Studies on Conditioned Responses in Fishes. Part VII. Temperature Perception in Teleosts.

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With 3 Figures in the Text.

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INTRODUCTION.

TEMPERATURE plays a large part in regulating the lives of all " cold-blooded " animals. It affects directly their rate of metabolism and their time of reproduction. Such effects are readily shown by *direct* physiological experiments on isolated tissues or organs and by simple observation of total behaviour. As to how far fishes may be supposed to *react purposively* to the temperature changes to which they are constantly subject we have no knowledge.

The present paper describes a series of experiments, using the method of the conditioned response, made with different kinds of fishes to find out whether they react in this way towards, or perceive objectively, small increases in temperature of the water surrounding them. The discussion at the end of the paper shows that a definite answer to this problem is of value in the successful prosecution of certain aspects of fishery research.

The experiments themselves were the first major research undertaken in the sound-insulated building erected for the purpose of these studies on conditioned behaviour. They could not have been carried out satisfactorily under any ordinary laboratory conditions. I wish therefore to record here, particularly, my deep appreciation of the action of H.M. Development Commissioners and of the Council of Armstrong College, University of Durham, in jointly providing this building for my researches. A description of the building is given in Part IV of these studies (**1**).

Outline of Method.

The general principles involved may be simply stated as follows. A slight increase in temperature of the water flowing past a fish is associated over a period of several weeks with the giving of food at a succeeding constant interval of time. The experiment is designed so that a well-marked motor response necessarily associated with the acquisition of food can be used as the registerable conditioned reaction and hence of discriminatory perception. Special tanks have therefore to be devised, for they have not only to be of such a size and shape as to be satisfactory for the application of a temperature stimulus, but they must also be such in which active fishes will live healthily and, as far as can be judged, "contentedly," for the several months required in coming to a reliable conclusion. The thermal stimulus has to be given in a way which precludes the possible operation of an associated factor as a "signalling" stimulus. It is difficult to do this in a way which will enable one to measure the temperature at the point of stimulation on an actively swimming fish, especially when the observer himself must remain concealed. It cannot be too strongly emphasised that reliable conclusions upon sensory perception in animals are, largely owing perhaps to the interference of unknown stimuli, extremely difficult to obtain.

It may well be that our present knowledge of the relationships between animals and their environment contains many serious misconceptions arising primarily out of these difficulties. It is believed that they have been overcome in the present work.

Apparatus.

Two arrangements were used, one for the larger, mostly free-swimming fishes (I), the other for small, mostly sedentary forms (II). In essentials these were alike, the differences between them being only of degree.

Arrangement I (photograph, Fig. 1; plan of arrangement in Fig. 2).

ABC and $A_1B_1C_1$ (fig. 2) are two similar strongly constructed wooden tanks with asphalt lining, 3 metres long, 15 cm. wide, 25 cm. deep, open at the top, and originally designed for a different purpose, but found quite serviceable for these experiments. The side of the one nearest the observer was continued upwards into a board inclined over the tank at 45° to form an effective screen (S_1, fig. 2) between the fish and the observer. The tanks rest in an inclined position on thick pads of felt which reduce sound conduction through the floor to a minimum (this itself was laid specially with the same end in view (see Pt. IV), **1**). By giving the tank this slope from A to C, a graduated depth of water is obtained from nil at A to a few cm. (varied according to species) at C. Sea-water from the Laboratory system enters at A through the tube D (fig. 2). It discharges through a fine jet, flows down the tank, and out to waste at C. The rate of flow was maintained constant for the duration of an experiment. The effect of the graduated depth of water is to limit the normal activities of the experimental fish to that part of the tank where it is covered with water (between B and C) and the depth at C was determined by this factor. This obvious restriction upon the normal activities of the fish decides the course of the experiments and makes it possible to use a simple but very striking conditioned response as evidence of discriminatory perception.

A fish placed in this tank for the first time swims for a while violently up and down, not as a rule passing upwards beyond the centre of the tank (i.e. where it begins to become uncovered). " Excitable " fishes occasionally persist (in those first few minutes) in splashing their way up-stream to the head of the tank in spite of the shallowing water and unless watched will stay there (and possibly die). They do not however attempt to do this after more than one or two such experiences and within a few hours settle down permanently near C. After they have thoroughly settled down, none of the fishes investigated have repeated this violent up-stream splashing or passed the centre of the tank, except for the special circumstances of the experiments as described on pp. 9, 10. It was decided to use this up-stream swimming and splashing response as the conditioned response to be elicited by association with an unconditioned stimulus which would itself evoke this action unconditionally. Considerable patience is needed for the successful conclusion of an experiment and many failures were had in the early stages for reasons which will appear.

Only a very strong incentive will induce a fish to make this difficult up-stream response. This is provided by the introduction of food at the head of the tank. For this purpose, a special food tube enters the outer screen at F. This is arranged so that the observer continues to be hidden from the fish whilst food is given, and so that there are no operations associated with its appearance which are visible to the fish. The tank is divided by a vertical partition (E, fig. 2) 25 cm. from the top end. An opening is cut in this partition so as to form an archway, the small portion AE of the tank constituting the " food chamber." To obtain the food in this chamber the fish must wriggle on its side through the arch, after which, in order to regain its normal position at C, it must either turn completely round in this chamber or go out again backwards, an act which involves much splashing. Even when thoroughly " conditioned " it does this typically with extreme rapidity and nervousness (as if eager to escape from the uncomfortable situation in which it finds itself).

The *temperature* increase which is to serve as the conditioning stimulus is given by the following device. The tube (of Pyrex glass) which carries the sea-water into the head of the tank from the main sea-water supply

