

# REACTIONS OF MARINE FISHES TO TEMPERATURE GRADIENTS <sup>1</sup>

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## INTRODUCTION

The ability of fishes to respond by movement to experimental gradients of various physical and chemical characteristics of water and so to exercise selection of their environment has been repeatedly demonstrated.<sup>2</sup>

Studies of this type have thrown much light upon the senses and the behavior of animals. Furthermore, many workers have held that selection in an experimental gradient is indicative of the nature of the most favorable environmental conditions for the organism in question, even when the detrimental effects of conditions which are rejected can not be demonstrated. The term "optimum" has frequently been used in this connection (M. M. Wells, 1914, 1915 *a, b*; Mendelssohn, 1895; Herter, 1924, etc.). Conclusions as to the relative importance of different characteristics of water as indices of the suitability of fish environments have been drawn from the relative vigor of the reactions of fishes to these stimuli (Shelford and Allee, 1913). Speculative attempts to explain the curious migration of fishes, such as those of the anadromous salmonids, in terms of reactions to physical and chemical gradients, have been made by most workers in this field.

One objection to the view that an optimum is selected, namely, that animals can become acclimatized to conditions which are rejected, and that such acclimatization may alter their reactions to a gradient, has been pointed out (Jewell and Brown, 1924; Brown and Jewell, 1926). Shelford (1929) recognized this objection and concluded that the gradient method is more useful as a measure of "acclimation," rather than of habitat preference. Owing to the lack of sufficient data relative to the influence of acclimatization, its importance could not be estimated. The present investigation was undertaken to obtain more complete data on the basis of which the physiological and ecological significance of selection in an experimental gradient could be evaluated.

<sup>1</sup> Contributions from the Scripps Institution of Oceanography, New Series, No. 42.

<sup>2</sup> For review of early literature see Chidester (1924).



Temperature has been regarded as having an important influence upon the migrations and distribution of fishes (Chidester, 1924; Ward, 1921; Creaser, 1930). Wells (1914), Shelford and Powers (1915), and Chidester (1922) found that fishes are very sensitive<sup>3</sup> and will react to this stimulus, but these reactions have not been adequately investigated. For these reasons most of the present experiments were performed with temperature (and a few with salinity) gradients.

I am indebted to Dr. F. B. Sumner and other members of the staff of the Scripps Institution for valuable advice and assistance.

#### MATERIAL AND METHODS

The material used was chiefly the young of the greenfish, *Girella nigricans* (Ayres). They were taken in rock-pools in the intertidal area near the Scripps Institution. Pacific killifish (*Fundulus parvipinnis* Girard) from False Bay near San Diego, young atherinids,<sup>4</sup> taken in the same locality as the *Girella*, and a few other species were also used.

The fishes were kept in the laboratory in flowing sea water, which was nearly at the same temperature as the surface water in which *Girella* were living in nature. In acclimatization experiments they were kept in constant temperature tanks, in which flowing sea water was maintained at any desired temperature by thermostatic control.

A satisfactory horizontal temperature or salinity gradient can not be maintained in a simple gradient tank of the type generally used. Owing to differences in density between the inflowing streams of water, stratification results in a steep vertical gradient. The tank which was devised for this purpose (Fig. 1) was a wooden one 80 inches long, 8 inches wide and 9 inches deep. It was subdivided by vertical partitions (*a*) into ten octagonal compartments arranged in linear series and communicating at their adjacent sides. Other vertical partitions (*b* and *e*) at the top and bottom further reduced the size of the openings (*p*) between adjacent compartments to two inches high by three inches wide. A horizontal wire screen (*s*) was placed over the lower partitions (*e*). The fishes were confined above this screen and, because of the shape of the compartments, could find their way from one compartment to the next without any difficulty.

Water in very small streams was introduced into and drawn out of each compartment at an equal rate through horizontal tubes (*i.t.*

<sup>3</sup> Excellent work of another type on the temperature sensitivity of fishes has been done by Bull (1928, 1936).

<sup>4</sup> These were either *Atherinops affinis* (Ayres) or *Atherinopsis californiensis* Girard. The specimens were lost before they had been identified.



and *o.t.*) with several perforations, so that no horizontal currents passing from one compartment to another were present. Sea water heated or cooled to a high, a low, and an intermediate temperature first flowed through three large tanks in which it was vigorously aerated with compressed air. From the aeration tanks the water was distributed to the

