

PROBLEMS OF FISH-LARVAE SURVIVAL IN NATURE AND THE REARING OF ECONOMICALLY IMPORTANT MIDDLE EUROPEAN FRESHWATER FISHES

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INTRODUCTION

In early times, when fish culturists began artificial brooding of fish eggs and consequent stocking of natural waters with fry, the value of these activities was unquestioned. It was naively taken for granted that if this practice were followed, one would more than make good the decrease of fish populations caused by commercial fishing. The complexity of the problems, as we now know them—or believe to know them—was not readily seen, but it seemed sound to believe that since eggs and fry were much more protected in the hatchery than in the wild, the percentage surviving to adult fish should be much greater. As we all know, the experiences with most methods and concepts did not lead to the expected successes. Many people working in fisheries management now think that the time is ripe for discarding the whole scheme.

Are they justified or would it be worthwhile to try again? Naturally not in the way it was done before, but with modern concepts based on special analyses. In my opinion, the effort should be made. What are the reasons for my optimistic views? At the beginning let me put forward two principal statements based on the results of studying fry of various salmonid fishes, but especially white fish (*Coregonus* spp.) and brown trout (*Salmo trutta*). (1) It is now firmly established that in our alpine lakes only one to ten adults will result from 10,000 naturally-spawned coregonid eggs. (2) On the other hand it is not difficult to raise the percent larval survival in the laboratory from 0.1 or 1 per thousand to practically 100 percent. No special devices are needed. One need only offer the fry enough light (over 100 lux) and a high enough density of zoo-plankters, preferably *Diaptomus* copepodites, and the mortality will approach zero. With a lowering of the food density and/or the light, survival will diminish and finally will reach zero. Therefore by varying these two natural environmental conditions, you may have 100 percent survival or none at all.

A series of experiments summarized in Table 1 which I performed 20 years ago show this double dependency. The experiments were carried out in glass tanks. Light intensity at the surface was measured with a Lange Photometer. The food concentration was chosen to approximate that found in the Mondsee in March.

At a light intensity of 600 lux, as seen in Table 1, the density of food organisms plays an important

role in influencing the *number* of fry that feed. If, however, an individual fry is able to capture food organisms at a high food density, it will also capture almost as many organisms in all except the lowest food densities.

TABLE 1
THE EFFECT OF LIGHT INTENSITY AND FOOD DENSITY (COPEPODITES) ON THE RATE OF SURVIVAL OF COREGONUS FRY

No. copepodites per liter	% of Fry feeding at lux							Relative feeding index								
	600	100	40	20	10	1	0.5	0.3	600	100	40	20	10	1	0.5	0.3
4.....	20	20	0	0	0	0	0	0	1.5	1.0	0	0	0	0	0	0
12.....	45	50	25	5	0	0	0	0	2.1	1.0	1.4	1.8	0	0	0	0
36.....	70	60	25	5	0	0	0	0	2.0	1.4	1.8	2.0	0	0	0	0
110.....	85	75	80	15	10	0	0	0	2.1	1.8	2.0	2.3	2	0	0	0
330.....	95	90	80	40	25	10	5	0	2.6	2.5	2.8	2.4	2.2	2.0	2.0	0
1000.....	100	95	100	60	35	20	15	0	2.8	2.9	2.7	2.4	2.4	2.5	1.3	0

Legend to Table: Coregonid fry of the Mondsee-race were used in this experiment. The left half of the Table shows the percentage of fry that fed at the different light intensities and the varying food-densities to which they were exposed. The right half of the Table gives the average relative amounts of food eaten by fry under the different conditions. Relative amounts are indicated by 0—none eaten; 1—one to three copepodites eaten; 2—gut partially filled; 3—gut well filled. Four copepodites per liter were chosen as a minimum experimental number on the basis of average numbers of copepodites per liter found in the Mondsee in March.

At a light intensity of 100 lux, one finds that there is practically no change in the percentage of feeding fry from that at 600 lux, although the relative *amount* of food that a fry eats is much lower at 100 lux than at 600 lux.

