Mouth and Body Form Relative to Feeding Ecology in the Fish Fauna of a Small Lake, Lake Opinicon, Ontario[1]

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ABSTRACT

In 14 cohabiting fish species in a small freshwater lake, mouth and body structures combine with food specializations and habitat preferences to greatly restrict interspecific competition within the fauna.

The species differ quantitatively in a large number of structures and, individually and in combination, these are clearly adapted for distinctive roles. The mouth is particularly plastic, varying in position, in aperture width, and in overall form, with structures as diverse as a scoop, a beak, and a tube being found. Six basic body types occur and these, combined with varying fin morphologies, result in a range of distinctive forms, including the following. *Micropterus salmoides*, with a compressed fusiform body and a wide mouth, is a strong-swimming, widely ranging piscivore. *Notemigonus crysopterus*, with a long, slender caudal peduncle, subfalcate pectoral fins, and a deeply forked caudal fin, has great maneuverability that permits it to catch individual zooplankters. *Lepomis macrochirus* is a "sedentary," gibbose-bodied water-hanger. *Umbra limi* has a stubby, cylindrical body that favours life in dense vegetation. *Labidesthes sicculus*, with an almost straight dorsal line to the body, a low dorsal fin, and a beak-like snout with tweezer-like teeth, is modified for surface feeding and leaping out of the water. *Ictalurus nebulosus* has chemotactile barbels that favour bottom feeding and paired fins that function partly as hydrofoils, keeping the body inclined downwards as the mouth sweeps the bottom.

The structural specializations give their owners a decided ecological advantage in certain situations. Only a few species, however, are limited by them to restricted ways of life. In most cases, a considerable measure of feeding flexibility is retained, presumably important for survival in cold temperate lakes.

INTRODUCTION

The objective of this paper is to describe and interrelate external morphological structure with way of life, feeding habits, and food. The fauna under investigation is that of a small (2200 acres) eutrophic lake, Lake Opinicon, Leeds County, Ontario.

Ichthyologists have paid little attention to the minor structural differences that separate cohabiting species of freshwater fishes, although the broad characteristics of the piscivore, the plankton feeder, the bottom feeder, and the swift and slow swimmer are well known. On this basis certain authors dealing with faunas have divided the species into a series of basic ecological types (Fryer, 1959; Lowe, 1964). Many freshwater fishes, however, differ from each other in minor morphological characters.

The situation in ichthyology contrasts to that in ornithology. Extensive research on birds has shown that minor differences in bill shape, form of wing, and length of tarsus are correlated with clear-cut differences in diet, feeding habits, and way of life (Lack, 1945; Hamilton, 1961; Osterhaus, 1962; and others). This knowledge has proven a valuable tool by means of which the ecology of species can be predicted. The mouth of fishes requires study since

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this is the structure whereby they obtain their food, and thus dictates the size and type of prey that can be handled. Its significance in leading to specialized feeding, and in reducing interspecific competition, needs assessing. Because there is a great deal of food overlap among cohabiting freshwater fishes, some workers have stated that these do not fit the Gausian concept (Gause, 1934) of ecological exclusion (Hartley, 1948; Larkin, 1956).

The present work draws upon a 4-year study of the food of the Lake Opinicon fish (Keast, 1965). A parallel study of the functional significance of differences in buccal and pharyngeal dentition, gill rakers, and intestinal structure in this fauna is near completion.

THE FAUNA

The species analysed in this study are as follows. Cyprinidae: *Notemigonus crysoleucas* (golden shiner), *Notropis heterodon* (blackchin shiner), *Pimephales notatus* (bluntnose minnow); Ictaluridae: *Ictalurus nebulosus* (brown bullhead); Umbridae: *Umbra limi* (mud minnow); Esocidae: *Esox lucius* (northern pike); Cyprinodontidae: *Fundulus diaphanus* (banded killifish); Percidae: *Perca flavescens* (yellow perch), *Percina caprodes* (log perch); Centrarchidae: *Lepomis macrochirus, L. gibbosus* (bluegill, pumpkinseed sunfish) (some hybridization), *Ambloplites rupestris* (rock bass), *Pomoxis nigromaculatus* (black crappie), *Micropterus salmoides* (largemouth bass); Atherinidae: *Labidesthes sicculus* (brook silverside). Four additional species occur in the lake, but were not included in the study. They are: *Ictalurus natalis* (yellow bullhead), which is structurally similar to *I. nebulosus*, relatively uncommon, and occupies a somewhat different habitat; *Pomolobus pseudoharengus* (alewife), a new immigrant which will be treated in detail elsewhere; *Etheostoma exile* (Iowa darter) and *Micropterus dolomieu* (smallmouth bass), both of which are very rare. Apart from dentition the characters of *Lepomis macrochirus* and *L. gibbosus* are closely similar, hence only the former is discussed.

METHODS

A series of criteria for comparing and measuring differences in mouth and body form were developed.

(1) *Standard length* (S.L.). The distance from the tip of the snout to the tip of the spinal column. This measurement, necessary for the calculation of body ratios, is taken as the criterion of body size. The food data quoted is based on total length, which includes the caudal fin (greatest length). A conversion factor for the two can be derived from Table I.

(2) *Mouth position*. Described as terminal, dorso-terminal or ventro-terminal.

(3) *Depth of mouth as seen from side*. The jaw angle is described as forming a deep, moderate, or shallow indentation.

(4) *Width of mouth aperture*. The distance across the inner sides of the open mouth at the jaw angles.

(5) *Premaxilla protrusibility.* In many fish the premaxilla is loosely attached to the maxilla by a median spinous process and a ligament. When the mouth opens, the premaxilla moves forward. This is possibly of some assistance in the seizure of prey, which is pulled inwards as the jaw closes. Fish with strong jaw margins have the premaxilla fused to the skull. Protrusibility is given as the percentage difference in distance from the anterior margin of the eye to the premaxilla as between the tightly closed and wide open mouth. The figures should be regarded as of relative value only, since fresh specimens were not always available for measurement.

(6) *Lower jaw extensibility.* When the mouth opens the lower jaw swings downwards and forwards, describing an arc. This is particularly noticeable when the mouth angle is strongly oblique; and the action may bring the lower jaw in advance of the upper to form a scoop-like structure. This is marked in some species. Alternatively, it may join with a protrusible premaxilla to form a tubular mouth. To obtain a measure of both the forward and downward movement, the distance from the anterior margin of the eye to the lower lip with mouth closed was deducted from the distance with the mouth open, and expressed as a percentage of the former. The figures are of broad comparative value only.

(7) *Dentition.* Only marginal dentition, that associated with the initial grasping of prey, is considered here.

(8) *Body height.* The deepest part of the body, excluding fins.

(9) *Body width.* The maximum width, which is characteristically in the region of the pectoral fins. In *I. nebulosus*, however, it is directly behind the head.

(10) *Body form.* The species are grouped into six categories: rounded fusiform, compressed fusiform, foreshortened tubular, elongate tubular, subgibbose, and gibbose (Fig. 1).

(11) *Pectoral-pelvic distance.* The horizontal distance between the midpoints of the bases of the paired fins, expressed as percentage of standard length.

(12) *Caudal peduncle length.* The horizontal distance from the anus to the end of the spinal column, expressed as percentage of standard length (Gray, 1953).

(13) *Fin form.* The basic types of pectoral fins occurring in this fauna are illustrated in Fig. 1. Nomenclature for these, as well as for caudal fin types, follows that of Norman and Greenwood (1963), with minor modifications. Dorsal and anal fins are described in terms of basal length, height or depth, and general shape.

(14) *Fin movements.* These are described in some detail because of their importance in maneuvering.

The measurements given in the study are based on 15 adult members of each species.

FOOD DATA

Series of the different size (year class) categories of each species were collected from Lake Opinicon at monthly intervals from May to October inclusive from 1962 to 1965. The number of stomachs examined ranged from 250 to 600 per species. Other food studies, involving similar numbers, were carried out in three other Ontario waterways: Jones Creek near Brockville, Fish Lake near Picton, and Kearney Lake in Algonquin Park. Thus, for about two-thirds of the species, comparable information was obtained. Data for other parts of the species range is from the literature. An understanding of food changes with growth is desirable since a structure could be of greater importance at one stage of life than another.

Feeding, general behavior, and habitat distribution of the Lake Opinicon fishes was studied in the lake using a canoe and snorkel. Indoor studies were conducted in large aquaria.

BODY AND FIN FORM IN FISHES

A brief review of existing knowledge of the significance of the common kinds of body forms found in fishes is a prerequisite.

The following is synthesized from various sources, but particularly Gray (1933, 1953, 1960); Harris (1936, 1938); Nursall (1958); Bainbridge (1958, 1960); Lagler et al. (1962); Young (1962); and Norman and Greenwood (1963).

