Studies on the Schooling Behavior of Fish—IV Some Discussions concerning Continuity of Swimming Speed and Response Time of Individuals

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The swimming speed and change of position of each individual in a school were measured in a water tank to discuss the swimming behavior, such as continuity of swimming speed, response time lag of motion and spatial distribution probability. The swimming speed lost its correlation in 2.0 seconds. The time lag for response was distributed within 0.5 to 5.0 seconds and about 20% of total combinations showed a 0.5 second response, which coincided with the latent period of swimming motion that had been reported in a previous paper.

It is very interesting problems to analyze the similarities of movement and response time lag among individuals in a school. The authors attempted to calculate them using the correlation coefficient of swimming speed. The data used in these analyses were as the same ones that had reported previously¹⁾, in which the relations between deformation and swimming speed of school have been discussed. The swimming speed were rearranged again discriminating each individuals.

1. Theoretical background of analyses.

1-i. The longest time during an individual persists in a swimming motion.

The communication between individuals of almost kinds of animal may be carried out by means of movements. If we want to attempt the quantitative description of these animal behaviors, it is necessary to apply the information theory. The entropy for an individual movement is introduced by the same method of the thermodynamics law, comparing the initial and following acts²⁾, that is, $H = - \sum_{i=1}^n P_i \log P_i$, where P_i is the probability chosen i -th movement (Q_i), n is total categories of behavior. The unit of movement most frequently used for information is the "bit"³⁾. A bit is the amount of uncertainty eliminated by answering a signal yes-no question, where the two answers are equally probable, often symbolized by the binary digits 0 and 1.

But the behavior of fishes are different from the other land animals, because the fishes usually show the three-dimensional change of positions, and its fact makes us difficult to establish categories of behavior giving careful attention to biological meaningfulness.

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Furthermore the behavioral motion does not so quite change in a short time period but maintain rather slight continuity though it shows a few random variation with time and space coordinates. It means the existence of the correlation between these swimming motions, and the probability to chose one movement in a unit time is not always priori probability.

The movement Q may be written as a functional form as follow,

$$Q = F(V, \theta) \quad 1),$$

where V is three-dimensional swimming speed (u_x, v_y, w_z), θ is the change of direction ($\alpha_x, \beta_y, \gamma_z$) and x, y, z are respectively axes of longitudinal, horizontal and vertical directions.

In these experimental series, we considered Q is

$$Q \simeq f(u_x, v_y) = V_i(t), (i=1, 2, \dots, 8) \quad 2),$$

$$V_i(t) = \sqrt{\left(\frac{dx}{dt}\right)^2 + \left(\frac{dy}{dt}\right)^2} \quad 3),$$

because any accurate measurement of θ and w_z was not carried.

Let $Y(t_0+t)$ be the distance traveled by an individual with starting time t_0 during the time interval t , which is changed by a characteristic movement. The variance of Y is obtained as follows^{4,5)},

$$\bar{Y}^2(t) = 2 \int_0^t \int_0^{t'} V(t_0+t') V(t_0+t'') dt' dt'' \quad 4).$$

Set $t'' - t' = \tau$, then

$$\bar{Y}^2(t) = 2V'^2 \int_0^t (t-\tau) R_L(\tau) d\tau \quad 5),$$

and right-hand side of 5) becomes

$$\int_0^t (t-\tau) R_L(\tau) d\tau = t \int_0^{t^*} R_L(\tau) d\tau - \int_0^{t^*} \tau R_L(\tau) d\tau \quad 6),$$

where $R_L(\tau)$ is Lagrangian auto-correlation coefficient, τ is lag time of movement, V' is the variance of swimming speed and t^* is the time for which $R_L(t^*) \simeq 0$. For $t \gg t^*$ the second term on the right-hand side of eq. 6) will become very small with respect to the first term, so it may be neglected. For the constant value of integrated time it can be written,

$$T^* = \int_0^{t^*} R_L(\tau) d\tau \quad 7).$$

We define T^* is a measure of the longest time during which an individual persists in a motion (Lagrangian integral time scale).

1-ii. Response time lag among the individuals.

Some mathematical simulations to estimate the change of fish school had been carried out and the result showed that the individuals maintained schooling form as long as the intensities of mutual and random forces were balanced⁶⁾. The mutual force that

control their separation distances will be brought as the responses of visual and lateral line sensation, the latter sense is said to recognize the variation of water particle deviation or pressure.

