# Regulation of food intake in the goldfish[1]

PAUL ROZIN[2] AND JEAN MAYER
*Department of Psychology, Harvard University, Cambridge, and Department of Nutrition, Harvard University School of Public Health, Boston, Massachusetts*

ROZIN, PAUL, AND JEAN MAYER. *Regulation of food intake in the goldfish.* Am. J. Physiol. 201(5): 968–974. 1961.— Goldfish were trained to press a lever. This response was followed by the delivery of a pellet of food. The fish were then allowed continuous access to the lever under controlled conditions, and their food intake was measured. Goldfish distribute their feeding responses fairly evenly over time, within the limits of the lighting cycle. Some fish eat mainly at night, some during the day, and others seem to be indifferent to the lighting cycle. Goldfish decrease their food intake by one-half to one-third in response to a drop in ambient temperature from 25 to 15 C, and show a corresponding increase in food intake when the temperature returns to 25 C. Goldfish increase their food intake significantly in response to dilution of their normal diet with kaolin, and thus seem to eat for calories or nutrient value.

SYSTEMATIC RESEARCH on the regulation of food intake has been conducted almost entirely on mammals. The excellent work of Dethier and Bodenstein (1) on the blowfly is the only major attempt to examine the regulation of food intake in a nonmammal. There is extensive literature on feeding in the major phyla of the animal kingdom, but this centers on problems such as nature of the diet and manner of obtaining and ingesting food. The research presented in this paper represents a beginning in the systematic study of the regulation of food intake in the goldfish.

Much work has been done on the feeding habits of fish, due to their economic importance and great numbers. Virtually no work has been directed specifically towards a study of the regulation of food intake. Some of the fundamental differences between fish and mammals open the possibility of experimental attacks on problems not easily dealt with in the usual laboratory animals. For example, it is probable that there is nothing corresponding to a thirst center in the fish. Research on the hypothalamic aspects of food intake of mammals has been confounded by hunger and thirst interactions (2, 3). The poikilothermic nature of fish permits a much more extensive examination of the relation of food intake to temperature. A thermostatic regulatory mechanism has been suggested in the mammal (4) and could be examined in a new light in a poikilothermic animal. Temperature change is also a valuable tool for the manipulation of metabolic rate in cold-blooded animals. The influence of telencephalic centers on various aspects of behavior often complicates experiments on mammals, and to date many telencephalic centers have been implicated in one way or another in feeding (5). The telencephalon of the fish is quite small and so far has been associated with little other than a purely olfactory function (6). It may be possible to observe the operation of subtelencephalic centers uncomplicated by higher centers in the fish.

Food intake regulation in the goldfish is being studied in a general framework established in a previous publication (7). Four basic questions can be asked about any such mechanism: *1*) Is there a regulation? *2*) How accurate is the regulation? *3*) What is regulated? *4*) How is it regulated?

In order to establish a situation in which food intake could be accurately measured, the techniques of operant conditioning were exploited. Fish were trained to press a lever by making the delivery of a single pellet of food contingent on this behavior. Their feeding behavior was monitored continuously under conditions of controlled temperature and lighting. Long-term food intake data can be obtained with this method with a minimum of disturbance to the experimental organism. This method also minimizes the problem of fouling of water that usually occurs when aquatic animals are fed freely.

## NORMAL FEEDING BEHAVIOR

*Method.* Five experimental units were employed in this study. Each unit consisted of a 4½- or 5-ft³ refrigerator containing a 5½-gal stainless steel aquarium (16 ×

Received for publication 12 June 1961.

[1] The work was supported in part by a grant from the Division of Research Grants (B-1941), National Institutes of Health and by the Fund for Research and Teaching, Department of Nutrition, Harvard School of Public Health.

[2] The data reported in this paper were incorporated in a thesis presented to the Graduate School of Arts and Sciences, Harvard University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The research was performed during tenure of a National Science Foundation predoctoral fellowship.

8 × 10 in.). A photograph of one of the experimental units is shown in Fig. 1. The aquarium was supported on a piece of ⅜-in. plywood which was attached to four Lord vibration-absorbing mounts. These mounts rested on the floor of the refrigerator and formed the only substantial contact between the body of the tank and the refrigerator. A ⅛-in.-thick sheet of translucent Plexiglas partitioned the tank; it was located 1½-in. from the left end. A hole, 1½ × 1½ in., was located in the center of the partition. The lever target was centered between this hole and the wall of the aquarium. This placement of the lever target required the fish to enter the hole in the partition with its head in order to push the lever and eliminated chance operation of the lever by the body and fins. The hole could be closed off by a piece of translucent Plexiglas. A small aluminum stimulus box (3 × 3 × 1½ in.) was attached to the refrigerator wall and faced the left end of the tank. The stimulus box housed two red 6-w light bulbs which illuminated the translucent Plexiglas partition in the aquarium for 3 sec when the fish pressed the lever.