The fusiform body, moderately elliptical in cross section (Figs. 1–3) is physically the most efficient for rapid progression through a liquid medium; hence, it is characteristic of fish species that swim more or less continuously

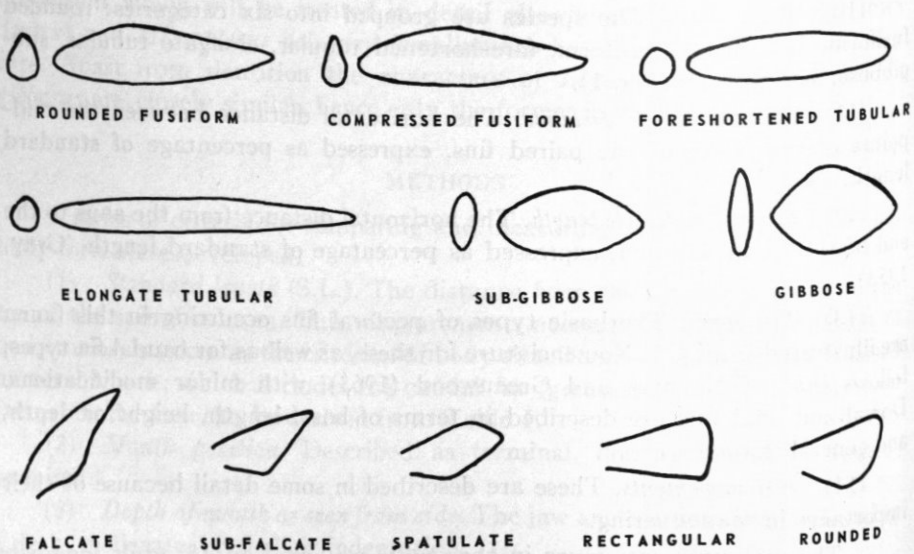

FIG. 1. Different kinds of body shapes, transverse sections and side views (upper), and kinds of pectoral fin (lower) of fishes of Lake Opinicon, Ontario.

and range widely. Propulsion is by means of alternating lateral contractions of the muscular body, plus the movements of the caudal fin, the latter providing a significant part of the forward thrust, estimated at 40% in the whiting, *Gadus merlangus* (Gray, 1933). There is a narrow, flexible caudal peduncle, muscular in generalized fishes, but largely tendinous in the pelagic tunas. The caudal fin is characteristically forked, thus serving to reduce turbulence and increase the fin's aspect ratio (ratio of span to length). However, for a fish accelerating to high speed from rest, too high an aspect ratio would cause the fin to stall. In such fish then, the caudal fin is usually wedge-shaped rather than crescentic, and, although it may be deeply indented, the posterior margin is convex rather than concave (Fig. 3). Generalized fishes like *Micropterus dolomieu* and *P. flavescens*, accordingly, have an aspect ratio between 2 and 4, whereas this reaches 6.1 in the continuously swimming marine tuna (Nursall, 1958). Furthermore, bass and perch, and others like them, can move the individual rays of the caudal fin independently. This facilitates hovering. Fish with truncated and rounded tails (and a low aspect ratio) are comparatively slow swimmers and, although capable of sudden bursts of speed, are unable to swim for long periods at high speed (Norman and Greenwood, 1963).

Paired and median fins function as stabilizing and maneuvering organs, the pectorals being the main medium whereby turning, banking, rising, diving, and stopping are accomplished. In swift fishes the pectoral fin is usually long and falcate, whereas in slow swimmers it is commonly rectangular, rounded, or spatulate (Figs. 1, 3). Median fins have a basic role as vertical keels. In species where the dorsal fin can be raised and lowered, it is elevated at the beginning of a turn, thus increasing the yawing movement (lateral oscillations about the path of progression) produced by the asymmetrical action of the body muscles, the unilateral braking action of a pectoral fin providing the fulcrum about which the turn is completed.

The gibbose body form (Fig. 1) has evolved independently in many suborders. Its possessor is "a very stable swimmer, since its large lateral area limits rolling, while pitching rotations can be controlled by the pectoral and pelvic fin forces: asymmetrical vertical forces can also be used to tilt the body laterally at any desired angle. The large lateral area demands large dorsal and anal fins to provide static stability in yaw during forward movement: normal propulsion is often produced by rowing with the pectoral fins". (Harris, 1938).

Where the pectoral fins are used for active propulsion, the amount of fin musculature is large with the adductors forming some 65% of the whole. There is free articulation of the first fin ray on the scapula to permit a "feathering" return motion. Fishes in which the pectorals function primarily as brakes have less fin musculature, most of the weight being made up of the adductors. Here the first fin ray, which takes most of the water force, rotates outward on a simple roller-bearing joint (Harris, 1938). Breder (1924) has drawn attention to a function of the pectorals in hovering fish like *L. macrochirus*: they move in rhythm with the respiratory movements, thus checking the forward thrust that results from expulsion of water from the operculum.

The pelvic fins are far forward in the gibbose fishes functioning here to neutralize the lift force of the relatively high pectorals. A compromise is involved: if the pelvics were far back, their downward force would depress the tail and lift the head (positive pitch). On the other hand if the pectorals were lower, their effectiveness as brakes would be reduced. Long-bodied teleosts with widely separated paired fins do not have this problem. The pectorals are ventral and situated well in front of the center of gravity, instead of close to it. The posteriorly located (abdominal) pelvic fins keep the tail end of the body from tipping up (negative pitch) when the fish stops (Lagler et al., 1962).

THE SPECIES, THEIR MORPHOLOGICAL CHARACTERISTICS, FEEDING HABITS, AND FOOD

The differences in body size of the species are indicated diagrammatically in Fig. 2, typical large adults being shown. The average standard lengths are given in Table I. The species range from large piscivores like *E. lucius*, which in this lake reaches slightly over 500 mm, down to small minnows like *N. heterodon* with a standard length of 50–55 mm.

The body and mouth forms of the species are illustrated in Figs. 3 and 4, their characteristics being compared quantitatively in Tables I and II.

UMBRIDAE

MUD MINNOW

In *Umbra limi*, the aperture of the terminal mouth is relatively wide, averaging 4.7 mm (8% S.L.) in the adult fish (Table I). The premaxilla is fixed, giving strength, the jaws are somewhat heavy, and the marginal dentition, consisting of a double row of sharp conical and recurved teeth, is moderately strong. The mouth is scoop-like (Fig. 4), and the feeding action is a snapping one.

The dominant foods are as follows. Lake Opinicon: Chironomid larvae and pupae (10–35% volume); Gastropoda (up to 40%); Ostracoda (5–10%); Amphipoda (up to 20%); small Ephemeroptera nymphs (up to 20%); Trichoptera larvae (up to 15%); and Coleoptera (up to 15%). Fish Lake: similar but less emphasis on chironomid larvae and slightly more on Ostracoda, small Odonata nymphs, and Hydracarina. Jones Creek: similar but Isopoda and Odonata nymphs more, and Ephemeroptera nymphs, less important. First-year fish (30–60 mm S.L.) have the same diet as adults but Cladocera make up a small proportion of the food (up to 20% volume). Such studies as have been carried out on the food of *U. limi* in other parts of its range (Pearse, 1916; and others) substantiate these findings. *Umbra limi* thus obtains its food from the bottom and rooted vegetation. The prey is relatively large and hard-bodied (note the wide gape, strong jaws, fixed premaxilla, and well-developed marginal (and buccal) dentition).

Measurements show that the body form of *U. limi* is foreshortened tubular (Fig. 3) the height: width ratio being 1.4 (Table I). In accordance with this, the paired fins are widely spaced and ventral. The single dorsal fin is medium-based,

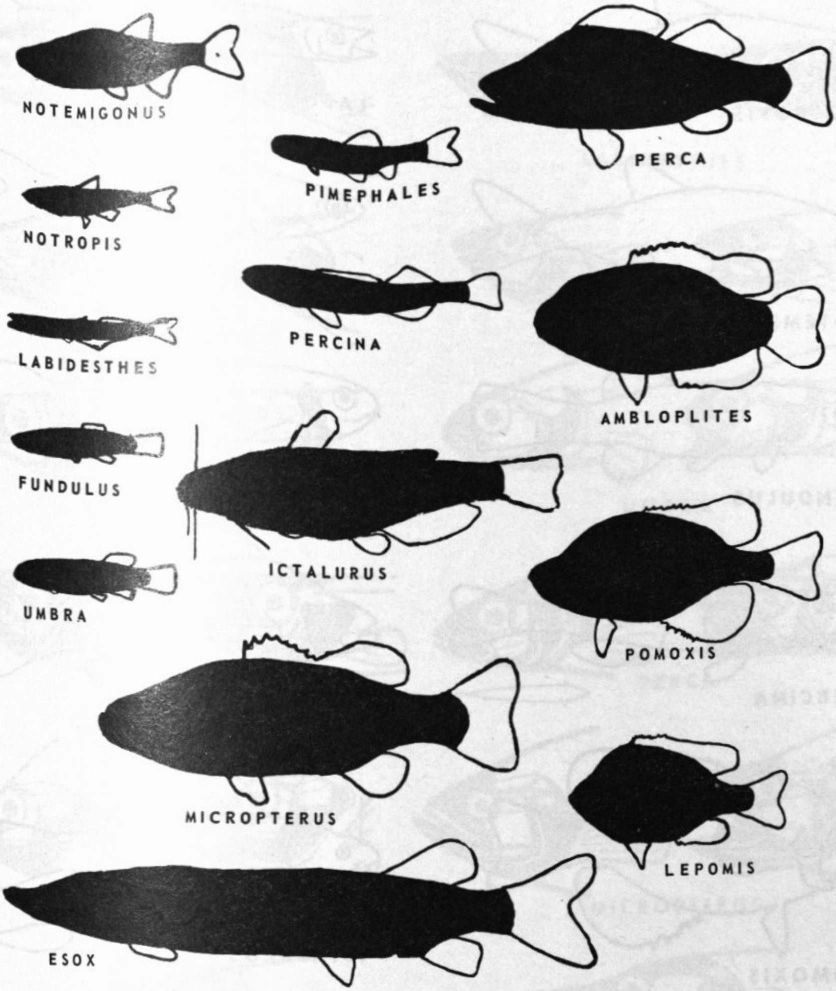

FIG. 2. General differences in body size of typical adult members of the cohabiting fish species in Lake Opinicon, Ontario. *Micropterus* and *Esox* are $\frac{5}{6}$ of natural size.

of intermediate height, rounded, and placed posteriorly; the anal is short-based, deep, and rounded. The whole body is thick, this presumably being of advantage amongst the tangled vegetation that forms its preferred habitat; this body form may also explain its ability to burrow into the soft mud to hibernate and escape predators. On the other hand, *U. limi* is a slow swimmer, as the thickened peduncle and rounded caudal fin indicate. The posterior dorsal and anal fins could supplement the propulsive action of the tail during sudden escape movements.

