

Abstract—The dynamics of the survival of recruiting fish are analyzed as evolving random processes of aggregation and mortality. The analyses draw on recent advances in the physics of complex networks and, in particular, the scale-free degree distribution arising from growing random networks with preferential attachment of links to nodes. In this study simulations were conducted in which recruiting fish 1) were subjected to mortality by using alternative mortality encounter models and 2) aggregated according to random encounters (two schools randomly encountering one another join into a single school) or preferential attachment (the probability of a successful aggregation of two schools is proportional to the school sizes). The simulations started from either a “disaggregated” (all schools comprised a single fish) or an aggregated initial condition. Results showed the transition of the school-size distribution with preferential attachment evolving toward a scale-free school size distribution, whereas random attachment evolved toward an exponential distribution. Preferential attachment strategies performed better than random attachment strategies in terms of recruitment survival at time when mortality encounters were weighted toward schools rather than to individual fish. Mathematical models were developed whose solutions (either analytic or numerical) mimicked the simulation results. The resulting models included both Beverton-Holt and Ricker-like recruitment, which predict recruitment as a function of initial mean school size as well as initial stock size. Results suggest that school-size distributions during recruitment may provide information on recruitment processes. The models also provide a template for expanding both theoretical and empirical recruitment research.

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Recruitment as an evolving random process of aggregation and mortality

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The study of recruitment processes has traditionally addressed mortality (predation and starvation) and the effects of patchiness on mortality (Vlymen, 1977; Beyer and Laurence, 1980; Hunter, 1984; Rothschild, 1986); hence the importance of aggregation and mortality in recruitment processes of marine fish populations has long been noted. Ecological processes of starvation, growth, and predation of larval fish, coupled with oceanographic factors show the inherent variability in these processes (Koslow, 1992; Mertz and Myers, 1994, 1995; Pepin, 1991; Rickman et al., 2000; Comyns et al., 2003). In particular Rickman et al. (2000) have indicated the importance of the magnitude of fecundity in the variability of egg and larval mortality. Indeed, Koslow (1992) argued that fecundity and the associated variability in egg and larval mortality will limit our ability to determine stock-recruitment relationships.

Stock-recruitment models have generally emphasized the static results of recruitment processes rather than the dynamics themselves. Indeed, although the classic stock-recruitment models such as the Beverton-Holt and Ricker have been related to microscale processes (Beverton and Holt, 1957; Ricker, 1958; Paulik, 1973; Harris, 1975), the dynamics at those scales were not explored, primarily because there was not a theoretical basis for doing so (Rothschild, 1986). Nevertheless, there is a need to develop a theoretical understanding of small-scale interaction processes during recruitment, particularly as they relate to group formation.

Group-formation (aggregation of fish into schools), schooling (shoaling) behavior, and the evolutionary motivations for formation of schools continue to be important research topics (Pitcher and Parrish, 1993; Landa, 1998). Schooling behavior has variously been attributed to predator-avoidance, predator-attack dilution, and hydrodynamic and foraging advantages (see Pitcher and Parrish, 1993, for a review). One of the first models for school formation was that of Anderson (1981) in which he empirically observed skewed distributions in which small schools were more prevalent than larger ones. Subsequently, Bonabeau and Dagorn (1995), Gueron and Levin (1995), Niwa (1998), and Bonabeau et al. (1999), developed group-size distribution models. In particular, Bonabeau et al. (1999) in comparing group-size distributions of tunas, sardinella, and buffalo suggested that power-law distributions may be quite generic. Niwa (1998) noted that Anderson's original model allowed for power-law distributions. Power-laws are termed scale-free because they exhibit no intrinsic scale. Similarly, existence of a power-law is often referred to as “scaling.”

Recently, power-law distributions have arisen in studies of the physics of small-world and evolving networks (for example the world wide web, actor collaborations, scientific citations [Barabási and Albert, 1999], biological cellular networks [Fell and Wagner, 2000], and ecosystem structure [Solé and Montoya, 2001]). In particular, Barabási and Albert (1999) demonstrated that a randomly evolving network would result in a scale-free degree distribution if the network is growing

(the number of nodes is increasing) and if the new nodes were linked to existing nodes by preferential attachment. Preferential attachment (or the “rich-get-richer” phenomenon) occurs when a new node is linked to an existing node with a probability proportional to the number of links already attached to that node. More formally, the Barabasi and Albert model is created by adding a new node at each time step and by randomly linking it to m existing nodes proportional to the number of links at the existing nodes. After a large number of time steps, the probability of a node having k links (the degree distribution) scales as a power-law $P(k) \sim k^{-\gamma}$, where $\gamma = 3$, independent of m . The Barabási and Albert result differs from the classic random network model of Erdős and Rényi (1960) in which nodes are linked randomly to existing nodes, leading to $P(k) \sim \exp(-\lambda k)$. Subsequent research has expanded on the Barabási and Albert model to examine aging, removal and rewiring of nodes, removal of links, fitness and attractiveness of nodes, and local modifications to preferential attachment (see Albert and Barabási, 2002, for a review of these developments)

The generic occurrence of scale-free school-size distributions suggest that modeling of aggregation and mortality processes using the analogy of random networks may be fruitful. The approach may provide insight into recruitment dynamics and a theoretical basis for further investigation. This study attempts to do that and is organized in the following manner. First, a simulation model of the recruitment process is developed in which aggregation and mortality occur based upon some simple rules of preferential attachment and random attachment. Attachment rules are presented as metaphors for more complex behaviors. Next, analytical models are created that mimic the simulations, and results of the simulations and analytical models are compared. Finally, the implications for existing stock-recruitment models and investigation of recruitment processes are discussed.

Methods

Simulation of individuals in ecology and population dynamics (individual-based models) have become increasingly popular (McCauley et al., 1993). However, it is often difficult to understand the dynamics of large individually based models (Pascual and Levin, 1999). Thus, it is important to obtain models that describe dynamics of groups that incorporate individual behavior (Flierl et al., 1999). The models that are developed here include an individually based model (simulation model) and an analytical model that describes “mean-field” dynamics of the individuals behavior.

Simulation model

The recruiting fish of a year class may be modeled as a network of fish in which a fish “links” to other fish to form schools. (Note that in this context it is assumed that a “school” includes aggregations consisting of a single fish). Thus, the process of aggregation is a process of adding links to nodes (aggregation of schools). Similarly, mortal-

ity is the removal of nodes (fish) and, if there are no more fish in the school, then the removal of schools. A simulation model with simple rules of mortality and aggregation was created to examine the dynamics of these processes.

The simulation model followed individual fish and schools through a recruitment period, i.e., the passage of time until an arbitrary time of recruitment. During a recruitment period fish and schools undergo encounters of mortality and aggregation. Starting at time $t=0$ with S fish, $N_{t=0}$ schools and $k_{i,t=0}$ fish in school i ($i=1,2, \dots, N_0$), simulations were conducted by randomly generating an encounter event (mortality or aggregation). If the event was a mortality, then a school was randomly selected by using the appropriate mortality rate model (m , discussed below). If the size of that school was greater than one, then that size was reduced by one. If the school size was equal to one, then the number of schools was reduced by one and this school was eliminated from the list.

If the event was an aggregation, then two distinct schools were randomly selected by using the appropriate aggregation rate model (w , also discussed below). The two schools were combined, leaving one school whose size was the sum of the two original ones and one fewer total number of schools. The probability of an event being a mortality was $m/(m+w)$ and the converse probability of an aggregation was $1-m/(m+w)$. Time increments of each event were computed using $\Delta t = m^{-1}$ for mortality events and $(mw)^{-1}$ for aggregation events. Results at time t were collated into the number of fish surviving to time t (denoted by R_t), the number of schools, N_t , the school size distribution, $P_t(k)$, and the average school size, \bar{k}_t . Note that $R_t = N_t \bar{k}_t$. Simulations were run until there were no fish left.

Encounter rates The encounter rates, m and w , were based upon random movements in statistical mechanics (Tolman, 1979) in which the encounter rate (U) of objects of type i with objects of type j is described by

$$U = (G_i + G_j) D_i D_j (v_i^3 + v_j^3)^{1/3}, \quad (1)$$

where G_i = the size of the detection space at which object detects object type j ;

D_i = the density of objects of type i ; and

v_i = the velocity (in three-dimensional space) at which object i moves in the environment.

For these simulations the G parameters were scaled to one and the velocity parameters (v 's) were collapsed into two encounter rates: μ for mortality encounters (scaled to unity) and α for aggregation encounters.

