

Possible universality in the size distribution of fish schools

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Motivated by the finding that there seems to be some universality in the size distributions of tropical tuna fish schools over several years and in various conditions, we conjecture that a simple model, inspired by a physical model of particle aggregation [H. Takayasu, *Phys. Rev. Lett.* **63**, 2563 (1989)], can be applicable to many instances of schooling in fish, or even of animal grouping in general. This model, which makes no assumption about the specific details of how fish aggregate to form a school but rather assumes that they are able to do so, predicts not only the power-law behavior observed in nature, but also its particular exponent as well as deviations from pure power-law towards exponential decay.

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I. INTRODUCTION

Some biological phenomena, especially those involving a lot of interacting entities, possess many similarities with physical processes and can be modeled with tools originating from physics [1]. In particular, aggregation or grouping phenomena in biology have numerous counterparts in physics, which have been and still are under intense investigation [2]. Finding bridges between aggregation phenomena in physics and biology may lead to a mutual enrichment of both fields [3]: besides the better understanding of empirical biological observations, common models may help extend the classes of natural phenomena sharing the same characteristic properties, such as “critical” exponents.

Groups of animals in general and schools of fish in particular have attracted a lot of interest for a long time [4] (see also Ref. [5] for a more mathematical review), but have been studied mostly from the viewpoint of the behavioral algorithms which govern their formation and dynamics [6]. Reference [7] is an exception. In the present paper, we propose a simple “statistical” (as opposed to behavioral) model of school formation, based on a physical model of particle aggregation introduced by Takayasu *et al.* [8]. Our approach was motivated by a striking feature of the size distributions $N(s)$ of tropical tuna fish schools (in which three species—yellowfin tuna *Thunnus albacares*, skipjack tuna *Katsuwonus pelamis*, and bigeye tuna *Thunnus obesus*—are mixed): in effect, many such distributions follow a power law $N(s) \propto s^{-\beta}$ up to a cutoff size s_c . The data have been obtained from commercial fisheries [9]: s is the quantity of fish (in tons) caught in a circular net whose perimeter is about 2 km. If s_c seems to depend on specific factors, the exponent β looks universal: from our field data, $\beta = \frac{3}{2}$ in most cases (β ranges from 1.39 to 1.67 with a peak at 1.5). A log-log plot of $N(s)$ over 7 years is represented in Fig. 1. The data have been binned so as to avoid large fluctuations in the graph: the original data exhibit a power-law behavior with fluctuations

over about or more than two decades. Other data (not represented here) originating from measurements performed in different conditions (such as in the vicinity of a fish-aggregating object—e.g., a wreck) confirm this observation.

In order to account for this apparent stability of β , a model should be simple and robust enough that it could apply to a wide spectrum of conditions and individual aggregation behaviors: this is precisely the case of Takayasu *et al.*'s model [8]. Note that this model has been applied to river network formation, to vortex aggregation in turbulence [10], or to cloud formation [11]. Alternative but related models of coagulation-fragmentation, based on a Smoluchowski rate equation including a breakup kernel, are also available with comparable results [12]. We chose Takayasu *et al.*'s model because the properties we are interested in can be easily and elegantly extracted. As we shall see, simple modifications of the model may destroy the critical nature of the process, but the exponent remains, e.g., $N(s) \propto s^{-3/2} e^{-s/s_c}$ (consistent with a number of numerical experiments [12], or more generally $N(s) \propto s^{-3/2} f(s/s_c)$, where the particular

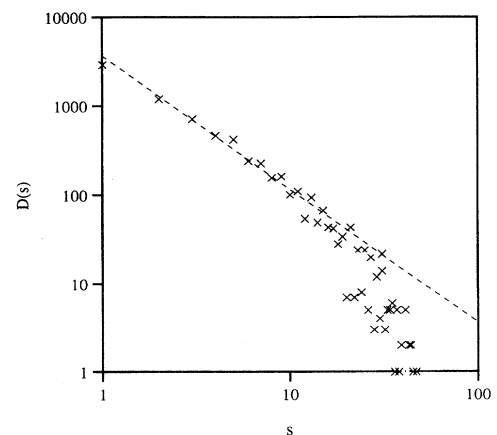


FIG. 1. Log-log plot of $N(s)$ vs s (in tons). Data from commercial fisheries in the vicinity of Cape Lopez, over 7 years (1976–1982) [9]. The dashed line corresponds to a pure power law with $\beta = \frac{3}{2}$.

