

Analysis of Fish Movements Using a Newton Rules Model: Possible Advantages of Schooling to Migration and Foraging

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力学モデルによる魚の行動解析：回遊および索餌に対する群れ形成の適応性
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Abstract

Pelagic fish commonly cruise as a school. A kinematic theory is presented to analyze erratic movements made by pelagic fish on the basis of a Newton rules model for fish schooling: individual fish are regarded as gas molecules with locomotion, inbuilt response to each other, and fluctuation of motion. This approach enables quantitative studies and development of predictive models of requirements and capabilities for oriented movements in homing migration and foraging in a stochastic environment in relation to individual behavior. Furthermore it offers possible explanations for adaptive advantages of schooling behavior, including error reduction in navigation and optimal food intake in the patchy environment. In this framework, the theory gives methods to predict ecological properties of fish schooling behavior from a knowledge of individual properties, e.g. variability in school size under food conditions, and also estimate numerical quantities quantifying individual behavior from ecological-scale data of fish school movements, e.g. orienting ability to external stimuli.

1. Introduction

The survival and reproduction rate of pelagic schooling fish, especially migrating species, will depend on their success at locating food resources (e.g. prey patches) and spawning site (e.g. natal stream for salmon). This success is determined largely by the manner in which individual fish search for their necessary items. Thus the need to quantify their search paths arises.

Pelagic fish commonly show schooling behavior. Various explanations for fish schooling have been put forward, including escape from predation (Brock & Riffenburgh, 1960; Clark, 1974; Pitcher, 1980; Partridge, 1982), energy saving (Weihs, 1973a), and facilitation of finding food in patchy environments (Pitcher, Magurran & Winfield, 1982). It is thought that schooling also confers advantages on fish in increasing efficiency orienting towards specific goal and foraging. Larkin & Walton (1969) have suggested that fish movements as a school may regulate their migratory paths, and estimated reducing error in navigation. Duffy & Wissel (1988) presented a theory which allows insights into the relation between environmental food supplies and school size.

Fish's search paths have a random pattern, so that it can be extremely difficult to quantify movement paths. A first step in such examinations of these advantages is the design of a quantitative description of fish movements when in school. Several authors have used the two-dimensional correlated random walk model to represent animals' movements with tendency to go forward (Kareiva & Shigesada, 1983; Bovet & Benhamou, 1988). These models quantify the movement path by means of only two simple parameters: move lengths and turning angles between successive moves. But to apply this approach to observations of animals' movements in the field, we need reasonable and consistent criteria for demarcating the end points of moves. Furthermore the formation of such models necessitates a better grasp of the natural occurrence of movements of animal individuals and groups. Therefore the need to mathematically formulate the mechanism of animal locomotion arises.

Here I introduce the Newton rules equation describing schooling of fish (Niwa, 1991, 1992, 1993). On the basis of this kinematic model I establish the statistical properties of the fish movement paths, considering schools as entities. In particular, I derive a formula for expected net squared displacement for the movement path. Thus we consider the evolutionary advantages of schooling on the migration and the foraging by examining that schooling reduces error in navigation of migratory fish towards a goal and improves the foraging efficiency for patchy food resources.

2. Newton Rules Model for Fish Schooling

The fish schools usually consist of individuals of the same size range (Inoue, 1970), and the same properties (with similar swimming speeds, as these depend on body length (Wu, 1977)). Schooling fish perform a well organized collective motion by some kind of mutual interaction. The individual motion appears to be deterministic in a statistical sense (Okubo, 1980). Now fish schooling can be modeled with the framework of Newtonian mechanics, and fish locomotion is described by Newton's law of motion: Mass \times acceleration = force. After dividing it by body mass the vector equation reads

$$\frac{dv_i}{dt} = \kappa(1 - \beta v_i^2)v_i + \sum_{j=1}^N f_{ij}^{(g)} + \sum_{j=1}^N f_{ij}^{(p)} + \eta_i(t), \quad (1)$$

where the fish school consists of N bodies, and v_i is the swimming velocity for the i th body in the school. The exerted forces on the fish body may be of physical, physiological, behavioral and ecological origin. Fish are regarded similarly as gas molecules with locomotion, and interacting with each other. Since swimming performance is unavoidably uncertain, it is assumed that the exerted force can be decomposed into a deterministic part and a stochastic part.

The first term of right-hand side of eq.(1) is locomotive force. A fish can swim forward by pushing its environmental water backward; the surrounding in turn reacts to provide thrust to the fish. Performance depends on the balance between thrust and hydromechanical drag. When an individual is moving in steady swimming, its speed is given by $\beta^{-1/2}$ at which the specific energy cost for cruising is a minimum (Weihs, 1973b; Wu, 1977). A parameter κ^{-1} is regarded as sensitivity of an individual behavior to surrounding fish or environmental.

The second term is attraction from other bodies analogous to intermolecular forces like a Lennard-Jones form (Breder, 1954). For aggregate fish the internal force is attractive except that it is repulsive in the very vicinity of bodies.