Other illuminating comparisons can also be made. In particular the one between feeding conditions (as expressed by light intensity and food density) and individual feeding capability (as expressed by the filling of the gut). The bottom horizontal row of figures in Table 1 shows that at a density of 1000 food organisms per liter, there is no significant difference in the percentage of fish feeding at light intensities of 600 to 40 lux; the percentage feeding then decreases rapidly. However, the amount that was eaten by those individuals which did feed was almost equal, down to a light intensity of one lux. These data are illustrative of the problem and the existence of individuality not only among the members of a single species, but also of a single race.

Two major questions seem to remain outstanding at this point. (1) What is the relation between the experimentally established data, illustrated in Table 1, and the natural ecological conditions of lakes contain-

¹ Translated by George O. Schumann.

ing coregonid fishes? and (2) In what way can the data provided by Table 1 be used to advantage in improving stocks of harvestable fish?

I shall discuss first the question of the relation between experiment and nature. Coregonid fishes spawn in cold water—some species and races on the falling water temperatures in the Fall, others during the Winter, and some upon rising temperatures in the Spring. The spawning habits and seasons of the same species may vary considerably in different lakes. In all cases, however, the spawned eggs sink to the lake bottom and, in most of them, spend all their developmental time at a temperature of 4° C. Approximately 75 to 80 days are required for development to hatching at this temperature, and fifteen days for the absorption of the yolk sac to a stage when the yolk-sac fry first begins to feed. The total developmental time from newly spawned egg to free-swimming fry is about three months. At this stage the fry are very small and live in open waters, or the pelagial zone of lakes. At the time of first feeding, a critical stage in the life history of the fry makes its appearance.

In most Austrian, South-German, and Swiss lakes coregonid fry are faced with the critical stage during February and March. The lakes may then still be covered with ice and snow and light intensities may reach very low levels at the water surface.

In the case of very deep lakes which do not freeze over, an unstratified condition exists and strong winds will cause a complete overturn of the water mass. Some deeper alpine lakes have an ice cover only once in three to seven years. Even though some deeper lakes may not freeze over—low temperatures reduce the amount of plankton to very low levels—in particular, copepodites are rare and nauplii are just beginning to appear. There may be as few as 30,000 to 50,000 copepodites below one m² of surface. Even these few organisms may be scattered into the depths by winds causing circulation of the lake water, resulting in densities of a few or only one “edible” crustacean per liter.

Feeding conditions for fry improve as the year proceeds. By the end of March the ice cover has left most of our lakes and from April on there will be more and more copepodites under one square meter of lake surface. The chances for a complete overturn of the lake occurring becomes less and less and by the end of April or early May, stable stratification is the rule. At this time copepodites concentrate between 0 and 7 m depth. Concomitantly, length of day and light intensity may rise above 100 lux and the number of copepodites per liter may increase to 20 or more. Should fry be stocked at this time it would seem that the chances of survival should be greater.

THE EFFECT OF TEMPERATURE

If it is true that the survival rate and feeding conditions are closely related as our experiments show, we should plant fry in late April or May to increase percent survival. The proper timing can be

achieved by manipulating temperature during development. I have been investigating the duration of development of fish eggs in relation to temperature on a broad scale. My results may be summarized as follows:

In general, European freshwater fish eggs develop within a temperature range of 0–27°C. Different fishes have different levels in this range. Coregonids and brown trout may be cultured at temperatures from 0–12°C with about equally good results. Char eggs produce exceptionally vigorous fry at 0°C, and losses begin to occur at 8–9°C caused by cracking of the egg-shells sometime before hatching. Northern pike has its safe interval between 6 and 18°C and carp between 15 and 27°C.

If the temperature is lowered by 10°C, developmental time increases by 5 times. This means that the time from fertilization to the feeding stage of coregonid eggs can be as short as 35 days or as long as six months. Therefore we are able to release feeding coregonid fry at a time when the chances for survival are maximal.

Formerly well water was used in many hatcheries because it is free of turbidity, relatively free of bacteria and not in danger of freezing. In our region well water has a fairly constant temperature (ca. 8°C). Coregonids take about 50 days to develop at this temperature which is at the upper range of their temperature tolerance. Because most coregonid races spawn between the second half of November and the first half of January, the fry from the hatcheries using well water had to be released in January or February. In performing this, holes had to be made through the ice and snow-covered lakes frequently. Stocking in this manner had little or no effect on the fish population!

