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Growth, maturity and Triaenophorus parasitism in relation to taxonomy of Lake Winnipeg ciscoes (Leucichthys).

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INTRODUCTION

Increased knowledge of variation and plasticity in the usual systematic characters of coregonine fish have resulted in a questioning of the current taxonomy of the ciscoes, Leucichthys (Coregonidae). In Lake Winnipeg, Dymond and Pritchard (1930) recognized four species: L. zenithicus, L. nigripinnis, L. tullibee, and L. nipigon. The status and relationships of the latter two species, as a result of investigations of other waters, have been challenged.

Morphological criteria heretofore have been used in developing the present conception of Leucichthys systematics, but a wider range of biological information seems applicable. The characters employed in this study are maximum size, curve of growth, sexual maturity, and incidence of parasitic infection. The problem considered is if these biological characters support the existing taxonomy of Lake Winnipeg Leucichthys.

Opportunity to reinvestigate the Lake Winnipeg ciscoes was provided by the Central Fisheries Research Station in connection with its programme of Triaenophorus research. Export of the coregonid production of Central Canada is adversely affected by the presence, in the flesh, of the Triaenophorus tapeworm. Ciscoes are regarded as the principal second intermediate host and their reduction has been advocated as a control measure (Miller, 1948). Knowledge of the bionomics of these species is essential to scientific experiments of this nature.

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TAXONOMY OF LEUCICHTHYS

The lake herring or ciscoes of North America were originally called Argyrosomus, the name given to them by Agassiz. Jordan and Evermann (1911) finding this name preoccupied, replaced it by Leucichthys. The generic name Leucichthys had been proposed by Dybowski for those coregonids with "der Mund vorderständig oder halb oberständig. Die Symphyse des Unterkiefer mit einer hockartigen Anschwellung" (Koelz, 1929). Dybowski, states Koelz, classified Leucichthys as a subgenus together with Coregonus sensu stricto in the genus Coregonus. Other European ichthyologists did not accept this splitting of the genus.

In their 1911 review Jordan and Evermann divided the ciscoes, Leucichthys into three subgenera--Thrissomus, Cisco and Allosomus. Koelz (ibid, p. 340) repudiated the division on the following grounds:

> The representatives of the subgenus Allosomus I regard as subspecies in the Thrissomus group. I find further no possibility of distinguishing structurally between the species of the latter group and those of Cisco and therefore do not subdivide the genus Leucichthys.

Both Dymond (1947) and Hubbs and Lagler (1947) follow Koelz's practice.

North American ichthyologists now consider the coregonids as a family Coregonidae separate from the salmonids, Salmonidae. This was initiated by Cope (1872). Gill (1895) who regarded Cope's osteological diagnosis of the difference between these two groups as erroneous, gave the coregonids only subfamily status. Jordan and Evermann (1896) apparently accepted Gill's suggestion but later (Jordan, Evermann and Clark, 1930) the coregonids were again raised to family rank. Among Europeans the family name Coregonidae fared as poorly as did the term Leucichthys. Regan (1914) and Berg (1947) both include the coregonids in the family Salmonidae. It is evident that the taxonomic position of the lake herring group differs according to the European or American taxonomists followed.

The lake herring, Leucichthys appear to be one group where caution is needed in the recognition of species. There has been much description and reduction to synonomy in the genus. Even today there is disagreement on the number of Leucichthys species that should be recognized. Since even the number of species is controversial no attempt is here made to list the described subspecies.

Nine species are listed in Jordan and Evermann (1896). Fifteen years later they (1911) recorded 19 species from North America. Jordan, Evermann and Clark (1930) list 30 species. This probably represents the peak in number of American species. The last named check list, however has been criticized by Myers (1935) as "unfortunate.....scarcely to be relied on". Although bearing the publication date of 1930 it does not contain Koelz's revision of the Great Lake coregonines.

In extensive surveys of the coregonine fauna of Eastern North America Koelz (1929, 1929b, 1931) recognized 11 species of Leucichthys. Hubbs and Lagler (1947) and where applicable Dymond (1947) concur with Koelz's species designations. The 11 species are as follows: artedi, alpenae, bartletti, hoyi, hubbsi, johannae, kiyi, nigripinnis, nipigon, reighardi and zenithicus. Six other species of ciscoes have been described from Northwestern America. Dymond (1943) examining Leucichthys specimens from this region, concluded that all of the six species were conspecific with other species. The following represents his revision:

L. pusillus synonymous with L. sardinella
L. laurettae synonymous with L. autumnalis
L. lucidus synonymous with L. artedi
L. entomophagus synonymous with L. zenithicus
L. athabascae synonymous with L. zenithicus
L. macrognathus synonymous with L. zenithicus

Recently two new species of Leucichthys, churchillensis and nueltensis have been described from Manitoba and Keewatin (Fowler, 1948).

In addition to this list, L. gemmifer may be mentioned. This species was described by Snyder in 1919 from specimens collected from Bear Lake, Idaho. Whether this species is still regarded as valid is not known to the author. The name is still used by the Idaho Department of Fish and Game (James C. Simpson, personal communication, June 1950).

The North American genus <u>Leucichthys</u> may then be regarded as comprizing 16 species. Critical investigations may reduce this number. As one ichthyologist has said, "some additional species are candidates for synonomy".

That there is difficulty in the assignment of common names to members of this group is no doubt owing to the difficulties of specific distinction.

The terms "lake herring" and "cisco" are applied collectively to the genus. The former term evokes a comparison to the marine herring of the family Clupeidae. Whenever "lake herring" is applied particularly, it is to <u>L. artedi</u>. The term "cisco" by itself is not used for any definite species. Chute et al. (1948) use the word when modified: deepwater cisco, <u>L. johannae</u>; large jaw cisco, <u>L. alpenae</u>; blackfin cisco, <u>L. nigripinnis</u>, etc. "Tullibee", the trivial name of Richardson's species is normally applied to all species of <u>Leucichthys</u> in western and northwestern Canada. On Lake Winnipeg, all coregonines other than the whitefish, <u>Coregonus clupeaformis</u> are known as tullibee. Dymond (1928) states, "where several species of the genus occur in the same body of water, as in Lake Nipigon, the largest form is locally called 'tullibee'".

SPECIES OF LEUCICHTHYS REPORTED IN MANITOBA

Review of the literature reveals that seven species of ciscoes have been reported for Manitoba: L. artedi, L. churchillensis, L. hoyi, L. lucidus, L. nigripinnis, L. nipigon and L. tullibee. The first Manitoban record of occurrence and notes on the taxonomy and distribution are presented for each species.

L. artedi (Le Sueur), L. lucidus (Richardson)

Le Sueur's description of L. artedi in 1818 made it the first cisco found in North America. The type locality is "Lake Erie and Lake Ontario" (Koelz, 1931). The variation in body form of L. artedi is considerable. This variation ranges from a slim, terete longish type called artedi artedi to the deep, slightly compressed type termed artedi albus (Koelz, 1929). Systematists have been confused by this plasticity, in particular the albus subspecies has been confounded with L. tullibee.

The first record of L. artedi in Manitoba appears to be Bean's (1882) who reported on specimens collected by Dr. Robert Bell at the mouth of the Nelson River. Bean believed that these specimens agreed with "typical artedi from the Great Lakes with the exception of its smaller eye". He states further, "It must not be inferred, however, that the species is at all like Coregonus tullibee for it is not closely related to this form".

Evermann and Smith (1896) concur in the designation of Bell's specimens as artedi. They also classified specimens seen in the United States National Museum from Labrador (L. M. Turner), Hudson Bay (Walter Haydon), Moose Factory (C. Drexler) as belonging to this species. Dymond (1933) identified 146 specimens received from the Hudson and James Bay areas as L. artedi. He observed that they belonged to the slim-bodied form of this species.

Bajkov (1932) identified 15 ciscoes from near the mouth of the Churchill River as L. lucidus. This name, given by Richardson in 1836, was applied almost always to the Great Bear Lake ciscoes (Dymond, 1943). In this paper Dymond considered lucidus as synonymous with L. artedi.

With respect to areas adjacent to Manitoba, L. artedi has been recorded from Reindeer Lake (Bajkov, 1932; Dymond, 1943) and Baker Lake, Keewatin (Dymond, ibid).

L. churchillensis Fowler

Fowler (1948) described L. churchillensis with the type locality as Churchill River at Churchill, Manitoba. Fowler compares his specimens with L. zenithicus but ignored the obvious comparison to L. artedi. It remains to be seen if Fowler's species is accepted.

L. tullibee (Richardson)

The first record of this species, and of the genus Leucichthys, in Manitoba is implicit in Richardson's description

(1836) of tullibee. The type locality is Pine Island Lake, Saskatchewan but it is stated, "the fish is very generally diffused through the waters of the fur countries". Richardson's type specimen is not extant; his description is not considered adequate to distinguish this species from other ciscoes (Koelz, 1925; Dymond, 1928). Consequently there has been a good deal of confusion in the recognition of this species.

Up to 1911 L. tullibee was regarded as occurring in the Great Lakes (Jordan and Gilbert, 1883; Evermann and Smith, 1896; Jordan and Evermann, 1896).

Jordan and Evermann (1911) taking as a representative of L. tullibee, a cisco from Waubegon Lake Oxdrift, Ontario stated:

> We have seen no specimens of the true tullibee from the Great Lakes, but we are told that it occurs in Lake Superior and the north channel of Lake Huron. Doubtless these statements refer to L. manitoulinus. The 'mongrel whitefish' of Lake Erie, once supposed by the present writers to be the true tullibee proves to be L. eriensis.