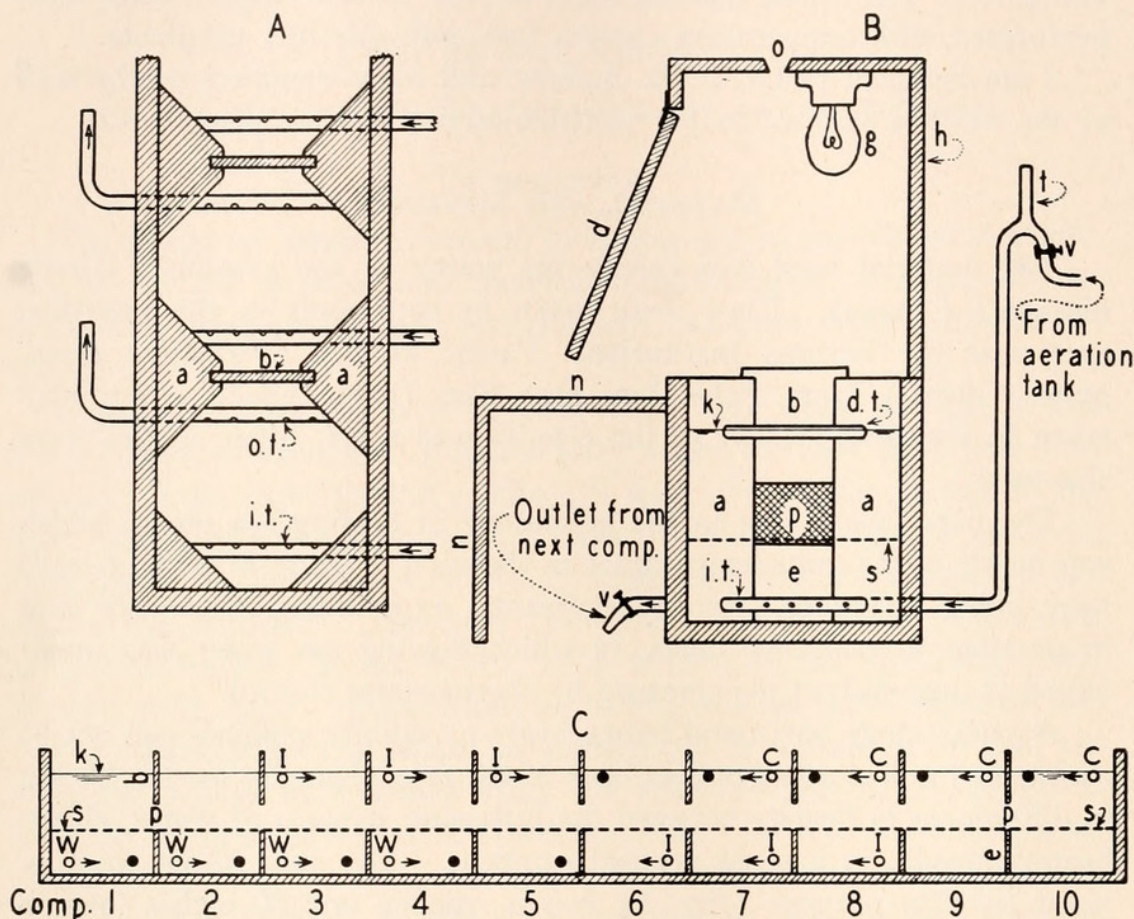


FIG. 1. Diagram of the gradient tank. *A*—Top view of a portion of the tank (Compartments 9 and 10). *B*—Cross-section through the tank (Compartment 2) and hood. *C*—Longitudinal section through the entire tank, showing arrangement of inlets and outlets. Cross-sections of outlet tubes are indicated by solid circles and inlet tubes by open circles. The relative temperature of the inflowing water is indicated above each inlet tube: *W* = warm, *I* = intermediate, *C* = cold. Dummy tubes are not indicated.

*a*, *b*, and *e* are partitions; *p*—opening between compartments; *s*—horizontal screen; *h*—hood; *d*—door of hood, *o*—observation slit, *g*—lamp; *i.t.*—inlet tubes; *o.t.*—outlet tubes, *d.t.*—dummy tube, *t*—air trap, *v*—screw-clamp, *n*—hood over outlets, *k*—water level.

gradient tank through 14 tubes, each of which was provided with a trap (*t*) to remove air bubbles and a valve (*v*) for regulating the flow. In every case water at a higher temperature than that maintained in any given compartment was introduced into it at the bottom (below the screen), while colder water was introduced at the surface. Dummy



inlet and outlet tubes (*d.t.*) were provided to make all compartments similar.

In this tank a very steep and uniform horizontal gradient could be maintained without the presence of vertical gradients. A difference of  $18^{\circ}$  was usually maintained between the two ends, or  $2^{\circ}$  between adjacent compartments.

A hood (*h*) was attached over the tank. The tank was illuminated by five small electric lights (*g*) attached to the top of the hood. The movements of the fish were observed through a narrow slit (*o*) in the top of the hood. The room was darkened while observations were made, and the observer was apparently invisible to the fish.

Observations were made in the following manner. One specimen at a time was put into the tank at any desired temperature (usually the temperature from which it had been taken), the fish being screened off from adjacent compartments. After a minute it was released and allowed to swim freely about the tank. The door of the hood (*d*) was then shut and, after the fish had been in the tank for a given length of time (usually one hour), the observation was begun. A bell metronome was then started and the position of the fish recorded at six-second intervals. The observation was generally continued for 30 minutes (300 recordings). The approximate percentage of the time that the fish had spent in each compartment was then calculated, and the temperatures in them recorded. About 600 such observations were made in the course of these experiments.

## RESULTS

### *Experiments with Girella Kept at Current Seasonal Temperatures ( $14.5^{\circ}$ to $22^{\circ}$ ) and Under Relatively Normal Conditions of Illumination*

Specimens kept in the laboratory under these conditions for many months were found not to differ in their behavior and reactions from those recently taken.

