INTERSPECIFIC COMPETITION BETWEEN RAINBOW TROUT (*Salmo gairdneri* Richardson) AND REDSIDE SHINERS (*Richardsonius balteatus* (Richardson)) IN TWO BRITISH COLUMBIA LAKES

by

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ABSTRACT

Competition is defined as the demand of two or more organisms for the same extrinsic resources in excess of supply.

The distribution, movements, behaviour and food of trout and shiners in Paul and Pinantan lakes were studied in order to determine the items and mechanisms of interspecific competition between them. Data from recent years were compared with data for years when trout alone inhabited the lake.

No interspecific aggression was observed. The possibility that the two species were competing for space was discounted.

Stomach contents of shiners in Pinantan Lake revealed a marked qualitative diurnal food cycle. In Paul Lake, shiners have drastically reduced the Gammarus population relative to its pre-shiner abundance. This overgrazing was caused by the concentration of large numbers of shiners over the shoals where Gammarus are also present in their highest concentrations and the ability of shiners to pursue food deeper into the weeds and to graze an area more thoroughly than trout. In Pinantan Lake shiners have apparently reduced the density of Daphnia to a point where trout are unable to feed on them as rapidly as in pre-shiner years. The ability of both species to utilize many types of food tends to reduce the intensity of competition.

The study demonstrates how false implications may arise from a delayed appraisal of competition. If observations had not been made on Paul Lake until after competition had been observed the importance of Gammarus as an item of competition would have probably been overlooked and the whole competitive relationship misconstrued.

Included among the basic mechanisms of competition is the consumption by one or more organisms of something in short supply before it reaches a potential habitat where it would become available to another organism or group.

Environmental factors and behaviour were shown to be important influences in the dynamics of competition. The physical and biological environment and the ditribution and behaviour of competitors may be in states of continual flux. Hence natural competitive relationships can be considerably more complicated and variable than situations described by the most elastic of theoretical models.

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INTRODUCTION

Interspecific competition is an important influence in the balance of mixed species communities. The role of interspecific competition in freshwater fish populations is a fundamental question in fisheries biology. The problem of competition of undesirable species with desirable ones (sports fishes) is dealt with at some length in the literature of pond fish culture (for example Bennet, 1952; Ricker and Gottschalk, 1941; Smith and Swingle, 1939; Swingle and Smith, 1941). These papers deal mainly with the end results of and remedies for undesirable competition. Field studies of competition almost always begin after the effects of competition are manifestly evident. The biology of the competitors before competition occurred and during the first phases of competition is lost to the observer. He is seriously handicapped in picking out the features of the competitors' biology which differ from those before competition occurred. Hence he is ill-equipped to determine what changes competition has wrought and through what mechanisms. As a result, attempts to describe the actual mechanisms of interspecific competition in freshwater fishes have been confined almost entirely to laboratory experiments and abstract, necessarily simplified mathematical models.

Several workers have pointed out the difficulties of demonstrating interspecific competition in freshwater fishes. Lagler (1944) emphasizes that to demonstrate that two species are drawing from a common food supply does not by itself prove that competition for food exists, for if the food is abundant and the populations are kept relatively low by other factors, the "feeding could have little effect on supply". Starret (1950) suggests that it is difficult to establish competitive relations between species because the fish may change their diets rather than enter into severe competition. Larkin (1955) states that it is difficult to separate interspecific competition as a factor in population control from other phenomena such as cannibalism and mutual predation. Wide habitat range in freshwater fishes and their consequent flexibility of feeding habits as well as their flexible growth rate and high reproductive potential also obscure competitive relations.

Crossman (1957) points out that mathematical approaches to competition deal mainly with population size, birth rates, mortality rates and reproductive potential, and neglect the effects of the reactions of fishes to the environment. These reactions "possibly create different interactions in nearly similar environments". The influence of factors such as distribution, movements and behaviour upon the interaction of the competitors will be discussed in the following sections.

The exact meaning of "competition" has troubled many authors (for instance Dobzhansky, 1950; Udvardy, 1952; Larkin, 1956) who have visualized the need for a precise definition of the term. Predation and parasitism are considered as separate interactions not falling within the bounds of competition by most recent writers (Solomon, 1949; Udvardy, 1952; Elton and Miller, 1954; Andrewartha and Birch, 1954, Larkin, 1956; and MacFadyen, 1957). Nicholson (1954) and Crombie (1947) on the other hand, prefer to consider all density dependent animal interactions including parasitism and predation as competitive phenomena. Most of these writers accept the definition of competition as "the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply," (Larkin, 1956).

The lack of agreement over whether or not predation and parasitism constitute competition centers around the interpretation of the word, "resource". Nicholson and Crombie consider the life of the host or prey to be a resource; most other writers do not. A conceptual standardization of the term competition can be accomplished only by ridding definition of its ambiguity.

If we choose a definition which admits all categories of unfavorable biological interactions,"it (can be) argued that every activity of each animal in a community in one way or another constitutes an act of competition with all other members of the community," (Larkin, 1956). The word is rendered so broad in meaning as to have little value as a precise scientific term. "The struggle for existence" serves just as well to express this general concept. Competition may be considered as one of the mechanisms in the struggle for existence along with predation, parasitism etc.

The insertion of one word in the definition so that it reads, ".... demand for extrinsic resources ...." helps clarify the concept. The problem of whether life is a resource or not is skirted. In a predatory or parasitic relationship the life of the host or prey is not extrinsic. Predation and parasitism are thus clearly excluded from competitive phenomena.

Competition is defined in this paper as the demand of more than one organism for the same extrinsic resources in excess of supply. It is divided into two phases; competition for space and competition for food.

Paul and Pinantan lakes near Kamloops, British Columbia, were chosen for this study. At the time of study both lakes contained only two species of fish, the rainbow trout, *Salmo gairdneri*, and the redside shiner, *Richardsonius balteatus*, providing a relatively simple example of interspecific fish competition. Limnological and fish biology studies have been carried on in the two lakes for many of the last thirty years and provided much background information for this investigation. The biology of the trout before and during the first years after the introduction of shiners is well documented and provides a unique opportunity to study the mechanisms of competition during their development. Pinantan Lake has since been poisoned and restocked with rainbow trout alone.

DESCRIPTION OF STUDY SITE

Paul and Pinantan lakes are situated about twelve miles northeast of Kamloops, B. C., at an altitude of about 2500 and 2860 feet respectively. The lakes are about four miles apart and connected by a stream, flowing from Pinantan into Paul, which occasionally stops running in the summer. Each lake has one outlet and one major inlet. A few mountain streams which dry up in the summer also enter Paul Lake. Larkin et al (1950) have described the physical features of Paul Lake. Rawson (1934) discusses the limnology of both lakes. Table I lists some limnological characteristics of the two lakes.

Table I. Limnological characteristics of Paul and Pinantan lakes.

	Paul Lake	Pinantan Lake
Area	*960 acres	□ 161 acres
Shoreline development	*5.55 units	□ 3.89 units
Maximum depth	• 182 feet	□ 62 feet
Mean depth	• 112 feet	□ 31 feet
TDS	+ 216 p.p.m.	□ 238 p.p.m.

• Larkin et al, 1950
* Crossman, 1957.
□ B. C. Game Commission, unpubl.
+ Rawson, 1942.

Rawson (1934) describes Pinantan Lake as highly eutrophic with high productivity. He considers Paul Lake as typically oligotrophic, but with relatively high productivity due to an extensive shoal area.

Mottley (1932) and Crossman (1957) discuss the sequence of events in Paul Lake after the liberation of trout fry in 1900. The history of Pinantan is similar. There was a rapid build up of a large underexploited population. The construction of a good road to the lakes led eventually to depletion of the stocks and fry-stocking programs were initiated.

Sometime after 1930 the Redside shiner, Richardsonius balteatus was introduced into Pinantan. A barrier was placed in the stream between Pinantan and Paul to exclude the shiners but by 1945 they had invaded the latter. A subsequent marked drop in the catch per unit effort, a decrease in the growth rate of yearling trout and an increase in growth rate of large trout in Paul Lake (see Figure 1) was attributed to their interaction with shiners (Crossman and Larkin, 1959). A noticeable decrease in the percent of one-year-old fish in the catch occurred (34% of the catch in 1946 to 49 compared with 6.1% in 1955 to 56). This was attributable to the slower growth rate of young trout; fewer one-year-olds attained sufficient size to enter the fishery.

The depression in the growth rate of yearling trout reached a maximum in 1952. Large trout did not start feeding on shiners until about 1951. In succeeding years shiners made up a successively larger quantity of the diet of trout over 10 inches fork length. The growth rate of these larger trout increased accordingly and surpassed that of pre-shiner years. By 1956 the growth rate of trout under ten inches, which did not feed appreciably on shiners, had also increased slightly from the 1951 level but was still lower than in pre-shiner years.

MacLeod (1957, MS) states that the growth rate of small trout in Pinantan in 1952 was considerably lower than the pre-shiner growth rate in Paul. The growth rate of Pinantan trout in 1957, calculated by this writer, was found to be slightly higher than in 1952 but still lower than in pre-shiner years in Paul Lake, (see Figure 1). Unfortunately no pre-shiner data on trout growth rates in Pinantan Lake were available and the deleterious effects of competition with shiners on growth can only be inferred.

