

Scaling behavior in a fish school and a school system*

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1. Introduction

Animal packing in social aggregations is of fundamental interest in ecology, and their conformations have been extensively studied. Parr [23] conducted pioneer tank observations of pelagic fishes (herring, sprat and mackerel), and noted the “persistently uniform density” of a school. Pitcher and Partridge [26] validated that all the fish in a school occupy a volume proportional to Nb^3 , where N is the number of fish and b is the mean nearest-neighbor distance (approximate to the mean fish-body length) in the school. Many models for social aggregations, however, predict that densities increase as the group size (in number) increases (overviews of such models are given in Ref. [27]). Mogilner et al. [17] mathematically tackled this problem of constant density and revealed the condition for a well-spaced group, i.e. what class of mutual interactions result in a relatively constant individual distance in the interior of the aggregate.

More recently, by means of underwater acoustics, the school sizes (in number or biomass of fish) have been quantitatively measured for different values of the dimensional size of schools in the wild. Precise data on conformations of large-sized schools of pelagic fishes became available rapidly, which were extremely helpful in elucidating a certain geometric law, i.e. the relation between dimensional and biomass sizes of pelagic fish schools, bringing about some important changes in our viewpoints. Misund and colleagues [1, 8, 10–15] found that the power-law scaling in dimension-to-biomass relationship exists, and is robust across a broad range of pelagic species (anchovy, herring, mackerel, pilchard, saithe, sardine, sprat, etc.) as well as across diverse environments. They demonstrated that if the biomass N in a school is, say, doubled, the cross-sectional area of a school is increased by a factor $2^{2\nu}$, i.e. the radius R of the school scales as

$$R = (\text{constant}) \times N^\nu \quad (1)$$

and that the exponent ν looks universal, reading 0.5 (from the field data ν ranges from 0.415 to 0.77). The geometric law they found implies that the mean density of a school scales as $N^{1-3\nu}$ in three dimensions of space and the conformation of social aggregations swells (i.e. $\nu > 1/3$). N , denoting the school biomass, is hereafter defined by the number of fish in a school.

It might come as a surprise that packing densities decrease as the group size increases, contrary to previous observations and predictions. Laboratory observations for school packing structure have been made exclusively in small tanks. In all set-ups, the factors resulting in homogeneous, cohesive school may

be especially pronounced. Pitcher and Parrish [25] claimed that homogeneity in schools has been over-emphasized. *In situ* observations of pelagic fish schools revealed that the packing structure within the schools is rather heterogeneous, and even empty vacuoles have been recorded [4, 9, 16]. Besides artificial environments in small tanks, the discrepancy in former observations could have been caused by too small numbers of fish in the schools. For instance, in Ref. [26], N takes a few tens of fish. Since such a geometric law above is always defined only in a certain limit [2], the scaling in the dimension-to-biomass relationship is expected to hold for large-sized schools of pelagics.

In this paper, the exponent ν is estimated according to the established universal scaling law in the school-size distribution of pelagic fishes [20, 21]: choose the suitable value of ν to achieve the best data-collapse on the size distributions in terms of the school dimension. Notice that the dimension-to-biomass relationship is a property of the single school and the scaling exponent ν is determined by the (social) interaction between fish, while the scaling in the school-size distribution emerges from the inter-school interactions at population level.

2. Scaling in school geometry

The biomass distributions $W(N)$ follow a power law with exponent $\beta = 1$ up to a cut-off size $\langle N \rangle_P$,

$$W(N) = N^{-\beta} P(N/\langle N \rangle_P), \quad (2)$$

where $P(x)$ is a crossover scaling function with a strong drop for $x > 1$, and the cut-off size (crossover size from power-law to exponential decay) is calculated from the biomass histogram data $\{(N_i, W_i) | i = 1, 2, \dots\}$,

$$\langle N \rangle_P = \frac{\sum_i N_i^2 W_i \Delta N}{\sum_i N_i W_i \Delta N}, \quad (3)$$

where histogram bins are chosen with width ΔN .