In control experiments, in which the water flowing into the gradient tank was at the same temperature throughout and, consequently, no gradient was present, no consistent preference was shown for either half of the tank nor for any compartment except the ones at the ends of the tank (Fig. 2, C). When, however, a suitable temperature gradient was established, the fishes showed a marked avoidance of the two ends of the tank. After a short time an apparent "preference" for one or two adjacent intermediate compartments was established, all others being avoided. When the percentage of time spent in each



compartment by a single individual in the course of a 30-minute observation was plotted against the temperature, a fairly regular, although frequently skewed, unimodal frequency distribution was obtained. The temperature at the mode of this distribution, located by a uniform procedure, will be referred to as the selected temperature.

While the temperatures selected in different observations by fishes taken from current seasonal temperatures varied considerably, a tendency to select high temperatures in the vicinity of  $26^{\circ}$  was observed.

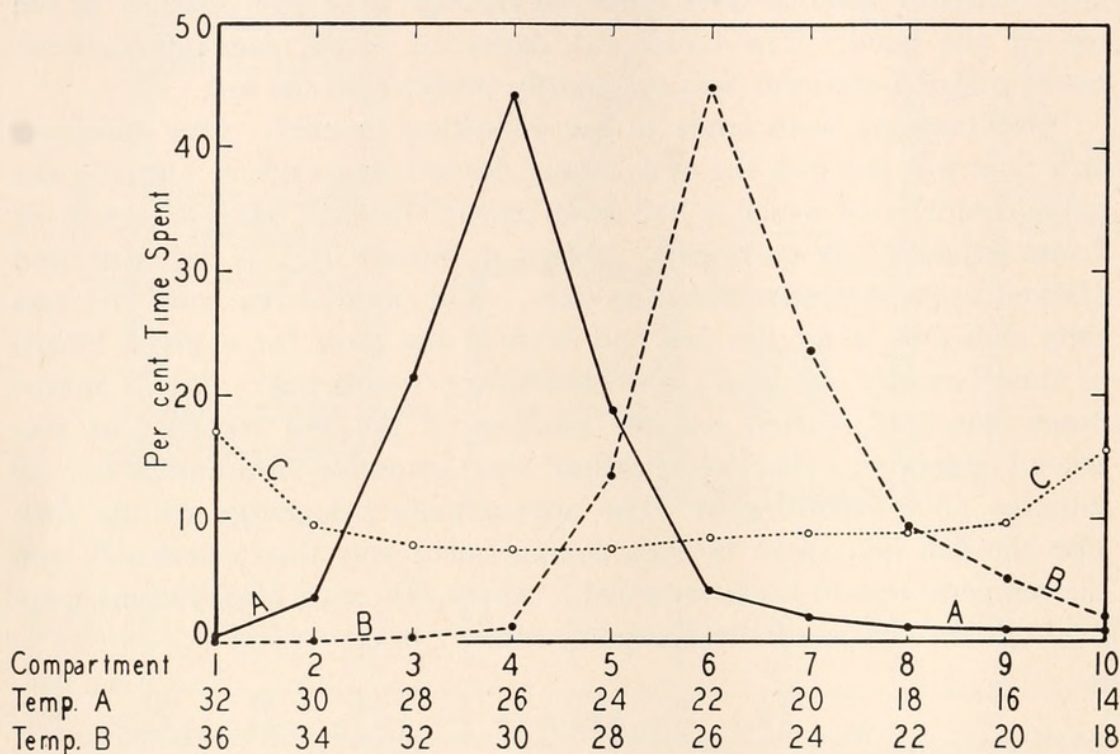


FIG. 2. Distribution of time spent in different compartments by *Girella* taken from sea water at the normal seasonal temperature and tested in *A*—a  $32^{\circ}$  to  $14^{\circ}$  gradient, *B*—a  $36^{\circ}$  to  $18^{\circ}$  gradient, and *C*—in the absence of a gradient (typical control experiment). Distributions *A* and *B* are based on the same eight specimens. The temperatures maintained in each compartment in the two experiments are indicated. Distribution *C* is based on five specimens. Observations made one hour after introduction of the fish.

So long as the two ends of the gradient were cold and warm enough to be invariably strongly repellent, the mean selected temperature was found not to be affected by changes in the range of the gradient used. This result is illustrated in Fig. 2. It will be observed that the modes of both distributions *A* and *B* are at  $26^{\circ}$ . In a number of such experiments the same result was always obtained. This shows that the fish were attracted to the selected compartments by the temperatures present there, rather than by any other differences (such as convection currents, etc.).



Figure 3 shows the distribution of selected temperatures obtained in 100 experiments in various gradients (usually  $14^{\circ}$ – $32^{\circ}$  or  $15^{\circ}$ – $33^{\circ}$ ). The mean ( $25.7 \pm 0.1^{\circ}$ ) is somewhat lower than the modal temperature ( $26.4^{\circ}$ ). Experiments were performed to determine the possible influence of size, recency of feeding, and season, which could account for the variability and the skewness of the distribution, since such skewness would result from unequal representation of specimens so differing. The mean temperatures selected by three size-groups of 14 specimens each (with mean weights of 9.6, 3.8, and 1.7 grams), taken at the same

