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Super-individuals a simple solution for modelling large populations on an individual basis

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Abstract

Modelling populations on an individual-by-individual basis has proven to be a fruitful approach. Many complex patterns that are observed on the population level have been shown to arise from simple interactions between individuals. However, a major problem with these models is that the typically large number of individuals needed requires impractically large computation times. The common solution, reduction of the number of individuals in the model, can lead to loss of variation, irregular dynamics, and large sensitivity to the value of random generator seeds. As a solution to these problems, we propose to add an extra variable feature to each model individual, namely the number of real individuals it actually represents. This approach allows zooming from a real individual-by-individual model to a cohort representation or ultimately an all-animals-are-equal view without changing the model formulation. Therefore, the super-individual concept offers easy possibilities to check whether the observed behaviour is an artifact of following a limited number of individuals or of lumping individuals, and also to verify whether individual variability is indeed an essential ingredient for the observed behaviour. In addition the approach offers arbitrarily large computational advantages. As an example the super-individual approach is applied to a generic model of the dynamics of a size-distributed consumer cohort as well as to an elaborate applied simulation model of the recruitment of striped bass.

Keywords: Fish; Individual-based models; Population dynamics

1. Introduction

The many advantages of individual-based models in ecology have been pointed out extensively by Huston et al. (1988), by Hogeweg and Hesper

(1990), and by various authors in the recently published book on this subject (DeAngelis and Gross, 1992). To mention a few:

- Parameters needed in the models (like speed of movement, amount eaten per day, etc.) as well as the predicted variables (like individual numbers, diets and conditions) are typically of the type measured by experimental biologists.
- Model behaviour is often rather robust to variations in formulation of the processes.

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- Instead of implicitly assuming information processing on the population level, individuals are taken as the natural units, which is more realistic and intuitively straightforward.

Individual-based models seem a promising way to fill the gap between modellers and experimental biologists. They explain often complex population phenomena from common knowledge about individual behaviour, rather than mimicking the patterns by means of mathematical constructs that hardly appeal to the average biologist. The obvious disadvantage of modelling populations individual by individual is that it takes impractically much computation time to simulate realistic numbers for most populations, especially if the individual behaviour is rather elaborate like in many applied models. There are basically three ways out of this problem: wait until computers are faster; use continuous distributions to represent the population structure rather than separate individuals; or use a smaller number of individuals to represent the population. We will neither attempt to speculate on the development of computer technology, nor mingle in the discussion about the various advantages and disadvantages of distribution models as opposed to individual-by-individual models (Metz and Diekmann, 1986; DeAngelis and Rose, 1992). Instead, we address the common approach to represent the population by a smaller number of individuals. The problems associated with various methods to do this are discussed, and the concept of “super-individuals” is presented as a convenient solution.

2. Problems of following a subset of the population

Results from simulations with a randomly drawn subset of individuals can differ significantly from full set runs for a number of reasons. Importantly, the represented range of most individual features will be reduced (Fig. 1). This can be especially influential when outliers, like large individuals, play a key role in the population (Huston et al., 1988). A bothersome effect of small numbers from the modellers point of view,

Fig. 1. Loss of variance with decreasing size of a random subset from the population due to the fact that one individual is the smallest unit.

is that simulation outcomes can be quite different depending on the values of seeds of random number generators. A third problem of reduced numbers is that in smaller populations, events like the death of important individuals are increasingly influential to the dynamics of the system. The introduced noise tends to prevent the manifestation of point, cyclic or strange attractors that may be clear in systems with large numbers (Scheffer et al., 1995). Obviously, these “problems” are exactly the reason why individual-by-individual models are a tool par-excellence to study the mechanisms in real small populations. However, when studying large populations, they need to be avoided.