Aquarium studies reveal that *U. limi* has the characteristic habit of holding still in midwater for long periods, often with the body inclined upwards. The former is achieved not by a regular beat of the pectoral fins but by a

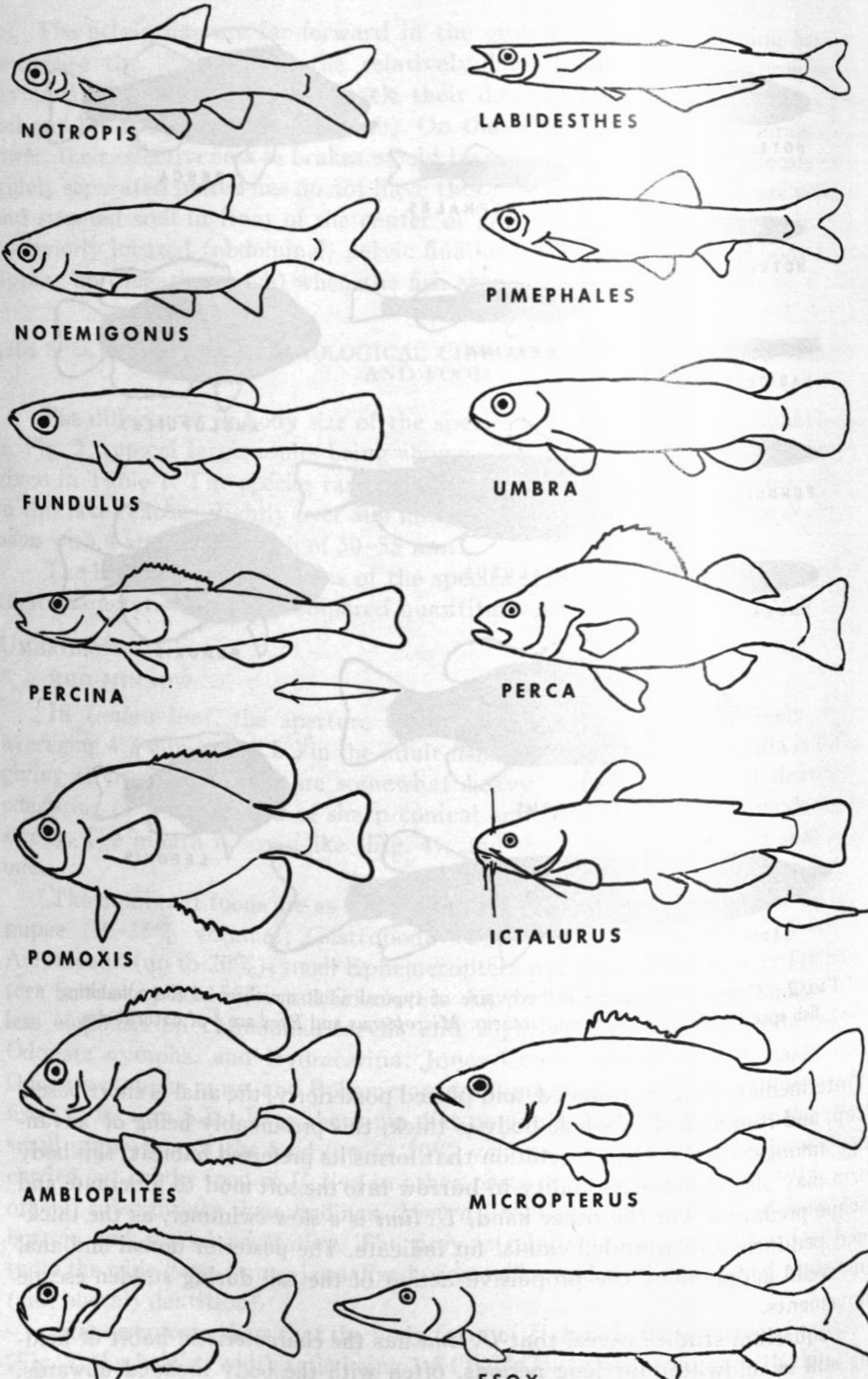

FIG. 3. Comparative body and fin morphology of fishes of Lake Opinicon, Ontario.

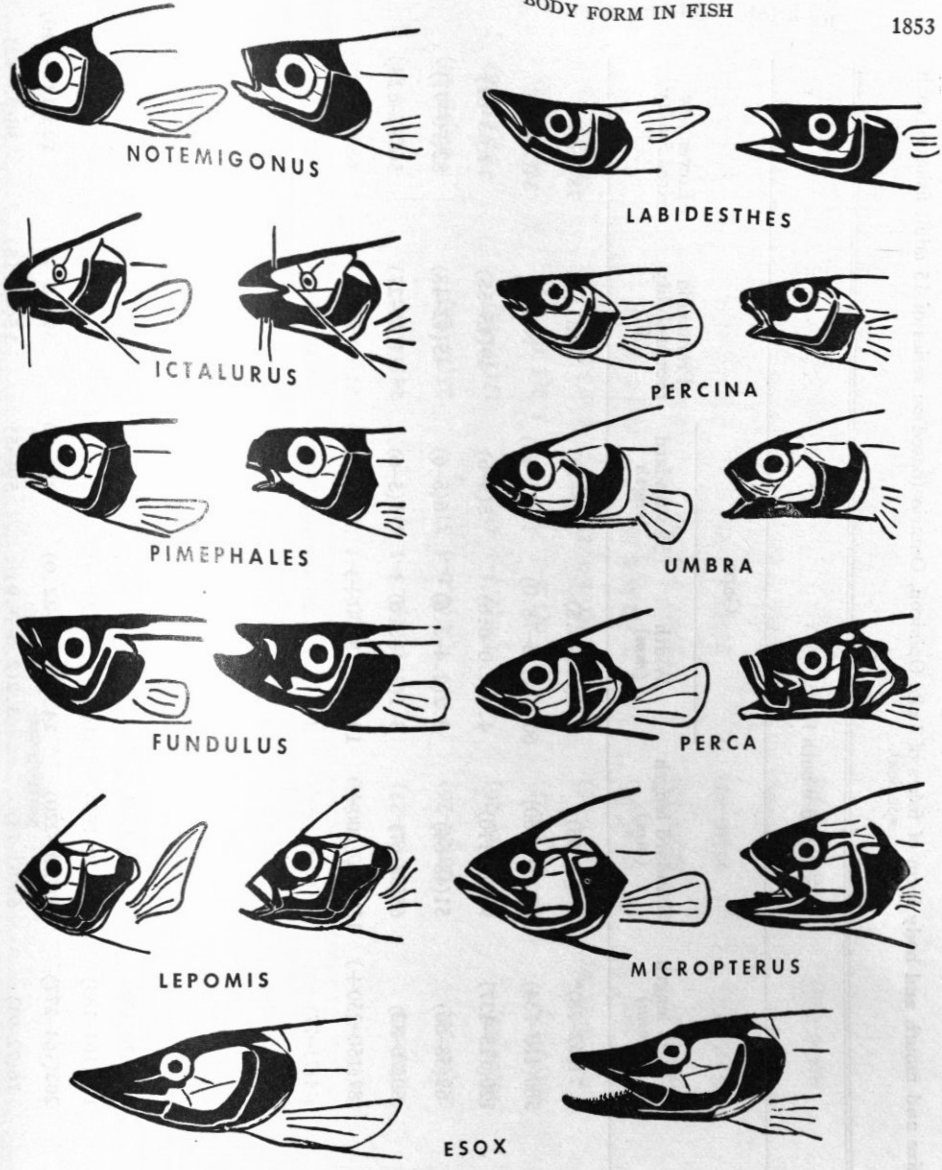

FIG. 4. Mouth morphology (closed on left, open on right) of fishes of Lake Opinicon, Ontario

continuous rippling movement (Table II), undulating waves passing anteroposteriorly across the extended fin surface. There is a simultaneous oscillation of the large dorsal fin. By contrast, terminal movements in the expanded anal fin are slight. When feeding, *U. limi* maneuvers close to its prey, then seizes it with a sudden strike. This, and the subtle fin movements which cause a minimum of turbulence, may be significant in stalking prey with the capacity for making rapid escape movements (such as Ephemeroptera nymphs and Coleoptera).

TABLE I. Quantitative data on size and mouth and body form of fishes of Lake Opinicon, Ontario (based on series of 15 adult fishes of each species).

