Studies on the Schooling Behavior of Fish—V. Note on the Dynamics of Fish Schooling^{*1}

Akira OKUBO^{*2}, Wataru SAKAMOTO^{*3}, Tadashi INAGAKI^{*4},
and Toshiro KUROKI^{*5}

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A dynamical model for fish schooling is presented. The basic equation of motion of individual fish contains mutual attraction or repulsion of fish around its equilibrium position, frictional force due to locomotion, and the swimming force. The concept of an average time lag ("latency") is introduced to the swimming force. As a result, the speed of school and the dimension of school obey the same dynamical equation correct to the first order of the time lag, and accordingly the corresponding frequency spectra behave in the same manner. The theoretical spectrum shows a minus four power law at large values of frequency. The cross-correlation between the change of the school form and the school speed has a time lag about one second on the positive side from the origin. These theoretical results compare favorably with the experimental results obtained in the previous studies.

SAKAMOTO, AOKI and KUROKI¹⁾, INAGAKI, SAKAMOTO and KUROKI²⁾, INAGAKI, SAKAMOTO, AOKI and KUROKI³⁾, and SAKAMOTO, INAGAKI and KUROKI⁴⁾ (1976) have recently made a series of studies on the schooling behavior of fish, in which interaction between individual fish, relationship between speed and form variations in schooling behavior, continuity of swimming speed, and response time of individuals are precisely analysed. We believe that a serious look at modeling for the dynamics of fish schooling is now warranted so that the model may be used to interpret some of the measurements of detailed movements of schooling fish.

Dynamical Model for Schooling Fish

Dynamical equations for centroid movement and separation distance of fish schools.

For simplicity we take a two-fish school; the following treatment may well be extended to a many-fish school. First consider the dynamics of schooling in one direction, say x -axis (Fig. 1).

^{*1} Contribution No. 201 from Marine Sciences Research Center, State University of New York at Stony Brook.

^{*2} Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794, USA (大久保 明: ニューヨーク州立大学).

^{*3} Department of Fisheries, Kyoto University, Sakyo-ku, Kyoto 606, Japan (坂本 直: 京都大学水産学教室; 京都市左京区北白川追分町).

^{*4} Ocean Research Institute, University of Tokyo, Nakanoku Tokyo, 164, Japan (稲垣 正: 東京大学海洋研究所; 東京都中野区南台 1-15-1).

^{*5} Department of Ocean Environmental Engineering, Tokyo University of Fisheries, Minatoku Tokyo, 108, Japan (黒木敏郎: 東京水産大学; 東京都港区港南 4-5-7).

Let $x_1(t)$ and $x_2(t)$ be the positions of a pair of fish at time t , x_2 -fish being ahead of x_1 -fish, and also $x_1^*(t)$ and $x_2^*(t)$ be the positions of the two fish at time t when they swim together in a state of "equilibrium," i.e. the attractive and repulsive forces balance with each other (PARR⁵⁾, BREDER⁶⁾), and the "equilibrium swimming force" of fish balances to the frictional force due to locomotion.

Fig. 1. Coordinate system for two-fish schooling.

As the resultant force vanishes at the equilibrium, a pair of fish will move with a constant velocity U_0 (which might be zero) if the fish maintain the equilibrium position. We thus take a new coordinate system moving with the velocity U_0 so that x_1^* and x_2^* may be fixed to the system. With respect to this new coordinate define the following quantities:

- $x_c(t) \equiv (x_1(t) + x_2(t))/2$: centroid
- $V(t) \equiv dx_c/dt$: centroid velocity
- $x'_1(t) \equiv x_1(t) - x_1^*$: deviation of the position of x_1 -fish from its equilibrium position
- $x'_2(t) \equiv x_2(t) - x_2^*$: deviation of the position of x_2 -fish from its equilibrium position
- $r(t) \equiv x'_2(t) - x'_1(t)$: relative separation between two fish

In practice the "leadership" may change during the time of observation. Thus x_1 -fish may become ahead of x_2 -fish. However, our treatment followed can cover all the cases if we regard x_2 -fish as a momentary leader and x_1 -fish as a momentary follower.