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form of the scaling function f depends on the details of the aggregation and breakup processes. From the field data, we also find in one case (out of 14) an exponentially decreasing size distribution (year 1981: see Fig. 2), therefore characterized by no well-defined exponent: the present model can also explain these deviations from power-law behavior through several possible modifications which tend to decrease s_c . The cutoff size s_c within this model could simply be a side effect of the general aggregation process combined with the finiteness of the number of fish. In reality, however, the cutoff size may stem from additional factors, such as some heterogeneity in the speed capacities of the fish composing the school (the slower fish cannot follow the leaders), or the capacity of a school to maintain its integrity over a certain amount of time, or can be computed from optimality considerations (tradeoff between school size and prey density [13]). Implicit inclusion of such additional factors into the model is easy: it suffices to assume that, e.g., a school of size s has a probability $P_{\text{split}}(s) \propto 1 - e^{-s/\sigma}$ to split, where the characteristic size σ is an explicit parameter of the model integrating all of the above mentioned factors. The observed cutoff size in the distribution will then result from the competition between aggregation and breakup. How schools split (even from a simple statistical viewpoint) is yet another challenging question that can be tested only numerically, for lack of clear experimental data.

II. MODEL AND RESULTS

The only biological assumption underlying the model is the tendency of schools of fish to aggregate when they meet. Such a tendency can be viewed as an extension of the concept “biosocial attraction,” i.e., a mutual attraction of individuals (usually associated with polarization as a condition for school formation) (see the review by Shaw [14]). This assumption is clearly minimal.

We further assume for modeling purposes that there are N sites (coarse-grained zones of space) between which n fish move. A single fish is considered as a 1-school; m fish swimming together form an m -school. One (tuna) fish may not be the right atomic unit, since field observations suggest that no

school exists under a certain “minimal” size: a 1-school should then be considered as an atomic object, which may contain a certain number of or correspond to a certain weight of fish. When an m -school and an h -school happen to move to the same site, they aggregate to form an $(m+h)$ -school. At each discrete time step, all schools move towards a randomly selected site. They may move to any site with equal probability. This corresponds to the mean-field theory of Takayasu *et al.*’s model [8], which is justified here because of the high potential speed of the fish: they can swim from 1 up to 100 km within one single day. We may therefore assume that there is no spatial effect so that the mean-field theory is most appropriate. It can be shown analytically that in the presence of injection, this simple aggregation process, in which “particles” move randomly and aggregate to form a larger mass particle when they encounter, leads to a stationary power-law distribution with the desired index [8]. Introducing the characteristic function of the size distribution $Z_1(\rho, t) \equiv \langle \exp[i\rho s] \rangle$ where $\langle \dots \rangle$ denotes the average over all possible realizations of the process, we have $Z_1(\rho, t+1) = \Phi(\rho) e^{Z^{-1}(\rho, t)-1}$ where $\Phi(\rho)$ is the characteristic function of the injection random variable. To see this, let us write the distribution $D(s, t+1)$ of s -schools at time t , as a function of $D(s, t)$:

$$D(s, t+1)$$

$$= \sum_{r=1}^N \binom{N}{r} \left(\sum_{s_1+s_2+\dots+s_r=s} p(s_{\text{inj}}) \prod_{i=1}^r D(s_i, t) \right),$$

where s_{inj} is the size of a particular realization of the injection. This formula is equivalent to