The dimension data of fish schools are binned with width ΔR , giving the set of frequencies $\{(R_i, W_i^{(G)}) | i = 1, 2, \dots\}$. From Eqs.(1) and (2), the distribution of geometric dimensions of fish schools is represented as

$$W^{(G)}(R) = R^{-1} P^{(G)}(R/\langle R \rangle_P), \quad (4)$$

where

$$\langle R \rangle_P = \langle N \rangle_P^\nu, \quad (5)$$

and

$$P^{(G)}(x) = P(x^{1/\nu}). \quad (6)$$

Therefore, the school-dimension distribution follows a power law with the same exponent “-1” as the

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school-biomass distribution. The power-law distribution $W^{(G)}(R)$ is truncated at a cut-off size $\langle R \rangle_P$, which is also calculated from histogram data of school geometric dimensions,

$$\langle R \rangle_P = \left[\frac{\sum_i R_i^{2/\nu} W_i^{(G)} \Delta R}{\sum_i R_i^{1/\nu} W_i^{(G)} \Delta R} \right]^\nu. \quad (7)$$

The following normalizations are adopted for the scaling function $P^{(G)}(x)$ and the histogram data of geometric dimensions of fish schools, because the cut-off size $\langle N \rangle_P$ is proportional to the total number of fish in the school system [20, 21, see also Eq.(18)]:

$$\int_0^\infty x^{\nu-1} P^{(G)}(x) dx = 1, \quad (8)$$

and

$$\sum_i R_i^{1/\nu} W_i^{(G)} \Delta R = \langle R \rangle_P^{1/\nu}, \quad (9)$$

respectively.

Since the size $\langle R \rangle_P$ depends on the exponent ν following Eq.(7), so that we can determine the value of ν by evaluating the location of the cut-off in the power-law distribution $W^{(G)}(R)$. I make use of the data collapse to extract the exponent. From Eqs.(4) and (8), when $y = W^{(G)}\langle R \rangle_P$ is plotted against $x = R/\langle R \rangle_P$ with correct parameter ν , all the empirical data should collapse onto each other. The power-law exponent of school-dimension distributions, ν , is then evaluated through data collapse. Let us search for the value of ν that places all the points most accurately on a single curve. We use a set of histogram data of vertical dimension of Japanese sardine *Sardinops melanostictus* schools, from 22 acoustic surveys by Hara [7] off south-eastern Hokkaido for seven years, 1981–1987. Hara [6] reported that Japanese sardine migrate as a huge-sized school in number from a few hundreds of thousands to a few million of fish. To obtain the best data collapse, the x -axis is divided into bins (Fig.1a), and for each bin two-dimensional variance

$$\epsilon = (\sigma_x/\mu_x)^2 + (\sigma_y/\mu_y)^2 \quad (10)$$

is calculated, where σ_x and σ_y denote the standard deviation of the mean μ_x and μ_y , respectively. The parameter ν is then estimated at value that minimize the mean of two-dimensional variance for the bins (Fig.1b). The mean of two-dimensional variance, $\bar{\epsilon}$, is a measure to determine the goodness of collapse [21]. A good data collapse can be obtained by using the value $\nu \approx 0.6$. The resulting plot of empirical school data is shown in Fig.1a. Experimentally fitting the parameter ν to achieve a good data collapse, “3/5”, is reminiscent of the Flory value of the exponent in a power-law dependence of the coil radius of a polymer chain (in three-dimensional solutions) on the degree of polymerization [2].

3. FSS in school-biomass distributions

The acoustic-survey data are converted into a school-biomass histogram as follows

