

RHEOTAXIS IN FISH, WITH PARTICULAR REFERENCE TO
EFFECTS OF TEMPERATURE AND SOME HORMONES ON
THIS REACTION IN YOUNG PACIFIC SALMON

by

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ABSTRACT

Several species of fish swim upstream into the area of greatest turbulence in artificially created currents of water. This reaction is most pronounced with young salmon and trout.

Treatment with thyroxine, testosterone and three estrogen compounds slightly increases the rate at which coho and sockeye salmon smolt jump upstream over a dam.

Elevated temperatures increase the amount of negative rheotaxis shown by chum fry and coho smolt in circular currents.

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INTRODUCTION

In order not to be carried about passively by currents, aquatic animals are variously adapted to maintain position in their particular ecological niches. Many invertebrates can live in fast-flowing waters, and some fishes have well developed ventral sucking structures which enable them to live in highly turbulent mountain streams (Hora, 1930). The Pacific lamprey uses its sucking mouth to hold onto rocks as it moves into fresh water from the ocean to spawn. Some fish, such as chum and pink salmon fry, are highly active in fresh water and exhibit a strong tendency to swim vigorously against fast currents, thus holding position in particular areas during daylight. Other active fish like coho salmon fry show territorial behaviour and tend to stay in quieter waters where they remain close to particular objects in the environment (Hoar, 1951 a).

Swimming against the current is the method used by most fishes to hold position in flowing streams. This is not a novel idea. Such activity has been recognized by fishermen and nature lovers for a very long time, and is now usually referred to in the scientific literature as rheotaxis. A taxis is a directed orientation reaction in which movement is towards or away from a source of stimulation (Fraenkel and Gunn, 1940). Thus, positive and negative phototaxis are movements by an animal straight towards and away from a light

source. It is suggested here that positive rheotaxis is the movement by fish upstream against a current of water, and negative rheotaxis is swimming movements with the current. It should be emphasized that rheotaxis is not confined to the fishes, but is also exhibited by reptiles and many invertebrates. Buddenbrock (1952) presents a brief outline of the occurrence of rheotaxis throughout the animal kingdom.

One of the aims of this thesis is to determine how widespread among fishes is the tendency to swim actively with or against currents of water and to determine how uniform the type of response is among several species. As many species as possible were utilized, and, although a large number of experiments was not performed with each species, the answers to several questions were sought by observing their behaviour in artificially created turbulent flows in long narrow troughs. Some of these questions are: Do these fish swim against the current all or most of the time? If so, is there variation in the rate of initial response, and is the response consistent? Do they prefer turbulent or quiet water when both are available? Is there variation in the degree of activity shown by the different species when in turbulent waters? Do some fish, but not others, jump out of the water? Some correlation was also sought between the activity of the animals in these currents and the natural habitat in which they are found. In other words, do young salmon that swim about in lakes and rivers show a higher degree of positive response in artificial currents

than sculpins and eels, which live mostly on the bottom ?

Many of these questions may be important if we are eventually to understand the mechanisms governing long-distance movements of some fish. Russell (1937) has shown that some marine fishes regularly move with or against the direction of flow at different times during their life histories. Such generalizations do little to further our understanding of the basic factors involved in the delicate balance between fishes and their environment; factors which initiate, direct and control such outstanding movements of fish as those occurring in some diadromous (Myers, 1949) species. However, Russell's ideas do serve to emphasize that the movements of fishes in direct relation to currents are not uncommon.

The metabolism, activity and daily life of poikilothermic animals are probably governed to a greater extent by temperature than by any other variable in their external environment. Such a generalization need not be elaborated on here. The relationship of temperature to the reactions of fishes to currents is of more particular interest, however, when dealing with species such as the Pacific salmon that have complicated life histories. Of perhaps greater importance in understanding the complex of events that leads to these fish moving successfully from fresh to salt water and back again is the role played by hormones.

Tinbergen (1950) has described the reproduction of the male three-spined stickleback, starting with migration and ending with the reproductive act, as an example of the

hierarchical pattern in which the nervous mechanisms underlying instinctive behaviour is laid out. Emphasis is placed on the fact that appetitive behaviour (or, in this case, migration from salt or deep, fresh water into shallow, fresh water) is the highest or primary level of the instinctive reproductive act. This behaviour is initiated by the action of the gonad hormone level of the blood on nervous centres in the brain. The gradual increase in length of day in springtime acts on the pituitary gland, which in turn activates the gonads of the stickleback to secrete increasing amounts of their hormones. This initiates, through the brain, the most generalized type of appetitive behaviour, i.e. migration, which continues until certain sign stimuli (or releasers), of which higher temperatures is one, release a more specialized type of appetitive behaviour, in this case, holding and defence of a territory. Wandering about the territory continues until further sign stimuli release the next most specialized act, either fighting or nest building. Thus, hormone level is of prime importance in the initiation of the most generalized type of appetitive behaviour, and temperature is one of the external releasers helping to direct the behaviour of the fish along proper lines. Such an analysis is, in part, similar to Fontaine's (1948) theory that hormonal changes in fish create internal stresses which lead to a movement out of one area into another.

It has been suggested that the spawning migrations of adult Pacific salmon are basically no more complicated than this

reproductive migration of the stickleback (Hoar, 1951 b). It might not be too rash, then, to propose that the downstream movement of young salmon is also due to the presence of a hierarchically organized system of nervous centres in the brain which are activated in turn by internal media such as hormones and by external stimuli such as temperature. A detailed analysis similar to Tinbergen's work on the stickleback has not been attempted with Pacific salmon; however, Hoar (1951a) has made many contributions to our knowledge of the comparative behaviour of these young fish and it is in the hope of furthering our understanding of the part played by such factors as hormones and temperature on the reactions of these fish to currents that the latter part of this study has been conducted.

In summary, then, the purpose of this thesis is threefold. Firstly, an attempt was made to determine, with several species, how widespread rheotaxis is among fishes, to what extent the activities of fishes vary in flowing streams, and whether both positive and negative rheotaxis occur. Secondly, the effects of thyroxine, testosterone and three estrogen compounds on the activity of coho and sockeye smolt in turbulent water were studied. Thirdly, the possibility was considered of sudden temperature changes radically modifying the rheotactic reaction of coho and sockeye smolt.

MATERIALS AND METHODS

Experiments were carried out at the University of British Columbia from May 1952 to April 1953. Fish were held in cement hatchery troughs in the basement of the Biological Sciences building. Water entering the hatchery was run through gravel and charcoal filters set up at the head of each trough. Mortality from chlorine in the water was thus avoided. Food, in general, consisted of canned salmon mixed with pablum and commercial fish meal. Some fish, such as eels, fed more readily on a diet of earthworms, whiteworms (Enchytraeus), Daphnia or meal worms (Tenebrio).

Table I lists the common and scientific names of the species used, together with the locality where each was caught. Under each group of experiments to be described below, the species utilized are listed, with corresponding size data.

General Responses to Currents of Water.

The fishes studied in this and the next series, and their mean lengths, are listed in Table II. The experimental period lasted from August 1 to December 15, 1952, during which time the temperature in the hatchery troughs fell from 18 to 8° C.

Metal troughs 242 cm. long, 26 cm. wide and 19 cm. deep were employed for observations of fishes in linear currents. Figure 1 shows two of these troughs set up for the hormone experiments to be described later. An overflow pipe 2 cm. in

Table I.

Fishes used for studying rheotaxis.

Species	Common name	Where obtained
<u>Oncorhynchus</u> <u>kisutch</u> (Walbaum)	coho salmon	Brunette and Alouette Rivers, B.C.
<u>O.</u> <u>tshawytscha</u> (Walbaum)	spring salmon	Nile Creek hatchery, B.C.
<u>O.</u> <u>keta</u> (Walbaum)	chum salmon	" " "
<u>O.</u> <u>nerka</u> (Walbaum)	sockeye salmon	Marblemount hatchery, Wash.
<u>Salmo</u> <u>gairdnerii</u> <u>kamloops</u> Jordan	kamloops trout	Smith Falls hatchery, Cultus Lake, B.C.
<u>Cottus</u> <u>asper</u> Richardson	prickly sculpin	Deer Lake, B.C.
<u>Ameiurus</u> <u>nebulosus</u> (Le Sueur)	brown catfish	Stave River, B.C.
<u>Anguilla</u> <u>bostoniensis</u> Le Sueur	american eel	Becaguimic River, N.B.

Table II. Names and fork lengths of fishes studied
for general response to currents.

Common name	Mean length cm.	Standard deviation cm.
coho salmon	7.7	± 0.67
spring salmon	6.2	± 0.58
brown catfish	4.5	± 0.71
prickly sculpin	4.3	± 0.99
atlantic eel	29.7	± 10.26
kamloops trout	6.2	± 1.15

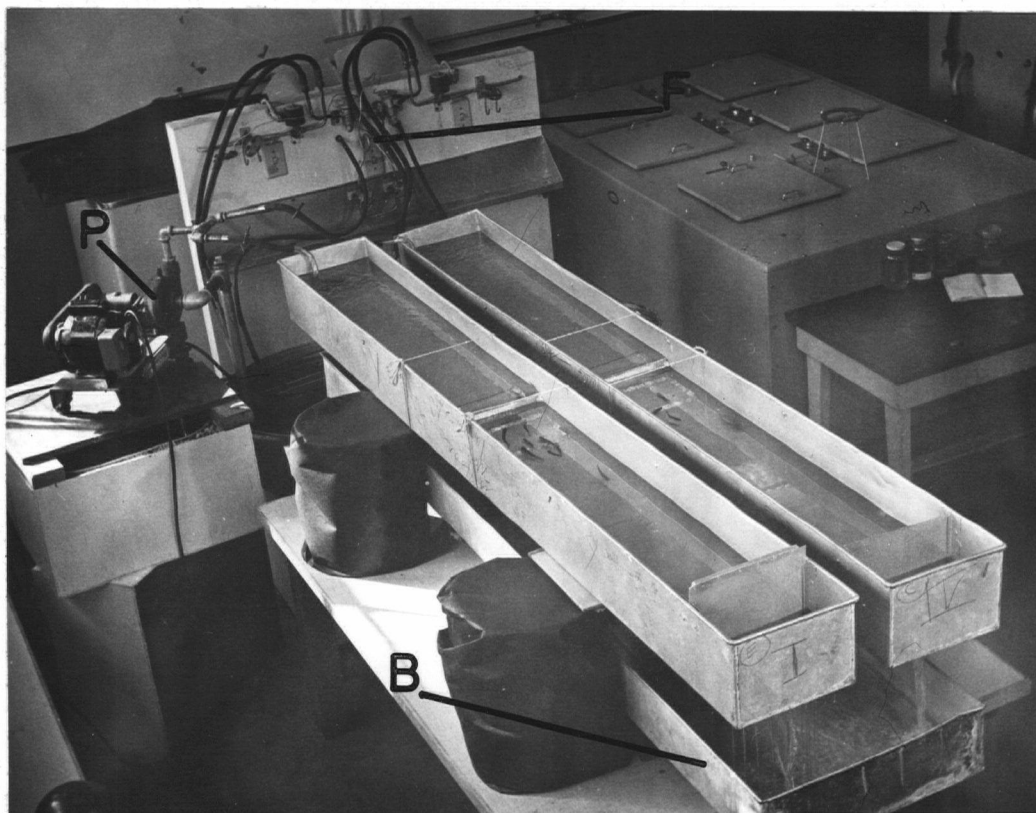


Figure 1. Apparatus for observing jumping of young salmon. Troughs were also used for studying general responses to currents, and preference of fish for flowing or quiet water. P, 1/4 horsepower centrifugal pump; F, freezing unit; B, sloping metal catch-basin returning water from experimental troughs to cooling reservoir below freezing unit.