	Size and mouth form					
			Gape			
Species	Total length (*mm*)	Standard length (*mm*)	Width (*mm*)	% standard length	Premaxilla protrusibility (%)[b]	Lower jaw extensibility (%)[b]
Umbra limi	71(62–78)[a]	59(52–65)	4.7(2.9–6.5)	8(7–10)	Nil	78(75–90)
Esox lucius	580(410–754)	500(350–650)	60.0(49.5–78.0)	12(11–12)	Nil	34(29–39)
Notemigonus crysoleucas	120(115–137)	96(92–110)	4.6(4.0–6.6)	5(5–6)	49(45–55)	74(63–82)
Notropis heterodon	62(58–66)	51(48–54)	3.2(2.4–3.6)	6(5–6)	45(42–48)	82(70–91)
Pimephales notatus	80(76–82)	65(62–67)	3.1(3.1–3.6)	5(5–6)	24(21–27)	56(51–62)
Ictalurus nebulosus	187(150–250+)	150(120–200+)	19.5(14.4–30+)	13(12–15)	Nil	63(54–66)
Fundulus diaphanus	74(71–77)	62(60–65)	3.9(3.0–4.2)	6(5–6)	35(28–40)	65(54–74)
Perca flavescens	159(147–295)	135(125–250)	10.8(8.8–5.0)	8(7–10)	20(18–29)	55(46–78)
Percina caprodes	104(93–116)	90(80–100)	4.5(3.2–5.0)	5(4–5)	Nil	61(50–70)
Micropterus salmoides	540(420–600)	450(350–500)	64.0(50.0–85.0)	16(16–17)	17(16–18)	104(90–118)
Lepomis macrochirus	170(158–189)	135(125–150)	8.1(6.2–12.0)	6(5–8)	48(42–58)	100(98–105)
Ambloplites rupestris	176(164–189)	140(130–150)	16.8(13.0–21.0)	12(10–14)	20(16–24)	107(99–112)
Pomoxis nigromaculatus	202(164–277)	160(130–220)	14.4(10.0–22.0)	9(8–10)	39(38–40)	123(114–130)
Labidesthes sicculus	76(72–91)	65(62–78)	3.2(2.5–3.9)	5(4–5)	15(11–18)	38(33–42)

Species	Body form				
	Width : length ratio	Height : length ratio	Height : width ratio	Pectoral-pelvic distance, % of standard length	Caudal peduncle, % of standard length
Umbra limi	16(15–17)	23(23–24)	1.4(1.3–1.5)	26(24–28)	28(27–29)
Esox lucius	13(12–15)	18(16–19)	1.3(1.0–1.4)	25(24–26)	23(22–24)
Notemigonus crysoleucas	12(12–13)	24(23–25)	2.0(1.9–2.0)	22(21–23)	35(34–37)
Notropis heterodon	13(13–14)	23(22–24)	1.7(1.5–1.7)	21(20–22)	32(29–34)
Pimephales notatus	15(14–15)	20(19–22)	1.4(1.3–1.4)	24(23–26)	32(32–34)
Ictalurus nebulosus	20(19–21)	25(24–26)	1.2(1.0–1.3)	23(20–25)	37(34–40)
Fundulus diaphanus	15(14–15)	19(19–20)	1.3(1.3–1.4)	17(17–18)	35(35–36)
Perca flavescens	16(16–17)	27(26–27)	1.6(1.6–1.7)	5.2(5.1–5.4)	32(32–33)
Percina caprodes	14(14.0–14.2)	17(17–18)	1.2(1.1–1.2)	3.4(3.0–3.9)	37(36–38)
Micropterus salmoides	18(18–20)	37(36–39)	2.1(2.0–2.5)	0.6(0.4–0.7)	34(33–35)
Lepomis gibbosus macrochirus	21(21–22)	52(51–53)	2.6(2.5–2.9)	6.0(5.4–6.2)	40(40–42)
Ambloplites rupestris	19(18–19)	41(40–42)	2.1(2.1–2.2)	3.2(3.0–4.0)	41(39–42)
Pomoxis nigromaculatus	15(15–16)	42(41–44)	2.8(2.7–2.9)	0.7(0.6–0.8)	49(47–51)
Labidesthes sicculus	9(8.9–9.1)	12(11–12)	1.3(1.2–1.4)	16(15–16)	48(47–48)

[a]Average and range.

[b]See text.

TABLE II. Mouth, body, and fin structures of fishes of Lake Opinicon, Ontario.

Species	Body form	Mouth			Caudal peduncle form	Pectoral fin		Caudal fin
		Position	Aperture	Form		Form	Movement	
Umbra limi	Foreshortened tubular	Terminal	Moderate	Scoop	Thick	Rectangular	Undulating	Rounded truncate
Esox lucius	Elongate tubular	Terminal	Wide	Broad beak	Short	Rectangular	Undulating when small	Deeply forked; rounded tips
Notemigonus crysoleucas	Compressed fusiform	Dorso-terminal	Narrow	Scoop	Long and slender	Sub-falcate	Synchronized beat	Deeply forked; pointed tips
Notropis heterodon	Compressed fusiform	Dorso-terminal	Narrow	Scoop	Long and slender	Sub-falcate	Synchronized beat	Deeply forked; pointed tips
Pimephales notatus	Rounded fusiform	Ventro-terminal	Very narrow	Tubular	Long and slender	Sub-falcate	Synchronized beat	Deeply forked; rounded tips
Ictalurus nebulosus	Flattened head; compressed body; sensory barbels	Terminal	Wide	Broad but low scoop	Short	Rounded	Extended as hydrofoils; intermittent, synchronized beat	Emarginate
Fundulus diaphanus	Rounded fusiform	Dorso-terminal	Narrow	Sub-tubular	Long	Spatulate	Independent beat; rapid	Truncate
Perca flavescens	Compressed fusiform	Terminal	Moderate	Scoop	Moderately long	Rounded	Alternating beat, horizontal plane; mild wrist action	Shallowly forked
Percina caprodes	Elongate tubular; snout knob	Ventro-terminal	Narrow	Small; snapping action	Moderately long	Spatulate	Synchronized, oar-like sweep; bottom props	Emarginate
Micropterus salmoides	Compressed fusiform	Terminal	Very wide	Cavernous scoop	Functionally short	Rounded	Alternating beat; minor wrist action	Shallowly forked, rounded tips
Lepomis macrochirus	Gibbose	Terminal	Narrow	Sub-tubular, snapping or nipping action	Functionally short	Falcate, large	Independent beat; marked wrist action	Shallowly forked, rounded tips
Ambloplites rupestris	Sub-gibbose	Terminal	Wide	Scoop	Functionally short	Rounded	Independent beat; slight wrist action	Shallowly forked, rounded tips
Pomoxis nigromaculatus	Gibbose	Dorso-terminal	Moderate	Scoop	Functionally short	Rounded, large	Independent beat; slight wrist action	Shallowly forked, rounded tips
Labidesthes sicculus	Elongated tubular	Dorso-terminal	Narrow	Fine beak	Long	Falcate, high on body	Independent beat; wide sweeping movements	Deeply forked; pointed tips

Esocidae

NORTHERN PIKE

In *Esox lucius*, the mouth aperture is wide, averaging 60 mm in a 500 mm fish (i.e. 12% S.L.). The mouth is terminal. From the side, the jaw angle forms a deep indentation, this being achieved by a flattening of the head to produce a snout similar to a "duck bill". The premaxilla is fused and the lower jaw moves in a downward, rather than a downward and forward plane. The jaws are massive. The premaxilla bears a single row of small, slender, conical teeth, strongly recurved; these are duplicated on the lower jaw but the lateral "canines" are much enlarged, compressed, triangular in shape, and have attenuated, recurved points. The marginal (and buccal) teeth are so angled that, once grasped, the prey can only move backwards towards the throat. Like other fish, *E. lucius* begins life as a plankton feeder but this phase is brief and limited to fingerlings below 30 mm in length. The species is largely piscivorous beyond 45 mm (Hunt and Carbine, 1950). Size of the prey increases as the pike grows; in Lake Opinicon the smaller fish take minnows (*P. notatus*, *N. heterodon*) and darters (*Etheostoma exile*), the larger fish sunfish (*L. machrochirus*) and alewife (*Pomolobus pseudoharengus*). Pike also occasionally take take small birds and rodents.

The body of *E. lucius* is elongated tubular, having a height: width ratio of 1.3. Accordingly, the pectorals and pelvics are widely separated and ventral. The single dorsal fin is high and short-based, the anal short-based, deep, and rectangular. Placed far posteriorly, these fins supplement the deeply forked caudal fin in forward propulsion. The caudal peduncle is short, but this is compensated for by the flexibility of the posterior part of the trunk. The concentration of power represented by the combined dorsal, anal, and caudal fins probably underlies the ability of *E. lucius* to make swift strikes from rest, for prey is usually rushed from a short distance away. The tubular body form is also effective in negotiating vegetation.

In the adult pike the extended, or semi-extended, pectoral fins, ventral in position and rectangular in form, have a stabilizing function. In small fish, however, they exhibit pronounced rippling movements similar to those that have been observed by us in *U. limi* and *Esox americanus vermiculatus*.

All aspects of the body and mouth form of *E. lucius* show great specialization for a piscivorous way of life.

Cyprinidae

The cyprinids are characterized by the absence of marginal teeth and possession of soft fin rays.