The centroid velocity can be expressed in terms of the deviations of the position

$$\begin{aligned} V(t) &= \frac{1}{2} \frac{d}{dt} (x_2(t) + x_1(t)) = \frac{1}{2} \frac{d}{dt} (x'_1(t) + x_1^* + x'_2(t) + x_2^*) \\ &= \frac{1}{2} \frac{d}{dt} (x'_1(t) + x'_2(t)) \end{aligned} \quad (1).$$

We now apply Newton's second law of motion to the movement of individual fish. According to INAGAKI, SAKAMOTO and KUROKI (1976),

$$m \frac{d^2 x'}{dt^2} = F = F_1 + F_2 + F_3 + F_4 + F_6 \quad (2).$$

Where m is the mass of individual fish, x' is the displacement from the equilibrium posi-

tion, F is the total force which consists of the common swimming force, F_1 , random part of swimming force, F_2 , mutual attraction or repulsion around the equilibrium position, F_3 , external force due to the change of environmental conditions, F_4 , and the frictional force (drag), F_5 .

We further assume that the mass of individuals is constant ($m=m_0$), $F_4=0$, and the frictional force is proportional to the velocity (OKUBO⁷⁾). The common swimming force and random force are related to some extent (see INAGAKI, SAKAMOTO, AOKI and KUROKI, 1976; hereinafter referred to as Paper III), and hence the sum $F_s=F_1+F_2$ can adequately be defined as "swimming force." Note that F_s no longer includes the equilibrium swimming force. The mutual attractive or repulsive force can be approximated by a type of harmonic oscillation, i.e. proportional to the displacement vector (Paper III).

The equations of motion for a pair of fish are thus expressed as follows:

$$\frac{d^2x_1'}{dt^2} = -k \frac{dx_1'}{dt} - \omega^2 x_1' + A_1(t) \quad (3),$$

$$\frac{d^2x_2'}{dt^2} = -k \frac{dx_2'}{dt} - \omega^2 x_2' + A_2(t) \quad (4),$$

where k is the coefficient of friction (T^{-1}), ω is the frequency (T^{-1}), and A_1 and A_2 are respectively the swimming forces per unit mass of x_1 -fish and x_2 -fish (LT^{-2}).

Adding (3) to (4), differentiating the sum with respect to time and making use of (1), we obtain

$$\frac{d^2}{dt^2} V = -k \frac{d}{dt} V - \omega^2 V + \frac{1}{2} \frac{d}{dt} (A_1 + A_2) \quad (5).$$

Subtracting (3) from (4), we obtain

$$\frac{d^2}{dt^2} r = -k \frac{d}{dt} r - \omega^2 r + (A_2 - A_1) \quad (6).$$

To proceed further, the swimming force needs specification. In our model for schooling, x_1 -fish follows x_2 -fish; thus as x_2 -fish accelerates, x_1 -fish responds to the leader with a small but finite amount of time lag, ϵ say. According to HUNTER⁸⁾, the average time lag ("latency") for two-fish experiments with jack mackerel was 0.17 sec.

We now express the swimming forces for two fish as

$$A_2(t) = A_1(t + \epsilon) \equiv A(t + \epsilon), \quad \epsilon > 0 \quad (7).$$

SAKAMOTO *et al.*¹⁾ classifies the response or reaction into two types: linear and non-linear. The linear response means that the fish responds directly to the other's movement, and the nonlinear response means that one individual receives the effect of the other's reaction and in turn, affects the movement of the other, i.e. mutual interference. In our model we assume that the response is primarily linear. By the use of (7), eqs. (5) and (6) are rewritten as

$$\frac{d^2}{dt^2}V + k \frac{d}{dt}V + \omega^2 V = \frac{1}{2} \frac{d}{dt} (A(t+\epsilon) + A(t)) \quad (8),$$

$$\frac{d^2}{dt^2}r + k \frac{d}{dt}r + \omega^2 r = A(t+\epsilon) - A(t) \quad (9).$$

Smallness of ϵ permits us to expand $A(t+\epsilon)$ into a Taylor series of ϵ . As a result, eqs. (8) and (9) can be expressed as

$$\frac{d^2}{dt^2}V + k \frac{d}{dt}V + \omega^2 V = \dot{A}(t) + \frac{1}{2}\epsilon \ddot{A}(t) + \frac{1}{4}\epsilon^2 \ddot{\ddot{A}}(t) + \dots \quad (10),$$

$$\frac{d^2}{dt^2}(r/\epsilon) + k \frac{d}{dt}(r/\epsilon) + \omega^2(r/\epsilon) = \dot{A}(t) + \frac{1}{2}\epsilon \ddot{A}(t) + \frac{1}{6}\epsilon^2 \ddot{\ddot{A}}(t) + \dots \quad (11),$$

where $\dot{A}(t) \equiv \frac{d}{dt}A$, etc.

