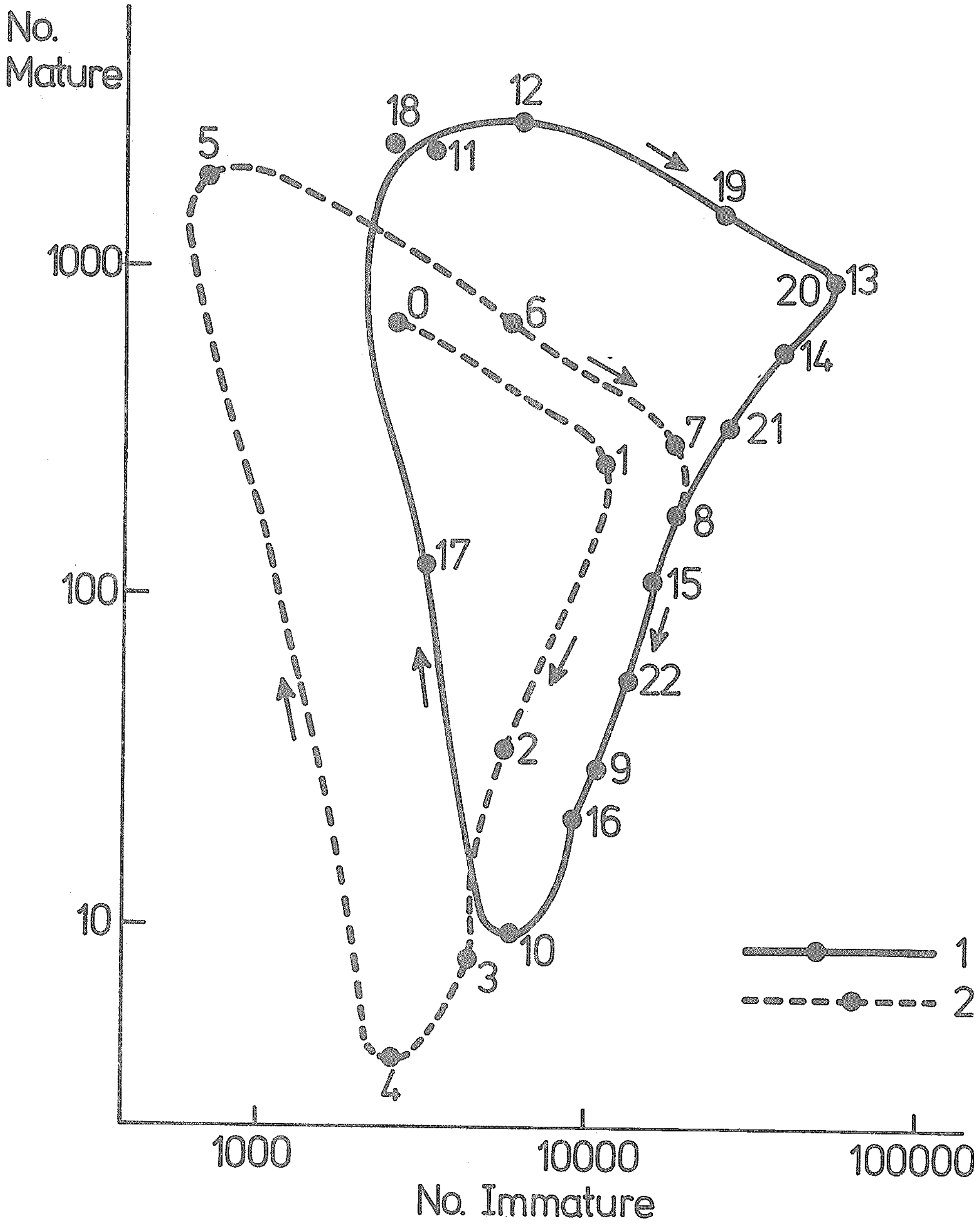


Fig. 42 The successive changes of state of Menshutkin and Zhakov's model population (Variant I)

1: Established cycle
2: Introduction into the cycle

Other numbers refer to the successive annual states of the population (after Menshutkin and Shakov 1964)