The third term is arrayal interaction. Two neighboring fish tend to swim parallel with each other and to equalize their velocities. Since each individual effectively interacts with the average velocity of the entire school (Partridge, 1980), the arrayal force is supposed to be expressed as

$$\sum_{j=1}^N f_{ij}^{(p)} = \frac{J}{N} \sum_{j=1}^N (v_j - v_i), \quad (2)$$

where J is the coefficient of arrayal interaction.

The last term is fluctuating force. It will of course have a certain influence on the movement of fish school. Thus we consider the system coupled to an environment as a noise source. We assume that the correlation time of the fluctuating force is very short on the typical macroscopic time scale of the equation of motion ($\approx \kappa^{-1}$), and the fluctuating forces acting on each body are independent of each other. This allows us to pass to the idealization of Gaussian white noise. So we have δ -correlated fluctuating force

$$\langle \eta_i(t) \rangle = 0, \quad \langle \eta_i(t) \eta_j^T(t') \rangle = 2\epsilon \delta_{ij} \delta(t - t') I, \quad (3)$$

where ϵ denotes the strength of the fluctuating force, and the bracket $\langle \dots \rangle$ the ensemble average.

In order to investigate collective properties of the system described by the nonlinear stochastic equation (1), by averaging over all individuals in the school, eq.(1) can be considerably simplified. Considering fish swimming in two-dimensional space, we then have the equation for the centroid velocity of the school, $\mathbf{V} = \frac{1}{N} \sum_{i=1}^N \mathbf{v}_i$, as the stochastic dynamical equation:

$$\frac{d\mathbf{V}}{dt} = \kappa \left(1 - 4 \frac{\beta\epsilon}{J} \right) \mathbf{V} - \kappa\beta \mathbf{V}^2 \mathbf{V} + \bar{\boldsymbol{\eta}}(t), \quad (4)$$

where stochastic force $\bar{\boldsymbol{\eta}}(t) = \frac{1}{N} \sum_{i=1}^N \boldsymbol{\eta}_i(t)$ satisfies the following relation:

$$\langle \bar{\boldsymbol{\eta}}(t) \bar{\boldsymbol{\eta}}^T(t') \rangle = \frac{2\epsilon}{N} \delta(t - t') \mathbf{I}. \quad (5)$$

Then we can derive the following general formula associated with the fish school movement. For the most probable value of moving speed as a whole, we have

$$|\mathbf{V}_m| = \sqrt{\frac{1}{\beta} \left(1 - 4 \frac{\beta\epsilon}{J} \right)}. \quad (6)$$

By using eq.(4) we can write down the equation for the mean square velocity

$$\frac{d}{dt} \langle \mathbf{V}^2(t) \rangle = 2\kappa \left(1 - 4 \frac{\beta\epsilon}{J} \right) \langle \mathbf{V}^2(t) \rangle - 2\kappa\beta \langle \mathbf{V}^2(t) \rangle^2 + \frac{4\epsilon}{N}, \quad (7)$$

then we have the stationary solution

$$\langle \mathbf{V}^2 \rangle_{st} = \frac{1}{\beta} \left(1 - 4 \frac{\beta\epsilon}{J} \right) + \frac{2\epsilon/N}{\kappa(1 - 4\beta\epsilon/J)}. \quad (8)$$

For the two-time correlation coefficient, we have

$$c_{|t-t'|} = \frac{\langle \mathbf{V}(t) \cdot \mathbf{V}(t') \rangle}{\langle \mathbf{V}^2 \rangle_{st}} = \exp \left(- \frac{2\epsilon/N}{\langle \mathbf{V}^2 \rangle_{st}} |t - t'| \right) \quad (9)$$

(see Appendix I). The fish school has a tendency to continue moving in the same direction to a certain degree. A measure of the degree of continue moving in the same direction is provided by the correlation time relating eq.(9):

$$\tau = \frac{\langle \mathbf{V}^2 \rangle_{st}}{2\epsilon/N}. \quad (10)$$

In other words, τ gives an average time interval of changing direction of moving school.

Fish schools typically traverse circuitous routs. Using the formulae above, we now develop the relationship between a fish school's movement behavior and its expected square displacement. Let us imagine that a school released from the point \mathbf{r}_0 at $t = 0$ reaches the point \mathbf{r}_t after t time has elapsed. Taking the average square of the total displacement $\mathbf{R}_t = \mathbf{r}_t - \mathbf{r}_0$, we then have

$$\langle \mathbf{R}_t^2 \rangle = \frac{\langle \mathbf{V}^2 \rangle_{st}^2}{\epsilon/N} t - \frac{1}{2} \frac{\langle \mathbf{V}^2 \rangle_{st}^3}{(\epsilon/N)^2} \left\{ 1 - \exp \left(- \frac{2\epsilon/N}{\langle \mathbf{V}^2 \rangle_{st}} t \right) \right\} \quad (11)$$

(see Appendix II for details; see also Kareiva & Shigesada, 1983). As time t becomes large, the second term of right-hand side of eq.(11) becomes negligible. Namely, in the limit the mean-square displacement depends linearly on time, and is given by the Einstein value:

$$\langle \mathbf{R}_t^2 \rangle = \frac{\langle \mathbf{V}^2 \rangle_{st}^2}{\epsilon/N} t = (2\tau)^2 \langle \mathbf{V}^2 \rangle_{st} \frac{t}{2\tau}. \quad (12)$$