GOLDEN SHINER

In *Notemigonus crysoleucas*, the mouth aperture is relatively narrow, averaging 4.6 mm in adults (5% S.L.). The mouth is dorso-terminal. From the side, the jaw angle forms a shallow indentation, though the latter is compensated for by a protrusible premaxilla and extensible mandible to produce a scoop-like structure. In Lake Opinicon the main foods are Cladocera, which account for 20–90% of the volume, depending on the month, flying insects (20%), chironomid pupae (10–30%), along with some filamentous algae (important in late summer). Very small numbers of Odonata nymphs, Coleoptera, and Hydracarina are taken. These foods are also characteristic in Fish Lake, where Mollusca also occur in the diet, Kearney Lake, and Jones Creek, as well as in Wisconsin (Pearse, 1916), Oklahoma (Carter, 1949), and various other parts of the range (Dobie et al., 1948). There is no significant difference in the basic diets of adults and young. It is obvious that *N. crysoleucas* is almost entirely a middle water and surface feeder, a prediliction that can readily be observed in aquaria. The position of the mouth is an adaptation for this as is the narrow gape for selecting items of relatively small size.

The body is compressed fusiform, the height:width ratio being 2.0. The caudal peduncle is long and slender and the caudal fin deeply forked. The pectorals and pelvics are widely separated and placed low on the body. A feature is the angular form of the fins. The pectorals are subfalcate, the short-based dorsal is high and triangular, and the short-based anal is deep and triangular.

Individually and in combination the body characters of this species are those of a very mobile fish and in Lake Opinicon the schools move over wide areas. The major feature, however, is its great maneuverability, the individuals twisting and turning with great rapidity as they feed. Small Cladocera are snapped up individually. Marked mobility of the fins is apparent at this time, the pectorals moving with sharp, synchronized, oar-like beats, and the dorsals being constantly raised and lowered as they initiate turns. *Notemigonus crysoleucas* does, on occasions, swim slowly or hold still, at which time position is maintained by a slow beat of the pectorals, a fluttering action of the upper lobe of the caudal fin, and an occasional twitching of the dorsal and anal fins.

BLACKCHIN SHINER

Notropis heterodon, in its mouth, body, and fin forms, is a small replica of the foregoing. Adults reach a standard length of only 50–55 mm, compared with 110 mm in *N. crysoleucas*. The gape, averaging 3.2 mm (6% S.L.), restricts the species to small food items such as Cladocera (from 20–50% volume), flying insects (10–80%), and filamentous algae.

The height:width ratio of the body (1.7) is somewhat less than that of *N. crysoleucas*, whereas the pectoral-pelvic distance and caudal peduncle are somewhat shorter. The significance of these minor differences is not clear. However, *N. heterodon* is much less widely ranging, being found mainly in the shallows close to shore. Like *N. crysoleucas* it is highly maneuverable.

BLUNTNOSE MINNOW

The mouth is ventro-terminal, tubular, and narrow, the aperture averaging only 3.1 mm (5% of the S.L.). In Lake Opinicon *Pimephales notatus* subsists almost entirely on organic detritus from the bottom (20–50% volume), small chironomid larvae (5–30%), and Cladocera (10–75%). In Kearney Lake the stomachs contain mostly chironomid larvae and algae (Sheppard, 1965). "Bottom ooze" is an important item of diet in most parts of the range, as recorded by Kraatz (1927) for Ohio and Starrett (1950) for Iowa. Thus the diet reflects this species structural specializations for bottom feeding. Aquarium observations confirm its ability to take Cladocera from the water column and show that it is quite unable to get its mouth into the necessary position to pick up items from the surface.

The body form of this species is more rounded and tubular than that of the other two cyprinids in the lake, the height:width ratio being 1.4. The pectoral–pelvic distance and relative length of the caudal peduncle are comparable. The fins, especially the caudal, are more rounded. Although retaining a measure of maneuverability, *P. notatus* definitely does not have the capacity for rapid acceleration, the restless mobility, nor the graceful gliding movements of *N. crysoleucas* and *N. heterodon*. It is a rather local species in Lake Opinicon, being found in the shallows over areas of sandy and muddy bottom.

Ictaluridae

The ictalurids are adapted for life in muddy water and/or nocturnal feeding, depending on chemosensory barbels, rather than vision, to locate food. The eyes are small and sight is poorly developed.

Brown bullhead

In *Ictalurus nebulosus*, the terminal mouth aperture extends for almost the entire width of the broad, flat head, averaging 19.5 mm (13% S.L.) in fish of 150 mm. From the side, the jaw angle forms a shallow indentation. The premaxilla is fixed, and the marginal dentition consists of several ill-defined rows of relatively long, conical, slightly recurved teeth.

In Lake Opinicon, fish 30–60 mm total length feed mainly on chironomid larvae (up to 50% volume), Cladocera (60%), Ostracoda, Amphipoda, Hemiptera, and small Ephemeroptera. These same items characterize the 70–120 mm group but Cladocera are replaced by increased amounts of Hemiptera, Ostracoda, and, in July, some newly hatched fish fry. Large fish of 130–240 mm total length feed on chironomid larvae (up to 80% volume), Mollusca (40%), Ostracoda (30%), small crayfish (20%), and Amphipoda (16%). In Jones Creek the diet is similar but leeches replace decapods. This versatile pattern of feeding agrees with findings in other parts of the species range (Baker, 1916; Nurnberger, 1930; and Moore et al., 1934).

Ictalurus nebulosus is hence mainly a bottom feeder, obviously capable of handling small items (chironomids) as well as larger hard-bodied prey. In aquaria, feeding is done by "nosing" along the bottom at a declined angle, somewhat in the manner of a vacuum cleaner, the ventral barbels just touching the substratum. When food is detected, the fish turns quickly and seizes it with a snapping action. A degree of suction appears to be involved in the case of smaller prey because a fish will often draw up detritus, mouth it, and then expel the residue. Since the mouth is terminal the fish may have to tilt to the vertical to seize an item on the bottom. The great dependence of this species on its chemotactile barbels is seen when aquarium fish are presented with small pieces of liver. They immediately go into vigorous searching movements of a random nature, threshing about until one happens to touch the item with its barbels or body. As often as not the object will be missed and fall to the bottom, to be obtained later by systematic searching.

The body of *I. nebulosus* is flat anteriorly, compressed posteriorly, and the pectorals and pelvics are widely separated. The whole posterior half of the body is used in propulsion, the swimming movements being sinuous and sub-anguilliform. The caudal fin is large and emarginate, as in many relatively slow-swimming fish. The high, short-based, dorsal fin is far anterior at the point where the body narrows where it can be of maximum advantage both as a keel and a turning aid. The anal is posterior, long-based, deep, and rounded, and such a fin in the catfishes, like the heterocercal tail of sharks, gives lift and negative pitch (Young, 1962). The paired fins are shark-like, being large, low on the body, and held outwards in a horizontal plane. Although they beat periodically with a synchronized action their main function is that of hydrofoils, effecting the tilting of the body necessary in bottom feeding and counteracting the lifting force of the enlarged anal.

CYPRINODONTIADAE

In typical cyprinodonts, the head is flattened anteriorly and the mouth opens dorsally, both adaptations for surface feeding (Hubbs and Lagler, 1958).

BANDED KILLIFISH

In *Fundulus diaphanus* the mouth aperture is relatively narrow, 3.9 mm (6% S.L.) in fish of 60–65 mm S.L. From the side, the jaw angle forms a shallow indentation. The mouth is sub-tubular, the premaxilla being protrusible. The marginal dentition consists of two rows of long, sharp, conical, and recurved teeth.

This species is a most versatile feeder. Small individuals of 30–40 mm total length take mostly chironomid larvae (up to 60% volume), Ostracoda (35%), Cladocera (25%), Copepoda (30%), Amphipoda (5%), and flying insects (5%). In adults of 60–80 mm these same items predominate but small, newly hatched Odonata and Ephemeroptera nymphs, Mollusca, and Turbelaria are also taken. This is the only species to prey upon ostracods to a significant degree. The diet in Fish Lake is similarly diverse. *Fundulus diaphanus*, accordingly, feeds effectively at all levels despite the dorso-terminal position of its mouth. However, when the mouth is fully open its position becomes almost terminal. The body is rounded fusiform, having a height: width ratio of 1.3. The caudal peduncle is moderately long and slender and the pectorals and pelvics are well separated. The pectoral fins are low and spatulate. The dorsal is single, medium-based, of intermediate height, and centrally placed on the body, and the anal is short-based, rectangular, and of intermediate depth. With the exception of the truncate caudal, the body and fin forms are thus not unlike those of *P. notatus*. The rather long caudal peduncle, however, may serve to compensate for the absence of a forked tail.

Feeding in *F. diaphanus* is as a member of a school. Although the schools are mobile they keep largely to shallow areas of sandy bottom. Individually, the species is characterized by swift darting and evasive movements and moderate maneuverability. It lacks, however, the continuous twisting and turning of *N. heterodon* and *N. crysoleucas* and since it only takes Cladocera at times of superabundance, it is possibly a much less efficient hunter of these organisms. Its ability to handle hard-bodied items is favoured by the marginal teeth. To sum up, *F. diaphanus* may be classified as a species that is rather generalized in body form as well as food and feeding habits.

Fundulus diaphanus frequently rests in the middle water or near the surface. Position is maintained during this time by a continuing series of sharp, rapid beats of the pectorals (synchonously or independently), and sharp flicking movements of the distal portion of the caudal fin. There is little movement in the extended dorsals and anals at this time.

PERCIDAE

YELLOW PERCH

In *Perca flavescens*, the mouth aperture is of moderate width, averaging 16.0 mm (8% S.L.) in fish of 200–250 mm S.L. The mouth is terminal, and from the side, the jaw angle forms an indentation of intermediate depth. The bones of the jaw margin are stout, but the premaxilla is somewhat protrusible. The jaw action can be described as a snapping scoop. The marginal teeth, set in three or four rows, are stout, sharp, conical, straight, and angled posteriorly.