A Fenwal (no. 17300) thermostat was suspended at the right end of the tank. The thermostat operated a 50-w submersible gravel-filled aquarium heater that rested on the floor of the aquarium. Two filters were attached to the back wall of the tank. One was a standard aquarium filter that circulated the tank water through activated charcoal and glass wool. The other filter circulated the water through a porous cartridge. Both filters were operated continuously.

Food pellets were dispensed by a Gerbrands pellet feeder which had a capacity of 144 pellets. The pellet feeder was attached to the top of the refrigerator. This minimized the effect of noise and mechanical disturbance associated with the operation of the feeder, and, as the feeder did not reload automatically, permitted reloading without opening the refrigerator. A ⅝-in.-diameter Tygon tube conducted the dispensed pellets through the top of the refrigerator to a point about 2 in. above the tank, near the back wall of the tank and just to the right of the partition.

The pellets were the standard rat food tablets manufactured by P. J. Noyes Co., Lancaster, N. H. Pellets weighing 20 mg were used as standard reinforcement. Occasionally, 45-mg pellets of the same composition were used, as were pellets diluted with kaolin. These pellets were the only food provided for the fish. The fish grew substantially on this diet.

A 10-w clear bulb was mounted near the top of the refrigerator and provided the only illumination. One could observe the fish without disturbing it by looking through a "Mystery Door Guard" (1-way window) mounted in the door of the refrigerator. The door was normally kept closed. The lever that the fish had to press to obtain food was a simple mechanical device. Pressure on the lever target broke a normally closed pair of contacts. The experimental contingencies were controlled by circuitry typical of operant conditioning experiments.

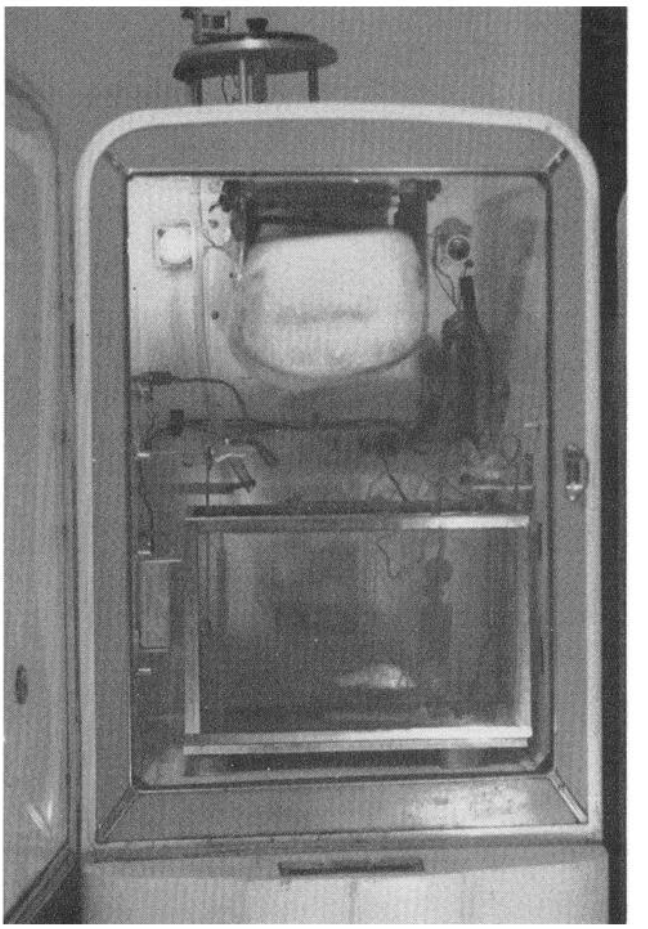

FIG. 1. Photograph of one experimental unit.

Aquaria were filled initially with Cambridge tap water. Additional tap water was added, as needed, to replace water lost through evaporation. If the tank appeared cloudy, the fish was removed, and the water in the tank was replaced with fresh tap water. Distilled water was added to replace evaporated water in aquaria that had not had a complete water change in more than a month, in order to prevent a buildup of electrolytes in the water. The two filters in each tank were operated continuously. Feces and occasional pieces of uneaten food were siphoned from the bottom a few times a week, if necessary, and the water removed in this process was replaced with tap water. The temperature was maintained at 25±0.2 C. A 12-hr-daylight, 12-hr-moonlight lighting cycle was controlled by an electric timer. The 10-w bulb in the aquarium was lighted at its rated intensity from noon to midnight of each day (daylight). From midnight to noon the light was operated in series with a 2,000-ohm resistor, which decreased the intensity of the light considerably (moonlight). An experimental day began at noon, with an increase in illumination. Data were collected at this time. Lever pressing responses were recorded on an Esterline-Angus operations (event) recorder. A separate channel was provided for each

