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The piscivore feeding guild of fishes in small freshwater ecosystems

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Synopsis

Analysis of the piscivore guild in fish species-rich lake and stream systems in eastern Ontario showed the co-occurrence of three types: (1) specialists that became piscivorous at the age of a few weeks *(Esox, Micropterus);* (2) 'secondary' piscivores that are fish-eaters only later in life *(Perca, Ambloplites);* and (3) species in which fish consumption is limited to taking some larvae *(Lepomis macrochirus).* In the first group the basic series of dietary shifts that characterize many long-lived fish (i.e. zooplankton followed by small invertebrates then large invertebrates and finally fish); is greatly accelerated. Prey size increases with growth. Overall prey selection was on the basis of body size and abundance. Most piścivores took a range of fish prey. There was little evidence of specialization at the species level. *Esox* and *Micropterus* spawn some weeks ahead of their major prey species. This is seen as adaptive. Their young harvest the larvae of the latter. The ensuing predator/prey association with growth is highly advantageous to the piscivore as prey of optimum body size are thus continually available.

Introduction

Piscivory among fishes is a major feature of all freshwater ecosystems. Piscivores have evolved repeatedly and from a wide range of fish stocks. In Nearctica at least eight families (Centrarchidae, Percidae, Cyprinidae, Amiidae, Salmonidae, Cottidae, Anguillidae, Ictaluridae), in addition to the specialized Esocidae and Lepisosteidae, have produced them. An extreme situation is represented by *Haplochromis* of Lake Victoria which has evolved more than 35 piscivore species (Greenwood 1974).

The piscivore adaptive zone is highly advantageous. Fish prey is of large size, energetically rewarding, and usually abundant. Being long-lived it is always available, even if varying seasonally in mean body size. On the debit side structural specializations for piscivory such as the large mouth limits efficiency in taking smaller prey and piscivores potentially suffer some of the constraints of a specialist (Alexander 1967, Werner 1977).

The co-occurrence of several piscivore species in many Canadian fresh water systems, and of different kinds and levels of piscivory, invites analysis. How do the patterns develop in the longer term evolutionary context? Do individual piscivores specialize on different prey species? Do patterns of piscivory change with age of the fish? Is there any evidence of coevolution of predator and prey?

The present paper investigates these questions in two small Ontario freshwater ecosystems, a lake and a stream.

Materials and methods

The study sites were Lake Opinicon, a 2200 hectare, 10 m deep lake in Leeds County, Ontario; and Jones Creek, a small 5 km long stream that enters the St. Lawrence River near Brockville, Ontario. The former has 18, and the latter 12, species of fish.

Data were developed at four levels: (a) age at which each species became piscivorous and extent to which it developed the habit; (b) the prey species eaten by each; (c) changes in sizes of prey with age; and (d) spawning times of piscivore relative to non-piscivore (i.e. prey) fish species. The first two sections are synthesized from previously published diet data (Keast 1965, 1966, 1968, 1977a, b, 1978a, b). The prey eaten by each year class of each species was grouped into the broad categories of zooplankton, small-bodied invertebrates (length <10 mm), large-bodied invertebrates (length > 10 mm), and fish. The last two sections are based on new data.

Food data relative to growth are from stomach analyses using standard procedures (see references above). The fish were collected from three sites in monthly series, May-October, and grouped into year (age) classes. The numbers of stomachs processed were as follows: *Esoc lucius* 220; *Micropterus salmoides* 570; *Pomoxis nigromaculatus* 469; *Ambloplites rupestris* 1477; *Lepomis machrochirus* 3200; *Perca flavescens* 2200; *Ictalurus natalis* 320; *Esox americanus vermiculatus* 281; and *Semotilus atromaculatus* 654. The data on *Esox lucius, Micropterus salmoides,* and *Ictalurus natalis,* are previously unpublished.

Spawning data on the piscivores and their prey were taken from Amundrud et al. (1974), Duckworth (1978), and Keast (1980) for Lake Opinicon, and Duckworth (1978), and Keast (unpublished) for Jones Creek. The Opinicon data is for the years 1969-1970, and Jones Creek, 1977.

Results

Lake Opinicon has six piscivores: *Esox lucius* (Esocidae); *Ictalurus natalis* (Ictaluridae); *Micropterus salmoides, Ambloplites rupestris, Pomoxis nigromaculatus* (Centrarchidae), and *Perca flavescens* (Percidae). Jones Creek has two: *Esox americanus vermiculatus* (Esocidae), and *Semotilus atromaculatus* (Cyprinidae).

