12 Modeling zooplankton dynamics

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12.1 INTRODUCTION

Modeling is a useful tool to relate abundance, distributions, fluctuations, and production of living organisms to variations in the abiotic environment, food conditions, and predation. Mathematical models integrate the dynamics of several variables into a single representation via interactions of processes (Wroblewski 1983). Nowadays models represent a continuum of complexity from simple response curves to complex marine food webs (Steele 1974; Walsh 1976; Kremer and Nixon 1978). Models are used prognostically or diagnostically, they serve to test different scenarios, and to understand the discrepancies between models and data. When models have been sufficiently tested and are considered robust, they can serve to predict future states.

Zooplankton models are built for three main objectives:

1) to estimate the flow of energy and matter through a defined ecological entity, for example an organism, a population or zooplankton community
2) to estimate the survival of individuals and the persistence of populations in their physical and biological environments, and to look at the factors and processes which regulate their variability
3) to study different aspects of behavioral ecology.

The core of this review is a description of models dealing with marine mesozooplankton. Models dealing with limnic zooplankton, or with fish larvae or meroplanktonic larvae are also partially described, and are only included to elucidate technical details or general principles. Models of microzooplankton are not described here. We aim to present detailed, specific applications of models on bioenergetics or demography of zooplankton rather than a general mathematical study of modeling. For general principles we refer the reader to papers and books listed in section 12.2.4.

Models dealing with a range of system components are reviewed in Table 12.1. The system components can be the internal components of the individual body, the individuals of a population, the populations of a single species, or the functional groups of zooplankton species. Process models dealing with physiological functions of individual organisms or specific links between physiological parameters and biological functions will also be presented. In section 12.2 we present general strategies for building

Table 12.1 Overview of the different models and their objectives following the levels of organization.

Type of models	Objectives
Process models	to define rate expressions or parameterization
Models of individuals	to calculate individual budget and growth
Models of groups of individuals	to simulate their trajectories in the physical environment to simulate individual variability in behavior, growth and development
Models of populations	to simulate population dynamics, to simulate dispersion of a population in a physical structure
Models of metapopulations	to simulate interactions between species to simulate succession of species
Models of ecosystems including zooplankton communities	to simulate the role of the zooplankton community in the functioning of an ecosystem

models, writing the mathematical relations and applying numerical methods to integrate the equations of the mathematical expressions of the model.

The rest of this chapter is devoted to the presentation of models relating to different levels of biological organization: individual (section 12.3), population (section 12.4) and community (section 12.5). Models coupling biological entities (individual, population, functional groups of zooplankton) with the physical environment to simulate spatial dynamics are presented in section 12.6.

12.2 MODELING APPROACHES AND TECHNIQUES

12.2.1 Steps of model building

The first step in building a model is to be clear exactly what the objectives are. These objectives will determine the scope of the model, as well as the kind of model to use and the output required from the model. The general method for building a model of a complex system is to identify simpler components of the system and to describe the interactions among these components and external variables of the system and among the components themselves (Wroblewski 1983).

CHOICE OF STATE AND FORCING VARIABLES

The first step is the identification of the components (*functional units*, or *compartments* or *subsystems*) of the system, and depends on the purpose of constructing the model. The level of complexity in the representation of the system (number of components, number of interactions in the model) depends on what we really understand, on the available knowledge for building specific details of a model, and on the capacity to represent details at the same level for the different parts of the system. In choosing the components, modelers must attempt to reduce the complexity of nature to manageable portions, whilst retaining sufficient structure to model processes that are of interest to them. There is no golden rule for doing this and, to a large extent, success will be judged by the ability of the model to predict observations and increase understanding. Adding

more compartments to a model adds to the dynamic complexity and can make model interpretation difficult. Thus, a stepwise approach is recommended, beginning with a model containing the minimum number of compartments required to tackle the problem in hand, and only adding further components as necessity dictates.

Determining the appropriate model is sometimes more difficult than parameter estimation. The pertinent variables (quantities that may vary with time and space) fall into two categories. First, the *internal variables* (or *state variables*) are those related to processes governing the system dynamics, for example the internal compartments of the body of an organism, the developmental stages of a population, and the trophic levels of an ecosystem model. Second, the *external variables* control some of the internal variables of the system. Temperature, light, and food concentration are typical external forcing variables of biological systems.

CHOICE OF MODEL UNITS

The next choice that must be made is the units or currencies of the model. For example carbon, nitrogen, phosphorus, or dry weight can be used if the variable is mass, whereas densities or numbers of individuals can be used if the variable is abundance. The choice of units will depend on the problem being studied. Many models have mixed units. Element ratios are usually assumed constant but Anderson (1992) presents a model for studying the influence of the modeled $C:N$ ratio.

CHOICE OF MATHEMATICAL FUNCTIONS TO MODEL THE INTERACTIONS BETWEEN VARIABLES

The study of interaction patterns is frequently helped by the use of various types of diagrams. Each variable is connected to other internal or external variables. The way in which each variable changes through the influence of one or more of the others must be known and the interactions described by mathematical functions. An important step is to determine the specific forms of these functions. In biological modeling, the relationships between variables are mostly established empirically, and the mathematical functions used to describe these relationships are not always derived from first principles. Empirical relationships should be used with caution. Each empirical relationship is only valid in certain space–time ranges, and should not be used outside these ranges without experimental tests. However, modelers frequently neglect this aspect. If several functions can describe a relationship between two variables, the simpler mathematical expression, i.e. the one with fewest parameters, should be chosen.

IDENTIFICATION OF PARAMETERS

An important process is the estimation of the values of the parameters (often called *calibration*). Such estimates often result from curve fitting of experimental data to the variables. If the model components represent large biological entities (e.g. the phytoplankton and zooplankton compartments of a pelagic ecosystem model), the function representing the relationship between the variables (e.g. the general grazing of phytoplankton by zooplankton) cannot be fitted from data. The form of the function is extrapolated from more specific studies, and possible parameter values are chosen from a large range of values due to the numerous species represented in the experiments. Most of the physiological parameters (e.g. ingestion rates, excretion rates, etc.) are experimentally obtained using small groups of animals of a given species.

Some parameters such as mortality rates are difficult to estimate experimentally. Because each situation is unique, one can only guess a mortality rate and examine the

model solution to see how well it fits the observations. This is called 'tuning' the model. It is a valid modeling technique when all but one set of parameters is well known. For instance, mortality can initially be set to zero to determine whether observed shifts in life-history stages of zooplankton could be simulated without mortality.

In more sophisticated methods models can be used for identifying values of parameters. In this case the properties of the model (its structure, the biological function used, etc.) need to be well understood. As an example, Jellison *et al.* (1995) present a comparison of cohort models for identifying demographic parameters.

12.2.2 The mathematical description of the system

SYSTEMS OF EQUATIONS

If the system is specified by the values of n state variables, the mathematical model of the system requires n equations. Equations are built by introducing rules for the interactions between variables of the system (state variables) and variables outside of the system (forcing variables). These rules are deduced from particular knowledge of the processes involved. There is no equivalent in biological models of physical laws such as the Navier–Stokes equation for fluid dynamics that provide the basis for physical oceanography; there is no set way to define how material is transferred between variables. Most of the models reviewed in sections 12.3–12.6 are dynamic simulation models, which allow time-dependent development of the state variables, either with no space dependence or with one to three space dimensions. Thus, most of the models considered here consist of time-dependent differential equations. The state of the system at any given time t depends upon what the state was at a previous time $t - dt$ and upon the conditions that prevailed and influenced the direction and rate of change from $t - dt$ up to but not including the instant t. In some cases, steady state conditions are considered by solving *time dependent* equations; usually the equations are not solved analytically, but numerically using computers. Ordinary differential equations (ODEs) are much more frequently used than partial differential equations (PDEs). This is a consequence of the availability of numerous routines for solving ordinary differential equations and of the greater simplicity of the equations. Reducing the dependence of the state variables to time or to one space dimension yields ordinary differential equations. Including more than one independent variable results in partial differential equations with greatly increased complexity for the numerical solving schemes.

In describing the way in which a dynamic system changes, two distinctions must be made: (1) continuous versus discrete state variables and (2) deterministic versus stochastic descriptions.

Biological state variables (e.g. the individual weight of an organism) are continuous, but many state variables of interest in zooplankton ecology are not continuous (e.g. the developmental stage of copepods). In the latter case, the value of the variable changes by discrete jumps. The treatment of discontinuous variables can be diverse, and they can be treated as though they were continuous if the scale at which we observe the system is coarse relative to the scale at which the jumps occur.

Biological functions can be built with two components: a deterministic component and a stochastic component in which the additional effect of variability due to randomness is added to the deterministic component. Stochasticity is used to represent known and not well understood effects on a process, and is added to a deterministic component. When the model is structured to account for such uncertainties in some of its functions, the model is referred to as a *stochastic model* (as opposed to a

deterministic model). They yield a probability distribution over the output sample space. In deterministic descriptions, the behavior of the system is completely determined by its state and by the specified conditions. As a result, a deterministic description of a dynamic system and its evolution through time usually gives a description of a particular trajectory. In a stochastic description, the additional effect of variability due to randomness is added to the deterministic component. This results in a distribution of probabilities for each set of possible behaviors. The connection between deterministic and stochastic descriptions is made by considering the expected or average behavior.

NUMERICAL METHODS

There are two ways of solving differential equations: analytical and numerical methods. Many differential equations cannot be solved analytically and must be solved numerically. Numerical techniques for solving differential equations are inexact, and involve approximations that allow a solution to be found by iterative calculations. There are many different numerical methods, but all can be implemented using a range of computer programs (e.g. Press *et al.* 1992). A good way to understand the principle of numerical methods is to use it for equations having a known analytical solution. The basis of the numerical solution of a differential equation is a difference equation that relates successive values of the solution at closely spaced intervals with the general form given by:

$$\frac{dN}{dt} = f(N(t), t) \tag{12.1}$$

with initial value $N(0)$ at time $t = 0$. f is the symbol of a function, N is the studied variable.

The numerical solution uses the difference equation:

$$\bar{N}(t + \delta t) = \bar{N}(t) + \frac{d\bar{N}}{dt} \delta t \tag{12.2}$$

where $\bar{N}(t)$ is a calculated value which is an approximation to the true value $N(t)$. The difference equation is iterated starting with the known value $N(0)$ at time $t = 0$ to produce the numerical solution $\bar{N}(\delta t), \bar{N}(2\delta t)$ and so on. Thus the numerical method produces an approximate solution to the differential equation which consists of a series of values at time intervals determined by the choice of the time increment. In practice the time increment δt is made small enough to achieve a satisfactory approximation.

One of the simplest approximations of an ODE by a difference equation is called Euler's method. The accuracy of the solution obtained by such a simple technique is related linearly to the step length δt, and generally can be improved by making δt smaller. However, the smaller the value of δt, the more calculations are required. This not only increases computer time, but the rounding errors of the computer can start to become significant, and introduce errors into the solution. There are other practical numerical methods for solving ODEs (see Press *et al.* 1992). An efficient recursive method approximating a Taylor series expansion is the Runge–Kutta technique.The fourth order Runge–Kutta method succeeds virtually always and is commonly used in many models.

For studying advection-diffusion processes PDEs have to be written. It is often difficult or impossible to find analytical solutions to PDEs, and we are forced to rely on

numerical approaches. There are many different techniques for obtaining numerical solutions to PDEs (see Press *et al.* 1992 for some that work reasonably well).

In some cases, it is possible to transform a PDE to an ODE (see for instance Sewell 1988, for a review of methods; and see Botsford *et al.* 1994, for an application). If not, finite difference methods are the most common applied numerical solution techniques (see Press *et al.* 1992). Many algebraic models are in fact discrete approximations to PDEs (Sinko and Streifer 1967), and certain integral formulations can also be shown to be equivalent to PDEs (Streifer 1974). The escalator boxcar train technique (Goudriaan 1986; De Roos 1988) is an example of an approximation to PDEs.

12.2.3 Computer programing and languages

The choice of which computer language to use for zooplankton modeling is usually determined by personal preference. However, there are a few practical implications associated with the choice. Relatively complex models can be developed using spreadsheet programs, where little active programing is required, and where good graphics are readily available. However, for increased flexibility and speed, it is often useful at some stage to write your own programs. The most commonly used programing languages in zooplankton modeling are BASIC, PASCAL, C, and FORTRAN. Existing computer routines for applying different numerical methods are available in these four languages. Many ocean models, particularly 3-D ocean models, are written in FORTRAN, so it is easier to link your zooplankton model to such a model if it is coded in a similar fashion. However, for developing individual-based models, an object-oriented language such as C++ or JAVA might be preferred.

There are various graphical programing languages available that are specifically designed to facilitate modeling of non-linear, dynamic systems. Among the most versatile of these languages is the graphical programing language STELLA II (Costanza *et al.* 1998; Hannon and Ruth 1997; Richmond and Peterson 1994). Some examples of models built with STELLA will be mentioned in this chapter.

12.2.4 Further reading

Several recent books are useful for introducing biological oceanographers to ecological models but the examples given are rarely taken from plankton:

Brown, D. and Rothery, P., 1993. *Models in biology: mathematics, statistics and computing.* Wiley, Chichester, 688 pp.
Edelstein-Keshet, L., 1988. *Mathematical models in biology.* Random House, New York, 586 pp.
Gold, H.J., 1977. *Mathematical modelling of biological systems. An introductory guidebook.* Wiley and Sons, New York, 357 pp.

Concerning the use of mathematical functions for fitting data for plankton processes:

Abramowitz, M. and Stegun, I.A., 1972. *Handbook of mathematical functions.* Dover Publications, New York, 1046 pp.

Concerning numerical methods and codes of these methods:

Press, W.H., Teukolsky, S.A., Vetterling, W.T. and Flannery, B.P., 1992. *Numerical recipes in*

FORTRAN. The art of scientific computing. Cambridge University Press, Cambridge, 963 pp. (This is also available for BASIC, PASCAL and C)

Sewell, G., 1988. *The numerical solution of ordinary and partial differential equations.* Academic Press, London, 271 pp.

Several books give examples of comparisons between stochastic and deterministic models of the same modeled system. In addition to those listed above we recommend:

Renshaw, E., 1991. *Modelling biological populations in space and time. Cambridge Studies in Mathematical Biology.* Cambridge University Press, Cambridge, 403 pp.

12.3 MODELS OF INDIVIDUAL BIOENERGETICS AND LIFE-HISTORY TRAITS

To construct a realistic population model one begins by formulating submodels for the individuals in the population. In order that a population model be predictive, it must represent the demographic effects of the physiological processes at the level of individuals (Streifer 1974).

12.3.1 Individual bioenergetics

BUDGET OF INDIVIDUAL ZOOPLANKTON

Several examples of trophodynamic formulations can be found in models of individuals, populations and ecosystems. The basis of many models of individuals and population-level individual-based models is the standard bioenergetic supply–demand function (Beyer and Laurence 1980, 1981; Batchelder and Miller 1989; Carlotti and Sciandra 1989; Caparroy and Carlotti 1996; Carlotti and Hirche 1997). In this function, growth is represented as the difference between the amount of food absorbed by an organism and the metabolic costs of its daily activities. Conover (1978) provides an extensive review of the different processes of the individual energetic balance of zooplankton (see also Mauchline 1998, for calanoid copepods). The principal functional forms used in models of biological energetics will be outlined in this section, and selected applications in recently published models will be provided.

The general balance equation of input and output fluxes of matter (or energy) in an organism is:

$$\text{Growth } (G) = \text{Ingestion } (I) - \text{Egestion } (Eg) - \text{Metabolic losses } (ML)$$
$$- \text{ Release of gametes or eggs } (RG)$$
$$- \text{ Other losses (molts, etc.)} \tag{12.3}$$

where

$$\text{Metabolic losses } (ML) = \text{Respiration}(R) + \text{Excretion } (Ex) \tag{12.4}$$

The assimilation efficiency is obtained as:

$$\text{Assimilation } (A) = (\text{Ingestion} - \text{Egestion})/\text{Ingestion} \tag{12.5}$$

Most models of individual bioenergetics consider input–output fluxes of matter. Ingestion is the process whereby animals acquire organic matter. Assimilation is the

Ingestion related to fluctuations of food concentration

Mayzaud and Poulet (1978) demonstrated a near linear response of five neritic copepod species to changes in food levels. This lack of saturation was thought to be due to variations in gut enzyme levels in response to varying phytoplankton concentrations. Franks *et al.* (1986) gave a mathematical formulation of this grazing response derived from Mayzaud and Poulet (1978) as:

$$I = I_m \alpha C \left(1 - e^{-\alpha C}\right) \tag{12.12}$$

As C gets larger, the formulation becomes linear with slope $I_m \alpha$, which is the initial slope of the Ivlev formulation. When C is large, the Ivlev curve shows saturation while the Mayzaud–Poulet curve does not. When C is small, the herbivore grazing rate is lower using the Mayzaud–Poulet formulation than the Ivlev. Franks *et al.* (1986) compared the effect of the choice of such ingestion functions on the dynamics of herbivore-zooplankton interaction in an N–P–Z (nutrient–phytoplankton–zooplankton) model.

Ingestion related to food quality – grazing on several resources – switching behavior
One severe limitation of studies in which only a single species of food is utilized is the possibility that the results obtained do not represent the complete spectrum of feeding behavior of copepods. The effect of food size on grazing efficiency has been considered in some models (Steele 1974; Steele and Mullin 1977; Bartram 1980). Bartram (1980) developed a model involving a general filtration rate and an efficiency of retention, itself a function of cell size, and tested it experimentally for two copepods. He applied the model to a population of copepods of different age classes feeding upon an assemblage of food particles of different sizes. Based on optimal foraging theory, Lehman (1976) proposed a model for filter-feeding behavior in mixtures of particle types and used it to evaluate selective ingestion of particles based on their comparative abundances, size and digestibility. Both these examples illustrate how food quality can be as important as food quantity in determining ingestion rates of copepods.

In their ecosystem model, Fasham *et al.* (1990) discuss the problem that arises when zooplankton modeling deals with parameterizing grazing on multiple prey of different types. For example in their model, the zooplankton graze on phytoplankton, detritus and bacteria, and it is necessary to specify how much of each prey is grazed at any time. One approach to this problem is to define a measure of total food, as:

$$F = p_1 P + p_2 D + p_3 B \tag{12.13}$$

where p_1, p_2, p_3, are constants determining the zooplankton preferences for various food types. P is phytoplankton, D is detritus and B is bacteria. A Michaelis–Menten expression can be used to define the grazing rate on, for example, phytoplankton as:

$$G_1 = gZ \frac{p_1 P}{K + F} \tag{12.14}$$

where g is the maximum specific grazing rate, Z is the zooplankton biomass, and K is the half-saturation constant for grazing.

Zooplankton preferences can be constant, but Fasham *et al.* (1990) chose to assign preference as a function of the relative proportion of the food based on Hutson's (1984) switching expression:

$$p_i = \frac{p_i' f(X_i)}{\sum_k p_k' f(X_k)}$$

where X_k is the concentration of kth food type and p'_i is defined as the preference for each of the different food types when the concentrations of these foods are equal. In their model, the simplest functional expression used is $f(X_k) = X_k$ which results in the model zooplankton selecting the most abundant food organism. Another possible functional type is the normalized limitation function describing zooplankton ingestion of the ith food type as suggested by Pace *et al.* (1984). Fasham *et al.* (1990) outline the properties of the non-prey-switching function and those based on Hutson's (1984) and Pace *et al.*'s (1984) switching expressions. Evans (1988) emphasizes that the model predictions can be very sensitive to the parameter values used in the switching function, whereas there are very few data on zooplankton feeding preferences to provide such values.

Ingestion related to predator and prey swimming activities and turbulence effects Several models have been developed to simulate the different steps of the feeding process of a swimming organism catching prey in the natural environment. The first models were developed for fish larvae, and then applications were extended to zooplankton in relation to the effect of turbulence. Most of the models described below refer to fish larvae. The amount of food ingested is a function of the number of prey encountered, captured and eaten, the levels of turbulence, light and prey aggregation.

The number of prey encountered and prey ingested are functions of the local prey concentration modified by local turbulence (Rothschild and Osborn 1988; MacKenzie and Kiørboe 1995). The behavior of the larvae (e.g. whether they exhibit cruise behavior or pause–travel behavior) also affects the encounter rate and these aspects are summarized next.