TABLE 1

| Fish | Mean No. Pellets Eaten Per Day (3 Days) | | Ratio* |
|---|---|---|---|
| | 20 mg | 45 mg | |
| *G11* | 106 | 35 | ·33 |
| *G13* | 33 | 23 | ·70 |
| *G25* | 62 | 28 | ·45 |
| *G2* | 39 | 18 | ·46 |
| *G14* | 48 | 21 | ·44 |

* Ratio of 45-mg pellets to 20-mg pellets. If nutrient content was controlling lever pressing behavior, the ratio should equal 0.44.

apparatus. The number of responses in daylight and moonlight for each fish was tabulated separately.

Untrained fish were placed in the experimental aquarium when training began. They were left in the aquarium for 1 day before magazine training commenced. The lever was absent at this time. Magazine training consisted of the delivery into the tank of about 100 pellets at irregular time intervals over a period of 2–3 days. The red lights in the stimulus box were turned on for 3 sec each time a pellet was delivered. The onset of illumination coincided with the operation of the pellet dispenser. After magazine training, the lever was placed in the tank; it was baited with a few food pellets (8). These pellets were held to the surface of the target facing the fish by a piece of plastic screening. The screening was attached to the target by rubber bands. Fish ordinarily struck at the target in an attempt to obtain the food behind the screen. In so doing, they broke the lever contacts, and a pellet was delivered into the tank, along with the onset of the red light stimulus. When the food and screening were removed from the target after a few hours, the fish usually continued to press the black Bakelite target. Fish received one pellet for each lever press (continuous reinforcement). The fish were allowed continuous access to the lever for at least 5 days before any experiments were begun.

Fish were weighed approximately once a month. Weighings were timed to occur between experiments, or sessions of experiments, so as not to disturb the fish in the middle of an experimental session.

Each fish lived in its experimental box and was removed from its aquarium only for weighing, or when the aquarium water was completely changed. There is a considerable amount of evidence (9) indicating that handling of fish for short periods of time affects their respiratory rate for a number of hours. In view of such data, it was considered advisable to move the fish as little as possible.

Subjects for all experiments were common or comet goldfish, *Carassius auratus*. They were purchased locally. The goldfish ranged in weight from 15 to 100 g and in length from 2½ to 5 in. (measured from tip of head to base of tail). Fish of both sexes were employed.

Lever pressing was used in this experiment to describe and measure food intake. This method has been used successfully in studies on food intake in the mammal. It has been found to be reliable and sensitive to changes affecting the energy balance of the subjects concerned. In the mammal the amount eaten in a lever pressing situation correlates well with the amount eaten ad libitum.

The techniques of operant conditioning have been successfully applied to the fish (10, 11). Food reinforcement has been used in these studies, but the emphasis was on learning rather than on the determination of food intake.

*Results and discussion.* It was important to determine whether, at the outset of this experiment, the fish's lever pressing behavior was indeed controlled primarily by the food reinforcement. It is unlikely that the fish activated the lever in the course of normal activity and exploratory behavior, as untrained fish practically never pressed the lever. A direct comparison of ad libitum and lever pressing food intakes would be difficult to perform, because of the difficulties involved in the long-term measurement of ad libitum food intake in fish. Bitterman, Wodinsky, and Candland (10) have compared ad libitum and instrumental (lever pressing) food intakes in African mouthbreeders, *Tilapia macrocephala*, for short periods. The two measurements were in fair agreement.

A control experiment was performed to confirm that the fish used in these experiments were, in fact, pressing for food. After 3 days of lever pressing for 20-mg pellets, a number of fish were switched over to 45-mg pellets. For the following 3 days, these fish received one 45-mg pellet for each lever press. If food is the predominant factor controlling lever pressing behavior, one would expect the number of lever presses followed by 45-mg pellets for 3 days to be less than half of the number of presses for 20-mg pellets for the same period. As shown in Table 1, an effect of this order was obtained.

It does, in fact, appear that under certain circumstances lever pressing is under the control of variables other than those relating to food or hunger motivation. A number of fish consistently left a considerable number of pellets uneaten on the floor of the aquarium. This "overpressing" appeared in two fish that had performed quite adequately in the experimental conditions for a period of months. These two fish never returned to their original "tidy" eating habits, and had to be discarded. All the other fish that showed overpressing developed it very shortly after their initial training. In general, overpressing could not be eliminated once it had appeared.