A trivial way to control the side effects of small numbers is to try simulations with different numbers of individuals and select the smallest sample size that does not seem to produce spurious results for further simulation. Obviously, this is a rather arbitrary approach. Furthermore, the required number of individuals will frequently still be very large. Especially in cases where survival is low (e.g. $\ll 1\%$ in early life of many fish, Bailey and Houde, 1989) initial numbers should be huge to allow sufficient survivors, unless scaling is adjusted in some way over time (Rose et al., 1993). Finding a reasonable compromise in scaling is also difficult when different considered groups of animals have very different individual densities, as is often the case with predators and prey. This can be partially solved by following the more abundant groups in smaller hypothetical subspaces (Fig. 2a). By choosing the volume ra-

Fig. 2. Two approaches of reducing computational costs in individual-by-individual models.

tios correctly, the different groups can then be followed in the same amount of detail. The coupling between the two scales is via the assumption that what happens in the subspace is representative for the rest of the volume. Although tricks like dynamic and multiple scaling reduce the problems associated with following small subsets, they cannot eliminate them.

3. The super-individual concept

The problem of any scaling approach is that there is essentially no free lunch. The effects of reduced numbers can be limited by cutting corners in the smartest way, but they can not be eliminated. We therefore propose to pay for the lunch by adding an extra feature to each model individual, the amount of individuals that it actually represents (Fig. 2b). Thus, the resulting “super-individuals” are in fact nothing else than classes of individuals (‘generalized individuals’ *sensu* Metz and de Roos, 1992).

A first decision to be made in this approach is, which individuals in the population should be combined in one super-individual. If simulations start of with a population where the individual properties like weight and length are defined by one or more frequency distributions, an obvious choice is to define super-individuals that combine population individuals within fixed intervals of these properties. This approach is illustrated by the first example given below. Often, however, it may be useful to fuse individuals one or more times during the simulation process. This is typically necessary when reproduction episodes cause large increases in individual numbers. The most pragmatic solution is to select a random subset of the new individuals and turn them into super-individuals by assigning “internal amounts” (i.e. the number of population individuals each of them represents) computed as the inverse of the sample fraction so as to keep the balance correct. This approach is illustrated by our second example below. A more sophisticated approach is to check the state of each individual first and subsequently fuse clusters of similar individuals into super-individuals with an internal amount set by the cluster size and an individual state set by the cluster centroid. An example of an efficient algorithm to fuse individuals according to their similarity can be found in Stage et al. (1993).

In the course of the simulation the internal amount should of course be affected by loss processes like death and immigration. Often, there will be a fixed background probability of mortality due to causes that are not explicitly modelled, in addition most individual-based models contain conditional mortality depending on explicitly modelled processes (i.e. individuals die from starvation when they lose more then a critical proportion of their weight). Typically, background mortality is realized in individual-by-individual models by drawing the answer to the to-die-or-not-to-die question for each individual from a Bernoulli distribution. In stead of repeating this procedure n times (n being the internal amount) for each super-individual, we can draw the number of survivors directly from a binomial probability density distribution with a sample size of n . Handling conditional mortality like the death of

individuals from starvation is slightly more complicated. The simplest way of handling it is to let a super-individual die completely when its conditions for mortality is fulfilled (i.e. when it lost half its weight due to starvation). This assumes all population individuals represented by the super-individual to be equal in their sensitivity to the mortality cause. Obviously, individuals being equal in a number of aspects still differ in many others that may not be explicitly modelled or measured, but still influence their fitness and their sensitivity to threats. Even in relatively uniform laboratory populations used to test the toxicity of chemical agents, for instance, some individuals die sooner than others, which is why the results of such tests are usually presented in statistics like the concentration of the substance that, after a standard time, leads to mortality of 50% of the individuals ("lc-50"). Therefore, it is more realistic to account for such background variance in fitness by letting some individuals die sooner than others within the same super-individual. There are several possible ways of handling this.

A pragmatic solution is to set the mortality probability to a fixed (high) value for as long as the super-individual is in the danger condition. The lower the variance in fitness within a super-individual, the higher this conditional mortality probability should be. The extreme situation is a 100% instantaneous die-off representing a situation again in which all animals represented by the super-individual are equal with respect to their sensitivity to the considered mortality cause.