Rothschild and Osborn (1988) discussed the role of turbulence in affecting (enhancing) encounter rates with planktonic prey. Subsequent studies, for example Sundby and Fossum (1990), MacKenzie and Leggett (1991), Muelbert *et al.* (1994), explored the role of turbulence in oceanic conditions, finding an effective increase in contact rates of 2 to 10 times under various wind- and tidal-driven flows. With this formulation, an estimate of $N(i)$ the number of ith prey of concentration $p(i)$ encountered over a 24 h period in a turbulent environment is

$$N(i) = \sum_{24h} LA(i)D(i)p(i)\Delta t \tag{12.15}$$

The effect of the turbulent velocity ω enters in the determination of $A(i)$, the velocity of a larval fish relative to its prey

$$A(i) = \frac{[\sigma^2_{prey}(i) + 3\tau^2 + 4\omega^2]}{3(\tau^2 + \omega^2)^{1/2}} \tag{12.16}$$

where the larval fish swimming speed τ, and the ith prey swimming speed $\sigma_{prey}(i)$ are assumed to be on the order of one body-length per second. The parameter L is a binary day/night switch and

$$D(i) = (2/3)\pi\rho^2 \tag{12.17}$$

is the cross-sectional area of perception of the larva, where $\rho = (3/4)L$ is the prey encounter radius and is related to L the larval fish length (e.g. Werner *et al.* 1996).

The turbulent velocity (squared) is

$$\omega = 3.615(\varepsilon r)^{2/3} \tag{12.18}$$

where the separation distance r can be approximated as a function of the concentration $p(i)$ of the ith prey item (Rothschild 1992) as:

$$r = 0.55p(i)^{-1/3} \tag{12.19}$$

and ε is the turbulent kinetic energy dissipation rate specified as a function of space and time. No single formulation has yet parameterized the precise nature of small scale turbulence affecting predator–prey encounters, and different formulations may better represent different limiting cases (Osborn 1996). The definition of the appropriate length scale to estimate the contribution of turbulence to predator–prey contact rates (e.g. equation 12.16) is still a matter of discussion (Dower et $al.$ 1997). The length scale has been variously defined as the average distance between prey particles (Sundby and Fossum 1990; MacKenzie and Leggett 1991; Sundby 1995; Werner et $al.$ 1996), the Kolmogorov scale (Muelbert et $al.$ 1994), the eddy separation distance (Davis et $al.$ 1991) and the larval fish reactive distance R (e.g., Evans 1989; MacKenzie et $al.$ 1994; Denman and Gargett 1995; Kiørboe and MacKenzie 1995).

For larvae that are pause–travel predators, and defining the effective encounter spatial scale as the larval reactive distance, MacKenzie and Kiørboe (1995) formulated an expression for the encounters E_{p-t} (no. prey sec^{-1}) as

$$E_{p-t}(i) = \frac{2}{3}\pi R^3 p(i)P_F + \pi R^2 p(i)(\tau^2 + 2\omega^2)^{0.5}P_F P_D \tag{12.20}$$

where R is the larval reactive distance (e.g. a fraction of the larval body-length), P_F is the pause frequency (no. sec^{-1}), P_D is the pause duration (sec), and $p(i)$ and τ are as given above. Finally, the estimate of prey encountered is

$$N(i) = \sum_{24h} LE_{p-t}^{(i)}\Delta t. \tag{12.21}$$

A model for the influence of small-scale turbulence on post-encounter processes in larval fish indicated that turbulence can have an overall beneficial or detrimental effect on larval fish ingestion depending on the magnitude of the turbulence and on larval behavior (MacKenzie et $al.$ 1994). A dome-shaped relationship is found where ingestion rates are maximum at intermediate rather than high levels of turbulence; the decrease in pursuit success in highly turbulent environments negates the increase in ingestion rate caused by the increase in encounter rate. The implementation of this formulation is achieved by scaling the number of prey encountered by the estimated probability of successful pursuit P_{sp}. The value of P_{sp} depends on the turbulent velocity ω, the pursuit time t_p and the larval reactive distance R. The intersection of the prey excursion sphere (of radius ωt_p) and the larval encounter sphere (of radius R) define appropriate values of P_{sp} (see MacKenzie et $al.$ 1994 for details).

Some models have attempted to represent the effect of microscale turbulence on the ingestion of copepods (Davis et $al.$ 1991; Saiz and Kiørboe 1995; Caparroy and Carlotti 1996). In their model, Caparroy and Carlotti take into account different processes implicit in the process of ingestion: encounter rate, capture rate, and ingestion $sensu$ $stricto$, i.e. when a prey is in the mouth. The encounter rate is related to relative displacement between prey and predator, which is the consequence of swimming behavior and the microscale fluid motion (Rothschild and Osborn 1988). Different models have represented simple swimming behavior and derived encounter rate expressions for linear swimming (Gerritsen and Strickler 1977) or random-walk swimming (Evans 1989; Yamazaki et $al.$ 1991). Kiørboe and Saiz (1995) introduced several types of swimming in their model.

Effect of temperature on ingestion   Temperature has an important effect on all physiological functions. As the ingestion process is the input of matter into the individual, the effect of temperature on ingestion is crucial both at the individual level and also at higher levels of organization. Providing that energy and other resources are not limiting, physiological rates usually increase with temperature within the range normally encountered by the organism until a sudden decline near the upper limits when enzyme systems become damaged.

Most of the time only the increasing part of the curve is considered in models, and the function usually used is a power function of temperature:

$$Y_T = AB^T \tag{12.22}$$

Other functions which mimic the complete curve with the increasing and decreasing parts are presented in Table 12.3.

Responses of organisms to temperature have been expressed quantitatively in terms of the temperature coefficient Q_{10} generated from the Arrhenius equation which denotes the ratio of the rate of a metabolic process (e.g. ingestion) at one temperature to the rate at a $10\,^{\circ}C$ change in temperature, i.e.

$$Q_{10} = \frac{Y_{T+10}}{Y_T} = B^{10} \tag{12.23}$$

The Q_{10} can be calculated as soon as rates are measured for two temperatures as:

$$\log(Q_{10}) = \frac{10}{T_2 - T_1} \log\left(\frac{Y_{T2}}{Y_{T1}}\right) \tag{12.24}$$

By measuring the rate at successive temperatures, it is usually observed that Q_{10} is not independent of temperature over the temperature range in question. The Q_{10} values generally decline with increasing temperature. The Q_{10} of ingestion is generally found to be around two. The effect of temperature on gut clearance rate also may be represented by different models (Dam and Peterson 1988), and the Q_{10} is again found to be slightly above two (Ikeda 1985; Dam and Peterson 1988).

Combined effects of external factors on ingestion
In their copepod growth model, Carlotti and Nival (1992) considered the effects of food concentration, temperature and weight on ingestion and they multiplied the effects of the three functions. Such combinations should be made with caution because the biological responses of combined parameters can differ from the effects studied separately. For example, Thébault (1985) showed that the effect of temperature can differ with food concentration.

Light limitation
The effect of light on prey ingestion rates for certain larval fish has been studied in the laboratory by Huse (1994). For young larvae, ingestion rates were observed to decrease at low and at high light intensities (too much light reduces the required contrast for the larvae to sense their prey). The penetration of light in the water column and its modulation by cloudiness and suspended matter in the water can affect the vertical position of feeding organisms (as they seek adequate light levels for feeding). Combined with the vertical structure of the flow, the effect of light may have an indirect effect on the dispersal of organisms. The inclusion of the effect of light limitation on the capture of prey by recently hatched cod larvae is discussed in the modeling studies of Lough *et al.* (1997) and Quinlan *et al.* (1997).

scaling studies deserves careful consideration (Anderson and Hessen 1995). Dry weight is the traditional measure for ecological variables such as growth, but Vidal and Whitledge (1982) suggest that dry weight-based scaling relationships may be biased if animals have large proportions of metabolically inactive tissue, such as lipid stores. Others have chosen to express body size in terms of carbon (e.g. Ikeda and Skjoldal 1989; Schneider 1990). Schmidt-Nielsen (1984) and Cammen et al. (1990) have recommended the use of body nitrogen content as a mass variable, protein content provides an easily determined measure of body nitrogen. Because metabolism–size relationships can change with the size index selected (Berges et al. 1990), metabolic measurements based on different mass variables are not easy to compare, and need careful consideration before inclusion in models.

Integrating the metabolic budget of copepods during their lifetime, i.e. under various food conditions, Steele and Mullin (1977) identify three main components of respiration in zooplankton: basal or routine metabolism, the costs associated with foraging and capturing food, and the cost of assimilating and biochemically transforming the food. The last two components are often grouped as active metabolism. Carlotti and Sciandra (1989) suggest that the basal metabolism is related to weight, and the active metabolism is a proportion of the ingestion rate. In their growth model of a ctenophore, Kremer and Reeve (1989) use similar components.

Caparroy and Carlotti (1996) present a deterministic model of a copepod's energy budget to study the effect of turbulence on ingestion and on the related physiological processes. In such a model, taking into account the swimming speed of the predator, the specific cost of swimming is of primary importance in estimating the consequences of feeding strategies in different turbulent conditions. Several models evaluate the energetic cost of swimming activity by copepods and the effect of buoyancy on this cost (Vlymen 1970; Morris et al. 1985) and fish (Laurence 1985). Tiselius and Jonsson (1990) used theoretical hydrodynamic models to investigate costs and benefits of different feeding strategies (see also Haury and Weihs 1976). In his model of fish feeding, Laurence (1985) takes into account the cost of processing and utilizing the digested food.

Anderson (1992) presents a bioenergetic model of marine heterotrophs (zooplankton and bacteria) and determines food quality (in terms of C and N content) on growth and nitrogen excretion. This model illustrates the close link between nitrogen excretion and respiration, because excretion varies with the type of substrate respired.

The effect of temperature on metabolic rates can be represented by various functions, such as those presented in Table 12.3. The Q_{10} is generally found to be between two and four.

GROWTH AND EGG PRODUCTION MODELS
Individual growth is simulated by integration of the equation

$$G = \frac{dW}{dt} = \text{Ingestion} - \text{Egestion} - \text{Excretion} - \text{Respiration} \qquad (12.27)$$

Growth and egg production generally do not occur simultaneously; when the matter budget is positive, it is used for either growth or reproduction. A time step of 1 h is generally sufficient to simulate the dynamics of physiological processes and growth over several days. At each time step, the calculated growth increment is integrated over time.

Growth models based on allometric relations to weight
The rates of metabolic losses in non-limiting food conditions and constant temperature

are usually considered as allometric relationships (Laurence 1978; Beyer and Laurence 1980, 1981; Peters 1983; Huntley and Boyd 1984; Moloney and Field 1989; Kiørboe and Sabatini 1995; Hirst and Sheader 1997). Von Bertalanffy (1960) produced the gross equation that expresses the rate of growth (G) as the difference between anabolism and catabolism:

$$G = \frac{dW}{dt} = kW^c - jW^b \qquad (12.28)$$

where W is the body mass, t is time, and k and j are indices specific to particular combinations of genotype and environment, and c and b are 'scaling exponents'. A scaling exponent of less than 1.0 means that larger animals demonstrate lower rates of metabolism per unit weight than do smaller animals.

If $c \neq b$ there is an optimal growth for the body mass M_{opt} and an optimal mass for a balance between losses and gains M_{max}:

$$M_{opt} = \left(\frac{jb}{kc}\right)^{\frac{1}{c-b}} \qquad (12.29)$$

$$M_{max} = \left(\frac{j}{k}\right)^{\frac{1}{c-b}}. \qquad (12.30)$$

The highly simplified growth equation 12.28 described by von Bertalanffy (1938) summarizes many different processes, with the influence of several external parameters. Temperature affects metabolism, and several empirical relationships (exponential, linear, power) relate the four parameters of equation 12.28 to temperature (Atkinson 1994). The exponential function of temperature is the most common (Huntley and Boyd 1984).

Allometric relationships, with or without their temperature-dependent effects, are based on regression models that can be derived from data sets using single species or groups of several species, and obtained under various conditions. Furthermore, not all authors proceed in the same way in calculating these regressions. For example, after log transformation of the values of rate processes and corresponding weight values, Moloney and Field (1989) fixed the values of the allometric exponents, rather than allowing these to be estimated by regression. Thus, allometric relationships should be used with caution in any model.

Growth and egg production models in changing environmental conditions

These models should take into account detailed physiological functions of those rates that vary with fluctuations of external variables. Food and temperature are usually taken into account in budget models of zooplankton (Kremer and Nixon 1978; Carlotti and Sciandra 1989; Carlotti and Hirche 1997). Table 12.4 presents a list of publications containing growth models for different zooplankton groups and species.

In Carlotti and Sciandra's (1989) model of the copepod *Euterpina acutifrons*, food and temperature affect ingestion which, in turn, influences the rate of excretion, so that the excretion rate is influenced indirectly by temperature and food. Because the physiological connections are numerous and non-linear, it is important to test the consequences of an hypothesis in relation to a given process. By comparing model output and data under different external forcing conditions, different scenarios in the hierarchy of the physiological processes can be tested. For example, Huntley *et al.* (1994a) developed a physiological model of growth of Antarctic krill *Euphausia superba* in terms of C and N

Table 12.4 Zooplankton growth models.

Species	Authors
Ctenophore	
Mnemiopsis leidyi	Kremer and Nixon (1978)
Mnemiopsis mcradyi	Kremer and Nixon (1978)
Meroplanktonic larvae	
Crassostrea virginica	Dekshenieks *et al.* (1993)
Pectinaria koreni	Carlotti (1996a)
Cladocera	
Daphnia sp.	Gurney *et al.* (1990)
CRUSTACEA	
Copepods	
Copepods	van den Bosch and Gabriel (1994)
	Omori (1997)
	McLaren (1997)
	Broekhuizen *et al.* (1994)
Euterpina acutifrons	Carlotti and Sciandra (1989)
	Carlotti and Nival (1992)
Calanus sp.	Steele and Mullin (1977)
	Steele and Frost (1977)
Calanus finmarchicus	Slagstad (1981)
	Carlotti and Radach (1996)
	Carlotti and Hirche (1997)
	Carlotti and Wolf (1998)
Calanus glacialis	Slagstad and Tande (1990)
Metridia pacifica	Batchelder and Miller (1989)
Metridia lucens	Batchelder and Williams (1995)
Mysidacea	
Mysis mixta	Gorokhova (1998)
Decapoda	
Hyas araneus	Anger (1990)
Euphausiacea	
Euphausia superba	Astheimer *et al.* (1985)
Fish larvae	
Engraulis mordax	Wroblewski (1984)
Gadus morhua	Werner *et al.* (1993)
Melanogrammus aeglefinus	Werner *et al.* (1993)
Melanogrammus aeglefinus	Cushing and Horwood (1994)
Theragra chalcogramma	Hinckley *et al.* (1996)
Theragra chalcogramma	Rose *et al.* (1996)
Theragra chalcogramma	Rose and Cowan (1993)
Theragra chalcogramma	van Winkle *et al.* (1993)

to study different scenarios of the life strategy of krill during winter. In this case, the time step was one day, and the simulations were run over a four month period.

Budget models can be used as a tool to test the importance of newly explored environmental factors such as microscale patchiness and turbulence to growth and

recruitment of planktonic consumers (Davis *et al.* 1991; Tiselius *et al.* 1993; Nonacs *et al.* 1994).

Egg production can be related to the mass budget of females. The simplest formulation is to consider that above a given mass (mass of mature females), all assimilated matter is used for egg production and not for growth (e.g. Carlotti and Nival 1992).

Carlotti and Hirche (1997) present a model of the individual bioenergetics of *Calanus finmarchicus* females with details of the oocyte maturation steps. Their model considers the transfer of matter to different parts of the body from the ingested matter in the gut. The matter is directed toward either the structural weight, the lipid reserves sac, or the gonads. Four steps of oocyte maturation are considered. By comparison with data, the model suggests that, for this species, egg production cannot be dependent only on external parameters but is also strongly linked to the state of internal compartments.

Egg production models related to external parameters

Several empirical relationships relating observed egg production directly to external variables have been proposed, mainly in relation to temperature and food. Corkett and McLaren (1978) defined a temperature dependent empirical equation

$$F(T) = \frac{E_s \cdot S}{t_1 + S_n \cdot t_S} \tag{12.31}$$

where $F(T)$ is the daily egg production per adult female, E_S is the number of eggs in one sac, S_n is the total number of sacs produced over life time, t_1 is the time from reaching adult to the appearance of the first sac, and t_S is the time between the appearance of successive sacs (Davis 1984b). The values of t_1 and t_S are expressed as a percentage of the embryonic duration which depends on temperature following a Belehrádek's equation (see page 590). Uye (1981) also defined an empirical relationship between copepod egg production and temperature and food. Checkley (1980a, 1980b) suggested a relationship between copepod egg production and female length and temperature. These empirical relationships are useful for population models which do not consider individual budgets (e.g. Davis 1984b).

12.3.2 Vital rates

Vital rates (e.g. development rates and mortality rates) can be obtained from cohort development studies either in laboratory controlled conditions, in mesocosms, or *in situ*. Aksnes *et al.* (1997) discuss obtaining data for life tables from cohort analyses of populations of copepods. Such data allow the estimation of durations of successive developmental stages of species under various environmental conditions (temperature, food, and salinity). In this section, we present empirical functions of development rates and mortality rates commonly used in population dynamics models. Inverse methods are described that estimate vital rates by fitting simulations of a population model to data.

Vital rates are usually linked directly to external parameters (e.g. temperature, food concentration) which are experimentally easy to control. Indeed, vital rates depend on physiological states of the organisms which vary with the external factors. The modeling of functional biological properties which modify vital rates (i.e. Carlotti and Sciandra 1989, their Figure 1) results in more efficient simulation of the dynamics of organisms if the external conditions of temperature and food are highly variable.

DEVELOPMENTAL STAGE DURATIONS OF CRUSTACEAN ZOOPLANKTON

In non-limiting food conditions, development time of stages from egg to C5 as a function of sea water temperature is commonly fitted using Belehrádek's equation (McLaren 1963, 1978; Mauchline 1998):

$$D_i = a_j(T + b)^c \qquad (12.32)$$

where D_i is the development time of stage i (days) and T is temperature (°C). Parameter a_i (days °C^{-1}) governs the mean slope, b (°C) allows for shifts in the temperature scale and c (dimensionless) determines the curvature of the response. The parameters b and c are considered as characteristics of the species and are equal for all the stages. Values of a_1, b and c are obtained by fitting embryonic durations (stage 1) at different temperatures. In the absence of sufficient data, c is often assumed to be -2.05 (Mauchline 1998, see his table 48), and b is set to a reference value (e.g. 13.87 for *Pseudocalanus*, Davis 1984a, 1984b; Corkett and McLaren 1970, 1978).

Parameter a_i depends on stage i and is determined by knowing stage durations D_i at a given reference temperature:

$$a_i = a_1 \frac{D_i}{D_1} \qquad (12.33)$$

The adult duration also changes with temperature but it is more difficult to estimate, because it is fixed by mortality. Davis (1984a) considers the adult female life D_{12} to be twice the length of the reproductive period.

Several empirical models have related stage duration to temperature (Heip 1974; Guerrero *et al.* 1994). The latter authors carried out a comparative analysis of several equations (Belehrádek's equation, linear equation, hyperbolic and power equations, and exponential equations) used to describe the dependence of the development of organisms on temperature. McLaren (1995) and Blanco *et al.* (1995) discuss the biological significance of the different equations. These equations fit the observed development time in a range of temperatures that are not the extreme temperatures. At the optimal temperature a minimum development time is observed, and above this optimal temperature the development time increases for higher temperatures.

Under fluctuating temperature conditions, the molting cycle can be modeled by approximating the stage duration over short time steps with constant temperature. If the time step of the model is dt, the fraction of the molting cycle completed after dt at time t (MC_t) is:

$$MC_t = \frac{dt}{a_i(T + b)^c} \qquad (12.34)$$

where T is the temperature during dt. By summing the molting fractions MC_t over the time since entry of the organism into that particular stage, the completed portion of the molting cycle is obtained. The molting cycle is completed when the sum is 1, and the stage duration can be calculated by summing the number of time steps. Miller and Tande (1993) modeled the development time for a single cohort of *Calanus finmarchicus* over one year in this way (see also section 12.4).

Stage duration also can be considered as the time period necessary for an organism to grow from a starting weight to a final weight, as modeled by Carlotti and Sciandra (1989). In doing so, there is an implicit hypothesis that development and growth are completely linked, which is not true in many cases. Nevertheless, models such as this allow the investigation of possible effects of external factors on development.

MORTALITY RATES

The representation of mortality in zooplankton modeling and the estimation of parameter values is difficult for population dynamics models as well as ecosystem models. The importance of emphasizing mortality when studying the dynamics of natural populations is expanded by Ohman and Wood (1995, 1996). The importance of the mortality term in bulk models is discussed in section 12.5.