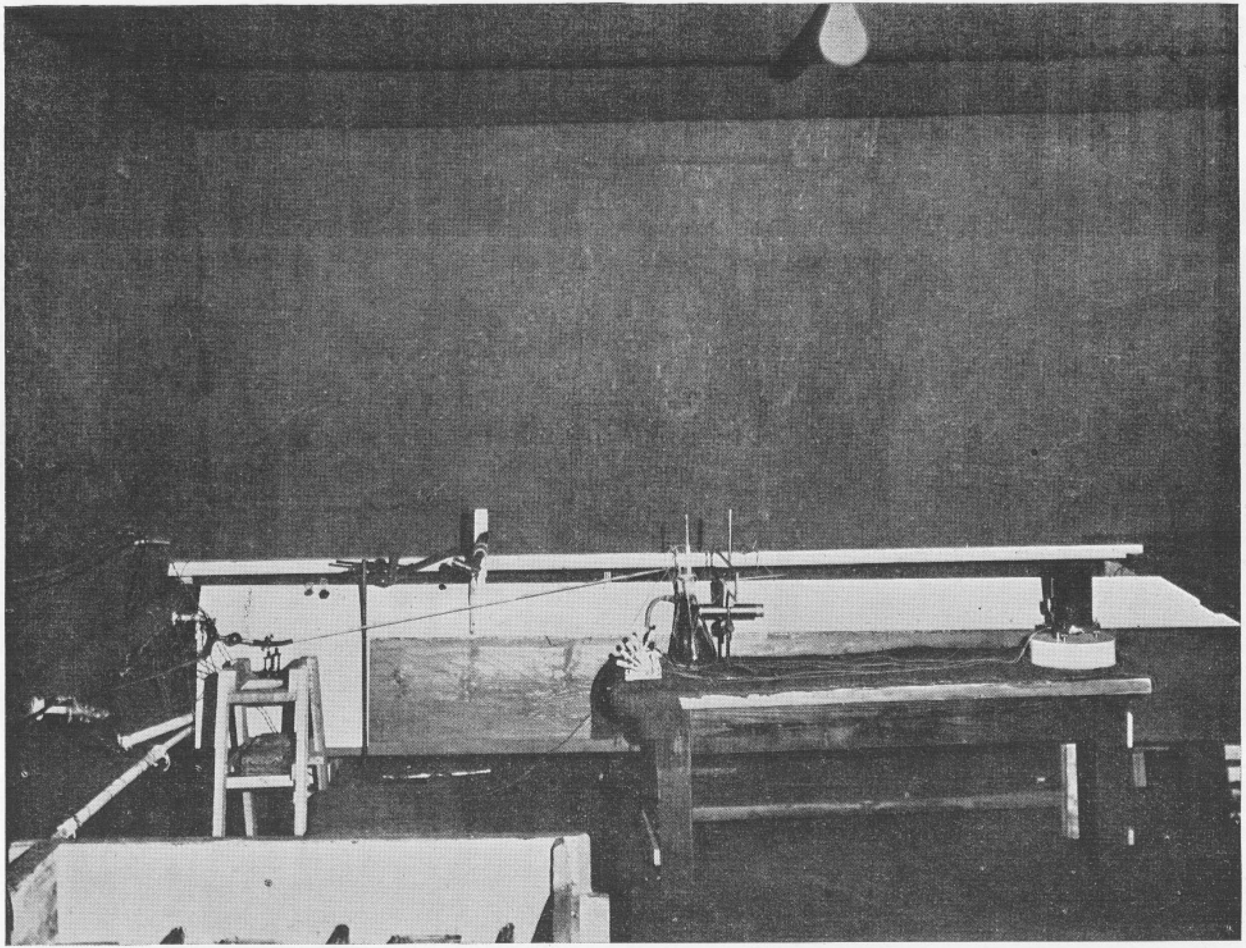

FIG. 1.—Photograph of interior of special building showing the larger tanks (Apparatus I) used in experiments on temperature perception in fishes.

N.B.—The smaller tanks (Apparatus II) were added after this photograph was taken.

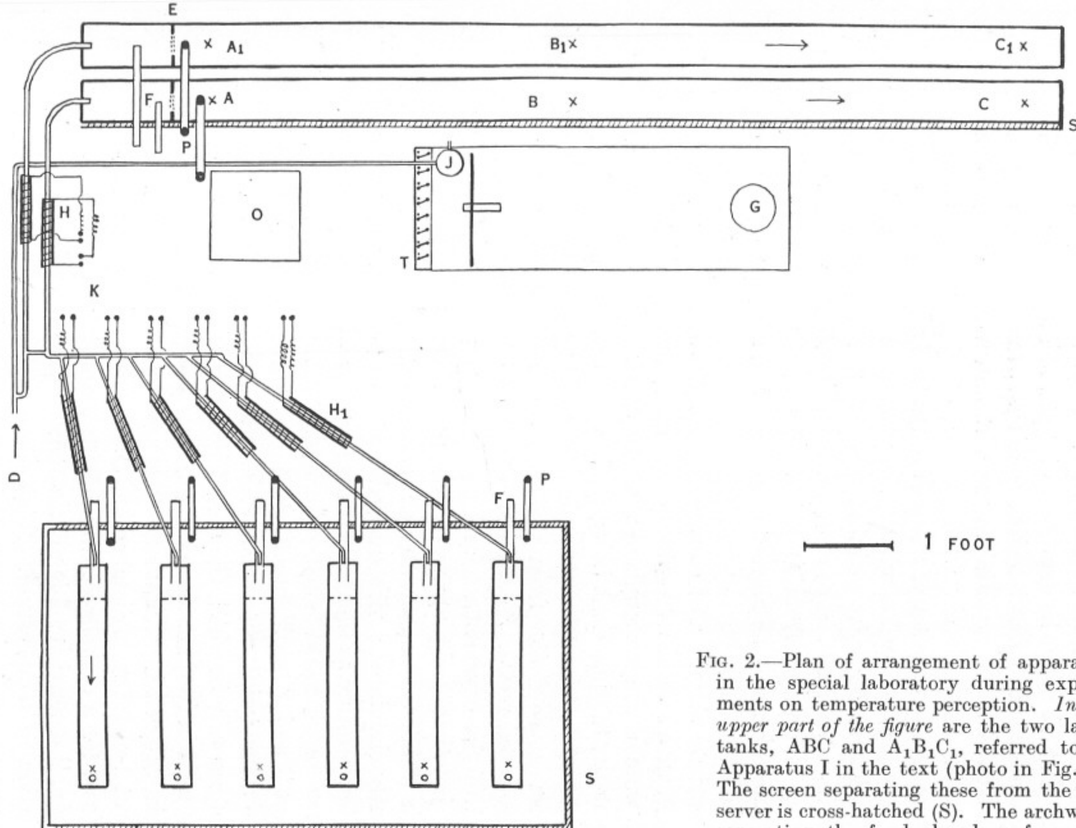

FIG. 2.—Plan of arrangement of apparatus in the special laboratory during experiments on temperature perception. *In the upper part of the figure* are the two large tanks, ABC and $A_1B_1C_1$, referred to as Apparatus I in the text (photo in Fig. 1). The screen separating these from the observer is cross-hatched (S). The archways separating the food chambers from the main bodies of the tanks are labelled E. To the left of these are the food tubes F, and to the right the periscopes for observation (P). Each tank has its separate sea-water supply from D. *In the lower part of the figure* are the six smaller tanks (Apparatus II), enclosed within their common screen S. Each of these is provided with its separate sea-water supply, food tube (F) entering the food compartment, and periscope (P). The taps separating the sea-water supply to each tank are *not* shown: G=mirror galvanometer; H and H1=heating coils (one each for the two large tanks and six small tanks) operated by switches from mains supply; O=observer's seat from which all observations and manipulations can be made; T=Thermo-couple switch board; X="hot-water junctions" of thermo-couples; all the "cold-water junctions" are immersed in J (provided with standard thermometer). The wiring of the thermo-couples is omitted, in order to avoid unnecessarily complicating the diagram. The direction of water flow is shown by arrows.

(D, fig. 2) is wound with a coil of ni-chrome wire (H, fig. 2) connected with the main heating circuit through a soft copper knife switch (K, fig. 2). By closing this circuit for varying lengths of time the water may be heated to varying extents on its passage through the tube into the tank. The heated water then flows down the tank, past the fish, and out to waste. It was found that, as might be expected, the path of this heated water is somewhat complex. This fact itself is not of importance in carrying out the experiments, it being essential to measure only the temperature at the surface of the fish.

For the proper appreciation of the performance of the experiments it is however necessary to outline what takes place at various positions in the tank. It has to be borne in mind that the fish has no restriction placed upon its movements in the tank, other than that effected by the shallowing of the water from C to A. The temperature-recording mechanism must therefore be both easy to move and without any serious time-lag.

For this purpose a system of copper-constantin thermo-couples, used in conjunction with a sensitive mirror galvanometer, were found suitable. The couples were of single strands of No. 34 S.W.G. Constantin and No. 38 S.W.G. copper, the junctions being made with a small bead of silver, using dry borax as flux. Each couple was entirely enclosed in glass tubing to prevent corrosion from the atmosphere which here rapidly attacks unprotected metal. The thermo-couples were thus constant for the duration of the experiments, and no replacements were necessary. The " cold " junction (J, fig. 2) was immersed in a conical flask with side tube through which the same water as that entering the experimental tank constantly circulated ; this ensured that this junction was always of the same temperature as the unheated tank water with possibly a very small difference for which the necessary correction could always be applied. At both " hot " and " cold " junctions the enclosing glass tubing was drawn out to a fine point, the end of which was sealed and filled with a small drop of mercury in which the actual junction was immersed. The couples were used in conjunction with an Onwood reflecting moving-coil galvanometer (Gambell Bros., Pattern 3041) used aperiodically. This had a sensitivity at 1-metre scale distance of 130 mm. per micro-amp. with a timing of 7 sec. for a complete swing. With a shunt resistance of 150 ohms, a " null " deflection of approximately 6 mm. was obtained for 0·1° C. variation in temperature. Each thermo-couple was separately calibrated against " A " N.P.L. certified thermometers over the range required and under the exact conditions of the experiment. This was done by attaching the thermometers to the thermo-couples with the bulbs of the thermometers in close contact with the junctions. Galvanometer readings were then taken for the whole range of differences in temperature used in the experiments, i.e. nil to 5·0° C. As only the " rise " in temperature was wanted, no " ice " junction was required. One of the standard thermometers remained in the " cold-water " junction for the duration of the experiments to give the " resting " temperature of the water.