The correlation coefficient $c_{|t-t'|}$ is a decreasing function of the time interval $|t-t'|$, and decays exponentially at large $|t-t'|$. Thus the correlations of fish school's movements are of finite range. Then the distribution function for \mathbf{R}_t has a Gaussian shape (Doi & Onuki, 1992):

$$P(\mathbf{R}_t) = \frac{1}{\pi \langle \mathbf{R}_t^2 \rangle} \exp \left[-\frac{\mathbf{R}_t^2}{\langle \mathbf{R}_t^2 \rangle} \right], \quad (13)$$

where we are in two-dimensions. Thus when we investigate the movements of a fish school in a time region where $t \gg \tau$, the probability of finding the fish school at \mathbf{R}_t is the random walk distribution. Hence, at spatial scales $R \gg 2\tau\sqrt{\langle \mathbf{V}^2 \rangle_{st}}$, we can regard the fish school's movement as the diffusion or the random walk of step length

$$l = 2\tau\sqrt{\langle \mathbf{V}^2 \rangle_{st}}, \quad (14)$$

which is also called the correlation length or the mean free path. We then see that the "sinuosity" (Bovet & Benhamou, 1988), which is a numerical index quantifying the spatial pattern of erratic paths of animal's movements, is equal to $2/\sqrt{l}$.

2. Evolutionary Advantages of Schooling

Compass Orientation in Migratory Fish

The return of Pacific salmon across the open ocean to their spawning grounds covers thousands of kilometers and constitutes one of the classic examples of animal migration. For mechanisms guiding migrations it is suggested that homing salmon orient to the geomagnetic field using the magnetic sensitivity (Quinn, 1984). Recent experiments have shown that there exist crystalline particles of the biogenic magnetite in the head and areas covering the lateral line of chum salmon (Ogura et al., 1992). Here assuming the compass orientation to a goal, we consider the oceanic homing migrations in terms of the forces, which are supposed to operate on the individuals and to govern their motions. This orienting force provides migratory fish a tendency of navigating homeward. Now making an analogy to Lorentz force acting on charged particles moving in magnetic fields, we may write the orienting force acting on a fish moving with velocity \mathbf{v} as

$$\mathbf{f}^{(H)} = -\frac{\mathbf{v} \times (\mathbf{v} \times \mathbf{H})}{v^2}, \quad (15)$$

where the vector \mathbf{H} is in the homeward direction, and its magnitude H represents the degree of direction-finding ability of individual fish. Then the orienting force vector $\mathbf{f}^{(H)}$ is in the direction perpendicular to the moving direction \mathbf{v} , and its magnitude is proportional to the sine of the angle between \mathbf{v} and \mathbf{H} . When a group of fish is migrating as a school of size N , the equation for orienting motion of the i th body is expressed as

$$\frac{d\mathbf{v}_i}{dt} = \kappa(1 - \beta v_i^2)\mathbf{v}_i + \sum_{j=1}^N \mathbf{f}_{ij}^{(g)} + \sum_{j=1}^N \mathbf{f}_{ij}^{(p)} + \mathbf{f}_i^{(H)} + \boldsymbol{\eta}_i(t). \quad (16)$$

Then the azimuthal angle Θ of the centroid velocity \mathbf{V} relative to the homeward direction \mathbf{H} changes with time according to the following equation:

$$V^2 \frac{d\Theta}{dt} = -VH \sin \Theta + V\bar{\eta}_\perp(t), \quad (17)$$

where $V = |\mathbf{V}|$, and $\bar{\eta}_\perp$ refers to the component of the fluctuating force $\bar{\boldsymbol{\eta}}$ perpendicular to \mathbf{V} (see Appendix III). Thus we can establish the probability density function which describes the stationary

distribution of angular deviations Θ from the true direction:

$$P_{st}(\Theta) = \mathcal{N} \exp\left(\frac{\mathbf{V} \cdot \mathbf{H}}{\epsilon/N}\right), \quad (18)$$

where \mathcal{N} is a normalization factor (Haken, 1983).

Now let us imagine the migratory path with end points at \mathbf{r}_0 and \mathbf{r}_t . A fish school's wanderings can be decomposed into a series of straight line moves. For such a discretization, we recommend using the time interval 2τ to define moves. On the supposition of weak orientation, using the convention of straight line moves, we can write the distribution function for the j th displacement \mathbf{a}_j as

$$p_j(\mathbf{a}_j) = \frac{1}{2\pi l} \delta(|\mathbf{a}_j| - l) \exp\left(\frac{\mathbf{V}_j \cdot \mathbf{H}}{\epsilon/N}\right). \quad (19)$$