Zooplankton mortality arises for a number of reasons. These can be classified as internal (developmental stage, senescence, genetic background), external (starvation, predation, parasitism) and the combination of external and internal factors (e.g. efficiency of enzymatic activity is a function of temperature) (see Ohman and Wood 1995 for a review). As a consequence there are a variety of formulations to represent mortality.

The simplest formulation is to consider a constant mortality for the whole population. This approximation neglects the fact that different stages may have different sensitivities during critical periods such as molt or starvation, and that individuals in a given stage may have different mortality rates depending on their physiological state. Numerous models consider constant stage-dependent mortality rates that decrease with life stage (i.e. Cushing 1975; Wroblewski 1980; Batchelder and Miller 1989). Mortality values used in population models are estimated from field data using different methods (see Aksnes et al. 1997; Wood and Nisbet 1991), and the range of estimated values is often large enough to simulate very different dynamics. By running simulations over successive years, it is possible to reduce the range to values giving stable population cycles. The use of different data sets to compare simulated and observed population abundance and structure is the best way to reduce the parameter range.

Mortality rates probably vary within stages for several reasons, and detailed formulations have been used in several models. Mortality caused by starvation can be related either directly to food concentration (Andersen and Nival 1986) or to an index of the physiological state of organisms in terms of their specific growth rates (Wroblewski 1984; Carlotti and Sciandra 1989; Bryant et al. 1997). An average value of specific growth rates over the previous few days could be introduced to represent the ability to buffer short starvation periods. Bryant et al. (1997) add a complementary effect of temperature in their mortality function.

Predation is often believed to be the major source of mortality for herbivorous zooplankton (Ohman 1986). Davis (1984a, 1984b) presents model simulations of copepod seasonal cycles on Georges Bank investigating the role of predation by chaetognaths (size selective), ctenophores (non selective) and carnivorous copepods, in the control of population growth. Mortality caused by each predator is represented as the product of predator abundance and the consumption rate (number of copepods eaten daily by one predator) which is temperature dependent. A formulation of the size selective chaetognath predation is developed in detail in Davis's (1984b) paper. The model runs were made with various consumption rates until the model output matched observed seasonal cycles.

Fiksen and Giske (1995) divide the contribution to mortality by predation into visual and tactile fractions. The visual component mainly consists of fish and the tactile component of invertebrate carnivores and omnivores like medusae, chaetognaths and predatory copepods. They use a process model of predation by visual predators on zooplankton (Aksnes and Giske 1993; Giske et al. 1994; see also Aksnes et al. 1997). The model consists of a set of equations that calculate the visual range of a planktivore from the prevailing light conditions, influenced by irradiance at the surface, the fraction

reflected at the air–water interface, turbidity, depth, prey characteristics and planktivore eye sensitivity threshold for prey recognition. In Fiksen and Giske's (1995) model, tactile predation is assumed to be a size-dependent mortality rate which can be represented by a negative power function of weight (Peterson and Wroblewski 1984; McGurk 1986). Hansen *et al.* (1994) present a synthetic study of the size ratio between predator and prey in zooplankton. The integrated effect is likely to be a decline in tactile predation pressure with age and stage (Ohman 1988), although this may not apply in all cases. Size dependent cannibalism is part of this tactile predation and is probably an important source of mortality for eggs and nauplii (Kremer and Nixon 1978; Peterson and Kimmerer 1994).

INVERSE METHODS TO ESTIMATE VITAL RATES

Population dynamics models presented in section 12.4 can be used to estimate stage durations (or development rates) and mortality rates by fitting the model to observed data. A wide variety of inverse methods can be used to do these fits (Manly 1989). Inverse methods estimate parameters by fitting simulations to data.

Although many methods employ analytical manipulations of the basic equations, most can be solved through parameter estimation techniques widely employed in system identification: Parslow *et al.* (1979) illustrate these techniques in a comparative analysis of four different cohort models. They found uncertainty in the estimates of both stage duration and mortality to increase with increasing sampling error and decreasing sampling intensity. Hay *et al.* (1988) also used a model to describe the birth, growth and mortality rates of small copepods reared in enclosures. They found that uncertainty in the estimates of mortality could be reduced by aggregating the stages. Jellison *et al.* (1995) use systems identification techniques to compare parameter estimates from stage-structured population models with different degrees of complexity to represent the development rate. Development and mortality rates were estimated in all three of their models using standard non-linear estimation techniques. The best values were determined by minimizing the weighted squared errors between modeled and simulated data using the Levenburg–Marquardt algorithm (Press *et al.* 1992). In a similar way, Rothschild *et al.* (1997) developed a numerical method for separating and estimating growth and mortality coefficients using a stage- or size-structured population model and an optimization formulation. A basic assumption when using inverse methods is that the rates of mortality and development are constant within each stage. Rothschild *et al.*'s (1997) method permits the incorporation of time-related functions of the rates.

Inverse techniques have been used to estimate vital rates from field data. Huntley *et al.* (1994b) used analytical solutions of a population dynamics model to estimate stage-specific mortality and development of *Calanoides acutus*, an Antarctic species, as the population emerged from overwintering diapause. Miller and Tande (1993) also compared simulations with an age-within-stage model to stage abundance data of *Calanus finmarchicus*. They determined stage durations by examining the temporal progression of fractional abundances of the stages, and discuss the quality of sampling in these estimations.

12.3.3 Evolutionary forces on the organism

Imagine a population of copepods or any other biological species. Within this population assume a limited number of genetic recipes: DNA-based codes for building a body, making enzymes for digestion, setting rules for allocation of surplus food to

body tissues and to reproduction and so forth. Let us term such a recipe a 'genetic strategy'. Offspring inherit the genetic codes from their parents; let us for simplicity assume they inherit everything from their mothers. We can calculate the instantaneous rate of increase ρ of each such strategy i by

$$\rho_i = \frac{\ln\left(\frac{N_i(t)}{N_i(0)}\right)}{t} \tag{12.35}$$

where N is the number of individuals carrying i and t is the time period. If the environment remains stable, or if the time period t is sufficiently long, then ρ_i describes the growth rate of strategy i. As there always will be a maximum number of individuals possible in any population (either because of resources, competitors, predators, parasites, or a combination of all) the total population will gradually be dominated by those strategies that have the highest rates of increase:

$$N(t) = \sum_i N_i(0)e^{\rho_i t} \tag{12.36}$$

The fitness of a strategy may be defined as the difference between its rate of increase and the average rate of increase (r) of the whole population (the whole gene pool of strategies) (Giske *et al.* 1993):

$$\Phi_i = \rho_i - r \tag{12.37}$$

Over evolutionary time only those strategies that on average produce the highest rates of increase may persist. Hence all strategies of life that exist among copepods or other species, are the results of natural selection, where the criterion for long term survival is maximization of the rate of increase ρ.

Evolution through natural selection introduces a biological *force* on the individuals (Dawkins 1995; Giske *et al.* 1998a). Although this is a completely passive and unconscious process, genetic codes will tend to produce individuals that live for the maximization of their reproductive rates (Sibly 1989; Figure 12.1). This also means that the lives of the individual organisms may be understood by the logic of natural selection, and sometimes also predicted from ecological factors. By resolving equation 12.37, we could find optimal decisions and trade-offs among developmental, physiological and ecological variables. This could enable us to model how an organism will lead its life.

The three main demographic variables controlling the rate of increase of the strategy are the fecundity (b), probability of survival from egg to reproduction (S), and the generation time (α):

$$\rho_i = \frac{\ln(bS)}{\alpha} \tag{12.38}$$

The survival can again be expressed as a function of the instantaneous mortality rate M

$$S = \exp(-\alpha M) \tag{12.39}$$

By substituting for S in equation 12.32, we can write

$$\rho_i = \frac{\ln(b)}{\alpha} - M \tag{12.40}$$

which is an expression of what can be maximized through natural selection (Sibly 1989). From equation 12.40 we can evaluate the fitness value of an action, and we can decide
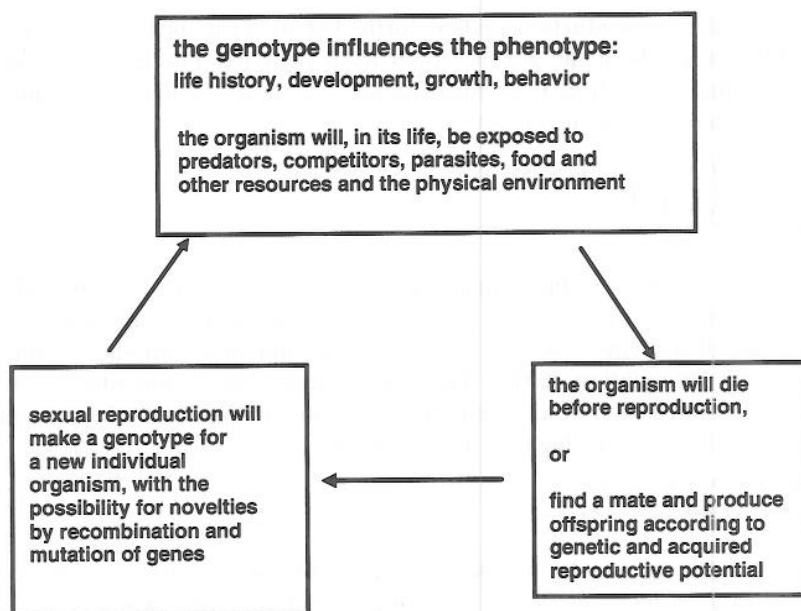
the genotype influences the phenotype:
life history, development, growth, behavior

the organism will, in its life, be exposed to predators, competitors, parasites, food and other resources and the physical environment

sexual reproduction will make a genotype for a new individual organism, with the possibility for novelties by recombination and mutation of genes

the organism will die before reproduction,

or

find a mate and produce offspring according to genetic and acquired reproductive potential

Fig. 12.1. The evolutionary premise for optimization theory in ecology: evolution leads to adaptation by natural selection. Although evolution cannot be sure to find the optimal solutions, it creates adaptations.

what to do among several alternatives. For instance, if a copepod could 'choose' among several depths with variable food concentrations (impacting fecundity), temperatures (impacting generation time) and light intensities (impacting mortality risk), then equation 12.40 can be used to calculate the fitness effects of the decisions. In many cases, the benefit of staying in warm, food-rich surface waters will be higher at night (with low light intensity and predation risk from visual predators) than during daytime, and there will be a benefit of diel vertical migration.

We can further split this equation into age-dependent processes by the Euler–Lotka equation (Euler 1760; Lotka 1907; Stearns 1992):

$$1 = \sum_{Y=1}^{\infty} m_Y l_Y e^{-eY} \tag{12.41}$$

Here we see that the optimal life-history strategy will depend on how behavior may impact fecundity (m_Y) or survival (l_Y) in this time period as well as in later periods. Heavy reproduction may in some instances impact both current mortality risk and future fecundity (e.g. by depleting energy reserves). Fitness maximization has implications far beyond these demographic variables. All aspects of life (biochemistry, morphology, anatomy, physiology, life cycle, and behavior) can be optimized by natural selection in order to maximize the expected rate of increase.

The Euler–Lotka equation will only find the precise value of ρ in an environment that repeats itself from generation to generation. In variable environments, fitness is maximized by a strategy that also minimizes intergenerational variation in the rate of increase (Yoshimura and Clark 1993; Tuljapurkar and Caswell 1997). But for ecological

modeling of zooplankton, the Euler–Lotka equation or a derivative of it will suffice in most cases.

12.3.4 Further reading

Books with descriptions of individual budget dynamics:

Kremer, J.N. and Nixon, S.W., 1978. *A coastal marine ecosystem. Simulation and analysis.* Springer-Verlag, Berlin, 217 pp.

Clark, C.W. and Mangel, M., 1999. *Dynamic state variable models in ecology: methods and applications.* Oxford University Press, Oxford, in press.

Kooijman, S., 1993. *Dynamic energy budgets in biological systems. Theory and applications in ecotoxicology.* Cambridge University Press, Cambridge, 350 pp.

Mangel, M. and Clark, C.W., 1988. *Dynamic modelling in behavioural ecology.* Princeton University Press, Princeton, NJ, 308 pp.

Metz, J.A.J. and Diekmann, O., 1986. *The dynamics of physiologically structured populations. Lecture Notes in Biomathematics 68.* Springer-Verlag, Berlin, 511 pp.

Tuljapurkar, S. and Caswell, H., 1997. *Structured-population models in marine, terrestrial, and freshwater systems.* Population and Community Biology Series 18, Chapman and Hall, New York, 643 pp.

For a review of knowledge on calanoid copepods, useful for parameter calibration, see:

Mauchline, J. 1998. *The biology of calanoid copepods.* Academic Press, San Diego, 710 pp.

12.4 POPULATION MODELS

12.4.1 Populations described by one variable

The simplest and earliest models describe populations in terms of one variable, the total number of individuals in that population. These models postulate that the rate of change of the population number, N, is proportional to N (Malthus 1798; Pielou 1969):

$$\frac{dN}{dt} = rN \tag{12.42}$$

Verhulst (1838) modified this equation by adding a non-linear term, giving the logistic equation (Pielou 1969):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{12.43}$$

By adding a time delay term to the logistic equation, oscillations of the population can be represented (Cunningham 1954).

12.4.2 Populations described by several variables – structured population models

Life cycles of zooplankton species are complex with individuals developing through different life stages. They are relatively long compared with bacteria, phytoplankton and microzooplankton. Some modeling approaches use variables that structure the popula-

tion with respect to age (age structured population models – ASM), stage (stage structured population models – SSM), size (size structured population models – SiSM) and weight (weight structured population models – WSM).

DISCRETE-TIME DIFFERENCE EQUATION MODELS AND MATRIX MODELS

Matrix models constitute a class of population models that incorporate some degree of individual variability. In a recent overview, Caswell (1989) showed that they are powerful tools for analyzing, for example, the impact of life-history characteristics on population dynamics, the influence of current population state on its growth potential, and the sensitivity of the population dynamics to quantitative changes in vital rates. Matrix models are convenient for cases where there are discrete pulses of reproduction, but not for populations with continuous reproduction. They are not suitable for studying the dynamics of populations that live in fluctuating environments.

Age structured matrix models (ASMM)

One of the first representations of age-structured dynamics was obtained by working with discrete age-classes, often referred to as a *Leslie matrix* (see Caswell 1988, 1989, 1997). Suppose there are m age classes numbered $1, 2, \ldots, m$, each covering an interval τ. If $N_{j,t}$ denotes the number of individuals in age class j at time t and G_j denotes the fraction of the population in this age class that survive to enter age class $j + 1$, then

$$N_{j+1,t+1} = G_j N_{j,t} \tag{12.44}$$

Individuals of the first age class are produced by mature individuals from older age classes:

$$N_{1,t+1} = \sum_{j=1}^{m} F_j N_{j,t} \tag{12.45}$$

where F_j is the number of age class 1 individuals produced per age class j individual during the time step τ.

The system of equations 12.44 and 12.45 can be written in matrix form:

$$
\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{pmatrix} (t+1) =
\begin{pmatrix}
0 & F_2 & F_3 & \cdots & F_m \\
G_1 & 0 & 0 & \cdots & 0 \\
0 & G_2 & 0 & \cdots & 0 \\
\vdots & \ddots & \ddots & \cdots & \vdots \\
0 & 0 & G_{m-1} & & 0
\end{pmatrix}
\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{pmatrix} (t). \tag{12.44}
$$

Such models were originally formulated for populations in which the individual age was the main source of variability (Leslie 1945, 1948).

Stage- (SSM), size- (SiSM) and weight- (WSM) structured matrix projection models

The Leslie matrix has been modified to deal with size classes, weight classes and developmental stages as the key individual characteristics of the population. Organisms grow through a given stage or size/weight class for a given duration.

The population projection matrix, often referred to as a *Lefkovitch matrix* (Lefkovitch 1965), has the form:

$$
\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{pmatrix}(t+1) = \begin{pmatrix} P_1 & F_2 & F_3 & \cdots & F_m \\ G_1 & P_2 & 0 & \cdots & 0 \\ 0 & G_2 & P_3 & \cdots & 0 \\ \vdots & \ddots & \ddots & \cdots & \vdots \\ 0 & 0 & & G_{m-1} & P_m \end{pmatrix}\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{pmatrix}(t).
\tag{12.45}
$$

where F_i is the size- (or weight- or stage-) specific fertility, G_i the probability of surviving and growing into the next size class, and P_i the probability of surviving and remaining in the current size class. G_i and P_i can be written in terms of the size-specific survival probability σ_i and the size-specific growth probability (or probability of molting) γ_i:

$$
G_i = \sigma_i \gamma_i
\tag{12.46}
$$

$$
P_i = \sigma_i(1 - \gamma_i)
\tag{12.47}
$$

The parameter γ_i can be estimated from the distribution of durations within each size class (or weight class or stage). Caswell (1988, 1989) presented the use of different stage duration distributions to estimate γ_i: geometric distributions, fixed stage durations for all individuals, variable stage durations, and negative binomial distributions.

For a stable population, the dominant eigenvalue λ of the matrix represents the population growth rate and the corresponding eigenvector is the stable size (or weight or stage) distribution (see Caswell 1989).

Structured matrix models including both stage, size, weight and age

The construction of models using both stage, size, weight, and age is possible (Caswell 1983, 1988, 1989) but such models are difficult to manipulate because of the large number of categories required. For zooplankton species, individuals proceed through a series of developmental stages with the probability of moving from one stage to the next dependent on the time already spent in the stage, but independent of the time spent in any previous stage. In such a model, individuals are classified by age within stages (or size/weight classes), as was first done by Parslow *et al.* (1979).

There are several variations of these matrix models, differing mainly in the expression of vital rates, which can vary with time depending on external (e.g. temperature, food concentration, competitors, predators) or internal (e.g. density-dependent) factors.

Examples of applications of matrix projection models for zooplankton population studies are given in Table 12.5. Two examples are described below.

Davis (1984a) presented a copepod model that simulates the movement of individuals through stages with a good representation of the duration of each stage. The model considers age-classes, one for each time step, separating new recruits in a stage from older individuals in the stage.

The transfer from one age class j to the next for non-molting individuals is given by:

$$
N_{i,j+1} = \sigma_i(1 - \gamma_{i,j})N_{i,j}
\tag{12.48}
$$

where i is the stage, σ_i is the stage-specific survival rate and $\gamma_{i,j}$ the stage- and age-within-stage-specific probability of molting.

Table 12.5 Population dynamics models of zooplankton and ichthyoplankton.
MM matrix model; ASMM age structured matrix model; SSM stage structured
model; CASM continuous-age structured model; CASiSM continuous-age and size
structured model; SASM stage and age structured model; WSM weight structured
model; SiSM size structured model; IBM individual based model; LEM Lagrange
ensemble model; CM cohort model.