Dietary changes with age are shown for *Micropterus, Ambloplites* and *Pomoxis* and for *Lepomis macrochirus* (non-piscivore) in Figure 1, and for *Perca, Ictalurus, Semotilus,* and *Esox vermiculatus americanus* in Figure 2. The data are expressed in terms of % volumes. Year 0 fish are those in their first summer of life, Year I in their second summer, and so on.

The following patterns emerge:

Micropterus salmoides. The zooplankton and small invertebrate feeding phases are confined to the first summer. Large invertebrates (crayfish) make up about 15% by volume of the diet throughout life. Piscivory begins in the first summer with the consumption of *Lepomis* larvae. The smallest *Micropterus* to contain fish prey were 23 mm in length and the prey 4.5-6.0 mm. Many juveniles of 28-35 mm contained these young fish. The prey taken became larger as *Micropterus* and the young *Lepomis,* grew. Fish made up 50% of the stomach volume in year 1, 70% in Year II, and 85% or more, thereafter.

Pomoxis nigromaculatus. Zooplankton dominated the diet of the year I fish and thereafter fell progressively, accounting for only 5% volume in the larger fish. Small invertebrates (especially *Chaoborus* and chironomid larvae) dominated the diet after Year I. Large invertebrates (Ephemeroptera nymphs) were never significant. Fish eating began in Year I but represented less than 10% of the diet until Year IV. It stabilized at about 30% in the older fish.

Ambloplites rupestris. The pattern of dietary changes with age was similar to *Pomoxis* except that zooplankton and small invertebrate eating was inconsequential in this large-mouthed species. Beyond Year II *Ambloplites* are large invertebrate (Anisoptera nymphs, crayfish) feeders. Fish only became a regular item of diet in Year IV, stabilizing at 20% by volume thereafter.

Ictlurus natalis. Zooplankton was of no significance. Diets of the younger fish were dominated by small invertebrates (especially chironomid larvae). After Year II large invertebrates (Odonata nymphs, crayfish) and fish were taken. Fish accounted to 45% by volume.

Perca flavescens. Zooplankton and small invertebrates dominated the diet in Years 0 and I, these items and large invertebrates (Odonata and

