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Stream Fertilization

Huntsman

Fertility and Fertilization of Streams

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ABSTRACT

Streams in a rather rocky and barren region in Nova Scotia were found to have almost no algae and fish except in relation to farm operations. Placing of bags of chemical fertilizer along the shore was followed in a year or two by increased quantities of algae and fish downstream, the maximum effect only 150 yards away. It is concluded that fertilizing materials are held locally in flowing water in relation to finely divided bottom material, as with soils.

Certain streams draining into Grand (Shubenacadie) lake, Nova Scotia, at the head of the bay of Fundy, were observed in 1944 to show striking differences in numbers of marked yearling salmon in September after having been planted rather uniformly with these in June. Factors found elsewhere to be correlated with survival of young salmon did not seem to explain the differences observed. There were similar differences in numbers of native young salmon and of other kinds of fishes.

The two streams showing the greatest contrast were the lower part of the Beaver river with rather many fish and the lower part of the Upper Rawdon river with no fish at all found in September. The lower part of the Beaver river runs through a farm, and abundance of fish seemed to be related to the farm operations. It is crossed at two points by fords, the lower of which is for traffic directly downhill from the barn. While some fish were found related to the upper ford and to a watering place for pastured cattle somewhat farther up, the greatest concentration of fish was just below the lower ford with scarcely any fish just above. For experimental purposes, an attempt was made on August 25, 1947, to seine out all the fish in this part of the river. The numbers of fish of various kinds and sizes obtained within 125 yards (1 yd. = 0.91 m.) downstream and 100 yards upstream from the lower ford were as given in the table below.

Table I. Numbers of fishes of different sizes obtained on August 25, 1947, in the Beaver river, N.S., within 110 yards above and 125 yards below ford from a barn.

	Length in centimetres					
Kind	2.5-4	4-6	6-10	10-14	14-22	22-33
	Above ford					
Salmo.....		3	1	1		
Anguilla....					3	
	Below ford					
Salmo.....		33	7	4	3	
Anguilla....					3	4
Catostomus .	11	72	24			
Fundulus...	8	2	8			
Cyprinidae .	155	29	3			

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The number of fish taken below the ford was 366 while only 8 were taken above, which was a very striking contrast.

The difference in growth of algae was equally striking. Masses of green filamentous algae were generally present on the bottom and coating the stones below the ford, but none were found above. There was, therefore, a considerable production of both plants and animals below the ford, but no evidence of any particular production above, since the few salmon and eels found there may well have moved into that section of the stream.

Beaver river discharges into Beaverbank lake, as do also several smaller streams that drain the land for about four miles (1 mi. = 1.6 km.) along the Beaverbank road that has a number of dwellings and partial farms. The water from Beaverbank lake flows down the Upper Rawdon river, which is half-a-mile long. Although the lower half of this river was barren of fish, there were some in its upper half, but they decreased in number from the lake outlet down as if they were related to food carried out of the lake. There are neither dwellings nor cultivated land along this river and human traffic is confined to a wood road along one side. With any fertilizing effect from above held by Beaverbank lake, the Upper Rawdon river seems not to have been fertilized by man until now.

Anadromous fishes have been considered to carry up from the sea fertilizing materials that are set free when spawning fish die. Cascades halfway up the Upper Rawdon river are said to be the upper limit for ascent of gaspereaux (*Pomolobus*) and bass (*Roccus*). It would seem that neither these nor any other migrating fish, such as eels (*Anguilla*), suckers (*Catostomus*), white perch (*Morone*), salmon (*Salmo*), trout (*Salvelinus*) and lampreys (*Petromyzon*), all of which are to be found in these waters, have served to fertilize the river.

The surrounding country is of Cambrian or Precambrian age. It is very rocky and the rocks are gold-bearing and of quartzite and slate (Goldenville and Halifax formations). The nearness of the city of Halifax (15 to 20 miles) is mainly responsible for such little cultivation of the land as is done by those who live along the roads that lead from the city to richer districts.

There is little spring water, but a great many lakes. The Upper Rawdon river drains an area of 37 square miles (1 sq. mi. = 2.59 sq. km.), of which 2¼ square miles are made up of lakes. The hills, in which the area abounds, rise to from 300 feet to 700 feet above sea level (1 ft. = 0.3 m.), with lakes nearly 500 feet up. Beaver river drops 30 feet in about a mile and Upper Rawdon river 46 feet in half-a-mile. These are fairly swift streams with successions of pools and rapids. However, the volume of flow varies greatly with rainfall. In a 17-year period (1921 to 1938), the mean flow of the Upper Rawdon river was 104 cu. ft. per sec. (1 cu. ft. = 0.028 cu. m.), the range being from 0.1 to 1,450 cu. ft. per sec. (Chisholm 1942). The monthly mean has been as high as 356 and as low as 0.5 cu. ft. per sec. In 1946 the means for July and August were 0.9 and 0.7, yet the July mean has been as high as 137 and the August mean as high as 145 cu. ft. per sec.

In 1945, it was decided to test the effectiveness of fertilizing the lower part of the Upper Rawdon river. Dr. M. W. Smith and Dr. S. A. Beatty, who had had experience in fertilizing lakes and ponds, were consulted. Inquiry failed to reveal that any attempt had ever been made to fertilize a stream. It was feared that

the fertilizing materials might merely be carried down into the lake below. Therefore, gradual introduction of the fertilizer seemed desirable. Circumstances were against taking any more than the simplest measures. Two methods were used. On July 24, 375 lb. (1 lb. = 0.45 kg.) of "C. I. L. 4-12-6" were scattered over a small area of the river bank below the cascades and a 125-lb. bag was placed upright in a pool against the bank a short distance down. On September 20, bottom samples were taken and given to Dr. F. P. Ide for assessment of the insect larvae. The results indicated that the fertilization, no matter of which sort, had been effective, particularly at the lower end of the stream, in producing a rather large population of small insect larvae of kinds that live upon locally grown plants. Circumstances did not permit very accurate assessment. The discharge during this period had varied from 2.3 to 14.8 cu. ft. per sec. On September 5, 1946, a brief attempt was made to discover any effect in occurrence of fish. No fish were found except at the head of the pool in which the bag of fertilizer had been placed, and there a dozen small cyprinids, a yearling sucker and a 9-in. (22.9 cm.) eel were taken. This seemed at the time too local an effect to be properly referable to the fertilization.

In 1946, on July 3, a second fertilization was carried out by placing three 125-lb. bags of "C. I. L. 4-12-6" on one side of the pool at the foot of the cascades, one under water, one at the water's edge and one on the bank to be covered by high water. On August 12, 1947, no trace was found of the lowest bag, there were slight remains of fertilizer from the middle bag and the fertilizer of the highest bag was largely still in place and covered with a heavy growth of algae. Cursory seining gave the first native salmon to be found in this part as well as other fish (eels and Cyprinids), and at all places tried. On August 22, 203 seine hauls were made over the quarter-mile stretch from the cascades to the river mouth. Salmon, eels, suckers, *Fundulus* and Cyprinids were taken. The number of fish per 10 hauls was graded, being greatest within 150 yards downstream from the points of fertilization in 1946 (3.75; 7.5; unseined; 4.14; unseined; 2.9; 2.5).

A possibly better measure of abundance is the number of fish taken per 100 yd. on the basis of 6 hauls per 10 yd. This gives a similarly graded distribution, the numbers for successive sections being: 23; 45; unseined; 25; unseined; 17;15. This result is illustrated graphically in figure 1. Masses of filamentous green algae were conspicuous at this time, and most were found where there were most fish. There was a definite relation of algae to relatively quiet water with silt bottom. In the extreme case, a solid bank of algae from bottom to surface stretched across the 11-yd. mouth of, but not inside, a side water with mud bottom and growth of pickerel weed and other aquatic plants. The algae were to be found all the way to the mouth of the river and for some distance along the adjacent lake shore.

Since farm operations seemed to have fertilized Beaver river effectively, a farm fertilizer was used. It is stated that "C. I. L. 4-12-6" contains 4 lb. total nitrogen, 12 lb. available phosphoric acid and 6 lb. water soluble potash per 100 lb. The nitrogen is obtained from ammonium nitrate, ammonium sulphate and cyanamide. The available phosphoric acid is obtained from superphosphate (20% P_2O_5). The potash is obtained from potassium chloride. The conditioner

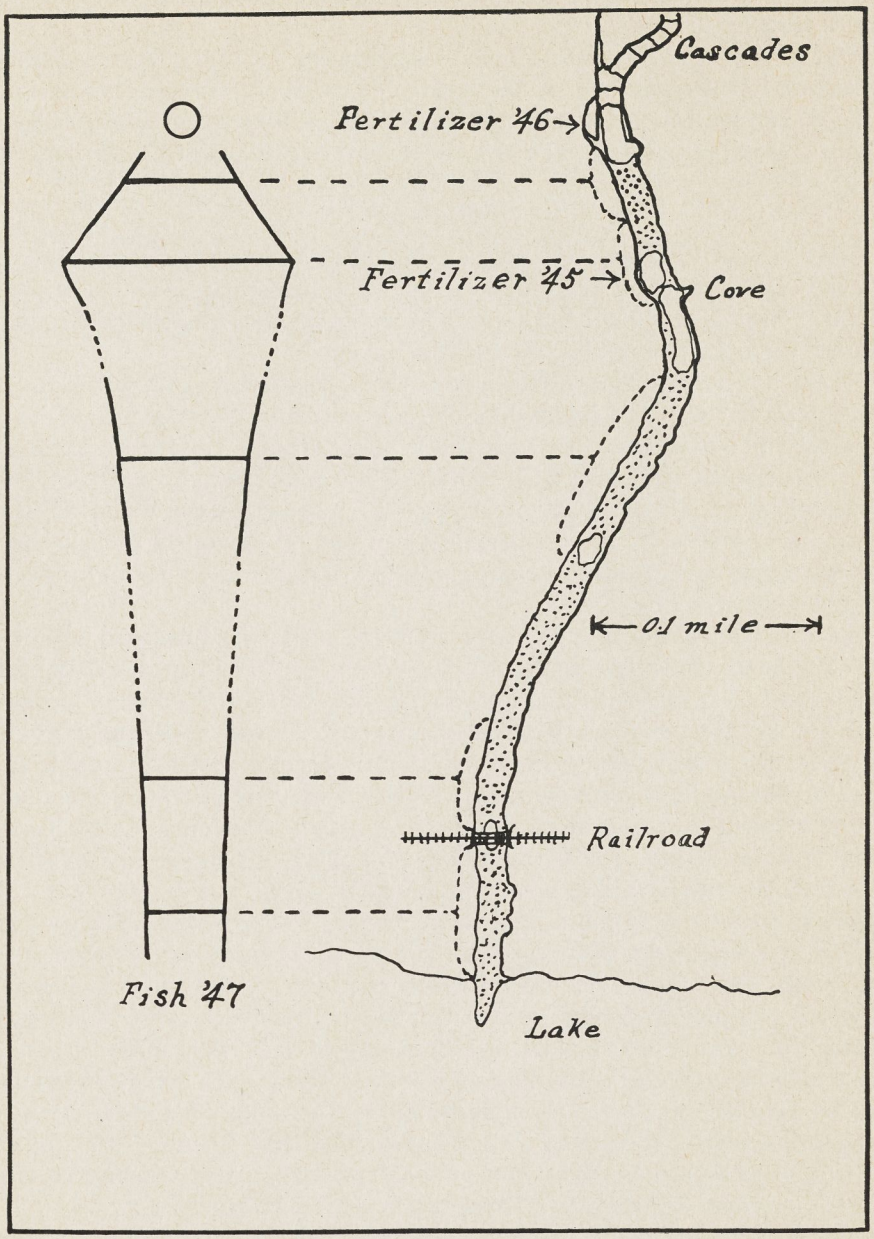

FIGURE 1. Lower part of Upper Rawdon river, N.S., on right, showing where fertilizer was placed in 1945 and 1946 and what parts were seined in 1947. Diagram on left shows relative abundance of fish as represented by numbers per 100 yds. with 6 hauls per 10 yds.

is dolomitic limestone—approx. 40 to 45% magnesium carbonate and 45 to 50% calcium carbonate.

The flow of the river subsequent to fertilization in 1946 was very slight for three months (less than 7 cu. ft. per sec. for 82 days) and ranged from as low as 0.1 cu. ft. per sec. in August to a fall high of 255 in September, a winter high of 1,100 in December, a spring high of 1,190 in May and down to 1.2 by Aug. 22.

DISCUSSION

That the fertilization would have some effect was to be expected, but that the chief effect would be such a short distance downstream was not expected. The experiment and the conditions with farm operations agree in showing a pronounced effect just below the point of application.

There is a welter of possibilities as to how the effect was produced. Experimental analysis, for which no opportunity presents, is much to be desired in order to reveal what substances were responsible, in what state they were transported and in what state they were held locally. Were they in solution or not? Were they in solid form, adsorbed on bottom material, chemically combined with other substances, or taken up by organisms? It can merely be stated that significant plant nutrients were fixed by bottom material, but not so firmly as to prevent their being absorbed by plants.

An outstanding point is the demonstration of remarkably local fertility in shallow streams. This means that fertility is not dependent upon substances in the flowing water, but upon the bottom material. It is a soil problem in spite of the steady leaching to which that soil is subjected. As with soils, the chief effect was where there was most very finely divided bottom material presenting an immense solid-liquid surface for action. The striking illustration of this was the bank of filamentous green algae, nearly a foot high, extending from bottom to surface and for 11 yds. across the mouth of a short, triangular side-water only 150 yds. below the fertilizing point. The bank of algae was so firm that a frog was sitting on the top. It was neither in the flowing water of the stream nor inside the sidewater, but where they joined and where silt brought down by the stream would settle. That these algae merely rested on the bottom is worth noting, since the rooted aquatics growing in the mud inside the sidewater were in a different category. The way in which plant nutrients may be held very locally by soils has been shown by long agricultural experiments. "Even when heavy dressings of dung are annually applied at Rothamstead there is, after fifty years, no appreciable enrichment of the subsoil in nitrogen (Table 40)" (Russell 1937, p. 223). This was found also for application of ammonium salts. The purification of sewage by land treatment and the filtration of water show similar effects.

It may be presumed that this picture would not have developed, or at least would not have been so clear, if the region had not been so barren of nutrient materials for plants. This barrenness seemed to provide a favourable background for experiment.

Attention may be called to the favourable conditions that streams present for experiments in fertilization. On the one hand, the effects will be only down-

stream from the point of application, leaving upstream water to serve as a control. On the other hand, there is the ready possibility of separating the action of the water and of varied bottom materials.

ACKNOWLEDGEMENTS

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REFERENCES

CHISHOLM, K. G. Atlantic drainage . . . 1936-37 and 1937-38. *Dom. Water and Power Bur., Water Res. Pap.* **83**, 1-66, 1942.

RUSSELL, E. J. Soil conditions and plant growth. Ed. 7, 1-655, London, etc., 1937.

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A TEST OF THE SOLUNAR TABLES

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Abstract

A study was made to determine whether the anglers fishing during solunar periods were more successful than those fishing between solunar periods. The raw data consisted of boat-rental ticket stubs on which the anglers of Loch Raven, Baltimore County, Maryland, were requested to enter their catches and on which were stamped the hours during which they used the boat. Stubs showing 2 and 1/2 through 4 and 1/2 hours fishing time were used for the study, but these only when the times stamped totally encompassed a solunar period or were entirely between two periods. The data, representing 1538 fishing trips were divided into classes according to anglers fishing during:

(1) a "major" solunar period, lasting about two hours;
(2) a "minor" solunar period, lasting about one and a half hours; and
(3) the interval between solunar periods.

The anglers of the first group spent 51 percent of their time during a "major" period, the second group spent 40 percent during a "minor" period, and the third group 0 percent during a solunar period. It was reasoned that, if fishing were significantly better during solunar periods than during the intervals between periods, the average solunar period angler would catch an appreciably greater number of fish per unit of effort than the average inter-solunar period angler.

The test showed that fishing in general was not demonstrably better during solunar periods. Crappies and bass seemed to be taken less readily and sunfish, yellow perch, and carp more readily during solunar periods. Apparently the catchability of catfish was not affected one way or the other.

Introduction

The Solunar Theory, which says that the activity of fish and game is affected by the position of the sun and moon, was first propounded in 1935 by John Alden Knight, an outdoor writer (see Knight, 1935a). Disclaiming credit for the original observations which gave rise to the theory, he stated only that he had improved upon and formulated a theory that had long been held by market hunters and some tribes of American Indians (Knight, 1950). He told of being introduced to the crude hypothesis by a fishing guide at Lake Helenblazes, Florida, about 1926, but found that, in its original form it would not hold outside Florida, and he was forced to make modifications to fit his new observations. Once having arrived at the "correct" explanation, he spent four years testing before publishing his theory. Unfortunately, Knight (1935a) did not present the data upon which he based his conclusions.

The theory evoked widespread interest, according to its author, and 1000 booklets giving the best fishing times (the Solunar Tables) were printed to satisfy the demand of

curious sportsmen (Knight, 1952). The demand increased until, to quote Knight (1950), "Today, instead of there being only a few thousand readers of the SOLUNAR TABLES, the schedules of Solunar Periods are read literally by the millions. Foreign editions are published in Canada, France, Germany, England, Denmark and South Africa. The novelty of 1935 is now a fixture." The Solunar Tables also, as of October 1, 1952, appeared as a syndicated feature in 91 American and Canadian newspapers.

There have been other attempts to commercialise the prognostication of fishing conditions. Most notable of these is the "Coble's Fisherman's Calendar" (Coble, 1952), which shows, by means of fish symbols, whether fishing will be good, bad, or indifferent on any day of the year. In addition, it indicates the time of day, to the nearest minute, when that day's fishing will be the best. Its prophesies are based on the phases of the moon (Lincoln, 1951) and would seem to be similar, fundamentally, to Knight's theory. A careful comparison, however, shows that they do not agree exactly on the best periods for fishing, Coble's best times occurring from 1:15 to 2 hours after the beginning of one of Knight's major periods. Coble's calendar is widely used for advertising purposes (Galleghar & Burton 1952), but there are at least two other systems used on advertising calendars (Distributors Advertising Promotions, 1953) (Cortland Line Co,, 1953) which do not agree with each other or with Coble. Unfortunately, no information is available on the theories behind these latter systems, but probably they do not differ radically from that of the former. One other indicator of fishing conditions is worth mentioning. A fishing tackle company, as an advertisement, and it is hoped, with tongue in cheek, presents a small blotter on which is printed a fish with an eye that changes color with changes in humidity (Enterprise Mfg. Co., 1952). When the eye is blue, fishing is supposed to be good; when it is red, fishing is poor.

Apparently there has been no critical examination of any of these prediction systems, but in recent years there has been some testing of certain widely held beliefs about fishing and the movements and feeding of fish. One of these studies was carried on in Illinois by Dr. David H. Thompson, about 1946 (correspondence from Dr. George W. Bennett, Urbana, Ill.). Thompson, using the records of a private fishing club and the records of nearby weather stations for a twelve-year period, could find no correlation between the quality of fishing and the behavior of the barometer. Apparently, he did not publish the results of his study.

Parsons and Sieh (1950) working with gill nets in Cedar Lake, Iowa, found that "No correlation could be detected between the periods of activity of the fish and barometric changes, wind, sky cover, or solunar periods.", although they did find that walleyes, Stizostedion v. vitreum, and yellow bass, Morone interrupta, were more active at dawn and dusk than at other times of the day.

E. L. Cooper (1953) reports that a study of fishing on the Pigeon River in Michigan showed that trout were as easy to catch when the barometer was falling as when it was rising. Phases of the moon had no effect on fishing but there was a correlation between water temperature and the rate at which anglers caught trout.

Courtemanche (1953), using hoop nets, gill nets and wire traps in Lake Lauzon, Quebec, found that "White Suckers entered nets and traps much more freely when the moon was full, but showed no effect one way or the other as the barometer changed."

The test reported here was engendered by an excellent opportunity to examine virtually complete anglers-catch records from a Maryland reservoir. These records

were gathered for the purpose of ascertaining total harvest of fish and the use of them for testing the Solunar Tables was of a secondary nature.

The Solunar Theory

The Solunar Theory, as explained by Knight (1935b) is, "Other conditions not being unfavorable, fresh-water fish tend to feed more readily during 'solunar periods' than at other times. The solunar period for any spot is the period, usually lasting about two hours, when the pull of the sun and the moon, as exerted at that point, would create either high or low tide, if that point were, in fact, on a seacoast." In other words, fish bite best on the turn of the tide, even where no tide is discernible.

Fish are allegedly able to determine solunar periods by perceiving slight variations in buoyancy. Again quoting Knight (1935b), "A short time ago a mining engineer told me that the bulk of the cave-ins of mine shafts and tunnels have been coincidental with solunar periods. It is not unreasonable therefore to assume that a fish, suspended as he is in the water in perfect balance between the pull of gravity and the push of buoyancy or water displacement, should be able to feel this pull without any difficulty. It is his constant job, if he wishes to maintain this state of balance, to inflate or deflate the air sac which lies along his backbone in order to compensate for the continual variations in atmospheric pressure. It must require a certain amount of correction also to meet the altering intensity of tidal or solunar conditions four times each day. Thus he is able to determine the solunar periods which are also his feeding periods."

Solunar periods are of two kinds, labeled "major" and "minor", corresponding to low tide and high tide. respectively. The major periods last about two hours while minor periods "last from an hour and a half to forty-five minutes" (Knight, 1953). Because of rotation, these periods sweep around the earth in an east-west direction at the rate of one circuit in twenty four hours and fifty minutes. Thus at any one place the solunar periods appear about fifty minutes later each day. Figure 1 shows the progression of solunar periods for the area under test for the first ten days of June 1952, together with the interval of time between any two periods.

Method of testing

Insofar as can be determined, no test of this theory directly on angling has been reported in fishery biology literature. This is perhaps because of the difficulty of setting up a bias-free experiment. The most obvious method of testing is to keep records of one's own fishing success, listing the exact time at which each fish was taken, but such a test would be subject to the criticism that one's fishing ability might vary according to his convictions concerning the Solunar Theory. Such objections would be valid in any case where the data taker was aware of the reason for keeping records. A further difficulty of such method would be the gathering of sufficient data to cancel fluctuations due to randomness and to such factors as weather and diurnal fish activity.

A valid test then, would have to obey the following rules: (1) The angler must be unaware of the reason for reporting his catch; (2) there must be enough fishing hours recorded to give statistically significant results; and (3) the test must run over a period long enough to cancel out effects of weather, diurnal activity, temperature changes and all the other factors which conceivably might have some influence on the rate at which fish take the hook.

The raw data for the present test consisted of the catch records of 1538 fishing trips on Loch Raven, Baltimore County, Maryland (see Table 1), during the 184-day fishing season of 1952. This amount of data is felt to be adequate and the period covered long enough for a fair test. Bias was forestalled by the simple expedient of not informing anyone of the experiment until all the data had been collected. In fact, it did not occur to the author to conduct the test until about half way through the fishing season and much of the data had already been turned in. After that time no one connected with the gathering of the records was informed of the decision to test the theory. If there is any weakness in the data it is the fact that errors in the original records were not completely controlled, but as any error had an equal chance of falling in favor of or against the theory, it would not mar the statistical significance of the results.

Table I
Descriptive data of Loch Raven, Baltimore County, Maryland

Location. . . . .about 10 miles north of downtown Baltimore	
Area.	2500 acres
Maximum depth	69 feet
Average depth . . . . . approx.	40 feet
Total alkalinity	12 ppm
pH	7.0
Thermocline . . . . . .poorly developed, at about	30 feet
Oxygen below thermocline. . . . . .4 ppm to 0 ppm at bottom	
Water level . .fluctuates irregularly according to rainfall	
Average draw-down . . . . . less than	2 feet
Maximum draw-down recorded . . . . . in 1930	6½ feet
Type of lake. . . . . .water-supply reservoir	
Age . . . . . dam built in 1923	
Fish reported taken on 10,136 fishing trips in 1952	
765 Smallmouth Bass*	
189 Largemouth Bass	
36,421 Crappies (both White and Black)	
3,009 Sunfish (Bluegill, Pumkinseed, Yellowbelly and Green)	
413 Yellow Perch	
1 Walleye	
1,129 Catfish (Brown Bullhead and White Catfish)	
6 White Suckers	
564 Carp	
33 Eels	
Number of fish harvested per acre	17.0
Pounds of fish harvested per acre	4.6
Total hours fished.	55,859
Average hours fished per angler	5.8
Number of fish harvested per man-hour of angling	0.76
Number of fish harvested per fishing trip	4.0
Portion of unsuccessful fishing trips	48%
Pertinent angling regulations:	
Fishing season in 1952 . . . . . May 3 to Nov. 2	
Bass season . . . . . opened June 1	
Legal lengths, black bass . . . . . 10 inches	
Creel limits, black bass . . . . . .10 per day	

* Nomenclature follows American Fisheries Society recommendations

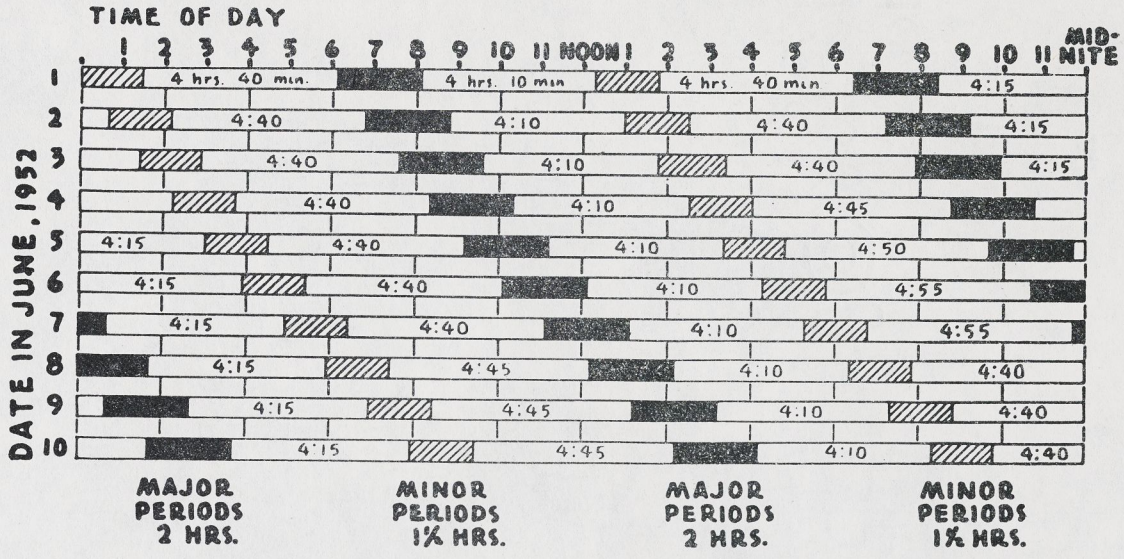
Since fishing was first allowed on Loch Raven it has been under the control of the League of Maryland Sportsmen, a federation of rod-and-gun clubs. The League maintains one boat livery with a supply of 75 boats; in addition, provision is made for the

beaching of privately-owned boats. As fishing is not permitted from banks or bridges and there are no cottages on the lake, all fishermen must pass through the boat livery area. It is estimated that 95 percent of the total fishing is done by people who rent boats, and it is from this group that the data for this study has been drawn.

All boat renters were given a ticket stub, as a receipt for their boat deposit, to which was attached a form for recording their catch. The front of the form contained blanks on which to enter the number and kind of fish taken and the number and kind of fish taken but returned to the water. The boat renters were also expected to record the number of anglers in the boat, their place of residence and the lengths of all bass caught. Stamped on the back of the form was the time at which they checked out the boat and the time at which they returned it; the stamping being done by the boat livery operators, using a hand-set circular time stamp. The form, with a typical entry, is reproduced in Figure 2. Very few of the anglers (about 0.15%) failed to return their forms. The portion of anglers failing to fill them out, or doing it incorrectly was much larger, but the livery attendants checked each form as it was turned in and were able to rectify most errors and omissions.

The ticket stubs were divided into three groups, designated "major period", "minor period" and "blank period": the first of these was composed of those forms on which the stamping indicated that their boats had been checked out for a time which entirely encompassed a major solunar period; the second group which covered a minor period; and a third which was entirely within the interval between two periods. The name "blank period" was adopted because it is less cumbersome than the more appropriate term "interval between solunar periods". Because the greatest length of time that a boat containing blank period fishermen could be rented (under the conditions imposed) was 4 hours and 55 minutes (figure 1), and allowing ten minutes for checking out and getting to its fishing site and another ten minutes for returning, the maximum angling time for a blank period fisherman was considered to be 4 hours and 35 minutes. Therefore, in order to make valid comparisons, <u>all</u> records from boats regarded as fishing more than this time were discarded. At the lower end of the scale, all records from boats rented less than 2 and 1/2 hours were discarded because that was the minimum time for which an angler could check out a boat and fish entirely over a major period (again allowing ten minutes for coming and going). All assumed fishing times were then rounded-off to the nearest half hour. This selection reduced the data to records from 2 and 1/2 through 4 and 1/2 hour anglers, about 15 percent of its original volume.

To illustrate the method of data selection, figures 2, 3 and 4 are presented. The form shown in figure 2, which is a photograph of an actual ticket-stub form, was interpreted in this manner; the boat was checked out about 8:20 a.m. and fishing was considered to have begun about 8:30 a.m. It was checked in again at 11:45 a.m. so fishing stopped at about 11:35 a.m. The first solunar period that day began at 6:35 a.m. and lasted until 8:05 a.m. (a minor period) while the next period did not start until 12:55 p.m. Therefore the boat contained blank period fishermen. Figure 3 is a reproduction (slightly modified) of the forms used in the primary study for the determination of fishing pressure patterns, and on which the fishing period of each party of anglers is represented by a horizontal line. The solunar periods for the daylight hours have been shaded in for illustrative purposes. The records represented by lines number 10, 13, 15, 20, 21 and 22, while of the appropriate length, had to be discarded because they start or stop within a solunar period. Figure 4 shows the relation of the solunar-test sample to the Loch Raven data as a whole.

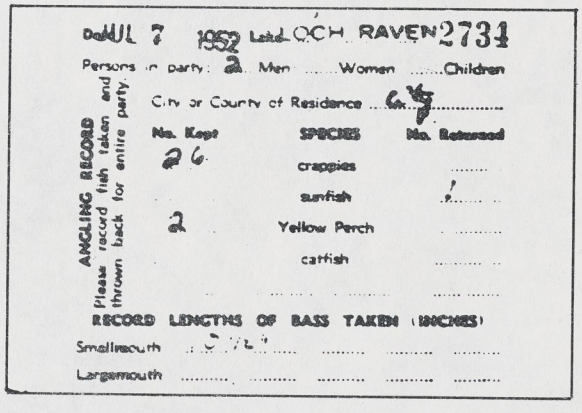


POSITION AND DURATION OF SOLUNAR PERIODS WITH TIMES BETWEEN, FIRST TEN DAYS OF JUNE, 1952

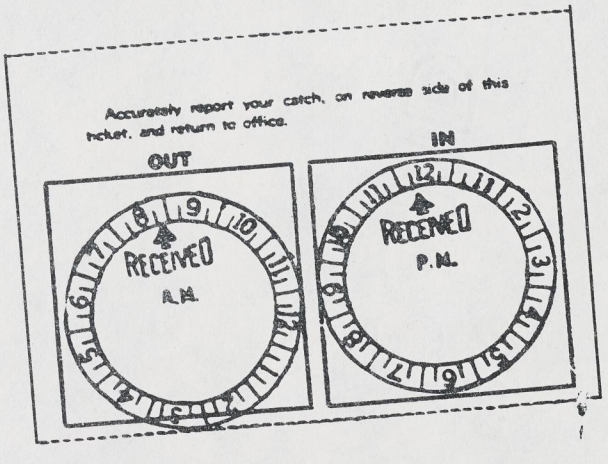
DATA FROM JOHN ALDEN KNIGHT "THE SOLUNAR TABLES" 18th ED.

FIGURE 1

Front

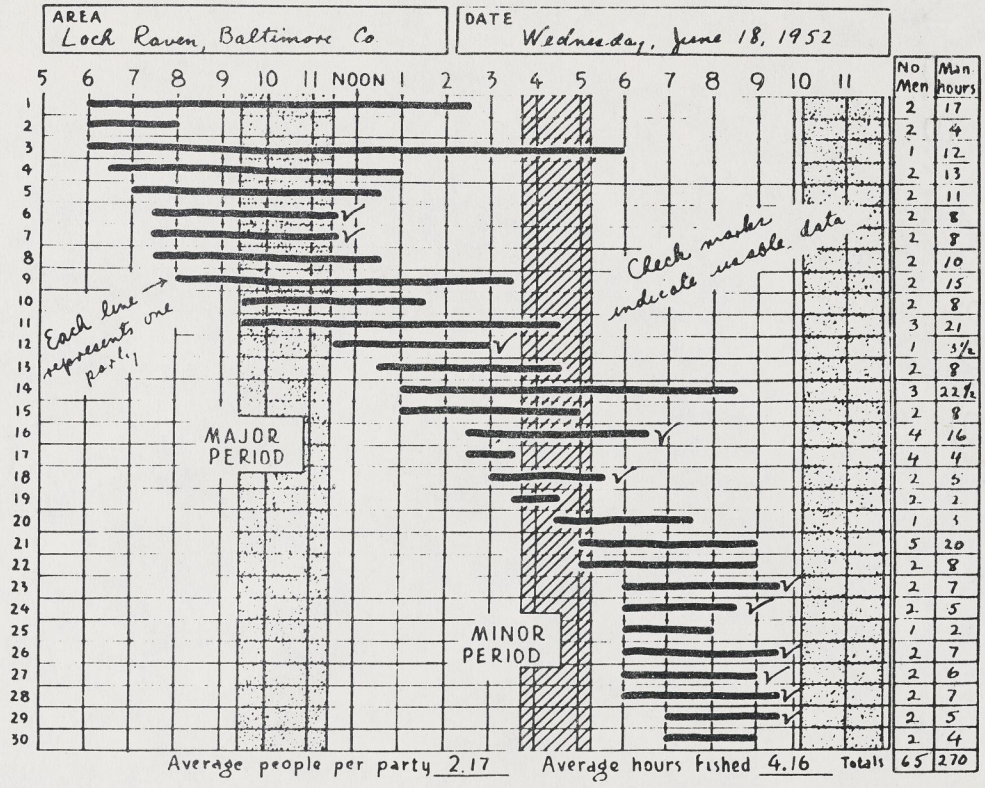


Back



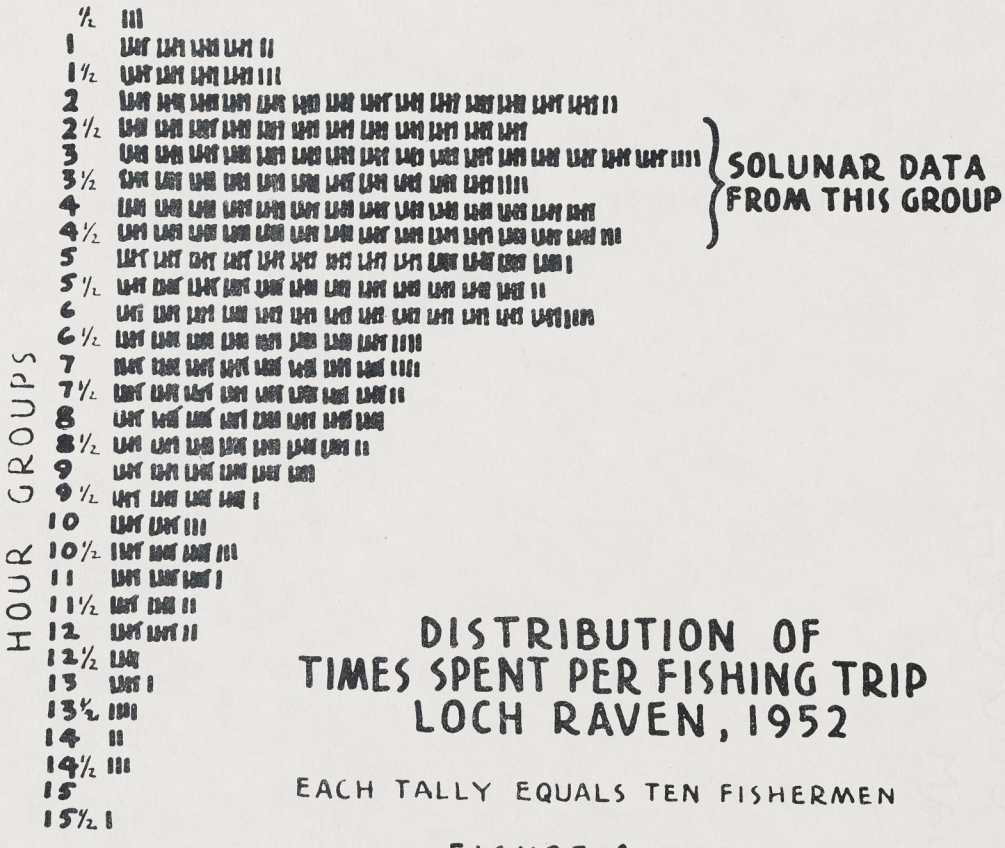
Example of the ticket stubs used as raw data for test of Solunar Tables

FIGURE 2



ANALYSIS FORM, MODIFIED, SHOWING METHOD OF SAMPLE SELECTION

FIGURE 3



DISTRIBUTION OF TIMES SPENT PER FISHING TRIP LOCH RAVEN, 1952

EACH TALLY EQUALS TEN FISHERMEN

FIGURE 4

The selected data was analysed by period-groups, by length-of-time groups and by months in the same manner as was the data from the primary study. It was tested in every way available to locate possible bias for or against the Solunar Theory. The opportunity for such testing was very limited, but there was little to indicate relevant bias in the solunar sample. For instance, the portion of total fishing effort expended in each month of the season for the solunar-test sample was quite similar to that of all the Loch Raven data, thus:

	Solunar sample	All Loch Raven anglers
4 weeks in May	20.4%	18.8%
4 weeks in June	28.0	26.9
5 weeks in July	25.9	23.5
4 weeks in August	12.3	12.6
5 weeks in September	10.3	13.4
4 weeks in October	3.1	4.9

The solunar sample percentages were a little larger early in the season and a little smaller after August, because of the greater proportion of short time fishermen early in the season.

To ascertain whether there was a reasonable distribution of anglers over the various subdivisions of the solunar sample, the expected number of anglers in each category was calculated. This was accomplished with the following procedure:

(a) The number of possible intervals (by half-hour steps) in a 24-hour day in which a fisherman of each hour-period category could fish was counted, and their ratios within each hour-grouping were established. Example - On June 1, there were two possible times at which a 2½-hour major-period angler could start his fishing trip; 6:00 a.m. and 6:00 p.m. (see Figure 1). Minor-period anglers fishing for 2½ hours had 4 possible starting times, 11:00 and 11:30 the night before, 11:30 a.m. and 12 noon. Blank-period 2½-hour anglers had 16 possible positions, starting at 1:30, 2:00, 2:30, 3:00, 3:30, 8:30, 9:00, and 9:30 a.m. and 2:00, 2:30, 3:00, 3:30, 8:30, 9:00, 9:30 and 10:00 p.m. The ratios of possible positions in the 2½-hour-group, then, was 2:4:16 (major 2: minor 4: blank 16).

(b) On the basis of 1538 fishermen (the solunar sample) the expected number of anglers in each hour-group was calculated, using the ratios of hour-groups within the Loch Raven angling population (as indicated by figure 4). Example - For Loch Raven, the 2½-hour group contained 19.4 percent of the fishermen in the 2½ through 4½-hour groups. This percent (19.4) of 1538 anglers is 266, the expected size of the 2½-hour group.

(c) The expected number of anglers in each hour-group was divided according to the ratios found by step (a). Example - The 266 expected anglers of the 2½-hour group, when portioned by the ratio 2:4:16 becomes 24:48:194, after rounding off.

The expected number of fishermen in each hour-period category together with the observed number is as follows:

Hour Group	Major period Expected	Major period Observed	Minor period Expected	Minor period Observed	Blank period Expected	Blank period Observed	Totals Expected	Totals Observed
2½	24	26	48	41	194	180	266	247
3	68	50	102	101	204	202	374	353
3½	72	53	96	121	96	110	264	284
4	113	111	141	116	56	71	310	298
4½	135	176	162	146	27	34	324	356
Totals	412	416	549	525	577	597	1538	1538

With the exception of the 4 and 1/2 hour major period category, the differences between expected and observed are not statistically significant (99% level), which indicates there was no marked preference on the part of the Loch Raven fishermen to fish according to the Solunar Tables. The significant discrepancy in the one category is perhaps due to sampling variations and probably is not important.

The type of fishermen, as far as the data allows comparison, shows, again with an exception, no essential difference between solunar groups and the Loch Raven fishermen as a whole, thus:

	Major Period	Minor Period	Blank Period	Loch Raven
Men	76.7%	78.3%	73.4%	78.0%
Women	10.3	9.7	9.9	11.0
Children (under 15)	13.0	12.0	16.7	11.0

The difference between the percent of children fishing during the blank periods and the percent that would be expected if the blank period sample were chosen at random from the Loch Raven fishermen is explained in this manner: parties with children tend to fish a shorter average time than those without, and as the solunar sample was chosen from the shorter-time fishermen, a high proportion of children is to be expected. Among the three solunar-period groups, the blank period contains the most anglers in the lower hour-groups (see preceding table).

The solunar-sample fishermen came from the same places as did the Loch Raven fishermen, and in roughly the same proportions:

	Major Period	Minor Period	Blank Period	Loch Raven
Baltimore City	67.7%	67.9%	58.2%	62.2%
Baltimore County	29.4	29.9	38.6	32.8
Other Maryland	1.3	1.7	1.9	2.3
Pennsylvania	1.1	0.4	0.6	1.3
Other out-of-state	0.5	-	0.7	0.4

The residence proportions of the blank period fishermen are significantly different from the others, but this fact does not seem relevant to the test.

Results

The 1538 fishermen of the solunar-test sample fished for a total of 5464 hours; an average of 3.56 hours. Broken down by period groups:

416 major period anglers fished 1636 hours, 60.9% (832 hours) during a solunar period.
525 minor period anglers fished 1950 hours, 40.4% (788 hours) during a solunar period.
597 blank period anglers fished 1878 hours, 0.0% (0 hours) during a solunar period.

The number of fish taken (all species), as reported by the anglers of each hour-period category was:

Hour group	Major Period	Minor Period	Blank Period	Hour-group totals
2½	1	14	442	457
3	190	168	278	636
3½	153	193	185	531
4	308	494	131	933
4½	287	264	71	622
Period totals	939	1133	1107	3179

There was a widely variable number of fishermen from one hour-group to another and from one period-group to another, and in order to make the catch figures validly comparable, they must be reduced to a common denominator. The obvious denominator is, of course, fish taken per man-hour of angling. This is the key of the test -- the key which determines whether the Solunar Tables were able to indicate the best fishing times on Loch Raven in 1952.

The following table lists the number of fish harvested per man-hour of angling, by hour-groups and by solunar-period groups, from Loch Raven during the fishing season of 1952:

Hour-group	Major Period	Minor Period	Blank Period	Hour-group averages
2½	0.02	0.14	0.98	0.74
3	1.27	0.55	0.46	0.60
3½	0.82	0.28	0.48	0.53
4	0.69	1.07	0.46	0.78
4½	0.36	0.40	0.46	0.39
Period averages	0.57	0.58	0.59	0.58

Confidence limits for the various entries in the preceding table were not calculated because of the peculiar nature of the curve formed by the frequency distribution of anglers in fish-per-man-hour classes. The curve resembles a hyperbola in which a few extreme values may materially affect the mean. Means of small samples from such a curve would normally show a much wider variation than comparable samples from normal or Poisson distributions.

Another measure of the "goodness" of fishing is the ratio of successful fishermen to the whole, defining a successful fisherman as one who catches at least one fish. In general, this is not as good a reflection of fishing conditions as is fish-per-man-hour, because a catch of one fish carries the same weight as a catch of a hundred. Never-

theless, it is a measure of the recreational value of a body of water so it has considerable value in some situations. In this case it indicates that major-period fishermen were, on the average more successful than the blank period fishermen. In the table that follows, the percent of successful fishermen for each hour-period category is listed:

Hour group	Major Period	Minor Period	Blank Period	Hour-group averages
2½	3.8%	21.9%	30.6%	26.3%
3	48.0	36.6	30.9	34.9
3½	34.0	34.7	38.2	35.9
4	45.1	40.5	40.8	42.3
4½	46.0	41.1	44.2	43.8
Period averages	41.8%	37.2%	34.1%	37.2%

There are only about 1.3 chances out of a hundred that the difference between the major-period and the minor-period averages is a chance difference due to sampling (the formula for calculating such probabilities is given in Arkin and Colton, 1939). The probability that the difference between the major and the minor period averages is a chance variation is about 0.147, or, 14.7 chances out of a hundred, and between the minor and blank periods it is 25.0 chances.

Although it is not necessary to the test, the breakdown of fish-caught by species is of some interest. There was no way of determining the number of fishermen who were fishing for bass, or for crappies, etc., but assuming that the various types of fishing were proportionately very much alike in the three periods, some significant differences are shown in the catch between periods. The following table shows the breakdown of the catch of each period, by species:

	Major Period	Minor Period	Blank Period	Loch Raven
Smallmouth Bass	0.7%	1.5%	1.6%	1.3%
Largemouth Bass	0.1	0.5	0.3	0.5
Crappies	86.9	84.4	91.3	90.8
Sunfish	8.7	9.1	4.0	5.9
Yellow Perch	1.9	1.4	0.3	0.4
Catfish	1.5	0.9	1.6	0.8
Carp	0.2	1.8	0.5	0.5

Highly significant differences (99% level) are shown between the percentages for crappies, sunfish and yellow perch for either solunar period and the blank period, and between the carp for the minor period and the other two periods. No such significance is shown for bass or catfish.

The assumption that the types of fishing effort were proportionately alike in the three period-groups may legitimately be questioned, for the analysis shows that the blank-period group had the largest proportion of children. It may be argued that children are predominately panfish anglers, so that it is to be expected that the blank period show a higher ratio of crappies. Acting on this new assumption, and combining yellow perch, sunfish, and catfish with the crappies in a panfish grouping, and the two species of bass opposed to them in a game-fish group, the figures of the preceding table take the following form:

	Major Period	Minor Period	Blank Period
Game-fish	0.8%	2.0%	2.2%
Panfish	99.0	96.2	97.3
Carp	0.2	1.8	0.5

The new combination of figures shows that the blank-period and the minor-period groups caught significantly more game-fish but less panfish than the major-period group. If the figures are combined into two classes, solunar-periods and blank period, we have:

	Solunar Periods	Blank Period
Game-fish	1.5%	2.2%
Panfish	97.4	97.3
Carp	1.1	0.5

which shows a significant difference in the catch of game-fish and carp between the two divisions but not in the panfish catch.

In the light of the above facts, it is difficult to accept the proposition that a higher proportion of children means a higher proportion of panfish in the catch. The facts would argue, rather, that either children are better fishermen than adults (which seems unlikely) or bass are easier to catch during blank periods.

Another line of reasoning which may explain why game-fish appear in greater proportions in the blank-period catch has been offered by Knight (1950), "It is not uncommon for bait fishermen, to complain that The Solunar Tables are useless and that more fish are caught between solunar periods than during the scheduled feeding times. While these criticisms are no doubt well founded, the explanation is not difficult. Fish, particularly game fish, find most of their food in the shallows. When a feeding period arrives, game fish leave the deeper water and move into the feeding grounds. Bait fishermen, who almost always make it a point to anchor their boats in fairly deep water, actually are fishing in practically barren water during the solunar periods. Only after these periods draw to a close and the fish leave the shallows to return again to their resting stations, do the bait fishermen find a market for their wares in deep water."

There was no data available to indicate the ratio of bait to bass fishermen on Loch Raven in 1952, but observations at the lake indicated that a substantial part of the fishing population was made up of bass fishermen, perhaps as much as 30 or 40 percent. Some evidence pertinent to Knight's explanation may be gleaned from an analysis of the ticket-stub forms turned in by fishermen who reported catching only bass. Assuming that these people were bass fishermen and dividing the group by periods we find that:

11 major-period anglers, fishing 45½ hours, reported 7 bass -- 0.15 per man-hour
13 minor-period anglers, fishing 50 hours, reported 9 bass -- 0.18 per man-hour
12 blank-period anglers, fishing 47 hours, reported 9 bass -- 0.19 per man-hour

This is not enough data to show significance, nor does it take into account the hours spent fishing by bass fishermen who went home empty handed. As bass fishermen at Loch Raven habitually fish "the shallows" this analysis tends to show that Knight's explanation is not valid for bass. It may be valid for crappies, but it did not hold for sunfish, perch or carp as shown by the breakdown of species caught.

To test the effect of the solunar periods on the size of bass taken, the records were analysed for average length of bass taken during solunar periods and the blank periods, with the following result (the figures in parenthesis refer to the number of bass whose lengths were reported):

	Major period	Minor period	Blank period
Average length, all bass hooked	8.9 in. (24)	9.6 in. (61)	11.0 in. (40)
Smallmouth	8.9 " (23)	9.4 " (51)	10.9 " (31)
Largemouth	10.8 " (1)	10.6 " (10)	13.4 " (9)
Average length, legal size only	11.6 in. (7)	11.9 in. (22)	13.5 in. (24)
Smallmouth	11.8 " (6)	12.0 " (16)	13.5 " (19)
Largemouth	10.8 " (1)	11.8 " (6)	13.4 " (5)

Conclusions

The hypothesis tested in this study may be stated formally: Fish are easier to catch during solunar periods than at other times. In view of the fact that the best measure of fishing success, fish caught per man-hour, shows no essential difference between solunar periods and blank periods, we can not conclude that our hypothesis is tenable. On the other hand, we have not proved the solunar periods to have no effect at all, as it would be entirely possible for a very small but real effect to exist but be masked by statistical error in the data.

The results of the analysis for ratios of successful fishermen shows that the catch of fish was spread over more anglers during major periods than during blank periods. This does not mean that fishing was better during the major periods, because it does not take into account either the number of fish taken by the successful fishermen or the time it took to catch them.

The test seems to indicate a difference in response to the solunar periods by various species of fish. Crappies and bass seem to respond negatively, while sunfish, yellow perch and carp respond positively. Catfish are apparently not affected one way or the other.

No indication was found to support an hypothesis by Knight that fish, particularly game fish, are found in shallow water during solunar periods and are more easily caught there at those times.

Acknowledgments

A study of this kind requires aiding and abetting. Among those who aided were Miss Sarah T. Grinnell, who did much of the preliminary analysis work, and Edwin Harvey, manager of the boat livery at Loch Raven who kept a watchful eye on the data as it was turned in. Among those who abetted were several of my colleagues, chiefly Romeo Mansueti, Rudolph Scheltema, Earl Walker and R. D. Van Deusen.

Literature cited

Arkin, H. and R. R. Colton
1939. An outline of statistical methods. Barnes and Noble, Inc., N. Y. 224 pp.

Coble, Grady W.
1953. Coble's Fishing Calendar for 1953. Published by author, Greensboro, N. C. 32 pp.

Cooper, Edwin L.
1953. Time to fish for trout. Weatherwise, Vol. 6 (1): 15-17.

Courtemanche, Albert
1953. Moon affects fish, barometer does not. Press release from Quebec Biological Bureau. Feb. 1953. (To be elaborated in Ann. Rept., Que. Biol. Bur., Montreal, Quebec).

Distributors Advertising Promotions, Inc.
1953. (Advertising catalogue). Philadelphia, Pa., 32 pp.

Enterprise Mfg. Co. (Pflueger Fishing Tackle)
1952(?) Old fish eye. (Advertising blotter). Printed by Lester B. Martin Assoc. Columbus, Ohio. 1 p.

Gallagher and Burton
1953. Fishing calendar. (Advertising folder.) Bristol, Pa., 4 pp. (Copyright by G. W. Coble, Greensboro, N. C.)

Knight, John Alden
1935a. Ocean tides and freshwater fish. The Sportsman (Concord, N. H.) pp. 23, 50-51, Jan. 1935.

1935b. The new Solunar Fishing Theory. The Sportsman (Concord, N. H.) pp. 27-28, 73-74, April, 1935.

1950. The Solunar Theory, in The Fisherman's Encyclopedia, I. N. Gabrielson and F. Lamonte, editors. Stackpole and Heck, New York and Harrisburg, pp 244-248.

1951. The Solunar Tables. Seventeenth Annual Edition. Forecast of the daily feeding times of fish and game for each day of the year, 1951. Published by author, Williamsport, Pa. 30 pp, ill.

1952. The Solunar Tables. Eighteenth Annual Edition. Ibid.

1953. The Solunar Tables. Nineteenth Annual Edition. Ibid.

Lincoln, R. P.
1951. Solunar Theory, in The Wise Fishermen's Encyclopedia, A. J. McClane, editor. Wm. H. Wise & Co., New York, pp. 1082-84.

Sieh, James G., and John Parsons
1950. Activity patterns of some Clear Lake, Iowa, fishes. Iowa Acad. Sci. Vol. 57: 511-518.

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THE ENDEMIC FISH FAUNA OF LAKE LANAO, AND THE EVOLUTION OF HIGHER TAXONOMIC CATEGORIES [1]

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Received January 25, 1960

INTRODUCTION

The present paper is concerned only incidentally with speciation. Its purpose is to point out some striking but neglected features of lake-fish evolution that illustrate the rapid origin of genera and still higher categories going on at the present time. I have selected the Lanao fishes as an example for several reasons. First, I have examined the fishes myself. Second, the Lanao fishes are in a recognizable stage of what has been called "explosive" evolution. Third, the age of the lake can be determined geologically, and its relative youth cannot be in serious dispute. Fourth, the remarkable zoogeographical situation of Lanao and of Mindanao Island excludes any reasonable possibility that more than one still existing species could have given rise to the 18 endemic species and four endemic genera now inhabiting the lake. The endemic Lanao fish fauna is without parallel, so far as known, in demonstrating explosive specific and generic evolution from a known and still existing ancestral species.

I am deeply indebted to my long-time friend and colleague, Dr. Albert W. Herre, discoverer and describer of the Lanao fish fauna, for many discussions regarding Lake Lanao and its fishes, extending through a period of 30 years. The late Professor Bailey Willis of Stanford, well known for his geological researches on four continents, did me the honor of employing his extensive first-hand knowledge of Philippine geology to prepare the brief geological account of Lake Lanao quoted below. Finally I must present my best thanks to my present graduate student, Mr. Angel Alcala, Instructor in Zoology at Silliman University, Dumaguete, Oriental Negros, for making further collections of Lanao fishes for Stanford. Mr. Alcala was working under National Science Foundation Grant G4381, made to Dr. Walter C. Brown for herpetological research in the Philippines.

THE LAKE

Lake Lanao lies at an altitude of approximately 2,100 feet in the midst of a volcanic area in central Mindanao, the largest island of the southern Philippines. Its exact area is in dispute, Herre giving it 375 square kilometers and others as many as 900. The late Professor Bailey Willis, who had given much attention to Philippine geology, as well as to that of the African Rift Valley and its lakes, investigated what was known of the geological history of Lake Lanao and prepared the following statement for me:

"The island of Mindanao has risen from the ocean gradually and unequally since the Miocene. It now consists of plateaus, hill country, swamps, and volcanoes. The streams were initially small and isolated from each other. The headwaters were, and are, generally swift and the lower courses estuarine.

"A north-central region was built up by basalt flows to a plateau, on which a small system of rivers developed. Some of them flowed southwesterly to Illana Bay, others northwesterly to Iligan Bay. The divide between them ranged from southwest to northeast.

[1] Abstract published in: Proc. XVth Internat. Congr. Zool., 151–152, 1959.

"Volcanoes were built up across the southwesterly flowing streams and they were dammed. Their headwaters gathered in the basin thus formed until they overflowed a low pass in the divide at Camp Keithly and discharged into Iligan Bay on the north coast.

"The impounded waters constitute Lake Lanao. The basin is probably shallow, 200 to 300 feet, perhaps, where deepest. The outlet at Camp Keithly plunges over a fall into a short canyon, indicating an age of 10,000 years, more or less. The principal tributaries to the lake enter from the southeast, from young but dormant volcanoes, and may at times have brought in quantities of ash."

While I have no specific reason to doubt Dr. Willis's estimate of the age of Lake Lanao, 10,000 years seems to be a very short time for the evolution of the Lanao fish fauna. When I brought up this question, Dr. Willis replied that the length of the canyon worn by the Agus River indicated a very brief erosional period. The possibility remains that more than one volcanic damming has been involved in the history of Lake Lanao, but the relative youth of the lake cannot be seriously doubted. The geology of the Lanao Plateau obviously needs more geological investigation.

The Fishes

Dr. A. W. Herre collected fourteen species of the Lanao fishes and described them formally in 1924, without mentioning the peculiar evolutionary features concerned. Before the publication of his 1924 paper, he had prepared an account of the zoogeography of Philippine freshwater fishes, in which he implicitly recognized the autochthonous nature of the Lanao fish fauna. However, this distributional paper was not published until considerably later (Herre, 1928). Dr. Herre visited the lake upon later occasions, adding two more species in 1926 and two in 1932.

After Dr. Herre joined the Stanford Museum staff in 1928, I urged upon him the value of preparing an account of the evolutionary features of the Lanao fauna. This resulted in the proposal of a new genus for one remarkable Lanao species (Herre and Myers, 1931) and, finally, in Herre's well-known paper of 1933. Since that time, nothing of importance has been published on these fishes save for Dr. Brooks' review of 1950.

This history is important because of the destruction of Herre's earlier material when the Bureau of Science was dynamited and its collections totally destroyed by Japanese troops in February, 1945, during the battle of Manila. The only sizable collection of Lanao fishes presently available is that in the Natural History Museum of Stanford University. This consists of a few specimens obtained by exchange from the Bureau of Science before World War II; the excellent collection made by Dr. Herre in 1931, including the types of two of his species; and a small collection made at my request in 1959 by Mr. Alcala. Two of the endemic genera (*Mandibularca* and *Spratellicypris*) and the majority of the species are represented. The only other collection of Lanao fishes known to exist in any museum is a small one obtained in 1908 by Dr. Hugh M. Smith and Dr. Paul Bartsch, and now in the U. S. National Museum. This collection was not reported upon *in extenso* until long after Herre's work was completed (Fowler, 1941). I am unable to accept some of Fowler's identifications and have not considered them in the present paper. Two of Herre's endemic genera (*Cephalakompsus* and *Ospatulus*) are known only from the destroyed types.

I have examined the Stanford collection and have had much unpublished information from Dr. Herre. Despite the unavailability of several of the described species, I am convinced that most if not all of the species described by Herre are distinct, some of them remarkably so. Unfortunately, little ecological information

is on record. Most of the collections obtained from the lake have been purchased from the native fishermen. The lake is extensively fished, and some of the endemic forms are highly prized as foodfishes by the local Moros.

The endemic forms are all members of the Cyprinidae, the largest family of primary fresh-water fishes. The large species flock consists of 13 known species of the genus Dr. Herre called *Barbodes,* better called *Puntius* (see Weber and de Beaufort, 1916) but in my opinion not easily distinguished from the widespread genus *Barbus* (Myers, 1960). Five more species are placed in four genera, *Spratellicypris* (1), *Mandibularca* (1), *Ospatulus* (2), and *Cephalakompsus* (1), all of them obviously immediately derived from stocks of *Barbus* within the lake. Other still undescribed species are probably present in the lake. Two non-endemic predators are present, *Channa striata,* perhaps introduced by man, and one diadromus eel (*Anguilla celebesensis*). Eels of this group are known to be able to ascend rapids and waterfalls impassable to other fishes. The North American black bass (*Micropterus salmoides*), a voracious predator, is said to have been introduced in recent years.[2]

Derivation of the Mindanao Cyprinidae

Herre (1928 and 1933) has outlined some of the distributional history of the Philippine Cyprinidae, and I have published a general study of the zoogeography of the fresh-water fishes of the region (Myers, 1951). The essential facts are as follows:

Central and southern Borneo teems with Cyprinidae, but the cyprinid fauna of North Borneo is relatively depauperate. Cyprinids have entered the Philippines from North Borneo in two widely different directions, through the Palawan-Calamianes chain to Mindoro, and through the Sulu chain to Mindanao. Cyprinids got no farther. The family is absent in the rest of the Philippines, and in Celebes. The Palawan-Mindoro cyprinids do not concern us here.

That Cyprinidae reached Mindanao via a sweepstakes route, across a series of salt-water gaps, is unlikely. My own studies (Myers, 1938, 1949, 1951) indicate that fresh-water fishes are less likely to cross such gaps, especially a series of them, than any terrestrial animals, although they must have done so (probably only once, across a very narrow barrier) at Lombok Strait (Myers, 1951). The Lombok crossing, if not by the hand of man, was almost certainly by means of a local cyclone (Darlington, 1938; Myers, 1951), for the salt-water gap at Lombok Strait, although probably broader now than in the Pleistocene, cannot have been bridged very recently (see Bruun and Kiilerich, 1957). Nor is it likely that hurricane (typhoon) winds could have aided the fishes invading Mindanao. The typhoon tracks shown by Dickerson (1928: 40) are all westerly in direction. Finally, fresh-water fishes are not well adapted to raft-dispersal across seas!

The obvious conclusion is that fresh-water fishes entered Mandanao across a dry-land filter bridge, through the Sulu chain. Just what lowering of sea-level occurred there during the Pleistocene, or what elevations or depressions of the Sulu chain may have occurred, is not known. The region is a volcanic, unstable one.

That few or no remains of the cyprinid migration are to be found today on the islands of the Sulu Archipelago is not too surprising. Dr. Herre fished the largest island, Jolo. He found the streams small and without Cyprinidae, but believes that relatively recent volcanic activity has wiped out the fresh-water fishes of the island (Herre, 1928).

[2] It is difficult to see why such an introduction should have been considered. Ecologically, and as a measure for increasing food production, it is clearly unsound. Scientifically, in view of the unique nature of the endemic Lanao fish fauna, it becomes a crime!

Quite clearly, then, North Borneo itself, together with the Sulu Archipelago, acted as a filter bridge to limit the access of fresh-water fishes to Mindanao. Only three genera of Cyprinidae reached Mindanao (*Barbus, Rasbora,* and *Nematabramis*) and these three are still the dominant cyprinid genera in the streams of North Borneo. Probably only one species of each genus reached Mindanao.

The cyprinid fauna of Mindanao Island outside the Lanao Plateau is very small. There is a single endemic *Rasbora* (*R. philippina*) confined to the western part of the island and closely related to a North Borneo species (Brittan, 1954: 127–131). There are two species of *Nematabramis* (*N. alestes* and *N. verecundus*), very closely allied to each other and to the species of North Borneo (Herre, 1953). Finally, there are four nominal species of *Barbus* (or *Puntius*). *Barbus binotatus* is widespread in Mindanao, and, according to Herre (1953: 123), has been erroneously reported from Lake Lanao by Fowler. *Barbus montanoi* is a doubtful form known only from the type from the Agusan River drainage, eastern Mindanao. *Barbus quinquemaculatus* from the Zamboanga Peninsula is probably a geographical subspecies of *B. binotatus*. *Barbus cataractae* (see Fowler, 1941: 797), also from the Zamboanga Peninsula, is probably a localized variant of *B. binotatus*. After examining the evidence, I suspect that there are really only three well-established cyprinid species in Mindanao outside the Lanao Plateau, one *Rasbora,* one *Nematabramis,* and one *Barbus,* each possibly represented on the island by several subspecies.

Nature of the Lanao Fish Fauna

Barbus binotatus is the commonest, most widespread, and probably the most variable cyprinid of Sundaland (see Weber and de Beaufort, 1916). It ranges from Siam to Singapore, and throughout Sumatra, Java, and Borneo. It is one of the three cyprinids that have been able to cross Wallace's Line at Lombok Strait; the others are forms of *Rasbora* (Brittan, 1954). *Barbus binotatus* exists in most or all of the lowland streams of Mindanao. It exhibits innumerable local races throughout its range.

With no other large endemic lake fish fauna is it possible with such certainty to identify the ancestral species. Lake Lanao was clearly formed rather rapidly, by volcanic action. The ill defined races of *Barbus binotatus* surrounding the Lanao Plateau form the only local source of invasions. Multiple invasions by dissimilar species of *Barbus* or other cyprinid genera are ruled out, unless one wishes to postulate a series of aerial invasions from Borneo, which dropped fishes only on the Lanao Plateau without colonizing the remainder of Mindanao!

Nor are any cyprinids known from Borneo or elsewhere which parallel or are similar to the strange Lanao genera *Mandibularca* and *Spratellicypris.* The same may be true of the genera *Cephalakompsus* and *Ospatulus,* but the types and only known specimens of these two genera were destroyed in Manila.

We are thus forced to the conclusion that *Barbus binotatus* alone gave rise to at least 18 species on the Lanao Plateau, including four new genera. All of the species that I have examined give evidence of derivation from *Barbus binotatus* or at least a close relative. Two or three of the species are only slightly differentiated from *binotatus* and occur both in the lake and its tributary streams. The most distinctive species are known only from the lake itself. *Mandibularca* occurs only in highly turbulent water at the outlet. One or two of the species are said by local fishermen to inhabit only the deeper waters of the lake, while others are found only in the shallow *Potamogeton* beds. *Barbus binotatus* is not known to occur on the plateau, nor are any of the lake species known from below María Cristina Falls, 65 meters in

height, in the Agus River which drains the lake.

The Supralimital Specializations

In 1936, in connection with a report on fishes from Lake Tanganyika, I briefly pointed out (perhaps for the first time) some of the general features of fish evolution in large lakes throughout the world—the African lakes, Titicaca, Baikal, and Lanao. Brooks (1950) has reviewed the subject of speciation in ancient lakes, including Lanao, but Lanao is not an ancient lake, geologically speaking, and the particular features I wish again to stress are neither limited to ancient lakes nor recognized by Brooks.

In Lake Lanao, the peculiar but quite different lower jaw modifications evolved in the genera *Mandibularca* and *Spratelli-cypris* (and probably in *Ospatulus* as well) are approached nowhere else in the very large family Cyprinidae, which is generally distributed throughout Eurasia, Africa, and North America, and exhibits many remarkable specializations. In other words, the jaw modifications of some Lanao cyprinids transcend the familial limits of all the 1,500 to 2,000 non-Lanao cyprinid species in the world. For want of a better term I am calling these supra-limital specializations.

That peculiar supralimital specializations are not confined to Lanao, but are a common and general feature of the evolution of endemic fish faunas in large lakes, is easily demonstrated. The remarkable scaleless cyprinid *Sawbwa* of the Inlé Lake in Burma (Annandale, 1918), the highly modified species of *Orestias* in Titicaca, the extraordinarily modified cichlid genera of Nyasa and Tanganyika, and many of the cottoids of Lake Baikal, all transcend, in one way or another (often strongly and in many characteristics) the limits of specialization of the large, widespread, and varied families to which they belong.

One illustration will suffice. The Percomorphi form the largest order of bony fishes, containing nine thousand species or more. Within the order, many families are defined by relatively few characteristics, of which dentition is often of considerable importance. The fresh-water percomorphs of the family Cichlidae form a large family of perhaps 700 species, distributed throughout Africa, Syria, Madagascar, southern India, and tropical America. Their dental characteristics are generally rather uniform, the modifications usually of small degree. Yet in some of the endemic cichlid genera of Lake Tanganyika, the dental modifications (especially the great, double pointed, heavy-based teeth of *Perissodus* and the utterly strange leaf-like teeth of *Plecodus*) far transcend the limits of dental modification not only of the family Cichlidae, but also of the order Percomorphi and of the entire class of bony fishes. Nothing remotely like them exists. Nor are dental characters the only ones involved. Specializations of the pelvic fins for bottom living (genera *Asprotilapia, Enantiopus*), which elsewhere are considered to be taxonomically of great importance, occur. Indeed, some of the Nyasa and especially the Tanganyika cichlids have come to resemble closely such diverse percomorph families as the Blenniidae (*Telmatochromis*), Girellidae (*Tropheus*), and certain European Percidae (*Asprotilapia*), representing a radiative divergence, and convergence towards different families, entirely unknown elsewhere in the entire gigantic order Percomorphi.

Both *Perissodus* and *Plecodus,* as well as certain other African lake cichlids, might easily be held to represent monotypic families, as has indeed been done with the Comephoridae and (by some) the Cottocomephoridae of Lake Baikal. The late Dr. David Starr Jordan, when shown the jaw of the Lanao genus *Mandibularca,* remarked that a family might well be set up for this genus alone. While I cannot quite agree with this opinion, Jordan's remark is indicative of the situation.

It may be noted that supralimital specializations in fishes are not confined to lake faunas. Any specialization peculiar to one species or genus is, in a sense, a supralimital specialization. However, the general or perhaps the invariable occurrence of extreme and unique specializations in the fishes of lakes that have existed long enough to have produced considerable endemic fish faunas, is notable. Still more notable is the fact that species possessing striking supralimital specializations form a much higher percentage of older lake faunas than they do of stream faunas in general.

The reason for this seems obvious. Most fresh-water fishes inhabit streams and are adapted to life in running water. When lakes are formed, only species already adapted to the slow moving, quiet backwaters are able to take immediate and full advantage of an extensive still-water environment. This extensive new environment usually provides many biotypes not represented in streams, and, in addition, geographical barriers (especially in larger lakes) which may either be present originally or develop with the evolution of the lake itself. The inability of biologists, who are terrestrial animals, to envision these subaquatic facts has greatly hindered studies of fish evolution in lakes.

Stages of Lake Fish Evolution

It is possible to point out sequential steps in the evolution of lake fish faunas, using different existing large lakes as examples; it seems worthwhile to do so. I have specifically refrained from any attempt to evaluate the probably numerous instances in which a relatively small or recent lake has obviously permitted the evolution of one or a few species, sometimes of diverse groups. One such lake is Lake Waccamaw in North Carolina (Hubbs and Raney, 1946). Another is Bear Lake, on the Utah-Idaho boundary, in which three distinct coregonids have evolved (Snyder, 1919). The coregonids have been especially prone to apparent endemism in northern glacial and alpine lakes, but doubt as to the real distinctiveness of many such forms in Postglacial lakes has often been expressed.

In the North American Great Lakes, which have become generally available to fishes only since the geologically recent retreat of glaciation, the coregonids of the "lake herring" (*Leucichthys*) type have experienced a burst of evolution, but many of the endemic species and races are still difficult to separate (Koelz, 1929), if indeed they are really distinct. The fauna is still too young to show anything very definite in the way of supralimital specializations, but the development of species flocks of coregonids is evident. Except for the "lake herrings," no other group of fishes so well preadapted to very cold, still water was present, and this one gained ascendancy.

A similar situation, but probably of greater age because of the greater distinctiveness of the species, is seen in the athernids (*Chirostoma*) of Lake Chapala and other lakes in Mexico (Regan, 1906–1908; Jordan and Hubbs, 1919; Alvarez, 1950) and the cichlids (Meek, 1907; Regan, 1906–1908) of Lakes Nicaragua and Managua. Supralimital specializations among the Cyprinodontidae are clearly foreshadowed in the dwarf, deep-bodied species of *Orestias* in Lake Titicaca (Tchernavin, 1944), which are unlike any of the non-Titicaca *Orestias*.

A clearly more advanced stage is represented by Lake Lanao, in which a single ancestral species of cyprinid has given rise to a species flock, five members of which have become so distinct as to be referable to four endemic genera. Their supralimital specializations have been mentioned above. The excellent work of Mr. Greenwood on the Cichlidae of Lake Victoria shows that the Victoria cichlids are in a state more or less comparable to that of the Lanao cyprinids, although evolution is proceeding on a far grander scale. The species flocks are much larger

and there are four distinctive endemic genera (Greenwood, 1956, 1959), but the ancestral types are either lost or unidentifiable. However, as in Lanao, endemics of families other than the dominant one are absent.

A much older stage is represented by the fishes of Lake Nyasa, which Brooks (1950: 135) estimates to be approximately 500,000 years old. Fryer (1959: 264) gives evidence pointing to greater age. As in all other large Central African lakes, the cichlids (Trewavas, 1935; Fryer, 1959) are dominant. They present the greatest of all known species flocks among lake fishes—over 100 species of the widespread genus *Haplochromis*. In addition, there are over 70 cichlid species belonging to 20 endemic genera, several of which exhibit remarkable supralimital specializations. However, fishes of other families have entered the lake and established endemic species, but only one endemic genus (Worthington, 1933; Jackson, 1959). Most large lakes are drained by physiographic evolution before they attain any age such as that of Nyasa, and it alone remains to represent the evolutionary stage of its fish fauna. The same is true of the two still older lake fish faunas, those of Tanganyika and Baikal.

Lake Tanganyika is at least 1,500,000 years old and may be even older (Brooks, 1950: 148). Its fish fauna (Poll, 1946; 1953) indicates a much later evolutionary stage than that of Nyasa, this being especially notable because of the comparable size and geographical proximity of these two immense Rift Valley lakes. The cichlids are still dominant; they are fewer in number of species than in Nyasa, but the vast majority belong to endemic Tanganyika genera. The only group that could be called a "species flock" is formed by the 19 species of *Lamprologus,* a genus also represented in the Congo.[3] Several of the endemic genera, as has already been noted, are morphologically worthy of familial or subfamilial groupings, and several have come to resemble quite different families of Percomorphi. In non-cichlid fishes, Tanganyika has had time to develop, in addition to a number of endemic species belonging to non-endemic genera, two endemic genera of Clupeidae, two of Bagridae, two of Clariidae, one of Cyprinodontidae (representing a distinctive subfamily; Myers, 1936) and one (*Luciolates*) of Centropomidae (Worthington and Ricardo, 1937; Poll, 1953). Evolution of some of these must have been accomplished in the face of strong competition by the entrenched Cichlidae.

Lake Baikal is the oldest of all, perhaps as much as 75,000,000 years old; its southern basin is Paleocene or possibly even late Cretaceous in age. However, the present lake basin was enlarged and deepened as late as the Pleistocene (Brooks, 1950: 33), and it is doubtful that even the most distinctive Baikal fishes arose prior to the Mid-tertiary. The Cottidae and their derivatives are dominant in Baikal; species of no other fish families are endemic to the lake (Taliev, 1955). The absence of non-cottoid endemics is notable; it is probably due to the poverty of the Siberian fish fauna. The 26 endemic cottoid species belong to nine endemic genera, eight referred by Taliev to two endemic subfamilies of the Cottidae and one genus with two species to the endemic family Comephoridae.

Other lake fish faunas might be fitted into the sequence, but this seems unnecessary.[4]

In all the larger endemic lake-fish faunas, from the youngest to the very

[3] The interesting possibility presents itself that Lamprologus is an autochthonous Tanganyika genus which has colonized the Congo basin.

[4] Some other lakes, with the families to which the dominant endemics belong, are: Lake Biwa, Japan (Cyprinidae); the Celebes lakes (Atherinidae, usually); various Mexican lakes (Atherinidae); the African lakes George, Albert, etc. (Cichlidae); various Central Asiatic lakes, such as Lop Nor, Koko Nor, etc. (Cyprinidae or Cobitidae); Utah Lake (Catostomidae).

oldest, a single family group, preadapted over other stream fishes for lake life, has gained dominance over all others and has retained it. This accounts for my former belief (Myers, 1936) that access to lakes dominated by a single fish family must have been restricted. Access was restricted in Lake Lanao, but probably this has only rarely been true in other lakes. Moreover, in all except the youngest lake fish faunas, supralimitally specialized forms are evident and continue to become more striking until some of them, in the older lakes, could be or are accepted by taxonomists as distinct families.

One other important point should be made. The greater richness in genera and species of the older lake fish faunas, insofar as the dominant family is concerned, compared to the fluviatile fauna of the same family in the same region, is always striking. The Lanao cyprinid fauna dwarfs the cyprinid fauna of Mindanao outside the lake. More than half the African species and far more than half the African genera of the large family Cichlidae are endemics in the lakes of East Central Africa. The greater part of the North American forms of *Leucichthys* are lake endemics. Probably the same is true of Mexican atherinids of the genus *Chirostoma*. The forms of *Orestias* in Lake Titicaca are more numerous than those in the rest of the Andean Altiplano. The cottoid genera of Baikal comprise over three-fourths of the known genera of fresh-water cottoids in the world.

Isolated Endemics

Whether the strange little mastacembelid-like *Chaudhuria caudata* (Annandale, 1918) of the Inlé Lake, sole representative of the family Chaudhuriidae, and the possibly even stranger *Indostomus paradoxus* (Prashad and Mukerji, 1929) of the Indawygi Lake, sole representative of the family Indostomidae, are to be considered as vastly modified relicts of autochthonous lake-fish families, is unknown. If so, they would be the ultimate examples of lake fish specialization, but neither species has any known close relatives, and both may be mere survivors of once widely distributed families. The two genera and three known species of the strange family Adrianichthyidae, from Lake Posso and Lake Lindu in Celebes (see Weber and de Beaufort, 1922), which are undoubtedly derivatives of the family Cyprinodontidae, likewise have no known close relatives by which to judge their exact origin. I would suspect them to be derivatives of the subfamily Oryziatinae, members of which are still widely distributed in fresh waters from India and Japan to Timor, and which have given rise, in India, to the remarkable fish *Horaichthys*. Isolated lake-fish endemics are not too rare, often in lakes in which fishes of another family have become dominant, but the endemic nature of the genus or higher category represented by them is sometimes in doubt. ~~The cottid *Triglopsis* in the American Great Lakes is an example~~. Perhaps some of these isolated endemics are relicts of previous cycles of lake-fish evolution in the same basins, cycles which were terminated by great changes in the basin itself.

New Areas, New Groups

What has happened, in the normal course of evolution, when one or more representative of an animal group not hitherto represented in the fauna has suddenly gained access to a large area replete with numerous available and unoccupied biotopes, seems to be clear. If the invaders are unable to withstand the competition of the older fauna, they disappear. If they can overcome competition, or especially if there is little or none, rapid or tachytelic evolution occurs, evolution that was impossible in their old home, where better balanced ecological conditions and a balanced fauna held evolutionary divergence more tightly in check. New genera, often utterly unlike their ancestors in one or more strik-

ing characteristics, appear with great rapidity. The rapid proliferation of proboscideans, and their development of supralimital specializations after their invasion of America, is a case in point.

The same sort of evolution has happened time and again when island groups were colonized. The supralimital bill specializations of the Galápagos finches, and (whatever their ancestors may have been) especially those of the drepanidid birds in Hawaii, are well known instances. Island evolution of this kind, like lake-fish evolution, is often striking, because the original colonizers found abundant biotopes totally unoccupied when they arrived.

However, the situation differs somewhat in lakes. The colonizers and founders of evolutionary dynasties in lakes must contend not only with the same types of problems that confront island or continent colonizers. In addition, they must face the change from a flowing to a still-water environment, and, in many instances, problems of depth, pressure, and salinity, perhaps new or inimical to them. In fact, it seems possible that gradually increasing salinity in a closed lake basin might eventually check the evolution of some fresh-water fish groups very severely (Myers, 1938; 1949).

The tachytelic evolution of lake fishes, in part at least representing quantum evolution in Simpson's sense, seems to point out in a really striking way how genera, families, or even higher categories of different animal groups have evolved. If they could get out of their lakes and use their supralimital specializations in other lakes or in streams, as some undoubtedly have done in the past, many existing lake fishes could easily become the founders of large and flourishing new groups at new adaptive levels. Terrestrial groups are not usually as limited in their ability to escape their ranges as are lake animals. As Simpson has so ably pointed out, the tachytelic evolution of new superior groups has seldom left a fossil record because of the speed with which events progressed, and, we may add, because of the probable localization of those events.