Mortality rate In the simulations, mortality of fish is perpetrated by mortality agents. If the mortality agents randomly encounter schools of fish, then the probability of a successful mortality (the removal of a fish from the system) is proportional to the school size k . Under these conditions Equation 1 reduces to Equation 2 with

$$\begin{aligned} G_i &= G_j = 1, (v_i^3 + v_j^3)^{1/3} = \mu; \\ m &= 2\mu ENk, \end{aligned} \quad (2)$$

where E = the density of mortality agents; and
 μ = the encounter rate of fish with mortality agents.

Note that on average Equation 2 reduces to $m = 2\mu E_t N_t \bar{k}_t = 2\mu E_t R_t = -dR/dt$. Hence, if the density of mortality agents is constant throughout the recruitment period, then mortality is density independent and mortality is proportional to abundance. An alternative interpretation of Equation 2 is that the mortality agents randomly encounter fish and that all encounters result in a successful mortality. The mortality model (Eq. 2) will be referred to as m_{di} (for density-independent). It is not expected that m_{di} is the most realistic, but rather it provides a basis for comparison.

A second mortality alternative is where mortality agents randomly encounter schools, whereupon they always perpetrate a successful mortality: $m_N = 2\mu E_t N_t$. This model, like m_{di} , assumes that the density of mortality agents are constant throughout the recruitment period.

For purposes of simulation, the density of mortality agents at the onset of the recruitment process was specified to be unity ($E_0=1$). For the two mortality models, m_{di} and m_N , this meant that $E=1$ throughout a simulation.

More realistic density-dependent mortality models are immediately suggested. The first is a density-dependent model in which the ratio of mortality-agent density to the number of schools remains constant throughout the recruitment period, i.e., E_t/N_t remains constant throughout the recruitment period. This leads to $m_{dN} = 2\mu N^2 k$, where E_t/N_t was set equal to one. In this model the ratio of mortality agents to schools is constant, agents and schools randomly encounter one another, and the probability of a successful mortality (given there is an encounter) is proportional to the number of fish that are in the school that is encountered (mortality success is related *preferentially* toward larger schools).

A second density-dependent model is where the mortality agent density is proportional to the number of fish (E_t/R_t is a constant set equal to one, $m_{dR} = 2\mu R^2 = 2\mu N^2 k^2$). In this model the ratio of mortality agents to the number of fish in the population is constant; agents and schools randomly encounter one another; and the probability of a successful mortality (given there is an encounter) is proportional to the number of fish that are in the school that is encountered (mortality success related *preferentially* toward larger schools). Another interpretation of this model is that agents randomly encounter fish, at which time the fish suffers mortality at a probability independent of school-size characteristics.

A third density-dependent model depicts mortality-agent density proportional to school size (E_t/k_t is a constant set equal to one, $m_{dk} = 2\mu N k^2$). In this model the ratio of mortality agents to mean school size is constant, agents and schools randomly encounter one another, and the probability of a successful mortality (given that there is an encounter) is proportional to the number of fish that are in the school that is encountered. Another interpretation of this model is that agent density is proportional to the number of schools, agents encounter schools *preferentially* according to school size, and the probability of a

successful mortality (given that there is an encounter) is proportional to the number of fish that are in the school that is encountered.

Subsequently it will be shown that the first density-dependent model is related to a Ricker-like stock-recruitment model and the second model is exactly equivalent to a Beverton-Holt model. Definitions of the mortality models are summarized in Table 1. Note that in the initial applications of these mortality models, it is assumed that a mortality encounter results in mortality of one fish. More detailed mortality models in which a number of fish greater than one are removed by mortality may be implemented in the future. Clearly, these would be more biologically realistic in many instances. However, the emphasis of this study is on the possible scaling behavior of school-size distributions. Barabasi and Albert (1999) showed that the scaling behavior of a growing random network is independent of the number of randomly selected links at each time step. With this analogy, simple increases in mortality per encounter are not expected to alter the scaling behavior of the school-size distributions. Therefore, the one-fish-per-mortality-encounter approach was used in these initial simulations.

Aggregation rate

Similar to mortality-rate encounters, aggregations were investigated as 1) random attachment of two unique schools ($w_N = 2\alpha N(N-1)$) and 2) preferential attachment of two unique schools i and j ($w_{pa} = 2\alpha N(N-1)k_i k_j$; [Table 1]). Note, the trivial alternative where there was no attachment, ($\alpha=0$), results in equivalence between the mortality models m_{dN} and m_{dR} ; whereas m_{di} becomes a simple proportional mortality rate. Thus, results of models with $\alpha=0$ are uninteresting in the context of this study and are not presented.

Initial conditions Each simulation was conducted with one of two alternative initial conditions. The first alternative was one of complete disaggregation in which simulations were initiated with S fish, S schools, and one fish in each school ($N_0=S$, $\bar{k}_0=1$). The second alternative initial condition was constructed from the population dynamics of a typical fish population. The main assertion of this alternative is that the eggs or larval fish produced by one female during spawning constitutes one school at the onset of the recruitment process. Thus, the fecundity per female at age is a measure of initial school size and the abundance of females at age is a measure of the frequency of schools of that size. More precisely, the initial condition was constructed for a population of females greater than five years of age (age of maturity), where their fecundity at age, F_{age} , is proportional to weight at age determined from a von Bertalanffy growth equation with parameters $K=0.2$ and $L_\infty=10$, and an allometric parameter of 3: ($F_{age}=1000[(1-\exp(-age(0.2)))]^3$). Abundance at age, A_{age} , was computed with an instantaneous mortality rate of 0.2: [$A_{age}=X\exp(-0.2(age-5))$]. The scalar X was obtained from the approximate solution to $S = \sum F_{age} A_{age}$, where F and A were integer values and S was the initial number of fish

Table 1
Summary of definitions of the mortality models used in this study.

Model	Definition
Mortality rates ¹ :	
$m_{di} = 2\mu Nk$	density-independent
$m_{dN} = 2\mu N^2k$	density-dependent, mortality agents proportional to N
$m_{dR} = 2\mu N^2k\bar{k}$	density-dependent, mortality agents proportional to R
$m_{dk} = 2\mu Nk\bar{k}$	density-dependent, mortality agents proportional to k
$m_N = 2\mu N$	random encounters with schools
Aggregation rates:	
$w_N = 2\alpha N(N-1)$	random encounters with schools
$w_{pa} = 2\alpha N(N-1)k_i k_j$	preferential attachment of schools i and j
Initial conditions:	
Disaggregated	$N_0 = S, \bar{k}_0 = 1$
Aggregated	(see text and Table 2)
Mean field equivalents used in analytical model (see text):	
$m_{di} = 2\mu N\bar{k}$	$m_{dN} = 2\mu N\bar{k}^2$
$m_{dk} = 2\mu N\bar{k}^2$	$m_{dR} = 2\mu N^2\bar{k}^2$
$w_{pa} = 2N(N-1)\bar{k}^2$	
Key to figures of simulation results:	
Figure 1: <i>disaggregated</i>	$m_{di} \quad w_{pa} \quad \alpha = 10^{-6} \quad S = 10^6$
Figure 2: <i>disaggregated</i>	$m_{di} \quad w_N \quad \alpha = 10^{-6} \quad S = 10^6$
Figure 3: <i>aggregated</i>	$m_{di} \quad w_{pa} \quad \alpha = 10^{-6} \quad S = 10^6$
Figure 4: <i>aggregated</i>	$m_{dN} \quad w_{pa} \quad \alpha = 1.5 \times 10^{-6} \quad S = 2 \times 10^6$
Figure 5: <i>aggregated</i>	$m_{dN} \quad w_N \quad \alpha = 1.5 \times 10^{-6} \quad S = 2 \times 10^6$

¹ In all simulations, μ was set equal to 1.

Table 2

The aggregated initial school-size distribution, when $S = 1,000,000$. Per capita female fecundity at age is a measure of school size, number of females at age is a measure of frequency of schools. See text for details of computation.

School size	Freq. of schools	Freq. × size	School size	Freq. of schools	Freq. × size
252	348	87,696	857	47	40,279
341	284	96,844	882	38	33,516
427	233	99,491	903	31	27,993
508	190	96,520	920	25	23,000
581	156	90,636	934	21	19,614
596	1	596	946	17	16,082
646	128	82,688	955	14	13,370
703	104	73,112	963	11	10,593
751	85	63,835	970	9	8,730
793	70	55,510	975	7	6,825
828	57	47,196	979	6	5,874

Sum of freq. × size = $S = 1,000,000$.

of a simulation. Then one school of an appropriate magnitude, M , was added such that the $M + \sum F_{age} A_{age}$ was exactly equal to S . Note that under this construction the school sizes in the distribution do not vary with S (except for the one school of size M), whereas the frequency of schools by size do. An example of the initial distribution with the use of this construction is given in Table 2.