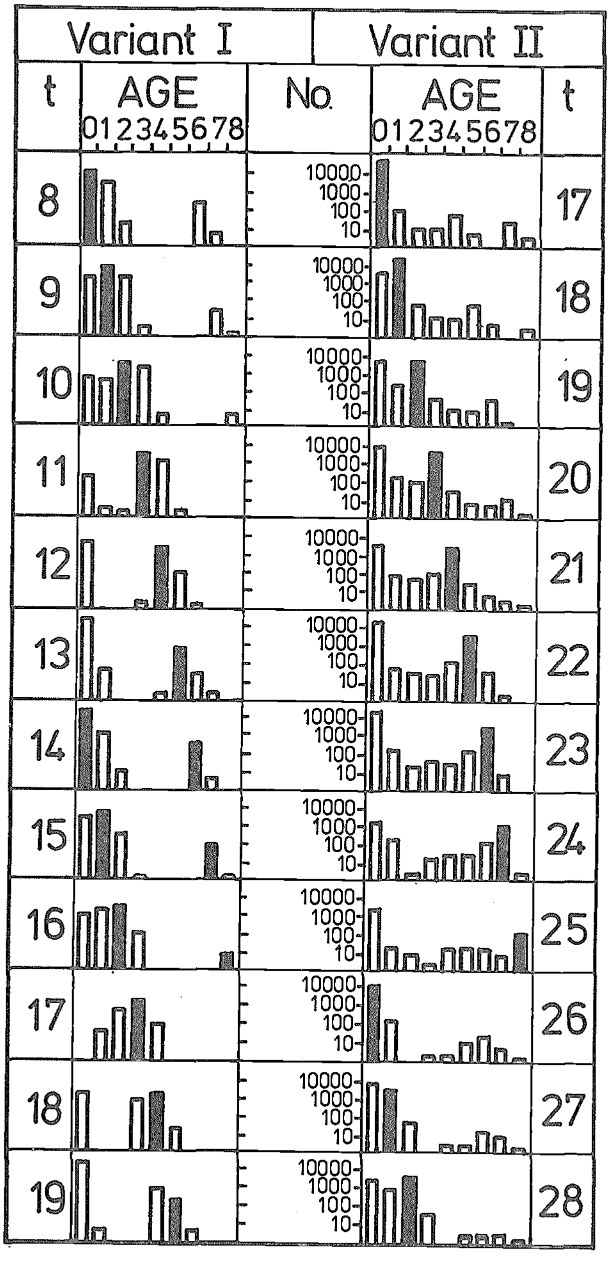


Fig. 43 Age group distribution in both variants of Menshutkin and Shakov's population model. Solid columns indicate the dominant year-classes: t is in years (from Menshutkin and Shakov 1964)

Tesch (1955) implied that reduced predation by Leucichthys was the cause. It has been noted above (section 4.2.1) that perch colonize new reservoirs rapidly and may become the numerically dominant fish for a few years before declining again. In Rybinsk Reservoir, Vasilev (1955) recorded that perch formed a constant proportion of 11-12 percent by number of the total fish catch during the first 12 years life of this water body, but that with time these fish became smaller (19.3 percent of catch of trash fish after 11-12 years).

4.6.3 Interrelations within the community

Zakharova (1955) considered perch undesirable as a competitor with more valuable commercial species and a consumer of eggs and fry of bream (Abramis brama), pike and roach. Nümann (1939) believed perch had an adverse effect on stocks of Coregonus lavaretus in Lake Constance, but Hartmann (1974) showed that numerical fluctuations of the two species paralleled one another with a two-year displacement, but the controlling factor was not identified.

A more positive functional role is identified by several workers. Herman et al. (1964) regarded perch as an important intermediate link in the food chain, being a converter of small invertebrates to fish flesh, themselves being eaten by walleye, pike, muskellunge (Esox masquinongy) and lake trout (Salvelinus namaycush). Thorpe (1974, In press a) calculated that perch fry made up 30 percent of the food of adult trout (Salmo trutta) between June and September in Loch Leven and 13 percent of food of adult perch in the same interval. These fry were thus acting as converters of zooplankton into a form usable by fish predators. Forney (1974) found that the abundance of perch fry governed the intensity of predation by walleye on other forage fish and thus indirectly controlled the size of the walleye population by regulating cannibalism.

5 EXPLOITATION

5.1 Fishing equipment

The types of gear used in perch fisheries are listed by countries in Table XXIX. Besides standard methods of gill-netting, seining, trawling, fyke-netting, trammel-netting and angling, perch are also taken regularly in cage traps particularly at the spawning season when the males enter them very readily and by drop-lines through the ice in winter. The ice-fishery of Lake Mendota yielded more than 50 kg per ha in 1956 (Herman et al. 1964).

The Jazgarnik of Poland is a 60-m long dragnet used for removal of ruffe (Gymnocephalus cernua L.) and perch, and consists of wings of 15 m length and 5 m depths, and a 30-m bag. The mesh size varies from 12 mm in the bag to 18 mm in the wings (Leopold pers. comm.).

The Naseki of Lake Dojran, Macedonia, are described by Apostolski (1958). In this lake, the perch aggregate in littoral reedy areas in winter. The fishermen throw into the water small bushes (Quercus coccifera L.) which serve to concentrate these shoals and then enclose these areas with a wall of reeds. The fish are then crowded into a progressively smaller area by building further walls of reeds within the enclosure until they are finally netted out of a small area (the Kolidor). A hundred and fifty metric tons of perch are harvested annually from the lake by this means.