Hence in the homing migration the distribution function for the total displacement $\mathbf{R}_t = \mathbf{r}_t - \mathbf{r}_0$ is expressed as

$$P^{(H)}(\mathbf{R}_t) = \int \cdots \int \delta\left(\sum_{j=1}^n \mathbf{a}_j - \mathbf{R}_t\right) \prod_{j=1}^n p_j(\mathbf{a}_j) d\mathbf{a}_j, \quad (20)$$

where $n = t/2\tau$. Consequently, as is shown in Appendix IV, we arrive at the following form in the continuous scheme:

$$P^{(H)}(\mathbf{R}_t) = \mathcal{N} \exp\left(-\frac{\mathbf{R}_t^2}{\langle \mathbf{R}_t^2 \rangle} + \frac{\mathbf{R}_t \cdot \mathbf{H}}{\langle \mathbf{V}^2 \rangle_{st}}\right). \quad (21)$$

Then we have the characteristic length l_H defined by

$$l_H = \frac{\langle \mathbf{V}^2 \rangle_{st}}{H}. \quad (22)$$

For spatial scales $R < l_H$ the force \mathbf{H} (measured by the dimensionless number $H \cdot R / \langle \mathbf{V}^2 \rangle_{st}$) is a weak perturbation. A computer simulation by Saito & Shappy (1963) indicated that the migrations of Pacific salmon from high seas to the coastal vicinity of their natal stream may be accomplished with only slight homeward orientation. Hence we can assume that $l < l_H$. Thus the migration path breaks up into a series of "segments" each of spread l_H . Since at scales where $l \leq R \leq l_H$ the mean-square displacement of fish school's movement is given by the Einstein value, we then have

$$l_H^2 = \frac{\langle \mathbf{V}^2 \rangle_{st}^2}{\epsilon/N} \tau_H, \quad (23)$$

where τ_H is the characteristic time related to l_H . The supposition of weak orientation reads $\tau < \tau_H$. In a time region where $t < \tau_H$ the movement paths of the homing migratory fish school remain the local correlation of eq.(9). Comparing eq.(23) with eq.(22) we see

$$\tau_H = \frac{\epsilon/N}{H^2}. \quad (24)$$

On the other hand, at larger scales $R > l_H$ the migratory path of homing fish school elongates toward home site. These segments then come into line in the homeward direction. Since the total number of segments in the present migratory path is t/τ_H , the longitudinal average elongation parallel to \mathbf{H} is evaluated as

$$\langle R_{\parallel} \rangle \cong l_H \frac{t}{\tau_H} \cong \tau_H t \quad (25)$$

(see Appendix V for rigorous expression). Thus the average speed of homing is given by

$$\bar{V} = \tau_H. \quad (26)$$

It is also of interest to ascertain the lateral spread of the homing migratory path, R_{\perp} , in elongation. The projection of the sequence of segments on an axis normal to H is a random walk of step length l_H , and thus

$$\langle R_{\perp}^2 \rangle \cong l_H^2 \frac{t}{\tau_H} \cong \frac{1}{2} \frac{\langle V^2 \rangle_{st}^2}{\epsilon/N} t \quad (27)$$

(see Appendix V for rigorous expression). We then define the diffusivity by

$$D = \frac{1}{4} \frac{\langle V^2 \rangle_{st}^2}{\epsilon/N}. \quad (28)$$

Hiramatsu & Ishida (1989) evaluated diffusivity and mean homing speed of migrating salmon from the open ocean towards their natal stream using data from tagging experiments. According to them, for pink salmon (*Oncorhynchus gorbuscha*) originated from North America, $V_m = 58.7 \text{ cm} \cdot \text{sec}^{-1}$, $\bar{V} = 22.7 \text{ cm} \cdot \text{sec}^{-1}$, and $D = 8.55 \times 10^7 \text{ cm}^2 \cdot \text{sec}^{-1}$. Using the approximation $\langle V^2 \rangle_{st} = V_m^2$, we then have $\epsilon/N = 3.5 \times 10^{-2} \text{ cm}^2 \cdot \text{sec}^{-3}$, $H = 4.6 \times 10^{-4} \text{ cm} \cdot \text{sec}^{-2}$, $\tau = 5.0 \times 10^4 \text{ sec}$, $\tau_H = 1.7 \times 10^5 \text{ sec}$, $l = 5.8 \times 10^6 \text{ cm}$, and $l_H = 7.5 \times 10^6 \text{ cm}$. Here these values should be regarded as the averages over ensemble composed of various size of the salmon schools, or the values expected for the most probable size of the salmon schools. Moreover we can see that a degree of orientation to an outside stimulus is low, that is, the assumption $l < l_H$ is valid. They also estimated a coefficient of directed versus undirected movement, $A = 0.77$. Using the coefficient A , the distribution function (18) can be expressed as $P_{st}(\Theta) = \mathcal{N} \exp(A \cos \Theta)$.

Now for the question of accuracy in navigation we have

$$\frac{\sqrt{\langle R_{\perp}^2 \rangle}}{\langle R_{\parallel} \rangle} = \frac{1}{H} \sqrt{\frac{2\epsilon}{Nt}}. \quad (29)$$

We see that error in navigation is reduced as $1/\sqrt{N}$. When a group of fish is migrating as a school there are opportunities for the errors of individuals to be compensated, so that as the size of school increases, the error in navigation for the school will be lessened. This agrees with Larkin & Walton's (1969) conjecture. They estimated this effect from the consideration of the statistical properties, similar to the central limit theorem, of the circular normal distribution which was supposed to describe the accuracy of navigation, that is, the angular deviations of their moving vector from the direction of goal, under the assumption that the individuals jointly orient to a group mean direction.