Eggs of the European brown trout need 1.6 times the time for development needed by coregonid eggs at any temperature; however, considering only the interval from hatching to ready-to-feed size, trout fry need about 3 times as many days as the coregonid fry.

The velocity of development is increased or diminished 15 to 16% by a 1°C difference. The rate stays the same over the whole temperature range. Thus in coregonid and trout eggs this percentage is the same at the freezing point and 8 or 9°C above it. Furthermore the temperature coefficient (Q_{10}) of developing fish eggs may be as high as 5 while simple chemical reactions speed up 2 to 3 times by raising the temperature 10°C. All of the chemical and physical reactions occurring in embryological development may occur harmoniously and at very high rates, which is a remarkable achievement indeed.

THE FOOD SITUATION IN ALPINE LAKES

In Alpine lakes the feeding situation for coregonid fry does not improve continuously as the year proceeds. Rather there is a turning point in May. Toward the end of May diurnal plankton migration sets in and carries the crustacean plankton down to 10–20 m

during the daytime. The critical light intensity for the fry may be at 5 m and is certainly too low below 10 meters.

Two other "negative" factors may also exist. The size of zooplankters may be inappropriate. In our "home lake", the Mondsee, *Daphnia longispina* prevails in May, comprising 95% of the whole zooplankton mass. *Daphnia*, however, is too big to be eaten by coregonid fry.

SURVIVAL OF ALPINE FISHES

Thus far my intention has been to show how environmental conditions seem to determine the rate of survival in coregonid larvae. In the field these can be shown even more convincingly.

Carp ponds

To be suitable for coregonids, carp ponds should not be too small nor too shallow. They should have an area of several acres and a depth of 2 to 3 m, and be situated in regions where it does not get too hot, so that the water will not warm up above 20° C.

If one stocks a carp pond with coregonid fry, even right after the ice is gone, not less than 10 or 20% of the fry survive; a very good survival. But natural reproduction in these ponds is not possible because the eggs fall to the muddy bottom, are covered by silt and die.

Creeks

Stocking of brown and rainbow trout fry in creeks results in poor yields. Removal of the adults which are predators and also competitors for food will change the percentage of survival drastically. This was shown by the following field experiment. If we remove all the trout of a creek by means of electrical fishing gear and then stock it with fry, half a year later up to 50% of the fry may be harvested as fingerlings 7.5–13 cm long. Floods may diminish this percentage because the young fish may be driven downward into the bigger main river while simultaneously larger specimens living in this area may swim up and enter the stocked area, acting as predators. The rate of survival of stocked trout fry may be cut down to 10 to 20% but compared with the natural survival these figures are still very high.

Summarizing our trout fry creek-stocking results the following criteria are now used: Creeks should be 1) about 1–3 m wide; 2) 15–30 cm deep; 3) "summer cool"; 4) pass through agricultural areas which allow continuous "homeopathic" fertilization; 5) flow at a moderate speed not exceeding 32 cm/sec; 6) not endangered by floods; 7) have bottoms covered with gravel 2.5–10.5 cm in size; 8) interrupted by waterfall-steps (of a height of 12.5–30 cm) followed by small pools; 9) and have frequent hollows in their shoreline.

In such creeks, previously freed of all trout, then stocked with 50,000 fry per mile, it is sometimes possible to harvest 15,000–20,000 fingerlings per mile, with an average length of 10 cm each.

POPULATION DYNAMICS AND PHYSIOLOGY OF COREGONID RACES IN AUSTRIAN LAKES

It is not without reason that I place Ecology and the study of population dynamics foremost in fisheries research. A particularly good demonstration of this is offered by studies on the ecology of the young of various races of coregonid fishes.

Small physiological and morphological differences may, in certain biological situations, decide whether a larva lives or dies, hence these differences probably arose in response to factors influencing survival. Death or survival is determined by the interplay of two groups of conditions: the milieu and the innate larval character.

The principal deciding factors in the dynamics of space and time in the milieu have already been discussed; now the characteristics or peculiarities of the larvae will be considered. We have heard previous speakers discuss some aspects of the biology of her-ring, sardine and flounder larvae. The freshwater fish I have been discussing (*Coregonus* spp.) somewhat resembles the marine herrings in form and habit.