$$W(N)\Delta N \propto W^{(G)}(R)R^{1/\nu-1}\Delta R. \quad (11)$$

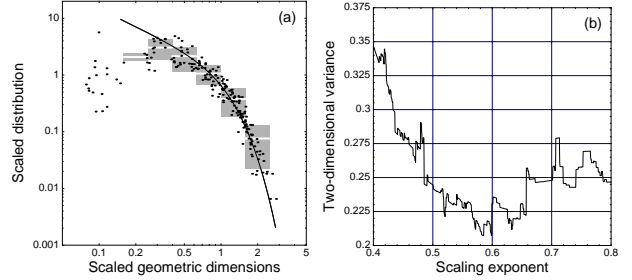


Figure 1: Data collapse to extract the exponent ν . (a) Scaled distribution of geometric dimensions of sardine schools. $y = W^{(G)}\langle R \rangle_P$ is plotted versus $x = R/\langle R \rangle_P$ with $\nu = 0.6$ on double-logarithmic scale. The bins are chosen equally spaced on a logarithmic scale as $x \in [10^{-1+k/5}, 10^{-1+(k+1)/5})$ with $k = 1, 2, \dots, 6$. The rectangle in gray reads the interval $\mu_y \pm \sigma_y$, i.e. the error σ_y on the mean μ_y (indicated by the slit) for each bin. The solid line is a prediction of the mean-field theory [20]. (b) The mean of two-dimensional variance, $\bar{\epsilon}$, versus the power-law exponent ν . Although $\bar{\epsilon}$ shows noisy fluctuations, it takes a minimum around $\nu = 0.6$. Data from Ref. [7] are analyzed.

We now crosscheck the value of ν through finite-size scaling (FSS) analysis of school-biomass distribution [21]. Since the finite population size causes the truncation of power-law distribution $W(N) \propto N^{-\beta}$, there is a well-defined quantity

$$L = \frac{\sum_i N_i^{1+\beta} W_i \Delta N}{\sum_i N_i^\beta W_i \Delta N}, \quad (12)$$

which depends on the system population size. In order to characterize the finite size effects, FSS hypothesis is used: the distribution function depends on N only through the ratio N/L^A ,

$$W(N; L) dN = L^{-B} F(N/L^A) d(N/L^A), \quad (13)$$

where $F(x)$ is a universal function independent of fish population size. The prefactor L^{-B} is required to ensure the normalization

$$\sum_i N_i^\beta W_i \Delta N = 1, \quad (14)$$

where $P(N) [\equiv N^\beta W(N)]$ now represents the probability distribution of school-biomass sizes. From the FSS hypothesis, it is expected that when WL^{A+B} is plotted against N/L^A with correct parameters A and B all the data collapse onto a single curve. The power-law exponent of biomass distributions, β , is then evaluated through FSS analysis. The value of B/A is the estimate of the power-law exponent β . Let us analyze a set of 22 acoustic-survey data of sardine schools (same as Fig.1) converted into biomass histograms by using Eq.(11) with $\nu = 3/5$. In a simultaneous best-fitting procedure (Fig.2), a good data collapse can be obtained by using the values $A \approx 1$ and $B \approx 1$. The power-law exponent derived from the FSS collapse is $\beta \approx 1$. The resulting plot is shown in Fig.2a. The school-biomass distribution follows a power-law decay with exponent -1 , and is truncated at the cut-off size

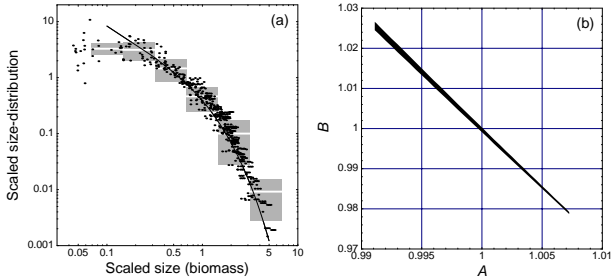


Figure 2: FSS analysis of school-size data. (a) FSS plot of the biomass distribution on double-logarithmic scale. Dimension data of sardine schools (same as Fig.1) are converted by Eq.(11) with $\nu = 3/5$. Here $y = WL^{A+B}$ is plotted versus $x = N/L^A$ with $A = B = 1$. Two-dimensional variances [same as Eq.(10)] are calculated for bins chosen equally spaced on a logarithmic scale as $x \in [10^{-1+(k-0.5)/3}, 10^{-1+(k+0.5)/3})$ with $k = 0, 1, \dots, 5$. The rectangle in gray is same as Fig.1. The solid line is a prediction of the mean-field theory [20]. (b) The region of the AB -plane in which the minimum of the mean of two-dimensional variance exists. A measure of data collapse for scaling, i.e. the mean of two-dimensional variance, $\bar{\epsilon}$, takes a minimum $\bar{\epsilon}_{\min}$ for the right choice of (A, B) . The minimum is found with the precision i.e. width of the minimum, $\Delta\epsilon = 10^{-3}$ in black region ($\Delta\epsilon/\bar{\epsilon}_{\min} \approx 3.12 \times 10^{-3}$). The values of the parameters lie in the intervals $A = 0.999 \pm 0.008$ and $B = 1.003 \pm 0.024$, and therefore $\beta = 1.004 \pm 0.032$.

of Eq.(3). The FSS collapse confirms the scaling laws for school sizes, Eq.(1) with $\nu = 3/5$ and Eq.(2) with $\beta = 1$.