Strategy for Foraging

Analysis of animals' movements has been shown to be worthwhile in the framework of Optimal Foraging Theory. We now examine the constraints put on school size by food supply. Schooling is common among long distance swimming species. Long stretches of these search paths for feeding are often crossed without food intake so that efficient foraging is essential to survival. Here I show that the habit of schooling is an advantage to foraging. Of course, disadvantages of schooling include being increased intraspecific competition for food within schools (Eggers, 1976). Then, is schooling impossible under certain food environment? Does food limit school size? Is there an optimal school size? These questions are also investigated by using the present kinematic model of fish schooling.

Duffy & Wissel (1988) have presented a mathematical theory on school sizes, in which they assumed that a school should be as large as possible to facilitate finding food in patchy environments (Pitcher, Magurran & Winfield, 1982), to confuse or evade predators when attacked (Pitcher, 1980), and to reduce the individual's chance of being eaten (Brock & Riffenburgh, 1960; Clark, 1974), given that all individuals must obtain enough food to satisfy their energetic requirements. They did not explicitly consider the intraspecific competition within schools. They discussed maximum school sizes in relation to the total

amount of food resources or the average food density in a feeding area. Here we discuss the size of a school as the outcome of optimizing food intake, assuming that each individual in a school always attempts to maximize its food intake, and that obtaining food is a greater selective constraint on individuals than predation.

We now consider the random search movements of fish over large distances for food items when in school of size N . Here we do not take into account school splitting and amalgamating. Let us assume that food supplies are clumpy and randomly distributed. Biotic populations are usually distributed heterogeneously in their habitats, and the distribution itself is often patchy (Cassie, 1963). When a fish school forages during some period T , e.g. one day, the per capita total food intake is proportional to the foraging efficiency, that is, the chance of encounter with prey patches in searching unit. Then the per capita total food intake is expressed as

$$Q_N \cdot T = S_N \cdot (T - \Delta T) \cdot q_N, \quad (30)$$

where Q_N is the average rate of per capita food intake, S_N the foraging efficiency, ΔT the total time exploiting food patches during T time, that is, the handling time, and q_N per capita food intake per prey patch.

When the fish school explores the feeding area, the foraging efficiency S_N is defined by the probability of encountering a prey patch. Therefore S_N is proportional to the number density of prey patches and the sweeping area of the search path made by the fish school per unit period. The foraging fish school statistically spreads over the area of $\langle R^2 \rangle$, where R is an end-to-end vector of movement path in searching unit and the mean-square of R is given by eq.(12). Namely considering the ensemble of fish schools of size N which are released at a point r_0 , we have the mean dispersal area per unit period, $\langle R^2 \rangle$. It is similar to a drop of ink spreading in water. Hence let us suppose that the search path's sweeping area is comparable with its net square displacement. We then have

$$S_N = b \langle R^2 \rangle, \quad (31)$$

where b is the number density of prey patches in the feeding area. The foraging efficiency is also written as

$$S_N = 2b\tau \langle V^2 \rangle_{st} = bl\sqrt{\langle V^2 \rangle_{st}} = 4bD, \quad (32)$$

by using the correlation time, the correlation length, or diffusivity. Thus the randomness of search paths will reflect the adaptation of fish's foraging behavior to the stochasticity of the environment.

The time required to handle food items when encountering a prey patch is proportional to q_N , hence the total time spent feeding during T time is proportional to the total number of encounters with prey patches during T time and q_N , assuming the amount of food in any prey patch is constant. Then we have

$$\Delta T = \frac{q_N}{\gamma} \cdot S_N \cdot (T - \Delta T), \quad (33)$$

where γ means the rate of food intake, that is, the efficiency of prey consumption. Hence the available time for foraging is given by

$$T - \Delta T = T \left(1 + \frac{q_N}{\gamma} S_N \right)^{-1}. \quad (34)$$

Thus we have the average rate of per capita food intake

$$Q_N = S_N \cdot \left(1 + \frac{q_N}{\gamma} S_N \right)^{-1} \cdot q_N. \quad (35)$$

Considering the expression of q_N , the followings are now supposed: Any fish individual in a school of size N takes the same quantity of food from a prey patch, so they all have the same q_N ; When a prey

patch is attacked by a fish school, it begins to disperse; When the prey density in a patch becomes a certain value, fish give up it, and begins to search other prey patches. Therefore the whole intake per prey patch of the school, i.e. Nq_N , becomes larger as the size of the school increases. However Nq_N will saturate at a certain size N_0 because of the limited volume of the prey patch. Moreover Nq_N will be lessened for $N > N_0$ because of increasing intraspecific competition for food within the school. Thus for a change of school size, the whole intake per prey patch changes as

$$\delta(Nq_N) = q_N \cdot [1 - \gamma_d \varphi(N, \gamma)] \cdot \delta N, \quad (36)$$

where $\varphi(N, \gamma)$ quantifies the intraspecific competition, γ_d the rate of patch dissipation. Here we expect φ to depend only on the school size N and on the feeding rate γ . We then have

$$\frac{\partial q_N}{\partial N} = -\frac{q_N}{N} \gamma_d \varphi(N, \gamma). \quad (37)$$

