## LAKE OPEONGO

# The Ecology of the Fish Community and of Man's Effects on It 

by

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## FOREWORD

This paper is one of seven lake case histories-Lake Superior, Lake Michigan, Lake Huron, Lake Erie, Lake Ontario, Lake Opeongo, and Lake Kootenay. Concise versions of these papers, together with other lake case histories developed for and by an international symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) appeared in a special issue of the Journal of the Fisheries Research Board of Canada (Vol. 29, No. 6, June, 1972).

While this and each of the others in this series is complete in itself, it should be remembered that each formed a part of SCOL and is supplemented by the others. Because much detail of interest to fisheries workers in the Great Lakes area would not otherwise be available, this and the other case histories revised and refined in the light of events at the symposium are published here.

SCOL symposium was a major exercise in the synthesis of existing knowledge. The objective was to attempt to identify the separate and joint effects of three major stresses imposed by man: cultural eutrophication, exploitation, and species introduction on fish communities. Recently glaciated oligotrophic lakes were chosen as an "experimental set." Within the set were lakes which have been free of stresses, lakes which have been subjected to one stress, and lakes which have been subjected to various combinations of stresses. The case histories provide a summary of information available for each lake and describe the sequence of events through time in the fish community. Some of these events were inferred to be responses to the stresses imposed. Lakes Opeongo and Kootenay were included in this set somewhat arbitrarily, with the case histories of the Laurentian Great Lakes, to illustrate similarities and differences in the problems associated with other recently glaciated oligotrophic lakes.

We began organizing SCOL in 1968 and were later supported by a steering committee: W. L. Hartman of the U.S.A., L. Johnson of Canada, N.-A. Nilsson of Sweden, and W. Nümann of West Germany. After two years of preparation, a work party consisting of approximately 25 contributors and a similar number of interested ecologists convened for two weeks in July, 1971 at Geneva Park, Ontario, Canada.

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N. V. Martin and F. E. J. Fry


#### Abstract

Lake Opeongo, lying on the Algonquin Highlands of the Canadian Shield, is located in Algonquin Park, Ontario, on the headwaters of the Madawaska River, a tributary of the Ottawa. The combination of relatively high altitude, severe climate, and infertile soils make the lake rather unproductive. It has an area of $58.6 \mathrm{~km}^{2}$, a maximum depth of 52 m and is moderately oligotrophic. Its fauna is typical of waters in the highlands of southern Ontario.

The smallmouth bass was introduced to Lake Opeongo in 1928, with no apparent major effect on the salmonids. Its presence has reduced fishing pressure on the lake trout, the other main sports fish in the lake. Plantings of various salmonids have been largely unsuccessful but may have served to alter gene pools in the native salmonids. The cisco introduced in 1948 contributed to faster growth, better condition, and higher fecundity of lake trout; lake trout maturity, however, has been delayed. Initially, poundage of lake trout in the catch increased and then decreased when several exceptionally strong year classes became available. The cisco seems to have been a factor in the decline of populations of perch and of benthic insects; growth rates and abundance of certain other fishes may have been affected also.

The sport fishery has removed from 600 to 2,700 and 700 to $4,300 \mathrm{~kg}$ of lake trout per year since 1936-a long term yield of 0.33 kilo/ha. Mean total mortality rate is about $50 \%$ per year. Tagging data indicate that exploitation from angling doubles the mortality rate after the trout enter the fishery. Year-class production is correlated with numbers of lake trout that survive to spawn, which in turn is related to levels of exploitation.


## INTRODUCTION

Lake Opeongo, Algonquin Provincial Park, Ontario, has provided one of those rare situations where the history of a lake and its fisheries has been more or less completely recorded since the lake first became accessible to serious exploitation. The study of these fisheries has been facilitated by a number of factors: a fisheries research station has been established at the lake since the beginning of the intensive fishery; the lake is in a Provincial Park, where various control measures can be rather easily applied; there is only one major point of access to the lake; and there is practically no development of cottages or lodges on the lake.

Lake Opeongo is in the south-central part of Algonquin Park, which lies in the northeastern corner of southern Ontario (Fig. 1); the lake is centered

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Figure 1. Map of southern Ontario showing location of Lake Opeongo. Dotted lines indicate contour lines at 500 foot ( 152 metre) intervals. Hatched line shows southern limits of Canadian Shield.
at about $45^{\circ} 42^{\prime} \mathrm{N}$ lat and $78^{\circ} 22^{\prime} \mathrm{W}$ long. It is one of the major headwaters of the Madawaska River system which eventually enters the Ottawa River at Arnprior some 160 air kilometers to the east of Lake Opeongo.

Geologically the lake lies on the Madawaska or Algonquin Highlands of the Canadian Shield. This area is a high peneplain of moderately to strongly broken relief. The rounded granitic hills are remains of mountains ground down by Pleistocene glacial action. This higher area was never covered by glacial lakes although glacial Lake Algonquin approached the easterly border of Algonquin Park and marine submergence by the Champlain Sea almost reached the easterly side (Martin and Chapman, 1965).

Lake Opeongo lies at an elevation of 403 m and is surrounded by hills ranging up to 100 m above the lake surface. Some of the highest land in Ontario, with elevations up to 595 m lies in the immediate vicinity of Lake Opeongo. The glacial history of this region and the high relief of the area have been prime factors in establishing the present day fauna in Algonquin Park.

Considerable exposed bedrock of the Grenville Series is found in the area and the hills are covered with a 1 to 3 m layer of stony to bouldery granitic till of sandy to silty sand texture (D. Burger, pers. comm.). To the north and east of the East Arm and Annie Bay of Lake Opeongo are found glacial outwash plains and associated eskers with tine to coarse granitic sands. These soils are acidic and low in fertility. The generally low productivity of the waters is related in part to the geological background of the area (Ryder, 1964 a, b).

When latitude is taken into account, climatological conditions may be considered as rather severe in the Opeongo area. The Algonquin Park area has the lowest mean temperature, lowest recorded temperature, and shortest growing season in Southern Ontario (Anon. 1967). Mean annual air temperature is 3.4 C and mean annual seasonal temperatures are 16.7 C in summer (June, July, August) and -11.4 C in winter (December, January, February). Mean annual precipitation is of the order of 84 cm of rain and 254 cm of snow. The length of the growing season (above 5.5 C ) is approximately 172 days. Ice cover in Lake Opeongo usually persists from about mid-December to late April or early May but breakup has been as late as mid-May. On the average the lake is covered by ice for $4-1 / 2$ to 5 months.

The Algonquin Park area lies in a transitional zone between the northern boreal forests and the more southern deciduous forests. The predominant trees are sugar maple (Acer saccharum), yellow birch (Betula lutea), and hemlock (Tsuga canadensis); locally abundant species include balsam fir (Abies balsamea), white spruce (Picea glauca), white birch (Betula papyrifera), and aspen (Populus tremuloides) among others. Before the advent of the lumbering industry in about the mid-1800's, white pine (Pinus strobus) and red pine (Pinus resinosa) were dominant species. Large forest fires occurred, particularly in the areas west and south of Lake Opeongo, about 1900-20 and a number of smaller fires have occurred on the shores of Lake Opeongo in more recent years. The specific effects of these fires on the aquatic environment are unknown.

A number of large bogs or swamps around Lake Opeongo, particularly along the margin of the upper parts of the South and North Arms support such species as black spruce (Picea mariana), tamarack (Larix laricina), sphagnum (Sphagnum sp.), Labrador tea (Ledum groenlandicum), and leather leaf (Chamaedaphne calyculata). These areas no doubt contribute colour and acidity to the lake waters.

The relatively small watershed covers $189.6 \mathrm{~km}^{2}$ (excluding Lake Opeongo). One major lake, Happy Isle Lake, and about a dozen smaller lakes (each less than 60 hectares) drain into Lake Opeongo.

## DESCRIPTION OF LAKE OPEONGO

Physical and chemical characteristics.
Lake Opeongo (Figure 2) consists of four major basins, each limnologically distinct-the South, North, and East Arms and Annie Bay. These are joined by shallow, restricted channels. The East Arm and Annie Bay Narrows have distinct currents and remain open throughout the winter. It is known from tagging studies that lake trout (Salvelinus namaycush) and smallmouth bass (Micropterus dolomieui), the two main game fish in the lake, move freely among the various arms, at least seasonally.

Table 1 presents basic data on the morphometric characteristics of the lake and its basins. Lake Opeongo, for its size, is only moderately deep ( 52 m ), a characteristic typical of many Algonquin Park lakes where repeated glacial action has tended to have a levelling effect on the topography. The


Figure 2. Map of Lake Opeongo showing depth contours and various geographic features.