We now choose the normalization

$$\sum_i N_i W_i \Delta N = \Phi, \quad (15)$$

where Φ denotes the total fish population in the school system ($\sum_i W_i \Delta N$ gives the total number of schools). Since Eq.(12) implies $L^A \propto \Phi^\gamma$ with a scaling exponent γ , the FSS relation for the school-biomass distribution is written as

$$W(N) = N^{-\beta} P(N/\Phi^\gamma). \quad (16)$$

Accordingly, the normalization of Eq.(15) yields the scaling relation

$$2 - \beta = 1/\gamma. \quad (17)$$

The best-fitting value in data collapse, $\beta \approx 1$, gives $\gamma \approx 1$. As a consequence, the location of the cut-off in the power-law distribution of school sizes simply reads

$$\langle N \rangle_P \propto \Phi, \quad (18)$$

which is verified by means of extensive numerical simulations [20, 21].

4. Newton-rules model

4.1 Gaussian school

Let us now investigate cohesive motion of schools in a three-dimensional space from the viewpoint of the behavioral algorithms which govern their formation

and dynamics: attraction between neighbors maintains cohesion of the school; a tendency to align with neighbors produces collective motion of the school. The minimal model of cohesion is a linkage of neighbors consisting of harmonic spring, because the inter-fish distance follows a Gaussian distribution [3, 19, 24]. Using the relative coordinates to the center of school, the equation of motion of fish (as noisy self-propelled particles) in a large school of size N is written by a one-body approximation as the following Langevin equation [18, 19]:

$$\frac{d^2 \mathbf{r}}{dt^2} = \mathbf{f}(\mathbf{r}) - J \frac{d\mathbf{r}}{dt} + \boldsymbol{\eta}(t), \quad (19)$$

providing that individuals are sufficiently sensitive to behavior of their neighbors, where $\mathbf{f}(\mathbf{r})$ is the cohesive force; J denotes the strength of alignment; and $\boldsymbol{\eta}$ is a random perturbation of the velocity with strength ϵ_v and a δ -correlated time dependence.

The attractive interaction force acting on one body due to a system of bodies is the neighbor-joining harmonic spring. One essential approximation is to replace the many-fish problem by the problem of solving the motion of one fish in a certain self-consistent field. The cohesive force is then written in the following form by the one-body approximation:

$$\mathbf{f}(\mathbf{r}) = -\frac{\tilde{k}}{N^\alpha} \mathbf{r}, \quad (20)$$

where $\tilde{k}N^{-\alpha}$ is the effective spring constant for the springs strung out from the center of the school to a fish: the number of consecutive springs joining the fish to the center of the school via other companions is proportional to N^α . The total ‘‘elastic energy’’ of inter-fish bonds in the school depends linearly on number N of individuals in the school. The overall elastic energy after integration over a sphere of radius R (denoting the average radius of the school) results $E_{\text{el}} \propto R^4 N^{-\alpha}$, which is derived from the ideal harmonic spring, Eq.(20). Therefore, the exponent α will be determined self-consistently,

$$\frac{R^4}{N^\alpha} \propto N. \quad (21)$$

The solution of the Langevin equation (19) with Eq.(20) takes the following asymptotic forms:

$$\sigma_v^2 \left[\equiv \left\langle (d\mathbf{r}/dt)^2 \right\rangle \right] \approx 3\epsilon_v/J \quad (22)$$

(fluctuation-dissipation relation), and

$$\langle \mathbf{r}^2 \rangle \approx \frac{\sigma_v^2}{\tilde{k}} N^\alpha, \quad (23)$$

where the root-mean-square $\sqrt{\langle \mathbf{r}^2 \rangle}$ gives the average radius of the school, R . From Eq.(21) together with Eq.(23), the self-consistent value of the exponent α is obtained:

$$\alpha = 1. \quad (24)$$

As a consequence, the self-consistent cohesive force reads

$$\mathbf{f}(\mathbf{r}) = -\frac{\sigma_v^2}{b^2 N} \mathbf{r}, \quad (25)$$

where b denotes the effective inter-fish distance (a constant independent of N): $b^2 \equiv \sigma_v^2/\tilde{k}$. The average radius of the school is then given by $bN^{1/2}$.