As argued, mortality can be handled by drawing the number of survivors within each super-individual from a binomial distribution with a sample size equal to the internal amount n . For $n = 1$ this is the same as the traditional drawing of the answer to the to-die-or-not-to-die question from a Bernoulli distribution (which is just a special case of the binomial). This implies that if we start simulations giving each super-individual an initial internal amount of 1, we simply have a full-scale individual-by-individual approach.

Drawing a number A from a binomial distribution sounds easier than it is. The computationally fastest way is to use the recursive notation of the

binomial frequency distribution. First compute a pseudo-random number r . Then compute the probability of zero mortality:

$$P_0 = (1 - p)^n.$$

Proceed through the subsequent classes using the recursive notation:

$$P_x = P_{x-1} \frac{(n - x + 1)p}{x(1 - p)}$$

until:

$$\sum_{x=0}^A P_x \geq r.$$

If the product of n and p is larger than 5, the binomial distribution can be approximated by a normal distribution with a mean of p and a standard deviation of $(np(1 - p))^{0.5}$, reducing the computational burden further.

It can be useful for some applications (e.g. the reconstruction of complex cycles or strange attractors) to get rid of the stochasticity completely. This can be achieved in the super-individual approach by considering the internal amount as a real instead of an integer and computing the mortality fraction simply by multiplying its value with the probability of mortality. This also speeds up the computations further. For high n the difference between the approaches is small since the stochasticity becomes especially apparent if the remaining number of individuals is small. Therefore a hybrid approach can be convenient, switching to drawing from probability distributions only below a certain value of n , combining high computational speed with essential stochasticity at low individual numbers. The latter approach is used for the examples given in the final section of this paper.

The possibility of changing from a full-scale individual-by-individual approach to a super-individual one without changing the model formulation can be very useful. The computational burden imposed by the pure individual-by-individual version can be reduced at any time by decreasing the number of super-individuals while increasing their internal amounts, allowing quick simulations that represent huge numbers of individuals.

But perhaps more importantly, the flexibility of switching between the two approaches facilitates the detection of computational artifacts imposed by either of the two. Another useful feature of the super-individual concept is that in the extreme case a whole population or cohort can be represented by just one super-individual. This allows a quick and easy check whether individual differences are indeed essential to produce the observed patterns. Although, in theory, this can also be done by making all individuals initially the same in an individual-by-individual model, it appears difficult to realize that in practice since there will always be an increase of variance over time if there is stochasticity in the events experienced by different individuals.

4. Related solutions

Among the solutions that have been proposed to reduce the computational problems associated with individual-based modelling, two deserve some special attention here because they appear closely related to the super-individual approach: the resampling algorithm of Rose et al. (1993) and the cohort representation of Metz et al. (1988).

To a certain extent, the resampling algorithm is indeed quite comparable to the super-individual idea presented here. Resampling also uses super-individuals. There is, however, a crucial difference in the way mortality is handled. In the resampling algorithm, mortality always leads to the complete elimination of a “super-individual” rather than reduction of the number of population individuals it represents. To keep the number of super-individuals in the simulated subset of the population constant the perished super-individual is replaced by a copy from a randomly selected surviving super-individual. The number of individuals represented by this survivor is then divided among the original and the cloned version. By definition, this resampling algorithm leads to a decrease of diversity in the simulated set of individuals due to the cloning. When the modeled subset is still large and when cloned individuals quickly diverge because of stochastic-

ity in, for instance, their interaction with the environment, the diversity loss will be minor. Indeed, Rose et al. (1993) show for a model of young striped bass that a version with resampling closely mimics the behaviour of the original model. However, in other cases the diversity loss may become more pronounced. While sharing the advantages of the resampling algorithm, the super-individual approach we propose now avoids this side effect.