After an initial stage of feeding on Cladocera, Ostracoda, and chironomid larvae, *P. flavescens* passes, by the end of the first year, to a mixed diet of Odonata nymphs (up to 40% volume in some months), Ephemeroptera (30%), newly hatched Mollusca (35%), Ostracoda (30%), chironomid larvae (20%), and fish fry (30%). Thereafter, there is a steady transition to the adult diet which, in fish of over 150 mm total length, is made up of Decapoda (up to 70% in some months), small fish (75%), and Odonata nymphs (40%). The diet in Lake Opinicon corresponds to that recorded for other parts of the range (Nurnberger, 1930; Ewers and Boesel, 1935; Langford and Martin, 1940; Parsons, 1950; Pycha and Smith, 1954). The species thus is a middle-water and bottom feeder. The prevalence of relatively large and hard-bodied items accords well with the general jaw structure and dentition.

The height:width ratio of the body is 1.6, so that it is compressed fusiform. The pectoral–pelvic distance is relatively short, as in all percoids, and the caudal peduncle is moderately long. The pectorals are low and rounded. The dorsal, long-based and of intermediate height, is double, being composed of separate anterior spiny-rayed and posterior soft-rayed segments, as in other percids. The anal is short-based, rectangular, and of intermediate depth. The caudal fin is shallowly forked.

In the aquarium this is a somewhat restless species, never remaining still for long, and preferring to patrol in the lower parts of the tank. Such a hunting pattern must favour the catching of decapods and Odonata nymphs since these organisms have a patchy distribution. Patrolling is a prerequisite also for the piscivorous way of life, although fish do not become important in the diet until *P. flavescens* is large.

When hanging in mid-water, which it does from time to time, *P. flavescens* holds its pectoral fins outwards, almost at right angles from the body. They beat alternately with an oar-like action and a degree of "wrist" movement reminiscent of the sunfishes. Simultaneous movements of the upper regions of the dorsal and caudal fins, characteristic of many other fishes, are lacking. The shallowness of the pectoral beat of *P. flavescens*, terminated before the fin reaches the body, may partly compensate for this. *P. flavescens* sometimes rests on the bottom.

LOG PERCH

In *Percina caprodes*, the mouth aperture is narrow, averaging 4.5 mm (5% S.L.) in large individuals of 80–100 mm S.L. The mouth is ventro-terminal. The jaw angle forms a shallow indentation from the side and the premaxilla is fixed. The marginal teeth are proportionately shorter and more numerous than in *P. flavescens*. The mouth closes with a snapping action. *Percina caprodes* has a rounded knob on the snout that it uses to roll over leaves and small stones to expose the organisms underneath and is the only species in the lake with this feature.

Young *P. caprodes* feed partly on Cladocera (Ewers and Boesel, 1935; Turner, 1921). The adults in Lake Opinicon take a variety of bottom organisms: chironomid larvae (70% volume in some months), Amphipoda (up to 40%), Isopoda (20%), small Anisoptera nymphs (15%), and Ephemeroptera nymphs (10%). This accords with the food in other regions (e.g. Pearse, 1916). The position, diameter, and structure of the mouth correlates well with a diet of exclusively bottom-dwelling organisms of small size.

The body has a height: width ratio of 1.2 and can be described as elongate tubular. It is thus a typical member of the Etheostomatinae which, with the partial exception of the piscivorous Luciopercinae, are the longest-bodied members of the Percoidea. The caudal fin of *P. caprodes* is shallowly forked. The median fins resemble those of *P. flavescens* though the anal, which functions as a prop, is rounded. As in all percoids the pectoral and pelvic fins lie close together, the distance between the two being only 3% of the standard length. This condition is anomalous for a long-bodied fish; compare (Table I) with *Labidesthes sicculus* (16%), *E. lucius* (25%), and *Ictalurus nebulosus* (23%). The pectoral fins are low on the body, exaggerated in size, spatulate or fan-shaped, and are reinforced anteriorly with stout spiny rays. When moving rapidly, these fins sweep the water with synchronized oar-like action. When resting on the bottom, in which position *P. caprodes* spends most of its time, the laterally projecting pectorals, along with the median pelvics, function as angular supports.

Percina caprodes is incapable of prolonged swimming. Its movements are rapid and erratic, amounting to a jerky zig-zag action. After a short period of violent activity, the fish drops back to the bottom, unable to maintain a position in midwater. This instability probably results from the positions of the paired fins, together with the tubular body form. A tubular body, as compared with a fusiform, does not, however, necessarily prevent its possessor from being an active swimmer (*E. lucius* and *Labidesthes sicculus* are examples). The perciform paired fin distribution has, however, probably determined the direction that evolution could take. The body form and enlarged pectorals are possibly secondary developments. The outcome is a successful evolutionary line of bottom dwellers lacking sustained swimming and directional ability but with well-developed ventral supports for resting, and a powerful muscular body permitting sudden escape movements from this position. The enlarged pectoral fins lack the refined "wrist-action" movements of *P. flavescens*.

Such feeding as has been observed in *P. caprodes* has consisted of a series of short, forward searching movements with intervening rests on the bottom. When a prey item is sighted, it is secured by a sudden dart forward. A leaf or stone is turned over in the same way, the fish pausing an inch or two distant, then quickly pushing the object out of the way.

In Lake Opinicon *P. caprodes* has a very restricted distribution, being confined to areas of pebbly bottom.

Centrarchidae

In the centrarchids, the body form ranges from compressed fusiform to gibbose. The pectoral and pelvic fins lie close together and are lateral. The caudal peduncle is functionally short (though at least 34% of the body length) because the gibbose body trend involves an expansion posteriorly to include much of it. Because of the method of measurement used (anus to end of spinal column), however, it appears long. The centrarchids have a long-based dorsal of intermediate height made up of anterior spiny-rayed and posterior soft-rayed portions. The two are separated in *M. salmoides*. The anal, which also has these subdivisions, varies from a short-based, rectangular structure in this species, through intermediate types in *L. macrochirus* and *A. rupesrtis*, to a long-based fin with greatly expanded posterior lobe in *P. nigromaculatus*. The caudal fin is large and tends to be emarginate.

Largemouth bass

In *M. salmoides*, the mouth aperture is exceptionally wide, averaging 50–85 mm (16% S.L.) in fish of 400–600 mm S.L. From the side, the jaw angle forms a deep indentation. The jaw margin is strong, with little protrusibility of the premaxilla. The marginal dentition consists of four to five rows of sharp, conical, and backwardly directed teeth, with those of the anterior row considerably enlarged. In opening, the lower jaw swings well forward and downward to form a snapping scoop.

Micropterus salmoides passes through the Cladocera- and insect-eating stages in the first month or two of life, with fish-eating commencing at about 50 mm total length (Turner and Kraatz, 1920; Ewers and Boesel, 1935; Cooper, 1937). Changes in food with growth in Lake Opinicon have been discussed by Keast (1965). Fish of 30–50 mm total length have a diverse diet of Cladocera (up to 50% volume), newly hatched Ephemeroptera nymphs (60%), Amphipoda (25%), chironomid larvae (20%), along with small quantities of Hemiptera, Copepoda, and Trichoptera nymphs. Slightly larger fish (50–70 mm) feed predominantly on Ephemeroptera nymphs (up to 40%), Odonata nymphs (20%), crayfish (20%), plus smaller quantities of Amphipoda, chironomid larvae, and small fish. Fish above 80 mm are predominantly piscivorous, small fish accounting for between 50% and 90% of stomach volumes and crayfishes for the remainder. At first the chief prey are minnows (*P. notatus* and *N. crysoleucas*), smaller *M. salmoides*, and *L. sicculus* (Keast, 1965). Sunfishes (*L. machrochirus*) and crayfishes form the bulk of the diet of the largest fish (Gilbert, 1962).

The body has a height:width ratio of 2.1 and hence approaches the compressed fusiform type. The separation of the two parts of the dorsal fin permits them to function independently. Thus, when the fish is moving forward, the anterior segment can be seen to lie flat against the back, reducing friction; during turns, however, it is erected (see introductory section for significance).

Adult *M. salmoides* are widely ranging in Lake Opinicon, tagged bass having been recovered 3½ miles away after a lapse of 6 weeks (Curran et al., 1947). First year individuals, however, are largely local in the shallows. In aquaria they spend much of their time patrolling slowly or hanging in midwater. The species obviously has not the maneuverability of the cyprinids.

Micropterus salmoides maneuvers into a favourable position close to its prey before striking. During this time the pectorals beat alternately in a horizontal plane, with only a hint of the "wrist action" seen in *L. macrochirus*, additional stability being obtained from terminal movements in the soft-rayed portion of the dorsal fin and upper lobe of the caudal fin. *Micropterus salmoides* is well adapted for the piscivorous way of life, particularly in mouth form.

SUNFISH

In *Lepomis macrochirus*, the mouth aperture is relatively narrow, averaging 8.0 mm (6% S.L.) in fish measuring 125–150 mm S.L. This is about one-third that of *M. salmoides* and half that of *A. rupestris*. From the side, the jaw angle forms a shallow indentation. The premaxilla is relatively protrusible, accounting for the rather tubular form of the terminal mouth. The marginal teeth resemble those of *M. salmoides* but are smaller. Food is obtained by a sharp snapping of the jaws possibly supplemented sometimes by a sucking action.

