

Percid Fishes

Systematics, Ecology and Exploitation

John F. Craig

Dunscore, Scotland

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Blackwell
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Percid Fishes

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For Nicholas, Stephen, Alastair and Rachel

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Series Foreword

Fish researchers (a.k.a. fish freaks) like to explain, to the bemused bystander, how fish have evolved an astonishing array of adaptations, so much so that it can be difficult for them to comprehend why anyone would study anything else. Yet, at the same time, fish are among the last wild creatures on our planet that are hunted by humans for food. As a consequence, few today would fail to recognise that the reconciliation of exploitation with the conservation of biodiversity provides a major challenge to our current knowledge and expertise. Even evaluating the trade-offs that are needed is a difficult task. Moreover, solving this pivotal issue calls for a multidisciplinary conflation of fish physiology, biology and ecology with social sciences such as economics and anthropology in order to probe new frontiers of applied science. The *Blackwell Science Series on Fish and Aquatic Resources* is an initiative aimed at providing key, peer-reviewed texts in this fast-moving field.

While bony fish stem from a great radiation that followed the invention of the swimbladder in the Cretaceous period 100 million years ago, some fish groups, such as the sharks, lungfish and sturgeons are more ancient beasts. Survivors from earlier eras may be more widespread than we think: the deep sea coelacanth, formerly known only from the Indian Ocean, have recently turned up in Indonesia. Also, these fishes may be more effectively adapted to specialised niches than their ancient body plans would suggest. For example, rays and angel sharks have perfected the art of the ambush predator, while most cartilaginous fishes can detect electric discharges in the nerves of their prey.

Bony fish themselves have evolved into an amazing array of habitats and niches. As well as the open sea, there are fish in lakes, ponds, rivers and rock pools; in deserts, forests, mountains, the great deeps of the sea, and the extreme cold of the Antarctic; in warm waters of high alkalinity or of low oxygen; and in habitats like estuaries or mudflats, where their physiology is challenged by continuous change. Air-breathing climbing perch (regularly found up trees), walking catfish and mangrove mudskippers are currently repeating the land invasion of their Carboniferous ancestors. We can marvel at high-speed swimming adaptations in the fins, tails, gills and muscles of marlins, sailfish and warm-blooded tunas; gliding and flapping flight in several groups of fish; swinging, protusible jaws providing suction-assisted feeding that have evolved in parallel in groupers, carps and cods; parental care in mouth-brooding cichlids; the birth of live young in many sharks, tooth carps, rockfish and blennies; immense migrations in salmon, shads and tunas; and even

the so-called four-eyed fish, with eyes divided into upper air and lower water-adapted sections.

In addition to food, recreation (and inspiration for us fish freaks), it has moreover recently been realised that fish are essential components of aquatic ecosystems that provide vital services to human communities. But, sadly, virtually all sectors of the stunning biodiversity of fishes are at risk from human activities. In fresh water for example, the largest mass extinction event since the end of the dinosaurs has occurred as the introduced Nile perch in Lake Victoria eliminated over 100 species of endemic haplochromine fish. But, at the same time, precious food and income from the Nile perch fishery was created in a miserably poor region. In the oceans, we have barely begun to understand the profound changes that have accompanied a vast expansion of human fishing over the past 100 years.

John Craig's *Percid Fishes*, the third volume in the Blackwell Science Series on *Fish and Aquatic Resources* is a comprehensive monograph summarising the biology, ecology, exploitation and economic importance of all groups of this remarkable assemblage.

From over 9300 member species of the Perciformes, a principally marine order of advanced bony fish, the Percidae, comprising the perch, ruffe, percarina, zander, apron and darter groups, are an ancient Northern hemisphere family with about 189 freshwater species, dating back to a bass-like ancestor 38 million years ago near the cataclysmic start of the Oligocene period. Many freshwater habitats are almost evanescent in geological time and exhibit spatial connections that may form and reform, so the percid group's subsequent evolution has been driven by the complex series of Northern hemisphere glaciations, so much so that some consider the group polyphyletic. An early radiation in European freshwater appears to have been suppressed when cyprinids evolved, but in North America the darters have carried a high diversity through to the present day. In general, percids live in acid, oxygen-rich freshwaters, but one species, the Caspian pike-perch, lives in salt water, and several species in the Baltic and the Danube delta regularly invade brackish waters.

Most of the book is concerned with perch and zander. A chapter by Lawrence Page reviews the North American darters (Etheostomatinae), and ruffe, percarina, asprete and zingel are covered in a self-contained chapter at the end of the book. John Craig has written chapters that thoroughly survey percid morphology, anatomy, growth, mortality, reproduction, development, feeding, ionic balance, swimming, migrations, parasites, diseases, population dynamics, community structure, biomanipulation and fisheries. A chapter on aquaculture by Patrick Kestemont and Charles M elard provides a bonus.

For me, highlights of the book are descriptions of the sturdy and flexible perch skeleton, the protrusible jaw suction feeding mechanism and the advanced closed swimbladder. The optic area of the perch brain (the mid-brain tectum) has 'on' and 'off' cell responses that parallel the similar but more famous neurones in the fore-brain of mammals; one set is tuned to respond maximally to the three vertical dark stripes of the perch flanks. Perch don't swim fast, but are extremely manoeuvrable.

After stalking and chasing, perch seize their prey sideways and turn them before swallowing – a system that reduces the effect of anti-predator spines. Another mechanism behind perch success is that they appear to have a flexible life history response to crowded conditions induced by productive environments; they reduce growth rate and mature at earlier ages and smaller size, resulting in populations that have almost constant biomass. In addition, percids exhibit an opportunistic diet; although larger percids are characteristically piscivorous, both perch and zander will eat invertebrates and plankton if they have to and chitinase is produced by the pancreas. Perch shoal to catch prey, and although cooperative hunting has not been unequivocally demonstrated, my hunch is that a reward awaits a clever graduate student who can devise the right controls and experiments.