Table 1. physical Characteristics of Lake Opeongo

| Lake basin | Area (km | Shoreline length (km) | Mean depth (m) | Max. depth (m) | Shoreline development (including islands) |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  | e | i | ? |
| South | 22.1 | 49.0 | 14.6 | 51.8 |  | 2.94 |  |
| North | 14.0 | 21.1 | 15.2 | 39.6 |  | 1.59 |  |
| East | 18.1 | 29.0 | 16.3 | 45.7 |  | 1.92 |  |
| Annie Bay | 4.4 | 10.2 | 9.6 | 21.3 |  | 1.37 |  |
| Total | 58.6 | 109.3 | 14.8 | 51.8 |  | 4.03 |  |

various arms, each of which is in effect a lake, have a relatively low shoreline development. The moderately high shoreline development of the lake in toto results from the convention of giving the complex a single geographic name. The arms differ somewhat in general physical characteristics. The East Arm has the most precipitous basin, with few shallow bays or swampy areas around its periphery. Sands, gravels, and rocky shoals are more common here than in the other basins and are probably related to the slight geological differentiation of this area. This arm has the most important lake trout fishery and has the chief spawning grounds for both lake trout and the lake whitefish (Coregonus clupeaformis). It is somewhat more transparent than the other arms and dissolved oxygen concentration tends to be higher. The water temperature regimes may vary somewhat from arm to arm as might be expected from their different wind exposures and configurations.

Ryder, (1964a, 1964b, 1965, 1972) has summarized some of the physical and chemical characteristics of Lake Opeongo. The lake is considered to be moderately oligotrophic as compared with a variety of other lakes accross Canada. Total dissolved solids ( 33 ppm ), total alkalinity ( $10 \mathrm{mg} / \mathrm{l}$ ), and turbidity ( 0.5 J.T.U.) are all rather low, in common with many Algonquin Park lakes, when compared with other lakes across Canada. Ryder related these low values to the glacial history of the area. The lake water is at about neutrality and is moderately clear, with Secchi disc readings ranging up to about 6 m .

Water levels in Lake Opeongo have been influenced by a series of dams at the outlet, at the foot of Annie Bay. In earlier years logging dams caused fluctuations in the lake level, and in more recent years the lake has served as a storage basin for hydroelectric facilities lower down the Madawaska River. Ordinarily water is now held in the lake in the spring and summer and drawn off in the fall. Maximum drawdowns are generally less than 1 m and, as Martin (1955) has pointed out, have probably had little effect on the reproduction of the fall-spawning species. In general the water level of Lake Opeongo is higher than it was in the years before major logging in this area began in the mid-1800's.

## BIOLOGICAL CHARACTERISTICS

In spite of the long term studies on Lake Opeongo no exhaustive faunal survey has been made; consequently the list of fishes (Table 2) is probably incomplete, particularly with regard to the cyprinids and other less obvious species. The American eel, never abundant in the lake, is believed to be absent now; the construction of a series of major hydro-electric dams on the Ottawa and Madawaska Rivers in recent years has probably prevented its upstream migration. The hybrid trout or splake first introduced in 1955, was occasionally taken in the lake for a number of years but has not been observed recently. The cisco or lake herring was first introduced into Lake Opeongo in 1940 but apparently unsuccessfully. A further introduction in 1948, however, was successful. Two populations of lake whitefish in Lake Opeongo were termed "dwarfs" and "normals" by Kennedy (1943). These differ in size at maturity, rate of growth, length of growing season, and in

Table 2. List of fishes occurring in Lake Opeongo'

| Scientific Name | Common Name |
| :---: | :---: |
| Anguillidae |  |
| Anguilla rostrata | American Eel |
| Salmonidae |  |
| Coregonus artedii | Cisco ${ }^{2}$ |
| Coregonus clupeaformis | Lake whitefish |
| Prospopium cylindraceum | Round whitefish |
| Salvelinus fontinalis | Brook trout |
| Salvelinus namaycush | Lake trout |
| Salvelinus fontinalis x S. namaycush | Hybrid trout ${ }^{2}$ |
| Cyprinidae |  |
| Hybognathus hankinsoni | Brassy minnow |
| Notemigonus crysoleucus | Golden shiner |
| Notropis cornutus | Common shiner |
| Phoxinus eos | Northern redbelly dace |
| Phoxinus neogaeus | Finescale dace |
| Pimephales notatus | Bluntnose minnow |
| Pimephales promelas | Fathead minnow |
| Semotilus atromaculatus | Creek chub |
| Semotilus margarita | Pearl dace |
| Catostomidae |  |
| Catostomus catostomus | Longnose sucker |
| Catostomus commersoni | White sucker |
| Ictaluridae |  |
| Ictalurus nebulosus | Brown bullhead |
| Gadidae |  |
| Lota Iota | Burbot |
| Gasterosteidae |  |
| Culaea inconstans | Brook stickleback |
| Centrarchidae |  |
| Lepomisgibbosus | Pumpkinseed |
| Micropterus dolomieui | Smallmouth bass ${ }^{2}$ |
| Percidae |  |
| Perca flavescens | Yellow perch |
| Etheostoma exile | Iowa darter |
| Cottidae |  |
| Cottus cognatus | Slimy sculpin |
| Cottus ricei | Spoonhead muddler |

[^1]numbers of lateral-line scales and gill rakers. Many of the cyprinids listed have been found only in creek mouths, bog areas, and small bays marginal to the main open lake but are probably at least occasional residents of Lake Opeongo itself. The smallmouth bass was first noted in Lake Opeongo in the late 1920's. Its presence here, as is discussed in the following section, is a result of man's activities.

In general the fish fauna of Lake Opeongo is typical of many of the waters in the highlands of Ontario. The precipitous nature of the watersheds
on the south-central Algonquin Park dome has apparently prevented the invasion since glacial times of many forms such as the northern pike (Esox lucius), the walleye (Stizostedion vitreum vitreum), and a variety of other warm water forms which occur at lower altitudes in the Park and within a distance of 30 air kilometers from Lake Opeongo.

No attempt is made here to document other aspects of the biota of Lake Opeongo. Studies have been carried out on bottom fauna by Miller (1937), and on phyco-periphyton by Foerster and Schlichting (1965); the few plankton investigations have generally not been of a qualitative nature.

## THE ROLE OF INTRODUCTIONS

## Smallmouth bass

The first known introduction to the Lake Opeongo fish fauna was the smallmouth bass. Christie (1957) has documented the events resulting in the presence of this species in the lake. A series of introductions each progressively closer to Lake Opeongo was made in lakes along the Opeongo River early in this century. By 1915 the bass were present in a lake only 15 km downstream from Lake Opeongo. Whether they made the final ascent of the Opeongo River and the dam at the foot of the lake or whether they were transported to the lake by man is unknown. At any rate the first record we have of bass in Lake Opeongo is in 1928.

Because smallmouth bass were present before any specific information was available on Lake Opeongo, the immediate effects of the introduction on the general biota of the lake are unknown. By 1936, the first year of studies on Lake Opeongo, however, this species had only been in the lake about 8 years and presumably only 3 or 4 year classes had resulted since its arrival. Hearsay reports indicate that numbers of brook trout were taken from the lake before the arrival of the bass but since that time brook trout have been taken only rarely. Similarly a small brook trout fishery existed in Happy Isle Lake (connected by river to Lake Opeongo) in earlier years. The bass were first noted in Happy Isle Lake in the late 1930's and early 1940's and brook trout catches have been rare in this lake since then also.

The smallmouth bass of Lake Opeongo are heavily parasitized by the cestodes Proteocephalus ambloplitis (Bangham, 1941) and Proteocephalus fluviatilis (Fischer, 1968) and presumably were so infected when they entered the lake. The introduction has imposed a new parasitological load on other fishes. The yellow perch, pumpkinseed, and brown bullhead are now serving as carrier hosts for the larval stages of this parasite (A. Dechtiar, pers. comm.) although the deleterious effects, if any, of this incidence are unknown.

Although the smallmouth bass may have affected the brook trout, there is no evidence that it had any appreciable effect on other elements of the salmonid community. No lake trout or whitefish or their eggs have ever been observed in bass stomachs. The bass eat only limited amounts of insects and yellow perch, which are important forage for trout and whitefish. The spatial separation of these species for much of the year and the size and variety of habitats available in Opeongo probably mitigate against any direct or indirect conflict between the bass and many of the colder water species. Since the
prime food of the bass is crayfish (about $80 \%$ ), it may have competed with the burbot to some extent for this forage.

The impact of the smallmouth bass on Lake Opeongo has probably been of significance in more indirect ways. Before the smallmouth was introduced, anglers fished for lake trout only. The presence of the bass no doubt attracts a greater number of anglers to the lake, particularly family groups and those who have neither the proficiency nor the required tackle to angle for lake trout. The bass fishery has also served to buffer fishing pressure on the trout, as the fishermen often seek small mouth when angling for trout is poor.

## Salmonids

Plantings of hatchery and wild stocks of salmonids have been made for many years. Although most of these are not introductions in the usual meaning of the word, they may be considered so in the sense of the possible introduction of different genetic characteristics to the existing populations. Brook trout of hatchery origin have been planted in Lake Opeongo since at least 1939 (possibly much earlier) but their survival has been apparently negligible. Extensive plantings of lake trout fingerlings and yearling have been made in Lake Opeongo in the period 1948-64. Hatchery lake trout stock from a wide variety of sources such as Great Slave Lake, Lake Superior, Lake Manitou, Lake Simcoe, and other Algonquin Park lakes have been used. About 158,000 yearlings and 51,000 fingerlings have been planted over these years but again survival has been very low (less that $0.01 \%$ ). An introduction of 303 adult lake trout from Lake Louisa, another Algonquin Park lake, to Lake Opeongo was carried out in 1961 and 1962 (Martin, 1966).

In 1955-57 a total of 15,400 hybrid trout (splake) yearlings were introduced into Lake Opeongo (Martin and Baldwin, 1960). These hybrids, their parents of varied origins, have offered limited returns to the Opeongo fishery.