$$Z(\rho, t+1) = \Phi(\rho) \sum_{i=1}^N \binom{N}{r} [Z(\rho, t)]^r,$$

hence the result. $\Phi(\rho)$ can be expanded as $\Phi(\rho) = 1 + i\langle I \rangle \rho - (\langle I^2 \rangle / 2) \rho^2 + \dots$. Taking the limit $N \rightarrow \infty$, one obtains the steady-state characteristic function $Z_1(\rho) = 1 - \sqrt{2} \langle I \rangle^{1/2} |\rho|^{1/2} i^{-1/2} + \dots$, so that the size distribution satisfies $D(s) \propto s^{-3/2}$ [15] for large enough s ($s \gg \langle I \rangle$). It can be shown that this steady-state distribution is also an attractor of the dynamical process described above, and that *any* perturbation is absorbed [10,16]. Therefore, starting from any initial condition, one should converge towards the power-law distribution. Computer simulations show that this prediction is robust and holds, up to a cutoff size, when the model is modified so as to take various factors into account: schools may split or disintegrate in many ways, fish may die, etc.

Let us take the following example, where n is maintained constant over time: we assume that a fraction p of each school is separated from the school, and that the corresponding pn fish are reinjected to the N sites. Consequently, the expectation of the injection is pn/N . To see how the previous model without loss is affected by the breakup process, let us write, once again $D(s, t+1)$: in the present case, we have

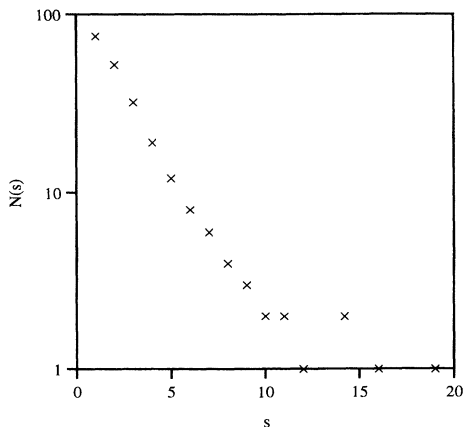


FIG. 2. Same as Fig. 1, but with a semilogarithmic scale and only for 1981.

$$D(s, t+1) = \sum_{r=1}^N \binom{N}{r} \left((1-p)^{(s_1+s_2+\dots+s_r+s_{\text{inj}})=s} p(s_{\text{inj}}) \right. \\ \left. \times \prod_{i=1}^R D(s_i, t) \right),$$

since it takes a total weight of $s/(1-p)$ hopping onto the same site to get a weight of s at that site after the removal of a fraction p (we have assumed for simplicity that the removal of particles occur after the injection, but another choice leads to essentially similar results). We then obtain $Z_1(\rho, t+1) = \Phi((1-p)\rho) e^{Z_1((1-p)\rho, t)-1}$. Note that this last equation does not ensure the conservation of the total weight in the process for *arbitrary* Φ , but we chose here a *specific* injection function, represented by the characteristic function Φ , which precisely conserves the total mass. It follows from this equation that $Z_1(\rho) = 1 - i\langle s' \rangle \rho + \dots$. Therefore the size distribution is short ranged with a finite mean $\langle s' \rangle = [(1-p)n]/N$. $\langle s' \rangle$ is a mean taken over occupied *and* empty sites, i.e., it includes the statistics of 0-schools. The mean $\langle s \rangle$ we are interested in does not include empty sites, and is related to $\langle s' \rangle$ through $\langle s \rangle = \langle s' \rangle (N/N^+)$, where N^+ is the number of occupied sites. To evaluate N^+ in the stationary state, let us write the evolution equation of N^+ , neglecting encounters of order higher than 2:

$$N^+(t+1) \approx N^+(t) + pn - \frac{[N^+(t) + pn][N^+(t) + pn - 1]}{2N^2},$$

provided N is large enough. We therefore obtain $\langle s \rangle \propto [(1-p)/p^{1/2}](n^{1/2}/N)$. We see that $\langle s \rangle$ increases with decreasing p . In the present case, the total mass of fish being conserved, there must be a finite mean, but what is more important is that the size distribution retains some of its power-law characteristics: in effect, the distribution is exponentially decreasing only for large sizes, but follows $D(s) \propto s^{-3/2} e^{-s/(s)}$, exhibiting a power-law behavior for medium sizes $0 \ll s \ll \langle s \rangle$. Of course, when $\langle s \rangle$ is small, the power law is not observed, but only an exponential decay. To illustrate this, we have performed simulations with different values of p . For a relatively small value of p (e.g., $p=0.1$), we observe a clear power law up to a cutoff size (Fig. 3), while for larger p (e.g., $p=0.5$) the distribution is exponentially decreasing (Fig. 4). In a related model (of cloud formation), the authors of Ref. [12] observed only the exponential decay because their simulations, though different, were similar to those we performed with a high value of p .

In the previous calculations, we have assumed that all “splitting” fish were equally redistributed between all sites, while this may not be the case: a group of fish separating from their school can very well stay together and be reinjected into the system as a whole; the size distribution of splitting groups can also be a parameter on its own. Moreover, as mentioned in the Introduction, the probability for a school to split may be related to its size. As an illustration, Fig. 5 represents the size distribution with $p=0.01$ and a uniform splitting for any school with a size greater than a maximum allowed size $s_{\text{max}}=50$ [i.e., $P_{\text{split}}(s)=0$ if $s \leq 50$

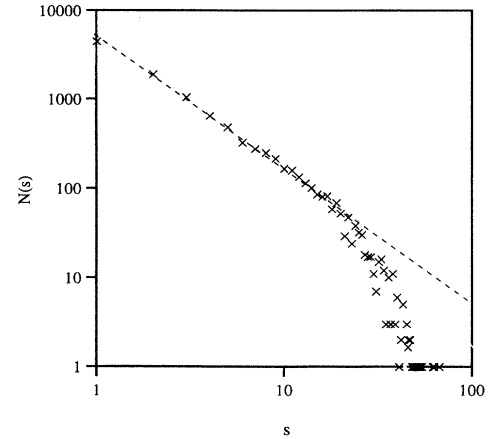


FIG. 3. Log-log plot of $N(s)$ vs s . Simulation with $N=300\,000$ sites, $n=80\,000$ individuals, $p=0.1$. Simulation run = 10^6 time steps. This curve is obtained from 1 run; all runs yield similar curves.

and $P_{\text{split}}(s)=1$ if $s>50$]. But all simulations show that these additional parameters do not qualitatively modify the results: a power-law behavior with index $\beta=3/2$ is observed, with a (somewhat more complicated) crossover to an exponential decay around a given size which depends on the values of the parameters. In particular, the cutoff size results from a competition between aggregation and disintegration and therefore crucially depends on the associated time scales. For instance, a tropical tuna fish school such as those studied in this paper is capable of maintaining its integrity over several days to several weeks (low disintegration rate, certainly related to migratory capacity), while other fish, such as the spottail shiner (*Notropis hudsonius*) [17], are only “occasional” schoolers [18,5], whose schools can hardly be maintained beyond a minute. In the first case, we observe a clear power-law distribution up to the cutoff size, while in the second case the distribution is clearly exponential. A purely exponentially decreasing distribution may also occasionally appear in the first case, e.g., in a period of intense fishing: this model then predicts an exponentially decreasing distribution, such as the one observed in 1981.