diameter, at one end, held the water level at 8 cm., while water was pumped in at the other end through 1.2 cm. glass tubing, at the rate of 8 to 10 liters per minute. A General Electric 1/4 horsepower centrifugal pump or two smaller Eastern centrifugal pumps were used to maintain a constant and identical flow of water in the two troughs. The overflow was screened off so the space available to the fish was 225 cm. long. All surfaces in contact with water were covered with aluminum paint. By using four of these troughs at one time a greater number of experiments was possible.

The procedure was to place 12 fish of one species in the central third of any trough between two perforated partitions with no water current in the trough. After one hour pumps were turned on, the inflow regulated to the desired volume, the partitions removed, and observations of the fishes' movements immediately begun from a position where the fish were not startled. Red wax pencil lines marked the division of the area of the trough into three equal sections. The number of fish in each of these sections was noted every 30 seconds for 15 minutes. This recording procedure was repeated after one hour and again two hours later. The fish were then returned to the holding troughs. Water temperatures were taken and the light intensity at the water surface in the centre of each trough was recorded with a Weston Light Metre after each experiment. A total of six experiments for each species was performed with coho and spring salmon, sculpins and eels, while catfish were used for eight replications.

In all experiments involving eels and young salmon plastic screening covered the trough to prevent the fish from escaping.

In analysing the data, the mean percent of fish in the inflow third of the troughs every 30 seconds was determined for each species.

Preference for Turbulent or Quiet Water.

A modification of the above apparatus was designed to determine whether fish will move into turbulent or quiet water. A piece of plywood 75 cm. long and 24 cm. wide was placed in the inflow end of the trough to form a central longitudinal partition down one third of its length. Inflowing water could be directed into either side of the plywood, thus creating turbulence on one side only. Addition of methylene blue dye showed that movement of inflowing water to the opposite side of the partition was negligible. The volume of water pumped into the trough was held at 10 liters per minute.

In any experiment the inflow of water was started on one side of the partition. Twelve fish were placed in the outlet end and permitted to roam freely in the trough. After one hour the numbers of fish on each side of the plywood were recorded every 30 seconds for 15 minutes. The inflow was then switched to the other side and one hour later similar records made for another 15-minute period. Water temperatures and illumination were recorded after each experiment.

Coho salmon, kamloops trout, eels, sculpins and catfish were used in these preference tests. Six experiments

were carried out with the salmon and trout, and five with each of the other species. The mean percentage of fish on each side of the partition at the end of one hour and again at the end of two hours was calculated for each species. t and P values were calculated to show the significance of the difference between means (Snedecor, 1946).

Modification of Rheotaxis by Hormone Treatment.

Coho and sockeye salmon smolt were immersed for varying periods of time in hormone solutions to determine whether or not this would alter their reactions to flowing water. The following hormones were used:

synthetic thyroxine-sodium (BDH)	1	:	2,500,000
methyl testosterone (BDH)	1	:	2,000,000
Dienoestrol (BDH)	1	:	1,600,000
Stilboestrol (BDH)	1	:	1,600,000
Ethinyl Oestradiol (Nylestin)(BDH)	1	:	20,000,000

The concentrations of thyroxine and testosterone used were based on previous experiments with salmon (Hoar et al, 1952). Concentrations of the three estrogens were dictated by availability and by some potency data supplied by the British Drug Houses, but were not based on previous work with fish.

Groups of 20 fish were immersed in 20 liters of aerated solution in 22 litre glass battery jars. They were fed twice daily, except on week ends, and the solutions changed every second day. Control groups were kept under identical conditions in hatchery tap water. To control temperatures the

jars were set in one of the cement hatchery troughs and surrounded by running water. Experiments were carried out from January to April, 1953, and temperatures in the hatchery varied from 6 to 9° C.

Fish treated with hormones were coho salmon smolt (8.9 ± 0.54 cm.) and sockeye salmon smolt (8.2 ± 0.53 cm.) Measurements were mean fork lengths.

Jumping behaviour was selected as a test for studying changes in activity following hormone treatment. The long metal troughs described previously were again utilized. In these tests a centrally placed vertical dam divided them into equal-sized upper and lower pools. Water was recirculated by a 1/4 horsepower G.E. pump from a reservoir, where a Parmetic freezing unit (using freon gas) maintained the temperature equal to that in the hatchery. From the outlet ends of the troughs water was returned to the cooling reservoir (figures 1 and 2). The height of the dam above the lower pool was regulated by changing the height of the overflow pipe. Coho were made to jump over a 2 cm. dam, and sockeye, being smaller fish, had to jump 1.5 cm. to reach the upper pool. The water volume entering each trough was held at 14 liters per minute and plastic screening prevented fish escaping over the sides. All parts of the apparatus were covered with aluminum paint and periodically thoroughly cleaned to remove slime.

In any experiment fish from two battery jars were placed in separate containers in quiet water for one hour. Water circulation was started in the troughs, water levels were adjusted so the dams were the appropriate height, and one group

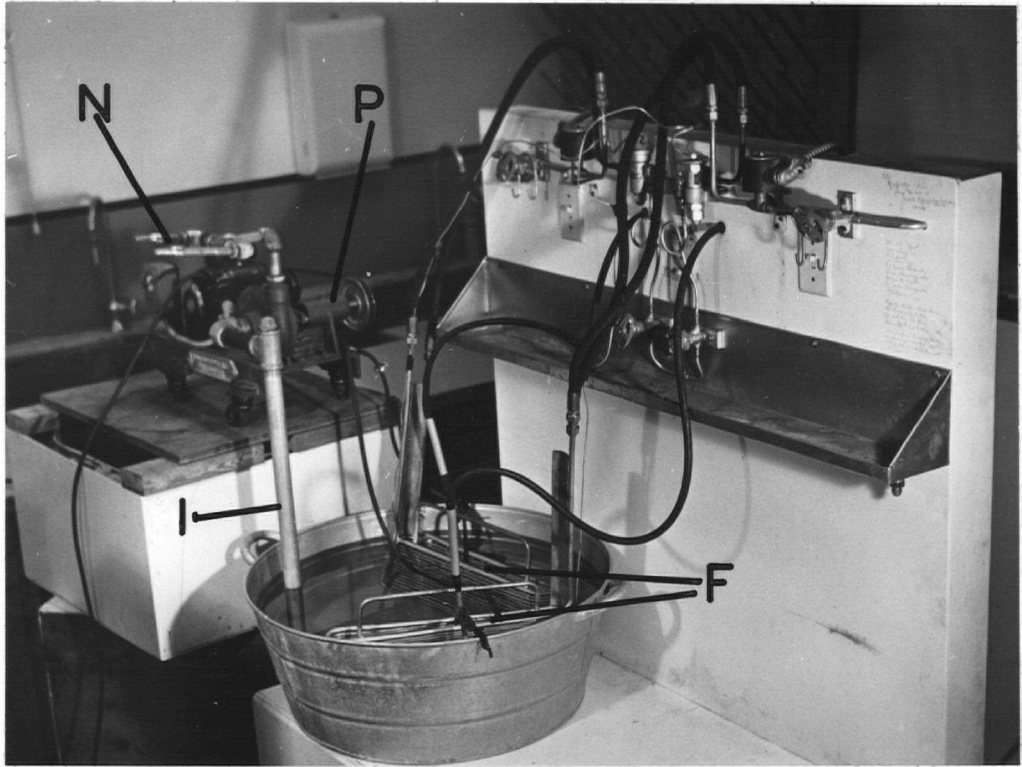


Figure 2. Apparatus used to pump a constant volume of water of required temperature through experimental troughs. P, 1/4 horsepower G.E. centrifugal pump; I, intake pipe; N, nozzles; F, twin coil Parmetic freezing unit.

of fish was put in the lower pool of each trough. Observations were begun at once from a point out of sight of the fish and the time necessary for 50 percent (10 fish) to jump to the upper pool was recorded. Fish were then returned to the appropriate battery jar. Water temperatures, light intensity and current speed were recorded at the conclusion of each experiment. Figure 3 shows a group of trout immediately below a dam.

Experiments commenced at the beginning of the second week of treatment and were repeated five or six times a week. After four weeks of treatment experiments were discontinued. Fish were then placed in the metal tubs described later to observe their behaviour in circular currents following hormone treatment. Then the fish were anesthetized in ethyl urethane solution, measured and preserved in 10 percent formalin.

The period of experimentation was arbitrarily divided into three weekly stages and mean times (in minutes) for 50 percent of the fish to jump over the dam were calculated for each stage. A t-test was used to determine the significance of the difference between the mean values for experimental and control fish. The calculations for thyroxine and testosterone treated fish cover pooled results from two series of experiments, while only one series was completed with the three different estrogens.

Effects of Temperature Changes on Rheotaxis.

Chum salmon fry (4.9 ± 0.43 cm.) and coho salmon smolt (8.9 ± 0.54 cm.) were used in this series. These



Figure 3. Kamloops trout swimming in turbulent water below vertical dam. Most fish are facing current. D, dam.

species were chosen because they show strong positive rheotaxis and changes occurring in the response to direction of flow were easily detected in the apparatus described below. Experiments with chum salmon were carried out during the summer of 1952 and those with coho in the spring of 1953.