In the cohort representation (Metz et al., 1988; De Roos et al., 1992) or, more generally, in the *i*-space distribution models (Metz and Diekmann, 1986) with a discrete distribution function, the individuals are grouped in classes and a density function keeps track of the actual number of individuals in each class. Although this suggests a similarity with the super-individual formalism, the approaches differ widely for all practical purposes. The cohort representation belongs in the family of *i*-space distribution models. In these models, partial differential equations are used to follow the frequency distribution of attributes of individuals in the population through time. The various advantages and disadvantages of explicit simulation of individuals relative to the partial differential equation approach are outlined extensively by DeAngelis and Rose (1992). They conclude that, while both approaches have their pros and cons, a key advantage of the actual simulation of individuals is that it allows for much greater flexibility in model formulation. A main caveat of this approach is that computational artifacts tend to arise when a small subset of the population is followed to keep the simulation computationally feasible. As argued in this paper the simple trick of using super-individuals is a practical way to eliminate many of these problems.

5. Two examples

To illustrate the power of the super-individual approach we give two examples of its application. In the first example the method is applied to a relatively simple generic model of the dynamics of a developing cohort of animals and their food.

In the second case the approach is tested on an elaborate realistic model of the recruitment of a population of striped bass (an American fish species). Although its complexity prohibits an exhaustive description of its formulation within the scope of this paper, we include this example as this model may be considered typical of many applied individual-based models.

5.1. Starvation in a size-distributed consumer cohort

As a first example of the application of the super-individual approach we use a model that describes the dynamics of a size-distributed cohort of animals foraging on a logistically growing food population. The model is written in the object-oriented language SMALLTALK using a toolkit for ecological modelling called ECOTALK (Baveco and Smeulders, 1994).

The consumer individuals have a weight, W_i (g), which is governed by simple energetic rules accounting for consumption, C_i (g day⁻¹), respiration, R_i (g day⁻¹), and an efficiency for converting food to body weight, e (g g⁻¹):

$$W_{i,t+1} = W_{i,t} + e \cdot C_i - R_i$$

Since small animals have higher weight-specific metabolic rates, the daily ration relative to that of a 1-g animal, c_{ref} (g day⁻¹), declines with body weight. The actual uptake is also a function of food density, F_t (g m⁻³), formulated as a Monod function with a half-saturation constant, H (g m⁻³), after subtraction of the lowest exploitable food level, Q (g/m⁻³):

$$C_i = c_{\text{ref}} \cdot W_i^{2/3} \cdot (F_t - Q) / (F_t - Q + H)$$

Respiration, like consumption, is computed relative to that of a 1-g animal, r_{ref} (g day⁻¹), and is dependent on the body weight of the animal:

$$R_i = r_{\text{ref}} \cdot W_i^{2/3}$$

During periods of food shortage, respiration can exceed energy uptake, resulting in weight loss. When animals lose more than 25% of their weight, they are put in a starvation mode. Whether an animal in this mode dies or not is decided by drawing from a Bernoulli distribution with a mean of 0.1 each day.

Growth of the food population is formulated in a logistic fashion as a function of the current density, F_t (g m⁻³), the maximum growth rate, g_{max} (day⁻¹) a carrying capacity K (g m⁻³), and the losses due to consumption:

$$F_{t+1} = F_t + g_{\text{max}} \cdot F_t \cdot (K - F_t) / K - \sum C_{i,t}$$

If we run the model for a large number of individuals, some interesting patterns emerge. A time plot of food biomass and the total biomass of the consumer cohort shows cycles of increasing period (Fig. 3). Each cycle starts with an increase of consumer biomass due to individual growth. At a certain moment food collapses due to the increased consumption and subsequently the consumer individuals begin to lose weight. When the weight loss exceeds 25%, starvation mortality speeds up the decline in total consumer biomass. The resulting decrease in grazing pressure allows the food population to recover, saving the survivors from further starvation. Their resumed growth sets off a new cycle. In each new cycle, the maximum biomass of the consumer cohort becomes higher. This is because the cohort consists of increasingly fewer but bigger individuals,

Fig. 3. Cycles in the total biomass of a consumer cohort and its food produced by an individual-based model.