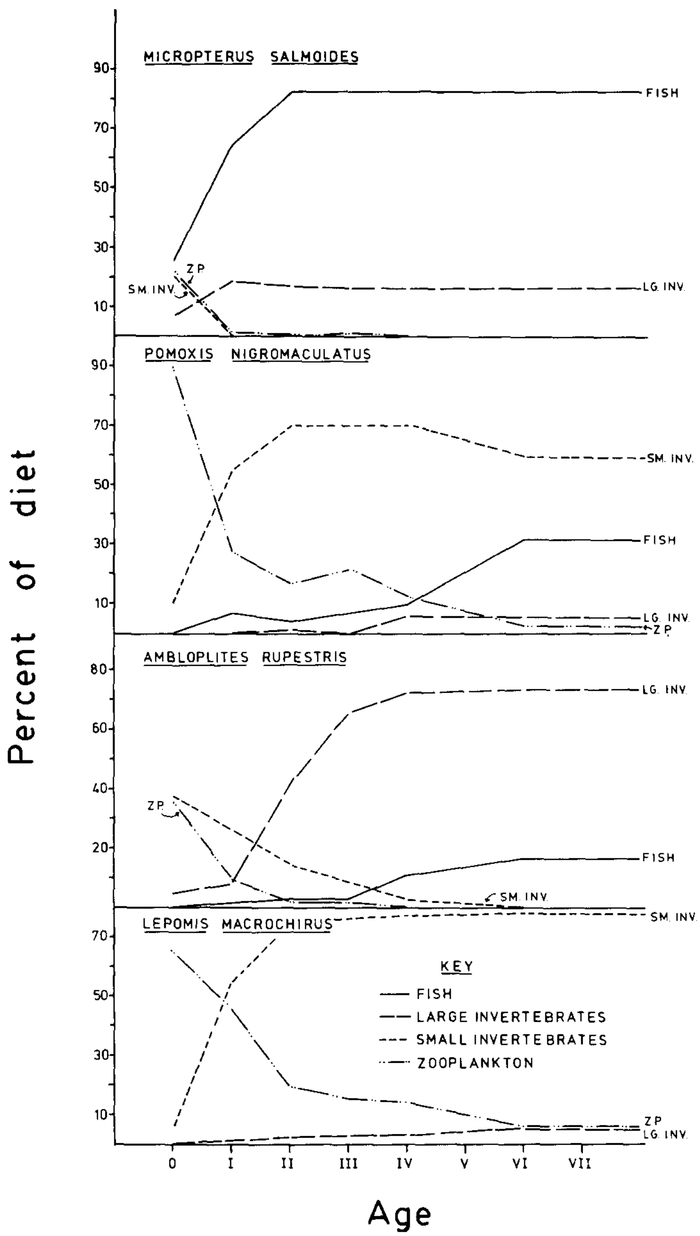

Fig. 1. Major diet shifts with age for four centrarchids, *Micropterus salmoides* (largemouth bass), *Pomoxis nigromaculatus* (black crappie), *Ambloplites rupestris* (rock bass), and *Lepomis macrochirus* (bluegill), in Lake Opinicon, Ontario, May-October, based on % volumes of 4 food categories: zooplankton, small invertebrates (< 10 mm), large invertebrates (> 10 mm), and fish. Sample sizes as in text.

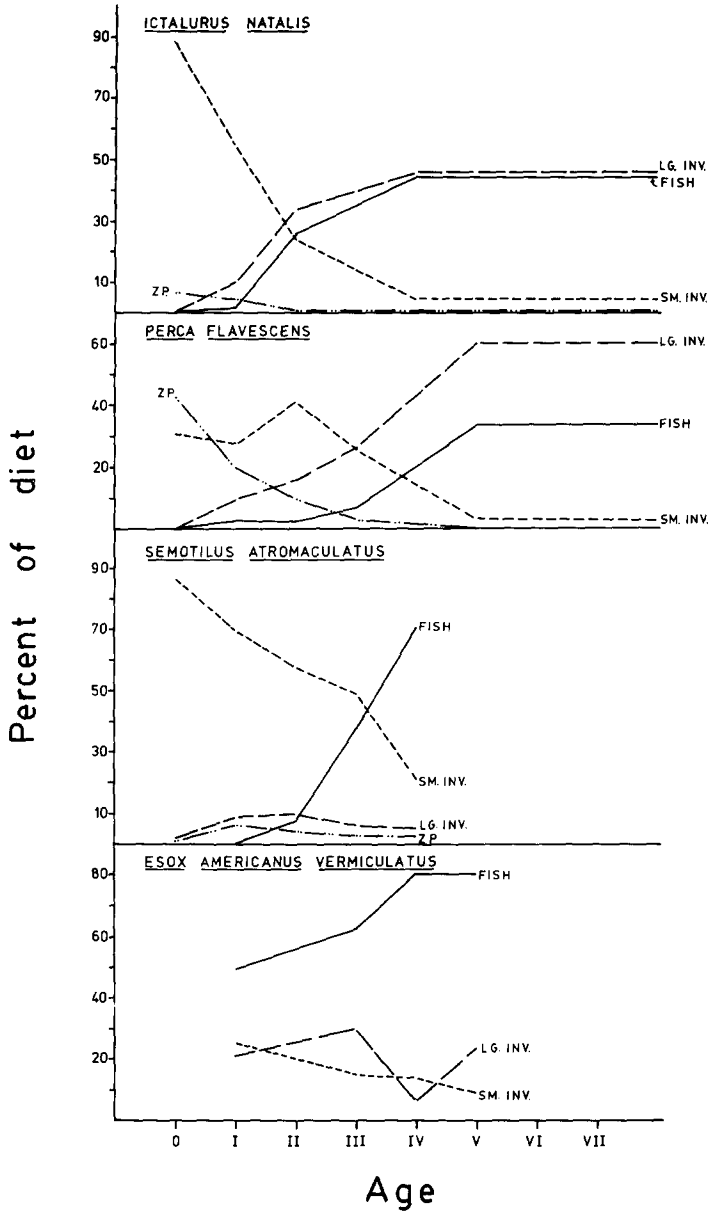

Fig. 2. Major diet shifts with age for *Ictalurus natalis*, yellow bullhead (Ictaluridae), and *Perca flavescens*, yellow perch (Percidae), in lake Opinicon, and *Semotilus atromaculatus*, creek chub (Cyprinidae), and grass pickerel *Esox americanus vermiculatus* (Esocidae) in Jones Creek, May-October, based on % volumes of 4 food categories: zooplankton, small invertebrates (< 10 mm), large invertebrates (> 10 mm), and fish. Sample sizes as in text.

Ephemeroptera nymphs, some crayfish) in Year II. Beyond Year IV large invertebrates were dominant. Fish formed a major item from Year V onwards making up 25% by volume of the diet.

