

## The Dynamics of Structured Populations

by Odo Diekmann

Physiological processes within individuals and behavioural patterns displayed by individuals are some of the subjects studied by biologists. Matters like growth, the succession of larval stages and reproduction are pieces of a sometimes remarkably complicated jig-saw puzzle called the life cycle.

On the other hand biologists also study the past and present state of large populations and try to predict their future development by calculating how the number of individuals changes as a consequence of reproduction and interaction (for example, competition for food).

Structured population models are intended to bridge the gap between the individual and the population level. The aim is to derive information about the dynamics of the population from information about the dynamics of the individuals or vice versa (cf. [1]).

The following three examples illustrate some of the main ideas.

1. If a predator eats (too) much prey he is not hungry any more and he will hunt with less zeal. Thus one expects that the functional response  $F$  (i.e., the number of prey eaten per predator per unit of time as a function of the prey density  $x$ ) will be given by a graph as shown in Figure 1.

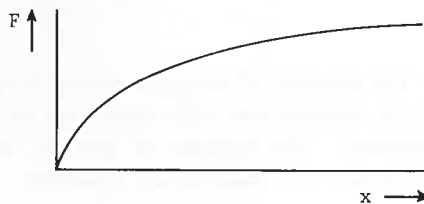


Figure 1.

Assuming that the state of each predator can be completely characterized by its satiation  $s \geq 0$  (i.e., some measure for the contents of stomach and gut) the population can be described by the satiation-density function  $s \rightarrow n(t, s)$  depending on time  $t$ . Thus  $\int_{s_1}^{s_2} n(t, s) ds$  represents the number of predators with satiation between  $s_1$  and  $s_2$  at time  $t$ .

One can then derive the following equation:

$$\frac{\partial n}{\partial t}(t, s) = -\frac{\partial}{\partial s} (g(s)n(t, s)) - x(b(s)n(t, s) - b(s-w)n(t, s-w))$$

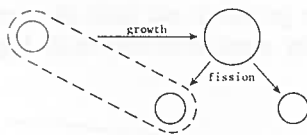
The first term at the right hand side describes the changes due to digestion (with rate  $g(s)$ ), and the second term describes changes due to the consumption of preys of constant weight  $w$  which are caught with rate  $xb(s)$ . Handling times and changes in prey density  $x$  are neglected here because of differences in time-scale: prey capture and digestion are fast processes compared with reproduction, and slow processes compared with the actual handling of the prey.

As  $t \rightarrow \infty$  the solution approaches a stable distribution  $\hat{n}(s)$  and the functional response is explicitly given by

$$F(x) = x \int_0^{\infty} g(s)\hat{n}(s) ds.$$

Numerical calculations based on this formula confirm the qualitative form of Figure 1. Moreover, one can use experimental measurements of  $g$  and  $b$  to determine  $F$  quantitatively and subsequently use the result as an input for a prey-predator total population model at the time-scale of reproduction. We refer to [2] for further details.

2. Consider a population of unicellular organisms (bacteria or algae) and assume that the physiological state of an arbitrary cell is completely described by one quantity  $x$  which obeys a physical conservation law (for



example, total mass or the amount of nitrogen atoms in the cell). We shall call  $x$  'size'. Furthermore, assume that cells reproduce by binary fission into two exactly equal daughters. The balance of growth, death and division (with rates  $g$ ,  $\mu$  and  $b$ , respectively) leads to the equation

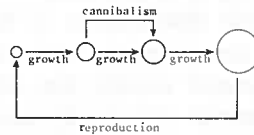
$$\frac{\partial n}{\partial t}(t, x) = -\frac{\partial}{\partial x} (g(x)n(t, x)) - \mu(x)n(t, x) - b(x)n(t, x) + 4b(2x)n(t, 2x),$$

which shows marked mathematical similarities to the equation in the first

example. It turns out that the existence of a stable distribution hinges on the biologically interpretable condition that  $x \rightarrow g(2x)$  and  $x \rightarrow 2g(x)$  are not identical.

Density dependence (as a consequence of limited resources) can be incorporated by specifying how  $g$  depends on the available nutrients and how, conversely, the food supply is influenced by consumption. References [3] are an elaborate presentation of this example.

3. Predators may prefer mature prey above young prey or they may, on the contrary, eat only eggs. Individuals of many species change their diet at various stages in the life cycle and thus one may have to distinguish the



predator according to its maturity. Cannibalism seems to be a major regulating mechanism for many species. In all of these situations one needs a population structure (in terms of age, size, larval stadia ...) in order to describe the interaction properly. See [4] for some models and results.

The first step in building these models consists of finding a suitable explicit parametrization of the state of the individuals (satiation, size, age, ...). The state of the population is then given by the density function  $n$  describing the distribution in the individual state space.

In the course of time the state of each specific individual changes (owing to digestion, growth, aging, ...). Moreover, individuals are born and die. (These words have to be interpreted broadly: in the first example a predator which consumes a prey "dies" while at the same time a new predator with  $w$  added to the satiation "is born".) In the second step one draws up the balance of these processes to derive a (first order partial) differential equation for the infinitesimal change in the population state. The coefficients in the equation describe the functioning and the behaviour of the individuals but the solution describes (properties of) the population as a whole. Starting from biological knowledge one can incorporate the interaction of the population and its environment (including other populations) by specifying in detail how the birth, death and growth processes depend on environmental quantities. Thus, as a rule, the equations become nonlinear.

When suitable boundary conditions are added, an initial condition  $n(0, x) = \phi(x)$  at  $t=0$  singles out a unique solution  $n(t, x; \phi)$ . It is mathematically convenient to conceive of  $\phi$  and  $n(t, \cdot; \phi)$  as elements of a function space  $X$  (such as  $L_1$  or  $C$ ) and to write

$$n(t, \cdot; \phi) = S(t) \phi.$$

The family  $\{S(t)\}_{t \geq 0}$  forms a semigroup of (continuous) mappings from  $X$  into  $X$  (i.e.,  $S(0) = I$  and  $S(t_1)S(t_2) = S(t_1 + t_2)$ ,  $t_1, t_2 \geq 0$ ) such that the balance equation can be interpreted as

$$\frac{dn}{dt} = An$$

with  $A$  the infinitesimal generator of  $\{S(t)\}_{t \geq 0}$ . Thus, these problems fit into the general framework of dynamical systems on infinite dimensional spaces [5,6]. An important special feature of these population models is the occurrence of *non-local terms* (such as the ones with the transformed arguments  $s - w$  and  $2x$ ) and this gives the problems a certain flavour reminiscent of functional differential equations, see [8].

The linear theory of stable distributions is based on positivity (Krein-Rutman Theorem) and on compactness arguments [2,3]. The qualitative theory of *nonlinear age-structured* models has developed rather rapidly in recent years [4,7]. For the general case hardly any work on nonlinear problems has been done. The objective of the project 'Dynamics of structured populations' at CWI is to develop parts of a qualitative theory little by little, by applying general techniques, such as bifurcation theory [9], to concrete problems in this area.

A recent colloquium at CWI has brought about cooperation with several biologists. Team-work has produced a set of examples (such as the ones above) which are as simple as possible but yet biologically relevant. Their mathematical analysis is now in progress. Step by step complexity and realism will be built up in the hope that eventually a coherent general theory will arise.

#### References

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