DIURNAL RYTHM OF THE FEEDING ACTIVITY OF GOLDFISH IN AUTUMN AND EARLY WINTER

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Many reports have been published on the correlation between feeding activity of fish and either light intensity or water temperature or both of them. However, the announced experimental results have not always agreed with one another as Hoar discussed in his paper[1]. Accordingly, it is presumable that the influence of environmental factors on the pattern of feeding activity in fish is not so simple. In fact, Hathaway[2] has found in his experiments on pumpkinseed, bluegill and bass that the food consumption on any one day apparently has little significance, since a day of heavy feeding is often followed by a day on which little or no food is taken. So, to clarify the normal pattern of the feeding activity in a given fish, both the diurnal rythm and the annual variation of the said activity must be studied first from the ecological point of view. Further, unless such a study on fish feeding is executed by means of continuously prolonged observations or recordings, the correlation between any certain sort of behaviour and the environmental factors would not be obtained, since the diurnal rythm of the former is often distorted heavily by the latter which fluctuate not only day by day but also hourly.

The writers have devised an automatic feeding recorder in fish as reported in the preliminary experiment[3]. Using this apparatus, the diurnal rythm of the feeding activity in the goldfish was recorded, and the results obtained were analyzed in relation to some environmental factors.

Nowadays, very little information is available on fisheries meteorology; the only book in this field has been published by Uda[4]. In many guide books for anglers the correlation has been described between angling-rate and climatic factors. However, all such descriptions are those based on the angler-writer's own experiences. The results obtained in the present experiment may offer some scientific evidence for both the fisheries meteorologists and the anglers.

The writers wish to express their thanks to the staff members of the Hakodate Marine Observatory for supplying the data of climatic observations used in the analysis of the present experiment.

MATERIAL AND METHOD

The feeding recorder used is the same as that reported in the preceding paper[3]; that is, it was designed to make an automatic recording on a kymograph when fish pecked a bait box suspended in a tank of water. The feeding frequency was calculated by examining the repeated marks of the kymographic record, as indicated in the preliminary report. A bait box packed with minced dry crustacean larvae was suspended in water to tempt the fish to peck it. The bait was changed every morning for the fresh material. Although by this changing of the bait the feeding behaviour of the fish appeared to be disturbed a little for a short time, the decrease in number of feedings which might be caused to occur seems to be negligible. Immediately after the substitution of the fresh bait, the fish appeared, in most cases, to peck it more frequently for a short time than they had done before the exchange was made.

All the experiments were performed in the same tank set in a greenhouse of the Faculty of Fisheries. The size of the tank is as follows: 140 cm long, 70 cm broad and 45 cm deep. The depth of the water was maintained at about 35 cm, a very little well-water flowing into the tank constantly. Throughout the present experiment 30 young goldfishes were used which had been acclimatized to this tank for about a month before the experiment started.

The feeding records cited in the present paper are those which were taken every day during the period extending from September 20 to December 10, 1955. The average total body length of the fishes used was 43 mm at the outset of the experiment and 52 mm at the end. Comparing the growth of these fishes with that of the control which were fed in the usual manner, no differences were found between them.

As the environmental factors, the water temperature, the air temperature, the atmospheric pressure, the solar radiant heat and the duration of sunshine were measured. Of these factors, the data of the latter three are those which were measured at the Hakodate Marine Observatory which is situated about 4 kilometers apart from the Faculty of Fisheries. So, exactly speaking, the values of the factors concerned may differ slightly from those measured at the location of the Faculty of Fisheries. In most cases, the water temperature was measured several times a day, and sometimes every hour day and night. To avoid the disturbance of the experimental fishes, the water temperature was measured by reading the thermometer which was inserted into a rubber tube, through which the water of the tank was constantly flowing out. The atmospheric pressure was measured every three hours all day. In measuring the solar radiant heat a Robitsch-Actinograph was used. The duration of sunshine was indicated by the every-hour index of from 0 to 10, calculating from the records by a Jordan's Heliograph.