Archaeological work shows that perch and zander fished along the Baltic shores in 6000 BP were much bigger than today's fish (no surprise there!). Today, Finland catches the most percids, followed by Kazakhstan, Russia and Turkey. Walleye and yellow perch are also caught and marketed in Canada and the USA. Such fisheries provide a great product: I have greatly enjoyed a German perch (barsch) dish with salt bacon and celery washed down with one of those appley dry Rieslings that the Germans never seem to export. Craig discusses the issues that face these freshwater fisheries in their endeavours to be sustainable.

Towards the end of the book, the reader will find four interesting case histories of percid ecology to compare: Oneida lake, New York; Western Lake Erie, Canada; Lake Ijssel, Netherlands; and Windermere, United Kingdom, where the author spent the early part of his career. Indeed, there is much fascinating detail in this book, and John Craig has assembled over 1250 references to the primary literature with which to support his lucid prose. I am confident that this important book will provide a valuable source of ideas and reference for percid fishes for many years to come.

Professor Tony J. Pitcher
Editor, Blackwell Science Fish and Aquatic Resources Series
Director, Fisheries Centre, University of British Columbia, Vancouver, Canada

Preface

This monograph provides a comprehensive coverage of percid biology. This very important family of fishes inhabits the temperate Northern hemisphere and provides a renewable resource for commercial and recreational fisheries and suitable candidates for aquaculture.

It is over fifteen years ago that I started to assemble information which formed the basis of my book *The biology of perch and related fish*, published in 1987. The number of publications on percids since that time has been considerable, although it is interesting to note that gains in knowledge have not been in proportion to the prolific output. Indeed, the foundations in all aspects of percid taxonomy, morphology, physiology, ecology and fisheries management were well established by the mid 1980s.

The most important and novel research in the last ten years includes molecular genetics and the use of DNA in stock identification. The techniques have been used to trace the ancestry and evolution of the family. There have been rapid developments in aquaculture and rearing of several members of this group. Knowledge has been gained in reproductive physiology and constraints in culture have been identified and overcome. Fishes are not domesticated like farm animals so their culture requires special attention. Patrick Kestemont and Charles Mélard have written a detailed account of this technology. This area of development is very pertinent as percid capture fisheries continue to decline.

There is now greater appreciation of the role of percids in the context of communities. A greater understanding of the effects of predation and both inter- and intra-competition has enabled managers to make improved predictions about their stocks and how they should be cared for. The application of bioenergetic and ecosystem models, which are becoming more sophisticated and more realistic, has aided the formulation of fishery policy and conservation. A quantitative approach is necessary to predict and manage the effects of varying harvest rates, climate change, pollutants and stocking with both indigenous and exotic fishes. Models rely on good, accurate data usually collected over an extended period. A number of percid populations have been monitored on a long-term basis which has provided very valuable and necessary information. However, the direct causative factors controlling population dynamics, in particular recruitment, are still poorly understood. In addition, the role played by percids in the ecosystem and how they can be used in biomanipulation needs further investiga-

tion. They are unpredictable in how they respond to natural and human induced perturbations.

There is a need to conserve our present day fish fauna which have an important function in many food webs. The darters, which are confined to North America but exhibit extensive diversity, are a case in point. Larry Page has provided a comprehensive chapter on this colourful group. There is also a need to understand other members of the family such as zingels and the asprete which are rare and threatened by extinction. The diversity of fishes continues to be threatened not only by adverse abiotic factors affecting habitat but also by elements such as introductions of exotics. The recent introduction of the ruffe into the North American Great Lakes and into water bodies outside its normal range in Europe has provoked interest and attention to a fish that was in the past considered to be somewhat innocuous.

I am privileged to have been able to work with these attractive fish for over thirty years and on two continents. As a biologist I continue to find them fascinating and worthy of further study.

John F. Craig

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Chapter 1

Taxonomy and Distribution

1.1 Introduction

The perch family, the Percidae, belongs to the order Perciformes and suborder Percoidei. The order Perciformes, the largest group of vertebrates, encompasses 18 suborders of fish, 148 families about 1496 genera and about 9293 species (Nelson 1994). The members of this huge group of spiny-rayed fish have a world-wide distribution and are especially common in tropical and subtropical seas and are less abundant in temperate waters. They normally inhabit marine inshore areas although 1922 species (mainly cichlids) occur only in freshwater. Individuals of about 2185 species enter freshwater for at least part of their life cycle (Nelson 1994). The members of the Perciformes are very varied in size and shape but in general have the following common characteristics. They usually have laterally compressed bodies and most have ctenoid scales (tooth-like processes are present on their free edge) although cycloid scales are found in some species: e.g. the scales of *Epinephelus* Bloch (Serranidae) above the lateral line are nearly all ctenoid, and those below it are cycloid. The Perciformes are physoclists (the duct connecting the swim bladder to the gut is closed). There are usually two dorsal fins but never an adipose fin. The first dorsal fin is supported by spines and the second by soft rays. The anal fin has two or three spines and a series of soft rays. The caudal fin has 17 or fewer principal rays, 15 are branched. Pelvic fins, when present, are jugular or thoracic in position, each with one spine and five or fewer soft rays. The pelvic girdle is often attached to the cleithra. The pectoral fins are elevated on the sides of the fish with the base of the fins more or less vertically oriented. The skull is elongate and well ossified. The upper jaw is bordered by the premaxillae and both jaws contain well-developed teeth. The post-temporal is usually forked and articulates with the skull; the orbitosphenoid and the hypocoracoid are absent. There are four to seven branchiostegal rays and gill rakers are toothed. Perciformes have 24 or more vertebrae and inter-muscular bones are absent.