The information received through such methods will contain some time lag in the course of communication, and for the recognition of the time lag it is necessary to calculate the cross-correlation function. The random component of movement will be contained in their swimming motion, then the coherency between their swimming speeds must be considered. If the coherency is 1.0, the behaviors of two individuals are very similar and in this case, we can observe the synchronized changes of motion in the individuals. On the other hand, when the coherency becomes 0.0, it means the individuals have no interest to each other in swimming. And also when the number of data is too small amount to consider the cross-correlation function, the coherency may be shown as very low value.

2. Results and Discussions.

2-i. Continuity of swimming speed and time lag of response.

In the previous paper, we reported that the schooling form did not disperse but repeated longitudinal shape and circular one, and the maximum period of the repeating

Fig. 1. Trajectories of "Tamoroko" in the experimental tank taken from the arbitrary parts in motion picture series. The number beside circles denotes the processes of movement in each particular frames.

was 12.5 seconds (8×10^{-2} Hz)¹⁾. This fact means that each individuals would have been able to near together once for twelve seconds, in other wards, one schooling form maintain during 10 seconds or so. Fig. 1 is an example of trajetries taken for an arbitrary time

Fig. 2. Auto-correlation coefficient of swimming speed and number means members in a school.

Table 1. Integral time scale of auto-correlation

No. of individual	$\int_0^{t^*} R(\tau) d\tau$ (sec)
1	0.9
2	1.4
3	1.8
4	1.4
5	2.5
6	2.0
7	1.5
8	2.5

intervals, the numbered courses of actions show the processes from following to separation of two individuals. The back side individual began to follow to the prior one for 10

seconds (from 11-th frame) when their separation distance had become shortest in the group, then after 10 seconds the pair separated again. The behavior of changing their nearest neighbor was occurred commonly in the experimental tank and the longest time length to follow the other was about ten seconds.

Auto-correlation coefficient and integral time scale of each individuals are shown in Fig. 2 and Table 1. The time length, T^* were distributed between 0.9 to 2.5 seconds and the average value was 2.0 seconds respectively. The individual would have lost its statistical correlation of swimming speeds in a few seconds. The integral time scale of auto-correlation coefficient seemed to be nearly equal to the time length during which the individuals had been maintained the polarized schooling form. From the results of observation, we found that usually they did not swim along a corner to corner in the water tank but randomly changed their directions, and the time to keep polarized one was about several seconds.

Fig. 3. Cross-correlation function of two swimming speeds. Number means each combination of two individuals. The abscissa is time lag (sec) and the ordinate is rate of correlation ($\text{cm}^2 \cdot \text{sec}^{-2}$).

The individuals who sometimes put in the front position of the school, applicable to "feeler" were shown large value of T^* , such as NOs. 5, 6 and 8. Also these individuals moved widely in the water tank (Fig. 5). But the equal chance to occupy the forefront

position of the school was not given in these experimental duration.

Lag times of response (ξ) are in Fig. 3 and Table 2, and coherency is shown in Fig. 4. The shortest time lag of several pairs indicated 0.5 seconds response, which was coincide with the latent period of behavior. The other pairs were shown between 2.5 to 5.0 seconds

Table 2. Characteristic time lag obtained from cross-correlation function

No. of individual former follower		lag time (ξ) (sec)
6	1	0.5
8	2	0.5
5	3	0.5
6	3	4.0
8	3	0.5
6	5	2.5
7	5	2.5
8	5	0.5
7	6	2.5
7	1	4.0
2	5	5.0

responses. But these facts did not always mean that an individual was aware of the other specific one with following acts of lag time 2.5 to 5.0 seconds. For discussion of this phenomenon, it is necessary to measure of behavior in more longer time than these experimental series, since the coherency of each pairs were not so high values, in which the existence of considerable random noise were suggested (Fig. 4).

These cross-correlation function were only calculated every two individuals in combination of the members (${}_8C_2$), but it is necessary to consider about moreover the effects of complexed behavior or interactions between one individual and the other member of plural numbers.

2-ii. Measurement of spatial limitation effected on the behavior.