In 1955 the Institute of Fisheries, University of British Columbia, initiated a program of study of the interaction of the two species. Crossman

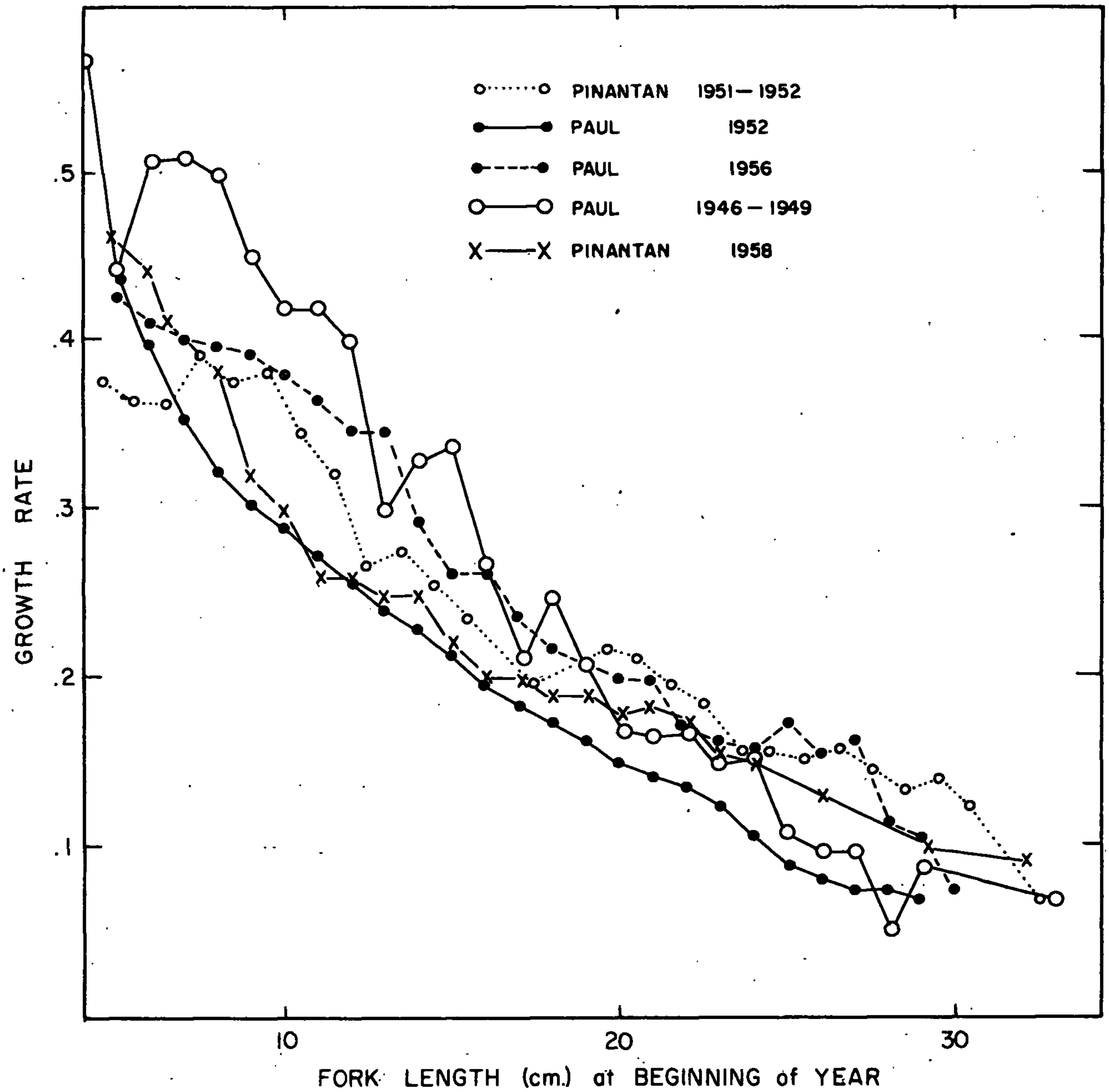

Figure 1. Instantaneous growth rate ($\log_{10}$ fork length at age $_{n+1}$ minus log fork length at age$_n$) in relation to fork lenth at the beginning of the year for rainbow trout in Paul and Pinantan lakes.

1946 and 1952 Paul Lake curves from Larkin et al (1957)
1955-56 curves from Crossman (1957)
1952 curves for Pinantan Lake from MacLeod (1957 MS).

(1957) dealt with the predation of trout on shiners and concluded that this predation had no significant influence on the size of the shiner population, but that it resulted in an increased growth rate of trout over ten inches long.

The present study deals with competition between the two species. Because of the importance of the rainbow trout as a sports fish and because of the large amount of research done on its biology in Paul Lake previous to the introduction of shiners, this study deals mainly with the effects of the shiners on trout. The effects of the trout on shiners were studied only casually.

METHODS

To establish the mechanisms involved in competition between the two species the study was divided into two facets.

1. What, when, where and how much do shiners and trout eat?
2. When the two species come in contact how do they influence each other?

Competition for Food

The stomach contents of 168 shiners caught in gillnets and a dipnet over the summer were analyzed to evaluate the seasonal, diurnal and spatial differences in their choice of food. About 20 stomachs from shiners taken in each of 1946 and 1948 in Pinantan Lake and in 1950, 1952 and 1959 in Paul Lake were also examined. The contents of stomachs from 335 trout caught by angling and gillnetting in the Pinantan Lake throughout the summer were analyzed.

To determine the qualitative and quantitative availability of food, three horizontal plankton tows at each of 3, 10 and 20 feet were made at noon and again at midnight during the first week in September, 1958, with a Clarke-Bumpus plankton sampler. Ten bottom dredgings on the shoal in depths from 1 to

10 feet were taken in June and again in August in Pinantan. Preliminary dredgings in the *Chara* with an Ekman dredge proved unsatisfactory. The dredge would not close properly over the weeds. Consequently a rake was used to gather the samples. Each sample consisted of the amount of *Chara* that would fit into a two litre container. Six-sided, (i.e. completely enclosed) pens 3' by 3' by 3' were used in experiments to study the utilization of a known amount of introduced food.

Factors Affecting the Time and Place of Competition

The seasonal and diurnal movements of shiners in Paul Lake have been described by Crossman (1957). Studies were carried out on Pinantan Lake in 1958 to corroborate and extend these findings. Direct observations were made throughout the summer. Diurnal movements were recorded using two gillnets, one set near shore, the other offshore, for one hour every four hours throughout 24 hours.

Crossman also discusses the distribution and movements of trout in Paul Lake. Direct observations and overnight gillnet sets were made throughout the summer both in Paul and Pinantan lakes.

Behavioural Factors in Competition

Shiners and 3 to 6 inch trout were held in enclosures in the lake for observation and feeding experiments. Four-sided pens, 6' by 6' by 5' deep and built of door screen on a wooden frame, were placed on *Chara* beds near shore and anchored firmly to the bottom in about 4 feet of water. The bottoms of the pens were open, hence the enclosed fish were swimming over natural *Chara* beds and had access to the bottom.

In order to test the possible effect of shiner odor on trout, two channels flowing into a box containing ten 3 to 6 inch trout in two cubic feet of water was constructed. In one channel a shiner was placed in a wire cage. The other channel contained no shiner. The number of trout orienting in each of the two currents was observed and the test repeated ten times.

Many hours during the summer were devoted to direct observation of the two species on and around the shoal in Pinantan Lake.

EVIDENCE FOR THE EXISTENCE OF COMPETITION

In the literature of fisheries biology, competition is commonly divided into three aspects; competition for food, space and spawning area (Larkin, 1956). Food is a well delineated subdivision. Competition for space however is a phrase often loosely applied to any situation where overcrowding occurs. What is often in short supply is not space *per se*, but some resource contained *within* a circumscribed space,e.g. feeding area (as distinct from food) shelter , shade, sunlight, oxygen, warmth, etc. and also, logically, spawning area. Any thorough study of competition for space must sort from a wide range of possibilities just what attributes of the space are in contention.

A. Competition for Space.

The possibility that trout may exclude shiners from parts of the lake they would otherwise occupy was not examined. A knowledge of the distribution of trout before (Mottley and Mottley, 1932) and after (Crossman, 1957) the introduction of shiners into Paul and Pinantan lakes led the writer to all but discount the possibility that shiners exclude trout from any part of their former range. However, some species of cyprinids have been shown to be repelled by the odor in the water of certain other species, (Hasler, 1954) and tests were carried out to determine whether shiners might repel trout in such a manner. Trout made no distinction in choosing between a current containing a shiner and another current without a shiner in it. Two-hundred choices were made; twenty by each of ten 3 to 6 inch trout. The shiner was switched from one current to the other after one-hundred choices had been made. Exactly one hundred movements were made into each of the two currents. The possibility that shiners might, over a period of time, "condition" the water and thus repel trout was not examined.

It is highly unlikely that trout and shiners compete for spawning space. Shiners are known to spawn in streams as well as in lakes (Lindsey, 1950) but in Paul and Pinantan lakes it appears that most spawning takes place in the lakes on the shoals. All trout spawning is done in the streams.