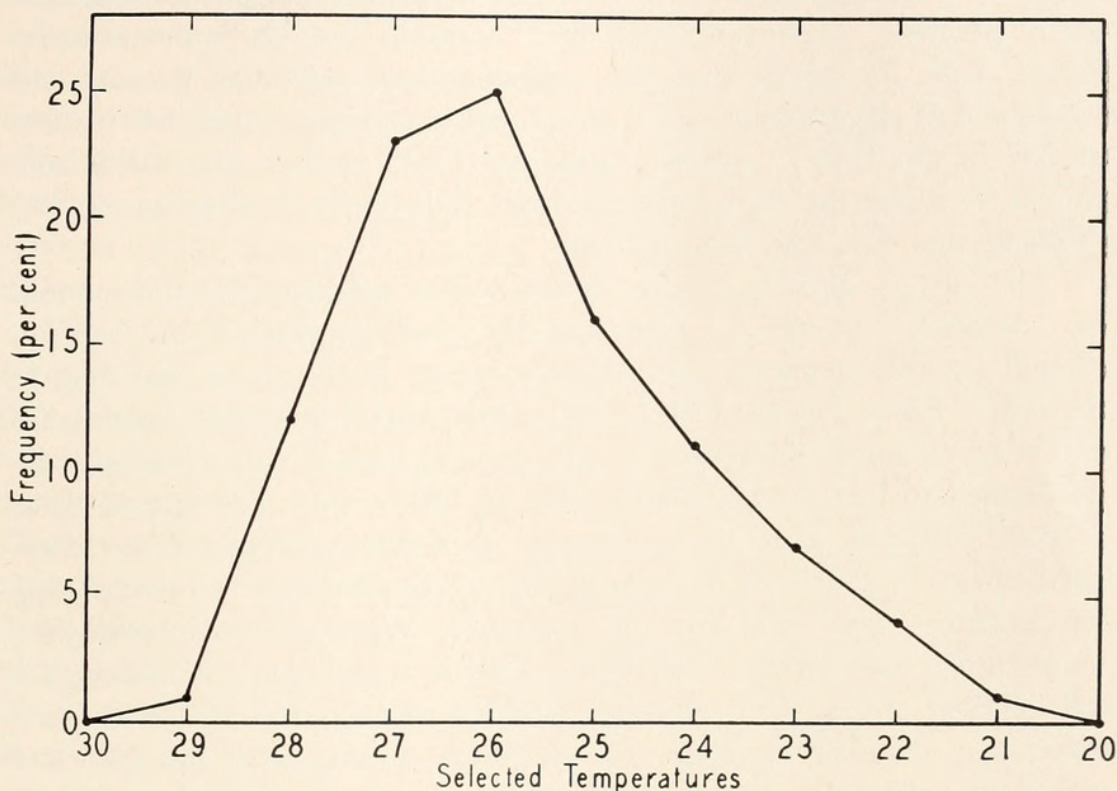


FIG. 3. Distribution of temperatures selected by *Girella* taken from current seasonal temperatures. (Based upon 100 thirty-minute observations, made one hour after introduction of fish into the gradient tank.)

time, did not differ significantly. Similarly, groups of fishes which had been recently fed, starved for two to three days, and starved for two weeks selected, on the average, practically identical temperatures. Specimens tested in early fall and in early spring did not differ appreciably. The former had been living through the summer at  $19^{\circ}$  to  $22^{\circ}$  and, when tested, were taken from  $20^{\circ}$ . The mean temperature selected by 24 specimens in a  $14^{\circ}$ – $32^{\circ}$  gradient was  $26.0^{\circ}$ . The latter had been living through the winter at  $14^{\circ}$ – $16^{\circ}$  and were taken from  $15^{\circ}$ – $16^{\circ}$ . Their mean selected temperature in the same gradient was  $25.8^{\circ}$  (22 observations). This indicates that, over a wide range of



temperatures, previous temperature history has no influence upon selection. The temperature of the compartment into which the fishes were introduced was found to have no influence upon the temperatures which were finally selected.

Since the temperature gradient was, of necessity, accompanied by other gradients, the possibility that the fishes had been reacting to some factor other than temperature was investigated. No gradient of oxygen or nitrogen tension was present, the water being brought to the saturation point at all temperatures by "aeration," as described earlier.<sup>5</sup> On the other hand, a gradient of the *concentration* of these gases was necessarily present. However, when the "aeration" of the water was reduced, with the result that the oxygen concentration at the extreme warm end of the gradient (32°) was equal to or higher than that present at 26° in the fully "aerated" gradient (4.75 cc./l.), the fishes continued to reject the high temperatures. Obviously, it was not to this gradient that they had been reacting.

The carbon dioxide tension could not be equalized by the amount of "aeration" provided. Consequently the CO<sub>2</sub> tension and the hydrogen ion concentration were slightly higher at the warm end than at the cold. Since Powers (1921) and others have found that some fishes will react to small differences of pH or CO<sub>2</sub> tension, experiments were performed to test the possibility that the fishes were reacting to these gradients instead of to temperatures. A shorter gradient (four compartments), in which the fish was given a choice between two contrasting temperatures, was used for this purpose. Water at an intermediate temperature was aerated and then passed at a constant rate through a tall cylinder, where CO<sub>2</sub> gas was bubbled through it. It then passed through a chamber, to allow for thorough mixing with the gas, and was then distributed to two lead coils immersed in flowing cold and warm water. The cooled and heated streams of CO<sub>2</sub>-treated water were distributed, out of contact with air, to the cooler and warmer halves, respectively, of the gradient tank. No difference of pH was detected when samples of water from the two ends of the gradient were brought to a common temperature, showing that no difference of CO<sub>2</sub> content had been present. In a preliminary experiment, in which the water was not treated and a gradient of 26° to 32° was maintained, ten specimens invariably selected the cooler half of the gradient, spending 92 per cent of the time there. The gradient was then changed so that