The " hot " junctions of three such couples were placed at various positions along the tank in the median line—one just past the entrance to the food chamber, one in the centre of the tank, and the other as near as possible to the normal resting site of the fish ; another was added if this latter was not fairly definite.

A typical picture of the temperature changes induced in the tank during an associative experiment is shown in Fig. 3, p. 8.

In this figure the data relate to three thermo-couples placed (1) at the entrance to the food chamber, (2) In the centre of the tank, (3) At the deep end of the tank, and usually touching the fish. The junctions are placed at a depth of 1 cm., 3 cm., and 4 cm. respectively at these three points.

A completely different picture is found on the surface of the water.

As the usual position of a fish in the early stages of the experiments is at C, several minutes elapse before the warmed water reaches the fish. The whole of this time provides valuable opportunity for noting " unstimulated " behaviour. It follows that whilst the actual temperature at the moment the heated water first reaches the fish is the only aspect of this factor which is of importance to the experiment, the fish is actually under the influence of a much higher temperature for a further and subsequent period of up to nearly fifteen minutes, during which the reactions described later (p. 9) are carried out. The conditioning temperature stimulus acts continually, therefore, up to the completion of the reactions involved in food getting. It may further happen that by the time the fish actually fetches the food in the food chamber the temperature at that point is back to normal, whilst that at the lower end still remains high. In later stages of conditioning the fish not infrequently comes to take up a resting position much higher up the tank, and may acquire a habit of resting as high up as the centre of the tank adjacent to the thermo-couple at B.

Arrangement II (lower portion of fig. 2).

A modification of arrangement I was used for smaller fishes, but in all that has been said in regard to observation and temperature measurement it was essentially the same. Instead of the large wooden type of tank, a small shallow oblong zinc trough (80 cm. long $\times$ 11·5 cm. wide) was used. This was similarly inclined to give a graduated depth of water as in the larger tank. It had, in addition, an L-shaped end (omitted in the diagram), but this was a feature introduced primarily for another purpose, and of no material importance in the present series of experiments. Its presence may be entirely disregarded. The normal sea-water entered at the head of the tank, flowed along the length of the tank, becoming deeper on its way, and out to waste at the deep end. In this smaller type of tank all the fishes used took up permanent positions close to the exit so that only one thermo-couple was required. For sedentary fishes such as *Blennius pholis* this was placed so that the fish naturally rested as a rule with its head in contact with the junction. The difficulty of measuring the precise temperature at the point of stimulation was therefore much less in this arrangement than in the larger. As in arrangement I food was

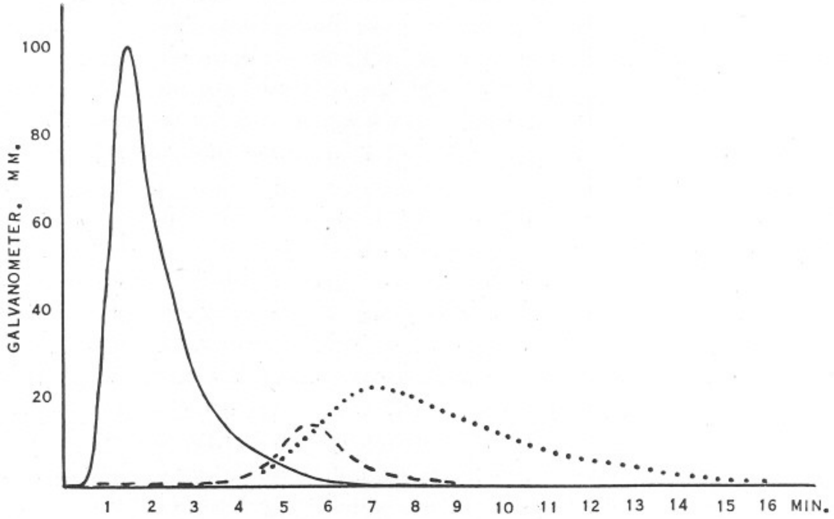

FIG. 3.—Typical record of the passage of the temperature "wave" along the larger tanks (Apparatus I) at each conditioning experiment. Continuous line=thermo-couple at A1; broken line=thermo-couple at B1; dotted line =thermo-couple at C1. Times are reckoned from the moment of putting in the switch of the heating circuit.

introduced into the shallow water through special tubes (F, fig. 2) into a separate food chamber. It was found possible to carry out six experiments simultaneously in six separate tanks of this type owing to their smaller size. All were enclosed in one common surrounding screen, 6 ft. high, and observations made with periscopes of the pattern described in part VI (**2**). The thermo-couples from all these tanks and the two larger tanks were all immersed at their " cold-water " junctions in the same vessel. They were connected up to the same galvanometer, their circuits being interrupted by knife switches arranged on the galvanometer table at a point convenient for the experimenter who carries out all manipulations and observations whilst seated as quietly as possible in one position where all the eight periscopes can be viewed, food given in any of the eight tubes, and the galvanometer scale read without change in position.

General Procedure in making the "Conditioning" Experiments.

After being put into the tanks the fish is left to "settle down," for which a period of at least two weeks is usually needed. During this time the fish is supplied daily with food, but generally refuses it for many days, and so long as it continues to do so the food is left until the end of the day when, if still uneaten, it is removed. When the fish is taking food readily this indiscriminate feeding is stopped for a few days before starting the process of "conditioning" or association of the temperature stimulus with the subsequent giving of food. The general behaviour of fishes during the preliminary "settling down" has been already noted on p. 3. The indiscriminate feeding during this time does not involve passage upstream, the food being dropped into the deeper end of the tank near the fish. The conditioning experiments are carried out as follows :—

The observer enters the special building and locks both doors. The tanks are inspected to see that water flow, etc., is all in order. He then takes up his position (wearing rubber shoes throughout the tests) on the stool O (fig. 2) and notes the behaviour and positions etc. of the fishes during at least fifteen minutes, the temperature of the cold-water junction is read, and the galvanometer readings for each thermo-couple are taken. Then the following operations are carried out for each tank. The switch of the heating circuit (K, fig. 2) is closed to heat the water very slightly as it enters the tank. In the early stages of conditioning the heating circuit is closed for 60 sec. for the larger tanks, and 15 sec. for the smaller, these times being reduced when the minimum temperature rise which the fish can perceive is being found. Records of the galvanometer readings for each thermo-couple in the larger tanks are then noted down at 15, 30, and 60 sec. intervals, at the same time watching the fish closely. The moment the temperature at the thermo-couple closest to the fish begins to fall away from its maximum (see fig. 3 and p. 7 for typical example of changes), food is introduced into the distant food chamber by "washing" it noiselessly down the food tube with water. Pieces of mussel of a uniform size for each type of fish are used as food, one piece at each association. To the first of the two stimuli—the temperature increase—the fish shows no signs of response for a large number of tests. To the second—the food lying in the food chamber—it shows no signs of response until it is perceived (by sight, smell, etc., according to the habit of the fish). A fish such as the cod, for instance, does not react to it for several minutes (i.e. until perceived either by smell or taste or, less likely, by sight) owing to the distance of the food, but when it is perceived the fish at once starts upstream "seeking" movements, and so persists directly upstream until it gets half-way up the tank where it begins to get uncovered.

In the early stages of conditioning, it now returns to its normal position, and shortly after again goes through the same performance, repeating it several times. Its actions become progressively more excited, at each attempt going further upstream nearer to the food, and in so doing becoming more and more uncovered with water. Finally it makes a rapid splashing swim, or rather, wriggle, right into the food chamber, where it makes an attempt to seize the food, acting throughout as if in a state of great agitation. In these early stages it is usual for this to result in failure to acquire the food, whereupon the fish splashes back at great speed to its resting position without the food for which it has struggled. For several days it is not usual for the fish to go through these actions in their entirety more than once in one day, although the food is still present in the food compartment and the fish is free to fetch it. If this remains uneaten by the end of the day I remove it before leaving the laboratory. As these associations are continued day after day the fish becomes more persistent in its efforts to reach the food and less agitated by its own vigorous splashing. Eventually, when thoroughly conditioned, it takes the food without hesitation, but always, or so it appears, with great excitement, and to the end of the experiments makes the return journey with very great rapidity and "nervousness." The movements involved in getting food from the food compartment have been already described on p. 3. By continuing this regular association of temperature increase with food there comes a time when, as soon as the thermo-couple nearest to the fish shows that the temperature increase has reached that point, the fish shows an obviously "anticipatory" reaction. With fishes such as the gadoids, which maintain posture by gentle undulation of the pectoral fins, the earliest sign of conditioned response is a quickening of their undulation, followed by a rapid swim upstream, of varying extent and in its final form the whole response occurs in the way already described as the act of food-getting. It must be remembered that this now takes place before the introduction of food. In the later stages the fish, having arrived in the food chamber, continues to wait there practically "high and dry" until food is given, which it then seizes sharply and swims and splashes violently back to its normal position.

