

# Power-law scaling in dimension-to-biomass relationship of fish schools

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## Abstract

Motivated by the finding that there is some biological universality in the relationship between school geometry and school biomass of various pelagic fishes in various conditions, I here establish a scaling law for school dimensions: the school diameter increases as a power-law function of school biomass. The power-law exponent is extracted through the data collapse, and is close to  $\frac{3}{5}$ . This value of the exponent implies that the mean packing density decreases as the school biomass increases, and the packing structure displays a mass-fractal dimension of  $\frac{5}{3}$ . By exploiting an analogy between school geometry and polymer chain statistics, I examine the behavioral algorithm governing the swollen conformation of large-sized schools of pelagics, and I explain the value of the exponent.

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## 1. Introduction

### 1.1. Brief history of studies on the packing geometry of fish schools

Animal packing in social aggregations is of fundamental interest in ecology, and their conformations have been extensively studied (Parr, 1927; Symons, 1971; Okubo and Chiang, 1974; Graves, 1976; Pitcher and Partridge, 1979; Aoki, 1980; Partridge, 1980, 1982; Dill et al., 1981; Aoki and Inagaki, 1988; Misund, 1993a; Parrish and Hamner (Eds.), 1997). Pioneer tank observations of pelagic fishes (herring, sprat and mackerel) were conducted by Parr (1927), and the “persistently uniform density” of a school was noted. From experiments on schools of saithe *Pollachius virens*, herring *Clupea harengus* and cod *Gadus morhua* cruising in a 10 m circular gantry tank, Pitcher and Partridge

(1979) 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. Misund (1993a) reported from field observations that the number densities of herring schools are almost independent of the dimensional size of school but are an order of magnitude lower than the packing densities observed when schooling in small tanks.

Tauti and colleagues (Tauti and Miyosi, 1929; Tauti and Hudino, 1929; Tauti and Yasuda, 1929; Tauti and Yasuda, 1929, 1930, 1933a, b) had experimentally shown that a fish school can be viewed as a group of inorganic particles and treated with the methods of physics. Breder (1954) explicitly applied physical equations to such fish schools. Recently, a number of theoretical and numerical models of schooling and flocking behavior have been studied by biologists, mathematicians and physicists (Okubo and Levin, 2001; Camazine et al., 2001; Vicsek (Ed.), 2001). As for the animal group geometry, many models for social

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aggregations, however, predict that densities increase as the group size (in number) increases [overviews of such models are given in Refs. (Warburton and Lazarus, 1991; Beecham and Farnsworth, 1999)]. Mogilner et al. (2003) mathematically tackled this problem of constant density and revealed the condition for a well-spaced group, i.e. what class of mutual interactions results 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 (Misund, 1990; Misund et al., 1992; Misund, 1993b; Misund et al., 1995, 1996; Coetzee, 2000; Misund and Coetzee, 2000; Misund et al., 2003) found that the power-law scaling in dimension-to-biomass relationship exists, and is robust across a broad range of pelagic species 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.

$$\text{cross-sectional area} \propto (\text{biomass})^{2\nu}, \quad (1)$$

and that the exponent  $\nu$  looks universal, reading 0.5 (from the field data  $\nu$  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.  $\nu > \frac{1}{3}$ ). Such a relationship as Eq. (1) with  $\nu = 0.5$  has been utilized for the dimensions to biomass conversion (e.g. transforming the school diameter  $R$  to the number  $N$  of fish) in analysing school-size distributions (Anderson, 1981; Niwa, 1996b, 1998, 2003, 2004a).

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 geometry and internal structure have been made exclusively in small tanks, which generally show the constant density of fish that the school volume is proportional to the number of individuals. In all set-ups, the factors resulting in homogeneous, cohesive school may be especially pronounced, and it therefore seems that the quantified structure is skewed. Pitcher and Parrish (1993) claimed that homogeneity in schools has been over-emphasized. In situ observations of herring and sprat schools with a high-resolution sonar revealed that the packing structure within the schools is rather heterogeneous (Cushing, 1977). This has been confirmed by measurements of free-swimming schools using photography and high-resolution echo integration,

which showed that the packing density distribution in capelin *Mallotus villosus* and clupeoid schools varies considerably (Fréon et al., 1992; Misund, 1993a). Regions of high density are usually found within the schools, and even empty vacuoles have been recorded. Misund and Floen (1993) observed by repeated echo integration that there were large variations in internal packing density of herring schools (i.e. high-density regions or empty lacunas within a school), and that the packing density structure was quasi-stationary. 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 Pitcher and Partridge (1979),  $N$  takes a few tens of fish. Since such a geometric law above is always defined only in a certain limit (de Gennes, 1979), the scaling in the dimension-to-biomass relationship is expected to hold for large-sized schools of pelagics.

In this paper, the exponent  $\nu$  is estimated according to the established universal scaling law in the school-size distribution of pelagic fishes (Niwa, 2003, 2004a): choose the suitable value of  $\nu$  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  $\nu$  is determined by the behavioral algorithm of fish schooling at individual level, while the scaling in the school-size distribution emerges from the inter-school interactions at population level (i.e. a global property of the interacting school system).

## 1.2. Scaling in school-size distributions

Animal group size is a focal issue in ecology that, in contrast to scaling, has introduced a single preferred size (i.e. optimal or compromise size) for any organism living in groups (Pulliam and Caraco, 1984; Higashi and Yamamura, 1993; Niwa, 1996b; Hoare et al., 2004). Fig. 1 shows an example of the histogram of school dimensions of Japanese sardine *Sardinops melanostictus*. A peak frequency and a right skew are typical of pelagic fishes (Anderson, 1981; Niwa, 1996b, 1998). Their linear dimension, e.g. the vertical thickness, of the school falls into a certain range below a few tens of meters. One fish may not be the right atomic unit in schooling, since field observations suggest that no school exists under a certain minimal size. This may cause binned data of school sizes to exhibit the fake peak frequency. Anderson (1981) and Niwa (1996b) have ignored slowly decaying (or fat-tailed) distributions, including scaling laws, in such data of school sizes short ranged with a fake peak frequency (the possibility of power laws was already presented in their models but not exploited). A traditional, widely used Gauss statistics says that, for the data from Hara (1990) shown in Fig. 1, finding sardine schools ranging from 18 to 20m in vertical