Species	Authors	Type of model
Salps		
Thalia democratica	Ménard *et al.* (1994)	MM
Salpa fusiformis	Andersen and Nival (1986)	SSM
Medusa		
Pelagia noctiluca	Morand *et al.* (1992)	MM
Annelids (larval stages)		
Streblospio benedicti	Levin *et al.* (1987)	ASMM
Nephtys incisa	Zajac and Whitlatch (1989)	ASMM
Owenia fusiformis	Thiébault and Dauvin (1991)	ASMM
Pectinaria koreni	Carlotti (1996a)	SSM
Cladocera		
Daphnia sp.	Frank (1960)	ASMM
	Sinko and Streifer (1967)	CASM
	Streifer (1974)	CASiSM
	Argentesi *et al.* (1987)	CASM
	De Roos *et al.* (1992)	SSM
	Hogeweg and Richter (1982)	IBM
	Mooij and Boersma (1996)	IBM
Cirripeds (larval stages)		
Balanus glandula	Roughgarden and Iwasa (1986)	ASMM
Copepods		
Copepod sp.	Woods and Barkmann (1993)	LEM
	Caswell and Twombly (1989)	SSMM
	Hogeweg and Richter (1982)	IBM
Diaptomus sanguineus	Hairston and Munns (1984)	ASMM
Eurytemora affinis	Gaedke (1990)	SSM
Euterpina acutifrons	Sciandra (1986)	SASM
	Carlotti and Sciandra (1989)	SASM
	Carlotti and Nival (1992)	SASM
Acartia tonsa	Gaedke (1990)	SSM
Acartia clausi	Wroblewski (1980)	SSM
Paracalanus sp.	Hofmann and Ambler (1988)	SSM
Paracalanus parvus	Davis (1984b)	SASM
Pseudocalanus sp.	Davis (1984a, 1984b)	SASM
Calanus sp.	Steele and Mullin (1977)	CM
	Steele and Frost (1977)	CM
Calanus finmarchicus	Slagstad (1981)	WSM
	Davis (1984b)	SASM
	Miller and Tande (1993)	SASM
	Carlotti and Radach (1996)	SASM

Table 12.5 *Continued*

Species	Authors	Type of model
Calanus finmarchicus	Carlotti and Wolf (1998)	IBM
	Bryant *et al.* (1997)	WSM
	Heath *et al.* (1997)	WSM
	Tande and Slagstad (1992)	WSM
Calanus marshallae	Wroblewski (1982)	SSM
Calanus glacialis	Slagstad and Tande (1990)	WSM
Calanoides acutus	Huntley *et al.* (1994b)	SSM
Calanus chilensis	Marin (1997)	SSM
Metridia pacifica	Batchelder and Miller (1989)	IBM
Metridia lucens	Batchelder and Williams (1995)	IBM
Decapoda		
Shrimps		
Penaeus astecus	George and Grant (1983)	SiSM
Penaeus sp.	Grant *et al.* (1988)	MM
Philocheras trispinosus	Labat (1991a, 1991b)	IBM
Krill		
Euphausia superba	Astheimer (1986)	SiSM
Euphausia superba	Hofmann *et al.* (1992)	IBM
Crabs (larval stages)		
Cancer magister	Moloney *et al.* (1994)	SiSM
Fish larvae		
Engraulix mordax	Lo *et al.* (1995)	SSMM
Sardinops sagax	Lo *et al.* (1995)	SSMM
Striped bass	Levin and Goodyear (1980)	ASMM
Gadus morhua	Werner *et al.* (1993)	IBM
Malanogrammus aeglefinus	Werner *et al.* (1993)	IBM
	Heath and Gallego (1998)	IBM
Theragra chalcogramma	Hinckley *et al.* (1996)	IBM
	Rose *et al.* (1996)	IBM
	Rose and Cowan (1993)	IBM
	van Winkle *et al.* (1993)	IBM

Transfer to the first age class of the next stage by molting individuals is given by:

$$N_{i+1,1} = \sum_j \sigma_i \gamma_{i,j} N_{i,j} \tag{12.49}$$

Egg production by adult females (stage 12), contributing to the first age-class (eggs, stage 1), is calculated as:

$$N_{1,1} = \sum_j \sigma_{12} F_{12,j} N_{12,j} \tag{12.50}$$

In this model, the time step is 1 day. There is a matrix calculation with a finite-difference equation system. The transfer of animals from stage to stage and the mortality at each stage are expressed as simple linear functions. The transfer rate $\gamma_{i,j}$ (day^{-1}) (or probability of molting) from stage i to $i+1$ depends on the stage but also on the age-

class. The transfer rate is determined from stage duration, using a polynomial approximation to the cumulative normal distribution function with mean equal to a calculated mean duration (D_i) and a standard deviation equal to 10% of the mean. The function is monotonic and is equal to zero for the first age and sharply increases at D_i. The mean duration D_i varies with temperature according to Belehrádek's equation (see page 590). The mortality rate σ_i (day^{-1}) is constant for each stage i, but among stages, mortality varies according to the susceptibility of that stage to physiological death, cannibalism, and predation.

The fecundity F is based on the temperature-dependent empirical equation of Corkett and McLaren (1978) (see section 12.3). Davis's (1984a) model gives a good representation of the duration of each stage and the model is a convenient basis for modeling species of animals with stage development.

Miller and Tande (1993) present a population model of *Calanus finmarchicus* with two matrices, one for the abundance in each age class of each stage and one for the associated molt cycle fraction. At each time step Δt, the stage duration D in the age class j of stage i is determined by temperature using Belehrádek's equation (equation 12.32):

$$D_{i,j+1} = D_{i,j} + \frac{\Delta t}{a_j(T + b_i)^{c_i}} \quad \text{and} \quad D_{i,1} = 0. \tag{12.51}$$

Individuals are transferred to the next age class $j + 1$ of stage i if $D_{i,j} < 1$, and

$$N_{i,j+1} = \left(\sqrt[1/\Delta t]{1 - \mu_i} \right) N_{i,j} \tag{12.52}$$

If $D_{i,j} \geqslant 1$, the molt cycle is completed, and the individuals molt to the first age class of stage $i + 1$, such that:

$$N_{i+1,1} = \sum_j \left(\sqrt[1/\Delta t]{1 - \mu_i} \right) N_{i,j} \tag{12.53}$$

With this model, it is possible to simulate the movement of individuals through stages, with a realistic representation of the duration of each stage.

Hairston and Munns (1984) developed a model with interacting copepod and fish populations using matrix projections to study the effects of copepod diapause switching on system dynamics.

CONTINUOUS-TIME STRUCTURED POPULATION MODELS

McKendrick (1926) introduced an entirely different type of model for an age-structured population. It describes the dynamics of the age distribution on a continuous-time basis using partial differential equations, and is usually referred to as the McKendrick–Von Foerster equation. This type of model has been developed to the extent that it can be used to describe the dynamics of a population that is living in a fluctuating environment. In addition, it can also be applied to situations in which more than one physiological trait of the individuals (e.g. age, size, weight, and energy reserves) have strong influences on individual reproduction and mortality. The movement of individuals through the different structural classes is followed over time. Age and weight are continuous variables whereas stage is a discrete variable.

The general equation (Sinko and Streifer 1967) is:

$$\frac{\partial n(t, a, m)}{\partial t} + \frac{\partial n(t, a, m)}{\partial a} + \frac{\partial g(t, a, m)n(t, a, m)}{\partial m} = -\mu(t, a, m) \, n(t, a, m)$$

(12.54)

where n is abundances of individuals of age a and mass m at time t.

Continuous-time and age structured population models (CASM)

The formulation which best introduces classical demographic modeling is the Von Foerster equation (Von Foerster 1959). This equation describes population processes in terms of continuous age and time as follows:

$$\frac{\partial n(a, t)}{\partial t} + \frac{\partial n(a, t)}{\partial a} = -\mu(a, t) \, n(a, t).$$

(12.55)

The equation has both an initial age structure φ at $t = 0$:

$$n(a, 0) = \varphi_0(a)$$

(12.56)

and a boundary condition of egg production at $a = 0$:

$$n(0, t) = \int_0^\infty F(a, S_R) \, n(a, t) \, da$$

(12.57)

F is a fecundity function that depends on age (a) and the sex ratio of the population S_R. These kinds of equations are mathematically and computationally difficult to analyze, especially if the environment is not constant (Nisbet and Gurney 1982). Equations 12.55 and 12.57 together constitute a continuous version of the entire Leslie matrix . Equation 12.57 corresponds to the first row of the matrix, and the rest of the matrix corresponds to equation 12.55 (see Caswell 1989, 1997).

Thus, a system of ODEs can be obtained as an equivalent to Von Foerster's PDE.

Gurney *et al.* (1983) developed a combination of the Von Foerster description with simple time-delay models to describe insect life history. The classical continuous-time description of the age structured population is described by PDEs with the integral boundary condition transformed by a set of ordinary delay-differential equations corresponding to a functional or developmental class of the species life history.

Continuous time and weight structured population models (CWSM)

The same type of equation as equation 12.55 can be used where age is replaced by weight

$$\frac{\partial n(w, t)}{\partial t} + \frac{\partial g(w, T, P)n(w, t)}{\partial w} = -\mu(w, t) \, n(w, t).$$

(12.58)

The weight of the individual w and the growth g are influenced by the temperature T, the food P and by the weight itself through allometric metabolic relationships.

The equation has both an initial age structure φ at $t = 0$:

$$n(w, 0) = \varphi_0(w)$$

(12.59)

and a boundary condition of egg production at $w = w_0$:

$$N(0, t) = \int_0^\infty F(w, S_R) \, n(w, t) \, dw$$

(12.60)

F is the fecundity function which depends on weight (w) and the sex ratio of the population S_R.

Bryant *et al.* (1997) present in detail the numerical realization of this equation. This requires a representation of the continuous distribution $n(w, t)$ by a set of discrete values $n_i(t)$ that are spaced along the weight axis at intervals $\Delta w_i = w_{i+1} - w_i$. Using upwind difference discretization to solve the equations, and recasting the representation in terms of the number of individuals in the ith weight class, $N_i(t) \approx n_i(t)\,\Delta w_i$, the dynamic equation becomes:

$$\frac{dN_i}{dt} = \left[\frac{g_{i-1}}{\Delta w_{i-1}}\right]N_{i-1} - \left[\frac{g_i}{\Delta w_i}\right]N_i - \mu_i N_i \qquad (12.61)$$

where $\mu_i(t)$ replaces $\mu(w_i, t)$. This describes the dynamics of all weight classes except the first ($i = 2$) and last ($i = Q$). If $R(t)$ represents the total rate of recruitment of newborns to the population, and all newborns are recruited with the same weight w_1, then the dynamics of the weight class covering the range Δw_1 are:

$$\frac{dN_1}{dt} = R - \left[\frac{g_1}{\Delta w_1}\right]N_1 - \mu_1 N_1 \qquad (12.62)$$

If we assume that individuals in only the Qth weight class are adult, and that adult individuals expend all assimilated energy on reproduction rather than growth, the population dynamics of the adult population is given by:

$$\frac{dN_{Q-1}}{dt} = \left[\frac{g_{Q-1}}{\Delta w_{Q-1}}\right]N_{Q-1} - \mu_Q N_Q \qquad (12.63)$$

and the rate of recruitment of newborns to the population is

$$R(t) = \beta(t)N_Q(t) \qquad (12.64)$$

where $\beta(t)$ represents the per capita fecundity of an average adult at time t.

The weight intervals Δw_i increase with class number i as an allometric function. The growth rate $g(w, t)$ can be calculated by a physiological model (see section 12.3).

Slagstad and Tande (1990) and Tande and Slagstad (1992) present other applications of weight structured population models (WSM) to *Calanus* sp. populations (see Table 12.5).

To demonstrate how various factors affect the pattern of recruitment of crab larvae, Botsford *et al.* (1994) transformed equation 12.58 into a set of ODEs by the method of characteristics, and developed an analytical solution to these ODEs.

STAGE-STRUCTURED POPULATION MODELS BASED ON ODEs

Zooplankton populations often have continuous recruitment and are followed in the field by observing stage abundances over time. A large number of zooplankton population models deal with population structures in terms of developmental stage, using ODEs.

Simple stage structured population models

A single ODE can be used to model each development stage or group of stages. An example of such a model is given by Wroblewski (1980) to describe the dynamics of

Acartia clausi. He subdivided the population into four groups: eggs, nauplii, copepodites and adults. The equation system is:

eggs $\qquad \dfrac{dN_1}{dt} = R - \alpha_1 N_1 - \mu_1 N_1$ $\qquad\qquad$ (12.65)

nauplii $\qquad \dfrac{dN_2}{dt} = \alpha_1 N_1 - \alpha_2 N_2 - \mu_2 N_2$ $\qquad\qquad$ (12.66)

copepodids $\qquad \dfrac{dN_3}{dt} = \alpha_2 N_2 - \alpha_3 N_3 - \mu_3 N_3$ $\qquad\qquad$ (12.67)

adults $\qquad \dfrac{dN_4}{dt} = \alpha_3 N_3 - \mu_4 N_4$ $\qquad\qquad$ (12.68)

where R is recruitment, α is the molting rate to next stage, and μ is the mortality rate.

The system of ODEs is solved by Euler or Runge–Kutta numerical integration methods, usually with a short time step (approximately 1 h). This ODE system is quite similar to the Lefkovitch matrix. In this model, the transfer of animals from stage to stage and the mortality at each stage are expressed as simple linear functions. The transfer rate α_i day^{-1} is constant. The underlying assumption is that there is a continuum of ages of individuals in each stage. Thus some animals are always ready to mature to the next stage while others still require a full development time. Wroblewski takes $\alpha_i = 2/D_i$, where D_i refers to the development time of the ith stage. Because of the exponential formulation of copepod development, 87% of the individuals present at time zero will progress to stage $i + 1$ in the time interval D_i and the remaining 13.5% will take longer to complete their development. If we take α_i day^{-1} equal to $1/D_i$ the proportion of laggards becomes 36.8%. Generally, this second formulation is used because this model cannot mimic realistic development time within a stage.

The mortality rate μ_i day^{-1} is also constant in each stage, but among stages mortality can vary according to the susceptibility of that stage to physiological death, cannibalism and predation.

Gaedke (1990) presented similar stage structured population models for two interacting populations (*Acartia tonsa* and *Eurytemora affinis*) with nine groups of stages of nauplii (N) and copepodites (C): eggs, N1 to N3, N4 and N5, N6 and C1, C2 and C3, C4 and C5, and adults. In her paper, mortality rates are based on starvation, low salinity, predation on nauplii by *Acartia tonsa*, and predation by fish and carnivorous invertebrates. The formulation of the different components is fully described in the annexe of her paper. The model gives unrealistic stage abundance, beginning with a synchronous cohort, because minimum durations within each stage are not enforced. Thus, the generation time is artificially shortened due to a numerical diffusion of individuals through the stages. In the case of a stable environment where populations develop over several generations (small species), this effect would not be significant, and in such cases this model would be a simple and useful approach.

A similar model was built by Marin (1997) to describe the dynamics of *Calanus chilensis*. His model was built and run using STELLA-II version 3.07 (High Performance Systems, Inc), an interactive, iconographic software package. The basic equations and the diagram of the stage structured population model are presented in full detail in Marin's (1997) paper.

Andersen and Nival (1986) present a model of the population dynamics of salps considering five stages of oozooids and five stages of blastozooids. Assuming that each stage represents individuals of a given weight range, they computed a growth rate based on physiological functions (feeding and excretion) that is temperature- and food-

dependent, and related the demographic parameters (transfer, mortality and reproductive rates) to growth rate.

Hofmann and Ambler (1988) modeled the population dynamics of *Paracalanus* sp. within a model of a pelagic ecosystem. They used five variables for five groups of stages, with the model unit being the biomass of individuals in each stage. The change in biomass in each stage was caused by movements of individuals through the stage and also by the flux of matter linked to metabolism of the individuals.

Stage and age-within-stage structured population models

Sciandra (1986) used an intermediate model to those of Wroblewski (1980) and Davis (1984a) to model copepod population dynamics. His model had subdivisions within each stage and the movement of individuals through these subdivisions was simulated using ODEs. Because individuals stayed for a set time in each subdivision, these subdivisions cannot be termed 'age-classes' as in Davis's (1984a) matrix model.

Carlotti and Sciandra (1989) and Carlotti and Nival (1992) developed a model with two types of equation: finite-difference equations to transfer organisms from one age class to the next in each stage, and ODEs to represent the movement of organisms from any age class of one stage to the first class of the next stage. The time step of the transfer from one age class to the next was set at 6 h, whereas the time step of the movement from any age class of stage i to the first class of stage $i + 1$ was set at 1 h. The system of ODEs was solved using a fourth-order Runge–Kutta numerical integration. The model formulations are described below.

The first age-class of stage i:

$$\frac{dN_{i,1}}{dt} = R_i - \alpha_{i,1}N_{i,1} - \mu_{i,1}N_{i,1} \tag{12.69}$$

Other age-classes of stage i:

$$\frac{dN_{i,j}}{dt} = -\alpha_{i,j}N_{i,j} - \mu_{i,j}N_{i,j} \tag{12.70}$$

The rate of recruitment of newborns to the population in the first age class of eggs is the number of eggs spawned by mature females in the adult stage. The rate of recruitment of newly molted individuals in the first age class of a stage is:

$$R_i = \sum_{j=1}^{m} \alpha_{i-1,j}N_{i-1,j} \tag{12.71}$$

When the transfer from one age class to the next occurs, the individuals of the last two age classes ($m - 1$ and m) are grouped in the last age class, the individuals of all age classes j are moved to those following, and the first age class is set to zero.

$$N_{i,m} = N_{i,m} + N_{i,m-1} \tag{12.72}$$

$$N_{i,j} = N_{i,j-1} \tag{12.73}$$

$$N_{i,1} = 0 \tag{12.74}$$

This process simulates the movement of cohorts of individuals through each stage. In a similar way to the matrix models that include stage and age, the structure of age-within-stage models allows the representation of different stage duration distributions to estimate molting probabilities. Mortality rates also can change with age within stage. Carlotti and his co-workers represented changes in the demographic parameters (molting rate,

mortality rate, egg production rate) as functions of individual properties of the organisms in the cohort (size, weight, growth rates), and the age distributions of the demographic parameters became a result of their simulations. Details of the different representations of the demographic processes in such structure are presented in the next sections.

Demographic parameters as functions of individual growth properties

In their model Carlotti and Sciandra (1989) represent the molting rate from stage i to stage $i + 1$ as a function of weight and growth rate. Molt determination is complex, but it is reasonable to believe that molting occurs only when a set of fundamental biological conditions are met (Carlotti 1996b).

The molting rate depends first on weight; animals should reach a critical molting weight. To represent a certain variability around the critical molting weight, S-shaped functions can be used. Carlotti and Sciandra (1989) used a Michaelis–Menten law with exponent. The increasing value of the exponent allows for reduced variability around the critical weight. Other S-shaped functions such as the hyperbolic tangent could be used. The molting rate depends also on the recent physiological condition of the organisms. Carlotti and Sciandra (1989) propose a linear function of the average specific growth rate (ASG) calculated over a given period Δt:

$$ASG_{i,j} = \frac{1}{\Delta t} \int_{t-\Delta t}^{t} \frac{G_{i,j}}{W_{i,j}} dt \tag{12.75}$$

where $G_{i,j}$ and $W_{i,j}$ are the growth of individuals in age-class j of stage i. Carlotti and Sciandra (1989) introduced a function whereby ingestion decreased when the weight of organisms in stage i was above the critical weight. As a consequence, individuals that reached the critical molting weight could molt, but those that remained in that stage diminished their probability of molting because of reduced ingestion and the decrease in the ASG value.

Mortality rate is usually considered constant in a stage. In fact, mortality rate varies as a function of food concentration, temperature and even age within stage (Carlotti and Nival 1992). Carlotti and Sciandra (1989) used an increasing hyperbolic function with mortality dependent on the specific growth rate. This function allowed for high mortality when energy budgets were unfavorable and low mortality when they were favorable. The average specific growth rate (ASG) could be used instead of the instantaneous specific growth rate to represent the effect of recent feeding history on the mortality rate. Egg production occurred when females reached a critical mature weight, following a sigmoidal function (similar to that used for the molting rate).

The links between physiological processes and demographic parameters suggested in this model resulted in stage duration distributions that were realistic (Carlotti and Nival 1992) as well as the frequently observed asymmetry of stage distributions in cultivated populations (Carlotti and Sciandra 1989).

Another type of continuous-time, physiologically structured population has been developed by De Roos et al. (1992) with the use of a numerical method called 'escalator boxcar train' (Goudriaan 1986). We do not know any examples where this has been applied to zooplankton species.

Demographic parameters as functions of age within stage

It is possible to simplify Carlotti and Sciandra's (1989) model, by developing age-dependent functions of molting rate, mortality rate and fecundity, and by removing all the physiological functions. The use of a gamma distribution to represent the age-

dependent molting rate, with its shape variations depending on food and temperature, appears to give a good parameterization (Souissi *et al.* 1997). In comparison with the simple model presented by Wroblewski (1980), the use of age-dependent molting rates allows for improved simulations of the time lags between stages in situations where cohorts are clearly identified. A similar model (called multi-transfer model) was used by Jellison *et al.* (1995) to identify stage durations and mortality rates.

DELAY DIFFERENTIAL EQUATION MODELS

Gurney *et al.* (1983), Nisbet and Gurney (1982), and Gurney *et al.* (1986) developed a modeling approach for species whose life history is made up of a number of well defined physiological stages, within which all individuals are assumed to be identical in feeding behavior and probability of death. The progress of an individual through a particular stage was quantified by a development index representing the state of development or the 'physiological age' of the individual within that stage at a particular time. The development index increased at the same instantaneous rate for all individuals in the stage at a given time. Maturation out of a stage occurred on achieving a fixed value of the development index.

Mathematically, this modeling approach is represented by a system of coupled ODEs for estimating population numbers, and delay-differential equations (DDEs) for estimating through-stage survival and stage duration. Crowley *et al.* (1987) give a complete description of such a model applied to a zygopteran with aquatic larval stages. No examples were found for copepods although the model structure is convenient for them. An extension of this model type was applied to the study of species with diapause stages (Gurney *et al.* 1992).