Analytical models

Analytical models of aggregation and recruitment are presented, where the models are developed from first principles and the parameters have an interpretation in the physics and biology of the recruitment process. Hopefully, the nature of the parameters can guide model selection,

and the estimates may provide a theoretical framework for empirical research on recruitment processes.

Noting that $R_t = N_t \bar{k}_t$, the recruitment dynamics depicted in the simulations may be modeled by using Equations 3–6 in which recruitment is dependent on the particular mortality and aggregation models that are chosen (m and w ; Table 1):

$$dR_t / dt = -m = d(N_t \bar{k}_t) / dt = (d\bar{k}_t / dt) N_t + (dN_t / dt) \bar{k}_t \quad (3)$$

$$dN_t / dt = -w - m_1 P_{1,t} \quad (4)$$

$$d\bar{k}_t / dt = m_1 P_{1,t} \left[(\bar{k}_t - 1) / (N_t - 1) \right] - (m - m_1 P_{1,t}) / N_t + w \bar{k}_t / (N_{t-1}) \quad (5)$$

$$\begin{aligned} dP_{k,t} / dt &= (m_{k+1} P_{k+1,t} - m_k P_{k,t}) / N_t - w_k P_{k,t} / N_t \quad k > 1 \\ &+ w \sum_{i=1}^{k-1} P_i P_{k-i} / N_t \quad (6) \\ &= m_2 P_{2,t} / N_t - m_1 P_{1,t} (1 - P_{1,t}) / (N_t - 1) \quad k = 1 \\ &- w_1 P_{1,t} / N_t, \end{aligned}$$

where $P_{k,t}$ = the proportion of schools with k fish in them at time t .

Also, m_k and w_k denote encounter rates appropriate to schools of size k , whereas unsubscripted m and w denote mean field dynamics and, thus, the $k_{i,t}$'s are replaced by \bar{k}_t 's (see Table 1).

The first term in Equation 4 denotes the reduction in number of schools due to aggregation events; the second term denotes a reduction due to mortality events on schools with one fish in them. Similarly, the first term in the mean school-size equation (Eq. 5) describes the change in mean school size due to mortality events on schools of size equal to one; the second term is due to mortality events on schools of size greater than one; and the third term is due to aggregation events. Finally, the first term in Equation 6 describes the change in probability of school size k due to mortality; the second term describes loss due to aggregation; and the third describes gain due to aggregation. Of particular importance is $P_{1,t}$: when $P_{1,t}$ is zero, the loss of schools occurs only due to aggregation. When $P_{1,t}$ is positive, then loss of schools is accelerated due to mortality (Eq. 4).

The goal is to obtain solutions to Equations 3–6 as functions of α , μ , and the initial conditions. If one can be assured that there will not be a school composed of one fish during a particular recruitment period ($P_{1,t} = 0$), then Equation 6 is eliminated, the $P_{1,t}$ terms drop out of Equations 4 and 5, and a numerical or analytical solution to the differential equations can be obtained, which is computationally feasible for use in fitting to stock-recruitment data. For example, when there is preferential aggregation (w_{pa}) and mortality agents are proportional to schools (m_{dN}), the equations reduce to

$$\begin{aligned} dN_t / dt &= -w_{pa} = -2\alpha N_t (N_t - 1) \bar{k}_t^2 \\ d\bar{k}_t / dt &= -m_{dN} / N_t + w_{pa} \bar{k}_t (N_t - 1) = -2\mu N_t \bar{k}_t + 2\alpha N_t \bar{k}_t^3. \end{aligned}$$

Analytical solutions were obtained for some of the mortality and aggregation models when $P_{1,t} = 0$ throughout the recruitment process (Appendix 1). In particular for m_{dR} and w_{pa} :

$$R_t = S / (1 + 2\mu t S) \quad (7)$$

$$N_t = N_0 + (\alpha / \mu) [S - S / (1 + 2\mu t S)] \quad (8)$$

$$\bar{k}_t = \bar{k}_0 / [1 + 2\mu t S + 2\alpha t S \bar{k}_0], \quad (9)$$

which is the Beverton-Holt stock-recruitment model expanded to include equations for the number of schools and the mean school size. Interestingly, Equation 9 indicates that monitoring the school-size distribution two or more times during a recruitment procession would yield estimates of the stock-recruitment parameters without having direct measures of the number of surviving fish. Equation 7 predicts recruitment by using one parameter, μ_t , the rate of mortality encounters during the recruitment period. However, spawning stock biomass is often used as a surrogate for the number of initial stock, S . Thus, another parameter is needed to convert spawning stock biomass to S in Equation 7. In that case the recruitment model becomes $R_t = aS / (1 + 2\mu t aS)$, where a is another parameter related to fecundity. The additional parameter will be needed for all the models discussed here, if spawning stock biomass is the measure of initial stock.

The assumption that $P_{1,t} = 0$ for all t of a recruitment period may not be justified in all situations. An approximation was developed (Appendix 2) to be applied when the initial conditions are disaggregated and when there is preferential attachment. In this circumstance, the differential equation (Eq. 6) when $k=1$ is replaced by

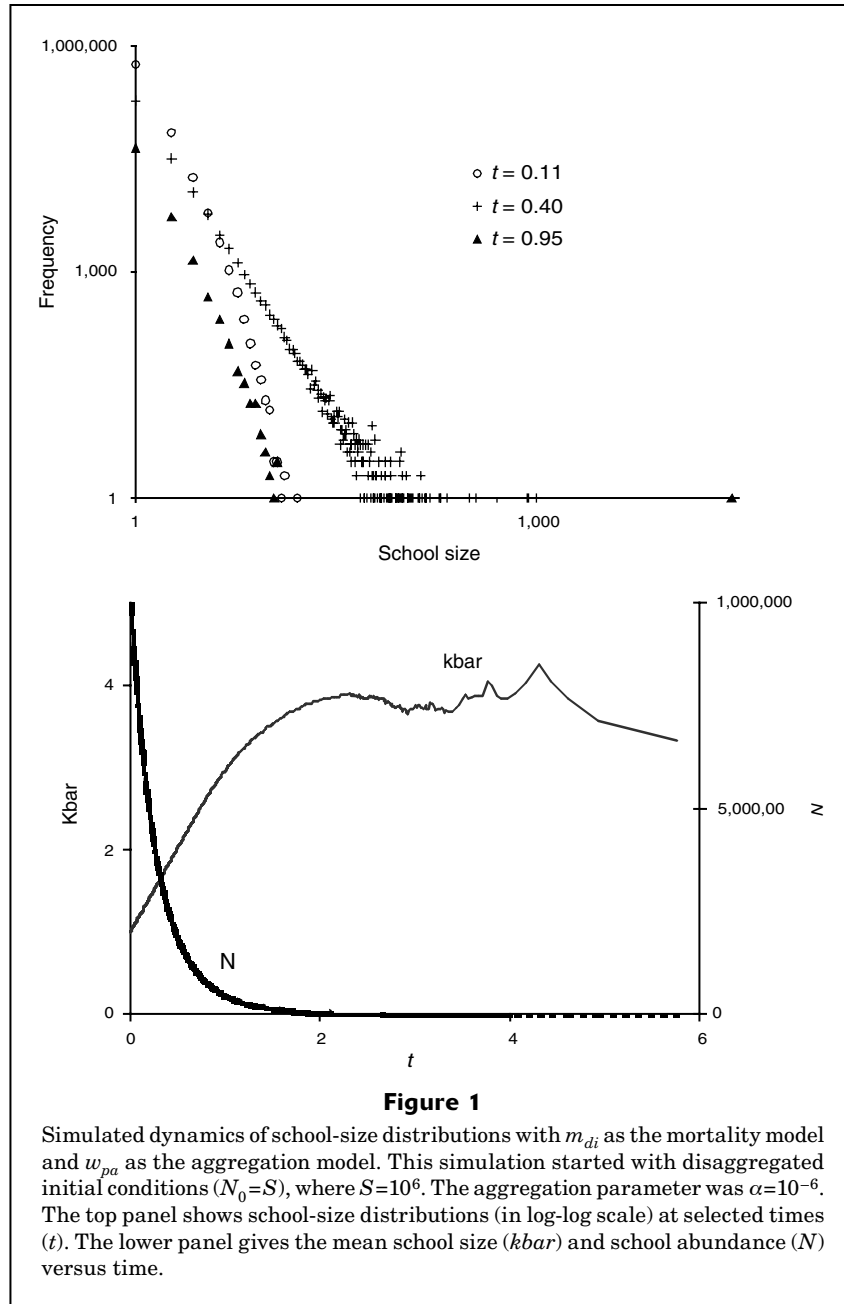
$$dP_{1,t} / dt = -w P_{1,t} / N_t + m(1 - P_{1,t}) / N_t. \quad (10)$$

Results

Simulations

Several hundred simulations were conducted under various initial stock sizes (S), aggregation parameters (α), initial aggregation conditions, and mortality and aggregation models (m and w). An example set of results are presented in Figures 1–5 (a key to figures is in Table 1).