5.2 Fishing areas

(See Table XXIX.)

5.2.1 General geographic distribution

(See section 2.1.)

Perch are variously prized, from very important food fish in the Laurentian Great Lakes and Finland, to fish of secondary importance (much of Europe and U.S.S.R.), to trash fish in areas given over primarily to sport fishing. Consequently, they are exploited unevenly over their entire geographical range, but are most prized in areas relatively remote from access to fresh supplies of marine fish. Müller (1961) refers to them as Konsumfische (together with roach and bleak, Alburnus alburnus L.) as opposed to Feinfische (Coregonids, eels, carp, tench (Tinca tinca L.) and pike).

5.2.2 Geographic ranges

(See section 2.1.)

5.2.3 Depth ranges

(See section 2.3.)

5.3 Fishing seasons

(See Tables XXIX-XXX.)

5.3.1 General pattern of seasons

Perch are fished for throughout the year over the greater part of their range, but in France, Belgium, Holland, Italy and parts of Czechoslovakia, Denmark and Bulgaria, closed seasons protect the fish during the spawning period (see section 6.1.2).

5.3.2 Dates of beginning, peak and end of seasons

(See Table XXIX.)

TABLE XXIX

Perch fisheries

Country	Exploitation	Gear	Areas	Seasons	Utilization	Authority
Australia	Sport, commerical (very little)	Rod and line	Lakes and reservoirs	All year round	"Bread and butter" species for 26% of anglers	Tilzey (pers. comm.)
Austria			(In Lake Constance only)	All year	Consumption	Hemsen (pers. comm.)
Belgium	Sport	Rod and line	Rivers: barbel and bream zone; ponds of central and lower Belgium	June–January	Recreation	Huet (pers. comm.)
Bulgaria	Sport, commercial	Rod and line, net	Rivers and dams of Danube, Maritza, and Tundja catchments, and rivers Ropotamo and Veleka	1 June–14 April	Recreation, consumption	Chervenkov (pers. comm.)
Canada	Commercial, sport	Trawls, gillnets, poundnets, angling	Great Lakes, commercially; smaller lakes for sport	Recreationally: all year, commercially	Food fish, fish meal, export	Scott and Crossman, 1973, FAO (1974)
Czechoslovakia	Commercial, sport	Trapnets, angling	In all waters of Bohemia and Slovakia to 800 m above sea level	Danube, Labe, and Vltava Rivers, all year. Elsewhere mostly 15 June–autumn	Consumption, recreation	Vostradovsky (pers. comm.)
Denmark	Commercial, sport	Fyke nets, pound nets, gillnets, seines, drifting hook lines; angling	Lakes and estuaries, with eel, pike, and pike-perch fisheries	Recreation, all year especially winter, through ice; commercial, April–November	Consumption, recreation	Dahl (pers. comm.)
Finland	Commercial	Gillnets, fyke nets, steel net weirs, rod and line, lines through ice	All inland waters, and coast of Baltic	All year, but expecially at spawning	Consumption	Sumari (pers. comm.)
France	Sport, commercial	Rod and line, gillnets	Cyprinid rivers, ponds and lakes; commercially in Lac Léman	Autumn–early spring	Recreation, consumption	Tuffery (pers. comm.)
Germany	Commercial, sport	Seines, gillnets, trap nets, electrofishing, angling	Commercially in most large lakes, lower reaches of large rivers, and along Baltic coast. Angling: nearly all types of inland and coastal waters except small rivers	Whole year angling	Consumption, recreation	Tesch (pers. comm.)

Country	Exploitation	Gear	Areas	Seasons	Utilization	Authority
Hungary				Spring-autumn		Donaszy (pers.comm.)
Ireland	Sport	Rod and line, gillnets, cage traps, seines	Everywhere except western side of the country	All year in gillnets; main fishery at spawning time in April-May; June-Oct. in seines	Sport: removal as management measure in trout waters	Fitzmaurice (pers. comm.)
Netherlands	Commercial, sport	Trammel nets, rod and line	Everywhere for sport; commercial chiefly in IJsselmeer	July/Aug.-16 Mar.	Sport, consumption	Willemsen (pers. comm.)
Poland	Sport, commercial	Rod and line, seines, gillnets, fykes, "Jazgarnik"	Everywhere	Maximum catches July-Sept. Season, 1 June-15 April	Consumption, sport. Also removal as management measure	Backiel (pers. comm.) Leopold (pers. comm.)
Romania	Sport, commercial	Pound nets, trawls, rod and line	Ponds in Danube Delta; Lake Razelm	All year	Consumption, recreation	Miron (pers. comm.)
Sweden	Sport, commercial	Fykes, trap nets, pound nets, gillnets, rod and line	Commercially, along Baltic coast	Chiefly April-June, plus perch in Sept., May-October	Consumption, recreation	Alm (1957)
Switzerland	Sport, commercial	Nets, rod and line	Lakes, 300-650 m above sea level	All year	Sport and consumption	Müller (pers. comm.)
Tasmania	Sport only	Rod and line	Lakes, such as Lake Leake, Zee Lagoon, Lagoon of Islands	1 August-30 April	Recreation	Lynch (pers. comm.)
U.K.	Sport only	Rod and line	ngland and Wales: lakes, rivers, canals	England and Wales 14 March-16 June	Recreation	
U.S.A.	Commercial, sport	Seines, pound nets, gillnets, trapnets, fyke nets, rod and line, droplines	Great Lakes chiefly: Lakes in northeast and upper Mississippi valley		Consumption, fish meal, recreation	
U.S.S.R	Commercial			R.Ob throughout year		Berg, 1965 Dryagin, 1948
Yugoslavia	Commercial	Gillnets, seine "Naseka", traps	Macedonia: Lake Dojran; Serbia: inundation area of Danube and Seva rivers, province of Banat and Srem; Croatia: no details	Winter and summer; spring and summer	Consumption	Apostolski (pers. comm. and 1958)