Koelz (1929) regarded manitoulinus and eriensis merely as local races of artedi. He classified Jordan and Evermann's representative of L. tullibee from Waubegon Lake as belonging to the artedi species group. In his 1929 publication he withheld judgment on the deep, compressed cisco found in Western Canada but in 1931 he designated various populations of these as L. artedi tullibee thereby regarding tullibee as a subspecies of artedi. Bajkov (1932), probably following Koelz, considers tullibee a subspecies of L. artedi.

In Koelz (1931) L. artedi tullibee is not listed as a new subspecies. The first person responsible for this reduction has not been determined. In Hubbs and White (1923) two fish are listed as L. artedi tullibee. These authors state that they have followed Surber (1920). This latter publication was not seen by the present author.

Dymond (1928) published a description of six ciscoes from Pine Island Lake which he regarded as topotypes of L. tullibee. At the time he considered these specimens as dinstinct from L. nipigon but made no reference of their relationship to L. artedi. Later Dymond (1943) directed attention to their similarity to L. nigripinnis:

> If the lengths of the head and eyes of the specimens whose measurements are given in this account (1928) are plotted on figure 1 it will be found that they approximate much more closely to the values for nigripinnis than those of L. artedi.

His conclusion was that Koelz's assumption of tullibee being a subspecies of artedi may be "unwarranted".

Dymond's topotypes are probably the only ones that will ever be collected. Doan (1946) was unable to secure additional specimens from this locality. The maximum depth found was seven and a half feet, the Saskatchewan River having broken into the lake in 1912. "An old fisherman, a lifelong resident of the district said he never took more than three or four tullibee in a year from Cumberland Lake in recent times". (Doan, ibid).

L. nipigon Koelz

Koelz's record (1925) of occurrence of nipigon in Manitoba was the earliest found. Specimens, he reported, were obtained from Lake Winnipeg in early 1919. The source is not mentioned.

L. nipigon has a restricted distribution. The species was described from Lake Nipigon specimens. It has been recorded from Black Sturgeon Lake (Koelz 1929), Lake Abitibi (Dymond and Hart, 1927) and Lac Seul (Dymond and Pritchard, 1930). It is not known to occur in any of the Great Lakes (Koelz, op. cit.) nor in Lakes Winnipegosis or Manitoba (Bajkov, 1932).

The taxonomic status of L. nipigon has been challenged. Jordan, Evermann and Clark (1930) regarded this species as synonymous with L. tullibee (Richardson). Fry (1937) remarks that the Lake Nipissing cisco, identified as L. artedi, also resemble strongly the species, L. nipigon. "In view of the resemblance of the Nipissing fish to both L. artedi wagneri and L. nipigon, it is felt that the problem of the relationship of the species artedi and nipigon is still an open question."

L. nigripinnis Gill

The first record of L. nigripinnis in Manitoba appears to be in Dymond and Pritchard (1930). It is known from all the Great Lakes except Erie (Koelz, 1929). Dymond and Scott (1941) record it from several localities in the Patricia portion of Ontario. Specimens identified as this species have been collected in Prince Albert National Park, Lake Athabasca (Dymond and Pritchard, op. cit.) and Reindeer Lake, Saskatchewan (Dymond, 1943).

The similarity between this species and L. tullibee as pointed out by Dymond has been mentioned.

L. zenithicus Jordan and Evermann

The type locality of this species is Lake Superior, off Isle Royale. Koelz (1929) records it from Lakes Michigan, Huron and Nipigon. As with the previous species the first Manitoban record is apparently in Dymond and Pritchard (op. cit.). These authors also record its occurrence in Lake Athabasca, Alberta. In Saskatchewan, it has been reported from Reindeer Lake (Dymond, 1943). The known range of zenithicus furthermore has been extended to include the Northwest Territories as a consequence of the reduction to synonomy of three species of ciscoes (cf. p.6).

L. hoyi Gill

Bajkov (1930, 1932) was the only taxonomist found that recorded L. hoyi from Manitoba. Its presence in Manitoba is recorded also in Jackson (1934) and Hinks (1943) admittedly on the strength of Bajkov's material. Bajkov (1932) writes, "this species has been found only in Lake Winnipeg (248 specimens examined), but probably occurs also in Lakes Winnipegosis and Manitoba....This fish is distributed throughout all Lake Winnipeg and is fairly common, but is of no commercial importance". From the key given in his paper it would be very difficult to separate this species from young L. zenithicus and L. artedi.

THE TAPEWORM, TRIAENOPHORUS CRASSUS

Triaenophorus cestodes are pseudophyllidean tapeworms completing their life cycle in freshwater teleost fish and copepod crustacea. They apparently do not infect humans since Nicholson (1932) could not infect dogs by feeding them T. crassus plerocercoids nor has there ever been a record of a human harbouring a T. crassus tapeworm (Newton, 1932).

Three species are recorded as occurring in Canada. T. crassus Forel, 1880 and T. nodulosus (Pallas), 1760 were described from Europe while the first North American records were Cooper's (1918). T. stizostedionis Miller, 1945 was described from Lesser Slave Lake, Alberta. Table I synopsizes the hosts of these three species.

Table I. Hosts for three species of Triaenophorus

Species	Definitive host	1st intermediate host	2nd intermediate host
T. crassus	Esox lucius[1]	Cyclops bicuspidatus[2]	coregonine fish[3]
T. nodulosus	E. lucius[1]	C. bicuspidatus[2]	Perca flavescens[4,7]
		C. strennus in Europe[2]	Lota lota[6]
T. stizostedionis	Stizostedion vitreum[5]	C. bicuspidatus[5]	Percopsis omiscomaycus[5]

References.

1. Miller, 1943 4. Cooper, 1918

2. Miller, 1943b 5. Miller, 1945c

3. Miller, 1945b 6. Miller, 1945

7. G. H. Lawler, personal communication, September, 1950.

Triaenophorus species have similar life cycles. All exist in America as procercoids in Cyclops bicuspidatus. T. crassus and T. nodulosus share definitive hosts but although mixed infections occur, each tends to infect different sized pike (Miller, 1943).

Differences occur in their morphological and biological characteristics. Shape of the scolex hooks differs in T. crassus and T. nodulosus (Ekbaum, 1935; Miller, 1943). T. stizostedionis is also distinctive in this feature (Miller, 1945c). Miller (ibid) describes differences in the male genitalia that exist among the three species. The most obvious difference between these tapeworms is in the infection of a second intermediate host (cf. Table I).

Having outlined briefly some relationships among the three species the remaining discussion will be limited to Triaenophorus crassus, the species encysting in the musculature of coregonine fish.

This adult tapeworm like most other fish cestodes lives for only one year (Miller, 1943). In the spring the adult, living in the intestine of the pike, Esox lucius, liberates its eggs. These hatch into free swimming ciliated larvae called coracidia. When ingested by a copepod, Cyclops bicuspidatus in Canada, they burrow into the body cavity be means of their coracidial hooks (Miller, 1943b). Upon arriving in the body cavity of Cyclops they increase in size (Miller, ibid). In about 10 days they are termed mature procercoids.

The next stage in the life cycle occurs if an infected Cyclops is swallowed by a coregonine fish. The larva encysts in the lateral musculature of the host's body and is now called a plerocercoid. Miller, (1945b) described this stage as follows:

> Each cysts consists of a wall of connective tissue supplied by the host; inside, surrounding the coiled plerocercoid, is a thick albuminous fluid made up of digesting host tissue and excretory products from the worm...The plerocercoid is a long (up to 300 mm.), thin (1mm.), unsegmented worm that has a fully developed scolex similar to that of the adult. Young plerocercoids still possess a frontal gland, which opens at the tip of the scolex. Sex organs are never developed. Often a cauda is present; this is a posterior appendage of variable length, characterized by poorly developed muscles and parenchyma and presenting a degenerate appearance.

Newton (1932) describes the position of these cysts in the flesh of the whitefish and Miller (op. cit.) lists the various shapes that may be encountered.

Pike receive the parasites by consuming infested coregonines. This completes the life cycle.

Triaenophorus crassus affords an opportunity to study host-parasite relationships. With respect to the second intermediate host, Miller (1945b) has observed some degree of specificity. Most frequently the plerocercoid encysts in ciscoes but several kinds of whitefish, Coregonus clupeaformis and Prosopium spp. may be infected. Other fish in which the occurrence of cysts has been recorded are lake trout, Cristivomer namaycush, inconnu, Stenodus leucichthys and northern pike, Esox lucius (Miller, ibid).

The extent of infection shows intergeneric differences. Where C. clupeaformis and Leucichthys occur together in infected lakes, Miller states that the latter are more heavily parasitized. Little consideration has been given to differential infection among species of ciscoes. Newton (op. cit.) determined for Leucichthys zenithicus and L. tullibee in Lake Winnipeg, percentages of infected fish and the number of parasites present in each individual.

MATERIALS

Collection

The present study deals with those ciscoes collected between June, 1947 and August, 1949. Data were secured from 887 specimens comprizing 504 L. zenithicus, 164 L. nigripinnis, 181 L. nipigon and 38 L. tullibee. Age determinations were not possible in the case of two zenithicus and four nipigon therefore in some instances the data from these six specimens are not considered.

Table II lists the number of each species collected from the various localities. Table XIII presents more detailed information than Table II with respect to Mukatawa locality specimens. Here the division is arranged according to biweekly periods for 1947 and according to net sets for 1948 and 1949.

Ideniification of specimens

Except for the practising taxonomist, the recognition of species can be made only by reference to artificial keys. Since the various species of ciscoes were indistinguishable to the author in the field, identification to species was made in the laboratory from the collected data. The identification of ciscoes used in this study is based on the keys given in Dymond and Pritchard (1930) and Dymond (1947). For the convenience of the reader the key in the former paper is reproduced here.