During these performances the attitude of the fish may be described as one of great excitement and its movements are rapid, alert, and vigorous; it may also show champing movement of the jaws. With sedentary fishes such as Blennius, Onos, Liparis, etc., which remain (under the conditions of these experiments) for hours or even days motionless in their tanks, the response is still more striking.

Results.

It will be useful if I restate here that, having first established that the particular type of conditioned motor response could in fact be built up, the experiments were planned to find out further whether fishes would form these conditioned motor responses to the smallest temperature increment which it was practicable to apply and to measure with reasonable accuracy under the peculiar circumstances of the experiment. They were therefore first conditioned to a relatively high temperature stimulus of a strength found to be effective (an increase of from 0·4° C. to 3·0° C.). After having formed the conditioned motor response to this stronger stimulus, the temperature rise was then gradually lowered at successive trials to the lowest practicable limit of between 0·03° C. and 0·1° C. If the fishes continued to give either a complete conditioned response or some essential part of it for a further large number of trials the object of the experiment was achieved. There were a number of deaths in the preliminary and early stages of an experiment, and these are not further considered. Such deaths would very likely have occurred just as readily had the fishes been living under ordinary aquarium conditions, and were regarded as failures to become acclimatised to the changed conditions. Of the fishes which became fully acclimatised, it may be said at once that each one had given, before the completion of the individual experiment, a well-marked conditioned motor response of the type outlined in the previous section to a temperature increase of between 0·05° C. and 0·10° C., and in some instances consistently to a rise of 0·03° C. for a large number of successive trials. This is the essential result of the whole series. As the experiments were lengthy, each individual being investigated for several months, it is proposed to give a " log " of one experiment only, that on the cod, *Gadus callarias*, and to give a summary of the remainder. These histories may be divided into two series corresponding to the two types of apparatus, large and small.

A. Experiments in Apparatus I.

Gadus callarias L.

The " log " of this experiment is condensed into Table I. In this record and in the brief descriptions of the other experiments a large number of subsidiary observations must of necessity be omitted, neither is it possible to give any detailed account of the temperature changes down the tank, for which the typical example quoted above (p. 8) must suffice. Throughout the paper I use such terms as " anticipatory," " sulking," " nervous," " attention," etc., in describing behaviour solely as a means to illustrate the behaviour of the fishes more graphically and in a manner which may be readily understood. The terms have merely a descriptive value.

TABLE I.

Record of Experiment on a Specimen of the Cod, *Gadus callarias* L., 20 cm. in length, showing the Process of Conditioning to a Temporary Slight Increase in the Temperature of the Surrounding Water.

size of specimen—20 cm. when started, 23 cm. when finished. Lived in the actual tank for several months before experiments were started. For full description of the actions of the fish under the various conditions see text pp. 9, 10. The times given in the "response" columns refer to the actual time subsequent to putting in the switch which starts to heat the water as it flows in. The maximum temperature rise used as stimulus from 12.v to 17.vi was 1·4° C., and was generally very close to this.

Date.	Time.	Behaviour of fish during 15 min. immediately prior to conditioning test. (Letters refer to position in tank, see Fig. 2.)	Position of fish when the observations in next two columns were noted.	Temperature increment of water in vicinity of fish at the instant of conditioned response.	Response to conditioning stimulus, e.g. temperature increment.	Response to unconditioned stimulus, e.g. food.	Notes.
12.v.3	12 00	Slow quiet swimming at C.	C	—	None during 22 min.	Fetched with very nervous actions after one preliminary attempt when it swam only half-way towards it.	Food given at B to get the fish accustomed to passing upwards.
13.v.32	14 30	do.	C	—	None during 20 min.	Fetched eagerly and at once.	do.
14.v.32	9 45	do. between B and C.	B	—	do 25 min.	do. leaving part behind.	Food given at entrance to food chamber.
17.v.	9 52	do. at C.	C	—	do. 15 min.	Fetched rapidly at once.	do.
[no further expt. between 15.v.32 and 3.vi.32 owing to personal illness.]							
4.vi.	12 10	do. at C.	C	—	do. 15 min.	do.	do.
5.vi.	11 05	do. at C.	C	—	do. 15 min.	do.	do.
6.vi.	10 20	do. between B and C.	B	—	do. 2 min.	do.	do.
8.vi.	12 30	do. at C.	C	—	do. 5 min.	Food given at 5 min. but not fetched until 18 min.	do.
9.vi.	12 35	do. at C.	C	—	do. 4 min.	do. [fetched at 15 min.]	Very active the whole time between giving of food and fetching it, dashing wildly up and down.
14.vi.	11 25	do. at C.	C	—	do. 4 min.	do. [do. 16 min.]	
15.vi.	10 15	do. at C.	C	—	do. 4 min.	do. [do. 12 min.]	
	15 05	do. at C.	C	—	do. 4 min.	do. [do. 6 min.]	
16.vi.	9 45	do. between B and C.	B	—	do. 2 min.	Food given at 3 min. fetched rapidly without hesitation.	Food now given inside food chamber, the return from which was made with great rapidity, much splashing, and signs of "nervousness."
	14 20	do. at C.	C	—	do. 4 min.	Food given at 5 min. do.	
	19 40	do. at C.	C	—	do. 4 min.	do. do.	
17.vi.	10 20	do. at C.	C	—	do. 4 min.	do. do.	
	12 50	do. between B and C.	B	—	do. 2 min.	Food given at 3 min. do.	
18.vi.	10 30	do. between B and C.	B	1·2° C.	Swimming became very rapid, excited dashing up and down.	do. 3 min. do.	
	12 30	do. do.	B	0·6° C.	Same excited actions as at 10 30.	do. do.	
20.vi.	16 30	do. do.	B	0·3° C.	Very excited swimming up and down, going almost to food chamber several times.	Food given at 5 min. Excited actions continued, food taken with great nervousness at 14 min.	
21.vi.	12 20	do. do.	B	0·3° C.	do.	do. fetched at 18 min.	
	17 20	do. do.	B	0·3° C.	do.	do. 12 min.	
22.vi.	11 45	do. do.	B	0·2° C.	do.	do. 8 min.	
	12 50	do. do.	B	0·4° C.	do.	do. 8 min.	
	16 10	do. do.	B	0·7° C.	do.	do. 14 min.	
23–24.vi. No expt.							
25.vi.	20 35	do. do.	B	0·23° C.	do.	do. 8 min.	
	21 20	do. do.	B	0·37° C.	do.	do. 8 min.	
26.vi.	11 05	do. do.	B	0·17° C.	do.	do. fetched immediately.	
	12 10	do. do.	B	0·25° C.	do.	do. fetched at 10 min.	
	15 20	do. do.	B	0·13° C.	do.	do. do. once.	
27.vi.	9 50	do. do.	B	0·10° C.	do.	Food given at 3·5 min. Fetched at once.	
	11 40	do. do.	B	0·15° C.	do.	do. do. 15 min.	
	12 50	do. do.	B	0·23° C.	do.	do. do. 15 min.	
	15 45	do. do.	B	0·23° C.	do.	do. do. 15 min.	Some adjustments made in apparatus after last test on 27th.