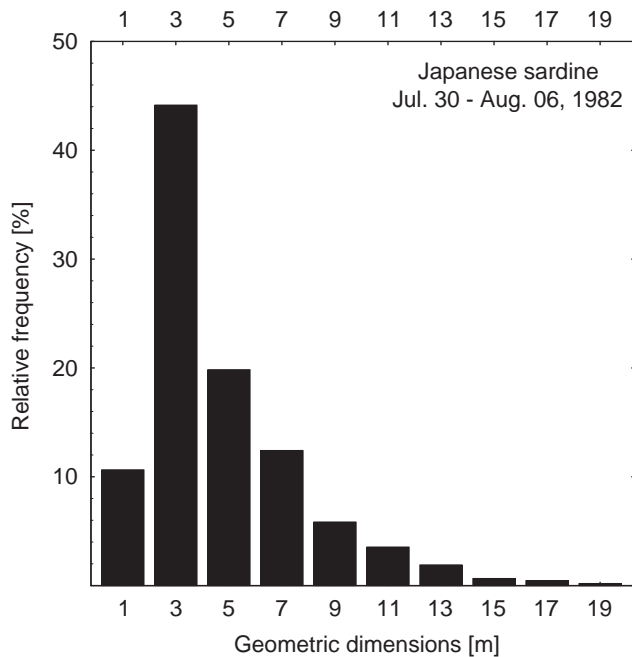


Fig. 1. Vertical dimension (in meters) of Japanese sardine schools. Data from the acoustic survey by Hara (1990) off southeastern Hokkaido in the summer, 1982. The same data are available in Hara (1984). Small schools of vertical dimensions in the first bin (<2 m) may be stray ones.

thickness should only occur about once every  $10^9$  detections of schools [for detail, consult Niwa (2004a)]. In other words, it is not the real world! Aquatic observations actually say that finding such schools occurs about once every 500 detections. The probability that such schools are found is  $10^6$  times as large!

The possibility of scaling in such distributions was found by Bonabeau and Dagorn (1995). Fat-tailed distributions have been found to quite generally characterize the size heterogeneity of pelagic fish schools (Niwa, 1998; Bonabeau et al., 1998, 1999). Only lately, Niwa (2003, 2004a) showed that the school-size distribution of pelagic fishes has the universal functional form of a power-law decay and a crossover towards the exponential distribution.

### 1.3. Scaling and data collapse in ecology

Scaling laws have been found to characterize many patterns in ecological systems (Azovsky, 2000; Chave and Levin, 2003; Halley et al., 2004). There is an empirical rule about the relationship between the areas ( $L$ ) of island and the numbers ( $S$ ) of species on them: whether counting birds, butterflies, plants or copepods in ponds, a tenfold smaller area contains roughly half the species. This can be fitted by a power-law function

$$S(L) \propto L^z \quad (2)$$

with the exponent  $z \approx 0.25$  (Preston, 1962; MacArthur and Wilson, 1967; Harte et al., 1999; May, 1999). The

species–area relationship is widely used in rough assessments of likely future rates of species extinction (because observed rates of tropical deforestation are equated to loss of habitat area, we can assess the annual production of species committed to extinction). So, a more secure understanding of such relationships has great practical importance (May, 1999). Banavar et al. (1999) applied finite-size scaling (Fisher and Barber, 1972; Binder and Heermann, 1988) to test the hypothesis of scaling invariance in the species–area relationship resting on a model proposed by Harte et al. (1999) for the species abundance distribution. Following the conventional notation in the physics literature, the system sizes are hereafter denoted by  $L$ .

The finite-size scaling (FSS) hypothesis assumes that the fraction of objects with size  $n$  for a finite system of size  $L$  is written, with a scaling exponent  $A$ , as

$$P(n; L) = L^{-A} F(n/L^A), \quad (3)$$

where  $F$  is a universal scaling function.  $P(n; L)$  reads, for instance, the species-abundance distribution, which defines the probability that any given species on a census patch of area  $L$  has  $n$  individuals, where  $P(n; L)S(L)$  is the expected number of species with  $n$  individuals.  $L^A$  is a measure of the width of the probability distribution  $P(n; L)$ , e.g. the mean or the standard deviation of the distribution. Eq. (3) expresses the principle that the behavior of the finite system, i.e.  $P(n; L)$ , is controlled by the ratio  $n/L^A$ . We test the FSS hypothesis by data collapsing: when  $y = L^A P(n; L)$  is plotted versus  $x = n/L^A$ , if the distributions across different  $L$ 's fall on a single curve (e.g. collapsing distinct abundance distributions measured in different areas and with different total numbers of individuals onto one scaling curve), then we should be able to identify a scaling function  $F(x)$ . In order to determine the exponent  $A$ , we try a best-fitting procedure such that the family of curves  $P(n; L)$  collapses onto a single curve as well as possible. We then obtain other scaling exponents (e.g.  $z$  of the species–area relationship) resting on the scaling relation between scaling exponents (Goldenfeld, 1992). By noting that the total number of individuals of all species is equal to  $\sum_n nP(n; L)S(L)$ , the species–area relationship leads to a scaling relation

$$A + z = 1, \quad (4)$$

assuming that the total number of individuals of all species is proportional to area  $L$  (Banavar et al., 1999).

The universal scaling is fundamental to data collapse. The power-law scaling emerges as ubiquitous properties in ecology. In statistical analysis in ecology, data collapsing across different environments or species has been, however, observed only lately in dynamics of breeding bird populations (Keitt and Stanley, 1998; Keitt et al., 2002), food web structure (Camacho et al., 2002), microbial body-mass spectra in marine

ecosystems (Rinaldo et al., 2002), school-size distributions of pelagic fishes (Niwa, 2003, 2004a), and in the context of ecological economics, capture fisheries productions of countries (Niwa, 2004b).