Several other models that include delay in stage recruitment have been used for the estimation of demographic parameters (for a review see Jellison *et al.* 1995)

STRUCTURED POPULATION MODELS TO ESTIMATE DEMOGRAPHIC PARAMETERS

A variety of cohort models have been developed for applying inverse methods; vital rates (e.g. mortality, stage duration) can be derived by fitting a population model to observed data (see Manly 1989 and 1990). All the structured models presented in the previous sections have been used for parameter identification: matrix models (Caswell and Twombly 1989), models with ODEs and models with DDEs (Rigler and Cooley 1974; Matthews *et al.* 1978; Parslow *et al.* 1979; Sonntag and Parslow 1981; Hairston and Twombly 1985; Saunders and Lewis 1987; Hay *et al.* 1988; Wood and Nisbet 1991; Jellison *et al.* 1995; Ohman and Wood 1996). The details of the techniques have been explained by Aksnes *et al.* (1997) and will not be repeated here.

STOCHASTICITY IN STRUCTURED POPULATION MODELS

Stochasticity can be included in structured population models either by influencing the environmental variable or the demographic process and vital rates. Stochastic events can be introduced into matrix models (Caswell 1989), as well as structured population models based on PDEs, ODEs and DDEs (Nisbet and Gurney 1982). However, no such examples have been found for marine zooplankton populations.

12.4.3 Individual-based models of a population

Individual-based models (IBMs), also called *i*-state configuration models (Metz and Diekmann 1986; Caswell and John 1992; Maley and Caswell 1993), describe population

dynamics by simulating the birth, development, and eventual death of a large number of individuals in the population. As powerful computers become more accessible, numerous IBMs of zooplankton populations have been developed, mainly to couple them with circulation models (see section 12.6.3). An increasing number of papers have appeared that have used this individual-based approach (De Angelis and Gross 1992; van Winkle *et al.* 1993).

BUILDING AN IBM

Maley and Caswell (1993) briefly presented the structure of IBMs, and the differences and the links between structured population models and individual-based models. Despite significant progress on model formulations for physiologically structured populations, several problems remain intractable. These problems include methods for dealing with the local character of many ecological interactions and the difficulty of jointly studying two complex ecological factors (i.e. investigating both the dynamic effects of age-structure and those of spatial variability). One solution to these problems is to focus on IBMs.

IBMs treat populations as collections of individuals, with explicit rules governing individual biology and interactions with the environment. Each biological component can change as a function of the others. Each individual is represented by a set of variables that store its *i*-state (e.g. age, size, weight, reserves, etc.). These variables may be grouped together in some data structure that represents a single individual, or they may be collected into arrays (e.g. an array of all the ages of the individuals, an array of all the sizes of the individuals, etc.), in which case an individual is an index number in the set of arrays. The *i*-state of an individual changes as a function of the current *i*-state, the interactions with other individuals, and the state of the local environment. The local environment can include prey and predator organisms that do not warrant explicit representation as individuals in the model. Population-level phenomena (e.g. temporal or spatial dynamics) or vital rates can then be inferred directly from the contributions of individuals in the ensemble.

The model starts with an initial population and the basic environment, then monitors the changes of each individual. At any time t, the i-state of individual j changes as:

$$X_{i,j}(t) = X_{i,j}(t - dt) + f(X_{1,j}(t - dt), \ldots, X_{i,j}(t - dt), \ldots, T, \ldots) \quad (12.76)$$

where $X_{i,j}(t)$ is the value of the i-state of individual j, and f is the process modifying $X_{i,j}$, as a function of the values of different i-states of the organism, and external parameters such as the temperature T. When the fate of all individuals during the time step dt has been calculated, the changes to the environment under the effects of individuals can be updated. Any stochastic process can be added to equation 12.76.

A simple example of a zooplankton IBM was presented by McLaren (1997) to study biases in estimating secondary production from copepod cohorts. This model needed three variables for each individual: the weight, the stage, and a variable specifying if the individual was dead or alive. The model was run with 50 000 individuals, each individual beginning with an initial weight drawn from a lognormal distribution. The weight of stage i at time t was

$$W_i(t) = (1 + G_i)W_i(t - 1) \quad (12.77)$$

where the growth rate G_i had been drawn from a random normal distribution. When the weight exceeded the critical weight for entering in a new stage, then

$$\text{Stage}_i(t) = \text{Stage}_i(t - 1) + 1 \quad (12.78)$$

The probability of death M_i was taken to be constant for each stage, but could vary among the stages. For each individual for each time step, a random uniform variate $U(0, 1)$ was generated, and if $U(0, 1)$ was greater than M_i, the individual survived to the next time step. Weight increments of individuals that lived to the end of the simulation period were accumulated as 'growth' production, whereas the weight increments of dead individuals were accumulated as 'lost' production. Actual production was the sum of growth and lost productions.

Batchelder and Miller (1989) presented an IBM of *Metridia pacifica*, with the basic equations 12.77 and 12.78, but with greater detail in the representation of physiological functions. Individual growth was calculated as assimilation less respiration according to functions presented in section 12.3. The inter-individual variation in physiology was represented because the characteristics (growth parameters, mortality coefficient, and parameters connected with reproduction) of each individual were chosen at random. In addition to a constant stage-dependent mortality, individuals could also die by starvation, when their weights fell below the mean weight of the previous stage. Daily egg production by mature females was generated from a normal distribution of parameters of clutch size, clutch frequency, and total number of clutches. The model described the development of individuals and generated a population history over one year. To solve the problem of an increasing number of individuals (to the result of reproduction), which becomes too large for storage and increases the computational effort, Batchelder and Miller (1989) randomly selected a fractional sample (1/5) of the population when it was close to a maximum number (100 000 individuals in their simulation). Subsequent abundance reports were then multiplied by five. Similarly, Rose *et al.* (1993) studied different aspects of such resampling techniques with an IBM of fish.

In a refined version of their IBM, Batchelder and Williams (1995) represented the effects of vertical food distributions on individual growth and vertical distribution. In this version, the effect of temperature (the external driving variable) on biological functions was also taken into account. The results were presented in terms of individual weight trajectories and stage frequency distributions over time. A similar example of an IBM with a stochastic component was presented by Labat (1991a, 1991b), where the population dynamics and temporal changes in size structure of a shrimp species was simulated.

With the aim of coupling an IBM of *Calanus finmarchicus* with a circulation model of the Georges Bank region, Miller *et al.* (1998) developed a simple model that had six variables: three for position, one to register the individual as dead or alive, one for the stage, and one to define the relative age in the stage. A temperature-dependent fraction of the molt cycle was incremented at each time step, as in equations 12.77 and 12.78. Copepodite stage 5 had the possibility of entering a resting stage. A reproductive function with a temperature-dependent maturation time for clutches, was added when individuals became females.

To represent both the dynamics of a zooplankton population with an IBM and its interactions with the trophic environment, realistic numbers have to be simulated. The techniques used by Batchelder and Miller (1989) in fractionating the population are not always convenient. Another method is to assume that the basic unit of an IBM (usually a zooplankton individual) actually represents more than one individual. The individuals in the unit should be identical, as for a group of individuals that are born almost simultaneously and have similar mothers. Hogeweg and Richter (1982) used this approach to group eggs produced by females of similar size. Woods and Onken (1982)

termed a similar approach the 'Lagrangian-ensemble method', which was a modeling technique in which identical individuals born at the same time were grouped in one unit (also called a 'family' or 'particle'). They first applied this method to phytoplankton cells, and then to zooplankton (Woods and Barkmann 1993, 1994, 1995).

Carlotti and Wolf (1998) presented an application of the Lagrangian-ensemble method to the population dynamics of *Calanus finmarchicus* coupled with a 1-D ecosystem model, where new units were formed by grouping the eggs produced by females that occurred in the same depth layer. To simulate the annual ecosystem dynamics with realistic numbers of copepods ($> 150\,000$ ind. m^{-2}), the number of units could not exceed 3000. Thus units could group up to 500 eggs at their time of creation. However, the number of units was large enough for producing realistic statistical distributions of the copepods in the water column. Carlotti and Wolf's (1998) model simulated the movements of organisms in relation to light (daily migration) and food concentration, similar to Batchelder and William's (1995) model for the physiology of organisms, but with a supplementary state of fatty reserves.

Several IBMs have been developed for the early life history of fish populations (see review by Tyler and Rose 1994). Techniques of resampling (Rose *et al.* 1993) or grouping of individuals (Scheffer *et al.* 1995) have also been presented for fish models. In recent studies by Hermann *et al.* (1996), Werner *et al.* (1996), Hinckley *et al.* (1996), Gallego and Heath (1997) and Heath and Gallego (1997), detailed physiological processes were introduced into IBMs of fish coupled with circulation models. These approaches attempted to derive conclusions about the population based on the distinct and unique life histories of the individuals. The coupling of IBMs to spatially explicit physical models adds the space dimension that is necessary to include environmental constraints that affect individuals as they move in an environment. These constraints include regions of poor growth, increased mortality, dispersion, etc. The approach integrates the unique temporal and spatial history of the individual larvae, each of which is exposed to different prey concentrations and physical parameters. In this manner, the growth of individual larvae can be understood in terms of a detailed time history of the food available to the larva, which itself is a function of the unique trajectory of each larva through the prey field, and the ability to encounter (and capture) the prey (see page 578).

OBJECT-ORIENTED PROGRAMING (OOP)

Object-oriented programing (OOP) is a technique that has been applied to IBMs recently. In OOP, the individuals, interaction structure, and environment are all defined as objects. Papers by Baveco and Lingeman (1992), Silvert (1993) and Maley and Caswell (1993) give good introductions to OOP illustrated by simple examples. There are very few examples of models using OOP for zooplankton populations. Laval (1995, 1996, 1997) presented such a model to simulate the development of a tunicate bloom, taking account of the physiology of salps and the colonization of space by its members with their spatial interactions. Population dynamics models based on OOP have been developed for cladocerans and copepods (Hogeweg and Richter 1982; Mooij and Boersma 1996).

CONSTRAINTS IN BEHAVIOR

IBMs are focused at resolving physiological and behavioral differences within populations. In this way, IBMs can describe population effects caused by individual variability more precisely than can SPMs. However, in standard IBMs this is done by specifying

how organisms respond to their environment, either by a fixed rule or by an elaborate IF-ELSE IF table. This may not always help the modeled individuals to behave in an evolutionarily optimal way. There are many things that can happen to a copepod, and it is not possible to combine all events in a predescribed decision matrix. Neither would the modeler know the appropriate response in many of these situations. Classical IBMs with defined behavioral rules are therefore best suited for simulations in rather simple and stable environments.

Alternatively, IBMs can derive their trade-off rules from life history theory, as suggested by Tyler and Rose (1994). A different approach would be to model the optimal decisions, and then let the population act accordingly on an individual basis, as in Stochastic Dynamic Programing (SDP; Clark and Mangel 1999). This type of forcing has been used by Fiksen and Giske (1995) and Fiksen and Carlotti (1998). However, SDP also has inherent weaknesses. The method can easily solve state-dependent or density-dependent optimal behavior in a changing environment, but cannot combine state- and density-dependencies in one model. The ING method (Huse and Giske 1998), described on page 627, can overcome many of these obstacles, but at a price of high CPU demand.

12.4.4 Models of interactions between zooplankton populations

In this section we look at models of direct interactions between species. Indirect interactions such as competition for food are treated in section 12.5. Direct interactions can be of different types: predation by one species on another, crossed predation of adults of several species on juveniles of other species, and cannibalism by adults on juveniles.

INTERACTION MODEL WITH TWO VARIABLES

Simple models of two-species interactions take the form:

$$\frac{dN_1}{dt} = r_1 N_1 - k_1 N_1 N_2 \tag{12.79}$$

$$\frac{dN_2}{dt} = r_2 N_2 - k_2 N_1 N_2. \tag{12.80}$$

These population models represent some special experimental situations or typical field situations. As an example, Legovic (1987) studied the dynamic properties and the steady state of a simple predator–prey model to represent the predation of the jellyfish *Pelagia noctiluca* (N_2 in mg C m^{-3}) on fish eggs and zooplankton (N_1 in mg C m^{-3}):

$$\frac{dN_1}{dt} = r N_1 \left(1 - \frac{N_1}{K}\right) - k_1 N_2 \left(\frac{N_1}{k_2 + N_1}\right) - k_3 N_1 \tag{12.81}$$

$$\frac{dN_2}{dt} = k_4 k_1 N_2 \left(\frac{N_1}{k_2 + N_1}\right) - k_5 N_2 \tag{12.82}$$

where r is the intrinsic growth rate of zooplankton (day^{-1}), K the carrying capacity of the prey population, k_1 the maximum specific predation rate of jellyfish (day^{-1}), k_2 the half-saturation constant (mg C m^{-3}), k_3 the specific mortality by other predators (day^{-1}), k_4 the conversion of prey biomass into jellyfish biomass (no units), and k_5 the specific mortality of jellyfish (day^{-1}). The results indicate different causes of an increase

in numbers of jellyfish, which include an increase in prey, the decrease of carnivorous competitors, and the decrease of jellyfish predators.

Gaedke and Ebenhöh (1991) presented an interaction model between two estuarine species of copepods *Acartia tonsa* and *Eurytemora affinis*, with equations similar to equations 12.79 and 12.80, but with (1) predation by *Acartia* on the two species (N_1 is replaced by N_2 in the second term on the right hand side of equation 12.80), (2) a term of biomass gain of *Acartia* by this predation, and (3) a density-dependent loss term caused by predation by invertebrates or starvation of the two species. This simple model did not result in stable coexistence between the two species with a reasonable parameter range under steady-state conditions. A more complex structured model was also built for comparison (see below).

Note that simple deterministic models of a number of ecological interactions can induce chaotic behavior, comparable with many field observations (Scheffer 1991).

POPULATION INTERACTIONS USING STRUCTURED POPULATION MODELS

Direct and indirect interactions between two estuarine copepods *Eurytemora affinis* and *Acartia tonsa* were studied by Gaedke (1990) and Gaedke and Ebenhöh (1991) using two stage-structured population models with stage-specific interactions (with similar equations to equations 12.65–12.68) and abiotic and biotic forcing variables: temperature, salinity, primary production, phytoplankton species composition, and seasonal abundance of fish, carnivorous zooplankton (mysids, chaetognaths and coelenterates) and *Noctiluca miliaris*. The stage-structured population models allowed the predation of large individuals of *A. tonsa* (copepodites 4 to adults) on nauplii of both species to be represented. Predation on nauplii depended on the combined abundances of predator (C4 to adults) and prey (eggs and nauplii) stages and was calculated for each stage. The results of this detailed numerical model were compared with results obtained using a simpler model with two variables. Greve (1995) presented a model of mutual predation between *Calanus helgolandicus* and *Pleurobrachia pileus*.

Carlotti and Slagstad (1997) developed an ecosystem model of the Greenland Sea in which zooplankton was represented by two copepod populations of *Calanus hyperboreus* and *Oithona similis*. The simulations indicated that the predation of *Calanus* on *Oithona* was necessary to sustain the *Calanus* population. *C. hyperboreus* is assumed to feed preferentially on phytoplankton, but supplements its diet with *Oithona*. A first grazing value (G1) with phytoplankton as the only food item was calculated with a type I feeding function (see Table 12.2). Then a second grazing value (G2) was calculated on the food constituted by phytoplankton plus the biomass of *Oithona* above a threshold biomass. The real predation was calculated as the difference between the two calculated grazing values (G2 − G1).

Cannibalism has been shown to occur in zooplankton (Daan *et al.* 1989), and a few theoretical models have investigated the consequences for the population dynamics (Gabriel 1985; Van den Bosch *et al.* 1988).

12.4.5 Further reading

Cushing, J.M., 1977. *Integrodifferential equations and delay models in population dynamics. Lecture Notes in biomathematics 20*. Springer-Verlag, Berlin, 196 pp.

McDonald, N., 1978. *Time lags in biological models. Lecture notes in biomathematics 27*. Springer-Verlag, Berlin, 112 pp.

Metz, J.A.J. and Diekmann, O., 1986. *The dynamics of physiologically structured populations. Lecture notes in biomathematics 68*. Springer-Verlag, Berlin, 511 pp.

Wood, S.N. and Nisbet, R.M., 1991. *Estimation of mortality rates in stage-structured populations. Lecture notes in biomathematics 90*. Springer-Verlag, Berlin, 101 pp.

12.5 MODELS OF ZOOPLANKTON COMMUNITIES

12.5.1 Zooplankton bulk models in ecosystem models

THE REPRESENTATION OF HERBIVOROUS ZOOPLANKTON IN NPZ-TYPE ECOSYSTEM MODELS

Modeling of ocean biogeochemical processes developed rapidly in the last decades and a number of text books on marine ecosystem modeling and related techniques (e.g. data assimilation) have been published. The book by Evans and Fasham (1993) presents a synthesis of the model-building process at the ecosystem level and linked aspects: level of resolution, linkage between physical, chemical and biological components, representation of trophic functional units and associated processes. A chapter devoted to zooplankton modeling describes the difficulty of representing very diverse groups of organisms with one or two variables. Previous monographs by Steele (1974), Kremer and Nixon (1978), Platt *et al.* (1981), Nisbet and Gurney (1982), Walsh (1988) and Fransz *et al.* (1991) also provide useful introductions for the student.

In the last two decades, ecosystem models have been developed to simulate more site-specific situations (Fasham *et al.* 1990; Hofmann *et al.* 1980; Hofmann 1988; Hofmann and Ambler 1988). These models have mainly used deterministic differential equations to describe ecosystem dynamics, although some papers have explored stochastic approaches to modeling (Fasham 1977; Kremer 1983). Models of pelagic ecosystems have been reviewed by Totterdell (1993) and the modeling of the zooplankton compartment in ecosystem models has been treated by Anderson *et al.* (1993).

The representation of zooplankton

In ecosystem models, the zooplankton compartment corresponds to a highly aggregated entity with organisms covering a large size range (Table 12.6). In Fasham *et al.*'s (1990) model, a one-compartment zooplankton model integrated organisms from bacterivorous flagellates through ciliates, copepods, and euphausiids (all of which may be partly herbivorous or carnivorous), to wholly carnivorous chaetognaths. To take into account the functional diversity of zooplankton, some modelers have divided zooplankton into two or more size classes (e.g. Frost 1987; Moloney and Field 1991), and such models will be described further in sections 12.5.2 and 12.5.3.

The ultimate goal of many ecosystem models is to embed the ecosystem model in a 3-D general circulation model from the mesoscale (e.g. Flierl and Davis 1993; Dadou *et al.* 1996) to basin scale (Wroblewski *et al.* 1988). The models have to be as detailed as necessary but as simple as possible (see Evans and Fasham 1993).

The simplest model has three components: nutrient (N), phytoplankton (P) and herbivorous zooplankton (Z). Such models are termed 'NPZ' models. They are driven by physical processes such as mixing or upwelling, which introduce nutrients into the euphotic zone and are closed at the upper level by some 'mortality' of herbivores (e.g.

Table 12.6 Groups of organisms, taxon or species represented in bulk zooplankton variables of ecosystem models.
N nutrients; P phytoplankton; Z zooplankton; D detritus; M microzooplankton and/or bacteria; F fish; DON dissolved organic nitrogen.