The order contains a widely developed assemblage of fishes and may be paraphyletic, consisting of distinct lines which evolved in parallel to a perciform grade of organisation (Nelson 1994). A thorough and detailed examination of the classification and distribution of the Perciformes is provided by Johnson (1993) and Johnson & Patterson (1993).

1.2 The Percoidei

The largest suborder of the Perciformes, the Percoidei, contains 71 families (Table 1.1), about 528 genera and 2860 species. Nelson (1994) considers it to be the basic group of the Perciformes from which others evolved. Approximately 338 (12%) species live in freshwater. There is no general agreement on how the percoid families might be interrelated. Some series of families appear to be more similar to one another than to most other percoid families (e.g. Carangidae, Nematistiidae and Coryphaenidae, or Lutjanidae, Haemulidae and Sparidae) but there are no sharp morphological discontinuities demarcating such groups, nor is it clear whether the similarities are the result of families being related or from evolutionary convergence.

Table 1.1 Families of the suborder Percoidi (After Nelson 1994.)

Family Name	Common Name
(1) Pomatomidae	Bluefishes
(2) Rachycentridae	Cobia
(3) Coryphaenidae	Dolphins
(4) Lobotidae	Tripletails
(5) Echeneididae	Remoras
(6) Caritsiidae	Manefishes
(7) Bramidae	Pomfrets
(8) Nematistiidae	Roosterfish
(9) Centrarchidae	Sunfishes
(10) Percidae	Perches
(11) Percichthyidae	Temperate basses
(12) Centropomidae	Snooks, glassfishes and perches
(13) Serranidae	Sea basses
(14) Grammidae	Basslets
(15) Pempheridae	Sweepers
(16) Apogonidae	Cardinalfishes
(17) Lutjanidae	Snappers
(18) Malacanthidae	Tilefishes
(19) Haemulidae	Grunts
(20) Gerreidae	Mojarras
(21) Inermiidae	Bonnetmouths
(22) Cirrhitidae	Hawkfishes
(23) Chaetodontidae	Butterflyfishes
(24) Mullidae	Goatfishes
(25) Sciaenidae	Drums or croakers
(26) Carangidae	Jacks and pompanos
(27) Sparidae	Porgies
(28) Centracanthidae	<i>Centracanthus, Spicara</i>
(29) Coracinidae	Galjoen fishes
(30) Lactariidae	False trevallies
(31) Priacanthidae	Bigeyes
(32) Pseudochromidae	Dottybacks

Cont.

Table 1.1 Cont.

Family Name	Common Name
(33) Pomacanthidae	Angelfishes
(34) Monodactylidae	Moonfishes or fingerfishes
(35) Leiognathidae	Ponyfishes, slimys or slipmouths
(36) Teraponidae	Grunters or tigerperches
(37) Plesiopidae	Roundheads
(38) Menidae	Moonfish
(39) Bathyclupeidae	<i>Bathyclupea</i>
(40) Oplegnathidae	Knifejaws
(41) Pentacerotidae	Armourheads
(42) Toxotidae	Archerfishes
(43) Nandidae	Leaffishes
(44) Nemipteridae	Threadfin breams
(45) Banjosidae	<i>Banjos</i>
(46) Cepolidae	Bandfishes
(47) Kuhliidae	Aholeholes
(48) Glaucosomatidae	Pearl perch, <i>Glaucosoma</i>
(49) Sillaginidae	Smelt-whitings
(50) Cheilodactylidae	Morwongs
(51) Latrididae	Trumpeters
(52) Kyphosidae	Sea chubbs
(53) Arripidae	Australian salmon
(54) Leptobramidae	Beachsalmon
(55) Chironemidae	Kelpfishes
(56) Aplodactylidae	Sea carp; also called marble fishes
(57) Enoplasidae	Oldwife
(58) Dinolestidae	<i>Dinolestes</i>
(59) Emmelichthyidae	Rovers
(60) Lethrinidae	Scavengers or emperors
(61) Chandidae	Asiatic glassfish
(62) Moronidae	Temperate basses
(63) Acropomatidae	Temperate ocean-basses
(64) Ostracoberycidae	<i>Ostracoberyx</i>
(65) Callanthiidae	<i>Callanthias</i>
(66) Notograptidae	<i>Notograpus</i>
(67) Opistognathidae	Jawfishes
(68) Dinopercidae	<i>Centrarchops</i> and <i>Dinoperca</i>
(69) Epigonidae	Deepwater cardinalfishes
(70) Polynemidae	Threadfins
(71) Drepanidae	<i>Drepane</i>

1.3 Percidae taxonomy and distribution

The family Percidae, unlike most of the 71 percoid families, is confined to freshwater, in the temperate and subarctic regions of North America and Eurasia (Nelson 1994). Some introductions of species of the family have been made into the Southern hemisphere. Percid fossils occur as far back as the Oligocene in both northern landmasses (Romer 1966). The existence in eastern North America, of the

subfamily Etheostomatinae Agassiz (four genera, c. 173 species) (Chapter 12) is further evidence of a long, independent history of the family in North America. Similarly, the existence of the endemic European genera *Zingel* (three species) and *Romanichthys* (one species) of the subfamily Luciopercinae Jordan and Evermann and *Gymnocephalus* (four species) and *Percarina* (one species) of the subfamily Percinae Bonaparte (Song *et al.* 1998), is evidence of a long, independent period of evolution there.