A typical example of the evolution of the school-size distribution is given in Figure 1 for the disaggregated initial condition, $\alpha = 10^{-6}$, $S = 10^6$, mortality model m_{di} and aggregation model w_{pa} . In this example both the mortality and aggregation models exhibit preferential attachment, and the school-size distribution approaches scale-free behavior $P(k) \sim k^{-\gamma}$, although γ evolves over time. Eventually, a so-called “giant cluster” is formed by the aggregation process, in which all the fish attach to one school. This has

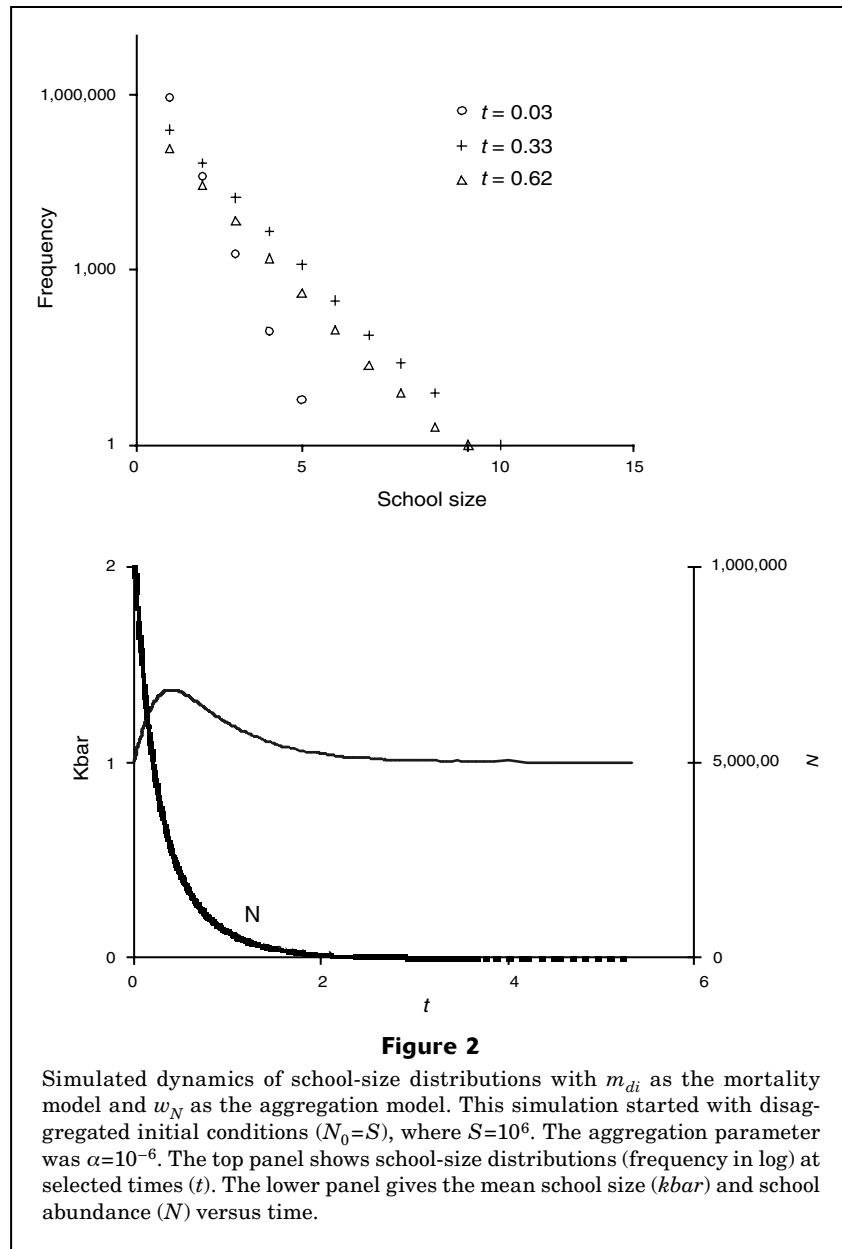


been shown to be an analog of Bose-Einstein condensation (Bianconi and Barabási, 2001; Dorogovtsev and Mendes, 2002) and gelation (Krapivsky et al., 2000). Greater mixing rates (α 's) and larger densities (N 's) accelerate the aggregation process and the formation of the giant cluster. The average size, \bar{k} , increases over time from the disaggregated initial condition until a giant cluster is formed. The number of schools declines over time because of both aggregation and the mortality of fish in schools that only have one fish in them.

When there is random aggregation beginning from a disaggregated initial condition ($\alpha=10^{-6}$, $S=10^6$, m_{di} , w_N ;

Fig. 2), the school-size distribution exhibits exponential behavior $P(k) \sim \exp(-\lambda k)$, with λ evolving over time. This is equivalent to the Erdős and Rényi (1960) results for random graphs. A comparison of Figure 2 with Figure 1 shows the difference between preferential attachment and random attachment, i.e., the difference between scale-free and exponential models.

Aggregated initial conditions (Figs. 3–5) result in a transition from the initial distribution to either scale-free or exponential distribution. During the transition, the size of the smallest school gradually becomes smaller until there is a finite probability of schools with one fish in



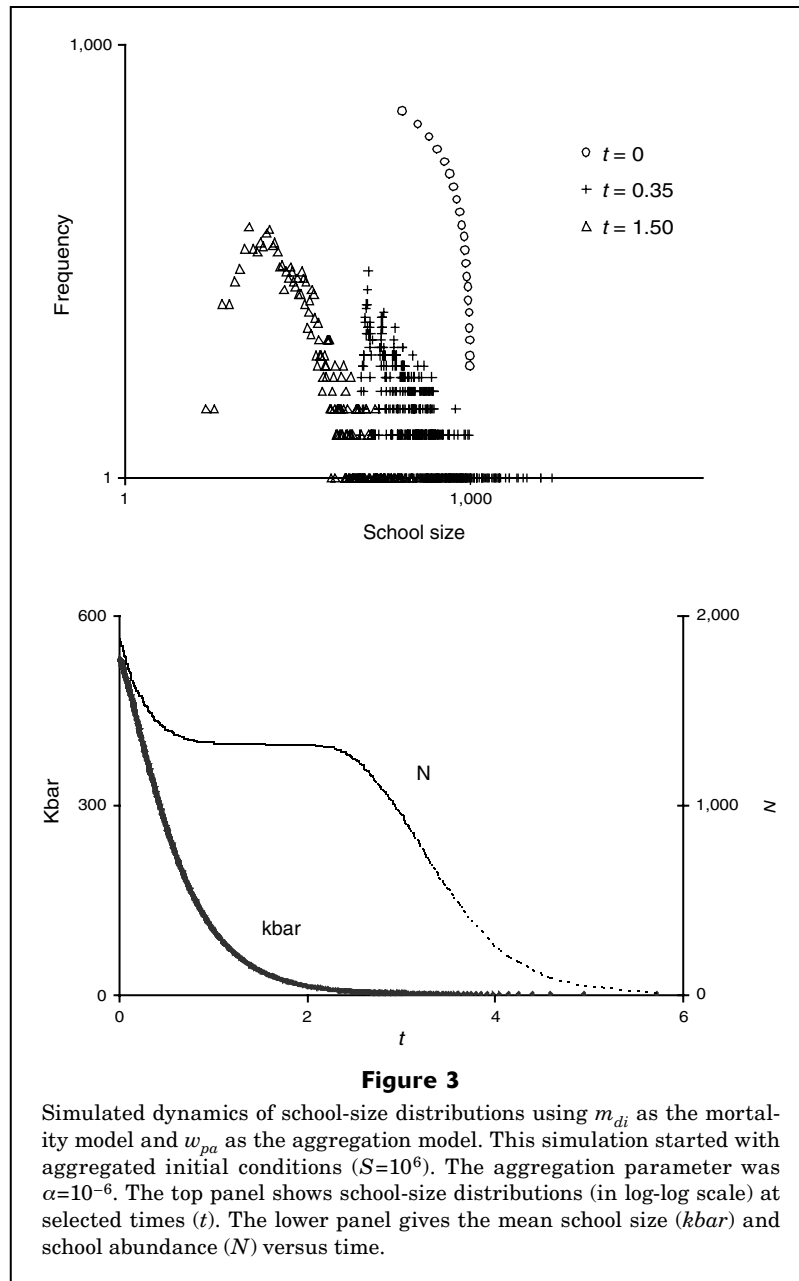
them. At this point the reduction in the number of schools is accelerated because of the mortality of fish that are in “schools” in which they are the only member, and because of the loss of schools attributed to aggregation.