Shiners have been observed thirty yards downstream from the Pinantan Lake outlet (McAllister, unpub.) and near the outlet of the stream flowing into Paul Lake. (Crossman, 1957). However, the shiners observed were few and occupancy of these areas not prolonged. The present writer observed no shiners in the spawning stream at any time during his investigation.

Shiners start spawning between the end of May and the end of June (Lindsey, 1950) just after the trout spawning run is over. Shiner eggs are broadcast fertilized rather than buried in the gravel and shed only at night (Lindsey, 1950) unlike trout eggs. No shiners have ever been observed with trout in Upper Paul Creek.

B. Competition for Food

(i) Food Available in Pinantan and Paul Lakes

Bottom Organisms

Table 2 shows the percent of the total volume of various food items in twenty Pinantan dredgings made on the shoal (in ten feet of water or less). The results are probably less precise than they might be because of the small number of dredgings. Anisoptera larvae were the most important single item in both June and August. Planaria dropped from 27% of the total volume in June to virtual absence in August. Hyallela and Physa made up most of the balance of the dredgings in both months. Shiner eggs, Sphaeridae and the larvae of Chironomidae, Ephemeroptera, Trichoptera and Enallagma were present in small numbers in June and absent in August. The total volume of bottom organisms in the dredgings in June was 35.6 cc's while it dropped steeply to 11.5 cc's in August. The difference is statistically significant ($p < .02$). All groups except Zygoptera larvae were present in fewer numbers in August than in June.

Table 2. Percent Total Volume of Food Items in Pinantan Lake Dredgings in June and August 1958.

Item	Anisoptera larvae	Planaria	Physa	Hyallela	Planorbis	Trichoptera	Hirudinea	Zygoptera
June	32.3	27	11.7	3.4	7.1	1.7	1.1	
Aug.	74.8		17.4	4.3				2.6

Dredgings were richest in volume and variety of organisms in the shallowest (1 to 2 inches) water and visible organisms were strikingly absent from two dredgings taken in water deeper than 8 feet in both June and August. This is in marked contrast to Paul Lake where abundance of organisms, although similarly greatest near the surface, tapers off much more gradually; all groups of organisms in the 0 to 5 meter depth zone were also found in the 5 to 10 meter zone and one-third of them were present in the 30 to 40 meter zone, (Larkin et al, 1950). Rawson (1934) attributes his finding no bottom organisms below the thermocline in Pinantan Lake to severe oxygen depletion. Paul Lake on the other hand has abundant oxygen at all depths.

Larkin et al (1950) recorded the bottom fauna of Paul Lake in 1948 and 1949. All groups found in Pinantan Lake were present in Paul Lake as well as Gammarus, Lymnaea, and Oligochaetes. Chironomids were the most abundant organisms numerically at all depths, from 0 to 50 meters. Percentage volumetric analysis of the various groups was not recorded. A marked decline in the numbers of Amphipods in the lake since the introduction of shiners was noted.

Plankton

Plankton tows made through the first week in September 1958 showed that sixty-five percent by volume of the plankton in the top 20 feet of Pinantan Lake (equivalent, approximately, to the epilimnion) consisted of Daphnia and 25% was Diaptomus. Aphanizomenon was unimportant in plankton tows made at 3 feet and 10 feet but made up 45% of the plankton at a depth of twenty feet. Similarly Anabaena was unimportant except at 20 feet where it made up 10% of the total volume. About 5% of the midnight tows at all three depths consisted of Chaoborus while none were recorded in 12 tows made during daylight.

Other organisms noted were Ceratium, Asplanchna, Spirogyra, Polyphemus, Pandorina, Protococcus, Ulothrix, Ghriodorus, Pediastrum, Dynobrion, Sphaerocystis, Staurastrum, Asterionella, Merismopedia, Cladophora, Anuraea, Colacium, Simocephalus, Tetradesmus and Conchostraca.

Rawson (1934) discusses the plankton in Paul Lake. Diaptomus and Daphnia in that order were the organisms of major importance. Two horizontal plankton tows just under the surface and two total vertical tows made in August 1959 indicated this was still the case.

(ii) The Food of Shiners

In preliminary tests groups of shiners were held foodless for various lengths of time before their stomachs were examined. Whereas 90% of the stomach contents from fish killed immediately on capture were identifiable, only 15.5% were identifiable after the fish were held foodless for an hour and 3.7% after two hours. It was concluded that almost all food in the stomachs of shiners killed immediately on capture had been eaten within two hours of capture. Hence any diurnal change in food habits can easily be detected in the stomach contents. Shiners were sampled at four hour intervalsthroughout the day in early August. A marked diurnal change in foods was discovered.

Figure 2 shows the gradual shift in dominance from _Daphnia_ to algae during the day and back to _Daphnia_ at night in the diet of Pinantan Lake shiners. The stomachs of 37 shiners taken at midnight contained 92.5% _Daphnia_ and 6.2% algae (mainly _Spirulina_, _Spirogyra_ and _Nodularia_).
In contrast the stomachs of 29 shiners taken at 5 p.m. contained only 19.1% _Daphnia_ and 69% algae.

The shift is more striking for offshore fish than for those on the shoals. At mignight offshore fish had virtually no algae in their stomachs while shoal fish had 14% algae and 84% _Daphnia_. But by 4 a.m. the offshore fish had 34% algae in their stomachs while shoal fish had only 8% algae. All shiners move back to the shoal at dawn; offshore shiners were caught only in the midnight and 4 a.m. sets.

Plankton consisting almost entirely of _Daphnia pulex_, made up 58.1% of the total diet and algae contributed 26.4%. Other food included _Hyallela_, various aquatic and terrestrial insects, _Planorbis_ and _Physa_. None of these foods ever composed more than 12% of the diet of a group of fish caught at one time and together they made up only 6.1% of the total diet. About 10% of the food was too well digested to be identified.

It is interesting to note that while shiner cannibalism has been observed in other lakes (Lindsey, 1950b) none of the 269 shiner stomachs from Paul and Pinantan taken from 1946 to 1959 contained a single shiner.

Stomachs of shiners collected in 1959 in Paul Lake by the writer and in various previous years in both lakes by members of the B. C. Game Commission were also examined. The gradual deterioration of all but the 1959 stomachs since their preservation made accurate stomach analysis difficult and the figures in Table 3, below, are just estimates. Apparently there was no marked qualitative diurnal variation in the feeding habits of Paul Lake shiners similar to that found in Pinantan shiners. Collections of shiners taken at

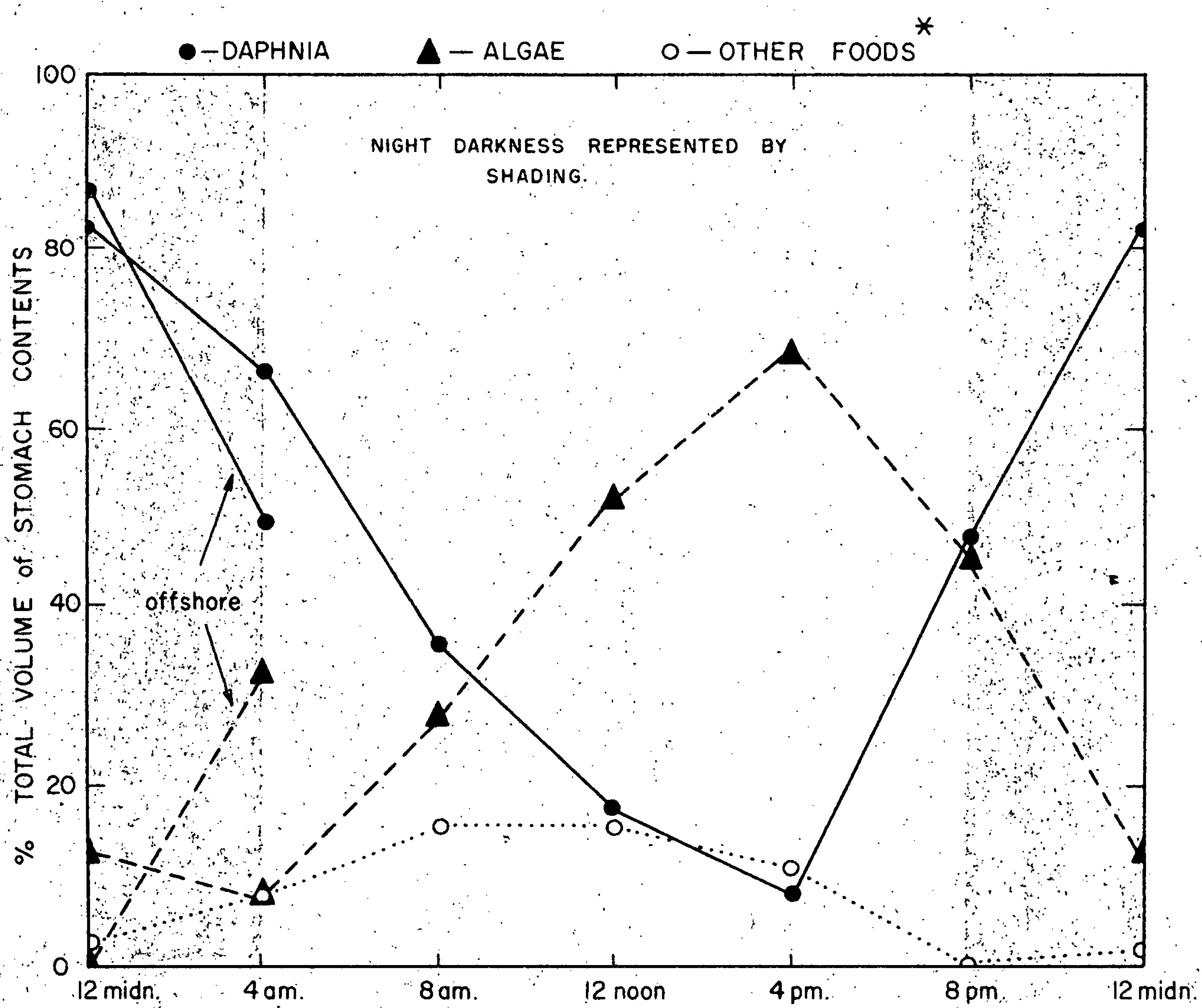

Fig. 2.