TABLE XXX

Seasonal distribution of perch catches
(Percent of total annual catch)

Area	Month												Authority
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Lake Dojran: < 12 cm	10.5	20.6	14.8	0.2	14.2	28.1	2.3	2.6	4.4	2.0	0.0	0.3	Apostolski (pers. comm.)
Lake Dojran: 12-20 cm	1.1	1.4	1.3	0.9	0.3	0.0	22.8	11.2	12.6	37.6	17.6	5.0	
Lake Dojran: > 20 cm	28.9	44.5	24.0	1.8	0.4	0.0	0.0	0.0	0.0	0.0	0.3	0.0	
Total	14.2	22.4	12.8	1.2	2.4	4.0	10.2	5.3	6.1	16.6	7.7	2.2	
Saginaw Bay, Lake Huron	3.2	1.5	3.3	5.6	0.7	2.8	2.1	2.7	13.1	42.9	19.0	3.1	El-Zarka (1959)
Polish Lakes:													
Commercial		17.2			26.0			39.2			17.6		Leopold (pers. comm.)
Recreational		2.9			34.8			49.9			12.4		

5.3.3 Variation in date or duration of season

Fluctuations in the sizes of the catch have been minimized to some extent by price-support measures taken by the Canadian Government to maintain the price of perch to the fishermen at about U.S.$ 0.1 per lb when sold to the processing plants for filletting and freezing (Anon. 1966-70).

5.4 Fishing operations and results

5.4.1 Effort and intensity

Besides the data for catches of perch with various gears in Polish lakes (Table XXXI: Leopold pers. comm.), Mackenthun and Herman (1949) quoted an average daily catch of 10 perch per man-day of angling through the ice on Lake Mendota with hardly any variation through the winters of 1947-49. Bardach (1951), comparing catches by gillnet in the same lake between 1916 and 1947, calculated catches as shown in Table XXXII.

In Ontario's Lake Erie, commercial fishery perch are now the mainstay, accounting for 60-70 percent of the total landings (Lambert 1975). Total fish landed in 1972 amounted to 16 700 t of which 3.6 percent was sold live, 18.2 percent freshly packed and 78.2 percent processed. The landed value of the fish harvest was U.S.$ 5.4 million, representing a value added (the activity's contribution to the local economy) of U.S.$ 3.2 million. This primary activity involved 601 people or 378 man-years of employment, and generated work for 599 more (516 man-years) in the packing and processing industry, and 15 (12 man-years) in transportation. This secondary stage accounted for a further U.S.$ 7.2 million in value added from packing and processing, and U.S.$ 79 000 from transportation. Thus, the total value added was U.S.$ 10.5 from 906 man-years of employment for 1 215 individuals.

Rudenko (1969) pointed out that the size of fish yield depended on the age-composition of the population as well as on its trophic level, the species composition of the water-body and the total ichthyomass. The fish crop is higher and the ichthyomass lower in lakes where young fish predominate so that in perch lakes, the yield must change yearly in accordance with the irregular changes in age-composition of the stock.

5.4.2 Selectivity

Selective properties of gear: Table XXXIII shows the changes in distribution of perch catches by size and month in a single Polish lake when the mesh of roach-perch gillnets was changed from 30-40 mm to 40-50 mm. Such changes also reflect activity and feeding changes by season, and the specific selective properties of nets in any one locality will depend heavily on the feeding opportunities and condition of the fish.

Selectivity of cage-traps during the spawning season was investigated by Thorpe (unpubl.) and some data are given in Table XXXIV. The traps used were as described by Worthington (1942) and were covered with 2 mesh sizes of wire, 2.5 cm or 0.8 cm; had 2 entrance sizes, 7.5 cm or 12.5 cm diameter; and were either 75 cm or 150 cm in length. No differences in size ranges of perch occurred between the catches in traps of differing mesh-size; no differences in quantity of perch were caught by traps of differing lengths; but, the size of entrance hole began to be selective among perch above a length of 25 cm.