Species or groups	Authors	Type of ecosystem model	Process studied
Herbivores			
copepods	Evans and Parslow (1985)	NPZ	Annual plankton cycle
copepods	Klein and Steele (1985)	NPZ	Spatial simulation of the pelagic ecosystem
copepods	Evans (1988)	NP(2)Z	Annual plankton cycle
copepods	Aksnes and Lie (1990)	N(2)P(2)ZD	Annual plankton cycle in a fjord
copepods	Aksnes and Wasmann (1993)	PZD	Role of zooplankton grazing in export production
copepods	Walsh (1975)	N(4)PZDF	Spatial simulation of the Peru upwelling ecosystem
copepods	Wroblewski (1977)	N(2)PZD	Spatial simulation of the Oregon upwelling ecosystem
copepods	Slagstad (1985)	NPZD	Plankton dynamics in the marginal sea ice zone
copepods	Fransz and Verhagen (1985)	N(3)P(2)ZD	Annual plankton cycle in the southern North Sea
copepods	Franks et al. (1986)	NPZ	Effect of a food-level acclimatation by copepods
copepods	Andersen et al. (1987)	N(2)P(2)Z(2)C	Plankton dynamics in mesocosms
copepods	Wroblewski and Richman (1987)	NPZF	Plankton dynamics during wind mixing events
copepods	Andersen and Nival (1988)	NPZ(2)D(5)	Sedimentation of biogenic particles
copepods	Wroblewski (1989)	NPZ	Plankton dynamics in the North Atlantic basin
copepods	Fasham et al. (1990)	N(2)PZDM and DON	Plankton dynamics at station India
copepods	Steele and Henderson (1992)	NPZ	Role of predation in plankton models
copepods	Kawamiya et al. (1995)	N(2)PZD and DON	Plankton dynamics at station Papa
copepods	Ross et al. (1993)	NPZC and DON	Annual plankton cycle in a fjord
copepods	Robinson et al. (1993)	NPZ(2)	Annual plankton cycle
Calanus sp.	Wasmann and Slagstad (1993)	N(3)P(2)MZD(2)	Annual dynamics in the Barents Sea
salps	Andersen and Nival (1988)	NPZ(2)D(5)	Sedimentation of biogenic particles
appendicularians	Andersen et al. (1987)	N(2)P(2)Z(2)C	Plankton dynamics in mesocosms
Carnivores			
ctenophores	Parson and Kessler (1987)	NPZ(3)DM(2)F	Plankton and fish production
ctenophores	Andersen et al. (1987)	N(2)P(2)Z(2)C	Plankton dynamics in mesocosms
ctenophores	Ross et al. (1993)	NPZC and DON	Annual plankton cycle in a fjord
euphausiids	Robinson et al. (1993)	NPZ(2)	Annual plankton cycle
chaetognaths	Andersen et al. (1987)	N(2)P(2)Z(2)C	Plankton dynamics in mesocosms
anchovy	Walsh (1975)	N(4)PZDF	Spatial simulation of the Peru upwelling ecosystem
anchovy	Wroblewski and Richman (1987)	NPZF	Plankton dynamics during wind mixing events
salmon	Parson and Kessler (1987)	NPZ(3)DM(2)F	Plankton and fish production

Steele and Henderson 1981; Evans and Parslow 1985). The interactions between the three components can be expressed in mass units per m^3:

$$dN/dt = \text{input} - \text{phytoplankton uptake}$$
$$+ \text{zooplankton metabolic losses} \qquad (12.83)$$

$$dP/dt = \text{phytoplankton uptake} - \text{zooplankton grazing} \qquad (12.84)$$

$$dZ/dt = \text{assimilated food} - \text{zooplankton metabolic losses}$$
$$- \text{predation} \qquad (12.85)$$

where:

- input $= p(No - N)$, p being the mixing rate from a deep high-nutrient source of constant concentration No
- phytoplankton uptake $= n(N)f(P)$, where $n(N)$ is some nutrient uptake function and $f(P)$ is a function representing self-shading
- zooplankton grazing $= g(P)Z$, where $g(P)$ is the grazing function
- zooplankton egestion $= a(P)Z$, where $a(P)$ is the egestion rate and $a(P) = (1 - \alpha)g(P)$
- assimilated food $=$ grazing $-$ egestion $= \alpha g(P)Z$, where α is the assimilation rate
- zooplankton metabolic losses $= e(P)Z$, with $e(P) = \beta \alpha g(P)$, where β is the excretion rate
- predation $= \alpha(1 - \beta)g(P)h(Z)Z$, where $h(Z)$ parameterizes predation by higher trophic levels.

Explanations for the formulations of processes and the values of parameters concerning nutrients and phytoplankton can be found in Steele and Henderson (1981). Here, we will focus on the processes relating to zooplankton. Some formulations for $g(P)$, $a(P)$, $e(P)$ and $h(Z)$ are presented in Table 12.7.

Steele (1974) represented zooplankton as a single growing cohort (age class) of mesozooplankton. The cohort was represented by two equations, one equation for the rate of change of individual weight from W_1 to W (in mass unit per individual), and one equation to represent the decrease of individual numbers in the cohort from N_1 to N (in numbers of individual per m^3) as a result of density dependent mortality and predation.

$$dW/dt = \text{assimilated food} - \text{metabolic losses} \qquad (12.86)$$

$$dN/dt = \text{density dependent mortality} + \text{predation} \qquad (12.87)$$

where:

- assimilated food $= \beta g(P)W^{0.7}$, where β is the assimilation rate and $0 < \beta < 1$
- metabolic losses $= \lambda g(P)W^{0.7} + \gamma W^{0.7}$, with the first term proportional to the assimilated food and the second term independent of food intake
- density dependent mortality $= -v(N - N_1)(W - W_1)/(H + NW)$
- predation $= h'(N)N$, and $h'(N)$ parameterize the predation by higher trophic levels.

The combination of the two equations gave the changes in zooplankton biomass. When the weight reached the maturity weight, the growth rate became storage for reproduction, and reproduction occurred after a given delay. The adults were then lost to predation and a new cohort was born. Landry (1976) presented a slightly extended version of Steele's (1974) model with the creation of a cohort each day and some modification in the processes. Note that the mortality function (h') in Steele's (1974)

Table 12.7 Mathematical formulation of processes linking zooplankton to other variables in ecosystem models.
P phytoplankton or food; Z zooplankton; $g(P)$ grazing rate; $a(P)$ assimilation rate; $e(Z)$ excretion or respiration rate; $h(Z)$ predation rate. (See quoted references for the meaning of parameters.)

Formulation	Authors	Zooplanktonic organisms
Zooplankton grazing		
$g(P) = I_{max}P$	Andersen and Nival (1988)	salps
$g(P) = I_{max}(1 - e^{-\alpha P})$	O'Brien and Wroblewski (1973)	copepods
	Wroblewski and O'Brien (1976)	copepods
$g(P) = I_{max}\alpha(1 - e^{-\alpha P})$	Franks *et al.* (1986)	copepods
$g(P) = I_{max}(1 - e^{-\alpha(P-P')})$	Wroblewski (1977)	copepods
	Andersen *et al.* (1987)	copepods and appendicularians
$g(P) = \dfrac{I_{max}P}{\alpha + P}$	Scheffer (1991)	zooplankton
	Doveri *et al.* (1993)	zooplankton
$g(P) = \dfrac{I_{max}P^2}{\alpha + P^2}$	Steele and Henderson (1981)	zooplankton
$g(P) = \dfrac{I_{max}(P - P')}{\alpha + (P - P')}$	Steele (1974)	copepods
	Walsh (1975)	copepods
	Evans and Parslow (1985)	copepods
	Frost (1987)	microzooplankton and copepods
	Robinson *et al.* (1993)	copepods and euphausiids
Zooplankton assimilation		
$a(P) = \alpha g(P)$	Steele and Henderson (1981)	copepods
$a(P) = \dfrac{E_{max}\epsilon\, e^{\alpha(P-P')}}{E_{max} + \epsilon(e^{\alpha(P-P')} - 1)}$	Wroblewski (1977)	copepods
Zooplankton excretion and/or respiration		
$e(Z) = \theta$	Fasham *et al.* (1990)	copepods
$e(Z) = \theta\gamma^T$	Andersen *et al.* (1987)	copepods
$e(Z) = \delta g(P)$	Walsh (1975)	copepods
	Evans and Parslow (1985)	copepods
	Wroblewski and O'Brien (1976)	copepods
$e(Z) = \delta g(P) + \theta$	Steele (1974)	copepods
	O'Brien and Wroblewski (1973)	copepods
Food-dependent mortality		
$h(Z) = a$ if $P \leq P'$	Andersen and Nival (1988)	mortality of copepods and salps
$h(Z) = \dfrac{b}{P} + c$ if $P > P$		
$h(Z) = a\exp\left(-b\dfrac{P}{Z}\right)$	Andersen *et al.* (1987)	appendicularian mortality

(Continued)

An important feature of mesozooplankton behavior is diel vertical migration. Many species migrate from daytime depths below 200 m up to the surface at night where they feed on the phytoplankton. There has been little modeling of this migration (Wroblewski 1982; Andersen and Nival 1991; Steele and Henderson 1998). However,

the migration patterns depend on species-specific behavior, and are difficult to represent in bulk-mass models of zooplankton.

Simulation results

It should be stressed that, in order to fully understand the dynamics of a model, it is important to analyze inter-compartment flows. If observational data of flow rates are available then they provide strong constraints on the model. Without such observations, modeled flows can be used to calculate bacterial or zooplankton growth efficiencies to check that they lie within the known range of experimental observations. The technique of 'flow analysis' provides a powerful tool for the analysis of either observed or modeled flow networks (Fasham 1985; Wulff *et al.* 1989). The mathematical analysis of simple food chain systems with three components (PZF) by Scheffer (1991) and five components (NPZF(2)) by Doveri *et al.* (1993) indicates that the dynamics of the model can be very complex.

The main biogeochemical functions of herbivorous (omnivorous) zooplankton, identified through field and modeling studies (Totterdell *et al.* 1993), are:

- control of lower trophic levels (phytoplankton, microzooplankton, bacteria) and the transfer of material to higher trophic levels
- the transfer of material from upper ocean layers to depth with the production of fecal pellets and carcasses
- a downward flux of matter linked to diel vertical migrations.

Aksnes and Wasmann (1993) showed the significance of zooplankton grazing for export production in a theoretical PZD model.

Other functions have been identified and depend on the organisms, such as the production of shells by pteropods, or detritus consumption by copepods.

FROM A SINGLE GRAZER TO SEVERAL GRAZERS

Functional groups of zooplankton

The NPZ-type models generally treat one copepod species as the herbivore in a simple food chain, whereas there is usually a succession of species (Davis 1987). Moreover, other herbivorous organisms, like salps or appendicularians can have a shorter and stronger impact on the ecosystem than do copepods. Copepods themselves develop through developmental stages and the ratio between the adult weight and the egg weight can be three orders of magnitude. However, Totterdell *et al.* (1993) recommended that life-history strategies should only be modeled explicitly if their effects are indispensable for the results and predictions sought, and they cannot be reproduced by some implicit formulation. The subdivision of zooplankton into several functional groups is treated in this subsection because the representation of processes is similar to that presented in section 12.5.1. The subdivision of zooplankton based on size or stage-development is presented in sections 12.5.2 and 12.5.3.

General formulation of a biological component

If we group several functional groups into one compartment, organisms with very different turnover times should not be combined (turnover time is defined as the organism pool size divided by the flux of biomass through that pool). Fasham (1993)

presented a general equation for change in bulk-biomass X of a zooplankton group k, based on an equation formalized by Wiegert (1979):

$$\frac{dX_k}{dt} = \sum_{i=1}^{m} e_{ik}\tau_k p_{ik} f_{ik} X_k - (\mu_k + \phi_k + \rho_k)X_k - \sum_{l=1}^{n} \tau_1 p_{kl} f_{kl} X_l \qquad (12.88)$$

The first term on the right side of equation 12.88 represents the assimilated ingestion or uptake by species k from all the other modeled species or abiotic sources. The second term represents physiological losses, and the third term represents predation on species j by other species. The parameters are defined as follows:

- e_{ik} assimilation efficiency of species k using the resource i
- τ_k the maximum specific ingestion uptake rate of species k
- p_{ik} the preference of species k for the resource i (if predators are dynamically switching between resources then p_{ik} will be a function of the other resources as well (see section 12.3.1)
- f_{ik} the limitation of ingestion of species k by resource i, which is usually a function of X_i
- μ_k specific loss rate due to excretion
- ϕ_k specific loss rate due to natural mortality
- ρ_k specific loss rate due to respiration.

The form of the different processes is similar to those presented in Table 12.7 and section 12.5.1.

The equations governing the biological processes can be linked to physical models that provide environmental forcing.

Examples

Several models studying the role of lower trophic levels in material cycles have changed the zooplankton bulk compartment into several compartments to represent the diversity of microorganisms (e.g. Pace *et al.* 1984). Moloney *et al.* (1986) and Moloney and Field (1991) subdivide the group of heterotrophic organisms into the components mesozoo-plankton, microzooplankton, heterotrophic flagellates, and bacteria. Mesozooplankton feed on large phytoplankton and on microzooplankton following a Michaelis–Menten hyperbola above a threshold concentration of food. Food in their models is the sum of phytoplankton and microzooplankton. Metabolic losses are composed of two terms, the first proportional to ingestion and the second proportional to biomass. The second term also includes zooplankton mortality which is not explicitly represented.

In some models, different categories of large mesozooplankton are considered. Andersen *et al.* (1987) modeled plankton dynamics of an enclosed water column, based on the CEPEX project. A simple NPZC model with one herbivore compartment (copepods) and one carnivore compartment (chaetognaths and ctenophores) did not adequately represent the development of plankton populations in the enclosure, and a second version taking into account separate categories of nutrients, of phytoplankton and of herbivores was developed. Herbivores were divided into copepods and appendicularians. Ingestion rates of both herbivore groups followed an Ivlev relationship (see Table 12.7), and the food consisted of the two phytoplankton categories with different capture efficiencies for prey and predators. Excretion rates of the two herbivore groups were temperature dependent. Mortality of copepods was caused by carnivorous predation whereas the mortality of appendicularians was a function of the ratio of phyto-

plankton biomass over appendicularian biomass (see the formulations in Table 12.7). The second model gave a better fit of the observed dynamics.

In a pelagic ecosystem model of the Ligurian Sea, Andersen and Nival (1988) took into account two important groups of grazers: copepods and salps. Whereas copepod grazing is described by an Ivlev function, the grazing rate of salps was proportional to the phytoplankton concentration. Excretion by the two groups was temperature-dependent and food-independent, and mortality was an inverse function of food concentration (see Table 12.7).

A few attempts have been made to model estuarine/marine and shelf ecosystems as a whole, taking into account benthic and pelagic processes as well as advection and dispersion (Kremer and Nixon 1978; Radford and Joint 1980; Baretta and Ruardij 1988; Baretta *et al.* 1995). In these models, the biological components have been aggregated into functional groups. Each functional group is represented by a sub-model. Broek-huizen *et al.* (1995) developed a zooplankton submodel taking into account omnivorous zooplankton (copepods) feeding on phytoplankton and microzooplankton, and carnivorous zooplankton (copepods and gelatinous plankton). Planktivorous fish ate both omnivorous and carnivorous zooplankton. Each prey taxon of any zooplankton group was consumed in proportion to its instantaneous relative abundance, and the grazing function was given by a type II functional response to the total food concentration. The assimilation rate and active metabolism were proportional to ingestion, and the basal metabolism of a group was proportional to its biomass. Mortality other than predation by fish was proportional to biomass.

The ECOPATH II model (Christensen and Pauly 1992) is an example of a modeling technique in which higher trophic levels that feed on zooplankton, especially commercially exploited fish, are well represented.

12.5.2 Size-structured zooplankton community

SIZE-STRUCTURED ECOSYSTEM MODELS
An alternative approach to using functional groups in models, is to subdivide zooplankton into groups that are based on organism size. There is a theoretical basis for defining size-related compartments, because growth and metabolic rates are often found to be dependent on organism size (Peters 1983). Several models represent size-structured zooplankton communities. Because some models defined functional groups on the basis of size (Pace *et al.* 1984; Moloney *et al.* 1986), they can also be considered as size-structured models.

One of the first size-structured models was developed by Vinogradov *et al.* (1972) to simulate the time evolution of a community in the Pacific equatorial upwelling zone. This model is built on the basis of eight functional groups. Zooplankton are subdivided in small-sized herbivores, large-sized herbivores, omnivores, small-sized carnivores and large-sized carnivores.

Steele and Frost (1977) simulated the size structure of herbivorous zooplankton and their prey, and their interactions, in a nutrient–phytoplankton–herbivore–carnivore dynamics model. Their study focused mainly on the population structure of filter-feeding copepods (*Calanus* and *Pseudocalanus* sp.) and the relative abundance of species which, at any developmental stage, differ markedly in body size.

Moloney and Field (1991) and Moloney *et al.* (1991) presented a size-based plankton model of the Benguela ecosystem, but general enough to simulate interactions within plankton communities of any ecosystem. Community structure and transfer processes

were all size-dependent, and all model parameters were determined by body size, using empirically determined relationships calculated from published data (Peters 1983; Moloney and Field 1989). In the original model (Moloney and Field 1991), autotrophic and heterotrophic groups comprised organisms in size ranges from 0.2 to 200 μm ESD (equivalent spherical diameter) and 0.2 to 2000 μm ESD respectively, and were divided into size classes using a logarithmic scale. A logarithmic scale of 10 was used because the resulting size classes were similar to traditional categories described by Sieburth *et al.* (1978). In the size range 0.2–2 μm ESD, picophytoplankton and bacterioplankton were considered, in the size range 2–20 μm ESD nanophytoplankton and heterotrophic flagellates, in the range 20–200 μm ESD net phytoplankton and microzooplankton, and in the range 200–2000 μm mesozooplankton. Moloney and Field's model simulated flows of carbon and nitrogen.

In the model, ingestion rate of heterotrophs was a function of prey concentration between a range of size classes, and following a Michaelis–Menten relationship:

$$g(P_i) = \frac{I_{max}(P_i - P_i')}{\alpha + \sum_{i=min}^{max} (P_i - P_i')} \tag{12.89}$$

where the specific ingestion rate of size class i by size class j was determined by the maximum mass-specific size-dependent ingestion rate of size class j (I_{max}). P_i is the standing stock of size class i, and P_i' is the threshold. Assimilation was taken to be constant, and respiration and excretion were proportional to biomass.

SIZE SPECTRUM THEORY

The biomass size spectrum model initially proposed by Sheldon and Parsons (1967) and Sheldon *et al.* (1972, 1973) has been developed in successive steps by Platt and Denman (1978) and Silvert and Platt (1978, 1980). Heath (1995) presented a synthesis of biomass size spectrum theory (see also Gaedke 1992, 1993; Gaedke and Straile 1994; Blanco *et al.* 1994, 1998).

The size distribution of organisms in the pelagic food chain can be described by the following time-dependent equation (Silvert and Platt 1980):

$$\frac{\partial N}{\partial t} + w \frac{\partial}{\partial w}(bG) + bM = 0 \tag{12.90}$$

where $\beta(w, t)$ is a biomass density function such that

$$b(w, t) = \beta(w, t)dw \tag{12.91}$$

$b(w, t)$ is the mass of particles per unit volume in the size interval from w to $w + dw$ at time t. Silvert and Platt (1980) assumed predation scales in a perfectly isometric fashion, i.e. the range of particle sizes acceptable as prey scales as w. Thus $dw \sim w$.

The function $G(w)$ is the specific growth rate of particles:

$$G(w) = \frac{1}{w} \frac{\partial w}{\partial t} \tag{12.92}$$

and the function $M(w)$ is the specific rate of change in numbers of particles due to mortality and reproduction:

$$M(w) = \frac{1}{N} \frac{\partial N}{\partial t} \tag{12.93}$$

and $N = \beta/w$.

The basic assumptions of the size spectrum theory (Silvert and Platt 1980) are that the system is in steady state, with no immigration and emigration of biomass, predation is the only source of mortality, large organisms eat only smaller ones that are a constant fraction of their own size, there is a constant input of energy to the smallest size classes in the spectrum, and the flow of energy (biomass) is in one direction only, from small particles to large ones.

Silvert and Platt (1980) showed that one possible solution to equation 12.90 is

$$\beta(w)G(w) \sim w^{-c} \tag{12.94}$$

where the exponent c is such that:

$$K_1 c = q^{c-1} \tag{12.95}$$

and parameter K_1 is the growth efficiency, i.e. growth divided by ingestion. Specific growth rate can be expressed as:

$$G(w) = kw^{-x} \tag{12.96}$$

where k and x are constants.

Combining equations 12.93 and 12.95,

$$\beta(w) \sim w^{x-c} \tag{12.97}$$

Silvert and Platt (1980) showed that

$$M(w) = \frac{G(w/q)}{K_1 q} \frac{\beta(w/q)}{\beta(w)} \tag{12.98}$$

and from equations 12.94 and 12.95

$$M(w) = \frac{k}{k_1} q^{c-1} w^{-x} = ckw^{-x} \tag{12.99}$$

Somatic growth represents the difference between the assimilated ration and losses due to metabolism and reproduction (reproductive loss is small relative to metabolic losses and is therefore ignored). Metabolism is found to take the form αw^γ and $\gamma = 1 - x$. Thus

$$\frac{dw}{dt} = pI - \alpha w^{1-x} = G(w)w = kw^{1-x} \tag{12.100}$$

for all w.