Semotilus atromaculatus. This Jones Creek species initially fed on small invertebrates but by Year IV it became a major predator of small fish which then made up 70% of the stomach contents.

Esox americanus vermiculatus. Small- and large-bodied invertebrates initially were important. Fish made up 50% of the diet in Year I and 80% from Year IV onwards.

Esox lucius. The northern pike is also piscivorous in its first summer (see also Hunt & Carbine 1950, Frost 1954). In Lake Windemere, Great Britain, piscivory commences at 35 mm (Frost 1954).

Thus, in Lake Opinicon two species, *Esox lucius* and *Micropterus salmoides* begin piscivory in their first summer, and in Jones Creek one, *Esox americanus vermiculatus*. These species are structurally specialized for piscivory, being of large size, having large mouths and fusiform bodies and, in *Esox*, recurved teeth.

Contrasting with them are five species that become piscivorous only in Year III or IV (Year II in *Ictalurus natalis)*. Even so they are never more than partly piscivorous. Fish reached only 30% of the diet by volume in *Pomoxis*, 20% in *Ambloplites*, 30% in *Perca*, 40-45% in *Ictalurus natalis* and, in Jones Creek, 70% in *Semotilus*.

The prey species eaten

Data on prey species eaten by each of the six piscivore species in Lake Opinicon are given in Table 1. *Lepomis macrochirus* and *L. gibbosus* are grouped since the two are initially difficult to distinguish. These two species are, respectively, the most common and second most common species in the littoral zone.

Lepomis was the most important prey type. Seven species ate it compared to six taking *Micropterus*, five *Perca*, and five *Notemigonus*. Most of the *Micropterus* eaten were years 0 and I. *Lepomis* ranged in importance in individual diets from 14% in *Pomoxis* to 60% in *Ictalurus natalis*. However, when the 'unidentified' centrarchids, most of which were *Lepomis*, were added, these figures rose to 17% and 100%.

All the fish species in the lake entered the diets of the piscivores. Most piscivores consumed several species. *Esox, Micropterus, Ambloplites*, and *Perca* took nine.

In no case did a piscivore specialize on a particular prey species. Rather, consumption was influenced by body size, abundance, and probably by habitat and habits. The selection of *Lepomis* by *Ictalurus natalis* probably stems from the habit of the former of sleeping near the bottom (Helfman 1981) where it is presumably vulnerable to the nocturnal, tactile-feeding *Ictalurus*. *Notemigonus, Alosa*, and *Labidesthes* are nocturnally active and don't rest on bottom. The consumption of the first two by the larger *Micropterus* and *Esox* can be linked to that. The commoner of the two *Ictalurus* in the lake, *I. nebulosus*, was eaten when young. *Ictalurus* can increase its body breadth by lateral extension of the spring pectoral fins. making it more difficult to swallow.

The small-bodied inshore- and weed-dwelling *Fundulus, Pimephales* and *Notropis* were consumed mainly by the smaller *Micropterus* and by the 'secondary' piscivores.

In Jones Creek, the major prey of *Esox vermiculatus americanus* were *Umbra limi*, small *Lepomis, Notemogonus* and *Esox*. The other piscivore in the system, *Semotilus atromaculatus*, consumed primarily *Chrosomus eos, Eucalia inconstans*, and small *Catostomus commersonii.*

Prey size selection

The size relationship between the various Lake Opinicon piscivores and their prey are shown in Figures 3 and 4. Data on *Esox lucius* is limited to individuals of 300 mm and over, few smaller fish being taken. In *Micropterus* by contrast, fewer older individuals were obtained and data are limited to year 0-IV. In all cases prey size increased significantly with age. There was much variation in prey size in all age series (see standard deviations). It was least in the perch.

Esox took prey up to 150 mm in length. This included all but the very largest lepomines. The largest *Micropterus* commonly took prey up to 100 mm in length, and rarely to 120 mm. *Ambloplites, Pomoxis*, and *Perca*, by contrast, took no prey larger than 40-50 mm.

Micropterus and *Esox* initially consumed the smaller centrarchids, the small cyprinids, and *Fundulus*. As they grew, lepomines and *Notemigonus* of increasing size dominated the diet. By contrast, the secondary piscivores took the small-

Table 1. Fish species eaten by the different piscivores, L. Opinicon, Ontario, % of individuals of different species.