Percent total volume of stomach contents of shiners taken at 4 hour intervals over 24 hours on the shoals and at 12 midnight and 4 a.m. offshore.

* Unidentified food not included.

2 p.m. and 2 a.m. both contained about 15% Gammarus and 85% terrestrial insects. The times of day of capture were not recorded for the other collections.

No algae or Daphnia was found in the stomachs of any Paul Lake shiners. The striking differences in the diets of shiners in the two lakes is not unusual. Lindsey (1950b) mentions the wide varieties of food eaten by shiners, in different lakes and streams. He states furthermore that in lakes inhabited by both rainbow trout and shiners, the shiners were found to eat all types of food eaten by the trout.

Table 3. Percent composition by volume of stomach contents of shiners in Paul and Pinantan lakes in various years.

Month	Year	Lake	Number of fish examined	Daphnia	Algae	Terrestrial insects	Gammarus	Trout Fingerlings*	Unidentified
July	1946	Pin.	22	5	90				5
Aug.	1948	Pin.	36	90					10
July	1950	Paul	20			70			30
Aug.	1952	Paul	4					50*	50
Aug.	1959	Paul	17			85	15		

* Fingerling trout had been planted in the area of capture of these shiners the same day. Two of the four fish examined contained trout fingerlings.

(ii) The Food of Trout

The stomach contents of 335 trout taken from Pinantan Lake in the summer of 1958 were examined. Daphnia constituted 63% of the food of trout of 10 inches fork length and under. The relative importance of Daphnia diminishes as the trout grow larger. Shiners constituted the major food item of trout over 14 inches long (70% by volume for the summer) although they dropped markedly in importance in September while Daphnia and Anisoptera increased proportionally in importance. Fish under ten inches long fed negligibly on shiners. Bottom organisms, mainly dragonfly nymphs, made up the bulk of the rest of the food of all three size groups.*

In Paul Lake in 1955 and 1956 Crossman (1957) reports a similar increase in importance of shiners and decrease in importance of plankton as the trout frow larger. Bottom organisms, assumed a greater importance than in Pinantan making up about 50% of the total diet.

Few Gammarus or Hyallela were present in either Paul or Pinantan trout. Larkin et al (1950) point out that in Paul Lake this is in marked contrast to 1931, a pre-shiner year, when amphipods made up 39.8% of the diet of Paul Lake trout.

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* Diaptomus were conspicuously absent from the stomachs of both trout and shiners despite the fact that they were one of the two most abundant plankters in both lakes. The very low availability to salmonids of Cyclops - a very similar copepod - has also been mentioned by Southern (1933), Lindstrom (1955) and Nilsson (1955). Nilsson reports that while high production of plankton species is in general connected with high consumption of that species by char, Cyclops composed as much as 90% of the plankton in Lake Blajon yet constituted less than 1% of the diet of char. Diaptomus, though present in small numbers in the lake was never taken in the stomachs of char.

A simple experiment explained this anomaly. Adult Daphnia and Diaptomus were placed in a glass of lake water. The writer attempted to capture single individuals of each species from the glass with an eye dropper. Daphnia were relatively easy to catch but it was virtually impossible to capture Diaptomus. They invariably dodged the eye dropper with great agility. Undoubtedly they do the same when a fish approaches. This reaction appeared to be a response at least in part to the sight of the approaching eye dropper. Ricker (1932) supposed that the appearance of Cyclops in plankton hauls in Cultus Lake in numbers relatively too few was due to a rheotropic response. The above observation suggests that this occurrence was due at least in part to the ability of this animal to flee quickly on sighting an approaching object.

Table 4. Average volume of stomach content of Pinantan Lake rainbow trout according to month and length group in 1958. Number in bracket under length group is number of trout in that group for whole year. Number in bracket beside month is the number of trout of all sizes in that month.

Length group (fork length in inches)	ITEM	JULY (104)							
		Shiners	*Daphnia*	Antisoptera nymphs	Chironomid larvae	Other insect larvae	Other bottom organ.	Terrestrial insects	Miscellaneous
6-10" (122)	Number of stomachs with item	2	21	4	2	4	-	2	9
	Percentage with item	6	69	11	6	11	-	6	25
	Percentage of total volume	8	61	9	+	7	-	+	14
10-14" (116)	Number of stomachs with item	12	8	6	4	3	-	2	3
	Percentage with item	40	27	20	13	10	-	7	10
	Percentage of total volume	52	17	+	1	10	-	4	4
14-14+ (97)	Number of stomachs with item	25	3	11	1	4	4	-	9
	Percentage with item	65	8	29	3	10	10	-	24
	Percentage of total volume	76	1	9	+	3	5	-	4

Length group (fork length in inches)	ITEM	AUGUST (162)							
		Shiners	*Daphnia*	Anisoptera nymphs	Chironomid larvae	Other insect larvae	Other bottom organ.	Terrestrial insects	Miscellaneous
6-10" (122)	Number of stomachs with item	7	48	8	24	8	1	5	10
	Percentage with item	13	86	14	43	14	2	9	18
	Percentage of total volume	22	63	9	1	+	+	29	2
10-14" (116)	Number of stomachs with item	14	33	16	12	12	3	2	13
	Percentage with item	23	54	26	20	20	5	3	21
	Percentage of total volume	33	28	18	+	14	5	+	2
14-14+ (97)	Number of stomachs with item	29	19	16	16	7	1	5	14
	Percentage with item	64	42	36	36	16	4	11	31
	Percentage of total volume	68	10	15	1	1	+	2	3

Length group (fork length in inches)	ITEM	SEPTEMBER (69)							
		Shiners	*Daphnia*	Anisoptera nymphs	Chironomid larvae	Other insect larvae	Other bottom organ.	Terrestrial insects	Miscellaneous
6-10" (122)	Number of stomachs with item	-	21	4	4	2	-	11	12
	Percentage with item	-	70	13	13	7	-	37	40
	Percentage of total volume	-	65	2	2	1	-	18	13
10-14" (116)	Number of stomachs with item	2	17	3	3	2	-	4	2
	Percentage with item	8	68	12	12	8	-	16	8
	Percentage of total volume	5	32	12	1	4	-	25	5
14-14+ (97)	Number of stomachs with item	4	5	5	5	-	-	4	4
	Percentage with item	29	36	50	36	-	-	29	29
	Percentage of total volume	30	20	40	+	-	-	6	5

(iii) Evidence of Competition for Food between Young Trout and Shiners

Pinantan Lake

Daphnia was the major food of shiners and young trout in Pinantan Lake. This in itself is not sufficient evidence to demonstrate the existence of competition conclusively. As Lagler (1947) stated, if the food is abundant and the fish population kept relatively low by other factors, feeding has little effect on supply.

It is impossible to determine the effects of the shiners on the abundance of Daphnia in Pinantan Lake directly as there are no data from pre-shiner years. Their probable effects however may be inferred from a comparison of the present situation with one described by Ricker (1936) in Cultus Lake.

Ricker showed that the consumption of Daphnia by young sockeye salmon in 1934 in Cultus Lake was sufficient to reduce the available supply and cause a reduction in the growth rate of the sockeye. The concentration of shiners present at night in the pelagic feeding ground in Paul Lake is between 1 in 6 cubic meters and 3 in 1 cubic meter (calculated using data from Lindsey, 1953). Direct observations of the densities of shiners on the shoals in both Paul and Pinantan lakes suggested that their concentrations in these two lakes were roughly similar. This is of the same order of magnitude as the concentration of sockeye in Cultus Lake during Ricker's observations (from 2 in 3 to 2 in 7 cubic meters).

Adult shiners in Pinantan Lake consumed about 2200 Daphnia per day*-- $4\frac{1}{2}$ times as many per individual as the sockeye in Cultus Lake as estimated by Ricker. The concentration of Daphnia in Pinantan Lake in August 1958

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* This estimate is based on previously described digestion rate experiments, volumetric stomach analysis and a count of the number of Daphnia per cubic centimeter of pure Daphnia in a trout stomach. Stomach contents of trout rather than shiners were used because the pharyngeal teeth of shiners fragment their food so much that the enumeration of individual plankers is impossible.

was about 1.2 per litre—about ½ the concentration in Cultus Lake. The rate of turnover of plankton in Pinantan may be somewhat higher than that of Cultus however due to its higher summer temperature and total dissolved solid content.