The apparatus consisted of two galvanized iron wash tubs 68 cm. in diameter across the top, 212 cm. in circumference and 27 cm. deep. These were placed side by side to facilitate comparative observations (figure 4). A vertical pipe 1 cm. in diameter attached to the inside of each tub was perforated along its length so that water entering at the top was forced out the series of holes, in a direction parallel to the side of the tub and produced a comparatively uniform circular current. A central overflow pipe maintained the water level at 19 cm. and drained water back into a reservoir while an Eastern centrifugal pump forced it up again into the perforated inlet pipe. Tubs and reservoirs were set in deep cement troughs where water surrounded the reservoirs to maintain appropriate temperatures. The surface speed of the current in each tub was held at 25 - 30 cm. per second, measured at the periphery. Aluminum paint covered the inner surfaces of both tubs and reservoirs.

The procedure followed in any experiment was to hold two groups of one species separately for an hour in quiet water at the temperature of the hatchery water. Currents as described above were started in the tubs, the temperature in



Figure 4. Rheotaxis tubs with kamloops trout orienting in circular currents. R, reservoir surrounded by water to control temperature; P, Eastern centrifugal pump.

one tub being equal to the holding temperature, and that in the other 4 or 5° C. above or below. A group of fish was placed in each tub and observations begun immediately from behind a screen. Chum salmon were observed in groups of 12 and coho in groups of 10. No attempt was made to obtain a quantitative measure of the activity of the fish in this apparatus, but over a 10 to 15-minute period careful observations were made of the rheotactic response of each group. Fish were described as showing negative rheotaxis when they swam faster than the surface flow, and in the same direction. If the fish faced the current, swimming into it or holding position in the flow, they were said to be showing positive rheotaxis. Occasionally an individual drifted with the current. This is not referred to as negative rheotaxis. Fish behaving in this way were classed with those showing positive rheotaxis. Light intensity at the water surface was recorded after every experiment. Thirty-six separate experiments were carried out with chum salmon and 12 with coho.

RESULTS

General Responses to Currents.

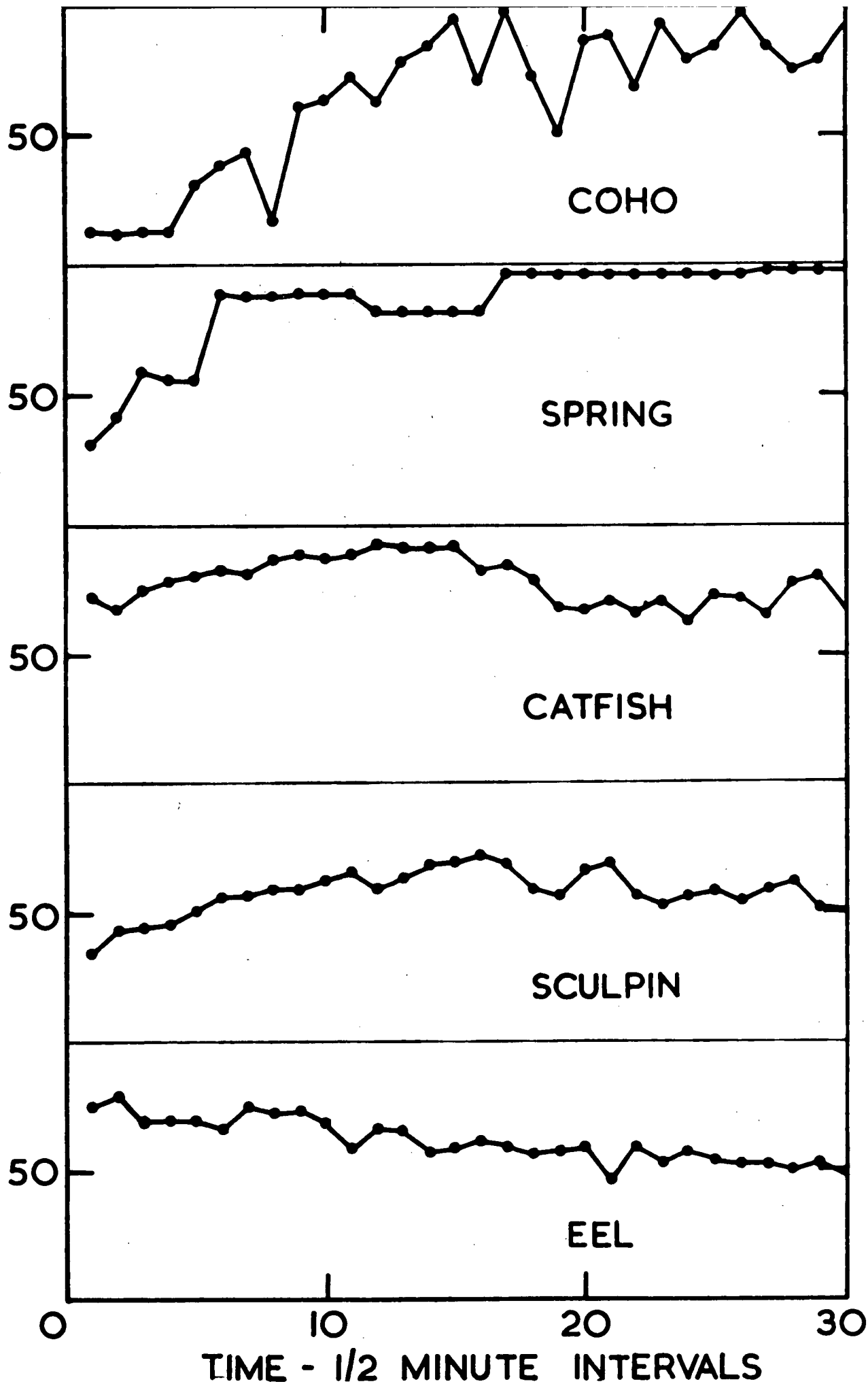
Figure 5 shows the proportion of five species in the area of greatest turbulence of the long troughs for 15 minutes after the flow was started. Each point on any curve represents the mean percentage of fish in the inflow third of the trough over a number of experiments. These five curves have been presented together to emphasize the fact that, although there are variations among species, all of these fish move close to the inflow and stay there at least 50 percent of the time.

On removal of the partitions holding the fish at the centre of the trough, the immediate response was usually a general movement by all fish toward the outflow end. The length of time for movement toward the inlet tube from this position varied among the species (figure 5). Both eels and catfish showed a rapid initial response, moving into the most turbulent area within one minute of release from the centre of the trough. In contrast the spring salmon moved into the inflow end in an average of four minutes and the coho in seven minutes.

Throughout these experiments the spring salmon fry showed the greatest activity. They swam most consistently into the turbulent zone and jumped out of the water in this area more often than any other species except the eels. When the spring fry moved away from the inflow, they swam quickly in

Figure 5. Mean percent of five species of fish in the inflow end of the long metal troughs at intervals of 30 seconds over a 15-minute period. See text.

PERCENT FISH IN INFLOW



close aggregates to the outlet end of the trough and back again. Coho fry, on the other hand, showed a less consistent positive response to the inflowing water. They moved back and forth from inflow to outlet more often than the spring fry, and in looser aggregations. Jumping near the inflow occurred less often with coho than with spring salmon. Nipping and defence of territory (Hoar, 1951 a; Stringer, 1952) by the coho were occasionally seen, but neither reaction was shown by the spring fry.

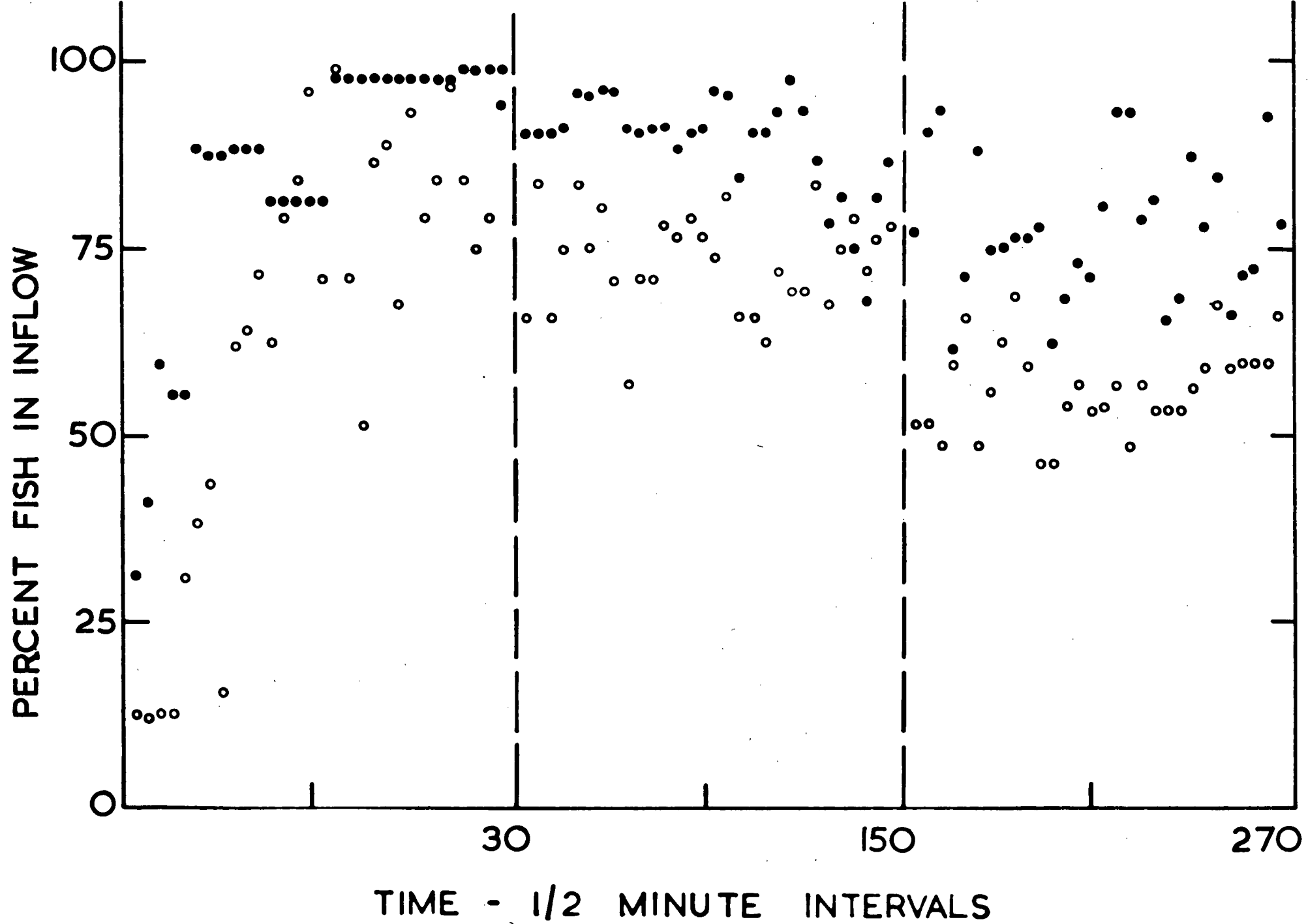
In general, catfish, sculpins and eels behave like the two species of salmon discussed above. The percent of these three species in the inflow end is more consistent than that of coho. This is partly explained by the fact that the former moved singly or in small groups, and over the first 15 minutes there were some fish at the inflow end most of the time, while others were scattered throughout the trough. On the other hand, the coho moved about in aggregates and there were often no fish near the inflow. The eels were the most difficult to hold in the troughs. They are active fish and escaped over the sides by jumping and working under the plastic screening.