It seems probable that events of the sort I have been discussing account for the almost unbelievably rich fauna of characid fishes of the greatest of all rivers, the Amazon. In its present form the Amazon is not an old river. In its lower course it is probably a reversed river; its old structural basin plunges westward. Its Peruvian reaches formed a great lake in relatively recent geological times, and the immense but fluctuating lakes that now line its lower course comprise one of the largest areas of ponded fresh water now existing on earth.

Finally, we cannot forbear to mention the largest of all bodies of still, quiet water, the deep seas. The supralimital specializations exhibited by the highly modified deep-sea descendants of invaders from more turbulent shallow waters have long been the wonder of all zoologists.

It follows that opportunity—the absence of well-adapted competing groups—is extremely important as a factor in the evolution of higher categories. The importance of such a conclusion in relation to the early, rapid evolution of the main animal phyla is obvious.

Summary

1. The endemic fish fauna of Lake Lanao, all belonging to the family Cyprinidae, consisting of a species flock of 13 species and five species referred to four endemic genera, has evolved in a relatively short time, possibly as little as 10,000 years.

2. The distributional facts permit the identification, beyond reasonable doubt, of the single, still-existing, ancestral species that gave rise to the entire endemic fish fauna.

3. Certain specializations of the endemic Lanao genera are paralleled or approached by no others in the large,

widespread family Cyprinidae; because they transcend the morphological limits of all non-Lanao cyprinids, these are termed supralimital specializations.

4. Supralimital specializations are shown to be very characteristic if not invariable features of all large, older, endemic lake-fish faunas; some are so distinctive as to provide characters worthy of family rank.

5. The stages of endemic lake-fish evolution are illustrated by examples, the youngest being the American Great Lakes, the oldest Lake Baikal.

6. A single preadapted fish family represented in the surrounding fluviatile fish fauna assumes dominance in the evolution of large endemic lake fish faunas.

7. The evolution of lake-fish faunas is compared to that of island faunas, and to the evolution of any groups newly admitted to extensive areas where competition is light or absent, and shown to be essentially similar in the relatively rapid production of supralimitally specialized forms.

8. The latter are often capable of becoming the founders of new genera, families, or perhaps even higher categories, at new adaptive levels. They have unquestionably already done so in the older lake-fish faunas, where certain endemic Tanganyika and Baikal genera are worthy of subfamilial or familial rank.

9. It is suggested that the origin of the excessively rich characid fauna of the Amazon River, and of the striking forms and groups of deep-sea fishes, has been due to similar tachytelic or quantum evolution.

10. It follows that opportunity for rapid radiative evolution is of very great importance in the evolution of higher categories, and that such opportunity still may occur from time to time through geological changes.

Literature Cited

Alvarez, J. 1950. Claves para la determinacion de especies en los peces de las aguas continentales Mexicanas. Secretaria de Marina, Dirreción General de Pesca e Industrias Conexas, Mexico: 136 pp.

Annandale, N. 1918. Fauna of the Inlé Lake. Rec. Ind. Mus., **14**: 214 pp., 26 pls.

Brittan, M. L. 1954. A revision of the Indo-Malayan fresh-water fish genus *Rasbora*. Inst. Sci. Tech. (Manila), Monograph, **3**: 224 pp., 3 maps.

Brooks, J. L. 1950. Speciation in ancient lakes. Quart. Rev. Biol., **25**: 30–60, **131–176.**

Bruun, A., and A. Kiilerich. 1957. Bathymetrical features of the Bali-Lombok Strait. Marine Research in Indonesia, **3**: 1–6.

Darlington, P. J. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol., **13**: 274–300.

Dickerson, R. E., and others. 1928. Distribution of life in the Philippines. Bureau Sci. (Manila), Monograph, **21**: 322 pp., 42 pls.

Fowler, H. W. 1941. Fishes of the groups Elasmobranchii . . . Ostariophysi obtained by the . . . Albatross . . . chiefly in the Philippine Islands. U. S. Nat. Mus. Bull., **100** (13): 879 pp.

Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. Proc. Zool. Soc. London, **132**: 153–281, 2 pls.

Greenwood, P. H. 1956. The monotypic genera of cichlid fishes in Lake Victoria. Bull. Brit. Mus. (Nat. Hist.), **3**: 295–333.

——. 1959. Evolution and speciation in the *Haplochromis* (Pisces, Cichlidae) of Lake Victoria. Proc. XVth Int. Congr. Zool. London, pp. 147–150.

Herre, A. W. 1924. The Philippine Cyprinidae. Philippine J. Sci., **24**: 249–307, 2 pls.

——. 1926. Two fishes from Lake Lanao. Philippine J. Sci., **29**: 499–502, 2 pls.

——. 1928. True fresh-water fishes of the Philippines. In: Dickerson, 1928 (which see): 242–247. [This paper was written previous to the publication of Herre's 1924 paper, and some of the fish names do not agree with those of the 1924 paper.]

——. 1932. Five new Philippine fishes. Copeia, **1932**: 139–142.

——. 1933. The fishes of Lake Lanao: a problem in evolution. Amer. Nat., **68**: 154–162.

——. 1953. Check list of Philippine fishes. U. S. Fish and Wildlife Service, Research Report, **20**: 977 pp.

Herre, A. W., and G. S. Myers. 1931. Fishes from southeastern China and Hainan. Lingnan Sci. J., **10**: 233–254.

HUBBS, C. L., AND E. C. RANEY. 1946. The endemic fish fauna of Lake Waccamaw, North Carolina. Misc. Publ. Mus. Zool. Univ. Michigan, **65**: 30 pp.

JACKSON, P. N. B. 1959. Revision of the clariid catfishes of Nyasaland, with a description of a new genus and seven new species. Proc. Zool. Soc. London, **132**: 109-128.

JORDAN, D. S., AND C. L. HUBBS. 1919. Studies in ichthyology: a monographic review of the family of Atherinidae or silversides. Leland Stanford Jr. Univ. Publ., Univ. Ser., 87 pp., 12 pls.

KOELZ, W. 1929. Coregonid fishes of the Great Lakes. Bull. U. S. Bur. Fisher., **27** (2): 297–643.

MEEK, S. E. 1907. Synopsis of the fishes of the Great Lakes of Nicaragua. Field Columbian Museum, Zool. Ser., **7** (4): 97–132.

MYERS, G. S. 1936. Report on the fishes collected by H. C. Raven in Lake Tanganyika in 1920. Proc. U. S. Nat. Mus., **84**: 1–15, 1 pl.

——. 1938. Fresh-water fishes and West Indian zoogeography. Ann. Rep. Smithsonian Inst., **1937**: 339–364, 3 pls.

——. 1949. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdr. Dierk., **28**: 315–322.

——. 1951. Fresh-water fishes and East Indian zoogeography. Stanford Ichth. Bull., **4**: 11–21.

——. 1960. Preface to any future classification of the fishes of the genus Barbus. Stanford Ichth. Bull., **7** (4). (In press.)

POLL, M. 1946. Revision de la faune ichthyologique de Lac Tanganika. Ann. Musée du Congo Belge, zool., (1) **4**: 145–364, 3 pls., map.

——. 1953. Poissons non Cichlidae. Explor. Hydrobiol. Lac Tanganika (1946–1947), Result. Scientif., **3** (5A): 251 pp., 11 pls.

PRASHAD, B., AND D. D. MUKERJI. 1929. The fish of the Indawygi Lake and the streams of the Myitkyina District (Upper Burma). Rec. Ind. Mus., **31**: 161–223, pls. 7–10.

REGAN, C. T. 1906–1908. Biologia Centrali-Americana. Pisces. London: xxxiv + 203 pp., 26 pls.

SIMPSON, G. G. 1953. The major features of evolution. New York: xx + 434 pp.

SNYDER, J. O. 1919. Three new whitefishes from Bear Lake, Idaho and Utah. Bull. Bur. Fisher., **36**: 1–9.

TALIEV, D. E. 1955. Bitschki-podkamenschtschiki Baikala (Cottoidei). Akademiia Nauk S.S.S.R., Moskva: 603 pp.

TCHERNAVIN, V. 1944. A revision of the subfamily Orestiinae. Proc. Zool. Soc. London, **114**: 140–233.

TREWAVAS, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. Ann. Mag. Nat. Hist., (10) **16**: 65–118.

WEBER, M., AND L. F. DE BEAUFORT. 1916. The Fishes of the Indo-Australian Archipelago. Vol. 3. Leiden: xvi + 455 pp.

——. 1922. *Ibid.* Vol. 4. Leiden: xiv + 410 pp.

WORTHINGTON, E. B. 1933. The fishes of Lake Nyasa (other than Cichlidae). Proc. Zool. Soc. London, **1933**: 285–316.

WORTHINGTON, E. B., AND C. K. RICARDO. 1937. The fish of Lake Tanganyika (other than Cichlidae). Proc. Zool. Soc. London, **1936**: 1061–1112.

World Distribution of Brown Trout, *Salmo trutta*[1]

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ABSTRACT

During the past century the Eurasian and North African range of the brown trout, *Salmo trutta* L., has been extended to include discontinuous populations on all continents except Antarctica. Primary factors affecting the establishment of naturalized populations are water temperature, precipitation, and suitable spawning grounds. Any future major expansion in the world distribution of the brown trout, with the possible exception of Asia, is unlikely.

INTRODUCTION

During the past century the pristine range of the brown trout, *Salmo trutta* Linnaeus, in Eurasia and North Africa, has been extended through introduction to include waters on all continents except Antarctica.

Linnaeus, when naming the trout of Sweden *Salmo trutta* in 1758, regarded the sea trout (*S. eriox*) and the brook trout (*S. fario*) as distinct species. The latter species must not be confused with the North American brook trout, *Salvelinus fontinalis* (American Fisheries Society, 1960). After that time various local representatives of the genus were given a variety of common and specific names (Regan, 1911) which included the common trout (*S. fario, ausonii, gairnardi, cornubiensis*), the English salmon trout (*S. trutta, eriox, cambricus, albus, phinoc, brachypoms*), the golden estuarian trout (*S. estuarius, orcadensis, gallivensis*), the great black lake trout (*S. ferox, nigripinnis*), the gillaroo (*S. stomachicus*), and the silver or Loch Leven trout (*S. caecifer, levenensis*). The exchange of brown trout stocks among European countries, such as the transfer of German brown trout to England in 1884 (Smiley, 1884) and to Italy in 1885 (Pavesi, 1887), further complicated the problem of speciation.

Modern ichthyologists, however, generally accept the concept of Günther (1866), Regan (1911), Jordan (1926), and Hubbs (1930) that there is but one species, *Salmo trutta*, and that trout with distinctive features should be recognized at only the subspecific level, if at all.

Most populations of brown trout now resident in hatcheries and natural waters throughout the world stem from the following three sources: sea run specimens of the European trout (*Salmo trutta trutta*), European trout permanently resident in fresh water (*Salmo trutta fario*), and the trout (*Salmo rutta levenensis*) from Loch Leven, and other waters of Scotland and northern

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England. Because of interbreeding in fish culture programmes, and the introduction of hybrids or several stocks to many waters, it would seem imprudent for practical purposes to identify the brown trout beyond the specific level (Wiggins, MS, 1950).

The objectives of this paper are: firstly, to present an account of known attempts to introduce the brown trout (*Salmo trutta* L.) beyond its native range; and secondly, to document the present world distribution of the species which has resulted from these introductions.

NATIVE RANGE

The native range of the brown trout (Fig. 1) has been established essentially from published material by Seeley (1886), Bean (1888), Dahl (1918,

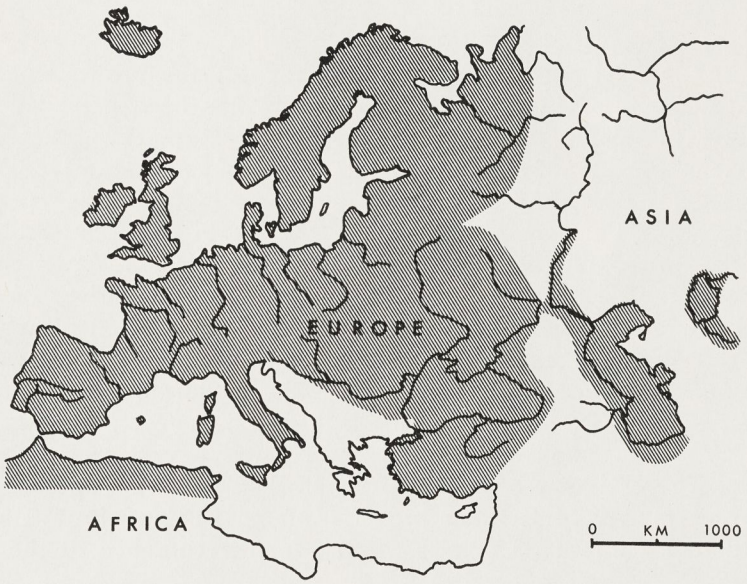

FIG. 1. Native distribution of *Salmo trutta*.

1919), Berg (1932), Tchernavin (1939), Wiggins (MS, 1950), Nikolskii (1937, 1961), and Vladykov (1931, 1963).

The early distribution of the species is believed to have extended from Iceland and the northern coasts of Europe southward to the countries fronting on the Mediterranean Sea, the islands of Corsica and Sardinia, and Algeria in northern Africa. The range extended eastward from the Atlantic drainage towards the northern slopes of the Himalayas. Migratory brown trout inhabited the Black, Caspian, and Aral seas and their tributaries.

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RECORDS OF YELLOW AND SPOTTED SNAKE-EELS (GENUS *OPHICHTHUS*) FROM SAN FRANCISCO BAY, CALIFORNIA[1]

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A northern range extension of approximately 400 miles, description, and illustration of the yellow snake-eel, *Ophichthus zophochir* (Jordan and Gilbert), is presented from a specimen 647 mm *TL* collected in April, 1964, from San Francisco Bay. Recent records indicate the yellow snake-eel is rather common in southern California waters. The spotted snake-eel, *Ophichthus triserialis* (Kaup), is recorded from San Francisco Bay on the basis of three specimens collected on three separate occasions.

A yellow snake-eel, brought to the University of California for identification by Joseph Tiner of Oakland, was caught by an unidentified fisherman with hook and line from Berkeley Pier, Alameda County, California, on April 16, 1964. It extends the northern geographical limits of the species by approximately 400 miles. Previous records for California have all been based upon specimens from southern California (Hubbs, 1916: 154; Fowler, 1923: 287, 296; Radovich, 1961: 22; Outdoor California, 1962: 14). The species is known as far south as Panama (Jordan and Gilbert, 1883: 632; Gilbert and Starks, 1904: 37).

The occurrence of the yellow snake-eel in southern California in 1957, along with many other tropical species of fishes, indicated to Radovich (1961) a warm period for the northeast Pacific Ocean. Recent records from southern California now indicate this species is not as rare as previously believed. Since 1953, the California State Fisheries Laboratory on Terminal Island has received seven yellow snake-eels:

1) 4 March 1953, Long Beach Harbor, seaward side of Pier A, caught in a suction dredge in 30 feet of water, Frank Luciene coll. (822 mm TL; size record for the species, *see* Outdoor California, 1962);
2) 11 December 1957, Santa Monica Bay in a lampara net by boat *Josie Lena* (645 mm TL);
3) 28 May 1961, Alamitos Bay, hook and line, Edward Ramsey coll. (720 mm TL, 405 grams);
4) 21 June 1961, Pierpoint Landing, Long Beach, hook and line by a small boy, saved by J. E. McClintock (580 mm TL, 245 grams);
5) 29 June 1961, San Clemente Pier, hook and line, William Martens coll. (510 mm TL, 155 grams);
6) 13 January 1962, Alamitos Bay, hook and line using squid for bait, piece of clam in stomach, James Ryan coll. (585 mm TL, 260 grams);
7) 30 June 1962, Belmont Shore Pier, hook and line using cut sardine, saved by Leo Pinkas (625 mm TL).

[1] Submitted for publication January 1965.

Some of these eels were mentioned and one illustrated in *Outdoor California* (1962). Specimens were deposited in the collections of either the University of California at Los Angeles or the Los Angeles County Museum. During June 1962, as many as three to five yellow snake-eels per week were caught from Belmont Shore Pier, Long Beach. This "minor fishery," reported by Biologist Leo Pinkas while conducting a pier fishery survey, lasted for perhaps 5 or 6 weeks (John E. Fitch, pers. commun.). Jordan and Gilbert (1882: 385) claimed the yellow snake-eel to be "rather common in the rocks about Mazatlan" on the western coast of Mexico.

The spotted snake-eel, *Ophichthus triserialis* (Kaup), is the only other member of the genus known from California. This species can be distinguished from the yellow snake-eel by the large, black spots on its body and its uniserial vomerine teeth. The yellow snake-eel completely lacks spots on the body and possesses biserial vomerine teeth. Both species possess biserial jaw teeth (note error in the description of *O. triserialis* on p. 384 of Jordan and Evermann, 1896). The range of the spotted snake-eel is from the Galapagos Islands (Jordan and Evermann, 1896) north to Tomales Bay (Hubbs, 1916: 153). A spotted snake-eel in the collections of the California Academy of Sciences (CAS 12649), ca. 1060 mm TL and 667 grams after preservation, is labelled "coast of Northern California" and was collected by C. Kofoid in September 1930.

Records of the spotted snake-eel from San Francisco Bay are as follows: CAS 11062 (presently in the collections of the University of California at Los Angeles) : 1 skeleton, Tiburon near Richardson's Bay, Marin County, no date of collection, Thomas Foley; CAS 19770: 1, ca. 1040 mm TL and 1191 grams after preservation, Black Point, Marin County, September 14, 1931, gift of J. M. Harrity; CAS 23715: 1, 886 mm TL and 744 grams after preservation, Point San Quentin, Marin County, May 15, 1948, caught by Robert W. Johnston with hook and line (sardine bait).

The preceding records for yellow and spotted snake-eels indicate that all three species of snake-eels known for the state of California occur in San Francisco Bay. Harry (1948:145) recorded the tiger snake-eel, *Myrichthys tigrinus* Girard, from San Francisco Bay.

The present specimen of yellow snake-eel is deposited at the California Academy of Sciences (CAS 23683). Color before preservation in formalin was maroon above and yellowish-brown to yellow below. Dorsal and anal fin margins were edged with black. After preservation, dorsum appeared brown and venter brownish-white. Lateral line pores were rimmed with black, slightly darker than the background color. Snout, lower jaw, gular, and cheek regions also were tinged with black. Throat region was white, much lighter than remainder of body.

Total length was 647 mm (644.5 mm SL) and weight 265 grams after preservation. Body measurements, expressed in thousandths of total length, are as follows: head length (to upper edge of gill opening) 089; head depth (in throat region) 038; snout length 014; orbit length 008; least interorbital distance 012; upper jaw length (from snout to rictal commissure) 030; snout tip to tip of lower jaw 004; dorsal fin base 861; dorsal origin to snout 132; dorsal origin to pectoral

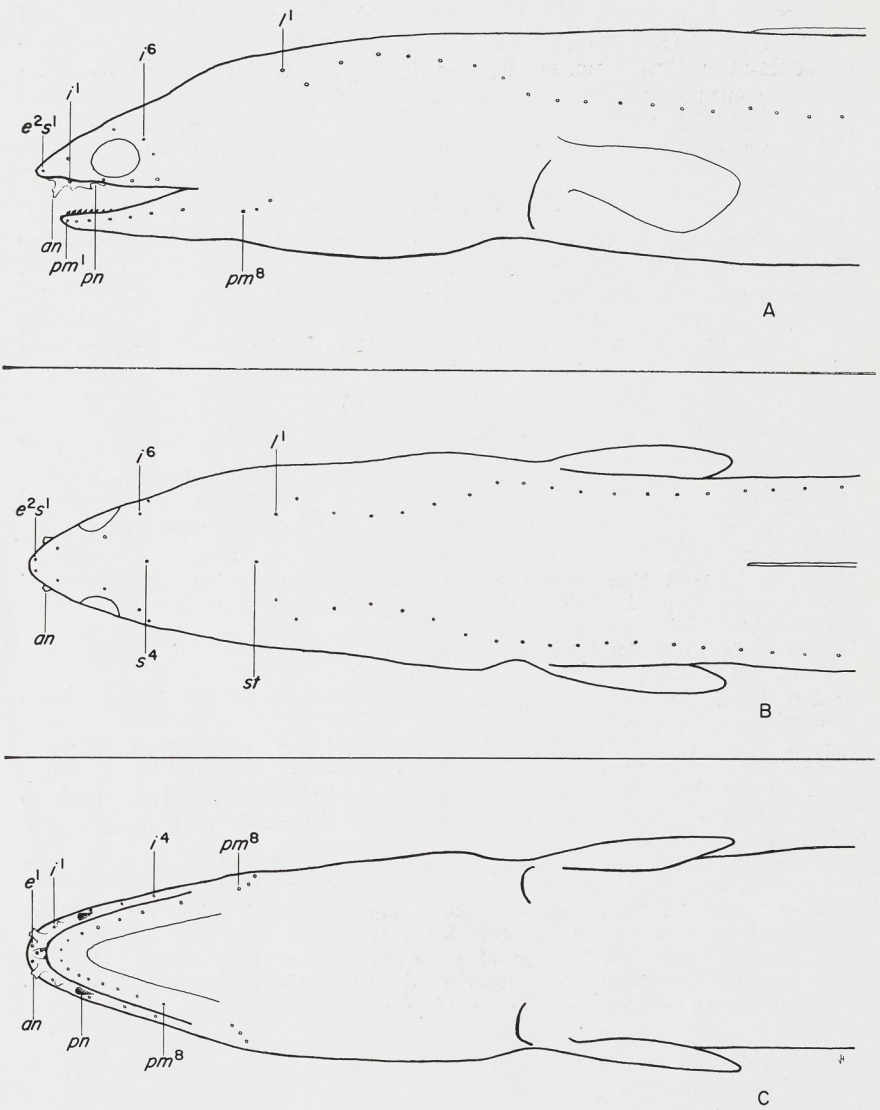

FIGURE 1. Distribution of sensory pores on the head of *Ophichthus zophochir* in (A) lateral, (B) dorsal, and (C) ventral view. Symbols: *an*, anterior nostril; *pn*, posterior nostril; *st*, supratemporal pore; l^1, first lateral line pore; i^1, first infraorbital pore; e^1, first ethmoidal pore; e^2s^1, compound pore formed from second ethmoidal and first supraorbital pores; pm^1, first preoperculomandibular pore. Terminology after Allis, 1903, and Kanazawa, 1963. *Drawings by the author.*

origin 046; dorsal origin to anal origin 251; post-dorsal distance 009; greatest body depth (region between pectoral origin and anal origin) 043; pectoral origin to snout 093; and fin base 615; anal origin to snout 376; post-anal distance 009; height of gill opening 013.

Laterial line pores 148 (149 on right side): 51(51) before anal origin and 97(98) behind anal origin; supratemporal pore 1; preoperculo-mandibular pores 10(11); 3(3) preopercular and 7(8) mandibular; supraorbital pores (including ethmoidal) 4(4); infraorbital pores 6(6) (Figure 1).

Vertebrae 153; 46 precaudal and 107 caudal; pectoral fin rays 16(16).

ACKNOWLEDGMENTS

I am indebted to W. I. Follett, California Academy of Sciences, for X-raying the specimen and for information on distribution. Lillian J. Dempster of the Academy assisted in locating pertinent literature. John E. Fitch contributed substantially to this paper by allowing me to use his unpublished records of yellow snake-eels from southern California.

LITERATURE CITED

Allis, E. P. 1903. The lateral sensory system in the Muraenidae. Intern. Monats. Anat. Physiol., 20 :125–170.

Fowler, H. W. 1923. Records of West Coast fishes. Acad. Nat. Sci. Phila., Proc., 75 :279–301.

Gilbert, C. H., and E. C. Starks. 1904. The fishes of Panama Bay, Calif. Acad. Sci., Mem., 4 : 1–304.

Harry, R. R. 1948. New records for the fish, *Myrichthys tigrinus*, a snake eel of the eastern tropical Pacific, with a relocation of the type locality. Copeia, 1948(2) :145–146.

Hubbs, C. L. 1916. Notes on the marine fishes of California. Univ. Calif. Publ. Zool., 16 : 153–169.

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America. Part 1. U.S. Nat. Mus., Bull., (47) :1–1240.

Jordan, D. S., and C. H. Gilbert. 1882. Descriptions of thirty-three new species of fishes from Mazatlan, Mexico. Proc. U.S. Nat Mus., 1881, 4 :338–365.

———. 1883. List of fishes now in the Museum of Yale College, collected by Prof. Frank H. Bradley, at Panama, with descriptions of three new species. Proc. U.S. Nat. Mus., 1882, 5 :620–632.

Kanazawa, R. H. 1963. Two new species of ophichthid eels from the Western Atlantic. Proc. Biol. Soc. Washington, 76 : 281–288.

Outdoor California, 1962. Yellow snake-eel stage small scale slippery invasion of California waters. Outdoor California, 23(3) :14.

Radovich, J. 1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures particularly during 1957 through 1959. Calif. Dept. Fish and Game, Fish Bull., (112) :1–62.

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A LAHONTAN REDSIDE, *RICHARDSONIUS EGREGIUS* (GIRARD), LACKING PELVIC FINS

A Lahontan redside which lacked pelvic fins was collected from Independence Lake, Sierra and Nevada Counties, California, on 1 July 1964. Independence Lake is at the headwaters of a tributary of the Little Truckee River, which is part of the Lahontan drainage system. The specimen measured 72.9 mm SL and weighed 7.6 g. It appeared normal in all respects except for the missing pelvic fins. An X-ray revealed that the basipterygia were absent. Scales completely covered the body where the pelvic fins normally occur, and no scars or aberrations were observed in this region. The specimen, X-rays, photographs, and field data are deposited in the Ichthyological collection of the California Academy of Sciences, catalog number CAS 23718.

—*Robert N. Lea, Department of Zoology-Fisheries, University of California, Berkeley, California.*

To Bob Behnke with the best regards of the author.

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Chromosoma (Berl.) 18, 455—466 (1966)

COMPARATIVE DNA VALUES AND CHROMOSOME COMPLEMENTS OF EIGHT SPECIES OF FISHES*

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Received February 8, 1966

Abstract. The present study appears to indicate that a series of polyploidization of the original vertebrate genome took place while vertebrates were still aquatic forms. The polyphyletic evolution of terrestrial vertebrates is suggested. The lung fish revealed close kinship to present-day members of the order *Caudata* of the class *Amphibia*. The DNA value was 3,540 per cent that of mammals. The trout had the DNA value similar to that of mammals and also to that of members of the orders *Crocodylia* and *Chelonia* of the class *Reptilia*. The DNA value of the gold fish, on the other hand, was very similar to that of birds and of snakes and lizards as well. It was 50 per cent that of mammals. Flat fishes and the swordtail had the undistinguished diploid complement made of 48 acrocentrics and the lowest DNA value merely 20 per cent that of mammals. They were regarded as the retainers of the original vertebrate genome.

Introduction

Placental mammals as a whole constitute one uniform group with regard to DNA content (considered in this study as 100 per cent), and various avian species constitute another uniform group with the comparative DNA value 44 to 59 per cent that of placental mammals (Ohno, Beçak and Beçak, 1964; Ohno, Stenius, Christian, Beçak and Beçak, 1964; Beçak, Beçak, Nazareth and, Ohno 1964; Atkin, Mattinson, Beçak and Ohno, 1965). These findings were interpreted to mean that extensive speciation from a common ancestor of each of the two classes of warm-blooded vertebrates was carried out without substantial change in total genetic content.

In the class *Reptilia*, two fairly discrete groups were discerned. The order *Crocodylia* and *Chelonia* had a DNA value only slightly below that of mammals, while the order *Squamata* demonstrated a DNA value only slightly above that of the class *Aves*. We then postulated that among ancient reptiles of the Mesozoic era, two different lineages with regard

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to total genetic content already existed, one eventually giving rise to placental mammals, the other the avian species. Thus, present-day reptiles also belonged to one or the other of these two lineages.

On the other hand, an extensive survey of comparative DNA values of amphibians (carried out by Joseph Gall of Yale University and quoted here with his kind permission) revealed that they possess much higher DNA values than reptiles, birds, and mammals. The lowest DNA value of this class, possessed by the family *Bufonidae* of the order *Salientia*, was 140 per cent that of mammals. Extraordinarily high values were obtained on members of the order *Caudata*, ranging from 705 per cent for *Plethodon cinereus* to 2,789 per cent for *Necturus maculosus*. The very fact that these members of the order *Caudata* have only 24 to 28 chromosomes in their complements makes doubtful any propinquity of descent between present-day amphibians and members of higher classes. It seems more reasonable to assume that the evolution of terrestrial vertebrates from aquatic vertebrates was polyphyletic.

If this assumption is correct, diverse DNA values might be found among present-day members of the class *Pisces*, some corresponding to those possessed by various terrestrial vertebrates of today. Our preliminary survey on chromosome complements of diverse species of fishes indicated that this might indeed be the case. Accordingly, eight species of the class *Pisces* representing two subclasses, six orders, and eight families were chosen for study. The comparative DNA value and the diploid complement of each species will be presented.

Materials and Methods

The eight species belonging to the class *Pisces* chosen for the present study are listed in Table 1.

Table 1. *Species of the Class Pisces Included in Present Study*

Subclass	Order	Family	Species, diploid number
Crossopterygii	*Dipnoi*	*Lepidosirenidae*	*Lepidosiren paradoxa*, $2n = 38$
Neopterygii	*Isospondyli*	*Salmonidae*	*Salmo irideus*, $2n = 60 \pm$
	Ostariophysi	*Cyprinidae*	*Carassius auratus*, $2n = 102 \pm$
	Percomorphi	*Cichlidae*	*Symphysodon aequifasciata* $2n = 60$
		Centrarchidae	*Lepomis cyanellus*, $2n = 46$—48
	Microcyprini	*Poeciliidae*	*Xiphophorus helleri*, $2n = 48$
	Heterosomata	*Pleuronectidae*	*Pleuronichthys verticalis*, $2n = 48$
		Bathidae	*Xystreurys liolepis*, $2n = 48$

Chromosoma (Berl.) 23, 1—9 (1967)

Diploid-Tetraploid Relationship among Old-World Members of the Fish Family *Cyprinidae**

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Received June 24, 1967

Abstract. Evidence suggesting that the goldfish and the carp of the family *Cyprinidae* are tetraploid species in relation to other members of the same family were presented. The two barb species, *Barbus tetrazona* and *Barbus fasciatus*, were chosen as representatives of diploid members of the family *Cyprinidae*. These barbs had the diploid chromosome number of 50 and 52 and the DNA value 20—22% that of placental mammals, while the goldfish (*Carassius auratus*) and the carp (*Cyprinus carpio*) had the diploid chromosome number of about 104 and the DNA value 50—52% that of placental mammals.

Introduction

Speciation from an immediate ancestor has no doubt been accomplished by allelic mutations at already existing gene loci. When evolution from one vertebrate class to another is considered, however, allelic mutations are no longer sufficient to account for all the changes that have taken place. Gene duplication now emerges as a prime factor in evolution.

Our previous studies on chromosome complements and DNA values of members of different vertebrate classes indicated that various degrees of gene duplication both by regional duplication of chromosomal segments and by polyploidization took place while vertebrates were still aquatic nearly 300 million years ago. Subsequent development of the chromosomal sex-determining mechanism tended to stabilize various genome lineages at characteristic degrees of gene duplication. Hence, evolution of terrestrial vertebrates from aquatic forms was polyphyletic.

Among ray-finned fishes (*Neopterygii*) of today, many were found to have a diploid chromosome complement of 48 acrocentrics. However, diverse DNA values were found. Flatfish of the order *Heterosomata* and members of the order *Microcyprini* had the DNA value only 20% that

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of placental mammals, while certain members of the order *Percomorphi* had the value 31% that of mammals and members of the suborder *Clupeoidea* the value 42% that of mammals (Ohno and Atkin, 1966, unpublished data). This increase in DNA value without a noticeable change in the diploid chromosome complement can be taken as evidence of gene duplication accomplished exclusively by repeated regional duplication of chromosomal segments. Rothfels and his colleagues (1966) have shown the similar situation in species of *Anemone* and related genera.

Suggestive evidence of polyploid evolution was furnished by certain teleost fishes which possessed approximately double the DNA value and twice the chromosome number of their close relatives. For instance, salmonoid fish had the DNA value 80% that of mammals and diploid complements made of 100 to 104 chromosome arms (Ohno and Atkin, 1966), while the DNA value of clupeoid fish was approximately 40% that of mammals and their diploid complements as a rule contained 48 acrocentrics (unpublished data).

Within the family *Cyprinidae* of the order *Ostariophysi*, the goldfish (*Carassius auratus*) has been shown to contain about 100 chromosomes in its diploid complement (Ojima *et al.*, 1966; Ohno and Atkin, 1966), and its DNA value was 52% that of placental mammals (Ohno and Atkin, 1966). While the goldfish's closest relative, the carp (*Cyprinus carpio*) has been reported to have a similarly high diploid chromosome number of 104 (Makino, 1939), the diploid chromosome number reported on other members of the family *Cyprinidae* was approximately 50 (Nogusa, 1960; Post, 1965; Chen, 1966). It was felt that the carp and the goldfish might represent the tetraploid state in relation to other members of the family *Cyprinidae*. Accordingly, the chromosome complements and DNA values of the goldfish and the carp were compared with those of the two species of barbs, *Barbus tetrazona* and *Barbus fasciatus*.

Materials and Methods

Five specimens each of the tetrazona barb, the fasciata barb, the goldfish and the carp of colored variety were used for the present experiment. Both sexes were represented in each species.

For chromosome analysis, each specimen received an intramuscular injection of 0.1 to 0.5 cc of 0.5% colchicine solution depending upon its body size 50 minutes prior to the time of sacrifice. For recovery of mitotic metaphase figures, gills and spleen of each fish were cut into small cubes of about 3 mm^3 in size. These cubes underwent hypotonic pretreatment in pH 7.0 distilled water for 15 minutes at room temperature. They were then transferred to a 50% acetic acid fixative. After 30 minutes of fixation, a squash preparation was made from each cube. Each preparation underwent 15 minutes of hydrolysis in 1N HCl at 50° C. Giemsa solution was employed for staining the preparations. Meiotic figures of the male were recovered from sexually mature testes in the same manner.

Comparative DNA values of the four species were obtained by measuring the Feulgen stain content of erythrocyte nuclei using the Deeley integrating microden-

Chromosoma (Berl.) 24, 59—66 (1968)

On the Diploid State of the Fish Order *Ostariophysi**

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Received December 29, 1967

Abstract. Our previous study on the order *Ostariophysi* was limited to members of the family *Cyprinidae*, suborder *Cyprinidea*. It was shown that the carp and the goldfish with 104 chromosomes and a DNA value of 50% that of mammals are tetraploid, as the diploid species of this family has 50—52 chromosomes and a 25% DNA value. In order to obtain some idea as to how many changes in DNA values and chromosome complements have occurred among diploid members of *Ostariophysi*, the study was expanded to cover members of the families *Cobitidae* and *Characinidae* of the suborder *Cyprinidea* as well as members of the families *Ictarulidae* and *Loricaridae* of the suborder *Siluroidea*. Diploid chromosome numbers varied from 50 to 98 and DNA values from 27—51% that of mammals. Apparently, diploid members of *Ostariophysi* underwent extensive chromosomal rearrangements as well as steady increases in DNA contents by regional duplication of chromosomal segments.

Introduction

On the basis of our comparative studies on DNA contents of various vertebrate classes and primitive chordates (Atkin, Mattinson, Beçak, and Ohno, 1965; Ohno and Atkin, 1966; and Atkin and Ohno, 1967), it was proposed that an ancestral vertebrate of the Ordovician period nearly 400 million years ago had a DNA content which was only 20% of the value (7.0×10^{-9} mg) possessed by placental mammals of today, and that its diploid complement was made up of 48 acrocentric chromosomes (Ohno, Atkin and Wolf, in press). This original karyotype and the 20% value which represents the lowest value of all vertebrates are still maintained by many specialized species of teleosts such as the flatfish of the order *Heterosomata* as well as the swordtail of the order

* In Duarte, this work was supported by a grant CA-05138 from the Nationa Cancer Institute, U.S. Public Health Service, and in part by a research fund established in honor of General James H. Doolittle. Contribution No. 21—67, Department of Biology. In Northwood, this project was supported by the British Empire Cancer Campaign.

** Fellow of the Institute for Advanced Learning of the City of Hope Medical Center.

Microcyprini (Ohno and Atkin, 1966). Diversification from this original state appears to have begun at the jawless state of vertebrate evolution, for lampreys and hagfish of the order *Cyclostomata* have DNA values considerably higher than the 20% value (Atkin and Ohno, 1967).

The following three mechanisms have contributed to the diversification in DNA contents and karyotypes. 1) Increase in DNA by regional duplication of chromosomal segments without changing the original karyotype. The original diploid complement of 48 acrocentrics was also found in the sunfish of the order *Percomorphi*, the anchovy of the suborder *Clupeoidea* and the hagfish of the order *Cyclostomata*. Yet, their DNA values were 30%, 40% and 80% that of mammals, respectively (Ohno and Atkin, 1966; Ohno, Muramoto, Klein, and Atkin, in press; Taylor, 1967; and Atkin and Ohno, 1967). 2) karyotypic changes with or without an increase in DNA content by regional duplication of chromosomal segments. The discus fish of the order *Percomorphi* has 60 chromosomes, 44 of which are metacentrics, yet it has the same DNA value as the sunfish with 48 acrocentrics. 3) Polyploidization. Tetraploid species were found among generalized teleosts of the orders *Isospondyli* and *Ostariophysi*. Within the order *Isospondyli*, herrings and anchovies of the suborder *Clupeoidea* and smelts of the family *Osmeridae*, suborder *Salmonoidea*, represented the diploid state, while trouts, salmons and whitefish of the families *Salmonidae* and *Coregonidae* having DNA values of 80—90% that of mammals were tetraploids (Ohno, Wolf, and Atkin, in press). Within the family *Cyprinidae* of the order *Ostariophysi*, the carp and the goldfish had 104 chromosomes and a DNA value 50% that of mammals, while other members had 50—52 chromosomes and a 25% DNA value. For this reason, the carp and the goldfish are considered to be tetraploid (Ohno, Muramoto, Christian and Atkin, 1967).

Our study on the order *Isospondyli* has made it evident that the diploid state of this order is represented by different DNA values and karyotypes. The herring and smelt have 52 chromosomes, 8 of which are metacentrics, and DNA values of merely 21 to 28%. Only the anchovy with 48 acrocentrics and a 40% DNA value represented a particular diploid state from which trouts, salmons and whitefish could have evolved by tetraploidization.

The present study on the order *Ostariophysi* was undertaken to determine the range of variability to be found among diploid species of this order.

Materials and Methods

The seven species presently studied are listed in Table 1. These represent five families and two suborders of *Ostariophysi*.

SUSUMU OHNO, ULRICH WOLF and NIELS B. ATKIN

EVOLUTION FROM FISH TO MAMMALS BY GENE DUPLICATION

Hereditas 59:169—187 (1968)

EVOLUTION FROM FISH TO MAMMALS BY GENE DUPLICATION

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(Received August 15th, 1967)

I. INTRODUCTION

WHILE speciation from an immediate common ancestor can be explained by allelic mutations at already existing gene loci, when evolution of the sub-phylum *Vertebrata* is considered *in toto,* allelic mutations are no longer sufficient to account for all the changes that have taken place during the past 300 million years. Gene duplication now emerges as the prime factor of evolution. It is becoming increasingly clear that in higher organisms such as mammals, one particular function is more often assigned to a group of several gene loci rather than to a single gene locus. Products of these several genes which arose by duplication from an ancestral gene perform the same function but in slightly different ways. These slight differences are exploited during ontogeny. Each somatic cell type at a given stage of development preferentially activates a few from the group of duplicated genes which fit the particular need of that cell type.

Pyruvate kinase is an essential enzyme for it is involved in glycolysis. If mammals are endowed with only a single gene locus which codes for a polypeptide of this enzyme, a deficient homozygous condition would surely be lethal. Yet, such a human homozygote merely suffers

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from nonspherocytic hemolytic anemia (TANAKA *et al.*, 1962). A homozygote escapes more catastrophic consequence, simply because man apparently possesses two separate gene loci for pyruvate kinase. Among many cell types of the human body, only erythropoietic cells exclusively utilize one gene locus with an amorphic mutant allele, while other cell types make use of either the other gene locus or both gene loci (KOLER *et al.*, 1964).

Aside from the above mentioned benefaction conferred by gene duplication, the most important role gene duplication played in vertebrate evolution was in the creation of new genes. The ability to produce immunoglobulin molecules is a unique property of vertebrates. Each immunoglobulin molecule is made of two subunits, the light-chain with the molecular weight of 20,000 and the heavy-chain with the molecular weight of either 50,000 or 70,000. The gene loci coding for these light- and heavy-chains must have arisen anew at the beginning of vertebrate evolution. For among jawless fish of today, the hagfish is totally incapable of gamma-globulin production, while the lamprey can produce 19S gamma-globulin molecules (PAPERMASTER *et al.*, 1962). Recent analysis of the amino acid sequence of light- and heavy-chains indicated that the heavy-chain is actually the duplicate and triplicate of a light-chain, and that the light-chain itself has an internal homology (LENNOX and COHN, 1967). An ancestral gene was probably coding for a polypeptide with the molecular weight of 10,000.

Gene duplication can be accomplished by the following four means: 1) by unequal exchange between the two sister chromatids of one chromosome, 2) by unequal crossing-over between the two homologous chromosomes during meiosis, 3) by regional redundant duplication of DNA molecules, and 4) by polyploidization. When gene duplication is accomplished by the first three means, the two duplicated gene loci should be arranged in tandem on the same chromosome. The gene loci for beta- and delta-chains of human hemoglobin are very closely linked (CEPPELLINI, 1959). The delta-chain gene must have been derived by unequal exchange or unequal crossing-over from the beta-chain gene.

If tetraploidization was responsible for gene duplication, on the other hand, the two duplicated genes should be located on two different chromosomes which were initially homologous to each other. The fact that the gene locus for alpha-chain of human hemoglobin is not linked to those for beta- and delta-chains and that in both man and the rabbit, the gene loci for light-chains of immunoglobulin are not linked with those for heavy-chains (KUNKEL, 1963—64; OUDIN, 1966) led us to

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CHAPTER 4

The Role of Gene Duplication in Vertebrate Evolution

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I. Introduction 109
II. Why Gene Duplication? 110
A. Allelic mutation and the limitation imposed by the assigned function . 110
B. Gene duplication, redundancy and greater freedom to mutate . . 111
C. Fusion of duplicates which further facilitates functional divergence . 114
D. The more immediate advantages of gene duplication 114
III. Hemoglobin and Immunoglobin Genes as Examples 115
A. Birth of hemoglobin genes by duplication 116
B. Creation of immunoglobin genes by duplication and fusion . . . 118
IV. Mechanisms of Gene Duplication and their Relative Advantages . . 122
A. Unequal exchange between two chromatids of the same chromosome . 122
B. Unequal crossing-over between two homologous chromosomes during meiosis 125
C. Regional redundant replication of DNA 125
D. Polyploidization 127
E. The stage of polyploidy in vertebrate evolution 129
V. Summary 130
References 131

I. Introduction

Evolution is the result of natural selection as envisaged by Charles Darwin. Natural selection in turn depends upon individual variability which is heritable.

The cause of heritable variability is mutation. While the structural gene (cistron) comprises DNA that specifies the amino acid sequence of a polypeptide, each mutation very often involves a single base substitution affecting one of the triplets in a cistron. Thus, a mutation leads to the replacement in the peptide chain of one amino acid by another.

By mutation is generally meant an allelic change at an already existing gene locus. Although allelic mutations can account sufficiently well for the origin of species from an immediate common ancestor, the evolution of mammals from fish could not have been due to allelic mutations alone. This is because big leaps in evolution were the consequence of the creation of new gene loci which arose from duplicates of an old one.

Higher vertebrates are an incredible complex of many different kinds of somatic cells. Indeed, it is no exaggeration to state that gene duplication

made such a great organization possible. Moreover, it is becoming evident that in higher vertebrates, a particular function is more often assigned to several gene loci rather than to a single gene locus. Products of these several genes arising by duplication from an ancestral gene carry out the same function but in significantly different ways. These differences are exploited during ontogeny, as each somatic cell type at a given stage of development preferentially activates a few from the group of duplicated genes which fit the particular need of that cell type.

This chapter which is concerned with the part played by gene duplication in vertebrate evolution falls into three parts: (1) Why gene duplication? (2) hemoglobin and immunoglobulin genes as examples of duplication, and (3) different mechanisms of gene duplication and their relative advantages.

II. Why Gene Duplication?

A. *Allelic mutation and the limitation imposed by the assigned function*

The function of a particular gene is defined by the amino acid sequence of the peptide chain it produces. The function assigned to a particular structural gene locus imposes severe restrictions on that gene's freedom to mutate, since natural selection eliminates the type of amino acid substitutions that hinder the given function of a polypeptide. It is not surprising, therefore, that the results of the complete analysis of the amino acid sequence of several different polypeptides in man and other vertebrates indicate the extremely conservative nature of structural genes.

Although every peptide chain has a part (or parts) that is vital to function, other parts are not as critical. It is only the non-critical parts that tolerate certain amino acid substitutions; and as a rule, short peptide chains consist almost entirely of a critical part upon which the assigned function depends. Thus, a structural gene which codes for a very short polypeptide would be expected to be most resistant to mutations. Insulin for example consists of two subunits, A and B, which are linked by two disulphide bridges. The A-chain has 21 amino acid residues, while the B-chain includes 31 amino acids. Studies of insulin of the horse, cattle, the pig, the sheep, the sperm whale and the sei-whale show that the B-chains are alike and that within the A-chains, substitutions had occurred only at the 8th, 9th and 10th positions (Harris *et al.*, 1958; Ishihara *et al.*, 1958). Furthermore, cytochrome *c* in vertebrates is a single peptide chain 104 residues in length. Such remotely related species as man and the tuna fish are found to differ only at 21 of the 104 sites (Margoliash, 1963).

A comparison of the sequences of shorter polypeptides of diverse vertebrate species confirms the extremely conservative nature of structural genes. Longer peptide chains such as hemoglobulin subunits show some tolerance toward amino acid substitutions at non-critical points in the chain.

Many of the alleles in human populations occur at the gene locus for the

α-chain and the β-chain of hemoglobin. Some are isoalleles which are functional equivalents of the species specific wild-type allele of that locus; others are deleterious alleles which, in the homozygous state, cause severe disease. Isoalleles bring about amino acid substitutions at non-critical sites of a peptide chain. Chronic methemoglobinemia, for example, is a disease caused by substitutions at critical sites. It will be remembered that histidine at the 58th and 87th positions of the α-chain and the same amino acid at the 63rd position of the β-chain represent the points of attachment of the peptide chains to the heme group. Substitution of a histidine residue at any of these three critical positions by a tyrosine residue, leads to methemoglobinemia. Hemoglobin is oxidized to methemoglobin at all times, but normally methemoglobin is easily reduced back to hemoglobin. However, a tyrosine residue mutationally introduced in place of a histidine residue at any of these positions resists reduction, since it forms a stable complex with the ferric iron of the heme group (Gerald and Scott, 1966).

Although such substitutions are known to cause disease and they are important in medicine, they have no bearing on the future course of evolution of the human species. For natural selection tolerates only those mutant alleles that continue to perform the function assigned to that gene locus. For this reason, tolerable allelic changes also contribute very little to the future evolution of a species.

Figure 1 compares the amino acid sequences of the α-chains of hemoglobin of man and the horse. It can be seen that these chains are 141 residues long, two of which differ only at 17 of the 141 sites (Braunitzer and Matsuda, 1963). Similarly, the β-chains of man and the horse are 146 residues long and only 25 sites are different, as shown in Fig. 2 (Smith, 1964). These differences reflect base substitutions (mutations) which have been accumulated independently by each species at the two gene loci. These base substitutions date back to the time Primates and Perissodactyla diverged from a common ancestor some 70 million years ago. Even so, a salient fact is that the α-chain of man resembles more closely that of the horse than its own β-chain. α- and β-chains of the horse produce hemoglobin molecules which are neither better nor worse than those of man, because despite millions of years of separation, the corresponding peptide chains maintained nearly identical sequences at parts critical to their assigned function. Clearly, big leaps in evolution could not have possibly taken place by allelic mutations at already existing gene loci, because evolution requires change and not conservation.

B. *Gene duplication, redundancy and greater freedom to mutate*

As long as a single gene locus discharges its vital function, natural selection always restricts that gene's freedom to mutate. Only when the genome (haploid set) incorporates two doses of the same gene by duplication is the severe restriction for a duplicate lifted. An original gene continues to

Horse and Human α-Chains

```
                1                                  10
Horse  α  Val-Leu-Ser-[ALA]-Ala-Asp-Lys-Thr-Asn-Val-Lys-Ala-Ala-Try-[SER]-
Human  α  Val-Leu-Ser-[PRO]-Ala-Asp-Lys-Thr-Asn-Val-Lys-Ala-Ala-Try-[GLY]-

                       20                                  30
Horse  α  Lys-Val-Gly-[GLY]-His-Ala-Gly-Glu-Tyr-Gly-Ala-Glu-Ala-Leu-Glu-
Human  α  Lys-Val-Gly-[ALA]-His-Ala-Gly-Glu-Tyr-Gly-Ala-Glu-Ala-Leu-Glu-

                                   40
Horse  α  Arg-Met-Phe-Leu-[GLY]-Phe-Pro-Thr-Thr-Lys-Thr-Tyr-Phe-Pro-His-
Human  α  Arg-Met-Phe-Leu-[SER]-Phe-Pro-Thr-Thr-Lys-Thr-Tyr-Phe-Pro-His-

                  50                                  60
Horse  α  Phe-Asp-Leu-Ser-His-Gly-Ser-Ala-Gln-Val-Lys-[ALA]-His-Gly-Lys-
Human  α  Phe-Asp-Leu-Ser-His-Gly-Ser-Ala-Gln-Val-Lys-[GLY]-His-Gly-Lys-

                                        70
Horse  α  Lys-Val-Ala-Asp-[GLY]-Leu-Thr-[LEU]-Ala-Val-[GLY]-His-[LEU]-
Human  α  Lys-Val-Ala-Asp-[ALA]-Leu-Thr-[ASN]-Ala-Val-[ALA]-His-[VAL]-

                                   80
Horse  α  Asp-Asp-[LEU]-Pro-[GLY]-Ala-Leu-Ser-[ASN]-Leu-Ser-Asp-Leu-
Human  α  Asp-Asp-[MET]-Pro-[ASN]-Ala-Leu-Ser-[ALA]-Leu-Ser-Asp-Leu-

                  90                                  100
Horse  α  His-Ala-His-Lys-Leu-Arg-Val-Asp-Pro-Val-Asn-Phe-Lys-Leu-Leu-Ser-
Human  α  His-Ala-His-Lys-Leu-Arg-Val-Asp-Pro-Val-Asn-Phe-Lys-Leu-Leu-Ser-

                                   110
Horse  α  His-Cys-Leu-Leu-[SER]-Thr-Leu-Ala-[VAL]-His-Leu-Pro-[ASN]-
Human  α  His-Cys-Leu-Leu-[VAL]-Thr-Leu-Ala-[ALA]-His-Leu-Pro-[ALA]-

                       120
Horse  α  [ASP]-Phe-Thr-Pro-Ala-Val-His-Ala-Ser-Leu-Asp-Lys-Phe-Leu-
Human  α  [GLU]-Phe-Thr-Pro-Ala-Val-His-Ala-Ser-Leu-Asp-Lys-Phe-Leu-

                130                                 140
Horse  α  [SER]-Ser-Val-Ser-Thr-Val-Leu-Thr-Ser-Lys-Lys-Tyr-Arg
Human  α  [ALA]-Ser-Val-Ser-Thr-Val-Leu- Thr-Ser-Lys-Lys-Tyr-Arg
```

FIG. 1. The amino acid sequence of the human α-chain of hemoglobin is compared with that of horse α-chain. The amino terminal of the chain is placed at the top left and the carboxyl terminal at the bottom right. Two chains differ only at 17 of the 141 sites. The positions outlined demonstrate the differences between the two chains.

Horse and Human β-Chains

```
                1                                                  10
Horse  β  Val- GLU -Leu- SER - GLY -Glu-Glu-Lys- ALA -Ala- LEU -
Human  β  Val- HIS -Leu- THR - PRO -Glu-Glu-Lys- SER -Ala- VAL -

                                                  20
Horse  β  VAL -Ala-Leu-Try- ASP -Lys-Val-Asp- GLU - GLU -Glu-Val-Gly-
Human  β  THR -Ala-Leu-Try- GLY -Lys-Val-Asp- VAL - ASP -Glu-Val-Gly-

                        30                                         40
Horse  β  Gly-Glu-Ala-Leu-Gly-Arg-Leu-Leu-Val-Val-Tyr-Pro-Try-Thr-Glu-Arg-
Human  β  Gly-Glu-Ala-Leu-Gly-Arg-Leu-Leu-Val-Val-Tyr-Pro-Try-Thr-Glu-Arg-

                                          50
Horse  β  Phe-Phe-Glu-Ser-Phe-Gly-Asp-Leu-Ser- GLY -Pro-Asp-Ala-Val-Met-
Human  β  Phe-Phe-Glu-Ser-Phe-Gly-Asp-Leu-Ser- THR -Pro-Asp-Ala-Val-Met-

                    60
Horse  β  Gly-Asp-Pro-Lys-Val-Lys-Ala-His-Gly-Lys-Lys-Val-Leu- HIS -
Human  β  Gly-Asp-Pro-Lys-Val-Lys-Ala-His-Gly-Lys-Lys-Val-Leu- GLY -

          70                                                   80
Horse  β  SER -Phe- GLY - GLU -Gly- VAL - HIS -His-Leu-Asp-Asp-Leu-
Human  β  ALA -Phe- SER - ASP -Gly- LEU - ALA -His-Leu-Asp-Asp-Leu-

                                    90
Horse  β  Lys-Gly-Thr-Phe-Ala- ALA -Leu-Ser-Glu-Leu-His-Cys-Asp-Lys-Leu-
Human  β  Lys-Gly-Thr-Phe-Ala- THR -Leu-Ser-Glu-Leu-His-Cys-Asp-Lys-Leu-

                    100                                        110
Horse  β  His-Val-Asp-Pro-Glu-Asp-Phe-Arg-Leu-Leu-Gly-Asp-Val-Leu- ALA -
Human  β  His-Val-Asp-Pro-Glu-Asp-Phe-Arg-Leu-Leu-Gly-Asp-Val-Leu- VAL -

                                              120
Horse  β  LEU -Val- VAL -Ala- ARG -His-Phe-Gly-Lys- ASP -Phe-Thr-Pro-
Human  β  CYS -Val- LEU -Ala- HIS -His-Phe-Gly-Lys- GLU -Phe-Thr-Pro-

                                    130
Horse  β  GLU - LEU -Glu-Ala- SER -Tyr-Glu-Lys-Val-Val-Ala-Gly-Val-Ala-
Human  β  PRO - VAL -Glu-Ala- ALA -Tyr-Glu-Lys-Val-Val-Ala-Gly-Val-Ala-

          140
Horse  β  Asp-Ala-Leu-Ala-His-Lys-Tyr-His
Human  β  Asp-Ala-Leu-Ala-His-Lys-Tyr-His
```

FIG. 2. The amino acid sequence of the human β-chain of hemoglobin is compared to that of the horse β-chain. The two chains differ only at 25 of the 146 sites.

carry out the function assigned to that locus, thereby resulting in a redundant duplicate. This redundant locus has the ability to accumulate independent base substitutions, many of which had been forbidden. Because of random accumulation of mutations, the redundant locus might begin to code for a degenerate peptide chain which is useless. In such an event, nature's experiment is a failure, and the redundant gene locus in this sense joins a collection of inactive DNA molecules which every vertebrate species carries in the form of so-called "constitutive heterochromatin". Conversely, the drift might bring about a change in the base sequence of that cistron in such a way that a polypeptide when produced acquires a useful function which though related, is different from that assigned to the original gene locus. A new gene locus is thus born, but to conserve it, natural selection again imposes new but equally severe restrictions on this gene's freedom to mutate.

C. *Fusion of duplicates which further facilitates functional divergence*

Redundancy alone allows of a duplicate to accumulate otherwise intolerable base substitutions. But so long as a duplicate has the original number of triplets, its function cannot diverge too much from that assigned to an original gene, since the number of amino acid residues limits the function of that peptide chain.

However, a drastic divergence in function is possible provided the duplicate undergoes a significant change in length. In fact the available evidence indicates that in evolution, fusion between two duplicates has occurred rather often. A new cistron whose length is twice that of an original gene has been subjected by nature to bolder experiments, including not only base substitutions but also deletions and insertions. The gene which has ultimately emerged from such a fused duplicate may code for a peptide chain with a function vastly different from that coded by an original gene; the homology between the two peptide chains may not at all be obvious until the complete amino acid sequences of the two chains are examined.

D. *The more immediate advantages of gene duplication*

Besides creating new genes, gene duplication confers on the organism certain immediate benefits. For example, if mammals had only a single gene locus which codes for a polypeptide of the enzyme, pyruvate kinase, a deficient homozygous condition would prove to be lethal. Yet, a human homozygote suffers only from non-spherocytic hemolytic anemia (Tanaka *et al.*, 1962). That is to say, a homozygote escapes more catastrophic consequences, simply because man possesses two separate gene loci for pyruvate kinase. Of the many cell types, only erythropoietic cells exclusively utilize one particular gene locus in which an amorphic mutant allele exists. Other cell types use either the other gene locus or both gene loci (Koler *et al.*, 1964).

Lactate dehydrogenase is a tetrameric molecule. In most of the vertebrates

studied, two separate gene loci coding for A- and B-subunits of this enzyme have been found. A- and B-subunits associate indiscriminately and form five tetrameric forms (A_4, A_3B, A_2B_2, AB_3 and B_4). These two gene loci arose by duplication from a common ancestor and the products of two gene loci are still capable of recognizing each other and themselves with equal ability.

The kinetics of the five molecular forms of the A- and B-subunits when studied as a function of substrate concentration and oxygen tension are not the same. In fact each somatic tissue exploits these differences by producing the five forms in appropriate ratios. This can be done by regulating the relative output of A- and B-subunits. If, for instance, a particular cell type produces A- and B-subunits in equal amounts, the ratio of these forms would be 1:4:6:4:1. If, however, four times more A-subunits than B-subunits are produced, the ratio would shift to 256:256:94:16:1 (Markert, 1964).

Another immediate advantage which the organism can derive from gene duplication is that a single duplication may provide a heterozygous advantage to members of a species. It is believed that an allele for an abnormal β^S-chain of human hemoglobin persists in African populations with a remarkably high frequency, because relative resistance to falciparum malaria is passed on to β/β^S-heterozygotes (Allison, 1954). As long as the normal β-chain and the abnormal β^S-chain gene exist as two alleles of the same gene locus, production of desirable heterozygotes is invariably accompanied by the production of deleterious β^S/β^S-homozygotes suffering from severe sickle-cell anemia. By gene duplication, the β-allele and a β^S-allele can be placed on the same chromosome to become two separate gene loci in extremely close linkage. If this occurs, then every member of a population would have a heterozygous advantage without ever having to produce a deleterious homozygous type. The fact that this type of duplication has never been observed among African people suggests that doubling of the β-chain gene dosage without simultaneously also increasing the α-chain gene dosage does more than offset the advantage gained by placing β- and β^S-alleles on the same chromosome. The almost exclusive formation of $\alpha_2\beta_2$-tetrameric hemoglobin molecules requires that α-chains and β-chains be produced in nearly equal amounts. Were the β-chain locus not to have to coordinate its activity with the α-chain locus, it is almost certain that the population would utilize such a gene duplication.

III. Hemoglobin and Immunoglobulin Genes as Examples

The techniques commonly used for the genetic study of proteins and their component polypeptides emphasize an existing difference between two related gene products. Electrophoresis, immunology and mapping of peptides obtained from digested proteins are frequently ways of detecting a single amino acid substitution. However, they are of little use in ascertaining homology between the products of two separate gene loci. Only by analysing the amino acid sequence, is it possible to know the homology. Furthermore,

when the complete amino acid sequence of each of the polypeptides coded by a group of duplicated genes becomes known, attempts at comparing these chains of the same species and at comparing the corresponding peptide chains of different species enable us to roughly determine at what stage of vertebrate evolution each gene duplication occurred. They also make it possible to know what changes followed each duplication. At present, this approach to the study of the evolutional process is being pursued with various hemoglobin polypeptides, and to a lesser extent with light- and heavy-chain subunits of immunoglobulin.

A. *Birth of hemoglobin genes by duplication*

While vertebrates from the most primitive hagfish to man are endowed with hemoglobin molecules, urochordates and cephalochordates lack hemoglobin. It is likely that the earliest gene for a hemoglobin polypeptide came into being at the onset of vertebrate evolution. On the other hand, the existence of hemoglobin in diverse invertebrate species suggests that a primordial gene capable of becoming a gene for hemoglobin has long been present in the animal kingdom.

It is the view of Ingram (1963) that this primordial gene had coded for a monomeric heme-containing protein. In vertebrates, the available evidence indicates that the first duplication of this locus gave rise to myoglobin and a hemoglobin gene. X-ray diffraction studies have shown that a myoglobin peptide chain and a hemoglobin polypeptide are folded around the heme group in a nearly identical way (Perutz *et al.*, 1960; Kendrew *et al.*, 1960). The assumption that both arose from a common ancestor is well founded, the cardinal difference between the two being that myoglobin remained a monomer, and hemoglobin a tetramer. There is good evidence that hemoglobin peptide chains acquired the ability to recognize each other. This having been acquired by a deletion, since all the known hemoglobin polypeptides of vertebrates that can polymerize are considerably shorter than the myoglobin peptide chain. These peptide chains are 141–146 amino acid residues long, and the myoglobin peptide chains about 152 residues.

A deletion involving several triplets from an ancestral hemoglobin cistron appears to have occurred after the development of a jaw by vertebrates. Monomeric hemoglobin is still found in the hagfish and the lamprey representing the most primitive jawless state in vertebrate evolution. A hemoglobin peptide chain of the lamprey has in fact been shown to be 156 residues long (Rudloff *et al.*, 1966). In the case of the hagfish, an undeleted ancestral hemoglobin gene had undergone further duplication, for this fish has several gene loci for hemoglobin polypeptides. Nevertheless, it is interesting that the product of each locus has remained a monomer (Ohno and Morrison, 1966).

The question of further duplication of a deleted ancestral hemogoblin gene giving rise to five separate hemoglobin gene loci in man, is perhaps clarified by descending the ladder of evolution from man to fish. Among the

five hemoglobin peptide chains of man, the α-chain stands apart from the rest in two respects. First, while the α-chain is produced by hemopoietic cells throughout the pre- and postnatal life of man, the ε-, γ-, and β-, δ-chains arise in sequence. Embryonic hemoglobin is $\alpha_2\varepsilon_2$, fetal hemoglobin $\alpha_2\gamma_2$ and two types of adult hemoglobin are $\alpha_2\beta_2$ and $\alpha_2\delta_2$. Second, the α-chain consists of 141 amino acid residues, while other chains consist of 146 residues.

It is interesting that the α-chain of the horse and of the mouse has also been shown to have 141 residues, while the β-chain of the horse, the mouse and the pig have 146 residues. In comparing the human α-chain shown in Fig. 1 with the human β-chain in Fig. 2, the two differ by as much as 84 substitutions and deletions. However, when the human α-chain is compared with that of the horse (Fig. 1), only 17 substitutions are discernible (Braunitzer and Matsuda, 1963). Similarly, when the human β-chain is compared with the horse β-chain, as indicated by Fig. 2, only 25 substitutions are found (Smith, 1964). It would thus appear that when the primordial mammal first emerged more than 70 million years ago, it already possessed two separate gene loci for hemoglobin polypeptides; one coding for the 141 residue long α-chain and the other for 146 residue β-chain.

In addition, information on the amino acid sequences of several segments of hemoglobin peptide chains of the carp (*Cyprinus carpio*) indicates that this species has two separate hemoglobin gene loci. One of the two chains can be considered homologous to the mammalian α-chain since it lacks six amino acid residues which correspond to those occupying 51st–56th positions in the mammalian β-chain. Deletion of these positions is one of the main features distinguishing the mammalian α-chain from the β- and other chains. Since the other chain of the carp has these six residues, it is regarded as homologous to the mammalian β- or γ-chain (Hilse *et al.*, 1966). These considerations imply that the second gene duplication which created the gene locus for the α-chain and the gene locus for a β-like chain, must have occurred when the future mammalian line was represented by a particular type of crossopterygian fish.

It is not yet known when in vertebrate evolution the third duplication responsible for the diversification of the original gene into the β-chain proper and the γ-chain gene had occurred. The human β- and γ-chains differ by 39 substitutions (Schroeder, 1963), thereby suggesting that these loci have led separate existences for some time. It has frequently been suggested that of the two, the γ-chain shows a closer kinship to the α-chain. In other words, the γ-chain locus is the direct descendant of the original gene locus for the β-like chain, while the β-chain locus is its duplicate. But not all mammals have the gene locus for the γ-chain. With Professor Hector Marquez-Monter of Mexico City, we have examined nearly 50 horse fetuses in various stages of development, the youngest being only 90 mm in crown-rump length. Even when globin subunits were subjected to urea gel electrophoresis, we were unable to distinguish the horse fetal hemoglobin

from that of the adult. Barring the possibility of the horse β- and γ-chains having the same net molecular charge, this observation suggests the absence of a gene locus for the γ-chain. Cattle, unlike the horse, have the γ-locus. Cattle β- and γ-chains differ only by 23 substitutions (Babin, 1966). Compared to the human β- and γ-chains, cattle β- and γ-chains are much more closely related to each other. It could be that the gene locus for the γ-chain is a fossil gene which has long been inactivate in most mammals. Only in man and possibly other primates have a series of base substitutions in this locus, provided the γ-chain with a special property, namely of $\alpha_2\gamma_2$ hemoglobin molecules being particularly capable of sustaining fetal life. For this reason, this vestigial gene remains active. The γ-chain locus of cattle may not be homologous to that of man. Possibly, it arose *de novo* in a primordial ruminant by an independent duplication involving the β-chain locus. Hence, it would be more appropriate to call it the fetal β-chain locus rather than the γ-chain locus.

Among the hemoglobin polypeptides of man, the β- and δ-chains are the most closely related, since the two differ only by 10 substitutions (Ingram and Stretton, 1962). There is little doubt that the δ-chain locus arose from the β-chain locus as the result of the occurrence of duplication in primordial man. This δ-chain gene is a very inefficient producer: Hb A_2 ($\alpha_2\delta_2$) amounts to only 1·5–4·0% of the total adult hemoglobin. Were the δ-chain gene as efficient a producer as the β-chain gene, this duplication would probably not have been tolerated, for β- and δ-chains produced in excess of α-chains would most likely exert deleterious effects. Thus, a new duplicate is sometimes not eliminated by the species, because it is harmless, and not because it confers an immediate selective advantage.

The main point to be emphasized here is that both the first and second gene duplication in vertebrates had led to the occurrence of tetrameric hemoglobin long before the emergence of terrestrial vertebrates. The first duplication was responsible for a myoglobin gene and an original hemoglobin gene. The second duplication produced the α-like chain and the β-like chain genes. These two peptide chains became able to recognize each other and to form tetrameric molecules. Indeed these two duplications are regarded as major leaps in evolution.

B. *Creation of immunoglobulin genes by duplication and fusion*

The ability of vertebrates to produce immunoglobulin molecules is a unique property. The gene loci coding for polypeptide subunits of these molecules are traceable to ancient ostracoderm fish, since the survivors of the most primitive jawless animals include the lamprey which does produce immunoglobulin and the hagfish which does not (Papermaster *et al.*, 1962).

Mammals produce three major types of immunoglobulin subunits: the light (L)-chain which is 210 to 220 amino acid residues long, the heavy (H)-chain which is about 450 residues long and a special μ-heavy chain which

is 650 or so residues long. There are tetrameric and decameric forms of immunoglobulin molecules. IgG, IgA, IgD and IgE classes are represented by tetrameric molecules, each consisting of two identical L-chains and two identical H-chains, as schematically illustrated in Fig. 3(*a*). The IgM class, on the other hand, consists of decameric molecules. A special μ-chain is used in place of the ordinary H-chain to combine with the L-chain (Fig. 3 (*b*)).

The cistrons which code for subunits of immunoglobulin molecules have the special ability of providing immensely variable amino acid sequences to the polypeptide chain they produce. Two antibodies of distinct specificity produced by the same individual differ by a contiguous, variable amino acid sequence of both the L-chain and H-chain. Mammals are capable of producing several thousand kinds of antibodies directed against numerous antigens to which they are exposed. These great variations in amino acid sequences which determine the antibody specificity of individual immunoglobulin molecules appear to be brought about by substitutions which occur at the fixed sites of the L- and H-chains. These sites are included in the region of a peptide chain of about 105 amino acid residues long, starting from the amino terminal. If the variable region of the L- or H-chain includes 40 such sites, and if one of three different amino acids can occupy each of these sites, the region will generate 3^{40} different variable sequences which are more than sufficient to account for the many different kinds of antibodies produced. The remaining region of a L- or H-chain which does not have variable sites is known as the constant region.

Since the mechanism responsible for these variabilities is not yet clear, we will exclude this aspect from the discussion, and will instead treat the cistrons for L- and H-chains as ordinary structural genes.

Man, the mouse, the rabbit and presumably most other mammals have at least two separate gene loci which code for k- and λ-L-chains. Both chains are about 210–220 amino acid residues long; the difference in length is due to the fact that a clone of plasma cells often produces a light chain without certain variable sites. The k-chain of man as well as that of the mouse has cysteine as the carboxyl terminal, while the λ-chain has one more amino acid, serine in the case of man, after cysteine. Complete amino acid sequences have been determined on several k- and λ-chains produced by monoclonal myelomas of man and the mouse (Hilschmann and Craig, 1965; Milstein, 1966; Porter, 1966; Baglioni, 1967; Gray *et al.*, 1967). A comparison of these sequences shows a great deal of homology between k- and λ-chains of man. Obviously these two gene loci arose by duplication in a primordial mammal. When the constant region (from the carboxyl terminal to the 106th position) of the mouse and human k-chains are compared, there is roughly a 60% homology, while the human k- and λ-chain show only a 48% homology (Lennox and Cohn, 1967). A more striking result suggested by a sequential study of light-chains is that if substitutions at the variable sites identified with antibody specificity are discounted, the light-chain itself shows internal homology. Various amino acids occupying non-variable sites

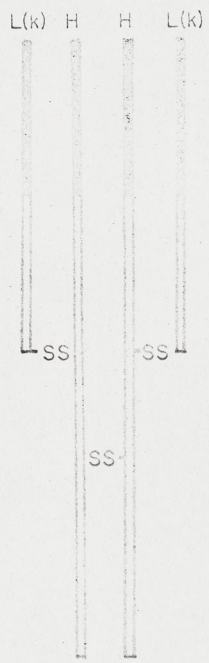

FIG. 3(a)

X5

FIG. 3(b)

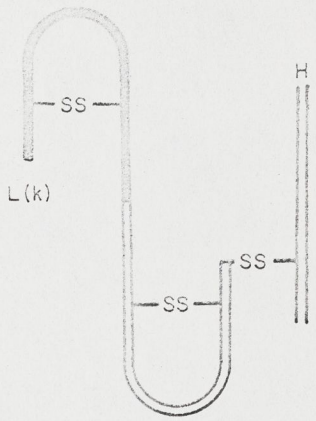

FIG. 4

FIG. 3. Schematic illustration of immunoglobulin molecules.

FIG. 3 (*a*). A tetrameric molecule of IgG, IgA, IgD and IgE classes. Two L-chains are bound to two H-chains by disulphide bridges. The length of the H-chain is twice that of the L-chain. The amino half of the L-chain represents the variable region (painted solid black) and the carboxyl half, the constant region (outlined). Since this L-chain is drawn to have cysteine at the carboxyl end, it is a k-type L-chain.

FIG. 3 (*b*). A dimeric unit of decameric molecules of IgM class. A special μ-heavy-chain used by the IgM class has three times the length of the L-chain.

FIG. 4. A more realistic representation of L-chain. One internal disulphide bridge occurs between cysteines in the variable region, with the other internal disulphide bridge between cysteines of the constant region. An obvious symmetry that exists between the variable and constant regions suggests that the L-chain gene arose by tandem fusion of two identical cistrons.

within the variable region (from the amino terminal to the 105th position) are often found in the corresponding sites in the constant region (from the 106th position to the carboxyl terminal which can be the 212th–218th) (Lennox and Cohn, 1967). Cysteine occupies the 22nd and 87th positions in the variable region and the 132nd (105+27) and 192nd (105+87) in the constant region of a human k-chain. This indicates that an original cistron for light-chain arose by tandem fusion of two duplicates, as shown in Fig. 4 (Milstein, 1966; Baglioni, 1967).

It is generally believed that man, the mouse and other mammals possess nearly ten separate gene loci which code for H-chains of IgG IgA, IgD and, IgE classes. For instance, four separate gene loci code for γ^a, γ^b, γ^c and γ^d H-chains of IgG, and yet another two gene loci code for α^a and α^b H-chains of IgA. These heavy-chains are about 450 amino acid residues long. The available data on partial sequences of H-chains indicate that an original cistron for this type of H-chain arose by tandem fusion of two L-chain cistrons (Doolittle *et al.*, 1966). The μ-chain of IgM is about 200 amino acid residues longer than other H-chains. For this reason, the gene locus for μ-chain can be considered a triplicate of L-chains.

Apparently, all these gene loci for L-chains, H-chains and μ-chain were already present in the genome of the primordial mammal. The frog, too, has gene loci for all three types of immunoglobulin subunits. It has at least one gene locus for the L-chain, the H-chain of the IgG class and the μ-chain of the IgM class (Marchalonis and Edelman, 1966*a*).

We have now to descend further the ladder of evolution to the class *Elasmobranchii* in order to find a situation where the organism is capable of producing only two types of immunoglobulin subunits. Studies by Marchalonis and Edelman (1966*b*) have shown that the smooth dogfish produces only an IgM class of immunoglobulin. This is because the species has the gene loci for an L-chain and μ-chain, and is not provided with the gene locus for the H-chain of IgG class. While the tandem fusion of three L-chain cistrons which produced the gene locus for μ-chain had occurred in an ancestor of this class, the second and independent fusion of two L-chain cistrons leading to a gene locus for the H-chain of the IgG and other classes developed after the emergence of bony fish of the class *Osteichthyes*.

When the ostracoderm fish first emerged, its genome probably contained a gene locus coding for a peptide chain consisting of 100 odd amino acids. While the function of this primordial gene may never be known, the first step was its doubling by duplication and fusion. Thus, a gene locus for L-chain of about 210 residues long was born. Unless the gene locus for μ-chain appeared in quick succession, the organism would not have been able to maintain a newly created L-chain locus. This is because the L-chain alone is an ineffective antibody.

The first duplication and fusion creating an L-chain locus, and the second duplication and fusion creating a μ-chain locus occurred before the emergence of bony fish. By the time the terrestrial vertebrate came into

being, the third duplication and fusion had already taken place and the organism was endowed with the gene locus for the H-chain. It would thus appear that a particular type of crossopterygian fish which eventually gave rise to mammals had at least one gene locus for each of the three classes of immunoglobulin subunits.

IV. Mechanisms of Gene Duplication and their Relative Advantages

Of the four different mechanisms by which gene duplication occurred during evolution, the first two result in a duplicate in the immediate vicinity of an original gene. This tandem arrangement of an original and a duplicate gene is essential if a new cistron is to be created by fusion of the two. The third mechanism also leads to tandem duplication, but it involves a segment of a chromosome containing a number of different gene loci. These three mechanisms have in common certain shortcomings, such as instability caused by the close linkage of duplicates, at a time when there is a tendency to further duplication and deletion of that segment of a chromosome. Without stabilization, duplicates can not diverge from each other so as to acquire different functions. More often than not, protein molecules are made of two different subunits coded by separate gene loci. For such a pair of gene loci, tandem duplication of one locus without concurrent duplication of the other would be deleterious.

The fourth mechanism involves the duplication of every gene locus simultaneously and the placing of an original and a duplicate on separate chromosomes. Thus, the first three mechanisms and the fourth are complementary. Indeed, the evidence indicates that during vertebrate evolution, these mechanisms were utilized alternately. In the case of mammalian immunoglobulin genes, the L-chain gene loci are not linked to the H-chain gene loci, but two gene loci for (K-) and λ-L-chains are closely linked, and so are the nearly ten gene loci for H-chains.

A. *Unequal exchange between two chromatids of the same chromosome*

When for the first time, Taylor *et al.* (1957) studied the DNA replication pattern of individual chromosomes by utilizing radioactive thymidine, they unexpectedly noticed frequent exchanges between two chromatids of the same chromosome. The arrangement of DNA strands in the chromosome is such that each metaphase chromosome of a daughter cell whose mother cell has incorporated tritiated-thymidine into its DNA includes a labelled chromatid and an unlabelled one. The observed pattern, however, was unexpectedly complicated. Both chromatids of a chromosome consisted of labelled and unlabelled parts, and when a part of one chromatid was labelled, the corresponding part of the other chromatid was not labelled. Clearly, during the synthetic phase of the mitotic cycle, frequent exchanges between two chromatids of the same chromosome occur. Two chromatids

of the same chromosome are assumed to be absolutely identical. On the surface, this type of exchange seems to be of no consequence, but since it does occur frequently, it could on occasion be unequal, as indicated by Fig. 5. Even the slightest unequal exchange would lead to the placement of

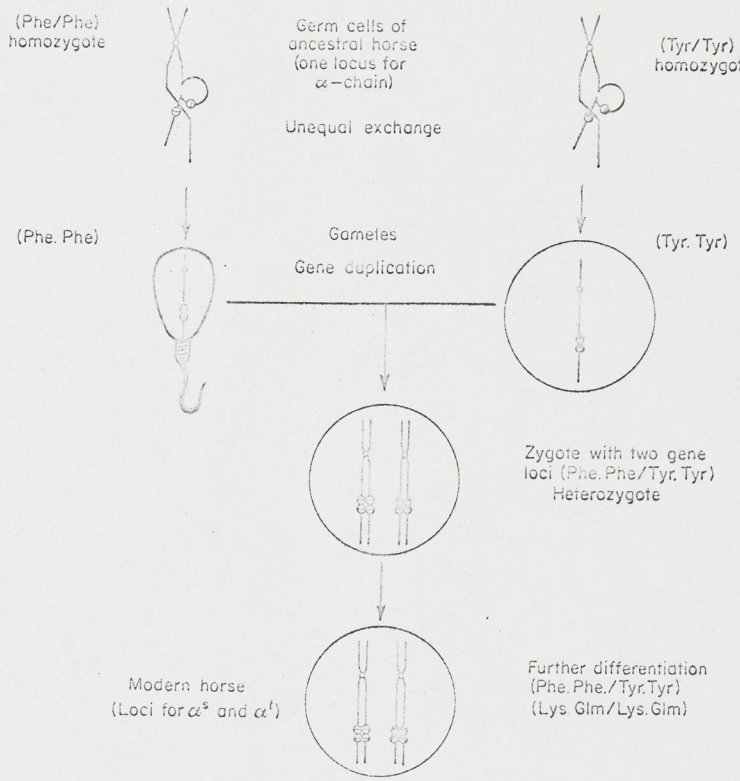

FIG. 5. Gene duplication by unequal exchange between two sister chromatids of the same chromosome can result in a unique situation in which two closely linked duplicated gene loci share the same allelic alternatives. This is schematically illustrated using the gene loci for horse α-chains as examples. A small open circle denotes the centromere of the chromosome, while each large circle represents an α-chain cistron. A cistron which codes for phenylalanine at the 124th position is drawn as a circle, having an outlined upper half while the cistron which codes for tyrosine at the 24th position is drawn as a circle having a solidly black upper half. When the bottom half of a circle is outlined, it indicates that the cistron codes for lysine at the 60th position. The shaded bottom half, on the other hand, indicates that the cistron codes for glutamine at the 60th position.

two identical cistrons on one chromatid and the deletion of that locus from the other chromatid. The exchange would result in one of the daughter cells becoming heterozygous for a gene duplication and the other daughter cell hemizygous for that locus. Were this to occur during mitosis of germ cells and were duplication to confer an immediate selective advantage on the offspring, the entire population would in time become homozygous for this duplication. Such a mechanism of gene duplication can result in a very

unique situation characterized by two duplicated loci sharing similar alleles.