Fig. 4. Snapshots of the size distribution of the consumer cohort after each of the cycles shown in Fig. 4. (a) A simulation starting off with 500 individuals; (b) a simulation starting off with 10 000 individuals; (c) a simulation starting off with 10 super-individuals. Note that in the latter case each bar represents one super-individual.

and since bigger individuals have a lower weight-specific metabolism, a higher total biomass of them can be tolerated by the food population before it collapses. A thorough treatment of the phenomenon of periodic die-off in consumer cohorts and its relevance to natural populations is given elsewhere (Scheffer et al., 1994).

If we make snapshots of the size distribution of the consumer cohort after each die-off cycle, it can be seen that with the loss of individuals the shape of the size distribution deteriorates quite fast (Fig. 4a). The problem can be postponed by scaling up the system and increasing the number of individuals in the simulation from 500 to 10 000 (Fig. 4b), but this also increases the computation time from 6 min to more than 2 h (on a 486 computer). If we think of the consumer cohort as young of the year fish in a lake, the real number of individuals involved will be order of millions rather than thousands. The corresponding computation time in case of this extremely simple model would be a few months and expansion of the model to include a more realistic behaviour of the individuals would easily blow up the computation time to a few years.

In order to overcome such computational problems we change the individuals into super-individuals by introducing the extra feature “internal amount”, S_i , being the number of individuals that it actually represents. Instead of drawing the initial size of the animals from a normal distribution, we now shape the size distribution by assigning appropriate internal amounts. If a super-individual enters the starvation mode its internal amount is decreased by 10% each day. When S_i falls below 1, the actual moment of extinction is decided by drawing from a Bernoulli distribution with a mean of 0.1 each day like in the plain individual-by-individual case. The simulation with super-individuals (Fig. 4c) takes less than one minute while preserving a smooth pattern in the size distribution throughout the observed period.

5.2. Recruitment of striped bass

The striped bass model is typical of many of the more elaborate applied individual-based sim-

ulation models. A detailed description of the model can be found in Rose and Cowan (1993).

The striped bass model begins with the spawning of individual females and simulates the growth and mortality of the spawned striped bass as they develop through the life stages of egg, yolk-sac larva, larva, and juvenile during their first year of life. The model represents these dynamics on a daily basis in a single, well-mixed compartment (700 m × 700 m × 4 m deep). Model simulations are of one year duration beginning on April 10. The environmental conditions in the compartment consist of daily water temperature, fraction of the day there is daylight, and the daily densities of zooplankton and benthic prey types.

Each female's spawn of eggs is followed as an individual entity (i.e., female's cohort of eggs) with daily temperatures determining hatching into yolk-sac larvae and then, with initiation of exogenous feeding, development into larvae. Upon initiation of first feeding, initial weight (mg dw) and length (mm) of feeding larvae in each female cohort are determined from egg weight which varies with female size. The number of eggs and then yolk-sac larvae in each female egg-cohort are reduced daily according to the fraction dying.

Daily growth of each individual larva beginning with first feeding is represented with a difference form of a bioenergetics equation.

$$W_t = W_{t-1} + p \cdot C_{\max} \cdot A - R_{\text{tot}} \quad (1)$$

where W_t = individual weight at day t (mg dw); p = proportion of $C_{\max}$ realized; $C_{\max}$ = maximum consumption rate (mg dw d⁻¹); A = utilization efficiency; R_{tot} = total metabolic rate (mg dw d⁻¹). The proportion (p) of $C_{\max}$ realized by a larva on a given day is determined based on stochastic prey encounters. Multiple zooplankton prey groups for larvae and benthic prey groups for juveniles are represented in the model. $C_{\max}$ and R_{tot} depend on larvae weight and temperature.