As has been indicated, these salmonid plantings may not be considered introductions in the sense of the importing of a non-indigenous species. However, from the viewpoint of their possible effects on the gene pools of existing native trout they may be considered as new elements in the biota. Both hybrid trout (splake) and lake trout from the Lake Louisa transfer have been taken in ripe condition on the spawning beds in Lake Opeongo together with native lake trout. Various studies in recent years, such as those of Lindsey (1964) and Khan (1968), indicate a number of refugia for lake trout during glacial times. Morphometric and meristic differentiation among lake trout from various regions has been indicated by Khan, and physiological differences may exist also. In brief, the genetic complement of the native Opeongo lake trout may have been changed over the last 30 or 40 years through the infusion of different genes from stocks from a wide variety of sources.

Since no detailed faunal survey of fishes in Opeongo has been made, it is not known whether changes have occurred in the species composition of lesser fishes, particularly with reference to the introduction of bait fishes. Although the Algonquin Park Act forbids the possession of bait fishes, it has not been rigidly enforced; consequently some non-native fishes, may have been
brought into these waters as bait. Such introductions would have been particularly likely during those years when the lake was open to a winter fishery for lake trout, a type of fishery in which live bait fish are used almost exclusively.

## Cisco

Another introduction that has had a major impact on Lake Opeongo has been that of the cisco. The use of the cisco as a forage for lake trout was first suggested by Fry $(1939,1949)$, who noted a depression in the growth curve and a high percentage of infertile fish (see below) at lengths where the trout were transferring from a diet of small perch and whitefish to larger forage. This observation suggested a deficiency in the diet which the cisco might fill. In 1940 approximately 250 adult ciscoes were planted in Lake Opeongo. The source of these fish was a spring run up the North Muskoka River near Huntsville (Fig. 1), some 80 air kilometers to the south-west of Lake Opeongo. This planting was thought to have been unsuccessful and was repeated in 1948 with an additional 400 adult cisco from the same source. The ciscoes became established and were first observed in the lake trout stomachs in the early 1950's; a few years later they had become the main food of the trout. They are now probably the most abundant fish species in Lake Opeongo.

As the following discussion points out, major changes apparently took place in the Lake Opeongo ecosystem in the late 1940's and early 1950's. To what degree, if any, these can be attributed to the cisco introduction is difficult to assess, largely because all levels of the biota have not been extensively or consistently monitored, and much of what is said must be perforce speculative.

The lake trout, however, has been consistently studied and its response to the cisco introduction has been clearly evident. Figure 3 illustrates the changes that have taken place in the lake trout diet in the period 1936-71. These data are largely an extension of a more detailed study (1936-65) by Martin (1970). As indicated in the upper panel of the figure, the proportions of trout with fish content and with empty stomachs have fluctuated around mean values of 55 and $40 \%$, respectively. The insect element of the diet, however, sharply decreased in the diet in the early 1950's and only recently has shown signs of regaining significance as food for lake trout.

Although the proportion of lake trout subsisting on fish has remained generally constant, the relative importance of the various forage species making up this part of the diet has changed markedly (Fig. 3). The frequency of perch in the stomach contents of the lake trout decreased sharply in the early 1950's. For a number of years the trout fed extensively on whitefish and then, as the cisco population increased after its 1948 introduction, ciscoes became the prime food of the lake trout.

These dietary changes have had marked effects on the biology of the Opeongo lake trout (Figs. 4-6). In brief, the length-weight relationship and rate of growth of the lake trout have improved significantly, and ovary weight, egg size, and egg number have increased. Fry and Kennedy (1937) and Fry (1949) observed that as many as $17 \%$ of the lake trout in Lake Opeongo in the


Figure 3. Percentage frequency of occurrence of forage fish, insects, and empty stomachs in Lake Opeongo lake trout, 19364971. Upper panel as percent of all trout examined, lower panel as percent of trout with forage fish in stomachs.


Figure 4. Length-weight (logarithmic) and age-weight (arithmetic) relationship of Lake Opeongo lake trout for the years 1937-1947 and 1953-1961(1965).
approximate size range $50-80 \mathrm{~cm}$ and in age classes $9-13$ failed to produce gametes in certain years although they were sexually mature. These fish were termed "infertile" but it was considered likely they would spawn again in later years. After the introduction of the cisco, the percentage of infertile fish decreased to only $2 \%$ by 1960 , and no infertile fish have been noted since that time.

There has, however, been a trend to later maturity in the lake trout. For example one trout in three was mature at age 6 in 1937-48, whereas only one in ten had reached maturity at this age in later years. This phenomenon may possibly be explained in part, at least, on the basis of Alm's (1959) finding that an initial good growth, when followed. by a slower rate, may result in maturity at a smaller size and younger age. In Lake Opeongo a somewhat parallel situation may exist, as initial rapid growth and slow late growth patterns have been reversed. Similarly Martin (1970) found that planktivorous lake trout, which have relatively rapid early growth and slow late growth mature earlier than piscivorous trout with inverse growth patterns.


Figure 5. Rate of growth of Lake Opeongo lake trout for the years 1937-1949 and 1955-1961.

The effects of the cisco introduction on the lake trout apparently reached a plateau in the early 1960 's, some five years or so after they had become well established in the lake. Length-weight and maturity data indicate the population has become somewhat stabilized in these respects. The 1966-71 length-weight curve, for example, superimposes on that for 1953-65. Although no further age data and gonad data are available since the 1936-65 analysis, it is likely the age-fecundity relationship also has become relatively stable.

The importance of food habits on the biology of lake trout in Lake Opeongo has been further demonstrated by the results from the transfer of adult trout from Lake Louisa to Lake Opeongo which has been referred to earlier. In Lake Opeongo, with its greater abundance of forage, the slow growing, short-lived, plankton-feeding trout of Lake Louisa grew faster and lived longer. This study further emphasized the plasticity of the lake trout in its response to qualitative changes in food.

The effects of differences in forage on the growth and production of lake trout in Algonquin Park waters has been discussed by Kerr and Martin (1970) and Kerr (1971). Kerr suggested that increased trout production in Lake Opeongo up to 1965 was the result of the cisco introduction. Although the available energy resource in the lake remained essentially the same after


Figure 6. Fecundity (upper panel) and egg size (lower panel) in Lake Opeongo lake trout for the years 1938-1946 and 1955-1963.
the establishment of the cisco, the growth efficiency of the trout increased materially, resulting in greater production. Since 1965 the annual production on a weight basis has decreased substantially, although the numbers caught have remained generally the same or increased and there is evidence of exceptionally strong year classes entering the population. It appears therefore that the increased growth efficiency of the trout was first expressed in improved weight production as indicated by Kerr, and then by contributing towards greater recruitment to the trout population because of the improved fecundity.

The effects of the cisco introduction on other parts of the ecosystem in Lake Opeongo are less fully understood. The other major piscivore in the lake, the burbot, is apparently utilizing the cisco. In the 1940's and 1950's the perch and then the crayfish were its main food, but more recently the crayfish has become the most important, followed by perch and cisco in that order. Preliminary analysis of data on this species (P. Hackney, pers. comm.) indicates that burbot are considerably larger now than in earlier years; this difference may be a reflection of an improvement in growth rate.

The frequency of occurrence of perch in trout stomachs decreased sharply about 1950 (Fig. 3). Population studies (unpublished) for perch in 193840 and 1959 suggest that this decrease was a reflection of a decrease in their actual numbers in the lake. Whether this decrease can be attributed to the 1948 cisco introduction is uncertain. The perch decline started about 1950, and it is doubtful that the cisco became abundant enough in the two years after its introduction to have a major influence on the perch population. The abruptness of the perch decline suggests the failure of one or more year classes, with the possibility that the cisco effectively suppressed its subsequent recovery. The perch and cisco inhabit the same general stratum in Lake Opeongo and, although no detailed studies have been made of the food of ciscoes in the lake, it is possible that they feed extensively on larval perch.

Similarly, the insect fauna decreased sharply in the early 1950's, judging by the contents of trout stomachs. It is of course dangerous to assume that food content reflects abundance; the decline in insect fauna in the trout stomachs may indicate only a preference by the trout for ciscoes. However, an analysis of bass stomachs over the years 1937-71 indicates that the trend in the proportion of insect bottom fauna in the diet closely paralleled that for the lake trout-that is, there was a sharp decrease in the 1950's followed by a gradual increase in the 1960's. Ciscoes can feed extensively on bottom organisms, and may have heavily cropped this forage when they became abundant in Lake Opeongo. Fry (1937) and Langford (1938) have shown that mayfly nymphs (the main insect food of Opeongo trout) are an important constituent of the cisco diet in Lake Nipissing.

The cisco is probably a serious competitor for the invertebrate resource with a number of other fishes. Adults and/or young of such species as lake trout, whitefish, bass, perch, and burbot rely heavily on this forage. As noted by Martin (1970) the rate of growth of young lake trout has decreased in recent years. The rate of growth of smallmouth bass also appears to have declined since the mid 1950's. It has been suggested that the perch may have been a factor in controlling the density of the bass population; when numbers of perch declined, over-crowding in the bass population may have resulted in
reduced growth (Emery, 1971). Sandercock (1964), in a study of the interaction between lake whitefish and round whitefish in four Algonquin Park lakes, noted that these two species fed extensively on bottom-dwelling forms in Lake Opeongo, and not on plankton as they did in the other three lakes. On the basis of the four lakes studies, rate of growth was directly correlated with the extent of plankton utilization, the "normal" (see Kennedy, 1943) Opeongo whitefish population had the slowest growth. Sandercock suggested that the cisco in Opeongo is occupying the mid-winter plankton feeding niche. Growth rates of lake whitefish during the first few years of life were slower in 1963 (Sandercock, 1964) than in 193940 (Kennedy, 1943).