The European species of coregonids have been isolated since the end of the last glacial period, and although a species may have a wide distribution, in many cases each lake has evolved a distinct form or race. Sometimes more than one species may be found in the same lake but in this case each species has adapted to a particular niche. Presumably in like manner each lake has presented specific ecological demands to a species upon its entry into the ecosystem with the resultant evolutionary tendency, noteworthy in this family, to differentiate. Many of the racial characteristics such as egg size, oxygen requirements, etc., have become genetically fixed, while other characters, usually morphological, may be quite plastic.

Physiology

In this respect some of the physiological phenomena in the further development of coregonid larvae may be considered.

Catabolism (measured by loss of dry weight) and water uptake.

- a. Continual weight measurements beginning with the first day after hatching in unchanging temperature show that the dry substance of larvae is steadily reduced.
- b. If an unfed larva dies after utilizing all of its yolk reserve and other absorbable body tissue the body generally is reduced, depending upon races, to 40–60% of its hatching dry weight.
- c. The fresh body weight, on the other hand, behaves quite differently. During the passage of the first quarter of life after hatching the fresh weight increases slightly (about 10%), then decreases until death. Immediately before dying, the fresh weight is still 80% of the hatching weight. The water content of the larvae, beginning with hatching, continually increases. In this context the water content after hatching

amounts to 75%; at death about 90% of the fresh weight.

If one investigates eggs and larvae of the various coregonid races, one notices, first of all, a marked size difference. Egg and larval weights of the ten coregonid races investigated in the region of the northern Alps, vary in the relationship 1:2, or between 3.5 and 6.5 mg. Since the larval weight is proportional to the third power of the length, the length varies far less when expressed in absolute numbers. At the stage of first feeding, the length of the smallest coregonid larva is 9 mm and those of the largest group 11 mm. These small differences are significant. Since he is concerned with law and order, the theoretical biologist has an immediate interest in creating a biological model and this often means that small differences are overlooked. How little a model would indicate the heart of coregonid larval biology is shown by the results of the following simple comparative investigations.

An equal number of feeding sized coregonid larvae of various races were placed in groups of aquaria, and supplied with a known, and always equal number of crustacean plankters. The size of the zooplankters was varied in the various groups of experimental aquaria. Food density and illumination were judged to be optimal in all tests (levels of illumination exceeded 600 lux in all tests and food density was high). The results are summarized below and in Table II.

1. Tests with extremely large food organisms resulted in only a small percentage of the most capable race of larvae (the lake Hallstätter fish) being able to capture food and survive; the remainder starved.

2. Races of larvae only one mm smaller than the Hallstätter failed completely under such feeding conditions.

3. With the food size reduced, conditions would be easily established by which the Hallstätter larvae survived for the most part (75%) while about 10% of the larvae averaging one mm smaller (Mondsee fish) succeeded in finding food. The smallest race of larvae (Attersee fish) with a length of about 9 mm, still found nothing to feed upon and eventually all starved.

4. When in the course of the tests an even smaller sized food was offered (principally small to medium-sized stages of *Daphnia*) an increased feeding capability was observed for the smaller larvae. One could, on the other hand, increase the test sensitivity to food size at will by combination with graduated light intensity.

The simple determination of size differences in the larvae of various coregonid races naturally does not offer a key to the biology of the various races. Various sized food organisms were obtained from the Mondsee by the use of graded plankton nets. The measurements given in microns in Table 2 represent the mean opening of the net mesh. Each test ran for two hours during which fish were allowed to feed. The data on stomach contents given in the table refer to relative numbers; i.e., the "fullest" stomachs were equated to 100.

TABLE 2
PERCENTAGE OF FEEDING COREGONID LARVAE IN RELATION TO SIZE OF THE FOOD ORGANISM

Food Size in Microns	Hallstätter fish Av. Wt. 5.6 mg		Mondsee fish Av. Wt. 4.4 mg		Attersee fish Av. Wt. 3.7 mg	
	% Feeding	Fullness of Stomach	% Feeding	Fullness of Stomach	% Feeding	Fullness of Stomach
470-----	15	10	0	--	0	--
370-----	75	60	10	5	0	--
250-----	100	75	45	25	40	20
180-----	100	90	65	55	65	40

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In the laboratory, newly hatched larvae of all but one of the races investigated showed not the slightest interest in food—no matter how ideally offered. Only when the yolk sac is absorbed to a certain degree (thus the passage of a definite time-temperature span) is there awakened an interest for food in the larvae which begin feeding.