Goldfish were never observed to "stuff" themselves with food. Visible distention of the body outline attributable to large amounts of food ingested were not observed. Such distention has been seen in *Betta splendens* by Hogan (12) and one of us (P.R.).

As mentioned under *Method*, the lever pressing behavior was recorded on an Esterline-Angus operations recorder. The data from the Esterline-Angus charts were transcribed on standard pieces of graph paper, so that

they could be easily visualized. A reproduction of one of these transcriptions can be seen in Fig. 2. Examination of these transcriptions indicates that each fish had a characteristic response pattern. This pattern tended to be similar from day to day, in a given fish, but it tended to shift gradually over time.

Most fish showed a characteristic distribution of responses in daylight as opposed to moonlight. The percentage of daylight responses for a given fish remained relatively constant for periods of a few weeks to several months. In preliminary studies, with the use of complete darkness in place of moonlight, 100% daylight responses were not uncommon. Under the daylight-moonlight cycle, some fish distributed their feeding responses equally throughout the day, while others showed a preference for either daylight or moonlight. The relative orderliness and reliability in individual behavior, as opposed to the greater variations among different fish, is also reflected in data on the activity of goldfish. Spoor (13) reports: "The goldfish were quite variable in their patterns and rates of activity under the experimental conditions. Some fish were diurnally active and nocturnally quiescent, others followed the opposite pattern and still others were arrhythmic throughout the observation periods. Some fish showed both rhythmic and arrhythmic periods when studied over a few months or weeks." Spencer (14), using a different measure of activity, obtained results similar to those of Spoor. Spoor used goldfish in the same size range as those used in the experiments described in this experiment. His quoted description of the relation between activity and light cycle matches very closely the observations presented here on feeding pattern and light cycle. Fish *G14* showed consistent arrhythmic feeding for a long period followed by clear diurnal feeding a few months later.

Records of the day-to-day food intake of each fish show that some fish have a relatively reliable base line, with comparatively small day-to-day variability (Fig. 3). Other fish show large variations in their day-to-day intake (Fig. 3). Occasional shifts from one pattern to another do occur in individual fish.

Some fish underwent periods of very low food intake, in comparison with their normal levels. The intake occasionally dropped to zero (Fig. 3). These anorexic periods tended to occur more in some fish than in others. At the termination of such periods, which usually lasted for 1–8 days, there was no clear compensation effect. That is, intake returned approximately to the normal level. There was no evidence of increased eating in response to the energy deficit that was presumably induced by anorexia.

The most striking characteristic of the time distributions of responses (e.g., Fig. 2) is the apparent absence of "meals." Within the limits set by the lighting cycle for any given fish, feeding seems to be fairly evenly distributed over time.