## 2. Scaling in dimension-to-biomass relationship

### 2.1. Estimation of the exponent $\nu$ through data collapse

In order to understand the geometric properties of school configurations, the school biomass  $N$  must be measured for different values of dimensional size  $R$ , and we must compare them. Misund and colleagues extensively performed the simultaneous observations of the values of  $R$  and  $N$  for pelagics by the following two methods: (i) two-dimensional (cross-sectional) acoustic measurements (unit in square meters) and subsequent purse seine capture (unit in tonnes) of schools (Misund, 1990, 1993b), and (ii) acoustic measurements of the three-dimensional structures and backscattered echo energy (Misund et al., 1992, 1995, 1996; Coetzee, 2000; Misund and Coetzee, 2000; Misund et al., 2003). The surveys were conducted on stocks of anchovy *Engraulis capensis*, herring *Clupea harengus*, horse mackerel *Trachurus trachurus capensis*, mackerel *Scomber scombrus*, pilchard *Sardinops ocellatus*, round herring *Etrumeus whiteheadi*, saithe *Pollachius virens*, sardine *Sardinops sagax*, and sprat *Sprattus sprattus*, in different seasons and geographic regions (the Barents Sea, the North Sea, the Norwegian Sea, the northeastern Atlantic and off Namibia, and off the coast of South Africa). They found that there is some biological universality in the dimensions-to-biomass relationships, Eq. (1). Their finding implies that the radius  $R$  of the school scales as

$$R = (\text{constant}) \times N^\nu \quad (5)$$

in a statistical sense.  $N$ , denoting the school biomass, is hereafter defined by the number of fish in a school.

Now I propose another way to establish the scaling law for school dimensions, Eq. (5), by applying universal scaling law in fish school-biomass distributions (Niwa, 2003, 2004a). The biomass distributions  $W(N)$  follow a power law with exponent  $\beta = 1$  up to a cut-off size  $\langle N \rangle_P$ ,

$$W(N) = N^{-\beta} P(N/\langle N \rangle_P), \quad (6)$$

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  $\{(N_i, W_i) | i = 1, 2, \dots\}$ ,

$$\langle N \rangle_P = \frac{\sum_i N_i^2 W_i \Delta N}{\sum_i N_i W_i \Delta N}, \quad (7)$$

where histogram bins are chosen with width  $\Delta N$ .

The dimension data of fish schools are binned with width  $\Delta R$ , giving the set of frequencies  $\{(R_i, W_i^{(G)}) | i = 1, 2, \dots\}$ . From Eqs. (5) and (6), the distribution of geometric dimensions of fish schools is represented as

$$W^{(G)}(R) = R^{-1} P^{(G)}(R/\langle R \rangle_P), \quad (8)$$

where

$$\langle R \rangle_P = \langle N \rangle_P^\nu, \quad (9)$$

and

$$P^{(G)}(x) = P(x^{1/\nu}). \quad (10)$$

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

$$\langle R \rangle_P = \left[ \frac{\sum_i R_i^{2/\nu} W_i^{(G)} \Delta R}{\sum_i R_i^{1/\nu} W_i^{(G)} \Delta R} \right]^\nu. \quad (11)$$

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 [Niwa (2003, 2004a); see also Eq. (23)]:

$$\int_0^\infty x^{1/\nu-1} P^{(G)}(x) dx = 1 \quad (12)$$

and

$$\sum_i R_i^{1/\nu} W_i^{(G)} \Delta R = \langle R \rangle_P^{1/\nu}, \quad (13)$$

respectively.

Fat-tailed school-size distributions are necessarily truncated because the population is finite. Since the size  $\langle R \rangle_P$  depends on the exponent  $\nu$  following Eq. (11), so that we can determine the value of  $\nu$  by evaluating the location of the cut-off in the power-law distribution  $W^{(G)}(R)$ . The ordinary least-squares regressions might, however, lead to a “wrong” estimation of the exponent (Niwa, 1998; Bonabeau et al., 1998, 1999). I make use of the data collapse to extract the “right” exponent. From Eqs. (8) and (12), when  $y = W^{(G)}(R)/\langle R \rangle_P$  is plotted against  $x = R/\langle R \rangle_P$  with correct parameter  $\nu$ , all the empirical data should collapse onto each other. The power-law exponent of school-dimension distributions,  $\nu$ , is then evaluated through data collapse. Let us search for the value of  $\nu$  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 (1990) off southeastern Hokkaido for seven years, 1981–1987. Hara (1986) 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. 2a), and for each bin two-dimensional variance

$$\varepsilon = (\sigma_x/\mu_x)^2 + (\sigma_y/\mu_y)^2 \quad (14)$$

is calculated, where  $\sigma_x$  and  $\sigma_y$  denote the standard deviation of the mean  $\mu_x$  and  $\mu_y$ , respectively. The parameter  $\nu$  is then estimated at value that minimize the mean of two-dimensional variance for the bins (Fig. 2b).