Serious competition for food occurred at the described level of food and feeders in Cultus Lake. It may be inferred from the above comparison that the Daphnia in Pinantan Lake may also have been kept at a relatively low level, by shiners, and that since the food requirements of young rainbow trout are similar to those of sockeye fingerlings, competition for food occurred in Pinantan Lake. That the growth rate of young Pinantan Lake trout was in fact even slower than the shiner-retarded growth rate of young Paul Lake trout supports this view.

In summary, there were probably no fewer than ¼ the concentration of shiners in Pinantan as there were sockeye in Cultus Lake during the years being compared. These shiners ate over four times as much Daphnia per individual per day as sockeye. The concentration of Daphnia in Pinantan Lake is ½ that of Cultus Lake though the rate of production is probably greater. Competition for food was demonstrated in Cultus Lake. Competition for food is inferred in Pinantan Lake from this comparison.

Paul Lake

Competition for food in Paul Lake has centered mainly around Amphipods. Gammarus and Hyallela have decreased in abundance in Paul Lake and have decreased markedly in importance as trout food since the introduction of shiners.

In 1949, amphipods in bottom dredgings were less than one third as abundant as in the pre-shiner year 1931 (Larkin et al, 1950). Before the introduction of shiners into Paul Lake, amphipods made up 39.8% of the food of trout. In 1931 Mottley and Mottley (1932) report that the average trout stomach contained 167 amphipods. Afterward, in 1947—1948, they made up only

9.4% of the food of trout (Larkin et al, 1950) and in 1955—1956 "even individual gammarids were rarely present" in the stomachs of trout (Crossman, 1957).

Figure 3 shows the decline of importance of amphipods in the diet of trout.

It was supposed that shiners had cropped off the amphipods to this low level. Pen feeding experiments were carried out to substantiate this hypothesis. After 500 Gammarus had been introduced into each of the holding boxes and allowed to seek shelter in Chara placed in the bottom, trout and shiners were introduced. All other visible food had been washed from the Chara. After twenty-four hours the boxes were lifted and the remaining Gammarus counted.

Ten 3 to 6 inch trout and ten $1\frac{1}{2}$ to 3 inch shiners consumed approximately the same number of Gammarus during this time. From the trout pen 119 Gammarus were recovered, 105 from the shiner pen and 315 from a control pen containing no fish. Apparently, both shiners and trout eat large quantities of Gammarus when they are available.

The potential grazing intensity of these shiners on Gammarus is many times that of the trout population. Lindsey (1953) states that the number of shiners in Paul Lake was too great for accurate estimation from fin-clipping experiments but that in 1950 the number was somewhere between five million and one hundred million. Larkin and Smith (1953) estimated the number in 1952 to be "several million". Crossman (1957) estimates that in 1955-56 there were about 16,000 trout over six inches in length in Paul Lake. Even if there were five times this many trout under six inches long in the lake there were probably at least fifty times as many shiners as trout in the lake. During the summer months thousands of shiners can often be seen at one glance along the shoal areas. This large number of shiners in the lake, their readiness to eat amphipods and their congregation over the area of greatest concentra-

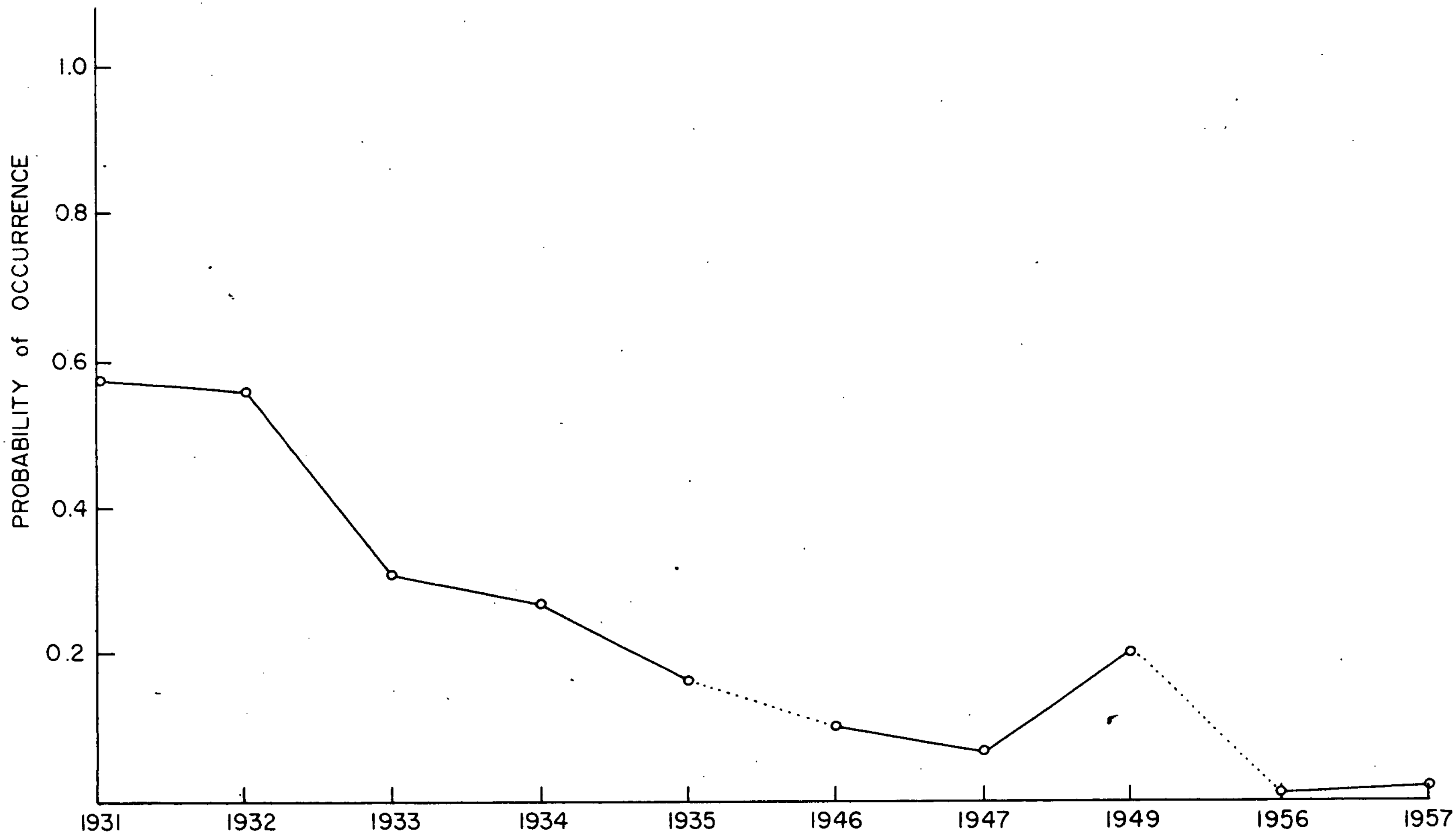


Figure 3. Probability of occurrence of Amphipods in stomach contents of rainbow trout, Paul Lake, 1931 to 1957.

tion of amphipods points to a major item of competition.

FACTORS AFFECTING TIME AND PLACE OF COMPETITION

A study of the distribution and movements of shiners and trout provides knowledge of the areas where both species occur and hence where competition is most likely to take place.

A. Distribution and Movements of Shiners

Crossman described the seasonal and diurnal movements of shiners in Paul Lake. Their movements in Pinantan Lake were similar although the trends were not so clear cut.

(i) Seasonal Movements

Data on the distribution of shiners in Pinantan Lake were derived from direct observations made day by day during June through August 1958, as well as from gillnet sets on the shoal and offshore.

The fish first appear on the shoals in schools in May or June. In May 1957 McAllister (unpub.) observed a huge "school of 2-3" shiners" about 50 yards down the outlet stream. Nothing is known of their winter distribution. Observations commenced on Pinantan Lake in the middle of June. The shiners on the shoal exhibited the same vertical and horizontal stratification noted by Crossman (1957) in Paul Lake and Lindsey (1950a) in Rosebud Lake: the smallest shiners were closest to the surface and closest to shore; the large fish progressively deeper and farther offshore. On cloudy days all but the ½ inch long, newly-hatched fry moved into deeper water just off the shoal. The shiners were most frequently seen in schools of from 30 to 500. Occasional individuals swimming lethargically by themselves were noted throughout the summer. Dead shiners were also seen frequently. Presumably some disease was affecting these fish, although no cause was found. The incidence of the tapeworm <u>Ligula</u> which varies from almost 100 to almost 0 per cent in various years was negligible in 1958.

In early July the vertical stratification in all but the 1958 fry seemed to break down gradually. Fry still stayed in segregated schools of 50 to 100 within about six inches of the surface. Otherwise, different sized fish intermingled in 1 to 8 feet of water, 1 to 4 feet from the surface. Later in July the fry gradually broke up and moved farther off the shoal mingling with the larger fish. By July 20 the schools were diminishing noticeably in size and number; the fish were visible offshore up to 30 yards or more and in deeper water. The largest fish left the shoals first. An estimated 50% of the fry remained on the shoal during this general offshore movement.