RESULTS

Diurnal rythm of the feeding activity in autumn and early winter

The diurnal frequency of the feeding was highly variable. So, to show the general appearance of the diurnal rythm of the feeding activity, the average frequency per hour was calculated for every ten-day period of the months during which the observations were continued. The results are illustrated in Fig. 1, A-H. As is clear from these figures, the feeding is almost restricted to the daytime throughout the experimental

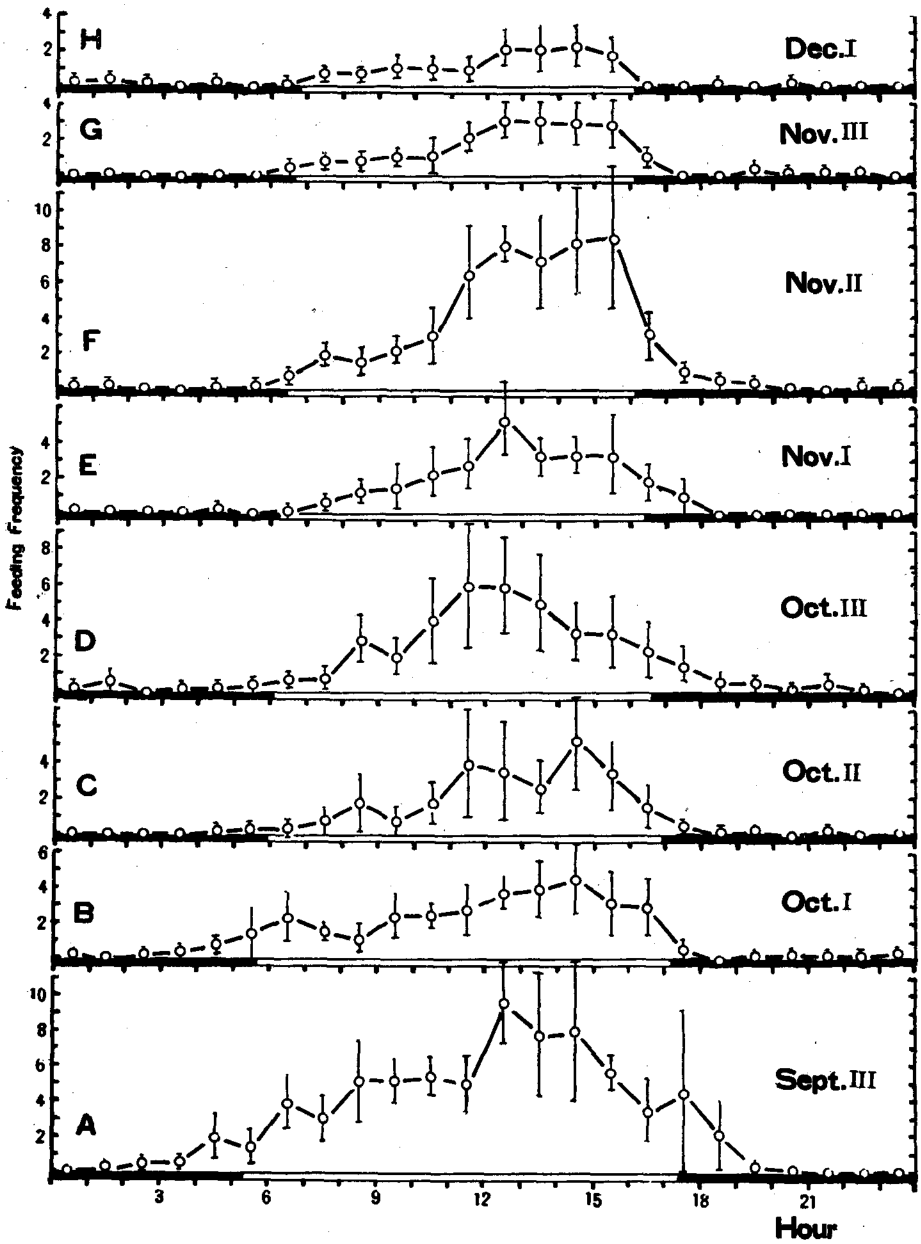


Fig. 1. Time and diurnal rythm of the feeding activity in the goldfish are shown in the average of every decade of days from September to December. The Roman numerals I, II and III mean the first, middle and last decade of every month, respectively. Each bar indicates the standard deviation of the feeding frequency.