For the large race of the Hallstättersee this stage is reached at a dry weight of larvae of about 20% of the fresh weight. The larvae of the large pelagic race of *Coregonus* in the Traunsee behave similarly. In both cases we are dealing with relatively large larvae with an average fresh weight of about 6 mg. Investigations such as these were carried out during many periods of the year. It was demonstrated repeatedly, that the established values were quite nicely replicated.

In smaller races of larvae it was generally established that they only begin feeding very late in development; i.e. at a low percentage dry weight. The smallest larvae, the Attersee race, begin their feeding last at a dry weight of 16% of the fresh weight.

If one determines the time at which only 50% of a group of starved larvae are still capable of feeding, the sequence for the various races of larvae is reversed from that of the "first feeding" test. The larvae which began feeding last were also the earliest to become too weak to feed. Thus, for example, 50% of the large pelagic coregonid larvae of the Traun- and Hallstättersees still fed at a mean relative dry weight of 13%, while the small larvae of the Attersee reached this state with a relative dry weight of 15%.

Larvae from the Lake Hallstätter race were so weak at a relative dry weight of 10%, and those of the Attersee race at 14%, that all the members of test groups were unable to capture food when these weights were reached.

In other words, the various races of larvae remained capable of feeding for varying lengths of time after a period of starvation. If one expresses the times in days (at the uniform temperature of 5° C) then one obtains a time of 2 days in the most unfavorable case, and 23 days in the most favorable case (Table 3, vertical column to the right). During these times, of

course, conditions of optimal food density, food size and intensity of illumination prevailed.

TABLE 3
DEVELOPMENTAL RATES OF COREGONID LARVAE TESTS WERE CONDUCTED AT A TEMPERATURE OF 5° C

Coregonid Race	Fresh Weight of newly hatched larvae (mg)	Time at which 50% of the larvae begin feeding (days)	Duration of feeding capability after starvation (days)
Hallstättersee.....	5.6	33	23
Traunsee.....	5.8	33	23
Bodensee*.....	6.5	31	12
Obertrumersee.....	5.6	25	10
Bodensee†.....	4.6	17	4
Mondsee.....	4.5	23	5
Attersee.....	3.7	12	2

* Littoral form.

† Pelagic form.

It seems pertinent to mention here two exceptions, because these show that one can never be certain whether laws or conformities established for a particular situation also apply in general. In this case, the exceptions concern the larvae of the Bodensee whitefish *Coregonus macrophtalmus* and the larvae of the whitefish living in the Obertrumersee near Salzburg.

The noteworthy thing about the Bodensee whitefish and one which earlier investigations noted, was that the embryonic development took longer than is usual for the European coregonids. In fact, the longer developmental time means that those larvae at hatching are considerably more physically advanced than the larvae of any other European whitefish. The relative dry weight of the Bodensee whitefish is, just after hatching, somewhat more than 18% of the fresh weight. This is smaller than the relative dry weight of the Hallstätter whitefish larvae in a stage when 50% of these larvae begin feeding.

The Bodensee whitefish has the largest larvae of all the investigated European coregonids, and unlike most coregonids begins feeding almost immediately after hatching. One can, by means of a simple manipulation, induce the Bodensee whitefish eggs to hatch prematurely. This is done by raising the water temperature above 10° C near the end of the embryonic period of these eggs, which causes hatching at the same time as other races of coregonids. The relative dry weight of these newly hatched Bodensee larvae was found to be not the normal 18%, but in this case 25% of the fresh weight. The Bodensee larvae caused to hatch prematurely, but otherwise normal, showed no more interest in food than newly hatched Traunsee or Hallstättersee larvae. Most interestingly, however, they began to feed first, at a relative dry weight of 18.2%; thus at precisely the dry weight with which they normally begin to feed. (The Hallstätter larvae begin feeding at 20%).

We can see, therefore, that the general principle of the largest larvae feeding first does not always hold true.

Noteworthy peculiarities came to light during the investigation of Obertrumersee coregonid larvae. The size of the larvae of this race is about the same as the Hallstätter and Traunsee larvae. Against all expectations, however, the Obertrumersee larvae reached the stage of first feeding considerably later than any of the other larvae investigated, and on the other hand, became too weak to feed in a shorter time. As can be seen in Table 3, the duration of full-feeding capability lasted only 10 days.