All species showed much the same response to the inflow over a two hour period as they did during the first 15 minutes. Figure 6 shows the response to current demonstrated by coho and spring salmon fry over two hours. Similar data for the other three species are given in the appendix.

Preference for Flowing or Quiet Water.

The results of the experiments using the long troughs

Figure 6. Mean percent of two species of salmon in the inflow end of the long metal troughs; records were taken at the time intervals shown. Solid circles, spring salmon fry; open circles, coho salmon fry; vertical broken lines, one hour periods during which no observations were made.



with longitudinal partitions at the inflow end are given in Table III. Figures shown are for average percentages of fish in the turbulent and the quiet areas over a series of experiments. With one exception, the sculpin, these figures indicate that a greater proportion of each species will move into a strong flow of water than into a quiet area. Coho salmon are most marked in their preference for turbulence. The experiments were carried out in the late fall when spring salmon were no longer available, and there was no possibility of comparing coho with spring fry. Kamloops trout fry were used instead for comparison with coho.

Various observations were made on the behaviour of the fish during these experiments. The kamloops trout fry usually remained in aggregations, but some evidence of territorial behaviour was seen. This sometimes led to confusing results. Territorial behaviour and occasional nipping in the turbulent water by several trout during the first hour of some experiments led to inconsistent results and a relatively high P value compared to that for the second observation period. As before, the coho fry moved about in loose aggregations. They moved actively up and down the length of the trough and entered the inflow side of the partition more consistently than the other species. The young catfish also moved into turbulent rather than quiet water, but more frequently stayed in groups near the outlet screen. The eels were difficult to keep in the trough. Some eels tried vigorously

Table III. Mean percent of fish on each side of partition.

Flow changed to opposite side of trough after one hour.

Species	No. of experiments	Percent fish before change				Percent fish after change			
		turbulent water	quiet water	t	P	turbulent water	quiet water	t	P
coho	6	37.8	5.0	6.934	<0.01	39.5	9.2	5.499	<0.01
trout	6	27.3	12.4	1.242	0.25	28.8	11.0	2.438	0.04
catfish	5	20.4	12.2	1.206	0.27	24.1	4.8	3.063	0.016
eel	5	24.4	11.6	1.123	0.30	21.1	14.1	0.986	0.36
sculpin	5	27.9	16.7	1.349	0.22	10.3	11.3	0.400	0.5

to work their way out under the screening, especially when in the most turbulent water. This "escape" behaviour led to increased activity on the inflow side of the partition and the proportion of eels on this side was decreased. Sculpins tended to stay near the corners of the trough. During the first hour the proportion of sculpins was slightly higher in the turbulent than in the quiet area. By the second hour no preference was seen. Sculpins and catfish did not jump out of the water in the turbulent area.

Hormones and Rheotaxis

The effects of testosterone and thyroxine on the rate at which coho smolt jump over a 2 cm. dam are summarized in figure 7. The four week treatments were duplicated with different fish and the graphs are the results of lumping the two sets of data. The difference in jumping time between treated fish and controls varies. The significance of this difference for each week has been determined statistically and t and P values are presented in Table IV. In only one case, the 3rd week of testosterone treatment, is this difference statistically significant at the 0.01 level for coho. However, the tendency of experimental fish to move over the dam faster than controls is consistent, except for the final week of treatment with thyroxine, where the treated fish seemed in poor condition.

Figure 8 graphically presents data for an identical series using sockeye smolt. Here again the overall result is

Figure 7. Histograms showing the effects of two hormones on the rate at which coho salmon smolt jump upstream over a 2 cm. dam. Open bars, control experiments.

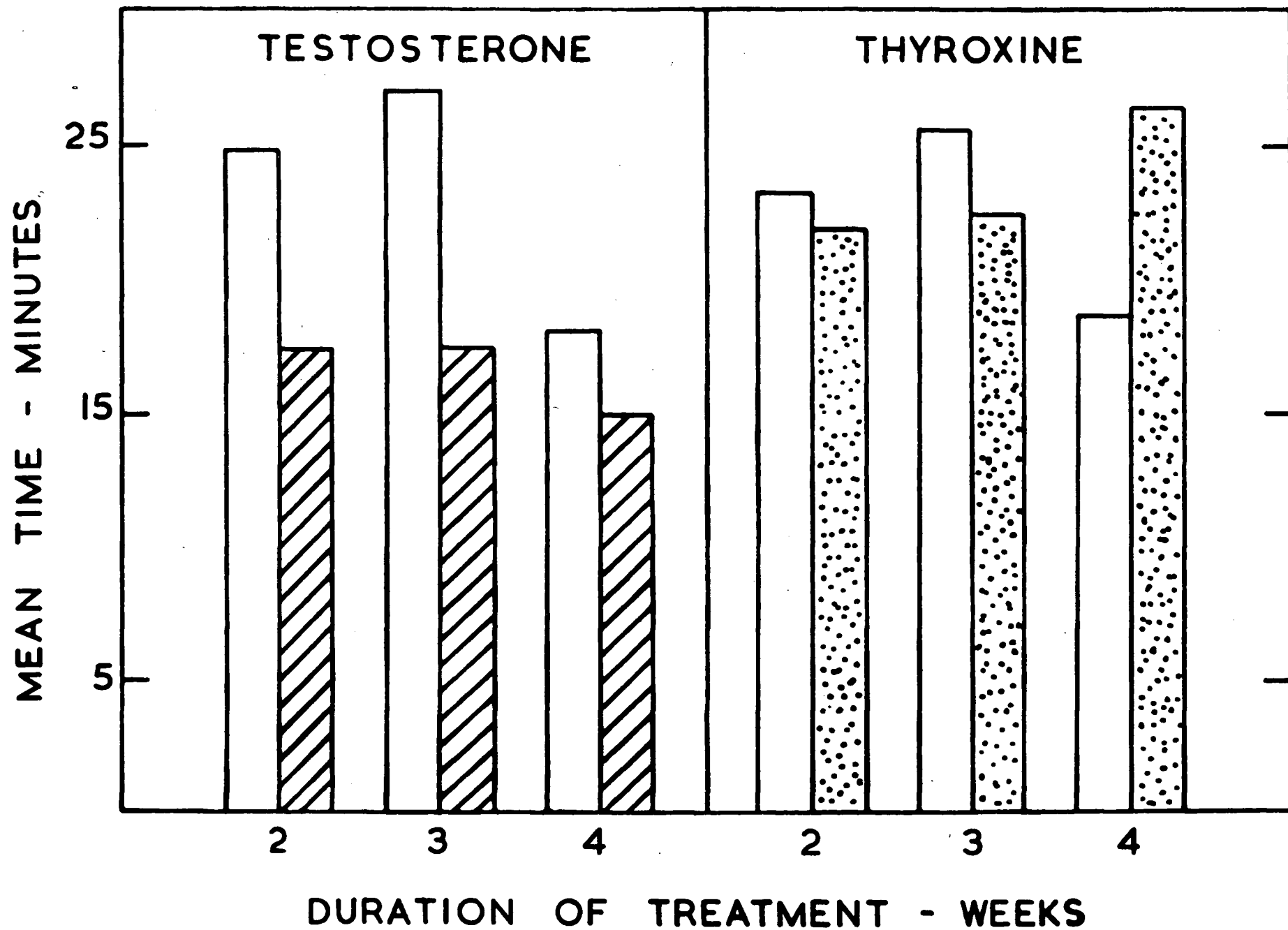
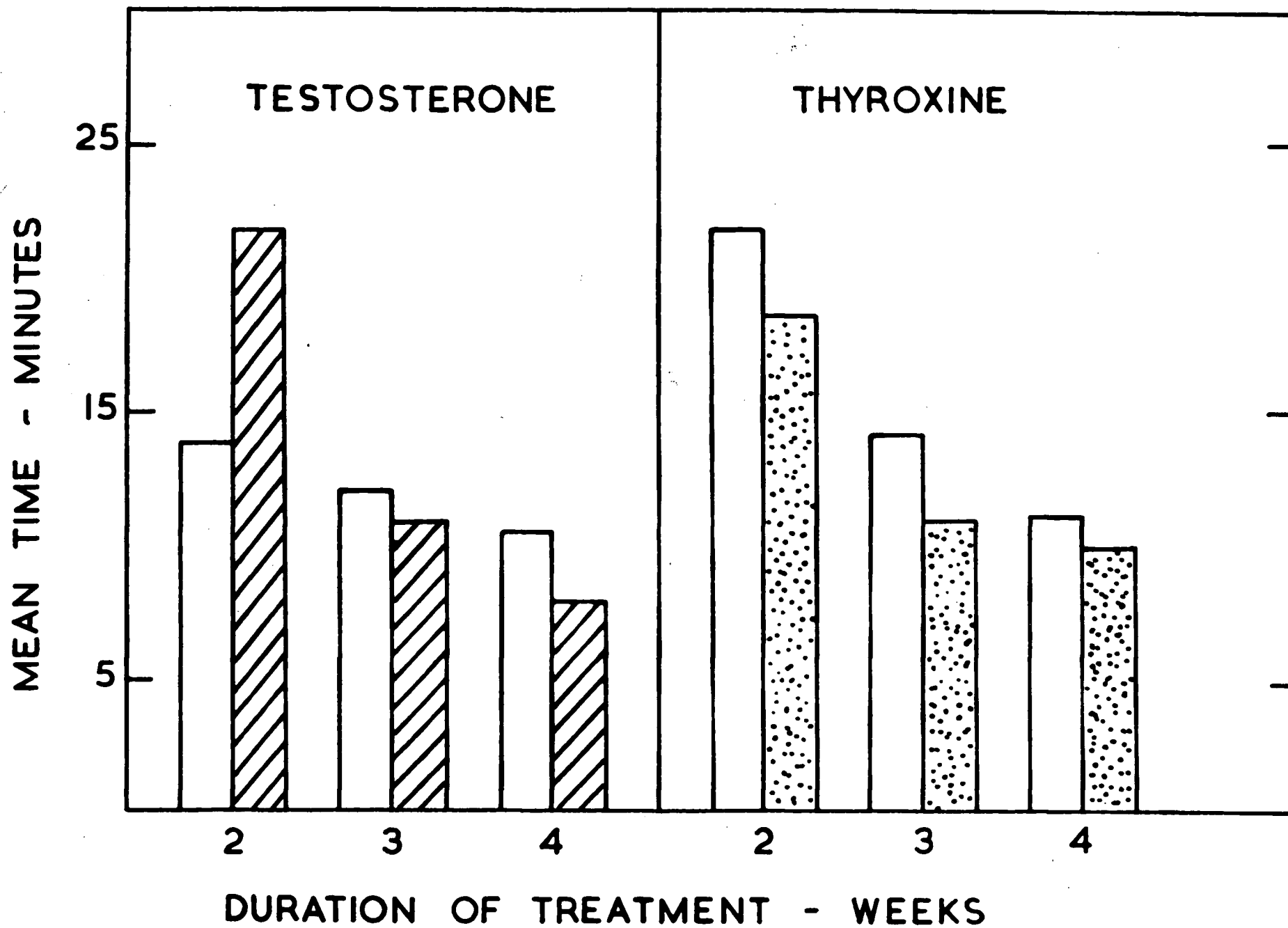


Table IV. Time taken for 50 percent of coho smolt to jump from lower to upper pool during thyroxine and testosterone treatment.