period. That is, generally saying, the fishes begin to feed at about daylight, and the feeding frequency increases gradually in the forenoon, then reaches to the maximum in the time extending from about the 11th hour to the 15th, thereafter decreases, and finally, the feeding ends towards nightfall. It may be natural that the feeding activity decreases gradually according to the passage of the season from autumn to early winter, though the cause of a higher activity of the feeding in the middle decade of November is not clear at present. It is noteworthy that between the seasons of the autumn and early winter there was found a different pattern of the feeding activity in both the time before sunrise and that after sunset. It was found that in the period extending from the last decade of the September to the first decade of October, the feeding begins usually one or two hours before sunrise, while thereafter such a feeding decreases gradually and becomes rare in the period of the early winter. Similarly, the feeding in the evening time continues furthermore one or two hours after sunset during the period extending from the last decade of September to the middle decade of November, while thereafter it comes to a stop with the time of sunset. Further, until the last decade of October, one or two feedings were often recorded in the night time, while such a behaviour becomes rare thereafter.

Correlation between the feeding activity and the environmental factors

As already described in the above, the feeding activity of the goldfish was found to be definitely restricted to the daytime throughout the period of the present experiment. Even from this fact only, it seems to be clear that the light is the main factor controlling the diurnal rythm of the feeding activity in the goldfish. Possibly the other environmental factors may influence the said activity either to accelerate or to inhibit it. Further, it is conceivable that the environmental factors themselves are closely correlated with one another. For example, both solar energy and duration of sunshine are not only related to the light environment in the daytime, but they also influence the

Table 1. Daily fluctuation of the feeding frequency of the goldfish in the period extending from the last decade of September to the first decade of December. Number and the mark of + mean that the recording was interrupted in the course of the experiment on that day.

Month	Decade \ Date	1	2	3	4	5	6	7	8	9	10	11
Sept.	III	95	80	47	—	155	79	—	66	25	62	
Oct.	I	44	45	43	65	43	37	10.	24	26	38	
	II	1	53	68	60	44	2	(17+)	0	26	0	
	III	0	—	(42+)	43	58	46	105	61	52	36	5
Nov.	I	40	6	—	(39+)	20	15	24	15	39	51	
	II	29	36	15	116	82	47	85	41	69	30	
	III	3	14	34	18	33	32	15	2	2	40	
Dec.	I	33	6	28	17	27	6	2	3	2	21	2

temperature.

Although the diurnal rythm of the feeding activity was clearly recognized, it was highly variable with days. It was not rare that a day of little feeding was followed by a day on which a very high activity of feeding was recorded, as indicated in Table 1. Such a variability might possibly be produced by the effects of some environmental factors. In other words, it may be presumable that the normal form of the diurnal rythm of the feeding activity in the fish is distorted variously by some environmental factors. Although the correlation between the feeding activity and the environmental factors will be studied statistically in future, some brief notes are presented as below.

1. Typical form of the diurnal rythm of the feeding activity

Some examples of the typical form in the diurnal rythm of the feeding activity which were most frequently recorded are illustrated in Fig. 2, A–C, together with the diurnal variations of the water temperature, the atmospheric pressure, the solar radiant heat and the duration of sunshine.