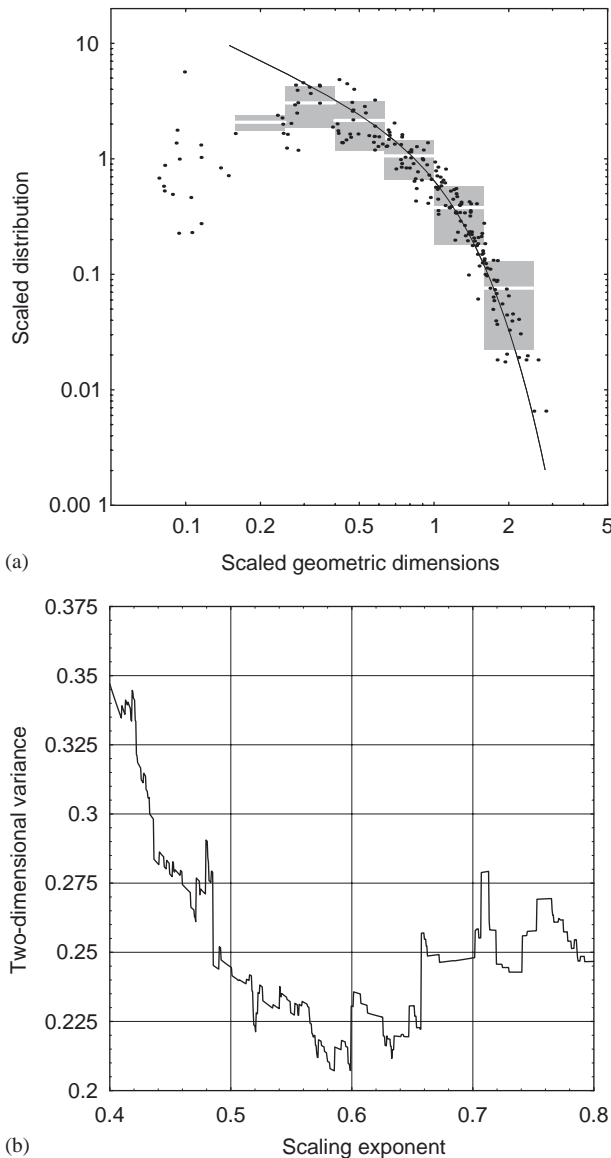


Fig. 2. Data collapse to extract the exponent  $\nu$ . (a) Scaled distribution of geometric dimensions of sardine schools.  $y = W^{(G)}(R)_P$  is plotted versus  $x = R/(\langle R \rangle)_P$  with  $\nu = 0.6$  on double-logarithmic scale. The bins are chosen equally spaced on a logarithmic scale as  $x \in [10^{-1+k/5}, 10^{-1+(k+1)/5})$  with  $k = 1, 2, \dots, 6$ . The rectangle in gray reads the interval  $\mu_y \pm \sigma_y$ , i.e. the error  $\sigma_y$  on the mean  $\mu_y$  (indicated by the slit) for each bin. The solid line is a prediction of the mean-field theory (Niwa, 2003). (b) The mean of two-dimensional variance,  $\bar{\varepsilon}$ , versus the power-law exponent  $\nu$ . Although  $\bar{\varepsilon}$  shows noisy fluctuations, it takes a minimum around  $\nu = 0.6$ . Data from Hara (1990) are analysed.

The mean of two-dimensional variance,  $\bar{\varepsilon}$ , is a measure to determine the goodness of collapse (Lillo et al., 2002, 2003; Niwa, 2004a). 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. 2a. Experimentally fitting the parameter  $\nu$  to achieve a good data collapse, “ $\frac{3}{5}$ ”, 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 (Flory, 1953; de Gennes, 1979).

Here we see that the power-law regime of the distribution is too short, which misled Anderson (1981) and Niwa (1996b) into overlooking the power-law distributions of school sizes. Notice that many power laws that appeared in the ecology literature span less than two orders of magnitude of scale (Halley et al., 2004). The power-law range of too few scales is not unique to ecology; the largest numbers of power laws reported in the physical science are for small ranges (Hamburger et al., 1996).

## 2.2. Retest of the FSS in school-biomass distributions

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

$$W(N)\Delta N \propto W^{(G)}(R)R^{1/\nu-1}\Delta R. \quad (15)$$

We now crosscheck the value of  $\nu$  through FSS analysis of school-biomass distribution (Niwa, 2004a). Since the finite population size causes the truncation of power-law distribution  $W(N) \propto N^{-\beta}$ , there is a well-defined quantity

$$L = \frac{\sum_i N_i^{1+\beta} W_i \Delta N}{\sum_i N_i^{\beta} W_i \Delta N}, \quad (16)$$

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  $N/L^A$ ,

$$W(N; L) dN = L^{-B} F(N/L^A) d(N/L^A), \quad (17)$$

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

$$\sum_i N_i^{\beta} W_i \Delta N = 1, \quad (18)$$

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,  $\beta$ , is then evaluated through FSS analysis. The value of  $B/A$  is the estimate

of the power-law exponent

$$\beta = \frac{B}{A}. \quad (19)$$

Let us analyse a set of 22 acoustic-survey data of sardine schools (same as Fig. 2) converted into biomass histograms by using Eq. (15) with  $\nu = \frac{3}{5}$ . In a simultaneous best-fitting procedure (Fig. 3), 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. 3a. The school-biomass distribution follows a power-law decay with exponent  $-1$ , and is truncated at the cut-off size of Eq. (7). The FSS collapse confirms the scaling laws for school sizes, Eq. (5) with  $\nu = \frac{3}{5}$  and Eq. (6) with  $\beta = 1$ .

Finite-size scaling techniques have been applied to ecology and shown to predict scaling relations between scaling exponents in relative abundance of species [Eq. (4)] (Banavar et al., 1999; Aji and Goldenfeld, 2001), in dynamics of breeding bird populations (Keitt et al., 2002), in biomass-size distributions of seston (Rinaldo et al., 2002), and in exploitation of fish stocks (Niwa, 2004b). In school-size statistics, we expect to have a scaling relation. We now choose the normalization

$$\sum_i N_i W_i \Delta N = \Phi, \quad (20)$$

where  $\Phi$  denotes the total fish population in the school system ( $\sum_i W_i \Delta N$  gives the total number of schools). Since Eq. (16) implies  $L^A \propto \Phi^\gamma$  with a scaling exponent  $\gamma$ , the FSS relation for the school-biomass distribution is written as

$$W(N) = N^{-\beta} P(N/\Phi^\gamma). \quad (21)$$

Accordingly, the normalization of Eq. (20) yields the scaling relation

$$2 - \beta = 1/\gamma. \quad (22)$$

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

$$\langle N \rangle_P \propto \Phi, \quad (23)$$

which is verified by means of extensive numerical simulations (Niwa, 2003, 2004a).