A. Gill rakers 55 or more on first branchial arch - L. nipigon

AA. Gill rakers fewer than 43 on first branchial arch - L. zenithicus

AAA. Gill rakers 43 to 54 on first branchial arch

B. Head long, in specimens 10 inches and more in length 3.8 - 4.0 - L. nigripinnis

BB. Head short, 4.1 - 4.4 - L. tullibee

The frequency distribution of the gill-raker counts of the 887 ciscoes is given in Table XIV. The table shows that 181 ciscoes had a gill-raker count of 55 or more, consequently from the key were regarded as Leucichthys nipigon. Five hundred and four specimens had fewer than 43 gill-rakers and were designated as L. zenithicus. The number of ciscoes possessing 43 to 54 gill-rakers was 202.

Table II. Number of ciscoes collected from Lake Winnipeg localities. Figures refer to number of individual examined.

Locality	Year collected	zenithicus	nigripinnis	nipigon	tullibee	Totals
Mukatawa River	1947	271	95	104	21	491
Mukatawa River	1948	119	13	62	2	195
Mukatawa River	1949	41	15	2	12	70
Black Bear Island	1948	20	5	0	2	27
Gimli	1948	18	23	2	0	43
Matheson Island	1948	35	13	11	1	60
Totals		504	164	181	28	887

The above key is ambiguous with respect to the separation of L. nigripinnis and L. tullibee. Does the head length (4.1 - 4.4) given for L. tullibee refer only to specimens 10 inches and over? The key apparently gives no characters to identify specimens of L. nigripinnis under 10 inches.

Those ciscoes possessing 43 to 54 gill-rakers were identified by the key in Dymond (1947). They comprised 164 L. nigripinnis and 38 L. tullibee.

METHODS

Collection of material

From June 19 to July 31, 1947 Mr. David Peterson and the author stayed at the Booth Fisheries fishing station, operated by Mr. Levy Hallgrimson, at the mouth of the Mukatawa River. This station, on the east shore of the northern part of Lake Winnipeg, is approximately 60 miles north of Berens River. Here, during June and July each year, some twenty boats fish primarily for whitefish. Ciscoes are taken incidentally. It was these fish, captured in commercial gill-nets of 5¼-inch stretched mesh, that we examined, having no nets or boat to collect our own.

We stayed briefly at Black Bear Island in September, 1947. This island is 5 miles north of the Lake Winnipeg "Narrows".

One gill-net was set from the twelfth to the fifthteenth in 15 feet of water. No ciscoes were captured. Few ciscoes were reported by the commercial fishermen who were fishing at that time fo yellow pike-perch, Stizostedion vitreum. This scarcity of ciscoes paralleled our experiences the following autumn.

During 1948, three weeks were spent at Mukatawa River and two weeks at Black Bear Island. That year, however, our specimens were collected with 1½ and 3-inch gill-nets.

On October 27, 1948 Dr. W. A. Kennedy collected some ciscoes in gill-nets of 1½ and 3-inch mesh set near Gimli in 25-28 feet of water. These specimens were held frozen in cold storage until examined at the Winnipeg laboratory in December.

During November of the same year ciscoes were collected with gill-nets by a local resident off Matheson Island. Matheson Island, locally called Snake Island, is directly south of Black Bear Island. Subsequent examination of the gonads revealed the fis to be ripe or spent. These specimens were likewise frozen and stored until they were examined on June 1-8 and August 12, 1949.

During 1949 field work was confined to the Mukatawa River locality where from June 17 to June 29, seventy specimens were collected. The Central Fisheries Research Station's vessel "Coregonus" was available for the first week and this facilitated collecting. During this period the size of the gill-nets were 1½, 3 and 5¼-inch stretched mesh.

Scale samples and morphometrical data (16 measurements and 6 counts) were collected on ciscoes examined. In addition, the sex and number of cysts were noted. Total length, sex, weight, vertebral and infection counts were recorded on scale envelopes while morphometrical data were entered on standard sheets. All information later was transferred to individual cards, 8 by 5 inches, for sorting and enumerating the data.

Sex was noted by an examination of the gonads when the fish were being filleted. Gonads of a small size, approximately one-fifth of an inch wide, were classified as immature. Immature females were recognized by the presence of minute eggs and the transverse folding on the ventral surface of the gonads. Immature males lacked these two features. Mature females were distinguished from mature males by the presence of eggs. The gonads of mature males usually had a smooth, creamy-white appearance.

Examination for Triaenophorus cysts was done in the same manner as in the Federal Department of Fisheries inspection. The fish were filleted by cutting both sides of the body away from the vertebral column. The ribs then were removed. Each fillet was systematically cut into small pieces of one-quarter inch thickness. The number of cysts seen during these operations was recorded.

Age determination

Scales, collected from the fish's left side above the lateral line in the region below the dorsal fin, were stored in coin envelopes. Before reading, the individual scales were cleaned by immersing them for 10 to 20 minutes in a 5 per cent solution of "Javex". I am indebted to Dr. W. B. Scott of the Royal Ontario Museum of Zoology for this suggestion. Three or four scales were mounted "wet" between microscopic slides and magnified by a Bausch and Lomb micro-projector. Magnification used was 26 times.

Over 500 scales were examined to learn to distinguish the annuli. Three different series of 50 scales each were read twice to determine the degree of accuracy in reading the age of any one fish. It was found that 60 per cent of the readings were identical. Where the first and second reading were dissimilar nearly always there was only year's disagreement. Thus, individual age determinations may be in error by one or possibly two years.

After this preliminary examination all the scale samples were read once and at that time a definite age was assigned. The data from six specimens were not used in some instances because no age determination was possible. During age determinations no reference was made to the species, length or weight of the specimens.

Ages were recorded as the number of completed years. The year class is considered to be the year the fish hatched. Thus fish hatched from eggs spawned in the fall of 1944 would be regarded as members of the 1945 year class and if captured in 1947, '48 or '49 would be designated as 2, 3 or 4 years old respectively.

Treatment of data

The object of an investigation will always dictate the manner of treating and discussing the data. The comparison of some characteristics of three species of ciscoes, present in the same lake, has been the object of the present study. Rather than consider the species separately, each characteristic will be discussed in turn so that similarities and differences among the species will emerge.

The restrictions of the data also will affect their treatment. The chief limitation in these data is their paucity. The procedure to be followed is that when two samples cannot be demonstrated to be heterogenous they are combined. Their value is thereby increased. When sampling from a homogenous population, extension of sample size increases the precision of the statistical measures (Snedecor, 1946).

In particular, the classification of the data according to sex will be examined to determine the possibility of combination. For a specified character, there is no necessity to keep the sexes separate when it cannot be established that they are different.

When growth is being investigated, a reason for combining data taken at different years has been stated by Van Oosten (1929, p. 373):

> In order to obtain the norm of growth in a long lived species, which is not influenced by seasonal changes of growth or annual fluctuations in it, we must combine the rates of growth for corresponding ages of all year classes.

Terminology and measurement of cisco parasitism

The parasitism of coregonine fish by the plerocercoids of Triaenophorus crassus has been termed "infection" or "infestation". An infection originally connoted invisible and internal agents whereas the term "infestation" was applied to external parasites. Later, in the nineteenth century, when infestation referred to internal parasites it was restricted to those not multiplying in the host.

Apparently there is now a confusion in the usage of these two terms. The Committee on Terminology of the Amercian Society of Parasitologists (Hertiz, Taliaferro and Schwartz, 1937) recommend the following:

> ...'infest' and 'infestation' ought to revert to their original use in connection with external and in most cases, visible agents...the terms 'infect' and 'infection' are properly applicable wherever the parasite invades and establishes itself within the body of the host...We fail to see any reason for continuing the use of the term 'infestation' as applied to internal parasites...

In order to be in accord with recognized authorities the term "infection" will be used in connection with Triaenophorus parasitism.

The measurement of infection, with reference to the parasitism of the second intermediate host, is directed to ascertaining the number of parasites present. The most accurate and unequivocal measure, it is believed, is the number of cysts per number of fish.

The determination of infection in number of cysts per weight of fish, as presently used by the Dominion Department of Fisheries, has certain objections for biological studies. Since poundage can be based on round dressed or filleted weight the units used must be specified if ambiguity is to be avoided. Secondly, the weight of a fish increases with its age. If a fish harbouring 6 cysts over a two year period doubles its weight it does not become less infected. If one does not agree with this view then he must say that a 200 pound man is less infected than one weighing 100 pounds when each harbours a Diphyllobothrium tapeworm.

A third objection to expressing degree of infection on a poundage basis is that one of the assumptions is not always realized. This assumption, in the opinion of the author, is that when samples are compared they should have the same average weight. To illustrate an example is presented.

In Lake Winnipeg 100 ciscoes, L. zenithicus and 100 whitefish, Coregonus clupeaformis could be examined for parasites. We could expect the cisco sample to contain 125 cysts and the whitefish sample 80. L. zenithicus is thus 50 per cent more parasitized than C. clupeaformis. The total round weights of the zenithicus and clupeaformis samples would be 56 and 250 pounds. On a 100 pound basis the ciscoes would have 223 cysts while the whitefish would have 50. Hence because of the different mean weight of the samples the ciscoes are considered now to possess four and one-half times as many parasites as the whitefish.

In the opinion of the author, comparable and precise measures of infection result only when the number of parasites present is based on the number rather than the weight of fish parasitized. Miller (1945b) calculates infection as the number of cysts per 100 fish. In the present study, infection refers to the number of cysts per single fish because of the small sample sizes.