Hence V and r/ϵ obey the same dynamical equation correct to the first order of ϵ . It is thus shown that to the first order the time behavior of V will be identical to that of r if both start with the same initial conditions. In this context HUNTER⁹⁾ speculated that the distance between fish should be influenced by swimming speed.

Relation between r and H (rate of form variation). Let us take x -axis momentarily in the direction of the movement of school and y -axis momentarily in a horizontal direction perpendicular to x . Note that in Paper III we chose y -axis in the direction of the school movement and x -axis perpendicular to y .

Our experimental data suggest that when a fish school moves in equilibrium, the mean separation in x -direction, $a \equiv x_2^* - x_1^*$, is somewhat larger than that of y -direction, i.e. $|y_2^* - y_1^*| = pa$ ($0 < p < 1$). Also a relative separation r in x -direction may be associated with the corresponding separation $-qr$ ($0 < q < 1$) in y -direction. The precise mechanism for this behavior remains unknown. We suspect that hydromechanics of fish schooling might have something to do with it (WEIHS¹⁰⁾, BREDER¹¹⁾). It is unimportant for the present discussion, however.

According to Paper III, the school form is defined by the rate of form variation, $H(t)$, which can be expressed as follows:

$$H(t) = 100 \times \frac{a+r}{a+r+(pa-qr)} = \frac{100}{1+p} \left(1 + \frac{r}{a}\right) \left(1 + \frac{1-q}{1+p} \frac{r}{a}\right)^{-1} \quad (12).$$

Under the experimental conditions we may assume

$$|r|/a \ll 1 \quad (13).$$

So that (12) can be approximated to the first order of r/a by

$$H(t) = \frac{100}{1+p} \left\{1 + \frac{p+q}{1+p} \frac{r}{a}\right\} \quad (14).$$

For a long time average the variation r vanishes, $\langle r \rangle = 0$, so that

$$\langle H \rangle = \frac{100}{1+p} \quad (15).$$

Since $0 < p < 1$, $\langle H \rangle$ lies between 50 and 100 (see Fig. 4, Paper III). The fluctuation of H is given by

$$H'(t) = H(t) - \langle H \rangle = 100 \frac{p+q}{(1+p)^2} (r/a) \quad (16).$$

Also note that $\langle V \rangle = 0$ since the coordinate system is fixed to the system moving with the velocity U_0 . Hence the fluctuations of V and H obey the same dynamical law correct to the first order of ε and r/a .

Spectra for the fluctuations of V and H . We consider a stationary random function $z(t)$ of time t which satisfies the differential equation

$$\frac{d^2 z}{dt^2} + k \frac{dz}{dt} + \omega^2 z = B(t) \quad (17),$$

where $B(t)$ is a stationary random forcing function.

The stationary random functions $z(t)$ and $B(t)$ can be expressed in the form of a random Fourier-Stieltjes integral with random complex amplitudes, i.e. Fourier-Stieltjes modes (BATCHELOR¹²), TATARSKI¹³):

$$z(t) = \int e^{ift} d\Gamma(f), \quad B(t) = \int e^{ift} d\Lambda(f) \quad (18),$$

where f is a radian frequency variable (T^{-1}). That stationarity requires that the random amplitudes must satisfy the relations

$$\overline{d\Gamma(f) d\Gamma^*(f')} = \delta(f-f') \Phi(f) df df' \quad (19),$$

$$\overline{d\Lambda(f) d\Lambda^*(f')} = \delta(f-f') \Psi(f) df df' \quad (20),$$

where $*$ indicates a complex conjugate, $\delta(f-f')$ is a Dirac function, and $\Phi(f) \geq 0$, $\Psi(f) \geq 0$ are the spectral density functions of $z(t)$ and $B(t)$, respectively (TATARSKI¹³).