It has been known for some time that upon electrophoresis, blood of every adult horse yields two distinct hemoglobin bands of equal intensity. This is attributable to the fact that the horse produces two different kinds of α-chains, α^f and α^s. The faster moving band represents $(\alpha^f)_2\beta_2$ tetramers, and the slower moving band $(\alpha^s)_2\beta_2$ tetramers. These two α-chains differ by a single substitution at position 60 of a polypeptide chain. Lysine of α^s is substituted by glutamine in α^f. Thus, the amino acid sequence of the α-chain appearing in Fig. 1 is that of α^s. It has also been observed that there is an allelic substitution from tyrosine to phenylalanine at position 24 of both α-chains. With regard to the α-chain, mating between a homozygous (Tyr/Tyr) stallion and a homozygous (Phe/Phe) mare produced heterozygous (Tyr/Phe) offspring. The most intriguing fact is that such a heterozygote produces two kinds of α^s-chains and two kinds of α^f-chains (Kilmartin and Clegg, 1967).

It could be that an ambiguous coding at position 60 of a single gene locus is responsible for the production of α^s-chain and α^f-chain. An alternative explanation is that α^s and α^f are coded by an original and a very recently arisen duplicate that share the same allelic alternatives. An immediate ancestor of the modern horse (*Equus caballus*) may have produced only one kind of α-chain, since it had only a single gene locus. This is not an unreasonable assumption, as the donkey, the horse's cousin, makes only one kind of α-chain. At the single locus stage, the horse may have already maintained two alleles, one coding for tyrosine and the other for phenylalanine at position 24. If duplication of this locus was accomplished by two separate events involving an unequal exchange within the same chromosome, an original and a duplicate loci on the same chromosome must have received the same codon for the 24th position. Thus, the two different kinds of homologous chromosomes came into being within the population: an original and a duplicate on one chromosome that codes for phenylalanine at the 24th position, and both on the other chromosome that code for tyrosine at the 24th position. Since an original and a duplicate are closely linked, there would be no recombination. A duplicate diverged subsequently from an original by replacing glutamine with lysine or *vice versa* at the 60th position. In this manner, the modern horse came to have one gene locus for α^s and another locus for α^f, with both loci on the same chromosome invariably sharing the same allelic change.

Professor Kurt Benirschke enabled us to examine blood samples of two Przewalski horses. We found that they too possess two kinds of α-chains. The Przewalski horse (*Equus przewalskii*) has 66 chromosomes (Benirschke *et al.*, 1965), while the horse of all breeds has 64 chromosomes. It must be that either duplication of the α-chain locus or a mutation which causes an ambiguous coding at the 60th position of the α-chain cistron occurred before a common ancestor diverged into two different horse species.

It is hoped that the phenomenon of two or more duplicated loci on the

same chromosome sharing the same allelic alternative will be substantiated by more unequivocal evidence in the future.

B. *Unequal crossing-over between two homologous chromosomes during meiosis*

In order to produce haploid gametes (eggs and spermatozoön) germ cells of a diploid organism pass through meiosis. During meiosis, two homologues pair side-by-side and form chiasmata between the two. Consequently, an exchange of genetic material takes place between the paternally derived and maternally derived elements. Again, an exchange of this sort might occasionally be uneven, the result being duplication on one chromatid and deletion of a gene locus from the other chromatid as illustrated by Fig. 6. If such an unequal crossing-over were to occur to a heterozygous individual during meiosis, two different alleles of the same locus would be placed on one chromosome as two separate gene loci. It thus becomes immediately evident that a single gene duplication of this type has the ability to confer a heterozygous advantage on every member of a species (Fig. 6).

Indeed, unequal crossing-over resulting in two alleles on one chromosome has occurred in man at the gene locus for haptoglobin α-chain. In this case, the problem of excessive gene dosage was solved by making one cistron out of two tandemly placed alleles. It has been known for some time that there exist in human populations at least three alleles of this gene locus, viz. Hp^{1F}, Hp^{1S} and Hp^{2}. Smithies *et al.* (1964) showed that the α-chain coded by Hp^{2}-allele has about twice the molecular weight of that coded by Hp^{1}-alleles, and that the amino terminal half (of the Hp^{2}-α-chain) consists of Hp^{1F} peptide chain and the carboxyl terminal half of Hp^{1S} peptide chain.

C. *Regional redundant replication of DNA*

Normally, replication of chromosomal DNA occurs only in preparation for mitosis, and newly synthesized DNA strands are divided evenly between two sister chromatids. If DNA molecules are arranged in a series of rings, however, it is conceivable that DNA replication might sometimes result in the growth of an individual ring, for the old and newly replicated strands may fuse in tandem fashion. Were this to occur, longitudinal duplication of an entire set of cistrons constituting an original ring would result.

On the basis of the following findings, Keyl (1966) holds that gene duplication by this mechanism has in fact played a part in the evolution of dipteran insects. This investigator observed that two subspecies of the midge (*Chironomus thummi*), although having an identical diploid complement, showed a marked difference in DNA content. The diploid nucleus of *Ch. th. thummi* contained 27% more DNA than that of *Ch. th. piger*. When the DNA contents of individual homologous bands of the two subspecies were compared on giant salivary gland chromosomes, it was noted that

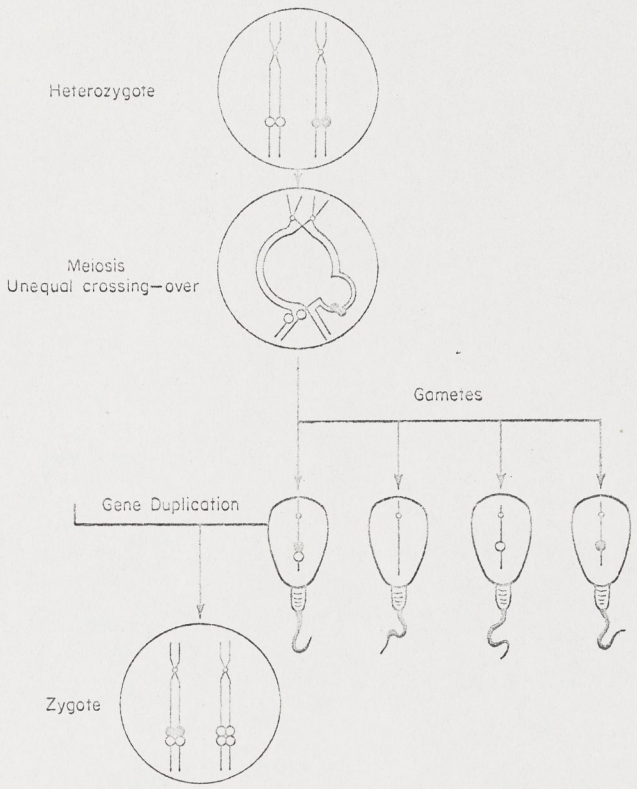

FIG. 6. Gene duplication by unequal crossing-over between two homologous chromosomes during meiosis is schematically illustrated. If this occurs in a heterozygote, two alleles of the same gene locus become two independent gene loci in extremely close linkage. A small circle denotes the centromere of the chromosome, while a large circle indicates a cistron. Initially, a solid black circle and an outlined circle exist as two alleles of the same locus (Top). Unequal crossing-over during meiosis of a heterozygote places two alleles on the same chromatid (Second from top). One of the four gametes produced by such a germ cell carries this duplication (Third row). If this duplication means a selective advantage, in time, every member of the population would become homozygous. The heterozygous advantage is thus permanently conferred on a population (Bottom).

certain bands showed as much as a 16-fold difference, while certain other bands showed no difference at all.

Regional redundant DNA replication as proposed by Keyl may have been a useful means of achieving gene duplication only if vertebrate genomes contained operons. In bacteria, as has been shown, the genes coding for a series of catalytic enzymes of the same metabolic pathway are often clustered and coordinated as a group, because they are coded by a polycistronic messenger RNA. Such a group is defined as an operon (Jacob and Monod, 1961). If vertebrate genomes contain operons, it follows then that for a chromosomal segment which contains an operon, duplication of a whole segment is infinitely more advantageous than duplication of an individual gene in an operon.

At the moment, there is no evidence that verifies this mode of gene duplication but such evidence may well be forthcoming.

D. *Polyploidization*

A diploid chromosome complement becomes a haploid complement (genome) after a diploid species becomes tetraploid. Thus, every gene locus is duplicated simultaneously. There is no problem with excessive gene dosage, and a duplication does not bring about further duplications, because an original and a duplicate lie on two separate chromosomes.

When we consider the different mechanisms of gene duplication occurring in evolution, we realize that in order to be able to produce the three types of immunoglobulin subunits, viz. L-chains, H-chains and a μ-chain, the genome had to go through at least one tetraploidization (Fig. 7).

When the ostracoderm fish first emerged, its genome probably contained a primordial gene locus which coded for a peptide chain of about 100 amino acid residues in length. The first step was an unequal exchange or crossing-over involving this locus followed by a fusion. The original L-chain cistron was thereby created. The next step was the creation of a long cistron for the μ-chain. In this case, however, a μ-chain gene could not be created at the expense of a newly made L-chain locus, because to produce immunoglobulin molecules of the IgM class, at least one gene locus for the L-chain had to remain as it was. Here then was a need for tetraploidy.

As a result of tetraploidization, an original and a duplicate of the L-chain cistron were placed on separate chromosomes of the haploid (diploid) set. One could continue to code for an L-chain while the other could participate in two successive unequal crossing-overs or exchanges and thus triple its length, and become a cistron for μ-chains.

Subsequently, H-chains involved in the formation of immunoglobulin molecules of IgG and other classes had to be produced. This could occur by one of two mechanisms. First, an original H-chain locus could have been formed anew from a redundant L-chain cistron by duplication and fusion. This would have required a second tetraploidization. Had this been the mechanism, the gene locus for μ-chain could not have been linked either to the loci for H-chains or to the L-chain loci. There is no information on this point from studies on man, the mouse and the rabbit. Second, an original H-chain locus might have been derived from a redundant μ-chain locus by a partial deletion. The placement of an original and a duplicate of the μ-chain cistron on the same chromosome by a simple unequal crossing-over or exchange is a prerequisite. Were this the case, it could then be predicted that the μ-chain locus and a group of gene loci for H-chains would be intimately linked.

Figure 7 schematically depicts the evolutionary mechanism outlined above which gave to mammals two separate gene loci for L-chains, nearly ten separate gene loci for H-chains of the IgG, IgA, IgD and IgE class, and one locus for the μ-chain of the IgM class. Also shown is that an ancestral

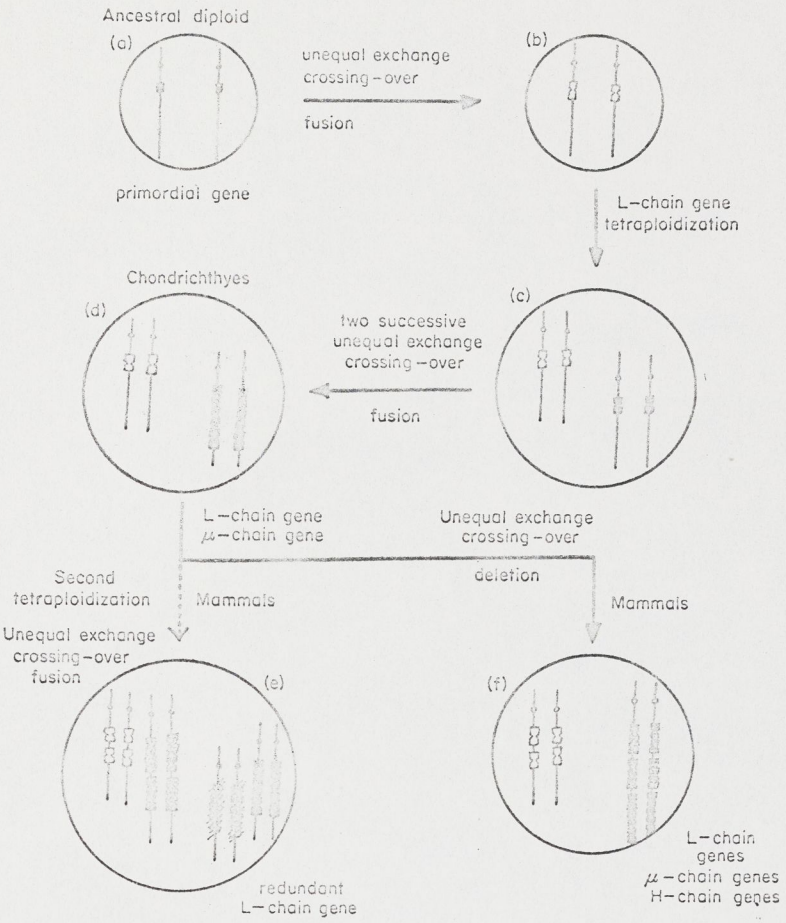

FIG. 7. A hypothetical scheme which reconstructs the formation of immunoglobulin genes by gene duplication. The diploid state is indicated by a pair of homologous chromosomes, the tetraploid by four chromosomes and the octaploid by eight chromosomes. (*a*) In an extinct diploid species which was a common ancestor to all vertebrates, there was a primordial gene which coded for a peptide chain about 105 amino acid residues long. This primordial gene is indicated by a square filled by vertical lines. (*b*) Unequal exchange or crossing-over placed an original and a duplicate of this primordial gene in tandem, and fusion of the two produced a gene locus for the L-chain (the outlined oblong square). (*c*) By tetraploidization, one L-chain locus became redundant (Black on oblong square). (*d*) This redundant L-chain locus passed through two successive tandem duplications and fusions and became a gene locus for the μ-chain (black oblong square three times the length of the L-chain square). Thus, an organism attained the ability to produce immunoglobulin of the IgM class. This much appears to have been accomplished before the emergence of bony fish.

Bottom row. Subsequent creation of the gene locus for H-chains may have been accomplished by one of the two alternatives shown in this row.

(*e*) Conversely, the H-chain locus may have been created anew from a redundant L-chain locus. This requires second tetraploidization, and also silencing of a redundant μ-chain locus (crossed out). Were this the case, then the H-chain gene loci would be linked neither to the L-chain loci nor to a μ-chain locus.

(*f*) The H-chain locus may have been derived from a tandem duplicate of the μ-chain locus. Intracistronic crossing-over between redundant duplicates of the μ-chain gene resulted in one-third deletion, thus establishing the locus for the H-chain which is twice the length of the L-chain (a shaded oblong square twice the length of the outlined L-chain square). In mammals, further duplication of an original L-chain locus created k-L and λ-L chain loci on one chromosome, and nearly 10 H-chain loci on the other chromosome. In this scheme, only two gene loci for H-chains are shown.

vertebrate which ultimately gave rise to a primordial mammal must have passed through at least one stage of tetraploid evolution.

It thus stands to reason that not only in man but also in the rabbit, the gene loci for the L-chains would be located on one chromosome and a group of gene loci for H-chains on another chromosome (Kunkel, 1964; Oudin, 1966).

E. *The stage of polyploidy in vertebrate evolution*

Since it is now certain that gene duplication by polyploidization played a role in the evolution of higher vertebrates, we would like to know at what stage of vertebrate evolution this occurred.

Polyploidy is incompatible with the well-established chromosomal sex-determining mechanism. When diploid organisms with the XY/XX-scheme of sex-determination become tetraploid, in addition to the 4AXXYY-male and the 4AXXXX-female, a high proportion of 4AXXXY-intersexes are invariably produced.

Mammals have a well-entrenched XY/XX chromosomal sex-determining mechanism. Hence, despite the wide diversity in diploid chromosome number, different mammals have the same amount of DNA in each of their diploid nuclei (Mandel *et al.*, 1950; Atkin *et al.*, 1965). This implies that extensive speciation from a primordial mammal was acquired mainly by allelic mutations of already existing gene loci with little or no change in the total genetic content. Furthermore, a group of surviving reptiles have a DNA content comparable to that of mammals, thereby indicating that since the advent of the reptilian ancestor, there has been little or no change in the total genetic content of the mammalian lineage (Atkin *et al.*, 1965).

Previous studies showed that major changes in gene duplication took place before the emergence of terrestrial vertebrates (Ohno and Atkin, 1966). While vertebrates were still aquatic, the chromosomal sex-determining mechanism was either non-existent or in its infancy. This is inferred from what we know of surviving fish. Thus, at this stage, there was nothing to hinder extensive experiments with gene duplication, employing all of the four known mechanisms, including polyploidization.

From the data on urochordates and cephalochordates of today (Atkin and Ohno, 1967), it is possible to deduce that a primitive chordate which was our prevertebrate ancestor had a DNA content which was only 10% of that found in mammals, and a diploid complement consisting of 24 one-armed (acrocentric) chromosomes. The evolution of the first vertebrates from this primitive chordate was probably accompanied by tetraploidization. Our results reveal that the lowest DNA content in vertebrates is 20% of the mammalian content, a value found in diverse species of teleost fish, many of which have a diploid complement of 48 one-armed chromosomes. Taking this value as our starting-point, we noticed a gradual rise in DNA content involving repeated unequal exchange, unequal crossing-over and regional redundant DNA replication. For instance, both the hagfish which represents the most primitive jawless state and the anchovy which is a teleost, continue

to have the original vertebrate karyotype of 48 one-armed chromosomes. Yet their DNA values had risen to 78% and 44% of the mammalian value, respectively.

Present evidence suggests that the second tetraploidization occurred independently in the case of diverse aquatic vertebrates whose diploid DNA content had variously risen above the 20% base-line as the result of unequal exchange and crossing-over. For example, the lamprey, a jawless fish, has a DNA content of 40% of the mammalian value, and a diploid chromosome number of 94–96. Thus, the lamprey can be considered as a tetraploid directly evolved from the base-line diploid state identified by a 20% DNA value and by 48 one-armed chromosomes. By contrast, the hagfish is not a tetraploid, despite having a higher DNA content. The hagfish is also incapable of producing immunoglobulin, which is not the case in lamprey, since it has gene loci for L- and μ-chains.

The carp and the goldfish have a DNA content of 50% of that of mammals and a chromosome number of 104. They are tetraploid with respect to members of the same family, Cyprinidae; this is because these other members have a 25% DNA value, and a diploid chromosome number of 50–52.

The salmonoid fish including salmon, trout and white-fish have DNA contents of 80–90% of the mammalian value and diploid complements consisting of 100–104 chromosome arms. They are tetraploid species having arisen from a diploid with a DNA value of 40% and 48 one-armed chromosomes. This diploid state is represented by the anchovy, an ally of the salmonoid fish.

It is believed that ancient crossopterygian fish which sought to live on land, thus becoming terrestrial vertebrates, were of different kinds, and only one kind was a direct ancestor of mammals. This ancestor probably had a DNA content similar to that of present-day salmonoid fish. For this reason, it is suggested that while every vertebrate passed through one initial tetraploidization, the line directly ancestral to mammals involved a second stage of tetraploidization.

A more detailed discussion of this subject can be found elsewhere (Ohno *et al.*, 1968).

V. Summary

At each gene locus, natural selection tolerates those allelic mutations that do not drastically alter the function of that locus. Because of this, allelic mutations at already existing gene loci can not change the basic character of a gene. Truly meaningful mutations resulting in new genes are those which are accumulated by redundant duplicates of original genes. Thus, big leaps in evolution have been accompanied by gene duplication.

In the course of vertebrate evolution, hemoglobin as well as immunoglobulin genes arose *de novo* by a series of duplication from a single primordial gene. Four mechanisms leading to gene duplication are envisaged: (1) unequal exchange between two sister chromatids of the same chromosome during mitosis, (2) unequal crossing-over between two homologous chromosomes

I 55

during meiosis, (3) regional redundant DNA replication, and (4) polyploidization. Both unequal exchange and unequal crossing-over place a duplicate right next to an original gene. This tandem arrangement is necessary for the creation of a new and longer gene by fusion of an original and a duplicate. Regional redundant DNA replication duplicates a small chromosomal segment containing many different cistrons. It is thus evident that for a chromosomal segment which contains an operon, duplication of a whole segment is infinitely more advantageous than duplication of an individual gene within an operon. The first three mechanisms, however, have certain shortcomings: the close linkage of duplicates invites further duplication and deletion of that segment of a chromosome. Many of the proteins, furthermore, are formed by polymerization of the products of two separate gene loci. For such a pair of genes, the duplication of one without the concurrent duplication of the other would be deleterious. The fourth mechanism of polyploidization, on the other hand, duplicates every gene locus within the genome simultaneously and places an original gene and its duplicates on two separate chromosomes. Thus, the first three mechanisms of gene duplication and the fourth mechanism complement each other.

Since evolution by polyploidy is incompatible with a well-established chromosomal sex-determining mechanism, the major alterations occurring in vertebrate evolution by gene duplication were carried out when the chromosomal sex-determining mechanism of vertebrates in the aquatic stage was still in its infancy.

Acknowledgement

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References

Allison, A. C. (1954). *Trans. R. Soc. trop. Hyg.* 48, 312.

Atkin, N. B., Mattinson, G., Beçak, W. and Ohno, S. (1965). *Chromosoma, Berlin* 17, 1-10.

Atkin, N. B. and Ohno, S. (1967). *Chromosoma, Berlin* 23, 10-13.

Babin, D. R., Schroeder, W. A., Shelton, J. R., Shelton, J. B. and Robberson, B. (1966). *Biochemistry* 5 (4), 1297-1309.

Baglioni, C. (1967). *Biochem. biophys. Res. Commun.* 26, 82-89.

Benirschke, K., Malouf, N. and Low, R. J. (1965). *Science, N.Y.* 148, 382-383.

Braunitzer, G. and Matsuda, G. (1963). *J. Biochem., Japan* 53, 262-263.

Doolittle, R. F., Singer, S. J. and Metzger, H. (1966). *Science, N.Y.* 154, 1561-1562.

Gerald, P. S. and Scott, E. M. (1966). In *The Metabolic Basis of Inherited Disease* (J. B. Stanbury, J. B. Wyngaarden, and D. S. Frederickson, eds), 2nd ed., pp. 1090-1099. McGraw-Hill Book Co., New York.

Gray, W., Dreyer, W. and Hood, L. (1967). *Science, N.Y.* 155, 465-467.
Harris, J. I., Sanger, F. and Naughton, M. A. (1958). *Archs. Biochem. Biophys.* 65, 427-438.
Hilschmann, N. and Craig, L. C. (1965). *Proc. natn. Acad. Sci., U.S.A.* 53, 1403-1409.
Hilse, K., Sorger, U. and Braunitzer, G. (1966). *Z. physiol. Chem.* 344, 166-168.
Ingram, V. M. (1963). *The Hemoglobin in Genetics and Evolution.* Columbia University Press, New York.
Ingram, V. M. and Stretton, A. O. W. (1962). *Biochim. biophys. Acta* 62, 456.
Ishihara, Y., Saito, T., Ito, Y., and Fujino, M. (1958). *Nature, Lond.* 181, 1468-1469.
Jacob, F. and Monod, J. (1961). *J. molec. Biol.* 3, 318-356.
Kendrew, J. C., Dickerson, R. E., Strandberg, B. E., Hart, R. G., Davies, D. R., Phillips, D. C. and Shore, U. C. (1960). *Nature, Lond.* 185, 422-427.
Keyl, H. G. (1966). In *Chromosomes Today* (C. D. Darlington and K. R. Lewis, eds), Vol. I, pp. 99-101. Oliver and Boyd, Edinburgh.
Kilmartin, J. V. and Clegg, J. B. (1967). *Nature, Lond.* 213, 269-271.
Koler, R. D., Bigley, R. H., Jones, R. T., Rigas, D. A., Vanbellinghen, P. and Thompson, P. (1964). *Cold Spring Harb. Symp. quant. Biol.* 24, 213-221.
Kunkel, H. G. (1963-64). *The Harvey Lectures* 59. 219-234.
Lennox, E. and Cohn, M. (1967). *A. Rev. Biochem.* 36, (1) 365-406.
Mandel, P., Métais, P. and Cuny, S. (1950). *C.r. hebd. Séanc. Acad. Sci., Paris* 231, 1172-1174.
Marchalonis, J. and Edelman, G. M. (1966*a*). *J. exp. Med.* 124, 901-913.
Marchalonis, J. and Edelman, G. M. (1966*b*). *Science, N.Y.* 154, 1567-1568.
Margoliash, E. (1963). *Proc. natn. Acad. Sci., U.S.A.* 50, 672-679.
Markert, C. L. (1964). In *Congenital Malformations*, pp. 163-174. The International Medical Congress, New York.
Milstein, C. (1966). *Biochem. J.* 101, 338-351.
Ohno, S. and Atkin, N. B. (1966). *Chromosoma, Berlin* 18, 455-466.
Ohno, S. and Morrison, M. (1966). *Science, N.Y.* 154, 1034.
Ohno, S., Wolf, U. and Atkin, N. B. (1968). *Hereditas.* 59, 169-187.
Oudin, J. (1966). *J. cell. Physiol.* 67, (Suppl. 1), 77-108.
Papermaster, B. W., Condie, R. M., Finstad, J. and Good, R. A. (1962). *Nature, Lond.* 196, 355-356.
Perutz, M. F., Rossmann, M. B., Cullis, A. F., Muirhead, H., Will, G. and North, A. C. T. (1960). *Nature, Lond.* 185, 416-422.
Porter, R. R. (1966). *Proc. R. Soc.* B, 163, 113-243.
Rudloff, V., Zelenik, M. and Braunitzer, G. (1966). *Z. physiol. Chem.* 344, 284-288.
Schroeder, W. A. (1963). *A. Rev. Biochem.* 32, 301.
Shaw, C. R. (1965). *Science, N.Y.* 149, 936-943.
Smith, D. B. (1964). *Can. J. Biochem.* 42, 755-762.
Smithies, O., Cornell, G. E. and Dixon, G. H. (1964). *Cold Spring Harb. Symp. quant. Biol.* 29, 309-319.
Tanaka, K. R., Valentine, W. N. and Miwa, S. (1962). *Blood* 19, 267-268.
Taylor, J. H., Woods, P. S. and Hughes, W. L. (1957). *Proc. natn. Acad. Sci., U.S.A.* 43, 122.

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Duplication of the Autosomally Inherited 6-Phosphogluconate Dehydrogenase Gene Locus in Tetraploid Species of Cyprinid Fish

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Among members of the fish family Cyprinidae, *a diploid–tetraploid relationship exists. The present study on electrophoretic patterns of 6-phosphogluconate dehydrogenase indicates that such diploid members as* Barbus tetrazona *maintain allelic polymorphism at a single gene locus for this enzyme. Tetraploid members such as the carp and goldfish are endowed with two separate gene loci for 6-PGD. Tetraploid evolution apparently fixed two former alleles of the same locus as two separate gene loci. Furthermore, it appears that after becoming tetraploid, the carp and goldfish developed a separate regulatory mechanism for each locus; thus preferential activation of one or the other 6-PGD locus occurs in different tissues of tetraploid species.*

INTRODUCTION

The enzyme 6-phosphogluconate dehydrogenase (6-PGD) catalyzes the second step of pentose phosphate shunt of carbohydrate metabolism. This enzyme has been found in many vertebrates to be controlled by a single autosomally inherited gene locus. The coexistence of two or more alleles at this locus which produce electrophoretically distinct subunits has been reported in man (Parr, 1966), the rat (Parr, 1966), the deer mouse (Shaw, 1965), the cat (Thuline, Morrow, and Motulsky, 1967), and the Japanese quail (Ohno, 1967). In addition, unpublished findings of various colleagues indicate that allelic polymorphism at this locus is a rule rather than an exception among diver-

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gent species of vertebrates. Such widespread polymorphism conceivably indicates that heterozygosity at this autosomally inherited locus carries some advantage.

If a substantial number of members in a given population enjoy the heterozygous advantage at a particular gene locus, natural selection is expected to favor duplication of that locus, for a duplication permits the genome to incorporate two former alleles as two separate gene loci. By this mechanism, every member of a species would carry the heterozygous advantage permanently, and this has been postulated in the evolution of isozymes (Brewer and Sing, 1969).

We have previously reported that, among members of the fish family *Cyprinidae*, the carp (*Cyprinus carpio*) and the goldfish (*Carassius auratus*), with 104 chromosomes and a DNA content of 50% that of mammals, are regarded as tetraploid species since the barbs (*Barbus tetrazona* and *Barbus fasciatus*) have 50–52 chromosomes and a DNA content of 20–22% that of mammals (Ohno *et al.*, 1967). The present report suggests that the barb (diploid species) maintains allelic polymorphism at a single 6-PGD locus, while the carp and goldfish (tetraploid species) are endowed with two separate gene loci for this enzyme. Thus, tetraploids appear to enjoy a permanently heterozygous state.

MATERIALS AND METHODS

Barbus tetrazona was chosen as a representative diploid species. The twenty specimens studied ranged from 2 to 6 cm in body length. Two hundred goldfish and 18 carps were studied as representative of tetraploid species. Most of the goldfish were immature specimens measuring less than 7 cm in body length, while carps measured approximately 15 cm. Because these fish were purchased at a local pet shop, their breeding background is unknown.

Small specimens were homogenized *in toto*. From larger fish, various organs were sampled separately: erythrocytes, liver, kidney, gonads, brain, eyes, gills, muscle, and heart. Slices of tissues were first rinsed in physiological saline and homogenized in an equal volume of 0.01 M potassium phosphate buffer, *p*H 7.0. Homogenate was centrifuged at 27,000 × *g* for 30 min at 4 C. The clear supernatant extract was employed for study.

Vertical starch gel electrophoresis was carried out at *p*H 8.6 using a continuous system of borate buffer. Each starch gel plate contained 5 mg NADP. Electrophoresis was continued for 16 hr at 4 C with a gradient of 10 v/cm. The staining solution contained 10 mg 6-phosphogluconate disodium salt, 2 mg phenazine methosulfate, 2 mg 3(4,5-dimethyl thiazolyl 1-2)2,5-diphenyltetrazolium bromide, and 2 mg NADP in 10 ml 0.1 M tris-HCl buffer, *p*H 8.0.

RESULTS

Coexistence of Three Alleles at a Single Gene Locus in *Barbus tetrazona*

As shown in Fig. 1, five different 6-PGD phenotypes were encountered among twenty specimens of *Barbus*; assuming single-band patterns to represent homozygotes and

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Duplication of the LDH Gene Loci by Polyploidization in the Fish Order Clupeiformes*

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Summary. Within the order *Clupeiformes*, chromosome analysis and DNA measurements have indicated a diploid-tetraploid relationship among closely related species. To confirm the presence of polyploidization at single gene loci we studied the LDH isoenzyme system. The results obtained are in agreement with the hypothesis of polyploidization. While the diploid species show two gene loci for LDH, the tetraploid species exhibit four separate gene loci.

Introduction

A major prerequisite for the evolution of organisms during phylogeny is the increase of genetic material. For this process two different mechanisms may be considered:

1. The duplication of single genes or small segments of chromosomes as a result of unequal crossing-over and other mechanisms.

2. The duplication of the complete genome by way of polyploidization.

While the first mechanism remained operative unlimitedly during evolution the mechanism of polyploidization is thought to have been succesful only on certain levels of organisation.

As soon as the sex chromosomes become heteromorphic, polyploidization will lead to intersexuality; consequently, this mechanism will be excluded as a factor in evolution (Ohno, 1967).

Among vertebrates, the sex chromosomes are still isomorphic on the level of fishes. It may hence be expected that polyploidizations still occured among this class. That polyploidizations have taken place can be considered as probable when closely related species differ in their ploidy level. Assays of the DNA-content per cell revealed that closely related species differ from each other by integer multiples. Within the order *Clupeiformes*, Ohno and Atkin (1966) found that a representative of the salmonoids, *Salmo irideus*, has 104 chromosome arms and a DNA value of 80% that of mammals, while a representative of the clupeoids,

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THE INFLUENCE OF SOME ENVIRONMENTAL FACTORS ON STANDING CROP AND HARVEST OF FISHES IN U. S. RESERVOIRS

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Abstract

The effects of nine environmental factors on standing crops of fish, as measured by recovery following rotenone treatment, and on sport and commercial fish harvests in U. S. reservoirs were explored by multiple regression analyses. The mean standing crop in 127 reservoirs was 186 pounds per acre; mean sport fish harvest in 121 reservoirs, 22.6 pounds per acre; mean commercial harvest in 46 reservoirs, 10.2 pounds per acre.

Environmental factors considered were: reservoir area, mean depth, total dissolved solids, storage ratio, shore development, age, water level fluctuation, outlet depth, and growing season. Most of the multiple regressions accounted for less than 50 per cent of the total variability in standing crop or harvest, but significance levels were high.

Environmental factors which appear to exert greatest positive influence are: dissolved solids on both standing crop and sport fish harvest; age of reservoir on clupeid standing crop and commercial harvest; storage ratio on sport harvest; shore development on standing crop and sport harvest. Factors of greatest negative influence are: age of reservoir on sport harvest; storage ratio on clupeid standing crop and commercial harvest; area on sport harvest; mean depth and shore development on commercial harvest.

Multiple regressions of greatest apparent predictive utility are: a) standing crop on dissolved solids divided by mean depth; b) standing crop on dissolved solids, shore development, and storage ratio; c) sport harvest on dissolved solids, growing season, age, area, and shore development; and d) commercial harvest on growing season, mean depth, storage ratio, age, and fluctuation.

Introduction

ONE of the major duties of science is the prediction and control of human interventions into nature. This maxim is particularly applicable to fishery scientists responsible for predicting effects of planned water development projects on fishery resources and for the management of the impoundments created. Estimates of resource-loss mitigation and needed enhancement measures resulting from reservoir construction have necessarily rested largely on qualitative judgments. Fortunately, an increasing backlog of quantitative fishery data has accrued on a great variety of reservoir projects since World War II, providing river basin evaluators and planners with better bases for prediction.

A primary aim of the reservoir research program of the Bureau of Sport Fisheries and Wildlife since its inception four years ago has been the collection and analysis of all available biological information on large U. S. impoundments. Emphasis has been placed on obtaining fish harvest and standing crop data on a wide variety of reservoirs where information on physical, chemical, and other biological characteristics is available for possible identification of cause and effect relationships.

Hopefully, much of the variation in standing crop and sport fish harvest among reservoirs can be explained by differences in a few environmental factors. Once identified, research and management efforts can be focused more directly on those factors which appear to be most vital to the welfare of the fish populations. Recommendations concerning design and operation of reservoirs to enhance fishery resources can stem from a firmer base.

Readily-measured keys to potential fish production of aquatic environments have been sought by fishery biologists for over thirty years. Welch (1935) listed average depth, rooted submerged vegetation, plankton, bottom fauna, turbidity, dissolved salts and gases, and dissolved organic matter as individual aquatic productivity indices which had been proposed by other workers. He concluded that no *single* usable index had been found and probably does not exist.

Rounsefell (1946) was the first to attempt to predict large reservoir standing crops and yields. Using data available from ponds and natural lakes, he derived a negative logarithmic regression (—0.39) between sport and commercial fish harvests and lake area. On this basis, reservoirs over 10,000 acres were not expected to yield more than 2 pounds per acre of sport fish annually. Commercial yields were calculated to range from 30 pounds per acre in a 10,000-acre lake to 12 in a 100,000-acre lake.

After analyzing fifteen years of Minnesota lake survey data, Moyle (1954) demonstrated highly positive curvilinear relationships between standing crop and total alkalinity, salinity, phosphorus, and nitrogen. He theorized that the positive alkalinity and salinity curves probably reflected the natural tendency of lesser elements (P, N) necessary for growth to increase as they increased. Moyle cautioned that the apparent relationships are complex and probably a combination of coincidence and cause and effect.

In a nationwide analysis of environmental factor effects on standing crop in lakes, Carlander (1955) observed that although standing crops of fish do not necessarily bear a close relationship to fish production, they are usually the only available estimates of production. Furthermore, he concluded that "since the annual rate of turnover probably varies less from one fish population to another than does the standing crop, standing crop data are probably fairly good estimates of fish production." Using cove rotenone sample data from 13 southern reservoirs with a

mean standing crop of 256 pounds per acre, Carlander obtained a positive logarithmic regression (0.017) of standing crop on surface area, but it was not significant at the 0.05 confidence level. Data from 19 small (< 150 acres) midwestern reservoirs yielded a negative logarithmic regression (—0.131) of standing crop on maximum depth.

Rawson (1958) listed the following factors as probable indices to reservoir productivity: area, mean depth, shoreline development, storage ratio, water level fluctuation, highest mean temperature, average near bottom oxygen at midsummer, average Secchi disc depth visibility, total dissolved solids, average standing crop of plankton and bottom fauna per unit area, average catch of fish in a standard gill net and a list of a few of the dominant plankters, bottom organisms, and fish. Earlier, Northcote and Larkin (1956) had described a positive relationship between standard net haul catches and total dissolved solids in 100 British Columbia lakes.

A number of pond studies concerning environmental factor effects on fish standing crop, estimated by rotenone recovery of marked fish, have been reported in the past decade. Jenkins (1958) found an average standing crop of 341 pounds per acre in 42 Oklahoma ponds, with positive logarithmic regressions of standing crop on age of pond (0.616), number of species (0.830), and MO alkalinity (0.509). Turner (1960) reported a mean standing crop of 385 pounds per acre in 22 Kentucky ponds, and described positive correlations between standing crop and total alkalinity ($r = 0.67$), and potassium ($r = 0.44$) and phosphorus ($r = 0.72$) present in watershed soils. Isaac and Bond (1963) reported bass-bluegill mean standing crop in 10 Oregon ponds of 281 pounds per acre. They found no clearly-defined relation between standing crop and total dissolved solids, MO alkalinity, or total phosphorus.

Larkin (1964), in summarizing findings on big Canadian lakes, concluded: with increase in area, there will be a relatively smaller contribution of plankton from rich shoreline areas; with increase in area and depth there will be advantages for limnetic production as a result of greater depth of circulation; with further increase in area and depth to "large" (e.g., 6 million acres) lakes, deep circulation will have disadvantages and production will decrease.

Expanding on a 1957 attempt to derive a lake "Productivity Index" (PI), Hayes and Anthony (1964) computed a series of regressions between PI and surface area, mean depth and MO alkalinity. This multivariable analysis represents the first reported use of an electronic computer in performing the huge number of computations required to explore new relationships between fish production and environmental factors. The most highly significant equation they derived accounted for 67 per cent of the variability in PI, of which 20 per cent was attributed to lake area, 29 per cent to depth, and 18 per cent to MO alkalinity. The analysis was based on 41 lakes or lake groups.

Ryder (1965) recently advanced a tidy, straightforward method for estimating lake fish production. For 23 north-temperate (Canadian) lakes, log "morphoedaphic index" — which is total dissolved solids (ppm) divided by mean depth (feet) — versus log annual sport and commercial harvests (pounds/acre), yielded a highly correlated ($r = 0.856$), positive regression (0.446). Ryder did not attempt to relate production of species at various trophic levels (short, medium, and long food chains) as did Hayes and Anthony (1964), reasoning that the removal of fish at one trophic level is usually compensated for by the interaction of other species at other levels.

If progressively more complex indices would have higher information output in the form of predictive reliability, analysis of available data on a number of factors recognized as probable influences on standing crop and harvest of reservoir fishes should prove rewarding. The goal is to develop manageable mathematical models involving 5-10 variables which would provide better bases for understanding, predicting, and modifying reservoir fish populations.

Materials and Methods

In 1963, we began to compile and analyze all available pertinent information on the biological, physical, and chemical characteristics of U. S. reservoirs. The primary aim is to describe and correlate pronounced fish production differences in terms of standing crop as estimated by cove rotenone samples and by sport and commercial yields with such variables as: drainage basin geology, soils and vegetation, climate, reservoir size, age, uses, shore development, depth, water level fluctuation, water chemistry, storage ratio, outlet depth, turbidity, thermocline position, dissolved organic matter, plankton and bottom fauna crops, and other biological parameters.

Physical data have been collected on 1,065 reservoirs over 500 acres at average annual level (and where if dam is placed at natural lake outlet, the water volume is at least doubled by impoundment), totaling 8,950,000 acres. To date, usable standing crop and/or harvest data have been obtained on 210 reservoirs which are included in this study.

Data sources. Physical descriptions of the reservoirs were obtained primarily from the 1964 revision (advance printout) of "Reservoirs of the United States," U. S. Geological Survey; Corps of Engineers District Office and Bureau of Reclamation publications; evaluation reports of the Division of River Basin Studies, Bureau of Sport Fisheries and Wildlife; Federal Aid to Fish Restoration (D-J) completion reports from forty states; annual "Surface Water Records," 1961-64, cooperative reports of the Geological Survey and state water resource agencies; Tennessee Valley Authority Technical Monographs; private power company publications and correspondence; fishery papers and reports on individual reservoirs; summary reports prepared by the Reservoir Committee, Southern Division, American Fisheries Society; and from correspondence with state fishery agencies.

Chemical descriptions were obtained principally from the following sources: Geological Survey "Quality of Surface Waters of the U. S.," Water Supply Papers, 1958-1963, and the bulletins "Chemical Character of Surface Waters" issued cooperatively with state agencies; the reservoir fishery literature; U. S. Public Health Service "Water Pollution Surveillance System" annual data compilations; Duke Power Company; Tennessee Valley Authority.

Standing crop figures are based on studies from 19 states of recovery of fishes in measured coves, or open-water areas enclosed by block net, following rotenone treatment. In general, field methods used in rotenone sampling have undergone gradual changes in the past 15 years, but technique innovations have quickly spread throughout the nation to maintain a relatively standard methodology (Hall, 1962). Values listed for individual reservoirs represent means of annual estimates, and are based on up to 12 years of records.

All sport fishery harvests cited were reported as statistically reliable, based on systematic sampling and analysis methods. Commercial harvest figures represent complete census, or are compulsory records submitted by commercial fishermen to the state agencies. Harvest figures also represent means of two or more years in many instances.

The standing crop and harvest data represent work done by 33 state fishery agencies, the Tennessee Valley Authority, and the Fish and Wildlife Service, with occasional financial aid from reservoir operating agencies.

The data were obtained from the published literature, from Federal Aid to Fish Restoration (D-J) completion reports, state administrative reports, and from correspondence with state fishery agencies and the Tennessee Valley Authority. A complete bibliography will be published in a subsequent paper along with recognition of individuals and agencies who supplied unpublished data. Most of the source material is cited in a reservoir bibliography (Jenkins, 1965) under the subject headings: Harvest Rates, Management Techniques Evaluation, Population Dynamics, Summaries, and Surveys.

Sample characteristics. Usable information on standing crop and harvest was collected on 210 reservoirs representing nearly one-half of the total reservoir area in the U. S. (Table 1). About two-thirds of the reservoirs are located in the mid-South between latitudes 31° and 38° N, and longitudes 79° and 98°W (Figure 1). Of the total, 127 are represented by standing crop estimates, 121 by sport fishery harvests, and 46 by commercial fishery harvests (Table 2). Reservoir area represented in the standing crop subsample equals 24 per cent of the total in the U. S., that in the sport harvest subsample equals 20 per cent, and in the commercial harvest subsample, 18 per cent.

About 92 per cent of the standing crop data is from reservoirs in Tennessee, Oklahoma, North Carolina, Louisiana, Alabama, Kentucky,

Table 1. Morphometric, edaphic, fish standing crop and harvest data on 210 reservoirs. Reservoirs are listed alphabetically within States, arranged first by chemical type (1 thru 4) and then major use (1 thru 4) within chemical types. Definitions of parameters listed in column headings are:

a) Reservoir - official name of impoundment; "Lake" omitted from name when occurring as part of official name.

b) State - abbreviation of State name where reservoir located; e.g., AL - Alabama, WY - Wyoming. Interstate reservoirs are placed in State where dam is located, or in State from which most fishery data were obtained.

c) Use - arbitrary classification of reservoirs into major or principal use types.
Key: 1. Hydropower and/or navigation
2. Flood control
3. Irrigation
4. Water supply, recreation or fish and wildlife

d) Year - first year in which significant volume of water was stored.

e) Drainage area - in square miles.

f) Surface area - in acres at average annual pool level where data were available; otherwise, conservation pool, summer pool, operating pool, or power pool area is listed.

g) Mean depth - in feet, at listed surface area.

h) Maximum depth - in feet, at listed surface area.

i) Outlet depth - midline depth in feet of principal outlet. Where multiple level outlets exist, mean depth of all outlets is listed.

j) Thermocline depth - in feet, of top of thermocline (water temp. change of 1° C/meter) on or about 1 August. A plus sign (+) signifies that a stable thermocline does not form. A dash (-) indicates no data.

k) Elevation - in feet above mean sea level, of reservoir surface at listed area.

l) Fluctuation - mean annual vertical fluctuation of reservoir surface level in feet.

m) Storage ratio - the ratio of the reservoir volume at the listed elevation in acre-feet to the average annual discharge in acre-feet.

n) Shore development - the ratio of shoreline length to the circumference of a circle equal in area to that of the reservoir.

o) Dissolved solids - residue on evaporation at 180° C, in ppm. Mean values calculated from available data; rounded to nearest 5 ppm where data were limited. Primary data sources - U. S. G. S. Water-Supply Papers, 1957-1963.

p) Chemical type - prevalent chemical type of inflowing rivers, according to Rainwater, F. H. 1962. Composition of rivers of the conterminous United States. Atlas HA-61. Plate 2. U. S. Geol. Survey. Delineation based on 50 percent breakpoint of major constituents, computed as equivalents/million.
Key: 1. Ca-Mg, CO_3-HCO_3 3. Na-K, CO_3-HCO_3
2. Ca-Mg, SO_4-Cl 4. Na-K, SO_4-Cl

q) Sediment load - sediment concentration (annual load/annual streamflow) of inflowing rivers according to Rainwater, F. H. 1962. (Reference above.) Plate 3.
Key: 1. 0-280 ppm 4. 6300-14000 ppm
2. 280-1900 ppm 5. 14000-28000 ppm
3. 1900-6300 ppm 6. 28000-38000 ppm

r) Growing season - average number of days between first and last frost. U. S. Weather Bureau data.

s) Sport harvest - estimated harvest of fishes by sport fishermen, in pounds per acre per year. Where data are available for two or more years, a mean value is listed.

t) Age - of impoundment in years at time of sport fish harvest estimate. Where data are available for two or more years, a mean reservoir age is listed.

u) Commercial harvest - estimated harvest of fishes by commercial fishermen or rough fish removal crews in pounds per acre per year. Where data are available for two or more years, a mean value is listed.

v) Age - of impoundment in years at time of commercial harvest estimate. Where data exist for two or more years, a mean age is listed.

w) Standing crop - estimated total standing crop of fish in pounds per acre, derived from recovery following rotenone treatment of coves or open areas enclosed by blockoff nets. Estimates based on recovery of marked fishes are not included. Where data are available for two or more years, a mean value is presented.

x) Clupeids - estimated standing crop of Clupeidae (gizzard shad, Dorosoma cepedianum; threadfin shad, Dorosoma petenense; and herrings, Alosa spp.) in pounds per acre.

y) Age - of impoundment in years at time of standing crop estimate. Where data for two or more years are available, mean age is listed.

Table 1

Reservoir	State	Use	Year	Drainage Area	Surface Area	Mean Depth	Maximum Depth	Outlet Depth	Thermocline Depth	Elevation	Fluctuation	Storage Ratio	Shore Development	Dissolved Solids	Chemical Type	Sediment Load	Growing Season	Sport Harvest	Age	Commercial Harvest	Age	Standing Crop	Clupeids	Age
Guntersville	AL	1	1939	24450	69100	14	54	18	+	594	2	0.04	26.1	105	1	1	200	19	2	12	20	277	164	19
Wilson	AL	1	1924	30750	15930	37	108	36	+	507	3	0.02	8.7	95	1	1	200	-	-	16	36	303	144	34
Walter F. George	AL	1	1962	7500	45180	20	96	80	-	190	5	0.13	21.5	35	1	1	240	-	-	-	-	96	20	1
Jordan	AL	1	1928	10200	4900	39	112	100	-	245	-	0.02	11.2	80	1	1	240	-	-	-	-	146	44	23
Lay	AL	1	1914	9087	6000	22	75	40	-	382	-	0.02	11.0	90	1	1	220	-	-	-	-	144	58	39
Martin	AL	1	1926	2963	39000	42	143	90	-	490	20	0.48	25.3	31	1	1	220	-	-	-	-	61	20	32
Mitchell	AL	1	1923	9827	5850	30	72	40	-	312	-	0.02	10.5	90	1	1	220	-	-	-	-	415	237	31
Weiss	AL	1	1961	5270	30200	21	56	55	-	564	12	0.10	18.3	75	1	1	210	-	-	-	-	467	282	1
Wheeler	AL	1	1937	29590	67100	17	58	0	+	556	6	0.04	29.3	100	1	1	200	-	-	10	18	365	114	16
Beaver	AR	1	1964	1186	24310	58	204	140	20	1120	20	1.19	19.1	125	1	1	190	24	2	-	-	-	-	-
Bull Shoals	AR	1	1951	6036	45440	67	201	120	30	654	16	0.69	21.8	145	1	1	190	54	5	-	-	201	130	7
Catherine	AR	1	1923	1516	1940	18	50	30	15	305	10	0.03	8.0	57	1	1	220	-	-	-	-	195	102	35
Hamilton	AR	1	1931	1441	7195	26	100	90	15	400	7	0.07	7.6	57	1	1	220	-	-	-	-	129	58	27
Norfork	AR	1	1943	1806	22000	57	177	105	28	552	18	0.85	18.3	166	1	1	200	39	16	-	-	166	89	16
Ouachita	AR	1	1952	1105	36740	51	200	80	30	572	13	1.79	24.6	50	1	1	220	-	-	-	-	129	67	6
Folsom	CA	1	1955	1875	9500	66	230	120	40	430	65	0.25	5.5	45	1	1	280	8	7	-	-	84	0	6
Spaulding	CA	1	1912	120	670	111	-	-	-	5000	-	. -	1.9	60	1	1	200	1	50	-	-	-	-	-
Beardsley	CA	1	1957	303	650	150	245	240	-	3390	140	0.29	6.0	40	1	1	240	8	6	-	-	-	-	-
Ice House	CA	1	1959	27	570	80	157	150	-	5447	120	0.87	2.4	40	1	1	180	3	3	-	-	-	-	-
Seminole	FL	1	1957	17150	37500	10	34	30	-	77	2	0.02	9.0	40	1	1	250	-	-	-	-	129	21	5
Allatoona	GA	1	1950	1100	11860	31	150	75	25	840	20	0.30	17.7	37	1	1	200	5	6	-	-	95	14	8
Bartlett's Ferry	GA	1	1926	4200	5850	32	-	-	-	521	10	0.04	14.6	45	1	2	220	-	-	-	-	175	59	34
Blackshear	GA	1	1930	3750	8515	9	-	-	-	-	2	0.04	10.0	40	1	1	240	-	-	-	-	80	36	32
Sidney Lanier	GA	1	1956	1040	38000	50	156	139	30	1070	6	1.28	16.0	40	1	2	200	4	4	-	-	72	8	5
Sinclair	GA	1	1952	2840	15350	22	-	-	25	340	15	0.14	15.0	40	1	2	220	5	10	-	-	129	23	11
Blue Ridge	GA	1	1931	232	3320	60	150	100	25	1690	90	0.47	16.0	20	1	2	180	3	31	-	-	62	6	32
Kentucky	KY	1	1944	40200	158300	17	60	25	+	360	5	0.06	13.5	85	1	1	200	15	21	24	16	389	127	14
Herrington	KY	1	1925	437	1600	70	205	170	25	735	30	0.50	12.0	150	1	2	180	7	35	-	-	256	129	31
Conowingo	MD	1	1928	27098	8560	36	90	60	+	107	10	0.01	3.0	160	1	1	200	2	31	-	-	-	-	-
Lake of the Ozarks	MO	1	1931	14000	59700	33	130	50	30	655	10	0.28	38.0	150	1	1	180	22	26	-	-	-	-	-
Table Rock	MO	1	1958	4020	43100	63	220	140	30	915	30	0.90	25.6	130	1	1	180	28	4	-	-	215	90	4
Taneycomo	MO	1	1913	4362	1730	11	50	10	10	700	2	0.01	8.3	140	1	1	180	49	46	-	-	314	150	47
Ennis	MT	1	1900	2180	3800	11	37	14	-	4841	1	0.04	1.3	160	1	1	100	5	50	-	-	-	-	-
Hebgen	MT	1	1915	905	12670	30	62	20	30	6529	15	0.55	4.0	160	1	1	100	1	37	-	-	-	-	-
Georgetown	MT	1	1905	50	3000	-	-	-	-	6430	5	1.00	.-	60	1	1	100	26	53	-	-	-	-	-
Badin	NC	1	1917	4160	5970	40	196	50	50	572	25	0.07	5.5	40	1	2	200	-	-	-	-	53	0	40
Blewett Falls	NC	1	1912	6600	2560	37	92	30	+	139	1	0.02	4.0	50	1	2	200	-	-	-	-	93	38	46
High Rock	NC	1	1927	3980	15180	17	60	40	+	655	30	0.08	15.0	55	1	1	200	3	33	-	-	223	50	33
James	NC	1	1919	380	6510	44	127	85	20	1200	27	0.63	13.3	35	1	1	180	-	-	-	-	100	78	40
Lure	NC	1	1925	200	1500	30	92	0	10	992	3	0.30	5.0	50	1	1	180	-	-	-	-	186	97	34

Table 1 Continued

Reservoir	State	Use	Year	Drainage Area	Surface Area	Mean Depth	Maximum Depth	Outlet Depth	Thermocline Depth	Elevation	Fluctuation	Storage Ratio	Shore Development	Dissolved Solids	Chemical Type	Sediment Load	Growing Season	Sport Harvest	Age	Commercial Harvest	Age	Standing Crop	Clupeids	Age
Rhodhiss	NC	1	1925	1090	3515	19	68	30	20	995	10	0.06	10.8	35	1	1	190	-	-	-	-	109	55	35
Tillery	NC	1	1928	4600	5294	31	70	50	+	240	10	0.04	6.2	60	1	1	220	4	35	-	-	95	39	32
Apalachia	NC	1	1943	1018	1120	52	130	40	8	1280	15	0.04	6.6	26	1	2	180	-	-	-	-	77	52	16
Hiwasse	NC	1	1940	968	4680	66	251	200	+	1503	100	0.23	16.2	25	1	2	180	-	-	-	-	19	2	18
Fort Gibson	OK	1	1950	12492	19100	19	72	54	25	554	4	0.07	11.6	165	1	1	215	46	4	4	10	361	137	8
Lake O' the Cherokees	OK	1	1940	10298	46300	25	120	63	25	745	10	0.32	20.7	178	1	2	200	-	-	4	20	498	262	14
Tenkiller Ferry	OK	1	1953	1610	12500	50	140	125	30	630	12	0.57	8.3	100	1	1	190	44	4	1	8	428	214	5
Clark Hill	SC	1	1952	6140	71500	35	155	75	35	330	12	0.44	28.3	40	1	1	230	6	8	-	-	119	43	9
Hartwell	SC	1	1961	2088	56400	45	185	105	25	660	6	0.80	28.9	30	1	1	210	-	-	-	-	118	39	3
Marion	SC	1	1942	14700	100500	12	35	0	+	77	6	0.11	6.7	50	1	1	280	-	-	-	-	140	84	21
Murray	SC	1	1929	2420	50800	42	189	171	20	360	15	1.08	16.5	45	1	1	240	-	-	-	-	308	115	32
Wateree	SC	1	1919	4750	13710	22	76	45	20	226	7	0.09	11.6	50	1	1	230	-	-	-	-	250	193	43
Boone	TN	1	1952	1840	4880	44	125	80	15	1385	3	0.10	13.2	111	1	1	180	-	-	-	-	324	112	10
Douglas	TN	1	1943	4541	19700	36	100	87	20	970	30	0.15	22.3	90	1	1	190	-	-	17	17	125	38	18
Fort Loudoun	TN	1	1943	9550	14560	25	117	78	15	813	6	0.04	21.2	135	1	1	200	-	-	8	17	225	108	18
Fort Patrick Henry	TN	1	1954	1903	890	30	97	77	12	1263	5	0.01	8.8	115	1	1	180	-	-	-	-	311	121	7
Hales Bar	TN	1	1940	21790	6420	21	64	0	+	634	2	0.01	14.4	91	1	1	200	-	-	18	20	322	76	20
Melton Hill	TN	1	1964	3343	5720	21	70	45	20	800	10	0.04	13.6	105	1	1	200	-	-	-	-	98	90	1
Norris	TN	1	1936	2912	34200	60	200	150	25	1020	60	0.65	30.8	93	1	1	200	15	28	1	24	124	66	22
Ocoee No. 1	TN	1	1911	595	1760	47	120	25	40	832	15	0.09	3.0	50	1	2	190	-	-	-	-	34	0	49
Pickwick Landing	TN	1	1938	32820	42700	22	74	50	+	414	6	0.02	17.1	90	1	2	200	-	-	21	22	359	174	25
South Holston	TN	1	1951	703	7580	84	257	129	30	1729	80	0.88	13.8	110	1	1	190	-	-	-	-	225	130	9
Watauga	TN	1	1949	468	6430	89	259	170	20	1959	100	1.10	9.4	65	1	1	180	-	-	-	-	115	66	10
Center Hill	TN	1	1949	2195	18220	73	178	90	30	648	18	0.48	19.5	117	1	1	200	16	5	1	10	115	67	11
Cheatum	TN	1	1949	14070	7450	14	40	21	+	385	3	0.01	15.4	100	1	1	200	11	12	15	12	505	283	10
Dale Hollow	TN	1	1943	935	27700	49	147	81	25	651	14	1.16	25.2	138	1	1	190	10	11	1	16	86	22	16
Old Hickory	TN	1	1956	11620	22500	19	73	48	+	445	3	0.03	17.6	96	1	1	200	20	5	-	-	403	226	5
Inks	TX	1	1938	31300	830	20	90	80	+	888	2	0.02	5.0	530	1	3	250	32	18	8	24	-	-	-
John H. Kerr	VA	1	1953	7800	53100	31	112	67	30	302	11	0.27	23.9	70	1	1	220	-	-	-	-	111	46	8
Pleasant	AZ	2	1927	1459	890	20	35	35	10	1530	20	0.90	5.3	270	1	5	330	21	35	-	-	-	-	-
Isabella	CA	2	1954	2093	4800	31	-	-	-	2555	100	0.28	2.9	150	1	2	220	55	10	-	-	-	-	-
Millerton	CA	2	1941	1633	4000	80	230	155	15	530	100	0.20	4.9	40	1	1	280	7	10	-	-	-	-	-
Pine Flat	CA	2	1952	1542	3400	145	-	190	20	850	150	0.36	6.4	30	1	1	270	12	12	-	-	-	-	-
Granby	CO	2	1949	311	5900	56	183	80	20	8248	25	3.00	4.0	44	1	1	150	27	12	-	-	-	-	-
Green Mountain	CO	2	1943	599	2000	70	247	140	40	7950	70	0.42	1.8	104	1	1	150	2	7	-	-	-	-	-
Merritt	KS	2	1964	600	529	38	110	71	70	2941	10	2.30	5.9	190	1	2	150	24	1	-	-	-	-	-
Gibson	MT	2	1929	575	1360	77	180	170	-	4712	100	0.18	2.9	170	1	3	100	1	22	-	-	-	-	-
Pishkun	MT	2	1919	+	1000	33	60	25	-	4370	10	0.16	2.7	170	1	1	100	1	32	-	-	-	-	-
Willow Creek (Harrison)	MT	2	1938	153	860	45	74	70	-	4736	15	0.50	2.5	380	1	1	100	17	23	-	-	-	-	-
Willow Creek (Sun River)	MT	2	1911	160	1450	22	60	40	-	4142	-	2.89	1.8	170	1	1	120	1	40	-	-	-	-	-

Table 1 Continued

Enders	NB	2	1950	820	1700	27	78	30	30	3112	15	0.86	3.2	320	1	4	150	38	9	-	-	-	-	-
Harlan County	NB	2	1952	20755	13600	25	71	50	+	1946	6	1.46	3.9	260	1	3	160	22	8	-	-	-	-	-
Harry Strunk	NB	2	1949	850	1770	22	64	25	30	2366	15	0.87	6.0	320	1	4	150	58	4	-	-	-	-	-
Swanson	NB	2	1953	4900	4960	24	59	40	50	2752	10	0.90	3.1	240	1	4	150	6	8	-	-	-	-	-
Wild Horse	NV	2	1938	209	1830	18	60	50	20	6189	16	1.09	.-	-	1	2	110	26	23	-	-	-	-	-
Storrie	NM	2	1919	90	1400	16	50	35	+	6500	38	1.52	2.0	200	1	3	160	1	41	-	-	-	-	-
Medina	TX	2	1913	609	5570	36	150	100	20	1064	50	2.40	10.0	590	1	3	240	3	42	-	-	-	-	-
Scofield	UT	2	1926	163	2800	26	40	25	-	7617	25	1.70	2.3	500	1	6	120	27	30	-	-	-	-	-
Strawberry	UT	2	1912	150	6900	25	-	25	-	7540	25	1.00	2.6	450	1	3	120	16	45	-	-	-	-	-
Deer Creek	UT	2	1941	560	2130	55	130	100	-	5410	60	0.50	5.4	300	1	2	50	18	16	-	-	-	-	-
Utah Lake	UT	2	1885	2570	75000	7	12	0	+	4489	3	1.50	2.5	800	1	1	100	2	75	-	-	-	-	-
Fall River	KS	3	1949	585	2600	10	48	20	+	949	20	0.11	5.6	350	1	2	190	6	5	-	-	-	-	-
Barren	KY	3	1964	940	9200	25	75	30	20	552	40	0.21	16.0	100	1	2	180	-	-	-	-	197	67	1
Nolin	KY	3	1962	703	5800	30	100	30	18	515	30	0.28	16.1	100	1	1	180	5	1	-	-	159	1	2
Rough River	KY	3	1959	454	4860	21	65	55	15	495	30	0.20	22.0	140	1	2	180	16	4	-	-	235	103	3
Lac Qui Parle	MN	3	1937	6100	14600	8	16	0	+	931	15	0.28	3.2	610	1	1	140	-	-	33	20	-	-	-
Ross Barnett	MS	3	1963	2970	31000	10	50	0	+	296	30	0.11	2.3	50	1	2	230	1	1	-	-	295	149	1
Arkabutla	MS	3	1941	1000	8700	8	25	0	+	215	20	0.07	7.0	35	1	1	225	-	-	-	-	143	53	22
Enid	MS	3	1952	560	11000	14	45	0	+	242	20	0.26	5.9	30	1	1	225	6	9	-	-	147	50	10
Granada	MS	3	1954	1320	24900	13	48	0	+	208	24	0.27	3.9	40	1	1	230	15	7	-	-	191	81	7
Sardis	MS	3	1940	1545	22800	15	60	0	+	265	30	0.21	4.3	30	1	1	230	10	24	-	-	318	106	22
Clearwater	MO	3	1948	898	1650	13	50	0	20	494	30	0.03	4.8	125	1	1	180	31	9	-	-	154	103	10
Wappapello	MO	3	1941	1310	8200	7	30	10	+	358	20	0.04	14.2	225	1	1	200	6	10	-	-	329	160	14
Charles Mill	OH	3	1936	216	1350	5	15	0	10	997	8	0.06	6.3	290	1	2	160	5	12	-	-	-	-	-
Hulah	OK	3	1951	732	3600	9	48	0	+	733	15	1.00	7.4	260	1	2	200	-	-	9	8	368	122	6
Benbrook	TX	3	1952	430	1200	15	45	30	+	665	10	1.90	2.8	400	1	3	240	169	2	-	-	-	-	-
Fort Smith	AR	4	1936	74	525	23	72	14	25	825	12	0.10	2.5	50	1	2	200	4	23	-	-	60	0	23
Decatur	IL	4	1922	906	2600	5	15	0	+	600	2	0.03	5.0	280	1	2	180	-	-	7	30	-	-	-
Beshear	KY	4	1964	30	712	15	35	35	15	410	5	1.00	5.7	80	1	1	180	9	1	-	-	52	0	1
Malone	KY	4	1961	29	692	21	40	40	10	460	5	1.00	7.4	60	1	1	180	-	-	-	-	160	85	4
Bussey Brake	LA	4	1958	+	2200	11	30	15	+	115	4	0.20	1.2	75	1	1	230	121	5	-	-	213	145	4
Loch Raven	MD	4	1914	303	1900	28	90	65	8	240	8	0.20	6.4	190	1	2	200	10	38	-	-	-	-	-
Triadelphia	MD	4	1943	78	790	24	75	41	16	360	10	0.20	6.7	190	1	1	200	12	9	-	-	-	-	-
Adams-McGill	ND	4	1961	-	625	2	7	0	+	5152	2	. -	.-	300	1	3	80	3	3	-	-	-	-	-
Buckeye	OH	4	1832	46	3140	8	16	0	5	750	5	0.90	3.7	210	1	2	160	16	115	-	-	-	-	-
St. Marys	OH	4	1841	93	13440	7	12	0	-	870	2	1.80	3.7	350	1	1	200	14	103	38	50	-	-	-
Eucha	OK	4	1952	358	2880	28	83	60	20	778	8	0.34	6.1	110	1	2	190	37	7	1	7	178	131	5
Greenleaf	OK	4	1937	81	900	14	45	0	12	510	3	0.25	3.1	150	1	1	220	-	-	5	20	508	300	14
Spavinaw	OK	4	1923	389	1637	19	57	12	20	680	3	0.12	2.8	110	1	2	190	10	35	7	35	540	424	30
Woods	TN	4	1952	263	3910	20	65	0	20	960	3	0.25	7.3	100	1	2	200	-	-	-	-	117	5	6
Carvin Cove	VA	4	1945	18	630	30	70	30	20	70	15	1.00	3.4	75	1	1	200	6	10	-	-	-	-	-
Lewis Smith	AL	1	1961	944	21200	66	245	155	15	510	15	1.70	24.6	22	2	2	210	-	-	-	-	70	4	1
Mead	AZ	1	1935	167800	115000	200	530	150	70	1163	20	2.21	10.0	640	2	1	260	7	28	-	-	-	-	-
Mohave	AZ	1	1950	169300	26100	62	128	90	30	640	15	0.16	11.5	640	2	1	280	6	13	-	-	-	-	-
Cumberland	KY	1	1950	5810	50250	80	184	92	25	723	34	0.62	34.6	80	2	1	190	9	11	-	-	150	76	12

Table 1 Continued

Reservoir	State	Use	Year	Drainage Area	Surface Area	Mean Depth	Maximum Depth	Outlet Depth	Thermocline Depth	Elevation	Fluctuation	Storage Ratio	Shore Development	Dissolved Solids	Chemical Type	Sediment Load	Growing Season	Sport Harvest	Age	Commercial Harvest	Age	Standing Crop	Clupeids	Age
Deep Creek	MD	1	1924	64	3900	27	70	47	22	2462	14	1.20	7.1	20	2	2	140	-	-	-	-	106	0	35
Fort Peck	MT	1	1937	57725	212000	74	209	130	-	2234	25	2.36	23.1	440	2	2	120	1	12	-	-	-	-	-
Johnson	NB	1	1940	+	2420	23	55	-	-	-	-	1.00	4.0	730	2	4	160	-	-	7	18	-	-	-
Carry Falls	NY	1	1953	872	3170	36	55	40	35	1385	40	0.10	3.2	30	2	1	140	1	3	-	-	-	-	-
Garrison	ND	1	1953	180940	329000	56	177	65	+	1837	15	1.39	16.3	460	2	3	130	-	-	1	8	-	-	-
Moultrie	SC	1	1941	15000	60000	18	75	50	+	77	6	0.08	3.4	50	2	1	280	-	-	-	-	142	58	22
Francis Case	SD	1	1952	263000	104000	50	135	60	+	1365	20	0.29	11.9	440	2	2	150	1	10	4	10	-	-	-
Oahe	SD	1	1958	243500	250000	58	200	70	70	1600	15	1.18	27.4	440	2	2	145	-	-	2	6	-	-	-
Cherokee	TN	1	1942	3428	19100	41	123	48	25	1043	60	0.23	18.8	130	2	1	200	-	-	3	18	211	67	17
Chickamauga	TN	1	1940	20790	34500	17	55	35	+	683	6	0.02	31.1	100	2	1	200	-	-	7	18	160	70	20
Watts Bar	TN	1	1942	17310	38600	25	70	50	+	741	6	0.05	28.3	123	2	1	200	-	-	6	19	146	92	18
Cachuma	CA	2	1953	421	3100	60	145	80	30	745	25	1.00	4.9	550	2	5	300	8	5	-	-	-	-	-
Piru	CA	2	1956	424	500	30	100	100	-	1000	150	1.00	4.1	300	2	2	300	94	4	-	-	-	-	-
Sterling	CO	2	1908	+	1500	20	50	50	+	3700	30	. -	.-	1550	2	3	140	4	49	-	-	-	-	-
Maloney	NB	2	1935	+	1550	13	31	15	+	3004	4	1.00	2.1	1000	2	4	160	20	14	35	8	-	-	-
Conchas	NM	2	1939	7409	9600	38	76	45	30	4201	30	0.52	7.0	470	2	2	180	76	20	-	-	-	-	-
Alamogorodo	NM	2	1937	4390	4500	27	70	75	+	4275	20	0.77	6.2	1400	2	3	200	-	-	-	-	186	0	24
Bluewater	NM	2	1927	215	550	15	60	30	+	7326	20	5.00	3.0	400	2	5	140	92	33	-	-	-	-	-
Elephant Butte	NM	2	1916	28900	36000	61	185	35	+	4325	35	0.40	9.4	1730	2	1	140	-	-	4	49	326	178	40
Altus	OK	2	1944	2515	6575	21	79	69	+	1559	10	1.43	4.3	1635	2	4	225	-	-	-	-	236	93	12
Angostura	SD	2	1949	9100	4830	33	127	40	45	3187	10	0.82	4.3	980	2	3	140	16	3	-	-	-	-	-
San Angelo	TX	2	1952	1490	4000	20	68	10	+	1900	20	2.00	2.6	500	2	2	233	11	3	-	-	-	-	-
Alcova	WY	2	1938	10800	2250	90	180	140	+	5500	19	0.22	3.5	330	2	1	100	2	13	-	-	-	-	-
Pathfinder	WY	2	1909	10700	4500	50	176	135	+	5790	40	0.28	5.5	400	2	1	100	3	42	-	-	-	-	-
Buckhorn	KY	3	1961	408	1230	18	64	40	25	782	60	0.07	13.3	50	2	1	170	18	2	-	-	82	1	2
Dewey	KY	3	1950	207	1100	17	53	40	15	650	30	0.11	11.5	60	2	1	180	6	10	-	-	145	68	8
Canton	OK	3	1948	12483	7500	13	39	0	+	1614	15	1.80	3.6	730	2	4	205	30	13	1	11	258	54	14
Fort Supply	OK	3	1942	1494	1800	6	15	0	+	2002	15	0.20	4.4	600	2	4	200	14	20	-	-	324	150	10
Wister	OK	3	1949	993	4000	7	35	0	15	472	5	0.40	8.5	30	2	2	210	-	-	12	10	236	41	8
Sutton	WV	3	1960	537	1520	42	125	100	15	925	75	0.08	7.3	50	2	1	160	29	3	-	-	65	0	4
Quabbin	MA	4	1939	186	24700	52	150	65	30	530	5	5.60	7.7	10	2	1	140	2	21	-	-	13	0	25
Meander	OH	4	1932	85	2000	16	45	0	25	905	1	0.50	6.3	190	2	2	150	-	-	17	10	-	-	-
Mogadore	OH	4	1940	14	900	10	25	15	+	1087	5	0.70	4.5	120	2	1	200	47	5	-	-	-	-	-
Humphreys	OK	4	1957	28	880	16	50	30	25	1100	5	2.10	5.0	280	2	3	220	-	-	-	-	155	58	3
Lawtonka	OK	4	1905	93	2400	26	80	30	25	1345	8	0.80	2.3	175	2	3	220	-	-	12	56	-	-	-
Murray	OK	4	1937	54	5000	11	75	0	20	747	5	2.00	10.0	100	2	3	230	-	-	1	23	308	115	16
Overholser	OK	4	1917	8300	1700	10	18	12	+	1242	5	0.10	1.3	500	2	4	220	9	44	24	36	-	-	-
Shawnee	OK	4	1935	21	1330	18	50	40	15	1000	8	5.90	4.0	110	2	4	210	-	-	-	-	271	72	14
Nasworthy	TX	4	1930	2659	1430	8	35	10	+	1872	10	0.12	5.3	500	2	2	230	3	24	-	-	-	-	-
Hickory	NC	1	1928	1310	4110	31	92	35	20	935	5	0.10	11.7	40	3	2	200	-	-	-	-	103	69	31

Table 1 Continued

Lookout Shoals	NC	1	1915	1450	1023	26	76	43	20	838	10	0.02	8.7	40	3	2	200	-	-	-	-	111	57	43
Mountain Island	NC	1	1923	1860	3235	18	80	32	20	648	5	0.04	7.7	45	3	2	200	-	-	-	-	103	68	35
Norman	NC	1	1963	1790	32510	34	110	80	20	760	12	0.79	20.6	40	3	1	200	-	-	-	-	72	17	1
Glenville	NC	1	1941	37	1460	50	-	90	25	3492	30	0.80	4.7	25	3	1	170	-	-	-	-	54	7	18
Nantahala	NC	1	1942	91	1380	80	230	132	25	2993	55	0.40	5.5	22	3	1	180	-	-	-	-	30	0	17
Santeetlah	NC	1	1928	176	2860	55	180	80	50	1939	45	0.41	11.3	16	3	2	180	-	-	-	-	53	25	31
Fontana	NC	1	1944	1571	8680	128	440	215	30	1675	130	0.41	17.2	30	3	2	180	-	-	-	-	52	22	17
Fishing Creek	SC	1	1916	3810	3370	18	58	31	30	417	8	0.02	4.4	45	3	2	220	-	-	-	-	214	189	47
Greenwood	SC	1	1940	1150	10500	21	65	35	30	440	18	0.21	14.6	50	3	2	240	-	-	-	-	189	108	23
Wylie	SC	1	1925	3020	12455	23	86	48	20	569	4	0.12	20.9	45	3	1	220	-	-	-	-	169	108	36
Heart Butte	ND	2	1950	1710	3400	22	60	30	+	2065	12	0.77	6.7	500	3	2	120	7	11	-	-	-	-	-
Lahonton	NV	2	1915	+	16000	26	100	90	40	4162	33	0.95	4.8	240	3	1	150	1	47	-	-	-	-	-
Crowley	CA	4	1941	437	4800	32	110	100	-	6781	10	0.70	2.0	187	3	1	130	28	17	-	-	-	-	-
Apache	AZ	1	1927	5940	2600	95	264	250	30	1914	40	0.45	5.9	780	4	3	300	9	26	-	-	-	-	-
Canyon	AZ	1	1925	6100	950	60	142	130	15	1660	25	0.10	6.5	780	4	1	330	14	38	-	-	-	-	-
Roosevelt	AZ	1	1910	5830	10000	70	200	180	30	2136	30	1.00	4.8	780	4	1	300	-	-	3	48	-	-	-
Saguaro	AZ	1	1930	6220	1260	55	160	140	12	1529	25	0.12	4.5	780	4	1	330	15	32	-	-	-	-	-
Texoma	OK	1	1944	39720	91200	30	116	102	+	617	10	0.75	12.8	840	4	3	230	-	-	1	16	174	29	14
Possum Kingdom	TX	1	1941	22550	16000	35	125	75	40	993	10	0.80	15.7	1180	4	4	240	13	15	-	-	-	-	-
Whitney	TX	1	1952	17700	15800	25	90	30	+	520	10	0.30	10.8	600	4	3	240	149	4	2	5	-	-	-
Diversion	TX	2	1924	2100	3420	11	35	30	+	1051	10	0.50	2.0	1870	4	4	220	-	-	-	-	124	53	35
Ocean Lake	WY	2	1922	+	6100	15	31	0	+	5223	3	2.00	1.7	2000	4	1	110	15	26	55	30	-	-	-
Kanopolis	KS	3	1948	7857	3550	14	60	40	+	1459	20	0.18	3.6	450	4	3	180	33	7	-	-	-	-	-
Carl Blackwell	OK	3	1940	75	3300	16	46	0	18	1200	10	2.80	5.0	430	4	4	220	-	-	2	18	-	-	-
Heyburn	OK	3	1950	123	980	8	65	0	20	762	10	1.10	9.1	165	4	3	220	-	-	-	-	178	26	7
El Capitan	CA	4	1935	190	500	30	-	60	16	750	15	1.00	3.6	200	4	3	300	78	20	-	-	-	-	-
Hodges	CA	4	1919	300	500	22	-	-	15	-	-	1.00	4.0	220	4	3	300	140	30	-	-	-	-	-
San Vicente	CA	4	1943	75	850	64	-	-	25	650	10	1.00	3.0	150	4	3	300	21	15	-	-	-	-	-
Sutherland	CA	4	1954	181	500	27	90	-	20	2070	10	1.00	3.3	200	4	3	300	84	5	-	-	-	-	-
Bayou DeSiard	LA	4	1937	32	1215	11	37	8	+	71	1	0.10	13.5	2200	4	1	250	30	24	-	-	375	220	25
Bistineau	LA	4	1938	1410	17200	7	30	0	6	-	2	0.11	2.9	190	4	1	260	-	-	-	-	122	67	18
Black Bayou	LA	4	1945	231	3960	4	15	0	+	183	0	0.10	3.9	2100	4	1	250	-	-	-	-	86	45	14
Black Lake	LA	4	1933	1377	13800	8	20	6	+	100	3	0.11	3.1	75	4	1	240	-	-	-	-	80	33	22
Caddo	LA	4	1915	2744	32500	6	28	0	+	168	4	0.10	5.2	865	4	1	240	2	40	1	40	52	10	44
Cane River	LA	4	1917	34	1044	11	25	0	+	76	2	0.10	15.5	300	4	1	250	-	-	-	-	262	197	42
Corney	LA	4	1940	443	1900	4	22	0	+	114	3	0.03	2.2	1190	4	2	230	-	-	-	-	13	0	16
Lafourche	LA	4	1958	+	1000	6	18	0	+	52	3	0.10	10.8	225	4	1	240	19	5	-	-	169	68	6
Monroe	LA	4	1937	-	2000	6	12	0	+	71	1	0.20	4.6	2200	4	2	230	107	26	-	-	260	148	27
Spring Bayou	LA	4	1955	-	1500	6	15	0	+	31	6	0.20	9.7	312	4	1	240	-	-	-	-	316	115	8
Chicot	LA	4	1943	57	1625	6	15	0	8	46	4	0.10	3.0	30	4	1	260	-	-	-	-	57	18	16
Anacoco	LA	4	1951	209	2600	9	19	0	+	194	6	0.11	2.0	32	4	1	260	-	-	-	-	35	13	10
Hefner	OK	4	1943	+	2580	29	100	-	50	1240	10	1.00	3.2	375	4	4	220	6	18	7	10	144	47	13
Okmulgee	OK	4	1928	40	560	17	50	40	15	625	3	0.80	10.0	165	4	3	200	-	-	-	-	186	68	28
Lavon	TX	4	1953	770	11100	9	39	8	+	472	20	0.66	5.6	420	4	3	240	-	-	2	7	166	40	2
Sheldon	TX	4	1957	9	1200	4	15	0	+	100	2	0.50	2.0	100	4	2	300	28	3	-	-	-	-	-

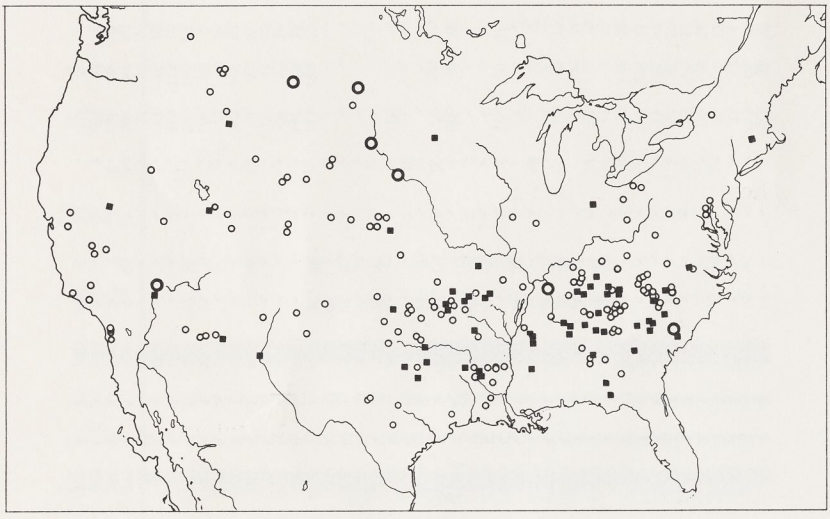

Figure 1.