28.vi.	12 10	Fish " sulking " in deepest corner of tank at C.	C	[1·12° C. (max.)]	No reaction whatever in 11 min.	Food given at 11 min. Not taken and no signs of interest taken in it. Removed at 13 05.	
	17 20	do.	C	[1·35° C. (max.)]	do.	do. Removed food at 18 30.	
29.vi.	No expts.	Deepened water slightly to facilitate passage completely into food chamber.					
30.vi	do.	Fish still " sulking " as on 28th.					
1.vii.	15 40	do. up till midday, then swimming as usual between B and C.	B	0·90° C.	Very excited swimming response as before the 27th.	Food given at 4 min. but not taken by 17 00 so removed.	
2.vii.	No expt.	Fish " sulking " and not looking well.					
3.vii.	do.	Fish apparently normal again in appearance and behaviour.					
4.vii.	6 50	Fish now swims more frequently at about centre of tank, near B.	B	0·08° C.	Very excited, went directly to food chamber, stayed there till food was given 10 sec. later.	Food taken at once.	
	12 05	do. almost stationary	B	0·08° C.	Exact repetition of last.	do.	
	16 50	do. do.	B	0·05° C.	do.	do.	
5.vii.	9 15	do. do.	B	1·00° C.	do.	do.	
	12 00	do. do.	B	1·00° C.	do.	do.	
	19 50	do. do.	B	1·00° C.	do.	do.	
6.vii.	11 45	Moving slowly about near T.C. 2 (B).	B	0·05° C.	Went immediately to food chamber.	do.	
	15 10	do.	B	0·05° C.	do.	do.	
7.vii.	9 50	Keeping more or less still with dorsal part of body out of water, about 1 foot above B.	See last col.	0·05° C.	do.	Food delayed for 5 min., during the whole of this time the fish stayed on its side in the food chamber, wriggling and nosing about for food. Response now very powerful.	
	12 10	do.	do.	0·08° C.	do.	do. [same delay].	
	19 45	do.	do.	0·05° C.	do.	do. [do.]	
8.vii.	15 45	do.	do.	0·05° C.	do	Food given immediately on entering food chamber.	
[Owing to the habit this fish now had of keeping well up the tank the level of the water was now reduced to its previous height (i.e. as before 28.vi).]							
9.vii.	10 05	Swimming slowly between B and C as before, but occasionally passing B.	B	0·05° C.	Repeated rapid and excited dashes to mouth of food chamber, but no actual entry.	Food given 2 min. after first rapid swim to entrance but it was not actually fetched for a further 2·5 min. The lower water level necessitates much more splashing in reaching the chamber.	
10.vii.	No expt.						
11.vii.	10 05	Swimming rapidly up and down [possibly due to hunger, as no food yesterday].	B	0·05° C.	Extremely violent dash straight into food chamber.	Food given immediately on entering food chamber, snapped up at once.	
	11 05	Swimming slowly between B and C.	B	0·05° C.	Exactly as on 9.vii.	do.	
12.vii.	10 50	do.	B	0·05° C.	Immediate swim directly into food chamber.	Food given at once and taken quickly. The fish continued to make repeated swims into the food chamber during the next 20 min., until an even temperature again supervened.	
	16 05	do.	B	0·08° C	do.	do.	do.
13.vii.	11 00	do	B	0·10° C.	do.	Food given and taken at once. Then rested quietly between B and C.	
	15 10	do.	B	0·05° C.	do.	do.	do.
14.vii.	10 35	do.	B	0·05° C.	do.	do.	do.
[15.vii.	No expt.	Demonstrations to Mr. Storrow caused a certain amount of disturbance.]					
16.vii.	9 25	Kept almost still by T.C. 2 (B).	B	0·05° C.	Dashed wildly up into food chamber, and then back to very opposite end of tank with extreme rapidity. It then continued to make repeated dashes from C to B, but there stopped suddenly short, as though violently inhibited.	Food taken with nervousness only after 15 min.	This very remarkable response is clearly connected with the demonstrations of yesterday.
17.vii.	10 00	Watched during 30 min. fish swimming slowly around at B, occasionally making short rapid swims (as if in anticipation) between B and the food chamber. It sometimes stayed there for nearly a minute showing evidence of keen attention.	B	0·16° C.	Almost exactly as yesterday, continuing even longer, for 30 min.	Food taken at 30 min.	do.
[17.vii. At noon raised the level of the water back to the level of between 28.vi. and 8.vii. The fish now took up its old position well above T.C. 2, between the mid-length of the tank and the food chamber, showing continuously signs of keen attention.]							
18.vii.	No expt.						
19.vii.	9 20	Swimming slowly between B and C, sometimes motionless for several minutes just above B.	B	0·05° C.	Immediate swim into food chamber, where it stayed waving its tail and nosing about until food was given.		
	15 30	do.	B	0·22° C.	do.	do.	do.
20 vii.	Fish removed to aquarium tanks prior to my going on leave. While I was away it jumped out of its tank and died on Aug. 8th, 1932.						

Among the more interesting points in the experiment with this fish are the following. The earliest signs of conditioning appeared at the 18th association of temperature with food (18.vi). This was followed by a period when the conditioned response was incomplete—lasting until the 37th association (1.vii). The first complete conditioned response occurred at the 38th association (4.vii). It may be readily seen that a temperature of 0·05° C. was sufficient to produce the conditioned response throughout the greater part of the experiment, which was brought to a premature conclusion on 19th July, 1932.

Gadus merlangus L.

Individual whiting were found to be difficult to acclimatise to these conditions. This experiment was therefore begun with a group of three young specimens, each of a length of 12 cm., which together settled down readily, after being placed in the apparatus on April 30th, 1932. Like the cod just described they normally swam slowly up and down at the deeper end of the tank, and there was also, as with that fish, considerable hesitation over the performing of the final part of the act involved in getting food until the experiment was well advanced. One fish (which could be easily recognised as having a darker mouth than the others) was generally the first to respond both to the temperature and to the food stimulus, as well as being the first to show any signs of conditioning. The first conditioning experiment was made on May 13th. On June 14th (at trial 10) the three fishes were swimming slowly about when the " leader " (for so we may conveniently call the dark-nosed individual) happened to arrive at the middle thermo-couple at the same time as the warmed water which was passing slowly down. It at once rapidly increased its rate of swimming and went without hesitation straight on and into the food chamber, but not waiting, however, for the food which was shortly to follow. It fetched this very nervously after a few minutes. The other two fishes showed no conditioned reactions, nor did they fetch the food for some considerable time. For the next three days this was a typical picture of events at each association. On June 18th all three, beginning still with the leader, showed conditioned responses before food was given. At the 25th trial (June 25th), the leader and one other gave a complete response, together swimming with extreme rapidity direct to the food chamber, the third following shortly afterwards. The next day all three gave a complete conditioned response at the same instant. From the earliest signs of conditioning all three showed evidence of extreme nervousness when carrying out the responses. On June 27th one of them was found to be very inflated and died during the night after removal to one of the aquarium tanks. Another died on July 2nd, leaving the experiment to be concluded with the " leader." By the 42nd trial this fish was giving complete conditioned responses to temperatures of 0·05° C. During the course of the experiment various adjustments of depth of water were made from time to time with results similar to those with the cod. I was absent on vacation between July 20th and August 16th. For this period the fish was removed to one of the aquarium tanks where it was fed with others in the usual routine manner. On returning it to the experimental apparatus in the special building it refused food and "sulked" until August 23rd. The following day this came to a sudden end when the fish gave a complete conditioned response, going directly to the food chamber in response to the temperature increment. This showed complete retention of the conditioned response after thirty days' absence from the apparatus. Between August 25th and Sept 6th temperature increases of 0·03°–0·07° C. consistently gave perfect conditioned responses, and again on Sept. 12th., after I had been away from the laboratory since Sept. 7th, during which time the fish was left in the apparatus without food and entirely free from disturbance. It was now necessary to go more fully into the question as to whether the temperatures given above (and indeed throughout the whole series) were those of the actual point of stimulation. This cannot be satisfactorily answered until more is known about the distribution of the end-organs for temperature perception. But the problem was narrowed down by placing thermo-couples at very short intervals between the surface and bottom, for it has already been mentioned that relatively warm water travels down the surface layer very much more rapidly than in the lower layers. It was definitely established that the response began only when the thermo-couple which was placed at a depth corresponding to the upper part of the body of the fish (excluding the dorsal fin) gave the readings from which the temperature increments were calculated. The experiment was concluded on Sept. 24th, 1932. Since Sept. 12th temperature increments of 0·03°–0·13° C. (with one occasion when no response was shown until a rise of 0·33° C. was indicated) had been adequate stimuli. Total number of associations 73.