We reported that the mutual force to balance with the separation distance between two individuals would have to change by the effect of the size limitation in water tank⁷⁾. For the purpose to discuss the behavior in water tank, it is necessary to show the spatial distribution of each individuals during the experiment. Fig. 5 is joint probability density distribution, in which the spatial distribution of behavior is shown neglecting the time function.

The joint probability $S(j, k)$ existed in unit area A is shown,

$$S(j, k) = \frac{m(j, k)}{M \cdot A} \quad (j, k = 1, 2, \dots, 30) \quad 9),$$

where M is total data number of series, $m(j, k)$ is number of members of the series that fall into j -, k -range, A is unit area and given as follows,

Fig. 4. Coherency, which is defined, $r^2(f) = [A(n)]^2 \{P_1(n)/P_{1+1}(n)\}$. ($A(n)$: frequency response function; $P_1(n)$, $P_{1+1}(n)$: auto-power spectra of i -th and $(i+1)$ -th individuals' swimming speeds). The abscisa is time lag (sec).

$$A = \Delta h_x \times \Delta h_y \quad (10),$$

and

$$\Delta h_{x,y} = \frac{\delta_{\max} - \delta_{\min}}{K} \quad (11),$$

where x, y are lengths measured longitudinal (x) direction and latitudinal (y) one respectively from the origin put on the water tank¹⁾, $\delta_{\max}$ and $\delta_{\min}$ are the positive and negative maxima of variances from average, K is total number of division and we chose $K=30$.

When an individual moves widely around the water tank with the uniform speed, the unit area A becomes large and the value of $S(j, k)$ is uniformly distributed, on the other hand, when the individual stay in narrow area for long time, A becomes very small and

$S(j, k)$ concentrates into a partial. In these experiments, the individuals were seemed to move in the central part of water tank and sometimes swam along the side wall.

If the change of swimming speed in a school would have been quite synchronized during five minutes, it would be very polarized school, in other words, the whole joint probability distribution patterns would have become the same; but there were some differences among them. For instance, the individual named NO. 1 did not move widely but swam in the narrow area, NOs. 2 and 6 individuals, on the other hand, moved widely and passed many times the upper and central parts of water tank. The difference of the patterns show that the schooling form was not so synchronized and polarized, which will give us some suggestions concerning to the characteristic appearance of fresh water fish school. But the recording time length is too short to make sure these facts, since the activity difference of individuals caused by the periodical nature of bio-rhythms are sometimes observed, and it has longer period than our experimental series. Recording of these behavior for the longer time will make sure whether these partialities are occurred usually or not.

Although these experimental series has many limitations both of recording time and observation tank, we believe that some analysing methods to describe quantitative informations on the schooling behavior could be obtained about a kind of fresh water fish *Gnathopogon elongatus elongatus* (tamoroko). But it is necessary to continue furthermore

Fig. 5. Joint-probability density distribution of each individuals. One part of cross-sectioned area shows unit A.

●: $> 10^3$, ⊗: $10^3-5 \times 10^2$, ⊙: $5 \times 10^2-3 \times 10^2$, //: $3 \times 10^2-10^2$,
 0: $< 10^2$ (per 10^6 times).

these analyses and to compare quantitative difference of movement between fresh water fish school and ones of marine fish. For succession of these works, more additional new methods are needed to measure fish movement, such as bio-telemetry system and marine acoustic measurement.

References

- 1) T. INAGAKI, W. SAKAMOTO, I. AOKI, and T. KUROKI: This bull. **42**, 629-635 (1976).
- 2) L. BRILLOUIN: in "Science and information theory. (translated in Japanese by H. SATO)", Misuzu Shobo., 11-26 (1969).
- 3) H. DINGLE: in "Behavior of marine animals". **1**, Plenum press., 126-156 (1972).
- 4) J. O. HINZE: in "Turbulence (2nd edition)", McGraw-Hill Inc., 48-58 (1975).
- 5) A. OKUBO: *Tech. Rep.*, **78**, Johns Hopkins Univ., 1-33 (1972).
- 6) T. INAGAKI, W. SAKAMOTO, and T. KUROKI: This bull., **42**, 265-270 (1976).
- 7) W. SAKAMOTO, I. AOKI, and T. KUROKI: *ibid.*, **41**, 945-952 (1975).