Week of treatment	Thyroxine		Control		t	P
	No. of experiments	Mean time minutes	No. of experiments	Mean time minutes		
second	4	21.9	4	23.3	0.179	> 0.5
third	8	22.4	8	25.6	0.941	0.36
fourth	8	26.4	8	18.7	2.406	0.03

Week of treatment	Testosterone		Control		t	P
	No. of experiments	Mean time minutes	No. of experiments	Mean time minutes		
second	4	17.3	4	24.8	3.000	0.02
third	9	17.5	9	26.9	3.357	< 0.01
fourth	9	14.9	9	18.1	1.067	0.3

Figure 8. Histograms showing the effects of two hormones on the rate at which sockeye salmon smolt jump upstream over a 1.5 cm. dam. Open bars, control experiments.



for treated fish to move upstream faster than controls.

A notable exception occurs with testosterone treated fish in the second week of treatment. The t and P values are calculated for sockeye and presented in Table V.

The results of identical experiments with sockeye smolt using three estrogen compounds are shown in figure 9. All three hormones stimulated the activity of the fish, but the change was most pronounced with one group. Those immersed in Stilboestrol were the most active fish seen in this apparatus. This increase in activity was also noticeable in the battery jars, and when the fish were carried in pails. Nylestin, on the other hand, seemed to have a detrimental effect. Fish immersed in solutions of this compound appeared to be under stress and their movements in the troughs were erratic; while in the battery jars they were less active than controls. It is interesting to note, however, that the mean time for half of this group to cross the dam is still less than for controls. Table VI presents the t and P values for significance of the difference between mean values.

Figures 7, 8 and 9 show that with few exceptions, both control and experimental sockeye and coho move upstream faster in the later stages of treatment than at first. This was especially noticeable after the first two or three experiments with each group. The possibility of a learning process being involved in this increase in jumping rate will be discussed later.

During the many hours of observations necessary

Table V. Time taken for 50 percent of sockeye smolt to jump from lower to upper pool during thyroxine and testosterone treatments.

Week of treatment	Thyroxine		Control		t	P
	No. of experiments	Mean time min.	No. of experiments	Mean time min.		
second	5	18.7	5	21.9	0.561	>0.5
third	8	10.9	8	14.2	1.100	0.3
fourth	8	9.9	8	11.1	0.857	0.4

Week of treatment	Testosterone		Control		t	P
	No. of experiments	Mean time min.	No. of experiments	Mean time min.		
second	6	21.8	6	13.8	1.951	0.08
third	9	10.8	9	12.1	0.929	0.37
fourth	7	7.9	7	10.5	1.857	0.09

Figure 9. Histograms showing the effects of three estrogens on the rate at which sockeye salmon smolt jump upstream over a 1.5 cm. dam. Open bars, control experiments.

MEAN TIME - MINUTES

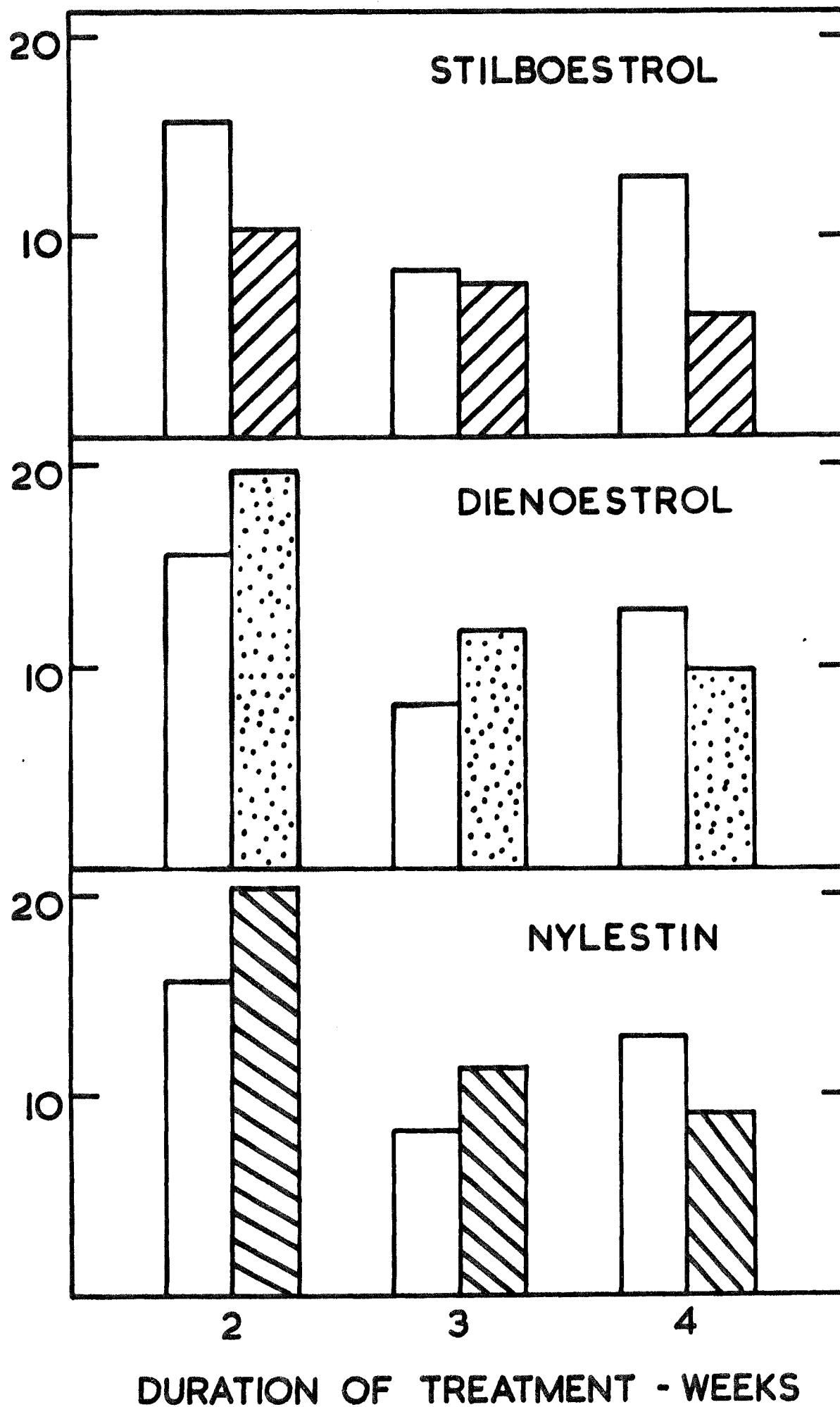


Table VI. Time taken for 50 percent of sockeye smolt to jump from lower to upper pool during three estrogen treatments. t and P values show the difference in time between each treated group and the same control.

Week of treatment	Control		Stilboestrol		Dienoestrol		Nylestin	
	No. of experiments	Mean time min.	No. of experiments	Mean time min.	No. of experiments	Mean time min.	No. of experiments	Mean time min.
second	3	15.8	4	10.3	4	19.9	3	20.3
t			2.037		0.569		0.803	
P			0.1		> 0.5		0.46	
third	6	8.2	6	7.5	6	11.9	6	11.4
t			0.854		3.083		1.975	
P			0.4		0.01		0.08	
fourth	5	13.0	5	6.1	5	10.0	5	9.2
t			3.833		1.667		2.000	
P			< 0.01		0.12		0.08	

to compile the data presented here some contrasts in behaviour of sockeye and coho were evident. Although both species moved about the troughs in aggregates, the young sockeye stayed in more compact groups than the coho. One characteristic of both species during the first few minutes of any experiment was for all fish to swim back and forth in close groups from the outlet screen to the face of the dam. This movement was at first rapid and regularly timed, the fish staying below the dam for a few seconds only. However, within a few minutes the time spent struggling in the turbulent water below the falls gradually increased. The closer grouping by sockeye was then emphasized as the coho aggregates broke up more readily, some fish staying immediately below the dam and others swimming to the outlet.

In the area above the falls this more compact grouping among sockeye was again evident. Whereas some of the coho in the upper pool often rested near the bottom in front of the dam, the sockeye stayed mostly in the area of greatest turbulence, and when swimming to the dam and back again moved as a group.

Another feature of the behaviour of these young salmon is the marked tendency of several fish to jump over the dam-together. It was repeatedly noticed that several minutes would pass with no fish jumping, then five or six fish would move over the barrier within several seconds. This happened more often with sockeye than coho.

Two further peculiarities of coho behaviour in this apparatus are worthy of comment. One is the movement of

fish back over the vertical face of the dam from the upper to the lower pool. This activity was seen in 26 different coho experiments of which 15 were with treated fish and 11 with controls. The other activity peculiar to coho was chafing, which has been described previously for a species of cyprinid (Keenleyside, 1952) and was seen in 10 separate experiments in this study. Chafing occurred both above and below the dam, among control and test coho, and by fish that were either facing or moving with the current. Neither downstream movement over the dam nor chafing was seen among sockeye.

The prolonged, 4-week treatment with hormones produced evidence of stress. The fish often showed erratic movements in the later stages of treatment. For example, coho smolt during the fourth week of treatment with thyroxine, were very slow to move over the barrier. Their jumping below the falls was weak and erratic and the same fish often had to jump six or eight times to cross the dam. Controls usually reached the upper pool on the first try. Furthermore, at this stage many coho stayed at the outlet end of the trough and did not attempt to jump. In contrast, some of the treated sockeye showed increased, but more erratic, general activity, swimming speed and jumping. The fish jumped vigorously, but in various directions below the dam and the result was slower movement to the upper pool than the degree of activity warranted.