It was commonly found that the maximum activity of the feeding occurs within the time extending from the 11th hour to the 15th, while the water temperature showed usually the highest degree. From this fact, it is conceivable that the feeding activity in

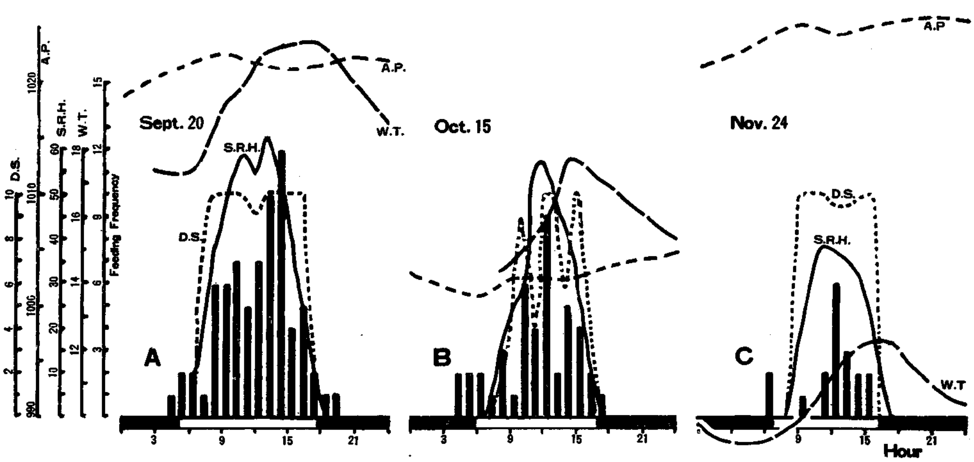


Fig. 2. Examples of the typical form of the diurnal rythm in the feeding activity of the goldfish in correlation with the environmental conditions. Environmental factors: ——·—— water temperature (W. T., C°); ——— solar radiant heat (S. R. H.,cal/cm^2); — — — atmospheric pressure (A. P., mb); - - - - duration of sunshine (D. S., every-hour index of 0–10)

the goldfish is closely related with the diurnal variation of the water temperature. Judging from the records which showed the typical rythm of the feeding activity, it can be said generally that the feeding is found to be normal when the water temperature varied diurnally with a normal rythm, i. e., one which shows high temperatures in the daytime and low in the night time. Further, it appears that when such a diurnal rythm of the water temperature varied more distinctly with higher peaks and lower dips, the feeding rythm is more active and also more distinct. Although it is natural that the feeding activity decreases gradually according to the passage of the season from autumn to early winter, the influence of low water temperature on the said activity was clearly found in the time both before sunrise and after sunset in the period of the late autumn and early winter, as already noted in the preceding section.

Solar radiant heat is considered to be a factor of the temperature environment. When the weather is fine, the diurnal rythm of the solar radiant heat is very distinct, showing maximum at about noontime and minima at about sunrise and sunset, both. Generally, in a typical fine day the water temperature also varied with a distinct diurnal rythm throughout the day, and likewise, the typical form of the diurnal rythm of the feeding activity was usually found. As a rule, the diurnal variation of the solar energy was found to be parallel with that of the duration of sunshine. Naturally, the solar radiant heat decreases from autumn to winter, similar to both the air temperature and the water temperature. The average total solar energy in each decade of the months experimented in Hakodate was as follows: the last decade of September 304 cal/cm^2, the first decade of October 168, the middle 256, the last 263, the first decade of November 151, the middle 186, the last 154, and the first decade of December 186.

The atmospheric pressure of the three days illustrated in Fig. 2, A–C changed diurnally in the range of from 1020 to 1023 mb (September 20), from 1001 to 1005 (October 15) and from 1020 to 1026 (November 24), respectively. In all these observations, in relation to this environmental factor, the feeding rythm was recorded in the typical form, though the seasonal differences were found. Although the absolute value of the atmospheric presssure in the case of October was much lower than the other two, it is commonly characteristic that the pressure varied through the whole day without any marked fluctuation. Therefore, it seems that, regarding the atmospheric pressure which influences the feeding activity of the fish, the absolute value of the pressure itself is not important, but the pressure gradient is really the important factor.

2. Atypical form of the diurnal rythm of the feeding activity

During the experimental period there were found abnormal cases of the feeding rythm which are quitely different from the typical ones described above. Such a few cases are illustrated in Fig. 3, A–C.