Although no intensive study of cisco diet has been made in Lake Opeongo it is likely the cisco has also played a more direct role in the abundance of other fishes by preying directly on their eggs or fry. As suggested earlier, the yellow perch may be particularly susceptible to this predation. Field studies currently being carried out indicate a scarcity of burbot fry in Opeongo as compared with other lakes in Algonquin Park. The possibility that cisco predation, particularly in late winter and early spring limits recruitment in this species, is being considered (P. Hackney, pers. comm.). Similarly, lake trout larvae and fry may be vulnerable to predation by the cisco in late winter. Pritchard (1931) found that the cisco fed on the fry and eggs of whitefish and burbot in Lake Ontario and Reckahn (1970) noted that it preyed on larval and post-larval alewives (Alosa pseudoharengus) in South Bay, Lake Huron.

As Figure 3 indicates, however, the perch population is now recovering in Lake Opeongo. Although no recent quantitative study of perch abundance has been made, random observations and netting operations also have suggested an increase in numbers. Similarly, the aquatic insect faunaparticularly the mayflies-may be increasing. It appears then that an equilibrium is now being reestablished in the Lake Opeongo ecosystem.

## THE ROLE OF EXPLOITATION

As has been indicated, Lake Opeongo was only lightly exploited before 1936, the year the area became accessible by road. In general the Algonquin Park area was largely overlooked in the development of Southern Ontario. Because the area lies on the rugged height of land between the waterways of Georgian Bay and the Ottawa River, history bypassed it for centuries. Itinerant bands of Indians made hunting and fishing excursions to the area but did not establish permanent settlements. At the East Arm Narrows of Lake Opeongo (Fig. 2) artifacts of the Laurentian culture dating back to 2500 B.C. have been located (G. Taylor, pers. Comm.). Early explorers and surveyors passed through the 'area in the early 1800's but their exploitation of the fishery resource was surely negligible. By the mid-1800's the square-timber industry had moved up the Ottawa valley into the highlands of Algonquin Park. This in turn was succeeded by the sawlog industry in the late 1800 's. Workers in these lumber camps and the accompanying supply and depot farms, one of which was at the East Arm Narrows in the 1870's and 1880's, subsisted partly on fish, but probably had no major impact on the fish
populations. When Algonquin Provincial Park was established in 1893, some measure of control over the use of its resources was initiated (Anon. 1967).

During the First World War, Lake Opeongo, along with a number of other inland Ontario lakes, was opened to commercial fishing to provide additional food under the emergency conditions of the times. One operator was licensed to fish the lake in 1916 but no records of the catch can be located. Between 1918 and 1936, the year a highway was completed to the area, Lake Opeongo was fished by anglers with increasing regularity. Since the lake could be reached only by a circuitous and laborious travel route however, fishing pressure was probably relatively light.

As has been indicated earlier, a fisheries research station (now the Harkness Laboratory of Fisheries Research) was established on Lake Opeongo at the time it first became subject to serious exploitation. A creel census was started immediately on the lake and is still in effect. This census has provided catch statistics of the lake trout and smallmouth bass fisheries of Lake Opeongo for 36 years. Through the census and other studies various biological data have been, collected to provide a more nearly complete picture of the character of the fish populations and their dynamics.

The basis and modus operandi of the Lake Opeongo creel census has been fully described by Fry and Kennedy (1937), Fry (1939) and Fry (1949). The only point of ready access to the lake is at the foot of the South Arm. Here is located the fish checking station and also an outfitting establishment which over the years has variously provided accommodations, supplies, guides, and boats, to anglers. No other cottages, lodges, or other sites of human development are to be found on the lake except for primitive individual camp sites. Only a few of these sites were present in the earlier years but they now total over 30 .

Anglers are routinely interviewed as they return to the foot of the lake. Data collected include the number of fish caught, the time spent fishing, the area fished, the numbers of anglers and boats, and any other general information related to the catch. In return for having their fish cleaned the anglers usually permit the census staff to measure and weigh the fish, collect scale samples and stomachs, determine gonad development, examine the fish for tags, clipped fins, and parasites, and obtain other biological information.

Although the preceding account suggests that the arrangements for carrying out a creel census program and assessing a fishery are ideal, a number of problems have arisen over the years which have complicated the interpretation of the information that has been collected. The problems are outlined here because they have a bearing on the subsequent discussion.

In the early years of the fishery nearly all anglers returned to the lodge at the foot of the lake each day and consequently their angling activities could- be easily and accurately recorded. In the last 10 years there has been an increasingly greater trend away from this pattern as many more anglers are camping at the lake and their fishing habits are far less regular. In view of this change it is likely that catch and fishing effort figures for these years may be somewhat low. Fry (1949) estimated that the census encompassed $80 \%$ of the fishing activity in the lake in 193647; this estimate has been accepted in the discussion that follows.

A more critical and less easily resolved problem from the view-point of assessing the fishery has been the change in the efficiency of the basic fishing unit. In earlier years many anglers were skilled in the specialized techniques required for lake trout fishing and were familiar with the most productive fishing areas of the lake. In the last 10 or 15 years there has been an increasingly higher proportion of unskilled anglers, many without proper fishing gear and often unfamiliar with the lake. An illustration of the change in the quality of angling effort is indicated by the change in the number of guides on the lake. Up to the mid 1950's 10 or more guides were constantly employed on Lake Opeongo, whereas in recent years 1 or 2 have been available, and their services have not been in great demand. In brief then, from the viewpoint of effective angling effort, values in the following presentation should be somewhat lower and fishing success values somewhat higher for the more recent fishery.

## Lake trout exploitation

As has been indicated earlier the lake trout is the only salmonid subject to exploitation in Lake Opeongo and the effects of the sports fishery on this species is discussed in detail in the following account.

Figure 7 presents basic catch data on the Lake Opeongo lake trout sport fishery for 1936-71, as collected through the creel census.

Harvest figures have been variable, reflecting in various degrees the amount of fishing effort, abundance of lake trout, angler skill, and the efficiency of the census. A general parallel is evident between catch and effort for most years. This parallelism, however, deteriorated somewhat in 1969 and 1970 when the creel census was extended to include campers and probably a less skilled segment of the anglers on the lake (Regier, 1971). The effect of fishing pressure on the lake trout population was immediately evident when the lake was opened to intensive fishing; the removal of 2600 and 2700 trout in 1936 and 1937 ( 0.7 and 0.6 kg per hectare) seriously affected the quality of angling in subsequent years (Fry, 1939).

Total estimated catch has varied between 630 and 2700 trout with an annual mean for the 1936-71 period of about 1300 fish and a weight removal varying from 700 to 4300 kg with a mean of about 1900 kg . In terms of yield per unit of surface area, annual harvest has varied from 0.12 to 0.73 kg per hectare ( 36 -year mean, 0.33 ).

The amount of fishing effort, on the basis of two men in one boat as the fishing unit, has also been variable but generally shows an upward trend. The low exploitation rates during the war years (1940-44) were the result of restricted travel. There is no explanation for the later fluctuations about the general trend except that the marked decline following 1957 may be the result of the excellence of the bass fishing in that period, which may have diverted some would be lake trout anglers to this species. In addition the quality of the trout angling was generally low at that time. The higher levels of the last few years again reflects the extension of the creel census to the contact of fishing parties on the lake itself. Estimated fishing effort for lake


Figure 7. Estimated numbers and weight of lake trout caught \{lower panel) and fishing effort in boat hours (upper panel) in Lake Opeongo, 1936-1971.
trout in 1936-71 has varied from about 600 to 6100 boat hours a year and averaged about 2700 hours.

The catch-per-unit-ofeffort index (Fig. 8) decreased steadily and markedly from a plateau in 193644 to the early 1960's but has remained thereafter at a nearly constant level, fluctuating around approximate mean values of 0.3 lake trout and 0.6 kg of trout per boat hour.

The average length and average weight varied greatly from year to year (Fig. 9) in part at least as a result of the entry of strong year classes into the fishery. Although average length showed no trend, average weight of the trout caught increased by over $60 \%$ from the mid-1950's to the mid-1960's, probably reflecting the change in the length-weight relationship brought about by the cisco introduction. Both averages dropped sharply in recent years. Although no age determinations have been made since 1961, the length composition data (Fig. 9) indicate the entry of exceptionally strong year classes in the last few years. An unusually high proportion of small and young fish (generally under 40 cm and 5 years) was caught in this period. The average age (Fig. 10), as might be expected showed considerable annual vari-


Figure 8. Numbers and weight caught of lake trout caught per boat hour (upper panel) and per hectare (lower panel), Lake Opeongo, 1936-1971.


Figure 9. Average length and average weight of lake trout caught in Lake Opeongo, 1936-1971.