South Carolina, Arkansas, Georgia, Mississippi, and Missouri. Sport harvest estimates are more widely distributed, with the greatest number from California. Over one-half of the commercial harvest estimates are from Oklahoma and Tennessee (Table 2).

Average area (at average annual level) of the reservoirs in the total sample is 17,170 acres, compared to 17,030 acres in the standing crop subsample, 14,500 acres in the sport harvest sample, and 35,000 acres in the commercial harvest sample (Table 3). Average area of the 1,065 reservoirs in the U. S. is 8,400 acres.

Reservoirs were first subdivided by prevalent chemical type of inflowing tributaries as defined by Rainwater (1962). Preliminary analysis suggested significant reservoir differences in standing crop between the four types where most of the dissolved solids are of the substances specified as follows: Type 1. Calcium-magnesium, carbonate-bicarbonate; 2. Calcium-magnesium, sulfate-chloride; 3. Sodium-potassium, carbonate-bicarbonate; 4. Sodium-potassium, sulfate-chloride. River water in about 13 per cent of the U. S. is one of the sodium-potassium types compared to about 22 per cent in our total reservoir sample. Dissolved-solids concentration for this type of water is usually higher than for calcium-magnesium types. Sodium-potassium water above 800 ppm dissolved solids may contain concentrations of calcium and magnesium that make it very hard.

Exploratory analysis indicated that total standing crop was highest in chemical type 1 reservoirs in Oklahoma (Figure 2). Most of the difference was due to higher crops of shad, suggesting that plankton production may be correlated with chemical type. This clue was considered worthy of further consideration in multivariable analysis.

TABLE 2. Geographical distribution, by State, of reservoirs in the study with data on standing crop and harvest

State	Number of reservoirs represented in study			
	Total	Standing Crop	Sport Harvest	Commercial Harvest
Oklahoma	21	18	8	15
Tennessee	19	19	5	11
North Carolina	17	17	2	
California	14	1	14	
Louisiana	13	13	5	1
Alabama	10	10	1	3
Kentucky	10	10	8	1
Texas	10	2	8	3
South Carolina	9	9	1	
Montana	8		8	
Arizona	7		6	1
Arkansas	7	6	4	
Georgia	6	6	4	
Nebraska	6		5	2
Mississippi	5	5	4	
Missouri	5	4	5	
New Mexico	5	2	3	1
Ohio	5		4	2
Maryland	4	1	3	
Utah	4		4	
Colorado	3		3	
Kansas	3		3	
Nevada	3		3	
South Dakota	3		2	2
Wyoming	3		3	1
North Dakota	2		1	1
Virginia	2	1	1	
Florida	1	1		
Illinois	1			1
Massachusetts	1	1	1	
Minnesota	1			1
New York	1		1	
West Virginia	1	1	1	
Total	210	127	121	46

TABLE 3. Physicochemical characteristics (mean values) of reservoirs in subsamples and total samples

Independent variable	Subsample means				Total sample	
	Chem. type 4					
	Total standing crop	standing crop	Sport harvest	Commercial harvest	Mean	Median
Number of reservoirs	127	18	121	46	210	210
Area (in 1,000s of acres)	17.0	10.6	14.5	35.0	17.2	4.6
Mean depth (feet)	29	10	36	26	33	25
Dissolved solids (ppm)	220	750	320	375	280	125
Storage ratio	0.46	0.34	0.73	0.59	0.64	0.29
Age of reservoir (yrs)	18	19	20	20	—	—
Shore development	12.7	6.6	8.3	12.0	—	—
Fluctuation (feet)	18	5	25	12	21	11
Outlet depth (feet)	52	11	61	20	—	—

FIGURE LEGENDS

Figure 1. Location of 210 U. S. reservoirs represented in this study of the effects of environmental factors on standing crop and harvest of fish. Relative size range categories are symbolized as follows: • 500-10,000 acres. ■ 10,000-100,000 acres; ● greater than 100,000 acres.

Figure 2. Mean standing crop of fish in 16 Oklahoma reservoirs, grouped by chemical type of inflowing stream. "Sport fishes" includes all centrarchids and catfishes, white bass and walleye.

Figure 3. Logarithmic plot and curvilinear regressions of log standing crop on log morphoedaphic index (total dissolved solids divided by mean depth) for 127 reservoirs. Key: Open circles - chemical type 1 reservoirs; solid circles - chemical type 2 reservoirs; triangles - chemical type 3 reservoirs; crosses - chemical type 4 reservoirs. Regression equations for the model log(standing crop) = log (total dissolved solids/mean depth), coefficients of determination, and probability of obtaining an R^2 as large or larger by chance when the hypothesis of no correlation is true; are:

a) Total sample (solid line; N = 127):
$\log Y = 2.003 + 0.616 \log X - 0.250 (\log X)^2$
$R^2 \times 100 = 40$; $P(R^2 \geq .40) = 1.0 \times 10^{-9}$

b) Total sample, less chemical type 4 reservoirs (dashed line; N = 109):
$\log Y = 2.005 + 0.655 \log X - 0.230 (\log X)^2$;
$R^2 \times 100 = 54$; $P(R^2 \geq .54) = 1.0 \times 10^{-9}$

c) Chemical type 4 (dotted line; N = 18):
$\log Y = 0.889 + 1.631 (\log X) - 0.480 (\log X)^2$;
$R^2 \times 100 = 27$; $P(R^2 \geq .27) = 0.09$

Figure 4. Regressions of standing crop of carp (solid line) and clupeids (dashed line) on impoundment age in nine South Carolina reservoirs varying in age from 3 to 47 years. Plotted values represent means of cove rotenone standing crop estimates from 3 to 5 years of sampling for individual waters.

Addendum to "Influence on Standing Crop and Harvest"

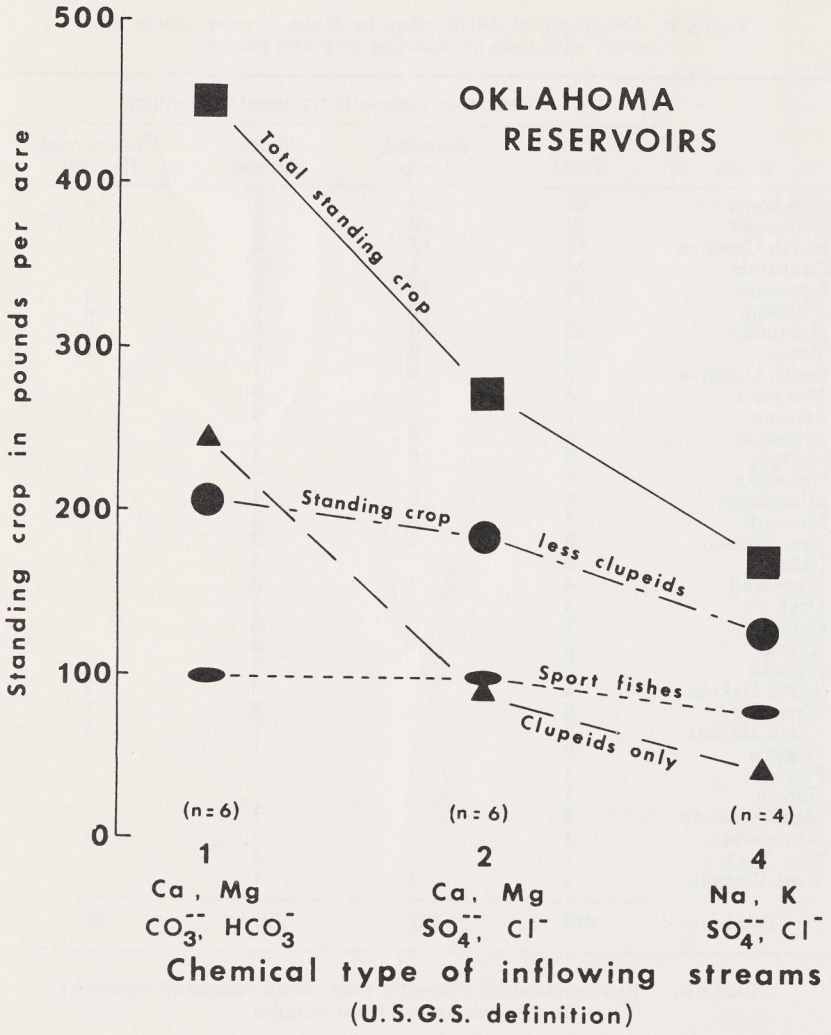

Figure 2.

The sample was further subdivided into use type in anticipation of significant differences in variables between reservoir groups operated primarily for hydropower, flood control, irrigation, or water supply purposes. Within use types, reservoirs are listed alphabetically by state.

All variables considered in the study are defined in Table 1 legend. Area is expressed as a reciprocal in the regressions; hence, a positive regression coefficient represents a negative relation. Data are essentially complete except for outlet and thermocline depths.

The only trophic level separation reported in this study is that of

the clupeids from the remainder of the species. In subsequent multivariable analyses, about 80 species or closely-related species will function as dependent variables.

The mean standing crop of fish in 127 reservoirs was 186 pounds per acre (Table 4). Weighted by area, the mean was 206 pounds per

TABLE 4. Mean standing crop and annual harvest of fish in U. S. reservoirs, unweighted and weighted by surface area of reservoirs in subsamples

	Number of reservoirs	Pounds per acre		
		Unweighted mean	Mean, weighted by area	Range
Standing crop				
Total	127	186	206	13–540
Total, clupeids present	116	198	210	19–540
Total, clupeids absent	11	63	53	13–186
Clupeids	116	91	90	1–424
Total, less clupeids	116	108	121	8–262
Annual harvest				
Sport	121	22.6	13.9	<1–169
Commercial	46	10.2	7.0	<1– 55

acre, suggesting a positive relation between standing crop and reservoir size. Clupeid standing crops averaged 91 pounds per acre, or about 45 per cent of the total crop in reservoirs where they were present.

The mean annual sport fish harvest in 121 reservoirs was 22.6 pounds per acre. It was 13.9 pounds per acre when weighted by area of reservoirs represented, indicating an inverse relation between harvest and reservoir size. Commercial harvest displayed a similar relationship, with the unweighted mean in 46 reservoirs being 10.2 pounds per acre compared to an area weighted mean of 7.0.

Regression Analyses

In an attempt to clarify interrelationships of environmental factors and fish production in reservoirs, a series of regressions between six independent and five dependent variables was computed. With the exception of area, all data were transformed to logarithms for computation. Programs were written for an IBM 7040 computer by Dr. James E. Dunn, Department of Mathematics, University of Arkansas, whose advice was of inestimable aid during the course of the analysis.

Single variable analysis. To identify single environmental factors having a significant influence on fish production, 24 variable combination regressions were calculated (Table 5). Most of the coefficients of correlation were lower than 0.33. When expressed as per cent of total variability ($r^2 \times 100$) in standing crop or harvest which might be explained by the effect of an environmental factor, none of the single variables accounted for more than 21 per cent of total variability. In comparison, Hayes and Anthony (1964) found that 35 per cent of the variability in

their fish "Productivity Index" in 41 lakes could be attributed to area, 46 per cent to depth, and 3 per cent to MO alkalinity. The factor values in both studies are interdependent and therefore not additive.

However, some regressions had high levels of significance (Table 5), affording clues to variables which should prove most important in a multivariable approach. Variables with the greatest influence on total standing crop appear to be dissolved solids, area and shore development (positive effects). Shad crops were positively influenced by increases in age and dissolved solids and decrease in storage ratio. Sport harvest was

TABLE 5. Regression coefficients (a), correlation coefficients (b), and constants for simplified model (c), showing relation between single environmental factors and standing crops and harvests. All data, except area, were converted to logarithmic expressions. The area expression is based on the assumption that allocthonous nutrient levels are inversely related to the square root of the area.

Independent variable		Dependent variable (pounds/acre)			
		Total standing crop	Clupeid standing crop	Sport harvest	Commercial harvest
Number of reservoirs		127	116	121	46
$\sqrt{10^8/\text{area in acres}}$	a	—0.001	—0.0002	0.001	0.002
	b	—0.24**	—0.03	0.21*	0.23
	c	2.26	1.78	0.85	0.58
Mean depth (feet)	a	—0.105	—0.136	—0.123	—0.765
	b	—0.10	—0.09	—0.08	—0.46**
	c	2.29	1.95	1.19	1.76
Storage ratio	a	—0.066	—0.180	0.085	—0.281
	b	—0.13	—0.22*	0.10	—0.27*
	c	2.10	1.61	1.06	0.55
Shore development	a	0.231	—0.103	0.187	—0.379
	b	0.23*	—0.04	0.12	—0.28
	c	1.92	1.86	0.87	1.11
Dissolved solids (ppm)	a	0.235	0.255	0.169	—0.154
	b	0.32**	p.22**	0.14	—0.12
	c	1.69	1.26	0.64	1.10
Age of reservoir (years)	a	—0.042	0.319	—0.336	0.749
	b	—0.06	0.28**	—0.29**	0.40**
	c	2.20	1.41	1.37	—0.18

*Correlation significant at 0.05 level.
**Correlation significant at 0.01 level.

negatively related to age and area. Commercial harvest was positively related to age, but negatively to mean depth and storage ratio.

A regression of sport harvest on standing crop in 49 reservoirs resulted in a positive regression (0.032) with a low correlation ($r = 0.158$). The Kendall "tau" test indicated that the regression was of low predictive value; i.e., a high standing crop is not necessarily associated with a high sport harvest.

Morphoedaphic index. Ryder's (1965) morphoedaphic index (dissolved solids/mean depth) for estimating potential sport and commercial yield in lakes was tested in relation to reservoir standing crop. The efficiency of dissolved solids and mean depth as independent variables in such an index was reduced on reservoirs, as they were correlated (r =

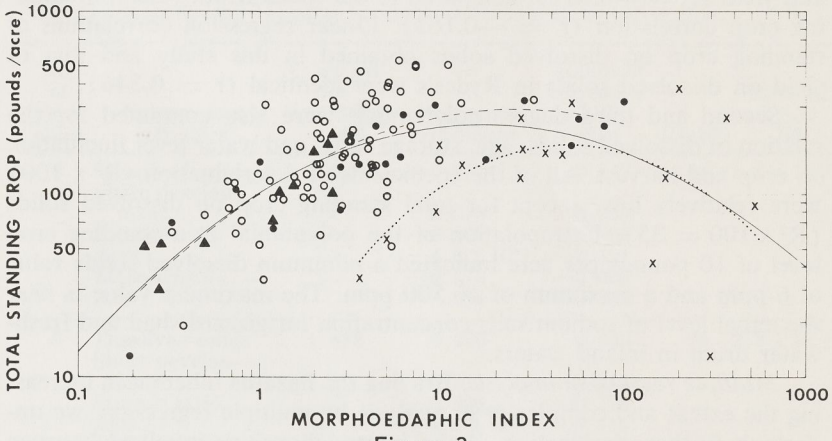

Figure 3.

—0.370). The equation for reservoir standing crop on morphoedaphic index (N = 127) is Y = 2.07 + 0.164X, where Y equals log (standing crop) and X equals log (morphoedaphic index). The coefficient of correlation (r) is 0.325, significant at the 0.01 level. Regression of sport harvest in 121 reservoirs on morphoedaphic index was Y = 0.88 + 0.183X; r = 0.23; significant at the 0.02 level. Commercial harvest versus the index in 46 reservoirs is expressed by Y = 0.52 + 0.210X; r = 0.21; not significant at 0.05 level. Ryder's yield regression on 23 lakes resulted in an r of 0.856, significant at 0.01 level and of greater predictive value.

Plotting of the reservoir data on logarithmic paper revealed that the relationship was actually curvilinear. A second-degree polynomial expression of the standing crop-morphoedaphic index relation (Figure 3) resulted in a much better fit, with about 40 per cent of the variability in standing crop being explained by the index.

Separation of reservoirs classified as chemical type 4 (Na-K, SO_4-Cl) water (Table 1) further clarified the relationship. The standing crop distribution of these 18 reservoirs located in Louisiana, Oklahoma, and Texas was significantly different from the rest of the sample. About 27 per cent of the variability in chemical type 4 waters is explained by the morphoedaphic index, at 0.09 significance level. With removal of chemical type 4 reservoirs, the quadratic expression for the remaining 109 reservoirs (in chemical types 1, 2, and 3) is improved, with 54 per cent of the standing crop variability explained by the morphoedaphic

index, compared to 74 per cent in Ryder's yield relationship based on 23 lakes.

The apparent reasons for the better fit obtained by Ryder are a) fewer observations included in his study (23 versus 109), and b) the much higher correlation which he obtained between mean depth alone and yield ($r = -0.830$), compared to our mean depth-reservoir standing crop correlation ($r = -0.163$). Linear regression correlations of standing crop on dissolved solids obtained in this study and that of yield on dissolved solids in Ryder's were identical ($r = 0.346$).

Second and third degree polynomials were also computed for the relation of dissolved solids, age, storage ratio, and water level fluctuation on crop and harvest. All of the coefficients of determination ($R^2 \times 100$) were relatively low, except for total standing crop on dissolved solids ($R^2 \times 100 = 35$). Extrapolation of the polynomial at a standing crop level of 10 pounds per acre indicated a minimum dissolved solids value of 6 ppm and a maximum of 16,500 ppm. The maximum value is near the lethal level of sodium salts concentration for gizzard shad and freshwater drum in inland waters.

Multiple regression analysis. Braving the hazards inherent in increasing the extent and complexity of analysis by multiple regression, we undertook further clarification of the interrelationships involved between six environmental factors and standing crop and harvest in reservoirs having complete data. A series of regressions between total standing crop, clupeid standing crop, sport and commercial harvest and area, mean depth, storage ratio, shore development, dissolved solids, and age was computed and tested for significance. By a step-down procedure, wherein all combinations of the environmental variables were tested at six- through one-variable levels, the most highly significant (0.01 level) multiple regressions were selected. The results are illustrated by regressions of standing crop on various environmental factor combinations in Table 6. The equation involving three independent variables was selected for further analysis and possible development of a new multi-factor index. Following the same procedure, single equations were also selected to relate clupeid standing crop, and sport and commercial harvest to the most influential environmental factors (Table 7).

None of the regressions provided an explanation of more than 37 per cent of the total variability in standing crop or harvest, although the correlations were highly significant. This is not surprising in view of the wide span of environmental conditions represented. Some general relationships were apparent in the multiple regressions, which will be explored in subsequent analyses as more variables are added and more subdivisions made by similar reservoir types. These were:

a) With increase in total dissolved solids, an increase in standing crop and sport fish yield;

TABLE 6. Summary of equations relating total standing crop to various combinations of six physicochemical factors in 116 reservoirs. Only the most highly significant regressions selected by a step-down process from all possible multiple combinations are presented. $R^2 \times 100$ is the coefficient of determination times 100, and reflects the percent of variability in the dependent variable explained by each multiple regression. The significance level listed is the probability of obtaining an R^2 as large or larger by chance when the hypothesis of no correlation is true. Equation form[2] log (dependent variable) = constant for simplified model (a) + regression coefficient (b_1) times log (independent variable) (x_1) + $b_2x_2 \ldots . + b_n x_n$.

No. of variables	Independent variables	Constant for Simplified model	Regression coefficient	Standard regression coefficient	$R^2 \times 100$	Prob. of a larger R^2
6	Dissolved solids	1.508	0.253	0.347	24	5.2×10^{-5}
	Shore development		0.273	0.268		
	Storage ratio		—0.099	—0.190		
	Area		-4.0×10^{-4}	—0.121		
	Mean depth		—0.072	—0.069		
	Age		—0.034	—0.045		
5	Dissolved solids	1.488	0.250	0.343	23	2.2×10^{-5}
	Shore development		0.287	0.282		
	Storage ratio		—0.090	—0.175		
	Area		-4.0×10^{-4}	—0.119		
	Mean depth		—0.087	—0.083		
4	Dissolved solids	1.363	0.267	0.366	23	1.0×10^{-5}
	Shore development		0.250	0.246		
	Storage ratio		—0.105	—0.023		
	Area		-4.0×10^{-4}	—0.125		
3	Dissolved solids	1.218	0.279	0.383	22	6.8×10^{-6} (selected)
	Shore development		0.318	0.312		
	Storage ratio		—0.100	—0.192		
2	Dissolved solids	1.348	0.267	0.367	18	1.9×10^{-5}
	Shore development		0.289	0.285		
1	Dissolved solids	1.694	0.235	0.323	10	5.2×10^{-4}

b) With increased age of reservoir, an increase in clupeid crop and commercial harvest, but a decrease in sport harvest and little effect on total standing crop;

c) With increased storage ratio (i.e., lower water exchange rate), a decrease in standing crop and commercial harvest and an increase in sport harvest;

d) With increase in reservoir area, a decrease in sport harvest;

e) With increase in mean depth, decreases in total standing crop, and sport and commercial harvest;

f) With increased shore development, increases in total standing crop and sport harvest, but a decrease in commercial harvest.

TABLE 7. Multiple regression equations relating clupeid standing crop, sport and commercial harvest to various combinations of physicochemical factors which were selected by a step-down procedure as being most highly significant and with a relatively high R^2 value. All data except area are logarithmic expressions.

Dependent variable	Constant for simplified model	Independent variables	Regression coefficient	Standard regression coefficient	Multiple R^2 x 100	Prob. of a larger R^2
Clupeid standing crop	0.828	Dissolved solids	0.276	0.240	16	7.2×10^{-4}
		Age	0.247	0.221		
N = 102		Storage ratio	—0.154	—0.192		
Sport harvest	0.129	Age	—0.318	—0.270	20	3.0×10^{-4}
		Dissolved solids	0.305	0.245		
		Area	0.001	0.284		
N = 99		Shore development	0.378	0.251		
Commercial harvest	0.734	Mean depth	—0.612	—0.369	37	4.8×10^{-4}
		Storage ratio	—0.174	—0.230		
N = 41		Age	0.572	0.123		

Subsample analyses. In an effort to reduce the variability of crop and harvest data in total samples, the reservoirs were subdivided into chemical types (Table 1). This subdivision improved the coefficients of determination (R^2) resulting from a number of multiple regressions; the improvement was attributable in great measure to reduction in the number of reservoirs in each sample. Some of the subsample regressions with relatively high R^2 x 100 values (per cent of total variability explained by environmental factors in the equation) were:

	Chemical type	Reservoirs in sample	R^2 x 100
Standing crop versus:			
Diss. solids (+) and depth (—)	1	78	43
Age (+), storage ratio (+) and depth (—)	2	16	86
Depth (—)	3	11	73
Shore development (+)	4	18	51
Commercial harvest versus:			
Depth (—) and storage ratio (—)	1	23	55
Area (—) and storage ratio (—)	2	15	76

To illustrate the probable predictive value of these regressions, consider the eleven chemical type 3 reservoirs located in the western Carolinas which encompass such diverse environments as Fontana and Greenwood reservoirs. In spite of this diversity, 73 per cent of the variability in standing crop is attributable to mean depth. From the regression log (standing crop) = 3.24 — 0.830 log (mean depth), Fontana Reservoir with a mean depth of 128′ has a calculated standing crop of 31 lb/acre.

The mean standing crop determined from five years (1957-1963) of cove samples by North Carolina biologists was 52 lb/acre. The calculated standing crop of Greenwood Reservoir, with a mean depth of 21 feet, is 138 lb/acre, compared to a four-year mean value from South Carolina studies of 189 lb/acre. These two examples represent the farthermost departures from the calculated regression. Santeetlah Reservoir, for instance, had an observed value of 53 lb/acre and a calculated of 61; Hickory Reservoir an observed value of 103 and a calculated of 100.

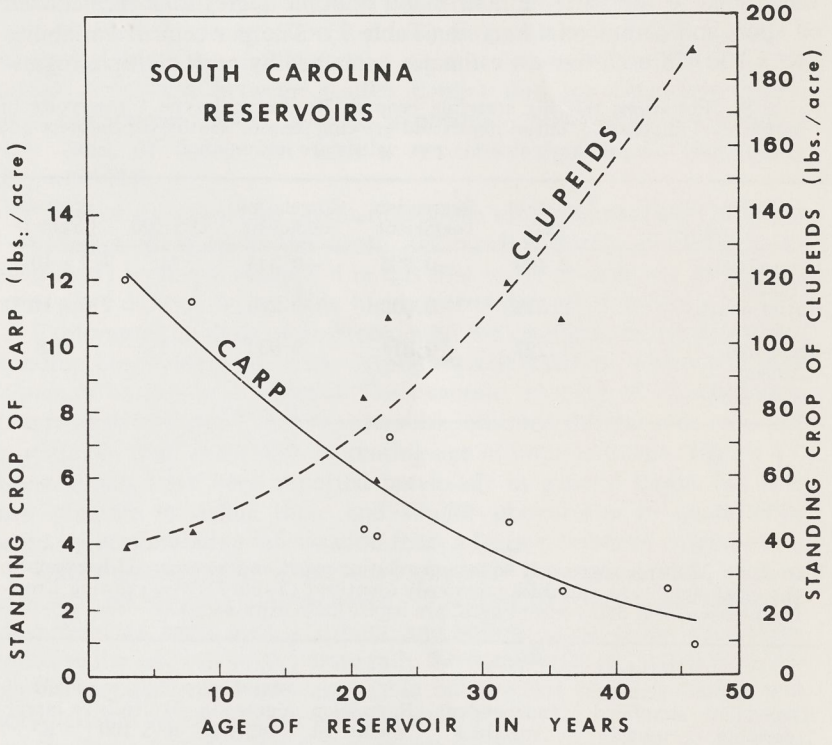

Figure 4.

In 18 chemical type 4 reservoirs, 51 per cent of the variability in standing crop was attributable to the effect of shore development. In other words, the greater the shoreline length in relation to reservoir area, the higher the standing crop.

The negative effects of increasing area and storage ratio in 15 chemical type 2 reservoirs accounted for 76 per cent of the variability in commercial fish harvest; i.e., the more river-like the impoundment, the higher the harvest. In 23 chemical type 1 reservoirs, the negative effects of increasing depth and storage ratio accounted for 55 per cent of the

variability in commercial harvest. The deeper and more lake-like the impoundment, the lower the yield.

Other variable effects. Three other variables, represented by incomplete data, were tested against standing crop in 70 chemical type 1 reservoirs (Table 8). Fluctuation and outlet depth negatively affected standing crop, but the correlations were low. Growing (frost-free) season positively influenced standing crop, but the correlation was very low. However, its probable importance in influencing yield and carrying capacity has been demonstrated (Thompson, 1941); so growing season was added to the variable matrix and multiple regressions recalculated on sport and commercial harvest (Table 9). The per cent of variability ($R^2 \times 100$) in both harvest estimates explained by each multiple regres-

TABLE 8. Equations relating standing crop in 70 chemical type 1 reservoirs to water level fluctuation, outlet depth and growing season. Outlet depths were not transformed to logarithms, as some zero values are represented.

Independent variable	Constant "a"	Regression coefficient	Correlation coefficient	$r^2 \times 100$	Prob. of larger r^2
Fluctuation (in feet)	2.460	—0.225	—0.335	11	4.7×10^{-3}
Outlet depth (in feet)	2.318	—0.002	—0.276	8	2.0×10^{-2}
Frost-free season (in days)	1.727	0.214	0.032	1	0.8

TABLE 9. Multiple regression equations relating sport and commercial harvests to the most significant variables previously identified (Table 7), plus growing (frost-free) season. All data, except area, are logarithmic expressions.

Dependent variable	Constant for simplified model	Independent variables	Regression coefficient	Standard regression coefficient	Multiple $R^2 \times 100$	Prob. of a larger R^2
Sport harvest	—2.041	$\sqrt{10^8/\text{area}}$	0.001	0.22	25	8.7×10^{-6}
		Shore development	0.152	0.10		
N = 116		Dissolved solids	0.339	0.29		
		Growing season	1.023	0.26		
		Age	—0.289	—0.24		
Commercial harvest	6.482	Mean depth	—0.492	—0.28	48	9.0×10^{-5}
		Fluctuation	—0.231	—0.18		
N = 45		Storage ratio	—0.204	—0.27		
		Growing season	—2.453	—0.37		
		Age	0.482	0.25		

sion was improved. Addition of growing season increased the sport harvest regression $R^2 \times 100$ value from 20 (Table 7) to 25, and the commercial harvest from 37 to 48. Increase in shore development, dissolved solids, and length of growing season positively influenced sport harvest. Decreases in mean depth, fluctuation, storage ratio, and growing season positively influenced commercial harvest. Increasing age of reservoir had a negative effect on sport harvest and a positive effect on commercial harvest. Area increase negatively affected sport harvest.

Outlet depth is correlated with mean depth (0.82). A multiple regression of standing crop on both mean and outlet depths of 95 reservoirs resulted in the equation log (standing crop) $=$ 2.800 $-$ 0.547 log (mean depth) $+$ 0.094 (outlet depth) with an $R^2 \times 100$ of 15. A partial correlation between (outlet depth) and log (standing crop), given log (mean depth), yielded a positive outlet depth on standing crop value of 0.062 but with a very low significance probability ($t_{(92)} = 0.63$).

Tests of the effects on production of the other factors listed in Table 1 (drainage area, maximum depth, thermocline depth, elevation, sediment load) were not attempted in this first series of analyses, as scattergram plots did not suggest any highly correlated relationships.

Exploratory analysis of environmental factor effects on single species standing crops suggested some important relationships which will subsequently be explored in detail. For example, plotting of standing crop data from nine South Carolina reservoirs indicated decreases in carp and increases in shad crops with increasing age of impoundment (Figure 4). These trends have been reported previously in general terms, but it is now possible to define these and similar phenomena in quantitative terms by accumulating information from a large number of reservoirs.

Data on many other important features of the environment, such as turbidity, phosphorus and nitrogen, dissolved oxygen, solar radiation, trace elements, basin soils, plankton, and bottom fauna crops, need to be added to the analysis to test more fully the complexity of factors influencing fish populations. However, usable information on such factors was not available on more than a few waters.

Similarly, factors such as fish growth rate and condition, species and size compositions, and fishing pressure and success rates should be incorporated into analyses. Relatively large masses of data are available on these important variables.

Conclusion

We have developed a few models describing the influence of some important environmental factors on reservoir fish standing crop and harvest. Those of greatest apparent utility are: a) curvilinear regression of standing crop on morphoedaphic index (dissolved solids in ppm/mean depth in feet), excluding chemical type 4 reservoirs; b) multiple regression of standing crop on dissolved solids, shore development

and storage ratio; c) regression of sport harvest on dissolved solids, growing season, age, area, and shore development; and d) commercial harvest on growing season, mean depth, storage ratio, age, and fluctuation.

Preliminary analyses suggest that predictive ability can be improved by further model subdivision of fish population structure and reservoir physicochemical "types" and by the inclusion of additional environmental factors. Reorganization of the data is now being accomplished.

To develop a general theory of reservoir biotic community structure, a multiplicity of models will be required to satisfy the demands of such a complex, heterogeneous group of waters. As Levins (1966) astutely observed: ". . . all models leave out a lot and are in that sense false, incomplete, inadequate. The validation of a model is not that it is 'true' but that it generates good testable hypotheses relevant to important problems."

Literature Cited

Carlander, Kenneth D. 1955. The standing crop of fish in lakes. J. Fish. Res. Bd. Canada 12(4): 543-570.

Hall, Gordon E. 1962. A survey of fish population sampling methods in Southern reservoirs. Report to the Reservoir Comm., So. Division, Amer. Fish. Soc., Aug. 1962. Mimeo. 16 pp.

Hayes, F. R., and E. H. Anthony. 1964. Productive capacity of North American lakes as related to the quantity and trophic level of fish, the lake dimensions, and the water chemistry. Trans. Amer. Fish. Soc. 93(1): 53-57.

Isaac, G. W., and C. E. Bond. 1963. Standing crops of fish in Oregon farm ponds. Trans. Amer. Fish. Soc. 92(1): 25-59.

Jenkins, R. M. 1958. The standing crop of fish in Oklahoma ponds. Proc. Okla. Acad. Sci. 28(1957): 157-172.

———. 1965. Bibliography on reservoir fishery biology in North America. U. S. Bureau of Sport Fisheries and Wildlife, Research Report 68: 57 pp.

Larkin, P. A. 1964. Canadian lakes. Vehr. Int. Verein. Limnol. XV: 76-90.

Levins, Richard. 1966. The strategy of model building in population biology. Amer. Sci. 54(4): 421-431.

Moyle, John B. 1954. Some aspects of the chemistry of Minnesota surface waters as related to game and fish management. Minn. Dept. of Cons. Invest. Report No. 151. Mimeo. 25 pp.

Northcote, T. G., and P. A. Larkin. 1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Canada 13: 515-540.

Rainwater, F. H. 1962. Composition of rivers of the conterminous United States. Atlas HA-61. U. S. Geol. Survey.

Rawson, D. S. 1958. Indices to lake productivity and their significance in predicting conditions in reservoirs and lakes with disturbed water levels. Invest. of Fish-Power Problems. H. E. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver, p. 27-42.

Reimers, N., J. A. Maciolek and E. P. Pister. 1955. Limnological study of the lakes in Convict Creek Basin, Mono County, Calif. U. S. Fish and Wildlife Service, Fishery Bulletin 103, vol. 56: 437-503.

Rounsefell, George W. 1946. Fish production in lakes as a guide for estimating production in proposed reservoirs. Copeia (1): 39-40.

Ryder, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Amer. Fish. Soc. 94(3): 214-218.

Thompson, D. H. 1941. In "A Symposium on Hydrobiology," pp. 206-217. Univ. of Wisconsin Press, Madison, Wisc.

Turner, William R. 1960. Standing crops of fishes in Kentucky farm ponds. Trans. Amer. Fish. Soc. 89(4): 333-337.

Welch, P. S. 1935. Limnology. McGraw-Hill. XIV + 471 pp.

Food and Feeding of Larval Dicamptodon ensatus from California

ABSTRACT: *Observations on 149* Dicamptodon ensatus *in aquaria showed that they fed readily upon* Ambystoma gracile. A. gracile *were frequently ingested by larger* Dicamptodon *in nature as shown in the analysis of 51 stomachs taken from salamanders immediately preserved upon capture. Cannibalism occurred commonly in captivity but not in nature.*

On 12 May 1967, larvae of *Dicamptodon ensatus, Ambystoma gracile* and *Taricha granulosa* were collected at Fern Lake on the Humboldt State College campus, Arcata, California. Fifty-one of the 200 *Dicamptodon* larvae were immediately preserved in 10% formalin; the rest were transferred to 500-gal aquaria in the Humboldt State College Fish Hatchery.

Metter (1963) summarized previous scanty information on feeding habits of *Dicamptodon,* and reported on the feeding habits of an Idaho population of larval *Dicamptodon* as related to larval size. Every animal over 95 mm snout-vent length contained an *Ascaphus truei* larvae; Trichoptera and Coleoptera larvae and adults, and Plecoptera and Ephemeroptera nymphs were also important in their diet.

In aquaria *Dicamptodon* fed readily upon *A. gracile* larvae. Usually the prey was swallowed rapidly, head first, but occasionally long periods (up to an hour) were required for ingestion, and some prey were swallowed tail first. Fighting over food was observed among large *Dicamptodon* (150 mm and over).

Dicamptodon did not eat *Taricha granulosa,* presumably because of their strong mucous integumentary poisons.

Cannibalism was observed. Anderson (1960) observed cannibalism among confined adult *Dicamptodon.*

TABLE 1.—Stomach contents of larval *Dicamptodon ensatus*

	Snout-vent length (mm)						
	61-80	81-100	101-125	126-185	Total	Frequency No.	Frequency %
Number of stomachs examined:	5	29	15	2	51		
Ambystoma gracile		11	11	1	23	20	39.2
Trichoptera larvae	2	23	3		28	10	19.6
Trichoptera adults		1			1	1	1.9
Coleoptera larvae	6	45	13	9	73	19	37.2
Coleoptera adults		26	34		60	11	21.6
Odonata larvae	18	90	24	11	143	36	70.5
Odonata adults			1		1	1	1.9
Ephemeroptera nymphs	4				4	1	1.9
Gammarid Amphipoda	2	1			3	2	3.9
Hemiptera adults	1	1	2		4	3	5.9
Arachnoidea (spiders)			3		3	2	3.9
Chironomidae	1	22	11	2	36	10	19.6
Oniscoid Isopoda		1			1	1	1.9
Miscellaneous*	1	7	4	1	13	13	25.5
Empty		1	1		2	2	3.9

*Detritus, rocks, etc.

Stomach content analysis of the preserved *Dicamptodon* (Table 1.) showed that those 81 mm or larger (snout-vent) fed upon *A. gracile* in nature; *A. gracile* apparently serves as a major constituent of their diet. The analysis suggests that cannibalism occurs only in confined *Dicamptodon* and not naturally. Unlike Metter's results, amount of detritus intake did not increase with body size. Odonata larvae occurred most frequently. Adult Coleoptera, primarily bark beetles (*Dendroctonus*), a common beetle in the area, were also prevalent. Larval Odonata, Coleoptera and chironomid larvae were ingested by all sizes of larval *Dicamptodon,* but adult Coleoptera were not found in individuals larger than 126 mm.

We thank Mr. Al Merritt for allowing this research to be carried out in the Humboldt State Fish Hatchery. Our thanks also go to Drs. John DeMartini, Humboldt State College, and Alan E. Leviton, California Academy of Sciences, for their review and suggestions concerning the manuscript.

REFERENCES

ANDERSON, J. D. 1960. Cannibalism in *Dicamptodon ensatus. Herpetologica,* **16**:260.

METTER, D. E. 1963. Stomach contents of Idaho *Dicamptodon. Copeia,* **1963**:435-436.

CLIFFORD RAY JOHNSON AND CARL B. SCHRECK, Department of Zoology, University of Queensland, St. Lucia, Brisbane, Australia, and Colorado Cooperative Fishery Unit, Colorado State University, Fort Collins 80521, respectively. *Submitted 15 April 1968; accepted 7 June 1968.*

Artificial Fertilization of a Small High-altitude Lake[1]

ABSTRACT: *A small shallow alpine lake was treated with diammonium phosphate for two summers. Nannoplankton were found to increase from several thousand organisms per liter before treatment to several million cells after fertilization. Apparent winterkill reduced the fish numbers so that it was difficult to ascertain to what extent fertilization played a role in increased food consumption and growth of the brook trout.*

An inorganic fertilizer was introduced into a small shallow alpine lake in an attempt to increase productivity and thus improve the growth rate of the brook trout population, *Salvelinus fontinalis.* I also fertilized three adjacent cirque lakes (Rabe and Gaufin, 1964), which were relatively deep with rock substrate, and observed only a slight increase in standing crop of plankton with little evidence of increased fish growth. Olive (1954) working in Colorado and Baxter (1959) in Wyoming both report increases of plankton after fertilization of high lakes but trout growth was not affected in either case.

Lake X-30 (elevation 3230 m) is located in the Swift Creek drainage of the Duchensne River system in the Uinta Mountains, Utah. It is 4.1 surface acres (1.66 ha) with a maximum depth of 3 m and a mean depth of 1 m. The substrate is mostly detritus. Spawning areas are sparse and little evidence of fish reproduction was noted. A total of 250 pounds (about 113 kg) of diammonium phosphate (35-7-0 and 21-53-0) was added to the lake during the summers of 1961-62.

[1] Study supported by the Utah Fish and Game Department, Departments of Zoology and Entomology at the University of Utah, and the U. S. Public Health Service (Division of Water Supply and Pollution Control).

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A limnological reconnaissance of Lake Lanao[1]

David G. Frey

With 6 figures and 3 tables in the text and on 2 folders

Lake Lanao on northern Mindanao in the Philippines is of great interest limnologically if for no other reason than that it contains endemic species of various kinds of animals, including a species flock of cyprinids that have evolved in the lake (most recent review by Myers, 1960, but see also Brooks 1950, and Herre 1933). Contrary to the opinion of Bailey Willis (quoted in Myers 1960) that the lake is only about 10,000 years old, based on the short length of the canyon below Maria Cristina Falls, evidence is accumulating that the lake is much older than this, possibly even deriving from the late Tertiary.

Relatively little has been published concerning the lake and its limnology, aside from taxonomic studies of the fishes by Herre (see bibliography in Myers 1960). The fragmentary and still incompletely published observations of the Wallacea Expedition in 1932 include a maximum depth sounding of 107 m, more than 1 ppm dissolved oxygen at 90 m on 7 May (in contrast to nearly all other deep lakes of the Philippines in which the oxygen completely disappears relatively close to the surface), and the inclusion of the lake by Woltereck in his group of deep tropical lakes with a complete circulation in winter (Woltereck 1933, 1941). This last statement is entirely presumptive, as up to now there have been no seasonal observations on the lake. Besides this there are partial lists of organisms (to genera in most cases, species in some) that occur in the inshore and offshore plankton, and to a lesser extent in the shallow-water benthos (Woltereck 1941). These observations, being very fragmentary, do more to suggest limnological processes than define them.

The present paper is a brief summary of limnological studies conducted from August 1967 through June 1968, during which time almost 40 half-day trips were made on the lake. A Koden echo sounder was used to map the bathymetry of the lake. The area of the lake and of the various tributary watersheds was measured with a planimeter from the

[1] Contribution No. 819, Department of Zoology, Indiana University, Bloomington. These studies were carried out while the author was a Ford Consultant at Mindano State University. The Ford Foundation (through Educational Projects, Inc., in Pittsburgh) also provided a really extensive suite of limnological equipment, not all of which, regretfully, arrived during my period of residence in the Philippines. This research would not have been possible without the cooperation of many persons. Participating in field trips and helping collect data were my class in limnology and volunteers from among the students, faculty, Peace Corps Volunteers, and British Volunteers Service Overseas. I am particularly indebted to Miss Asuncion Amila and Rodrigo Calva, who, besides faithfully helping out during the academic year, served as full-time assistants from mid-April to mid-June, and to Dean Domiciano K. Villaluz of the College of Fisheries. Persons outside the University include Engr. D. C. Paz of the National Power Corporation, Dr. Froilan Gervasio of the Bureau of Mines, Mr. Felix E. Encina of the Weather Bureau, and Mr. Galo B. Ocampo of the National Museum. Dr. Robert G. Wetzel of Michigan State University kindly determined the activity of the C^{14} used and made counts on the membrane filters from the photosynthesis runs. The Research Institute of Mindanao State University generously provided funds for rental of a boat and employment of the two full-time assistants in April—June. The Ford Foundation provided many services through its Manila office.

1 : 50,000 maps available from the Board of Technical Surveys and Maps in Manila. Data on the fluctuations in lake level and discharge of water from the lake were made available by the National Power Corporation. Also available are rainfall data for three stations and temperature data for one station located near the lake (obtained from the Weather Bureau in Manila) and short, although valuable, series of measurements of discharge of the major rivers tributary to Lake Lanao (Williams & Gochoco 1924).

Bathymetry

The lake basin is shallowest toward the north end and becomes progressively deeper toward the south (Fig. 1), with an extensive area east of the two southern islands greater than 110 m in depth and with a maximum depth of approximately 112 m, the same maximum depth quoted by Halbfass (1922: fide Hutchinson 1957). This datum undoubtedly derives from studies by the U. S. Army Engineers, when they were at Camp Keithley at Marawi City during the early decades of this century (Villaluz 1966). Based on a limited number of soundings, Woltereck (1941) concluded that the northern half of the lake (roughly north of a line between Uato and Tamparan in Fig. 3) was quite shallow, and that the bottom dropped off rapidly from here toward the south. Fig. 1 shows that there is a distinct increase in slope here, indicated by the closer spacing of the 10-m countours, but nothing approaching the gradient implied by Woltereck, nor is the northern half so shallow as inferred from the few soundings on his simple map. The maximum depth of 107 m recorded by Woltereck was to the east of the two islands in the south. The base datum for water depths on the bathymetric map is the mean lake level of 701.89 m as determined from records of the National Power Corporation.

During the period of the survey (January through May 1968) the monthly mean lake level varied from 701.12 to 701.40 m. These differences below base datum were overcompensated by a positive error in the echo sounder, which varied asystematically with depth. Since in addition the resolution of the echo sounder was not as great as desired for this work (80 mm of record for 150 m of water depth), the depths are not precise. These errors and others will be discussed in greater detail in the final reports of this study.

In most parts of the lake the bottom is monotonously lacking in relief away from shore. Most offshore bedrock structures have been masked by sediment accumulation, although there are a few areas where this is not so. One is indicated by the sinuosities of the 30- and 40-meter contours in the northern third of the lake. Here, even at this depth and distance from shore, the bottom is composed of coarse sand (with considerable magnetite and garnet) and small pebbles, with gastropods and other benthos abundant and diversified. Fishes, and hence fishermen, are also attracted to this region. Another such area is the structural ridge on which the two southern islands are located. Still others but without major influence on the bathymetry are indicated by subsurface reflections breeching the surface on the echo traces. Near shore, however, except along the east where the major rivers enter, the relief is controlled mainly by bedrock, with only a thin veneer of relatively coarse sediment. In general, the above-water topography is countinued below the surface, as required by a drowned land surface. Hutchinson (1957) lists Lanao as one of the best examples of a lake formed by a lava dam. Tectonic processes have also been involved, however, and are continuing, as evidenced by collapse associated with the 1955 earthquake. Hence, the basin must be considered volcano-tectonic in origin. The steepest slopes occur off the scarp along the south end of the lake, where a depth of 100 m is present barely 200 m offshore. This is the region of the lava dam. The typical deepwater sediments away from shore and away from offshore regions with bedrock at the surface are a fine gray clay. Much could be accomplished toward understanding the geomorphology and evolution of the region with an echo sounder having greater depth resolution and sufficient energy for penetrating the sediments.

Several morphometric statistics of the lake are: area — 357 km^2; volume — 21.5 km^3; maximum depth 112 m; mean depth (volume/area) — 60.3 m; replacement time (volume/mean annual discharge) — 6.5 years.

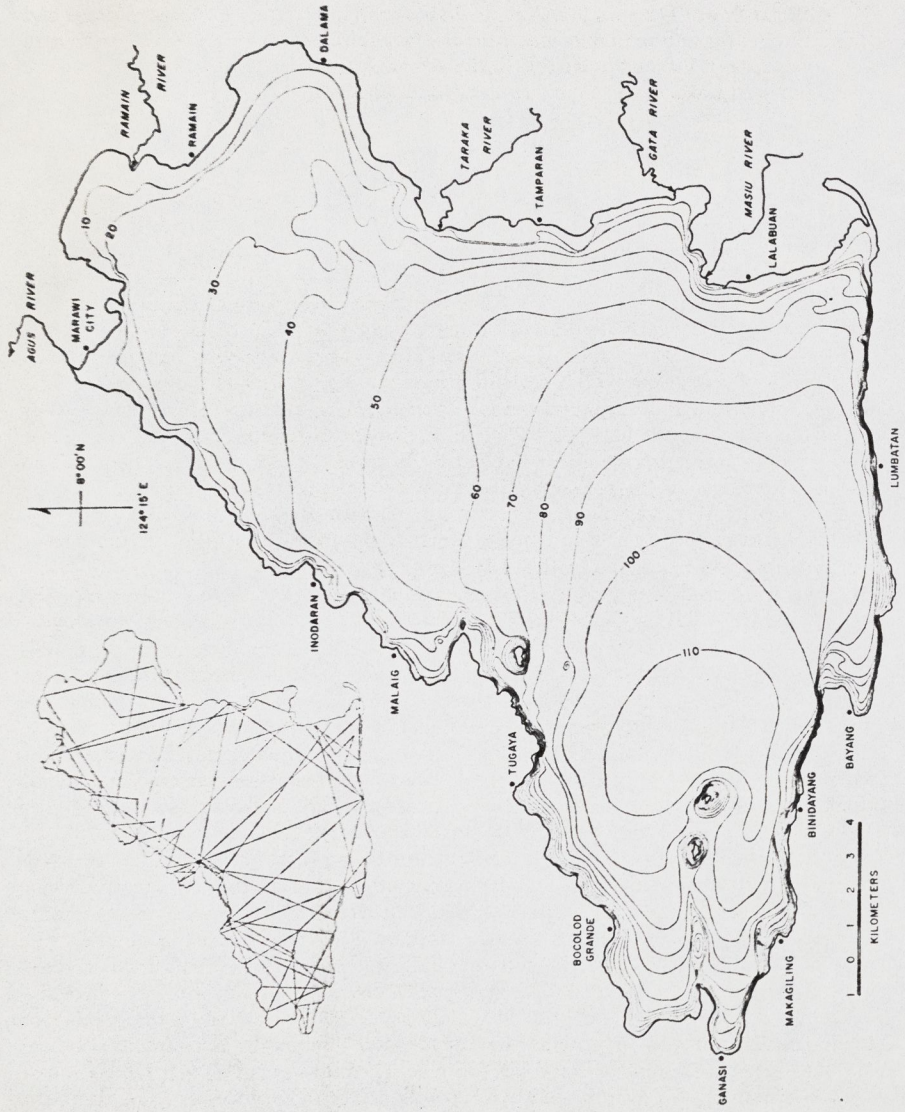


Fig. 1. Bathymetric map of Lake Lanao, prepared with the aid of a Koden echo sounder, model SR-390 D. The various sounding runs made with the boat are shown on the small insert map. Offshore contours are reasonably accurate because of the low relief here. Nearshore contours are only approximate on a map of this size. There are many topographic irregularities within several hundred meters of shore, reflecting bedrock control of a drowned land surface. Contour intervals are 10 meters below the mean lake level of 701.89 m.

Meteorology

Rainfall records are available for the Marawi City region (including Camp Keithley) at the north end of the lake for various intervals over the period May 1918 to January 1954, encompassing a total of about 25 years; for Ganasi at the southwest corner of the lake for the period May 1919 to January 1933; and for Lumbatan on the south shore from April 1919 to December 1932. Maximum and minimum temperatures are available only for Marawi City from January 1921 to December 1932. No official weather station is being maintained in the province of Lanao del Sur at the present time, although one is to be established at Mindanao State University.

The mean annual rainfall at these stations is remarkably consistent: Marawi City — 2865 mm, Ganasi — 2890 m, and Lumbatan — 2864 m, for an overall average of 2873 mm. The number of rainy days per year, however (a rainy day is defined as one with at least 0.1 mm precipitation), is not consistent: Marawi City — 237 days, Ganasi — 180 days, Lumbatan — 194 days. The average precipitation per rainy day varies inversely with these numbers. Thus Ganasi has fewer rainy days per year than Marawi City (and hence probably more hours of sunshine, although there are no data to substantiate this), but the rains when they do come are more intense.

The lake exerts considerable control over the local climate, which affects the insolation amount and pattern. Typically the sky is relatively cloudless until mid morning. The small updraft clouds that form over the land tend to dissipate as they move out over the cooler water. As a result the lake is frequently surrounded by clouds, but the sky overhead is clear. This permits almost maximum insolation and undoubtedly affects the primary productivity.

As is typical of many monsoon areas of the Philippines, the months December through April are relatively dry, the other seven months relatively wet. This is the pattern evident in the climatograph for Marawi City (Fig. 2), which also shows the markedly colder mean daily temperatures from December through March. This is the period during which the lake turns over, based on the records for this one year. Stratification is reestablished in late March and early April during the period of rapid warming. Peak precipitation occurs in June, with a lesser although substantial peak in September.

Hydrology

The Lake Lanao-Agus River system is presently unregulated. When the lake level is high, more water leaves the lake than when the level is low. This results in a stable lake but an unstable river. Over 27 years of record, the mean annual variation of lake level has been only 0.8 m (range 0.3—1.5 m), with an extreme range of 2.09 m. On the other hand, the monthly mean discharge from the lake over this period has varied from 233.0 m^3/sec. in December 1955 to only 12.8 m^3/sec. in May 1958 and even less than this in March and April 1966.

Based on data generously made available by the National Power Corporation, over the periods 1932—40 and 1948—66 the mean lake level was 701.89 m. The time of occurrence of the annual maximum and minimum monthly mean lake levels corresponds closely to the annual cycle of precipitation: 53 % of all maxima occurred during the months June through August, although each month of the year had at least one instance in which the annual maximum occurred in that month. Minimum lake level occurred 70 % of the time in March and April, and the months July through October never had a minimum for any year of record.

During the period July 1938 through December 1940, discharge measurements were made on the Agus River where it leaves the lake at Marawi City, from which a rating curve was established for approximating discharge for any given lake level. During this period the mean monthly lake level varied from 701.60 to 702.29 m and the discharge from 73.38 to 160.14 m^3/sec. A least-squares analysis of these data, assuming a linear relationship between discharge and lake level, gave the regression equation $Y = 118.375 X - 82{,}981.536$ (Y is discharge in m^3/sec. and X is lake level in meters), with a highly

significant correlation coefficient of 0.960 for Y as a function of X. This rating curve is slightly different from the one derived by the National Power Corporation, having approximately the same y-intercept but a somewhat steeper slope. Both curves yield zero discharge at 701.00 m, and yet in March and April 1966 when the mean monthly lake levels were 700.94 and 700.95, respectively, there was still a small discharge from the lake (based on verbal reports of a number of persons at Mindanao State University). Hence, discharge as a function of lake level may be approximately linear over most of the expected range but apparently not at extremely low lake levels.

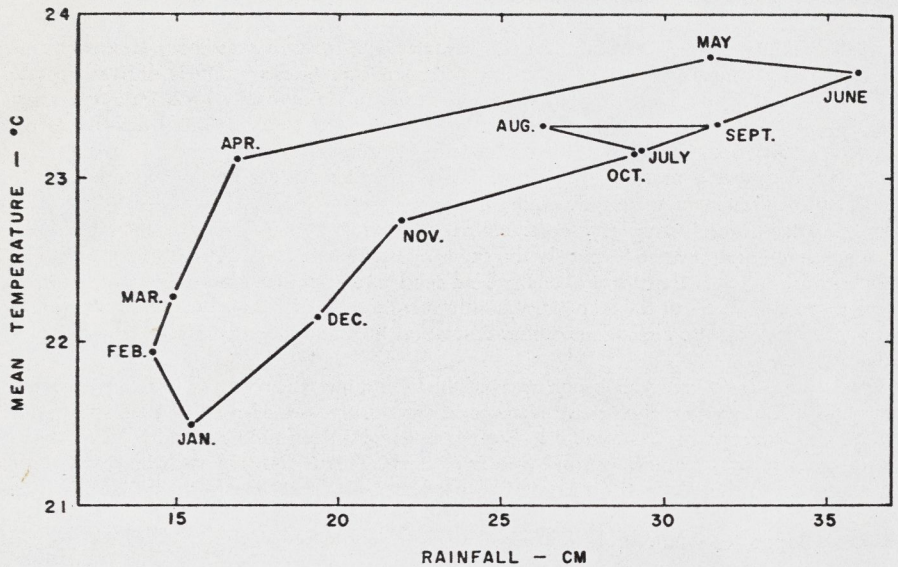
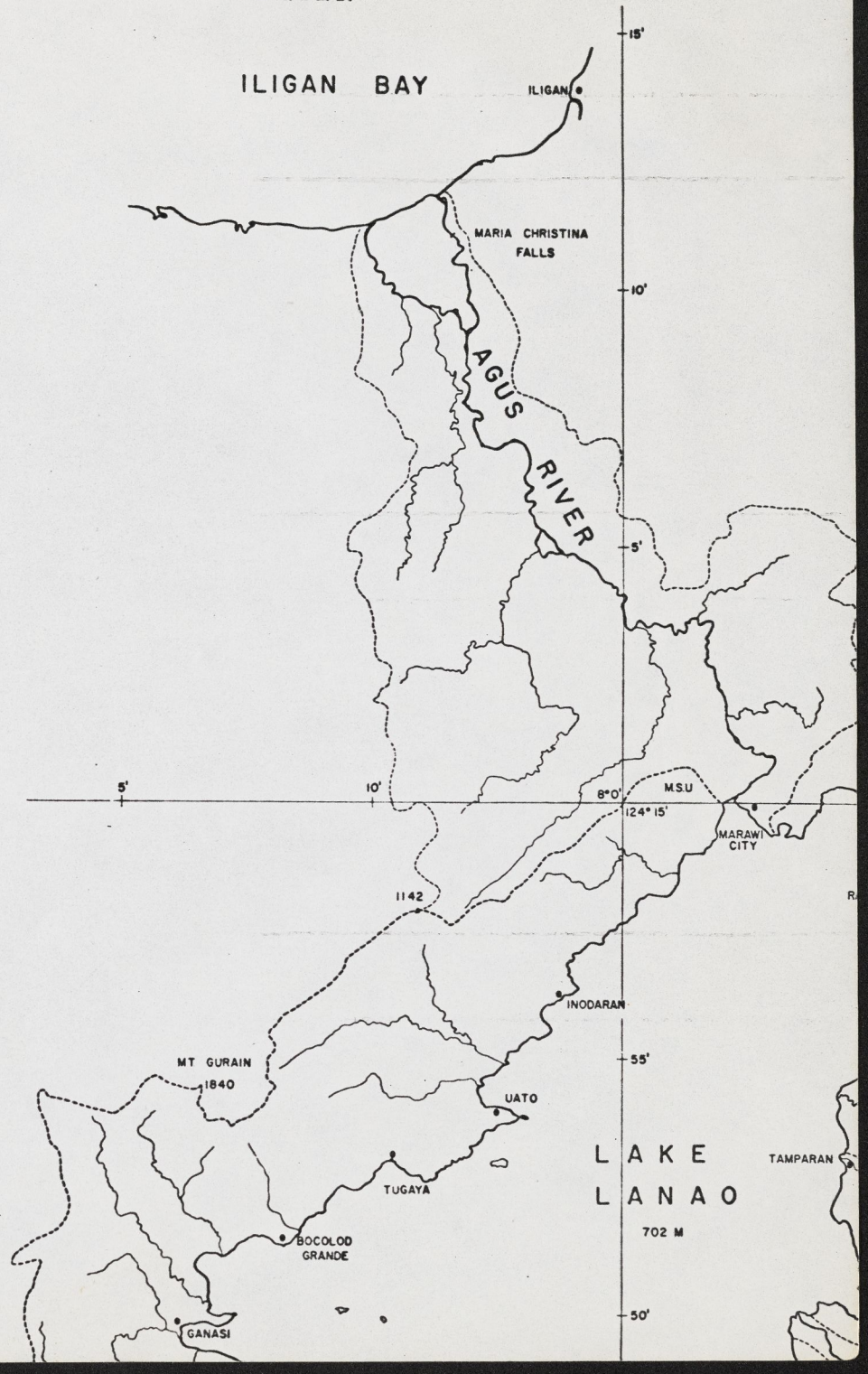


Fig. 2. Climatograph for Marawi City. Mean rainfall for the various months is based on 21 to 26 individual monthly totals over the period May 1918 to January 1954. Monthly mean temperatures are based on 8 to 10 averages for each month accumulated over the period January 1921 through December 1932. All data are from the records of the Weather Bureau, except rainfall data for July 1950 through January 1954, which are from the National Power Corporation.

From the regression equation given above, the mean discharge from the lake (at a mean water level of 701.89 m) is 104.71 m^3/sec., which yields an average annual discharge of 3.304 billion m^3. Since the area of the total watershed above the source of the Agus River at Marawi City is approximately 1.680 billion m^2, each square meter of watershed surface (including the lake) contributes roughly 1.97 m^3 to the discharge from the lake. Assuming a mean precipitation of 2.873 m for the entire watershed (although it may well be substantially higher than this), the difference of 0,90 m must be accounted for by evapotranspiration and other losses from the system.

The Lake Lanao watershed can be resolved into the major components shown in Tab. 1 (see also Figs. 3 and 4). Discharge measurements for the five major rivers draining the mountainous region to the east are available for the period September 1919 through June 1922. The discharge from the lake for this same period can be estimated from the discharge measurements of the Agus River made at Momumgan 23 km downstream from the lake. Tab. 2 shows that in general each watershed contributes to the total discharge from the lake in proportion to its area. The Masiu River and the Gata + Bacayawan Rivers (the Bacayawan is shown in Fig. 4 as the small elongated watershed — labelled S — between the Taraka and Gata watersheds) have a small excess contribution, the Ra-



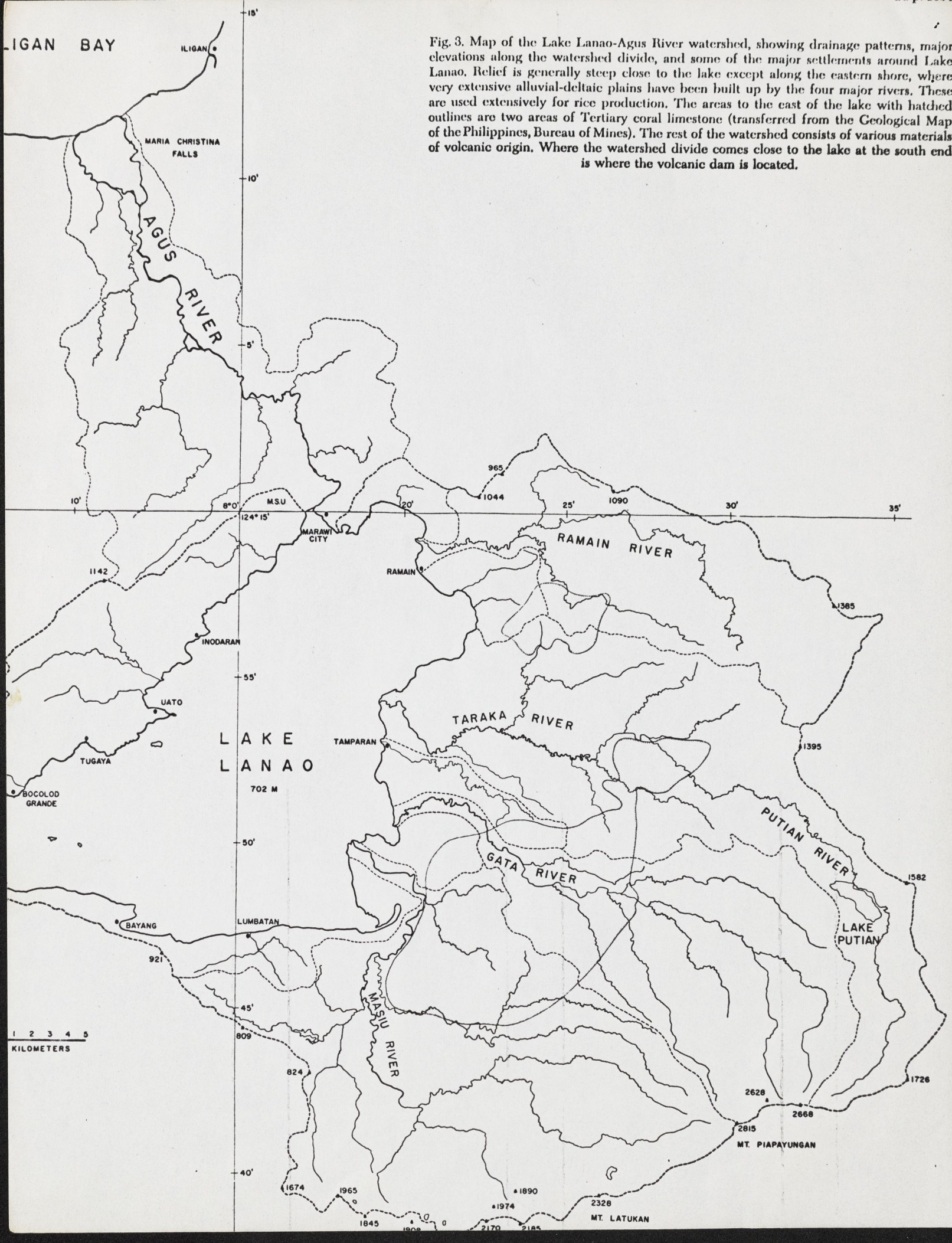


Fig. 3. Map of the Lake Lanao-Agus River watershed, showing drainage patterns, major elevations along the watershed divide, and some of the major settlements around Lake Lanao. Relief is generally steep close to the lake except along the eastern shore, where very extensive alluvial-deltaic plains have been built up by the four major rivers. These are used extensively for rice production. The areas to the east of the lake with hatched outlines are two areas of Tertiary coral limestone (transferred from the Geological Map of the Philippines, Bureau of Mines). The rest of the watershed consists of various materials of volcanic origin. Where the watershed divide comes close to the lake at the south end is where the volcanic dam is located.

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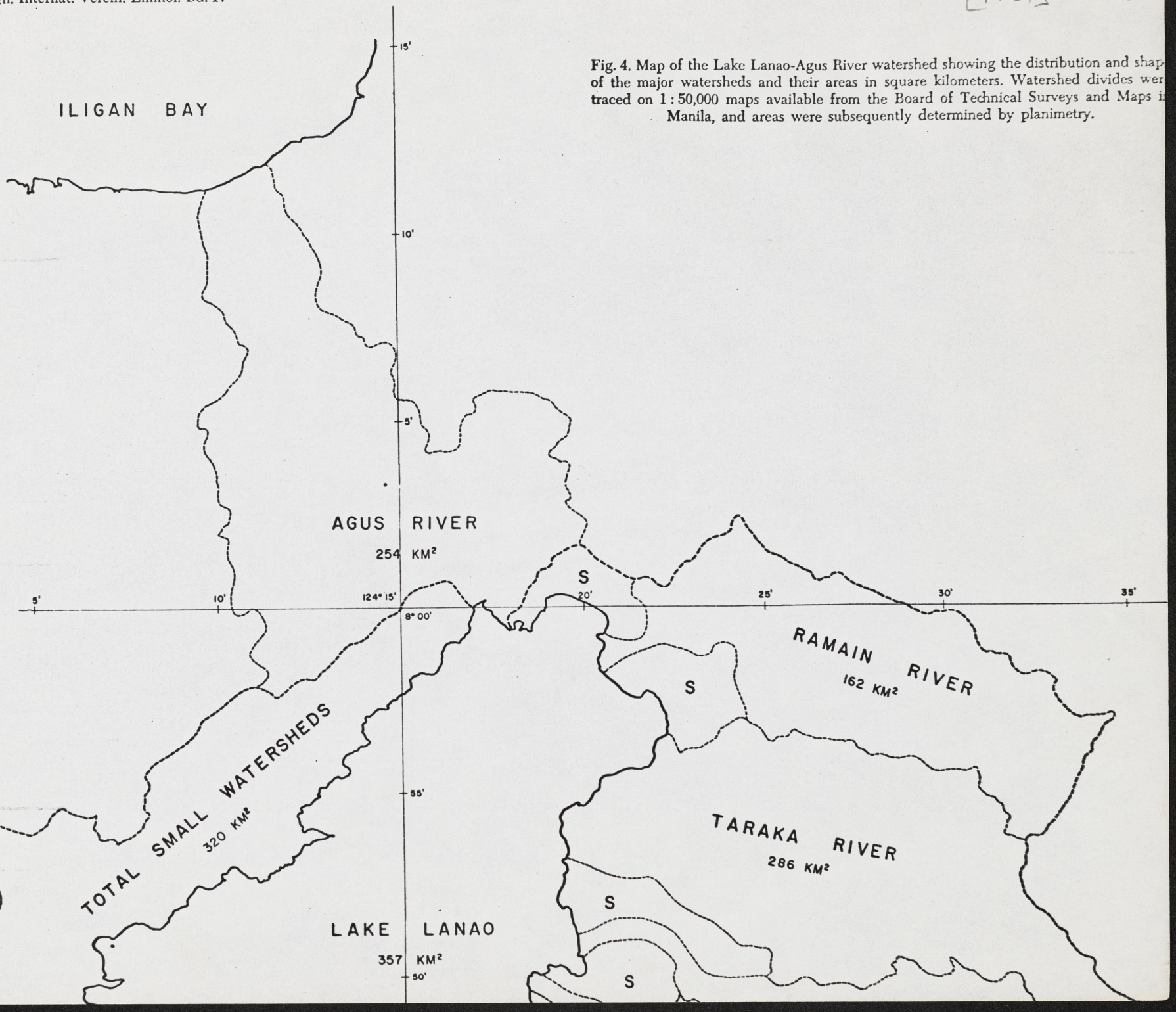
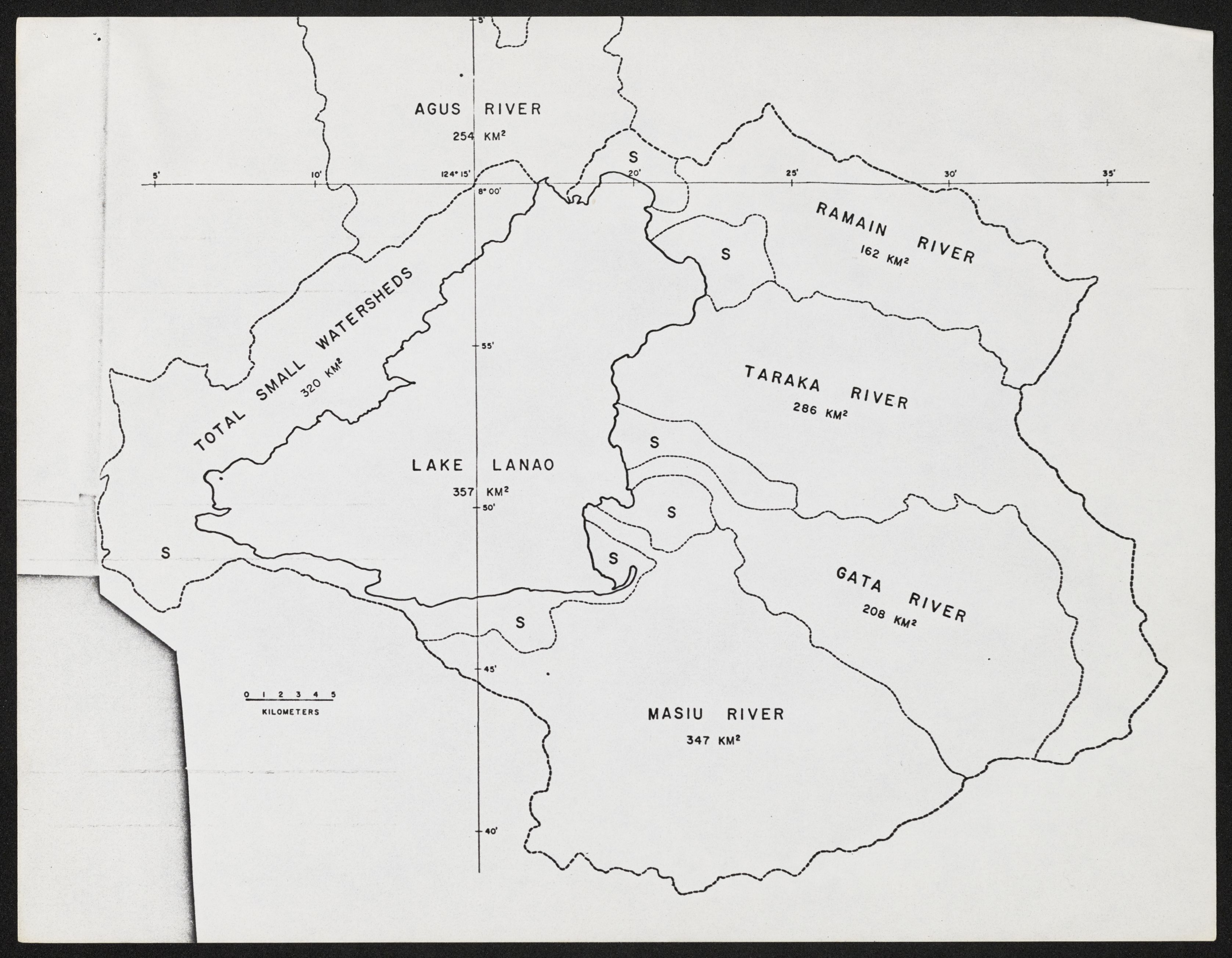


Fig. 4. Map of the Lake Lanao-Agus River watershed showing the distribution and shap of the major watersheds and their areas in square kilometers. Watershed divides wer traced on 1 : 50,000 maps available from the Board of Technical Surveys and Maps i Manila, and areas were subsequently determined by planimetry.


AGUS RIVER
254 KM²
S
RAMAIN RIVER
162 KM²
S
TOTAL SMALL WATERSHEDS
320 KM²
TARAKA RIVER
286 KM²
S
LAKE LANAO
357 KM²
S
S
S
S
S
GATA RIVER
208 KM²
MASIU RIVER
347 KM²
0 1 2 3 4 5
KILOMETERS
5'
10'
124° 15'
20'
25'
30'
35'
8° 00'
55'
50'
45'
40'

main and Taraka a small deficient contribution. The excess of the Bacayawan itself is undoubtedly explained by the water from the Gata River that flows into it through several distributaries where the river comes out of the mountains onto the Basak alluvial-deltaic plain.

Tab. 1. Breakdown of the Lake Lanao watershed into major components by area and percentage of the total area.

Watershed	Area km²	% of total
Lake Lanao	356.6	21.2
Bacayawan River	23.9	1.4
Gata River	208.3	12.4
Masiu River	347.0	20.7
Ramain River	162.4	9.7
Taraka River	285.6	17.0
Small marginal watersheds	296.5	17.6
Total	1680.4	
Agus River below Lake Lanao	254.1	

Tab. 2. Percentage distribution of total discharge for various periods of time, and comparison with the percentage distribution by area of the watershed involved.

Watershed	% discharge 1920	1921	1919 + 1922[1]	Total	% area[2]
Bacayawan	3.5	4.4	4.6	4.2	2.3
Gata	16.8	21.0	19.2	19.3	20.3
Masiu	37.5	34.2	35.8	35.6	33.8
Ramain	17.3	13.8	13.9	14.9	15.8
Taraka	25.0	26.5	26.6	26.0	27.8
Agus at Momungan	63.0	58.1	66.5	61.2	—
Agus at Marawi City[3]	69.1	63.7	72.9	67.1	61,1

[1] December 1919 plus January through June 1922.
[2] Determined by planimetry from 1 : 50,000 maps available from the Board of Technical Surveys and Maps, Manila.
[3] Flow at Momungan times 0.9117 (factor derived by Nation Power Corp.).

What these data suggest is that the rainfall pattern and distribution are reasonably uniform over the entire watershed, at least the land area. The data also show that these rivers comprising 61 % of the total watershed area contribute about 61 % of the water leaving the lake. Undoubtedly the small marginal watersheds, which are largely in agriculture and grassland, experience a greater rate of evapotranspiration. Many of these small streams do not maintain surface flow during the dry portion of the year. Furthermore, because of its suppressive influence on atmospheric convection, the lake might be expected to have somewhat less precipitation than the land.

These suppositions are supported by the meager data at hand. In 1920, which was a relatively "dry" year (total precipitation at Marawi City 2685 mm), the five major rivers contributed 63 % of the flow from the lake, whereas in 1921, a "wet" year (total precipitation 3262 mm), they contributed 58 %. Furthermore, during December 1919 and the period January through June 1922, which encompasses the "dry" season of the year, the five major rivers contributed 73 % of the flow leaving the lake at this time.

The Agus River is a high-energy stream, with a drop of 700 m over a distance of only 36 km. In order to develop a major portion of its hydroelectric potential of 750 mega-

watts, the Agus River would have to be regulated by the controlled release of water from the lake. Such stability in river discharge would be at the cost of stability in lake level, which could have severe economic and sociological repercussions on the region as well as marked influences on the limnology of the lake.

Temperature and light

If the 1967—68 year is representative, then Lake Lanao is a warm monomictic lake. The months December through March are so appreciably colder than the rest of the year (Fig. 2) that oligomixis is unlikely. During the year of study, the lake was actively circulating during January, February, and early March, interrupted by periods of temporary warming. From mid- February to mid-March the lake was essentially isothermal at 24.4° C. Over a three-week period from 10—31 March, coincident with the end of the winter foggy season, the uppermost 30 meters warmed rapidly to 26.5°, with a sharp thermocline between 21 and 23 m, which persisted through April (Fig. 5) at roughly the same depth. Such a sharp thermocline would be ideal for studying internal waves in the lake, except that during this period the winds apparently were not strong enough to generate seiches. A series of seven bathythermograph casts at roughly 2-km intervals along an east-west transect on 26 May gave almost precisely the same temperatures at corresponding depths. A Whitney thermistor was used for more precise temperature measurements of the uppermost 60 m.

During May and June the surface water warmed to almost 28°, which is probably near the maximum for the year. During this period also the thermal gradient moved downward and became less steep. However, temperatures at depths greater than 40 m remained at 24.3° or somewhat less throughout this period. In mid-August of 1967 when the first thermal profile of the lake was obtained, the temperature was 25.4° down to 30 m. Subsequently there was a minor warming of a few tenths of a degree in early October before the lake slowly cooled down to isothermal overturn in January.

Light was measured with a Whitney submarine photometer, which late in the study period was provided with a series of five Jena filters through the generosity of Prof. Heinz Löffler. The 1% level (without filters) varied from 11 to 25 m. Transparency was low during overturn, reached a maximum immediately after stratification was established in March, and then declined rapidly as a large bloom of nannoplankton developed (Fig. 5). Hence, the trophogenic zone is thick. Green light was transmitted best, followed in order by blue, orange, violet, and red. The approximate transmission maxima of the filters used are 420, 480, 530, 600, and 660 mμ. The Secchi disc reading on 7 May 1932 was 6 m, which made Lanao the most transparent Philippine lake of those studied during the Wallacea Expedition (Woltereck 1941).