### 3. Behavioral algorithm of fish schooling

#### 3.1. Gaussian model

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

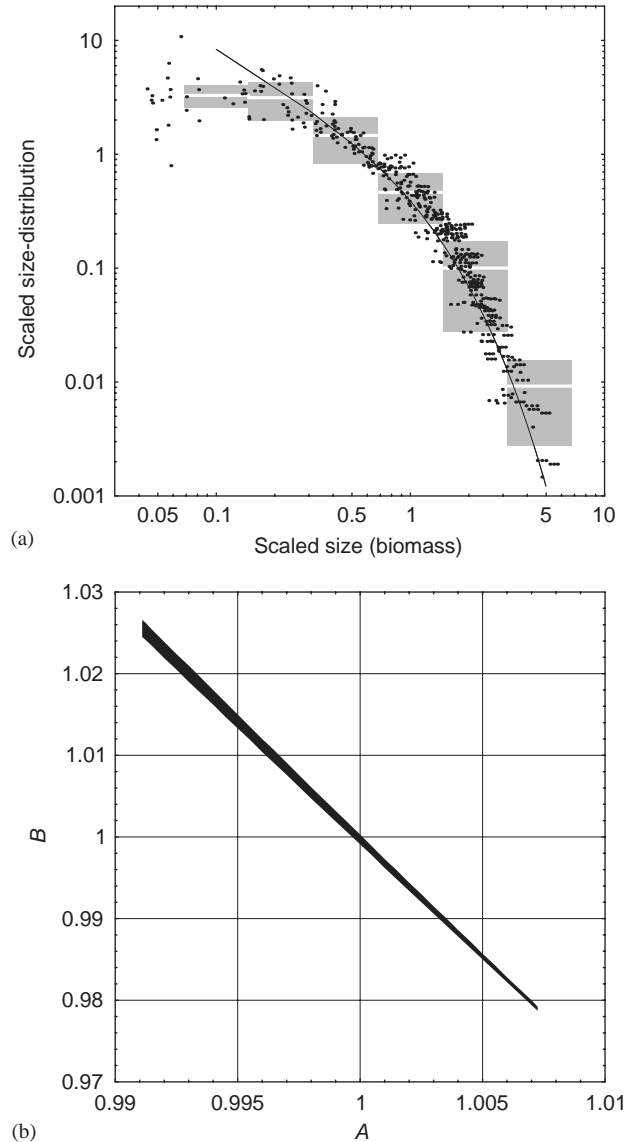


Fig. 3. FSS analysis of school-size data. (a) FSS plot of the biomass distribution on double-logarithmic scale. Dimension data of sardine schools (same as Fig. 2) are converted by Eq. (15) with  $\nu = \frac{3}{5}$ . Here  $y = WL^{A+B}$  is plotted versus  $x = N/L^A$  with  $A = B = 1$ . Two-dimensional variances [same as Eq. (14)] 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. 2. The solid line is a prediction of the mean-field theory (Niwa, 2003). (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,  $\bar{\varepsilon}$ , takes a minimum  $\bar{\varepsilon}_{\min}$  for the right choice of  $(A, B)$ . The minimum is found with the precision i.e., width of the minimum,  $\Delta\varepsilon = 10^{-3}$  in black region ( $\Delta\varepsilon/\bar{\varepsilon}_{\min} \approx 3.12 \times 10^{-3}$ ). The values of the parameters lie in the intervals  $A = 0.999 \pm 0.008$  and  $B = 1.003 \pm 0.024$ , and therefore  $\beta = 1.004 \pm 0.032$ .

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 (Dill et al., 1981; Partridge, 1982; Niwa, 1996a). 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 (Niwa, 1994, 1996a):

$$\frac{d^2 \mathbf{r}}{dt^2} = \mathbf{f}(\mathbf{r}) - J \frac{d\mathbf{r}}{dt} + \boldsymbol{\eta}(t), \quad (24)$$

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  $\varepsilon_v$  and a  $\delta$ -correlated time dependence.

### 3.2. Self-consistent calculation of cohesive force

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:

$$\mathbf{f}(\mathbf{r}) = -\frac{\tilde{k}}{N^\alpha} \mathbf{r}, \quad (25)$$

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  $N^\alpha$ . 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 in  $E_{\text{el}} \propto R^4 N^{-\alpha}$ , which is derived from the ideal harmonic spring, Eq. (25). Therefore, the exponent  $\alpha$  will be determined self-consistently,

$$\frac{R^4}{N^\alpha} \propto N. \quad (26)$$

The solution of the Langevin equation (24) with Eq. (25) takes the following asymptotic forms (Hori, 1977):

$$\sigma_v^2 [\equiv \langle (d\mathbf{r}/dt)^2 \rangle] \approx 3\varepsilon_v/J, \quad (27)$$

$$\langle r^2 \rangle \approx \frac{\sigma_v^2}{\tilde{k}} N^\alpha, \quad (28)$$

where the root-mean-square  $\sqrt{\langle r^2 \rangle}$  gives the average radius of the school,  $R$ . From Eq. (26) together with Eq. (28), the self-consistent value of the exponent  $\alpha$  is obtained

$$\alpha = 1. \quad (29)$$

As a consequence, the self-consistent cohesive force reads

$$\mathbf{f}(\mathbf{r}) = -\frac{\sigma_v^2}{b^2 N} \mathbf{r}, \quad (30)$$

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  $bN^{1/2}$ . Note that Eq. (27) is an example of a more general principle called the fluctuation–dissipation theorem (Kubo, 1966).

Notice that the above model has been developed in the absence of the excluded volume interactions. Social cohesion by harmonic spring interactions between neighboring fish reminds us of the classical picture of a polymer chain based on the bead-spring model (Rouse, 1953). The exponent  $\nu$  close to the value  $\frac{3}{5}$  may then be understood by taking the excluded volume effect (Doi and Edwards, 1986). Such a school without excluded volume effect may be called the “Gaussian” school in line with polymer physics.