Mortality of individual larvae and juveniles depends on weight and length. Weight-dependent mortality is based on laboratory data at low food levels without predators and therefore can be viewed as starvation-related mortality. The weight of an individual larva or juvenile is evaluated

Table 1

Average growth and mortality rates of larval striped bass in a full individual-by-individual simulation compared to simulations where the population is represented by increasingly few super-individuals. Results for three different random generator seeds are shown. The number of population individuals (and hence of individuals in the full run) is 209 992, 195 311 and 178 177 for seeds A, B and C respectively

Number of model individuals	Growth rate (mm day ⁻¹), random generator seed			Mortality rate (day ⁻¹), random generator seed		
	A	B	C	A	B	C
Full i-by-i run	0.553	0.564	0.568	0.166	0.162	0.162
10 000	0.552	0.565	0.567	0.165	0.163	0.162
1000	0.554	0.565	0.567	0.165	0.162	0.162
500	0.552	0.566	0.566	0.164	0.163	0.162
100	0.542	0.559	0.567	0.165	0.164	0.163
20	0.553	0.585	0.582	0.162	0.165	0.161

each day, and if its weight is less than some fraction (0.65 for larvae and 0.5 for juveniles) of the average weight for an individual of that length, the individual is assumed to die. Length-dependent mortality is estimated from field data and is therefore representative of predation and other losses. Probability of dying (P_d) is evaluated daily for each individual based on its length (L); $P_d = (1 - e^{-M})$, where $M = 0.003 + 0.295 \cdot \exp(-0.075 \cdot L)$. If a generated random number from a uniform distribution between 0 and 1 is less than P_d , the model individual is assumed to die.

In full individual-by-individual simulations all larvae are followed separately from the moment that they first start feeding (the transition from yolk-sac larvae to larvae). The total number of individual larvae in this stage differs slightly with

the randomly drawn sizes of the spawning females but is typically around 200 000. For the super-individual simulation, a sample of individual larvae at first feeding is taken from each female egg-cohort in proportion to the number of surviving first feeding larvae in that cohort. These larvae are converted into super-individuals by assigning them an initial internal amount (S_i), of T/N where T is the total number of surviving first feeding larvae obtained by summing over all female eggs-cohorts and N is the total number of super-individuals to be followed. Mortality in super-individuals is handled as in the former example.

To check how the use of super-individuals affects the model results we performed a simulation with the full individual-by-individual version followed by a series of simulations in which the

Table 2

Comparison between the loss of accuracy in the super-individual approach and in the resampling procedure of Rose et al. (1993) when the population is represented by an increasingly small number of model individuals. Absolute deviations from the growth and mortality rates produced by a full individual-by-individual run (about 200 000 individuals, see Table 1) are averaged for three simulation runs with different random seeds

Number of model-individuals	% deviation in growth rate		% deviation in mortality rate	
	super-i	resampling	super-i	resampling
10 000	0.2	0.1	0.4	0.8
1000	0.2	0.8	0.2	0.4
500	0.3	1.7	0.6	2.0
100	0.4	2.6	0.8	2.9
20	2.1	7.4	1.6	4.9

larval population was represented by an increasingly small number of super-individuals. We focus on the deviations in growth and mortality rates that occur relative to the full blown simulation (Table 1). Those larval rates are important as they greatly influence the overall model predictions of striped bass recruitment. Even if the 200 000 individuals are represented by as few as 20 super-individuals the deviation from the full individual-by-individual simulation is only about 2%. The results are more than three times as accurate as the results obtained by the already quite effective resampling procedure (Table 2) used in Rose et al. (1993), while taking slightly less computation time.

We conclude that in addition to being conceptually simple and attractive, the super-individual approach is also a powerful tool when it comes to reducing the computational burden of running elaborate individual-based models while retaining a high accuracy.

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