Chemistry

Only the simplest chemistry could be studied because of the lack or non-delivery of equipment and supplies. Methyl-orange alkalinity averaged about 1.2 m.eq. and conductivity (K_{25}) about 120 micromhos. Neither of these parameters showed any systematic variation with depth during stratification. The Ramain, Taraka, and Gata rivers have concentrations less than this, the Masiu greater, (probably

as a result of the Tertiary coral limestones in its watershed) so that the concentration in the lake is largely the resultant of these combined sources. The processes by which these inflowing waters become incorporated into the structure of the lake during stratification are not understood. Because of the lower temperature and frequently heavy tripton loads of the inflowing rivers, underflows with strong convergence lines developed at the mouths of the rivers when observed in May

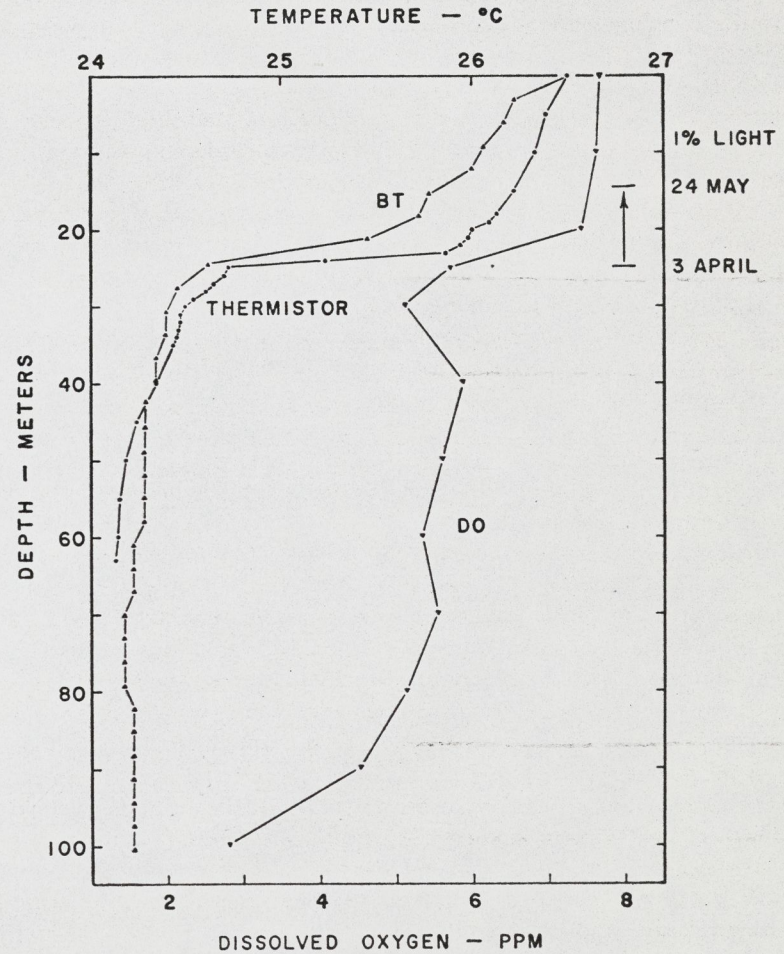


Fig. 5. Temperature and oxygen profiles in Lake Lanao on 19 April 1968. A Whitney thermistor and a Kahl bathythermograph were used for measuring temperature. The thermistor data are more reliable, as the instrument was standardized over its entire operating range against a calibrated mercury thermometer. Deepwater variations in the BT data are not significant because of the width of the stylus trace and the fact that the reading grid was not precisely drawn. Dissolved oxygen was determined by the unmodified Winkler method. Because the temperature difference between top and bottom is so small, the saturation curve closely parallels the curve shown. The top 20 meters at this time were slightly supersaturated (106% at the surface).

and June. There were no opportunities to study the propagation of these over the lake bottom.

Oxygen, although reduced well below saturation, apparently persists in the deepest water during stratification (Fig. 5). Oxygen saturation at 90 m on 14 June 1968 was 26 % (2.0 ppm). From mid-May through mid-June during the nannoplankton bloom and during relatively calm weather, the trophogenic zone (approx. 12 m) was slightly supersaturated (7.3—8.5 ppm). In mid-April the lake had a weakly developed minus-heterograde oxygen curve (Fig. 5), with a notch at the top of the hypolimnion. Saturation values in mid-June declined quite gradually from 60—70 % (4.3—5.3 ppm) at 20 m to the minimum value cited above. Possibly the lake is presently in a transitional state. Increased use of agricultural fertilizers, increased lumbering, and long duration of stratification (including the possibility of incomplete overturn or even non-turnover in an exceptionally warm winter) could make much of the hypolimnion anoxic.

Only a Fisher titrimeter was available for measuring pH, which was not very satisfactory. Triplicate measurements were made on each sample, with the instrument being restandardized for each measurement. The best series is that of 16 June 1968. On this date the pH within the top 10 m ranged from 8.2 to 8.9. From 7.6 at 15 m the pH the gradually declined to 7.2 at 45 m. These pH differences along with the oxygen saturation data give some indication of the intensity of photosynthesis at this time.

Biota

As the quantitative and taxonomic studies have not been completed, only general information can be presented. All specific names are from the report by Woltereck (1941), except as noted. There is very little net phytoplankton in the lake — chiefly *Botryococcus, Pediastrum, Melosira granulata, Ceratium,* and a filament that resembles *Leptothrix* very closely (not reported by Woltereck). Three radiocarbon runs on 26 May, 6 June, and 16 June, in the last two of which the plankton was fractionated by means of a 35 μ Nitex net, showed that considerably more than 80 % of the photosynthesis at this time was being accomplished by nannoplankton. Woltereck (1941) noted many small flagellates in the centrifuge plankton on 7 May 1932.

The zooplankton is abundant, consisting of both calanoid and cyclopoid copepods (with at least one endemic species of each — *Tropodiaptomus gigantoniger* and *Thermocyclops wolterecki*), several species of Cladocera *(Diaphanosoma modigliani, Moina micrura*[2]*, Bosmina longirostris,* and *Bosminopsis deitersi),* and a surprisingly large population of *Chaoborus* (not reported by Woltereck) living both planktonically and in the sediments. In terms of numbers the calanoids are dominant, forming populations as dense as 600/l during the bloom of nannoplankton. Adults migrate toward the surface at night, forming such a dense layer on the echo-sounder record as to obscure the echos from the sampling instruments. *Chaoborus,* palaemonid shrimps, and small fingerlings of the introduced goby also occur at the surface at night.

[2] This species was identified with the help of Goulden's 1968 monograph. Woltereck had reported the species as *M. microphthalma.*

Besides *Chaoborus* in the benthos there is a considerable variety of chironomids (with heavy emergences at times), oligochaetes, gastropods[3] on firm substrates down to at least 30—40 m, and in shallower water a large population of *Corbicula*[3]. Small palaemonid shrimp (7 species, according to Villaluz 1966) are abundant in the macrophyte zone and appear on the local markets in substantial quantities. Sponges and bryozoans are abundant on the macrophytes, and sponges have been found on gastropods as deep as 30 m.

The native cyprinids of the lake consist of approximately 20 species (perhaps more, but not yet described) of the genus *Barbodes* (also referred to as *Puntius* or *Barbus* by some authors) and several derived genera — *Mandibularca, Spratelliicypris, Cephalokompsus,* and *Ospatulus.* Most of these are endemic to Lake Lanao, although at least four species also occur in Lake Dapao (Kosswig & Villwock 1965) about 5 km to the southwest of Lake Lanao and at an elevation about 100 m higher. Lake Dapao is presently in a different drainage system. Herre (1933) and Myers (1960) argued that all these species evolved from a single progenitor, *Barbodes binotatus,* although Kosswig & Villwock (1965) suggest there may been several divergent populations of the species in the streams of the region before the lake was formed. They postulate that cyprinids (3, and possibly 4, genera) reached the southern Philippines from Borneo during one or more of the glacial lowerings of sea level. A matter of importance in the evolution of these fishes is whether the lake was already in existence at these times or was not formed until later.

A number of persons have collected (or, more commonly, purchased in local markets) specimens since Herre's time — W. L. Tressler in 1932 (Woltereck 1941: all these specimens have been lost, according to Kosswig, in correspondence), Angel Alcala in 1959 (Myers 1960), Charles E. Wood in 1962—63, Prof. Curt Kosswig and associates in 1963 (Kosswig and Villwock 1965), and ourselves in 1967—68. Wood (Wood & Wood 1963) has assembled a monograph of the cyprinid fishes of Lake Lanao (still unpublished), and Kosswig and colleagues (Kosswig, in correspondence) are still working on the systematics of the specimens they collected. Aside from Herre's original descriptions of the species, further taxonomic studies still underway, and speculations concerning the evolution of these fishes, virtually nothing else is known about them — their habitats (except for some general remarks by Herre & Kosswig), habits, behavior, food habits, and genetic relationships.

Those fishes endemic to the lake have evolved in the absence of any serious fish predators. Maria Cristina Falls about 57 m high and a correspondingly high falls on the Linamon branch of the Agus River have kept all predacious marine species — such as the gobies — from entering the lake. About 1962—64, however, the white goby (*Glossogobius giurus,* called kadurog locally) was accidentally introduced, presumably with milkfish fry planted by the Philippine Fisheries Commission (Villaluz 1966), and in the relatively few years since then has irrupted to

[3] Specimens sent to the National Museum in Manila have been provisionally identified as *Vivipara pagodula* Bartsch, *Vivipara mearnsi* Bartsch, *Vivipara* spp., *Pila ampullacea* Linné, *Thiara* spp., *Melania* spp., *Bulimus* spp., *Lymnaea* spp., and *Corbicula fluminea* Müller (correspondence from Mr. Galo B. Ocampo, Director, dated 30 July 1968). Hence, the fauna is quite diversified as well as abundant.

a large population, which has made serious inroads on the populations of some of the endemic cyprinids as well as on the palaemonid shrimps. The situation is reminiscent of the havoc created by the sea lamprey *(Petromyzon marinus)* in the St. Lawrence Great Lakes. Changes are proceeding so rapdily in Lake Lanao, according to the fishermen, that some of the species may be threatened with extinction. Hence, any detailed studies on the species other than taxonomic may well have to be accomplished within the next few years if we are to get any reasonable understanding about this experiment in evolution.

Other species occurring in the lake, many of which have been introduced, are the following (VILLALUZ 1966): the silurid *Clarias batrachus*, the anabantids *Anabas testudineus*, and *Trichogaster pectoralis*, the anguillid *Anguilla mauritiana*, the ophiocephalid *Ophiocephalus striatus*, the cyprinid *Cyprinus carpio*, the cichlid *Tilapia mossambica*, the centrarchid *Micropterus salmoides*, the chanid *Chanos chanos*, and *Glossogobius giurus*.

Productivity

Three radiocarbon series were run on 24 May, 9 June, and 16 June 1968. Light and dark bottles after inoculation with 1.89 μc of $Na_2{}^{14}CO_3$ each were incubated in situ at 0, 1, 3, 5, 7, 10, 15, 20, 25, and 30 m for three hours, approximately from 0900 to 1200 hours. On the second and third series two light bottles were run at each depth, one containing raw water and the other water that had been filtered through a 35 μ Nitex net to eliminate the macroplankton. The station utilized was off Nataron Point (the point just south of Inodaran in Fig. 3) in about 50 m of water. On all three dates the sky overhead was completely clear during the incubation period, so that photosynthesis should have been proceeding at near-maximum rates. On 24 May, which was a clear day at Mindanao State University where the pyrheliograph was located, the period from 0900 to 1200 comprised 67 % of the morning insolation. If relationships in the afternoon were the same, the total insolation, and hence total photosynthesis, would be 2.98 times that of the exposure period. Because of usual afternoon clouds and haziness, however, the factor was arbitrarily reduced to 2.4 for estimating total carbon fixation during these days.

The results in Tab. 3 and Fig. 6 show the marked buildup in phytoplankton over this period, both is terms of absolute amounts of carbon fixed and in the progressive upward displacement toward the surface of the zone of maximum (optimum) photosynthesis. On 24 May the 1 % level of surface light occurred at

Tab. 3. Carbon fixation by phytoplankton, based on C^{14} uptake. The mg C/m²/day is an estimate, based on the light received during the 3-hour exposure period beng. approximately 1/2.4 of the total light-day (see text).

Date 1968	Incubation period	mg C $m^{-2}3hr^{-1}$	mg C $m^{-2}day^{-1}$	V/O ratio	Depth — meters 1 % surface light	Depth — meters Max. photosynthesis
24 May	0905—1205	123	295	0.11	15.1	5
9 June	1015—1315	154	370	0.13	—	3
16 June	0930—1225	201	482	0.12	10.8	1—3

15.1 m, but only at 10.8 m on 16 June. Fig. 6 shows that there was a fair amount of net photosynthesis (approximated by the C^{14} estimates) at depths below 10 m.

The V/O ratio proposed by RODHE (1958) — the ratio of mg C/m³ at maximum to mg C/m² of lake surface — is approximately constant, as RODHE also found for Swedish lakes. On 9 June 82 % and on 16 June 88 % of the total photosynthesis was accomplished by nannoplankton (< 35 μ). Macroplankton (net plankton) was negligible in photosynthesis at depths of 7 m and greater.

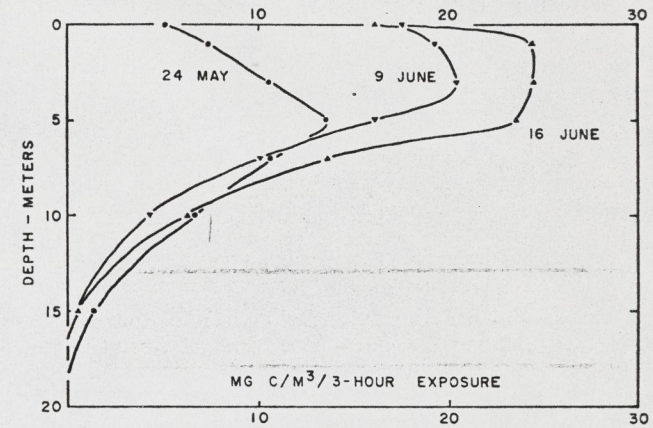


Fig. 6. Net photosynthesis, as calculated from C^{14} uptake. To convert to mg C/m³/day, the figures in the graph should be multiplied by the approximate factor 2.4 (see text). On 9 and 16 June more than 80 % of the total photosynthesis was accomplished by nannoplankton (< 35 μ). No larger algae were significantly active at depths of 7 m an greater.

One's subjective impression, based on benthos biomass, is that secondary productivity is quite high, although there are few substantiating data as yet. At irregular but rather frequent intervals except during the winter overturn, there were large emergences of midges, which could form windrows up to ½ inch thick on window sills at night when the wind was from the south. At times of such emergences the lake surface was densely populated with cast pupal skins and emerging adults. Fish were attracted toward the surface (recorded as blips on the echo sounder), and fishermen under these conditions fished their gill nets during the day rather than chiefly at night. According to the estimates of VILLALUZ (1966), more than 50 metric tons of shrimps and 200 metric tons of molluscs were caught in the lake in 1963—64.

Excluding these invertebrates, an estimated total of 1.7 million kg of fin fishes was caught in the lake in 1963—64, amounting to 48 kg/ha. The native cyprinids comprised 56.7 % of the fin-fish catch. The mudfish *(Ophiocephalus)* and the carp *(Cyprinus carpio)* each made up 13.7 % of the catch, *Glossogobius* 7.4 % and *Tilapia* 6.3 %. All together the introduced species comprised 27.7 % of the total catch of fin fishes. Considering the high level of primary production and the apparently high level of secondary production at the invertebrate level, the fish harvest seems low. Undoubtedly there will be demands to introduce other species of fishes to

utilize the food resources of the lake more effectively, but in light of what is happening to the native fishes since the accidental introduction of the kadurog, no further introductions should be permitted until the native fishes have been studied and the situation is better understood.

Large quantities of water hyacinth *(Eichornia crassipes)* grow on the lake surface. In clumps of various sizes up to large rafts they drift back and forth across the lake with changing winds and sometimes line up in distinct rows or bands along surface convergences. Removal of this material via the Agus River occurs continually, particularly when winds are from the southeast.

References

Brooks, J. L., 1950: Speciation in ancient lakes. — *Quart. Rev. Biol.* **25**, 30—60, 131—176.

Goulden, C. E., 1968: The systematics and evolution of the Moinidae. — *Trans. Amer. Phil. Soc.*, N. S. **58**, 6, 1—101.

Halbfass, W., 1922: Die Seen der Erde. — *Petermanns Mitt.*, Ergänzungsh. **185**, vi, 169 p.

Herre, A. W., 1933: The fishes of Lake Lanao: a problem in evolution. — *Amer. Nat.* **67**, 154—162.

Hutchinson, G. E., 1957: *A treatise on limnology.* Vol. I. Geography, physics, and chemistry. — New York, Wiley. xiv, 1015 p.

Kosswig, Curt, & Villwock, Wolfgang, 1965: Das Problem der intralakustrischen Speziation im Titicaca- und im Lanaosee. — *Verh. dt. Zool. Ges.* 1964, 95—102.

Myers, G. S., 1960: The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. — *Evolution* **14**, 323—333.

Rodhe, W., 1958: Primärproduktion und Seetypen. — *Verh. internat. Verein. Limnol.* **13**, 121—141.

Villaluz, D. K., 1966: *The Lake Lanao fisheries and their conservation.* — Bureau of Printing, Manila. iii, 53 p., **9 pl.**

Williams, A. D., & Gochoco, J. C., 1924: Surface water supply of the Philippine Islands 1908—1922. Vol. II. — *Water Supply. Bull.* No. 1, Bur. Public Works, Dept. Commerce and Communication, **414 p.**

Woltereck, W., 1933: Meine Forschungsreise nach Amerika und Ostasien zum Studium insulärer und lakustrischer Endemismen. — *Int. Rev. Hydrobiol.* **28**, 338—349.

— 1941: Die Seen und Inseln der „Wallacea"-Zwischenregion und ihre endemische Tierwelt. Zweiter Teil: Inseln und Seen der Philippinen. — *Int. Rev. Hydrobiol.* **41**, 37—176.

Wood, C. E., & Wood, J. C., 1963: A monograph of the fishes of Lake Lanao. — Unpublished. Hectographed, 1—120 p. (From Kosswig & Villwock 1965).

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Contribution à l'identification des zones piscicoles de quelques cours d'eau de Moravie (Tchécoslovaquie)

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Avec 8 figures et 1 tableau dans le texte

I. Introduction

L'influence du courant sur la distribution des poissons dans les eaux courantes est considérable (Huet 1962). Elle résulte de l'action mécanique et écologique du courant. Cette double action se fait sentir directement et indirectement, en agissant notamment sur la vitesse du courant et la température de l'eau, ainsi que sur les caractères physiographiques de l'habitat.

Il est possible de prévoir quelle doit être, théoriquement, la distribution des poissons dans un cours d'eau déterminé, en appliquant la «Règle des pentes» (Huet 1946) et en utilisant le «Graphique des pentes» (Huet 1949) élaboré pour les cours d'eau d'Europe occidentale tempérée.

La présente communication concerne quatre rivières de Moravie, étudiées sur place par les auteurs en 1967, à l'occasion d'un voyage d'étude effectué par M. Huet, à l'invitation de l'Académie des Sciences de Tchécoslovaquie. Les données physiographiques relatives au parcours et à la pente des cours d'eau on été élaborées en partant de documents préparés par les auteurs tchèques. Les données relatives à la composition des populations piscicoles résultent d'échantillonnages effectués en 1967 et antérieurement, à l'aide d'appareils de pêche électrique.

Il résulte de la présente étude que la règle des pentes est applicable aux cours d'eau de Moravie et qu'il est possible d'élaborer pour les cours d'eau d'Europe centrale un graphique des pentes différent quelque peu du graphique valable pour l'Europe occidentale.

II. Population piscicole de quelques cours d'eau de Moravie

1. La rivière Becva (Fig. 1 et 2). — La Becva est longue de 118,65 km. La source est située à 880 m d'altitude et son embouchure dans la Morava à 197,7 m. C'est une rivière rhéophile. La pente décroît régulièrement et passe de plus de 83,3 ‰ à l'amont à 0,9 ‰ dans le cours aval.

La rivière se présente successivement sous les caractères de la Zone à Truite, de la Zone à Ombre, de la Zone à Barbeau du type supérieur d'abord, du type inférieur ensuite.

Le Tab. 1 donne la composition de la population piscicole correspondant à divers emplacements reportés sur le profil en long de la rivière. Dans son cours supérieur, la Becva est un cours d'eau de la Zone à Truite. En aval de Hovezi (empl. 1, pente 5,9 à 4,5 ‰) la rivière appartient à la Zone à Ombre, ce qui résulte tant des observations sur le terrain que de la population piscicole, dans laquelle les salmonides dominent (51,1 %). En aval de Vsetin (empl. 2, pente 3,1 ‰) la Becva est à ranger dans le type supérieur de la Zone à Barbeau, près de sa limite avec le type inférieur de la Zone à Ombre; les salmonides sont encore présents (2,7 %), mais la masse de la population est formée par les Cyprins d'eaux vives (97,3 %).

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NOTES ON SMALL COLLECTION OF FISHES FROM AFGHANISTAN WITH A DESCRIPTION OF GLYPTOTHORAX JALALENSIS, SP. N. : (PISCES, SISORIDAE)

EUGEN K. BALON and KÁROL HENSEL

Received August 18, 1969

Abstract: The work presents a description and diagnosis of four species of fish from the Afghanistan territory — *Salmo trutta oxianus* Kessler, 1874, *Schizothorax intermedius fedtschenkoi* Kessler, 1872, *Glyptothorax jalalensis* sp. n., and *Ophiocephalus gachua* Hamilton, 1822. The *Glyptothorax jalalensis* sp. n. is simultaneously the first proof of the occurence of this genus in Afghanistan.

Through the courtesy of Prof. D. Povolný and Dr. J. Gaisler we have received a few specimens of fish collected in Afghanistan during an expedition of the Zoological Institute of the College of Agriculture, Brno, in 1967.

As the available studies on fish from Afghanistan (Day, 1880; Günther, 1889; McClelland, 1842; Annandale and Hora, 1920; Hora, 1934, 1935; Vijayalakshmanan, 1949) and from adjacent territories (Berg, 1949a, b; Turdakov, 1952; Sufi, 1957, 1963; Ahmad and Mirza, 1963, 1964) deal, for the most part, with individual specimens, and since more detailed diagnoses are often lacking, it is considered useful to present here a description of these fishes.

Two specimens of trout were caught on May 20, 1967 in the rapids of a mountain stream (2700 m above sea level) which joins the river Kunduz (a tributary of Amu-Daria) in the Bamian pass. Larger specimens are currently caught here, but only the smallest of them ended in formalin. The remaining fishes described here were cought in the lowland tributaries the Kabul river in the environs of Jalal-Abad (in the Indus watershed), in March and April of 1967.

The specimens are deposited in the collections of the Slovak National Museum in Bratislava.

Salmo trutta oxianus Kessler, 1874

Two specimens, 158 and 143 mm of standard length. The larger one is a female, the smaller one a male. Radii D III 10 and III 9, radii A III 8 in both, radii C VIII 17 VIII and IX 17 VIII, radii P I 11 and I 12, radii V I 8 in both. Lateral line scales 104 in both. Branchial spines 21/21 and 21/22 (external spines on the first branchial arch on left and right side of body) are thin, long and spiniform.

In % of standard length:
head length 29.1 and 29.4; praeorbital length 7.6 and 7.7; internasal distance 5.4 and 4.9; diameter of eye 6.0 and 6.3; interorbital distance 8.9 and 8.4; postorbital distance 17.1 and 16.8; praedorsal distance 46.2 and 49.6; praeventral distance 57.6 and 55.2; praeanal distance 76.6 and 75.6; length of caudal peduncle 17.1 and 16.8; distance P-V 32.3 and 30.1; distance V-A 20.2 and 21.0; length of D 14.6 and 12.6; legth of A 9.5 and 9.1; length of P 20.9 and 21.7; length of V 15.2 and 16.1.

Both specimens still show well defined juvenile dark spots on either side of their bodies. Both have an equally well developed annulus of the year 1966 on the scales, and a new annulus closely on their margin. Hence, they belong to the 2nd age class. Evidently there is question here of autochthonous trout found in and originally described from the Bamian river (McClelland, 1842), which were later found here and in the upper Amu-Daria river-basin by several authors (Kessler, 1874; Berg, 1905; Hora, 1933, 1935; Nikol'skij, 1938). The characters in our specimens agree with those already described. According to Balon's evolutionary hypothesis (1968) these trout are derived from the extinct Mediterranean species, whose "neotenic" populations penetrated through the continental river system thus far to the East and produced the *ezenami* and *oxianus* forms.

Schizothorax intermedius fedtschenkoi Kessler, 1872

The material from the tributary of the Kabul river contains two females of 178 and 121 mm standard length. Their counts and measurements are as follows: Radii D III 8 in both, radii A III 5 in both, lateral line scales 93 and 87 on the left, and 96 and 84 on the right, transversal rows of scales 19 and 18 on the left, and 16 and 14 on the tight, number of branchial spines 14 and 12 on the left, and 17 and 17 on the right, lower pharyngeals 2.3.5 and 2.3.5, on the third hard dorsal ray the larger has 13 and the smaller one 15 little denticles.

In % of standard length:

head length 27.0 and 25.6; praeorbital distance 11.2 and 9.1; 1-st barbel length 7.9 and 6.6; 2-nd barbel length 6.7 and 8.3; internasal distance 6.2 and 5.8; diameter of eye 3.9 and 4.5; interorbital distance 9.5 and 8.3; postorbital distance 12.9 and 12.4; depth of head 18.0 and 15.7; head length 17.4 and 14. 9; praedorsal distance 53.9 and 53.7; praeventral distance 50.0 and 52.1; praeanal distance 74.7 and 76.8; depth of body 23.6 and 24.0; width of body 15.2 and 14.9; length of caudal peduncle 20.2 and 18.2; depth of caudal peduncle 12.9 and 12.4; width of caudal peduncle 8.4 and 7.4; last heigh of body 10.7 and 10.7; P-V distance 27.5 and 28.9; V-A distance 24.7 and 24.8; length of D 13.5 and 11.6; length of A 6.7 and 4.9; length of P 20.8 and 19.8; length of V 17.4 and 18.2; heigh of D 20.2 and 20.7; heigh of A 19.1 and 19.8.

The larger specimen belongs to the 4th age class (annuli 3+) the smaller one to the 3rd (annuli 2+). The smaller one shows dark irregular spots on its body, while the larger one is free of them, but the upper half of its body is darker (after imbedding in formalin). The larger specimen has strong fleshy lips, divided in the centre of the mandible and lobed at the sides. Fleshiness of lips in the smaller one is only weakly indicated, without lobes.

Glyptothorax jalalensis sp. n. (fig. 1)*

Holotype: Female 73.2 mm long (Fig. 1), caught in a tributary of the Kabul river near the town of Jalal-Abad, in March 1967. It is deposited in the Slovak National Museum under No. RY 2176.

Description: Radii D II 6, radii A III 10, radii P I 8, radii V I 5, radii C XII 17 XII.

In % of standard length:

head length 27.3; praeorbital distance 15; diameter of eye 2.2; postorbital distance 12; depth of head 12.3; width of head 19.1; interorbital distance 6.3; internasal distance 4.0; length of nasal barbel 12.8; length of maxillary barbel 23.2; length of external mandibulary barbel 16.5; length of internal mandibulary barbel 10.4; praedorsal distance 39.6; praeventral distance 47.6; praeanal distance 65.6; depth of body 19.1; width of body 17.8; length of caudal peduncle 21.9; heigh of caudal peduncle 10.9; width of caudal peduncle 7.5; last heigh of body 9.3; P-V distance 27.3; V-A distance 16.4; length of D 11.6; length of A 12.0; length of P 20.5; length of V 16.4; heigh of D 15.3; length of D spine 11.5; heigh of A 20.0; length of addipose fin 19.1.

Derivation of the name: According to the town Jalal-Abad.

With the Author's Compliments

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EUGEN K. BALON and KAROL HENSEL

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*- see folder w/ data on rainbow, sockeye-Wenatchee [1971]
+ Wernsman's thesis

An Experiment with Medaka, *Oryzias latipes*, and a Critique of the Hypothesis that Teleost Egg Size Controls Vertebral Count

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LINDSEY, C. C., AND M. Y. ALI. 1971. An experiment with medaka, *Oryzias latipes*, and a critique of the hypothesis that teleost egg size controls vertebral count. J. Fish. Res. Bd. Canada 28: 1235–1240.

In each of two sets of experiments, two female medaka, *Oryzias latipes*, that laid different-size eggs were crossed reciprocally with two males. Vertebral counts of the offspring differed significantly between batches, but there was no consistent correlation between egg size and vertebral count. Both the highest and lowest counts resulted from crosses with females laying large eggs. Other experiments are reviewed, and it is concluded that within the same race of fish there is no causal connection between vertebral number and egg size, although between different races or related species large adult size is often correlated with high vertebral count. The possible advantages of variation in vertebral number are discussed.

LINDSEY, C. C., AND M. Y. ALI. 1971. An experiment with medaka, *Oryzias latipes*, and a critique of the hypothesis that teleost egg size controls vertebral count. J. Fish. Res. Bd. Canada 28: 1235–1240.

Au cours de deux séries d'expériences, deux medaka femelles, *Oryzias latipes*, pondant des oeufs de grosseurs différentes, furent croisées réciproquement à deux mâles. Le compte vertébral des descendants différa significativement, mais il n'y eu pas de corrélation constante entre la grosseur de l'oeuf et le nombre de vertèbres. Les comptes vertébraux le plus élevé et le plus bas ont tous deux été le produit de croisements de femelles à gros oeufs. Nous passons en revue d'autres expériences et en arrivons à la conclusion qu'au sein d'une même race de poissons il n'y a pas de relation causale entre le compte vertébral et la grosseur de l'oeuf. Par ailleurs, entre races différentes ou espèces apparentées, une grande taille à l'état adulte est souvent associée à un nombre vertébral élevé. Nous examinons les avantages possibles de la variation du nombre de vertèbres.

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MERISTIC variation in fishes has been the subject of quite a few experimental studies (recently reviewed by Fowler 1970) and of innumerable taxonomic investigations. Almost no satisfying hypotheses have resulted concerning either the evolutionary significance of meristic variation or the embryonic mechanisms that produce it. Latitudinal clines in the numbers of vertebrae, fin rays, or other meristic elements are widespread in nature, but their explanation is unknown. Meristic variation amongst the individuals of a wild fish population is often spectacular, yet its selective value remains inscrutible. Many different meristic series in fish can be altered by many different environmental factors, but few generalizations can be found either to predict these responses, or to ascribe them to any developmental laws.

There has been one hypothesis advanced that deserves attention but has not been adequately tested. This suggests that the size of the egg (or the amount of yolk) exerts an influence on the number of vertebrae in the larva. In 1926 Kyle wrote "··· it is the general rule that the smaller eggs yield the smaller larva and the smaller larva has the smaller number of vertebrae." Kyle offered no experimental evidence.

In 1959, Garside and Fry capitalized on a "natural experiment" by counting the myomeres on partly twinned salmonid embryos. They found that myomere counts were progressively lower in embryos that had a progressively more extensive

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degree of twinning; this correlation was significant in one species, *Salvelinus fontinalis*, but not in another that had a larger egg, *S. namaycush*. They concluded that there may perhaps be a certain critical yolk size, below which yolk size becomes limiting on the number of vertebrae formed, but above which (as in the *S. namaycush* eggs) yolk supply was ample for even complete twinned embryos each to form a full vertebral complement.

To test the hypothesis that egg size affects vertebral count, we have used a species of cyprinodont fish, *Oryzias latipes*, the medaka, which lays very much smaller eggs than do salmonids. Females have been chosen that produced eggs of significantly different sizes, and the vertebrae have been counted in offspring arising from these eggs when fertilized with different males. The results are compared, in the Discussion, with other studies that may be relevant to the relation of egg size to vertebral count in fishes.

Materials and Methods

Eggs were obtained from the same domestic stock of *O. latipes* (Timminck and Schlegel) that was used for experiments described by Lindsey and Ali (1965). Methods of obtaining eggs, rearing fish in cloth baskets suspended in a water bath held constant at 24 C, and counting vertebrae were as previously described. Two pairs of parents, females A and B, males E and F, were used in one set of reciprocal crosses, and two other pairs, females C and D, and males G and H, were used in a second set. For each set, two females had been selected that had different egg sizes (Table 1). Diet and living conditions were the same for all parents. Each individual egg was measured before it had completed first cleavage, using a binocular microscope and ocular micrometer. The diameter of the yolk (clearly visible through the transparent chorion) was recorded by averaging two measurements taken from different viewing positions. Neither measured diameter passed through the animal pole.

Each of the eight egg batches (Table 1) was the accumulation of the eggs laid by one female on two or more mornings. Previous experiment had shown that no significant vertebral differences occurred between young from two egg batches laid by the same mother on 2 days separated by as much as a 15-day interval (Ali MS 1962). Numbers of fertilized eggs per batch ranged from 98 to 164. Percentage of eggs that hatched ranged from 49 to 72%, and the percentage that survived to preservation from 34 to 59%. Time to 50% hatching ranged from 263 to 524 hr. Neither hatching time nor survival rate seemed to be correlated with egg size or vertebral count.

Results

Mean egg (i.e., yolk) diameters (shown in Table 1) differed significantly ($P < .01$) between females A and B, and also between females C and D. Mean vertebral counts differed greatly between different batches. The difference between the highest and lowest means, 1.51 vertebrae, is greater than the largest difference induced upon any single genotype within this stock of medakas by manipulation of temperature or other environmental factors (Ali MS 1962; Lindsey and Ali 1965).

Although egg diameters and vertebral counts each differed significantly between batches, no correlation was apparent between the two (Fig. 1). Two males (G and H) produced more vertebrae when crossed with *large* than with small eggs (both differences significant), but the other two males produced more vertebrae when crossed with *small* than with large eggs (one difference significant). Both the highest and lowest vertebral counts resulted from crosses (DH and BF) with

TABLE 1. Egg sizes and vertebral counts in two sets of reciprocal crosses.

Parents		Egg diam	Vertebrae				
♀	♂	(*mm*)	29	30	31	32	Mean
Exp 1							
A	E	1.03		4	30	4	31.00
A	F	1.06	1	23	12		30.31
B	E	1.13	1	19	15	1	30.44
B	F	1.14	3	28	5		30.05
Exp 2							
C	G	1.09		18	22		30.53
C	H	1.09		6	47	1	30.91
D	G	1.16		1	27	14	31.31
D	H	1.14			17	23	31.56

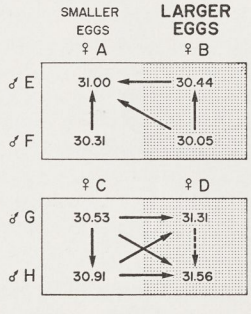

FIG. 1. Mean vertebral counts in two sets of reciprocal crosses. Arrows point towards significantly higher of two connected counts; solid arrows $P < .01$, broken arrow $P < .02$.

large eggs. Therefore, although females exerted some influence on vertebral count, the operative mechanism was evidently not yolk size. In all four tests two different males crossed with the same female produced significantly different counts (Fig. 1).

In three other meristic series (pectoral, dorsal, and total caudal ray counts) there was also no correlation between egg size and meristic count. No consistent parental influence was found in dorsal or total (i.e., major plus minor) caudal rays, but pectoral rays seemed to be more influenced by the father than by the mother. Only anal fin ray counts were correlated with egg size; the larger eggs in all four pairs of crosses yielded more anal rays than did the smaller eggs mated with the same male. Anal fin ray counts, however, were found (Ali MS 1962) sometimes to vary between successive daily egg batches from the same parent, and to be altered by mechanical shock and certain other external influences (none of which affected vertebral or pectoral ray counts), so the apparent correlation between anal ray count and egg size is of dubious significance.

Discussion

If a causal connection were demonstrated between the number of vertebrae in a fish and the size of the egg that produced it, there might be far-reaching implications. In many species the eggs laid by small females are smaller than those laid by large females (in *Clupea harengus harengus* (Hempel and Blaxter, 1967); in *Engraulis anchoita* (Ciechomski 1966); in *Salmo gairdneri* (Pennask Lake population, Scott 1962); in *Oncorhynchus nerka* (Bilton and Jenkinson MS 1966); and in *Platichthys flesus* (Solemdal 1967)). Eggs laid early in the season are commonly larger than those laid later (Hiemstra 1962). Hence, offspring of genetically similar fish, or of the same female in successive years, might have different mean vertebral counts even if reared under uniform conditions. One consequence would be to complicate the use by biologists of meristic characters in identifying discrete spawning stocks. Another would be the possibility that selection with respect to vertebrae might operate differentially on the offspring of young and of old spawners.

Salinity of the medium surrounding the female can alter the volume of the eggs that she produces (Solemdal 1967), although this would not necessarily alter the vertebral count of her offspring if count were dependent on dry weight rather than on overall volume of the egg. Bagenal (1969) suggests that egg size should always be measured as dry weight or chemical composition, since wet weight may be only a reflection of the time of spawning. In any event, *both* wet and dry egg weights were probably different in the experimental studies of egg size and vertebral count reported here, since neither salinity nor laying time differed consistently in the production of the large and small eggs studied.

If larger eggs produce fry that are longer and that have more vertebrae (Kyle 1926), then a correlation might be expected between the lengths of recently hatched fry and their vertebral counts. In wild fish such a correlation is frequently observed, but in many species it is probably attributable to temperature changes during a protracted spawning time. Templeman and Pitt (1961) cite several examples of species in which the larger fish within a year-class have more vertebrae, and these are all species that spawn on a rising temperature; conversely, in races of *C. harengus harengus* that spawn in autumn on a declining temperature, the larger fry have *fewer* vertebrae. However, these sorts of correlations are not necessarily due to direct modification of the embryo by temperature, since capacity for growth might be genetically linked to vertebral count. Amongst wild populations there are too many complexities for us to establish causal connection between egg size and vertebral count.

However, if egg size controls vertebral count, then amongst laboratory-reared fish that have been hatched from common parents and reared at uniform temperature we should expect to find a correlation between fry size and vertebral number. In fact *no* such correlation has been found in most of the experiments where it has been sought. Mottley (1937) showed that in one brood of *S. gairdneri* the longer fry had significantly more vertebrae, but since these fish were 5 months old before they were measured, their size hierarchy did not necessarily reflect the size hierarchy of the eggs from which they had hatched, and Mottley did not report whether a size–vertebral count correlation existed in the other 19 samples of *Salmo* that he raised. Dannevig (1950) found a correlation between vertebral count and length of fry from several females of *Pleuronectes platessa* that had spawned in an aquarium, but when he repeated the experiment the next year using a single female he found no such correlation. Other workers who have tested for this correlation in experimentally reared fish have found none: in *C. harengus harengus* (Hempel and Blaxter 1961), *S. gairdneri* (Canagaratnam MS 1959; Orska 1962 p. 331), *Salmo trutta* (Tåning 1952 p. 188), *O. nerka* (Canagaratnam MS 1959; Lindsey 1958), *Oncorhynchus gorbuscha*

(Canagaratnam MS 1959), *Catostomus commersoni* (Rough MS 1961), *O. latipes* (Ali MS 1962), and *Gasterosteus aculeatus* (Lindsey 1962).

In seeking a correlation between egg size and vertebral count, direct measurement of egg size differences would be preferable to inferring them from differences in fry length, but this has seldom been attempted. From the experiments on *O. latipes* reported here, vertebral count in this species is evidently controlled as much by the male as by the female, and some females with large eggs tend to produce fry with low counts. It has therefore been established that control of vertebral number has at least a large genetic component independent of egg size; it has not, however, been established that egg size has *no* effect, since large and small eggs with the same genotype were not compared.

In an earlier experiment on *S. gairdneri* taken from the outlet of Cultus Lake, B.C., in 1959, (referred to in Lindsey 1962 p. 307) the eggs from a single anadromous female were fertilized and sorted mechanically into small, medium, and large sizes by rolling them down an inclined trough whose bottom contained a tapering slot. The three lots of eggs were hatched and reared separately under identical conditions. Grading by this means was based on diameter of the hardened chorion, not of the yolk, but the two dimensions are probably correlated, and fry from the large eggs were significantly longer than those from the small eggs when all were preserved and stained about 4 months later. Meristic counts on samples (of 30, 35, and 37) from the three groups revealed no significant differences in numbers of vertebrae, dorsal rays, anal rays, or median pterygiophores.

Tåning (1952 p. 188) referring, without details, to experiments of *S. trutta*, wrote: "According to our investigations so far it may be said that the larger or smaller diameter of egg does not appear to have any certain influence on the number of vertebrae, and further that the size of the fry does not appear to mean anything either. It appears likewise that the number of vertebrae is the same in the first and last hatched fry of a batch of eggs."

The two preceding experiments dealt with salmonid eggs with large yolks, which might be supposed to lie above the critical limiting size hypothesized by Garside and Fry (1959). The eggs of *O. latipes* are in contrast very small, and yet they also failed to display a consistent correlation between egg size and vertebral count. The critical value, however, might be the ratio of the embryo size to the amount of yolk, concerning which we have no data.

If yolk size does not generally limit vertebral number, how are we to explain the intriguing results of Garside and Fry's investigation on twinned embryos? In the small-egged *S. fontinalis*, there was a significant negative correlation ($P < .01$) between the degree of separation of the twins and of the number of vertebrae formed in each twin. In the large-egged *S. namaycush* there was none. Yet, in *S. namaycush* eggs fertilized by *S. fontinalis* sperm, the same negative correlation existed as in the pure *S. fontinalis* cross, although it was less pronounced ($P < .05$). In other words, on the same (large) eggs, greater separation of twins produced greater reduction of vertebral count with one species of father but not with the other. Surprisingly, the reduction occurred only when the father was of the species that ordinarily has the lower vertebral count, so the result cannot be due to the *S. fontinalis* male having made a greater vertebral "demand" on a limited yolk supply. In any event, the factor that imposes a limit on vertebral count of twins seems to have been imparted in part from the male parent. What that factor is, remains quite unknown, but it cannot be solely the size of the egg.

Evidently the few studies based on egg measurements, and the more numerous but less satisfactory studies based on lengths of young fry, fail to support the hypothesis of a morphogenic mechanism linking vertebral count to egg size *amongst genetically similar fish*. On the other hand, there are many instances in which larger eggs do produce higher vertebral counts when comparisons are made *between genetically different units* within the same species, or genus, or family. For example, Garside and Fry (1959) found higher vertebral numbers in *Salvelinus namaycush* (which has a larger egg) than in *S. fontinalis*. That this difference was genetically determined by mechanisms other than egg size was demonstrated in a hybrid cross between an *S. namaycush* female and *S. fontinalis* male. The hybrids' vertebral counts lay between those of the parents and were strikingly lower than the pure *S. namaycush*, despite the fact that the hybrids were on the large *S. namaycush* eggs. In another series of hybridization experiments using sockeye salmon (the large-egged anadromous form of *O. nerka*, which has higher vertebral count) and kokanee (the small-egged lacustrine form), McCart (MS 1970) found that in one hybrid cross in which the eggs were from sockeye, the vertebral count was *lower* than in either parental form or in the reciprocal hybrid cross. He reports other crosses that gave opposing results, again demonstrating that determination of vertebral count is complex and not attributable solely to egg size.

In these and many other instances it is the species or race with the greater adult size that forms the higher vertebral count. *Salvelinus namaycush* adults

are larger than *S. fontinalis*; sockeye salmon are larger than kokanee. R. McV. Clarke has kindly provided us with calculations showing that in 10 races of Atlantic herring (*C. harengus harengus*) there is a striking correlation (r 0.85, $P < .01$) between average body length of spawning females and average vertebral count in each race (data from Schnakenbeck 1931, and Hempel and Blaxter 1967). There is an equally striking correlation (r 0.84) between average body length and average egg weight, but we suspect from artificial crossing (Hempel and Blaxter 1961) that vertebral difference between at least two of these races may be transmitted by the male and therefore cannot be attributable solely to egg size. There are many other examples (e.g., family Percidae (Bailey and Gosline 1955), and suborder Esocoidei) in which related species show a tendency for larger adult size to be associated with higher vertebral count. The larger species also often, but not invariably, lay larger eggs. Kyle's 1926 statement quoted in the Introduction may therefore be generally true when it is applied to different species, although not when it is applied to members of the same species in the same spawning group.

The selective values of vertebral differences in fish (as distinct from the embryonic mechanisms producing those differences) lie beyond the scope of this discussion. We are currently engaged in a general survey of the factors associated with vertebral variation. Tentatively, we suggest that amongst related species the vertebral count of each is adaptive to its average body size, and that the explanation may lie in the hydrodynamics of locomotion. If vertebral count has indeed been selected to match body size, then the reasons for the latitudinal clines often displayed by vertebral numbers may be associated with the striking latitudinal clines already demonstrated to occur in fish body sizes (Lindsey 1966). But regardless of what selective significance may eventually be attributed to vertebral count, the scattered evidence reviewed here suggests that morphogenic control of vertebral count does not reside in the egg size.

Acknowledgments

We are grateful to Dr D. P. Scott for useful discussions and for reading the manuscript. R. McV. Clarke kindly supplied calculations regarding herring data. Financial support was provided by the National Research Council of Canada.

Ali, M. Y. MS 1962. Meristic variation in the medaka (*Oryzias latipes*) produced by temperature and by chemical factors affecting metabolism. Ph.D. Thesis, Univ. of British Columbia, Vancouver, B.C. 237 p.

Bagenal, T. B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. J. Fish Biol. 1: 167–182.

Bailey, R. M., and W. A. Gosline. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Misc. Publ. Mus. Zool. Univ. Mich. 93: 1–44.

Bilton, H. T., and D. W. Jenkinson. MS 1966. Relationship between egg size and fish size in sockeye salmon (*Oncorhynchus nerka*). Fish. Res. Board Can. MS Rep. Ser. (Biol.) 848: 8 p.

Canagaratnam, P. MS 1959. The influence of light intensities and durations during early development on meristic variation in some salmonids. Ph.D. Thesis. Univ. of British Columbia, Vancouver, B.C. 130 p.

Ciechomski, J. D. de 1966. Development of the larvae and variations in the size of the eggs of the argentine anchovy, *Engraulis anchoita* Hubbs and Martini. J. Cons. Cons. Perma. Int. Explor. Mer 30: 281–290.

Dannevig, A. 1950. The influence of the environment on number of vertebrae in plaice. Rep. Norweg. Fish. Mar. Invest. 9(9): 1–6.

Fowler, J. A. 1970. Control of vertebral number in teleosts — an embryological problem. Quart. Rev. Biol. 45: 148–167.

Garside, E. T., and F. E. J. Fry. 1959. A possible relationship between yolk size and differentiation in trout embryos. Can. J. Zool. 37: 383–386.

Hempel, G., and J. H. S. Blaxter. 1961. The experimental modification of meristic characters in herring (*Clupea harengus* L.). J. Cons. Cons. Perma. Int. Explor. Mer 26: 336–346.

1967. Egg weight in Atlantic herring (*Clupea harengus* L.). J. Cons. Cons. Perma. Int. Explor. Mer 31: 170–195.

Hiemstra, W. H. 1962. A correlation table as an aid for identifying pelagic fish eggs in plankton samples. J. Cons. Cons. Perma. Int. Explor. Mer 27: 100–108.

Kyle, H. M. 1926. The biology of fishes. Sidgwick and Jackson, London, England. 396 p.

Lindsey, C. C. 1958. Modification of meristic characters by light duration in kokanee, *Oncorhynchus nerka*. Copeia 1958: 134–136.

1962. Experimental study of meristic variation in a population of threespine sticklebacks, *Gasterosteus aculeatus*. Can. J. Zool. 40: 271–312.

1966. Body sizes of poikilotherm vertebrates at different latitudes. Evolution 20: 456–465.

Lindsey, C. C., and M. Y. Ali. 1965. The effect of alternating temperature on vertebral count in the medaka (*Oryzias latipes*). Can. J. Zool. 43: 99–104.

McCart, P. J. MS 1970. A polymorphic population of *Oncorhynchus nerka* at Babine Lake, B.C., involving anadromous (sockeye) and non-anadromous (kokanee) forms. Ph.D. Thesis. Univ. of British Columbia, Vancouver, B.C. 135 p.

Mottley, C. M. 1937. The number of vertebrae in trout (*Salmo*). J. Biol. Bd. Can. 3: 169–176.

ORSKA, J. 1962. The influence of temperature on the development of meristic characters of the skeleton in Salmonidae Part I. Temperature-controlled variations of the number of vertebrae in *Salmo irideus* Gibb. Zool. Pol. 12: 309–339.

ROUGH, G. E. MS 1961. The effects of temperature and light intensity on the growth, and meristic and morphometric characters as related to utilization of yolk in the pro-larva of the common white sucker. Ph.D. Thesis. University of Pittsburgh, Pittsburgh, Pennsylvania. 242 p.

SCHNAKENBECK, W. 1931. Zum Rassenproblem bei den Fischen. Z. Morphol. Oekol. Tiere 21(3/4 Heft): 409–566.

SCOTT, D. P. 1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Bd. Canada 19: 715–731.

SOLEMDAL, P. 1967. The effect of salinity on buoyancy, size and development of flounder eggs. Sarsia 29: 431–442.

TÅNING, Å. V. 1952 Experimental study of meristic characters in fishes. Biol. Rev. (Cambridge) 27: 169–193.

TEMPLEMAN, W., AND T. K. PITT. 1961. Vertebral numbers of redfish, *Sebastes marinus* (L.), in the north-west Atlantic, 1947–1954. Rapp. Proces-Verbaux Reunions Cons. Perma. Int. Explor. Mer 150: 56–89.

[1971]

Lawrence B. Slobodkin

Scientific Sterility in Middle Age

Views

Time-consuming, prestigious, nonscientific work may lead to intellectual death at an early age

Perhaps half or more of all American science Ph.D.'s move into research or teaching positions in minor or second-rate institutions, and live lives of essential mediocrity. Perhaps they continue until retirement to repeat and slightly extend the research work that got them their doctorates, but they never have any real hope or prospects of making anything but a miniscule addition to knowledge. The remainder constitute what I will call the scientific middle class. From them are recruited the staffs of first-rate institutions, editors of journals, speakers at symposia, officers of societies, recipients of most research funds, and from them come most of the "good" articles in scientific journals.

They progress in income and reputation from junior to senior positions, they are in good enough repute nationally so that they can hold their own in academic infighting and by the age of 35 to 40 they have tenure positions, growing children, half-paid mortgages, and an air of solidity, if not prosperity. Some even have a hobby. At around this age, their graduate students start referring to them as Boss, Chief, The Old Man, or something equally pseudomilitary and capitalized.

Having defined my class, let me define my problem. I believe that most of the men of the scientific middle class enter on a period of relative sterility just when they have established their reputations and might have been expected to be at their most productive. Some of them recover, most do not. I believe the sterility period is almost inevitable but that effort devoted to aiding recovery from this sterility would be as valuable for maintaining and incrementing scientific accomplishment, dollar for dollar and man hour for man hour, as any procedure that can be imagined.

The typical problem of a middle class scientist seems to be that he has initially a certain fear of failure combined with the possibility that he really is another Einstein. The combination is enough to keep most graduate students working hard and productively. This is emphasized by the fact that almost any graduate student was the brightest boy in his high school class and still retains the memory of this position.

Very pleasant milestones are encountered by every young scientist. His first clearly defined problem, first successful experiments, first oral presentation to a class or at a scientific meeting. Fellowships, assistantships, and the vanishing of less effective classmates all give the student the sense that he is progressing. Reprints of his first published paper are sent to parents and grandparents; and the first reprint requests from strangers in Iowa or, better still, from agricultural stations in India or Brazil produce a tremendous elation. A brand new Ph.D. is ready to take on the world single-handed, and usually does, which accounts for the high mobility of college instructors.

Reprint requests are beginning to lose their spice when the first symposium invitation arrives, and for the next several years there is an almost visible swelling in stature both in and out of the home institution. The rate at which invitations arrive accelerates, since the people who organize symposia are generally cautious men who invite only those speakers who have already demonstrated their competence as symposium participants.

Concurrently, the home university, being also run by cautious men who have only been waiting for some external evidence, decide that the developing middle class scientist is a valuable asset and increase his salary, facilities, rank, and responsibilities. The grant advisory panels, by the

The author says:

"This little note, begun in Ann Arbor in 1960, completed in Jerusalem in 1961, and rediscovered while cleaning my desk in Stony Brook in 1971, indicates that I could foresee the problems of detours on the path of scientific investigation. Despite this foreknowledge, during the interval 1961 to 1971, I have been a Guggenheim Fellow at Jerusalem, Visting Professor at Tel Aviv, Editor of the American Naturalist, *Trustee of the University of Michigan Press, President of the General Systems Research Society, Vice-President of the American Society of Naturalists, consultant to the Smithsonian, AEC, NASA, FAO, WHO, the Italian Academy of Sciences, the Scottish Fisheries Research Board (among others), Instructor-in-charge of the Marine Ecology Course (Marine Biological Laboratory, Woods Hole), and Program Director of the Ecology and Evolution Program and Chairman of the Ecology and Evolution Department at the State University of New York at Stony Brook. I have not yet lectured in Australia, West Virginia, or Mississippi. I am under contract for three as yet unfinished books to patient but truculent publishers.*

"I believe this incomplete list is average for the scientific bourgeoisie. Unfortunately, none of the various jobs in the above list has been purely honorary and my performance has been mixed. Starting in 1969, I have been gently abandoning most of them to others. I hope it isn't too late since I am now forty-three and must very soon decide what to be when I grow up. My adolescent ambition to enter science as a career still persists. At present my research activities include field studies on coral reefs, laboratory studies on evolutionary strategy, and a program in the applications of ecology to practical problems of planning and environmental quality control. I would like to assure my publishers that I also count books as scientific work.

"This paper is contribution No. 42 from the Ecology and Evolution Program, State University of New York at Stony Brook; it was not supported by any research foundation. Now that I am a department chairman and my rate of publication is lower, it seems like the time to publish it."

Address: Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY 11790.

same cautious argument, decide to provide larger grants and perhaps use the talents of this obviously respectable citizen in evaluating grant requests from others. The journal editors become more generous in article acceptance and begin to send articles to be refereed.

Now the middle class scientist has arrived. He has relative affluence, and many props to his ego. All the fears and insecurities of the new Ph.D. are gone. To be sure, the work isn't as much fun as it had been. Hired technicians never do it quite right, but considering how much more he gets done, it is worth it. Also, lectures on research are getting dull, but one can't expect results as fast when one matures as when one was young.

We can't all be Einstein and we can't all do work; some of us must sacrifice ourselves, jet first-class, to lead the field, explain it to the others, popularize, write. And if our middle class scientist can believe that, he's dead already. If he hasn't read this far, the problem hasn't hit him yet.

It should be noted that, in one sense, frenetic activity does not stop scientific production. If a scientist is willing to keep turning the crank on the same machine that ground out his early research, he can be nominally productive for his entire life, but this is just another kind of death.

How do you stay scientifically alive? The motivation of a scientist is basically curiosity, in most cases overlain with other things, and these other things (particularly money, prestige, and security) are so important early in a career that when they must disappear as motivation, if the curiosity is to survive, it is difficult to let them go. This all may be projection. I myself am not really prestige-laden at the moment, but I am at the point where I can see that I do not need prestige. It will not aid me in my scientific activity, whatever it might do for my ego. Nevertheless, prestigeful, nonscientific activity attracts me. If this is not projection, there are others facing the same problem. Is there a recipe for preserving scientific values without being either Einstein on one hand or a graduate student on the other?

I don't believe I have really solved the problem, but I must discuss possible solutions in any case. Some of our very good scientists, including three Nobel prizemen I can think of off-hand, switched fields, thereby bringing their intellectual maturity to bear on completely fresh problems. This probably is not a reasonable solution, because the same concern for a fresh approach is probably intimately related to their getting the Nobel Prize in the first place. Furthermore, only scientists of very high prestige can afford to switch interests completely without hearing violent protest from their employers. It is almost surely the case that switching technique, approach, problem, or even species can prevent stagnation to some degree. Alteration in the teaching–research ratio may also help. An irrelevant question from an elementary student can, on occasion, be very stimulating, and conversely a year of isolation can counteract the comfortable adulation so freely given to histrionically gifted lecturers. But all of these solutions require that the research worker divest himself to at least some extent of his smothering security.

Another kind of trap which normal scientific progress provides is the unexamined samples, the unanalyzed data, and the outdated or nonfunctional equipment that fill laboratories and file cabinets. We all know men who have become lost in the attic of research, always about to finish some yellowing heap of numbers or drawings or manuscript. Research administrators may be of practical help here by encouraging the use of fellowship and sabbatical time for the purpose of finishing half-started projects, rather than for the initiation of new ones.

The implicit assumption I am making is that if a scientist is freed of secondary problems, so that he is confronted with the choice of being bored or being creative, he will be creative. This may not be so. Perhaps creativity in science is concomitant with attempts to solve personal, financial, and other problems that have nothing to do with science itself. I don't know. I am trying to avoid the problem in my own case by deliberately modifying my research goals, techniques, and teaching programs. I am also taking advantage of the liberality of the Guggenheim Foundation to live in a completely new social context while I finish up old work and clear up a series of half-formulated ideas.

Perhaps there is no problem. Perhaps these procedures that look attractive to me are utterly irrelevant to the problem. If the problem is real, certainly it is worth examining further.

"This new drug works on streptococci, pneumococci, and staphylococci. Now here's where you come in . . ."

Mitt. Hamburg. Zool. Mus. Inst.	Band 68	S. 177—194	Hamburg, April 1972

Biostatistische Untersuchungen externer Merkmale an Lanao-Cypriniden

Ein Beitrag zum Problem der intralakustrischen Speziation

Ellen Wahl[1] [2])

(5 Abbildungen im Text und Tafeln VI und VII)

Abstract

The development of a group of about twenty closely related species of Cyprinidae in Lake Lanao (Mindanao, Philippines) has been explained by two theories. Whereas one hypothesis defends the intralacustrine speciation of a single primitive form, the other explanation maintains multiple invasions of several closely related forms and their hybridization in Lake Lanao. These contradictory assumptions have incited the present investigation which, however, does not yet allow a final decision in favour of one of the theories mentioned above: The analysis of some external characteristics of those Lanao fishes — such as the number of scales and the proportions of the bodies — supports as well the possibility of an allopatric origin as a sympatric speciation of these cyprinids.

Inhalt

Problemstellung 178
I. Die Lanao-Cypriniden 178
a) Der Lanao-See 178
b) Die Cyprinidenfauna des Lanao-Sees 178
II. Untersuchungsbefunde 181
a) Material und Methode 181
b) Statistische Bearbeitung 183
III. Diskussion der Ergebnisse 186
a) Gruppierung der Lanao-Cypriniden 186
b) Zum Speziationsproblem der Lanao-Cypriniden 187
Zusammenfassung 190
Tabellenanhang 191
Literatur 194

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Problemstellung

Intralakustrische Speziation gilt als Ursache für das Vorkommen einer auffallenden Formenfülle von Cypriniden im Lanao-See auf Mindanao. Der dort endemische Speziesschwarm von etwa zwanzig Arten in fünf Gattungen – vier Gattungen endemisch – wurde von HERRE entdeckt und beschrieben (HERRE 1924, 1933) und soll sich nach seiner Darstellung von einer einzigen Art herleiten, die bei der Bildung des Sees in dem Gewässer isoliert wurde.

Vor allem der Zeitfaktor – für den Lanao-See wird ein Alter von nur 10 000 Jahren angegeben (MYERS 1960) – läßt Zweifel an der Richtigkeit dieser Interpretation aufkommen. Auch weitere Gründe wie die geringe Ausdehnung und geringe Gliederung des Sees sprechen gegen die Annahme einer intralakustrischen Artbildung im geforderten Umfange und machen genauere Untersuchungen zu diesem Problem wünschenswert (KOSSWIG und VILLWOCK 1964). Die vorliegende Arbeit soll einen Beitrag dazu liefern. Sie beschränkt sich im wesentlichen auf die statistische Analyse einiger morphologischer Merkmale dieser Fische und die daraus zu ziehenden Folgerungen.

I. Die Lanao-Cypriniden

a) Der Lanao-See

Der Lanao-See (Abb. 1) liegt im Hochland des westlichen Zentral-Mindanao, etwa 700 m hoch über dem Meer. Mit einer Oberfläche von über 300 km² – genaue Angaben fehlen – ist er der zweitgrößte See der Philippinen (PRATT 1916). Die Angaben über seine Tiefe sind widersprüchlich und schwanken zwischen 300 m (HERRE 1933; WOOD 1963) und etwa 100 m (PRATT 1916; WOLTERECK 1941). Nach WOLTERECKS Ergebnissen ist der nördliche Abschnitt sehr viel flacher als der übrige See, der rasch auf über 50 m abfällt und seine tiefste Stelle nahe dem Südufer mit 107 m erreicht (Abb. 1). VILLWOCK (mündliche Mitteilung) vermutet größere mittlere Tiefen im nördlichen Teil.

Alle Autoren sind sich über den vulkanischen Ursprung des Lanao-Sees einig: Während WOLTERECK (1941) den Lanao als Kratersee deutet, sieht ihn SMITH (1910) als natürlichen Stausee an, der sich nach Abriegelung eines Flußtales durch einen Lavastrom gebildet habe. Die aufgestauten Wassermassen verschafften sich mit dem Agus-River einen sekundären Abfluß nach Norden. Unweit der Mündung in die Iligan-Bay stürzt der Agus als 58 m hoher Wasserfall senkrecht in die Tiefe. – WILLIS (Zitat in MYERS 1960) äußert eine entsprechende Ansicht über die Entstehung des Sees und schätzt sein Alter auf nur etwa 10 000 Jahre. Er schließt diese Zahl aus der Länge des vom Agus-River ausgewaschenen Canons und dem Ausmaß der an den Lavamassen beobachteten rückschreitenden Erosion. WOOD (1963) bestätigt diese Angabe durch Altersbestimmungen eigener Bodenproben vom Seegrunde und aus der Umgebung.

b) Die Cyprinidenfauna des Lanao-Sees

Die Karpfenfische sind im philippinischen Archipel sehr schwach vertreten (KOCH 1965). Es gibt nur einen Ort, wo sie das beherrschende Element der Süßwasserfauna bilden: den Lanao-See auf Mindanao. HERRE, der diese für die Phi-

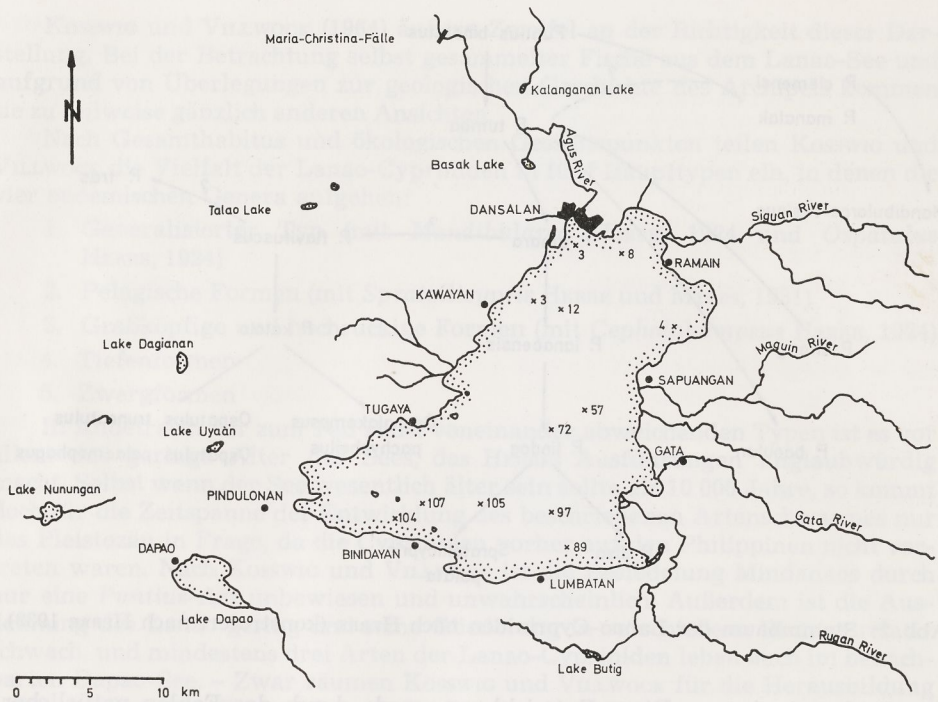


Abb. 1: Lanao-See und Umgebung (nach den Karten P.C.G.S. 2539 (1st ed., 1964) und P.C.G.S. 2544 (1st ed., 1964), kombiniert mit Tiefenangaben nach Woltereck 1941).

lippinen einmalige Cyprinidenfauna entdeckte und über Jahre ihr einziger Bearbeiter blieb, beschreibt insgesamt siebzehn Spezies, zwölf davon als zum Genus *Barbodes* Bleeker, 1859/60 (nach Herre 1953 = *Puntius* Hamilton Buchanan, 1822) gehörig. Für die fünf weiteren Arten stellt er vier neue Genera auf (Herre 1924, 1926, 1932; Herre und Myers 1931), wobei als Gattungskriterien jeweils ungewöhnliche Kieferbildungen herangezogen werden. Sie sind am deutlichsten in der monotypischen Gattung *Mandibularca* Herre, 1924, deren Vertreter sich durch einen schmalen, stark aufwärts gekrümmten Unterkiefer auszeichnen, und bei *Ospatulus* Herre, 1924, wo der Unterkiefer cranial wie abgeschnitten ist, so daß er nicht in den Oberkiefer „paßt" (Tafel VI b und c; Kosswig und Villwock 1964).

Herre (1933) ist sich ganz sicher in der Annahme, daß die gesamte Cyprinidenfauna des Lanao-Sees auf eine einzige Ausgangsart, auf *Puntius binotatus* (Cuv. und Val., 1842), zurückgeht. *P. binotatus* ist ein im Malaiischen Archipel weit verbreiteter Fisch von großer Variabilität (Weber and de Beaufort 1916). Er konnte über die während einer glazialen Meeresspiegelsenkung auftretenden Landbrücken von Borneo aus die ursprünglich acyprinide Region der Philippinen erreichen (Kosswig und Villwock 1964), verbreitete sich über ganz Mindanao und wurde bei der Absperrung des Lanao-Flußtales in dessen Oberlauf eingeschlossen. Mit der allmählichen Herausbildung und Vergrößerung des Sees wuchs die Anzahl der verschiedenen Biotope und begann – nach Herre – die Differenzierung des

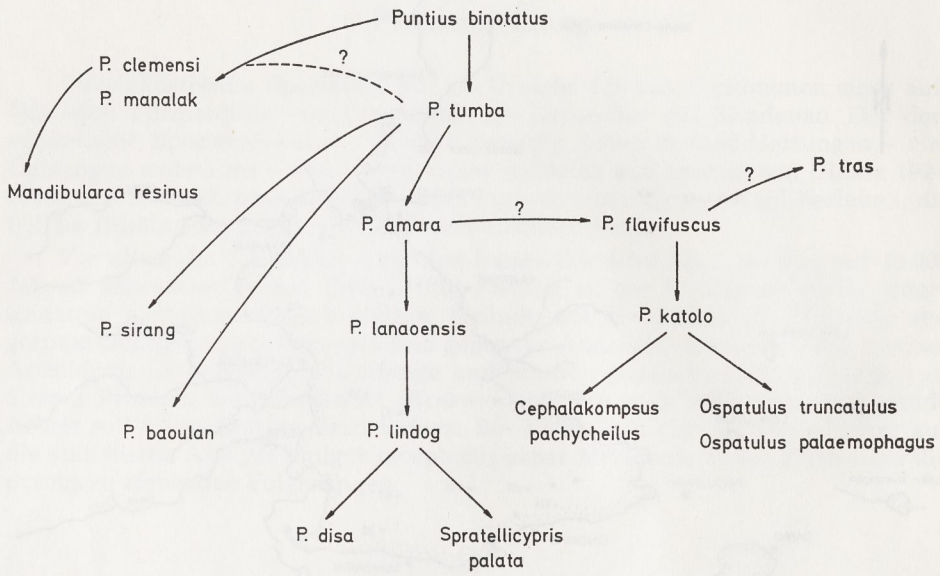


Abb. 2: Stammbaum der Lanao-Cypriniden nach HERRE (konstruiert nach HERRE 1933).

Cyprinidenschwarmes. Diese Entwicklung wurde durch das Fehlen natürlicher Konkurrenten begünstigt, da die für Fische (junge Aale ausgenommen) unpassierbaren Maria-Christina-Fälle den See und seine Zuflüsse gegen Zuwanderer aus dem Meer isolieren. Die Art *Puntius binotatus* selbst verschwand im Lanao, und an seine Stelle trat *P. tumba* (HERRE, 1924), der als Ausgangsform für alle weiteren Arten des Sees gilt. Abb. 2 bringt HERRES Vorstellungen über die Zusammengehörigkeit der Arten und die Entwicklungslinien innerhalb des Speziesschwarmes (HERRE 1933):

Von *Puntius tumba* führt eine gerade Entwicklungslinie über *P. amarus* (HERRE, 1924), *P. lanaoensis* (HERRE, 1924) und *P. lindog* (HERRE, 1924) zu *P. disa* (HERRE, 1932) und *Spratellicypris palata* (HERRE, 1924). Nach HERRE handelt es sich in dieser Gruppe um pelagische Formen, die in den uferfernen Gebieten des Sees in fünf bis fünfzehn Meter Tiefe in großen Schwärmen auftreten. – *P. baoulan* (HERRE, 1926) und *P. sirang* (HERRE, 1932) sind direkt von *P. tumba* abzuleiten, der erstere eine relativ selten gesehene Tiefenform, der zweite eine zwergenhafte Form aus flachen, schlammigen Buchten. In diesen Lebensraum gehört wahrscheinlich auch die Gruppe um *P. flavifuscus* (HERRE, 1924) und *P. katolo* (HERRE 1924), die sich vielleicht von *P. amarus* herleitet. Hier sind die Gattungen *Cephalakompsus* HERRE, 1924, und *Ospatulus* HERRE, 1924, anzuschließen. Die großen Formen *P. clemensi* (HERRE, 1924) und *P. manalak* (HERRE, 1924) leiten sich möglicherweise direkt von *P. binotatus* ab; *Mandibularca* HERRE, 1924, wird als weitere Spezialisierung des *P. clemensi* aufgefaßt und wurde bisher nur in den Stromschnellen des Agus gefunden.

Das sind – grob umrissen – HERRES Vorstellungen von der Entwicklung der Cyprinidenfauna im Lanao-See, denen sich MYERS (1960) anschließt. Beide Autoren vermuten noch weitere, bisher unbeschriebene Arten im See. –

Kosswig und Villwock (1964) äußern Zweifel an der Richtigkeit dieser Darstellung. Bei der Betrachtung selbst gesammelter Fische aus dem Lanao-See und aufgrund von Überlegungen zur geologischen Geschichte des Archipels kommen sie zu teilweise gänzlich anderen Ansichten.

Nach Gesamthabitus und ökologischen Gesichtspunkten teilen Kosswig und Villwock die Vielfalt der Lanao-Cypriniden in fünf Haupttypen ein, in denen die vier endemischen Genera aufgehen:

1. Generalisierter Typ (mit *Mandibularca* Herre, 1924 und *Ospatulus* Herre, 1924)
2. Pelagische Formen (mit *Spratellicypris* Herre und Myers, 1931)
3. Großköpfige und hochrückige Formen (mit *Cephalakompsus* Herre, 1924)
4. Tiefenformen
5. Zwergformen

In Anbetracht der zum Teil stark voneinander abweichenden Typen ist es vor allem das geringe Alter des Sees, das Herres Ausführungen unglaubwürdig macht. Selbst wenn der See wesentlich älter sein sollte als 10 000 Jahre, so kommt doch für die Zeitspanne der Entwicklung des beschriebenen Artenschwarmes nur das Pleistozän in Frage, da die Cypriniden vorher auf den Philippinen nicht vertreten waren. Nach Kosswig und Villwock ist die Besiedelung Mindanaos durch nur eine *Puntius*-Art unbewiesen und unwahrscheinlich. Außerdem ist die Ausdehnung des Lanao gering und seine Gliederung in verschiedene Biotope relativ schwach, und mindestens drei Arten der Lanao-Cypriniden leben auch im benachbarten Dapao-See. – Zwar räumen Kosswig und Villwock für die Herausbildung einander ähnlicher Formen innerhalb der einzelnen Haupttypen die Möglichkeit der intralakustrischen Speziation bzw. Differentiation ein, aber die Frage nach der sympatrischen Entstehung aller Lanao-Cypriniden wird von ihnen aus den genannten Gründen verneint.

Den Haupttypen entsprechend nehmen die Autoren wenigstens fünf bis sechs verschiedene *Puntius*-Vorfahren für die heutige Mannigfaltigkeit an. Entweder wurde Mindanao von mehreren *Puntius*-Arten erreicht, oder es bestanden möglicherweise in mehreren Glazialen für Süßwasserfische benutzbare Verbindungen von Borneo nach den Philippinen. Im letzteren Falle könnten aufeinanderfolgende Populationswellen derselben Art – mit teilweise verschiedenen Genbeständen und der Möglichkeit späterer Rekombination – die große Variabilität der Lanao-Fische erklären. –

II. Untersuchungsbefunde

a) Material und Methode

Für die Bearbeitung stellte Herr Prof. Dr. W. Villwock über tausend formolfixierte, in Alkohol aufbewahrte Exemplare der Lanao-Cypriniden zur Verfügung, die 1963 während einer von der Deutschen Forschungsgemeinschaft finanzierten Reise gefangen worden waren.

Die Vielfalt des Materials läßt vermuten, daß die meisten von Herre beschriebenen Formen vorhanden sind. Eine Identifizierung nach Herres Angaben erwies sich in vielen Fällen als unmöglich, und so bot es sich an, in Anlehnung an die von Kosswig und Villwock aufgestellten Haupttypen eine grob-morphologische Einteilung vorzunehmen. Dabei wurden die Gruppen 4 und 5 („Tiefenformen" und „Zwergformen") in den generalisierten Typ (= A) aufgenommen, während Herres Genera *Mandibularca* (= B) und

Ospatulus (= C) — der besseren Übersicht wegen — extra gestellt wurden. Gruppe 2 blieb im wesentlichen bestehen; in ihr wurden alle schlanken Formen zusammengestellt (= D). Der Versuch, Gruppe 3 in die hochrückigen Typen (= E) und die großköpfigen (= F) zu trennen, wurde wegen gleitender Übergänge wieder aufgegeben. — In jeder dieser Hauptgruppen wurden Untergruppen gebildet, die in sich homogen sein sollten. Meist handelte es sich dabei um einzelne Fänge, die zum Teil von WOOD benannt worden waren (alle Namensnennungen sensu WOOD). Wo solche Namen nicht vorhanden waren, traten andere Protokollbezeichnungen für die Kennzeichnung hinzu.

Folgende Aufteilung des Materials in Gruppen liegt der Auswertung zugrunde (vgl. Tafeln VI und VII):

A — A Norm (= „Tumba")
A Bal (= „Baoulan")
A Man (= „Manalak")
A Pal (= „Palata")
A Sir (= „Sirang")

B — (= *Mandibularca*), wegen geringer Individuenanzahl (n = 3) von den Berechnungen ausgeschlossen

C — (= *Ospatulus*), wegen geringer Individuenanzahl (n = 4) von den Berechnungen ausgeschlossen

D — A/D 7
D 19
D 39
D 41
D 43

E–F — E 38
E Mrw
E/F
F

Folgende Daten wurden ermittelt:

1. Ll: Linea longitudinalis = Anzahl der durchbohrten Schuppen in der Seitenlinie
2. Ltr: Linea transversalis = Anzahl der Schuppen in der Transversallinie, gezählt vom Beginn der Dorsalen aus, dorsale und ventrale Medianschuppe sowie Schuppe in der Seitenlinie nicht mitgezählt
3. Do: Flossenstrahlanzahl in der Dorsalen
4. An: Flossenstrahlanzahl in der Analen
5. Tl: Totallänge = Schnauzenspitze bis Schwanzflossenende, bei zusammengelegter Flosse
6. Stl: Standardlänge = Schnauzenspitze bis zum Hinterrand der letzten durchbohrten Schuppe der Seitenlinie
7. H: größte Körperhöhe
8. Kl: Kopflänge = Schnauzenspitze bis zum Hinterrand des Kiemendeckels
9. A⌀: horizontaler Augendurchmesser

(Alle Messungen in ganzen Millimetern, 5 und 6 auf der Fischmeßlatte, 7, 8 und 9 mit der Schublehre; alle Zählungen unter dem Binokular.)

Für die Anzahl der Flossenstrahlen in der Dorsalen und Analen ergaben sich keine Unterschiede: Allgemein gelten die Formeln D IV/8 und A III/5. Die Merkmale Do und An fanden daher keine weitere Berücksichtigung.

Aus den ermittelten Körpermaßen wurden folgende Indizes berechnet:

a) Stl/Tl: Schwanzlängenindex = Standardlänge in Prozenten der Totallänge
b) H/Stl: Höhenindex = Körperhöhe in Prozenten der Standardlänge
c) Kl/Stl: Kopflängenindex = Kopflänge in Prozenten der Standardlänge
d) A⌀/Stl: Augengrößenindex = Augendurchmesser in Prozenten der Standardlänge

(Alle Indizes auf eine Stelle hinter dem Komma berechnet, a bis c in Klassen von 0,5 % Breite zusammengefaßt.)

Da sich die Körperindizes zum Teil als streng größenabhängig erwiesen, blieb die statistische Analyse dieser Merkmale auf einzelne Größenklassen beschränkt. Die bei kleinerem Stichprobenumfang zunehmende Unschärfe der statistischen Aussagen wurde in Kauf genommen, um eine unüberschaubare Ungewißheit infolge von stark unterschiedlichen Größen der Vergleichsobjekte zu vermeiden.

Die Meßwerte folgender Größenklassen gingen in die weitere Bearbeitung ein:

1. 61— 80 mm Totallänge
2. 81—100 mm Totallänge
3. 101—120 mm Totallänge
4. 121—140 mm Totallänge
5. 141—190 mm Totallänge
6. 201—270 mm Totallänge

Kleinere Fische blieben unberücksichtigt, da bei ihnen am ehesten Verfälschungen der Maße durch Fixierungseinflüsse zu erwarten sind.

Als bemerkenswerte Tatsache zeigte sich bei der Aufteilung des Materials in Größenklassen, daß Jungfische von 20 bis 40 mm Länge ausschließlich in der Gruppe A Norm auftreten.

b) Statistische Bearbeitung

Die statistischen Maßzahlen der der Auswertung zugrunde liegenden Meßreihen — Mittelwert plus Konfidenzintervall, Varianz und Standardabweichung — gehen aus den Tabellen des Anhangs hervor. Unabhängig von Abweichungen von der Normalverteilung dient dabei die Standardabweichung als Streuungsmaß (Sachs 1969).