(A) September 29 (Fig. 3, A)

The water temperature varied throughout the day with the range of 16.3° to 17.8°C. Accordingly, considering only from the water temperature, it is not likely that such temperature is unfavorable for the feeding. However, the feeding was not active, and furthermore, a few feedings were recorded in the forenoon. It is noticeable that the

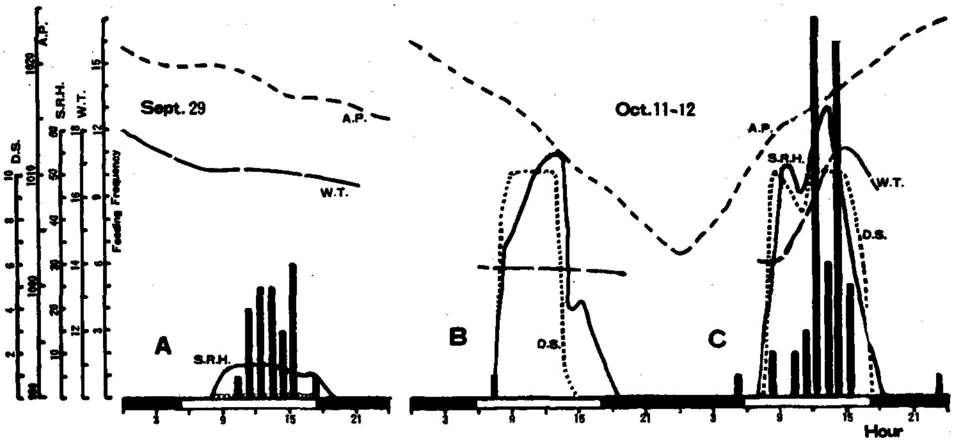


Fig. 3. Examples of the atypical form of the diurnal rythm in the feeding activity of the goldfish in correlation with the environmental conditions. Environmental factors: —— —— water temperature (W. T., C°); ——— solar radiant heat (S. R. H., cal/cm²); — — — atmospheric pressure (A. P., mb); - - - duration of sunshine (D, S., every-hour index of 0-10)

solar radiant heat fluctuated all that day during daylight hours with a low value. Such a low solar energy might produce an obscure diurnal rythm of the water temperature, and might result secondarily in the depression of the feeding activity. If so, it is presumable that a distinct diurnal rythm of the environmental temperature including solar radiant heat, air temperature and water temperature may be an essential factor controlling the feeding activity in the goldfish. This day, the duration of sunshine was zero throughout the daytime. Although the atmospheric pressure varied monotonously the whole day as in the figure, it is not known whether or not such an unusual feeding activity may have connection with the typhoon which struck the southern part of Kyûshû on that day.

(B) October 11 - 12 (Fig. 3, B - C)

On October 11, only one pecking of the bait box was recorded at about the 7th hour. The water temperature varied monotonously in the daytime with the range from 13.6° to 13.8°C. The solar energy dropped suddenly at about the 14th hour from 55 to 15 cal/cm², notwithstanding it had shown normally a rather high value in the forenoon. This day, the Kantô Region was visited by a typhoon, and the atmospheric pressure decreased in Hakodate also with a sharp fall of from 1022 to 1003 mb. Although the sudden depression of the solar energy at the beginning of the afternoon might affect the feeding activity, no feeding in the afternoon might be mainly due to some connection with the sharp depression of the atmospheric pressure. Next day, the good weather was restored as indicated in Fig. 3, C, and the feeding activity returned to the normal pattern of the diurnal rythm. The feeding frequency of this day appeared rather to exceed the average number of feedings in this season. However, it is not clear at present whether such an apparently compensatory increase of the feeding was due either to hunger or to the recovery of favorable climatic factors, or to both of them. Only, it seems interesting that this increase of feeding is somewhat similar to the fact that there have been, in most cases, good hauls of yellow-fishes in Sagami Bay and also in some other fishing grounds within from half a day to one day and a half after an pressure depression had passed over[4].