MAXIMUM SIZE ATTAINED

Of the many characters sought to distinguish between groups of animals, size is one of the first investigated. With fishes, some related groups are separated by size differences. As examples the following freshwater fish may be cited: Stizostedion vitreum, the yellow pike-perch and Stizostedion canadense, the sauger; Esox masquinongy, the muskellunge and E. lucius, the northern pike; Noturus flavus, the stonecat and Schilbeodes mollis, the tadpole madtom; Alosa sapidissima, the shad and Pomolobus psuedo-harengus, the alewife. Size is occasionally useful in distinguishing certain species of Leucichthys. Koelz (1929) found that the maximum size attained is a useful diagonostic character in some of the Great Lakes coregonines. Leucichthys kiyi and L. hoyi are relatively small while L. nipigon and L. nigripinnis attain a larger size than the other species of lake herring occurring in the Great Lakes.

Consequently, the species of Lake Winnipeg ciscoes as identified in the present study were arranged into length frequency distributions to show any possible differences in size (Table III). The smallest specimen collected was 105mm. in length (L. zenithicus) while the largest was 353 mm. (L. tullibee). Although the upper range limit of the four identified species is similar, the percentage of specimens of a given species attaining a standard length of 300 mm. appears to be different. The percentages of specimens of L. nigripinnis, nipigon, and zenithicus over 300 mm. found in this study are respectively 21.1, 212, and 0.6 per cent. Another reason for considering nigripinnis the largest is the slower decline, as compared with nipigon and zenithicus, in numbers of the frequency distribution beyond the 280-299 length interval. The degree to which this slow decline is representative of the population is not known.

Table III. Length-frequency distribution of Leucichthys collected from Lake Winnipeg, 1947-1949.

Standard length in mm.	zenithicus	nigripinnis	nipigon	tullibee
100-119	17	1	-	-
120-139	34	12	-	-
140-159	14	12	-	-
160-179	18	3	-	1
180-199	34	19	1	1
200-219	46	14	4	1
220-239	141	22	20	6
240-259	145	19	68	7
260-279	50	12	70	9
280-299	2	16	14	6
300-319	2	18	3	3
320-339	-	12	1	3
340-359	1	4	-	1
360-379	-	-	-	-
	504	164	181	38

Of 19 fish collected, 9 years and older, 12 were L. nigripinnis. Thus the observed size differences among species might be attributable to age. However, a more reasonable explanation is found when growth curves are examined. Figure I (p. 41) illustrates the growth curves for three species. This figure shows the growth rate of L. zenithicus starting to level off at the fifth year. This eventual decline is not initiated in nigripinnis until the seventh year. It is thus possible that the greater maximum size found in L. nigripinnis is not referable to age differences but results from the later age at which the reduced growth rate commences.

Discussion of the possible significance of the absence of small nipigon (less than 180 mm.) in the samples is deferrred until page 36. The size of L. tullibee will also be treated later (p.5).

The maximum size found for the Lake Winnipeg ciscoes may be compared with published reports. Koelz (1929) remarks that L. zenithicus in both Lakes Superior and Huron rarely exceed a length of 300 mm. A frequency distribution table is presented in Van Oosten's study (1937) of Koelz's Lake Superior specimens. Only 4 of the 859 specimens are 300mm. and over. Dymond (1926) does not present the size range of zenithicus found in Lake Nipigon. He implies that they are generally under 300 mm. The key to the species of Leucichthys (p. 60) reads: "Occasional specimens of artedi, zenithicus and reighardi of over twelve inches may be looked for, but the key under AA may be used for their identification".

Both Koelz (1925) and Dymond (op. cit.) agree on the large size attained by L. nipigon. Koelz's comments follow:

> The fish grows to a larger size than any species of Leucichthys seen from the Great Lakes, though it is possible that when these waters were virgin, as Lake Nipigon now is, some individuals of the larger species in the Great Lakes equalled those of the new form in this respect. The largest specimen I have seen is from the Toronto collection, and measures 447 mm. Examples longer than 300 mm. are common.

Although there has been no detailed account published of the size attained by L. nigripinnis, excerpts from Koelz's monograph (1929) substantiate our findings that this species also reaches a large size. "The blackfin (nigripinnis nigripinnis of Lake Michigan) is one of the largest of the deep water Leucichthys. It not infrequently reaches a length of 35 centimeters (13¾ inches) with a weight of a little more than 1½ pounds." He mentions 66 specimens over 300 mm. seen from Lake Superior (p. 426) and discusses data from 69 specimens 290 mm. and over from Lake Nipigon (p. 431). Dymond and Pritchard (1930) list the mean length of 5 specimens of nigripinnis from Lake Winnipeg as 294 mm.

A consideration of the length frequency distribution of the Lake Winnipeg ciscoes has revealed that nigripinnis attains a larger size than either zenithicus or nipigon. The difference is not entirely due to the greater number of older specimens but is attributed to the prolongation of a high rate of growth to a more advanced age. The Lake Winnipeg observations on maximum size attained by Leucichthys spp. find agreement with results published by other investigators.

GROWTH

Curves of growth

The growth of an individual or population may be represented in at least six different ways (vide Medewar, 1945). The two most utilized methods to illustrate the growth of fish are the curve of growth and the rate of growth. The curve of growth results from plotting of absolute magnitudes against time; when increments occurring between the time intervals are plotted the rate of growth is presented. As Thompson (1942) states, "one is the inverse of the other;.....each makes clear to the eye phenomena which are implicit, but less conspicious in the other".

It was decided that the most appropriate method of comparing the growth in length of the three Leucichthys species would be by presenting their curves of growth. Theoretically, the curve of growth results from a plotting of continous units. However, where discrete units are used, the resultant histogram can be altered to a curve by smoothing. The variates used for the growth curves presented in this study are the completed ages of the fish and their actual standard lengths at the time of capture. The presentation of curves of growth using these units has inherent difficulties. Distortion of the curve ensues when one variate is continuous and the other discontinuous.

The age of a fish is recorded in discrete units. Actually age is a continuous variate. Only on the day of annulus formation, the fish's "birthday", is a fish a specific age--for example four years. From that day until the formation of the next annulus the following year, it is designated as four years. Actually it progressively becomes 4 years 1 month, 4 years 2 months, etc. until it reaches five completed years. But unless the time of annulus formation is known, it is impossible to record the age of a fish as a continuous variate.

The magnitude of the fish should represent the size of the fish at a discrete age and nothing else. Using the length at capture does not do this. It is observable that fish captured early in the growing season will be smaller than specimens of the same age, expressed in descrete units, taken towards the end of the growing season. Actual lengths usually represent more than the size at a discrete age.

To eliminate the variation in size that arises from this extra growth that is added in the interval between the initiation of the growing season and the time of capture, the "calculated" length may be determined. The "calculated" length is the size of the fish at the beginning of the growing season. It is determined by calculating back to the length at the time of annulus formation. The determination of "calculated" lengths depends on the establishment of the relationship between the growth of the body and the growth of the scale. This is a very disputed subject. One point seems clear. The size of the fish when the scales are laid down must be established. Since no material was available to determine this size, "calculated" lengths are not used in this study.

Growth in different calendar years

The growth made by an individual fish or the population is influenced by environment conditions. Since environmental factors probably change in intensity from year to year, studies of the growth of a species should be conducted for several years to determine the range in growth that might be expected to occur. Table XV is presented to show the variation in mean lengths for each group during three calendar years. The specimens are from the Mukatawa River locality. For 6-year-old L. zenithicus females the mean lengths of the samples collected in 1947, 1948 and 1949 were respectively 245, 240 and 226 mm. The younger age group, the 5-year-olds, had mean lengths of 217 mm. in 1947, 248 mm. in 1948 and 206 mm. in 1949.

No attempt was made to determine if the exhibited differences within the mean lengths of an age group of each species collected in different calendar years are ascribable to sampling or to changes in the growth rate of the different year classes.

Growth differences between sexes

It is important biologically, and for future presentation of the data, to determine if differences exist in the growth between males and females of the same age and species. Table IV presents the data used. The differences in the means in millimeters (column 8) range from nil to 31, but are usually under 5. The differences in length between the two samples (males and females) of a particular age and species can be compared with the differences in sampling from a normally distributed population and from these comparisons it may be said that the differences in the size of male and female fish are or are not statistically significant. The statistical test employed is the "t" test (Snedecor 1946, 82). The one assumption made is that the variation in length within an age group is distributed normally about its mean value.

Table IV lists 17 comparisons that were tested. L. zenithicus made up 7 comparisons; nigripinnis, 7 and nipigon, 4. A variety of age groups was used. The youngest age group compared was 3 years, the oldest 9 years. Of the 17 comparisons, only 3 were on the borderline of significance (P value of .05). These 3 samples were nigripinnis, 5-year-olds; nigripinnis, 7-year-olds and nipigon, 6-year-olds. With regard to nigripinnis, in one case the females were larger (5-year-olds) and in the other, the males were larger (7-year-olds). From a biological standpoint, if differences in growth occur, it is expected that they would be consistent. On the basis of the above information, it was decided that the data for the sexes could be combined. Data from other localities will be likewise grouped and discussion hereafter, with regard to standard length, will be on combined material.

Table IV. Comparison of standard length of male and female Leucichthys. Samples collected Mukatawa River, Lake Winnipeg, 1947-49.

Species	Age	No. of males	Mean of males	Sum of squares	No. of females	Mean of females	Sum of squares	Difference of means	"t" value
zenithicus	3	19	138	13,559	14	131	2,875	7	.851
"	4	27	184	37,495	18	180	27,121	4	.339
"	5	65	226	17,338	49	222	35,162	4	.976
"	6	50	239	13,734	78	242	19,863	3	.414
"	7	30	249	16,714	50	253	14,127	4	.872
"	8	4	264	3,135	9	254	2,051	10	.766
nigripinnis	3	3	133	61	5	142	1,376	9	.796
"	4	7	196	11,055	5	183	9,811	13	.486
"	5	15	224	17,391	13	248	6,806	24	2.339*
"	6	15	263	18,616	11	263	7,108	0	-
"	7	7	307	2,442	8	276	4,822	31	2.534*
"	8	8	304	3,450	8	322	1,072	18	.971
"	9	4	309	2,185	10	318	4,664	9	.637
nipigon	4	5	225	506	5	228	985	3	1.305
"	5	26	252	7,422	29	254	220	2	.617
"	6	25	258	4,758	29	268	5,375	10	2.627*
"	7	15	268	2,030	23	268	10,074	0	-

Note: "t" values having "P" of .05, *; .01, ** (Snedecor, 1946, p. 65).