<sup>5</sup> Frequent oxygen determinations were compared with solubility values given by C. J. J. Fox (1909), corrected for vapor pressure. The untreated sea water was at an intermediate temperature and approximately saturated with air. The warmed sea water was, consequently, super-saturated with air, and "aeration," in this case, resulted in the removal of excess air.



the warm end was at 26° and the cold at 18°. The water was treated with enough CO<sub>2</sub> to raise the partial pressure of CO<sub>2</sub> and the H-ion concentration at the two ends (26° and 18°) to higher values than those which had been present in the preliminary experiment at the corresponding ends of the gradient (32° and 26° respectively). Only the pH at room temperature (22°) was determined. The change of pH necessary to satisfy the above requirements was readily calculated by the use of tables giving the relation between temperature, pH, partial pressure of CO<sub>2</sub>, and total CO<sub>2</sub> in sea water of constant chlorinity and titratable alkalinity furnished by Buch et al. (1932). The pH of the water (chlorinity 18.6‰) was lowered from 8.1 to 7.7, and later to 7.35. In both cases the change was more than sufficient to satisfy the requirements. Twelve specimens tested in the treated gradients invariably selected the warmer half (26°), spending 91.1 per cent of the time there. Had the fishes been reacting to CO<sub>2</sub> tension or to pH instead of temperature in the untreated gradients, they should now have selected the colder half (18°), as they did in the untreated 26°–32° gradient.

While *Girella* is quite resistant to low salinities, it is a typical marine fish and does not occur in situations where the water becomes appreciably diluted. Experiments were performed to compare its reactions to temperature and to salinity, in order to test the value of these reactions as an index of "habitat preference." In a salinity gradient, in which the temperature was the same throughout and the salinities ranged from 5.6‰ to 29.9‰, no consistent reactions were observed. A combined temperature and salinity gradient was then established, with salinities ranging from 2.6‰ to 32.3‰ and temperatures from 26° to 18°, the dilute water being at the higher temperature. Seven specimens taken from normal sea water (salinity 33.8‰, temperature 18° C.) invariably avoided the normal sea water and spent 94% of the time in the five compartments in which the water was warmer and more dilute. The mean temperature and salinity which were selected were 24.6° and 7.8‰ respectively. The salinity gradients were not entirely satisfactory, since the fresh tap-water used differed from the sea water in several other respects. The pH was approximately the same, but the CO<sub>2</sub> tension was slightly higher, and a small quantity of free chlorine (.02–.03 parts per million) was present. However, this circumstance only emphasizes the fact that the fishes were selecting unnatural conditions.

#### *Experiments with Girella from Constant-temperature Tanks*

Three constant-temperature tanks, maintained at 10°, 20° and 30°, were used. Figure 4 shows the relation between the temperatures of



acclimatization and the temperatures selected by specimens kept at the former temperatures for 3 to 4 months. It will be noted that the fishes from the 20° constant-temperature tank selected lower temperatures, on the average, than those from untreated sea water (discussed in the preceding section) taken from the same temperature in fall or taken from a lower temperature (15°–16°) and tested at the same time as the 20°-conditioned ones. Apparently, the small difference between the fishes from normal seasonal temperatures and those from the 20°

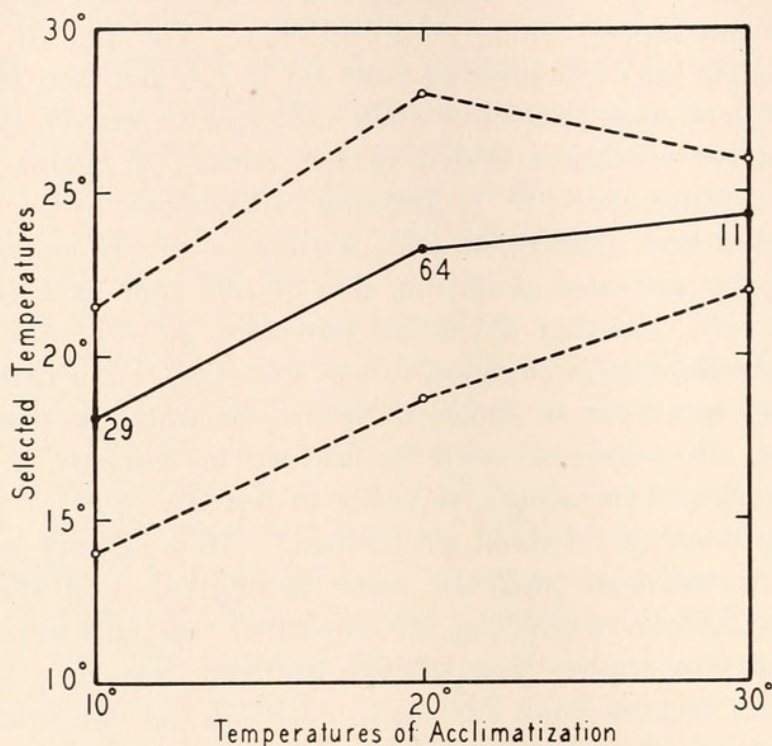


FIG. 4. Relation between temperatures of acclimatization and temperatures selected by *Girella* which had been kept for 3 to 4 months in three constant-temperature tanks. Solid circles, connected by solid lines, indicate mean selected temperatures. The number of observations in each group is indicated. Open circles, connected by broken lines, indicate the highest and lowest temperatures selected by specimens from each of these tanks. Observations made one hour after introduction of fish into gradient.