Worthington (1942) noted that perch avoided unpainted wire traps, but entered rusty ones. Von Brandt (pers. comm.) found that perch avoided light-coloured gillnets: Scidmore and Sheftel (1958) found that nylon gillnets were no more efficient than linen ones in catching perch, but Högman (1973) found nylon nets 1.2-1.33 times as efficient as cotton ones.

5.4.3 Catches

Total annual yields: The average annual yields in so far as records are available, are given in Table XXXV. Data taken from the FAO Yearbook of Fisheries Statistics for 1973 show that perch formed an approximately constant 7.3 percent by weight of the total catch of freshwater fish in Europe and North America (statistical areas 02, 05 and 27) from 1965-70 but decreased sharply thereafter to a new level at only 3.9 percent (Table XXXVI). The reduction was most noticeable in inland waters of Europe where the yield fell to 15 percent of its previous level. The cause of this decline is unknown, but reports of widespread (unidentified) disease among perch in British waters were current during 1970 (section 3.3.5), which, if general over the entire geographic range could have led to decreased yields over the subsequent years.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.1.1 Limitation or reduction of total catch

The only recorded limitation on catches of perch is that of a bag-limit of 2 kg imposed on anglers in Bulgaria (Chervenkov pers. comm.).

6.1.2 Protection of portions of population

Tesch (1955) noted that there was no good reason to protect perch by minimum catch sizes except perhaps in such stocks as those of the Baltic coast where the fish reach edible size ($>$20 cm) before maturing. Lassleben (1953)

TABLE XXXI

Perch fishing with various gears in Polish Lakes
(Data from Leopold pers. comm.)

Gear	Fishing Season	Size Class of lakes (ha)	Perch as % of total catch	Average catch per day (kg)	Intensity of Exploitation	Number of lakes
Winter seine with bag	January-April	up to 100	14.53	35.66	Very high	108
		100-500	7.75	25.10		
		over 500	11.69	58.53		
		total	11.17	43.70		
Summer seine with bag	July-December	up to 80	8.01	12.62	High	206
		80-500	10.09	17.95		
		over 500	12.31	31.06		
		total	11.01	22.81		
Perch-roach gillnets	April-December	All lakes	12.90	0.44	Average	21
Fyke nets	March-October and December	All lakes	5.86	0.09	Low	105
Jagarnik			50-100	up to 200	Very low	46

TABLE XXXII

Perch catches in gillnets in Lake Mendota (fish/100' of net/h)
(From Bardach 1951)

Season	1916	1947
Spawning Season (Nets inshore at 4-10 m depth)	15.5	3.6
Summer (Nets at 6-9 m depth)	33.5	14.2

TABLE XXXIII

Structure of perch catches by roach-perch type of gillnets as depending on mesh-size (in one lake)
(From Leopold pers. comm.)

Period	Mesh-size (mm)	Units	Months								Year	% of catch in weight		
			IV	V	VI	VII	VIII	IX	X	XI		above 0.5 kg	0.2-0.5 kg	below 0.2 kg
1958-62	30-40	kg	0.34	0.19	0.55	0.50	0.95	1.39	0.55	0.04	0.63	19.09	51.49	29.42
		%	6.58	4.40	22.98	21.35	51.27	52.56	31.08	5.22	21.69			
1963-67	40-50	kg	0.17	0.19	0.21	0.64	0.84	1.06	0.33	0.06	0.54	13.97	77.37	8.66
		%	7.58	9.40	15.93	41.54	49.48	62.81	33.20	7.03	31.92			

TABLE XXXIV

Relative catches of spawning perch in Loch Leven in paired cage-traps with entrance diameters 7.5 and 12.5 cm (data from Thorpe, unpublished)

Fish length (TL cm)	Trap entrance diameter (cm)	
	7.5	12.5
20.5	69.0	31.0
21.0	51.4	48.6
21.5	61.0	39.0
22.0	50.8	49.2
22.5	46.5	53.5
23.0	53.3	46.7
23.5	53.8	46.2
24.0	54.2	45.8
24.5	44.3	55.7
25.0	53.9	46.1
25.5	40.5	59.5
26.0	51.2	48.8
26.5	54.3	45.7
27.0	47.1	52.9
27.5	41.0	59.0
28.0	34.0	66.0
28.5	21.4	78.6
29.0	31.0	69.0
29.5	29.3	70.7
30.0	25.0	75.0