The ingestion rate becomes:

$$I = \frac{k+\alpha}{p} kw^{1-x} \tag{12.101}$$

and growth efficiency:

$$K_1 = \frac{p(k+1)}{\alpha} \tag{12.102}$$

Peterson and Wroblewski (1984) estimated the four parameters k, x, K_1, and q from the literature on a range of pelagic species and concluded that:

- $x \sim 0.25$
- $k = 4.23\ 10^{-3}\ \text{d}^{-1}$
- $c \sim 1.22$ with $K_1 = 0.14$ and $q = 3.45\ 10^{-4}$

The steady-state constraint on this basic model, with constant energy input to the smallest size classes, dictates that it can only be considered to represent some long-term average distribution of biomass across the full range of organisms in an ecosystem, such that temporal trends are eliminated. The shortest such time period over which the model could apply would be 1 year, thereby removing the dominant seasonal signal in the energy input (at high latitude), and several data sets supported this conclusion (see references in Heath 1995). However, Thiebaux and Dickie (1993a, 1993b) have suggested that within any trophic group in the ecosystem other factors are involved which cause the biomass spectrum to be non-linear. Considering variations in the biomass spectrum on some time scale shorter than one year, Silvert and Platt (1978, 1980) showed that perturbations in the energy input to the ecosystem must propagate up the spectrum as a damped wave. Feedback mechanisms, such as reproduction, will lead to smearing of the wave, but the mathematics of this process are complicated.

New technological developments such as the Optical Plankton Counter will probably encourage further development of the size-based approach to data analysis (Heath 1995; Zhou and Huntley 1997). Applications of biomass spectrum theory to fish larvae are presented by Beyer (1989).

12.5.3 Size- and stage-structured zooplankton populations in ecosystem models

The life cycle of dominant zooplankton species in ecosystems can be represented in detail in ecosystem models, when the representation of an average individual is not sufficient.

Steele (1974), Steele and Mullin (1977) and Steele and Frost (1977) have developed an ecosystem model in which the dynamics of *Calanus* were represented as successive cohorts. Hofmann (1988) used a stage structured model of *Paracalanus* sp. in five groups of stages which were feeding on two size categories of phytoplankton. Stage and age-structured population models (see page 602) have been coupled with ecosystem models (Fransz 1981; Davis 1984a, 1984b; Carlotti and Radach 1996).

Koslow (1983) studied the role of predatory interactions in the regulation of the size structure of marine zooplankton communities. The model contained size-structured populations of large (*Calanus* sp.) and small (*Paracalanus parvus* and *Acartia clausii*) herbivorous zooplankton, and invertebrate carnivores (chaetognaths). Planktivorous fish were represented by one compartment.

12.5.4 Further reading

Steele, J., 1974. *The structure of marine ecosystems*. Harvard University Press, Cambridge, MA, 128 pp.

Fransz, H.G., Mommaerts, J.P. and Radach, G., 1991. Ecological modelling of the North Sea. *Neth. J. Sea Res.*, **28**: 67–140.

Ulanowicz, R.E. and Platt, T., 1985. Ecosystem theory for biological oceanography. *Can. Bull. Fish Aquat. Sci.*, **213**: 260 pp.

Platt, T., Mann, K. and Ulanowicz, R.E., 1981. Mathematical models in biological oceanography. *Monogr. Oceanogr. Methodol. 7*, The UNESCO Press, Paris, 157 pp.

12.6 MODELING SPATIAL DYNAMICS OF ZOOPLANKTON

Spatial distribution, dispersion and patchiness of zooplankton are important features of the ocean (Mann and Lazier 1991). They are influenced by a set of biological and physical processes of which the relative contributions are difficult to extract. Mathematical models that include biological as well as circulation processes provide an approach for investigating and separating environmental and biological factors that control plankton distribution. Many of the examples found in the literature study the effect of some selected factors, assuming that other factors have negligible effects. Simulated plankton distributions obtained with models treating plankton as simple drifters and for which dispersion is determined solely by circulation, show strong differences from observed distributions. The primary conclusion from these models is the need to include biological effects, and a thorough effort has been made in this direction during the past decade.

12.6.1 Modeling active behavior and counter-gradient search

An organism's sensory systems are evolutionary adaptations that enable the organism to react to environmental variations. Zooplankton will benefit from organs that allow them to locate food and mates and to avoid predators and other harmful situations. The evolution of such organs is therefore under strong selection pressure. The simplest formulation of predator–prey contact rates is obtained by assuming that either the prey or the predator is stationary while the other is moving about with an average speed v and that the predator has a reaction volume with a surface A outside which it cannot detect prey (Gerritsen and Strickler 1977). Then the total number of encounters between predators and prey during a time period T is given by

$$E = TNPAv \qquad (12.103)$$

where N and P are concentrations of predators and prey respectively (Giske et al. 1994). This model can be easily reformulated to express feeding rates of predators and mortality rates of prey. It has been elaborated in two directions: models of contact rates and models of perception ranges (Table 12.8). Contact rate models can incorporate swimming of both predator and prey, pause swimming, and turbulent water motions.

The effect of small-scale physics on plankton ecosystems is a recent research topic (Yamazaki and Osborn 1988; Granata and Dickey 1991; Denman and Gargett 1995). Recent theoretical models suggest that small-scale turbulence is a significant component in the encounter rate between a larval fish and their planktonic prey (Rothschild and Osborn 1988; MacKenzie and Leggett 1991; McKenzie et al. 1994). Few studies of this effect have been found to date. Using numerical simulation methods, Yamazaki et al. (1991) demonstrated that the contact rate model of Rothschild and Osborn (1988) is valid. Lagrangian models which mimic the aggregation of planktonic organisms in turbulent flow allow one to take into account small-scale non-linear processes, and to study the behavior of planktonic organisms in conjunction with such structures (Yamazaki 1993).

Models of perception ranges focus on the sensory organs of predators and prey, and mathematical formulations are available for the lateral line, vision, hearing and olfaction. Although zooplankton use all sensory systems simultaneously (Bollens et al. 1994), no single model has yet incorporated all of these.

The sensory systems of fish take up information at several spatial and temporal scales.

Table 12.8 Models of sensory systems of fish and mortality risk of zooplankton.

Authors	Modeled processes
Passive and tactile encounter	
Gerritsen and Strickler (1977)	contact rate between a predator and a prey
Rothschild and Osborn (1988)	effect of turbulent motion on contact rates
MacKenzie and Leggett (1991)	effect of wind and tide on encounter rates between fish larvae and zooplankton
MacKenzie and Kiørboe (1995)	encounter rates for cruising and pause travel predators in calm and turbulent conditons
Kiørboe and Saiz (1995)	copepod feeding and predation risk in turbulence
Caparroy and Carlotti (1996)	energy budget for copepod in turbulent regime
Eiane et al. (1997)	comparison of tactile and visual predation in the vertical field
Fiksen et al. (1998)	combination of light and turbulence for predation by fish larvae
Olfaction	
Jumper and Baird (1991)	detection range of odor plume
Baird and Jumper (1995)	mate location by olfaction
Baird et al. (1996)	odor spread by diffusion, turbulence and advection
Moore et al. (1994)	odor spread in benthic boundary layer flow
Light and vision	
Aksnes and Giske (1993)	model of visual range of planktivorous fish
Aksnes and Utne (1997)	
Giske et al. (1994)	vision-based (light-dependent) mortality risk for zooplankton
Hearing, lateral line and pressure fields	
Rogers and Cox (1988)	underwater sound propagation and biological responses
Kalmijn (1988)	detection range of hydrodynamic and acoustic fields
Bleckmann (1993)	model of detection by lateral line system

The lateral line system can detect zooplankton movement at very small distances, and therefore can be the first tool available for prey detection by fish larvae (Blaxter and Batty 1985). Vision is also a near-field instrument, because the decay rate of images underwater is fast (Aksnes and Utne 1997). Sound propagates better in water than in air (Rogers and Cox 1988), and hearing is therefore a good long-distance tool. Olfaction can be used to trace prey or a mate along a concentration gradient (Baird and Jumper 1995) and it is the only sense to measure 'past experience'. It can also be used to indicate concentrations of predators and hence predation risk for prey (Larsson and Dodson 1993). The lateral line and vision systems give more precise information than hearing or olfaction, and final prey capture will most often rely on one of these. Hearing or olfaction is probably more important for the early phase of prey location and for predator avoidance.

12.6.2 Modeling behavioral mechanisms, aggregation, and schooling patches

MODELING ZOOPLANKTON BEHAVIOR AT THE 'MICRO-SCALE'

The simplest model of dispersion is a random walk model, where individuals move along a line from the same starting position (see Okubo 1980; Possingham and Rough-

garden 1990; Renshaw 1991; Brown and Rothery 1993). Below we describe models that are used to simulate movement of zooplankton individuals.

Random walk models (RWMs) have been used for the last 50 years (Yamazaki 1993). They involve a succession of movements along a line segment where the direction and the length of each move is randomly determined (Yamazaki and Okubo 1995). The RWM and its extensions, as well as numerous applications can be found in Okubo (1980) and Berg (1983). In plankton ecology, RWMs have been used mainly for the study of phytoplankton trajectories in mixing circulation or Langmuir cells (see Yamazaki 1993), and for behavior of fish larvae (Okubo 1986). There are few RWMs for zooplankton studies. Davis *et al.* (1991) presented a series of models exploring the role of swimming and patchy food supply on the growth of a predator (fish larvae preying on copepods, or copepods preying on phytoplankton cells). From a RWM, they derived an appropriate form for a diffusion term and combined this with a growth model (similar to those presented in section 12.3). A general analysis of the growth/swimming model showed the dependence upon the parameters and the patch structure. The authors used this model to study the effect of turbulence, which induces more frequent encounters but also dissipates prey patches. Tiselius *et al.* (1993) presented a model of individual copepods, taking into account the feeding process in a patchy prey environment, as well as growth and reproduction. In their model, copepod motility followed a RWM.

Yamazaki made initial attempts to simulate a zooplankter in a flow field, first as a passive particle, then with behavior based on a RWM (Yamazaki *et al.* 1991). These models showed that organism behavior must be integrated into studies of small-scale physics. The only way to properly account for the effects of small-scale physics (e.g. turbulence) is to develop Lagrangian models and implement these into realistic simulated flow fields, for example turbulent flow from direct numerical simulations based on the Navier–Stokes equations.

A different method for modeling the movements of organisms is by utilizing evolutionary theory (section 12.3.3). Tools for this approach will be discussed in Evolutionary modeling approaches for optimal spatial distributions, section 12.6.2.

From animal aggregation to patch dynamics models

Here we denote aggregation as a grouping of conspecific individuals without any implication of mutual attraction (Ritz 1994). Passive aggregations are caused by physical factors (e.g. currents, light). Active aggregations can be permanent or temporary, as a response to food concentration or predation, or for mating. Different types of models have been built, some of them focusing on the structure and shape of aggregations depending on internal and external physical forces, others dealing with the benefits for individuals of living in groups with regard to feeding (foraging models) and to predation. There are many models dealing with living in groups (see for review Pulliam and Caraco 1984), but few have been applied to marine zooplankton.

Models for studying aggregation size, structure and shape need the development of physical models to which can be added the swimming behavior of organisms. The focus of much modeling work has been the study of the maintenance of animal aggregations (swarms, patches, schools, etc.) in the face of dispersive forces acting on them from the environment (Okubo 1980).

The Lagrangian approach can take into account the behavior of individual organisms, and the effects of the physical environment upon them. The Lagrangian approach is straightforward, but the nature of the mathematics, i.e. 'n-particle motion dynamics', makes any analysis computer intensive with an increasing degree of non-linear aspects.

Yamazaki (1993) reviewed available Lagrangian simulations for animal groupings (presented with others in Table 12.8). Yamazaki (1993) introduced numerical Lagrangian models that incorporate an attractive force component in organism aggregations (see also Yamazaki and Okubo 1995). Yamazaki and Haury (1993) used such a model to find a generalized relationship between an organism's locomotion ability (e.g. swimming speed and 'motivation' to maintain a swarm), perception distance (measuring the ability to sense and orient toward neighbors), and the strength of diffusing forces (e.g. turbulence) in a zooplankton swarm.

Although Eulerian approaches are mathematically tractable, the methods do not explicitly address the density dependence of aggregating individual behavior within a patch. Okubo (1980, 1986) has reviewed much of the work in mathematical modeling of animal aggregations that use a Eulerian approach, incorporating diffusion and advection terms to represent random walk processes and attractive forces. Several models have emphasized the forces that internally maintain schools (Okubo 1980; Anderson 1981). Anderson (1981) represented a school size change by Fokker–Planck stochastic differential equations, having linear terms for school size increase and decrease.

Group living is an important feature for some zooplankton species and fish larvae. Group membership is supposed to be helpful for the individual in feeding and avoiding predators (Pulliam and Caraco 1984; Clark and Mangel 1986). Foraging and feeding in groups may give benefits for locating new or richer food patches, but also increases competition for resources within a prey patch. Clark and Mangel (1986) present a set of simple mathematical models to investigate the relationship between evolutionary fitness of individual foragers and the size of the foraging group.

Another important function of aggregation is to confer protection from predators upon its members. Swartzman (1991) approaches the formation and maintenance of fish groups under predation. He described a birth–death model that is expressed as a system of differential-difference equations describing the probability of having different numbers of schools in a $1 \, km^2$ study region. The equilibrium solution was obtained analytically, and results were presented for different combinations of prey and predator characteristics. These results were interpreted to indicate under what conditions schooling is likely.

EVOLUTIONARY MODELING APPROACHES FOR OPTIMAL SPATIAL DISTRIBUTIONS

The theory of evolution by natural selection predicts that the gene pools of populations will become adapted to their physical and biological environment (section 12.3.3 and Figure 12.1). Optimal spatial distributions have been investigated by several modeling approaches (see review by Giske *et al.* 1998a). The simple equation for population growth has branched into four bodies of theory (Figure 12.2), of which two have been utilized to predict individual behavior.

Optimization

The earliest theory for optimal spatial distributions of individuals within a population was the Optimal Foraging Theory (OFT) (Emlen 1966; MacArthur and Pianka 1966). OFT is not derived from any specific equation related to Darwinian fitness, but assumes that increased efficiency during feeding will benefit the organism by providing more time for other fitness-related tasks (such as mating or hiding). OFT was the major theory in use by behavioral ecologists in the 1970s, and diversified into theories of optimal diet, optimal habitat and several more (see review by Schoener 1987). In contrast, Zaret

Game theory

Game theory addresses optimal solutions to frequency-dependent problems, i.e. situations where the optimal decision depends on what other individuals do. Two game theoretic approaches have been utilized in ecological modeling, the evolutionary stable strategy (ESS) and the ideal free distribution (IFD). Game theory, like optimality theory in OFT, was introduced to ecology from economics (Maynard Smith 1982; Parker 1984). Commonly, the goal of a game is to find a strategy (pure or mixed) that can persist in a population, and the Evolutionary Stable Strategy (ESS) is a well-known example (Maynard Smith and Price 1973; Maynard Smith 1974). A strategy is an ESS if, once established in the population, a new mutant or immigrant cannot invade the population (see Box 12.2).

Iwasa (1982) constructed the first aquatic ESS model. He modeled the diel vertical distribution of zooplankton (that ate phytoplankton and were eaten by fish) and fish. The game between predator and prey led to light-dependent behavior at both trophic levels. Gabriel and Thomas (1988a, 1988b) developed this game further, but included negative density-dependent effects of competitors within each trophic level. Their model thus was both frequency- and density-dependent. Hugie and Dill (1994) also constructed a habitat-selection game between zooplankton and a planktivorous fish population. Their model links ESS and the other game theoretical approach, the IFD (see below).

Ideal Free Distribution

The Ideal Free Distribution (IFD) is a theoretical model for studying density-dependent effects on the spatial distribution of optimal individuals in a group (Fretwell and Lucas 1970). 'Ideal' means that each individual animal is able to choose the habitat that maximizes its fitness rewards, and 'free' means that there are no costs associated with entering this habitat. For animals that forage in a patchy environment, for convenience the rewards are often supposed to be equivalent to food intake rate. Generally, in classical IFD, all individuals are alike, but this constraint has been relaxed in several approaches (see review by Tregenza 1995). The relaxation of the original assumptions

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Box 12.2   The evolutionary stable strategy (ESS)

A strategy is an ESS if, once established in the population, a new mutant or immigrant cannot invade the population. This can be stated as

$$S_e(1 - \epsilon) > S_m(\epsilon) \tag{1}$$

where S_e and S_m are the pay-offs of the established and mutant strategies when their frequencies of occurrence are $(1 - \epsilon)$ and ϵ, respectively ($\epsilon \ll 1$). However, a mixed ESS, or an evolutionary stable polymorphism, can be established if the pay-offs of the two (or more) strategies are the same at some frequency of occurrence

$$S_e(x_s) = S_m(x_s) \tag{2}$$

and when a change in frequency of occurrence from this balance leads to reduced fitness of the strategy:

$$S_e(x) < S_e(x_s) \tag{3}$$

for x close to x_s.

usually leads to very computer-intensive models (e.g. Giske *et al.* 1997). A limitation of IFD is that it cannot explain the fluctuating motivation of individuals according to time and state. Combined effects of density and internal state may be studied by SDP. Giske *et al.* (1997) present in detail an IFD model of similar copepods in the water column which includes both density-dependent predation risk and food supply (See Box 12.3).

Box 12.3 The Ideal Free Distribution (IFD)

Under Ideal Free Distribution models with equal competitors, the total number of individuals distribute themselves among habitats so that the gain of an individual is equal in all habitats. In the classical version of the model, food was the resource, and the individual gain (S_i) in a habitat (i) declined from a density-independent maximum B_i by a habitat-specific function of competitor density d_i

$$S_i = B_i - f_i(d_i), i = 1, 2, \ldots, L(\text{habitats}) \tag{1}$$

The IFD is achieved when individual gain is equal among habitats

$$S_1 = S_2 = \ldots = S_i \tag{2}$$

and total numbers in the $K \leq L$ occupied habitats match population size N_T

$$N_1 + N_2 + + + N_K = N_T \tag{3}$$

For zooplankton in a natural environment we would not expect that food gradients alone could cause an IFD for three reasons: (1) there are combinations of low competitor density and high food production where individual feeding rate will not be influenced by a (minor) increase in competitor density, and more important, (2) one of the main resources for development and fitness of aquatic organisms may be environmental temperature and (3) predation risk will affect fitness in a density-dependent manner. Habitat profitability may then be expressed directly in terms of the habitats' expected contribution to the fitness (Φ) of the animal, and ideal free individuals will distribute so that

$$\Phi_1 = \Phi_2 = \ldots = \Phi_i \leftrightarrow \rho_1 = \rho_2 = \ldots = \rho_i \tag{4}$$

as r is a population parameter constant for all habitats and is the average of all ρ_i' (see equation 12.37). In a situation where feeding will be sufficient for growth and where reproduction may occur unhindered by, for example, seasonal constraints, fitness is proportional to the life-history trade-off g/M, as shown above. Then we may write

$$\Phi_1 = \Phi_2 = \ldots = \Phi_i \leftrightarrow g_1/M_1 = g_2/M_2 = \ldots = g_i/M_i \tag{5}$$

(Giske *et al.* 1997). In IFD terms we will find the relation between the optimum number in each habitat, so that gain is equalized by competition and predation risk dilution. Fecundity, growth and survival will be derived from mechanistical equations of the environment and density-dependent responses. The ideal free distribution – where no individual could increase its fitness by moving – is obtained when competitor density in each available habitat is adjusted so that the ratio g/M is equalized.