	Piscivore						
Prey	*Esox lucius*	*Micropterus salmoides*	*Pomoxis nigro-maculatus*	*Ambloplites rupestris*	*Perca flavescens*	*Ictalurus natalis*	*Lepomis macrochirus*
No. of prey individuals	109	407	139	288	284	127	53
Lepomis macrochirus & gibbosus	27	38	14	30	34	60	16
Unidentified *Centrarchids*	23	13	3	12	11	40	
Micropterus salmoides	3	4	9	22	11		66
Ambloplites rupestris	3			2			
Pomoxis nigromaculatus	2	2	1				
Perca flavescens	14	17	27		1		18
Ictalurus nebulosus		7					
Fundulus diaphanus			20	6	14		
Pimephales notatus		7	18		6	7	
Notropis heterodon		2	5	4	8		
Notemigonus crysoleucus	2	10	3	2	2		
Unidentified *cyprinids*	13			8	5		
Labidesthes sicculus				8	8		
Alosa pseudoharengus		11					
Esox lucius	2						

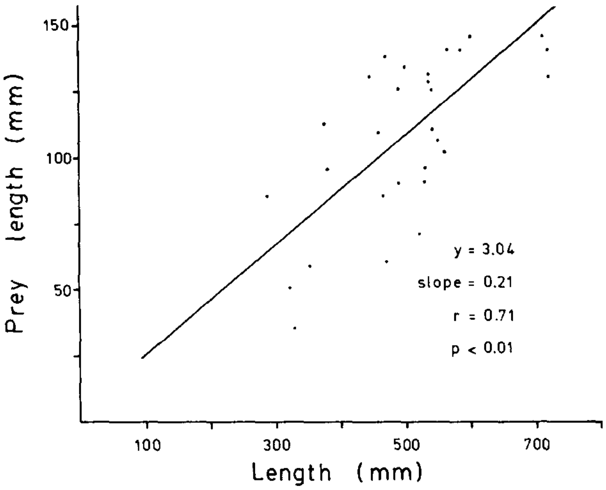

Fig. 3. Prey size selection as a function of length of pike, *Esox lucius*, in Lake Opinicon.

bodied cyprinids and *Fundulus*, and Year 0 centrarchids. Mean lengths of the perciform prey at the end of their first summer in Lake Opinicon were: *Pomoxis* 43 mm (Keast 1968); *Ambloplites* 45 mm (Keast 1977a); *Lepomis macrochirus* and *L. gibbosus* 42 and 48 mm (Keast 1978a); *Micropterus* 62 mm (unpublished data), and *Perca* 54 mm (Keast 1977b). These Year 0 fish made up 64% of prey individuals eaten by *Pomoxis*, 66% of *Ambloplites*, and 67% of *Perca*.

Correlation of spawning of piscivores and prey

Specialized piscivores like *Micropterus* and *Esox* owe their success as piscivores to a rapid growth rate and the achievement of large body size.