In a channel about eigth feet deep between an island and the shore a large school stayed about 30 feet offshore, for almost a month, without shifting during the day. In 0 to 3 feet of water was a school of about 500 fry; in 0 to 8 feet of water a school of one-year-old fish and in 2 to 8 feet of water a school of larger fish (about 3 inches and over). The three schools often intermingled through vertical mixing but invariably sorted themselves out within 10 to 15 seconds, into the three separate size groups. These schools were continuously preyed on by trout. Fishing and gillnetting for trout in this vicinity was very productive.

By the end of August the schools had reformed and stratified on the shoals again. The lake was poisoned in early September. Presumably the fish would have moved offshore en masse in October as they had been observed to do in previous years by the lodge owner and by Crossman (1957) in Paul Lake. Nothing is known of their winter distribution. Larkin (pers. comm.) has noted that they collect around holes cut in the ice during the winter.

In July and August several observation trips were made around the perimeter of the lake. Shiners were strikingly absent from the shoals of the south half of the lake, on all occasions. One could cruise for hundreds of yards at a time in this area without seeing a single shiner while at the same time the shoal of the north half was almost continuously populated.

When the shiners were concentrated on the shoals during June and early July, schools of large (over 3 inches F. L.) individuals were often seen 20 to 40 yards offshore on the northwest side. They would often vigorously dapple the surface. Either almost all the individuals in the school would participate in this activity or none at all. It could not be ascertained if they were feeding as no food was seen. In the schools near shore this dappling behaviour was noted only occasionally and was carried out only by single individuals.

(ii) Diurnal Movements

Similar to Crossman's findings, the shiners were observed to spread out all over the surface waters (0 to 25 feet deep) of the lake as nightfall approached and move back to shore at the first light of morning.

At 11:30 p.m., June 25, about one-twentieth of the daytime numbers were seen by flashlight on the shoal randomly distributed according to size horizontally and vertically, except for fry which were still in schools within six inches of the surface. At night shiners could be seen dimpling the surface sporadically all over the lake. It could not be ascertained if they were feeding.

Two possible reasons for this offshore movement present themselves; 1. The shiners move out in response to an upward migration of Daphnia on which they feed extensively at night. 2. They lose their orientation to the shore at night and swim about at random horizontally.

Larkin et al (1950) mentions a slight downward migration of Daphnia in Paul Lake from 4:30 to 10:30 a.m. and a compensatory upward migration from 7:30 p.m. to 4:30 a.m. However even at the peak of the downward migration the proportion of Daphnia below 12 meters never exceeded 25%. In Pinantan Lake a series of midnight and noon plankton tows at depth of 1 foot, 10 feet and 20 feet did not indicate any significant difference between night and day in the number of Daphnia in the upper ten feet of water, the area in which the shiners are concentrated at night. Hence the second explanation, a loss of orientation to the shore in the dark appears to be the more reasonable theory.

B. Distribution and Movement of Trout

Tagging studies done by Crossman (1957) in 1952 indicated that "at least in 1952 there were no discrete populations of trout at any one place at any one time" (except during the spawning migration) in Paul Lake. "The trout seemed to move about freely from place to place over the length of the lake, at times moving from one end to the other".

Observations and results of gillnetting on both Paul and Pinantan lakes indicate that during the summer the large trout (10 inches and larger) tend to stay around and, in Paul, below the thermocline. Mottley and Mottley (1932) state that the older fish in Paul Lake "seek great depths" during the summer. Recently planted hatchery fingerlings (2-5 inches F.L.) were seen however in large numbers on the shoals in as little as a foot of water, often swimming in company with schools of shiners, in July 1959.

Large trout were frequently observed by Crossman (1957) and this writer to make quick dashes into shallow water (as little as one foot deep) while chasing and feeding on shiners. They returned immediately into deeper water off the shoal when they had caught or lost their prey. This activity could be observed almost continuously in restricted areas of the shoals on warm bright days in late July and August in both lakes. These feeding movements are described in detail by Crossman (1957).

C. Time and Place of Competition

The only area where trout and shiners were both observed in any numbers during the summer was just off the shoals in the upper twenty feet of water. Trout but not shiners also ranged below this depth. No trout were ever taken along with shiners in the offshore gillnet sets. (The gillnet was suspended from the surface and was eight feet deep). Almost no surface feeding by trout was observed offshore by night (or day) during the summer observations in Pinantan Lake. Apparently shiners do not encounter many trout during their offshore night migrations.

Little is known of the distribution of shiners from late September to May. Lindsey (1950a) states that a few shiners have been found lying dormant in the mud and among bottom debris during the winter. Larkin (pers. comm.) observed shiners gathering around holes cut in the ice in Paul Lake. Except for this one observation shiners have not been seen on the shoals or at the surface during the winter. While shiners constitute the major food item for trout over 14 inches long in the summer, they were found in only two of 78 stomachs taken from Paul Lake trout over 14 inches long taken in December 1953 (Crossman, 1957). This would suggest that the winter distributions of trout and shiners in Paul Lake do not overlap appreciably. The diet of these trout was very similar to what it was before shiners had entered Paul Lake (Crossman, 1957). Probably competition for food is not intense during the winter.

BEHAVIOURAL FACTORS IN COMPETITION

The previous sections have dealt with what competition is for and where it occurs. Observation of the behaviour of the two species is important in order to determine how competition occurs and, if one species is more successful than the other, what abilities or habits it possesses which make it more successful.

Crossman (1957) states that he observed no interspecific aggression in nature. The shiners however "appeared to be more efficient feeders and when a trout and shiner darted after the same food item, the shiner invariably got it and while shiners would move right into the shore to feed, trout did not come into water shallower than 15 inches."

In the course of summer observations the present writer saw many trout 3 to 5 inches long swimming in company with, or in and out of, schools of shiners in 2 to 8 feet of water. There appeared to be no interspecific agression except in one instance when a six inch trout was "chased" for about three feet by a $1\frac{1}{2}$ inch shiner. Otherwise both species appeared to be oblivious to one another. Shiners however moved noticeably faster and hence ranged over a wider area per unit time in search of food than trout did.

A. Behaviour of Trout in a Pen Without Shiners

An observation pen was marked off horizontally in nine equal squares by strings stretched across the pen along the surface. Trout (3 to 5 inches F.L.) remained at the sides or corners of this open-bottom pen just above or down among the dense weed growth, except when they were feeding. Observations for several days showed that activity was greater during bright weather. In the brightest part of the day, out of ten trout, some single individual would move from the area under one square into another every one to two minutes. On dull days there was virtually no movement except when food was introduced.

Only 4 or 5 of the ten fish exhibited this behaviour over about two dozen fifteen minute observations spread over several days; some individuals remained continually hidden in the weeds. There was some establishment of territories, and nipping occurred as often as three times per minute in bright sunlight. The same territory was not held by a fish indefinitely. There appeared to be no unchanging order of dominance or "peck order" although the largest fish of the ten appeared to dominate all the others. Considerable individual variation was seen in these activities. In some cases one trout was observed chasing another trout larger than itself. (These observations on dominance, nipping, territories and the correlation of light intensity with activity agree well with those of Stringer and Hoar (1954) in the laboratory).

The fish preferred shaded areas in the pen about six to one over sunlit areas. During overcast days and in the evenings there were no signs of movement and the trout went deeper among the weeds.

There was never a territory established near the center of the pen. Occasionally a swimming trout on "finding itself" in the middle of the pen would appear frightened and dart quickly for cover among the weeks at a side or corner of the pen.

The trout were left in the pens for a week without any food except the natural food they might find in the weeds. At the end of this time no feeding was observed and it was assumed that the trout had eaten all available natural food. About 2000 Gammarus, most of which were alive, were placed in the pen with the trout which were at the time all down among the weeds. The largest (about 5 inches F.L.) trout immediately came out of the weeds and made 54 feeding movements (consisting of darting at and swallowing a Gammarus) in the space of four minutes. Three smaller trout (3 to 4 inches) started feeding within a minute but they appeared more wary than the large trout and returned immediately to their territory among the weeds after each feeding movement. The largest trout often made six to eight feeding movements before returning to his home territory. Within five minutes all ten trout were feeding with varying degrees of activity which seemed to be related to their size. Sometimes two trout would pursue the same shrimp and collide. The fish often nipped and chased each other even when neither fish was in its habitual territory.

At the end of fifteen minutes few Gammarus were in sight and feeding activity had dropped to three movements per minute. The trout often mistook the tips of Chara shoots for Gammarus, mouthed them, then spat them out.

Almost without exception no trout strayed farther than one square in any direction from its home territory. Food was usually captured by a sudden dash of two feet or less. Smaller trout (3 to 4 inches) occasionally spat out large Gammarus three or four times before finally swallowing them, or rejecting them completely. The trout took dead Gammarus resting on the weeds as well as Gammarus in motion. The trout seemed to feed at random, making erratic rushes here and there, often ignoring Gammarus near them and rushing after others farther away.

B. Behaviour of Shiners in a Pen Without Trout

Unlike the trout, shiners stayed in one compact school in an area of about 8 cubic feet just above and among the tips of the weeds. Only when frightened by quick movements of the observer did they scatter down into the weeds. The school moved very slowly over the whole area of the pen often staying more or less in one spot for ten minutes or more but never seeming to favor any spot nearer the sides or corners than the center of the pen. No feeding movements were seen after the first day in the pen--presumably they had cleaned out the food. No correlation of activity with light intensity was noted.