Figure 10. Average age (1936-1961) and percent mature (1936-1971) of lake trout caught in Lake Opeongo. Dotted line indicates 5-year mean.
ability in the period 1936-61. The apparent entry of exceptionally strong year classes during the last few years will undoubtedly cause the curve to drop markedly again in the late 1960's. Average length of trout caught has varied from 50.8 to 41.5 cm ( 36 year mean, 47.0 cm ), average weight from 2.15 to 0.97 kg ( 36 year mean 1.46 kg ), and average age from 6.9 to 9.1 years (1936-61 mean, 8.6 years).

As was indicated earlier, there has been a general trend towards later maturity in the Opeongo lake trout (Fig. 10). Although increasingly heavier exploitation of the population would result in greater cropping of younger, immature trout, the trend can also be attributed in part to the general tendency toward later maturity in the fish themselves. The fishery then is exploiting an increasingly higher proportion of immature trout now (70\%) than in earlier years.

On the basis of data from creel census returns (particularly on catch, catcheffort, and length), early analyses of the Lake Opeongo trout fishery were made by Fry and Kennedy (1937), Fry (1939), and Fry and Chapman (1948). Aging of the catch permitted a more refined appraisal of the dynamics of the fishery for 193647 by Fry (1949) and the following account is in part an extension of this analysis.

## Exploitation and mortality

Table 3 brings the estimated yield by age up to 1961, the last year for which age data are yet available. The estimates given are $125 \%$ of the reported

Table 3. Estimated age composition of lake trout catch 1936-1961, Lake Opeongo

| Year of Capture | 2 | 3 | 4 | 5 | 6 | 7 | Numb 8 | $\begin{aligned} & \text { ers at age } \\ & 9 \end{aligned}$ | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | Average Age | $\begin{aligned} & \text { Estimated } \\ & \text { Catch } \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1936 | 0 | 30 | 95 | 128 | 233 | 474 | 665 | 478. | 260 | 118 | 57 | 19 | 25 | 10 | 15 | 11 | 8.1 | 2600 |
| 1937 | 0 | 0 | 4 | 34 | 198 | 650 | 1025 | 555 | 176 | 38 | 4 | 8 | 8 | 0 | 0 | 0 | 8.0 | 2700 |
| 1938 | 0 | 12 | 74 | 127 | 275 | 420 | 439 | 195 | 90 | 3 | 9 | 3 | 0 | 3 | 0 | 0 | 7.1 | 1650 |
| 1939 | 0 | 39 | 36 | 116 | 221 | 321 | 393 | 223 | 90 | 47 | 24 | 13 | 15 | 4 | 4 | 4 | 7.7 | 1550 |
| 1940 | 0 | 20 | 84 | 82 | 224 | 434 | 364 | 120 | 46 | 14 | 6 | 0 | 6 | 0 | 0 | 0 | 7.1 | 1400 |
| 1941 | 0 | 8 | 79 | 144 | 275 | 235 | 200 | 104 | 22 | 11 | 11 | 11 | 0 | 0 | 0 | 0 | 6.9 | 1100 |
| 1942 | 0 | 7 | 18 | 46 | 117 | 217 | 121 | 53 | 28 | 8 | 9 | 2 | 2 | 0 | 0 | 0 | 7.1 | 630 |
| 1943 | 0 | 6 | 42 | 42 | 121 | 272 | 211 | 133 | 42 | 0 | 24 | 6 | 0 | 0 | 0 | 0 | 7.7 | 900 |
| 1944 | 0 | 8 | 26 | 84 | 114 | 197 | 202 | 198 | 93 | 44 | 31 | 9 | 22 | 9 | 4 | 4 | 8.1 | 1050 |
| 1945 | 0 | 0 | 11 | 32 | 69 | 170 | 352 | 373 | 159 | 84 | 37 | 21 | 43 | 16 | 37 | 16 | 9.0 | 1420 |
| 1946 | 0 | 19 | 30 | 78 | 116 | 240 | 325 | 217 | 93 | 47 | 26 | 11 | 7 | 0 | 7 | 4 | 9.1 | 1220 |
| 1947 | 0 | 3 | 30 | 55 | 85 | 217 | 221 | 153 | 76 | 18 | 12 | 3 | 0 | 6 | 3 | 3 | 7.8 | 885 |
| 1948 | 0 | 8 | 12 | 47 | 122 | 311 | 315 | 303 | 8 | 47 | 32 | 12 | 4 | 8 | 0 | 0 | 8.0 | 1230 |
| 1949 | 0 | 9 | 35 | 131 | 254 | 332 | 350 | 149 | 61 | 66 | 22 | 4 | 0 | 4 | 0 | 0 | 7.4 | 1416 |
| 1950 | 0 | 45 | 100 | 179 | 286 | 429 | 297 | 184 | 68 | 48 | 27 | 9 | 7 | 0 | 0 | 0 | 7.1 | 1678 |
| 1951 | 0 | 0 | 11 | 72 | 193 | 348 | 401 | 261 | 117 | 45 | 38 | 8 | 8 | 8 | 0 | 0 | 8.0 | 1510 |
| 1952 | 0 | 0 | 11 | 53 | 99 | 320 | 404 | 194 | 91 | 50 | 15 | 4 | 0 | 0 | 0 | 0 | 7.9 | 1243 |
| 1953 | 0 | 4 | 4 | 45 | 83 | 124 | 244 | 293 | 150 | 53 | 38 | 11 | 4 | 0 | 0 | 0 | 8.5 | 1050 |
| 1954 | 0 | 0 | 11 | 48 | 128 | 300 | 373 | 359 | 187 | 73 | 29 | 7 | 7 | 0 | 4 | 0 | 8.3 | 1528 |
| 1955 | 0 | 12 | 63 | 134 | 194 | 273 | 277 | 178 | 107 | 43 | 8 | 4 | 4 | 0 | 0 | 0 | 7.4 | 1295 |
| 1956 | 0 | 3 | 35 | 149 | 239 | 257 | 232 | 121 | 101 | 10 | 21 | 0 | 0 | 7 | 0 | 0 | 7.3 | 1176 |
| 1957 | 0 | 0 | 30 | 188 | 370 | 431 | 340 | 238 | 127 | 51 | 0 | 15 | 0 | 0 | 0 | 0 | 7.4 | 1791 |
| 1958 | 10 | 10 | 78 | 340 | 272 | 423 | 360 | 141 | 73 | 24 | 15 | 10 | 0 | 0 | 0 | 0 | 7.7 | 1753 |
| 1959 | 0 | 0 | 14 | 53 | 72 | 153 | 167 | 258 | 201 | 100 | 77 | 38 | 0 | 10 | 0 | 0 | 8.8 | 1143 |
| 1960 | 0 | 3 | 41 | 68 | 61 | 82 | 119 | 119 | 95 | 82 | 37 | 31 | 17 | 7 | 3 | 0 | 8.6 | 765 |
| 1961 | 0 | 20 | 26 | 51 | 48 | 67 | 70 | 96 | 109 | 42 | 77 | 13 | 3 | 3 | 0 | 0 | 8.5 | 625 |
| Total Catch | 10 | 266 | 1000 | 2526 | 4469 | 7697 | 8467 | 5696 | 2670 | 1166 | 686 | 272 | 182 | 95 | 77 | 42 | 8.6 | 35308 |
| Total Virtual Population | 35321 | 35311 | 35045 | 34045 | 31519 | 27050 | 19353 | 10886 | 5190 | 2520 | 1354 | 668 | 396 | 214 | 119 | 42 |  |  |
| Percent | 0.03 | 0.75 | 2.8 | 7.2 | 12.7 | 21.8 | 24.0 | 16.1 | 7.6 | 3.3 | 1.9 | 0.8 | 0.5 | 0.3 | 0.2 | 0.1 |  | 1358 |



Figure 11. Catch by age of lake trout in Lake Opeongo for the years 1936 through 1961. The straight line drawn as tangent to the descendinglimb represents a mean total mortality rate of 50 percent per year.
catch, following the convention used by Fry (1949). As pointed out above, changes in the nature of the fishery indicate that a lesser fraction of the catch was reported in the years after 1947. Yields given in the table for the years after 1950 are probably underestimated by as much as $20 \%$.

Lake trout of ages 7 and 8, which have been cropped most heavily, made up $45.8 \%$ of the total catch and fish of ages 6 and 9 contributed another $28.8 \%$. Since no more than $10 \%$ of the catch was drawn from fish below age 6 , exploitation can be considered negligible through age 5 .

Figure 11 gives the mean age composition of the catch over the years of record as a conventional catch curve. A tangent to the mid-region of the descending arm represents a mean total mortality rate for the section of the population under full exploitation of $50 \%$ per year or a coefficient of total mortality (Ricker's, 1958, instantaneous rate) of 0.70 .

Partitioning of total mortality into fishing and natural mortality has been carried out in two ways. On the basis of Fry's (1949) data on catch and fishing effort, Beverton and Holt (1957) estimated the natural mortality coefficient to be 0.248 and the fishing coefficient to be 0.583 for ages 8 and 9 in the years 193747. Paloheimo (1958), using the estimates of survival based on virtual populations (see above) instead of catch per unit effort,
obtained a coefficient of 0.215 in natural mortality and 0.0435 for fishing mortality over ages 9 and 10 for the years 1936-47. An extension of these estimates on the basis of more recent data is complicated by the fact the nature of the Opeongo trout fishery has changed considerably in recent years, particularly with reference to a decline in the effectiveness of fishing effort.