Substituting (18) into (17), we find

$$(-f^2 + ikf + \omega^2) d\Gamma(f) = d\Lambda(f)$$

or

$$d\Gamma(f) = d\Lambda(f) / (-f^2 + ikf + \omega^2) \quad (21).$$

From (19), (20) and (21) it is obtained

$$\Phi(f) = \Psi(f) / \{(f^2 - \omega^2)^2 + k^2 f^2\} \quad (22).$$

We shall apply the above result to the dynamical equations for the fluctuations of V and H by regarding V , H as z and $\dot{A}$ as B . Let $\Psi_1(f)$, $\Psi_2(f)$, $\Omega(f)$ be respectively the (normalized) spectral density functions of V , H and $\dot{A}$. We thus have

$$\Psi_1(f) = \Psi_2(f) = \Omega(f) / \{(f^2 - \omega^2)^2 + k^2 f^2\} \quad (23).$$

Concerning $\dot{A}$ ("jerk"), we will make an *ad-hoc* assumption that $\dot{A}$, not A , varies extremely rapidly compared with the variations of V and H , i.e. $\dot{A}$ is a Dirac function of time. Alternately we may say that $\Omega(f)$ has a white noise

$$\Omega(f) = \lambda^2 \text{ (constant)} \quad (24).$$

Hence

$$\Psi_1(f) = \Psi_2(f) = \lambda^2 / \{(f^2 - \omega^2)^2 + k^2 f^2\} \quad (25).$$

For small values of f , (25) tends to

$$\Psi_1(f) = \Psi_2(f) \sim \lambda^2 / \omega^4 \text{ (constant)} \quad (26),$$

while for large values of f , (25) tends to

$$\Psi_1(f) = \Psi_2(f) \sim \lambda^2 / f^4 \quad (27),$$

which demonstrates a *minus four relation to the frequency*.

Note that the frictional force plays no role in the limiting behaviors of the frequency spectrum. However, the shape of the spectrum at intermediate frequencies is determined

Fig. 2. Theoretical frequency spectra of $V(t)$ and $H(t)$ for various values of q .

by the ratio of k and ω . Fig. 2 shows the frequency spectrum for various values of k/ω . The peak of the curve for $k/\omega = 0$ at $f = \omega$ corresponds to the resonance of fish schooling without friction. The frictional force tends to suppress the occurrence of resonance. Thus, for $k/\omega \geq \sqrt{2}$ the peak disappears.

Power spectra of V and H show in Fig. 5 in Paper III agree fairly well to the theoretical spectrum with the value of k/ω in a range of $1 \sim 2$, and with $f/\omega = 2\pi n/\omega$ (n ; frequency) $= 5$ corresponding to $n = 1$ Hz. This gives $\omega = 1.26/\text{sec}$ or $2\pi\omega^{-1} \approx 5$ sec, and $k \approx 1.3 \sim 2.5/\text{sec}$. The minus four power relation was also observed in the frequency spectrum of fluctuation of separation distances between two individuals of fish in another experiment (see Fig. 7 in SAKAMOTO *et al.*¹¹⁾).

The above analysis for the spectrum is based on the dynamical equations that omit the terms of the order of ε or higher. Since ε is the order of 0.1 sec, the inclusion of the terms omitted would not change the spectral behavior in a range of frequency $f = 10$ Hz or smaller.

Cross-correlation function between H and V . Although the fluctuations of V and H

obey the same dynamical law correct to the first order of latency, their behavior differs to the high order. In fact the experiment shows a time lag between the fluctuations of H and V (Paper III), and the cross-correlation coefficient between $H(t)$ and $V(t+\tau)$ has a primary peak at $\tau=0.75$ sec, though this value may not be very accurate.

We can calculate the cross-correlation function or coefficient on the basis of eqs. (10) and (11), remembering (11) is equally applicable to H . To this end, use is made for

$$A(t)=2\pi\lambda\delta(t) \quad (28),$$

with $\delta(t)$ being a Dirac function.

The cross-correlation function between H and V depends only on the time difference, τ , and is expressed by

$$\overline{H(t)V^*(t+\tau)}=\overline{R(\tau)}=\int e^{ift}S(f)df \quad (29),$$

where $S(f)$ denotes the cross-spectral density function.