Age, length and curves of growth of Lake Winnipeg Leucichthys

For the Lake Winnipeg Leucichthys it has been shown that the males and females of the same age are essentially the same in standard length. An indication of the length differences at each age of the different year classes has been presented. In these discussions the data used were those collected off Mukatawa River. Data obtained from the other localities on Lake Winnipeg were inspected so as to employ all available material for the presentation of curves of growth. These specimens were collected in 1948 at Matheson Island, Gimli, and Black Bear Island. The number of each species of Leucichthys used from these localities has been recorded in Table II. The range and mean of lengths for each age and species were found to be similar to those for the Mukatawa River collection presented in Table XV. Therefore all the data could be combined. Tables V, VI, and VIII present length frequency distributions, grouped according to age, for L. zenithicus, L. nigripinnis and L. nipigon collected at all localities during the three years on Lake Winnipeg.

These tables illustrate the age composition of the samples. For all species the majority of the fish were 4 to 7 years old. No young of the year or yearlings of Leucichthys were collected. Even the two-year-old fish were not well represented; 13 in all having been taken. Twelve of these fish were zenithicus. The youngest nipigon collected were 4 years old.

The absence of the two and three-year-olds of this species, when these same age groups were represented in the *nigripinnis* and *zenithicus* samples, cannot be explained. From an examination of the growth curves (Figure 1) young *nipigon* would be expected to be larger than young *nigripinnis* and *zenithicus* so they could have been taken by the fishing gear. Possibly they live in different areas or depths than those sampled. Dymond (personal communication) did not collect *L. nipigon* specimens under 175 mm. in length during the Lake Nipigon investigation, 1921-24.

Lake Winnipeg *Leucichthys* appear to live approximately one decade. The oldest individual taken was a *nigripinnis* in its twelfth year. Kennedy (1949) found *L. artedi* in Great Bear Lake to be up to 13 years old (in their fourteenth year of life). The samples indicate that *nipigon* may be the shortest lived species since only 3 specimens completed 8 years of life while 30 specimens of *nigripinnis* and 22 specimens of *zenithicus* lived to that age.

Leucichthys vary somewhat in length within an age group. This variation is undoubtedly exaggerated because actual lengths are used (cf. page 31). In age groups 4 to 7 the range in length within an age group approximates 140 mm.

It is from the frequency distributions listed in Tables V to VII that curves of growth (Figure I) are derived. To facilitate comparisons only the mean lengths are used in plotting these graphs. However, as will be apparent, each variate is utilized in comparing the growth curves.

Table V. Relationship between length and age in L. zenithicus. Data from Lake Winnipeg, 1947-49. Age recorded in completed years and standard length in mm.

Midpoints of class interval	2	3	4	5	6	7	8	9	10	11
110	-	2	-	1	-	-	-	-	-	-
120	6	10	2	-	-	-	-	-	-	-
130	2	12	7	-	-	-	-	-	-	-
140	1	8	3	1	-	-	-	-	-	-
150	-	2	3	2	-	-	-	-	-	-
160	1	2	2	1	-	-	-	-	-	-
170	1	1	7	3	-	-	-	-	-	-
180	-	1	1	4	1	1	-	-	-	-
190	-	1	8	3	2	-	-	-	-	-
200	-	-	6	13	2	-	-	-	-	-
210	-	1	5	8	5	2	-	1	-	-
220	1	-	3	30	16	2	1	-	-	-
230	-	-	5	30	22	12	-	-	-	-
240	-	-	2	28	36	10	1	-	-	-
250	-	-	1	13	29	21	7	-	-	-
260	-	-	1	3	24	22	3	-	-	-
270	-	-	-	1	8	11	3	-	1	-
280	-	-	-	-	-	2	2	1	-	-
290	-	-	-	-	-	2	-	-	-	-
300	-	-	-	-	-	1	-	-	-	-
310	-	-	-	-	-	-	1	-	-	-
320	-	-	-	-	-	-	-	-	-	-
330	-	-	-	-	-	-	-	-	-	-
340	-	-	-	-	-	-	-	1	-	-
350	-	-	-	-	-	-	-	-	-	-
360	-	-	-	-	-	-	-	-	-	-
Totals	12	40	56	141	145	86	18	3	1	-
Mean	138	135	182	221	240	250	258	-	-	-
S.E. mean	8.86	3.33	4.90	2.08	1.45	1.96	4.38	-	-	-

Table VI. Relationship between length and age in L. nigripinnis. Data from Lake Winnipeg 1947-49. Age recorded in completed years and standard length in mm.

Midpoints of class interval	Age 2	3	4	5	6	7	8	9	10	11
110	-	-	-	-	-	-	-	-	-	-
120	-	2	-	-	-	-	-	-	-	-
130	-	4	2	-	-	-	-	-	-	-
140	1	4	3	1	-	-	-	-	-	-
150	-	2	3	-	-	-	-	-	-	-
160	-	1	2	-	-	-	-	-	-	-
170	-	1	1	-	-	-	-	-	-	-
180	-	-	2	2	-	-	-	-	-	-
190	-	-	5	3	-	-	-	-	-	-
200	-	-	5	7	3	-	-	-	-	-
210	-	-	2	3	1	-	-	-	-	-
220	-	-	1	3	1	-	-	-	-	-
230	-	-	2	6	3	-	-	-	-	-
240	-	-	1	3	7	1	-	-	-	-
250	-	-	-	6	3	3	-	-	-	-
260	-	-	-	2	1	-	1	-	-	-
270	-	-	1	1	3	2	-	-	-	-
280	-	-	-	4	2	1	-	2	-	-
290	-	-	-	-	1	3	1	1	-	-
300	-	-	-	-	4	1	1	2	-	-
310	-	-	-	-	3	-	5	1	1	-
320	-	-	-	-	-	3	5	-	-	-
330	-	-	-	-	-	2	1	2	-	1
340	-	-	-	-	-	-	1	2	-	-
350	-	-	-	-	-	-	1	1	1	-
360	-	-	-	-	-	-	-	-	-	-
Totals	1	14	30	41	32	16	16	11	2	1
Mean	-	138	183	225	256	287	313	313	-	-
S.E. mean	-	3.58	6.61	5.21	6.02	7.69	4.95	7.37	-	-

Table VII. Relationship between length and age in L. nipigon. Data from Lake Winnipeg, 1947-49. Age recorded in completed years and standard lengths in mm.

Midpoints of class intervals	Age 2	3	4	5	6	7	8	9	10	11
110	-	-	-	-	-	-	-	-	-	-
120	-	-	-	-	-	-	-	-	-	-
130	-	-	-	-	-	-	-	-	-	-
140	-	-	-	-	-	-	-	-	-	-
150	-	-	-	-	-	-	-	-	-	-
160	-	-	-	-	-	-	-	-	-	-
170	-	-	-	-	-	-	-	-	-	-
180	-	-	-	-	-	-	-	-	-	-
190	-	-	-	-	-	-	-	-	-	-
200	-	-	-	1	-	1	-	-	-	-
210	-	-	2	-	-	-	-	-	-	-
220	-	-	3	2	1	-	-	-	-	-
230	-	-	2	3	-	-	-	-	-	-
240	-	-	4	12	5	-	-	-	-	-
250	-	-	-	17	14	5	-	1	-	-
260	-	-	-	14	13	10	-	-	-	-
270	-	-	1	8	11	14	-	-	-	-
280	-	-	-	4	10	8	2	-	-	-
290	-	-	-	-	-	3	1	-	-	-
300	-	-	-	-	2	-	-	-	-	-
310	-	-	-	1	1	-	-	-	-	-
320	-	-	-	-	-	-	-	-	-	-
330	-	-	-	-	-	1	-	-	-	-
340	-	-	-	-	-	-	-	-	-	-
350	-	-	-	-	-	-	-	-	-	-
360	-	-	-	-	-	-	-	-	-	-
Totals	-	-	12	62	57	42	3	1	-	-
Mean	-	-	230	252	262	267	-	-	-	-
S.E. mean	-	-	4.94	2.10	2.10	2.68	-	-	-	-

In the investigation of the probability that these growth curves are the same, a definition of terms is necessary. The growth curves for the three species would be identical if each curve had a common shape and position or, if calculated, could be expressed by a single equation. Comparison of these characteristics of the curves would have limited utility. The methods, therefore, used in the comparison of the growth curves of the three species is the testing, by statistical techniques, of the differences observed in the mean size attained at each age. Within an age group, variation in length follows a describable distribution. The central tendency of these distributions can be recorded in terms of a mean, mode, or median. The mean was chosen to best express the central tendency of each distribution because methods are available to estimate the likelihood of error associated with that measure. The hypothesis being tested is that the differences in means will not be worthy of consideration unless they are greater than could be expected to occur in samples drawn from a homogenous population.

The test used is a modified difference of means test (Snedecor, 1946 p. 83). Table XVI gives the statistics and the results of these tests for 14 comparisons. Table VIII compiles the individual results for easy perusal.