The second method of partitioning natural and fishing mortality which is based on tag returns, depends on the following reasoning. A tagged sample is released and records are kept of the returns throughout the period until the sample has completely passed through the fishery. It is assumed that fishing mortality and natural mortality are competitive and constant during the time tagged fish are present, and that the ratio of total tags recovered to tags never seen after release represents the ratio between the coefficient of natural mortality and that of fishing mortality multiplied by the number of units of effort expended. It is further assumed that fishing effort is constant from year to year. "Natural mortality" now includes unidentified tag loss.

In 1948-50 and 1952, and again in 1961-62 lake trout were tagged with streamer tags affixed just posterior to the dorsal tin. In the earlier period the lake trout for tagging were captured with gill nets set in a wide variety of locations in Lake Opeongo; 90\% was taken in October and early Novemberwhile they were moving to, or while on the spawning beds. In 1961 and 1962 trout were captured in two trap nets set in the East Arm of the lake on spawning beds as part of egg-collection operations. Table 4 shows the numbers of lake trout tagged and the recapture data. Table 5 gives the length and age composition of the tagged fish for the two periods. All fish released with tags

Table 4. Summary of tagging and recapture data for Lake Opeongo lake trout

|  | Number <br> tagged | NUMBER RECAPTURED BY ANGLING |  |
| :--- | :---: | :---: | :---: |
| Year |  | From tagging of 1961-1962 |  |
| 1948 | 65 | 8 |  |
| 1949 | 238 | 37 |  |
| 1950 | 38 | 39 |  |
| 1951 |  | 24 |  |
| 1952 | 17 | 16 |  |
| 1953 |  | 11 |  |
| 1954 |  | 1 |  |
| 1955 |  | 6 |  |
| 1956 |  | 2 | 4 |
| 1957 |  | 1 | 17 |
| 1958 |  | 1 | 9 |
| 1959 |  |  | 8 |
| 1960 |  |  | 3 |
| 1961 | 77 |  | 160 |
| 1962 | 115 | 44.7 | 1 |
| 1963 |  |  | 42 |
| 1964 |  |  |  |
| 1965 |  |  |  |
| 1966 |  |  |  |
| 1967 |  |  |  |
| Number | recaptured |  |  |
| Percentage | recaptured |  |  |

Table 5. Length and age composition of tagged lake trout, Lake Opeongo

| Length group (fork-ems | Percent |  |
| :---: | :---: | :---: |
|  | 1948-1950,1952 | 1961-1962 |
|  | 0.3 |  |
| 28-29.9 | 0.9 |  |
| 35-39.9 | 4.0 |  |
| 4044.9 | 14.7 |  |
| 45-49.9 | 30.2 | 1.0 |
| 50-54.9 | 28.4 | 10.5 |
| 55-59.9 | 8.6 | 29.3 |
| 60-64.9 | 5.7 | 29.8 |
| 65-69.9 | 2.9 | 13.6 |
| 70-74.9 | 2.9 | 11.0 |
| 75-79.9 | 0.9 | 2.6 |
| 80-84.9 | 0.6 | 1.0 |
| 85-89.9 |  | 1.0 |
| Average length | 50.0 | 61.5 |
| $\mathrm{A}^{3} \mathrm{e}$ |  |  |
| 4 | 0.3 |  |
| 5 | 0.9 |  |
| 6 | 14.3 |  |
| 7 | 23.8 | 0.8 |
| 9 | 26.618 .0 | 30.21 .6 |
| 10 | 5.6 | 26.4 |
| 11 | 4.3 | 15.5 |
| 12 | 1.5 | 6.2 |
| 13 | 1.5 | 6.9 |
| 14 | 0.3 | 1.5 |
| 15 |  | 0.8 |
| Average age | 7.9 | 10.0 |

in the 1948-59, 1952 series were fin-clipped. In the total of 184 fish recognized on recovery, 32 ( $17 \%$ ) had lost their tags. It is presumed that a similar loss was suffered in the later series. Two tags, not included in the returns in Table 4 were recovered downstream from the Opeongo dam.

The angling fishery took $45 \%$ of the earlier series of tagged fish and $26 \%$ (corrected for tag loss) of the later. Results for the first series indicate approximately twice me yield per recruit found in the later series. The reason for this wide difference is not clear. The most plausible explanation is that the fish tagged in the second series were much larger than the general population (see Table 5 and Fig. 9). All but three of the fish tagged in 1961-62 were above the mean length of all the fish taken in the fishery in those years. The tagged trout in this series averaged 10 cm longer and 2 years older than those in the 1948-50, 1952 series.

Taking the $45: 55$ ratio of losses to angling and natural mortality obtained from the 1948-50, 1952 tagging series and a total annual mortality rate of $0.5 \%$ (coefficient 0.70 ) we arrive at a coefficient of natural mortality of 0.385 (Ricker, 1958, Appendix II). The value thus found is substantially
higher than the one derived by the method of Beverton and Holt (1957) Possible causes for discrepancy are unrecorded tag loss and handling mortality at the time of tagging.

Similar calculations applied to the 1961-62 series would indicate a natural mortality coefficient of 0.511 . We are reluctant to accept this value in the absence of supporting data, however, since it suggests a mortality rate substantially higher than that indicated by any other estimate. Moreover, the estimate of total mortality has not yet been made beyond 1961. Coefficients of natural mortality in Lake Manitou, Manitoulin Island, and South Bay, Lake Huron (Budd et al., 1968, 1969) were about 0.25.

The above data suggest that after the trout have entered the fishery the mortality rate is somewhat more than doubled as a result of exploitation.

## Variations in year class strength

As one method of estimating the size of the Lake Opeongo trout population and changes in trout abundance, Fry (1949) used the virtual population. When the total catch and age composition of the fishery are known for a period of time, the total contribution to the fishery of a year class can be made. It is calculated by summing successively younger age groups of a year class from its last appearance in the fishery. Thus the virtual population at any given age represents those fish present at that age which were subsequently taken by the fishery. The value given for the youngest age represents the total yield to be obtained from a given year class.

The biases inherent in the use of the virtual population as an index of abundance were pointed out by Bishop (1959). Among the most important is the effect of the level of exploitation during the passage of a year class through the fishery: the higher the exploitation rate the higher the virtual population estimate. Trends in the level of exploitation during the history of the Opeongo fishery are shown in Figure 7; however, since it is unlikely that effective fishing effort has remained constant, the trend in hours of fishing is not necessarily the trend in effective fishing. If there are no substantial changes in the rate of exploitation, the virtual population can be taken as representative of the true population and changes in virtual population from age to age give an estimate of total mortality rate. Since lake trout are relatively long-lived, they have a relatively low force of natural mortality in the years when they are vulnerable to exploitation, and thus the virtual population appears to be a suitable index of abundance of this species.

As Table 6 indicates the virtual populations at age 3 for year classes 193344 which have passed completely through the fishery, have varied from 1750 to 940 . Calculations at age 7 extend the series of observations back 4 years without losing much information, and by adding mean virtual populations beyond age 14 a further extension can be made into more recent years to the spawning year of 1949. The resulting data are plotted in the upper curve of Figure 12. The impression gained from the crude virtual populations is that year class success is cyclic-the data suggest that success was high at the beginning of the observations, declined irregularly until about 1937, then increased to 1943. A second decline and rise followed. The impression is

Table 6. Virtual populations of lake trout of various year classes at different ages. Figures underlined are means for their columns.