Song *et al.* (1998) classified the Percidae based on mitochondrial cytochrome b DNA sequence data. Their classification (Fig. 1.1) is similar to that of Collette and Bănărescu (1977) although the latter grouped Percini (*Perca*, *Gymnocephalus* and *Percarina*) and Etheostomatini (*Percina*, *Crystallaria*, *Ammocrypta* and *Etheostoma*) into the subfamily Percinae. The Percinae have the anterior-most interhaemal bone greatly enlarged (Fig. 1.2). Also, the lateral line usually does not extend onto the caudal fin and the anal spines are large and well developed. In the Luciopercinae, the anterior-most interhaemal bone is not larger than the other interhaemal bones, the lateral line does extend onto the caudal fin and the anal spines are not well developed (Collette & Bănărescu 1977). Song *et al.* (1998) believed that similarities between Etheostomatinae and some members of Luciopercinae (*Zingel* and *Romanichthys*) have resulted from convergent evolution as these fish have independently invaded benthic rheophilic habitats. Wiley (1992) had previously claimed that the Etheostomatinae and the small luciopercines were monophyletic.

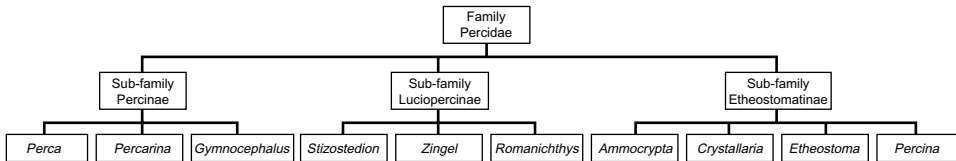


Fig. 1.1 Taxonomic relationships of the Percidae (based on Song *et al.* 1998).

There are three species of *Perca* Linnaeus. *P. fluviatilis* Linnaeus (Eurasian perch, referred to hereafter as perch; Russian = okun) is widely distributed throughout Eurasia but also has been introduced into South Africa, Australia and New Zealand. *Perca flavescens* (Mitchill) (yellow perch) is a North American perch and *P. schrenki* Kessler (Balkhush perch; Russian = Balkhushkii okun) is found only in eastern Kazakh (Russia) (Fig. 1.3).

There are four species of *Gymnocephalus* Bloch: *G. cernuus* (Linnaeus) (ruffe; Russian = ěrsh), *G. schraetser* (Linnaeus) (striped ruffe; Russian = polosatyĭ ěrsh), *G. acerinus* (Güdenstadt) (Don ruffe; Russian = Donskoiěrsh) and *G. baloni* Holčík & Hensel (Balon's ruffe; Slovak – hrebenačka Balonava) (see Holčík & Hensel 1974). The distribution of these four species of ruffe is shown in Figure 1.4.

The one species of *Percarina* Nordmann, *P. demidoffi* Nordmann (percarina;

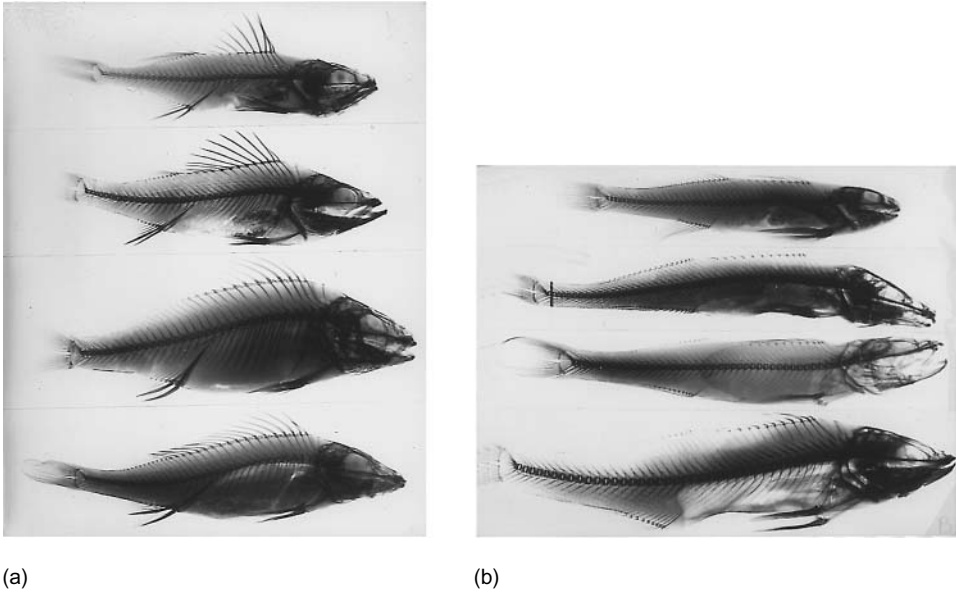


Fig. 1.2 Radiographs of (a) four species of Percinae from top to bottom: *Percarina demidoffi*, *Perca schrenki*, *Gymnocephalus cernuus* and *G. schraetser*, showing the enlarged anterior interhaemal bones, and (b) four species of Luciopercinae, from top to bottom: *Romanichthys vascanicola*, *Zingel zingel*, *Stizostedion canadense* and *S. volgensis*, with no enlargement of the interhaemal bones. (After Collette 1963.)

Russian = perkarina) is distributed in the Sea of Azov and parts of the Black Sea (Fig. 1.5).

There are four genera of darters which are distributed solely in North America (Fig. 1.6). These are *Percina* Haldeman (40 described species), *Crystallaria* Jordan and Gilbert (one species), *Ammocrypta* Jordan (six species) and *Etheostoma* Rafinesque (126 described species).

Stizostedion Rafinesque has five species: three in Europe, *S. lucioperca* (Linnaeus) (zander; Russian = sudak), *S. marina* (Cuvier) (sea pikeperch; Russian = morskoi sudak) and *S. volgensis* (Gmelin) (Volga pikeperch; Russian = bersh) and two in North America, *S. canadense* (Smith) (sauger) and *S. vitreum* (Mitchill) (walleye) (Fig. 1.7).