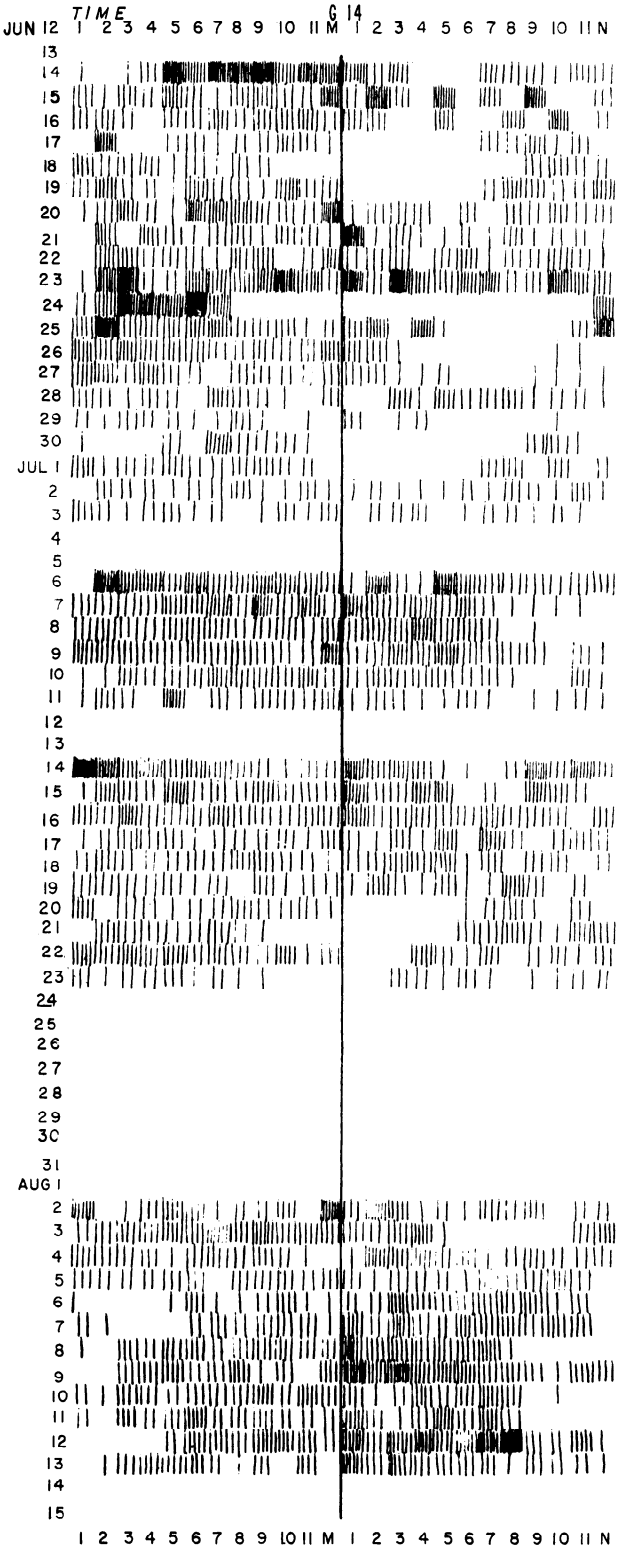


FIG. 2. Typical transcription of Esterline-Angus records. Each line represents 1 lever pressing response. Continuous dark line divides transcription into daylight on left and moonlight on right. Each row = 1 day. Blank rows = days of deprivation. Light does not seem to be an effective controlling factor in feeding pattern in this fish.

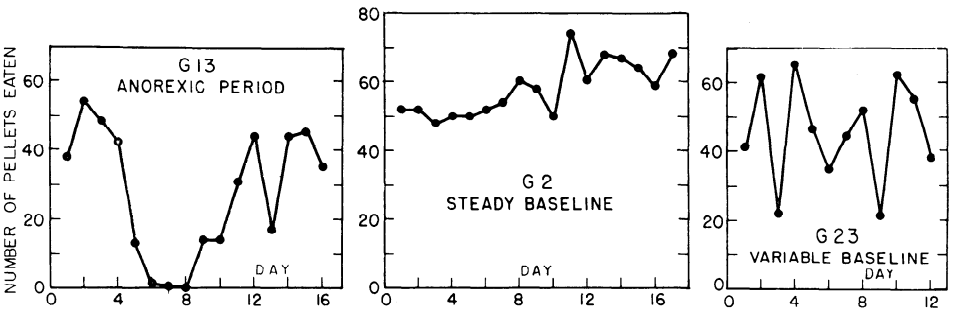


FIG. 3. Some characteristic daily food intake patterns.

EFFECTS OF TEMPERATURE CHANGE

If the goldfish regulates its food intake, the amount it eats should drop with decreases in temperature. A lower rate of metabolism indicates slower utilization of energy, and consequently lower energy need. The experiment described below was performed in order to determine if the food intake of the goldfish could be depressed reliably by a drop in ambient temperature of 10 C. Measurements were made of the steady state food intake at two different temperatures. Transient effects of temperature change were not examined in detail.

*Method.* The subjects were three goldfish; *G14*, *G23*, and *G24*. *G23* and *G24* had had no previous experience in other experiments. *G14* had been a subject in deprivation and diet-dilution experiments previous to its participation in this experiment.

The experimental units described in the general apparatus section were employed. The food intake of each fish was measured for 10 consecutive days at 25 C. At the beginning of the 11th day, the temperature in the aquarium was dropped gradually to 15 C, and always reached this value within 24 hr. *Days 11–14* were adaptation days. Food intake was recorded, but these data were not employed in comparisons of amount eaten shown in the results. Schlieper (15), studying trout (*Salmo trutta*) and swordtails (*Xiphophorus helleri*), has found that these species may take up to 3 days to reach a stable level of oxygen consumption when ambient temperature is changed by 10 C. It was hoped that the metabolic rate of the goldfish would stabilize during the 4-day adaptation period. Food intake was measured at 15 C from *days 15–24*, a 10-day period. At the beginning of *day 25*, the temperature was gradually brought back up to 25 C. Four days (*days 25–28*) were allowed for adaptation, with the lever always available. Daily food intake was measured for 10 more days (*days 29–39*).

*Results.* The results for all three fish are summarized in Fig. 4. Food intakes for 10 days at 25 C, 10 days at 15 C, and 10 days at 25 C are shown for each fish in the bar graphs. There is clearly a considerable drop in amount of food eaten after the 10-deg temperature drop. This is followed, in each fish, by a substantial rise in intake upon return to 25 C. There does not appear to be a systematic difference between food intake at 25 C before and after the period at 15 C. The day-to-day food intake of two of the fish is shown in Fig. 5. *G24* yielded a relatively high $Q_{10}$ of 3.2 (mean no. of pellets eaten per day at 25 C divided by mean no. eaten at 15 C). The $Q_{10}$ of *G23* was 2.0 and that of *G14* was 1.9.