(C) October 20

No feedings were recorded this day. The weather was somewhat like that of the combination of the cases (A) and (B). In detail, the water temperature varied evenly in the daytime within the range from 12.9° to 13.4°C; the solar radiant heat passed over the daytime with low value, showing the total 128 and the maximum 27 cal/cm² at the 10th hour; the total duration of sunshine was only 7; the atmospheric pressure depressed with a sharp fall of from 1019 to 1003 mb. Possibly, a complex of the changes of these environmental factors might distort the feeding activity in an unusual manner.

Effect of water temperature upon the cessation of the feeding activity

It is well known that water temperature by which fishes are forced to cease the feeding is closely related with the previous temperature for which they had acclimatized [1)2)5)7)]. At least under the present experimental conditions, it was clarified that the young goldfish ceases to feed in early winter at about 8.5°C water temperature. The evidence may be seen in Fig. 4.

In Hakodate, it gets cold towards the end of November. It is not rare in this season that the air temperature falls to about 4°－5°C, and the water temperature below 8°C at night or before daybreak, though in most days the former rises to higher than 10°C and the latter to higher than 8.5°C in the daytime. In early December, it snowed a few times but not heavily, and in such days the water temperature fell below 5°C at night or before dawn. The daily total solar radiant heat also decreased gradually in this season. That value which was more than 200 cal/cm² in the mean of every decade of both September and October (excepting only the first decade of October) fell to 154 and 186 cal/cm² in the last decade of November and in the first decade of December, respectively.

In such climatic conditions, the feeding activity depressed gradually with days, and then, in the first decade of December the feeding almost ceased for a few days. Further, on both December 10 and 12 a small number of feedings were recorded again, and then, the feeding almost ceased, thereafter.

Upon analyzing the feeding activity during the two weeks illustrated in Fig. 4, one may classify its pattern into the two different categories. The feeding records of the

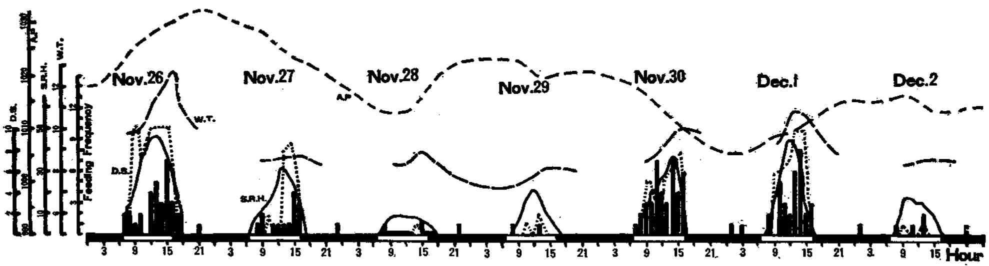


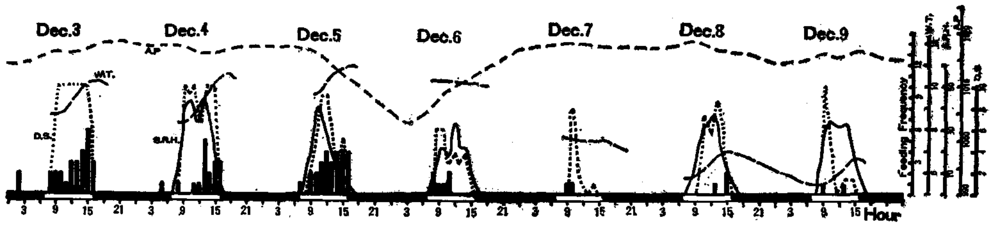
Fig. 4. Depression of the feeding activity of the goldfish in early winter in correlation with ——— solar radiant heat (S. R. H., cal/cm²); —·—·— atmospheric pressure (A. P., mb);

26th, 27th, 30th of November, the lst, 3rd, 4th and 5th of December belong to the first group. On these days, the feeding frequency was recorded to be more than 15 times. The second group is composed of the 28th, 29th of November, the 2nd, 6th, 7th, 8th and 9th of December, on which were recorded only less than 6 times of feeding (cf. Table 1).