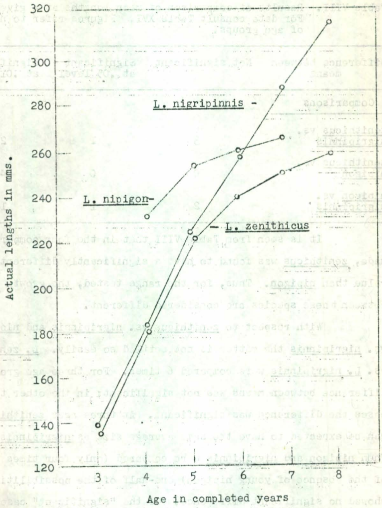

Figure I. Curves of growth of Lake Winnipeg ciscoes.

Table VIII. Results of comparison of mean lengths at a given age. For data consult Table XVI. Figures refer to number of age groups.

Difference between means	Not significant	Significant at .05 level	Significant at .01 level
Comparisons			
zenithicus vs. nigripinnis	3	1	2
zenithicus vs. nipigon	0	0	4
nipigon vs. nigripinnis	2	1	1

It is seen from Table VIII that in the four comparisons made, zenithicus was found to have a significantly different mean value than nipigon. Thus, for the range tested, the growth curves between these species are considered different.

With respect to zenithicus vs. nigripinnis and nipigon vs. nigripinnis the matter is not settled so easily. L. zenithicus vs. L. nigripinnis were compared 6 times. For three age groups the difference between means was not significant; in the other three cases the difference was significant. At three ages zenithicus can be expected to have the same average size as nigripinnis. When nipigon and nigripinnis were compared (only four times because of the absence of young nipigon) one-half of the possibilities showed no significant difference. Of the "significant" cases, one was at the .05 level and the other at the .01. As in the previous case nipigon can be expected not to differ in average size from L. nigripinnis in two age groups.

If only these tests were available, it might be concluded that the growth curve of zenithicus is not different from nigripinnis because in 50 per cent of the comparisons made, no significant differences between the means was demonstrated. The same reasoning applies to nipigon vs. nigripinnis. However, an examination of the manner in which these differences are distributed over the growth curves makes these conclusions untenable.

If Figure I is examined, the following considerations present themselves. At age two nigripinnis and zenithicus appear to be the same average size. This age was not tested for difference of means because only one individual of nigripinnis was taken. The size of L. nipigon at this age and at 3 years old is not known because no specimens were collected. Extrapolation of the nipigon growth curve suggests that this species is larger than either zenithicus and nigripinnis at two and three years of age. At age three the mean lengths of the samples of zenithicus and nigripinnis are 135 and 138 mm. The difference was found to be not significant. When the fish are 4 years old L. nipigon is significantly larger than either zenithicus or nigripinnis. Four-year-old zenithicus and nigripinnis are considered to be the same size; only 1 mm. difference in sample means was observed. The three species when 5 years old continue the trend shown in their fourth year. L. nipigon is the largest, being approximately 29 mm. longer than the other species. Although the difference of the mean lengths of the samples of nigripinnis and zenithicus has increased to 4 mm. the difference is not significant. It appears that at 6 years of age nigripinnis begins its trend of diverging in size from zenithicus. At this age the mean length difference between the species, as illustrated by the samples, is 16 mm. This difference could be expected once in twenty times if they were the same size and is termed "barely significant". Now nigripinnis and nipigon are the same average size. As in the previous age group zenithicus is smaller than nipigon. At 7 years of age the mean lengths of the three species differ significantly one from another. The zenithicus and nigripinnis samples differ by 37 mm. The size of nipigon is intermediate, being on the average, as judged by the samples, 20 mm. smaller than nigripinnis and 17 mm. larger than zenithicus.

Having described the mean size at each age of each species we can now discuss in what respects the three curves are different.

The growth curves of zenithicus and nigripinnis follow one another from the second to the fifth year. From that time on they diverge in size because zenithicus has reached its upper asymptote of growth. Indications are that the decline in the growth rate of nigripinnis commences at 7 years. Initially L. nipigon must grow faster than zenithicus or nigripinnis in order to be the longest at 4 years of age. It averages longer than either species also at 5 and 6 years of age. It, however, does not maintain this lead but is succeeded by nigripinnis after the sixth year. The eventual "final" size of L. nipigon is intermediate between nigripinnis and zenithicus.

SEXUAL MATURITY

Table IX tabulates the data on the sexual maturity of the ciscoes with respect to species, age, sex and condition. Owing to the absence of the younger age groups, apparent variation in the onset of sexual maturity with age and the limited number of specimens examined, no precise picture of sexual maturation can be presented.

Since mature specimens of each sex and species were taken at the earliest ages collected, it is not known at what age sexual maturity first occurs.

The three species, L. zenithicus, L. nigripinnis and L. nipigon are similar in two respects, relative scarcity of immature females and wide variation in the age of immature males. Only 4 of the 272 zenithicus and one of the 80 nigripinnis females were immature. No immature females of nipigon were collected. With only one exception (zenithicus, age 2) the percentage of immature males in each age group is greater than the percentage of immature females. The induction made from the data is that there is a tendency for the females to mature at an earlier age than the males. If the explanation of the sexes maturing at different ages

Table IX. Relationship between sexual maturity and age of Lake Winnipeg ciscoes. Figures refer to number of individuals.

Species	Sex	Condition	Age in completed years 2	3	4	5	6	7	8	9
zenithicus	males	immature	-	5	13	18	2	-	-	-
		mature	5	17	15	60	50	31	6	1
nigripinnis	males	immature	-	-	6	4	1	1	-	2
		mature	-	6	11	16	15	7	8	2
nipigon	males	immature	-	-	3	5	4	1	1	-
		mature	-	-	2	21	21	14	1	1
zenithicus	females	immature	1	1	-	-	2	-	-	-
		mature	5	17	24	63	89	55	12	3
nigripinnis	females	immature	-	-	-	1	-	-	-	-
		mature	-	7	13	18	15	8	8	10
nipigon	females	immature	-	-	-	-	-	-	-	-
		mature	-	-	6	34	32	27	1	-
zenithicus	undetermined	undetermined	1	-	4	-	2	-	-	-
nigripinnis	undetermined	undetermined	1	1	-	2	1	-	-	-
nipigon	undetermined	undetermined	-	-	1	2	-	-	-	-

is the correct interpretation of the data, in the first years (age groups 0, 1 and 2) the percentage of immatures should be greater in the females than in the males. Unfortunately this point cannot be verified because young specimens were not collected.

The explanation of the greater percentages of immature males in the age groups sampled may lie in a misjudgement of the sexual condition of the males. The majority of the ciscoes were collected in the period June to July (cf. p. 19). The males may have been classified as immature when in actuality they would spawn in the fall.

The Lake Winnipeg data suggest that there is a tendency for the female ciscoes to mature at a younger age than the males. Other instances of differential maturity of coregonine fish have been reported. Van Oosten (1929) postulated for the Lake Huron cisco, L. artedi, that the females matured earlier in life than the males. However, in the whitefish of Lake Huron (Van Oosten, 1939) and Lake Erie (Van Oosten and Hile, 1949) the males were reported to be the earlier maturing sex.

The author's observations on the sexual maturity of Leucichthys zenithicus do not agree with Bajkov (1930).

> .....neither of the two important species (L. zenithicus and L. tullibee) spawns before four years old, but in the third year the ovaries can be microscopically distinguished from the testes.....At the time of first spawning Black-backed tullibee reach about 300 mm. (12") in length, but the Light-backed (L. zenithicus) only 250 mm. (about 10").

Table IX shows that for L. zenithicus, 10 age two specimens were regarded as mature. The mean length fonnd for 2 year old zenithicus was 138 mm. (Table V).

Until more data become available, it is concluded that there are no noticeable differences in the age of onset of sexual maturity among three species, L. zenithicus, L. nigripinnis and L. nipigon. Within each species there appears to be, particularly in the males, a wide variation in the age of attainment of maturity.

INFECTION OF LAKE WINNIPEG CISCOES

Incidence

Since the number of parasites in each cisco was recorded it was possible to calculate the incidence of infection in Leucichthys zenithicus, L. nigripinnis and L. nipigon. The purpose of these calculations was to decide if the incidence of infection differed among the three species.

Examination of frequency polygon graphs, Figure 2, reveals that the occurrence of cysts per fish, in L. zenithicus and L. nigripinnis, follows a poisson-type distribution. Newton (1932) presents a graph showing similar skewed distributions for infection of three Lake Winnipeg coregonines. In the type of distribution displayed by L. zenithicus and L. nigripinnis the variance is not independent of the mean. Unless a suitable transformation of the variates is utilized, tests of significance by analysis of variance are not strictly allowable.

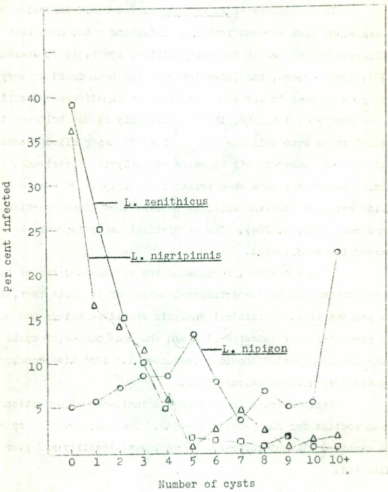

Figure 2. Frequency distribution in percentages of T. crassus infection of Lake Winnipeg ciscoes.

The incidence of T. crassus plerocercoid infection may be dependent upon various factors. Infection rates have been influenced by the age of the host (Miller, 1945b, 1948; Oakland, 1949). Furthermore, the infection rate has been found to vary from year to year in the same locality and in different localities in the same year (Oakland, ibid). Initially it was believed that the infection data collected on the Lake Winnipeg ciscoes could be analyzed for these effects by means of analysis of variance. Examination of the data when arranged in analysis of variance tables revealed that the subclass numbers were "disproportionate" (Snedecor, 1946, p. 284). The statistical analysis would be necessarily complicated.