When Gammarus were introduced shiners appeared to feed more efficiently and methodically than trout. They moved as a school eating every Gammarus near them that was visible to the observer as well as making feeding movements at objects too small for the observer to see. (This was not so with the trout. The observer could invariably see the objects on which they were feeding). The shiners fed more slowly than the trout, making approximately half the number of feeding movements per individual per unit time as did the trout. They pursued Gammarus several inches further down into the weeds than the trout would venture after them. They often spat out and rejected larger Gammarus.

C. Behaviour of Trout and Shiners Together

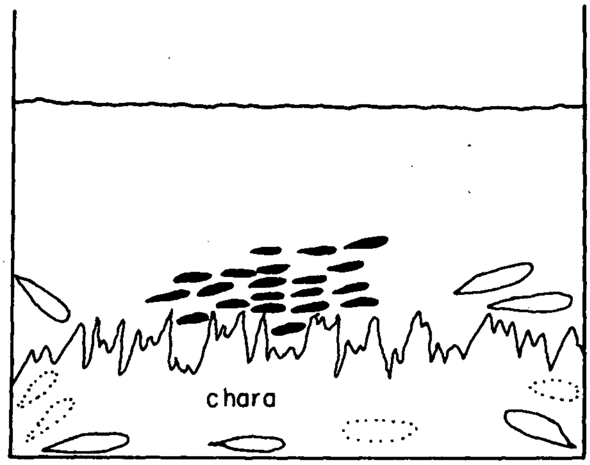
There was no observed difference between the behaviour of the two species in the presence of one another and their behaviour when in separate pens, with or without food.

The shiners, being at first higher above the weeds, were on the whole faster to notice the Gammarus and faster to start feeding than the trout. When the trout started feeding they ranged higher above the weeds than the shiners and the shiners ranged lower among the weeds than the trout, (see Figures 4 & 5).

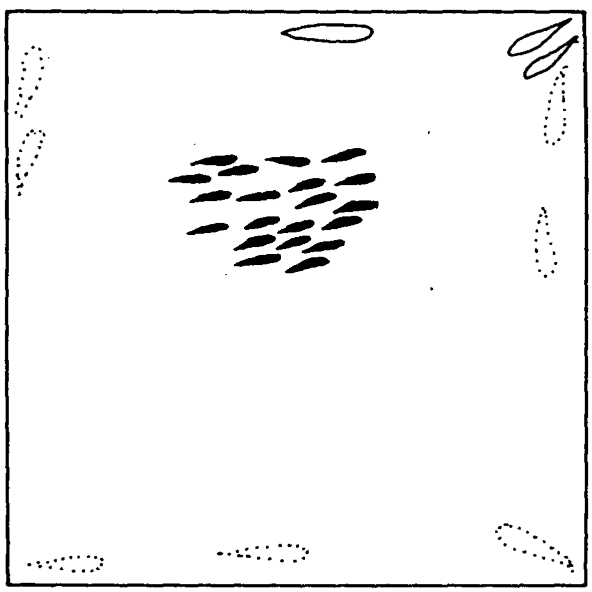
In the space of half an hour however, trout made only three movements right up to the surface to feed. Shiners made none. Five hours later there were still twelve large Gammarus floating on the surface. Trout often nipped and chased each other but never chased shiners. Occasionally a trout and shiner would collide while moving in search of food. As the trout were larger and moving faster, the shiners were usually pushed aside in this collision. Incidents of this nature appeared accidental however and were infrequent. In one-half hour of intermingled feeding of the two species no trout was observed to chase or nip a shiner. On one occasion only, one two-inch shiner chased a four inch trout for about one foot horizontally. Both, shiners and trout occasionally mistook the tips of Chara plants for Gammarus, mouthed them, then rejected them.

Occasionally when a trout mouthed a Gammarus then spat it out as described previously a shiner would eat it before the trout had a chance to mouth it again. This was the only type of overt competition for the same food item observed and was seen only twice in one-half hour.

Figure 4. Diagrams of the Distribution of Trout and Shiners in the Observation Pens when not Feeding.



Diag. A. Schematic Side View.

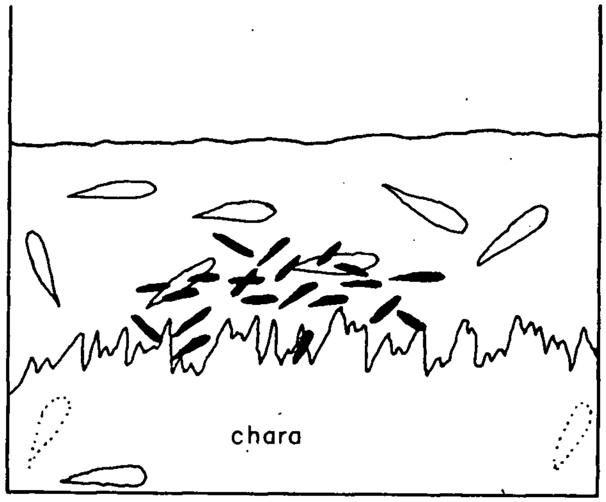


Diag. B. View Looking Down on Pen.

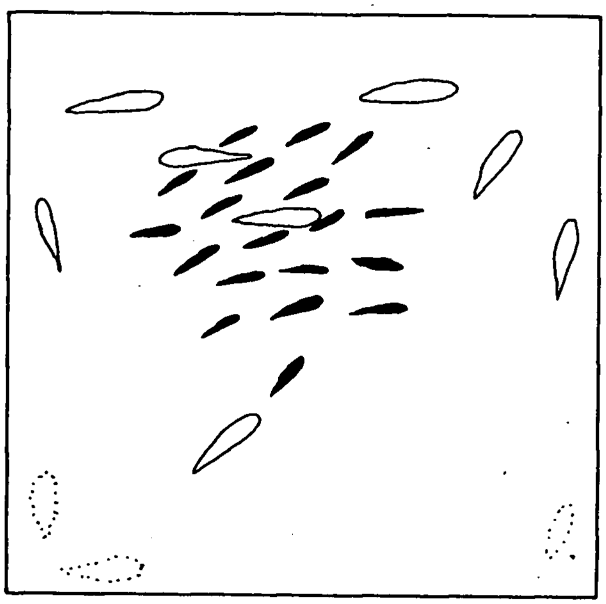
Trout remain at the sides or corners of the pen just above or down among the weeds.
Shiners hover in a compact school above and mong the weed tips, favoring neither center nor sides of the pen.

Shiner
Trout
Trout hidden in weeds

Figure 5. Diagrams of the Distribution of Trout and Shiners in the Observation Pens when Feeding.



Diag. A. Schematic Side View.



Diag. B. View Looking Down on Pen.

Trout range higher in the water than shiners. Shiners go deeper into the weeds for food than trout. (Trout pictured in the weeds have just returned from feeding excursion and do not feed while in the weeds). Shiners still school though less compactly than when not feeding. Trout do not school. The two species intermingle as though oblivious to each other.

Shiner
Trout
Trout hidden in weeds.

In subsequent observations the same activities were noted. Shiners seemed to feed more quickly when they had been starved for a longer per- priod of time.

MECHANISMS OF COMPETITION FOR FOOD

It has been stated that trout would not forage down among the weeds in search of food like shiners. A second line of evidence supports the general applicability of this observation in the lake. Gammarus were abundant down to a depth of 50 meters in Paul Lake in pre-shiner years of low trout abundance (Rawson, 1934). When the trout population was increased as a result of heavy stocking, Gammarus below the Chara zone decreased markedly in abundance while in the Chara zone they decreased only slightly (Larkin et al, 1950). Chara appears to provide amphipods with relatively effective shelter from the predation of trout.

Interspecific aggression is not a factor in competition for food between trout and shiners. None was observed in the lake nor in the observation pens.

There are five observations which suggest that trout are at a disadvantage when competing with shiners for amphipods in Paul Lake.

1. Shiners range deeper among the weeds in search of food than trout, cropping off many bottom organisms before they move out into areas in which they are available to trout.
2. Shiners appear to be able to utilize food items smaller than the smallest items taken by trout. Consequently they may graze off large numbers of smphipods before they reach a size at which they become available to trout. They may also graze off a much higher proportion of immature amphipods than trout, leaving fewer to survive long enough to reproduce and replenish the amphipod population. (Amphipods left by shiners during feeding experiments averaged three times as large as those left by trout).

3. In the summer during the day shiners are concentrated directly over the shoals. Trout tend also to be near the shoals, but farther offshore and in deeper water not so close to the main source of amphipods.
4. Shiners are more methodical feeders than trout, searching an area more thoroughly for their food.
5. There are probably 50 or more shiners for each trout in the lake.

Competition for Daphnia in Pinantan Lake does not facilitate study and description as readily as the above situation. Several facts are apparent however. Shiners spread out in the pelagic areas of the lake only at night. Trout appear to be in this area only during the day. This is evidenced by the angling success offshore during the day while no trout were ever caught in offshore gillnet sets during the night. Presumably the two species do not overlap appreciably in their occupancy of the pelagic feeding area.

At the present level of grazing there remained about 1200 Daphnia (2 cc's) per cubic meter in the epilimnion in late summer. Presumably trout were going short because the plankton was spread out relatively diffusely and they were unable to feed on it as rapidly as in pre-shiner years.