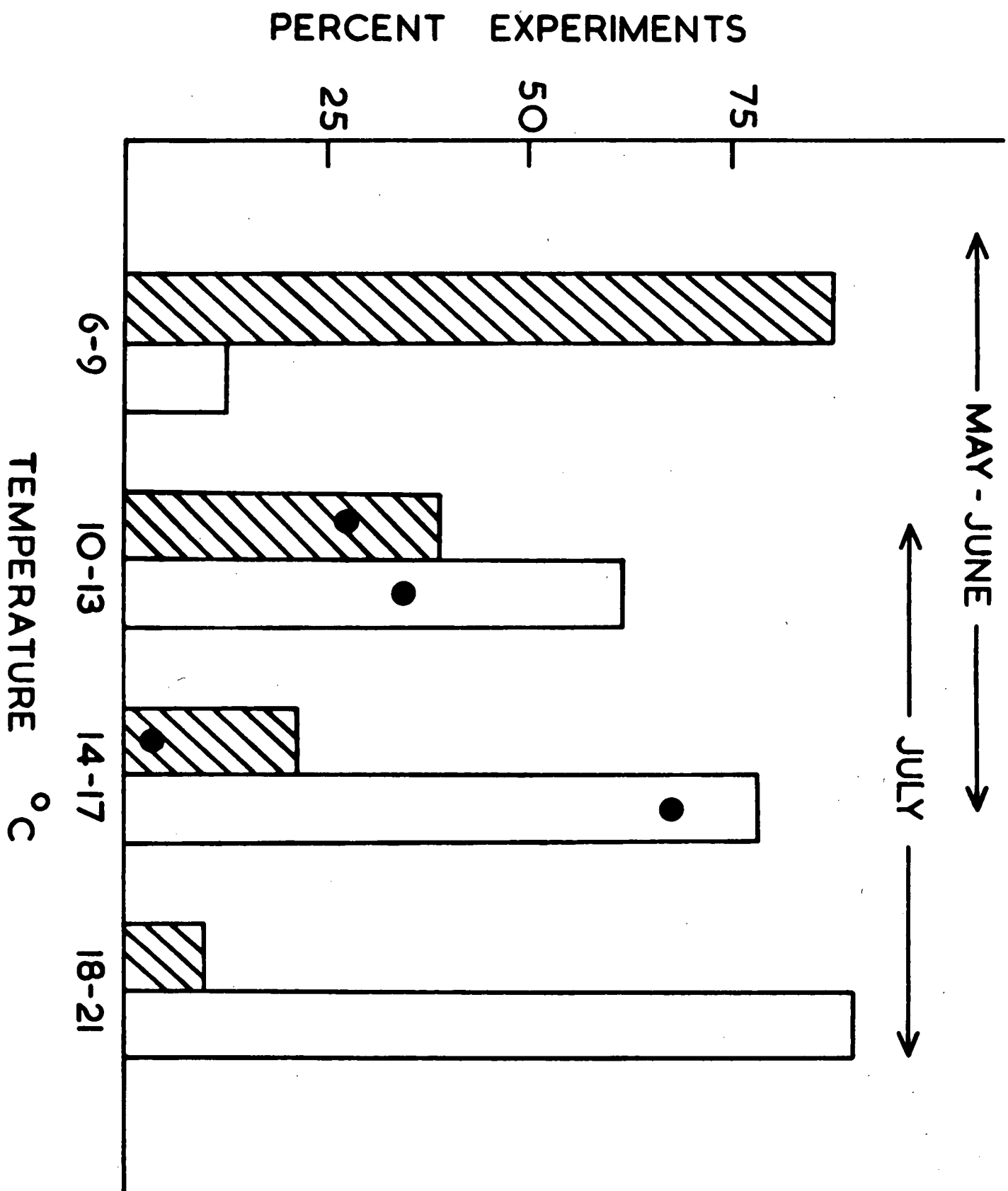
Such erratic behaviour was not consistent with any one group, but appeared occasionally among all treated sockeye.

When these experiments were terminated each group of fish was placed in the rotating current in one of the rheotaxis tubs described earlier. The control coho smolt stayed in a close group and held position in the fastest flow. Those coho from thyroxine solutions showed erratic movements and much darting about. This led to a scattered distribution both in fast and slow water. Testosterone treated coho, however, displayed vigorous positive rheotaxis in the fastest flow. The entire group moved as a loose aggregation around the tub against the current. No negative rheotaxis was observed among coho. In these circular currents the sockeye exhibited more inconsistent behaviour. Positive rheotaxis dominated, but both treated and control sockeye occasionally darted about and the grouping behaviour was less marked than expected. Those treated with Stilboestrol were the most active sockeye. They aggregated more closely than the others and showed a higher degree of positive rheotaxis. Sockeye did not show active negative rheotaxis in these tubs. It was not possible to carry out tests in this apparatus during earlier stages of treatment of sockeye and coho salmon.

Temperature and Rheotaxis

At elevated temperatures both chum fry and coho smolt show consistent negative rheotaxis in the circular tubs. In water colder than the holding temperature the dominant activity is positive rheotaxis. Figure 10 summarizes the results for 36 experiments with chum salmon. These were carried out from May to July, 1952 when temperatures in the

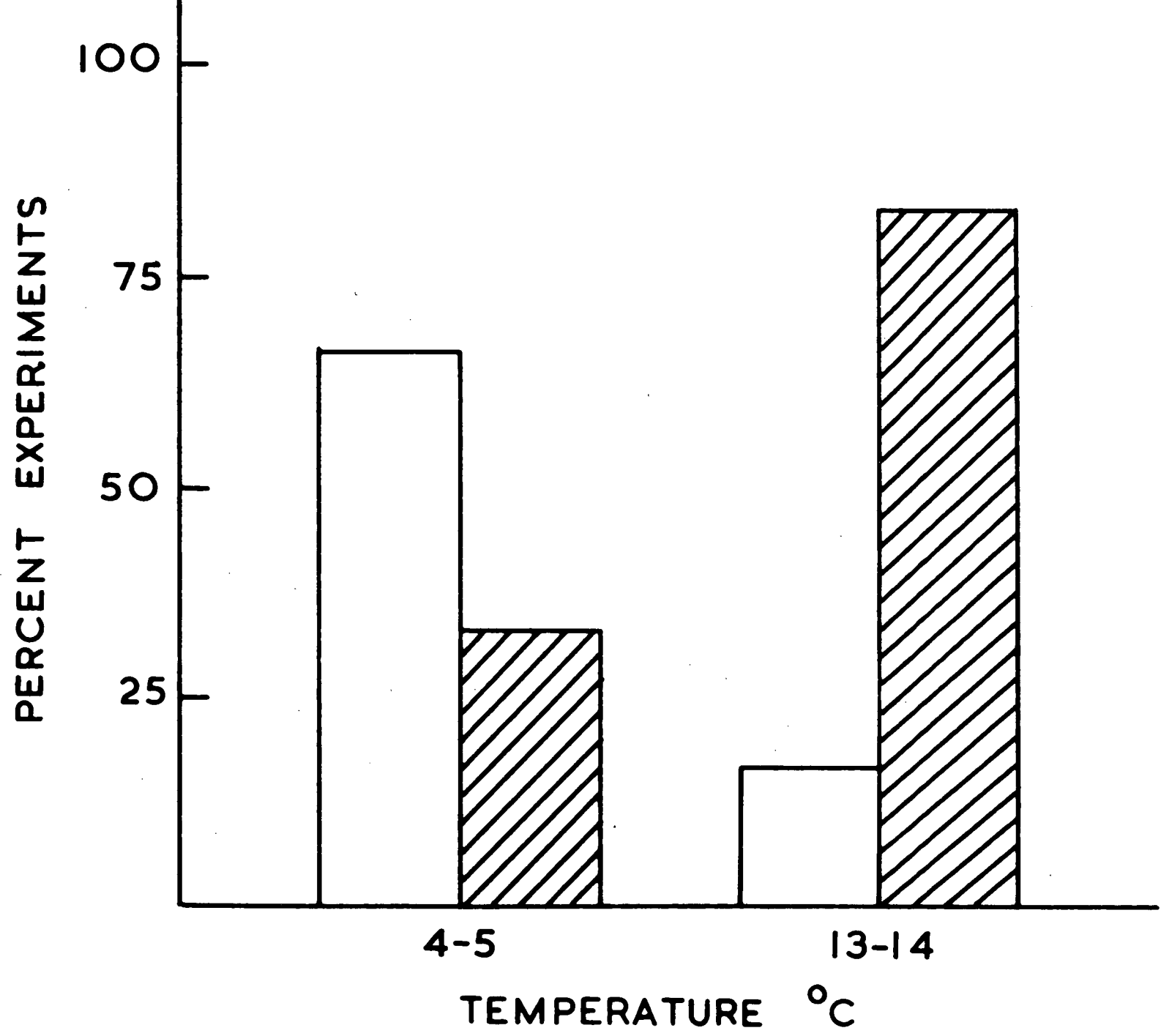
Figure 10. Histograms showing response of chum salmon fry to circular currents at different temperatures. Values shown are percent experiments at each temperature range. Cross-hatched bars, positive rheotaxis; open bars, negative rheotaxis; solid circles, proportion of experiments in each bar that were controls. See text.



hatchery increased from 10 to 16° C. Most of the chum fry showed negative rheotaxis during July when control temperatures were high. The four central bars in figure 10 contain solid circles. The proportion of the bar below the circle marks the proportion of experiments included in that bar that were controls. The 6 - 9° and 18 - 21° bars which include no controls show most clearly the different response to currents with elevation and lowering of temperature.

The results of 12 identical experiments in February and March, 1953, with coho smolt are shown in figure 11. Because the period of experimentation with coho covered about five weeks during early spring, the control temperatures were consistent at 9° C. Figure 11 covers only the experimental results, thus emphasizing the response at extreme temperatures. Some control coho showed negative rheotaxis also. It was found that startling the fish suddenly after the observation period by waving a white handkerchief over both tubs immediately enhanced the positive reaction regardless of the dominant response during the experiment.

Figure 11. Histograms showing response of coho salmon smolt to circular currents at different temperatures. Values shown are percent experiments at each temperature range. Cross-hatched bars, negative rheotaxis; open bars, positive rheotaxis.