It was decided, because of the skewness of two of the distributions and the nonorthogonal nature of the data that, at the present time, statistical analysis should be waived and only the percentages of infected fish and the mean number of cysts found in each species should be considered. Tentative conclusions are drawn from these calculations.

Table X presents data on the incidence of infection of three species for the years 1947-1949. The data for each species are combined without reference to age, sex, locality and year collected.

Table X. Triaenophorus crassus infection of Leucichthys collected from Lake Winnipeg, 1947-1949.

	zenithicus	nigripinnis	nipigon
No. of specimens	501	164	176
No. infected	309	105	167
Percentage infected	62	61	96
No. of cysts	778	399	1253
No. of cysts per fish	1.5	2.4	7.1
No. of cysts per infected fish	2.5	3.8	7.5

Line three of this table shows that the percentage of infected zenithicus, nigripinnis and nipigon was 62, 61 and 96 per cent respectively. The percentages of infected fish are such that, although not tested statistically, they appear to represent a real and significant difference in infection between L. nipigon and each of the other two species. L. zenithicus and L. nigripinnis are considered to be infected to the same degree.

In line five of this table is recorded the mean number of cysts per fish. The rate of infection as judged from these mean values is highest in L. nipigon and is considered to be different from the other two species. Whether there is a significant difference in the mean cyst count between L. zenithicus and L. nigripinnis has not been determined. It might be suggested that the postulated differences in infection between L. nipigon and the other two species is consequent upon the few number of non-parasitized nipigon in contrast to the greater percentages of clear L. zenithicus and L. nigripinnis. This undoubtedly is true in part but inspection of the mean cyst counts for infected fish only (line six) shows that the relative position of the means does not change for the three species.

In the author's opinion the presented data indicate that L. nipigon has the highest incidence of infection on the basis of the percentages of infected fish and average cyst count. The small differences in infection between L. nigripinnis and L. zenithicus do not warrant the conclusion of differential incidence existing between them.

Newton (1932) has discussed the infection of L. zenithicus in Lake Winnipeg. His data, presented on page 347, when recombined compare favourably with the author's data given in Table X. Newton's data, based on 4,149 specimens reveal 60 per cent of the individuals infected, whereas 62 per cent of the 1947-1949 L. zenithicus specimens were parasitized. The mean number of cysts per fish for Newton's specimens is 1.4; for infected fish only, the average is 2.4. Between these figures and the author's, there is only 0.1 difference in each case.

Relationship of infection to age of host

To ascertain the relationship between the incidence of infection and the age of the host, the infection of year classes as they increase in age should be calculated. To follow two different year classes from the time they increase in age from one to nine years necessitates the collection of samples for a period of ten consecutive years. Since specimens were collected only for three years it is not possible to use this approach.

As an alternative, the mean cyst count for each age group of the ciscoes, collected at Mukatawa River locality, is discussed. These data are recorded in Table XI. Figure 3 has been drawn to illustrate the 1947 data. The data for 1948 and 1949 are not graphed because of the small number of ciscoes collected. The standard error of the means was not calculated (owing to the nature of the frequency distributions), therefore the differences of the means within and between species were not tested.

Figure 3 reveals that in the samples collected in 1947 the infection of L. zenithicus shows no correlation with age, the mean cyst count fluctuating between 1.2 and 1.6 cysts per fish. In the L. nigripinnis sample there is an increase in the mean cyst count from the third to the fourth year and then a fluctuating but gradual decline in cyst count. It should be noted that the number of specimens representing ages three and four is particularly small. L. nipigon shows an increase in infection from age 4 (however, there are only 7 specimens in this category) to age 6. There is no difference in the infection of the 6 and 7 year olds.

Table XI. Mean Triaenophorus infection with age of <u>Leucichthys</u>. Specimens from Mukatawa River, 1947-1949. Figures in parenthesis are number of specimens.

Age in completed years	3	4	5	6	7	8	9
<u>L. zenithicus</u>							
1947	1.6(20)	1.4(31)	1.5(71)	1.2(73)	1.3(54)	1.5(10)	0.0(1)
1948	3.3(3)	1.3(6)	1.3(32)	1.6(47)	1.6(25)	5.0(1)	1.0(1)
1949	2.0(10)	2.0(7)	3.0(11)	2.2(8)	0.0(1)	1.0(2)	-
<u>L. nigripinnis</u>							
1947	2.0(3)	3.8(7)	2.8(20)	3.4(21)	1.8(13)	0.9(16)	0.9(11)
1948	1.0(1)	0.0(1)	4.2(5)	6.6(3)	11.0(1)	-	0.0(1)
1949	3.3(4)	4.0(3)	0.6(3)	8.0(2)	3.0(1)	-	1.0(1)
<u>L. nipigon</u>							
1947	-	3.2(7)	5.3(25)	8.3(38)	8.3(28)	14.3(3)	11.0(1)
1948	-	5.2(2)	6.3(29)	6.7(16)	8.0(10)	-	-
1949	-	4.0(1)	10.0(1)	-	-	-	-

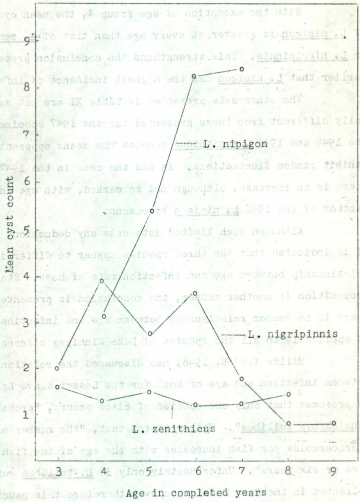

Figure 3. Age of host vs. mean cyst count in Lake Winnipeg Leucichthys.

With the exception of age group 4, the mean cyst count of L. nipigon is greater at every age than that of L. zenithicus or L. nigripinnis. This strengthens the conclusion presented earlier that L. nipigon has the highest incidence of infection.

The other data presented in Table XI are not substantially different from those presented for the 1947 specimens. In the 1948 and 1949 L. zenithicus samples the means apparently exhibit random fluctuations. As was the case in the 1947 specimens there is an increase, although not so marked, with age in the infection of the 1948 L. nipigon specimens.

Although such limited data make any deductions tentative, it is indicated that the three species appear to differ in their relationship between age and infection rate of host. Stating the proposition in another manner, the conclusion is presented that there is no common relationship between age and infection which is applicable to all the species of Lake Winnipeg ciscoes.

Miller (1945b, 1948) has discussed the relationship between infection and age of host for the Lesser Slave Lake cisco. He presumes that only one species of cisco occurs, "probably Leucichthys tullibee". Miller states that, "the number of plerocercoids per fish increases with the age of the fish up to five or six years". Unfortunately only 38 L. tullibee were collected in the Lake Winnipeg survey therefore this paucity of specimens prevents a reinvestigation of his conclusions with reference to that species.

However, as shown by Figure 3, the increase in infection up to five or six years appears not to apply to all species of ciscoes. L. nipigon follows such an increase but this is definitely not the case in L. zenithicus. Since adequate data are not available for young L. nigripinnis (age groups 0-3) it is not known if the high mean cyst count of later age groups is the highest for every year of life in this species.

In those situations where the older age groups of ciscoes are not more parasitized than the younger, it is expected a priori that diminution of infection in whitefish by overfishing of the ciscoes (vide Miller, 1948) would be rendered more difficult.

To recapitulate, it has been found that the species of Lake Winnipeg ciscoes differ not only in their incidence of infection but also in the relationship of infection to age of host. Although in some species, L. nipigon in Lake Winnipeg and L. tullibee in Lesser Slave Lake, the number of cysts increase up to a certain age this is not the universal rule. These considerations prompt the suggestion that identification of ciscoes be made whenever this group is investigated with reference to Triaenophorus programs.

LEUCICHTHYS TULLIBEE

Thirty-eight of the ciscoes collected are regarded as L. tullibee. Conclusions drawn from such limited data can be regarded only as tentative therefore consideration of this species has been omitted from the main portion of the text.

L. tullibee ranks with L. nigripinnis as being the largest species collected on Lake Winnipeg. The largest Leucichthys taken was a 10 year old tullibee with a standard length of 353 mm. Twenty-six per cent of tullibee were over 300 mm. long.

The mean length of the various age groups is presented in Table XII. With respect to the size at each age tullibee resembles more closely nigripinnis and nipigon than zenithicus. When 4 and 5 years old the average size of tullibee is considered the same as nipigon. It was noted (p. 43) that the average size of nipigon at ages 4 and 5 was significantly different from nigripinnis and zenithicus. L. tullibee is the largest in average size of the four species at age 6. The difference was not tested statistically. The size of nigripinnis at ages 7 and 8 was found to be significantly different from zenithicus and nipigon (p. 44). At these ages the size of tullibee is nearest to nigripinnis. The curve of growth of L. tullibee, if it were drawn, would be similar to nipigon at ages 4 and 5, at age 6 similar to both nigripinnis and nipigon and at ages 7 and 8 would be closest to nigripinnis.

Three of the 38 specimens were immature. One was a 6 year old male and the other two were 5 year old females. Twenty-three mature females were taken. The proportion of mature to immature females is greater than that observed in the other three species.

Table XII. Relationship of length, sexual maturity and Triaenophorus infection with age of Lake Winnipeg L. tullibee.

Age in completed years	3	4	5	6	7	8	9	10
Number of specimens	2	1	13	14	3	3	1	1
Mean standard length	206	230	249	270	291	308	325	353
Number of fish infected	2	1	6	9	3	1	0	0
Mean number of cysts per fish	3.0	1.0	0.6	2.1	1.6	1.3	0	0
Male immature	-	-	-	1	-	-	-	-
Male mature	1	-	4	3	1	1	1	-
Female immature	-	-	2	-	-	-	-	-
Female mature	1	1	7	10	2	1	-	1
Undetermined sex and condition	-	-	-	-	-	1	-	-

The incidence of Triaenophorus infection of L. tullibee was calculated. Twenty-two fish each contained one or more parasites. The percentage of infection was 58. The mean number of cysts per fish was 1.4. It is concluded that L. tullibee has the same incidence of infection as L. zenithicus and L. nigripinnis but differs from L. nipigon.