There are three *Zingel* Cloquet species: *Z. zingel* (Linnaeus) (zingel; Russian = tschop), *Z. streber* Siebold (streber; Russian = malyi tschop) and *Z. asper* (Linnaeus) (French = apron). Zingel and streber are found in the Danube and Vardar Rivers and apron is distributed in the Rhône River (Fig. 1.8). Zingel's close relative *Romanichthys* Dumitrescu, Bănărescu and Stoica, is monotypic and represented by *R. valsanicola* Dumitrescu, Bănărescu and Stoica (asprete) which was found in the Arges and Riul-Doamnei Rivers but is extinct there (Stanescu 1971) and is now only found in the Vilsan River (Fig. 1.8).

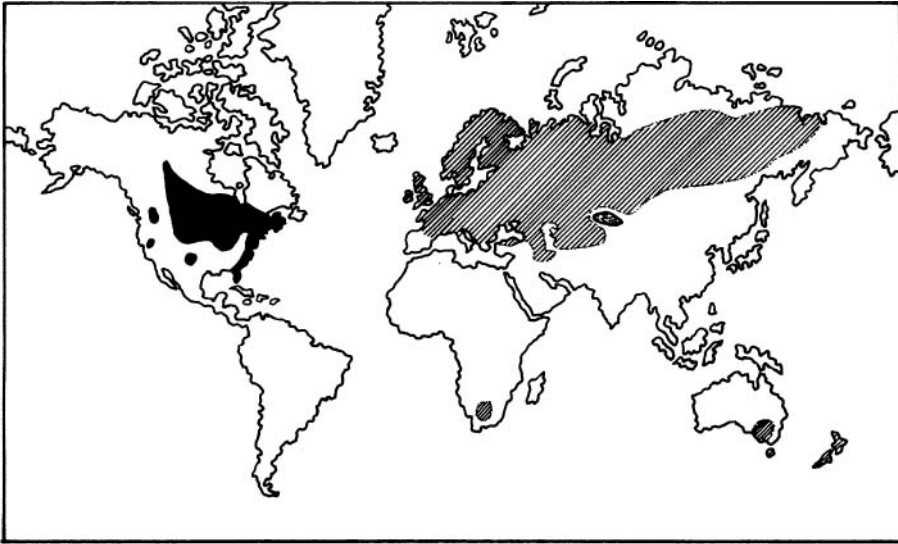


Fig. 1.3 The distribution of *Perca* species. ■ = *Perca flavescens*, ▨ = *P. fluviatilis* and □ = *P. schrenki*.

1.4 Some general characteristics of the percids

Percids are hardy species tolerating a wide range of environmental conditions. Water temperature limits their distribution through its effects on metabolic processes. The upper limit for *Perca* species is a summer air isotherm of about 31°C which is reached on the edge of their range in Italy, Greece, the USA and Australia. The lower limits of the temperature range may influence reproductive success rather than the survival of the adults. The northern distribution limit of walleye to about the summer air isotherm of 13°C probably is more a reflection of temperatures required for maturation and spawning success on a seasonal cyclic basis than limitations to metabolism. Perch and yellow perch eggs and young stages can tolerate low pH and have intermediate requirements in terms of temperature and oxygen concentrations when compared to other temperate freshwater fishes. High production, growth and survival of percids require appropriate food such as zooplankton, littoral invertebrates and prey fish, at the correct stage in the life cycle. Perch species are very successful animals within the limits of tolerable environmental conditions. They have relatively high fecundity, fairly unspecific spawning requirements and can expand rapidly in numbers when they are introduced to new bodies of water such as reservoirs and canals. The same criteria apply to *Stizostedion* species although zander appears to tolerate higher summer maxima than walleye; it may also be better adapted to spawning than walleye. Nest building and guarding leads to better fertilisation and hatching rate and to lower mortality of eggs and