It seems that these different patterns of feeding activity also might be produced by the diurnal changes of the environmental factors in this special season. In the first group except for the case of November 27, the water temperature measured higher than about 10°C during the time from the 12th hour to the 15th, at which the most active feeding was found. The total solar radiant heat in every day was much higher than that of the second group, showing the lowest 155 cal/cm² on November 27. Although that of December 3 was not measured, it is easily presumable that it might be nearly equal to that of the next day, 258 cal/cm², inferring from the same value of the total duration of sunshine, 77. On November 27, it was cold even in the noontime, both the air temperature and the water temperature showing equally 8.5°C. At any rate, it is noticeable that 15 times of the feeding were recorded this day at about 8.5°C of the water temperature.

On each of the three days extending from the 7th to the 9th of December which belong to the second group, 2 or 3 times of feeding were recorded between the 9th hour to the 15th, at which the water temperature was either approaching to or just at the maximum of the respective day. The maximum water temperature of these days were as follows: 7.5° on the 7th, 7.0° on the 8th and 6.6°C on the 9th. It snowed on the 7th, so the solar energy might be low though it was not measured. On the 8th, the weather cleared up after about the llth hour. and the total solar radiant heat was 178 cal/cm². In spite of such good weather, on that one day, a temperature environment favorable to feeding by the fish was not produced owing to the cold weather of neighbouring days.

Similarly, feeble feedings were recorded also on both days of November 28 and 29. The water temperature of the former day at the time of the feeding recordings was in



the environmental conditions. Environmental factors: ——·—— water temperature (W. T., C°); – – – – duration of sunshine (D. S., every-hour index of 0–10)

the range of from 8.3° to 8.9°; that of the latter day was from 7.4° to 8.1°C. On both days the total solar energy was low, being 63 and 103 cal/cm², respectively. In addition, the rain of the former day, and the rain and snow of the latter day might distort the feeding activity which had already been in a feeble state.

Six times of feeding were recorded on December 2. The water temperature when the feedings were recorded was in the range of from 8.3° to 8.4°C. The weather was cloudy all day long showing the total duration of sunshine only 3; the total solar radiant heat was 102 cal/cm². On December 6, the water temperature in the daytime varied in the range of from 10.0° to 10.2°C. The total solar energy was 155 cal/cm² and the total duration of sunshine 27. So, in view of the water temperature factor only, a feeding frequency of as many as the 17 times of December 4 might be expectable. However, only 6 times of feeding were recorded on this day (December 6) also. Possibly, the depression of the feeding activity in this case may be considered as effects of bad weather conditions such as the rather sharp drop in atmospheric pressure and, further, the forenoon's rain and snow.

From the results described above, it is presumable that the limit of the water temperature for the feeding in the case of goldfish is approximately 8.5°C. Moreover, it appears that in this early winter also the solar radiant heat is an important effective element of the temperature environment, so far as it can act on both the air temperature and the water temperature against the cold atmosphere. The atmospheric pressure, if it varies sharply, also appears to distort the feeble feeding activity in early winter as well as in autumn.

DISCUSSION

In spite of the fact that studies on both the annual variation and the diurnal rythm of the feeding activity in fish have been desired economically and practically for all fish-culturists, there have been very few experiments executed from the ecological point of view, so far as the writers are aware. The automatic recording apparatus used is still not a satisfactory one. For instance, it is a flaw that the number of the feedings are recorded as the same whether one fish pecked at the bait box or whether several fishes did at the same time. However, even by means of such apparatus the approximate tendency of the feeding activity in the fish may be understood, as described above. Considering from the fact that no difference in the fish growth was found between two groups of the fishes which were fed in a usual manner and reared by the present method, it can be said that the recording apparatus used is favorable for a prolonged experiment.

It is generally accepted in most animals that the diurnal rythm of the behaviour in many cases is not due to the creature's own nature, but that it depends mainly upon the diurnal changes of the environmental conditions[8)–10)]. Accordingly, the degree of the dependence of the feeding activity in the goldfish on the environmental factors must be studied by some analytical experiments in future. However, it can be said from the present experiment that the feeding activity in the goldfish shows a distinct diurnal rythm, and also that annual variation of the said activity may be found.