This fish is by far the most generalized feeder in Lake Opinicon, up to nine types of organisms commonly being found in a stomach at the 5% volume level or over (Keast, 1965). The different year classes consume the same foods, only the proportions varying. The major foods are chironomid larvae (up to 50% volume), Cladocera (30%), Amphipoda and Isopoda (10%), flying insects (35%), Odonata nymphs (20%), Ephemeroptera nymphs (10%), Trichoptera larvae (15%), Mollusca (15%), and fish fry (10%). Small quantities of Ostracoda, Copepoda, and algae, are also commonly present. Such diversity also characterizes other parts of the range (Moffett and Hunt, 1945; Ball, 1948; and Gerking, 1962). There is a large element of opportunism in the feeding of *L. macrochirus*, the dominant food usually being the resource that is most abundant at the time. *Lepomis macrochirus* feeds at all levels in the water.

The body form is gibbose, with the height:width ratio 2.5. Like other species with this body type, *L. macrochirus* feeds by patrolling slowly or by hanging still in the middle water from which position it can readily rush to the surface or bottom. In the lake individuals hover a few feet apart, moving independently in search of food.

The structural attributes and fin movements are directly associated with hanging, or hovering, in the water (see previous discussion). Stability is achieved by undulations of the enlarged posterior lobes of the dorsal and anal fins and the upper lobe of the caudal fin. The large, graceful pectoral fins, by which maneuvering is accomplished, beat independently with a pronounced rotating or "wrist" action. Their falcate shape is probably associated with reducing water resistance on the recovery stroke.

Lepomis macrochirus is local in its distribution and individual fish can be observed in the same place for hours on end.

ROCK BASS

In *Ambloplites rupestris*, the mouth aperture is wide, averaging 16.0 mm (12% S.L.) in fish of 130–150 mm S.L. The form of the mouth and the dentition are similar to those of *M. salmoides* and the jaw margins are thick. The jaw angle, however, forms a moderate rather than a deep indentation. In Lake Opinicon fish up to 70 mm total length feed mainly on chironomid larvae (up to 50% volume), Ephemeroptera nymphs (35%), Odonata nymphs (30%), Cladocera (40%), Amphipoda (30%), Isopoda (15%), and surface insects (35%), along with small quantities of Copepoda and Hydracarina (Keast, 1965). Above 75 mm there is an abrupt shift in diet, Odonata nymphs (up to 75% volume), Ephemeroptera (35%), Trichoptera (35%), fish fry (30%), and crayfish (15% and over), making up the bulk of the food. Chironomid larvae, Amphipoda, and Isopoda are relatively unimportant. The larger *A. rupestris* (i.e. between 120 and 200 mm) subsist almost entirely on crayfish and Anisoptera nymphs.

Hence, in its diet, *A. rupestris* specializes on the larger bottom-dwelling insects. The correlation between this and the relatively strong mouth and moderate gape is obvious.

The body form is intermediate between those of *M. salmoides* and *L. macrochirus*, i.e. sub-gibbose, being relatively thick, and having a height:width ratio of 2.1. It cruises more than the latter, and shows more tendency to move from the deeper water into the shallows to feed at night. Nevertheless, the "hanging and rushing" habit is well-developed, although the pectoral fins are distinctly shorter and more rounded and show only slight wrist action compared with those of *L. macrochirus*. Despite the fact that minnows appear in the diet of the larger fish, aquarium tests show *A. rupestris* to be much less adapt at catching these than *M. salmoides*, having great difficulty securing them if the first strike is unsuccessful. Tadpoles, by contrast, present no problem.

BLACK CRAPPIE

In *Pomoxis nigromaculatus*, the mouth aperture is moderate, averaging 14 mm (9% S.L.) in 130–180 mm S.L. fish. From the side, the jaw angle forms a shallow indentation. The premaxilla is somewhat protrusible and the lower jaw swings well forward on opening. The marginal dentition is similar to that of the other centrarchids, but the jaws are structurally lighter than in either *M. salmoides* or *A. rupestris*.

The main foods in Lake Opinicon are *Chaoborus* larvae (up to 70% of stomach volumes), Cladocera (up to 50%), Copepoda (20%), fish fry (25%), flying insects (15%), chironomid pupae and larvae (25%), and Ephemeroptera nymphs (10%). These items characterize all age groups, the proportions alone changing. It is apparent that, although the species is predominantly a midwater feeder, some prey is taken at all levels. The numerous gill rakers of *P. nigromaculatus*, 26–30 on the first arch (Keast, unpublished data) account for the prominence of Cladocera in the diet. The food in Lake Opinicon accords with that from other parts of the species range (Forbes, 1878; Forbes and Richardson, 1920; Pearse, 1919; Bailey and Harrison, 1945; Mitchell, 1945, 1949). In Texas, Mitchell (1945) has noted that planktonic Crustacea make up 50% of the diet until a total body length of 180 mm is reached. The species subsists largely on small fish after it has reached 250 mm total length.

The body and head are narrower than those of *L. macrochirus*, the height: width ratio being 2.8, and associated with this the long-based dorsal and anal fins are larger, with greatly expanded posterior lobes. The pectorals are large and rounded. The swimming and general hunting actions are not unlike those of *L. macrochirus*, with the addition of plankton straining. The species inhabits the deeper waters in the lake and is more mobile. There is some movement into the shallows at night.

ATHERINIDAE

BROOK SILVERSIDE

Labidesthes sicculus, a small fish, has a flat head that is modified anteriorly into a beaked snout. The mouth is dorso-terminal and from the side the jaw angle forms a deep indentation. The premaxilla is moderately protrusible. The mouth aperture is narrow, averaging 3.2 mm (5% S.L.). The well-developed marginal dentition consists of three rows of long, slender, sharp, conical, and slightly recurved teeth. These probably function like the serrations on a pair of tweezers ensuring a good grip on flying insects seized at the surface. The mouth operates with a snapping action.

Labidesthes sicculus is a specialized feeder, the diet being made up of Cladocera (frequently up to 80% volume), small flying insects (up to 40%), and *Chaoborus* larvae (50%). Smaller individuals in the population take relatively greater amounts of Cladocera (Keast, 1965). Hubbs (1921) and Boesel (1938) also record that Cladocera and flying insects predominate in the diet. All the food, accordingly, is taken from the middle water or surface. *Labidesthes sicculus* may leap out of the water to catch hovering insects (Hubbs, 1921).

The elongate tubular body, not unlike that of a pike, has a height:width ratio of 1.3. Obvious adaptations for surface feeding are the almost straight dorsal body line, the small dorsal fin, and the compensatory long-based deep, triangular, and markedly enlarged anal fin. The pectorals are set very high on the body, a position reminiscent of the marine "surface-skipping needle fish" (*Tylosurus*). When *L. sicculus* is holding still in the water, or is swimming slowly, the pectorals move independently with wide upsweeping movements. The species is highly mobile, ranging widely over the lake. It is apparently pelagic in midsummer, as in Lake Erie (Hubbs, 1921). Both nocturnal and diurnal feeding were observed.

STRUCTURAL SPECIALIZATIONS, WAY OF LIFE, AND FOOD NICHE

The survey shows that each of the structures studied is subject to variation from one species to another, and most of the differences may be quantified.

No two species are identical in all their characteristics. The structures (Table II) include a series of distinctive body forms, fin features, types of movement, mouth positions and shapes, and these can be correlated with different ways of life, degree of maneuverability, swimming power and speed, feeding levels, and kind of foods eaten. Some specializations characterize all the members of a family studied but others apply only to genera and species.

Ultimately, the structural characteristics of species are related to their food niches. The major types of food available in the lake, and the characteristics of the species that utilize them may be summarized as follows.

(*a*) *Large-bodied Invertebrates.* Odonata and Ephemeroptera nymphs, and Decapoda are important foods of *A. rupestris* and *P. flavescens*. The piscivorous *M. salmoides*, above 80 mm in length, take many Decapoda. These are all large fish, and have compressed fusiform to sub-gibbose bodies (Table II) and shallowly forked tails (Fig. 3) and are somewhat widely ranging. All have terminal, scoop-like mouths (Fig. 4), moderate to wide mouth apertures, strong jaws, and numerous marginal teeth.

(*b*) *Small-bodied Invertebrates.* The fish feeding on these organisms range from small *U. limi*, with its somewhat strong, terminal, scoop-like mouth, to the large-bodied, wide-mouthed *I. nebulosus*, and *P. caprodes* with a small, ventro-terminal mouth. As noted, however, the feeding habits of the three differ considerably. *Umbra limi* takes many hard-bodied insects whereas *P. caprodes* seeks mainly chironomid larvae and amphipods. *Ictalurus nebulosus* depends on chemosensory barbels to locate prey, and its bottom feeding undoubtedly partly entails mouthing, or sifting, prey items from the mud. *Umbra limi* and *P. caprodes* are not strong swimmers. Small-bodied invertebrates, as a food type, obviously lend themselves to predation by fishes of relatively local habits.

(*c*) *Bottom Ooze.* The mouth of *P. notatus* is clearly adapted for this food. The species has a less maneuverable body than the other cyprinids.

(*d*) *Plankton.* *Notemigonus crysoleucas* and *N. heterodon* have compressed fusiform bodies and a range of other features conferring considerable mobility and maneuverability. These are obviously essential for the pursuit and capture of individual plankters. *Pomoxis nigromaculatus*, a gibbose "water-hanger", obtains them, however, by means of its gill raker screen. *Labidesthes sicculus*, a small fish with a tubular body also takes planktonic organisms individually; *Chaoborus* larvae replace them as the major food seasonally and when the fish increase in size.