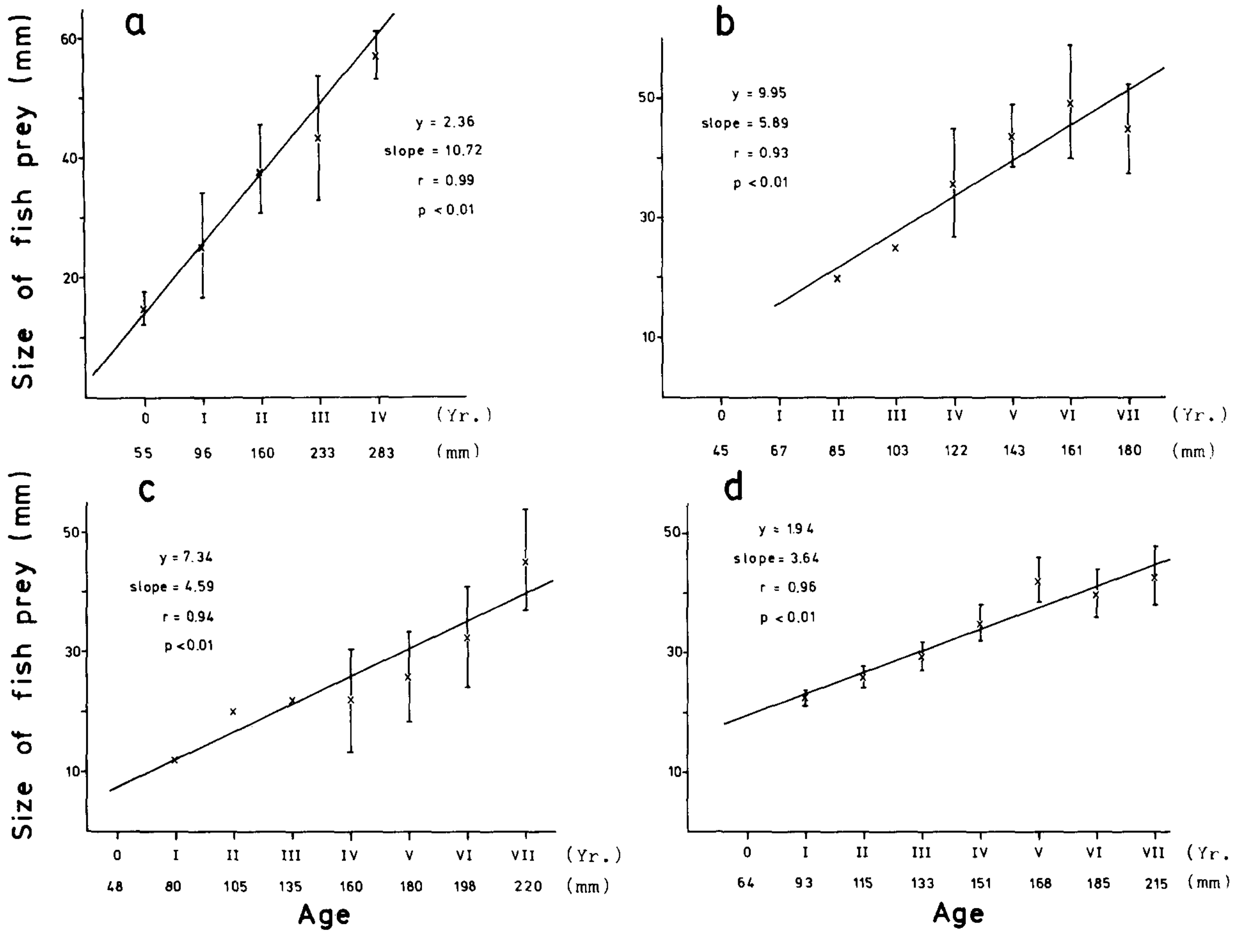

Fig. 4. Prey size selection as a function of age in the (a) largemouth bass; (b) rock bass; (c) black crappie; and (d) yellow perch in Lake Opinicon. Diets are from the first summer (Year 0) onwards. Means and standard deviations of prey size are shown. Mean lengths of predator at each age are given on ordinate.

Rapid growth is dependent on maximizing energy gain relative to expenditure.

One way a piscivore can achieve this is by spawning sufficiently early for its young to harvest young of prey species. The predator can then maintain the size differential as it grows. It is thus always assured of prey of appropriate size.

The spawning dates of the piscivores of Lake Opinicon and Jones Creek relative to that of potential prey species are shown in Figures 5 and 6. Young *Esox lucius* spawns in mid-April, those of *Perca flavescens* in late April – early May. *Micropterus* spawns in May and is the first of the centrarchids to do so. By contrast, most of the major prey species are late spring spawners and have a protracted spawning season. The most important prey, *Lepomis macrochirus,* produces young from late June until mid July (Keast 1980), three weeks later than *Micropterus.* In Lake Opinicon *Esox lucius* and *Micropterus salmoides* thus have a wide spectrum of young fish to exploit.

In Jones Creek *Esox americanus vermiculatus* is a late April -early May spawner. Amongst the prey species, *Umbra limi* is an early spawner and *Lepomis gibbosus* and *Notemigonus crysoleucus* are later spawners. The year 0 *Umbra limi,* a northern 'cold water' species, thus escape much of the predation of year 0 *Esox.*

In both systems the secondary piscivores, whose year 0 do not take fish, are generally later spawners.

Discussion

The results of this study raise several interesting questions. Why are there two distinct 'kinds' of piscivores and what is the nature of their coexistence? How can the system support so many? Why do all the piscivores go through an intermediate interval of invertebrate eating? How is it possible for the lake to support so many piscivore species especially when, as has been noted, the same basic prey species are eaten by all? Are there co-evolu-