Model comparisons

Numerical integration of Equations 3–5 matched the simulation results (Fig. 6, when $P_{1,t}=0$), indicating that the mathematical model describes the simulation dynamics. The numerical techniques are sufficiently efficient to be used in a curve-fitting context. Evaluations of the approximation (Appendix 2) indicate that the approximation may be useful for predictions of recruitment, when compared

with the simulations. However, the components of recruitment, \bar{k}_t and N_t , were biased (Fig. 7). Further research is needed to develop estimates of $P_{1,t}$ and, more generally, $P(k)$ under other models and initial conditions.

Recruitment was compared between mortality models and aggregation models (Fig. 8). If the mortality model was either m_{di} or m_{dR} , then the mortality rate was not affected by the school-size distribution: random attachment and preferential attachment perform equally as well in terms of survival at a given time. But if mortality encounters proportional to school density (m_{dN}) were imposed, then there were better survival rates with preferential attachment than with random attachment (Fig. 8, A and B). Conversely, mortality encounters proportional to school



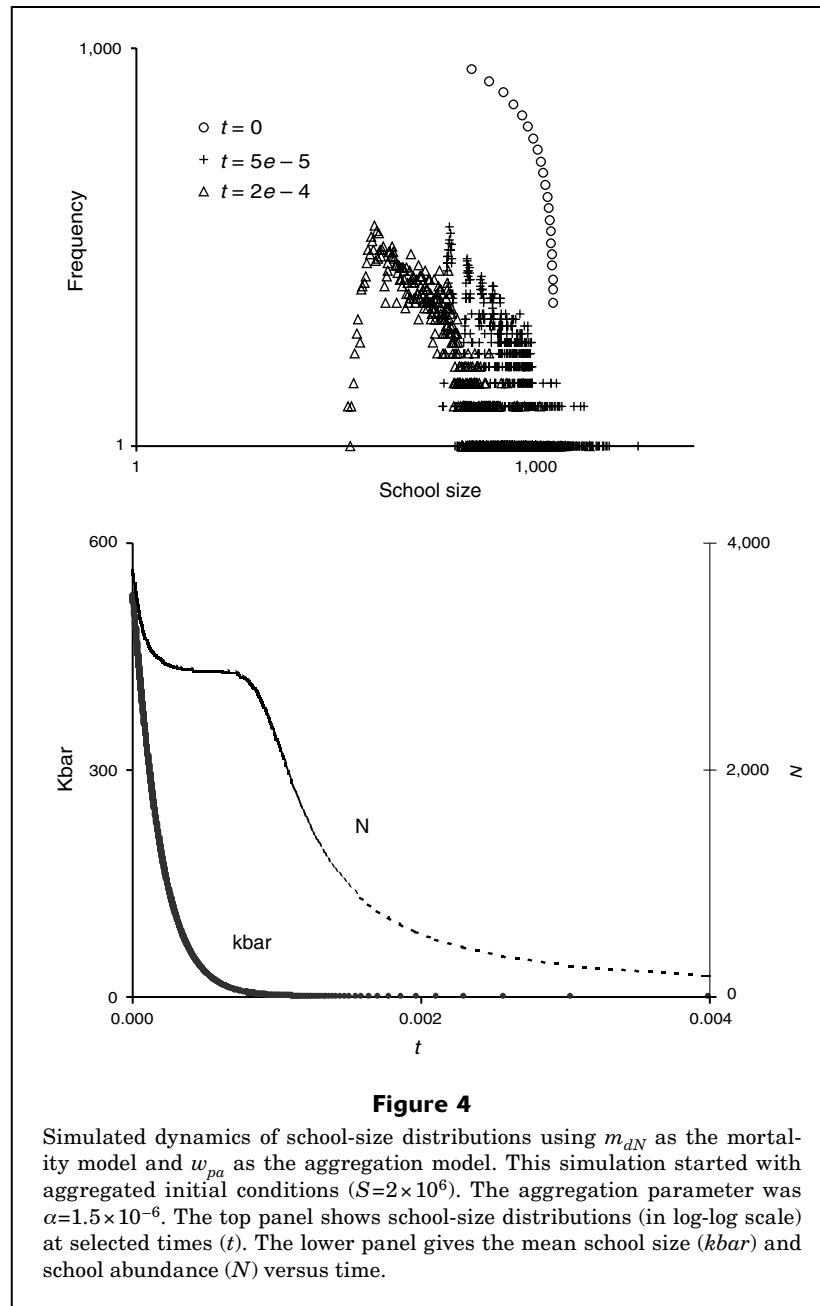
size (m_{dk}) led to poorer survival with preferential attachment (Fig. 8, C and D).

Discussion

Koslow (1992), Rickman et al. (2000), and others have commented on the inherent variability in stock-recruitment data and the limited predictive power of deterministic stock-recruitment models. Therefore, there is no expectation that one could select the models described here over other stock-recruitment models on the basis of fits to data. Although the aggregation-mortality models

may be fitted to stock-recruitment data, the real usefulness is as a guide to selection of stock-recruitment models used in management, as a mechanism for integrating research on recruitment processes, and as a tool for exploring the structure of recruitment variability.

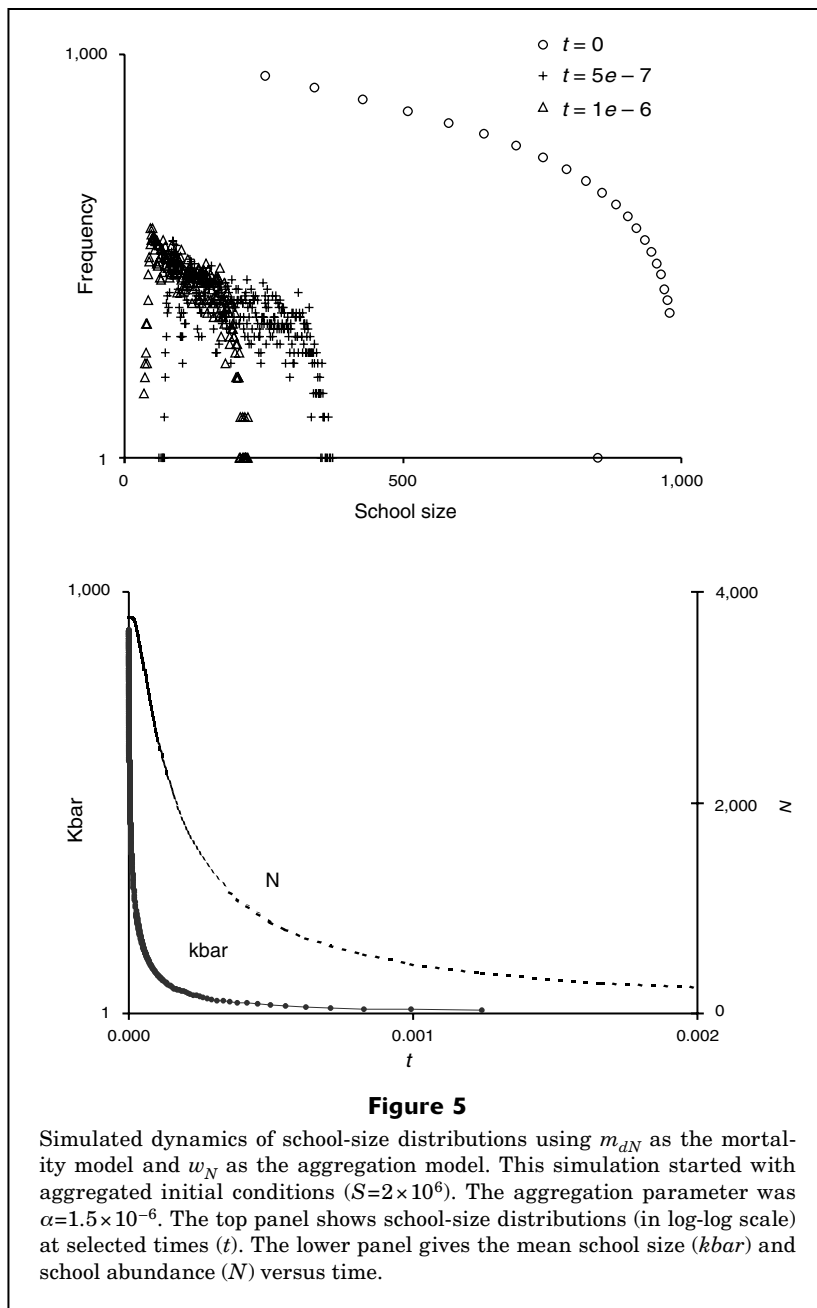
The aggregation-mortality models were introduced by using an analogy with evolving random networks (Barabási and Albert, 1999) and were shown to be analytically equivalent (Appendix 2). Modeled fish are subjected to competing forces of organization (aggregation) and decay (mortality), as in a network in which links to nodes in the network are created, destroyed, and rewired (Albert and Barabási, 2002). An important finding of Barabási and