The daily changes of the water temperature in the tank appeared to be controlled by the fluctuations of the two factors of air temperature and solar radiant energy, reaching the maximum two or three hours subsequent to the maxima of the latter two. The agreement of both maxima in the water temperature and the feeding activity suggests that they are very closely related with each other.

The solar radiant energy has been strongly emphasized by Kato[11)] as an important factor in the study of some insect behaviour. It was found in the present study that the said energy as a factor of the environmental temperature affects similarly the diurnal rythm of the feeding activity in the goldfish. That is to say, even if the water temperature itself were favorable, the feeding activity declined when the amount of solar radiant heat was little. In such a day the diurnal variation of the water temperature was monotonous, not showing the distinct rythm of high in the daytime and low in the night time. Accordingly, it may be said that such a distinct rythm of the water temperature environment is an important factor influencing the feeding activity in the goldfish; further, in some cases the rythm may be rather more important for the said activity than the absolute temperature value itself. In other words, similarly as in the studies on some other animals[10)], such a process of the change in the environmental factors must be taken up for the analysis of the fish behaviour as well as the absolute value itself.

Not only in insects[9)], but also in fishes, there are very few investigations concerning the influence of the atmospheric pressure on their diurnal activities. It was clarified from the present study that the day's progress of the atmospheric pressure with a sharp depression may distort the diurnal rythm of the fish activity, the feeding being inhibited heavily even if both the water temperature and the solar energy appear to be favorable. On the other hand, as described in the case of October 15, even if the atmospheric pressure were low, it may not influence the feeding activity of the fish when the pressure varies monotonously throughout the whole day.

The depression of the feeding activity in early winter appears to be mainly due to the low water temperature, as shown by Markus' study in the bass[6]. After the diurnal rythm of the feeding activity was distorted repeatedly by low temperature, the fishes are forced to cease the feeding and then to hibernate. Under the conditions of the present experiment, the limit of the water temperature at which the feeding was recorded may be said to be approximately 8.5°C.

Although by analysis of the feedings recorded in the night time they appear to be correlated with the intensity of moonlight, further studies are necessary before any conclusions can be reported on this problem.

SUMMARY

1. Using an automatic recording apparatus, the diurnal rythm of the feeding activity of goldfish was studied in the period from autumn to early winter.

2. The feeding activity is definitely restricted to the daytime; that is, the feeding begins one or two hours before sunrise, reaches the maximum in the hours from about the 11th to the 15th, and ends one or two hours after sunset. As a rule, the maximum in the diurnal rythm of the feeding activity is found in the time interval showing the highest water temperature.

3. From autumn to early winter, the daily feeding frequency decreases gradually with the passage of the days. The feedings before sunrise become rare after early November, and the feeding ceases with the time of sunset after late November. In Hakodate, the goldfish ceases to feed at water temperature below 8.5°C, in early December, after the lapse of several days in states of either no feeding or very feeble feeding.

4. The daily frequency of the feeding is highly variable. Even if the water temperature is apparently favorable for the feeding, the diurnal rythm of the said activity is distorted when the water temperature does not show a distinct diurnal rythm which is high in the daytime and low in the night time.

5. The solar radiant energy is an important factor influencing the environmental temperature. So, when it varies during an entire daylight period with a very low value, the water temperature shows an indistinct rythm without any marked ups and downs. The diurnal rythm of the feeding activity may be heavily inhibited on such a day.

6. When the atmospheric pressure falls sharply, the feeding activity may be severely distorted, its frequency being much decreased. However, even if the atmospheric pressure is low, it does not exert influence upon the feeding activity of the goldfish when the pressure varies monotonously through the whole day.

7. As well as the absolute value in each of the environmental factors, the relative magnitude of the diurnal variation must be taken up for the sake of comprehensive

analytical studies of the fish behaviour.

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