The school size N and the feeding rate γ play the same role to exploit the prey patch, namely, the effect of doubling N upon exploiting the patch is equivalent to doubling γ . Consequently the following scaling law holds:

$$\varphi(\nu N, \nu^{-1} \gamma) = \varphi(N, \gamma), \quad (38)$$

that is,

$$\varphi(N, \gamma) = \varphi(\gamma N). \quad (39)$$

We now have the form

$$\varphi(N, \gamma) = \gamma_c (\gamma N)^\alpha, \quad (40)$$

where γ_c indicates the intensity of competition. Assuming two-body interaction for the intraspecific competition within the school, we have $\alpha = 2$. Thus we obtain the expression for the per capita food intake when the fish school of size N encounters a prey patch:

$$q_N = q_0 \exp \left[-\frac{1}{\alpha} \left(\frac{N}{N_0} \right)^\alpha \right], \quad (41)$$

where the saturation size $N_0 = \gamma^{-1} (\gamma_c \gamma_d)^{-1/\alpha}$. q_0 is proportional to the prey population within a patch or the whole energy content per patch.

Assuming that $\epsilon/\kappa\beta V_m^4 \ll 1$, that is, a group of fish forages as a highly organized school, we then have the average rate of per capita food intake

$$Q_N = \left[\frac{1}{bq_0 V_m^4 / \epsilon} \frac{\exp \{ \alpha^{-1} (N/N_0)^\alpha \}}{N} + \frac{1}{\gamma} \right]^{-1} \quad (42)$$

The optimal size N_{opt} fulfills the condition

$$\frac{\partial Q_N}{\partial N} = 0, \quad (43)$$

which leads to

$$N_{\text{opt}} = N_0. \quad (44)$$

Besides optimal diffusivity (correlation time, correlation length) can be also determined for foraging.

Thus we see that the optimal size is the size at which the whole food intake per prey patch is a maximum, and the schooling regulates foraging in this sense. Fish then utilize patchy food resources most efficiently. We also see that N_{opt} depends on the ethological relations between fish and prey items, i.e. γ and γ_d . For example, when the available prey item is of great mobility (large value of γ_d) and

the fish consume it with high efficiency (large value of γ), the expected school size is small. Here it should be noted that N_{opt} is not directly dependent on the number density of prey patches, b , and the prey population within a patch, q_0 , therefore, the total amount of food resources in a feeding area. We can say the optimal school size is set by the quantity of food, not the amount of food supplies. Our results suggest that changes in food items will cause changes in school size. Hence seasonal or regional variability in food items need to be considered when examining the changes in observed school size with area and season (Misund, 1991).

4. Future Problems

We started with the Newton rules model for fish schooling (eq.(1)) and derived the expressions eq.(29) and eq.(42) for reducing error in navigation and per capita energy intake. These procedures analyzing fish movements as a school based on the kinematic equation were convenient to connect the individual behavior and the statistical properties (ecological phenomena), for instance, migration and variability in school size.

We investigated the homing migration by assuming directional orientation to the goal, although the precise orienting mechanism is not yet clear. Pacific salmon migrate from the open ocean to the home site well timed over thousands of kilometers in absence of any landmark indicating the location of this place. Hence salmon must determine their location relative to home. It then becomes necessary to postulate that salmon have a certain system of navigation which enables them to know where they are and where they are to go. This implies that salmon has to either possess a calendar as well as a compass (Quinn, 1984), or memorize the location of home site by means of an egocentric coding process, that is, by relating the distance and the direction of the home site to the salmon's own location and orientation by processing the route-based information about its ongoing path (Benhamou, Sauvé & Bovet, 1990). Here the following question arise: Does schooling improve these map senses?

We were also dealing with foraging search paths in a homogeneous stochastic environment, i.e. one where the prey patches are randomly distributed (according to Poisson's law). The search paths might be regulated by certain environmental features. When involving explicitly the effect of patchy resource dispersal structure in the theory, we wish to know the expected school size in relation to the food resource supplies. This is another important character of foraging fish schools.

Fish school sizes are randomly distributed over the range of school size in the wild (Anderson, 1981). Observations on the size-frequency distribution show a well-defined peak frequency. Towards larger and smaller sizes the frequency distribution decreases in an exponential-like manner. These frequency distribution may be determined by environmental conditions. Since interaction between fish schools may occur in the processes controlling the school size, the frequency distributions are likely to be set by fish stock size. Namely one school will split into some schools, and schools meet and amalgamate. Then the meeting chance must depend on the fish stock population. This problem must be reduced to a generalized diffusion problem in an abstract space within the framework of Optimal Foraging Theory. Then we may connect the size-frequency distribution and the per capita energy intake Q_N .