Albert (1999) was that scaling of the aggregate-size distribution was dependent on the type of aggregation, specifically preferential attachment. Bonabeau and Dagorn noted the generic occurrence of scaling of aggregation distributions in nature (Bonabeau and Dagorn, 1995) and this scaling of aggregation distributions motivated the development of the models presented here.

The emphasis of the aggregation models was on preferential attachment and on comparison of model results with results for models with random attachment strategies. The preferential attachment rule used in the simulations was that aggregation rates were proportional to the size of the school encountered. But, what is meant by preferential

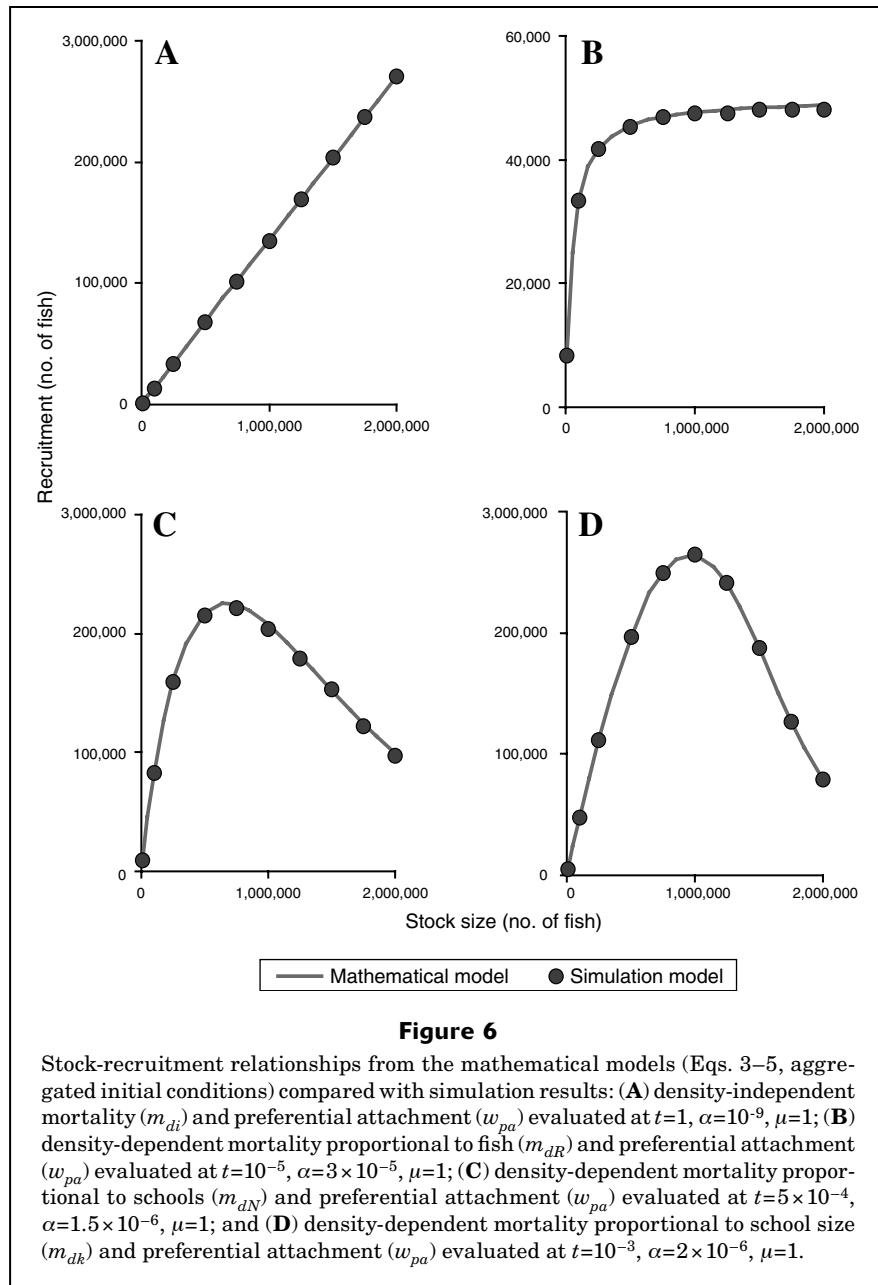
attachment and does preferential attachment occur in nature? Clearly, a fish, school or mortality agent has no global knowledge of the proportional size of a school that is encountered. However, preferential attachment in these models is a metaphor for aggregation strategies that are weighted toward larger school sizes. Indeed, studies of networks have shown that attachment may be proportional to a power of school size and still produce scale-free properties (Albert and Barabási, 2002). Also, network studies have shown that scale-free distributions occur when a wide number of attachment criteria are included, such as the “fitness” of the object being encountered and the attractiveness of local conditions (Bianconi and Barabási,



2001; Calderelli et al., 2002; Vazquez, 2003). Biological concepts of fitness, feeding behavior, predator-avoidance behavior, and habitat suitability appear to fall within the attachment criteria examined in physics literature. Oceanographic stability (Myers and Pepin, 1994), assortative schooling by color patterns (Crook, 1999), chemosensory stimuli (Quinn and Busack, 1985), and larval fitness indices from RNA/DNA ratios (Pepin, 1991; Suneetha et al., 1999) may be mechanisms that directly or indirectly influence aggregation size and, thus, distribution.

The geometry of the school size itself may be sufficient to produce preferential attachment behavior, as well. In the

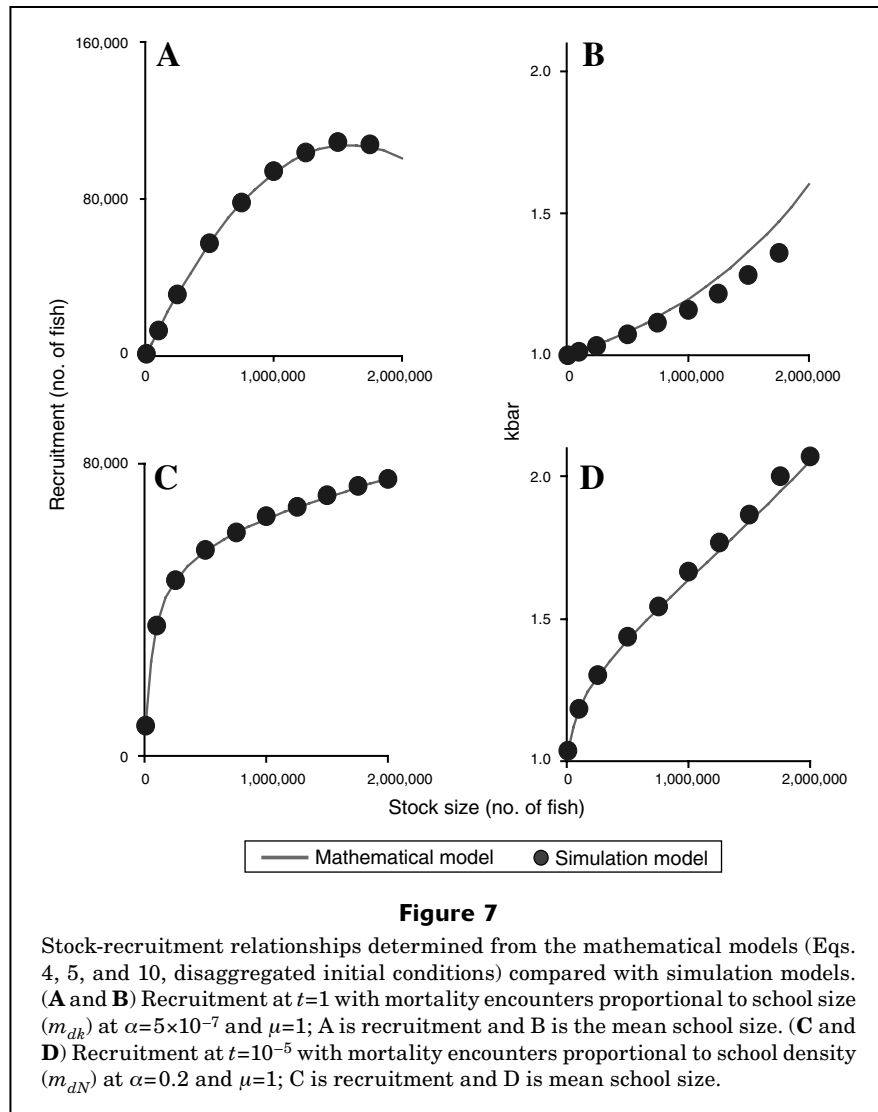
models of this study, the detection spaces ($G_i + G_j$ in Equation 1) were set to unity and assumed to be independent of school size. However, the detection space may be related to school size. For example, if a school of one fish has a spheroid detection space around itself with radius equal to 1, then using the geometry of an aggregation of k fish, the detection space of the aggregate would be proportional to $k^{1/3}$. Alternatively, if the detection space were a two-dimensional circle with a radius of 1, then the aggregate's detection space would be proportional to $k^{1/2}$. Substituting size-dependent detection spaces into the random mortality and aggregation models would be sufficient to induce pref-