Gadus virens L. Size 14 cm.

Started October 6th, 1933, and settled down readily. Two individuals of this species previously tried had refused to settle down. The first conditioning experiment was made on October 11th. Its general behaviour was closely similar to that of the other gadoids already described. The first sign of conditioned responses to temperature increments was shown on October 26th (24th association). These actions, both in their early and in their completed states, closely resembled those of the cod and whiting, i.e. in the early stages—short, rapid, to and fro swimming, passing once or more to the upper parts of the tank, but not actually entering the food-chamber, the whole action being carried out with signs of considerable

" nervousness." This incomplete response was given until November 9th. On this date (49th association) the complete conditioned response including entry to food chamber was made, but with great rapidity and nervousness, this type of reaction occurring until November 29th (71st association). Then followed a period lasting until December 5th, when the response was carried out completely but with less evident signs of nervousness, to be followed by the last period lasting until December 15th, during which the highly nervous type of response reappeared and persisted. The total number of associations was 83, of which at numbers 61 to 83 the adequate temperature stimulus was an increment of between 0·06° and 0·10° C.

Raniceps raninus (L.). 17 cm.

This is one of our rarer fishes and is not easy to keep in captivity. The specimen used was caught on a fisherman's line in November, 1931, and kept under aquarium conditions before being transferred to the experimental building on November 11th, 1932. During these twelve months it appeared to be in exceptionally fine condition, but after its transference it refused food for many weeks and was not feeding readily enough for experimental purposes until January, 1933, the first association of temperature and food being given on January 9th. Its normal resting behaviour was characteristic—" lurking " at the lowest corner of the tank (C), occasionally passing almost imperceptibly a short distance up the tank with slow waves of the tail, then backing again with the same smooth action. When disturbed it could be both vicious and vigorous in its actions. Temperature increments of approximately 0·4° C. were used in the early stages of conditioning.

No change in the normal resting behaviour was shown to any of these increments until the 31st (on February 2nd). At this trial the fish started to swim slowly upstream in response to the temperature stimulus and went straight on to take the food from the food chamber when it was given 30 sec. later. No further complete responses were given for several weeks—although the fish continued without exception to carry out the first parts of the reaction immediately following the temperature stimulus. From February 13th to March 14th food was entirely refused, but weak anticipatory responses continued to be shown to the temperature rise. On March 14th (trial 56) weak anticipatory responses were followed by actual consumption of the food—fetched from the food chamber. The 61st trial (March 21st) produced a complete conditioned response, the fish splashing rapidly upstream on reception of the thermal stimulus. With occasional modifications and periods during which no food was taken the fully formed conditioned response was given to most of the trials with the thermal stimulus from this date to the conclusion of the experiment on June 8th after 147 associations. The magnitude of the stimulus was lowered gradually between March 21st and April 18th, until by the latter date conditioned responses were given to increments between 0·05° C. and 0·10° C., and continued to be given to these small increases up to the end of the experiment.

Pleuronectes platessa L.

This species readily settles down to the experimental conditions. An experiment with a ♂, 17 cm. long, was started on August 24th, 1932. Its normal resting behaviour was generally to stay motionless in one position for long intervals of time mostly at about the centre of the tank, touching the central thermo-couple. The first conditioning experiment was made on August 26th, the fish showing no reaction whatever to the temperature increment (1·0° C.), but fetching the food readily from the food chamber in its slow, hesitant manner. Owing to the restricted size of the entrance to the food chamber the fish had difficulty in getting out of it again, and eventually backed out, a course which it was always compelled to adopt. The earliest evidence suggesting that the association between temperature and food was being formed was seen so early as the 11th association (September 6th), when, after making such anticipatory actions as eye-movements directed towards the food chamber, and characteristic forward jerks, the fish passed into the food chamber after ten minutes. The food was withheld until the responses ended at their goal. At the next two trials on the same day slight forward movements were the only response to the thermal stimulus. During the following three days no experiments were made, but a complete conditioned response of the slow, jerky nature typically given by this species was given at each of three separate trials on September 12th. Between September 13th and 15th (i.e. from trials 19 to 23) the temperature increase was lowered at each successive trial; from September 16th onwards it was kept at 0·1° C. or lower (minimum actually producing response 0·06° C.).

The experiment was finished on October 25th after 71 associations, temperature increments below 0·1° C. acting as stimuli from trials 24 to 71. The stationary habit of this fish permitted the measurement of the temperature increment at the moment of response to be made with a much greater degree of accuracy than with the fishes previously described.

A smaller specimen (8·5 cm.) of the same species was investigated in Apparatus II, between October 6th and December 15th, 1933, during which it was given 78 associations of temperature and food. The first conditioned responses appeared at trial 21, the complete response at the 27th, whilst temperatures below 0·1° C. (minimum 0·05° C.) were effective conditioning stimuli from the 35th association (November 18th) to the conclusion.

Cottus scorpius L. 22 cm., ♂.

Cottus scorpius and *C. bubalis* are fishes which are well-suited to this type of experiment, being ready feeders, easy to keep in good health, spending long periods motionless in one position, and such movements as they do make are sharp and decisive in character.

This specimen was placed in the apparatus on June 26th, 1933 and the first conditioning experiment made on June 28th. No signs of awareness of temperature increment were shown until the 12th association with food (July 4th). Shortly after the maximum increase of 0·6° C. had been reached the fish made a short jerky movement forward—rested a few seconds—then another movement—and so on until it reached the middle of the tank, at which moment food was given in the food-chamber.

It then completed the response and dashed wildly back to its normal position at the deeper end. The complete conditioned response was given so early as trial 16 (July 5th). By trial 20 (July 6th) the temperature stimulus was reduced to 0·2° C. and at trial 23 to 0·1° C. Until the conclusion of the experiment after 88 associations (September 7th) the effective stimulus remained between 0·05° C. and 0·1° C. Some modification of behaviour took place during the course of the experiment, the fish coming to adopt the habit of staying at a point midway in the tank in spite of the fact that under these conditions its head was well out of water. The conditioned responses given in the later stages were carried out with actions so rapid, and splashing so violent as to make it very difficult to observe both the galvanometer scale and the fish at the instant of reaction.

B. Experiments in Apparatus II.

Pleuronectes flesus L. 15 cm. long.

Experiment started on August 10th, 1933. This fish was stationary for long periods close to the outflow, and generally had the thermo-couple junction in direct contact with it. The first conditioning experiment was made on August 17th. No responses were shown to the temperature increment until the 20th association (September 1st), when the fish moved slowly round and looked "expectantly" towards the food chamber; it made no further move until food was given two minutes later. The next day it went rapidly to the food chamber when the temperature increase was 0·6° C. and remained there until food was given. No tests were made on September 3rd, whilst a negative result was given on September 4th. I was away from the laboratory for the following seven days during which time the fish was removed from the special building to an aquarium tank, being replaced in the apparatus on

September 13th. At two trials on September 14th, being the 24th and 25th since the beginning, no conditioned response was seen, but at the 26th and 27th (September 15th) the complete swim to the food chamber was made before food was given. The conditioned response then remained stable until the conclusion of the experiment at the 59th association (October 5th), for the last 20 of which no increment greater than 0·1° C. had been used as the conditioning stimulus, the minimum being 0·05° C. The experiment was ended mainly because the fish had become too long to turn round comfortably.

Pleuronectes platessa L. Length 8·5 cm.

Summarised above on p. 17.

Spinachia vulgaris Flem. Length 12 cm.

Put in apparatus on October 6th, 1933. For some time swam restlessly up and down, frequently getting entirely out of water at the food chamber, but settled down after a few hours. A small plant of Fucus was found useful in the deeper end of the tank, as the fish took cover among its fronds, and stayed amongst it throughout the experiment. Conditioning experiments were started on October 11th, the fish proving to be an easy subject as it fed readily and viciously. No response was given to the temperature increment until after 41 associations with food (November 5th). At the 41st temperature stimulus the fish turned awkwardly round (its normal position being head downstream at the deep end, concealed among the Fucus) and went directly to the food chamber where it was given food on its arrival. No further conditioned behaviour was seen until November 11th at association No. 53 when the fully formed response was again given. Such sudden changes in conditioned behaviour are unusual unless for some clear reason such as obvious loss of appetite. The temperature increment was lowered between November 11th and 25th until it was down to the range 0·05° C.–0·10° C. which was then used as stimulus and found effective up to the end of the experiment on December 15th after 84 associations.