| Year Class (Spawning) | 3 | 4 | 5 | 6 | 7 | 8 | $\mathrm{Age}_{9}$ | 10 | 11 | 12 | 131 | 141 | 1516 | 16 | 17 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1919 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 |
| 1920 |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | 0 |
| 1921 |  |  |  |  |  |  |  |  |  |  |  |  |  | 4 | 4 |
| 1922 |  |  |  |  |  |  |  |  |  |  |  | 15 | 7 | 4 | 0 |
| 1923 |  |  |  |  |  |  |  |  |  |  | 12 | 4 | 4 | 0 | 0 |
| 1924 |  |  |  |  |  |  |  |  |  | 22 | 18 | 15 | 0 | 0 |  |
| 1925 |  |  |  |  |  |  |  |  | 66 | 28 | 19 | 6 | 0 | 0 |  |
| 1926 |  |  |  |  |  |  |  | 207 | 31 | 28 | 4 | 4 | 4 | 4 | 4 |
| 1927 |  |  |  |  |  |  | 731 | 176 |  | 393 | 3322 | 220 | 02 | 20 | 16 |
| 1928 |  |  |  |  |  | 1387 | 362 | 167 | 77 | 63 | 525 | 505 | 50 | 41 | 4 |
| 1929 |  |  |  |  | 1432 | 782 | 343 | 120 | 74 | 63 | 54 | 482 | 26 |  | 3 |
| 1930 |  |  |  | 1240 | 1042 | 622 | 229 |  |  | 79 | 55 | 46 | 3 | 3 | 0 |
| 1931 |  |  | 1191 | 1157 |  | 561 | 197 |  |  |  | 34 | 13 | 6 | 0 |  |
| 1932 |  | 1181 | 1177 | 1050 | 829 | 395 | 195 | 142 |  | 056 | 619 | 8 | 8 | 0 | 0 |
| 1933 | 1117 | 1117 | 1043 | 927 | 703 | 468 | 347 | 214 | 12 |  | 711 | 8 | 4 | 0 | 0 |
| 1934 | 1261 | 1249 | 1213 | 1131 | 856 | 639 | 428 | 230 | 71 | 24 | 12 | 0 | 0 | 0 |  |
| 1935 | 1393 | 1354 | 1270 | 1126 | 1009 | 737 | 535 | 162 | 69 | 51 | 19 | 15 | 8 | 0 |  |
| 1936 | 1194 | 1174 | 1095 | 1049 | 928 | 731 | 379 | 162 | 86 | 39 | 17 | 8 | 0 | 0 | 0 |
| 1937 | 943 | 935 | 917 | 875 | 761 | 591 | 266 | 113 | 105 | 39 | 12 | 4 | 4 | 4 | 0 |
| 1938 | 1121 | 1114 | 1072 | 988 | 919 | 679 | 458 | 155 | 94 | 46 | 8 | 4 | 0 | 0 |  |
| 1939 | 1007 | 1001 | 975 | 943 | 827 | 610 | 295 | 146 | 78 | 33 | 18 | 7 | 0 | 0 | 0 |
| 1940 | 1250 | 1242 | 12311 | 1153 | 1068 | 757 | 407 | 223 | 106 | 56 | 18 | 11 | 7 | 0 | 0 |
| 1941 | 1274 | 1274 | 12441 | 1189 | 1067 | 735 | 438 | 177 | 86 | 33 | 4 | 0 | 0 | 0 | 0 |
| 1942 | 1605 | 1586 | 15561 | 1509 | 1255 | 826 | 425 | 231 | 81 |  | 0 | 0 | 0 | 0 | 0 |
| 1943 | 1757 | 1754 | 174216 | 1611 | 1325 | 977 | 573 | 280 | 93 | 50 | 29 | 14 | 14 | 4 | 1 |
| 1944 | 1476 | 1468 | 14331 | 1254 | 1061 | 741 | 497 | 138 | 31 | 21 | 21 | 11 | 11 |  | 1 |
| 1945 | 1184 | 1175 | 1075 | 1003 | 904 | 780 | 407 | 229 | 128 |  | 62 | 24 | 7 |  |  |
| 1946 | 1160 | 1115 | 1104 | 1051 | 968 | 668 | 391 | 270 | 143 |  | 4211 | 11 | 8 |  |  |
| 1947 | 1164 | 1164 | 1153 | 1108 | 980 | 707 | 475 | 237 | 164 |  | 271 |  |  |  |  |
| 1948 | 1360 | 1360 | 1356 | 1308 | 1114 | 857 | 517 | 376 | 175 |  |  |  |  |  |  |
| 1949 | 1623 | 1619 | 16081 | 1474 | 1235 | 804 | 444 | 186 | 91 | 49 |  |  |  |  |  |
| 1950 | 1492 | 1492 | 1429 | 1280 | 910 | 457 | 320 | 201 | $\underline{92}$ |  |  |  |  |  |  |
| 1951 | 1062 | 1050 | 1015 | 827 | 555 | 402 | 283 | 187 |  |  |  |  |  |  |  |

strengthened by consideration of data beyond the range of the curve. The 1928 year class was large, since the virtual population at age 8 was high (Table 6). At the other end of the series, the 1950 year class is of the same order as that for 1949.

As levels of exploitation could influence the size of the virtual population, it is possible that trends in fishing effort have brought about the apparent trend in year class success shown in Figure 12. A correction for the effect of fishing effort has been made to the virtual populations as follows. A regression of the virtual population at age 7 on mean annual weighted survival over the ages 7 through 9 was determined to eliminate the possible effects of changes in exploitation (Fig. 13). The weighting chosen was equivalent to a mean annual survival of 0.5 , that is a weight of 4 was assigned to survival observed in the virtual population over the years $7-8$, a weight of 2 to survival in the following year, and 1 to the third. The survival values so weighted were derived from the virtual population estimates in Table 6 and were calculated


Figure 12. Upper curve: virtual populations at age 7 for spawning years 1929-1949. Lower curve: deviations from trend corrected for mortality.


Figure 13. Virtual populations at age 7 in relation to weighted estimates of mean annual survival. Regression coefficient $b=8.9 \pm 4.8$.
as, survival year $\mathrm{n}=\frac{\text { virt. }(8 \text { through } 11 \text { year } \mathrm{n})}{\text { virt. }(9 \text { through } 12 \text { year } \mathrm{n}+1)}$
The lower curve in Figure 12 shows the deviations in virtual population from the trend in survival and indicates that the course taken by the uncorrected virtual populations is not a function of varying exploitation rates.

As Table 6 indicates the 1928 and the 1950 year classes which are not in the figure, were both large. The curves in Figure 12 therefore indicate a general cyclicity in year class strength in the Opeongo lake trout population, with strong year classes having occurred in the years of record at intervals of about 8 years and weaker ones between these peaks.

Spawning success in relation to spawning strength
Figure 14 shows the relationship between spawning escapement and year class strength in the Lake Opeongo trout population. The minimum spawning escapement in year N is calculated from the virtual population in year $\mathrm{N}+1$ together with sex ratio and egg count in relation to age (Fry, 1949, Table 10). The minimum strength of the year class resulting from a given spawning is represented by the virtual population assigned to the resulting year class.


Figure 14. Relation between spawning strength and year class production. The circled numbers indicate the relations for the 1935 through 1937 year classes. The solid lines extending to the origin represent success ratios of 1:000 and $1: 2000$, respectively. The hatched parallelogram encloses the range of egg escapement values for the years 1951-1957, the latest years for which estimates can be made. Yields for these years are not yet known but it can be presumed they will be similar to those shown for the earlier period.

There is a significant correlation between virtual spawning strength and virtual year class strength for the year classes beyond 1938 ( $\mathrm{r}=0.656$ $d f=11$ ). The year classes 1935 through 1937 weaken the general correlation but within themselves show a trend similar to the trend for the remaining estimates (but with a lower slope). Yields from these year classes can be expected to be lower because the ages for their peak vulnerability fell within the war years when exploitation of the fishery was curtailed (Fig. 7). Hence, on the basis of the observations by Bishop (1959), it can be expected that proportionately more of these year classes fell prey to natural mortality than did the later ones under consideration, the oldest of which (1938) entered the fishery in strength for the first time in 1945.

Any effect of exploitation in Figure 14 is otherwise more likely to contribute to scatter than to bias, since there is almost no overlap in the fishing years on which the respective estimates of parents and young were based. For this reason, with the exception of the three early years mentioned above which were excluded, the effect of fishing pressure has been disregarded and the correlation is accepted as a valid one.

From Figure 14 it can be taken that approximately one recruit to the fishery results from every 1500 surviving ripe ova. It does appear from the data that the Opeongo lake trout population is in a stage of exploitation where reproduction is being limited and that greater yields can be expected if reproduction and/or recruitment can be favoured.

The correlation shown in Figure 14 perhaps emphasizes the cyclicity suggested by Figure 12. Strong year classes would be expected to produce a strong year class 7-9 years later, since they would then be themselves at their maximum spawning strength.

As has been indicated, year class production, on the basis of the 192849 year classes is largely related to spawning escapement, which is in turn determined by fishing intensity. Although aging of the Opeongo trout has been completed only through 1961, an examination of the length compositions of the catches since 1961 suggests the entry of some substantially stronger year classes in 1967 through 1971. The average lengths of fish in the catch during these 5 years was substantially lower (except for 2 years) than those for all the preceding years. A high proportion of trout below about 40 cm (approximate ages, 3-5) were taken in these years.

The effect of the cisco introduction on the fecundity of the trout was at its maximum level in 1960-65, and may have resulted in an improvement in egg production with subsequent stronger year classes. This benefit, however, may have been at least partly offset by the fact the lake trout also matured about a year later in these years. It is possible too that lower harvests in 1960-63 (Fig. 7) resulted in greater spawning escapement and subsequent stronger year classes.

## DISCUSSION AND CONCLUSIONS

Lake Opeongo has escaped many of the stresses that may beset other aquatic communities including many of the lakes considered in the SCOL symposium. It is relatively free of human influences and there is no indication
of pollution or eutrophication. The soil and vegetation around the lake have remained relatively undisturbed and there is little evidence of erosion. Water levels fluctuate only to a minor degree and spawning facilities appear to be adequate for most resident species of fish. There have been no invasions by exotic species which have led to any apparent deleterious effects on the native fauna. Lake Opeongo has had the further advantage of being located in the Provincial Park since 1893, where emphasis has been placed on protecting the environment and fauna of the area. As a consequence there has been some degree of stability in the aquatic community in Lake Opeongo.

On the other hand there has been some measure of stress on the ecosystem by virtue of the infertile nature of the lake waters and their limited productive capacity. This is a result of the geological setting of Lake Opeongo in an area of infertile soils, its relatively high elevation and severe climate, and its small watershed. As a result any additional stress placed on the lake by man could presumably have marked effects on the equilibrium of the community structure.

Two main stresses that have been placed on Lake Opeongo by man have been introduction and exploitation. The lake trout has been the most consistently and thoroughly studied element in the ecosystem over 36 years and has served as the main bench mark in assessing changes in the community structure. Because other physical and biological characteristics have received only intermittent attention to date the authors have had to be somewhat conjectural in their consideration of other levels of the system.