By Fourier-Stieljes transformation of (10) for V and of (11) for H , we can solve for $d\tilde{V}(f)$ and $d\tilde{H}(f)$. It results

$$d\tilde{V}(f)=2\pi\lambda(1+i\varepsilon f/2-\varepsilon^2 f^2/4)df/(-f^2+ikf+\omega^2) \quad (30),$$

$$d\tilde{H}(f)=2\pi\lambda(1+i\varepsilon f/2-\varepsilon^2 f^2/6)df/(-f^2+ikf+\omega^2) \quad (31),$$

where

$$V(t)=\int e^{ift}d\tilde{V}(f) \quad (32),$$

$$H(t)=\int e^{ift}d\tilde{H}(f) \quad (33).$$

Since

$$S(f)=\overline{d\tilde{H}(f)d\tilde{V}^*(f)},$$

we obtain

$$S(f)=\frac{4\pi^2\lambda^2\{(1-\varepsilon^2 f^2/4)(1-\varepsilon^2 f^2/6)+\varepsilon^2 f^2/4-i\varepsilon^3 f^3/24\}}{(f^2-\omega^2)^2+k^2 f^2} \quad (34).$$

Substituting (34) into (29) and calculating the Fourier integral, we finally find

$$R(\tau)=4\pi^2\lambda^2(\alpha^2+\beta^2)^{1/2}e^{-1/2k\tau}\cos(\omega'\tau-\gamma), \quad \tau \geq 0 \quad (35),$$

where

$$\omega'^2=\omega^2-k^2/4 \geq 0$$

$$\alpha=1/k\omega^2-\varepsilon^2/6k-\varepsilon^3/24+\varepsilon^4(\omega^2-k^2)/24k$$

$$\beta=1/4\omega'\omega^2+\varepsilon^2/12\omega'+\omega\varepsilon^3/48\omega'+\varepsilon^4(k^2-12\omega'^2)/192\omega'$$

$$\gamma=\sin^{-1}\{\beta/(\alpha^2+\beta^2)^{1/2}\}.$$

The time lag τ_1 of $V(t)$ against the variation of $H(t)$ can be calculated from (35) as

$$\omega' \tau_1 = \gamma$$

or

$$\tau_1 = \gamma / \omega' \quad (36).$$

For three choices of $k=1.26, 2.0$ and $2.5/\text{sec}$ together with $\omega=1.26/\text{sec}$, and $\epsilon=0.2 \text{ sec}$, τ_1 takes respectively the values of $0.26, 0.75$, and 8.25 sec . The second choice, i.e. $k=2.0/\text{sec}$ yields the time lag which is exactly equal to the observed one (see Fig. 7 in Paper III).

We thus conclude that a best choice of the values of the parameters used in our dynamical model is given by

$$\omega = 1.26/\text{sec}$$

$$k = 2.0/\text{sec}$$

$$\epsilon = 0.2 \text{ sec}.$$

The frictional coefficient k may be evaluated independently by equating $k|\bar{V}|$ to the quadratic friction drag, $C_D/2\rho A|\bar{V}|^2/m$ with C_D, ρ, A, m being respectively the drag coefficient, density of water, area of the projection of the body, and the virtual mass of the fish in water (BATCHELOR¹⁴), OKUBO¹⁷). A numerical choice that $C_D/2 \approx 1$, $\rho A/m \approx (2L)^{-1} = (2 \times 7.5)^{-1}/\text{cm}$ (see Paper III for fish's body length, L), $|\bar{V}| \approx 20 \text{ cm/sec}$, gives $k \approx 1.3/\text{sec}$. As this evaluation should be considered valid only for an order of magnitude, the agreement between the two values of k is satisfactory.

Discussion

Our mathematical model is proven to be very adequate for describing the dynamics of fish schooling. Nevertheless, there is still some room left for the improvement of the model.

The drag of a swimming fish should be a quadratic function of its velocity relative to water flow rather than a linear function assumed in the model. Similarly the harmonic restoring force may be replaced by an anharmonic force. However, this refinement would not create a drastic change in the result but invite a severe difficulty in mathematical analysis.

Above all our model inclines to the physical aspect of fish schooling; the biological interpretation of the introduced parameters is left for future investigation.

It might be important to point out that the presented model is essentially the same as applied to insect swarming (OKUBO¹⁵). The only difference appears in the forcing function, $A(t)$; the deterministic element often dominates in fish schooling (SAKAMOTO *et al.*¹¹) while the random element dominates in insect swarming (OKUBO and CHIANG¹⁶).

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