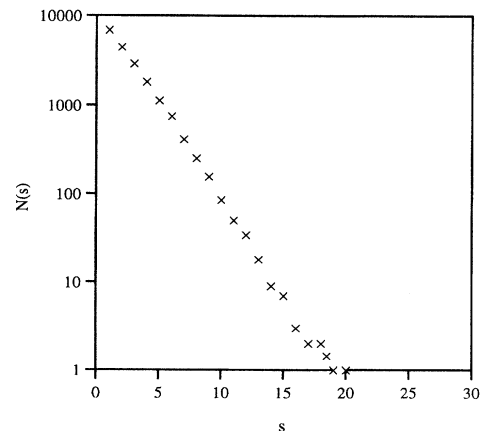


FIG. 4. Same as Fig. 3, but with a semilogarithmic scale and $p=0.5$.

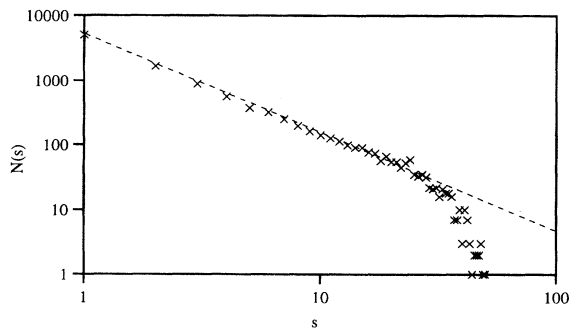


FIG. 5. Same as Fig. 3, with $p=0.01$ and with uniform splitting above $s=50$, i.e., any school with $s>50$ divides into two schools of sizes s' and $s-s'$ where s' is uniformly distributed in the interval $[1, s-1]$.

III. CONCLUSION

In conclusion we have presented evidence that a simple model of particle aggregation [8] can account for the observed power-law exponent in the size distribution of tropical tuna fish schools. The power law, up to a cutoff size, is robust enough to resist many modifications of the model necessary to take various biological or environmental factors into account. Purely exponential distributions appear as the disintegration rate increases in whatever form. Therefore we have shown that if the cutoff size certainly depends on factors external to the model, the exponent β appears to be universal. To speak of (biological) universality, however, one should test for the presence of this exponent in other species of fish, or even in other types of animal groups, such as herds of mammals or flocks of birds. Our prediction is that in most grouping phenomena in biology, the size distribution must either be exponential (or, in the vocabulary of Ref. [5], geo-

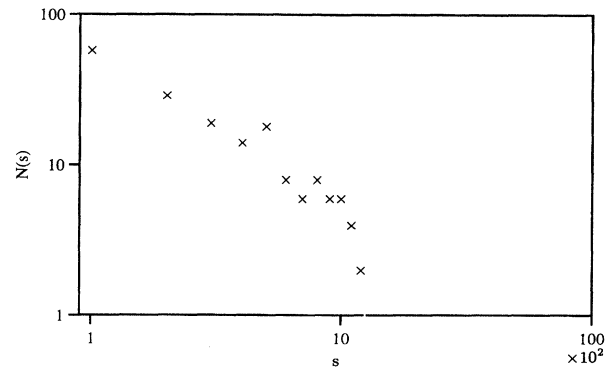


FIG. 6. Log-log plot of the size distribution of herds of African buffalos (s must be multiplied by 100, i.e., s ranges from 10 to 1200).

metric) or follow a power law with an exponent close to $-\frac{3}{2}$ up to a cutoff size if the mean-field theory can be considered biologically valid. In fact, other exponents can be obtained with more complicated combinations of aggregation and breakup kernels, even in the mean-field case [12]. Note that the possibility of power laws was already present in Anderson's model [7], but has not been exploited. A lot of available data seem to fall into the first category, i.e., geometric distributions, although we are certainly not aware of all possible data. Yet, our finding about tuna fish led us to reconsider some existing data, e.g., the size distribution of herds of African buffalos (*Syncerus caffer*) [19]: we found that this distribution is much better fitted by a power law than by a geometric decay, as was suggested in [5] (see Fig. 6). This clearly supports our conjecture. But the power index is closer to -1.2 than to -1.5 , indicating that spatial effects or other *relevant* factors (such as particular aggregation and breakup functions) must come into play.

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