### 3.3. The excluded volume effect

From Eq. (24), the probability of the school radius being between  $r$  and  $r + dr$  is given by the following (Hori, 1977):

$$\Psi_0(r) = 4\pi r^2 \left( \frac{3}{2\pi b^2 N} \right) \exp\left( -\frac{3r^2}{2b^2 N} \right) \quad (31)$$

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. (31), 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  $p(r)$ . The approach is due to Doi (1996). 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

$$p(r) = (1 - w/r^3)^{N(N-1)/2} = \exp\left( -\frac{wN^2}{2r^3} \right), \quad (32)$$

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

$$\Psi(r) = \Psi_0(r)p(r) \propto r^2 \exp\left(-\frac{3r^2}{2b^2N} - \frac{wN^2}{2r^3}\right) \quad (33)$$

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  $R_0 = (2b^2N/3)^{1/2}$ . The maximum of  $\Psi(r)$  occurs at  $R$ , which satisfies the following equation obtained by differentiating the logarithm of Eq. (33):

$$\left(\frac{R}{R_0}\right)^5 - \left(\frac{R}{R_0}\right)^3 = \frac{9\sqrt{6}}{16} \frac{w\sqrt{N}}{b^3}. \quad (34)$$

If  $N \gg 1$ , the second term on the left-hand side of Eq. (34) can be neglected and hence

$$R \simeq R_0 \left(\frac{w\sqrt{N}}{b^3}\right)^{1/5} \propto N^{3/5}. \quad (35)$$

The exponent  $\frac{3}{5}$  is the very value extracted through the data collapse.

The scaling in the relationship between geometric dimensions and biomass of pelagic fish schools is analogous to that developed in polymer physics (de Gennes, 1979). The result suggests that the dynamics are unexpectedly “simple” and depend primarily on common cohesive motion in these animate and inanimate systems. Though the above is a very rough theory of school conformation with the excluded volume effect, the overall statistical properties do not depend on the details of the model, which is a consequence of universality (Stanley, 1995).

### 3.4. Exploiting the analogy to a polymer chain model

As indicated in the Introduction, large internal variations in packing density occur within a school. Fréon and Misund (1999) pointed out that a source of substantial variation in internal school structure is the formation of subgroups. Such subgroups have been observed in saithe schools (Partridge, 1981), and in schools of minnow *Phoxinus phoxinus* (Pitcher, 1973) and herring (Pitcher and Partridge, 1979). 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” (de Gennes, 1979): the polymer chain behaves as a series of blobs. Based on the blob concept, for small value of the excluded volume  $w$ , a subgroup within a school, with a number of  $\lambda_B$  of fish, must be nearly Gaussian. We see this from Eq. (33) when we find no effect of  $w$  if  $w\lambda_B^{1/2}/b^3 < 1$ . There is a

certain value of  $\lambda_B[\sim (b^3/w)^2]$ , beyond which excluded volume effects become important. A single school will appear Gaussian at scales  $r < r_B$  where

$$r_B \simeq b\lambda_B^{1/2} \simeq b^4/w, \quad (36)$$

while at scales  $r > r_B$  it will show excluded volume effects. According to the “blob” approach, an  $N$ -sized school can be described as a cluster of  $N/\lambda_B$  subgroups. Inside the subgroup the core repulsion (by excluded volume effects) is a weak perturbation leading to a Gaussian state. The school radius is then written as  $R \simeq r_B(\lambda_B^{-1}N)^v$  in the native state.

Notice the plasticity of school geometry and internal structure. The compact, dense packing, as observed in artificial environments like small tanks, may be caused by the very strong stress. When the school is confronted by danger such as predators, the inter-fish distance decreases rapidly and all the vacuoles within the school collapse quickly (Fréon et al., 1992). This change may be closely related to the coil-globule transition in a polymer solution (Ptitsyn et al., 1968; de Gennes, 1975).

In real schools the nature of the short-range interaction is quite complicated like van der Waals-type intermolecular forces. Accordingly, all fish within a school interact via the two-body potential deformed from a parabolic potential of harmonic spring [grouping forces have been expressed as the gradient of a potential function in previous model studies (Mogilner et al., 2003)]. The potential change, denoted by  $\Delta U_{ij}$ , is given as the correction term to cohesive interaction potential between the  $i$ th and the  $j$ th fish:  $\Delta U_{ij}$  will include steric effects and also may involve weak attractions. The correction factor to the probability distribution  $\Psi(r)$  of the school radius  $r$ , in place of Eq. (32), is then given by the configuration integral

$$p(r) \simeq r^{-3N} \int \cdots \int \exp\left(-J \sum_{i < j} \Delta U_{ij}/\varepsilon_v\right) \times d\mathbf{x}_1 \cdots d\mathbf{x}_N, \quad (37)$$

where  $\mathbf{x}_i$  denotes the position vector of the  $i$ th fish, and  $\exp(-J\Delta U_{ij}/\varepsilon_v)$  is integrated over the school configuration space. We can estimate  $p(r)$  by means of the cluster expansion (Mayer and Mayer, 1940; Uhlenbeck and Ford, 1962). Introducing a function of separation between pairs,  $\mathbf{r}_{ij} = \mathbf{x}_j - \mathbf{x}_i$ ,

$$\zeta_{ij} = \exp(-J\Delta U_{ij}/\varepsilon_v) - 1, \quad (38)$$

we integrate Eq. (37) in the Mayer cluster expansion over diagrams up to the second irreducible cluster, yielding

$$p(r) \simeq \exp\left(-\frac{wN^2}{2r^3} - \frac{w_\Delta N^3}{6r^6}\right) \quad (39)$$

with the excluded volume parameter

$$w = - \int \zeta_{12} d\mathbf{r}_{12}, \quad (40)$$

and the other parameter defined by

$$w_{\Delta} = - \int \int \zeta_{12} \zeta_{13} \zeta_{23} d\mathbf{r}_{12} d\mathbf{r}_{13}. \quad (41)$$

The actual configuration is decided by maximizing the distribution function  $\Psi(r) = \Psi_0(r)p(r)$ , and this maximization condition leads to the equation determining the school radius  $R$ ,

$$\left(\frac{R}{R_0}\right)^5 - \left(\frac{R}{R_0}\right)^3 - \frac{27w_{\Delta}}{16b^6} \left(\frac{R}{R_0}\right)^{-3} = \frac{9\sqrt{6}}{16} \frac{w\sqrt{N}}{b^3}. \quad (42)$$