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Appendix I

Eq.(4) is formally solved as follows:

$$\mathbf{V}(t) = \exp \left\{ \int_0^t \kappa \left(1 - 4 \frac{\beta \epsilon}{J} - \beta \langle \mathbf{V}^2(t') \rangle \right) dt' \right\} \\ \times \left[\int_0^t \bar{\eta}(t') \exp \left\{ - \int_0^{t'} \kappa \left(1 - 4 \frac{\beta \epsilon}{J} - \beta \langle \mathbf{V}^2(t'') \rangle \right) dt'' \right\} dt' + \mathbf{V}(0) \right]. \quad (\text{A1})$$

Exploiting eq.(5), we find for the two-time correlation function immediately

$$\langle \mathbf{V}(t) \cdot \mathbf{V}(s) \rangle = \langle \mathbf{V}^2 \rangle_{st} \exp \left\{ - \frac{2\epsilon/N}{\langle \mathbf{V}^2 \rangle_{st}} (t - s) \right\}, \quad (\text{A2})$$

for $t > s$.

Appendix II

For the continuous travels, we designate the displacement of the fish school after a succession of some time intervals Δt as \mathbf{a}_j ($j = 1, 2, \dots, n; n \equiv t/\Delta t$). For $\Delta t \ll \tau$, each j th move \mathbf{a}_j takes $\mathbf{V}_j \Delta t$, where \mathbf{V}_j is the velocity observed at each j th beginning of the interval. Then the total displacement after n consecutive moves is given by $\mathbf{R}_t = \sum_{j=1}^n \mathbf{a}_j = \sum_{j=1}^n \mathbf{V}_j \Delta t$. The mean square of net displacement \mathbf{R}_t is then written by

$$\langle \mathbf{R}_t^2 \rangle = \left\langle \left(\sum_{j=1}^n \mathbf{a}_j \right) \cdot \left(\sum_{k=1}^n \mathbf{a}_k \right) \right\rangle = \langle \mathbf{V}^2 \rangle_{st} (\Delta t)^2 \sum_{j,k=1}^n c_{|j-k|\Delta t}. \quad (\text{A3})$$

Letting $r_{\Delta t} = \exp(-\Delta t/\tau)$, we have

$$\begin{aligned} \sum_{j,k=1}^n c_{|j-k|\Delta t} &= \sum_{j,k=1}^n r_{\Delta t}^{|j-k|} = n + 2 \sum_{j=2}^n \sum_{k=1}^{j-1} r_{\Delta t}^{j-k} \\ &= n \left(1 + \frac{r_{\Delta t}}{1-r_{\Delta t}} \right) - 2 \left(\frac{r_{\Delta t}}{1-r_{\Delta t}} \right)^2 (1-r_{\Delta t}^n), \end{aligned} \quad (\text{A4})$$

for small Δt . Thus the mean-square distance is given by

$$\begin{aligned} \langle \mathbf{R}_t^2 \rangle &= 2\tau \langle \mathbf{V}^2 \rangle_{st} t - 2\tau^2 \langle \mathbf{V}^2 \rangle_{st} (1 - e^{-t/\tau}) \\ &\quad - \langle \mathbf{V}^2 \rangle_{st} t \Delta t + 2\tau \langle \mathbf{V}^2 \rangle_{st} (1 - e^{-t/\tau}) \Delta t + \mathcal{O}(\Delta t^2). \end{aligned} \quad (\text{A5})$$

Going to the continuous limit $\Delta t \rightarrow 0$, we arrive at eq.(11).

Appendix III

The vector product of \mathbf{v}_i and eq.(16) gives

$$\frac{1}{N} \sum_{i=1}^N \mathbf{v}_i \times \frac{d\mathbf{v}_i}{dt} = \frac{1}{N} \sum_{i=1}^N \mathbf{v}_i \times \mathbf{f}_i^{(H)} + \frac{1}{N} \sum_{i=1}^N \mathbf{v}_i \times \boldsymbol{\eta}_i. \quad (\text{A6})$$

We separate \mathbf{v}_i into the two terms: $\mathbf{v}_i = \mathbf{V} + \delta\mathbf{v}_i$, where $\delta\mathbf{v}_i$ denotes fluctuations around the average $\mathbf{V} = \frac{1}{N} \sum_{i=1}^N \mathbf{v}_i$. Inserting it into eq.(A6) yields

$$\mathbf{V} \times \frac{d\mathbf{V}}{dt} = -\mathbf{V} \times (\mathbf{V} \times \mathbf{H}) + \mathbf{V} \times \bar{\boldsymbol{\eta}} \quad (\text{A7})$$

to the first approximation.