DISCUSSION

The widespread occurrence of rheotaxis among aquatic animals has been mentioned and this fact is emphasized many times in the literature (Fraenkel and Gunn, 1940; Buddenbrock, 1952). Among fishes, the phenomenon is universally recognized and, in some cases, is of direct importance to the fishing industry, and in the conservation of fish as a food and recreational resource. With some commercially valuable species the spawning migration is the only time when the fish are concentrated in an area small enough to make fishing profitable. Since it is believed that the ability of fishes, such as salmon, to orient themselves in currents is of fundamental importance in their spawning migration upstream, a detailed knowledge of their movements in relation to the water masses along their migration routes is desirable. Further, it is becoming increasingly desirable to direct the downstream movements of young salmon around power dams without great losses to the population, and here again knowledge of the ability of fish to orient in a fast stream is important.

Sensory Basis of Rheotaxis.

In attempting to understand an innate reaction such as rheotaxis one must be familiar with the sensory mechanisms involved. There are descriptions in the literature of experiments designed to determine what sense organs are primarily involved in rheotaxis. A brief review of some of the more penetrating of these will not be out of place here.

Lyon (1904) placed several fish in an enclosed bottle of water and suspended it in a river. When the bottle drifted with the current, the fish crowded to the upstream end, and when pulled upstream the fish/quickly moved to the downstream end. When the apparatus was held stationary, there was a lack of orientation. This experiment was carried out in shallow water where the bottom was visible to the fish, and it was clear that the observed reaction was due to loss of visual contact with objects on the bottom. Lyon further demonstrated the importance of the optical stimulus by placing fish in an aquarium with a movable background along each side. The fish swam along beside the moving field although no current was present. He later showed (1909) that blinding both eyes of the fish destroyed the latter reaction, but with only one eye blinded swimming with the background occurred as before. Lyon concluded that the eyes were of prime importance in holding position in a stream. Other workers have also emphasized the important role of the eyes in orientation to flowing waters (Garrey, 1904; Clausen, 1931).

The role of tactile organs in rheotaxis has also been stressed. Lyon (1904) found that blinded fish oriented in currents when they touched the bottom. Dykgraaf (1933) showed that fishes utilize the sense of touch to maintain position in a stream by placing blinded fish in an aquarium with a moving floor. When the fish touched the bottom they moved along with it, thus swimming through the still water. Others have argued that tactile stimulation is of prime importance in enabling the fish to detect pressure changes in currents of water.

Buddenbrock (1952) reviews this literature.

The function of the lateral line in rheotaxis has been emphasized. Dykgraaf (1933) showed that blinded fish could detect fine jets of water directed against their sides through a pipette, and that this detection ceased when the lateral line nerves were cut. He stressed the fact, however, that the cutaneous sense organs will detect sudden differences in water pressure in larger masses of water such as the fish meets in its natural habitat and thus overshadow stimulation of the lateral line. Dykgraaf concluded that sight and touch are the primary senses of orientation for fishes in currents, while the lateral line may be important in some situations.

The part played by the ear in rheotaxis is not yet clearly understood. Gray (1937) found blinded fish could orient in rotating but not linear currents and attributed this "pseudo-rheotropism" to asymmetrical stimulation of the semicircular canals. In a review of the sensory capabilities of the labyrinth Lowenstein (1950) concluded that the canals are sensitive to angular accelerations while the otoliths are capable of responding to any movement involving a change in momentum. Not all workers are agreed, however, that the semicircular canals cannot also detect linear movements (Lowenstein, 1950).

Jordan (1917) has observed the grouper Epinephelus striatus orienting to a stream of water by pointing its tail toward the flow. Cutting the lateral line nerves had no effect on this response, but anesthetizing the lips resulted in lack

of orientation. The lips of this fish are the most sensitive part of the body and Jordan argues that orientation with the head pointing away affords the greatest protection for the mouth region. This seems to be an unjustified conclusion, as the most sensitive area of any fish's body is probably some part of the head, but the grouper seems to be the only one showing this type of orientation.

After reviewing some of the literature on the sense organs involved in rheotaxis of fishes, it is evident that the majority of workers interested in this problem today believe the visual stimulus to be the strongest, although tactile and labyrinthine stimuli are also important. The lateral line may be called into play in some situations.

General Rheotactic Reactions.

Experiments involving different species in the long metal troughs have brought out several significant points. Coho and spring salmon, trout, sculpins, catfish and eels move towards the inflow when water is pumped through the troughs. However, the intensity of this positive rheotaxis varies among the five species. Such variation is not unexpected, and differences can probably be correlated with natural habits of the species.

Spring salmon fry are usually found in rivers during their first year of life, and many of them move out to sea before their second year. This movement is gradual, however, and in some areas many spring salmon stay in their home streams

until their second summer. A careful analysis of the mechanisms responsible for downstream movement of young spring salmon has not been published. However, it is tentatively suggested here that those fish which show the strongest tendency to move into fast water are those most likely to be swept away at night when visual stimuli disappear. A similar explanation has been offered for the seaward movement of chum salmon fry (Hoar, 1951a).

MacKinnon (1950) found that coho fry move into the faster of two flows, but that this preference is greatest during the first two hours of observations, after which the response to faster flow changes to an indifference. The coho used for this study moved readily into the inflow end of the long troughs, but did not show a consistent response, i.e. they moved up and down the length of the trough more often than did the spring salmon. It is suggested that this type of response would not lead coho fry into strong currents where they would be swept away readily at night. However, in the experiments where turbulent and quiet areas on either side of a partition are available, coho almost invariably move into the turbulent water. In these experiments, records of the positions of the fish were made one hour after the flow started on one side of the partition. If coho show indifference to faster flow only after two or three hours (MacKinnon, 1950), these results may not give a true picture of the rheotactic reaction. Figure 6 shows that whereas

spring fry continue to move into the inflow end over a two hour period, the coho response decreases more rapidly. It is suggested that consistent positive rheotaxis contributes to the early downstream movement of many spring salmon fry. The fact that most coho fry stay in fresh water longer is due in part to their less consistent positive rheotaxis.

Kamloops trout were studied only in the troughs with partitions at the inflow end, where they preferred the turbulent side. However, they moved into the quiet area more often than coho. These fish are hatched in streams leading into or out of lakes. While some stay permanently in streams, others may move into lakes as fry. From the few experiments performed here no conclusions can be drawn as to the likely fate of these particular fish in their native habitat. The larger percentage of fish in the inflow side suggests movement into fast water. There they would either be carried downstream into lakes at night or they would swim vigorously upstream into lakes during the day.

The high rheotactic response shown by young catfish is noteworthy. The fish used in this study were taken from a shallow, quiet part of the Stave River, typical of the waters anglers usually associate with catfish. Both large and small catfish were taken in the same hauls. Thus, there is no evidence that the different age groups prefer different habitats. The small fish seem to be more active generally than the larger ones and this activity may result in the younger fish moving into currents. However, the lack of catfish in

fast currents in nature suggests strong positive rheotaxis may be only temporary.

The prickly sculpin is a bottom dwelling fish that is widely distributed in fresh water. In the experiments with a straight flow of water about 50 percent of the fish were in the inflow end over a two hour period. In the partition apparatus they showed about equal preference for turbulent and quiet areas. The fish used in these experiments were caught on sandy sloping bottom immediately off the mouth of a small stream flowing into Deer Lake, Burnaby. It is suggested that sculpins prefer quiet water near flowing streams into which they dart for food. These fish often rest in contact with objects on the bottom and in corners of the troughs (thigmotaxis) and it is possible that in turbulent rivers they stay in quiet pools or behind rocks. Sculpins are known to descend rivers during the night at the time of seaward migration of young salmon. Active feeding behaviour may lead the sculpins into fast water where they are carried downstream.

The Atlantic eel lives on the bottom of rivers and estuaries of the east coast of North America, where it hides under cover during daylight and moves about more during the night. Figure 5 shows that about 50 percent of the eels are in the inflow end of the trough over a fifteen minute period. This proportion is maintained over a two hour period (see appendix). With a partition at the inlet end, they show slight preference for the turbulent over the quiet area. For a

species living in turbulent waters a greater positive response for strong flow might be expected, but it is possible that the eels, which repeatedly tried to escape, were under stress in this apparatus and that a true picture of their response to currents was not obtained.

Comparisons can be made on the length of time after the flow is started in the long troughs before the fish move towards the inflow. The threshold for this initial response is lower with catfish and eels than with the other three species. The meaning of this difference is not entirely clear, but it may be that catfish and eels are less sensitive to disturbances such as shadows and vibrations. It was evident that coho and spring salmon and sculpins were more easily disturbed by movements of the observer.

Data from experiments on the general rheotactic reaction of several species partly explains the behaviour of these fish in nature. The spring and coho salmon data is most consistent with the relation between these fish and currents of water in their environment.

Hormones and Rheotaxis.

Hormone treatment brings about changes in the responses of sockeye and coho salmon smolt to flowing water. The interpretation of these changes, however, is not a simple matter. One of the chief difficulties lies in the apparatus, which was designed to determine whether or not treatment with hormones affects the rate at which fish jump upstream over a dam. This change in rate of jumping should be a rough measure of

the change in general activity of the animals. The anomaly in this situation is that a change in activity of the fish does not necessarily lead to an increased number of successful jumps, even though the swimming speed may be increased. Some of the treated sockeye occasionally showed increased swimming speed, and an increase in numbers of jumps, but the latter were often more erratic than the jumps of the control fish, leading to slower movement of the group into the upper pool. An accurate quantitative description of the effects of hormone treatment on activity of young salmon will gradually be built up by the use of different types of apparatus until the most suitable is found.

Another obvious feature of these experiments was the gradual decrease over a period of four weeks in jumping time among control as well as experimental fish. This change is most apparent during the first three or four observations. Each group of fish shows a similar pattern, namely, moving over the dam very slowly for the first few trials, then gradually decreasing this jumping time. It is suggested that this speeding up of jumping time by all fish, including controls, is due to habituation to the presence of the dam and to the handling involved in transferring fish to the test trough. The tendency for sockeye and coho salmon smolt to move toward an area of increased flow is strong and it is felt that the adverse effect of the dam on this rheotactic reaction is soon decreased due to habituation (Thorpe, 1950).

Thyroid Hormone and Activity.