erential interaction even when encounters are random: schools are randomly encountered, but the encounter event itself is weighted toward larger schools. Thus, the shape of the detection space may be another mechanism by which preferential attachment may be exhibited.

In the models presented, it is blithely assumed that mortality is caused by undefined mortality agents. However, most larval recruitment research has been directed at starvation and predation as determinants of recruitment variability (Lasker, 1975; Hunter, 1984; Bailey and Houde, 1989; Chambers and Trippel, 1997, for example). The mortality models used here clearly fit within the predation paradigm: mortality from predation results from

encounters with mortality agents of specific density and size. Whereas, mortality from starvation ensues from a lack of encounters with prey agents of sufficient density and size. In certain situations starvation processes might be aptly described by the predation-encounter approach used in this study. However, further research is needed to evaluate their appropriateness and to develop alternative modifications to Equations 3–6. A mechanism to do this may be the inclusion of fragmentation of schools into the models. In the models as they are now characterized, new schools are not created, the number of schools only becomes smaller through either aggregation or through mortality on schools of a single fish. Fragmentation might

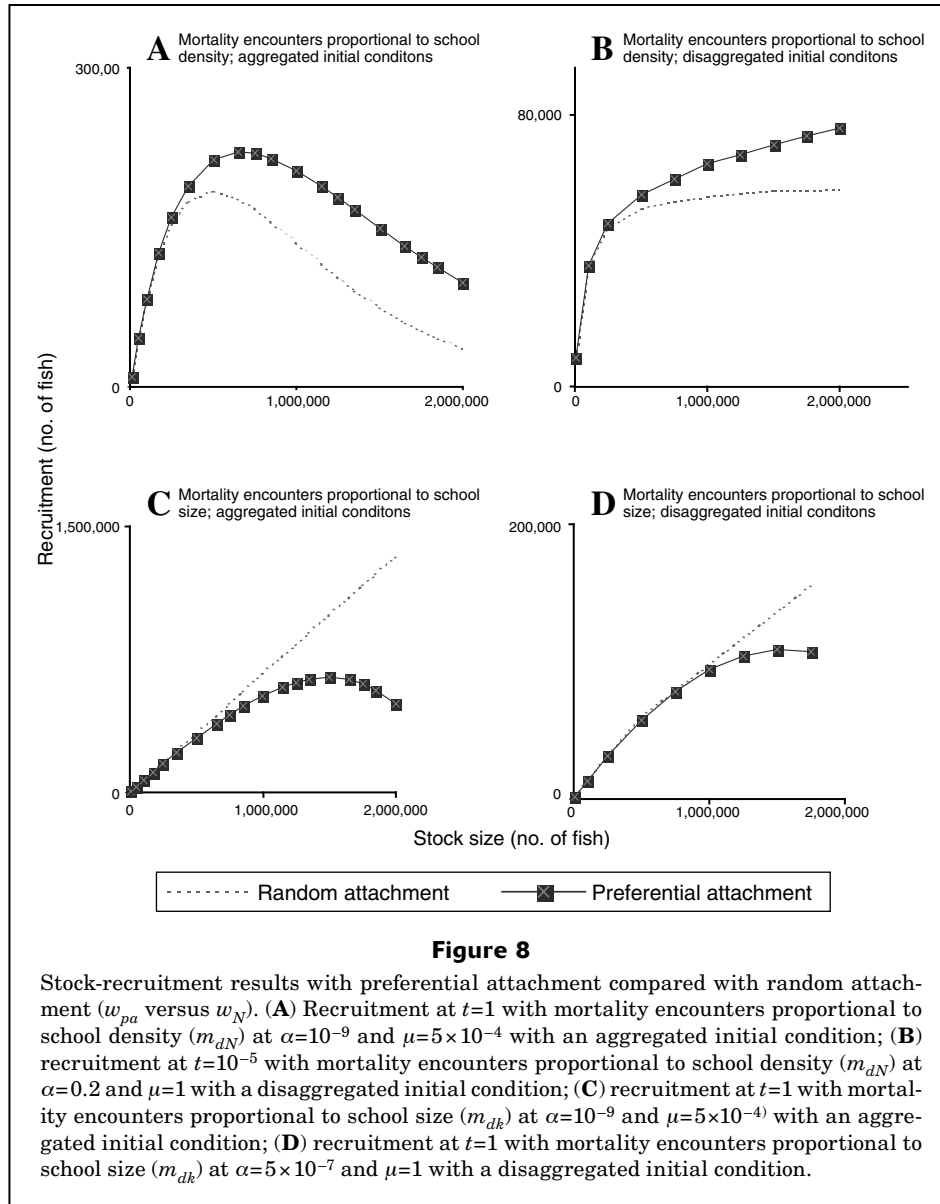


occur due to secondary effects of mortality encounters, as well as other factors such as starvation. For example, Sogard and Olla (1997) have shown predation-risk and hunger to be related to group cohesion.

The formation of a giant cluster (a single school encompassing all the fish) is an important feature of the attachment process. The simulations showed that with preferential attachment the recruitment process passes through a phase where the size distribution is scale free, then a critical point is reached where a giant cluster is being formed, i.e. a single school begins to attract all the fish. Research on complex networks has shown the conditions for formation of the giant cluster (Aiello et al., 2000; Albert and Barabasi, 2002). This should be investigated for the school aggregation models because it is likely that the mortality models used in the present study would no longer be appropriate once the giant cluster is formed. Indeed in some fish stocks, schools may aggregate into giant clusters on a local scale and then aggregation may stop for

reasons such as juveniles entering a benthic phase. The resulting distribution of school sizes may be the cluster distribution across benthic habitats. Spatial limitations of aggregation are an important feature of individually based models (Pascual and Levin, 1999). Again, this may be an important area for research.

What is the benefit of preferential attachment? If mortality encounters are proportional to school density, then recruitment survival rates are improved when there are fewer schools for a given number of fish, i.e. when preferential attachment is employed rather than random attachment (Fig. 8). Perhaps, preferential attachment strategies are a useful evolutionary hedge against uncertainty in the nature of the mortality dynamics. Conversely, when mortality encounters are proportional to school size, then better survival is achieved when schools are smaller, i.e. with random attachment (Fig. 8). If mortality by predators is related to larger schools, or if attainment of prey is inversely related to larger schools, then more solitary life



history strategies may evolve. Perhaps, the random aggregation model would be most effective for solitary predatory fish when their mortality is imposed by a m_{dk} -type model. For fish, this may be more likely to occur at later life stages than at recruitment. If mortality encounters are proportional to fish (m_{dR}), then results are intermediate and preferential attachment and random attachment perform equally as well.