Gobius (*Gobiusculus*) *flavescens* Fab.

(*Gobius ruthensparri* Euphrasén.) ♂, length 6 cm.

Put in apparatus on October 6th, 1933, and settled down at once, showing no signs of uneasiness whatever, and taking food readily the same day. Owing to its small size the depth of water for this species was reduced to 2·5 cm. at the deeper end and shallowing to nothing in the food chamber. Neither this species nor Spinachia showed any discomfort whilst wriggling along out of water and wriggled backwards readily with no undue haste after taking the food. The normal resting behaviour consisted of alternate rests and sallies, and it was frequently observed chasing bubbles or any small particles that might happen to fall on the surface of the water. Conditioning started on October 11th, the full conditioned motor response being given so early as October 18th after 14 associations. The temperature increment acting as conditioning stimulus was lowered to 0·1° C. by October 28th (after 26 associations) and was maintained between 0·05° C. and 0·1° C. from then until the conclusion on December 15th after 77 associations. Of these further 51 trials, 15 produced no response (December 6th to 12th) but food was also refused on those days. Only rarely did this fish show any of the very rapid nervous responses of the gadoids, generally going straight upstream into the food chamber with a series of rapid darts, the final six inches, which necessitated wriggling, excepted.

Crenilabrus melops (L.).

A young specimen, 6·5 cm. long, taken from a rock-pool at Cullercoats on October 4th, 1933, and put in the experimental apparatus on October 6th. Its normal behaviour was to rest in contact with one of the lower corners of the tank, but making occasional swims round the sides of the tank. Conditioning began on October 11th. Owing to the relatively greater depth of body, it was found that this species could not negotiate the final six inches of the passage to the food chamber unless there was sufficient water present to enable it to get along in at least a semi-vertical position. Probably for this reason it could not be conditioned to make the full swim, always stopping short when the dorsal part of the body was clear of the water. Anticipatory actions were seen after 29 associations (October 31st); these were champing of the jaws, upturning of the eyes to the food tube and waving of the pectoral fins. No further evidence of conditioning was seen until trial 39 (November 8th) when the anticipatory actions again appeared, whilst even partial swimming to the food chamber did not occur until trial 46 (November 15th) and the full swim (modified as above) not until trial 53 (November 21st). Temperature increments between 0·05° and 0·10° C. were then used successfully until the conclusion of the experiment on December 15th (total number of associations—71).

Liparis montagui (Don.). Length 9 cm.

This is a small and inconspicuous littoral fish with the ventral fins united to form an adhesive disc. In the apparatus the fish stayed motionless for many hours at a stretch, adhering to the bottom or sides of the tank, generally close to the outflow. Small pieces of shore-crab liver were used in place of mussel as food for this and the next species. The fish was put in the apparatus on October 6th, 1933 and the first conditioning experiment made on October 11th, but for a few days food was not as a rule eaten until many minutes had passed. Anticipatory reactions, consisting of curling and uncurling the tail (the body staying adherent and motionless), were given at the 26th association of temperature increase and food (October 28th). These continued to be given without any further motor response until the 36th association (November 6th) at which test, on perceiving the thermal stimulus the fish turned round and went upstream searching and " nosing about " with rapid circular movements as it went to the food chamber. This remained the general picture of the full motor response until the end of the experiment on December 15th after 71 associations. Only temperature increases between 0·03° C. and 0·10° C. were used after November 6th.

Cyclopterus lumpus L.

The specimen used was a very young one, only 3 cm. long, of a fish belonging to the same family as the last and characterised likewise by the union of the ventral fins to form a circular adhesive disc. Its general behaviour was closely similar to that of Liparis, and the experiment progressed in much the same way, the fish being put in the apparatus and receiving the first conditioned stimulus on the same dates. No anticipatory reactions were seen in this fish but this may have been due to the difficulty of observing such reactions in so small a fish with the low magnification of the periscope. It gave a full conditioned response of swim to and entry into the food chamber on November 4th (after 32 associations). Food was usually taken readily and quickly but was not infrequently ejected and reswallowed several times before the fish finally left the food chamber and returned to its usual position. Temperature increases of 0·05–0·10° C. only were used between November 5th and the conclusion on December 15th (after a total of 67 associations), the conditioned response remaining quite stable. It is interesting to find that so young an individual forms the conditioned response as readily as mature fishes.

Zoarces viviparus L.

Put in the apparatus on March 10th, 1934, but did not feed until March 17th, and the first conditioning experiment was made on April 3rd. Its general behaviour was well suited to the purpose as it remained motionless, curled up in one corner, for long intervals. The temperature stimulus evoked anticipatory reactions on April 14th after 25 associations with food, and the full conditioned response was given at the 26th at which test the increase in temperature used was 2° C. On April 18th the fish swam rapidly and excitedly to the food chamber in response to a rise of

0·03° C., and a stimulus of between 0·03° C. and 0·05° C. was used for the remainder of the experiment until May 28th (associations 31 to 95).

Blennius pholis L.

A specimen 15 cm. long was put in the apparatus on March 10th, 1934. The first association of temperature increase with food was made on April 3rd. No response was given to the thermal stimulus until the 33rd association with food (April 19th), when the temperature alone produced the anticipatory conditioned response typical of this species. A complete response following anticipatory movements was given at the 37th, the anticipatory responses occurring to a rise of 0·03° C., the full response to a rise of 1·0° C. The temperature increase at each association was then successively lowered; between associations 49 and 95 (the last), lasting from April 30th to May 28th, the stimulus was restricted to a rise of 0·03°–0·05° C., full conditioned responses being readily given since trial 37.

Onos mustela (L.).

A specimen 14 cm. long was put in the apparatus on the same date as the two last, and experiments began also on April 3rd, 1934. In normal behaviour it is somewhat similar, except in its response to food, the acquisition of which is determined by olfaction and gustation instead of by vision. When food was put in the food chamber the fish gave no sign of movement for a minute or so; it then started random circling movements, going steadily nearer to the food, and frequently passing close to it without apparently noticing it until some part of its body actually came into contact with it, when it would turn round sharply and sieze it. The conditioned response was dominated by these same features. After 12 associations of temperature increase with food (April 7th) these seeking movements were initiated by the temperature stimulus alone, continuing until food was acquired.

At the 15th trial it progressed in this way upstream in response to a temperature increase of 0·03° C. and remained in the food chamber "excitedly" floundering about until food was given. It continued so to respond to the same small increment until an accident caused its death after 29 associations on April 17th.

Centronotus gunnellus (L.), 19 cm. in length.

The general course of this experiment was not unlike that on Zoarces, both the normal and the conditioned behaviour of the two species being similar. It was put in the apparatus on March 10th, 1934, given its first association of temperature with food on April 3rd, and gave the full conditioned response on April 24th after 39 associations, continuing so to do until the conclusion on May 28th. From associations 47 to 95 (April 28th to May 28th) only temperature increments of 0·03–0·05° C. were used as conditioning stimuli. The fish showed no anticipatory reactions other than orientation of the whole body or an occasional tail movement which passed directly into the carrying out of the whole response.

Chirolophus galerita (L.) [=*ascanii* (Walbaum)].

A specimen 19 cm. long of this uncommon species was conditioned to a temperature increase as far as the early stages, but died accidentally before any attempt had been made to ascertain the minimum rise to which it would respond. Twenty-five associations were required for the production of the conditioned response, the behaviour of the fish throughout being very similar to Centronotus.

Nerophis lumbriciformis (Pennant).

