STABILIZATION OF PROLIFIC POPULATIONS THROUGH MIGRATION AND LONG-LIVED PROPAGULES

Byers, R.E. and R.I.C. Hansell

Department of Zoology,
University of Toronto,
25 Harbord St.,
Toronto, Ontario, M5S 1A1

Abstract

A spatial analogue of the logistic model is constructed, with sub-populations located on a 10 by 10 grid, with terms representing long lived propagules such as seeds left in the seed bank by plants or eggs left by many insects and other animals, and with terms representing migration between sub-populations. Both long lived propagules and migration proved sufficient, individually, to stabilize the population when \( r \) is set much greater than 4. The usual sequence of bifurcation to chaos is seen as \( r \) is increased to 4, but the degree of chaos diminishes greatly as \( r \) is increased beyond 4, ultimately becoming locked in a period 3 cycle. As would be expected, low migration rates allowed each sub-population to operate as an independent oscillator while high migration rates synchronized the sub-populations. Estimation of the correlation dimension is not feasible for this model since the combination of the memory induced by the persistent propagules with the spatial distribution results in very high dimensional behaviour.

Introduction

Schaffer (1981) showed that complex systems can be decomposed into relatively independent subsystems, for the purpose of modelling, and derived the dependance of the parameters of the model of a subsystem on the dynamics of those parts of the system which are excluded from the model. The criteria Schaffer used was that each subsystem was comprised of species which operate on similar time scales, with each subsystem in the ecosystem operating on different time scales. Other criteria, such as the degree of connectance between components of the system might also be used. In each case, the parameters of the estimated model will be functions of the ecosystem containing the modelled population. Baleen whales feeding on euphasiids may change their abundance so little during several generations of euphasiids that there is little point in modelling their dynamics in a model of euphasiid population dynamics, but the survival parameter that is appropriate for the euphasiid model will depend on whether the whales are common or scarce during the time for which the model is to apply. There is a strong connection between the whales and euphasiids, but the great disparity between the time scales on which the two organisms operate allows the study of them separately. Similarly, although birds of prey may, in a particular area, depend on trees for nest sites, the connection between birds of prey and trees is so weak that they can be studied independently: the dynamics of the birds of prey are much more likely to depend on the abundance of song birds and small mammals each year than a change in the number of trees, barring annihilation of the forest.

The simplest model which might be examined, in the process of decoupling an ecosystem into subsystems, is the logistic model. The diversity of behaviours which the logistic model can show, ranging from period one fixed points to chaos, is now well known, and it may be necessary to understand the dynamics of this simple model before a more complicated model can be understood. However, there are a variety of population processes which may alter the dynamics
of the population, and there are a number of problems with a direct application of the logistic
model to a population. First, the logistic model shows a series of period doubling bifurcations as
the population growth rate increases up to 400%. However, a growth rate of 400% is not
particularly fast since all it requires is the production of four offspring that survive to reproduce,
if the mother dies, or three if she doesn't. Many small mammals and birds produce more than
four offspring each year, sometimes breeding more than once each year, and may live to breed for
several years. With such species, the proportion of the population which doesn't breed, or the
death rate of both juveniles and adults would have to be very large in order to yield a net rate of
increase less than 400%. And there are many species which are much more prolific than mammals
and birds. Many species of fish, for example, may produce from several hundred thousand to
several dozen million offspring (e.g. 0.8-2.4 million for atlantic sturgeon, 60 million for a 300 kg
bluefin tuna) each time they reproduce, and live to reproduce dozens of times (e.g. bluefin tuna
may live 38 years, and atlantic sturgeon may live 60 years) (Scott and Scott 1988). For a species
that produces a million offspring in a year, 99.9994% of the offspring must die in order to reduce
the net annual growth rate to 400% (assuming a sex ratio of 1:1), and it is difficult to imagine a
predator, or a set of predators, being efficient enough to annihilate such a large proportion of, the
young produced. Trees, similarly are very prolific and long lived. For prolific, long lived species,
very high mortality rates are expected and observed, but it is questionable as to whether or not
the mortality rates are high enough to reduce population growth rates low enough to prevent these
populations from showing chaos.

A second problem in applying the logistic model is that many species produce propagules
that remain inert for a considerable period of time before producing an offspring. In plants, this
phenomenon is described as a seed bank (Harper 1977). Many zooplankton produce resting eggs.
Protists may use spores. These inert propagules are used to survive temporarily inhospitable
environments such as dense forest cover, in the case of shade intolerant plants that contribute to
the seed bank, or winter, in the case of zooplankton. They may also serve to preserve a prolific
species which has increased beyond the capability of the environment to support it: i.e. the
inevitable crash in the logistic model when \( r > 4 \).

Finally, the logistic model ignores spatial aspects of population dynamics. In a now classic,
simple experiment, Huffaker (1958) found that the predatory mite *Typhlodromus occidentalis*
usually annihilated the phytophageous mite *Eotetranychus sexmaculatus*. The principal feature of
his experimental system was that the phytophageous mites were fed on oranges arranged on a grid
intermixed with rubber balls. When few oranges were used, the system quickly crashed, the prey
being annihilated. However, when a large number of oranges were used in conjunction with a
variety of barriers to the dispersal of the mites, the system persisted. With a single population of
each of the predator and prey, the prey is annihilated quickly, but with a large number of
populations, connected with limited migration, local populations go extinct but the total system
persists. The spatial aspect of the population biology of these species, including dispersal, stabilized an otherwise unstable system.

In this study, the logistic model is extended to allow consideration of these three issues.
The effects of persistent propagules and migration on the dynamics of a population is examined.
In particular, the ability of each of these to preserve a population with a \( r > 4 \), and the degree of
synchrony between populations, is examined.

**Method**

A spatial logistic model is constructed consisted of 100 populations set up on a 10 by 10
grid on a 2d-torus. This is a two stage model in that given a population size at time \( t \), the number
of persistent propagules is calculated along with the number of emigrants and then the emigrants
are equally divided between the eight nearest neighbors of the population. Finally, the population
size at time \( t+1 \) is obtained by applying the logistic map \( rX(1-X) \) to the sum of the population
size at time \( t \) and the immigrants to the population, and the result (which is set to zero if it
becomes negative) is added to a contribution from the pool of persistent propagules that existed at
time \( t+1 \). The sequence of events within a time period (between \( t \) and \( t+1 \)) is 1) the production of
propagules, 2) emigrants leave, 3) immigrants arrive, and 4) a portion of the persistent propagules
produce new adults. Most of the simulations were run for 1000 iterations, although a few were
run for up to 100,000 iterations. The longer simulations were done primarily to verify the