DISCUSSION

Twenty years ago Dymond and Pritchard using limited material believed that the Lake Winnipeg ciscoes comprised four species: L. zenithicus, L. nipigon, L. nigripinnis and L. tullibee. Reinvestigation of these ciscoes was started for two reasons. Examination by the author of the morphometrical characters of a large series of specimens revealed them to be so provokingly similar that the discreteness of the species was doubted. As may happen in the case of sympatric groups, it was felt that arbitrary limits may have been placed on one exceedingly variable species. Furthermore, on the basis of investigations of other waters, suspicion has centered on the validity of nipigon and tullibee.

The taxonomy of the ciscoes has been investigated from a biological viewpoint. Instances may be noted where other fields of Zoölogy have been used as an aid in the recognition and definition of taxonomic groups. Drosophila simulans was recognized on account of its breeding behavior (Huxley, 1940). Ticehurst (cf. Mayr. 1942) found the nesting sites distinctive in two morphologically similar species of old world warblers. Kennedy (1943) discovered sibling species of the whitefish, Coregonus clupeaformis from the fact that they matured at different sizes.

In the Lake Winnipeg study, groups of ciscoes identified by taxonomic keys in Dymond and Pritchard (1930) were found to exhibit the following differences:-

L. nigripinnis and L. tullibee attain a larger size than either L. nipigon or L. zenithicus.

The curve of growth of nipigon differs from those of zenithicus and nigripinnis. In the latter two species the curves are not considered different from the second to the fifth year but differ from the sixth to the eighth. If the curve of growth of tullibee were drawn, the lower half would resemble nipigon and the upper half nigripinnis.

The incidence of Triaenophorus crassus infection differs between L. nipigon and the other three species. Of three species examined, there appears to be no common relationship between incidence of infection and age of host.

This biological study is directed to testing the validity of described species rather than the recognition of new forms. The conclusions, therefore, are restricted by the following consideration. Characters of two related species may be studied which have not been recorded as taxonomic characters of the scientific description. The validity of species is not questioned if characters of this nature are found not to be different in both species. Differences may support but similarities do not refute the species.

Although it is not known if the biological differences found among the four Leucichthys species are the expression of the genotype, the environment or the product of both, they reveal discontinuity which parallel morphological and morphometrical characteristics. Support for the original designation is afforded when groups which were assigned specific status by reason of morphological distinctiveness reveal also biological differences. It is in this correlation between biological and morphological characteristics that the present study corroborates Dymond and Pritchard's opinion that L. zenithicus, L. nigripinnis, L. nipigon, and L. tullibee occur in Lake Winnipeg.

SUMMARY

1. The ciscoes of Lake Winnipeg, Manitoba have been studied with respect to maximum size attained, curve of growth, sexual maturity and infection by the tapeworm, Triaenophorus crassus. The 887 ciscoes collected from 1947 to 1949 were found to comprise 504 Leucichthys zenithicus, 164 L. nigripinnis, 181 L. nipigon and 38 L. tullibee.

2. A historical survey of the taxonomy of Leucichthys is presented. The first record and notes on the distribution of those species reported as occurring in Manitoba is given.

3. L. nigripinnis and L. tullibee were found to attain the largest size. This is attributed mainly to prolongation of a high rate of growth to a more advanced age.

4. For the ages observed the differences in length between the sexes were found to be negligible in the three species examined. The range in length of a cisco of a given age was approximately 140 mm. The curves of growth of L. zenithicus, L. nigripinnis and L. nipigon were statistically compared. The growth curve of L. nipigon differs from those of L. zenithicus and L. nigripinnis. In the latter two species the curves are not considered different from the second to the fifth year but differ from ages 6 to 8. With respect to size at each age L. tullibee is similar to L. nipigon at ages 4 and 5 but more closely resembles nigripinnis than the other species at ages 7 and 8.

5. The data on the four species are not adequate to give a complete picture of sexual maturity. All species appear to mature over a period of ages. Females may mature at a younger age than males. No apparent differences in the age of onset of sexual maturity was observed among the four species.

6. The incidence of the plerocercoid stage of T. crassus in the four species was considered. Although such factors as the age of the fish, year and place of capture are reported to influence infection it was not possible to allow for these effects in the present study. Percentages of specimens infected and the mean number of cysts per fish have been the measures of infection. It was concluded that there were no differences in infection rates among L. tullibee, L. zenithicus and L. nigripinnis but that all

three differed from L. nipigon. There appeared not to be a common relationship between infection and age of host in three species examined.

7. The present study has shown that the ciscoes of Lake Winnipeg, which were identified on morphological and morphometrical characters differ in several biological characteristics. It is concluded that this parallelism between morphological and biological characteristics supports the opinion that four species of ciscoes occur in Lake Winnipeg.

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APPENDIX

Table XIII. Number of ciscoes collected near Mukatawa River, Lake Winnipeg, 1947-1949. Figures refer to number of individuals examined.

Date	Species				Totals
	zenithicus	nigripinnis	nipigon	tullibee	
June 19-July 3, 1947	114	25	21	12	172
July 3-July 17, 1947	46	26	29	3	104
July 18-July 31, 1947	111	44	54	6	215
June 15, 1948	10	6	25	0	41
June 19, 1948	3	4	16	1	24
June 28, 1948	106	3	21	1	131
June 17, 1949	14	0	0	1	15
June 18, 1949	4	0	2	0	6
June 19, 1949	1	1	0	0	2
June 22, 1949	6	7	0	4	17
June 24, 1949	6	3	0	5	14
June 25, 1949	5	2	0	0	7
June 28, 1949	3	1	0	0	4
June 29, 1949	2	1	0	2	5
Totals	431	123	168	35	757

Table XIV. The frequency distribution of gill-raker counts of 887 Lake Winnipeg Leucichthys.

Gill-raker count	Frequency	Gill-raker count	Frequency
33	1	51	8
34	11	52	7
35	23	53	7
36	62	54	8
37	95	55	10
38	83	56	31
39	71	57	26
40	72	58	37
41	57	59	23
42	31	60	16
43	29	61	18
44	31	62	6
45	24	63	8
46	26	64	2
47	21	65	1
48	13	66	1
49	16	67	2
50	10	68	0

Table XV. Variation in average length of <u>Leucichthys</u> during 1947-1949. Specimens collected off Mukatawa River, Lake Winnipeg. Figures in parenthesis refer to number of specimens.

Species	Year collected	Sex	Age in completed years 3	4	5	6	7	8	9+
zenithicus	1947	males	134(13)	177(20)	223(37)	235(28)	250(20)	274(3)	341(1)
"	"	females	125(7)	182(11)	217(34)	245(45)	251(34)	254(7)	-
"	1948	males	-	241(4)	230(20)	242(20)	246(10)	-	-
"	"	females	136(3)	182(2)	238(12)	240(27)	254(15)	246(1)	276(1)
"	1949	males	148(6)	156(3)	226(8)	253(2)	-	235(1)	-
"	"	females	136(4)	174(5)	206(3)	226(6)	287(1)	260(1)	-
nigripinnis	1947	males	136(1)	218(4)	216(11)	267(13)	312(6)	303(8)	297(3)
"	"	females	142(2)	218(3)	245(9)	273(8)	277(7)	322(8)	322(9)
"	1948	males	127(1)	-	241(3)	255(1)	275(1)	-	-
"	"	females	-	261(1)	257(2)	238(2)	-	-	280(1)
"	1949	males	137(1)	166(3)	250(1)	225(1)	-	-	345(1)
"	"	females	142(3)	135(1)	253(2)	233(1)	273(1)	-	-
nipigon	1947	males	-	235(2)	250(11)	261(15)	270(9)	283(2)	250(1)
"	"	females	-	228(5)	258(14)	269(23)	269(19)	276(1)	-
"	1948	males	-	223(2)	251(14)	253(10)	265(6)	-	-
"	"	females	-	-	250(15)	265(6)	269(4)	-	-
"	1949	males	-	208(1)	277(1)	-	-	-	-
"	"	females	-	-	-	-	-	-	-

Table XVI. Comparison of mean standard length of Leucichthys species at a given age. Data from Lake Winnipeg, 1947-1949.

Comparison	Age	Difference of means	t value $\frac{\bar{X}}{S_{\bar{x}}}$	t value if P is .05	t value if P is .01
zenithicus vs. nigripinnis	3	3	.61	2.09	-
zenithicus vs. nigripinnis	4	1	.12	2.03	-
zenithicus vs. nipigon	4	48	6.86**	2.10	3.38
zenithicus vs. nipigon	4	47	5.70**	2.10	2.88
zenithicus vs. nigripinnis	5	4	.71	2.01	-
zenithicus vs. nipigon	5	31	10.48**	1.99	2.63
nigripinnis vs. nipigon	5	27	4.80**	2.02	2.70
zenithicus vs. nigripinnis	6	16	2.59*	2.03	2.74
zenithicus vs. nipigon	6	22	8.03**	1.73	2.29
nigripinnis vs. nipigon	6	6	.94	2.03	-
zenithicus vs. nigripinnis	7	37	4.66**	2.12	2.93
zenithicus vs. nipigon	7	17	5.11**	2.00	2.67
nigripinnis vs. nipigon	7	20	2.46*	2.12	2.92
zenithicus vs. nigripinnis	8	55	8.32**	2.12	2.92