Also in other tests (for example, the determination of minimum oxygen concentrations, food size) Obertrumersee larvae averaged poorer than similarly sized relatives from other lakes. One must conclude that there are cases in which other factors besides size are important, a type of superior instinct, or vitality, or both must also play a role.

Minimum oxygen requirements

Various fish species require differing, but usually family characteristic demands on the minimum oxygen concentration of the habitat. The salmonids need at least 3-4 mg/liter, the cyprinids 0.5-1 mg/liter.*

If one investigates the larvae of various races of coregonid fishes with this in mind, one finds astonishingly large variation, although still within the generally high values required by all salmonid fishes.

The studies reported here were carried out in the following way: feeding larvae were placed in all glass aquaria and 1) the oxygen concentration measured when 50% of the larvae lay motionless on the bottom; and 2) the oxygen concentration at which all larvae lay motionless on the bottom. In general, ten tests were made with each group of larvae, and it is emphasized that the test replicates gave oxygen values which at the most diverged only 13% from each other. If one considers, on the other hand, the performance of each of the individuals tested within one race, one finds again important and characteristic differences. At a water temperature of 6.5° C, suffocation began at 6 mg O₂/liter while a few larvae held out until an oxygen concentration of 1.9 mg/liter.

We will see later, that the smaller races of larvae require a much higher minimum oxygen concentration than the larger races. One can legitimately connect these differences with innate resistance because when one conducts an oxygen test with coregonid larvae which are a few days away from dying, a 2-7 mg/liter higher minimum oxygen concentration is recorded.

At higher temperatures the required minimum concentrations are generally higher than at lower temperatures. One must therefore always work with the same temperatures when making comparisons.

Table 4 presents several characteristic oxygen values for larvae of the Hallstätter coregonid. The values given in Table 4 are average values which are reliably reproducible. On the other hand, however, the variation in the reactions of single individuals in a test is rather high, but also very reproducible. A test of the

* To convert mg O₂ to ml O₂ multiply by 0.7 (approximate).

latter type is given in Table 5. This test deserves special interest because here rather exact estimates of the variations in individual behavior were made at various temperatures on the larvae of Hallstätter whitefish.

TABLE 4
MINIMUM O₂ CONCENTRATION REQUIRED AT VARIOUS TEMPERATURES FOR HALLSTÄTTER LAKE COREGONID LARVAE

Temperature	O ₂ Concentration at which 50% of larvae lay motionless at the bottom of the aquarium, mg/liter	O ₂ Concentration at which 100% of larvae lay motionless at the bottom of the aquarium, mg/liter
6.5°-----	3.3	1.9
11.5°-----	3.7	2.1
19°-----	5.5 (†)	4.4 (†)

TABLE 5
THE O₂ CONCENTRATIONS AT WHICH THE FIRST 10% OF LARVAE LAY MOTIONLESS ON THE BOTTOM

Temperature	The first 10% of larvae on bottom at mg/L O ₂ .
6.5-----	6
11.5-----	6.9
19-----	7.5

TABLE 6
OXYGEN CONCENTRATION (MG/LITER) AT WHICH 50 TO 100% OF THE LARVAE OF DIFFERENT RACES DIED (11.5° C)

Race	Weight of Larvae in mg.	Oxygen concentration at which 50% lay motionless on bottom (Average values)	Oxygen concentration at which 100% lay motionless on bottom (Average values)
Hallstättersee-----	5.6	3.7	2.1
Traunsee-----	5.8	3.9	2.0
Bodensee*-----	6.5	4.3	2.6
Obertrumerssee-----	5.6	4.3	2.6
Bodensee†-----	4.6	4.3	2.6
Mondsee-----	4.4	4.3	2.8
Attersee-----	3.7	4.9	3.1

* Littoral form.
† Pelagic form.

In Table 6 all tests have been compiled which were made with larvae of various races. Among the various races of larvae, three groups are easily distinguishable: one particularly viable group of larvae (Hallstätter—and Traunsee); a homogeneous middle group on the basis of their oxygen requirements; and the race least vigorous in this respect, the whitefish of the Attersee.