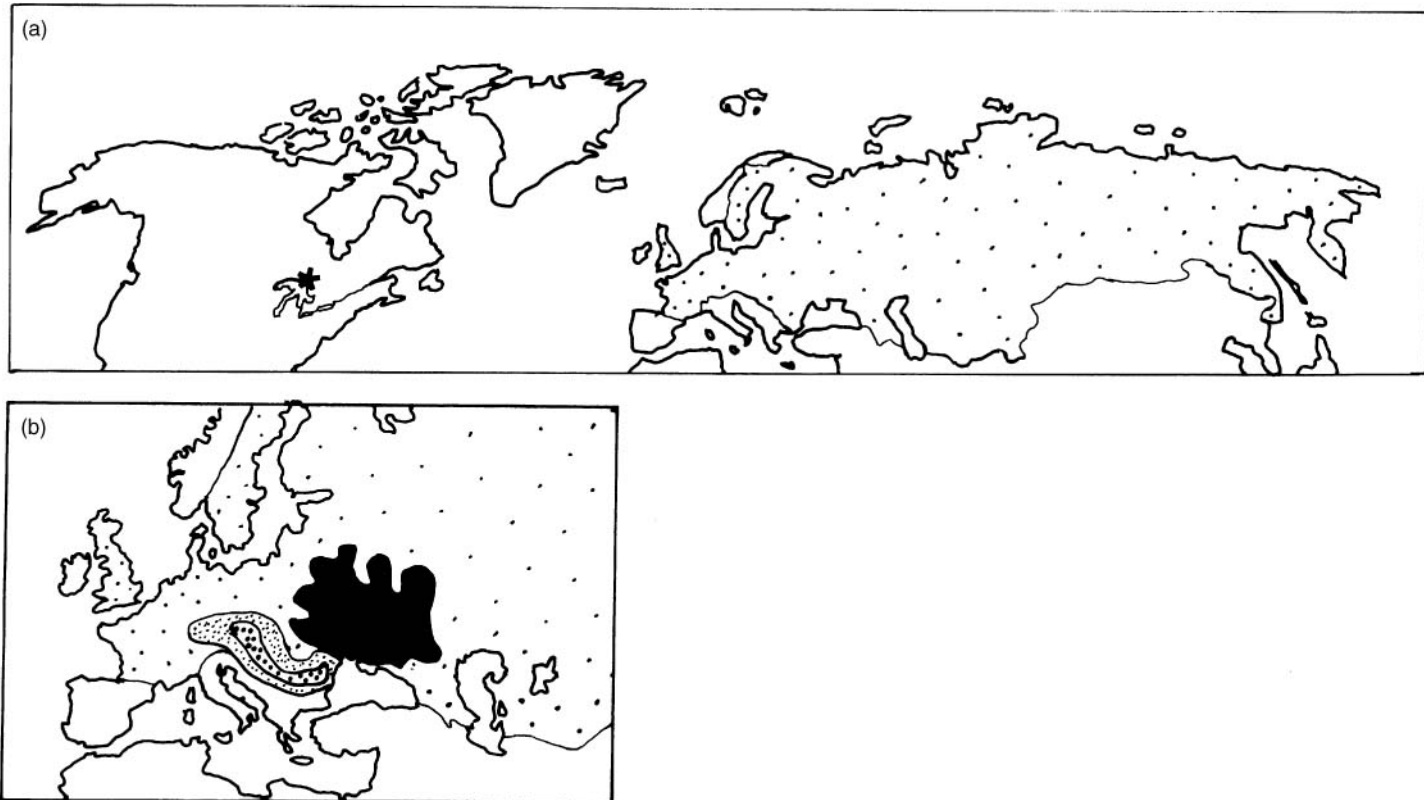


Fig. 1.4 The distribution of *Gymnocephalus* species. [•] = *Gymnocephalus cernuus*. It has been introduced into Lakes Superior and Huron (★). [•••] = *Gymnocephalus schraetser*, [••••] = *G. baloni* and *G. schraetser* combined and [■] = *G. acerinus*.

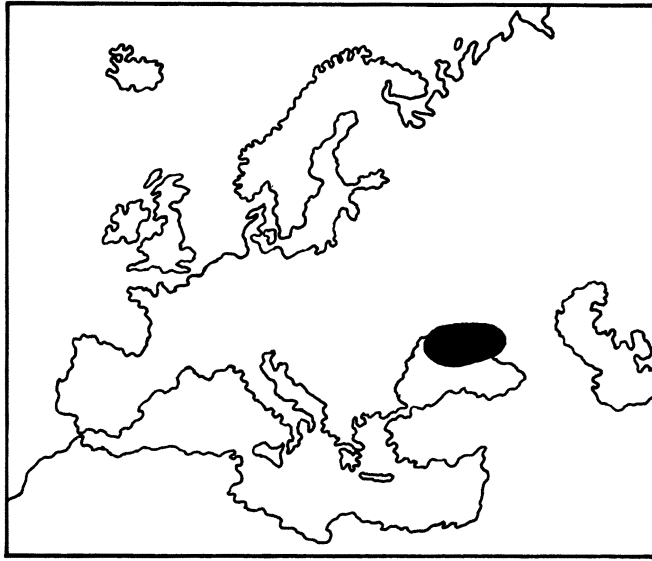


Fig. 1.5 The distribution of *Percarina demidoffi* ■.

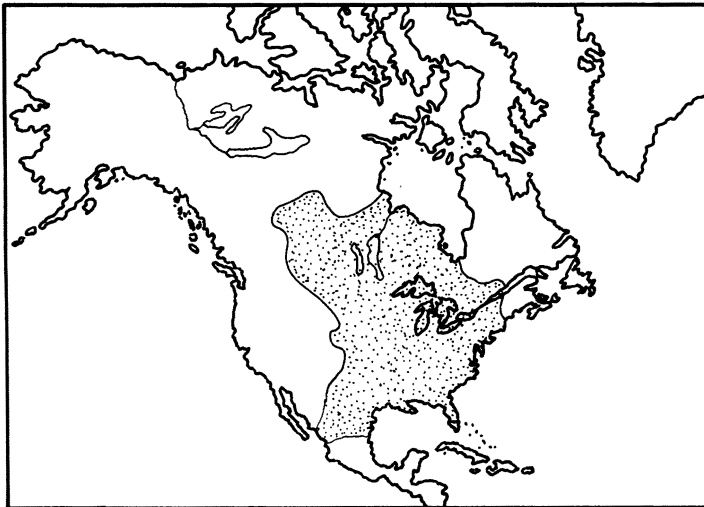


Fig. 1.6 The distribution of the *Etheostomatinae* ▤.

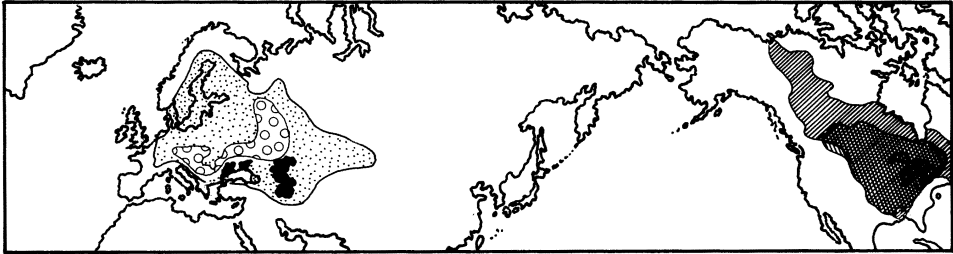


Fig. 1.7 The distribution of *Stizostedion* species. [···] = *Stizostedion lucioperca*, [■] = *S. marina*, [⊗] = *S. volgensis*, [▨] = *S. canadense* and [▧] = *S. vitreum*.

larvae. In addition the zander is more fecund than the walleye. These factors probably enable zander to spawn successfully under stressed conditions and to flourish in areas where it has been introduced. Both zander and walleye are particularly successful in lakes with low mean depth, where the water is mixed and there is no thermal stratification. *Stizostedion* species also may compete successfully with other predators because their activities are usually confined to twilight and night.