*Discussion.* The data on temperature dependence of food intake in *G14* and *G23* are in general accord with available data on the oxygen consumption of goldfish as a function of temperature. Ege and Krogh (16) computed a respiratory $Q_{10}$ of about 2.4 for narcotized or normal goldfish for the temperature interval 15–25 C. Fry and Hart (17) arrived at similar figures for the goldfish, measuring both standard (basal) and active rates of metabolism. Fry and Hart found that both active and standard metabolism increased uniformly over the 15–25 C range. Above 30 C the total active oxygen uptake does not increase with temperature, so that measurements on food intake in this range might yield values considerably different from those determined in this experiment.

There have been a few studies comparing amounts of food eaten by fish at various temperatures. Hathaway (18), studying three species of fresh water teleosts, reports that: "Fish were found to consume about three times as much food per day at 20° C. as at 10° C." Baldwin (19) fed minnows to brook trout, *Salvelinus fontinalis*, kept at various temperatures. He found that the weekly

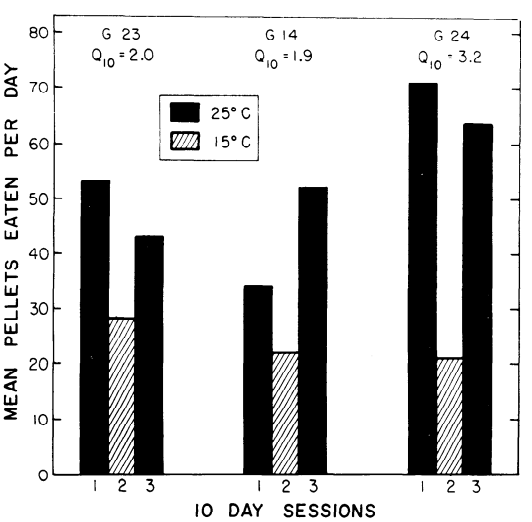


FIG. 4. Effects of temperature on amount of food eaten.

consumption of minnows approximately doubled for each 4 C rise in temperature, up to 13 C. The amount eaten dropped off above 17 C. This relatively steep increase in food intake with temperature, followed by a decrease in intake, is probably related to the stenothermal characteristics of this species. Correspondingly sharp rises in oxygen consumption for related fish have been observed (20). The data collected in this experiment are generally consistent with the results of Hathaway (18). There are some factors that may introduce systematic discrepancies between measures of metabolic rate and of food intake as a function of temperature. One such factor is variation in the efficiency of utilization of food as a function of temperature. Kinne (21) has recently reported systematic variations in the efficiency of conversion of food to fish as a function of temperature.

### EFFECTS OF DILUTION OF DIET WITH NONNUTRITIVE MATERIAL

This experiment is directed at clarifying what is regulated by the goldfish. Volume or weight of material ingested was pitted against the caloric or nutrient value of this material. Dietary dilution is, in principle, a very simple and powerful tool that can be used to assess the importance of digestive system distention factors in the regulation of food intake. In the past, it has been applied with success to mammals (22, 23). To our knowledge, it has never been applied to a nonmammalian form. This failure to use the dilution technique in nonmammalian forms probably stems from the lack of precise control over food material employed in the feeding studies, and a general lack of interest in the comparative problems of food intake regulation.

Goldfish will accept pellets composed of Purina and kaolin. In this experiment, the number of kaolin-diluted pellets eaten was compared with the number of standard Purina pellets eaten over equal periods of time.

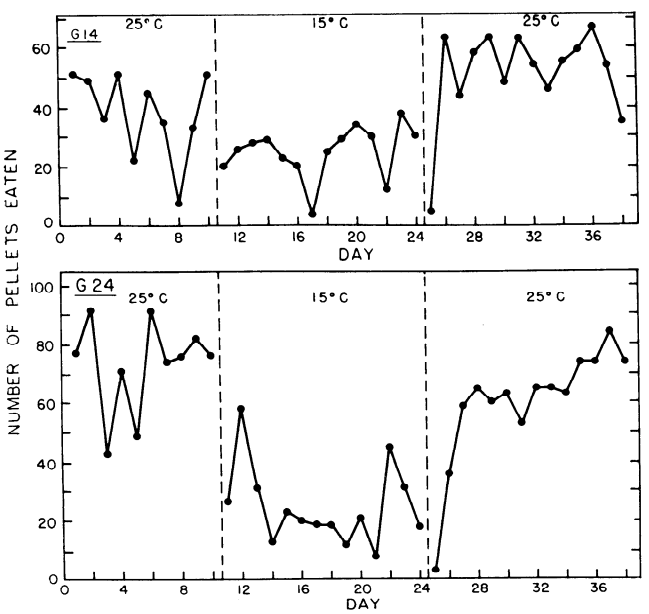


FIG. 5. Effects of temperature change on daily food intake of 2 fish.