constant-temperature tank ( $2.5^\circ \pm 0.23^\circ$ ) was due neither to season nor to the temperature of acclimatization. It was probably due to a slight difference of behavior.<sup>6</sup> The fishes in the constant-temperature tanks had been subject to conditions of dim and erratic illumination, and had been frequently disturbed. Some irrelevant factor of this nature was probably responsible for the slight change.

<sup>6</sup> The fishes from the constant temperature tanks were more active, in the sense that they moved about the gradient more freely and reacted less sharply and rapidly. The distribution of selected temperatures was symmetrical.



At any rate, the specimens in the three constant-temperature tanks had been subject to the same conditions with the exception of temperature and are, therefore, comparable. The mean temperatures selected by eleven 30°-conditioned and eleven 20°-conditioned fishes, acclimatized to these temperatures for three months and tested in alternation in a 15°–33° gradient, were 24.3° and 23.6° respectively. The difference was small and the probability that it was significant was not high (.8578).<sup>7</sup> The 10°-conditioned fishes, however, selected considerably lower temperatures. When sixteen of these and an equal number of 20°-conditioned specimens were tested in a 12°–30° gradient, the mean selected temperatures were 17.8° and 23.2° respectively. The difference was unquestionably significant, the probability being .9999 +.<sup>7</sup> The 20°-conditioned fishes were then transferred to 10° and the 10°-conditioned ones to 20°. They were tested again after they had been at the new temperatures for three days and again after 24 days. Other specimens, which had been kept continuously at 10° and 20°, were tested at the same time as controls. The result is shown in Fig. 5.

Results essentially the same as the above were obtained in other experiments, in which different periods of acclimatization and various gradients were used. When 10° and 20°-conditioned specimens were left in the gradient tank and repeated observations were made in the course of 24 hours, no appreciable changes of the mean selected temperature were observed after the first half hour, although the temperatures selected by single individuals in successive observations varied considerably.

#### *General Notes on the Behavior of Girella*

After the fishes had been introduced into the gradient, some were very active and showed little selection until they began to come to rest. As a general rule, however, a specimen taken from a relatively low temperature avoided, at first, the high temperatures which were later selected. As it moved back and forth in the gradient, its excursions into warmer water became more prolonged and extended, while those into colder water became more brief. The selected temperature thus moved up rapidly, until the fish came more or less to rest at a relatively high temperature. Thereafter, the selected temperature did not remain constant, but occasionally fluctuated up and down, so that the temperature which was selected at one time was avoided at another. The fish continued to make frequent excursions into other temperatures. A rapid excursion into a much higher or lower temperature was followed by a very rapid and violent reaction. But, if the fish moved into the same

<sup>7</sup> For method of computing probabilities see Tippet, 1931, pp. 80–82.



temperature gradually, the avoidance reaction was often markedly delayed and the excursion frequently followed by a temporary or a relatively permanent rise or fall, respectively, of the selected temperature. When the same specimens were tested more than once, no marked tend-