4.2 Excluded volume effect

From Eq.(19), the probability of the school radius being between r and $r + dr$ is given by the following:

$$\Psi_0(r) = 4\pi r^2 \left(\frac{3}{2\pi b^2 N} \right) \exp\left(-\frac{3r^2}{2b^2 N}\right) \quad (26)$$

in a stationary state in three dimensions (i.e. the position vector \mathbf{r} follows a Gaussian distribution). The Gaussian school model considered above permits fish to occupy the same region in space. Of course this is a physical impossibility since each fish possesses its own finite volume. Therefore, in the “excluded volume” school, there are a number of Gaussian school configurations which are disallowed due to the steric effect. Let $p(r)$ be the probability that a Gaussian school configuration, as counted in Eq.(26), is also allowable under the excluded volume condition. We now calculate the probability that no overlaps occur when we place N fish within a region of volume ($\sim r^3$), which will lead to an estimation for $p(r)$. Letting w be the volume which is effectively excluded to one fish by the presence of another ($w \lesssim b^3$), the probability that one particular fish will not overlap with another is then given by $(1 - w/r^3)$. Since there are $N(N - 1)/2$ possible combinations of pairs, the probability that no overlap occurs in all of these combinations is given by

$$p(r) = (1 - w/r^3)^{N(N-1)/2} = \exp\left(-\frac{wN^2}{2r^3}\right), \quad (27)$$

where $r^3 \gg w$ and $N \gg 1$. Therefore, the probability distribution of the school radius r can then be written as

$$\Psi(r) = \Psi_0(r)p(r) \propto r^2 \exp\left(-\frac{3r^2}{2b^2 N} - \frac{wN^2}{2r^3}\right) \quad (28)$$

for the excluded volume school.

Both $\Psi_0(r)$ and $\Psi(r)$ have a maximum at certain values of r . Let us estimate the average size of the school radius in each model by calculating the positions of these maxima. The maximum of $\Psi_0(r)$ occurs at $R_0 = (2b^2 N/3)^{1/2}$. The maximum of $\Psi(r)$ occurs at R , which satisfies the following equation obtained by differentiating the logarithm of Eq.(28):

$$\left(\frac{R}{R_0}\right)^5 - \left(\frac{R}{R_0}\right)^3 = \frac{9\sqrt{6}}{16} \frac{w\sqrt{N}}{b^3}. \quad (29)$$

If $N \gg 1$, the second term on the left-hand side of Eq.(29) can be neglected and hence

$$R \simeq R_0 \left(\frac{w\sqrt{N}}{b^3}\right)^{1/5} \propto N^{3/5}. \quad (30)$$

The exponent is modified strongly by the steric effect, and “3/5” is the very value extracted through the data collapse. Here we see an analogy between school geometry and polymer chain statistics.

5. Discussion

To understand the scaling law for school geometry, Eq.(1) with $\nu = 3/5$, it is essential to see what the value of ν represents. The number of fish in a school of radius R scales as $N(R) \sim R^{1/\nu}$: the packing structure within the schools is characterized by a non-integer (i.e. fractal) dimensionality of $1/\nu \approx 1.7$. As indicated in the Introduction, large internal variations in packing density occur within a school. Fréon and Misund [5] pointed out that a source of substantial variation in internal school structure is the formation of subgroups. Relatively independent movements of such clusters of individuals can open up empty spaces and cause large variation in school volume. The polymer-chain analogue of the subgroup in school conformation is the “blob” [2, 22]. Inside the subgroup the core repulsion by excluded volume effects is a weak perturbation leading to a Gaussian state.

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