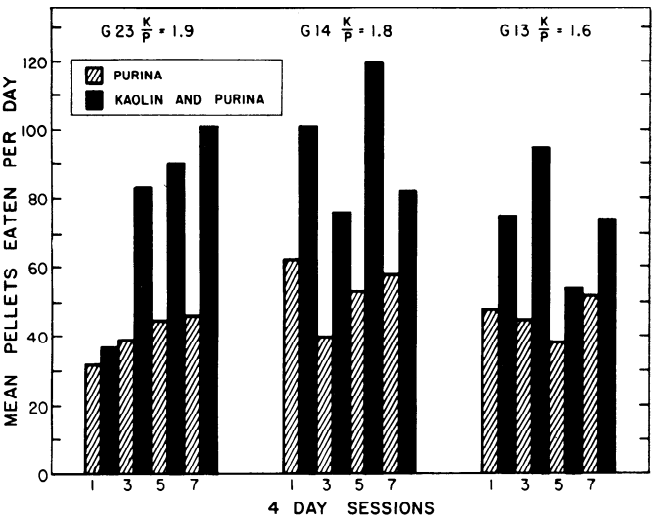


FIG. 6. Effect of dilution of diet with nonnutritive material on food intake. Purina pellets are standard 20-mg pellets used in all experiments. Kaolin and Purina pellets contain 11.3 mg kaolin and 11.3 mg Purina. K/P = 1.8 for perfect calorie (nutrient) compensation.

*Method.* The subjects were three goldfish, *G13*, *G14*, and *G23*. All had had some previous experience in the experimental units.

Two types of pellets were employed in this experiment. One type was the standard 20-mg Purina pellet used in the previous experiments. The other type was made on special order by the P. J. Noyes Co. This pellet, the kaolin pellet, was made from the same die as the 20-mg Purina pellet. It was 50% kaolin, 50% Purina by weight. Kaolin is heavier than Purina, so that the kaolin and Purina pellet weighed more than the Purina pellet. The kaolin pellet weighed 22.6 mg, and contained 11.3 mg kaolin and 11.3 mg Purina. In terms of nutritive value, 1.8 kaolin pellets are the equal of 1 Purina pellet.

The dietary dilution experiment lasted 32 days for each fish. The 32-day period was divided into eight 4-day sessions. During the 1st, 3rd, 5th, and 7th sessions, the fish received Purina pellets for each lever press. During the 2nd, 4th, 6th, and 8th sessions, kaolin pellets were dispensed. Each fish experienced alternating 4-day sessions of continuous reinforcement on Purina pellets and kaolin pellets.

*Results.* The intakes for each fish are presented in Fig. 6. The fish clearly ate more kaolin pellets than Purina pellets. It can be seen that each switch from Purina to kaolin involved an increase in the number of pellets eaten for the 4-day sessions, and that each switch from kaolin to Purina, with one exception, produced a decrease in the number of pellets eaten. The effect of switching from one type of pellet to the other was apparent on the 1st day of the change. A total of 21 changes from Purina to kaolin or from kaolin to Purina was

made. For 18 of these 21 changes either the intake on the last day of kaolin was higher than that on the 1st day of Purina, or the intake on the last day of Purina was lower than that on the 1st day of kaolin. In order to get some estimate of the quantitative effect of the compensation for dietary dilution, the ratio of the total number of kaolin pellets consumed to the total number of Purina pellets consumed in the 32-day sessions for each fish was computed. This ratio, called K/P, would equal 1.8 for perfect calorie compensation, as 1.8 kaolin pellets are equal to 1 Purina pellet in calories. The K/P ratio was computed for each fish and appears in Fig. 6. Values of 1.9, 1.8, and 1.6 were obtained for the three fish. This is certainly good evidence that these fish were responding primarily to calories or nutrient value.

There is no systematic trend within each 4-day session. In other words, there is no evidence that the fish took any appreciable time to adjust to the change in diet. Because of the considerable variability in the day-to-day pellet intake, it was necessary to combine the data over the eight 4-day sessions to arrive at a reasonable quantitative estimate of the response to dietary dilution.

It is not likely that the fish ate more kaolin pellets because they preferred them to Purina pellets. When given a choice of Purina or kaolin pellets in free feeding experiments, fish usually ingested the Purina. Fish deprived of food for 1 hr usually accepted at least 1 Purina pellet, and frequently refused 50% kaolin pellets.