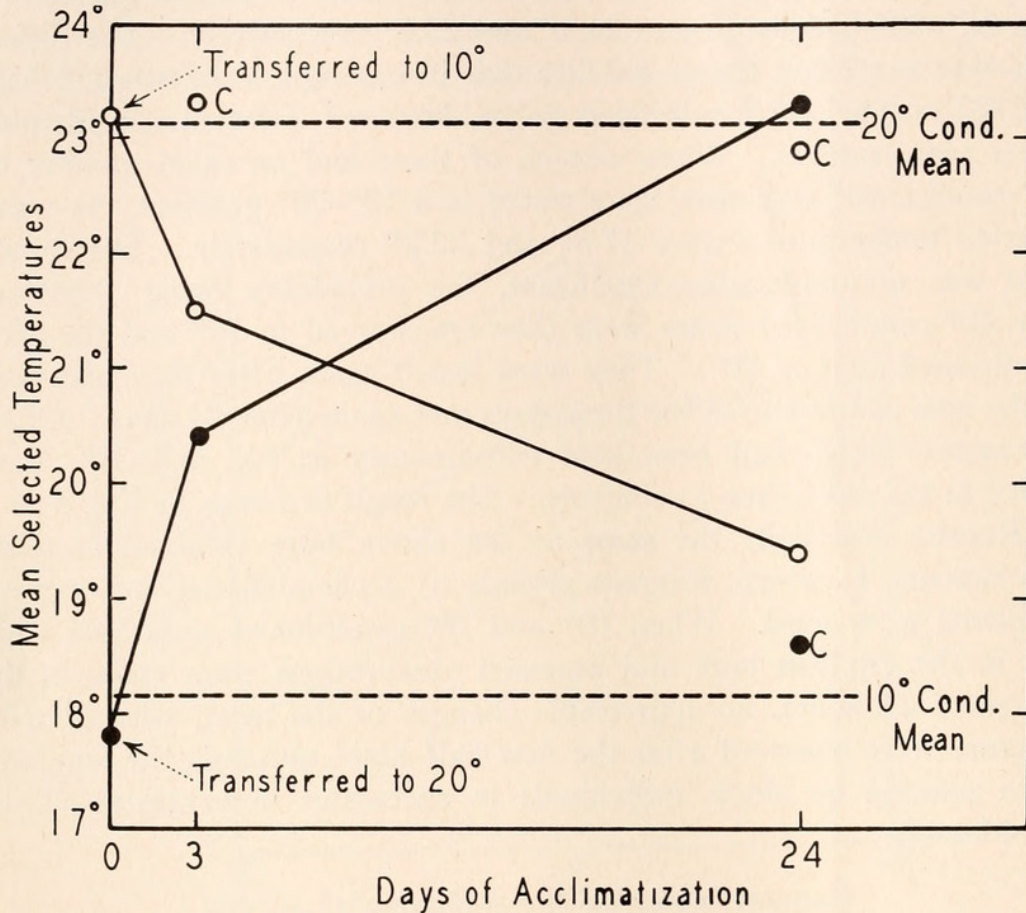


FIG. 5. Rate of change of mean temperatures selected by *Girella* as a result of acclimatization to 10° and 20°. Fishes originally conditioned for 100 days to 20° (open circles) and to 10° (solid circles). Circles connected by solid lines are mean temperatures selected in successive observations by 16 specimens of each group before and after transfer to the other temperature (as indicated). Days of acclimatization (abscissas) refer to time at new temperatures only. Points marked C are controls and are based upon 13 to 16 specimens which had been kept continuously at the original temperatures of acclimatization. These were obtained at the same time as those for recently transferred specimens on the same abscissa. Broken lines indicate mean temperatures selected by all the specimens which had been kept at 10° and 20° continuously for 100 days or more.

ency was observed for the same individuals to select relatively high or low temperatures in successive trials.

From these observations it appears that the variability of temperatures selected by different individuals with a similar history was not indicative of any permanent physiological differences, resulting in differences of "preference." A specimen could become "adapted" to,



and establish an apparent "preference" for any temperature within a fairly wide range. Thereafter, other temperatures were repellent by contrast. Over a wide range of temperatures, however, the influence of past experience was, apparently, of brief duration and past impressions were rapidly destroyed in the course of the random movements of the fish in the gradient. Consequently, the range of temperatures at which the fishes finally came to rest was largely independent of previous temperature history. Specimens conditioned to 10° were unable to tolerate rapid transfer to the highest temperatures selected by specimens which had not been subjected to this abnormal temperature. The observed change of behavior was obviously adaptive.

### *Experiments with Other Species*

In control experiments, in which no gradient was present, young atherinids behaved much like *Girella*, showing no "preference" except for the end compartments. In a temperature gradient their behavior was not quite as satisfactory as that of *Girella*, owing to a more pronounced tendency to move about in set patterns, rather than at random. Nevertheless, marked reactions to the gradient were observed. Nine specimens taken from untreated sea water at 21.5° and tested in a 14°–32° gradient spent, on the average, 74 per cent of the time in four adjacent compartments (22° to 28°). The mean selected temperature was 25.2°.

In experiments with *Fundulus parvipinnis* only specimens which had been kept for one to two months in the three constant-temperature tanks were used. This species inhabits shallow bays and sloughs, in which very high temperatures occur, and is more resistant to high temperatures than *Girella*. My specimens were originally taken from water at 27° in June, but temperatures several degrees higher are probably not uncommon in their habitat. While these fishes reacted to the gradient, their reactions were not nearly as sharp and consistent as those of *Girella*. They were frequently very inactive and "nervous," and showed such a strong tendency to move to the ends of the tank that it was not always possible to repel them from both ends, even though a steeper gradient was used. Nevertheless, a few interesting observations were made. In a 14° to 35.5° gradient, twelve 20°-conditioned and six 30°-conditioned specimens showed marked avoidance of the lower temperatures, but were not consistently repelled by the highest temperatures. In both cases about 75 per cent of the time was spent in the warm half of the gradient (26° to 35.5°). However, when the 20°-conditioned specimens were tested in an 18°–40° gradient, all avoided the warmest



water. Seven 10°-conditioned specimens tested in a 14°–35° gradient were very inactive, but all avoided both ends of the gradient and spent 75 per cent of the time in four intermediate compartments (18.5°–26°).

Several bottom-living forms (*Gillichthys mirabilis* Cooper, *Leptocottus armatus* Girard, *Clinocottus analis* (Girard), etc.) were tested in temperature and salinity gradients. They were very inactive, and no marked reactions were observed. Two specimens of *Clinocottus*, a fish which is little resistant to dilute water, moved into such water and remained there until they died. A single young specimen of the blenny *Heterostichus rostratus* Girard was tested in a salinity gradient. This fish was quite active and showed a marked avoidance of diluted water.

#### DISCUSSION AND CONCLUSIONS

The ability of the more active fishes to avoid harmful temperatures and to exercise selection in an experimental temperature gradient has been demonstrated.