The middle group is very close to the uppermost group in its minimum oxygen tolerance. However, it is highly noteworthy that the middle group contains larvae of considerable size variation. The Bodensee whitefish, and the whitefish of the Obertrumerssee seem to be out of sequence. If larval weight alone were

decisive, the Bodensee larvae would occupy the top position and the fish of the Obertrumerssee would also be in the upper group.

The sensitivity of various races for low oxygen concentrations is connected somehow with a "resistance factor", which would probably be shown in tests made with material having a poisonous effect, such as ammonia or chlorine. It is more than probable that one would find similar differentiating characteristics for the larvae of various races.

FROM LARVAE TO ADULT

When one reflects on the seemingly simple, but biologically complex fact, that survival among the larvae of many fishes is one in several thousand, while at the same time individuals once having attained a few centimeters in length stand a hundred or thousand fold chance of survival, one is led to the conclusion that a "species"—consists ecologically of many distinct though related parts. By this is meant that fish go through, on the way through larval to metamorphosed or adult forms, such important transformations, that it would appear rewarding, even necessary, to reinvestigate and describe them in certain time intervals.

It should be possible to test anew each stage in larval transformation, and possibly juvenile stages as well, to learn how and when the greatest losses in stock occur. One would surely learn that many of the dangers and sensitivities of one growth period are not so much lost in a succeeding period, but merely exchanged for new difficulties. Presumably, however, factors such as size and concentrations of food organisms along with intensity of illumination, become as always of less importance for survival at each succeeding growth stage. In coregonids, for example, fish of a length of about 25 mm and a weight of 100 mg are fully developed; the entire body is scaled, the swim bladder is filled, and the fins developed.

The differences between the index of survival or "stock potential" of larvae versus fully developed fry can be demonstrated most conclusively when one stocks lakes, which previously were without whitefish, with either feeding larvae or fully developed fry (of about 30 mm). We have performed this type of "big" experiment many times. The success of the experiment is determined naturally only by the later capture of grown fish. Although one cannot term this method an exact test of degree of development or maturity upon rate of survival, the scope of such biological experimentation leaves no other practical conclusion. In any event, some noteworthy results have been realized. In one lake we stocked one million whitefish larvae without a single grown fish being captured in the following years, despite all our efforts. In other similar cases the results were not much better. However, at least a few fish were later captured, but frankly 1 animal per ten thousand was never exceeded.

Stocking experiments utilizing fully developed fry gave completely different results. In one case we cap-

tured not less than 25% of the stocked fish as adults, and in other cases, which we could not hold so completely under our control, at least 10% of the fish were captured as adults. We naturally presume that the captures represent the minimum survival of stocked fish—as many, or more fish remained at large and therefore were not recognized as a surviving “percentage”.

Since we of this symposium are not dealing with special problems of management of whitefish lakes, I would like to point up, in closing, in the following special connection, some generally important facts. When one hopes to feed the larvae of any species of fish for any length of time and then release the fish in nature, a fundamentally important question arises: at what specific stocking size will the survival rate of cultured fish materially exceed that of the newly hatched, or wild fish? This question is at once clear when one considers the parallel increase in length and weight of growing larvae. The statement that a doubling of the length in young fish results in a 10 fold increase in weight, seems reasonably accurate upon examination. Young coregonids weigh about 15 mg at a length of 15 mm; at 20 mm, 40 mg; 30 mm,

150 mg; 40 mm, 400 mg, etc. It seems evident that, in light of these conditions, the expenditures necessary for rearing also increase about ten-fold with a two-fold increase in the length of the fish. Since as a rule, rearing of larval or juvenile fish deals with relatively very large numbers, a problem of considerable importance is to determine at which length, relative to rearing costs, the young fish achieve an optimum survival. One may attempt to determine this length or growth stage by experimentation. This length is that by which relative to the expenditure, a maximum yield can be expected. It is obvious that this type of experiment cannot alone deliver complete data. Thus, for example, nothing is said about the role of predators, disease, etc. on survival.

In any event, however, when fish are reared for the purpose of augmenting wild populations, the fluctuations of success will be determined when the young are released in nature. As I have shown in this paper, one may deduce important keys to the roles played by vague factors—complexes in population dynamics from variability and the different characteristics of natural waters. This should be so whether we are concerned with fish in a lake or the Pacific Ocean.