The plastic nature of percid adaptation to the environment undoubtedly has enabled them to expand within their niche both naturally and as a result of human influence. Specialisation often leads to the end of an evolutionary line. The amount of DNA in teleost haploid cells ranges from 0.4 to 4.4×10^{-12} g. It tends to decline the more specialised the fish becomes (Hinegardner 1968; Hinegardner & Rosen

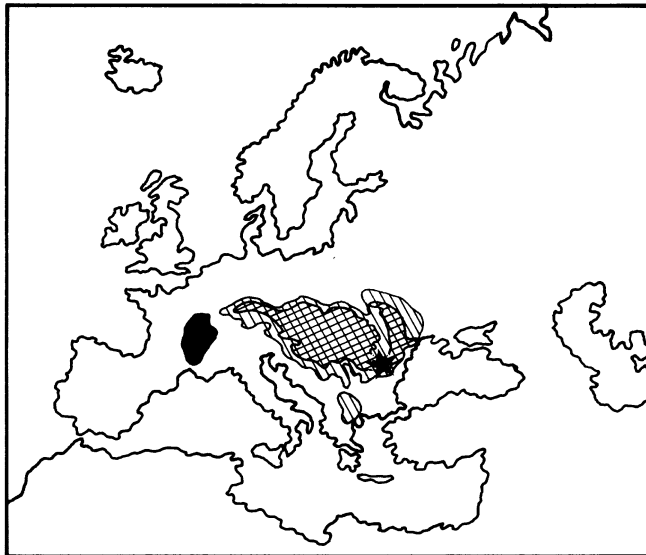


Fig. 1.8 The distribution of *Zingel* and *Romanichthys* species. [▨] = *Zingel zingel*, [⊗] = *Z. streber*, [■] = *Z. asper* and ★ = *R. valsanicola*.

1972). The Percoidei are a fairly specialised group of fish but within the group, members of the Percidae family are of a generalised form. Thus *P. flavescens* has a DNA content of 1.2×10^{-12} g compared to a more specialised species such as *Chaetodon ocellatus* Bloch (Chaetodontidae, butterfly fishes) which has a DNA content of 0.9×10^{-12} g. Specialisation usually means the loss of structures and possibly an evolutionary 'dead-end'. The generalised form of the percids makes them radially adaptive. However, they have certainly not been as successful as Cyprinidae. Up to the Miocene period the Percidae probably played a major role in the fish fauna in Europe. But the appearance of cyprinids at this time may have prevented diversification of the percids. This was not the case in North America where only one fairly primitive cyprinid appeared during the Miocene. Thus, some groups of percids were able to diversify leading to the present day extensive Etheostomatinae fauna (see Chapter 12).

A Perch ancestor probably evolved from an anadromous offshoot of the Serranidae during the Cenozoic. The basic form of the family Percidae is found in Europe. Fossils of *P. fluviatilis* have been discovered in Miocene deposits in the former USSR (Lebedev 1952; Yakovlev 1960), Pliocene deposits in the former USSR, Austria and Belgium (Newton 1908; Weinfurter 1950; Sychevskaya & Devyatkin 1960) and Pleistocene deposits in the former USSR and Germany (Weiler 1933; Gripp & Beyle 1937; Svetovidov & Dorofeeva 1963). Fossils of *P. flavescens* have been found from Pleistocene deposits in Oklahoma, USA. These deposits contain fossils of animals which inhabited the Great Plains at that time (Smith 1954).

It is generally accepted that *Perca* and *Stizostedion* species invaded North America by a north Pacific route across the Bering land bridge (Yakovlev 1961; Collette & Bănărescu 1977; Billington *et al.* 1990, 1991; Song 1995). A number of scientists believed that the route was from Europe across the Atlantic. Cihăr (1975) suggested that perch moved from Europe to North America during the late Pleistocene glacial Würm period, 13–15,000 BP, through brackish water along the foot of the receding ice sheet. The Rocky Mountains in the west and the Mackenzie Mountains in the northwest stopped their advance in North America. The spread eastward in Asia was halted by the Kolyma and Anadyr Mountains. Cihăr (1975) drew these conclusions from the fact that perch are not found in north Siberian rivers (the furthest east is the Kolyma River, Russia) nor the yellow perch in North American rivers running into the Bering Sea and Pacific Ocean. Recently (nineteenth century), yellow perch have been introduced by humans into water basins flowing into the Pacific Ocean.