Vergleicht man zwei Formen miteinander, so kann man in den Fällen, in denen sich die Konfidenzintervalle der Mittelwerte nicht überschneiden, die Mittelwerte auf dem gewählten Wahrscheinlichkeitsniveau (95 %) als signifikant verschieden ansehen. Entsprechend sind sie nicht voneinander zu trennen, wenn sich die Vertrauensbereiche vollständig überdecken; die dazwischen liegenden Fälle teilweiser Überdeckung sind mit dem t-Test für den Vergleich zweier Mittelwerte zu überprüfen (Sachs 1969).

Tabelle I bringt einen nach steigenden Mittelwerten geordneten Überblick über die Anzahl der Schuppen in der Seitenlinie, Abb. 3 die graphische Darstellung dazu.

Schon bei einer ersten Betrachtung fällt auf, daß die Variationsbreite der Normalform die gesamte Variabilität aller Untergruppen von A und E-F einschließlich A/D 7 umfaßt. Außerdem weichen die Mittelwerte dieser Formen maximal kaum mehr als eine Einheit voneinander ab: Ohne Ausnahme liegen sie bei 26 bis 27 Schuppen. Dagegen setzen sich die vier übrigen Gruppen des D-Typs erkennbar ab, sowohl durch erhöhte Variabilität als auch durch deutlich höhere Mittelwerte.

Im einzelnen ergibt sich für die Schuppenzahlen in der Seitenlinie folgendes Bild: Innerhalb der Gruppe A stimmen A Bal und A Man recht gut mit der Vergleichsgruppe A Norm überein. A Pal und A Sir sind untereinander sehr ähnlich; jedoch läßt sich A Pal im vorliegenden Material nicht sicher vom Normaltyp abtrennen, während zwischen A Sir und A Norm ein gesicherter Unterschied besteht. – Innerhalb E-F zeigt sich gute Übereinstimmung von E Mrw mit E 38 und auch noch mit E/F. Dagegen unterscheidet sich F von allen dreien signifikant durch erhöhte Schuppenzahlen. – Für die Gruppe der pelagischen Formen (D) läßt sich nach steigenden Schuppenzahlen die Reihe A Norm – A/D 7 – D 41 – D 43 – D 39 – D 19 aufstellen, wobei sich außer A Norm und A/D 7 bzw. D 41 und D 43 die jeweils aufeinanderfolgenden Formen sicher voneinander trennen lassen.

Das Merkmal Ltr ging in keine statistische Rechnung ein, bestätigt aber die in allen Haupttypen bestehende Tendenz zur Erhöhung der Schuppenzahl, wie die Zusammenstellung der am häufigsten vorkommenden Werte zeigt (Tab. VI). –

Der Vergleich der Körperproportionen aufgrund der berechneten Indizes erfolgt graphisch; die zugrunde liegenden Maßzahlen sind den Tabellen II-V zu entnehmen.

In Abb. 4 sind die vier Indizes dargestellt. Für jede untersuchte Gruppe und für jedes Merkmal wurde die Differenz des Mittelwertes zu demjenigen der Vergleichsform (A Norm) durch die Standardabweichung s der Vergleichsform dividiert. Ins Koordinatennetz übertragen ergeben die so normierten Werte ein graphisches Profil der Merkmalsabweichungen. Dabei werden die für die Vergleichsform geltenden Mittelwerte als auf der Abszisse liegend angenommen, und die Ordinate zeigt den in Vielfachen von s ausgedrückten Abweichungsgrad der Mittelwerte aller anderen Gruppen. Nimmt man für die Variation der Merkmale die Normalverteilung an, dann sind zwischen den

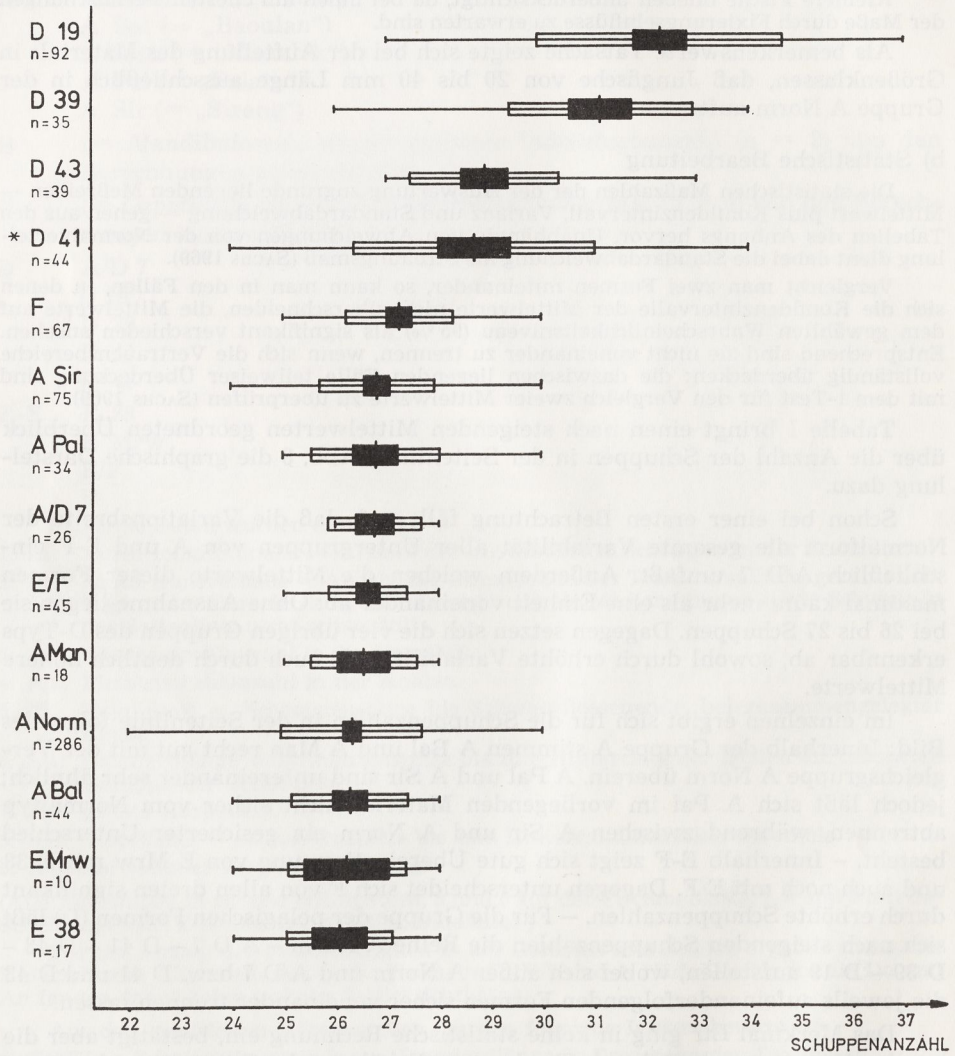


Abb. 3: Variationsbreite, Mittelwert mit 95 % — Konfidenzintervall (schwarz) und Standardabweichung (umrandet) für die Schuppenzahlen in der Seitenlinie.
*) Angabe des Konfidenzintervalls trotz Abweichung von der Normalverteilung.

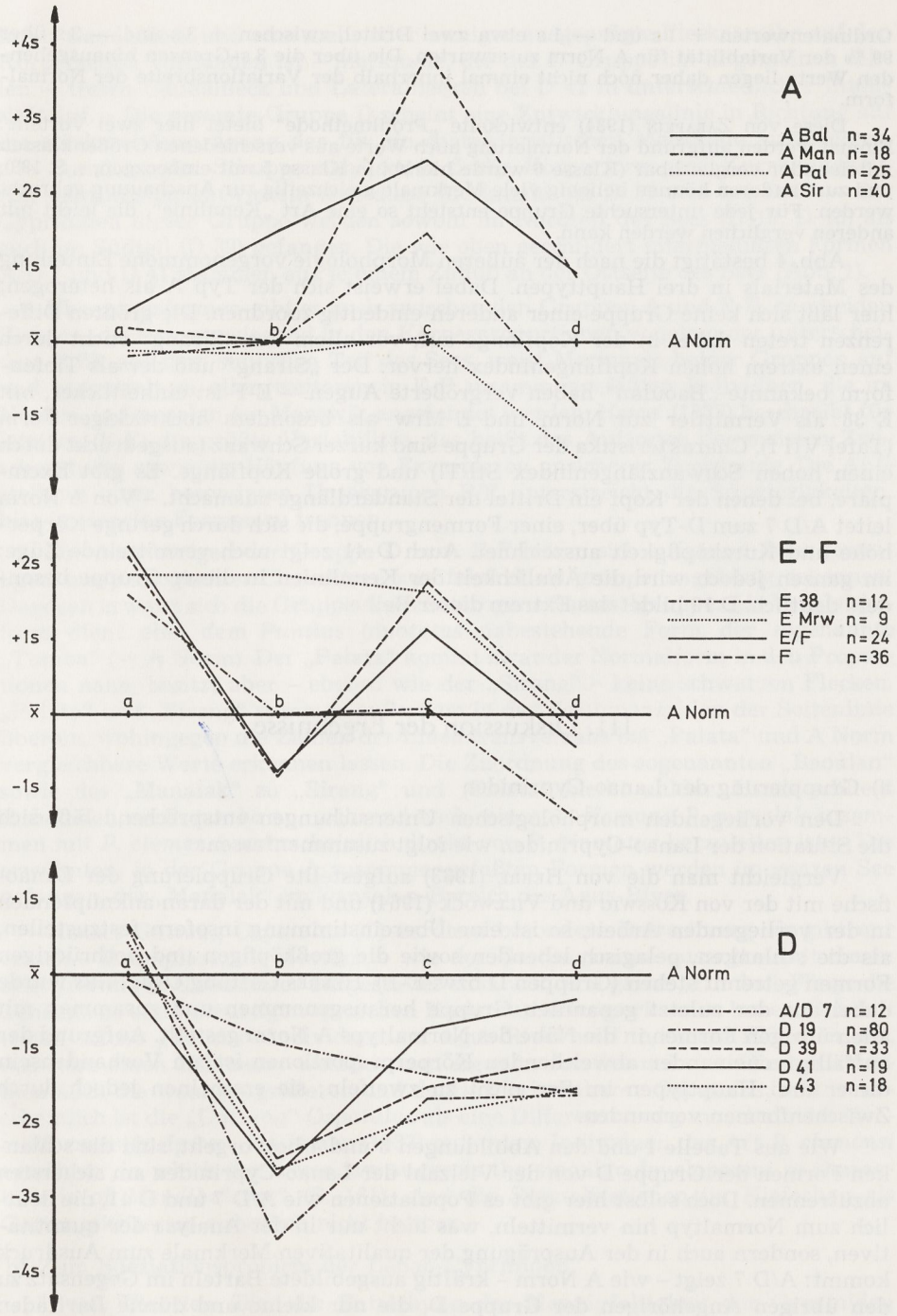


Abb. 4: Graphischer Vergleich der Körperindizes: a) Stl/Tl, b) H/Stl, c) Kl/Stl, d) A♂/Stl (Erklärung im Text).

Ordinatenwerten + 1 s und — 1 s etwa zwei Drittel, zwischen + 3 s und — 3 s über 99 % der Variabilität für A Norm zu erwarten. Die über die 3 s-Grenzen hinausgehenden Werte liegen daher noch nicht einmal innerhalb der Variationsbreite der Normalform.

Diese von ZARAPKIN (1934) entwickelte „Profilmethode" bietet hier zwei Vorteile: Einmal werden aufgrund der Normierung auch Werte aus verschiedenen Größenklassen miteinander vergleichbar (Klasse 6 wurde hierbei in Klasse 5 mit einbeozgen, s. S. 183), und zum anderen können beliebig viele Merkmale gleichzeitig zur Anschauung gebracht werden. Für jede untersuchte Gruppe entsteht so eine Art „Kennlinie", die leicht mit anderen verglichen werden kann.

Abb. 4 bestätigt die nach der äußeren Morphologie vorgenommene Einteilung des Materials in drei Haupttypen. Dabei erweist sich der Typ A als heterogen; hier läßt sich keine Gruppe einer anderen eindeutig zuordnen. Die größten Differenzen treten dabei in der Kopflänge auf, vor allem der „Sirang" sticht durch einen extrem hohen Kopflängenindex hervor. Der „Sirang" und der als Tiefenform bekannte „Baoulan" haben vergrößerte Augen. – E-F ist einheitlicher, mit E 38 als Vermittler zur Norm und E Mrw als besonders hochrückiger Form (Tafel VII f). Charakteristika der Gruppe sind kurzer Schwanz (ausgedrückt durch einen hohen Schwanzlängenindex Stl/Tl) und große Kopflänge. Es gibt Exemplare, bei denen der Kopf ein Drittel der Standardlänge ausmacht. – Von A Norm leitet A/D 7 zum D-Typ über, einer Formengruppe, die sich durch geringe Körperhöhe und Kurzköpfigkeit auszeichnet. Auch D 41 zeigt noch vermittelnde Züge; im ganzen jedoch wird die Ähnlichkeit der Kennlinien in dieser Gruppe besonders deutlich. D 19 bildet das Extrem dieser Reihe.

III. Diskussion der Ergebnisse

a) Gruppierung der Lanao-Cypriniden

Den vorliegenden morphologischen Untersuchungen entsprechend läßt sich die Situation der Lanao-Cypriniden wie folgt zusammenfassen:

Vergleicht man die von HERRE (1933) aufgestellte Gruppierung der Lanaofische mit der von KOSSWIG und VILLWOCK (1964) und mit der daran anknüpfenden in der vorliegenden Arbeit, so ist eine Übereinstimmung insofern festzustellen, als die schlanken, pelagisch lebenden sowie die großköpfigen und hochrückigen Formen getrennt stehen (Gruppen D bzw. E-F). HERRES Gattung *Ospatulus* wurde dabei aus der zuletzt genannten Gruppe herausgenommen und zusammen mit allen übrigen Formen in die Nähe des Normaltyps A Norm gestellt. Aufgrund der auffällig voneinander abweichenden Körperproportionen ist am Vorhandensein dieser drei Haupttypen im See nicht zu zweifeln; sie erscheinen jedoch durch Zwischenformen verbunden.

Wie aus Tabelle I und den Abbildungen 3 und 4 hervorgeht, sind die schlanken Formen der Gruppe D von der Vielzahl der Lanao-Cypriniden am sichersten abzutrennen. Doch selbst hier gibt es Populationen wie A/D 7 und D 41, die deutlich zum Normaltyp hin vermitteln, was nicht nur in der Analyse der quantitativen, sondern auch in der Ausprägung der qualitativen Merkmale zum Ausdruck kommt: A/D 7 zeigt – wie A Norm – kräftig ausgebildete Barteln im Gegensatz zu den übrigen Angehörigen der Gruppe D, die nur kleine und dünne Bartfäden aufweisen. D 41 dagegen vermittelt zwischen A Norm und den übrigen Seeformen durch die Art der Körperfleckung: Während bei A Norm typischerweise ein deut-

licher Caudalfleck und eine mehr oder weniger ausgeprägte Fleckenreihe auf den Körperseiten vorhanden ist – Merkmale, die der D-Gruppe im allgemeinen fehlen –, treten Caudalfleck und Lateralflecken bei D 41 in unterschiedlicher Intensität auf. – Die gesamte Gruppe D scheint eine Entwicklungslinie in Richtung auf die stärkere Ausprägung der für sie charakteristischen Merkmale aufzuzeigen, wie Zunahme der Schuppenzahl sowie flache Körperform und Kurzköpfigkeit. Am deutlichsten entwickeln sich diese Merkmale bei D 39 und bei D 19. – Die Cypriniden dieser Gruppe werden sowohl im Nordteil des Sees (D 19, D 43) als auch im Südteil (D 39) gefangen. Die wie oben geschildert intermediären Formen A/D 7 und D 41 stammen aus je einem Zufluß an der Ostseite des Sees (Abb. 1).

Übergangsformen gibt es auch zwischen den Gruppen A und E-F, den beiden Formen, die sich vorwiegend in den Körperproportionen voneinander unterscheiden. E 38, aus dem südlichen Teil des Sees, weist Merkmale beider Gruppen auf und vermittelt zu allen weiteren in E-F zusammengefaßten Individuen, die im Norden, in Dansalan (= Marawi), angelandet werden. Herre (1933) beschreibt für letztere (E-F) die größte Variabilität, das heißt das Auftreten der meisten Zwischenstufen sowie die Häufung von Exemplaren unsicherer Zuordnung. Die Aufstellung einer besonderen Untergruppe E/F unterstreicht die Schwierigkeiten, hier in einzelne Formen zu trennen.

Die Angehörigen der Gruppe D bzw. E-F lassen sich aufgrund ihrer jeweiligen morphologischen Charaktere zweifelsfrei als gruppenzugehörig erkennen. Dagegen erweist sich die Gruppe A als heterogene Sammelgruppe. Als Vergleichsform dient eine dem *Puntius binotatus* nahestehende Form, der sogenannte „Tumba" (= A Norm). Der „Palata" kommt zwar der Normalform in den Proportionen nahe, besitzt aber – ebenso wie der „Sirang" – keine schwarzen Flecken. „Palata" und „Sirang" stimmen außerdem in den Schuppenzahlen der Seitenlinie überein, wohingegen die Zahlen der Linea transversalis bei „Palata" und A Norm vergleichbare Werte erkennen lassen. Die Zuordnung des sogenannten „Baoulan" sowie des „Manalak" zu „Sirang" und „Palata" bleibt unklar. Herre schließt *P. baoulan* an *P. tumba* an, während nach seiner Auffassung *P. manalak* zusammen mit *P. clemensi* wahrscheinlich direkt von *P. binotatus* herzuleiten ist. – Die erwähnten, in der Gruppe A zusammengefaßten Formen werden im ganzen See gefangen, der „Manalak" im Dansalan-Bereich des Agus-River.

Herres Gattung *Ospatulus* (C) verdient besondere Betrachtung. Es gibt nur einzelne Exemplare, die deutlich – wie der Gattungsname aussagt – mit einem spatelförmigen Unterkiefer ausgestattet sind, während ganze „Tumba"-Fänge die Tendenz zu einer derartigen speziellen Kieferausbildung erkennen lassen. Gehäuft treten solche „Tumba"-Individuen im Agus-River und in einem Flüßchen auf, das etwa einen Kilometer westlich vom Agus in den See mündet. Hierher stammen auch die wenigen größeren und deutlich erkennbaren *Ospatulus*, und wahrscheinlich ist die „Gattung" *Ospatulus* als eine Differenzierung innerhalb der Normalform aufzufassen. Da Herre (1933) außerdem Individuen der Art *P. clemensi* erwähnt, „in which the lower jaw suggests the singular development so characteristic of *Mandibularca*" (S. 161), sind die Spezialisationen im Kieferbau als Gattungskriterien sicherlich nicht haltbar.

b) Zum Speziationsproblem der Lanao-Cypriniden

Zwei Theorien über die Entstehung der Mannigfaltigkeit der Cypriniden im Lanao-See stehen einander gegenüber, einmal die der Aufsplitterung einer einzigen Art (Herre 1933) und zum anderen die Vermutung verschiedener Ein-

wanderungswellen von Cypriniden nach Mindanao (KOSSWIG und VILLWOCK 1964). Die vorliegenden Untersuchungen bieten sowohl Anhaltspunkte für die allopatrische Herkunft als auch für sympatrische – hier intralakustrische – Speziation.

Die Verschiedenartigkeit der drei Haupttypen des Sees ist belegt. Dadurch wird die von KOSSWIG und VILLWOCK (1964) geäußerte Ansicht gegen eine rein intralakustrische Bildung dieser unterschiedlichen Typen gestützt, eine Ansicht, die sich ihrerseits auf die geologische Geschichte des philippinischen Archipels gründet.

Die große Variabilität der Lanao-Fische und das Auftreten von Intermediärformen lassen sich nach KOSSWIG und VILLWOCK einmal durch die Annahme verschiedener, in größeren zeitlichen Abständen aufeinanderfolgender Populationswellen derselben Art erklären. Eine weitere Möglichkeit besteht danach in der Annahme, daß mehrere, nahe verwandte Formen den Lanao-See gleichzeitig erreicht und besiedelt haben, wobei es in beiden Fällen zu einer sekundären Durchmischung kam. Diese Auffassung läßt sich möglicherweise durch eine nähere Betrachtung der Formengruppe D stützen, für die aufgrund von Schuppenanzahl (Abb. 3) und Kennlinien der Körperproportionen (Abb. 4) die Reihung A Norm – A/D 7 – D 41 – D 43 – D 39 – D 19 aufgestellt werden kann. Abb. 5 bringt dazu die prozentualen Häufigkeiten der Schuppenzahlen in der Seitenlinie, von oben nach unten in der angegebenen Reihenfolge der Gruppen. Dabei zeigt sich nicht nur die kontinuierliche Verschiebung der Varationsbreite in Richtung auf höhere Werte, sondern außerdem treten bezeichnenderweise bei D 41 und – weniger deutlich – bei D 43 zweigipflige Verteilungen auf, deren einer Gipfel zur Normalform tendiert, während der andere im Bereich der D-Typen liegt. Im Zusammenhang damit fällt die hohe Variabilität der Zwischenform D 41 auf, wie es für die einzelnen Merkmale aus den Werten der Standardabweichung abzulesen ist (Tab. I bis V). Diese Verhältnisse lassen zumindest die Möglichkeit offen, daß es sich um Intermediärformen sensu KOSSWIG und VILLWOCK handeln kann.

Zugunsten der von HERRE vertretenen Theorie von der intralakustrischen Speziation läßt sich anführen, daß im vorliegenden, recht umfangreichen Material Jungfische von 20 bis 40 mm Länge ausschließlich bei A Norm auftreten, d. h. bei der dem *Puntius binotatus* nahestehenden Form. Daraus ist folgende Vorstellung ableitbar: Bei der Bildung des betrachteten Cyprinidenschwarmes handelt es sich tatsächlich um eine schnell vollzogene bzw. noch nicht abgeschlossene Aufspaltung einer einzigen ancestralen Form, wobei die Jungfische der rezenten Lanao-Cypriniden ebenso unspezialisiert sind wie die vermutete Ahnform. Diese Verhältnisse erinnern an die schweizerischen Coregonen, wobei STEINMANN die schlechte Unterscheidbarkeit der Jungfische als ein Argument für die monophyletische Abstammung dieser Felchen heranzieht (1950/51).

Für die von HERRE vermutete Art und Weise der Speziation sprechen die von ihm für die systematische Einteilung benutzten Sonderbildungen in der Schnauzenregion. Diese lassen Spezialisationen bei der Nahrungsaufnahme vermuten. Bestärkt wird die Annahme von verschiedenartigen Ernährungsweisen durch die zum Teil sehr unterschiedliche Beschaffenheit der Muskulatur: Das rötlichgelbe und noch in der Fixierung fettige Fleisch von A Bal, A Man und D 19 zum Beispiel steht im Gegensatz zu der regelmäßig festen und fast weißen Muskulatur der Normaltypen. In Anbetracht dieser augenscheinlich ökologischen Differenzierungen innerhalb der Lanao-Cypriniden gewinnt die von HERRE (1933) postulierte monophyletische Abstammung an Wahrscheinlichkeit. Durch das Fehlen natürlicher Konkurrenten (s. S. 180) wurde es den Vorfahren des heutigen Cypriniden-

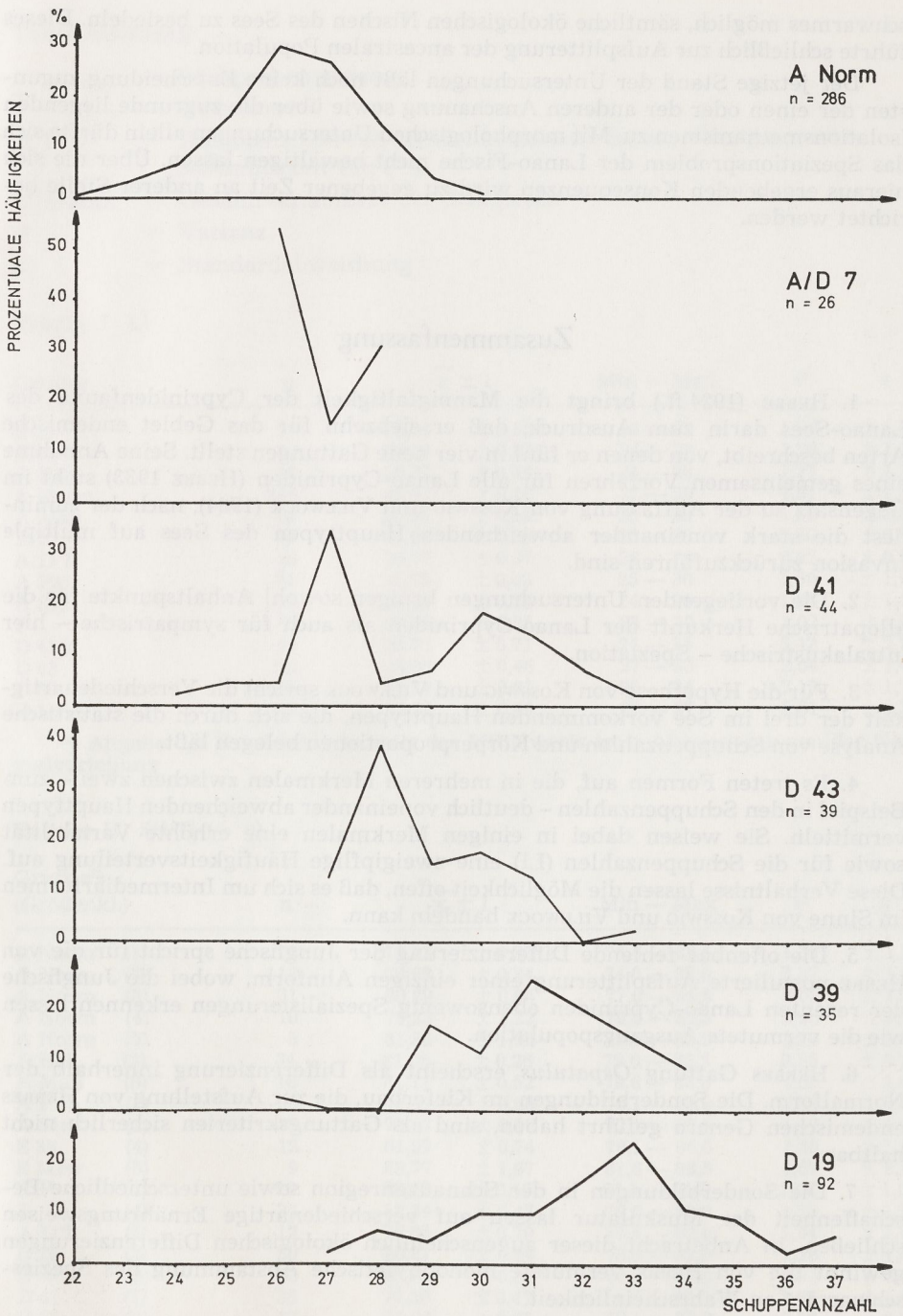


Abb. 5: Häufigkeitsverteilungen der Schuppenzahlen in der Seitenlinie für A Norm und Gruppe D.

schwarmes möglich, sämtliche ökologischen Nischen des Sees zu besiedeln. Dieses führte schließlich zur Aufsplitterung der ancestralen Population.

Der jetzige Stand der Untersuchungen läßt noch keine Entscheidung zugunsten der einen oder der anderen Anschauung sowie über die zugrunde liegenden Isolationsmechanismen zu. Mit morphologischen Untersuchungen allein dürfte sich das Speziationsproblem der Lanao-Fische nicht bewältigen lassen. Über die sich hieraus ergebenden Konsequenzen wird zu gegebener Zeit an anderer Stelle berichtet werden.

Zusammenfassung

1. HERRE (1924 ff.) bringt die Mannigfaltigkeit der Cyprinidenfauna des Lanao-Sees darin zum Ausdruck, daß er siebzehn für das Gebiet endemische Arten beschreibt, von denen er fünf in vier neue Gattungen stellt. Seine Annahme eines gemeinsamen Vorfahren für alle Lanao-Cypriniden (HERRE 1933) steht im Gegensatz zu der Auffassung von KOSSWIG und VILLWOCK (1964), nach der zumindest die stark voneinander abweichenden Haupttypen des Sees auf multiple Invasion zurückzuführen sind.

2. Die vorliegenden Untersuchungen bringen sowohl Anhaltspunkte für die allopatrische Herkunft der Lanao-Cypriniden als auch für sympatrische – hier intralakustrische – Speziation.

3. Für die Hypothese von KOSSWIG und VILLWOCK spricht die Verschiedenartigkeit der drei im See vorkommenden Haupttypen, die sich durch die statistische Analyse von Schuppenzahlen und Körperproportionen belegen läßt.

4. Es treten Formen auf, die in mehreren Merkmalen zwischen zwei – zum Beispiel in den Schuppenzahlen – deutlich voneinander abweichenden Haupttypen vermitteln. Sie weisen dabei in einigen Merkmalen eine erhöhte Variabilität sowie für die Schuppenzahlen (Ll) eine zweigipflige Häufigkeitsverteilung auf. Diese Verhältnisse lassen die Möglichkeit offen, daß es sich um Intermediärformen im Sinne von KOSSWIG und VILLWOCK handeln kann.

5. Die offenbar fehlende Differenzierung der Jungfische spricht für die von HERRE postulierte Aufsplitterung einer einzigen Ahnform, wobei die Jungfische der rezenten Lanao-Cypriniden ebensowenig Spezialisierungen erkennen lassen wie die vermutete Ausgangspopulation.

6. HERRES Gattung *Ospatulus* erscheint als Differenzierung innerhalb der Normalform. Die Sonderbildungen im Kieferbau, die zur Aufstellung von HERRES endemischen Genera geführt haben, sind als Gattungskriterien sicherlich nicht haltbar.

7. Die Sonderbildungen in der Schnauzenregion sowie unterschiedliche Beschaffenheit der Muskulatur lassen auf verschiedenartige Ernährungsweisen schließen. In Anbetracht dieser augenscheinlich ökologischen Differenzierungen gewinnt die von HERRE vermutete monophyletische Abstammung des Spezies-schwarmes an Wahrscheinlichkeit.

8. Der jetzige Stand der Untersuchungen läßt noch keine Entscheidung zugunsten der einen oder der anderen Anschauung zu.

Tabellenanhang

n	=	Stichprobenumfang
$\bar{x}$	=	Mittelwert
± l	=	Konfidenzintervall für den Mittelwert bei einer Irrtumswahrscheinlichkeit von 5 %
Min-Max	=	Gesamtvariabilität der Stichprobe
s^2	=	Varianz
s	=	Standardabweichung

Tabelle I: Ll

Gruppe	n	$\bar{x}$ ± l		Min — Max	s^2	s
E 38	17	26,06	± 0,35	24 — 28	1,06	± 1,03
E Mrw	10	26,20	± 0,82	24 — 28	1,29	± 1,14
A Bal	44	26,27	± 0,34	24 — 28	1,27	± 1,13
A Norm	286	26,31	± 0,16	22 — 30	1,91	± 1,38
A Man	18	26,54	± 0,52	25 — 28	1,09	± 1,04
E/F	45	26,64	± 0,23	25 — 28	0,60	± 0,77
A/D 7	26	26,77	± 0,37	26 — 28	0,83	± 0,91
A Pal	34	26,79	± 0,43	25 — 30	1,50	± 1,23
A Sir	75	26,80	± 0,26	24 — 30	1,23	± 1,11
F	67	27,25	± 0,25	25 — 30	1,07	± 1,04
D 41[1])	44	28,70	± 0,71	24 — 34	5,42	± 2,33
D 43	39	28,90	± 0,46	27 — 33	2,04	± 1,43
D 39	35	31,14	± 0,61	26 — 34	3,13	± 1,77
D 19	92	32,28	± 0,49	27 — 37	5,61	± 2,37

[1]) Angabe des Konfidenzintervalls des Mittelwerts trotz Abweichung von der Normalverteilung

Tabelle II: Stl/Tl (= a)

Gruppe[2]) (Größenkl.)		n	$\bar{x}$ ± l		Min — Max	s^2	s
A Norm	(1)	72	79,73	± 0,30	76,6 — 82,5	1,59	± 1,26
A Norm	(2)	113	79,68	± 0,34	74,0 — 85,0	3,37	± 1,83
A Norm	(3)	31	80,29	± 0,64	77,0 — 84,5	3,06	± 1,75
A Norm	(4)	10	79,25	± 1,22	76,6 — 82,5	2,90	± 1,70
A Norm	(5)	5	81,35	± 1,62	79,6 — 83,0	1,70	± 1,30
A Bal	(3)	34	81,05	± 0,26	79,6 — 82,5	0,56	± 0,75
A Man	(6)	18	81,11	± 0,52	79,6 — 83,0	1,09	± 1,04
A Pal	(2)	25	79,47	± 0,68	76,1 — 82,0	2,74	± 1,66
A Sir	(1)	38	79,97	± 0,36	77,1 — 82,5	1,17	± 1,08
E 38	(4)	12	81,97	± 0,74	79,1 — 84,0	1,36	± 1,16
E Mrw	(5)	9	83,77	± 1,67	81,6 — 88,5	4,69	± 2,17
E/F	(4)	23	83,07	± 0,45	81,1 — 85,0	1,08	± 1,04
F	(4)	34	82,84	± 0,47	79,6 — 88,0	1,79	± 1,34
A/D 7	(1)	12	79,63	± 0,79	77,6 — 82,0	1,54	± 1,24
D 19	(2)	80	80,81	± 0,24	78,0 — 82,5	1,16	± 1,08
D 39	(2)	33	80,85	± 0,34	79,0 — 83,0	0,91	± 0,95
D 41	(1)	38	79,50	± 0,47	74,6 — 82,0	2,05	± 1,43
D 43	(3)	17	81,02	± 0,45	79,1 — 83,0	0,76	± 0,88

[2]) Zur Aufteilung des Materials in Größenklassen s. S. 183.

Tabelle III: H/Stl (= b)

Gruppe[1] (Größenkl.)		n	$\bar{x} \pm 1$		Min — Max	s^2	s
A Norm	(1)	72	29,51	± 0,39	25,6 — 33,5	2,75	± 1,66
A Norm	(2)	113	30,13	± 0,28	25,6 — 34,5	2,53	± 1,59
A Norm	(3)	30	29,82	± 0,65	26,6 — 33,0	3,03	± 1,74
A Norm	(4)	10	30,75	± 1,87	28,1 — 37,5	6,84	± 2,62
A Norm	(5)	5	30,15	± 2,26	28,6 — 32,5	3,30	± 1,82
A Bal	(3)	34	32,43	± 0,54	28,6 — 35,5	2,41	± 1,55
A Man	(6)	18	30,16	± 0,84	28,1 — 33,5	2,84	± 1,69
A Pal	(2)	25	29,87	± 0,85	24,6 — 34,0	4,31	± 2,08
A Sir	(1)	40	29,53	± 0,49	26,6 — 34,0	2,33	± 1,53
E 38	(4)	12	30,72	± 0,85	28,1 — 33,0	1,79	± 1,34
E Mrw	(5)	9	33,55	± 1,49	30,6 — 37,0	3,75	± 1,94
E/F	(4)	24	28,72	± 2,03	26,1 — 33,0	2,32	± 1,52
F	(4)	36	28,55	± 0,72	24,1 — 35,0	4,57	± 2,14
A/D 7	(1)	12	27,97	± 0,63	26,1 — 29,5	0,99	± 1,00
D 19	(2)	80	24,44	± 0,25	21,1 — 27,5	1,24	± 1,11
D 39	(2)	33	26,19	± 0,55	22,1 — 29,0	2,36	± 1,54
D 41	(1)	39	25,04	± 0,89	20,6 — 31,5	7,57	± 2,75
D 43	(3)	18	25,27	± 0,68	22,6 — 29,0	1,86	± 1,36

Tabelle IV: Kl/Stl (= c)

Gruppe[1] (Größenkl.)		n	$\bar{x} \pm 1$		Min — Max	s^2	s
A Norm	(1)	72	26,77	± 0,26	24,6 — 29,5	1,19	± 1,09
A Norm	(2)	113	27,38	± 0,32	24,1 — 32,0	2,94	± 1,72
A Norm	(3)	31	27,20	± 0,64	23,6 — 30,5	3,10	± 1,76
A Norm	(4)	10	28,25	± 1,47	24,1 — 31,0	4,22	± 2,06
A Norm	(5)	5	27,95	± 1,42	26,1 — 30,0	1,30	± 1,14
A Bal	(3)	34	31,49	± 0,26	30,1 — 33,0	0,54	± 0,74
A Man	(6)	18	29,61	± 0,73	26,6 — 33,5	2,17	± 1,47
A Pal	(2)	25	27,51	± 0,45	25,1 — 29,5	1,21	± 1,10
A Sir	(1)	40	31,00	± 0,36	28,6 — 31,5	1,28	± 1,13
E 38	(4)	12	28,38	± 0,63	26,1 — 30,5	1,06	± 1,03
E Mrw	(5)	9	29,83	± 0,95	27,1 — 32,0	1,50	± 1,23
E/F	(4)	24	30,55	± 1,17	22,1 — 36,5	7,65	± 2,77
F	(4)	36	31,91	± 0,62	28,1 — 38,5	3,32	± 1,82
A/D 7	(1)	12	25,30	± 0,72	23,1 — 27,5	1,30	± 1,14
D 19	(2)	80	24,49	± 0,20	22,1 — 27,0	0,79	± 0,89
D 39	(2)	33	24,79	± 0,32	23,1 — 26,5	0,81	± 0,90
D 41	(1)	39	25,99	± 0,48	23,1 — 29,5	2,25	± 1,50
D 43	(3)	18	23,88	± 0,34	22,1 — 25,0	0,47	± 0,69

[1]) Zur Aufteilung des Materials in Größenklassen s. S. 183.

Tabelle V: A⌀/Stl (= d)

Gruppe[1] (Größenkl.)		n	$\bar{x} \pm 1$		Min — Max	s^2	s
A Norm	(1)	72	9,43	± 0,16	7,9 — 11,1	0,48	± 0,69
A Norm	(2)	111	9,21	± 0,13	7,7 — 11,1	0,48	± 0,69
A Norm	(3)	31	8,33	± 0,26	7,3 — 9,6	0,48	± 0,70
A Norm	(4)	10	8,10	± 0,45	7,1 — 9,1	0,40	± 0,63
A Norm	(5)	5	7,20	± 0,81	6,4 — 7,9	0,43	± 0,66
A Bal	(3)	34	8,98	± 0,15	8,2 — 9,8	0,18	± 0,43
A Man	(6)	18	6,66	± 0,32	5,8 — 8,1	0,41	± 0,64
A Pal	(2)	25	8,14	± 0,24	7,4 — 9,2	0,33	± 0,57
A Sir	(1)	38	10,04	± 0,21	8,8 — 11,5	0,42	± 0,65
E 38	(4)	12	7,22	± 0,23	6,8 — 7,8	0,13	± 0,36
E Mrw	(5)	9	7,02	± 0,28	6,5 — 7,5	0,13	± 0,36
E/F	(4)	24	7,82	± 0,23	7,0 — 8,7	0,29	± 0,54
F	(4)	36	8,01	± 0,18	7,1 — 8,9	0,29	± 0,54
A/D 7	(1)	12	8,34	± 0,21	7,8 — 8,9	0,11	± 0,33
D 19	(2)	80	8,10	± 0,10	7,3 — 9,2	0,21	± 0,46
D 39	(2)	33	8,44	± 0,16	7,7 — 9,2	0,19	± 0,44
D 41	(1)	39	9,20	± 0,22	8,1 — 10,4	0,45	± 0,67
D 43	(3)	18	7,24	± 0,21	6,5 — 8,2	0,17	± 0,42

[1]) Zur Aufteilung des Materials in Größenklassen s. S. 183.

Tabelle VI: Ltr

Gruppe	häufigster Wert	zweithäufigster Wert	dritthäufigster Wert
A Norm	4 / 3	4 / 2	5 / 3
A Bal	4 / 3	4 / 2	4 / 4
A Man	5 / 3	4 / 3	5 / 4
A Pal	4 / 3	4 / 4	5 / 3
A Sir	5 / 3	4 / 3	—
E 38	4 / 3	4 / 2	5 / 3
E Mrw	5 / 3	6 / 3	6 / 4
E/F	4 / 3	5 / 3	4 / 2
F	5 / 3	4 / 3	6 / 3
A/D 7	4 / 3	4 / 2	—
D 19	5 / 3	5 / 4	4 / 3
D 39	5 / 3	5 / 4	4 / 3
D 41	4 / 3	5 / 3	5 / 4
D 43	5 / 3	4 / 3	5 / 4

Literatur

HERRE, A. W. C. T., 1924: Distribution of the true fresh-water fishes in the Philippines. — Philipp. J. Sci. **24**, 249—306, Manila.

— , 1926: Two fishes from Lake Lanao. — Philipp. J. Sci. **29**, 499—502, Manila.

— , 1932: Five new Philippine fishes. — Copeia 1932, 139—142, New York.

— , 1933: The fishes of Lake Lanao: a problem in evolution. — Am. Nat. **67**, 154—162, Lancaster.

— , 1953: Check list of Philippine fishes. — U.S. Department of the Interior, Fish and Wildlife Service, Research Report 20.

HERRE, A. W., and G. S. MYERS, 1931: Fishes from southeastern China and Hainan. — Lingnan Sci. J. **10**, 233—254, Canton.

KOCH, H. J., 1965: Beiträge zur Biogeographie der Philippinen. — (unveröffentlichte Staatsexamensarbeit, Hamburg).

KOSSWIG, C. und W. VILLWOCK, 1964: Das Problem der intralakustrischen Speziation im Titicaca- und im Lanaosee. — Verh. dt. zool. Ges. in Kiel 1964, 95—102, Leipzig.

KREYSZIG, E., 1968: Statistische Methoden und ihre Anwendungen. — Göttingen (Vandenhoeck & Ruprecht).

MYERS, G. S., 1960: The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. — Evolution **14**, 323—333, Lancaster.

PRATT, W. E., 1916: Philippine lakes. — Philipp. J. Sci. Sec. A, **11**, 223—237, Manila.

SACHS, L., 1969: Statistische Auswertungsmethoden (2. Aufl.). — Berlin—Heidelberg—New York (Springer).

SMITH, W. D., 1910: Geologic reconnaissance of Mindanao and Sulu: II. Physiography. — Phillipp. J. Sci. Sec. A, **5**, 345—363, Manila.

STEINMANN, P., 1950/51: Monographie der schweizerischen Koregonen. — Schweiz. Z. Hydrol. **12**, 109—189, 340—491; **13**, 54—143, Basel.

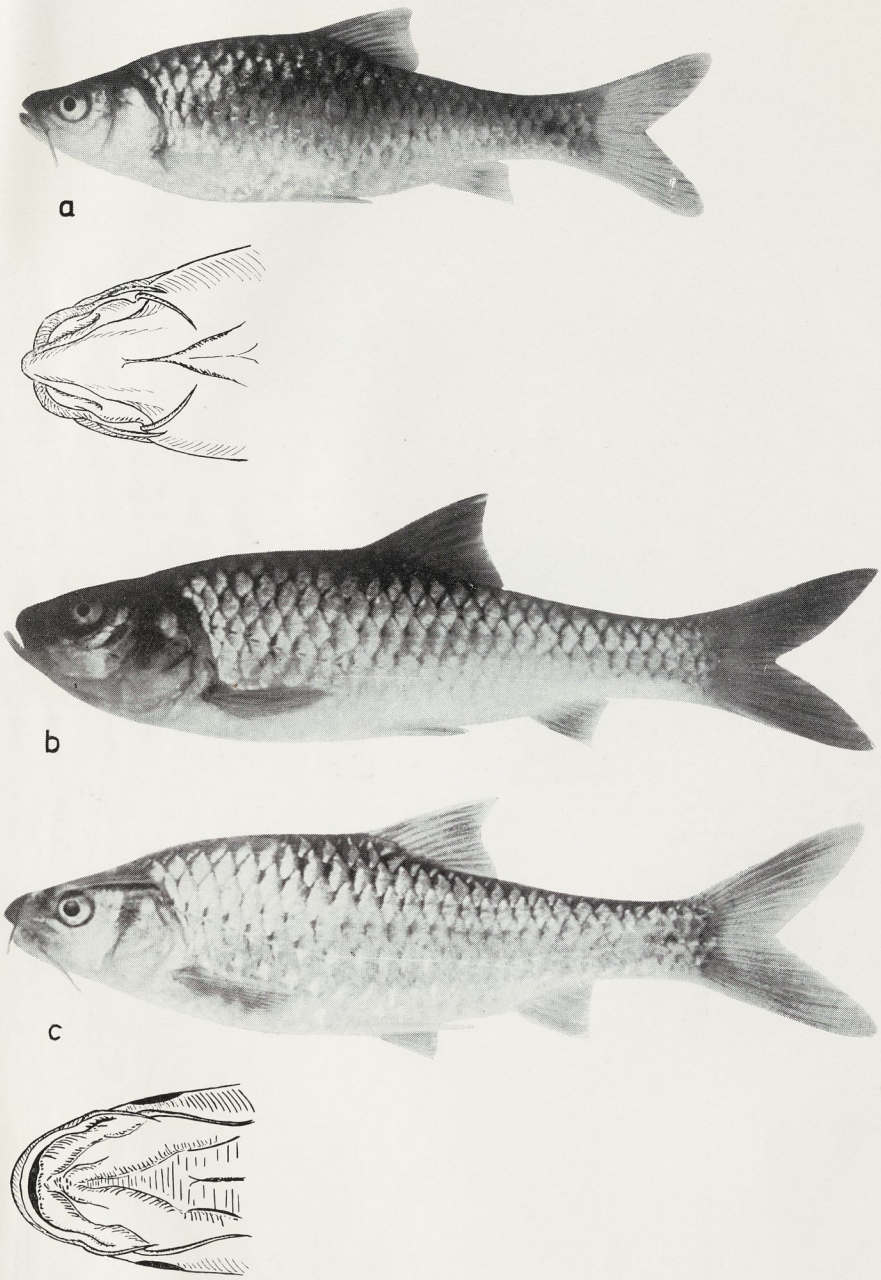
WEBER, M., and L. F. DE BEAUFORT, 1916: The fishes of the Indo-Australian Archipelago III. Ostariophysi II: Cyprinoidea, Apodes, Synbranchi. — Leiden (E. J. Brill Ltd.).

WOLTERECK, R., 1941: Die Seen und Inseln der „Wallacea"-Zwischenregion und ihre endemische Tierwelt. II. Teil: Inseln und Seen der Philippinen. — Int. Revue ges. Hydrobiol. Hydrogr. **41**, 37—176, Leipzig.

WOOD, C. E., and J. C. WOOD, 1963: A monograph of the fishes of Lake Lanao (unveröffentlichte Hektographie, Marawi).

ZARAPKIN, S. R., 1934: Zur Phänoanalyse von geographischen Rassen und Arten. — Arch. Naturgesch. N.F. **3**, 161—186, Berlin.

Wood, C.E. 1966. Two sp. Cyprinidae fm. N. Cent. Mindao - Phillipine J. Sci. 95(4): 411-



a) A Norm, b)*Mandibularca*, c) *Ospatulus* (fig. a: ca. 1:1 nat. Gr., fig. b u. c: ca. $^2/_3$ nat. Gr.; aus Kosswig und Villwock 1964).

Tafel VII

d) und e) D-Formen, f) E Mrw, g) E/F, h) F (fig. d bis h: ca. 1:1 nat. Gr.; aus Kosswig und Villwock 1964).

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THE DEFINITION OF SYSTEMATIC CATEGORIES IN BIOLOGY*

*Pierre Legendre***

Summary

Biological taxonomy, now combined with cytogenetics and mathematical philosophy, has become a new synthetic theory of evolution. The purpose of this paper is to derive a comprehensive, united series of formal descriptions of the results of evolution, which are the systematic categories as understood by biosystematics. In a first move, differences between individuals are found by comparing their chromosomal arrangements, and algebraic measures of feasibility of pairing are derived. Individuals are also compared with regard to their genes, and an algebraic measure of genic similarity between individuals is defined. A chain is also defined, which unites in clusters the groups of individuals which are equivalent with regard to a relation which is to be defined in each case. With these mathematical tools, a species is defined as a group of individuals which cluster when one applies on them a relation showing their possibility of crossing freely. A genus is defined as a group of species which cluster after a chain is formed on pairs of species between which there is a calculated possibility of occasional hybridization. A local population is defined as a group of organisms located within pairing distance of each other. A subspecies is defined as a major subdivision of the specific gene pool which corresponds to a geographical subdivision of the species' range. The usefulness of the semispecies as a category different from the subspecies is discussed according to biosystematic principles. It is also suggested that an environmental multi-dimensional space could be of major usefulness for determining the major adaptive peaks reached by supra-generic taxa.

Résumé

La taxonomie biologique, qui s'appuie maintenant sur la cytogénétique et la philosophie mathématique, est devenue une nouvelle théorie synthétique de l'évolution. Ce travail présente une série de descriptions formelles des résultats de l'évolution; ces résultats sont les catégories systématiques telles que comprises par la biosystématique. En premier lieu, les différences entre individus sont établies par comparaison de leurs chromosomes et leur capacité d'accouplement est décrite algébriquement. La comparaison des gènes des individus mène à une mesure algébrique de la similarité génique des individus. On définit aussi une chaîne qui groupe les individus qu'une relation (à déterminer dans chaque cas) définit comme équivalents. À l'aide de ces instruments mathématiques, les individus qui se groupent lorsqu'on leur applique une relation montrant leur capacité de croisement, sont définis comme formant une espèce. Les espèces qui se groupent à l'aide d'une chaîne montrant leur capacité de former occasionnellement des hybrides, sont définies comme formant un genre. La population locale est définie comme un groupe d'organismes situés à proximité suffisante les uns des autres pour qu'ils puissent s'accoupler. La sous-espèce est définie comme une subdivision génétique majeure de l'espèce qui correspond de plus à une subdivision géographique. L'utilité de la semi-espèce comme catégorie différente de la sous-espèce est évaluée selon les principes biosystématiques. L'on suggère aussi qu'un espace écologique multi-dimensionnel pourrait être très utile pour déterminer quels sont les sommets évolutifs atteints par les taxa de niveau supra-générique.

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* Part of a thesis (Legendre, 1971b).

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1. Logical background

Ten score years ago, any treatment of natural history would begin with the description of those parts of living nature that were most familiar and, therefore, supposed to be the most understood by humans — the beasts, the birds, the fishes, the flowers, and the trees, passing on perhaps to less well-known parts of life, the reptiles, the insects, the grasses, the fungi, and the algae; then it might go on to include the worms in the soil and even stones. The general guiding idea was that of degrees of perfection, the great ladder of life, beginning with man as nearest to the angels and going on to the less perfect realizations of the divine archetype.

With the triumph of the theory of evolution as presented by Darwin (1859), this approach was abandoned. From this point on, it was thought to be more appropriate to begin with the simple unicellular plants and protozoa and then to go on to the higher and more evolved species following the ever more branching evolutionary tree.

The question, how to proceed with the study of the evolution of life, has been dominated by experimental biologists, though it is no less the task of those recognizing the need of the theoretical approach. A combined experimental and theoretical approach is especially important in the field of classification, which has become considered by many as the poor relative of experimental biology. However, during recent decades biological taxonomy has been revitalized with its new role as an approach to evolutionary principles and results. Hence, its combination with cytogenetics and mathematical philosophy has helped to transform it into a kind of a new synthetic theory of evolution. As a first order, this synthesis uses and formalizes the concepts of classification which are the most important bases for the studies that may solve the problem concerning where to proceed with the explanations of the principles and processes of biological evolution.

We can consider this trend to have started with the later works of Darwin himself, or at least with the geneticists of the early decades of this century, even though they were more concerned with uncovering the principles of heredity and the processes of genetics than with speculations about their significance for the theory of evolution or the classification of living matter. A synthesis of such speculations and experiments was attempted by Turesson (1922), who proposed a new species concept which was essentially genetical but bore little relation to the ideas and experience of taxonomists. An equally abortive attempt was made by Danser (1929), who lost sight of the evolutionary synthesis in his jungle of unwieldy terms. The lack of a genetical background for the attempts at new definitions of the basic biological concepts by Du Rietz (1930) prevented their acceptance as a basis for the waiting synthesis, as did the same faults of numerous other such attempts, so that even when Hultén (1937, 1968) tried to replace cytogenetics with geographical observations, he was unable to apply the definitions without serious misgivings. The real experimental basis for a new theoretical synthesis that led to the discovery of reproductive isolation as the only basis for evolutionary classification was first furnished by Müntzing (1930) when he discovered, in *Galeopsis*, that differentiation within the species is based on gene mutation and genetic recombination, whereas that between species is caused by chromosomal rearrangements, linear or numerical. Unfortunately, his limited interest in theoretical taxonomy prevented him from seeing the significance of

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CONTRIBUTIONS TO THE LIFE HISTORY OF THE PIUTE SCULPIN IN SAGEHEN CREEK, CALIFORNIA[1]

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The Piute sculpin, *Cottus beldingi* Eigenmann and Eigenmann, is the dominant fish by number and weight in Sagehen Creek, a mountain stream on the east slope of the Sierra Nevada. Sculpins are at their greatest density in the middle part of the creek where they, along with brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*), find good foraging for bottom dwelling aquatic insect larvae. The numbers of sculpins are low in the precipitous headwaters of Sagehen Creek and also low in the lower reaches of the stream, which are frequented by their chief predator, the brown trout (*Salmo trutta*), and by other fishes. Sculpins in Sagehen Creek and Lake Tahoe exhibit minor differences in growth and reproduction but appear to occupy a similar ecological niche in the two areas.

INTRODUCTION

The Piute sculpin lives in lakes and streams of the Lahontan and Columbia River Basins of the western United States. Baker and Cordone (1969) and Ebert and Summerfelt (1969) described the biology of *C. beldingi* living in Lake Tahoe, an oligotrophic mountain lake. This report concerns the Piute sculpin in Sagehen Creek, a nearby mountain stream, and compares the biology of stream and lacustrine dwellers of this species.

Sagehen Creek is a spring-fed stream that is tributary to the Little Truckee River, itself tributary to the Truckee River draining Lake Tahoe. The creek rises in the Sierra Nevada at an altitude of 7,400 ft, flows through a watershed approximately 19.2 square miles in area, and after about 13 miles enters the Little Truckee River at 5,800 ft elevation. Climatic conditions are boreal. Between 1954 and 1961, minimum daily flows in Sagehen Creek in fall ranged from 1.0 to 2.6 cfs and momentary maximum daily flows in spring ranged from 27 to 212 cfs (Gard and Flittner MS).

ABUNDANCE

The Piute sculpin is the most common fish in Sagehen Creek and, by number and weight, is a significant part of the stream ecosystem. The population density (number of fish per acre) of sculpins in Sagehen Creek was estimated from the number of fish collected from 10 short sections of stream (Table 1). The sections, numbered from I (upstream) to X (downstream), totaled approximately 2,000 ft in length and were located at approximately 1-mile intervals along the course of the stream. The water flow was diverted from each section, the pools in the section drained with a pump, and the fish captured. Later the fish were returned to the stream, except for samples retained for study. Details of the collecting methods are given by Flittner (1953).

[1] Accepted for publication March 1972.

TABLE 1—**Population Density and Total Weights of the Piute Sculpin in Sagehen Creek in August and September of 1952 and 1953. (Data exclude age-group 0 sculpins which were not sampled representatively. The gradient and bottom type of each stream section and the dominant fish present in each section are from Flittner (1953) and Gard and Flittner (MS).)**

Stream section	Ft/100 ft	Bottom type	1952		1953		Dominant fish species by weight
			Number per acre	Pounds per acre	Number per acre	Pounds per acre	
I	6.8	Boulders	0	0	0	0	Brook trout
II	2.7	Rubble-gravel	67	1.0	33	1.0	Brook trout
III	3.6	Boulders	1,419	15.2	355	4.5	Brook trout
IV	1.6	Rubble-gravel	5,804	83.7	24,609	115.5	Sculpin
V	4.9	Boulder-rubble	2,859	38.6	4,847	32.4	Sculpin
VI	3.4	Gravel-rubble	6,098	59.5	8,463	85.4	Sculpin
VII	1.6	Rubble-gravel	9,443	92.1	22,970	76.8	Sculpin
VIII	0.8	Silt-gravel	3,738	44.5	8,976	48.8	Sculpin
IX	0.8	Mud-gravel-clay	376	5.0	782	6.2	Brown trout
X	1.0	Gravel-mud-clay	112	2.9	528	7.2	Suckers

TABLE 2—**Calcluated Age Composition of Piute Sculpins in Sagehen Creek in August and September of 1952 and 1953. (Data exclude age group 0 sculpins which were not sampled representatively. Dash indicates no age sample collected.)**

Stream section	1952						1953					
	I	II	III	IV	V	Total	I	II	III	IV	V	Total
I	--	--	--	--	--	0	--	--	--	--	--	0
II	33*	0	0	34	0	67	--	--	--	--	--	33
III	645	129	548	97	0	1,419	32	129	129	65	0	355
IV	106	2,427	2,110	1,055	106	5,804	21,777	0	531	1,770	531	24,609
V	--	--	--	--	--	2,859	4,094	0	282	471	0	4,847
VI	--	--	--	--	--	6,098	3,472	1,085	2,170	1,519	217	8,463
VII	--	--	--	--	--	9,443	21,534	0	574	862	0	22,970
VIII	516	2,449	644	129	0	3,738	7,944	0	516	516	0	8,976
IX	17	308	51	0	0	376	104	313	209	156	0	782
X	0	47	56	9	0	112	17	297	82	115	17	528

* Values indicate numbers per acre.

Sculpins were most abundant in middle Sagehen Creek, which included sections IV-VIII, where the stream gradient was intermediate, the bottom consisted of gravel-rubble and brook trout, rainbow trout, and brown trout were the only other fish present. (A few individuals of other species were present in section VIII as noted below.) Sculpins were absent or scarce in upper Sagehen Creek (sections I-III), which was the precipitous, boulder-strewn headwaters of the stream inhabited primarily by brook trout. Sculpins also were scarce in lower Sagehen Creek, which included sections IX and X, where the stream had a slight gradient, a bottom of gravel, mud and clay, and a fish population that included in addition to the 3 trouts, Tahoe suckers (*Catostomus tahoensis*), mountain suckers (*C. platyrhynchus*), Lahontan redsides (*Richardsonius egregius*), speckled dace (*Rhinichthys osculus*), and mountain whitefish (*Prosopium williamsoni*). The non-salmonid fishes in sections IX and X also occurred in reduced numbers in section VIII (Gard and Flittner, MS).

The apparent success of sculpins in middle Sagehen Creek may be due to a combination of favorable conditions; gravel riffle areas which provide cover for the sculpins and a substrate for their forage (bottom dwelling aquatic insect larvae) and the general absence or scarcity of predaceous brown trout. In Lake Tahoe sculpins ranged from the littoral zone to 700 ft in depth, but similarly were most common in the rubble-boulder areas of intermediate depth which offered protection from lake trout (*Salvelinus namaycush*), the sculpin's chief predator in the lake (Baker and Cordone 1969).

AGE COMPOSITION

Sculpins in Sagehen Creek reach 5 years of age, determined by counting annuli in otoliths. Calculated age distributions of the sculpin populations in sections I–X are shown in Table 2. In 1953, 1-year-old fish (the 1952 year class) made up 82% of the total number of sculpins sampled, but in 1952, 1-year-old fish made up only 11% of the total number of sculpins. Seegrist and Gard (in press) reported that the severe spring floods in 1952 decimated the eggs of spring-spawning rainbow trout. Our observations indicate that the high-water conditions present in the summer of 1952 may have benefited the survival of young-of-the-year sculpins. In sections IX and X, 1-year-old sculpins were less numerous than 2-year-olds in both 1952 and 1953; this suggests that reproduction in lower Sagehen Creek is relatively unsuccessful and that the sculpin population there is maintained partly by migration into the area.

REPRODUCTION

Piute sculpins spawn a small number of eggs which are relatively large in size. The fecundity of 70 fish from 65 to 86 mm TL ranged from 77 to 235 (average 132). The linear regression of fecundity on total length of fish was $Y = -151.59 + 3.81X$, $r = 0.69$, $P < 0.01$. Eggs taken from the ovaries of several unspawned females collected during the spawning season averaged 2.54 mm in diameter and water-hardened eggs collected from the two nests averaged 2.90 and 2.97 mm.

Measurements of the eggs were made after the fish had been preserved initially in 10% formalin and then transferred to 60% ethyl alcohol.

The spawning season of sculpins in Sagehen Creek in 1953 was short. At section VI the first spawned-out female was collected on June 2 and by June 8 all females collected in this section had spawned. Males also appeared to be in spawning condition for only a short time. Males from which milt could be extruded by applying pressure to the abdomen were collected in section VI only from June 1 to 8. The average daily maximum and minimum water temperatures at this location were 52.2 F and 38.3 F (May 25–31) and 57.0 F and 40.1 F (June 1–7). Water temperatures are lower upstream from section VI and higher downstream (Gard and Flittner MS), so that if spawning time is dependent on water temperature, spawning probably occurs at different times in different sections of the creek.

Sculpins in Lake Tahoe spawned primarily in May and June (Ebert and Summerfelt 1969). The report by Miller (1951) of ripe female sculpins in lake trout stomachs (which are inhabitants of the deeper, cooler water) as late as August 28 suggests that the spawning season in Lake Tahoe also varies in different parts of the lake in relation to temperature. The average fecundity of Lake Tahoe sculpins (123) (Ebert and Summerfelt 1969) was close to that of sculpins in Sagehen Creek.

The two sculpin nests observed in the spawning season of 1953 were located in riffle areas of the stream, under rocks 8 to 12 inches in diameter and in water 6 to 10 inches deep. Egg clusters were attached to the undersurface of the rocks. Each female sculpin apparently spawns only once per year and presumably deposits a single egg cluster, since the number of eggs in the two nests (122 and 160) was close to the average fecundity.

In the month previous to spawning, female sculpins contained two distinct size groups of ovarian eggs. The smaller, immature eggs were less than 0.60 mm in diameter and the mature eggs were 1.55 to 3.55 mm in diameter. (The preserved eggs were usually misshapen; and, as a result, their diameters had a greater than normal range.) After spawning, only immature eggs were present; enlargement of the ova preparatory to the next season's spawning was not noticeable until October.

GROWTH

Sculpins in Sagehen Creek grew primarily from May to October. Age group 0 sculpins sampled in section VI increased from 12.0 mm in August to 25.4 mm in October. Growth slowed after October; in January the average length was only 24.5 mm. Growth from January to May is probably also slow, since age group I fish collected in January 1954 (24.5 mm) were about the same size as age group I fish collected in May 1953 (24.8 mm). The length of age group I fish increased from 24.8 mm in May to 54.4 mm in October. By January the I age group had increased to only 58.0 mm. Older sculpins also increased most in length from May to October but little from October to May.

The increased growth rate of Sagehen Creek sculpins observed in spring and summer corresponds with the higher water temperatures in

these months; the mean daily maximum water temperature was higher than 50 F only in the months of May through October (Needham and Jones 1959). Ebert and Summerfelt (1969) concluded that the Piute sculpin in Lake Tahoe grows primarily in the spring and early summer and found a larger volume of food in their stomachs in spring and summer compared to fall and winter. Sculpins in Lake Tahoe were generally larger at a given age than those in Sagehen Creek, especially for younger age groups. No records of water temperature were available to interpret the seasonal growth patterns in Lake Tahoe as compared to Sagehen Creek.

The sculpins collected in August 1953 in the downstream sections of Sagehen Creek were larger than those in the upstream sections. This difference was probably because during most of the year water temperatures are higher in the downstream portion of the stream and as a result the growth rate is more rapid. Gard and Seegrist (in press) also found increased growth of brook, rainbow, and brown trout at lower elevations of Sagehen Creek.

Male sculpins grow faster than females. The difference in growth rate between the sexes was apparent in age group I individuals collected in August, when sexual differentiation of the gonads was first apparent from gross examination. The growth curve for males was $L = 44.4\ t^{0.5415}$, where L = total length (mm) and t = age (years). The growth curve for females was $L = 43.4\ t^{0.4793}$. Males apparently live longer than females; out of 12, 5-year-old fish collected, 11 were males.

The relationship between length (mm) and weight (g) of Sagehen Creek sculpins was $W = 8.8356 \times 10^{-6}L^{3.10617}$.

DISCUSSION

The Piute sculpin is the most abundant fish in Sagehen Creek and is the dominant species in the gravel-rubble parts of the stream where the gradient is intermediate. Brook trout and rainbow trout coexist with sculpins throughout the stream; brown trout, which inhabit primarily the lower sections of the creek, are their most important predator. Predation, food supply, and stream flow may be factors which limit population size. Growth and spawning time of sulpins in Sagehen Creek are related to the seasonal cycle of water temperature and are different in Sagehen Creek than in Lake Tahoe. Except for minor differences in biology, the Piute sculpin appears to occupy a similar ecological niche in the two areas.

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REFERENCES

Baker, Phillip M., and Almo J. Cordone. 1969. Distribution, size composition, and relative abundance of the Piute sculpin, *Cottus beldingii* Eigenmann and Eigenmann, in Lake Tahoe. Calif. Fish Game 55 (4): 285–297.

Ebert, Verlyn W., and Robert C. Summerfelt. 1969. Contributions to the life history of the Piute sculpin, *Cottus beldingii* Eigenmann and Eigenmann, in Lake Tahoe. Calif. Fish Game 55 (2) : 100–120.

Flittner, Glenn Arden. 1953. The composition and distribution of the fish populations in Sagehen Creek, Nevada-Sierra counties. MA Thesis (Zoology), University of California, Berkeley, 150 p.

Gard, R., and D. W. Seegrist. (In press). Abundance and harvest of trout in Sagehen Creek, California. Amer. Fish. Soc., Trans.

Gard, R., and Glenn A. Flittner. (MS). A ten-year study of distribution and abundance of fishes in Sagehen Creek, California. MS, Univ. of California, School of Forestry and Conservation.

Miller, Richard Gordon. 1951. The natural history of Lake Tahoe fishes. Ph. D. Thesis. Stanford University, 160 p.

Needham, Paul R., and Albert C. Jones. 1959. Flow, temperature, solar radiation, and ice in relation to activities of fishes in Sagehen Creek, California. Ecology 40 (3) : 465–474.

Seegrist, D. W., and R. Gard. (In press). Effects of floods on trout in Sagehen Creek, California. Amer. Fish. Soc. Trans.

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The Role of Fish in Research on Genetics and Evolution

C. Kosswig

For over 50 years fish have been used as experimental animals in the field of classical genetics. To quote only a few examples: the investigations of J. Schmidt on *Zoarces* (Schmidt, 1919) and *Lebistes* (Schmidt, 1919), Winge's now famous analysis of sex determination in the latter (Winge, 1930), and similar work on *Oryzias* by Aida (1930). In 1914, far ahead of his time, Gerschler (1914) published his sensational results of crosses between *Xiphophorus* and *Platypoecilus*. It is incomprehensible that studies on fish genetics are so seldom found in the summarizing literature despite the fact that the smaller fish species provide by far the best material, at least among the vertebrates, for studying inheritance. No other group of vertebrates is so easy to keep and breed in large numbers as the different orders of small fish. Moreover, bony fish of a number of species can be successfully crossed to produce fertile offspring, and in this respect fish are even superior to the otherwise ideal *Drosophila*. The goldfish, in the course of more than 1 000 years of domestication, has produced a hitherto unexploited wealth of mutants. Genetic laboratories in the USA, Europe and Russia have, over the past decades, bred many hundreds of thousands, and probably even millions, of controlled progeny, numbers which have never been attained in other vertebrates (excluding the mammals bred for medical research purposes, such as mice, guinea pigs and rats) and only rarely among insects.

The following survey of results of genetic and ichthyologic research is by no means exhaustive: its primary aim is to emphasize results obtained exclusively or mainly on fish. The literature cited is limited to review articles with the help of which further publications can readily be found.

Geologically, teleosts are a very old group. In the Eocene and Oligocene highly specialized genera of bony fish already occurred, from both salt- and freshwater, that are still in existence today. Nevertheless, they are still in a state of active evolution and are generally held to be the most species-rich class of vertebrates. The figure of 20 000, often cited in the literature for the number of morphospecies, is far too low. Each year new genera and often even families are discovered in regions difficult of access. Furthermore, if it is taken into consideration that, in many cases, the term morphospecies covers several biospecies (Scheel, 1968) whose members, on account of extensive phenotypic similarities, can only experimentally be shown to be sexually isolated, it becomes obvious how promising is the study of the genetics of bony fish.

In the past two decades, which have brought close contact between classical genetics and evolutionary research, population genetics has occupied the centre of interest. Panmictic populations are more or less heterozygous, two or more alleles of numerous genes occurring in their gene pools. Thanks to the possibilities offered by recombination, it is possible to produce individuals that vary in their fitness with respect to different external conditions. Territorial expansion and subsequent isolation in hitherto unoccupied ecological niches is, according to the concepts of population genetics, achieved by isolated individuals of a certain genotype. Emigrants that successfully founded

new populations possess, in all probability, only a fraction of the alleles of the mother population, and those in a modified proportion. So far, this has not been demonstrated unequivocally in fish, and obviously a different principle is involved here, which has probably been overlooked most readily in other groups of organisms. It seems that the conquest of new areas and of new ecological niches is achieved not by specially predestined genotype carriers, but can be carried out by any individual of a population or species thanks to a very wide reaction norm or range of adaptability which is part of the general genetic make-up of the species (Kosswig, 1972). A wide reaction norm guarantees the plasticity necessary to enable fish to adapt to permanent or temporary changes in environmental conditions. Since 1900, as a result of the opening of the Suez Canal in 1869, an ever-increasing number of fish and other animals have migrated from the Red Sea to the Mediterranean, have dispersed and reproduced there. Some of these erythraean immigrants have already reached the Aegean Sea and represent a considerable part of the fish caught there: in some cases the intruders even appear to be crowding out the original Mediterranean fauna. A very wide range of ecological situations is presented by the 100 km length of the Suez Canal. Temperature and salinity are not the same as in the Red Sea, the salt content in particular changing considerably: in the south it is higher than in the Red Sea, in the north lower, but in the Mediterranean it is again higher than in the northern part of the canal. If, in the course of its life span, an erythraean fish swims the length of the canal, this indicates that it has inherited a range of adaptability large enough for it to achieve the necessary physiological adjustments. According to population genetics migration along the canal in the course of more than one generation would have to be accompanied by selection for survival first in water of raised salinity, then in lowered salinity. This assumption seems to be less plausible than that of a simple wide reaction norm for all individuals of the immigrating species. This renders possible not only tolerance of a wide range of environmental conditions, but also the development of long-term modifications of a physiological and/or morphological nature. Many examples of extremely different phenotypes are known, especially among the salmonids (e.g. nationes fario, lucustris and marina of *Salmo trutta*), which have been shown to be merely modifications based on the wide reaction norm of the genotype.

Preadaptations, anchored in the genotype, even permit the conquest of extreme biotopes such as caves. From *Astyanax mexicanus*, a large-eyed fish that lives in swarms and exhibits a slightly negative phototaxis, originate typical cavernicolous populations of varying genotype, that have quite incorrectly been given a special genus name and whose various populations, again incorrectly, have been accorded the status of species. In the meantime it has transpired that although the epigeous *Astyanax* can swim actively into cave waters, passive transport is of primary importance in the genesis of its cavernicolous relatives. In karst regions of the Sierra de El Abra river beds may abruptly sink down into old underground river systems. Apparently every surface form of *Astyanax* is preadapted to find its way (Schemmel, 1967) and to reproduce (Wilkens, 1968) in perpetual darkness. Although optical orientation appears to be of decisive importance for a fish living in surface water, an experimentally blinded fish or one transferred to and kept in permanent darkness can thrive and reproduce even under the new conditions. All that is lost, is the optically governed swarming behaviour: the blinded fish behaves in this respect like its blind cave derivative and wanders about ceaselessly in the aquarium. In this case the morphological basis of the preadaptation to perpetual darkness is known to be a system of neuromasts, sense organs of current perception, distributed over the entire body. This system is so well developed in epigeous fish that no further increase is necessary in the blind, poorly pigmented sub-

terranean populations. Preadaptation has been demonstrated experimentally in a younger cave-dwelling form of *Poecilia sphenops* (Zeiske, 1968).

Nothing whatever is known about the genetic basis of this wide reaction norm or of preadaptability. Their large degree of stability, on the one hand, and their occurrence in all individuals of a species lead to the assumption that a highly polygenic system is involved in which numerous genes and + and - modifiers collaborate, and in which, besides additive and non-additive polymery, hierarchies of genes are involved, the entire system being held together by pleiotropy of its elements. The genotype of a higher organism, which a bony fish certainly is, is thus revealed to be more than the sum of its constituent genes. It is tempting to put forward the hypothesis that it is just that part of the genotype of every individual that cannot be analysed in a crossing experiment on account of its polygeny, which contains the characteristics determining those of the taxon, i.e. of the "type", in the morphological sense.

It was mentioned above that in teleosts, in contrast to almost all other groups in the animal kingdom, species crosses can be carried out. This means that genomes that have undergone divergent evolution over thousands of years can be combined with one another in the hybrid. If such hybrids prove to be fertile, inferences can be drawn as to the number of genes that have been modified since the separation of the two species from a common ancestor. The information which, thanks to the fertility of the F_1 offspring, is provided by crosses between two different species, is discussed in more detail below. Even complete or partial sterility of the resultant hybrids can, under certain circumstances, reveal some information as to the genetical basis of the species-separating mechanism. Various degrees of sterility of species hybrids can be distinguished:

1. The gonads of the F_1 hybrids contain scarcely any or no gonogonia. Whether the latter are not formed in hybrids or whether they simply do not enter the gonads at the right time is unknown. This type of sterility can only be attributed to the incompatibility of foreign genomes in general (Öztan).

2. In some crosses, such as, for example, the backcross of an F_1 hybrid of *Xiphophorus helleri* x *X. maculatus* with *X. helleri* the individuals that possess the gonosome of their *maculatus* grandparent remain sterile for years, irrespective of whether they are ♂♂ or ♀♀. Treatment of the otherwise sterile ♀♀ with gonadotropic hormone and of the ♂♂ with androsterone can render them fertile (Öztan, 1963). Thus it appears that certain combinations of genes can elicit hormonal imbalance, in this case not until F_2R, and that this can be overcome by appropriate treatment.

3. In some crosses, the gonads and sometimes even the phenotype (Villwock, 1958) of the ♀♀ can be shown to be intersexual. Animals of this type are able to produce fertilizable eggs whilst young. Later, spermatogenic tissue develops in the ovaries and disturbances in spermatogenesis typical for certain kinds of ♂♂ sterility then occur.

4. Sterility of ♂♂ following normal synapsis is due to irregular distribution of chromosomes on the two secondary spermatocytes and subsequent premature termination of spermatogenesis (Karbe, 1961). In many such cases of ♂♂ sterility the F_1 hybrid ♀♀ are normally fertile and can be backcrossed with the ♂♂ of the two original species. With an increasing number of such backcrosses the number of fertile ♂♂ progeny rises, from which it can be concluded that the normal course of spermatogenesis in both parent species is under different polygenic control.

5. In this type of cross ♂♂ occur in which spermatogenesis is normal but which are nevertheless sterile. It has been shown that, in such cases, hybridization results in a genetically conditioned lack of mobility of the spermatozoa (Karbe, 1961).

6. Within the *Xiphophorini* sympatric or allopatric species can be crossed with one another if no ♂♂ of the same species are present. It has been demonstrated in competitive experiments, and this is important in sympatric species, that the spermatozoa of foreign species are much inferior to those of the same species. Given simultaneous insemination with both types of spermatozoa the former have a smaller chance of achieving fertilization and a weaker chance of surviving in the oviduct of the ♀ of another species as compared to the spermatozoa of the same species (Zander, 1962). Since the 'foreign' spermatozoa in allopatric populations of the same species already exhibit inhibitory phenomena of a comparable nature, it can be assumed that an existing system of incompatible genes has been reinforced by new genes in the course of phylogenetic divergence.

The analysis of sex determination in viviparous cyprinodontids has brought new aspects to light and has shown that (Kosswig, 1964a) a far greater diversity of genetic principles is involved than had been assumed by M. Hartmann (1956). In many species sex determination is of the so-called monogenic type, for which Correns' classical interpretation holds true on principle. It was surprising to learn that among close relatives, in fact within one population of the same species, male and female heterogamety occur side by side. In *X. maculatus* XY and YY ♂♂, and XX, XW and YW ♀♀ are to be found (Kallman, 1965). Winge's (1930) results that in *Lebistes reticulatus* the decisive male-determining factor is in the Y holds for many other species. A potent female-determining factor (gene or complex of genes) is located in the W of the *maculatus* ♀♀. This principle of localization of the decisive gene for the heterogametic sex in the Y or W chromosome seems to be the rule in vertebrates. Winge (1934) knew already, however, that genes influencing sex differentiation occur not only on the gonosomes but on the autosomes as well. An increase in number of such genes is responsible, for example, for the occurrence of ♂♂ of XX constitution in *Lebistes*. A similar situation was later brought to light in *X. maculatus* (Öktay) and was termed polygenic sex determination. Years ago, sex determination was shown in *X. helleri* to be exclusively polygenic and was described in detail (Kosswig, 1964b). The same principle of polygenic sex determination has been revealed in a large number of invertebrates.

For reasons unknown, a differentiation of the opposite sex to that of the animal's gonosomic constitution occasionally occurs, and further the normal monogenic sex-determining mechanism can be put out of action by species crosses (Kosswig, 1936; Rust, 1941). With the aid of such exceptions even WW-♀♀, for example, can be produced by appropriate crossing. In the same way it is possible to obtain YY homogametic ♂♂ by crossing exceptional XY ♀♀ with normal XY ♂♂. For a long time it had seemed that in an animal group that, despite clear-cut differentiation into ♂♂ and ♀♀, is approaching hermaphroditism, morphologically differentiated gonosomes could not be expected. However, increasing numbers of reports are available of well differentiated gonosomes in various not particularly closely related Cyprinodonts. It is interesting that such cases appear in just those groups that are notable for a large degree of constancy in their typical chromosome number (n=24) (Miller and Walters, 1972).

Treatment with sex hormones during a critical period of early developing stages results in a complete inversion of the sex. Treatment of *Lebistes* (Zander and Dzwillo, 1969) and of *Oryzias* (Yamamoto, 1967)

with androsterone transforms ♀♀ (XX) into functional ♂♂ and vice versa ♂♂ (XY) can become functional ♀♀ under the influence of female sex hormone. In suitable crosses (e.g. transformed XY-♀ crossed with normal XY-♂) homogametic YY-♂♂ can be obtained which become functional ♀♀ by treatment with female hormone, etc.

These experiments have shown that the genetic constitution XY or XX of the gonogonia does not, as such, determine sex, but rather that the primary gonogonia in the young gonads are exposed to the influence of sex-determining substances, normally produced by the soma of the gonads. Experimentally, the effect of these substances is masked by that of the sex hormones added. This interpretation agrees with that proposed by Witschi (1929) for amphibia. Occasional, spontaneous cases of faulty sex differentiation, i.e. one contrary to the gonosome constitution, are interesting in regard to the phylogeny of various modes of sex determination among closely related animals (Kosswig, 1936).

Finally, it should also be mentioned that, among the teleosts, hermaphroiditism occurs in many species from various families: it can be either protandrous, protogynous or synchronous. The latter leads to cases of self fertilization, an example of which is provided by the small toothed carp *Rivulus marmoratus*.