The relationship between the thyroid gland and activity of fish is not clear. Treatment with thyroxine increases the metabolic rate of higher animals (Barrington, 1952, Schneider, 1939), but many workers have failed to demonstrate a change in metabolism, as measured by difference in oxygen consumption, in fishes treated with mammalian thyroid extract (Root and Etkin, 1937; Hasler and Meyer, 1942; Smith and Everett, 1943). The thyroid inhibiting drug, thiourea, has been shown to have no effect on oxygen consumption of Fundulus (Matthews and Smith, 1947). One author (Fleischmann, 1951) has concluded that most fish are very insensitive to thyroxine. However, at least one exception to this lack of metabolic stimulation has been published. Smith and Matthews (1948) increased the oxygen consumption of specimens of Bathystoma over 15 grams in weight by treatment with parrot fish thyroid extract. The suggestion is made by these authors that thyroxine from fish thyroid is more effective than that from the mammalian gland. The thyroid is known to be intimately associated with metamorphosis of amphibia and does modify some phases of fish metabolism (Hoar, 1951b).

In spite of the lack of conclusive evidence that thyroxine increases activity of fish through a change in rate of oxygen consumption, there is at least one example of increased activity of fishes after treatment with thyroxine. Hoar et al (1952) found that chum salmon fry treated for one week with synthetic thyroxine showed an increase in swimming speed,

and the swimming of those immersed in thiourea solution slowed markedly after two weeks. No attempt was made to measure the oxygen consumption of these fish.

It is now becoming increasingly evident that the thyroid gland is related in some way to fish migrations (Hoar, 1951 b). The change from parr to smolt stage is characteristic of young migrating salmonoids, and heightened activity of the thyroid has been recognized at this stage in some salmon and trout (Hoar, 1939, Robertson, 1948). Further, Robertson (1949), Smith (1949) and Hoar (1951b) have increased silvering among salmonoid parr by treatment with thyroid derivatives. No clear evidence of increased silvering was seen in either coho or sockeye smolt treated with thyroxine in this study. This may be due to the fact that the parr marks were already partly covered before treatment commenced and slight changes in the guanine deposition were difficult to detect. Hoar and Bell (1950) relate increased thyroid activity in chum salmon fry held in fresh water past their normal migration time with an upset osmotic balance at this time.

There is evidence in the literature of a relation between thyroxine and rheotaxis. Fontaine (1948) treated elvers of the European eel migrating into fresh water with phenylthiourea. After several days only 20 percent of these fish showed positive rheotaxis, while 90 percent of the controls still exhibited this reaction. Vilter (1944), however, attempted to show by histological inspection that the thyroid

gland of migrating elvers is in the same state as that of elvers raised in captivity. He concluded that the thyroid plays no part in rheotaxis. It is considered that Vilter's conclusion is not based on adequate experimental evidence.

The data on the rate at which thyroxine treated coho and sockeye salmon smolt jump upstream over a dam does not demonstrate clearly that such treatment results in altered rheotaxis. The results suggest, however, in conjunction with qualitative observations, that there may be an increase in rheotaxis which can be demonstrated by more refined apparatus. A method of quantitatively measuring the swimming rate of fish similar to that used by Fry and Hart (1948) might be advantageous in this respect.

Gonad Hormones and Activity.

There are many accounts in the literature of treatment of fishes with male and female sex hormones (Hoar, 1951b). Most of these describe the premature induction of secondary sex characteristics (Berkowitz, 1937; Bretschneider and Duyvene de Wit, 1947; Eversole, 1941) or sex reversal (Bullough, 1940; Taylor, 1948). However, there are some examples of change in activity of fishes after treatment. Stanley and Tescher (1931) greatly increased the activity of goldfish by feeding them mammalian testicular substance, and Hoar et al (1952) showed that the swimming speed of chum salmon fry was increased after one week of treatment with methyl testosterone. The treatments of sockeye and coho smolt in this study show that in general the gonad hormones increased the

activity of the fish. This increase was especially marked in those fish treated with Stilboestrol. The significance of the coincident change in rheotaxis is not entirely clear.

The increasing size of the gonads and the appearance of secondary sexual characteristics are well known features of adult salmon during their spawning migration. Increased activity of the gonads is not to be expected in young salmon moving to sea. However, interrelations between the endocrine organs may be very complex. It has been shown that maturation of the gonads of fish may reduce activity of the thyroid gland (Olivereau, 1949; Hoar, 1951). Barrington (1952) found that immersion of Lebistes in thiourea solution for several months resulted in failure of development of the germ cells and secondary sex characters. The latter appeared when the fish were fed thyroid. The pituitary is recognized as the site of production of both gonadotrophic and thyrotrophic hormones (Hoar, 1951), but the true picture of this complex interrelationship among pituitary, thyroid and gonads in fishes is little understood.

It should be stressed that the concentrations of estrogen solutions used varied widely and potency of the three compounds also varies. The differences that these variations might produce in the activity of the fish should not be overlooked.

Another variable in the sex hormone experiments was the sex ratio among the treated fish. The gonads of yearling Pacific salmon are well differentiated, but no method has yet

been devised for differentiating the sexes from external characteristics.

Temperature and Activity.

The role of temperature in the seaward movement of young salmon is still uncertain. Some workers are of the opinion that it is important as a departure stimulus (Foerster, 1937). Hoar (1951) found that chum fry show increased activity and a marked tendency to swim with the current as hatchery temperatures increase during the summer months. On the other hand, Huntsman (1948) states that at no time do salmon swim actively downstream with the current.

On the basis of many observations of chum fry and coho smolt in the rheotaxis tubs used for temperature experiments, it is concluded that negative rheotaxis does occur at high temperatures, and that active downstream movement in these tubs is not simply a failure of positive rheotaxis.

Foerster (1937) has shown that sockeye salmon migrate from Cultus Lake at temperatures of 4.4 to 5.0° C. As the warmer spring temperatures cause an overturn of the waters in the lake, the mean temperature increases, and at the above range, sockeye smolt move out of the lake. From the evidence in the literature and as a result of the experiments performed here it is suggested that sudden elevation in temperature may lead to active negative rheotaxis by coho smolt and chum fry in rivers, thus hastening their downstream movement.

In conclusion, positive rheotaxis has been shown in

several species of fresh water and diadromous fish. The degree of activity in currents of water varies, those fish normally living in the fastest flowing waters showing the most consistent response. Sustained positive rheotaxis, however, is not the only method used to maintain position in a stream. Some fishes, such as sculpins, hold position through strong positive thigmotaxis. Active positive rheotaxis may lead some young salmon and trout into fast waters where they will be swept downstream at night when visual stimuli are lost. The relation of thyroxine, testosterone and three estrogen compounds to rheotaxis is still not definite, but indications are that all of these hormones increase general activity and lead to more active positive rheotaxis. It is suggested that the appetitive behaviour leading to restless movements of such fish as sockeye yearlings about a lake may be initiated by the hormonal level in the blood. Temperature is probably an environmental releaser leading to a more specialized form of activity, which in some species at least takes the form of an active swimming downstream.

SUMMARY

1. The tendency of several species of fish to move into a flowing stream of water has been measured.
2. Some correlation has been suggested between the natural habitat of each species and the degree of activity in artificially created currents.
3. There is some evidence that increase in thyroxine and sex hormone level enhances the rheotactic response in sockeye and coho salmon smolt. This increase is reflected in the shorter time required by fish to jump upstream over a dam. An estrogen, Stilboestrol, has the most marked effect. Qualitative observations confirm these results.
4. Sudden elevation in temperature 4 to 5° C. above the holding temperature produces negative rheotaxis in chum salmon fry and coho salmon smolt.
5. Migration downstream of young Pacific salmon may be appetitive behaviour which is initiated by increase in some body hormones, controlled, in part, by temperature and directed by water currents.

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APPENDIX

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Table 1. Percent sculpins in inflow end during second and third hours of flow. Figures are mean Percentages for six experiments.

Second hour		Third hour	
Time - 30 second intervals	Percent fish	Time- 30 second intervals	Percent fish
1	55.6	1	65.3
2	59.7	2	59.7
3	47.2	3	50.0
4	50.0	4	55.6
5	50.0	5	54.2
6	54.2	6	55.6
7	58.3	7	54.2
8	51.4	8	55.6
9	47.2	9	51.4
10	33.3	10	56.9
11	48.6	11	51.4
12	51.4	12	56.9
13	44.4	13	50.0
14	50.0	14	40.3
15	43.1	15	44.4
16	34.7	16	51.4
17	44.4	17	54.2
18	45.8	18	50.0
19	33.3	19	48.6
20	36.1	20	58.3
21	56.9	21	56.9
22	52.8	22	54.2
23	34.7	23	65.3
24	45.8	24	61.1
25	41.7	25	50.0
26	54.2	26	56.9
27	52.8	27	63.9
28	34.7	28	56.9
29	37.5	29	66.7
30	45.8	30	56.9

Table 2. Percent eels in inflow end during second and third hours of flow. Figures are mean percentages for six experiments.

Second hour		Third hour	
Time - 30 second intervals	Percent fish	Time - 30 second intervals	Percent fish
1	43.1	1	51.4
2	41.7	2	55.6
3	40.3	3	52.8
4	44.4	4	52.8
5	54.2	5	48.6
6	54.2	6	50.0
7	51.4	7	58.3
8	45.8	8	52.8
9	48.6	9	52.8
10	55.6	10	50.0
11	40.3	11	52.8
12	58.3	12	48.6
13	59.7	13	50.0
14	61.1	14	56.9
15	63.9	15	58.3
16	54.2	16	55.6
17	54.2	17	59.7
18	51.4	18	54.2
19	55.6	19	55.6
20	56.9	20	55.6
21	56.9	21	56.9
22	55.6	22	54.2
23	45.8	23	54.2
24	59.7	24	56.9
25	55.6	25	52.8
26	59.7	26	68.1
27	56.9	27	58.3
28	55.6	28	58.3
29	56.9	29	61.1
30	61.1	30	62.5

Table 3. Percent catfish in inflow end during second and third hours of flow. Figures are mean percentages for eight experiments.

Second hour		Third hour	
Time - 30 second intervals	Percent fish	Time - 30 second intervals	Percent fish
1	87.5	1	61.5
2	74.0	2	71.9
3	71.9	3	70.8
4	77.1	4	64.6
5	72.9	5	62.5
6	70.8	6	71.9
7	76.0	7	60.4
8	58.3	8	67.7
9	69.8	9	69.8
10	76.0	10	58.3
11	55.2	11	61.5
12	65.6	12	65.6
13	63.5	13	74.0
14	65.6	14	67.7
15	70.8	15	75.0
16	69.8	16	75.0
17	74.0	17	71.9
18	77.1	18	71.9
19	63.5	19	74.0
20	66.7	20	72.9
21	80.2	21	77.1
22	79.2	22	80.2
23	78.1	23	66.7
24	80.2	24	74.0
25	81.3	25	76.0
26	76.0	26	81.3
27	79.2	27	76.0
28	61.5	28	78.1
29	74.0	29	76.1
30	83.3	30	83.3