(*e*) *Surface Insects.* The species to which surface insects are important are *L. sicculus*, *N. crysoleucas*, *N. heterodon* and, to a minor extent, *F. diaphanus* and *P. nigromaculatus*. All have dorso-terminal mouths. *Labidesthes sicculus* is far the best adapted structurally both in body and mouth form. *Fundulus diaphanus* and *N. crysoleucas*, which have curved backs have to swim at a shallow angle to the surface, in contrast to *L. sicculus*.

(*f*) *Fish.* *Esox lucius* and *M. salmoides* show a wide range of structural specializations for the piscivorous way of life. They reach the largest size, have stable fusiform or tubular bodies, narrow caudal peduncles of short or medium length, forked tails, and efficient propulsive surfaces. They are adapted for prolonged cruising and for making quick rushes. The mouth opening is wide, the jaws strong, and the teeth large.

Perca flavescens, it might be noted, has a body form convergent with that of *M. salmoides* (Fig. 3). The mouth width, however, is only 8%, instead of 16% of the standard length, restricting the size of food that can be handled and limiting its piscivorous activities until it reaches a large size.

(*g*) *Generalized feeders. Lepomis gibbose*, *L. macrochirus*, and *F. diaphanus* are by far the most diverse and versatile feeders in the lake, taking a wide range of foods and feeding at all levels in the water. The two are highly different in most of their bodily attributes (Table II, Fig. 3), and in their hunting habits. *Lepomis macrochirus* uses its "water-hanging" ability to place it in a favorable position to rush items on the bottom, surface, or middle water, as these appear. *Fundulus diaphanus*, a small, maneuverable species, patrols the shallows in schools. Since both species have relatively small mouths there is an upper limit to the size of organisms that can be handled.

It is obvious from the above survey that, apart from the many clear-cut correlations between form and way of life the species composing the Lake

Opinicon fauna show several instances of alternative structures serving to fill common ends.

CHANGING FOOD NICHE AND STRUCTURE WITH GROWTH

Many fish change diet as they grow. Instances of this in the present fauna have been given by Keast (1965). The correlation between changes in body form and ecology has been little studied except by Nikolsky (1963, fig. 84) in the cyprinid, *Rutilus rutilus caspicus*. The subject lies beyond the scope of the present paper, but some general comments may be made at this stage with respect to the Lake Opinicon fishes.

There is no case, in the present fauna, of a structure being significant at one growth stage but not another. However, increasing body size and mouth aperture width do permit a change in "food niche" and way of life. *Amblop-lites rupestris*, for example, changes from chironomid larvae and other small items to Odonata and Ephemeroptera nymphs between body lengths of 75 and 100 mm, and later to crayfish (Keast, 1965). The widespread use of Cladocera by fry and fingerlings of virtually all species is obviously associated with the ability to pursue and catch these small items.

One other aspect of ecological change with growth has been commented upon previously (Keast, 1965), that being the habit of first year *M. salmoides* and *A. rupestris* of keeping to the shallows, a habitat different from that occupied by the adults. Avoidance of predation is presumably the main reason for this but, structurally speaking, they could equally be said to be limited to this habitat by their relative slowness and inability to range widely and to handle the larger kinds of food available in the adult habitat.

STRUCTURE AND THE REDUCTION OF INTERSPECIFIC COMPETITION

The present study shows clearly that whereas structure does not prevent food overlaps in cohabiting species, it does serve to reduce interspecific competition because most species have specializations that place them at an advantage in certain situations, or in the obtaining of certain foods. Beyond this, it is a fair generalization to say that the greater the number of structural specializations, the more the species niche tends to be circumscribed.

Some of the best examples in the lake of structural specializations reducing interspecific competition are as follows.

(*a*) The extreme maneuverability of the body in the cyprinids *N. crysoleucas* and *N. heterodon* permits them to be specialized plankton feeders. Significantly they, unlike most of the other species, are able to obtain this resource even when it is rare. Competition between these two species is partly avoided by spatial separation and different behavioral patterns.

(*b*) *Labidesthes sicculus* has a range of structures permitting it to catch insects hovering over the surface, which the other species apparently cannot do. The cyprinids lack the extreme specializations for surface living:

the straight dorsal line, flattened, beak-like snout, and well-developed rows of marginal teeth.

(*c*) As noted, *A. rupestris*, *M. salmoides*, and *P. flavescens*, living on hard-bodied invertebrates, have relatively strong mouths. Although these are not identical in form (that of *P. flavescens* is smaller), ecological exclusion is enhanced by *P. flavescens* concentrating mainly on Zygoptera, and *A. rupestris* on Anisoptera nymphs (Keast, 1965). *Micropterus salmoides* more than 80 mm long are predominantly piscivorous.

(*d*) The small *U. limi* is adapted by its body form for life in weedy shallows and by its mouth for taking hard-bodied insects; the differences in habitat, structure, and food between this species and the cyprinids are marked. The marginal teeth of *U. limi* plus *F. diaphanus* and *L. sicculus* are undoubtedly of value in seizing and holding hard-bodied prey.

(*e*) The ventrally-placed, tubular mouth of *P. notatus* is an adaptation for bottom-ooze feeding. There is no question of competition here as it is the only fish in the fauna to utilize this resource.

(*f*) *Percina caprodes*, by means of its leaf- and stone-turning habits, is able to obtain foods not available to other species.

(*g*) *Ictalurus nebulosus* is unique in Lake Opinicon in body form and feeding habits. This nocturnal chemosensory bottom-feeder frequents somewhat deep waters, where it can obtain chironomid larvae much more effectively than other species relying on vision. It also has the habit of submerging itself in, and wriggling freely through, the ooze at the bottom of ponds (Loeb, 1964). It would seem likely that buried food may be obtained from the mud at this time.

(*h*) The piscivorous *E. lucius* and *M. salmoides* are structurally adapted for their role by a wide range of features. *Esox lucius* is the more specialized piscivore structurally and it lives almost entirely on fish beyond a size of 60 mm. Adult *M. salmoides*, by contrast, combine fish and decapod eating. *Esox lucius* can, apparently also feed at lower temperatures than *M. salmoides*, and the midsummer period of reduced feeding is less marked in the latter.

Although *E. lucius* and *M. salmoides* are well-armed with marginal teeth, and these are characteristic of piscivores generally, their absence is apparently not a barrier to the development of a fish eater; the piscivorous minnow *Ptychocheilus*, a west coast cyprinid, is an example.

The above examples emphasize that structure plays a basic role in channelling species into particular ways of life and feeding niches. Of equal importance in limiting interspecific competition, however, are the obvious limitations imposed by body size, poor swimming ability, type of mouth, and other factors.

Several important conclusions emerge from the present study and its predecessor (Keast, 1965). A clear degree of specialization in feeding structures, feeding behavior, habitat, and actual food consumed is indicated. This is in conflict with the statement of Forbes (1914) that fish have a common body of food resources which many of them draw upon according to the circumstances, and with the findings of Hartley (1948) that, in the Cam River in England, the members of the fish community were distinguished by no more than the varying proportions they drew from a common stock of food. These general conclusions of Forbes and Hartley are accepted by Larkin (1956), who quotes various studies in support. The difference in findings of the present works, relative to previous works, is significant. The explanation presumably lies in the superficial nature of most fish food studies, the majority of which have been based on limited series collected at irregular intervals, with little attempt to simultaneously study the food organisms in the environment or to take structure into account. Habitat specializations have not been given the degree of importance they merit, although various workers have discussed them; for example, Hile and Juday (1941) respecting certain Wisconsin lakes and Fryer (1959b) relative to Lake Nyassa.

Habitat and body form are, of course, interrelated; for example, fishes with gibbose bodies can only occur under conditions of relatively still water; riffle species and pelagic species have a readily identifiable shape. In a small lake, series of species are not separated into distinctive sub-faunas on the basis of habitat. Minor habitat differences do, however, separate individual species spatially. As noted in Keast (1965), *P. nigromaculatus* and *P. flavescens* are inhabitants of the deeper water, *L. macrochirus* and *F. diaphanus* the shallows. Thus, when the two are feeding on Cladocera, these organisms are, in part, being taken from different areas. The same applies to feeding on chironomid larvae by *F. diaphanus*, *P. caprodes*, and *I. nebulosus*, which live mainly over sandy shallows, areas of pebbly bottom, and in deeper sections of the lake, respectively. Interspecific competition cannot, of course, be defined on trophic relationships alone. Densities, spawning times, growth rates, capacity to withstand winter temperatures and low oxygen tensions, and ability to do without food for long periods, must be recognized as adaptive specializations.

A significant feature of the structural differences separating the Lake Opinicon fishes is that in few cases are specializations so extreme as to prohibit the owner from taking at least three distinct kinds of food. This flexibility reflects the environment, for it is obviously advantageous for all species to be able to take advantage of temporarily superabuntant resources. Cold temperate waterways, with their somewhat unpredictable temperature regimes, must favour retention of generalized features. This contrasts with certain tropical situations where species show a variety of bizarre tooth types and body forms, and true herbivores are well developed (Norman and Greenwood, 1963; Fryer, 1959a). The differences between the African Rift Lakes and the Great Lakes could, of course, in part be due to the greater age of the former.

The final conclusion from the present study is that a great deal can be predicated about the ecology of freshwater fish species from a study of body morphology. The situation is, then, similar to that in birds even though a great deal remains to be learnt of the significance of finer structural details.

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