TABLE XXXV

Perch catches

Country	Estimated annual catch (mean) (MT)				Authority
Austria	Lake Constance only			100.8	Hemsen (pers. comm.)
Belgium				19.2	Huet (pers. comm.)
Canada	1965–73			9 820.0	FAO (1974)
Denmark	1963–72:	Inland waters	21.5		
		Brackish waters	36.5		
		Total		58.0	Dahl (pers. comm.)
Finland	1965–73:	Inland waters	2 756		
		Baltic	1 811		
		Total		4 567.0	FAO (1974)
Germany, F.R.	Lake Constance only				
	1967–73			263.0	Tesch (pers. comm.)
German D.R.	1965–73:	Inland waters	156		
		Baltic	544		
		Total		700.0	FAO (1974)
Hungary				1.0	Donaszy (pers. comm.)
Ireland	1965–72:	Adult fish	33.5		
		Spawn	5.2		
		Total		38.2	Fitzmaurice (pers. comm.)
Netherlands	1965–73			222.0	FAO (1974)
Poland	1970–72			1 500.0	Leopold (pers. comm.)
Romania				680.0	Miron (pers. comm.)
Sweden	1965–73:	(Baltic only)		156.0	FAO (1974)
Switzerland	1971			1 335.0	Müller (pers. comm.)
U.S.A.	1965–73			2 411.0	FAO (1974)
Yugoslavia	1953–73:	Macedonia	95.5		
		Serbia	35.0		
		Total		130.5	Apostolski (pers. comm.)
TOTAL Recorded				22 001.7 1/	

1/ Underestimate: Lake Erie (Canada) produced an average of 10 405 MT in this interval (Colby pers. comm.)

TABLE XXXVI

Perch as a percentage by weight of the total catch of freshwater fish (from FAO 1974)

Area	Year								
	1965	1966	1967	1968	1969	1970	1971	1972	1973
North America	16.6	17.1	18.3	18.7	19.0	15.1	10.9	11.9	10.7
Europe (inland)	2.4	2.6	2.5	2.6	2.3	2.1	0.3	0.4	0.4
Europe (Baltic)	14.6	15.2	17.2	14.4	14.0	14.8	7.6	7.7	8.4
Total	7.1	7.3	7.4	7.6	7.8	6.6	3.7	4.0	3.9

commented that if perch were protected they ate one another, the perch being its own worst enemy.

By contrast, Herman (1964) noted that perch populations benefit from heavy exploitation with improvements in growth noticeable in such stocks as those of Lake Mendota and Lake Geneva. Hartmann (1974) predicted that introduction of a close season in Lake Constance would not be beneficial as it might lead to an increase in size of older perch with increasing cannibalism and an increase in the stocks of less valuable Cyprinids.

In South Green Bay, Lake Michigan, Hile (1953) recorded 150 percent increase in the retainable catch of perch after the size limit had been reduced from 8 in (20 cm) to 7½ in (19 cm) in 1952 without any change in the size composition of the population on the fishing grounds.

However, close seasons and size limits are in force in some areas as shown in Table XXXVII.

6.2 Control or alteration of physical features of environment

None used for the promotion of perch stocks.

6.3 Control or alteration of the chemical features of the environment

None used for the promotion of perch stocks.

6.4 Control or alteration of the biological features of the environment

Population manipulation: (See section 3.4.3.) Tesch (1955) recommended the removal of spawn as the most effective measure for promotion of good growth. This is achieved by setting branches as additional spawning substrates in the shallows and removing these subsequently together with the attached egg-strands. In some small ponds, planted eels (Anguilla anguilla) consume perch eggs very efficiently; although as noted in section 3.2.1, the natural predators of perch spawn are very few.

Thinning out the population reduces competition for food among the remainder which can grow large enough to feed on their own fry, and thus further restrict the growth of the population. However, Schneider (1972) from a study of experimental populations concluded that the yield from a perch fishery is limited by the food supply available to the larger perch, and that few perch will reach a large size unless recruitment of autumn fry is restricted. He recommended management measures to reduce recruitment and to improve available food resources:

(a) Reduction of recruitment

As fry growth is density-dependent, culling of the fry populations should be carried out in the autumn so that restricted growth rate up to that point enables the older cannibal fish to make maximum use of these progeny as food. Then the cull should be severe, leaving only enough survivors to achieve the optimal biomass of large fish, that is the carrying capacity of the environment, at recruitment to the fishery. Using observed values of growth and mortality for perch in Cassidy and Jewett Lakes, Michigan, he determined such an optimal stock structure for these lakes as shown in Table XXXVIII.