There were relatively few amphipods in Pinantan Lake compared with Paul Lake when shiners were first introduced, according to Rawson (1934). He attributed this to the absence of any extensive Chara zone in Pinantan. Since this time a very rich and extensive Chara zone has developed. This plant affords amphipods considerable protection from the predation of trout and it is probable that a large amphipod population would have developed along with the Chara had shiners not been present to graze them down. (It has already been mentioned that shiners penetrate weeds much deeper in search of food than trout).

In Paul Lake an extensive Chara zone and a large population of amphipods was already present when shiners antered the lake. It is possible that when the amphipods in Paul Lake are reduced by shiners to a level of abundance comparable to that in Pinantan Lake the shiners will shift to Daphnia as their main food. A second phase of competition paralleling that described in Pinantan Lake might then ensue. Nilsson (1955) reports that char in Swedish lake turn from a diet of bottom organisms to plankton when the former become scarce.

An alternative hypothesis is the possible development of a new relationship between trout and shiners in Paul Lake unpredictable on the basis of what has occurred in Pinantan. As Crossman (1957) has stated, reactions of animals to the environment may possibly create different interactions in nearly similar environements. Differences between the two lakes, i.e. depth, oxygen, profile, may be such that the future relationship of trout and shiners in Paul Lake will have little in common with the situation described in Pinantan Lake.

SUMMARY

A. Items Competed For

Trout and shiners do not compete for space or for spawning area in Paul or Pinantan lakes. The reduced growth rate of yearling trout since the introduction of shiners into the lakes is the result of competition for food. Shiners have drastically reduced the abundance of amphipods in Paul Lake. Shiners and yearling trout compete for Daphnia in Pinantan Lake.

B. Mechanisns of Competition

Yearling trout and shiners show no behavioural interference with one another when swimming together. Their behaviour is identical with what it is when only one species is present. Direct physical aggression plays a minimal role in competition between the two species.

During daylight in the summer the main concentration of shiners is over the food-rich shoal areas whereas the trout are somewhat deeper and farther offshore. Shiners go deeper into the weeds in search of food than do trout. They appear to include in their diet food particles smaller than the smallest size eaten by trout. It is these factors in the shiner's biology and distribution plus its enormous numbers which have caused the depletion of amphipods in Paul Lake and the decline in the growth rate of young trout.

In Pinantan Lake shiners have apparently reduced the density of Daphnia in the epilimnion to a point where trout are unable to feed on them as rapidly as in pre-shiner years.

DISCUSSION

While the present study covers particular situations in only two lakes the results have broader significance. The data will be considered below as they apply to the phenomena of interspecific competition in general and fish competition in particular.

Competiton in nature is usually first recognized only after its results have become apparent. Usually a noticeable change in one of the competing populations (i.e. reduction, extinction, emigration) must occur before the observer becomes aware that competition is taking place. Discovering the items and mechanisms of competition under these circumstances is like trying to understand a novel after reading only the last chapter.

The present situation in Paul Lake serves to illustrate how false implications may arise from a delayed appraisal of competition. In recent years amphipods were scarce in the lake and formed only a small fraction of the stomach contents of trout and shiners. On the basis of this observation alone an observer would hardly suspect that amphipods were the most important item of competition. What is more, as there is relatively little overlap in the present feeding habits of the two species one might conclude that competition for food was not occurring at all. The present case is an example of Hartley's (1948) statement that, "the finding of different foods in different species is not irrefutable proof of the absence of competition unless it can be shown that all selection of foods is by choice alone from diverse superabundant food stocks all equally accessible to the species studied." Observations made before and during the first phases of competition showed that shiners and trout were not feeding by choice alone. They have been forced by their depletion of amphipods to replace them in their diets with other, presumably less preferred foods.

This shift in the diets of trout and shiners in Paul Lake since competition began serves to caution against assuming that the present feeding habits of the two species in Pinantan Lake tell the whole story of competition there. Possibly the most important original items and mechanisms of competition in Pinantan were quite different from what they were at the time of this study.

Another important consideration in studying competition is: in what direction does one look to find causes and mechanisms? Theoretical approaches to population interactions deal mainly with the characteristics of the competing populations, i.e. numbers of competitors, birth rates, death rates and reproductive potentials. They have focussed little attention upon the behaviour of the competitors and the modifying effects of the environment.

The present study indicates that both these factors may have considerable bearing on the dynamics of competition. Environmental factors such as lake morphology, plant growth temperature and oxygen profiles and light intensity play important roles in determining the items, areas and times of competition. Indirectly they may also influence the intensity of competition by determining the distribution of the two species and their degrees of overlap.

Items of competition are at least in part determined by their availability and this in turn is strongly influenced by plant growth. In Paul Lake where Chara and consequently amphipods were abundant, the main food item in contention was amphipods. On the other hand, in Pinantan Lake, because of the relatively sparse Chara zone at the time of the introduction of shiners, few amphipods were present and competiton centered around Daphnia.

Environmental factors limiting the times and areas of competiton are:

1. the temporal and spatial distribution of food,

2. the summer hypolimnial oxygen deficit in Pinantan Lake which keeps

fish in the hypolimnion.

3. High summer temperatures on the shoal apparently preventing trout from occupying it more than momentarily.

4. Some diurnal variable - probably light intensity - which causes shiners to occupy offshore waters and feed appreciably on Daphnia only at night.

As well as these more of less constant or cyclic environmental influences there are also less predictable year to year influences. Some unknown epidemic caused a mass mortality of shiners in Paul Lake in August 1958. As a consequence shiners were found far less frequently in the stomach contents of trout in 1959 than in early 1958. Amphipods were significantly more abundant in the trout diet in 1959, presumably because there were fewer shiners to graze them down.

Infestation by the tapeworm, Ligula, in shiners varied from almost 100 to almost 0 percent in the lakes from year to year. Ligula-invested shiners are not only sluggish and more vulnerable to the predation of trout, but also they have extremely small amounts of food in their stomachs compared to uninfested fish. Probably shiners consumed significantly less food per individual in years when they were heavily parasitized.

Year to year differences in rainfall and atmospheric temperature cause an almost two-fold difference in the summer heat income of Paul Lake (Larkin et al, 1950) and a five degree fahrenheit difference in the summer epilimnal temperature (McAllister, unpub.). Annual fluctuations of this magnitude might be expected to exert a significant influence upon food production and fish distribution - both factors in the intensity of competition. Nilsson (1955) ascribed year to year differences in the foods of trout and char in three Swedish lakes at least in part to differences in temperature and lake levels in different years.

Many of the above factors act to make both competitors and items of competition non-randomly distributed both spatially and temporally in a highly complicated fashion

A more careful study would have undoubtedly uncovered more environmentally controlled aspects of competition in Paul and Pinantan Lakes. Why, for instance, are trout not found offshore like shiners in Pinantan Lake during the night?

A third often neglected factor in the dynamics of competition is the behaviour of the competitors. Shiners are more efficient feeders than trout; they seem to appreciate smaller food items; they go deeper into the weeds after food. The situation would be further complicated, as it undoubtedly is between many pairs of competitors, if there were any interspecific behavioural patterns which favored one species over the other.

Competition need not entail any physical conflict; the competitors need not even be in the same place at the same time to compete. Solomon (1949) noted this when he included among the mechanisms of competition, "the occupation or consumption by earlier arrivals of something in limited supply so that late comers are automatically excluded or deprived." The present study demonstrates this situation. Shiners eat plankton offshore only during the night. Trout are apparently present in the pelagic feeding ground only during the day. Also, shiners eat bottom organisms down among the weeds before they reach an area where they become available to trout. This suggests that competitors may be separated even a step further than that pointed out by Solomon and we can include among the basic mechanisms of competition, the consumption by one or more organisms of something in short supply before it reaches a potential habitat where it would become available to another organism or group.

Larkin (1956) has commented on the vague demarcation of ecological zones in freshwater environements and the lack of sharp demarcation of fish faunas within these zones. "Freshwater communities would seem to be characterized by more breadth than height in the pyramid of a food chain; a complexity in horizontal organization." No better example of this statement could be imagined than the present one. Both shiners and trout eat virtually all the organisms available in the lakes - including each other. At different times of the day and year fish may be found leading either a pelagic, a shoal, or a bottom existence with their food habits varying accordingly. The feeding habits of rainbow trout and shiners (Lindsey, 1950a and b, and others) in various lakes, reveal an enormous range of dietary tolerance. The ability of both species to change their distributions and diets tends to reduce the intensity of competition. While amphipods have been severely depleted in Paul Lake, both trout and shiners have replaced them in their diets. That this new diet is not as satisfactory as the old one for young trout may be inferred from their slower growth rate - but large trout now grow faster than beofre as a result of feeding on shiners (Crossman, 1957). Here the difference in abilities of large and small fish to change their diets results in completely opposite effects of competition within different size groups of the same species.

In conclusion, the present study indicates that competition in nature may be continually shifting in intensity and emphasis. The physical and biological environment and the distribution and behaviour of competitors may be in states of continual flux in which case the "niches" of the competitors cannot be considered constant as is a basic assumption in all theoretical models. Hence natural competitive relationships can be considerably more complicated and variable than situations described by the most elastic of existing models.

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