Perca fluviatilis and *P. flavescens* are very alike in morphology, physiology and behaviour and they are limited in their distribution by similar factors such as salinity, current speed and oxygen concentration. There has been much controversy over their taxonomy. Mitchill (1818), Gunther (1859), Steindachner (1878), Day (1880; 1886), Sterba (1962), Scott and Crossman (1973) and Collette and Bănărescu (1977) have classified *P. fluviatilis* and *P. flavescens* as separate species. Jordon and Gilbert (1877), Smith (1892), Berg (1905; 1949), Pokrovskii (1951) and Cihăr (1975)

have made *P. flavescens* a subspecies of *P. fluviatilis*, *P. fluviatilis flavescens*. Thorpe (1977) compared many aspects of the morphology and biology of the two animals and found them very similar. Collette and Bănărescu (1977) have pointed out that there is a difference in the position of the predorsal bone. In *P. fluviatilis* the bone is anterior to the first neural spine but in *P. flavescens* the bone is inserted between the first and second neural spines. MacCrimmon *et al.* (1989) found a specimen of yellow perch that was intermediate between these two types. The fish had a predorsal bone that was anterior to the first neural spine (as in *P. fluviatilis*) but the pterygiophore supporting the first dorsal spine extended between the second and third neural spines (as is typical in *P. flavescens*). However, Song (1995) compared the entire nucleotide sequences of cytochrome b gene and found a large genetic divergence between *P. fluviatilis* and *P. flavescens*. These two species probably became separated a long time ago, about eight million years BP. This would support the theory that *Perca* invaded North America from Siberia. They may have done this at a similar time to *Stizostedion*. The divergence times between the two North American species, *S. canadense* and *S. vitreum*, between two European species, *S. lucioperca* and *S. volgensis* and between the North American and two European species were calculated by Billington *et al.* from allozyme and mitochondrial DNA data (1990, 1992) (Table 1.2). The evidence supports the theory that *Stizostedion* ancestors invaded North America during the Pliocene via the Bering land bridge c. ten million years BP. *Stizostedion* was probably well established in North America by the mid Pliocene.

Table 1.2 Approximate divergence times (million years BP \pm S.E.) for North American and European *Stizostedion* species based on allozyme and mtDNA data. Studies are from: (i) Billington *et al.* (1991) and (ii) Billington *et al.* (1990). (After Billington *et al.* 1991, with kind permission of Academic Press.)

	Allozyme	mtDNA
North America (i)	1.58 \pm 1.14 (26 loci)	4.07 \pm 0.73
North America (ii)	3.12 \pm 1.33 (36 loci)	4.06 \pm 0.73
	2.85 \pm 1.22 (39 loci)	
European (i)	6.02 \pm 2.32 (26 loci)	1.98 \pm 0.47
North American & European (i)	13.28 \pm 3.78 (26 loci)	7.42 \pm 1.01
North American & European (ii)	10.59 \pm 2.74 (36 loci)	7.86 \pm 1.18

The Balkhash perch, *P. schrenki*, has developed in isolation since the Tertiary period, unaffected by glacial activity. However, when *P. schrenki* has been introduced into waters containing *P. fluviatilis*, hybridisation has occurred and the resulting populations exhibit convergence of morphological characteristics from the two species (Dukravets & Biryukov 1976; Dukravets & Mamilov 1993).

Stizostedion vitreum has been represented by two subspecies, *S. vitreum vitreum* Mitchill and the blue pike, *S. vitreum glaucum* (Hubbs 1926). The blue pike inhabited Lake Erie and Lake Ontario but is now extinct (McAllister 1970). As well

as competition from stocked exotic fish and selective fishing, the gene pool of the blue pike may have become mixed with that of *S. vitreum vitreum* by hybridisation and the subspecies lost (Regier *et al.* 1969). The environmental requirements of walleye are similar to those of yellow perch although the walleye extends further north than the yellow perch. Their niches are closely connected and probably these species have evolved together. Thus yellow perch is the chief food of walleye in many water-bodies and predation may play a part in controlling recruitment both for the predator and prey.

Stizostedion lucioperca originated in the Elbe River and the drainage basins of the Black, Baltic, Caspian and Aral Seas and in the Maritsa River which flows into the Aegean Sea (Sakovich 1986). It has spread throughout Europe as a result of human introductions. It also now occurs in western Turkey (Aksiray 1961) and Morocco (Brunet 1957). Many of the introductions have been recent and well monitored. The zander did not appear in French waters until the 1900s. In 1910 it inhabited the Rhine River and the canal connecting the Rhine and Rhône Rivers (Gagne 1977). By 1915 it was found in the Doubs River, by 1920 in the Saône River and by 1932 in the Rhône basin (Vivier 1951). In 1948 it inhabited the brackish waters of Etang du Vaccares, France, where it has now become very abundant. The zander spread through numerous introductions into canals, rivers and ponds. Today it is found in all river basins and a large number of lakes in France.

The zander was first introduced into England in 1878 (Sachs 1878). Several introductions were made and by 1910 a breeding population was established (Fitter 1959). The zander became established in the Great Ouse Relief Channel, England, in 1963 from the original, introduced, Woburn stocks (Wheeler & Maitland 1973; Linfield & Rickards 1979). The zander has spread uncontrollably from this open water system to many of the canals and rivers of East Anglia.

Stizostedion volgensis is an eastern European species while *S. marina*, a partially marine species, is found in the Black and Caspian Seas and the lower reaches of the River Bug and River Dnieper. Both species have probably evolved in partial isolation.

Within a percid species there are a number of races and stocks but the extensive variation in morphological characteristics within even a population makes it often difficult to differentiate between these stocks. Some attempts have been made in this direction, for example in comparing scale shape and brain mass to body mass ratio between populations. The latter was shown to vary between three populations of perch in the former USSR (Yakovleva *et al.* 1976). For example, two stocks of perch were identified in one lake by separation of their blood proteins (Kirsipuu 1967). This would be consistent with the theory that two forms of perch live in the same body of water, a predatory deep-water form and a littoral form living off invertebrates and small fish. Care must be taken to ensure that blood protein comparisons have a genetic basis (Kirsipuu 1971). Examination of 19 enzymatic loci using starch gel electrophoresis failed to show any differences in samples of yellow perch from Green Bay, Lake Michigan or nearby Keyes Lake, USA (Leary &