(b) Improvement of food resources

Establishment of a planktivorous fish, to transform some of the primary production into a form acceptable to adult perch, would augment the food supply both directly and possibly indirectly since the planktivore might reduce recruitment of perch fry through competition. He tested such a system, using fathead minnows (Pimephales promelas) as

TABLE XXXVII

Close seasons and size limits

Area	Close season	Minimum size	Authority
Belgium	1 Feb to Saturday before 2nd Sunday of Jun	Rivers north of Sambre and Meuse: 15 cm Rivers south of Sambre and Meuse: 18 cm	Huet (pers. comm.)
Bulgaria	Rivers only: 15 Apr to 31 May	–	Chervenkov (pers. comm.)
Czechoslovakia	(Most waters): 16 Mar to 15 Jun	–	Vostradovsky (pers. comm.)
Denmark	Rivers Gudeno and Randersfjord: 15 Apr to 31 May	Rivers Gudeno and Randersfjord: 19 cm	Dahl (pers. comm.)
France	(Effectively): 1 Feb to 15 Mar and 15 Apr to 15 Jun	(Recently: 14 cm)	Tuffery (pers. comm.)
German (D.R.)	–	15 cm	Tesch (pers. comm.)
Germany (F.R.)	–	15 cm (Bremen: 13 cm Saarland: 20 cm)	Tesch (pers. comm.)
Italy	Variously by regions: 15 Mar to 31 May	–	Bini 1962
Netherlands	16 Mar to 31 May	22 cm	Willemsen (pers. comm.)
Poland	15 Apr to 31 May	–	Leopold (pers. comm.)
Switzerland	–	15 cm	Müller (pers. comm.)
U.S.A.	Lake Huron: 15 Apr to 10 May (1948–56)	–	El Zarka 1959
	Commercial fisheries		
	Indiana, Lake Michigan: none	20 cm	Schneider (pers. comm.)
	Wisconsin, S. Green Bay: 9 Apr to 20 May	19 cm	
	Wisconsin, Lake Michigan: 9 Apr to 11 Jun	20 cm	
	Michigan, Saginaw Bay: none	none	
	Michigan, Ohio, Ontario; Lake Erie: none	20 cm (22 proposed)	
	Sport fisheries: none	none	

TABLE XXXVIII

Structure of a hypothetical perch population from which the harvest of perch 18 cm would be optimal (After Schneider 1972)

Age	Natural Mortality	Perch/ha		Average lengths (cm)
		Number	(kg)	
1		254	1.6	8.4
	0.15			
2		216	7.5	16.5
	0.41			
3		127	7.9	17.8
	0.41			
4		38[a]	3.5[a]	20.3

[a] The predicted perch population if fishing mortality is 0.5

planktivore, but the increased perch production was only marginal. Fry survival was reduced by 60 percent and their growth by 20 percent, and even though their vulnerability to predation by adults may have been extended, their numbers were still in excess of the optimum level at age 1.

He concluded also that the yield to man could be doubled if sterilization measures could be developed, as at present, approximately half the annual production of adults went into gonadal tissue.

6.5 Artificial stocking

6.5.1 Maintenance stocking

In general, the stocking of perch is not practised widely in areas in which it is native. However, in France, large quantities have been brought from Eastern Europe for stocking in impoundments (Tuffery pers. comm.), and some similar stocking has been carried out in Germany (F.R.) in small angling ponds and newly constructed reservoirs and on a small scale in Holland. In Denmark, perch are occasionally stocked as 2-3 year olds from wild populations into impoundments being developed as recreational fisheries. Winter-kill ponds may also be repopulated this way (Dahl pers. comm.). In Ireland (Fitzmaurice pers. comm.), Kiltullagh Lake was stocked with perch as food for pike.

It is possible that some perch stocking was practised in Finland before 1800, but none now (Sumari pers. comm.). Seeley (1886) quoted introductions of perch into trout ponds in Germany as food for trout.

In England, many canals have been stocked repeatedly to maintain angling stocks although this seems largely unnecessary.

Elsewhere in Europe, perch stocking is actively discouraged.

In the U.S.A., hatchery programmes in Pennsylvania, Ohio, Vermont, Michigan, Maryland, Minnesota, Wisconsin, Iowa and Illinois were operated for many years earlier this century. Eggs were collected from wild spawnings and incubated in screen-bottomed floating boxes to be stocked as eyed-eggs or yolk-sac fry in suitable rivers and lakes (Muncy 1959, 1962). Leach (1928 a) quotes an output for 1927 of 12 million perch eggs, 194 million fry and 1.25 million fingerlings, and in addition, 222 million eggs were collected from the wild. The perch were distributed to 15 states over an area from Virginia, Missouri, Montana and Vermont.

6.5.2 Transplantation, introduction

Within the U.S.S.R., perch have been transplanted into the Far East, into Lake Kenon, near Chita in the Amur basin (Berg 1965). Karpevich et al. (1961, 1963, 1965, 1972) reported no acclimatizations of perch within the U.S.S.R. between 1957 and 1972.

Within the U.S.A., numerous transplantations have taken place, increasing the distribution of perch into almost every state. Not all have been successful, but Scott and Crossman (1973) note flourishing colonies in California, Oregon, Washington, New Mexico, Utah and Texas. Curtis (1949) and Coots (1956) noted the introduction to California as taking place in 1891. Weatherley (1963 a) referred to introductions to several reservoirs in Georgia and to failures to acclimatize the fish in southern Ohio, probably due to high summer temperatures.