Two known introductions have been made to the Lake Opeongo fauna, the smallmouth bass and the cisco. The bass has had no major observable direct effects on the salmonid community although it may compete with other species in the lake for the crayfish as food. It has provided a second sport fishery in the lake and may have served at times to buffer fishing pressure on the lake trout.

The introduction of the cisco has apparently had considerable impact in Lake Opeongo. It has served to alter the biology of the lake trout, particularly with reference to growth, maturity, and fecundity. This has resulted in increased weight production in the fishery and may have contributed towards the generation of stronger year classes.

From the community standpoint the cisco introduction has apparently had profound effects in Lake Opeongo. It appears to have initiated a chain reaction which in one way or another may have affected many levels of the ecosystem. The generally synchronous nature of the declines in the perch population and insect fauna, the apparent changes in the growth rates of certain fishes, all concomitant with the build up of the cisco population, suggest a relationship between these events. Unquestionably the insertion of the cisco into the food chain has altered the dynamics and inter-relationships of the trophic system.

The second main stress on the Opeongo ecosystem brought about by man has been exploitation, which became intensive in 1936 with the completion of a highway to the area. The lake trout has been the main salmonid exploited in Opeongo over a period of 36 years. Fishing mortality is high after the lake trout enter the fishery. Year class strength is significantly correlated with spawning escapement which is in turn related to levels of exploitation.

What other effects exploitation of the lake trout has had on other parts of the salmonid community can only be surmised. The harvest of substantial numbers of the top predator in the food chain each year could presumably be of some significance in the abundance of animals at lower levels of the trophic system. Similarly the removal of some $2,000 \mathrm{~kg}$ of trout flesh per year may be of consequence in a lake such as Opeongo where nutrients and basic productivity are already limited.

In summary, both the factors of introduction and exploitation have had significant effects on the salmonid community in Lake Opeongo. From the specific viewpoint of the chief salmonid, the lake trout, exploitation has probably had the greater impact. From the viewpoint of effects on the salmonid community as a whole introductions have probably had more far reaching effects.

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## LITERATURE CITED

ALM, G.
1959. Connection between maturity, size and age in fishes. Rep. Inst. Freshwater Res. Drottningholm 40, 145 pp.

## AMERICAN FISHERIES SOCIETY

1970. A list of common and scientific names of fishes from United States and Canada. Spec. Publ. No. 6, 150 p.

ANONYMOUS
1967. A history of the Pembroke Forest District. Ontario Dept. Lands and Forests, District History Series, No. 21, 42 pp.

BANGHAM, R. V.
1941. Parasites of fish of Algonquin Park lakes. Trans. Amer. Fish. Soc., 70:161-171.

BEVERTON, R. J. H., and S. J. HOLT
1957. On the dynamics of exploited fish populations. U. K. Mm. Agr. and Fish. Invest., Ser. 2, 19, 533 pp.

BISHOP, Y. M. M.
1959. Errors in estimates of mortality obtained from virtual populations. J. Fish. Res. Bd. Canada, 16:73-90.

BUDD, J. C., F. E. J. FRY, and P. S. M. PEARLSTONE
1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Bd. Canada, 26:2413-2424.

BUDD, J. C., F. E. J. FRY, and J. B. SMITH
1968. Survival of marked lake trout in Lake Manitou, Manitoulin Island, Ontario. J. Fish. Res. Bd. Canada, 25:2257-2268.

CHRISTIE, W. J.
1957. The bass fishery of Lake Opeongo. M. A. Thesis Dept. Zoology, Univ. of Toronto, Toronto, Ont., 77 pp.
EMERY, A. R.
1971. Smallmouth Bass Unit. In: Research Review, Ann. Rept. Res. Br. for 1970, Ontario Dept. Lands and Forests.
FISCHER, H.
1968. The life cycle of Proteocephalus fluviatilis Bangham (Cestoda) from smallmouth bass, Micropterus dolomieui Lacepede. Can. J. Zool., 46:569-579.

FOERSTER, J. W. and H. E. SCHLICHTING, JR.
1965. Phyco-periphyton in an oligotrophic lake. Trans. Amer. Micros. Soc. 84(4):485-502.

FRY, F. E. J.
1937, The summer migration of the cisco, Leucichthys artedii (LeSueur), in Lake Nipissing, Ontario. Univ. Toronto Stud. 44, Pub. Ont. Fish. Res. Lab. 55:9-91.
1939. A comparative study of lake trout fisheries in Algonquin Park, Ontario. Univ. Toronto Biol. Stud. 42, Pub. Ont. Fish. Res. Lab. 58-69 pp.
1949. Statistics of a lake trout fishery. Biometrics 5:27-67.

FRY, F. E. J. and V. B. CHAPMAN
1948. The lake trout fishery in Algonquin Park from 1936 to 1945. Trans. Amer. Fish. Soc. 75:19-35.

FRY, F. E. J. and W. A. KENNEDY
1937. Report on the 1936 lake trout investigation, Lake Opeongo, Ontario. Univ. Toronto Biol. Stud. 42, Pub. Ont. Fish. Res. Lab. 54:20pp.
KENNEDY, W. A.
1943. The whitefish Coregonus clupeaformis (Mitchill), of Lake Opeongo, Algonquin Park, Ontario. Univ. Toronto Biol. Stud. 51, Pub. Ont. Fish. Res. Lab. 62:23-66.

KERR, S. R.
1971. A simulation model of lake trout growth. J. Fish. Res. Bd. Canada 28:815-819.

KERR, S. R. and N. V. MARTIN
1970. Trophic-dynamics of lake trout production systems, p. 365-376. In: Marine food chains (ed. J. H. STEELE), Oliver and Boyd, Edinburgh.

KHAN, N. Y.
1968. Intraspecific variations and postglacial distribution of lake trout. M. A. Thesis, Univ. of Ottawa, 72 pp .

LANGFORD, R. R.
1938. The food of the Lake Nipissing cisco, Leucichthys artedii (Le Sueur) with special reference to the utilization of the limnetic Crustacea. Univ. Toronto Stud. 45, Pub, Ont. Fish. Res. Lab. 57: 143-190.

LINDSEY, C. C.
1964. Problems in zoogeography of the lake trout, Salvelinus namaycush. J. Fish. Res. Bd. Canada 21:977-994.

MARTIN, N. V.
1955. The effect of drawdowns on lake trout reproduction and the use of artificial spawning beds. Trans. 20th North Amer. Wildl. Conf., pp. 263-271.
1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario lake trout. Trans. Amer. Fish. Soc. 95:415-422.
1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. J. Fish. Res. Bd. Canada 27:125-146.

MARTIN, N. V. and N. S. BALDWIN
1960. Observations on the life history of the hybrid between eastern brook trout and lake trout in Algonquin Park, Ontario. J. Fish. Res. Bd. Canada 17:541-551.

MARTIN, N. V. and L. J. CHAPMAN
1965. Distribution of certain crustaceans and fishes in the region of Algonquin Park, Ontario. J. Fish. Res. Bd. Canada 22:969-976.
MILLER, R. B.
1937. A preliminary investigation of the bottom fauna of five Algonquin Park lakes. M. A. Thesis. Dept. of Zoology, University of Toronto, Toronto, Ontario.

PALOHEIMO, J. E.
1958. A method of estimating natural and fishing mortalities. J. Fish. Res. Bd. Canada 15:747-758.

PRITCHARD, A. L.
1931. Taxonomic and life history studies of the ciscoes of Lake Ontario. Univ. Toronto Biol. Stud. 35, Pub. Ont. Fish. Res. Lab. 41, 77 pp.

RECKAHN, J. A.
1970. Ecology of young lake whitefish Coregonus clupeaformis in South Bay, Manitoulin Island, Lake Huron. In: Biology of Coregonid fishes. Univ. Manitoba Press, Winnipeg, Canada, pp. 437460.

REGIER, H. A.
1971. A mark-recovery method for estimating angler's catch, with an example from Lake Opeongo, Ontario. Trans. Amer. Fish. Soc. 100(3):495-501.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. J. Fish. Res. Bd. Canada Bull. 119:300 pp.

RYDER, R. A.
1964a. Chemical characteristics of Ontario lakes with reference to a method for estimating fish production. Ontario Dept. Lands and Forests, Res. Br. Sect. Rept. (Fish), 48:75 pp.
1964b. Chemical characteristics of Ontario lakes as related to glacial history. Trans. Amer. Fish. Soc. 93(3):260-268.
1965. A method for estimating the potential fish production of northtemperate lakes. Trans. Amer. Fish. Soc. 94(3):214-218.
1972. The limnology and fishes of oligotrophic glacial lakes in North America (about 1800 A.D.). J. Fish. Res. Bd. Canada 29(6):617628.

SANDERCOCK, F. K.
1964. A contribution to the ecology of the whitefishes Prosopium cylindraceum and Coregonus clupeaformis of Algonquin Park, Ontario. M.A. Thesis, Univ. of British Columbia, Vancouver, B. C., 63 pp.


[^0]:    'Contribution No. 71-28 of the Ontario Department of Lands and Forests, Research Branch, Maple, Ontario.

[^1]:    1 Names after American Fisheries Society (1970)
    ${ }^{2}$ Introduced