This is a very difficult species to work with on these lines, feeding being erratic ; only very small pieces of crab's liver were taken, and those but occasionally, although the fish appeared thoroughly healthy and is still alive (Dec. 1935) after more than three years' experiments with one stimulus or another. The specimen (22 cm. long) was placed in the experimental tank on March 10th, 1934 and received its first association of temperature with food on April 3rd. A small piece of the brown seaweed, *Halidrys siliquosus*, was provided as a natural means of the protective concealment characteristic of the pipe-fishes. Its normal resting behaviour was to remain with the greater part of its body concealed amongst this alga. The fish was not seen to be affected by any of the sudden increases in temperature (none exceeding 2·0° C.) until May 16th, 1934 (association 56), when the fish slowly uncurled its tail and then swam rapidly upstream to the food chamber. During a large number of these 56 associations the food was not taken nor was any apparent interest displayed when it was given. There can be little doubt that the long time (six weeks) taken to condition this fish is due to the difficulty of feeding. It was remarkable that the full response was given consistently to all the remaining trials, although these were few, as the experiment was finished on May 28th at the 76th association. From May 18th (association 59) temperatures of 0·07° to 0·10° C. were used as conditioning stimuli with no apparent reduction in the strength or constancy of the conditioned response.

Cottus bubalis Euphrasén.

The results with the larger specimen of the allied species, *Cottus scorpius*, were repeated with a smaller specimen of this species (8 cm. long), the experiment being started on March 10th, 1934. Twenty-seven associations were required for the production of the complete conditioned response. One hundred and eight associations in all were given between April 3rd and May 28th. The general nature of the conditioned response was similar to that of the larger species. For the last 54 trials (April 26th to May 28th) the effective stimulus was in no instance higher than 0·05° C. and was for the most part kept at 0·03° C.

General Summary of Results.

The main features of the individual experiments in both series may be conveniently summarised in the following table (Table 3).

TABLE 3.

Summary of Experimental Results.

Species.	Duration of expt.	Number of associations required for production of conditioned response to thermal increase.	Total number of associations in experiment.	Minimum effective thermal conditioned stimulus. ° C.
Spinachia vulgaris Flem.	6.x.33–15.xii.33	41	84	0·05
Nerophis lumbriciformis (Pennant)	10.iii.34–28.v.34	56	76	0·07
Gadus callarias L.	12.v.32–19.vii.32	18	61	0·05
Gadus merlangus L.	30.v.32–24.ix.32	10	73	0·03
Gadus virens L.	6.x.33–15.xii.33	24	83	0·06
Onos mustela (L.)	10.iii.34–17.iv.34	12	29	0·03
Raniceps raninus (L.)	11.xi.32–8.vi.33	31	147	0·05
Blennius pholis L.	10.iii.34–28.v.34	33	95	0·03
Chirolophis galerita (L.)	18.iv.34–9.v.34	25	33	—
Centronotus gunnellus (L.)	10.iii.34–28.v.34	39	95	0·03
Zoarces viviparus (L.)	10.iii.34–28.v.34	25	95	0·03
Gobius flavescens Fab.	6.x.33–15.xii.33	14	77	0·05
Pleuronectes flesus L.	10.viii.33–5.x.33	20	59	0·05
Pleuronectes platessa L.	24.viii.32–25.x.32	11	71	0·06
	6.x.33–15.xii.33	21	78	0·05
Cottus scorpius L.	26.vi.33–7.ix.33	12	88	0·05
Cottus bubalis Euphrasén	10.iii.34–28.v.34	27	108	0·03
Cyclopterus lumpus L.	6.x.33–15.xii.33	32	67	0·05
Liparis montagui (Don.)	6.x.33–15.xii.33	26	71	0·03
Crenilabrus melops (L.)	6.x.33–15.xii.33	29	71	0·05

Discussion and Conclusions.

More stress is now being laid upon the economic aspects of "fundamental" research than was done when these studies were begun. It is proposed therefore to briefly discuss here the bearing of these experimental results upon fishery research.

The present state of knowledge upon temperature and its relation to fishes can be put under three heads :

1. The direct effect of abnormally high or low temperatures.
2. Experimental demonstrations of temperature perception.
3. Observations made in the course of routine fishery research work at

sea or in the field from which it has been concluded that temperature affects movements or migrations of fishes.

To the standpoint of the present paper only the last two are relevant.

The published experimental work upon temperature perception *per se* is slight, and is limited to work carried out with the gradient tank of Shelford and Allee (**7**). Wells (**15**), working with fresh water fishes, concluded that they detected and reacted to variations in temperature of 1° C. (·1° C.?*) and found all the species equally sensitive. Shelford and Powers (**8**), using marine fishes, obtained " good reactions with a difference of 0·6° C. in the length of the tank. Fair reactions were obtained with a difference of 0·5° C. and since the fishes often turned round near the centre it appears that they recognised a difference of 0·2° C." These " preference " experiments must be regarded with caution. The mere fact of a fish turning round in the centre of a tank, at a point moreover where water is overflowing, is not a sufficient basis for the statement that they react to 0·2° C. or, as in Wells' experiments of 1° (·1° C.).*

Miles (**5**), using the same method, concluded : ". . . I made a slight investigation of the sensitivity of blennies to temperature changes using Shelford and Power's gradient tank, differing by 3° C. in a length of 35 cm." He says " it seemed unwise to use much of the limited time upon these experiments." . . . yet " it is probably true that blennies are not readily sensitive to small differences in temperature."

Under the third heading, *speculation* upon the effect of temperature on fish movement is frequent. It is not necessary to consider these papers in detail, and for a summary of them see Chidester (**3** ; pp. 87–89) ; many of them may be summarised in the remark " . . . under stress of circumstances, extreme heat or cold, fish *seek* deeper water " (Lumby and Atkinson, **4**). Direct observations of conditions in which fish are said to have responded towards situations through the action of temperature are few. Ward (**14**) says that salmon when ascending rivers to spawn, upon encountering streams with a difference of 1° F. or more *select* the stream with the lower temperature. The most lengthy, as well as the most recent, observations of this class are those of Thompson (together with those of Sleggs **9**) upon the relation of cod catches to water temperature in waters operated from Newfoundland. In his earlier papers on this subject Thompson (**10**, **11**, **12**) gives no downright statement as to the precise nature of the relationship (other than that of a positive statistical correlation) which the temperature bears to the fish. But he qualifies certain anomalies by saying (**11** ; p. 76) of certain shallow waters that they were such as " cod might be *wary*† of occupying owing to the liability

* It is not clear which of these figures is the correct one. He says 1° C. in one place, ·1° C. in two places ; one of these must be a misprint.

† The italics are mine.

of sudden temperature changes." Here he directly implies, as we would ordinarily put it, conscious selection of environment. Therefore, when he says (**11**; p. 76): "These results seem to be decisive and to indicate that for Grand Bank a sharp line of division can be drawn (in spring) between waters of just below and waters of just above zero temperature. Below zero cod are scarce, while at a mere half-degree above zero they can be plentiful" it would seem that, whilst it might just as well have been that the fish were found under these conditions merely through the "set" of hydrographical factors, Thompson considered that they were there because they chose to be there. That this is the interpretation he would give of the relationship is finally made clear in his last paper where he says (**13**, p. 25): "The 1934 results *clearly indicate the conscious quest for low temperatures*,* since the skipper found that at these only did they secure large cod." None of the psychological expressions italicised in these quotations are logical deductions from the observed facts. Before the facts may be even interpreted in this way it is essential to show that behaviour of a type which may be looked upon *ordinarily* in this manner is exhibited by fishes to such temperature conditions. In other words, it must be clearly established that small differences in temperature have, as E. S. Russell puts it, *valency* (Russell, **6**) for a fish.

These experiments have made it clear that in the discriminatory perception of temperature a fish is provided with a sensory field which is so acutely sensitive as to be of obvious value in directive movements. They establish in fact the first premise needed for the proof of such deductions as that fish make a "conscious quest for low temperatures" (Thompson, *vide supra*) and other speculative assertions of a like nature.

Those points of essential value to the primary object of this series of studies will be discussed at a later date.

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SUMMARY.

By the use of a "conditioned response" technique it has been shown that teleostean fishes respond "purposively" to an increase in temperature of the water surrounding them of between 0·03° C. and 0·10° C. It is probable that the former figure is true for all the species investigated, but it has only been practicable to establish it with certainty in a few sedentary forms.

The bearing of the results on fishery problems is discussed.

* The italics are mine.

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