The density-dependent mortality models implicitly incorporate a predator-prey interaction. Alternative predator-prey interactions examined were those in which predator density was proportional to fish, to schools, or to the number of fish within a school (school size) throughout a recruitment period. In reality mortality is perpetrated by a variety of agents at many different scales. Some agents act at the scale of the population ($N\bar{k}$), some at the scale of

schools (N), some at the scale of mean school size (\bar{k}), and some at the scale of a local school (k_i). The mixture of predatory agents and their densities can cause various kinds of dynamics including oscillatory, chaotic, and stable behavior (Wilson 1996, Pascual and Levin 1999). Therefore, it is unlikely that the models in this study, in which predator-prey ratios are constant, would be predictive of anything other than average behavior during recruitment. However, the analytical approach allows changes in the scale of predator-prey interaction over time. We can model this as $m_i = 2\mu N_i^a \bar{k}_i^b$, where a and b are dynamic (time-dependent) and, perhaps, correlated. Although we may wish to use the Beverton-Holt model ($a=b=2$) or the Ricker-like model ($a=2, b=1$) as a representation of average dynamics, it remains that recruitment variability will be influenced by the dynamics of the exponents, a and b . Numerical evalua-

tion of the differential equations by using random variates at each time step may be a mechanism to evaluate how the variability of a and b within a recruitment period are translated into the variability structure around a stock-recruitment relationship.

The model formulations used in the present study have been characterized from the underlying physical processes. By doing so, research may be directed at empirical and experimental measurement of specific stock-recruitment parameters, which opens the models to testing and verification. Additionally, results indicate that the school-size distribution contains a rich source of information on the mortality and aggregation processes and that monitoring of the distribution during recruitment could be useful for understanding recruitment variability and model structure.

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Appendix 1

Analytical solutions to Equations 3–5 for selected mortality and aggregation models. Solutions assume that $P_{1,t} = 0$ for all t evaluated and that the number of schools is large. No analytical solutions were found for (m_{dN}, w_{pa}) , (m_{dN}, w_{pa}) , or (m_{dk}, w_{pa}) .

Mortality proportional to fish: m_{dR}
Preferential aggregation: w_{pa}

$$R_t = \frac{S}{1 + 2\mu St}$$

$$N_t = \frac{S}{\bar{k}_0} + \frac{\alpha}{\mu} \left(S - \frac{S}{1 + 2\mu St} \right)$$

$$\bar{k}_t = R_t / N_t = \frac{\bar{k}_0}{1 + 2\mu St + 2\alpha S \bar{k}_0 t}$$

Mortality proportional to fish: m_{dR}
Random aggregation: w_N

$$R_t = \frac{S}{1 + 2\mu St}$$

$$N_t = \frac{S}{S - (S - \bar{k}_0)e^{-2\alpha t}}$$

$$\bar{k}_t = R_t / N_t = \frac{S - (S - \bar{k}_0)e^{-2\alpha t}}{1 + 2\mu St}$$

Density-independent: m_{di}
Preferential aggregation: w_{pa}

$$R_t = S e^{-2\mu t}$$

$$N_t = \frac{S}{\bar{k}_0} - \frac{S^2}{2} \frac{\alpha}{\mu} (1 - e^{-4\mu t})$$

$$\bar{k}_t = R_t / N_t = \frac{\bar{k}_0 e^{-2\mu t}}{1 - \frac{S \bar{k}_0}{2} \frac{\alpha}{\mu} (1 - e^{-4\mu t})}$$

Density-independent: m_{di}
Random aggregation: w_N

$$R_t = S e^{-2\mu t}$$

$$N_t = \frac{S}{S - (S - \bar{k}_0)e^{-2\alpha t}}$$

$$\bar{k}_t = R_t / N_t = e^{-2\mu t} (S - (S - \bar{k}_0)e^{-2\alpha t})$$

Mortality proportional to schools: m_{dN}
Random aggregation: w_N

$$R_t = S e^{-2\mu t} \left\{ \frac{\bar{k}_0}{S - (S - \bar{k}_0)e^{-2\alpha t}} \right\}^{\frac{\mu}{\alpha}}$$

$$N_t = \frac{S}{S - (S - \bar{k}_0)e^{-2\alpha t}}$$

$$\bar{k}_t = R_t / N_t = \frac{\bar{k}_0^{\mu/\alpha} e^{-2\mu t}}{\left[S - (S - \bar{k}_0)e^{-2\alpha t} \right]^{\frac{\mu}{\alpha} - 1}}$$

Mortality proportional to school size: m_{dk}
 Random aggregation: w_N

$$R_t = \frac{S}{1 + 2\mu St - \frac{\mu}{\alpha}(S - \bar{k}_0)[1 - e^{-2\alpha t}]}$$

$$N_t = \frac{S}{S - (S - \bar{k}_0)e^{-2\alpha t}}$$

$$\bar{k}_t = R_t / N_t = \frac{S - (S - \bar{k}_0)e^{-2\alpha t}}{1 + 2\mu St - \frac{\mu}{\alpha}(S - \bar{k}_0)[1 - e^{-2\alpha t}]}$$

Random mortality encounters: m_N
 Random aggregation: w_N

$$R_t = S - \frac{\mu}{\alpha} \ln \left\{ \frac{S}{\bar{k}_0} (e^{2\alpha t} - 1) + 1 \right\}$$

$$N_t = \frac{S}{S - (S - \bar{k}_0)e^{-2\alpha t}}$$

$$\bar{k}_t = R_t / N_t$$

Appendix 2

Characteristics of school-size distribution under preferential attachment

Much of the recent literature on evolving complex networks has been directed at determining the degree distribution, i.e., the probability $P(k)$ of a node having k links (Albert and Barabási, 2002). When the network grows or declines proportional to k or when links are rewired to be proportional to k , then $P(k)$ can be determined by using continuum theory (Dorogovtsev and Mendes, 2000; Albert and Barabási, 2002) leading to scale-free degree distributions. Therefore, when preferential attachment and nonrandom mortality are used, then the model may be couched as a scale-free network in the manner of Barabási

and Albert (1999), Dorogovtsev and Mendes (2000) and Albert and Barabási (2002).

When the aggregation model is *preferential attachment* (w_{pa}) (ignoring for the moment the nonstationarity of N and R), then the partial differential of a school of size k_{it} with respect to R_t has been shown by Dorogovtsev and Mendes (2000) to asymptotically be

$$\partial k_{it} / \partial R_t = \beta_t (k_{it} / R_t), \quad (\text{A1})$$

where β_t is the net rate of decay per each mortality event, i.e.,

$$\beta_t = 1 - w_{pa} / m. \quad (\text{A2})$$

With specific-mortality models, β_t is

$$m_{di}: \beta_t = 1 - (\alpha / \mu) (N_t - 1) \bar{k}_t \approx 1 - (\alpha / \mu) R_t$$

$$m_{dN}: \beta_t = 1 - (\alpha / \mu) (N_t - 1) \bar{k}_t / N_t \approx 1 - (\alpha / \mu) \bar{k}_t$$

$$m_{dR}: \beta_t = 1 - (\alpha / \mu) (N_t - 1) / N_t \approx 1 - (\alpha / \mu)$$

$$m_{dk}: \beta_t = 1 - (\alpha / \mu) (N_t - 1) \approx 1 - (\alpha / \mu) R_t / \bar{k}_t,$$

where the approximations on the right assume that the number of schools is large. The first term of (A2) denotes the removal of a fish proportional to school size for a mortality event; the second term denotes aggregation events proportional to school size. If β_t is independent of time ($\beta_t = \beta$), then Dorogovtsev and Mendes (2000) showed that under continuum conditions

$$P(k) \propto k^{-\gamma} \quad \gamma = 1 + 1 / \beta. \quad (\text{A3})$$

Equation A3 is equivalent to the results of Dorogovtsev and Mendes (2000), Krapivsky et al. (2000), and Albert and Barabási (2002) and suggest that β_t may be a useful approximation for determining the power-law tail of the school-size distribution (Appendix Fig. 1).

The simulation results showed the dynamics of P_{kt} . When the aggregated initial condition was imposed, at the start of the simulations there were no schools with only one fish in them ($P_{1t} = 0$). Eventually, as the number of schools and fish declined, P_{1t} became positive. Finally, as the distribution became scale-free, $-\partial P_{1t} / \partial k$ became negative and remained so throughout the remainder of the simulation or until a single giant cluster was formed (Appendix Fig. 1). Conversely, if the initial conditions began with schools being disaggregated, then $\partial P_{1t} / \partial k$ began as a negative number and remained so until either a giant cluster formed or there were no more fish remaining.

An approximation is suggested by the above results for circumstances when the initial conditions are disaggregated and when there is preferential attachment: the differential equation $dP_{k,t} / dt$ when $k=1$ (Eq. 6) is replaced by

$$dP_{1,t} / dt = -wP_{1,t} / N_t + m(1 - P_{1,t}) / N_t. \quad (\text{A4})$$