A unique sensation at the time was afforded by Hubbs' finding that *Mollienesia* (now *Poecilia*) *formosa* is a constant gynogenetic hybrid between *P. sphenops* and *P. latipinna*. In order to produce fertile offspring the *P. formosa* ♀♀ has to be fertilized by a ♂of one of the two original species. Gynogenetic development with the diploid maternal chromosome complement normally takes place following fertilization of the egg by a *sphenops* or a *latipinna* sperm: sperms of other species have the same effect. Normally, however, the genome of the sperm is not involved in the development of the gynogenetic progeny, which all possess the same genotype as the individuals of an asexually reproducing clone (Kallman, 1962). Under what particular conditions the gynogenetic *formosa* arose in nature is unknown. Crossing both parent species in the aquarium produces in F_1 *formosa*-like offspring of both sexes which, after further crossing, result in progeny of mixed polygenic recombination. In recent years similar cases of gynogenetic reproduction have been reported in several species of the genus *Poeciliopsis*, coupled, however, with triploidy (Schultz, 1969). It is noteworthy that in this genus the tendency is apparently widespread for species crosses to result in triploid, gynogenetic ♀♀, the eggs of which require fertilization although the genome of the sperm plays no part in development.

In passing, it should be mentioned that the presence of heterogametic males and females within one and the same species, as described in *X. maculatus*, has been proved to be of practical importance as well as of theoretical interest. The genus *Tilapia* is nowadays bred in fish ponds in all tropical and subtropical countries. In populations consisting of both sexes the growth of the ♂♂ slows down rapidly as soon as they begin to mate and breed in the presence of ♀♀. If, however, in the breeding pond a homogametic ♀ (XX) is paired with a homogametic ♂ (YY) the entire progeny is ♂♂ (XY), which in the absence of female sexual partners exhibit normal growth.

Many populations of the most varied species of small fish exhibit a more or less pronounced polymorphism for certain characteristics connected with form and particularly for characteristics of colour (Kosswig, 1964). In some cases the polymorphism, being humorally controlled, is restricted to one sex, as in *Lebistes*, whereas in other cases both sexes are to a greater or lesser extent obviously polymorph. Upon detailed investigation the polymorphism is seen to be due to genes or supergenes that may occur in several alleles or pseudoalleles, as

is the case with the colour genes in the Y of *Lebistes* or with those carried in the X or Y of *X. maculatus* and other species of *Xiphophorus*. Since the frequency with which some of these colour genes occur in natural populations does not change over a long period of time (Gordon, 1947) the possibility has been discussed of this being perhaps a case of balanced polymorphism as understood in population genetics.

Two or more quite distinct phenotypes, or the genes responsible for them, often occur in natural populations: examples are provided by albinism, xanthorism and other colour variants. In *Gasterosteus aculeatus* the extent of the scutaceous body covering is monogenically controlled (Münzing, 1963). The phenotype that is completely covered with scutes, trachurus, is homozygous TT for one pair of genes, the largely naked form, leiurus, is tt, and the heterozygous form with an intermediate degree of covering Tt is termed semiarmatus. In anadromic populations between the English Channel and the North Sea the frequency of tt and Tt individuals decreases from W to E, and from W to NE. Whether such a gradient is of adaptive value or merely the result of postglacial contact of a north european scutate 'subspecies' and a mediterranean naked 'subspecies' is unknown. Experimental crosses have revealed that the heterozygous semiarmatus does not always have the same type of body covering, which suggests the involvement of modifier genes. It is quite certain that the european *Gasterosteus* is a single species, whereas the situation on the Pacific coast of North America is probably different (Hagen and McPhail, 1970; Miller and Hubbs, 1969) and more complicated.

Polygenic differences are sometimes encountered in crosses of populations from separate river systems, and even occur regularly when species that have been crossed with one another produce a fertile F_1 so that F_2- and backcross generations can be obtained. In such hybrids genomes that have developed along different lines over longer or shorter periods of isolation from one another are united and later recombined. Some insight is thus provided into the extent of diversification of the genotypes since their separation from a common ancestor. Segregation in the F_2 and backcross generations only rarely permits of an approximate estimate of the number of allele pairs involved, and as a rule the verdict of 'higher polygeny' has to suffice. The inheritance of meristic characters and of body proportions was the subject of a classical investigation almost forty years ago (Breider, 1936) involving F_2 and F_2R analyses of hybrids between species of the genus *Limia* (now *Poecilia*): *nigrofasciata*, *vittata* and *caudofasciata*. Quite independently, in New York and in Istanbul, the mode of inheritance of differences in the structure of the gonopodia of *X. helleri* and *X. maculatus* was investigated. Fine differences in the individual anal fin rays that form a part of the gonopodium are probably polygenic (Sengün, 1950; Gordon and Rosen, 1951) and show free recombination. It has been demonstrated that one species of the genus *Macropodus*, *concolor*, possesses latent genes for a vertically striped pattern that is regularly seen in another species, *opercularis*.

In polymorphic populations of the killifish *Aphanius anatoliae* varying degrees of degeneration of the scaly covering can be observed. This is not the result of a gradual loss of scales but is due rather to a pronounced multiplication of the scale primordia in two main gradients, the one dorsad to the lateral line, and the other ventrad. Repeated division of the morphogenetic field of the individual scales results in delayed and imperfect formation of miniature scales or, in the end, in their total absence. Just how complicated is the genetic background of the reduction process can be demonstrated by crossing two individuals from certain populations with reduced scales which can result in progeny with more or less normal scales, whilst the mating of two individuals with normal scales can lead to offspring with reduced scales. The number of

genes involved and their mode of action is unknown (Aksiray, 1952; Villwock, 1958; Franz and Villwock, 1972). More is known about the genetic background of the phyletic reduction process leading to the differences between the surface form of *Astyanax mexicanus* and its cavernicolous relatives. (For systematicists this would be a genus cross *Astyanax* x *"Anoptichthys"*). The distribution in F_2 shows (Peters and Peters, 1966; Wilkens, 1968) that at least four and perhaps even seven genes or supergenes are responsible for eye reduction. The reduction of the number of melanophores depends in one population (Pachon) upon two alleles and in the other (Sabinos) upon one allele to those of the river fish (Wilkens, 1970a). In another allele pair one allele governs the presence of many melanin granula in the individual melanophores of surface fish, whilst the other is responsible for there being fewer in cavernicolous fish. It is probable that mutations at two loci led to the loss of the ability of cavernicolous fish to react to alarm substances. The number of genes responsible for the loss of morphological colour change in cave-dwelling fish is still unknown. Some populations of the latter possess a gene for albinism, which is usually regarded as a characteristic of domestication (Wilkens, 1970b). Partially, at least, the regression process of the eye of cavernicolous fish takes place by means of different, non allelic genes: a cross between populations of Sabinos and Pachon produced hybrids whose eyes, although blind, were better developed than those of their parents (Wilkens, 1970). Apart from this the genes for eyes and those for loss of pigment are to a large extent able to combine freely. Thus in the F_2 both well pigmented, blind individuals as well as poorly pigmented specimens with eyes are encountered among others. It can be assumed that following the transition of preadapted epigeous fish to caves, all of those genes that had no biological significance in the new environment could mutate. In other words, the typical formation of a normal eye capable of sight in surface fish is subject to the control of preservatory or stabilizing selection processes (Wilkens, 1968). Removal of the pressure of selection gives mutation pressure a free hand, with the result that all structures, and only those, that have become biologically meaningless can be lost. This holds true also for the aggressivity of ♂♂, which becomes superfluous in permanent darkness (Parzefall, 1969). Hearing (Popper, 1970) and sense of smell remain as well developed in the cavernicolous form as in its surface-dwelling relative. There is no evidence for the assumption that loss of the eye and of body pigment is of any selective value. Thus the phylogenetic age of cave populations can be regarded exclusively as the result of mutation pressure. If *Astyanax* was not able to migrate into Mexico until the transition from pliocene to pleistocene (following establishment of a land bridge between South and Central America) it follows that the differentiation of the genotypes of the cavernicolous fish required less than one million years, and perhaps even much less than this (Parzefall and Wilkens, 1972). A secondary sex characteristic of the males of certain species and subspecies of *Xiphophorini* is a black-edged sword, of up to body length, with an iridescent centre. The possession of such a sword can be regarded as a derived character. Those species of *Xiphophorus* possessing no such adornment can be termed primitive. Between the two extremes are species with the mere beginnings of a colourless sword, whilst in *X. pygmaeus nigrensis* the sword length is variable. There are ♂♂, for example, with a slight suggestion of a sword whereas in others it has attained at least half the length of the body and has a black ventral border. That the sword length is a polygenic character has been demonstrated in numerous crosses between eight different species of *Xiphophorini* (Zander and Dzwillo). Similarly, there are special genes responsible for the coloration of different portions of the sword. In the F_1 of swordless species with *X. helleri* the swords vary in length: the F_1 ♂♂ from *X. couchianus* and *X. helleri* have very short swords

whereas those of the hybrids from *X. maculatus* and *X. helleri* are of intermediate length. A clue as to the reason for this is provided by treating *couchianus* and *maculatus* with androsterone, which in the latter leads to a pronounced increase in the length of those caudal fin rays forming the sword in *helleri* (Zander and Dzwillo, 1969), whereas no such effect is seen in *couchianus*. From these results it can be concluded that the increased hormone level activates normally latent genes for sword formation in *maculatus*. The apparently orthogenetic development from a small protuberance up to the formation of a colourful structure body length has its origin in the possession of latent genes. It is noteworthy that in the F_2 of a cross between two species possessing well developed swords such as *X. helleri* and *X. montezumae cortezi*, ♂♂ occur with a sword shorter than that of the *cortezi*, and in some completely fertile F_2 ♂♂ the sword may be entirely absent. In two closely related species, *helleri* and *m. cortezi*, sword formation is therefore, at least in part, ensured by the presence of different, non-allelic genes (see above, eye genes in two cavernicolous strains of *Astyanax*). The entire problem of parallel evolution and its genetic basis thus gains fresh interest. If, in *Xiphophorini*, the sword is a new acquisition, that is to say, it reflects a constructive evolutionary process, the question immediately arises as to the biological significance of this secondary sexual character. There is no evidence that it has arisen by a process of sexual selection (Kosswig, 1963) and its possession cannot be said to be of any significance either in mating or securing a position within the hierarchy of a group of ♂♂. A premature anthropomorphic interpretation would only serve to obscure the facts. A well developed structure is only of secondary, if any, biological significance. Apart from *X. maculatus* the display of all other *Xiphophorini* is characteristic for the species (Frank, 1964). Gerschler (1914) already pointed out that in the F_2 from *helleri* x *maculatus* ♂♂ occur whose display, despite the absence of a sword, is typical for *helleri*. The genes for sword formation and for display, whereby the role of the sword is only an apparent one, are independently inherited. Certain individual features of display, too, in which, for example, *helleri* and *montezumae cortezi* differ from one another (Frank, 1970) can be recombined in the F_2 generation just like the parts of a morphological structure.

The surface form of *Astyanax* has taste buds only in the mouth zone of the upper and lower jaws. A blinded surface fish, dependent in its search for food upon its sense of taste, stands perpendicularly above the food under investigation. In blind cave-dwelling fish, however, the taste-bud area has, as a result of selection, spread far over the ventral side of the fish so that in its search for and inspection of food it stands at an angle of 45° and not 90°. In the F_2 generations of crosses between hypo- and epigeous fish, individuals occur, in which the genes for increase in number of taste buds have been separated from those responsible for their 'proper' use. This is apparently a polygenic effect involving recombination. As a result, some individuals, although possessing plentiful taste buds on the anterior ventral half of the body 'stand on their head' like a blinded surface fish, whilst others, despite a reduced number of taste buds, search for food in exactly the same manner as typical cave fish (Schemmel, 1967). Another example of constructive evolution in cave fish is provided by the ♀♀ of a cavernicolous population of *Poecilia sphenops*: with the help of a 'genital cushion' larger than that of the surface-dwelling form a ♂-attracting substance is probably produced in increased quantities (Parzefall, 1970).

Perhaps the most exciting chapter in ichthyological genetics is that of changes in the manifestation of colour genes of one species of *Xiphophorini* when combined with the hereditary material of another. So far, as in the genetic analysis of regressive and constructive evolution, com-

parable investigations in other groups of organisms are lacking. At least two loci for macromelanophore distribution and at least two more for the formation of pterinophores in various regions of the body are situated in close proximity in the gonosomes (X, Y, in W only in domesticated strains of *X. maculatus*)(Kallman, 1970). Whether a 'gene' is present in several allelic forms on each locus or whether it is a supergene with several pseudoalleles cannot be proved with certainty at the moment. For the sake of simplicity, the term 'gene' should be used without any implication as to its structure. It was very soon recognized that each one of these colour genes has its own polygenic system of modifiers (Kosswig, 1929) by means of which the characteristic manifestation of just this colour gene is guaranteed within the species (or even population). In the other species (Anders et al., 1972) and, in some cases, in other populations (Gordon and Gordon, 1957) allelic or non-allelic genes have to be postulated: they influence the degree to which a foreign colour gene is manifested, sometime inhibiting, but usually enhancing its effect. In 6 of the species of a total of 9 *Xiphophorini* investigated so far (*X. clementiae* has not yet been included) gonosomally localized colour genes of this type occur. Even the species that possess neither genes for macromelanophores nor for pterinophores possess specific modifier systems for the different colour genes of the other species (Zander, 1969). In decades of experimental work about 20 of these colour genes, many of them in several allele forms, have been carried over into other species. This could only be achieved due to the availability of these ideal experimental objects. Somebody who is not acquainted with the many details of the results obtained and who is not interested in studying the literature had better neglect the facts and pass over them silently. Investigations into the manifestation of colour genes of one species in a genotypic milieu of another are of particular interest because in certain invariably reproduceable crosses melanomas and occasionally erythromas are formed. The melanomas occurring subsequent to species crossing of *Xiphophorini* do not differ essentially in structure from human melanomas. They are definitely not the result of a virus infection, but rather of the combination of various completely healthy genomes. They can be produced at will and reversed by appropriate crossing. Such investigations have been going on for many years in Giessen under the direction of Anders. Apart from elucidation of their genetics, histological and cytological investigations have revealed the polyploidy (Vielkind et al., 1971) of the macromelanophores and, using the electron microscope, the fine structure of melanomas has been demonstrated (Vielkind et al., 1971). Of special interest are the investigations on amelanotic tumours, made possible by combining the genetic constitution producing the melanoma with that of the albino gene of *X. helleri*. This represents a great advantage as compared with similar investigations on *Homo sapiens*. We owe to Anders (1972) also the pursuance of a useful hypothesis concerning the cooperation of the colour gene with regulator genes of the same species and booster genes of other species. In the past few years this field of research has been extended by two further sets of facts. By means of a mutation on one of the macromelanophore loci the normal manifestation of a particular colour gene can, within the species, be so much enhanced that, in spite of the presence of modifier systems typical of the species, melanosis and even melanoma formation can occur (Anders et al., 1971). The mutation may be either a simple gene mutation or it may be the result of translocation of a macromelanophore gene of the same or another species. In both of the latter cases it still remains to be established whether this is a positional effect in the classical sense of the term or whether, in the course of translocation, the colour gene has been separated from a regulating gene normally adjacent to it. In some ♂♂ of *X. pygmaeus nigrensis* a gene occurs in the Y chromosome that is responsible for yellow coloration (Zander, 1968).

Yellow coloration results from the so-called G-(colourless, granula-bearing) xanthophores: the carotenoid pigment lies in the middle of the cell. Crossing with *X. maculatus* brings about the transformation of these G-xanthophores (Öktay, 1964) into typical erythroxanthophores, the granules of which become occupied by a red drosopterin instead of a colourless pterin. *X. maculatus*, which possesses limiting modifiers for the distribution of its special erythroxanthophore pattern, has, on the other hand, a modifier system that permits the transformation of yellow G-xanthophores (Öktay, 1964) over the entire body into drosopterin-containing erythroxanthophores. Gordon (1950) has described a case where an erythroma occurring in one and the same hybrid together with a melanoma was able to supplant the latter. Even if this is only a case of the devil chasing Beelzebub, the fact is of interest in that it reveals a close connection between melanin and pterin pigments based upon closely coupled genes in the gonosome of *X. maculatus*. So far a detailed analysis of the modifier genes, some of which have an enhancing some an inhibitory effect on the colour genes, has been impossible. Their large numbers and complicated interrelationships will probably also prevent their elucidation in the future. Hundreds of modifier genes for the colour genes are probably contained in each genome of each species. As regards genetic interpretation we are in the same position as Dobzhansky, who was forced to capitulate faced with an analysis of the 'modifier systems' responsible for the heterotic effect of certain inversion heterozygotes within a population of *Drosophila pseudobscura* (Dobzhansky, 1951). We are still far removed from a molecular interpretation of relatively simple gene effects.

A complete contrast to the recognition of the highly polygenic origin of even simple morphological characters such as the colour patterns of the *Xiphophorini* is offered by the results of molecular biological and biochemical investigations, which have come to play an ever-growing role in genetics over recent years. Whereas the systematicist, the morphologist and the classical geneticist aim, albeit with different methods, at elucidating the basis of organic diversity, the biochemist concentrates upon the unifying characteristics in nature. Functionally identical proteins, especially enzymes, are widespread in the organic kingdom. Their more or less largely identical functions are ensured by a remarkably similar sequence of amino-acids in their molecular make-up, at least at the points known as 'hot spots'. These similarities result from a similar coding and sequence of triplets in a gene (cistron), and it appears unlikely that they arose independently in each case. The presence of identical or merely constitutionally similar enzymes in organisms that cannot be crossed with one another (e.g. in bacteria and man) requires the assumption of 'homologous' genes in otherwise very different organisms. On account of the meaning attached to the word 'homology' by morphologists I suggested (Kosswig, 1961) the use of the term 'ubiquitous' genes in such cases some time ago. Present-day knowledge concerning so-called point mutations within a cistron justifies the use of the term allele genes instead of ubiquitous genes even in species between which insuperable sexual barriers were established long ago. The failure of one vital enzyme as a result of mutative changes in a structural gene involved must have a lethal effect. A feasible way out of this dangerous strait might lie in the possibility that by repeated tandem duplications a cistron can be replicated so that in the event of functional failure one of the duplicates can take over its role. What then becomes of the mutant gene is not clear. It might form part of the redundant 'junk' (as it is termed by Ohno, 1972) which is dragged on because of unknown reasons or it might achieve a new functional state by further processes of mutation, so contributing to the division of labour within an enzyme system, or it might even assume a completely new role. It remains to be seen whether or not fish are suitable objects for the investigation of such problems. Al-

though exhibiting a large degree of constancy at all the 'hot spots' of the molecule of certain structural genes they show a remarkable variability in the genes determining the so-called isoenzymes. In *Xiphophorini* (only 3 species so far investigated) 24 loci for the formation of different enzymes could be identified, of which 16 possess up to 4 alleles, each allele of the very same locus controlling a different isoenzyme. The analysis of the frequency of such alleles in natural populations has become a favoured method for tracking morphologically indistinguishable populations. Nevertheless, little is known of the biological significance of such heterozygosity. It could be demonstrated in *Astyanax* that the large surface populations (Avise and Selander, 1972) possess considerably more variability than the cave populations, which in all probability originate in a few individuals. The heterozygosity under discussion here was proved using the sequence of the bands produced by the various isoenzymes in electrophoresis experiments. In determining the species (and population-) specific content of free amino acids the Giessen group (Anders and Klinke, 1966) again encountered a highly polygenic system, of which it can be assumed that the genes play a boosting role in tumor formation following species crosses. This assumption is supported by the observation that elevation of the salt content of the water in the aquarium is paralleled by an increase in tumor formation and a rise in free amino acids. Yet another polygenic system of genes was discovered by Kallman (1964) in the course of transplantation experiments, which are only successful between individuals of isogenic stocks.

Isogenic stocks resulting from years of inbreeding offer ideal material for mutation experiments, which have so far made use of X-irradiation. The Giessen group succeeded in hitting with X-rays one of the polygenic systems influencing the manifestation of melanophore genes in *X. maculatus* ♀♀. Schröder (1969a, 1969b) has carried out extensive series of investigations on *Lebistes*, in which he tested, amongst other points, the effect of irradiation on vitality, differences in reactivity of inbred and hybrid stocks, occurrence of inheritable changes in number of vertebrae, structure of vertebral column and body proportions, frequency of small mutations correlated with the material started with, rise in cross-over value between X- and Y-chromosomes, as well as sensitivity of different stages of gametogenesis to intensity of radiation.

Cytological investigations on a large number of bony fish have brought sensational results, following the reactivation of this topic by Post. Improved methods enabled Scheel (1972) to carry out chromosome studies on somatic tissue in which, although the chromosome number is doubled, the individual chromosomes are considerably larger and more easily recognizable than in spermatogenesis. In contrast to the large degree of uniformity in chromosome numbers in the *Aphaniini* (n=24) or on the whole in the very varied forms of *Poeciliidae* (n=24, rarely 23) other groups of cyprinodontids exhibit amazing variability even among close relatives, such as, for example, the African and South American *Rivulini*, in which even the haploid numbers of different biospecies concealed within one morphospecies are very different. Even if two of these biospecies have the same number of chromosomes this does not necessarily indicate common ancestry. The reduction in chromosome numbers observed in such groups is due to the transformation of originally metacentric chromosomes into acrocentric elements by pericentral inversion and their refusion to form giant metacentric -, or perhaps following a still further transformation by pericentric inversion, giant telocentric-elements. Since such changes do not take place simultaneously, populations (biospecies) of the same morphospecies can form widely differing karyotypes when in isolation. If crosses are possible, meiosis presents the further complication that in the various karyotypes different arms of the old complement have fused with one another. The *Characidae*, just

like the *Rivulini*, present an abundance of different karyotypes within a close circle of relatives. No other class of vertebrates exhibit such variability. Polyploidy also arose polyphyletically. In all probability this is always a case of autotetraploidy (Uyeno and Smith, 1972), which is obscured by mutation in two of the four original homologues in a process termed diploidization by Ohno (1970). Clear-cut sexual differentiation of tetraploid individuals is ensured by the strength of the realisator gene on the Y or W chromosome of the heterogametic sex.

For decades innumberable species of ornamental fish have been kept by amateurs in aquaria. Such animals are often the offspring of only a few original imported individuals. It is small wonder that numerous mutations have arisen as a result of unintentional inbreeding under domestication. Some of these mutants have been further cultivated on account of their aberrations. In no case, however, has crossing and planned selection achieved the diversity seen in the goldfish after more than 1 000 years of domestication (Grzimek and Ladiges, 1970). Nevertheless, the number of variants and hybrid progeny of some of the more common ornamental fish is already large. Mutations such as albinism, xanthorism, melanism and elongated fins are especially frequent. In complete contrast to the polygenic nature of many characters of natural forms, these mutations of easily traceable monogenic characters are so nearly identical with their phenotypes that there is scarcely any doubt that they involve "ubiquitous" genes that, just like certain genes for biochemical characters, are part of the general make-up of the genotype of every bony fish or even of every vertebrate. A more detailed phenogenetic investigation would certainly yield results of scientific interest as well as providing pets for the aquarium. An immense diversity of aquarium strains of popular ornamental fish owe their origin to the principle of introgressive hybridization in *Xiphophorini* and *Poeciliini*. Unfortunately, many of these colourful variations are the result of species crosses, multiple backcrossing and perhaps crossing with yet a third species, so that their origins are no longer obvious and the breeders are unwilling to reveal their secrets. Some popular variations, however, have been produced in genetic laboratories and the methods published (Gordon, 1946).

At this point a phenomenon which is unparalleled in other vertebrates should be mentioned: this is selective fertilization, by means of which certain genes can be prevented from occurring in the homozygous state. This holds for the gene Fu in the Y-chromosome, responsible for producing melanosis in the 'pure' domesticated *X. maculatus* (Kosswig, 1938), as well as for autosomally inherited genes for elongated unpaired fins in domesticated strains of *"X. helleri"* (Schröder, 1966). In the ovoviviparous xiphophorine fish fertilization of the egg takes place in the ovary so that the spermatozoa have to penetrate the follicle epithelium. This presents unsolved problems of developmental physiology which can probably better be studied in oviparous forms for which phenotypically similar mutants are available.

Many expeditions in recent years have had the aim of collecting material from well-defined sites and incorporating this material into crossing experiments. Mexico and Central America have been visited repeatedly by investigators from the USA and twice by members of the Hamburg group. Parts of West Africa have often been visited by Scheel, and almost all the waters of Anatolia have been searched for *Aphaniini*. In recent years the latter subfamily has been sought by Villwock (Franz and Villwock, 1972) in the entire Mediterranean region, especially in hitherto unknown regions of N. Africa. In Hamburg extensive fixed material of *Orestiatini* (from Peru) is under investigation, besides endemic *Cyprinidae* from Lake Lanao on the island of Mindanao. These are probably the last collections from both regions, where, thanks to human folly, the

endemic species are doomed to extinction, if this has not already taken place. The latter investigations concentrated on sympatric species formation since much of what has appeared on this subject in the literature ignores the genetics involved. For the endemic 'species flocks' the problem of intralacustric speciation is still open to question only in the *Cichlidae* of the large East African lakes. It seems to be supported by some observations on aquarium fish and is only apparently disproved by others. The term 'preferential mating' and perhaps even 'Praegung' offer starting points for experimental solutions. As should already be clear, fish behave differently from other vertebrates in so many respects that conclusions as to evolutionary mechanisms drawn from other groups should only be applied with great caution.

References[1]

Aida, T. (1930): J. Genetics 15, 1-16.
Aksiray, F. (1952): Hidrobiologi (Istanbul) 1, 33-81.
Anders, A., Anders, F. et al. (1969): Zool. Anz. (Suppl.) 33, 333-339.
Anders, A. et al. (1971): Experentia 27, 931-932.
Anders, F. (1967): Experentia 23, 1-10.
Anders, F., Klinke, K. (1966): Verh. dtsch. zool. Ges. 1966, 391-401.
Anders, F. et al. (1972): Biologie in unserer Zeit. 2 Jg., 35-45.
Avise, J.C., Selander, R.K. (1972): Evolution 26, 1-19.
Breider, H. (1936): Z. ind. Abst. Vererbgsl. 71, 441-499.
Dobzhansky, Th. (1951): Genetics and the origin of species. 3. ed. New York: Columbia Univ. Press.
Franck, D. (1964): Zool. Jb. (Physiol.) 71, 117-170.
Franck, D. (1970): Z. Tierpsychol. 27, 1-34.
Franz, R., Villwock W. (1972): Mitt. ham. zool. Mus. Inst. 68, 135-176.
Gerschler, M.W. (1914): Z. ind. Abst. Vererbgsl. 12, 73-96.
Gordon, H., Gordon, M. (1957): J. Genetics 55, 1-44.
Gordon, M. (1946): Zoologica 31, 77-88.
Gordon, M. (1947): Adv. in Genetics 1, 95-132.
Gordon, M. (1950): Endavour 9, 26-34.
Gordon, M., Rosen, D.E. (1951): Bull. Am. Mus. Nat. Hist. 95, 413-464.
Grzimek, X., Ladiges, W. (1970): Grzimek Tierleben 4, 360 ff.
Hagen, D.W., McPhail, J.D. (1970): J. Fish. Res. Bd. Canada 27, 147-155.
Hartmann, M. (1956): Die Sexualität. Stuttgart: G. Fischer.
Holzberg, S., Schröder, J.H. (1972): Mutation Res. 16, 289-296.
Hubbs, C. L., Hubbs, L.C. (1946): The Aquarium Journal 17, 4-6.
Kallman, K.D. (1962): J. Genetics 58, 7-21.
Kallman, K.D. (1964): J. Genetics 50, 583-595.
Kallman, K.D. (1965): Zoologica 50, 151-190.
Kallman, K.D. (1970): Zoologica 55, 1-16.
Karbe, L. (1961): Mitt. hamb. zool. Mus. Inst. 59, 73-104.
Kosswig, C. (1929): Z. ind. Abst. Vererbgsl. 50, 63-73.
Kosswig, C. (1936): Biol. Zbl. 56, 409-414.
Kosswig, C. (1937): Roux' Arch. Entw.-Mech. 136, 491-528.
Kosswig, C. (1938): Rev. Fac. Sci. Instanbul 3, 1-7.
Kosswig, C. (1947): Nature 159, 605-606.
Kosswig, C. (1961): Zool. Anz. 166, 333-356.
Kosswig, C. (1963): Veröff. Inst. f. Meeresforsch. Bremerhaven (Sonderband), 178-196.
Kosswig, C. (1964a): Experentia 20, 1-10.
Kosswig, C. (1964b): Copeia 1964, 65-75.

[1] The number of reference works is so large (over 1 000) that only a sample can be listed here. This sampling, however, will lead the way to further publications.

Kosswig, C. (1972): XVII. Congr. internat. Zoologie Monaco (im Druck).
Kosswig, C., Villwock, W. (1964): Verh. dtsch. zool. Ges. Kiel 1964, 95-102.
Miller, R.R., Hubbs, C.L. (1969): Copeia 1969, 52-69.
Miller, R.R., Walters, V. (1972): Contr. in Science no. 233 (Nat. Hist. Mus., Los Angeles County).
Münzing, J. (1963): Evolution 17, 320-332.
Öktay, M. (1959): Rev. Fac. Sci. Istanbul, B 24, 225-233.
Öktay, M. (1964): Mitt. hamb. zool. Mus. Inst. (Erg.bd.) 61, 133-157.
Öztan, N. (1954): Rev. Fac. Sci. Istanbul, B 19, 245-280.
Öztan, N. (1963): Rev. Fac. Sci. Istanbul, B 25, 27-47.
Ohno, S. (1970): Evolution by gene duplication. Berlin-Heidelberg-New York: Springer.
Ohno, S. (1972): this symposium.
Parzefall, J. (1969): Behaviour 33, 1-37.
Parzefall, J. (1970): Z. Morph. Tiere 68, 323-342.
Parzefall, J., Wilkens, H. (1972): Z. Morph. Tiere 73, 63-79.
Peters, N., Peters, G. (1966): Roux' Arch. Entw.-Mech. 157, 393-414.
Pfeifer, W. (1960): Z. vergl. Phys. 43, 578-614.
Popper, A.N. (1970): Behaviour 18, 552-562.
Rust, W. (1941): Z. ind. Abst. Vererbgsl. 71, 336-395.
Sadoglu, P. (1955): Experentia 13, 394-395.
Scheel, J.J. (1968): T.F.H. publications, 473 p. New York
Scheel, J.J. (1972): Z. zool. Syst.-Evolutionsforsch. 10, 180-203.
Schemmel, Ch. (1967): Z. Morph. Tiere 61, 255-316.
Schmidt, J. (1919): J. Genetics 8, 147-153.
Schröder, J.H. (1966): Zool. Beitr. (NF) 12, 27-42.
Schröder, J.H. (1969a): Mutation Res. 7, 75-90.
Schröder, J.H. (1969b): Zool. Beitr. 15, 237-265.
Schultz, R.J. (1969): Am. Nat. 103, 605-619.
Sengün, A. (1950): Rev. Fac. Sci. Istanbul 15, 110-133.
Siciliano, M.C. et al (1972): XVII. Congr. internat. Zoologie Monaco
Uyeno, T., Smith, G.R. (1972): Science 175, 644-646.
Vielkind, J. et al. (1971): Cancer Reseach 31, 868-875.
Villwock, W. (1958): Mitt. hamb. zool. Mus. Inst. 56, 81-152.
Wilkens, H. (1968): Zool. Anz. 180, 454-464.
Wilkens, H. (1970a): Z. zool. Syst.-Evolutionsforsch. 8, 173-199.
Wilkens, H. (1970b): Roux' Arch. Entw.-Mech. 166, 54-75.
Wilkens, H. (1972): Zool. Anz. 188, 1-11.
Winge, Ö. (1930): J. Genetics 23, 69-76.
Winge, Ö. (1934): C.R. Lab. Carlsberg, Ser. phys. 21, 1
Witschi, E. (1929): Handb. Vererbgswiss., 11/10. Berlin: Bornträger
Yamamoto, T. (1967): Genetics 55, 329-336.
Zander, C.D. (1962): Mitt. hamb. zool. Mus. Inst. 60, 205-264.
Zander, C.D. (1968): Molec. Gen. Genetics 101, 29-42.
Zander, C.D. (1969): Mitt. hamb. zool. Mus. Inst. 66, 241-271.
Zander, C.D., Dzwillo, M. (1969): Z. wiss. Zool. 178, 276-315.
Zeiske, E. (1968): Z. vergl. Phys. 58, 190-222.

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KURT D. FAUSCH

Data on the Biology of Lake Trout from Great Bear and Great Slave Lakes, Northwest Territories, 1973

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by
M.R. Falk, D.V. Gillman and
L.W. Dahlke

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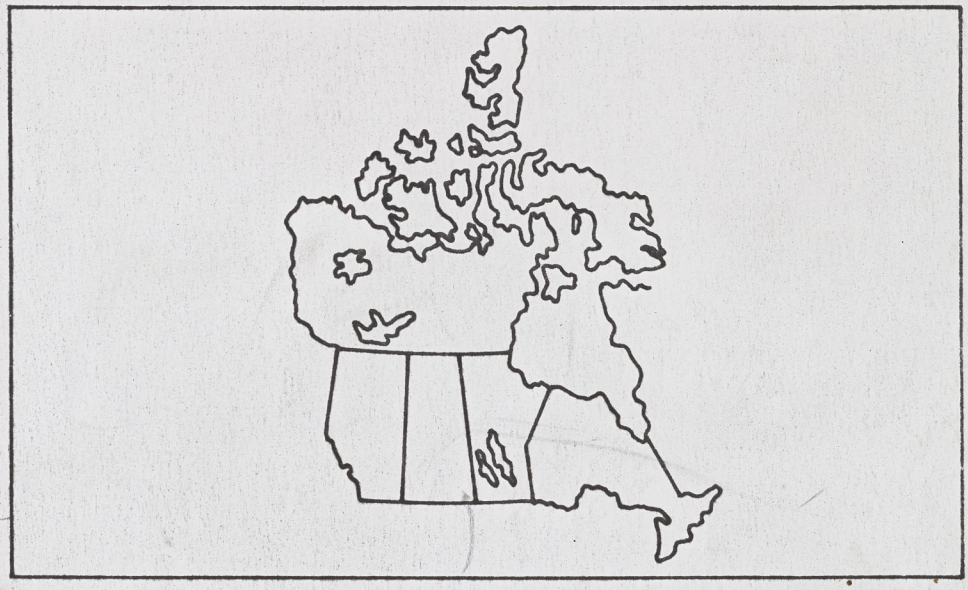
Data Report Series No. CEN/D-74-4

Resource Management Branch
Central Region



DEPARTMENT OF THE ENVIRONMENT

FISHERIES AND MARINE SERVICE

Fisheries Operations Directorate
Central Region

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by

M. R. FALK
D. V. GILLMAN
and
L. W. DAHLKE

Lake Management Section
Fishery Management Division
Resource Management Branch
Winnipeg, Manitoba

1974

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TABLE OF CONTENTS

	Page
Acknowledgements	ii
Table of Contents	iii
List of Figures	iv
List of Tables	v
List of Appendicies	vi
Introduction	1
Materials and Methods	2
Results	6
Length-Frequency Distributions	6
Length-Weight Relationships	6
Age and Growth	11
Sex and Maturity	17
Literature Cited	19
Appendix	20

LIST OF FIGURES

		Page
1.	Map of Great Bear Lake showing the sport fishing lodges censused during 1973	3
2.	Map of Great Slave Lake showing the sport fishing lodges censused during 1973	4
3.	Percent frequency distributions of length for lake trout sampled from Great Bear Lake lodges	7
4.	Percent frequency distributions of length for lake trout sampled from Great Slave Lake lodges	8
5.	Percent frequency distributions of age for lake trout sampled from Great Bear Lake lodges	12
6.	Growth in length and weight for lake trout from Great Bear Lake lodges	13
7.	Catch curves for lake trout sampled from lodges on Great Bear Lake	14
8.	Percent frequency distributions of age for lake trout sampled from Great Slave Lake lodges	15
9.	Growth in length and weight for lake trout from Great Slave Lake lodges	16
10.	Catch curves for lake trout sampled from lodges on Great Slave Lake	18

LIST OF TABLES

		Page
1.	Length-weight relationship summary for lake trout sampled from Great Bear Lake lodges	9
2.	Length-weight relationship summary for lake trout sampled from Great Slave Lake lodges	10

LIST OF APPENDICES

		Page
A-1.	Mean weight, maturity and sex ratio by length interval for lake trout from Great Bear Lake Lodge, 1973	20
A-2.	Mean weight, maturity and sex ratio by length interval for lake trout from Great Bear Lodge, Neiland Bay Outpost, 1973	22
A-3.	Mean weight, maturity and sex ratio by length interval for lake trout from Great Bear Trophy Lodge, 1973	24
A-4.	Mean weight, maturity and sex ratio by length interval for lake trout from Cameron Bay Lodge, 1972 and 1973 .	25
A-5.	Mean weight, maturity and sex ratio by length interval for lake trout from Great Slave Lake Lodge, 1973	26
A-6.	Mean weight, maturity and sex ratio by length interval for lake trout from Frontier Lodge, 1973	27
A-7.	Mean weight, maturity and sex ratio by length interval for lake trout from Arctic Star Lodge, 1973	28
A-8.	Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Bear Lake Lodge, 1973	29
A-9.	Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Bear Lodge, Neiland Bay Outpost, 1973	31
A-10.	Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Bear Trophy Lodge, 1973	33
A-11.	Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Cameron Bay Lodge, 1972 and 1973	35
A-12.	Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Slave Lake Lodge, 1973	37
A-13.	Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Frontier Lodge, 1973	38

Page

A-14. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Arctic Star Lodge, 1973 39

INTRODUCTION

From June to September, 1973 a creel census and sampling program was carried out at seven sport fishing lodges on Great Bear and Great Slave lakes. This was done as a part of a three year program (Falk et al. MS 1973) designed to monitor the harvest of lake trout (*Salvelinus namaycush*) from these lakes; to determine the effects of the past and present levels of exploitation on the fish populations; and to recommend remedial action if necessary. The objectives of the present study were to determine if interim measures taken by the lodge operators and the Fisheries and Marine Service during the 1973 season were effective in reducing the harvest of lake trout; to further define the effects of exploitation on the fish populations; and to explore the natural history of the lake trout in order to manage the fishery more effectively on a biological basis.

The creel census segment of the program afforded an opportunity to study the biology of lake trout and to determine the effects of exploitation on the populations without an extensive and expensive sampling program. Data from the sampling segment of the 1973 study are presented here pending the completion of the program in 1975 and to provide interested persons some insight into the biology of lake trout in northern lakes. In 1975 a final report will cover the results of the three year program in detail as well as the conclusions and recommendations for management direction and future studies.

MATERIALS AND METHODS

During 1973, Fisheries and Marine Service personnel were stationed at sport fishing lodges on both lakes as follows: Great Bear Lake, Great Bear Trophy and Great Bear (Neiland Bay Outpost) lodges on Great Bear Lake (Fig. 1) and Great Slave Lake and Frontier lodges on Great Slave Lake (Fig. 2). In addition a partial census was carried out at Cameron Bay Lodge on Great Bear Lake (Fig. 1) and Arctic Star Lodge on Great Slave Lake (Fig. 2).

Details concerning the lodge operation as well as the methods employed have been covered previously by Falk et al. (MS 1973). Upon returning from a days fishing, anglers and/or guides were questioned as to the number of fish caught, released and retained, the hours and locations fished and the gear used. At this time a fraction of the daily catch was sampled for fork length (tip of snout to distal end of shortest caudal ray) measured in millimeters, round weight (± 50 g), sex and stage of maturity. The relative stage of maturity was determined by examination of the gonads and coded by reference to a scale of maturity stages as follows:

Female	Male	Maturity Stage
1	6	Immature
2	7	Maturing
3	8	Mature
4	9	Ripe
5	10	Spent

Otoliths were obtained from the majority of sampled lake trout by splitting the skull and locating the sagittal otolith with tweezers. They were stored dry in envelopes marked with the sample information. In the laboratory the convex surface of the otolith was ground on a fine carborundum stone to expose the annual growth zones. The otolith was then immersed in a 3:1 solution of benzyl-benzoate and methyl salicylate on a depression slide and read under a dissecting microscope.

During 1973 only a partial creel census was carried out at Cameron Bay Lodge. As a result a small number of lake trout was sampled. In order to make comparisons with lake trout sampled from other lodges on the lake the 1972 and 1973 data were combined to obtain a larger sample size.

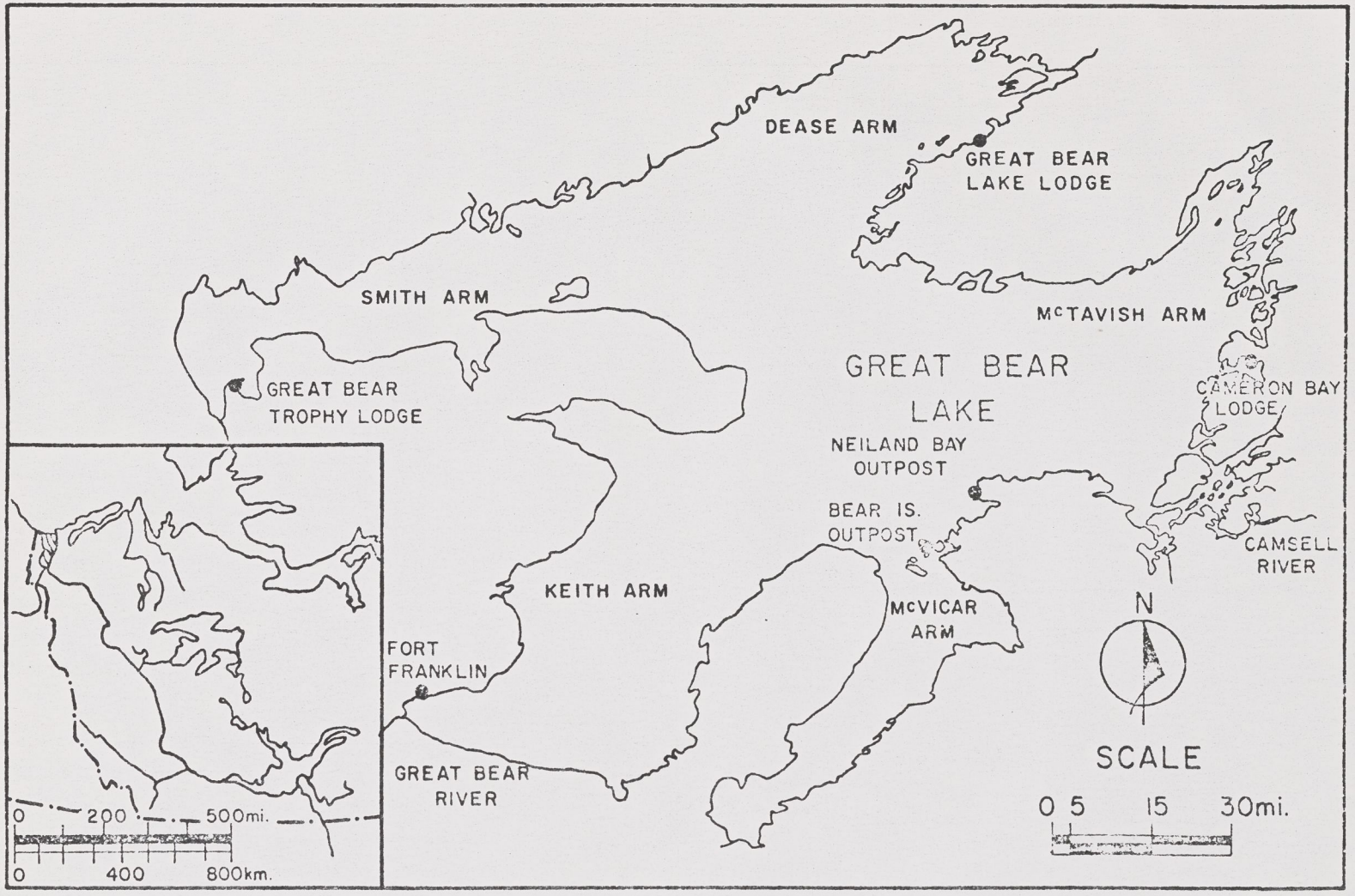


Figure 1. Map of Great Bear Lake showing the sport fishing lodges censused during 1973.

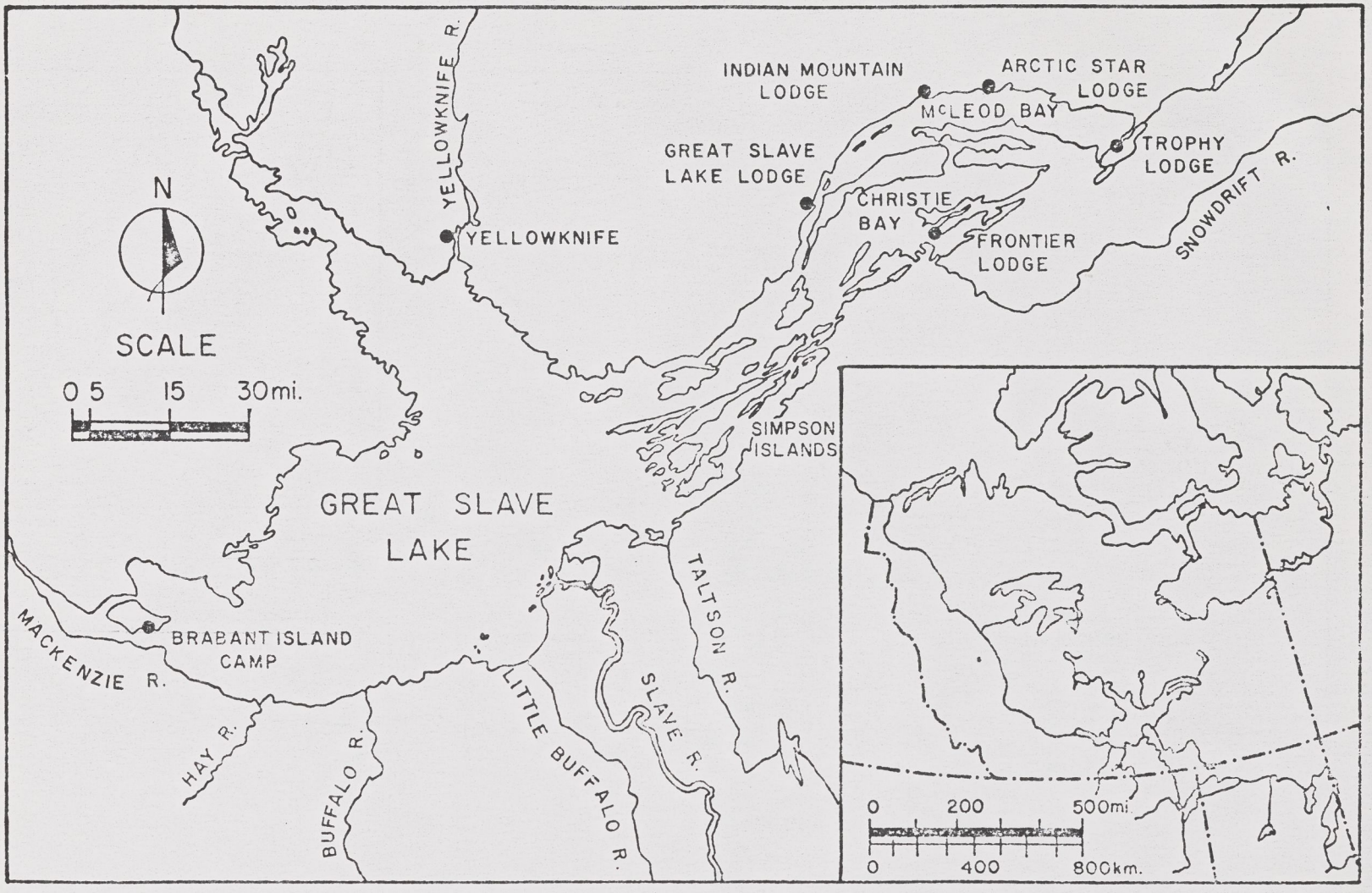


Figure 2. Map of Great Slave Lake showing the sport fishing lodges censused during 1973.

Data collected during the study were analysed using a programmable calculator (Hewlett-Packard Model 9810-A). Annual mortality rates (natural and fishing) were calculated using the methods outlined by Robson and Chapman (1961). Length-weight relationships were determined by the following power equation:

$$\log_{10}W = a + b\ (\log_{10}L)$$

Where: W = weight in grams (g)

a = Y-intercept

b = slope of the regression line

L = length in millimeters (mm)

Condition factors (K) were calculated from formula $K = W \times 10^5/L^3$. K - values, so obtained, are a measure of plumpness or condition of the fish.

RESULTS

Biological data on lake trout sampled from lodges on Great Bear and Great Slave lakes during 1973 are summarized in tabular form in the Appendices by length and age class. In the following sections the analysed data are presented in graphical and tabular form to illustrate the biological characteristics of the lake trout populations.

LENGTH-FREQUENCY DISTRIBUTIONS

The percent frequency distributions of length for lake trout from lodges censused on Great Bear Lake are shown in Figure 3. Lake trout averaged 664 mm (range 215-980 mm; mode 650 mm) from Great Bear Lake Lodge; 728 mm (range 320-1100 mm; mode 610 mm) from Great Bear Lodge; 647 mm (range 269-890 mm; mode 640 mm) from Great Bear Trophy Lodge and 624 mm (range 376-855 mm; mode 590 mm) from Cameron Bay Lodge. The length-frequency distribution described by Johnson (1973) for lake trout caught in 1963 using gill nets is also shown in Figure 3 for comparative purposes. The percent length-frequency distributions of lake trout from Great Slave Lake lodges are shown in Figure 4. Lake trout averaged 605 mm (range 385-970 mm; mode 550 mm) from Great Slave Lake Lodge, 545 mm (range 320-820 mm; mode 550 mm) from Frontier Lodge and 567 (range 415-878 mm) from Arctic Star Lodge. The length-frequency distribution described by Rawson (1951) for lake trout caught in the east arm of Great Slave Lake using gill nets is also shown in Figure 4 for comparative purposes.

LENGTH-WEIGHT RELATIONSHIPS

Data on the length-weight relationships for lake trout from lodges on Great Bear Lake are summarized in Table 1. The logarithmic relationship of weight to length for all lake trout sampled from Great Bear Lake is described by the following equation:

$$\log W = -4.2487 + 2.752 (\log L)$$

Length-weight relationship data for lake trout sampled from lodges in the east arm of Great Slave Lake are given in Table 2. The logarithmic relation of weight to length for lake trout from all lodges is described by the equation:

$$\log W = -6.3070 + 3.448 (\log L)$$

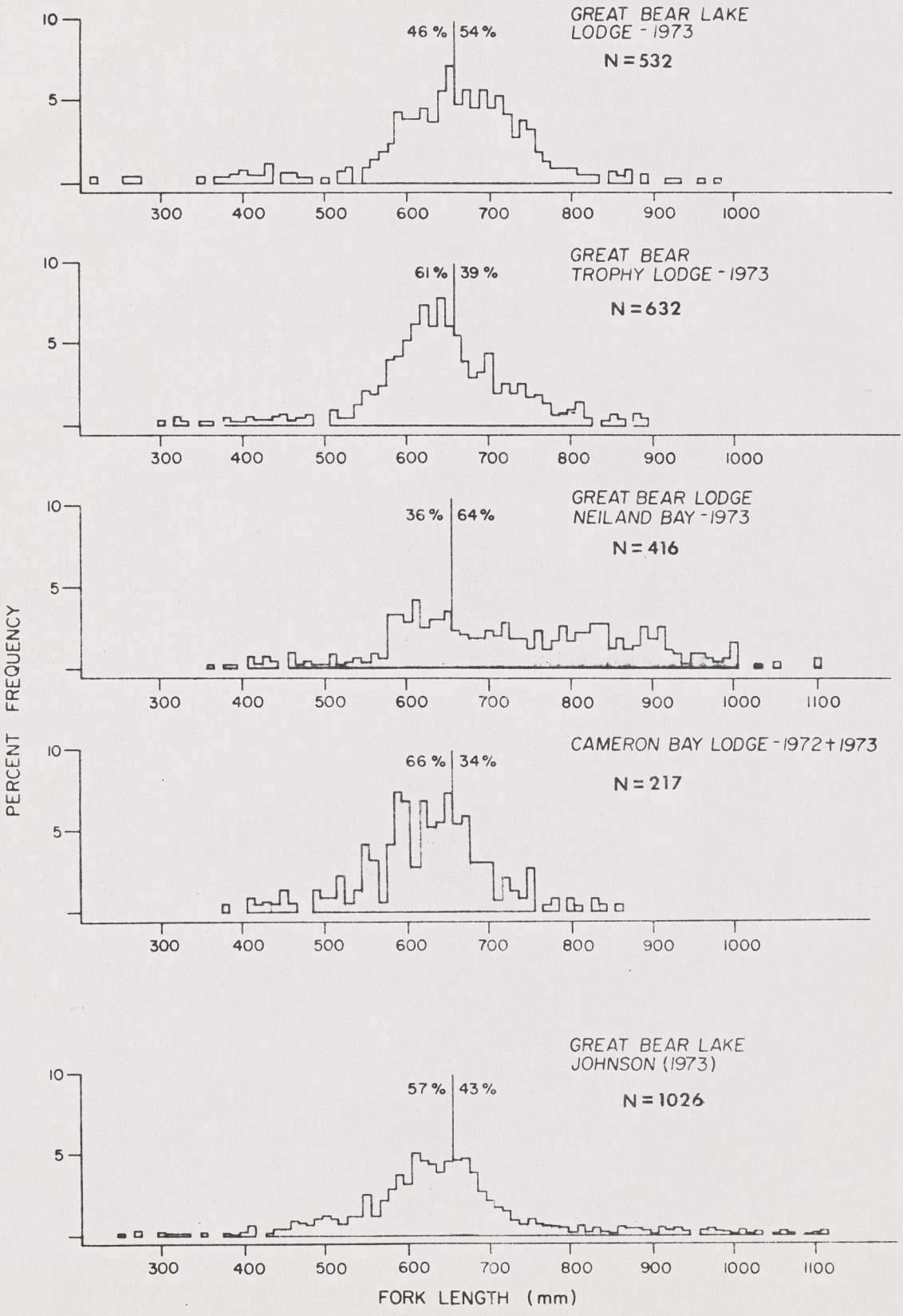


Figure 3. Percent frequency distributions of lake trout sampled from Great Bear Lake lodges.

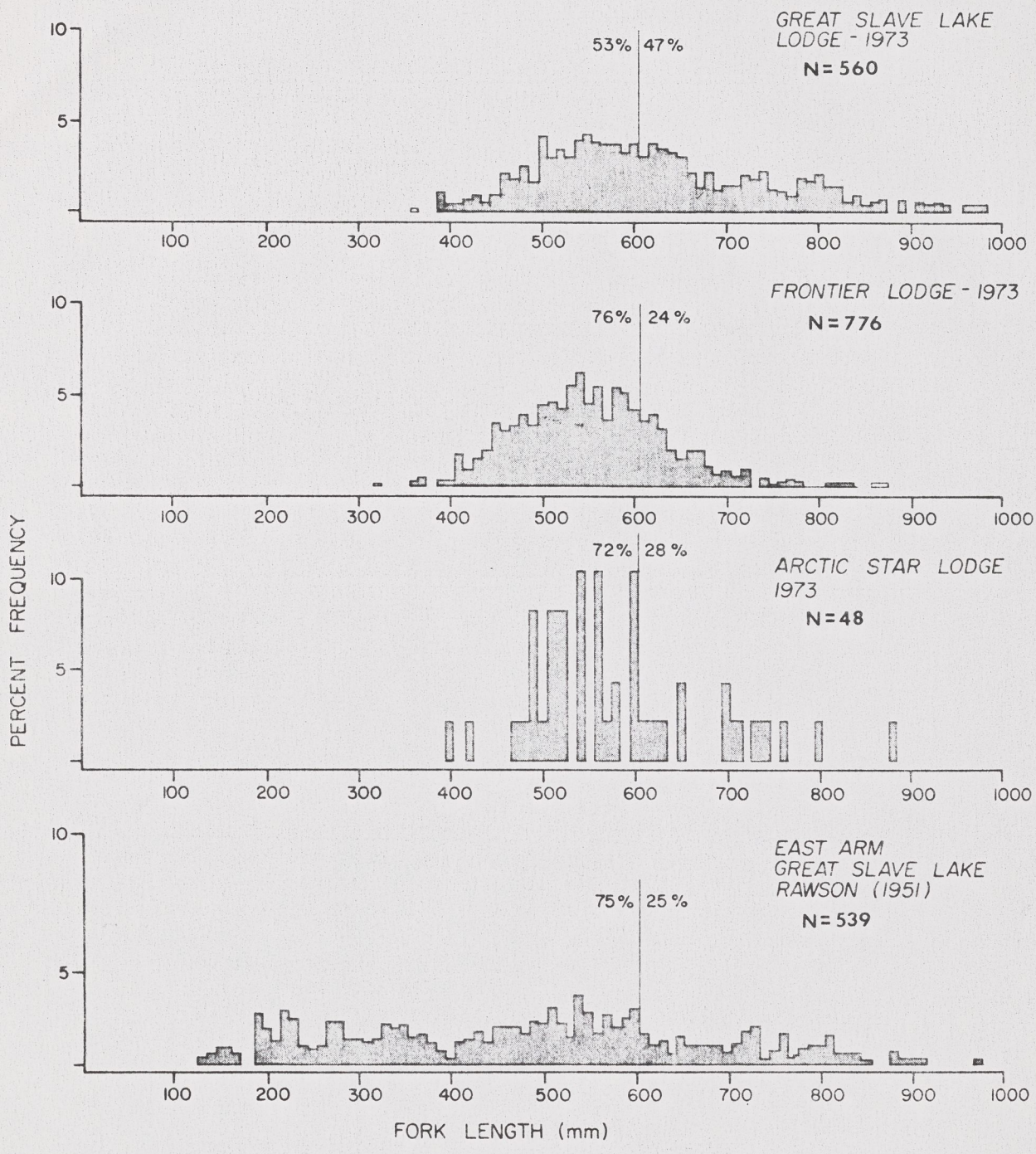


Figure 4. Percent frequency distributions of lake trout sampled from Great Slave Lake lodges.

Table 1. Length-weight relationship summary for lake trout samples from Great Bear Lake lodges, 1973 ($\log_{10}W = a + b\ [\log_{10}L]$).

Lodge	Sex	N	Y-intercept a	Slope b	S_b	95% C.I. of b
Great Bear Lake Lodge	Male	267	-4.0903	2.701	0.0621	2.579 - 2.823
	Female	233	-4.1762	2.738	0.0673	2.606 - 2.870
	Combined	500	-4.1333	2.720	0.0647	2.593 - 2.847
Great Bear Lodge	Male	213	-3.8000	2.599	0.0492	2.503 - 2.695
	Female	147	-3.6407	2.546	0.0457	2.455 - 2.637
	Combined	360	-3.7204	2.573	0.0475	2.480 - 2.666
Great Bear Trophy Lodge	Male	319	-4.8794	2.965	0.0610	2.845 - 3.085
	Female	253	-4.6697	2.874	0.0632	2.770 - 3.018
	Combined	572	-4.7746	2.930	0.0621	2.807 - 3.053
Cameron Bay Lodge *	Male	136	-4.6200	2.875	0.1285	2.623 - 3.127
	Female	144	-4.1158	2.700	0.1149	2.476 - 2.924
	Combined	280	-4.3679	2.788	0.1217	2.551 - 3.025
Total	Male	935	-4.3474	2.785	0.0752	2.638 - 2.932
	Female	777	-4.1506	2.720	0.0728	2.577 - 2.863
	Combined	1712	-4.2487	2.752	0.0736	2.608 - 2.896

* Includes 1972 and 1973 data.

Table 2. Length-weight relationship summary for lake trout samples from Great Slave Lake lodges, 1973.

Lodge	Sex	N	Y-intercept a	Slope b	S_b	95% C.I. of b
Great Slave Lake Lodge	Male	213	-5.3352	3.156	0.0545	3.046 - 3.266
	Female	259	-5.5558	3.230	0.0512	3.130 - 3.330
	Combined	472	-5.4529	3.195	0.0529	3.095 - 3.295
Frontier Lodge	Male	344	-7.0027	3.758	0.0888	3.588 - 3.928
	Female	346	-6.8286	3.692	0.0847	3.522 - 3.868
	Combined	690	-6.9134	3.724	0.0867	3.554 - 3.898
Arctic Star Lodge	Male	22	-5.9501	3.384	0.1494	3.084 - 3.684
	Female	24	-6.0970	3.433	0.1900	3.043 - 3.823
	Combined	46	-5.9774	3.392	0.1167	3.162 - 3.622
Total	Male	579	-6.3492	3.413	0.0781	3.260 - 3.566
	Female	629	-6.2765	3.492	0.0749	3.345 - 3.637
	Combined	1208	-6.3070	3.448	0.0756	3.300 - 3.596

AGE AND GROWTH

The percent frequency distributions of age (years) for lake trout from lodges on Great Bear Lake are shown in Figure 5. The average ages were 26.8 (range 7-53) from Great Bear Lake Lodge, 24.9 (range 4-45) from Great Bear Lodge, 23.2 (range 4-53) from Great Bear Trophy Lodge and 23.3 (range 9-48) from Cameron Bay Lodge. The modal age class for all lodges was age 20. Growth in length and weight varied little among the four lodges, with lake trout from Great Bear Lodge demonstrating a more rapid growth rate than from other areas (Fig. 6). Because of the extreme variation in length and weight per age class only those age classes containing data from five or more fish were used to plot the growth curve. Catch curves for lake trout sampled from Great Bear Lake lodges are shown in Figure 7. With the exception of Cameron Bay Lodge the peak of the catch curve occurred at age 20. Each curve assumed a very irregular appearance, being riddled with peaks and valleys. This is thought to be due to the small sample size considering the age span rather than actual fluctuations in year class strength. These may occur but they could not be detected. Despite irregularities in the catch curves they all appeared to be similar with a gradual decrease after age 20 to ages between 45 and 53. Variations among year classes made it difficult to accept estimates of annual mortality rates. A fairly successful attempt was made to smooth the descending limb of the catch curves using a moving mean. This is the average of two successive age classes. Using the moving mean the annual mortality rates were 9.5 percent (ages 22-53) from Great Bear Lake Lodge, 10.9 percent (ages 21-46) from Great Bear Lodge, 16.7 percent (ages 22-37) from Great Bear Trophy Lodge and 10.8 percent (ages 21-47) for Cameron Bay Lodge. Annual mortality rates for comparable ages of 22-37 were 14.5, 12.5, 16.7 and 14.7 percent, respectively. For all lodges on Great Bear Lake combined the annual mortality rate was 14.5 percent for both a moving mean and the unsmoothed data using ages 22 to 37.

Age frequency distributions for lake trout from Great Slave Lake lodges are illustrated in Figure 8. Average ages were 16.1 (range 7-30) from Great Slave Lake Lodge, 15.4 (range 5-30) from Frontier Lodge and 16.5 (range 10-28) from Arctic Star Lodge. Modal ages were 13, 11 and 16, respectively. Growth in length and weight for lake trout sampled from Great Slave Lake and Frontier lodges are shown in Figure 9. Again, the curves were plotted using ages where there were 5 or more fish. Lake trout from Great Slave Lake Lodge appeared to grow more slowly than those from Frontier Lodge up to age 13. After this age the growth rate was greater. A growth curve from Arctic Star Lodge was not plotted due to the small sample size. However, it was evident that the growth rate was slower

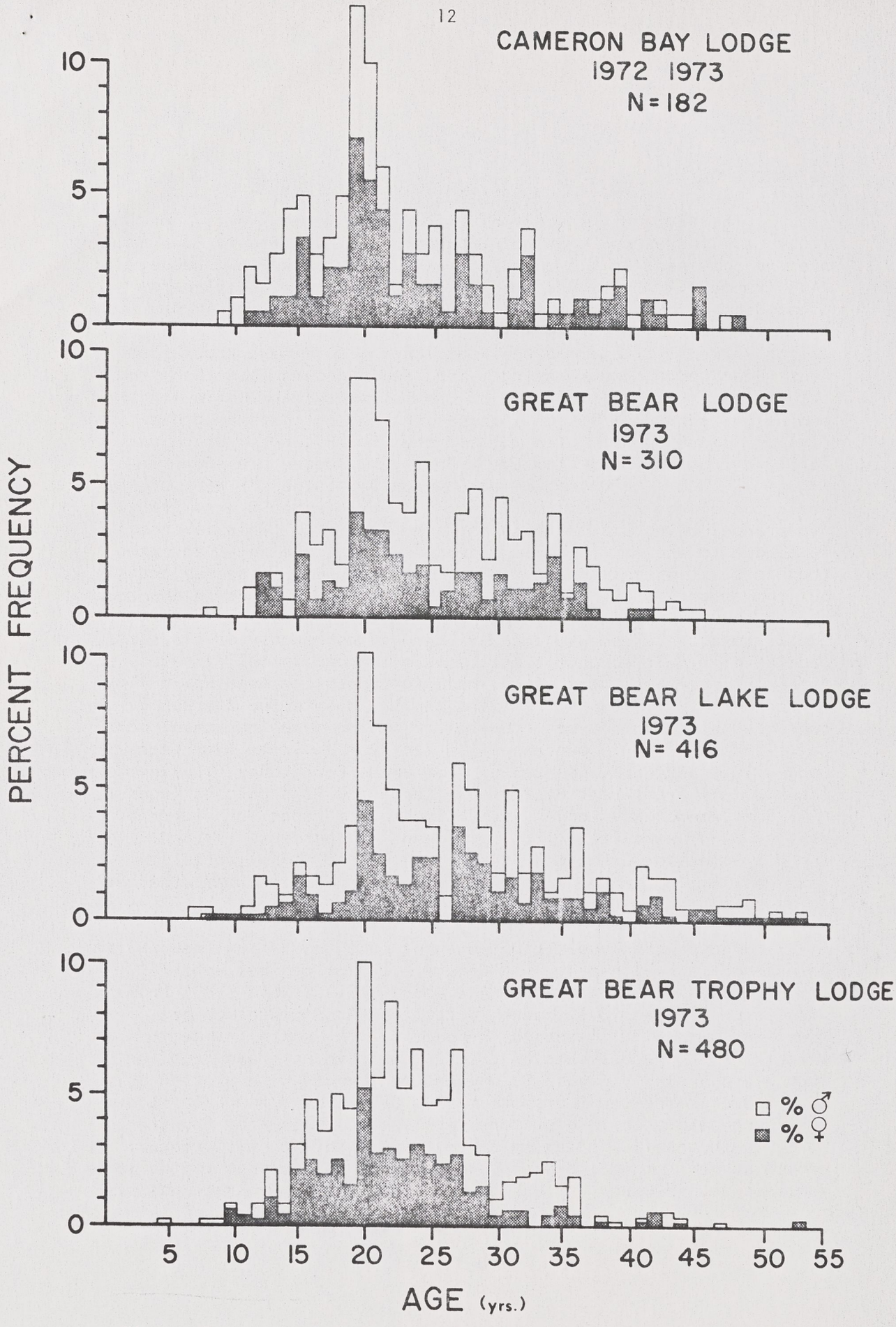


Figure 5. Percent frequency distributions of age for lake trout sampled from Great Bear Lake lodges.

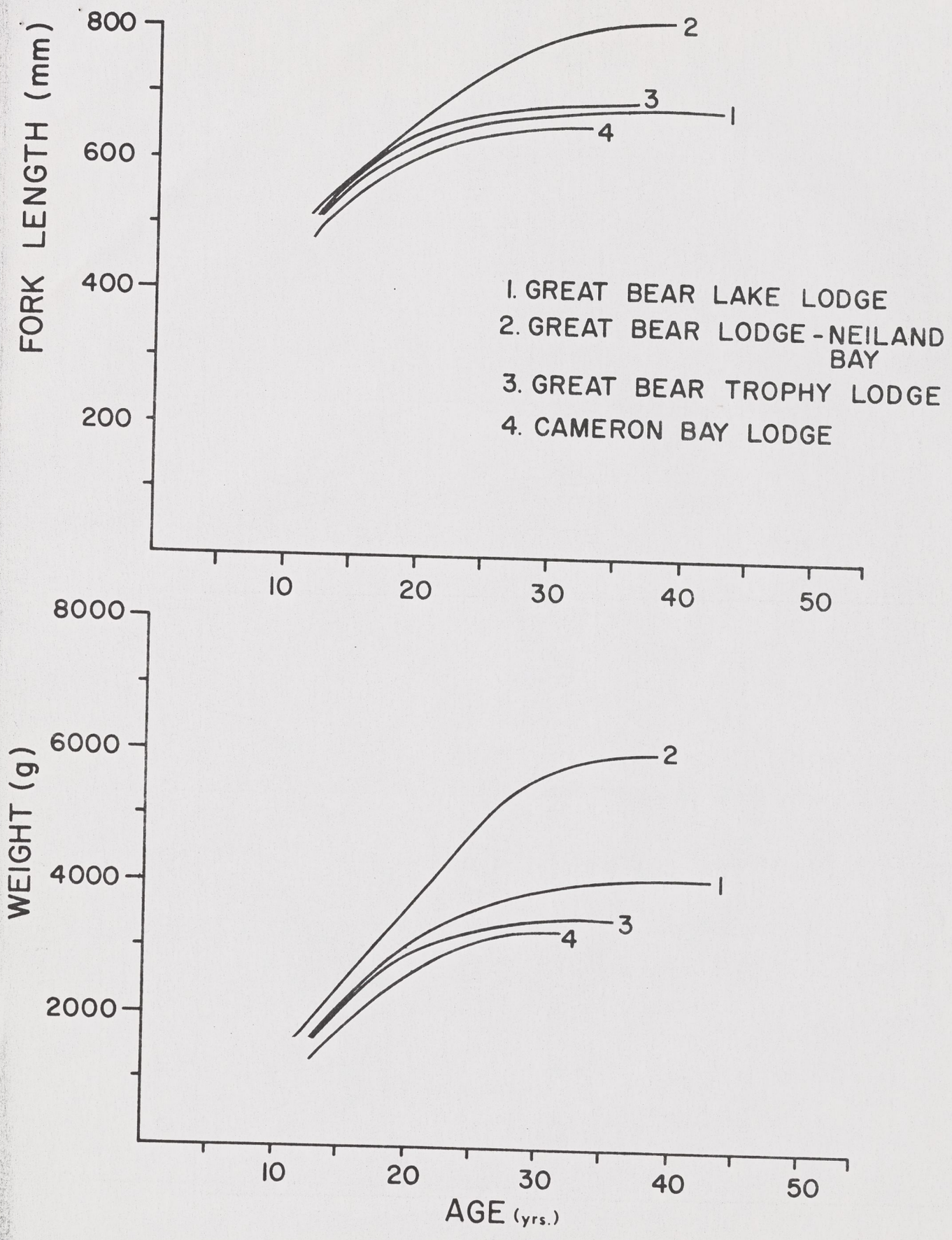


Figure 6. Growth in length and weight for lake trout from Great Bear Lake lodges.

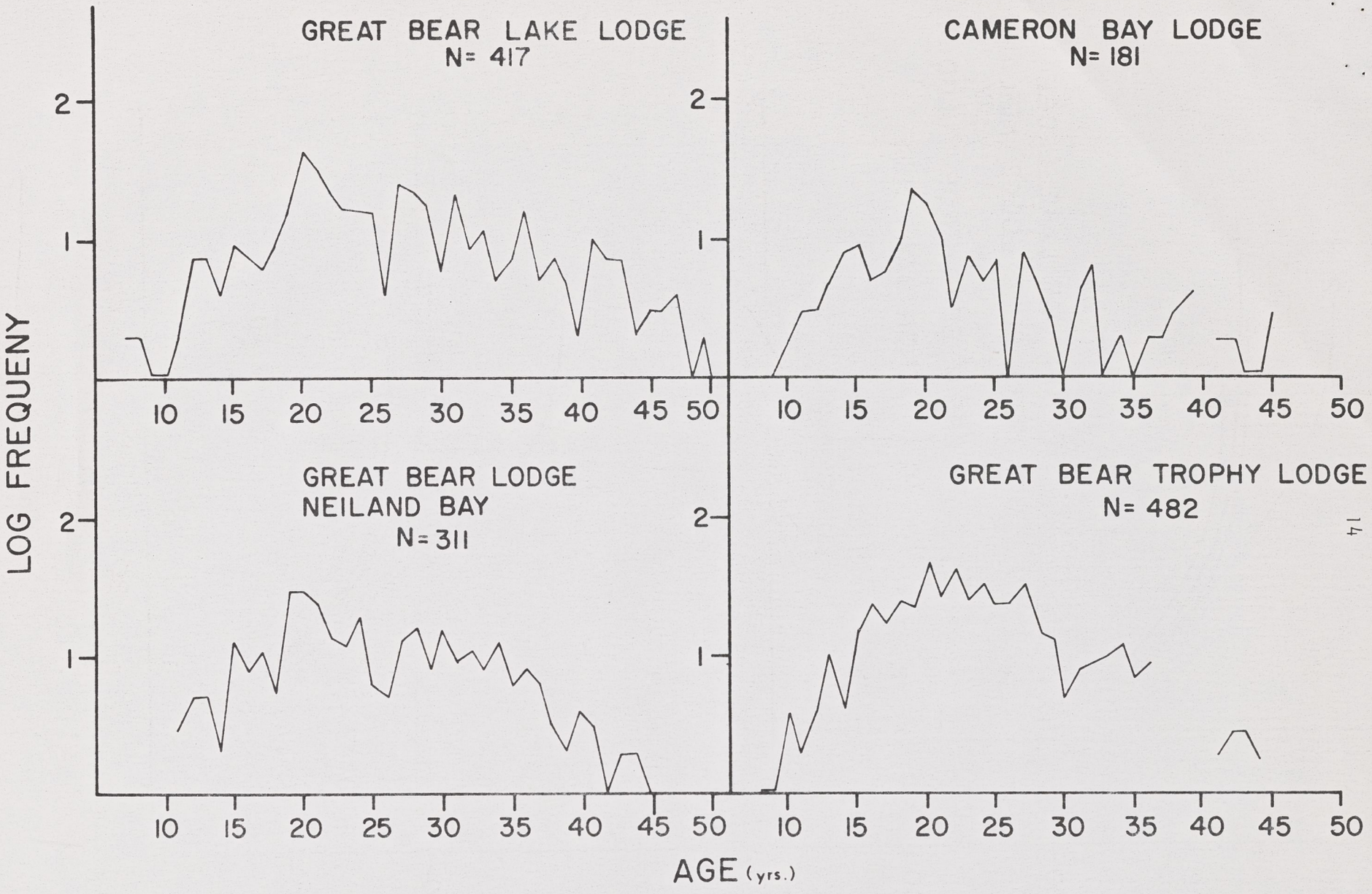
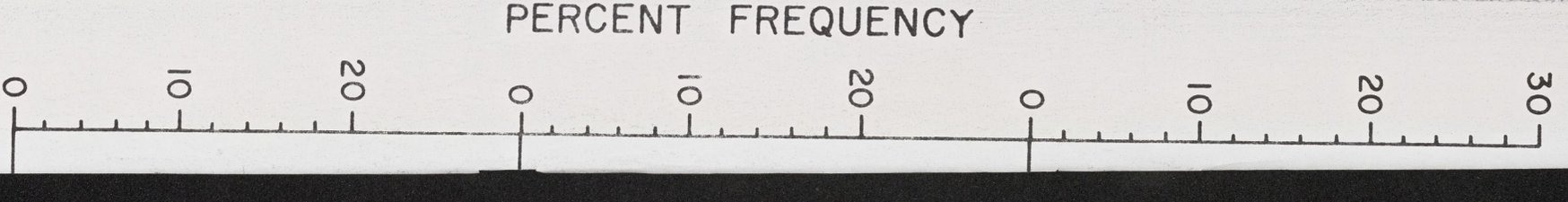


Figure 7. Catch curves for lake trout sampled from lodges on Great Bear Lake.



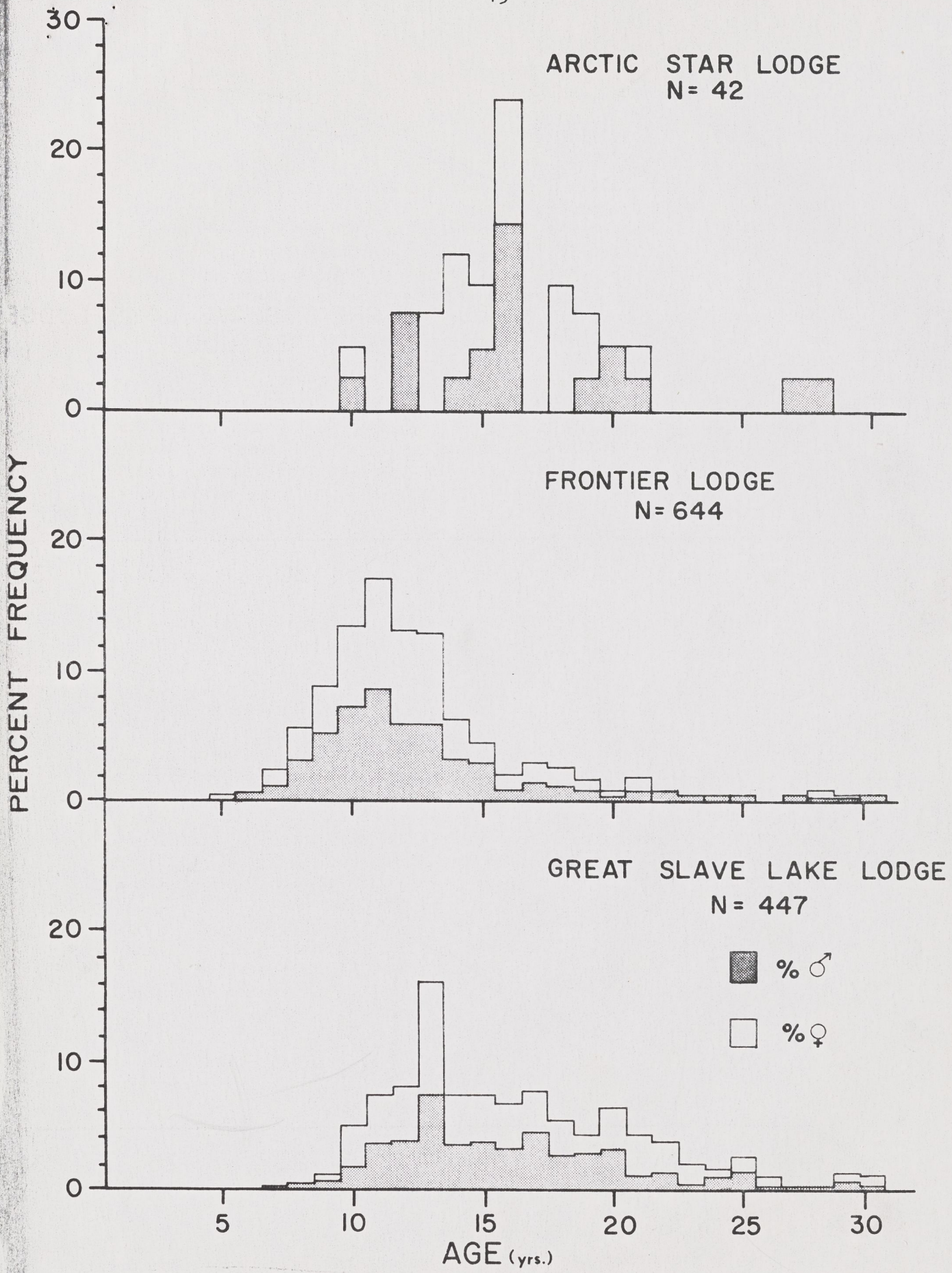


Figure 8. Percent frequency distributions of age for lake trout sampled from Great Slave Lake lodges.