Appendix IV

By using the form of Fourier integral

$$\delta \left(\sum_{j=1}^n \mathbf{a}_j - \mathbf{R}_t \right) = \int \frac{d\mathbf{k}}{(2\pi)^2} \exp \left\{ i \left(\sum_{j=1}^n \mathbf{a}_j - \mathbf{R}_t \right) \cdot \mathbf{k} \right\}, \quad (\text{A8})$$

the distribution function for \mathbf{R}_t is written down as

$$\begin{aligned}
P^{(H)}(\mathbf{R}_t) &= \int \frac{d\mathbf{k}}{(2\pi)^2} e^{-i\mathbf{k}\cdot\mathbf{R}_t} \prod_{j=1}^n \left[\int d\mathbf{a}_j p_j(\mathbf{a}_j) e^{i\mathbf{k}\cdot\mathbf{a}_j} \right] \\
&= \int \frac{d\mathbf{k}}{(2\pi)^2} e^{-i\mathbf{k}\cdot\mathbf{R}_t} \left[\int d\mathbf{a} \frac{1}{2\pi l} \delta(|\mathbf{a}| - l) \exp \left\{ \left(i\mathbf{k} + \frac{1}{2\tau} \frac{\mathbf{H}}{\epsilon/N} \right) \cdot \mathbf{a} \right\} \right]^n \\
&= \int \frac{d\mathbf{k}}{(2\pi)^2} e^{-i\mathbf{k}\cdot\mathbf{R}_t} \exp \left[n \ln \left\{ 1 + \frac{1}{2!} \frac{1}{2} \left(i\mathbf{k} + \frac{1}{2\tau} \frac{\mathbf{H}}{\epsilon/N} \right)^2 l^2 + \dots \right\} \right] \\
&= \int \frac{d\mathbf{k}}{(2\pi)^2} e^{-i\mathbf{k}\cdot\mathbf{R}_t} \exp \left[\frac{nl^2}{4} \left(i\mathbf{k} + \frac{1}{2\tau} \frac{\mathbf{H}}{\epsilon/N} \right)^2 \right], \tag{A9}
\end{aligned}$$

thus we arrive at eq.(21).

Appendix V

Describing the configuration of migratory path as a succession of position vector $\{\mathbf{r}_j\}$ observed at the j th end of some fixed interval $\tilde{\Delta}t$, s.t. $\tau \ll \tilde{\Delta}t \ll t$, we can write down the probability of the entire configuration of a path with end points at \mathbf{r}' and \mathbf{r} , that is, the probability of starting at the point $\mathbf{r}_0 = \mathbf{r}'$ at time $t = 0$ and coming into the point $\mathbf{r}_n = \mathbf{r}$ at time t :

$$G(\mathbf{r}, t; \mathbf{r}', 0) = \int d\mathbf{r}_0 \int d\{\mathbf{r}_j\} \delta(\mathbf{r}_0 - \mathbf{r}') \delta(\mathbf{r}_n - \mathbf{r}) \prod_{j=1}^n P^{(H)}(\mathbf{r}_j - \mathbf{r}_{j-1}), \tag{A10}$$

where $n = t/\tilde{\Delta}t$, $P^{(H)}$ is given by the distribution function (21). In continuous scheme, the probability $G(\mathbf{r}, t; \mathbf{r}', 0)$ is described by a path integral

$$G(\mathbf{r}, t; \mathbf{r}', 0) = \int_{\mathbf{r}(0)=\mathbf{r}'}^{\mathbf{r}(t)=\mathbf{r}} D[\mathbf{r}(s)] \exp \left[- \int_0^t \left\{ \frac{1}{\sigma^2} \left(\frac{d\mathbf{r}(s)}{ds} \right)^2 - \frac{\mathbf{V}(s) \cdot \mathbf{H}}{\langle \mathbf{V}^2 \rangle_{st}} \right\} ds \right], \tag{A11}$$

where $\sigma^2 = \langle \mathbf{V}^2 \rangle_{st}^2 / (\epsilon/N)$ (Khandekar & Wiegel, 1989). The most probable path $\mathbf{r}_m(t)$ is determined by maximizing the integrand to yield

$$\frac{d\mathbf{r}_m}{dt} = \frac{1}{2} \frac{\langle \mathbf{V}^2 \rangle_{st}}{\epsilon/N} \mathbf{H} = \tau \mathbf{H}. \tag{A12}$$

The variance $\langle [\mathbf{r} - \mathbf{r}_m(t)]^2 \rangle$ is obtained from the probability distribution for $\mathbf{y}(t) = \mathbf{r} - \mathbf{r}_m(t)$:

$$\hat{G}(\mathbf{y}, t) = \int_{\mathbf{y}(0)=0}^{\mathbf{y}(t)=\mathbf{y}} D[\mathbf{y}(s)] \exp \left[- \frac{1}{\sigma^2} \int_0^t \left(\frac{d\mathbf{y}(s)}{ds} \right)^2 ds \right], \tag{A13}$$

which is easily derived from eq.(A11). Consequently

$$\langle \mathbf{y}^2 \rangle = \frac{\langle \mathbf{V}^2 \rangle_{st}^2}{\epsilon/N} t. \tag{A14}$$

Hence the component perpendicular to \mathbf{H} is given by

$$\langle R_{\perp}^2 \rangle = \frac{1}{2} \frac{\langle \mathbf{V}^2 \rangle_{st}^2}{\epsilon/N} t. \tag{A15}$$