The occurrence of perch in Italy is suggested as due to introductions (Weatherley 1963 a), but their status here is not clear.

Introductions of perch well outside their normal range have been made on several occasions. Eleven fish survived the journey from England to Tasmania in tanks in 1861 and were held in ponds until they reproduced. The fry were then distributed fairly widely and have become abundant in the Macquarie - S. Esk river system in the north; in the Jordan, Derwent and Coal rivers in the south; and in the slower reaches of the few rivers to which they were added in the northwest. They also flourish in Lake Echo to which they were introduced about 50 years ago (Weatherley 1974).

Seven specimens were brought to Australia to Victoria in 1968. Perch were sufficiently well established there by 1882 that the mayor of Ballarat could give some to the New South Wales Zoological Society (Arentz 1966). However, these died in the heat en route, but successful introductions to New South Wales were made in the ensuing years and the fish now occurs throughout the Murray River system up to Wilcannia on the Darling River and in tributaries of the Snowy River (Lake 1959). Recently, introductions have continued, and Arentz (1966) reported 1 000 perch from Ballarat liberated into Lake George, New South Wales, resulting in regular catches of 3-4 lb (1.5-2 kg) fish by 1966. However, the general experience has been that the native species are extinguished and, with increasing density, the mean weight of individual perch declines with each new generation. However, in some areas which have been changed by the construction of weirs and dams to the disadvantage of native species, perch provide good fishing (Lake pers. comm.).

O'Connor (1886) reported the liberation of 36 specimens in Gold Creek River, Queensland, Australia, but with no subsequent success. A second liberation there was also unsuccessful (Weatherley 1963 a).

In South Africa, fry were imported in 1896 with only one survivor which grew to a "large size" over the next eleven years (Anon. 1945). Several further attempts were made to introduce perch over the next thirty years, but not until 1928 when a few fish were introduced to Paarde Vlei Lake, Somerset-West, was there much success. In 1930, largemouth bass (Micropterus salmoides Lacepède) were also introduced, and from then on, new year-classes of perch appeared. It is thought that perch eggs had been eaten by the indigenous fish Sandelia capensis, but this latter fish became prey for the bass. The numbers of perch began to increase by 1933, and a 5-lb (2.2 kg) fish was caught in 1934. Between 1934 and 1944, a "fair number" were caught by angling, but their numbers were less than those of largemouth bass. After the introduction of bluegills in 1940, both perch and bass improved in condition. Since 1945, the perch has gradually disappeared and none have been reported from Paarde Vlei "for many years" (D.F. Smith pers. comm.). Other populations in the province are likely to have been eliminated by drought.

Hey (1947) and Jubb (1967) reported stocking of perch at Florida Lake, Johannesburg and at a dam in Somerset East. The latter yielded 80 fish weighing 4-5 lb (1.8-2.2 kg) each (R.E. Boltt pers. comm.).

Perch have also been introduced into New Zealand, and are now widespread in the river-systems there (Allen and Cunningham 1957).

7 POND FISH CULTURE

In Europe, perch are not normally reared artificially in ponds. In Netherlands, there is some such production of perch but as an incidental extra from farms producing other species. The same applies in Belgium and France where some perch are produced incidentally in Cyprinid ponds. Recently in Czechoslovakia, some experiments were carried out into the cultivation of perch, but these were discontinued due to difficulties with feeding (Vostradovsky pers. comm.).

In the U.S.A., Leach (1928 a) described the incubation of perch eggs in a number of hatcheries. These eggs were obtained either from captive fish in tanks or floating boxes, or collected from vegetation as the floods subsided alongside the Mississippi River. In the hatcheries, they were either incubated in jars like whitefish eggs (2 qt per jar) or in wire baskets suspended in streams. These baskets were cylindrical, 15 in (38 cm) in diameter and 20 in (50 cm) long made of fine mesh wirecloth, attached in groups to 10-12 ft (3-3.7 m) planks as floats and anchored in situations where they were clear of the bottom at all times.

Mansueti (1964) described the Maryland incubation method, very similar to that given by Leach except that the containers were square wooden boxes with fine hardware cloth stretched across the bottom. The only husbandry was intermittent stirring and removal of dead eggs.

Trials are currently under way to establish the feasibility of rearing perch intensively to marketable size in Wisconsin (Downs 1975). Since the demand for perch from the Great Lakes has begun to outstrip supply, the operation may become viable. So far, acceptable sized perch have been reared in 9 months. The recommended stocking rate in farm tanks, 6 ft (1.82 m) wide and 3 ft (1 m or 0.90 m) deep was given as not more than $\frac{1}{2}$ lb (225 g) of adult fish to 2 gal (9 l) of water.

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