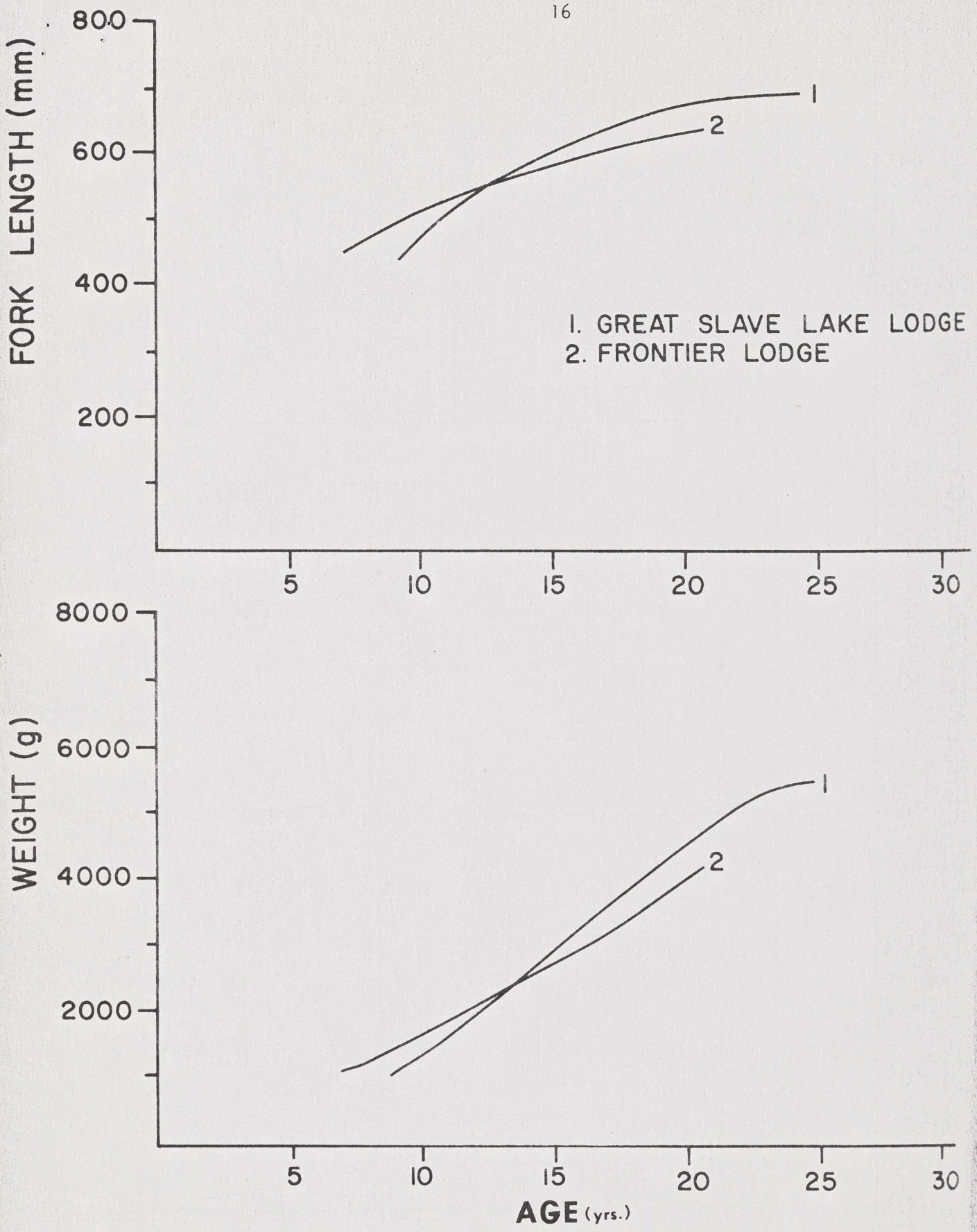


Figure 9. Growth in length and weight for lake trout from Great Slave Lake lodges.

than the two lodges illustrated. It was noted that lake trout older than age 22 from Frontier Lodge did not conform to the growth curve and were comparable in length and weight to trout aged 10 to 15 from the same sample. Accepting our age determinations as valid a plausible explanation escapes us. It is possible, however, that these trout were either caught in a region of Great Slave Lake which harbours extremely slow growing trout or that they were a form of "big-headed" trout. Whatever the cause, further study is necessary to determine the reason for this divergence. Catch curves for lake trout sampled from Great Slave Lake lodges separately and combined are illustrated in Figure 10. Peaks of the curves occurred at age 13 for Great Slave Lake Lodge, age 11 for Frontier Lodge, age 16 for Arctic Star Lodge and age 13 for the combined sample. Fluctuations were not as pronounced as those from Great Bear Lake. The larger sample sizes and shorter life span are thought to be responsible for this. However, a moving mean was again used to smooth the curve and facilitate calculations of annual mortality rates. These were 19.6 percent (ages 12-28) for Great Slave Lake Lodge and 27.4 percent (ages 12-27) for Frontier Lodge. Annual mortality rates using ages 15 to 27 were 17.8 and 25.7 percent, respectively. For the entire sample annual mortality rates were 21.8 percent using a moving mean and 22.2 percent using the unsmoothed data over ages 15 to 27.

SEX AND MATURITY

Sex ratios for lake trout from Great Bear Lake were 0.87 M:1F from Great Bear Lake Lodge, 0.66 M:1F from Great Bear Lodge and 1.07 M:1F from Cameron Bay Lodge. Sexual maturity was first reached at age 12 (448 mm; 1567 g) and was generally complete by age 20. Sex ratios for lake trout from Great Slave Lake were 1.25 M:1F from Great Slave Lake Lodge, 0.97 M:1F from Frontier Lodge and 1.09 M:1F from Arctic Star Lodge. Sexual maturity was first reached at 10 (484 mm; 1345 g) from Great Slave Lake Lodge and at age 9 (490 mm; 1243 g) from Frontier Lodge. Complete sexual maturity was attained at an earlier age and at a more rapid rate from Great Slave Lake Lodge. Lake trout from Great Bear Lake appear to spawn every third year while those from Great Slave Lake appear to spawn every second year after attaining sexual maturity.

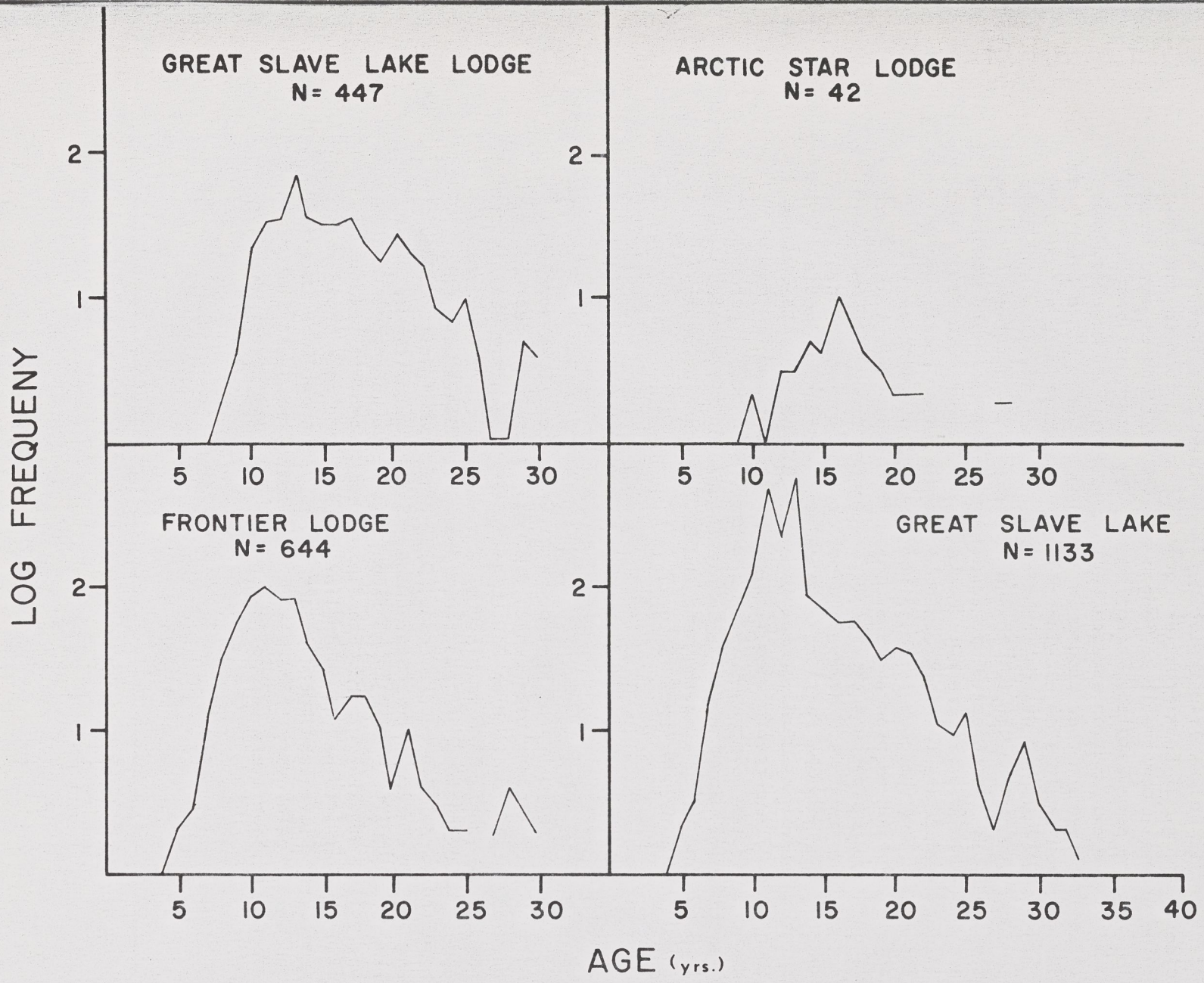


Figure 10. Catch curves for lake trout sampled from lodges on Great Slave Lake.

LITERATURE CITED

Falk, M. R., D. V. Gillman and L. W. Dahlke. MS 1973. The 1972 sport fisheries of Great Bear and Great Slave lakes, Northwest Territories. Canada Dep. Environ., Fish. Mar. Serv., Oper. Dir., Rep CEN/T-73-8: 100 p.

Johnson, L. 1973. Stock and recruitment in some unexploited Canadian Arctic lakes. R.P-V. Cons. Int. Explor. Mer. 164: 219-227.

Rawson, D. S. 1951. Studies of the fish of Great Slave Lake. J. Fish. Res. Board Can. 8(4): 207-240.

Robson, D. S. and D. G. Chapman. 1961. Catch curves and mortality rates. Trans. Amer. Fish. Soc. 90(2): 181-189.

APPENDIX

Table A-1. Mean weight, maturity and sex ratio by length interval for lake trout from Great Bear Lake Lodge, 1973.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Weight (g) S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
251 - 275	1	263	200	-	-	-	1	1	-
276 - 300	-	288	-	-	-	-	-	-	-
301 - 325	1	313	700	-	1	-	-	-	-
326 - 350	-	338	-	-	-	-	-	-	-
351 - 375	1	363	600	-	1	-	-	-	-
376 - 400	2	388	650	28.9	1	0	1	0	1:1
401 - 425	4	413	838	23.9	2	0	2	0	1:1
426 - 450	5	438	867	33.3	4	0	1	0	0.3 :1
451 - 475	2	463	1100	100.0	1	0	1	0	1:1
476 - 500	2	488	1300	-	-	-	2	0	-
501 - 525	2	513	1800	-	1	0	1	0	1:1
526 - 550	9	538	1862	88.5	5	20	4	0	0.8 :1
551 - 575	20	563	2375	83.3	14	64	6	17	0.4 :1
576 - 600	50	588	2602	55.1	30	77	20	35	0.7 :1
601 - 625	46	613	2907	77.9	19	84	27	52	1.4 :1
626 - 650	81	638	3411	55.5	41	90	40	68	1:1
651 - 675	65	663	3606	57.7	41	83	24	50	0.6 :1
676 - 700	72	688	3919	57.7	44	91	28	61	0.6 :1
701 - 725	53	713	4208	98.0	20	90	33	82	1.7 :1
726 - 750	45	738	4407	80.3	25	64	20	45	0.8 :1
751 - 775	15	768	4694	137.4	8	63	7	43	0.9 :1
776 - 800	14	788	5085	210.9	5	60	9	44	1.8 :1
801 - 825	5	813	5240	150.3	1	0	4	0	4:1
826 - 850	3	838	5933	328.3	1	100	2	0	2:1
851 - 875	2	863	6620	369.3	1	0	4	25	4:1
876 - 900	1	888	6400	1400.0	2	50	-	-	-

Table A-1. (Cont.)

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Weight (g) S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
901 - 925	1	913	7200	-	1	0	-	-	-
926 - 950	1	938	7600	-	1	100	-	-	-
951 - 975	1	963	9400	-	1	100	-	-	-
976 - 1000	1	988	9500	-	1	0	-	-	-
Total	509	-	-	-	272	75.9	237	51.5	0.87:1
Mean	-	-	3419	-	-	-	-	-	

Table A-2. Mean weight, maturity and sex ratio by length interval for lake trout from Great Bear Lodge, Neiland Bay outpost, 1973.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Weight (g) S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
351 - 375	2	363	825	75.0	1	0	1	0	1:1
376 - 400	1	388	900	-	1	0	-	-	-
401 - 425	5	413	921	47.6	2	0	3	33	1.5 :1
426 - 450	3	438	1113	51.5	2	0	1	100	0.5 :1
451 - 475	4	463	1250	74.2	3	0	1	0	0.3 :1
476 - 500	3	488	1583	101.4	1	0	2	0	2:1
501 - 525	6	513	1783	127.6	3	33	3	0	1:1
526 - 550	6	538	2092	100.4	4	25	2	50	0.5 :1
551 - 575	14	563	2419	68.1	10	60	4	0	0.4 :1
576 - 600	34	588	2742	64.7	17	53	17	59	1:1
601 - 625	33	613	2906	67.9	25	88	8	63	0.3 :1
626 - 650	35	638	3077	47.5	20	70	15	47	0.8 :1
651 - 675	25	663	3628	69.8	14	93	11	46	0.8 :1
676 - 700	22	688	3639	122.7	15	67	7	57	0.5 :1
701 - 725	22	713	3905	81.6	9	89	13	46	1.4 :1
726 - 750	19	738	4318	84.3	11	82	7	47	0.6 :1
751 - 775	18	763	4307	91.3	12	100	5	60	0.4 :1
776 - 800	22	788	5341	137.1	11	91	9	78	0.8 :1
801 - 825	22	813	6080	108.1	12	100	8	100	0.7 :1
826 - 850	26	838	6406	103.3	16	100	8	100	0.5 :1
851 - 875	16	863	6670	290.0	11	91	2	100	0.2 :1
876 - 900	23	888	7654	176.3	9	100	9	100	1:1
901 - 925	17	913	8261	172.4	5	100	4	100	0.8 :1
926 - 950	7	938	8893	243.1	-	-	2	100	-
951 - 975	8	963	9919	590.7	-	-	-	-	-
976 - 1000	11	988	11150	3014.5	2	100	-	-	-

Table A-2. (Cont.)

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Weight (g) S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
1001 - 1025	-	1013	-	-	-	-	-	-	-
1026 - 1050	3	1038	12987	767.8	-	-	-	-	-
1051 - 1075	-	1063	-	-	-	-	-	-	-
1076 - 1100	1	1088	13094	1093.5	-	-	-	-	-
Total	410	-	-	-	216	78.2	142	64.1	0.66:1
Mean	-	-	4847	-	-	-	-	-	-

Table A-3. Mean weight, maturity and sex ratio by length interval for lake trout from Great Bear Trophy Lodge, 1973.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Weight (g) S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
276 - 300	1	288	300	3.16	1	0	-	-	-
301 - 325	-	313	-	-	-	-	-	-	-
326 - 350	-	338	-	-	-	-	-	-	-
351 - 375	-	363	-	-	-	-	-	-	-
376 - 400	1	388	550	3.16	-	-	1	0	-
401 - 425	1	413	800	3.16	-	-	1	0	-
426 - 450	6	438	979	45.83	5	0	1	0	0.2:1
451 - 475	2	463	1200	100.00	2	0	-	-	-
476 - 500	3	488	1163	25.00	1	0	2	0	2:1
501 - 525	5	513	1325	51.23	3	33	2	0	0.5:1
526 - 550	19	538	1718	71.94	13	31	6	17	0.5:1
551 - 575	34	563	1952	24.30	19	53	15	40	0.8:1
576 - 600	65	588	2151	24.69	46	54	19	47	0.4:1
601 - 625	101	613	2504	27.51	57	64	44	39	0.8:1
626 - 650	109	638	2859	35.49	57	65	52	58	0.9:1
651 - 675	69	663	3132	46.73	35	74	34	59	1:1
676 - 700	57	688	3634	58.16	31	68	26	39	0.8:1
701 - 725	36	713	3860	82.51	20	65	16	21	0.8:1
726 - 750	23	738	4293	87.64	9	56	14	44	0.9:1
751 - 775	19	763	4430	120.71	10	70	9	13	0.9:1
776 - 800	12	788	5040	249.98	4	25	8	20	2:1
801 - 825	11	813	5436	172.16	6	50	5	50	0.8:1
826 - 850	4	838	6787	419.01	2	0	2	0	1:1
851 - 875	2	863	6675	75.00	2	0	-	-	-
876 - 900	4	888	6225	595.82	2	50	2	0	1:1
Total	583	-	-	-	325	58.6	259	42.5	0.8:1
Mean	-	-	3317	-	-	-	-	-	-

Table A-4. Mean weight, maturity and sex ratio by length interval for lake trout from Cameron Bay Lodge, 1972 and 1973.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Weight (g) S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
376 - 400	2	388	637.5	87.5	-	-	2	0	-
401 - 425	4	413	662.5	112.5	3	0	1	0	0.3 :1
426 - 450	10	438	1480.0	476.4	5	0	5	0	1:1
451 - 475	4	463	1243.8	182.1	3	0	2	0	0.7 :1
476 - 500	5	488	1270.0	165.3	4	0	1	0	0.3 :1
501 - 525	10	513	1387.5	121.9	5	0	5	20	1:1
526 - 550	17	538	1811.8	70.7	10	10	9	11.1	0.9 :1
551 - 575	11	563	2043.2	171.1	8	12.5	4	25.0	0.5 :1
576 - 600	40	588	2381.3	214.9	25	36.0	15	40.0	0.6 :1
601 - 625	31	613	2631.5	48.1	12	58.3	19	57.9	0.6 :1
626 - 650	41	638	2901.2	76.9	23	60.9	19	73.7	0.8 :1
651 - 675	31	663	3102.4	87.2	13	46.2	19	63.2	1.5 :1
676 - 700	23	688	3529.4	126.4	11	36.4	12	50.0	1.1 :1
701 - 725	17	713	3663.2	143.3	3	33.3	14	71.4	4.7 :1
726 - 750	15	738	4421.7	179.4	5	60.0	10	60.0	2:1
751 - 775	4	763	4725.0	131.5	1	-	3	33.3	3:1
776 - 800	4	788	5243.8	245.0	3	33.3	1	-	0.3 :1
801 - 825	3	813	5616.7		2	50.0	1	-	-
826 - 850	2	838	5287.5	787.5	-	-	2	-	-
851 - 875	1	863	6075.0	-	-	-	1	-	-
Total	275	-	-	-	136	35.3	145	47.6	1.07:1
Mean	-	-	2763.6	-	-	-	-	-	-

Table A-5. Mean weight, maturity and sex ratio by length interval for lake trout from Great Slave Lake Lodge, 1972.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Range	S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
351 - 375	1	363	500.0	-	-	1	0	-	-	-
376 - 400	9	388	673.8	454 - 900	49	4	0	5	0	1.3 :1
401 - 425	5	413	808.0	600 - 1100	85	2	0	3	0	1.5 :1
426 - 450	14	438	978.4	600 - 1500	59	8	0	6	0	0.8 :1
451 - 475	30	463	1211.7	502 - 3000	74	15	20	15	7	1:1
476 - 500	33	488	1522.1	1000 - 3500	100	10	10	23	13	2.3 :1
501 - 525	35	513	1605.4	1200 - 2200	95	19	16	16	0	0.8 :1
525 - 550	54	538	2092.7	1500 - 7000	107	23	22	29	31	1.3 :1
551 - 575	42	563	2225.0	1600 - 2800	49	19	42	23	35	1.2 :1
576 - 600	48	588	2509.2	1400 - 3600	62	23	30	24	29	1:1
601 - 625	38	613	2810.8	1900 - 3600	60	16	38	21	24	1.3 :1
626 - 650	38	638	3410.3	2100 - 4700	101	16	44	22	32	1.4 :1
651 - 675	15	663	3944.0	3240 - 8600	346	5	0	10	10	2:1
676 - 700	21	688	3847.7	2700 - 4960	123	7	57	14	29	2:1
701 - 725	23	713	4522.2	2500 - 6330	246	13	31	10	30	0.8 :1
726 - 750	19	738	4977.9	3250 - 6100	277	6	17	13	31	2.2 :1
751 - 775	12	763	5813.3	3100 - 8200	405	7	43	5	20	0.7 :1
776 - 800	21	788	6303.3	3300 - 8400	323	8	50	13	31	1.7 :1
801 - 825	12	813	6733.3	3500 - 9000	393	8	38	4	50	0.5 :1
826 - 850	7	838	7928.6	5700 - 9000	396	2	50	5	60	2.5 :1
851 - 875	5	863	8840.0	8600 - 9200	112	4	75	1	-	0.3 :1
876 - 900	3	888	7766.0	7000 - 8500	433	1	100	2	-	2:1
901 - 925	2	913	9350.0	-	-	-	-	2	-	-
926 - 950	2	938	9950.0	-	-	1	100	1	-	1:1
951 - 975	2	963	11500.0	-	-	-	-	2	50	-
Total	491	-	-	454 -11500	3894.7	218	28.4	273	24.5	1.25:1
Mean	-	-	3190	-	-	-	-	-	-	-

Table A-6. Mean weight, maturity and sex ratio by length interval for lake trout from Frontier Lodge, 1973.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Range	S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
301 - 325	1	313	400	-	-	-	-	1	0	-
326 - 350	-	338	-	-	-	-	-	-	-	-
351 - 375	6	363	500	400 - 600	36.5	3	0	3	0	1:1
376 - 400	4	388	537.5	400 - 700	68.8	3	0	1	0	0.3 :1
401 - 425	22	413	789.5	500 - 2900	122.5	13	0	9	0	0.7 :1
426 - 450	46	438	914.1	500 - 2500	51.9	17	5.9	29	0	1.7 :1
451 - 475	57	463	1083.3	600 - 2500	45	34	5.9	23	0	0.7 :1
476 - 500	68	488	1314.7	900 - 2100	35.6	39	12.8	29	3.4	0.7 :1
501 - 525	75	513	1597.3	1000 - 2500	38.2	33	15.2	42	9.5	1.3 :1
526 - 550	98	538	1836.7	1100 - 3200	33.1	49	38.7	49	8.1	1:1
551 - 575	69	563	2086.9	1300 - 4000	57.1	32	40.6	37	10.8	1.2 :1
576 - 600	84	588	2626.2	1400 - 4000	68.5	51	68.6	33	21.2	0.7 :1
601 - 625	60	613	3185.0	2100 - 5200	85.5	30	56.6	30	40.0	1:1
626 - 650	40	638	3527.5	2400 - 4700	97.5	17	88.2	23	34.7	1.4 :1
651 - 675	27	663	4218.5	2000 - 5600	133.4	14	78.5	13	53.8	0.9 :1
676 - 700	15	688	4640.0	3700 - 5500	160.3	9	66.6	6	33.3	0.7 :1
701 - 725	7	713	5185.7	3500 - 6500	338.4	1	100	6	33.3	6:1
726 - 750	4	738	6475	6500 - 7000	347.5	1	-	3	33.3	3:1
751 - 775	-	763	-	-	-	-	-	-	-	-
776 - 800	2	788	6150	5550 - 7500	1160	-	-	2	100	-
801 - 825	2	813	7250	6900 - 7600	350	2	100	-	-	-
Total	687	-	-	400 - 7600	3229.8	348	39.1	339	15.9	0.97:1
Mean	-	-	2364.1	-	-	-	-	-	-	-

Table A-7. Mean weight, maturity and sex ratio by length interval for lake trout from Arctic Star Lodge, 1973.

Length Interval (mm)	No.	Class Mark	Weight (g) Mean	Range	S.E.	No. Males	% Mature	No. Females	% Mature	F/M Ratio
376 - 400	1	388	600	-	-	1	0	-	-	-
401 - 425	1	413	1000	-	-	1	0	-	-	-
426 - 450	-	438	-	-	-	-	-	-	-	-
451 - 475	1	463	800	-	-	1	0	-	-	-
476 - 500	6	488	1483	1200 - 1600	60.0	3	33	3	67	1:1
501 - 525	8	513	1700	1350 - 1900	59.0	4	75	4	25	1:1
526 - 550	5	538	1710	1600 - 1800	45.8	1	100	4	0	4:1
551 - 575	8	563	2325	2100 - 2500	59.0	6	84	2	50	0.3 :1
576 - 600	4	588	2475	2100 - 3000	193.0	-	-	4	25	4:1
601 - 625	2	613	3100	2700 - 3500	400.0	1	100	1	100	1:1
626 - 650	2	638	4300	3600 - 5000	700.0	-	-	2	50	-
651 - 675	-	663	-	-	-	-	-	-	-	-
676 - 700	2	688	4900	4300 - 5300	600.0	1	100	1	100	1:1
701 - 725	1	713	5800	-	-	-	-	1	100	-
726 - 750	2	738	5550	5500 - 5600	50.0	2	100	-	-	-
751 - 775	2	763	6750	6100 - 7400	650.0	1	100	1	-	1:1
776 - 800	-	788	-	-	-	-	-	-	-	-
801 - 825	-	813	-	-	-	-	-	-	-	-
826 - 850	-	838	-	-	-	-	-	-	-	-
851 - 875	-	863	-	-	-	-	-	-	-	-
876 - 900	1	888	8780	-	-	-	-	1	-	-
Total	46		-	1200 - 8780	2816.8	22	68.2	24	41.6	1.09:1
Mean	-		2778	-	-	-	-	-	-	-

Table A-8. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Bear Lake Lodge, 1973.

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
7	2	382	7.5	650	50	1.16	2	0	-	-	-
8	2	392	2.5	700	0	1.16	1	0	1	0	1:1
9	1	265	-	200	-	1.07	-	-	1	0	-
10	1	495	-	1300	-	1.07	-	-	1	0	-
11	2	407	7.5	725	125	1.07	1	0	1	0	1:1
12	7	510	37.0	1614	338	1.21	6	0	1	0	0.2 :1
13	6	489	34.4	1414	323	1.21	4	0	2	0	0.5 :1
14	4	549	33.4	1850	333	1.11	1	0	3	0	3:1
15	9	573	10.3	2133	113	1.13	2	0	7	14	3.5 :1
16	7	597	46.8	2514	517	1.18	3	33	4	0	1.3 :1
17	6	581	37.1	2483	476	1.26	5	40	1	0	0.2 :1
18	9	587	25.3	2406	314	1.19	6	33	3	0	0.5 :1
19	15	634	12.7	3000	138	1.18	10	50	5	20	0.5 :1
20	42	629	80.0	3096	90	1.23	23	70	19	47	0.8 :1
21	31	638	11.6	3105	128	1.22	20	70	11	36	0.6 :1
22	21	653	14.7	3248	185	1.17	14	86	7	29	0.5 :1
23	16	647	13.8	3331	157	1.23	10	70	6	17	0.6 :1
24	16	703	22.5	4244	373	1.22	6	100	10	70	1.7 :1
25	15	698	22.4	4080	263	1.20	5	80	10	30	2:1
26	4	746	77.1	5325	1391	1.28	4	100	-	-	-
27	25	679	12.3	3996	153	1.27	10	100	15	47	1.5 :1
28	21	671	8.3	3771	153	1.25	10	100	11	73	1.1 :1
29	15	657	10.5	4244	194	1.26	6	100	9	67	1.5 :1
30	8	645	18.9	4080	584	1.40	3	100	5	60	1.7 :1
31	21	684	12.9	4325	130	1.19	14	100	7	57	0.5 :1
32	8	658	19.8	3996	242	1.20	5	100	3	0	0.6 :1
33	12	708	14.1	4367	172	1.23	4	100	8	50	2:1

Table A-8. (Cont.)

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
34	5	682	11.1	4370	125	1.17	1	100	4	100	4:1
35	7	671	26.1	4367	520	1.33	3	100	4	50	1.3 :1
36	15	715	18.5	4043	328	1.20	11	100	4	100	0.4 :1
37	5	709	13.5	4120	225	1.16	3	100	3	100	0.7 :1
38	7	721	13.3	4229	269	1.13	2	100	5	60	2.5 :1
39	5	684	24.2	3900	503	1.22	4	100	1	100	0.3 :1
40	2	760	-	4100	200	0.93	2	0	-	-	-
41	9	705	25.0	4111	412	1.17	6	83	3	67	0.5 :1
42	7	675	9.4	3507	187	1.14	3	67	4	75	1.3 :1
43	7	697	16.0	3743	143	1.10	6	67	1	100	0.2 :1
44	2	676	17.5	3750	450	1.17	2	50	-	-	-
45	3	687	31.8	3767	623	1.16	1	100	2	100	2:1
46	3	704	12.3	3933	120	1.13	1	0	2	50	2:1
47	4	719	48.0	4775	887	1.29	3	100	1	100	0.3 :1
48	1	670	-	3700	-	1.23	-	-	1	100	-
49	2	683	12.5	4850	650	1.53	1	0	1	100	1:1
50	1	750	-	4500	-	1.07	-	-	1	100	-
51	2	820	100.0	5650	1550	1.02	1	0	1	100	1:1
52	1	690	-	4300	-	1.31	1	0	-	-	-
53	2	640	10.0	3300	-	1.26	1	0	1	100	1:1
Total	416	-	-	-	-	-	227	73.6	189	48.1	0.83:1
Mean		664	-	3419	-	1.21	-	-	-	-	-

Table A-9. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Bear Lodge, Neiland Bay outpost, 1973.

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
7	1	410		900	-	1.31	-	-	1	0	-
8	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-	-
11	3	451	21.9	1283	235.1	1.39	3	0	-	0	-
12	5	504	25.5	1610	223.8	1.26	-	-	5	0	-
13	5	530	47.6	2000	525.4	1.34	2	0	3	0	1.5 :1
14	2	510	50.0	1500	500.0	1.13	2	0	-	-	-
15	12	605.4	20.2	2613	202.2	1.17	5	20	7	0	1.4 :1
16	8	607.3	17.6	2581	164.7	1.15	6	33	2	0	0.3 :1
17	10	628.3	14.7	2895	179.9	1.17	6	17	4	25	0.7 :1
18	6	680.0	24.4	3308	260.9	1.05	3	67	3	33	1:1
19	28	656.4	13.5	3275	149.7	1.16	16	69	12	25	0.8 :1
20	28	678.8	14.0	3670	183.9	1.17	18	72	10	80	0.6 :1
21	23	642.9	14.7	3287	184.3	1.24	13	85	10	10	0.8 :1
22	13	690.5	22.4	3942	241.3	1.20	6	83	7	86	1.2 :1
23	12	698.9	26.3	4017	329.1	1.18	7	86	5	60	0.7 :1
24	18	686.4	25.1	4014	352.6	1.24	12	92	6	67	0.5 :1
25	6	696.3	49.8	4483	693.0	1.33	5	60	1	100	0.2 :1
26	5	785.0	31.6	5560	521.9	1.15	2	100	3	100	1.5 :1
27	12	762.1	29.4	5244	444.0	1.19	7	86	5	80	0.7 :1
28	15	691.9	25.0	4200	373.0	1.27	10	100	5	100	0.5 :1
29	8	702.3	30.7	4044	390.0	1.17	6	100	2	100	0.3 :1
30	14	800.4	23.8	5886	438.0	1.15	9	100	5	100	0.6 :1
31	9	788.9	33.9	5658	583.0	1.15	6	100	3	100	0.5 :1

Table A-9. (Cont.)

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
32	10	754.8	37.9	5339	608.0	1.24	7	100	3	100	0.4 :1
33	8	801.9	23.0	6031	403.0	1.17	4	100	4	100	1:1
34	12	819.9	32.5	6204	556.0	1.13	5	100	7	100	1.4 :1
35	6	789.7	56.7	5783	960.0	1.17	4	100	2	100	0.5 :1
36	8	728.8	36.6	4356	672.0	1.13	4	100	4	75	1:1
37	6	809.7	35.0	6058	803.0	1.14	5	100	1	0	0.2 :1
38	3	711.7	80.1	4733	1408.0	1.31	3	100	-	-	-
39	2	813.5	71.5	5625	1125.0	1.04	2	100	-	-	-
40	4	783.8	32.1	5500	637.0	1.14	3	100	1	100	0.3 :1
41	3	754.0	65.6	5217	1380.0	1.22	2	100	1	100	0.5 :1
42	1	910.0	-	7600	-	1.01	1	100	-	-	-
43	2	882.5	42.5	7450	1050	1.08	2	100	-	-	-
44	2	632.5	52.5	3625	375	1.43	1	100	1	100	1:1
45	1	850.0	-	6250	-	1.02	1	100	-	-	-
Total	311	-	-	-	-	-	188	79.3	123	58.5	0.65:1
Mean	-	727.7	-	4847.4	-	1.19	-	-	-	-	-

Table A-10. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Bear Trophy Lake, 1973.

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
5	1	296	-	300	-	1.16	1	0	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-
8	1	448	-	950	-	1.17	1	0	-	-	-
9	1	443	-	900	-	1.04	1	0	-	-	-
10	4	456	14.0	1000	78	1.05	1	0	3	0	3:1
11	2	426	48.5	850	300	1.12	-	-	2	0	-
12	4	503	31.5	1387	206	1.08	3	0	1	0	0.3 :1
13	10	515	13.1	1445	94	1.03	5	0	5	20	1:1
14	4	539	19.6	1688	222	1.07	2	0	2	0	1:1
15	15	572	8.8	2018	98	1.07	5	20	10	20	2:1
16	23	595	7.9	2258	104	1.06	11	36	12	25	1:1
17	17	612	10.9	2499	152	1.09	8	38	9	67	1.1 :1
18	25	627	11.6	2675	151	1.08	13	39	12	25	0.9 :1
19	21	607	10.1	2337	130	1.04	14	50	7	14	0.5 :1
20	48	640	9.2	2825	126	1.09	23	65	25	44	1.1 :1
21	27	642	11.2	2812	148	1.06	14	57	13	39	0.9 :1
22	41	642	7.9	2948	142	1.12	27	48	14	50	0.5 :1
23	25	639	11.7	2840	179	1.09	13	69	12	75	0.9 :1
24	32	638	7.9	2820	106	1.08	17	65	15	53	9:1
25	22	679	15.1	3436	238	1.11	9	78	13	39	1.4 :1
26	23	661	12.7	3234	218	1.12	12	67	11	55	0.9 :1
27	32	674	10.5	3442	190	1.12	19	63	13	31	0.7 :1
28	15	661	13.8	3039	193	1.05	9	78	6	67	0.7 :1
29	13	682	18.3	3636	315	1.15	6	50	7	86	1.2 :1
30	5	685	49.7	3050	456	0.95	3	100	2	0	0.3 :1
31	8	666	16.1	3321	278	1.12	5	100	3	33	0.6 :1

Table A-10. (Cont.)

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
32	9	677	14.6	3256	181	1.05	6	50	3	67	0.5 :1
33	10	695	18.0	3875	391	1.15	4	50	6	33	1.5 :1
34	12	674	15.1	3398	194	1.11	10	70	2	0	0.2 :1
35	7	699	17.3	3807	354	1.11	3	67	4	0	1.3 :1
36	9	718	22.6	3938	377	1.06	7	57	2	0	0.3 :1
37	-	-	-	-	-	-	-	-	-	-	-
38	-	-	-	-	-	-	-	-	-	-	-
39	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	-	-	-	-	-	-	-
41	2	670	20.0	3325	575	1.11	1	100	1	0	1:1
42	3	690	36.7	3833	67	1.16	-	-	3	67	-
43	3	677	10.6	3333	333	1.07	3	100	-	-	-
44	2	707	12.5	5725	375	1.62	1	100	1	100	1:1
45	-	-	-	-	-	-	-	-	-	-	-
46	-	-	-	-	-	-	-	-	-	-	-
47	-	-	-	-	-	-	-	-	-	-	-
48	-	-	-	-	-	-	-	-	-	-	-
49	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	-	-	-	-	-	-	-
51	-	-	-	-	-	-	-	-	-	-	-
52	-	-	-	-	-	-	-	-	-	-	-
53	1	880	-	-	-	1.00	-	-	1	0	-
Total	477	-	-	-	-	-	257	56.0	220	40.5	0.86:1
Mean	-	647	-	3317	-	1.10	-	-	-	-	-

Table A-11. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Cameron Bay Lodge, 1972 and 1973.

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
9	1	560	-	1900	-	1.08	-	-	1	0	-
10	2	485	35.0	952	498	0.83	2	0	-	-	-
11	4	522	14.8	1646	261	1.16	3	0	1	0	0.3 :1
12	3	538	54.2	1567	682	1.00	2	0	1	100	0.5 :1
13	5	448	16.4	799	76	0.89	3	0	2	0	0.7 :1
14	8	557	37.6	1985	370	1.15	6	50	2	50	0.3 :1
15	9	596	24.9	2396	227	1.12	3	33	6	17	2:1
16	5	518	46.2	1720	340	1.24	3	0	2	50	0.7 :1
17	6	586	30.5	2144	244	1.06	2	0	4	50	2:1
18	9	586	36.0	2131	363	1.06	5	20	4	25	0.8 :1
19	22	597	18.6	2318	180	1.09	9	22	13	8	1.4 :1
20	18	602	20.9	2532	200	1.16	8	38	10	10	1.3 :1
21	11	647	22.3	3098	297	1.14	3	67	8	38	2.7 :1
22	3	723	18.3	4033	319	1.07	1	0	2	50	2:1
23	8	657	46.4	3280	541	1.16	3	33	5	60	1.7 :1
24	5	644	51.7	3906	654	1.46	2	0	3	67	1.5 :1
25	7	582	25.0	2266	825	1.15	4	25	3	67	0.8 :1
26	1	825	-	6525	-	1.16	-	-	1	0	-
27	8	605	36.9	2672	496	1.20	3	33	5	20	1.7 :1
28	5	610	38.7	2515	453	1.11	2	50	3	67	1.5 :1
29	3	657	14.8	2883	249	1.02	2	100	1	100	0.5 :1
30	1	675	-	3825	-	1.24	1	100	-	-	-
31	4	631	23.8	2716	457	1.08	2	50	2	100	1:1
32	7	702	280.0	3980	542	1.15	2	50	5	100	2.5 :1
33	1	600	-	2951	-	1.37	1	0	-	-	-

Table A-11. (Cont.)

Age	No.	Length (mm)		Weight (g)		Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	S.E.	Mean	S.E.						
34	2	630	15.0	2525	175	1.01	1	100	1	0	1:1
35	1	585	-	2350	-	1.17	-	-	1	0	-
36	2	675	-	3888	13	1.26	-	-	2	100	-
37	2	633	12.5	2638	63	1.04	1	0	1	100	1:1
38	3	647	37.1	2958	698	1.09	1	0	2	100	2:1
39	4	695	17.6	3701	463	1.10	1	100	3	100	3:1
40	-	-	-	-	-	-	-	-	-	-	-
41	2	660	25.0	3840	435	1.34	-	-	2	100	-
42	2	636	29.0	3200	400	1.24	1	100	1	0	1:1
43	1	620	-	3200	-	1.34	1	100	-	-	-
44	1	615	-	2575	-	1.11	1	100	-	-	-
45	3	730	8.7	4117	158	1.06	-	-	3	100	-
46	-	-	-	-	-	-	-	-	-	-	-
47	1	622	-	2450	-	1.02	1	100	-	-	-
48	1	738	-	5150	-	1.28	-	-	1	100	-
Total	181	-	-	-	-	-	80	33.8	101	44.6	1.26:1
Mean	-	624	-	2764	-	1.12	-	-	-	-	

Table A-12. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Great Slave Lake Lodge, 1973.

Age	No.	Length (mm)			Weight (g)			Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	Range	S.E.	Mean	Range	S.E.						
7	1	400.0	-	-	700.0	-	-	1.09	-	-	1	0	-
8	2	417.5	385-450	32.5	800.0	600-1000	200.0	1.10	2	0	-	-	-
9	5	439.8	391-500	21.0	1012.0	610-1500	148.9	1.19	3	0	2	0	1.5 :1
10	21	483.5	385-620	14.2	1344.9	454-2500	131.7	1.19	8	14	14	10	1.8 :1
11	33	530.1	360-652	15.0	1822.5	500-3600	157.9	1.22	15	13	18	0	1.2 :1
12	35	532.4	405-615	9.3	1881.7	700-3500	120.7	1.25	17	18	18	27	1.1 :1
13	73	553.6	384-755	8.5	2135.7	600-4900	129.7	1.26	32	13	41	10	1.4 :1
14	36	603.4	467-780	15.5	2848.1	1040-7400	272.4	1.30	15	20	21	19	1.4 :1
15	32	589.9	440-750	15.6	2586.3	1100-6300	222.5	1.26	16	6	16	19	1:1
16	32	623.7	440-785	18.5	3273.1	900-6080	270.9	1.35	14	14	18	22	1.3 :1
17	35	662.5	495-810	17.9	3903.5	1500-8000	314.5	1.34	20	15	15	40	0.8 :1
18	23	632.8	472-820	23.9	3755.5	1200-7940	468.3	1.48	11	36	12	17	1.1 :1
19	18	645.9	473-808	23.2	3819.4	1500-7300	416.0	1.42	12	50	6	51	0.5 :1
20	29	707.5	512-870	22.1	5125.4	1800-9000	515.0	1.46	14	57	15	47	1.1 :1
21	20	702.3	510-930	32.2	5047.4	1740-10500	645.0	1.46	5	40	15	54	3:1
22	16	697.0	540-939	30.3	4762.5	2100-10900	606.8	1.41	6	84	10	10	1.7 :1
23	8	617.4	540-736	29.2	3287.5	2000-5800	480.5	1.40	2	50	6	33	3:1
24	7	637.4	555-775	22.2	3637.1	1600-5600	519.6	1.40	5	60	2	0	0.4 :1
25	11	716.7	615-970	36.2	5421.8	3000-11600	855.3	1.47	6	84	5	60	0.8 :1
26	4	597.0	473-655	41.8	2810.0	1580-4100	519.9	1.32	2	100	2	50	1:1
27	1	835.0	-	-	8500.0	-	-	-	-	-	1	100	-
28	1	640.0	-	-	3500.0	-	-	-	-	-	1	100	-
29	5	710.0	620-755	23.5	4620.0	2900-6500	652.0	1.29	3	33	2	50	0.7 :1
30	4	797.0	710-905	44.6	7400.0	5100-9000	876.0	1.46	-	-	2	50	-
Total	447	-	385-970	497.1	-	454-11600	8523.7	-	208	26.9	243	24.8	1.17:1
Mean	-	604.9	-	-	3190	-	-	1.32	-	-	-	-	-

Table A-13. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Frontier Lodge, 1973.

Age	No.	Length (mm)			Weight (g)			Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	Range	S.E.	Mean	Range	S.E.						
5	2	407.5	370-445	37.5	700.0	400-1000	300.0	1.03	-	-	2	0	-
6	3	371.6	320-405	26.2	433.0	400- 500	33.3	0.84	2	0	1	0	0.5 :1
7	15	477.5	365-675	20.1	1236.6	400-4000	229.3	1.13	7	0	8	0	1.14:1
8	36	491.9	400-720	12.2	1213.8	500-3700	110.6	1.02	20	0	16	0	0.8 :1
9	60	489.8	354-750	8.7	1243.3	600-2600	62.2	1.06	33	12	27	4	0.8 :1
10	86	511.9	405-780	5.3	1512.9	600-3700	63.6	1.13	47	17	39	0	0.8 :1
11	110	538.4	440-670	5.1	1934.5	700-4900	79.3	1.24	55	33	55	5	1:1
12	83	545.4	415-680	6.7	2086.1	600-5600	105.4	1.29	38	34	45	13	1.2 :1
13	81	555.6	425-678	6.3	2224.7	600-4300	108.8	1.30	38	45	43	23	1.1 :1
14	40	564.8	395-665	10.6	2508.8	450-4600	167.2	1.39	20	50	20	40	1:1
15	28	590.0	470-715	10.5	2850.0	1000-5100	223.8	1.39	19	74	9	22	0.5 :1
16	13	598.1	505-720	17.9	2992.3	1100-5000	392.8	1.40	6	83	7	57	1.2 :1
17	18	608.8	530-680	11.3	3216.6	1500-4900	288.0	1.43	10	80	8	50	0.8 :1
18	17	626.2	560-695	8.1	3464.7	2100-5000	205.8	1.41	8	63	9	56	1.1 :1
19	11	630.9	520-710	16.0	3454.5	1900-5200	363.2	1.38	6	50	5	80	0.8 :1
20	4	622.5	500-720	57.2	4225.0	1700-6500	1088.0	1.75	2	100	2	50	1:1
21	11	650.9	530-770	22.8	4163.6	1500-7300	567.3	1.51	5	67	6	33	1.2 :1
22	4	676.3	615-740	31.4	4350.0	2900-7000	911.5	1.41	1	100	3	0	3:1
23	3	525.0	610-640	15.0	2800.0	2500-3100	300.0	1.15	1	100	2	100	2:1
24	2	600.0	570-630	30.0	2400.0	2100-2700	300.0	1.11	2	100	-	-	-
25	2	570.0	560-580	10.0	1850.0	1900-2000	150.0	1.00	-	-	2	0	-
26	-	-	-	-	-	-	-	-	-	-	-	-	-
27	1	620.0	-	-	2200.0	-	-	-	1	0	-	-	-
28	4	591.0	520-630	24.0	2000.0	1500-2400	187.0	0.97	1	0	3	33	3:1
29	3	565.0	555-580	7.0	2033.0	1800-2500	233.0	1.13	2	50	1	0	0.5 :1
30	2	597.0	540-655	57.0	2350.0	2000-2700	350.0	1.10	2	100	-	-	-
30+	5	654.0	630-820	43.0	3300.0	1900-6000	923.0	1.18	5	67	-	-	-
Total	644	-	320-820	-	-	400-7300	-	-	331	35.9	313	17.3	0.95:1
Mean	-	544.7	-	-	1900.0	-	-	1.23	-	-	-	-	-

Table A-14. Mean length, mean weight, condition factor, maturity and sex ratio by age for lake trout from Arctic Star Lodge, 1973.

Age	No.	Length (mm)			Weight (g)			Condition Factor	No. Males	% Mature	No. Females	% Mature	F/M Ratio
		Mean	Range	S.E.	Mean	Range	S.E.						
10	2	407.5	415-400	7.5	700.0	600- 800	100.0	1.03	1	0	1	0	1:1
11	-	-	-	-	-	-	-	-	-	-	-	-	-
12	3	505.3	468-535	19.7	1433.3	1000-1700	218.5	1.11	3	33	-	-	-
13	3	535.0	-	-	1783.3	1750-1800	16.6	1.17	-	-	3	0	-
14	5	514.0	475-600	22.7	1720.0	1200-2500	224.5	1.27	1	100	4	25	4:1
15	4	550.3	485-648	36.2	2200.0	1500-3600	484.7	1.32	2	0	2	0	1:1
16	10	562.2	490-730	27.1	2495.0	1600-5500	424.0	1.40	6	100	4	75	0.71:1
17	-	-	-	-	-	-	-	-	-	-	-	-	-
18	4	625.5	600-700	24.8	3375.0	2300-5500	722.0	1.38	-	-	4	50	-
19	3	682.6	615-878	99.1	4360.0	2100-8780	2210.0	1.37	1	100	2	0	2:1
20	2	530.0	505-555	25.0	2050.0	1700-2400	350.0	1.38	2	50	-	-	-
21	2	576.5	-	-	2250.0	-	150.0	1.17	1	100	1	0	1:1
22	2	605.0	-	-	3550.0	-	-	1.60	1	0	1	100	1:1
23	-	-	-	-	-	-	-	-	-	-	-	-	-
24	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	-	-	-	-	-	-
26	-	-	-	-	-	-	-	-	-	-	-	-	-
27	1	760.0	-	-	6100.0	-	-	-	1	100	-	-	-
28	1	740.0	-	-	5600.0	-	-	-	1	100	-	-	-
Total	42	-	415-878	280.6	-	600-8780	4800	-	20	65.0	22	31.8	1.1 :1
Mean	-	566.7	-	-	2780	-	-	1.38	-				

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NOTES

MISSISSIPPI SILVERSIDES AND LOGPERCH IN THE SACRAMENTO-SAN JOAQUIN RIVER SYSTEM

The Mississippi silversides, *Menidia audens* Hay, and the logperch, *Percina caprodes* (Rafinesque), are two species of fish recently introduced into California that are rapidly expanding their ranges in the Sacramento-San Joaquin River system. The logperch was accidently introduced in 1953, into three ponds on Beale Air Force Base, Yuba County, which overflow into tributaries of the Yuba River (McKechnie 1966). Farley (1972) collected a logperch from the San Joaquin River near Mendota, indicating their range in California had greatly expanded. Mississippi silversides were introduced into Clear Lake and upper and lower Blue lakes, Lake County, in 1967, largely to help control the Clear Lake gnat, *Chaoborus astictopus* (Cook and Moore 1970). The population in Clear Lake has exploded. Recent collections indicate that they are now the single most abundant littoral zone species. They have not previously been recorded in California outside the Clear Lake Basin. This paper reports recent collections of the two species in the main Sacramento-San Joaquin River system and their introduction into reservoirs in Alameda and Santa Clara counties, in drainages that are part of the Sacramento-San Joaquin system.

Between August, 1972 and November, 1973 numerous fish collections were made with small mesh seines in sloughs and creeks flowing into the lower Sacramento River and the Sacramento-San Joaquin Delta as part of various research projects on the native fishes. These collections show the logperch to be abundant and widely distributed and the Mississippi silversides to be present in Putah and Cache creeks, Yolo County (Figure 1). On 2 August 1972, a collection was made in a large pool on Cache Creek near Capay, about 25 miles upstream from the Sacramento River and about 55 miles downstream from Clear Lake. Along with numerous white catfish (*Ictaiurus catus*), several species of centrarchids, carp (*Cyprinus carpio*), and goldfish (*Carassius auratus*), the collection contained hundreds of Mississippi silversides and one logperch. The collection indicates that the Mississippi silversides has access to the main Sacramento-San Joaquin River system, because the logperch could only have moved upstream from the Sacramento River and the silversides downstream from Clear Lake. A similar conclusion can be reached from Putah Creek collections made on 20 July and 9 October 1973, in which a total of six Mississippi silversides and three logperch was taken from the creek on the University of California, Davis campus, about 15 miles upstream from the Sacramento River. Additional logperch have been collected there at other times. Fifteen other species were collected from the same area. Since Putah Creek below the dam at Winters (upstream from Davis) was completely dry in September 1972, these fish must either have moved upstream from the Sacramento River (including the logperch) or downstream via irrigation canals from Clear Lake (Mississippi silversides).

FIGURE 1. Recent records of Mississippi
California.

Both species are also found in
Francisco Bay. Logperch have b
Reservoir, Alameda County, wher
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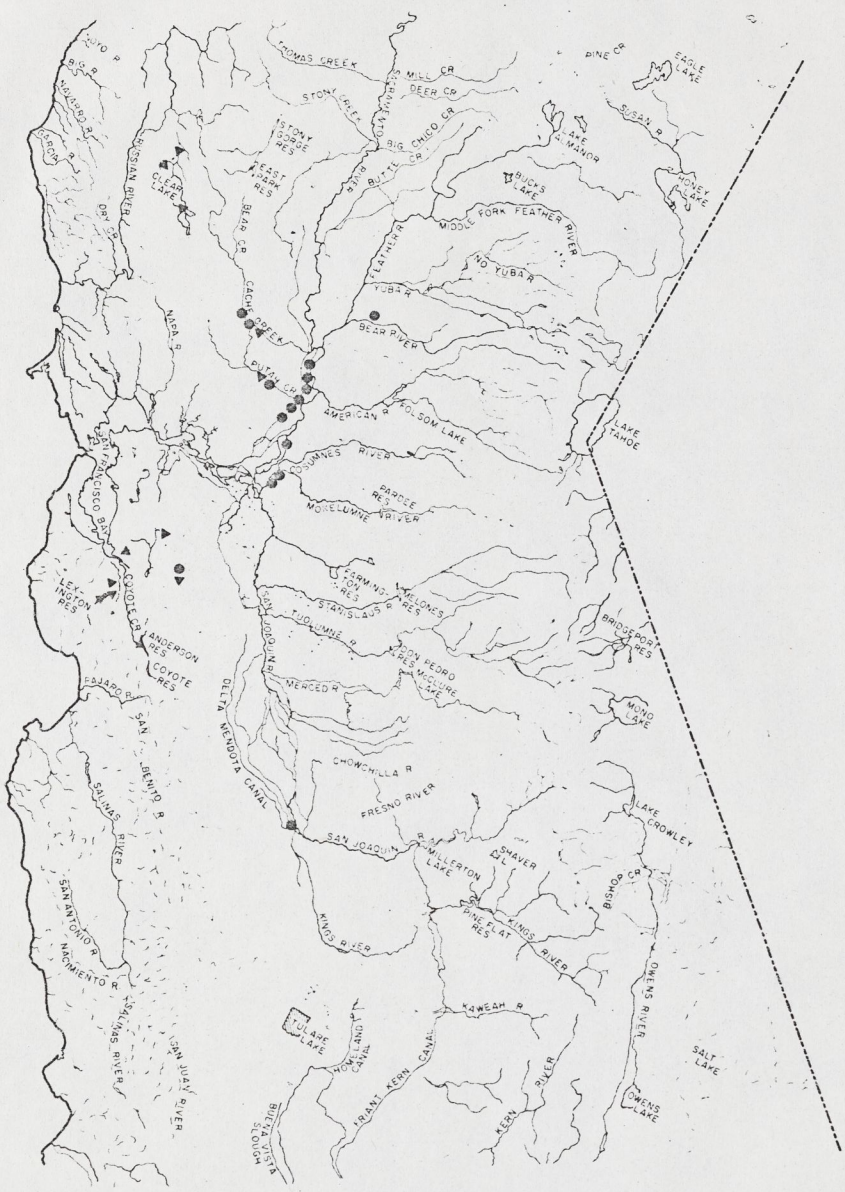

FIGURE 1. Recent records of Mississippi silversides (triangles) and logperch (circles) in California.

Both species are also found in reservoirs which drain into south San Francisco Bay. Logperch have been found thus far only in Del Valle Reservoir, Alameda County, where they are abundant. They presumably were pumped into the reservoir from the Sacramento-San Joaquin Delta via the Tracy pumping plant and South Bay Aqueduct. Mississippi silversides are now found in at least eight reservoirs and ponds

in Alameda and Santa Clara counties. All the fish apparently originated from an authorized experimental introduction into three ponds near Dell Avenue in Campbell, Santa Clara County, on 5 January 1968. The introduction consisted of 750 fish from Clear Lake. On 29 April 1969, 1,500 silversides were seined from the ponds and planted in Lake Elizabeth, in the Central Park of Fremont, Alameda County. On 27 May 1970, 1,000 fish were taken from Lake Elizabeth and planted in Shadow Cliffs Lake, Alameda County. Populations are now established at all three localities.

Although the above three introductions were authorized by California Department of Fish and Game personnel, a number of unauthorized introductions have been made into other reservoirs in the area, presumably by bait fishermen using fish from the original introduction sites. Silversides were collected from Lexington Reservoir, Santa Clara County, a large impoundment on Los Gatos Creek, in 1969. From Lexington Reservoir they have spread downstream to Vasona Reservoir and a series of ponds along Camden Avenue, Campbell. In September 1972, silversides were collected in Del Valle Reservoir, presumably the result of an unauthorized introduction. The numbers and size classes of silversides collected indicate they have been in the reservoir since at least 1971. Finally, on 12 October 1973, numerous silversides were taken from Anderson Reservoir, Santa Clara County, on Coyote Creek. Method and date of introduction are unknown, but the size classes present indicate they have been there at least one year.

Our information indicates that the logperch is well established and widespread in the lower Sacramento-San Joaquin River system, and that Mississippi silversides probably soon will be. The effect these two species may have on the fishes and invertebrates of the system, especially the Sacramento-San Joaquin Delta, is not known but neither is likely to be beneficial. The bottom living logperch has low value as a forage fish (Applegate, Mullan, and Morais 1966) and the presence of eggs in the stomachs of logperch collected from one slough (Moyle, unpublished data) indicates they can be significant predators on fish eggs, especially those of centrarchids. The effect of the Mississippi silversides on the Clear Lake ecosystem is controversial and has yet to be properly evaluated. However, as it is both a littoral and pelagic zooplankton feeder (Saunders 1959) and tolerant of brackish water (Hubbs, Sharp, and Schneider 1971), it could develop large populations in the Sacramento-San Joaquin Delta, adversely affecting the ecologically-similar Delta smelt (*Hypomseus transpacificus transpacificus*) and, perhaps, juvenile striped bass (*Morone saxatilis*). Although they can be important as forage fish in reservoirs (Mense 1967), they are unlikely to provide additional forage for game fishes but only replace species already present.

ACKNOWLEDGMENTS

Jamie Sturgess, Roderick Hobbs, Mark Caywood, David Dettman, and Ralph Elston made a number of the collections used in this study. The map was drawn by Chris Van Dyck.

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and H. W. Li, Division of Wil
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REFERENCES

Applegate, R. L., J. W. Mullan, and D. I. Morais. 1967. Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir. Proc. 20th Ann. Conf. S. E. Assoc. Game and Fish Comm., (1966) :469–482.

Cook, S. F., Jr., and R. L. Moore. 1970. Mississippi silversides, *Menidia audens* (Atherinidae), established in California. Trans. Amer. Fish. Soc. 99(1) :70–73.

Farley, D. G. 1972. A range extension for the logperch. Calif. Fish Game. 58(3) :248.

Hubbs, C., H. B. Sharp, and J. F. Schneider. 1971. Developmental rates of *Menidia audens* with notes on salt tolerance. Trans. Amer. Fish. Soc. 100(4) : 603–610.

McKechnie, R. J. 1966. Logperch, p. 530–531. *In* Alex Calhoun (ed.). Inland fisheries management. Calif. Dep. Fish and Game. 546 p.

Mense, J. B. 1967. Ecology of the Mississippi silversides, *Menidia audens* Hay, in Lake Texoma. Okla. Fish. Res. Lab. Bull. 6 :1–32.

Saunders, R. P. 1959. A study of the food of the Mississippi silversides, *Menidia audens* Hay, in Lake Texoma. M. A. Thesis, University of Oklahoma, 42 p. (unpublished).

Peter B. Moyle, Division of Wildlife and Fisheries, University of California, Davis, California 95616; Frank W. Fisher, California Department of Fish and Game, 3900 N. Wilson Way, Stockton, 95205, and H. W. Li, Division of Wildlife and Fisheries, University of California, Davis 95616. *Accepted January 1974.*

[1976]

Effect of the Introduction of the Mississippi Silverside (*Menidia audens*) on the Growth of Black Crappie (*Pomoxis nigromaculatus*) and White Crappie (*P. annularis*) in Clear Lake, California

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ABSTRACT

The growth of black crappie (*Pomoxis nigromaculatus*) and of white crappie (*P. annularis*) before a new forage fish, the Mississippi silverside (*Menidia audens*), became established in Clear Lake, California, was compared to their growth after the silverside had become established. Following the establishment of the silverside, growth rates of both species were slower than the presilverside growth rates for the first two years of life, and were apparently faster beyond year II. No correlation was found between changes in climatological conditions and crappie growth patterns. The overall impact of the silverside on the crappie fishery in Clear Lake may be negative if increased juvenile mortality rates result from the smaller sizes observed at the younger age classes.

The introduction of exotic planktivorous fishes into reservoirs and lakes is a common management tool used to convert underutilized zooplankton populations into forage fish that can be consumed by piscivorous game fishes. Such introductions commonly result in improved growth of adult game fishes (von Geldern and Mitchill 1975). However, planktivorous fishes tend to selectively remove the larger zooplankters from the zooplankton community (Brooks and Dodson 1965), so the growth and survival of juvenile game fishes that depend on such zooplankton may decline (von Geldern and Mitchill 1975). Thus the consequence of the introduction of a new forage fish must be evaluated on the basis of its impact on both adult and juvenile game fishes.

In the western United States, perhaps the most widely introduced forage fish has been the threadfin shad, *Dorosoma petenense*. Its effect on game fish growth is just beginning to be understood (von Geldern and Mitchill 1975). However, little is known about the impact of the more recently introduced Mississippi silverside. This fish has become established through introductions in a number of Oklahoma and California reservoirs and appears to be spreading rapidly (Moyle et al. 1974). It was first introduced into California in 1967 to control gnats and midges and to provide forage for game fishes in Clear Lake, Lake County (Cook and Moore 1970). The silverside selectively feeds on the largest zooplankters available (Elston 1976), and, in Clear Lake, constitutes 70 to 90 percent of the diet of adult black and white crappie (Li, Charters, and Roosa, unpublished). The purpose of this paper therefore is to evaluate the impact of the Mississippi silverside introduction on the growth of black and white crappie in Clear Lake throughout their life span.

STUDY AREA

Clear Lake, Lake County, with a surface area of 17,670 hectares, is the largest natural warmwater lake in California. It is located at a moderate elevation (440 m) on the eastern side of the geologically complex coastal foothills. It is shallow (maximum depth 18 m, average depth 8 m), with warm summer temperatures (20–25 C), and is highly eutrophic (Goldman and Wetzel 1963). Due to its shallowness and frequent strong winds Clear Lake is polymictic. Clear Lake has probably been in existence in one form or another for at least 100,000 years

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TABLE 1.—*Back-calculated growth increments of black crappie from Clear Lake, California, taken in 1968 (N = 78) and 1974 (N = 153) and the* t *values comparing the mean annual increments between the two samples. Underlined values were not used in the comparison because they would not have been affected by silverside introduction.*

Year class	N	Age group interval							
		0–I	I–II	II–III	III–IV	IV–V	V–VI	VI–VII	VII–VIII
				1968 Sample					
1962	1	86	35	17	18	19	18		
1964	6	82	36	30	22				
1965	35	76	56	28					
1966	33	76	68						
1967	3	86							
Mean increment		77	59	28	21	19	18		
				1974 Sample					
1966	2	62	40	39	30	21	24	28	20
1967	8	62	36	40	29	29	27	21	
1968	27	71	40	35	32	26	22		
1969	52	69	49	38	31	28			
1970	30	74	50	40	33				
1971	12	57	33	22					
1972	13	63	36						
1973	9	70							
Mean increment		69	44	37	32	27	23	27	20
df		219	215	171	124				
t		3.63	14.04	10	23				
$P \leq$		0.001	0.001	0.001	0.001				

(Moyle, in press) and so has endemic variants of the Sacramento-San Joaquin fish fauna (Hopkirk 1973). The present-day fish fauna is a mixture of native and introduced species, although the introduced species predominate.

METHODS

During March–May, 1968, 149 white crappie and 78 black crappie were collected from the lake using various sizes of seines. During August, 1974, 149 white crappie and 153 black crappie were collected using a 100 × 2.6 m, 0.13-cm mesh, beach seine. Standard lengths, weights, and scales were taken from all fish. Plastic impressions were made of all scales using an Ann Arbor Roller Press. The impressions were projected onto a wall with a 35-mm projector and each was read by at least two people. Disagreements were mediated by a third opinion. In order to make back-calculations of length, the width of the annulus on the right anterior lateral field of each scale (as projected) was measured. Criteria used in the identification of annuli were those of Vanderpuye and Carlander (1971).

The proportional method of back calculation was used because the relationship between scale length and body length in crappie has been demonstrated to be linear (e.g., Vanderpuye and Carlander 1971; Nelson 1974). Mean standard lengths of each age were first estimated by averaging the back-calculated lengths from all fish of each species. The back-calculated lengths for the first two years of life for the 1966 and 1967 year class fish collected in 1974 were not used in calculating the overall mean standard lengths for the 1974 samples because growth in these years could not have been influenced by the Mississippi silverside. A paired t test was used to compare the mean annual growth increments at each age between fish from 1968 and 1974. This test has the advantage that a growth model does not need to be assumed for comparative analyses (Casteel 1975). For black crappie, only the mean annual growth increments for the first four years of life were compared, because only one fish older than that was taken in 1968. The t test was also used to compare the growth rates of the two species to each other.

In order to see if there was any correlation between changing climatological conditions and changes in crappie growth that might confound the effects of the silverside introduction on their growth, annual climatological data from U.S. Weather Bureau records for the region were compared to the annual growth increments between ages I and II for

TABLE 2.—*Back-calculated growth increments of white crappie from Clear Lake, California, taken in 1968 (N = 149) and 1974 (N = 147) and the t values comparing the mean annual increments between the two samples. Underlined values were not used in the comparison because they would not have been affected by silverside introduction. NS = not significant.*

Year class	N	Age group interval						
		0–I	I–II	II–III	III–IV	IV–V	V–VI	VI–VII
				1968 Sample				
1962	2	64	24	24	39	22	19	
1963	2	66	101	36	25	26		
1964	49	63	53	44	29			
1965	60	74	86	35				
1966	35	73	89					
1967	1	70						
Mean increment		70	75	39	29	24	19	
				1974 Sample				
1967	3	51	39	43	31	31	17	27
1968	4	35	47	44	37	40	33	
1969	11	71	58	43	35	35		
1970	10	52	42	39	42			
1971	58	51	39	43				
1972	55	60	55					
1973	6	67						
Mean increment		56	47	43	37	35	26	27
df		294	287	197	79	20	7	
t		7.27	17	7.16	12.3	7.3	1.25	
$P \leq$		0.001	0.001	0.001	0.001	0.001	NS	

both species, for all years from 1962 to 1973. Spearman's test of rank correlation was used (Langley 1970, p. 199).

RESULTS

Following the introduction of the Mississippi silverside, the growth patterns of both black and white crappie changed in similar ways. Mean annual growth increments of both species to ages I and II were significantly smaller but most of the increments were significantly larger at subsequent ages (Tables 1 and 2). This resulted in the changes observed in mean length at each age class for both species (Table 3). Some discrepancies occur between the mean annual growth increments of age I and II black crappie of the 1966 and 1967 age classes listed under both 1968 and 1974 samples. We believe this is mainly attributable to small sample sizes, primarily in the 1974 sample.

The black crappie grew faster during the 0+ to age I interval than the white crappie but the white crappie always grew faster than the black crappie at succeeding ages (Tables 1 and 2). This was true both before and after the silverside was introduced. It is interesting to note that the negative effect of the silverside introduction was much greater on the white crappie and the stimulation of growth rate during later age classes was greater for the black crappie (Table 4).

Climatological conditions at Clear Lake varied little from year to year during the

TABLE 3.—*Mean back-calculated lengths of black and white crappie in Clear Lake, California, before (1968) and after (1974) the introduction of the Mississippi silverside. NS = not significant.*

Year	Age							
	I	II	III	IV	V	VI	VII	VIII
				Black crappie				
1968	77	136	158	168	175	193		
1974	69	113	150	186	210	225	245	255
df	219	215	171	124				
$P \leq$	0.001	0.001	NS	NS				
				White crappie				
1968	70	145	178	189	213	193		
1974	56	103	138	184	225	226	239	
df	294	287	197	79	20	7		
$P \leq$	0.001	0.001	0.001	NS	NS	NS		

TABLE 4.—*Average annual increments in length of black and white crappie in Clear Lake, California, before (1968) and after (1974) the introduction of the Mississippi silverside. NS = not significant.*

	Age interval					
	0–I	I–II	II–III	III–IV	IV–V	V–VI
	1968 Sample					
Mean increment						
black crappie	77	59	28	21		
white crappie	70	75	39	29		
Degrees of freedom	225	221	153	58		
Level of significance	0.001	0.001	0.001	0.001		
	1974 Sample					
Mean increment						
black crappie	69	44	37	32	27	23
white crappie	56	47	43	37	35	26
Degrees of freedom	285	281	215	115	53	42
Level of significance	0.001	NS	0.001	0.001	0.001	NS
	1968–1974					
Increment change						
black crappie	–8	–15	9	11		
white crappie	–14	–28	4	–3		

study period. No significant correlation ($P > 0.10$) was found when annual growth increments for both species were compared to mean annual temperatures, mean July temperatures (hottest months), mean December temperatures (coldest month), and total annual precipitation. A significant correlation ($P < 0.05$), however, was found between the annual growth increments of both species, indicating that both species were being affected in a similar fashion by environmental factors affecting the growth rates.

DISCUSSION

This study strongly suggests that the changes in the growth rates of the two crappie species observed during the study period are related to the establishment of the Mississippi silverside in the lake. The establishment of the large silverside population was the only major man-caused environmental change that took place, and there were no major climatological fluctuations.

The most significant change in the pattern of crappie growth following the silverside introduction was the reduction in growth in the first two years of life by both species. This may have been caused by interspecific competition for zooplankton among both crappie species and the silverside. After the first year of growth, crappies are able to prey upon the abundant silverside and thus 1974 growth rates to age III exceed those of 1968. We suspect that increased growth rates at older age classes were real and attributable to the abundance of prey in the form of silverside.

The overall impact of the Mississippi silverside on the crappie fishery in Clear Lake may be slightly negative, since slower growth in the first year of life is likely to be accompanied by increased juvenile mortality (Johannes and Larkin 1961; Murphy 1968). Slower growth rates during the first two years of life also probably reduces the reproduction contribution of first breeding crappie as fecundity is size dependent. Furthermore, both species typically first breed at lengths between 10 and 20 cm (Moyle, in press) and the age of first breeding may be delayed. Despite the apparent increase in growth rates of fish beyond age II, there may be little increase in reproductive capacity of the population because size increases conferred by the silverside introduction do not become manifest until ages IV and V for black crappie and white crappie, respectively. In fact we suggest that reduced and delayed recruitment into the population accompanied by heavy fishing mortality on the older age classes may reduce the reproductive potential of the population. An estimated 192,106 kg of white crappie and 524,234 kg of black crappie were removed from Clear Lake in 1969 and crappie fishing is the prime attraction of the lake to fishermen (Puckett 1972).

The changes in growth rates may also affect the population interactions between the two crappie species. Black crappie were introduced into the lake about 1915, whereas white crappie were introduced in the early 1950's (Moyle, in press), yet the two species now seem to be about equally abundant in the lake (Li, Charters, and Roosa, unpublished). We do not know to what degree these two species compete in the lake, but white crappie are known to replace black crappie under turbid conditions. Eutrophication has increased at Clear Lake because of agricultural and land development (Goldman and Wetzel 1963). Turbidity of the Clear Lake at the present time is high. We recorded secchi disk readings from June 1974

to August 1975. The average for 29 determinations was 0.9 m ± 0.73 with a range from 0.2 to 3.5 m. However, interactions between the two species may have changed as a result of silverside introduction.

White crappie, prior to the introduction of the silversides, grew considerably faster than the black crappie and may have been gradually replacing them by being able to utilize the resources more efficiently and to reproduce at a faster rate. The introduction of the silverside seems to have decreased white crappie growth early in life more than black crappie growth although white crappie still grow slightly faster than the black crappie. The black crappie in Clear Lake feeds more on zooplankton than the white crappie; whereas the white crappie is more piscivorous (Li, Charters, and Roosa, unpublished). This may explain the differences in growth patterns between the two species.

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LITERATURE CITED

Brooks, J. L., and S. Dodson. 1965. Predation, body size, and composition of plankton. Science 150(3692): 28–35.

Casteel, R. W. 1975. Growth rate of *Ptychocheilus grandis* in central California 1000–1600 years ago. Wasmann J. Biol. 32(2): 281–296.

Cook, S. F., and R. L. Moore. 1970. Mississippi silverside, *Menidia audens* (Atherinidae), established in California. Trans. Am. Fish. Soc. 99(1): 70–73.

Elston, R. A. 1976. Ontogeny of size selective predation and feeding habits of the Mississippi silverside, *Menidia audens*, in Clear Lake, California. M.S. Thesis Univ. of Calif., Davis. 284 pp.

Goldman, C. R., and R. G. Wetzel. 1963. A study of the primary productivity of Clear Lake, Lake County, California. Ecology 44(2): 283–294.

Hopkirk, J. D. 1973. Endemism in fishes of the Clear Lake region. Univ. Calif. Publ. Zool. 96. 160 pp.

Johannes, R. E., and P. A. Larkin. 1961. Competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*) in two British Columbia lakes. J. Fish. Res. Board Can. 18(2): 203–220.

Langley, R. 1970. Practical statistics. Dover Press, N. Y. 399 pp.

Moyle, P. B. In press. Inland fishes of California. Univ. Calif. Press.

———, F. W. Fisher, and H. W. Li. 1974. Mississippi silversides and logperch in the Sacramento-San Joaquin River system. Calif. Fish Game 60(2): 145–147.

Murphy, G. I. 1968. Pattern in life history and the environment. Am. Nat. 92(7): 391–403.

Nelson, W. R. 1974. Age, growth and maturity of thirteen species of fish from Lake Oahe during the early years of impoundment, 1963–68. U.S. Fish Wildl. Serv. Tech. Rep. 77: 29 pp.

Puckett, L. K. 1972. Estimated angler use and success at Clear Lake, Lake County, California in 1969. Calif. Dep. Fish Game Env. Serv. Admin. Rep. No. 72-1. 27 pp.

Vanderpuye, C. J., and K. D. Carlander. 1971. Age, growth and condition of black crappie, *Pomoxis nigromaculatus* (LeSueur), in Lewis and Clark Lake, South Dakota, 1954 to 1967. Iowa State J. Sci. 45(4): 541–555.

Von Geldern, C., and D. Mitchill. 1975. Largemouth bass and threadfin shad in California. Pages 436–449 *in* Henry Clepper and Richard H. Stroud, eds. National symposium on biology and management of centrarchid basses. Sport Fishing Inst. Washington, D.C.

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FEEDING ECOLOGY OF THE PIT SCULPIN, *COTTUS PITENSIS*, IN ASH CREEK, CALIFORNIA

HIRAM W. LI AND PETER B. MOYLE[1]

ABSTRACT: The diet of the Pit sculpin, *Cottus pitensis*, consists mainly of benthic invertebrates and is similar to the diet of other stream-dwelling members of the genus *Cottus*. They feed at all hours but show a peak of feeding intensity in the early morning. Electivity indices indicate that they are highly selective in their feeding but that the reasons they select particular organisms are complex. They appear to be ecologically segregated from the three species that commonly occur with them, speckled dace (*Rhinichthys osculus*), Sacramento sucker (*Catostomus occidentalis*), and rainbow trout (*Salmo gairdneri*).

Freshwater sculpins of the genus *Cottus* are important components of cold water stream ecosystems over much of North America. Consequently, as part of a much larger study of the ecology of the fishes of the great Sacramento-San Joaquin drainage system of California, we undertook an intensive study of the feeding ecology of Pit sculpin, *Cottus pitensis*. The Pit sculpin is one of the most abundant and widely distributed fishes of the Pit River and its tributaries, which drain much of the northeastern corner of California before flowing into the Sacramento River. In Oregon, the Pit sculpin is considered to be a rare, and potentially endangered, species because of its restricted distribution in the state (Bond, 1966). Little is known about the biology of this species, partly because it has been recognized only recently as being distinct from the more widely distributed riffle sculpin, *Cottus gulosus* (Bailey and Bond, 1963.) A major purpose of this paper is to report on its feeding habits. However, since the diets of most stream dwelling species of *Cottus* have been found to be similar (e.g., Bailey, 1952; Bond, 1963; Millikan, 1968; Jones, 1972; Novak and Estes, 1974; Small, 1975; Moyle, 1976), we examined the feeding chronology of the Pit sculpin, factors affecting its selection of prey organisms, and the diets of three other species of fish that commonly occur with it.

METHODS

Fish were collected from Ash Creek, Lassen and Modoc Co, one of the larger tributaries to the upper Pit River. This stream was chosen because of its moderate size (typical summer flows, 400–700 l/sec), accessibility, and substantial populations of native fishes. All fishes were collected with a Smith-Root type Va electrofisher. Daytime samples were taken on 5 May, 21 June, 24 July, and 28 October 1973, and a night time sample on October 27, 1973. On 7–8 June 1974, samples of fish were collected at four hour intervals for twenty-four hours. Most fish were taken in riffles near the middle of the stream. All fish were preserved immediately after capture in a four percent solution of buffered formalin. Although the main object of the sampling was to obtain Pit sculpins, samples of speckled dace, *Rhinichthys osculus*, juvenile Sacramento sucker, *Catostomus occidentalis*, and rainbow trout, *Salmo gairdneri* were preserved when they were taken in association with the sculpins. Sacramento squawfish, *Ptychocheilus grandis*, hardhead, *Mylopharodon conocephalus*, California roach, *Hesperoleucus*

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TABLE 1. Mean percent composition by weight of all bottom samples (N = 88) from Ash Creek, May 1973 to June 1974, and caloric values of invertebrates collected 21 June 1973. Number in parentheses under kilocalories per organism is the number of organisms upon which the determination was based.

Organism	Percent composition	Kcal per gm dry wt.	Kcal per organism
Ephemeroptera			
Baetis	< 1	–	–
Ephemerella	2	–	–
Isonychia	3	4.621	1.194(1)
Centroptilum	1	–	–
Ameletus	1	–	–
Heptagenia	1	6.744	0.022(2)
Iron	4		–
Plecoptera			
Acroneuria	8	5.395	0.100(26)
Isoperla	< 1	–	–
Hemiptera			
Ambrysus	2	9.664	0.218(4)
Megaloptera			
Sialis	< 1	–	–
Tricoptera*			
Hydropsyche	34	5.131	0.021(66)
Rhyacophila	6	5.792	0.055(29)
Brachycentrus	11	4.129	0.024(41)
Helicopysche	3	7.138	0.103(20)
Leptocella	< 1	–	–
Limnephilidae	5	0.893	0.737(4)
Lepidoptera			
Paragyractis	2	–	–
Coleoptera			
Eubrianax	< 1	–	–
Dystiscidae	< 1	–	–
Elmidae	< 1	–	–
Diptera			
Atherix	< 1	–	–
Limnophila	5	5.914	0.166(3)
Chrionomidae	1	–	
Gastropoda			
Physa	4	1.427	0.223(8)
Ancola	< 1	1.393	0.270(3)
Fluminicola	3	1.245	0.049(25)
Pelycepoda			
Sphaerium	2	–	–
Turbellaria	1	–	–
Hirundinea	1	–	–
Oligochaeta	1	–	–
Amphipoda	1	–	–
Dace larvae	1	–	–

* All case cadisflies were weighed without cases.