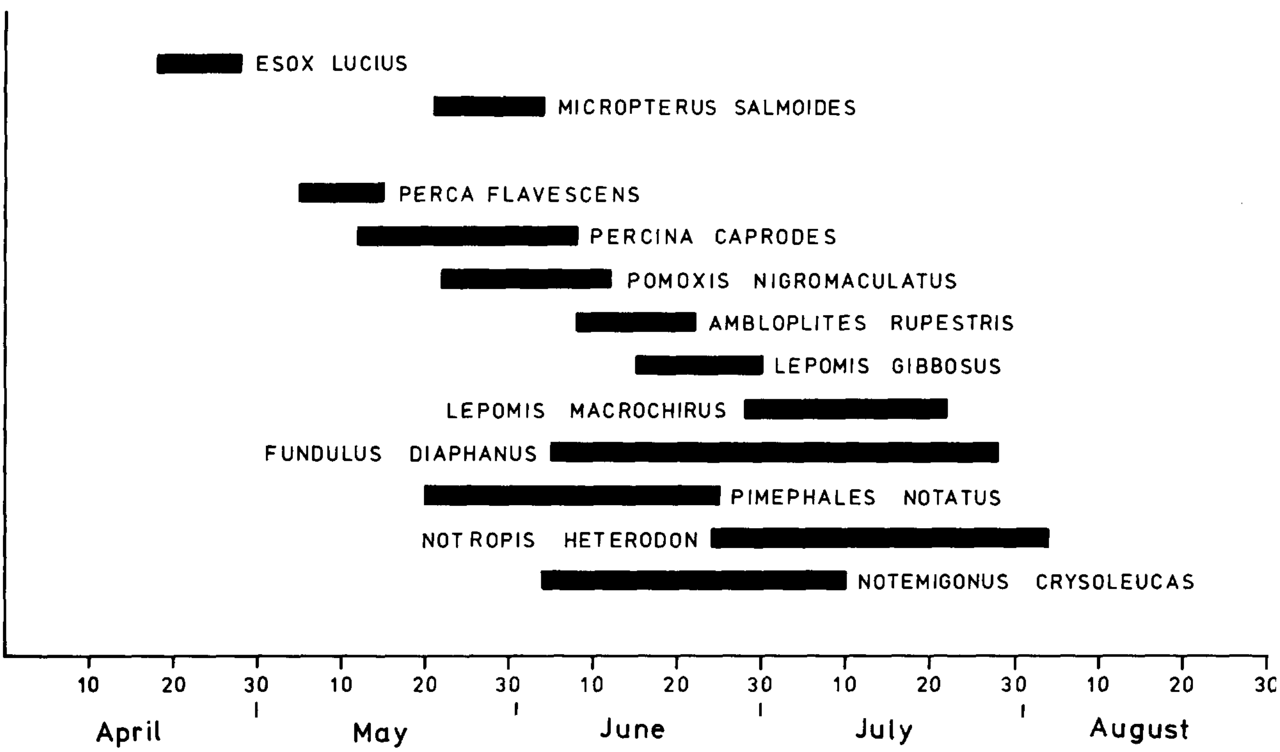

Fig. 5. Time of appearance of early juveniles, Lake Opinicon fish community, 1969-1970.

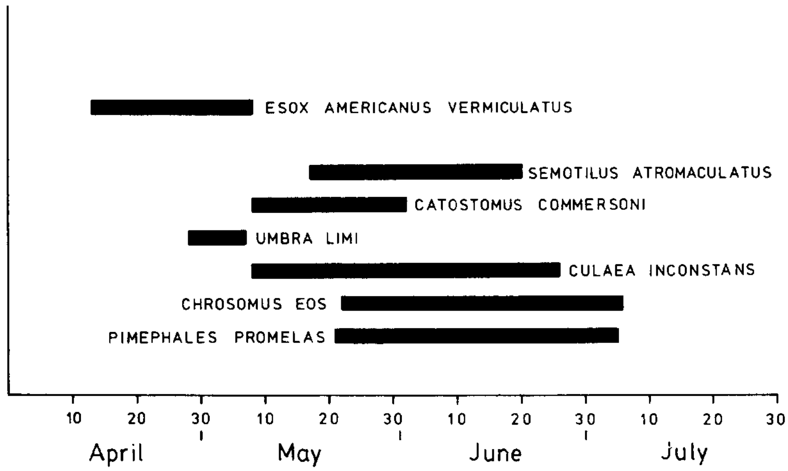

Fig. 6. Time of appearance of early juveniles, Jones Creek fish community, Ontario, 1977.

tionary relationships between predators and their prey? If there has indeed been coevolution, as for example between largemouth bass and bluegill, why does the latter not breed earlier so that the former cannot prey on its young?

The present finding of a series of co-occurring piscivores that vary in degree of specialization probably applies widely. In effect, the feeding guild within each water body represents a gradation from primary to secondary piscivores. The two are, obviously, very different entities. Secondary piscivores only eat fish when they are large. In order to maintain energetic efficiency as they grow, they should eat progressively larger prey and beyond a certain point fish are the only large prey available. These piscivores are in no way structurally specialized for piscivory, other than in acquiring a large mouth with age. The body form of the rock bass, black crappie, and yellow bullhead does not lend itself to pursuit or rapid strike; rather, they are relatively slow-moving. They are also nocturnal (Emery 1973, Helfman 1981). However, they are able to catch young centrarchids, (small prey of limited mobility) particularly in low light.