Notice that, when the first irreducible cluster integral in Mayer's expansion is only taken into account, the configuration integral, Eq. (37), is evaluated by Eq. (32). In case that  $\Delta U_{ij}$  consists of a hard core repulsion and a short-range weak attraction (i.e. at the distance of near-collision ( $r \sim w^{1/3}$ ) the attraction gradient between fish becomes steeper), Eq. (40) is estimated as  $w = w_0(1 - \varepsilon_{\theta}/\varepsilon_v)$ , expressing the dependence of  $w$  on the velocity-fluctuation  $\varepsilon_v$  of fish, where  $w_0$  and  $\varepsilon_{\theta}$  are constants (Doi and Edwards, 1986). During predation threats or laboratory observations, the value of excluded volume parameter  $w$  will change sign from positive to negative, provided that the velocity fluctuation  $\varepsilon_v$  is suppressed below a certain value  $\varepsilon_{\theta}$ . Decreasing  $\varepsilon_v$  below  $\varepsilon_{\theta}$ , the dimensional size of the school becomes much smaller than that of a Gaussian school, as depicted in Fig. 4. According to Eq. (42) the so-called “expansion factor”  $R/R_0$  is determined not by  $w$  but by  $wN^{1/2}$ , and so if  $N$  is large only a small change in  $\varepsilon_v$  will cause a big change in dimensional size. For example, for school of  $10^6$  fish, a small variation in  $\varepsilon_v$  will induce a dramatic change in the school radius. Eq. (42) states that when  $-wN^{1/2}/b^3 \gg 1$ ,  $R/R_0$  is proportional to  $(-wN^{1/2})^{-1/3}$  and hence the solution is as follows:

$$R \simeq R_0 \left( \frac{-wb^3\sqrt{N}}{w_{\Delta}} \right)^{-1/3} \propto N^{1/3}, \quad (43)$$

which shows the closest packing of fish in a school, i.e. the constant density independent of the number of individuals. This change may be called the swollen-dense packing transition of schools.

### 3.5. Configuration inside a swollen school

The approach of treating fish schools as interacting particle systems naturally leads to the idea of applying successful methods of statistical physics to the description of moving together without a leader (Vicsek, 2001). In statistical physics, the presence of non-trivial scaling is usually taken to mean that the dynamics are largely governed by simple geometric properties of the system

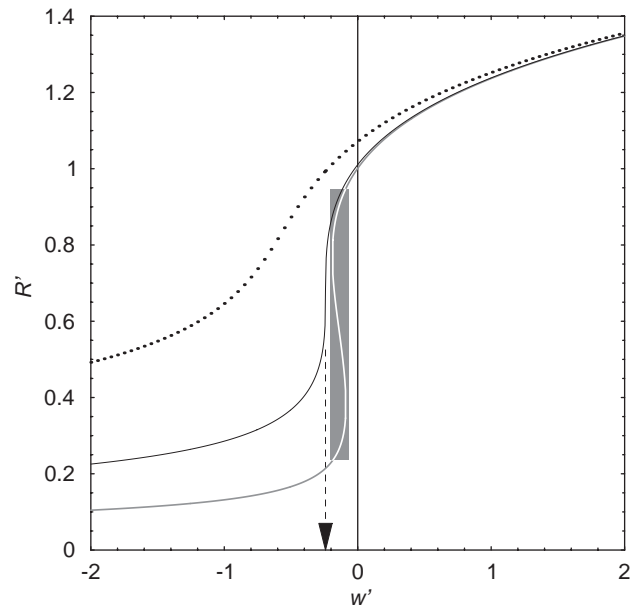


Fig. 4. Swollen-dense packing transition in the school geometry [the solution of Eq. (42)]. Here  $R' = R/R_0$  is plotted as a function of a combined variable  $w' = (9\sqrt{6}/16) wN^{1/2}/b^3$ . Shown is the transition region  $|w|N^{1/2}/b^3 \approx 1$ . At  $\varepsilon_v = \varepsilon_{\theta}$  the excluded volume parameter  $w$  equals 0. The repulsive excluded volume effect then balances the attractive forces between fish, and the school behaves as a Gaussian school. The property of the swollen-dense packing transition is quite different in the two regions separated by the critical value  $w_{\Delta}/b^6 = 0.0228$ . The transition between the swollen conformation and the compact packing is gradual when  $w_{\Delta}/b^6 > 0.0228$  (dotted line), while it becomes extremely sharp and the transition is discontinuous when  $w_{\Delta}/b^6 < 0.0228$  (gray line). The solid line shows the marginal transition behavior, and the crossover takes place when  $w' = -0.242$  (indicated by the arrow). Notice that the solution of Eq. (42) is multivalued [depicted by a sigmoid curve (white cutout)], showing a first-order discrete phase change (Ptitsyn et al., 1968; de Gennes, 1975), when  $w_{\Delta}/b^6 < 0.0228$ .

and do not depend strongly on detailed properties of the system components (Wilson, 1983).

As for the school geometry, the basic units are the effective inter-fish length  $b$  and the number of fish,  $N$ . We assemble  $\lambda$  neighboring fish in a school into  $N/\lambda$  groups, e.g. in the sense of the Voronoi–Dirichlet diagram (Dirichlet, 1850; Voronoi, 1908, 1909). The length between centers of neighboring subgroups is defined by  $\lambda^{\tilde{v}}b$  with an exponent  $\tilde{v}$ . After such a scale change as

$$N \rightarrow \lambda^{-1}N, \quad b \rightarrow \lambda^{\tilde{v}}b, \quad (44)$$

the macroscopic quantities which determine the overall properties of the school satisfy

$$g(\lambda^{-1}N, \lambda^{\tilde{v}}b) = \lambda^{\chi}g(N, b), \quad (45)$$

where  $\chi$  is an exponent which depends on the quantity under consideration. For this to hold true for arbitrary  $\lambda$ , the function  $g(N, b)$  must take the scaling form

$$g(N, b) = N^{-\chi}g^{(sc)}(bN^{\tilde{v}}), \quad (46)$$

where a new function  $g^{(\text{sc})}$  is introduced. This is the Widom–Kadanoff scaling law in critical phenomena (Goldenfeld, 1992). For example, the average radius of the school,  $R$ , should be unaltered under the transformation of Eq. (44):

$$R(N, b) = R(\lambda^{-1}N, \lambda^{\tilde{\nu}}b) = R^{(\text{sc})}(bN^{\tilde{\nu}}). \quad (47)$$

Because of Eq. (5),  $R^{(\text{sc})}(x) = x$  and we must have

$$\tilde{\nu} = \nu, \quad (48)$$

where  $\nu = \frac{3}{5}$  in three dimensions.