*Discussion.* Fish seem to respond more rapidly and more accurately to substantial dietary dilution than do rats (22) or dogs (23). Adolph (22) found that rats did not completely compensate for calories when fed pellets of less than 70% nutrient material (more than 30% kaolin). The weight of rats fed on 50% kaolin was 98% normal after 3 days. Adolph reports that the response to the kaolin dilution was moderately rapid in the rat. Janowitz and Grossman (23) found that the dog did not compensate well for calories when its diet was diluted. Compensation was frequently not complete, and it was often many weeks before their dogs settled at their highest level of diluted diet intake. The goldfish's response to dietary dilution seems more rapid and at least as precise as the response of the mammal.

## GENERAL DISCUSSION

The response of the goldfish to a drop in temperature gives evidence that a regulatory mechanism is operative. It does not give any information as to the nature of this mechanism. A fundamental control through sensitivity to distention of part of the digestive system is consistent with these results. Von Maltzan (24) has computed a $Q_{10}$ of from 2 to 2.2 for time of passage of food through the carp digestive system in the 15–25 C range. Depression of food intake with drop in temperature could be accounted for in terms of the lowered rate of intestinal clearance at low temperatures. The results of this experiment are also consistent with the notion that food intake is regulated by factors directly sensitive to the metabolic state of the fish. The rate of intestinal clearance and the rate of metabolism are affected similarly by temperature drop. The relative role of these two effects and the importance of other effects cannot be distinguished in the temperature experiment.

The dilution experiment provides positive evidence that distention factors are not primary in the regulation of food intake in the goldfish. The natural food of goldfish is calorically much less dense than the food employed in this experiment. It is possible that by employing calorically concentrated foods, the role of a distention factor has been minimized. Nevertheless, under the experimental conditions, food intake regulation in the goldfish can best be described as a regulation of calories or amount of nutrient ingested.

## REFERENCES


1. DETHIER, V. G., AND D. BODENSTEIN. *Z. Tierpsychol.* 15: 129, 1958.
2. MORRISON, S. D., AND J. MAYER. *Am. J. Physiol.* 191: 248, 1957.
3. VERPLANCK, W. S., AND J. R. HAYES. *J. Comp. Physiol. Psychol.* 46: 327, 1954.
4. BROBECK, J. *Yale J. Biol. Med.* 29: 565, 1957.
5. STELLAR, E. In: *Handbook of Physiology*, edited by J. FIELD. Washington, D.C.: Am. Physiol. Soc., 1960, p. 1501.
6. HEALEY, E. G. In: *The Physiology of Fishes*, vol. 2, edited by M. E. BROWN. New York: Academic Press, 1957, p. 1.
7. MAYER, J. *Ann. N. Y. Acad. Sci.* 63: 15, 1955.
8. LONGO, N., AND M. E. BITTERMAN. *Am. J. Psychol.* 72: 616, 1959.
9. FRY, F. E. J. In: *The Physiology of Fishes*, Vol. 1 edited by M. E. BROWN. New York: Academic Press, 1957, p. 1.
10. BITTERMAN, M. E., J. WODINSKY, AND D. CANDLAND. *Am. J. Psychol.* 71: 94, 1958.
11. MURRAY, A., AND P. E. FIELDS. University of Washington School of Fisheries Tech. Rept. no. 45, 1957.
12. HOGAN, J. G. Ph.D. thesis. Cambridge: Harvard University, 1961.
13. SPOOR, W. A. *Biol. Bull.* 91: 312, 1946.
14. SPENCER, W. P. *Ohio J. Sci.* 39: 119, 1939.
15. SCHLIEPER, C. *Biol. Zentr.* 69: 216, 1950.
16. EGE, R., AND A. KROGH. *Internat. Rev. ges. Hydrobiol. Hydrog.* 7: 48, 1915.
17. FRY, F. E. J., AND J. S. HART. *Biol. Bull.* 94: 66, 1948.
18. HATHAWAY, E. S. *Ecology* 8: 428, 1927.
19. BALDWIN, N. S. *Trans. Am. Fisheries Soc.* 86: 323, 1957.
20. GIBSON, E. S., AND F. E. J. FRY. *Can. J. Zool.* 32: 252, 1954.
21. KINNE, O. *Naturwissenschaften* 22: 525, 1960.
22. ADOLPH, E. F. *Am. J. Physiol.* 151: 110, 1947.
23. JANOWITZ, H. D., AND M. I. GROSSMAN. *Am. J. Physiol.* 158: 184, 1949.
24. VON MALTZAN, M. G. *Zool. Jahr. Abt. Allgem. Zool. Physiol. Tiere* 55: 191, 1935.