Secondary piscivores almost exclusively harvest first summer prey, and so are linked to the base of the numbers pyramid. It could be rationalized, hence, that they are not really 'competing' with each other, or with the primary piscivores, in that this resource is 'superabundant' in late summer. Moreover, as noted, secondary piscivores never become more than 30-40% piscivorous. This may explain why so many secondary piscivores can coexist.

A different set of selective pressures apply in the case of the primary piscivores. They are structurally adapted for piscivory. In contrast to the secondary piscivores that take several years to go through the diet sequence of small invertebrate to fish, the specialized piscivores, *Micropterus* and *Esox,* shorten this sequence and become partially piscivorous in the first months of life. They must nevertheless initially go through a short phase of invertebrate feeding because the smallest (larval) fish available are 4.5-5.0 mm in length (Keast 1980). To achieve rapid growth and large size, the transition to fish feeding has to be achieved as rapidly as possible.

There is now a considerable literature documenting how diet shifts to prey of increased size are linked to spurts in growth of the predator (e.g. Paloheimo & Dickey 1967) and that a fish diet is superior to a planktonic one. For example, in Algonquin Park, Ontario, both planktivorous and piscivorous stocks of lake charr *(Salvelinus namaycush)* exist. The latter grow more rapidly, reach a greater size, and mature at a larger size than the former (Martin 1966).

The tendency for specialized piscivores such as

Micropterus and *Esox* to spawn early enough that their young can eat the young of their prey has previously been noted. Frost (1954) observed such a relationship between pike and perch. Inferential data suggest that this also applies to walleye, *Stizostedion vitreum,* feeding on *Perca flavescens* (Forney 1971, 1976, Smith 1977, Nelson & Walburg 1977, and Forsythe & Wrenn 1979).

An alternative hypothesis is that piscivores breed early so that their larvae do not compete with those of other , later spawning fish species. The larvae of most fishes feed almost exclusively on zooplankton (Fig. 3. 1, 2 and Keast 1980) and competition could potentially occur if these resources were limited. However, whilst the zooplankton eating phase is very protracted in most fish species, it is exceedingly short in *Mirocpterus* (Keast 1980) and in *Esox lucius* (Frost 1954). Within days of the onset of exogenous feeding a zooplankton diet is forsaken for one that includes larger prey. This minimal dependence on Cladocera suggests that the avoidance of competition is not the primary force selecting for early spawning in these specialized piscivores.

Why do prey species not reduce their vulnerability by breeding earlier? Presumably there is an ecological trade-off. There may be several disadvantages to spawning early, e.g. development may be slower at the low temperatures early in the season, prey may be less abundant, and there is an absence of protective vegetation for the young.

A link between the breeding of a predator and its prey, so that the young of the former can exploit those of the latter, has been recognised in many systems. Examples include parasitic insects and their hosts (Price 1974), mink, *Mustela vison* and muskrat, *Ondatra zibethica* (Errington 1963); lynx, *Lynx canadensis* and snowshoe hare, *Lepus americanus* (Keith 1962, Tanner 1975), and Falconiformes and their prey. In England (a) the kestrel, *Falco tinnunculus,* lays from mid-April to mid-May, and rodents, its main prey, produce young from late May onwards; (b) the sparrowhawk, *Accipiter nisus,* a bird predator, breeds in May and young songbirds become plentiful in early June; and (c) the hobby, *Falco subbeteo,* an aerial hunter, lays in June, and its prey, young swallows, and dragonflies become plentiful in July (Newton 1979). In eastern Mediterranean the falcon, *F. eleonorae,* breeds so as to match the arrival times of the vast numbers of southward flying migrants (Walter 1970).

The results of this study also have implications for fisheries management. Failure to understand patterns of size structuring between predators and prey probably explains some of the difficulties fisheries managers have had in their efforts to improve productivity by stocking (Campbell 1979). For example, *Micropterus* and *Lepomis macrochirus* were once considered an ideal combination for artificial ponds (Swingle 1950). The limited success of this combination may, in part, have been due to the fact that the full range of prey sizes were not made available in the correct proportions (see also Hackney 1975). A better understanding of optimum prey size relationships could remove stocking from the 'trial and error' category into a more exact procedure.

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