As an example of the application of the above scaling law, let us consider the pair correlation function inside a school, where fish movement take place in a three-dimensional space. A pair correlation function  $\rho_2(r)$  is defined as follows. We pick one fish at random in the school, and we place it at origin. Then we ask, what is the number density of other fish at a (directional) distance  $r$  from the first, and we average the result over all choices of the first fish (and of directions). The function  $\rho_2(r)$  has an integral which is just the total number of fish per school,  $\int \rho_2(r) dr = N$ . Hence, from dimensional analysis, we can write

$$\rho_2(r) = R^{-3}g(N, r/b). \quad (49)$$

Under the transformation that neighboring  $\lambda$  fish are grouped to form one subunit in a school,  $\rho_2(r)$  will be reduced by  $1/\lambda$ , since the pair correlation function is proportional to the number density of fish. Therefore

$$g(\lambda^{-1}N, r/\lambda^{\nu}b) = \lambda^{-1}g(N, r/b). \quad (50)$$

Then, the function  $\rho_2(r)$  obeys a simple scaling rule

$$\rho_2(r) = NR^{-3}\rho_2^{(\text{sc})}(r/R), \quad (51)$$

where  $\rho_2^{(\text{sc})}$  is a dimensionless universal function, and  $NR^{-3}$  is the dimensional factor. Focusing on the limit  $r \ll R$ , we can reach the form of  $\rho_2(r)$  by a simple argument. In a sphere of radius  $r$  we have a certain number of fish,  $\tilde{N}$ , related to  $r$  by the excluded volume exponent:  $\tilde{N}^{3/5}b \simeq r$ . The function  $\rho_2(r)$  scales like the density of fish in the sphere,

$$\rho_2(r) \simeq \frac{\tilde{N}}{r^3} \simeq \frac{1}{r^{4/3}b^{5/3}} \quad (\text{for } r < R), \quad (52)$$

which gives  $\rho_2^{(\text{sc})}(x) \simeq x^{-4/3}$ .

The possible observable property, Eq. (51), tells us that if we were to measure  $\rho_2(r)$  for fish schools of different size  $N$ , there would be superposition of the curves obtained by plotting  $\rho_2(r)R^3/N$  against  $r/R$ . Thus this kind of scaling relation may be verified experimentally on large schools of pelagic fish.

## 4. Discussion

The power-law scaling generally exists in dimension-to-biomass relationship of pelagic fish schools in nature. Here I have estimated the power-law exponent  $\nu$  of the geometric relation, based on the dependence of the power-law regime of the school-dimension distribution  $W^{(\text{G})}(R)$  on  $\nu$ , i.e. Eq. (11). We have tested whether the distributions  $W^{(\text{G})}(R)$  are self-similar (i.e. exhibit scaling), relying on both the power law for the dimension-to-biomass relationship of Eq. (5) and the FSS relation in the power-law school-biomass distribution of Eq. (6). Plotting the scaled histogram data from the 22 in situ observations, we have found that the 22 curves do indeed collapse onto each other (Fig. 2a), suggesting that  $W^{(\text{G})}(R)$  follows a universal functional form [Eq. (8)]. We have extracted the power-law exponent of dimension-to-biomass scaling relationship via a minimization of a measure to quantify the nature of scaling collapse. Next I have explained the value of the exponent  $\nu$ , proposing the Gaussian school model for the fish with excluded volume  $w$ . By exploiting the analogy between fish-school and polymer conformations, we have examined the behavioral algorithm governing the swollen conformation of large-sized schools. We have seen that the exponent is modified strongly by the steric effect. What is universal in Eq. (5) is the exponent  $\nu \approx 0.6$ : it is independent of species as well as environmental conditions, and the same for all schools. The constant that multiplies  $N^{\nu}$  in Eq. (5) is non-universal [ $\sim (wb^2)^{1/5}$  with effective inter-fish distance  $b$ , predicted from Eq. (35)], and depends on the details of interactions between fish which may vary with species and environmental conditions (Morgan, 1988).

To understand the scaling law for school geometry, Eq. (5) with  $\nu = \frac{3}{5}$ , it is essential to see what the value of  $\nu$  represents. Obviously, for a regular object embedded into a  $d$ -dimensional Euclidean space, Eq. (5) would have the form  $N(R) \sim R^d$  expressing the fact that the volume of a  $d$ -dimensional object grows with its linear size  $R$  as  $R^d$ . Contrary to an integer dimensionality, it has been shown that the packing structure within the schools is characterized by a non-integer (i.e. fractal) dimensionality of  $1/\nu \approx 1.7$ : the number of fish in a school of radius  $R$  scales as  $N(R) \sim R^{1/\nu}$ . During the last decades of the 20th century it has widely been recognized by researchers working in diverse areas of science that many of the structures commonly observed possess a rather special kind of geometrical complexity; the name “fractal” was coined by Benoit Mandelbrot (Mandelbrot, 1982). for these complex shapes. Objects of biological origin are many times fractal-like (Vicsek (Ed.), 2001).

FSS plots of data lead to possibly important and practical insights in ecology. In the context of the fisheries mission, the demonstrated geometric relation

between dimensions and biomass of pelagic fish schools, when applied to mapping pelagic schooling fish, will largely improve the precision in the fish stock assessment. Because of the linear dependence of the fish population on  $\langle N \rangle_P$ , as given by Eq. (23), the fish stock abundance can be inferred from an index (i.e. cut-off size) that can be determined directly from observations [see Eq. (7)].

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