Fishes which had been taken from their normal environment could not be regarded as selecting temperatures to which they had been acclimatized. Differences of previous temperature history did not necessarily result in differences of behavior in the gradient. At most, the influence was only temporary. Thus, *Girella* which had been conditioned to 10° always moved into higher temperatures. Had they been left in the gradient, they would have become acclimatized to these higher temperatures and, in time, would have selected as high a temperature as specimens which had been kept continuously at 20° or 30°. The data in Fig. 5 indicate that a number of days would have been required for this change to take place. Obviously, selection in a gradient is not a reliable index or measure of acclimatization.

The term "optimum," as used to designate the most favorable condition for an entire organism (rather than for a single process or activity), has never been adequately defined. At any rate, a temperature "optimum" or "habitat preference" which changes with the temperature of the environment (and consequent acclimatization) is of questionable significance. However, the fishes did not select temperatures to which they were accustomed, but showed a marked tendency to move, in time, into a common range of temperatures. This range of temperatures must have some physiological significance. For the view that it represents an "optimum" or a "habitat preference," however, I find no evidence. The temperatures most frequently selected by normal *Girella* (26°–27°), even after they had been living in relatively cold water, are not normal in their habitat. The average surface temperature



to which these fishes are exposed in this locality is  $16.9^{\circ}$  (Mean for 18 years). The mean temperature for August, the warmest month, is  $20.8^{\circ}$ , while the highest monthly mean on record (July, 1931) was  $23.6^{\circ}$ . Under these (suboptimal?) conditions the species has been living and reproducing successfully for an indefinite period.

The negative response to extreme and obviously harmful temperatures is unquestionably adaptive. The assumption that the specific behavior of animals in response to all other thermal stimuli must necessarily have similar significance is open to question. Granting, however, that the sharp avoidance reactions were given to "unfavorable" stimuli, the conclusion does not follow that the selected temperatures were more "favorable" or "preferable" except under the special (and somewhat unnatural) conditions of the experiment. It is important to distinguish between the excitatory or detrimental effects of given rapid *changes* of temperature and the effects of given temperatures upon an organism which is exposed to them continuously. Particularly is this so in the case of poikilotherms.

In my discussion of the behavior of *Girella* (based upon several hundred prolonged individual observations), I have shown that the fishes did not move directly into a certain temperature and remain there. Instead, the phenomenon of selection and the fluctuations of the selected temperature were shown to be the result of a succession of characteristic avoidance reactions (turning and swimming back) of varying intensity to *contrasting* temperatures encountered in the course of random movements. These reactions were subject to modification by rapid "adaptation." The correspondence between this behavior and the familiar effects of "adaptation" and "contrast" in human cutaneous thermal sensations is obvious.<sup>8</sup> From the observed reactions, it appears that a rapid change, for example, from  $15^{\circ}$  to  $25^{\circ}$ , is less stimulating and repellent than (and, perhaps, is preferred to) the reverse change following exposure to the higher temperature. It does not follow, however, that the lower temperature is not entirely as "favorable" (physiologically) or "satisfactory" (psychologically) as the higher one in the absence of contrasting temperatures. The fact that all species tested selected relatively high temperatures indicates that, in general, within normal ranges of temperature rapid cooling is more detrimental or stimulating than a rapid rise of temperature. Whether this difference depends upon peculiarities of the cutaneous thermal sense or has more general physiological significance is not clear. The temperatures se-

<sup>8</sup> This rapid "adaptation" should not be confused with the more gradually produced and lasting changes affecting behavior, resistance, metabolic rate, etc., which I have referred to above as acclimatization (See Sumner and Doudoroff, 1938, and citations).



lected by different species may be expected to bear some approximate relation to the maximal temperatures which they can tolerate and, consequently, to the temperatures which occur in their natural environments. Thus, *Fundulus* was not repelled by high temperatures which were strongly repellent to *Girella*. This is hardly evidence that an "optimum" was selected in either case.

Analogies between experimental gradients and those which occur in nature should be regarded with caution. The former are usually much steeper. Fishes in them are so confined that their random movements bring them repeatedly into widely different conditions at a rate with which "adaptation" can not keep pace. No correspondence between the reactions to these two types of gradient can be assumed.

The above conclusions probably apply, to a large extent, to reactions to other stimuli than temperature. Certainly, the relative vigor of the reactions of fishes to different stimuli can not be relied upon to show what characteristics are more important as indices of the suitability of environments. My results with temperature and salinity gradients, in which *Girella* selected entirely unnatural conditions, support this conclusion. They indicate only that the fishes were more sensitive to changes of temperature than of salinity. This difference may depend, largely, upon the nature of the receptive apparatus involved.

#### SUMMARY

An apparatus is described whereby a steep horizontal temperature (or salinity) gradient can be maintained, without the presence of vertical gradients, for the study of the reactions of fishes. The reactions of several species of marine fishes, chiefly of *Girella nigricans* (Ayres), to these gradients have been studied. A marked selection was demonstrated of temperatures which were relatively high in comparison with the normal environment of the fishes. The influence of acclimatization and of other factors upon temperature selection was investigated. While acclimatization was found to influence selection, the effect was slight and only temporary, the selected temperature being, to a large extent, independent of past experience. The physiological and ecological significance of selection in the experimental gradient is discussed. The rôle of contrast and of rapid "adaptation" is indicated. It is concluded that selection is indicative of the relative stimulative or detrimental effects of given rapid *changes* of temperature, while the common view that such selection indicates the nature of "optimal" conditions or habitat preference is not tenable.



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