According to equation (1) habitat profitability is a decreasing function of concentrations of foragers, while in equation (5) the fitness may be maximal at some intermediate zooplankton concentration with low resource competition but with substantial dilution of predation risk. In the latter case, with a bell-shaped habitat profitability curve, there are two zooplankton concentrations that give the same fitness in each habitat. This makes it far more complicated to calculate the expected spatial distribution of a population. Methods for this calculation are discussed in Giske *et al.* (1997).
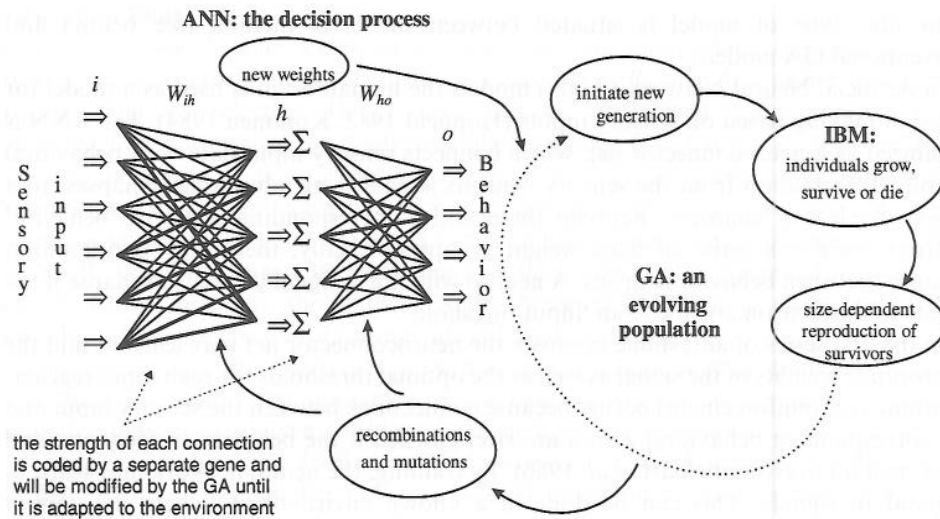
ANN: the decision process

the strength of each connection
is coded by a separate gene and
will be modified by the GA until
it is adapted to the environment

Fig 12.3. The ING concept: one or more artificial neural networks (ANN) code for the decision processes utilized in an individual-based model (IBM). A cohort of individuals with randomly set individual strings coding for the weighting of the ANN are initiated in the first time step. The strings are then adapted using the genetic algorithm (GA) through the principle of evolution by natural selection. Differences among the strings are expressed through differences in weights of the ANN, which leads to behavioral differences. The i, h, and o refer to input, hidden, and output layers respectively. The input layer consists of internal or environmental input. The output nodes fire if their values are above certain threshold values. The lines indicate the relationships among the different layers. Each of the nodes in the i-layer are connected to all the nodes in the h-layer which again are connected to all the nodes in the o-layer. W_{ih} and W_{ho} are the weight matrices of connection strengths between the nodes of the layers. Potential weight differences are indicated by the variation in line thickness of the connections. The GA will evolve the 'gene pool' to contain the best possible response to the combinations of sensory inputs received throughout the lives of the individuals, as measured by the fecundity that results from the IBM given a particular ANN. Modified from Giske *et al.* (1998a).

coefficient. Other examples are given by Nisbet *et al.* (1993) and Rothschild and Ault (1996).

GRID-BASED MODELS

Tischendorf (1997) gave a short review of modeling methods for spatially explicit simulations in heterogeneous landscapes. Grid-based models are starting to be used in spatial zooplankton dynamics, and are mostly associated with new modeling approaches of individual movements. Grids divide a continuous two-dimensional space into discrete units of equal size and shape, i.e. cells. Each cell can easily be selected by indices because of its defined position in a matrix. By this arrangement, cells relate descriptive information (e.g. state variables and transition rules) both to each other (by fixed neighborhood relationships) and to the area they cover. Movements of individuals are commonly expressed by rules that either assign individuals to other cells or change

cumulative cell state variables that describe a spatial class of individuals. Such movement rules can be influenced by landscape features associated with cells. Object-oriented modeling of individual movements uses grids to represent space (e.g. Laval 1997). Cellular automata represent such a class of models for population interactions in space (Phipps 1992; Caswell and Etter 1993), but there are very few examples in zooplankton ecology (Delgado and Marin 1998).

12.6.3 Coupling IBMs and spatially explicit models

PASSIVE PARTICLE TRAJECTORIES FROM LAGRANGIAN TRANSPORT IN MODEL CIRCULATION FIELDS

This approach uses simulated currents from sophisticated 3-D hydrodynamic models driving Lagrangian models of particle trajectories to examine dispersion processes.

The approach is relatively straightforward and is a first step in formulating spatially explicit individual based models (IBMs). Given a 'properly resolved' flow field, particle (larval fish/zooplankton/meroplanktonic larvae) trajectories are computed (generally with standard Runge–Kutta integration methods of the velocity field). Specifically, hydrodynamic models (Box 12.4) provide the velocity vector $v = (u, v, w)$ as a function of location $x = (x, y, z)$ and time t and the particle trajectories are obtained from the integration of

$$dx/dt = v(x, y, z, t). \qquad (12.104)$$

These trajectories could be modified by turbulent dispersion as described below. Once the larval/particle position is known, additional local physical variables can be estimated along the particle's path, for example temperature, turbulence, light, etc., and input to the IBM (see section 12.4.3). The physical quantities are then included in biological, for example physiological or behavioral, formulations of IBMs (see section 12.4.3).

In general, flows can be three-dimensional, baroclinic and time-dependent. Driving forces are the winds, tides, atmospheric heating and cooling and prescribed inflows. Estimates of local turbulence levels are derived from advanced turbulence closure models. The simulations can become quite intensive computationally and the model output of the physical model can be large if 3-D physical data is saved on the order of every hour.

Simulations considering trajectories of plankton as passive particles are a necessary step before considering any active swimming capability of planktonic organisms. They show the importance of physical features in the aggregation or dispersion of the particles (see as examples Ishizaka and Hofmann 1988; Oliver *et al.* 1992; Werner *et al.* 1993).

Effect of turbulence on dispersion

Small scale turbulence can be represented in various ways. Some Lagrangian models include a stochastic term to mimic diffusive processes (e.g. Walsh *et al.* 1981). Others use a diffusion coefficient using a random walk procedure as in Black and Gay (1990).

Werner *et al.* (1996) and Hannah *et al.* (1998) present a more complex representation. The dispersal of particles in heterogeneous turbulent fields (e.g. near or within turbulent boundary layers) can lead to aggregations that are not realistic if the dispersal process is not treated carefully (e.g. Thompson 1987; and Holloway 1994). Legg and Raupach (1982) proposed a Langevin equation to derive a Markov equation for the vertical velocity of a particle (or zooplankton organism) in a flow where the turbulence is heterogeneous.

Box 12.4 The hydrodynamical model equations

Acceleration in x direction:

$$\frac{\partial u}{\partial t} = fv - u\frac{\partial u}{\partial x} - v\frac{\partial u}{\partial y} - w\frac{\partial u}{\partial z} - \frac{1}{\rho}\frac{\partial p}{\partial x} + A_v\nabla^2 u + \frac{\partial}{\partial z}A_v\frac{\partial u}{\partial x}. \tag{1}$$

Acceleration in y direction:

$$\frac{\partial v}{\partial t} = fuv - u\frac{\partial v}{\partial x} - v\frac{\partial v}{\partial y} - w\frac{\partial v}{\partial z} - \frac{1}{\rho}\frac{\partial p}{\partial y} + A_h\nabla^2 v + \frac{\partial}{\partial z}A_v\frac{\partial v}{\partial x}. \tag{2}$$

Vertical velocity is found from the equation of continuity:

$$0 = \frac{\partial w}{\partial z} + \frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} \tag{3}$$

and surface elevation

$$h = \int w_1 dt \tag{4}$$

where

u, v horizontal velocity components in x and y direction, respectively
w vertical velocity component
w_1 vertical velocity of surface elevation, i.e. upper layer
h height of the free surface from the undisturbed mean
f Coriolis parameter
ρ density
A_h horizontal eddy diffusion of momentum
A_v vertical eddy diffusion of momentum
p pressure found by the hydrostatic equation

$$p = \int_z^h rgdz + P_a \tag{5}$$

where P_a is the atmospheric pressure.
 The space–time variations of water density ρ are found by the functional relationship

$$\rho = \rho(S, T) \tag{6}$$

where S and T are the salinity and temperature of the water, respectively. These scalar fields can be modeled by a balance equation of the form

$$\frac{\partial c}{\partial t} = \frac{\partial}{\partial x}(uc) - \frac{\partial}{\partial y}(vc) - \frac{\partial}{\partial z}(wc) + K_h\nabla^2 c + \frac{\partial}{\partial z}\left(K_v\frac{\partial c}{\partial z}\right) + \delta_c \tag{7}$$

where

c S or T
K_h horizontal eddy diffusion of salinity and temperature
K_v vertical eddy diffusion of salinity and temperature
δ_c thermodynamic interaction between the upper layer and the atmosphere ($c = T$) or supply of salt and fresh water during freezing or melting respectively ($c = S$) and the operator ∇^{-2} means

$$\nabla^2\Theta = \frac{\partial^2\Theta}{\partial x^2} + \frac{\partial^2\Theta}{\partial y^2} \tag{8}$$

where Θ is any function of x and y.
 Vertical mixing is calculated as a function of the Richardsons number, wave height and parametrization of tidal mixing in shallow areas. (From Giske *et al.* 1998b.)

The Langevin equation for the dispersion of particles is:

$$dw/dt = -\alpha w + \lambda \xi(t) + F \tag{12.105}$$

where $\alpha = 1/\tau_1$ and τ_1 is the Lagrangian integral time scale (or auto-correlation time scale) estimated from $N_q = \sigma_w^2 \tau_l$, where N_q is the turbulent exchange coefficient (see Galperin *et al.* 1988), σ_w is the Lagrangian velocity variance $(\sigma_w^2 = 0.3q^2/2)$; $\lambda = \sigma_w^2 \sqrt{2/\tau_1}$; $\xi(t)$ is Gaussian noise of zero mean and unit variance; and $F = \partial(\sigma_w^2)/\partial z$ is a term involving the gradient in the turbulent velocity variance.

The Markov chain for w_{n+1}, the turbulent vertical velocity at time step $n + 1$, becomes:

$$w_{n+1} = a_n w_n + b_n \sigma_{wn} \xi_n + C_n \tag{12.106}$$

where

$$a_n = \exp(-a_n/\tau_{1n}), b_n = [1 - \exp(-2\Delta t/\tau_{1n})]^{1/2} \tag{12.107}$$

$$C_n = (F/\alpha)[1 - \exp(-\Delta t/\tau_{1n})] \tag{12.108}$$

and Δt is the time step.

This approach was used in the studies of Hannah *et al.* (1998) wherein potential upper-ocean pathways for the supply of *Calanus finmarchicus* from the Gulf of Maine to Georges Bank were investigated by numerically tracking particles in realistic 3-D seasonal-mean and tidal flow fields. Hannah *et al.* (1998) found that upper-ocean drift pathways for biota in the southern Gulf of Maine are strongly sensitive to biological and/or physical processes (including turbulent dispersion) that affect vertical position (in relation to the surface Ekman layer) and horizontal position (in relation to topographic gyres).

TRAJECTORIES OF ACTIVELY SWIMMING PARTICLES FROM LAGRANGIAN TRANSPORT IN MODEL CIRCULATION FIELDS

Plankton transport models that include biological components typically use a prescribed vertical migration strategy for all or part of an animal's life history or a vertical motion (sinking or swimming) that is determined by animal development and growth (Hofmann *et al.* 1992; Werner *et al.* 1993; Verdier *et al.* 1997). The simulated plankton distributions from these models tend to compare better with observed distributions than models that use passive particles. Sensitivity studies show that behavior is an important factor in determining larval transport and/or retention.

Biological and physical models can be coupled in the following way. First, the physical model can be run with a particular physical scenario (winds, boundary conditions, etc.), then the biological model can be used. Organisms, considered as particles, can be tracked in the 3-D velocity field calculated by the physical model using a standard Euler or Runge–Kutta integration:

$$dx/dt = v_a(x, y, z, t) + v_b \tag{12.109}$$

where v_a is the velocity vector from the circulation model as a function of location $x = (x, y, z)$, t is time and v_b is the swimming speed of the organism depending on prescribed or dynamical biological properties. Hofmann *et al.* (1992) and Capella *et al.* (1992) present a time- and temperature-dependent model combining temperature effects on development times, physiology and density of krill embryos and larval sinking and ascending rates. Verdier *et al.* (1997) consider a prescribed age-dependent vertical swimming velocity of annelid larvae.

The coupling of IBMs of zooplankton and 3-D circulation models is a recent field of study, even for fish models (Tyler and Rose 1994). Generally, models that describe the spatial heterogeneity of the habitat have been designed to answer questions about the spatial distribution of a population rather than questions about the numbers and characteristics of surviving individuals. The simplest biological representation concerns the swimming ability of the planktonic organism. As questions concerning biological aspects of dispersion receive increasing attention through programs like GLOBEC, the number of models with biological detail (see section 12.4.3) is likely to increase.

The dispersion of several species on the Georges Bank has been studied recently (US-GLOBEC Georges Bank program): a *Calanus finmarchicus* model (Miller *et al.* 1998), a larval fish model applied to haddock and cod (Werner *et al.* 1996), and a model of scallop larvae (Tremblay *et al.* 1994). They all use the three-dimensional hydrodynamic model developed by Lynch and collaborators (Lynch *et al.* 1992, 1996). Other spatially explicit IBMs for fish larvae have been developed (see Tyler and Rose 1994 for a review; Hinckley *et al.* 1996). Verdier *et al.* (1997) presented a spatially explicit IBM for meroplanktonic larvae in the Bay of Banyuls.

Tyler and Rose (1994) emphasized that models that incorporate individual-based formulations and physical habitat modeling techniques not only increase our understanding of the link between spatial and temporal dynamics of zooplankton and fish populations, but also allow us to explore the potential effects of habitat alteration on these populations. Using this approach, biological mechanisms that are strongly dependent on habitat and that are not fully understood could be studied by examining different scenarios. For example, Moloney and Gibbons (1996) used an IBM of herbivorous zooplankton coupled with simplified 1-D profiles of food and temperature to study the effects of different scenarios of diel vertical migration on daily ingestion.

12.6.4 Spatial zooplanton dynamics with advection-diffusion-reaction equations (ADRE)

The general biological–physical model equation used to describe the interaction between physical mixing and biology is:

$$\frac{\partial C}{\partial t} + \nabla \cdot (v_a C) - \nabla \cdot (K \nabla C) = \text{'biological terms'} \tag{12.110}$$

where $C(x, y, z, t)$ is the concentration of the biological variable which is either a functional group (zooplankton), a species, or a developmental stage (in which case the number of equations would equal the number of stages) at position x, y, z at time t. The concentration can be expressed as numbers of organisms or biomass of organisms per unit volume, and

- $v_a(u_a, v_a, w_a)$ represents the advective fluid velocities in x, y, z directions;
- K_x, K_y, K_z are diffusivities in x, y, z directions;
- $\nabla = (\partial/\partial x, \partial/\partial y, \partial/\partial z)$ is the Laplacian operator.

On the left hand side of equation 12.110, the first term is the local change of C, the second term is advection caused by water currents, and the third term is the diffusion or redistribution term. The right hand side of equation 12.110 has the biological terms that

represent the sources and sinks of the biological variable at position x, y, z as a function of time.

The biological terms may or may not include a velocity component (swimming of organisms, migrations, sinking, ...) and the complexity of the biological representation can vary from the dispersion of one variable (the zooplankton biomass, or the concentration of a cohort) in NPZ ecosystem models (see section 12.5) to detailed population dynamics with stage-structured populations. The following sections give examples of passive and active dispersion of zooplankton biomass or targeted populations.

The numerical methods used to solve ADREs are finite difference techniques (see for instance Sewell 1988). Examples given by Okubo (1980, chapter 6) include solution methods for ADREs.

MODELING PASSIVE DISPERSION WITH ADREs

There are several examples of models of passive dispersion of planktonic organisms. The spatial dependence is usually reduced from three to two or one dimension depending on the question being asked, and the equations are solved analytically or numerically. However, the simultaneous partial differential equations that model such systems can be solved analytically only under very special circumstances, depending on the assumptions regarding the boundary conditions and on the functional forms used in the model. Results of analytical solutions are of interest because they can delimit parameter space for simple situations, and also because they can serve as a useful check to the solutions obtained by numerical methods.

Sundby (1983, 1991) presented a simple model of vertical egg distribution as a function of the properties of the water (density, current and turbulent diffusion) and physical properties of the eggs (buoyancy and dimension). The basic equation 12.110 is then reduced to the vertical component of the diffusion equation:

$$\frac{\partial C(z,t)}{\partial t} - \frac{\partial}{\partial z}\left[K(z,t)\frac{\partial C(z,t)}{\partial z}\right] = \text{mortality} + \text{spawning} - \frac{\partial[w_b(z,t)C(z,t)]}{\partial z}$$

$$(12.111)$$

where $C(z,t)$ is the concentration of eggs in numbers per unit volume, $K(z,t)$ is the vertical eddy diffusivity coefficient, and z is the vertical coordinate.

The biological terms are reduced to the mortality of eggs, the input from spawning, and the sinking of eggs with $w_b(z,t)$ as the vertical velocity of the eggs.

To solve equation 12.111, $w_b(z,t)$ and $K(z,t)$ must be known. The vertical velocity is expressed as $w_b = f(d, \Delta\rho, v)$, where d is the diameter of the egg, $\Delta\rho$ is the difference in density (buoyancy) between the egg, ρ_e, and the ambient water, ρ_w, and v is the viscosity of the water. Sundby presented the solutions in steady-state situations (first term equal to zero) and with an equal value for mortality and spawning.

To study the passive settlement of planktonic larvae onto bottoms of different roughness, Eckman (1990) and Gross et al. (1992) developed 1-D advection-diffusion models with particular attention to the effect of the turbulent boundary layers. The equations were solved with a finite-difference technique.

Hill (1990) presented a model of pelagic dispersion of lobster larvae in the horizontal plane. The model is two-dimensional in space and the concentration of larvae is depth-averaged. Current and turbulence fields are also considered as depth-averaged values.

The concentration $C(x, y, t)$ of larvae at a position x, y at time t, is governed by the following advection-diffusion equation:

$$\frac{\partial C(x, y, t)}{\partial t} + \frac{\partial [u_a(x, y, t) C(x, y, t)]}{\partial x} + \frac{\partial [v_a(x, y, t) C(x, y, t)]}{\partial y}$$
$$- \frac{\partial}{\partial x} \left[K(x, t) \frac{\partial C(z, t)}{\partial x} \right] - \frac{\partial}{\partial y} \left[K(y, t) \frac{\partial C(y, t)}{\partial y} \right] = m C(x, y, t)$$

(12.112)

where $u_a(x, y, t)$ and $v_a(x, y, t)$ are depth averaged water velocities in the x and y directions respectively, and $K(x, t)$ and $K(y, t)$ are the turbulent diffusion coefficients in the x and y directions. In his model, Hill (1990) assumed a constant current speed u_a in the x direction, no current in the y direction ($v_a = 0$), and constant and equal turbulent diffusion in both x and y directions. The biological term represented reduction of larval concentration because of mortality of organisms at an instantaneous mortality rate, m.

With the same assumptions, Hill (1990, 1991) studied the relative contributions of turbulent diffusion and advection, as well as mortality and dispersal, to the dispersion of the larvae. He used analytical solutions of simplified versions of equation 12.112, corresponding to idealized configurations.

Similar models have been used to investigate the advection, diffusion, and mortality of Pacific herring larvae (McGurk 1989), the movements of larvae released from a well-defined region into a tidal current (Richards *et al.* 1995), and the dispersal and recruitment of a larval population of barnacles in a coastal habitat (Possingham and Roughgarden 1990). Possingham and Roughgarden (1990) presented, in detail, the use of finite difference methods to solve numerically the differential equations describing the dynamics of the distribution and abundance of adult and larval barnacles.

Hofmann (1988) presented a two-dimensional spatially-dependent advection-diffusion model of biological variables of the pelagic ecosystem on the outer southeastern US continental shelf. The dynamics of the copepod *Paracalanus* sp. was taken into account in this model (Hofmann and Ambler 1988).

MODELING ACTIVE VERTICAL SWIMMING WITH ADREs
The swimming behavior and/or buoyancy effects of organisms are included in equation 12.110 by the addition of a Laplacian term $\nabla(v_b C)$ for the swimming velocities, with $v_b(u_b, v_b, w_b)$ representing the swimming velocities in x, y, z directions. However for zooplankton organisms (not for fish larvae) the horizontal effect is negligible ($u_b = v_b = 0$).

Dekshenieks *et al.* (1996) presented a vertically structured and time-dependent model to investigate the effects of changes in the physical environment on the vertical distribution of oyster larvae, as determined by vertical stratification in temperature and salinity. The vertical distribution of a given size class, C_i, was assumed to be governed by:

$$\frac{\partial C_i(z, t)}{\partial t} + \frac{\partial [w_a(z, t) C_i(z, t)]}{\partial z} - \frac{\partial}{\partial z} \left[K(z, t) \frac{\partial C_i(z, t)}{\partial z} \right]$$
$$= \text{growth}_{i-1} - \text{loss}_i - \frac{\partial [w_b(z, t) C_i(z, t)]}{\partial z}.$$

(12.113)

The first term on the left hand side represents the rate of change of the number of larvae in a particular size class i in a size-structured population model. The second term

represents the effect of advective vertical transport by the fluid flow. The value of w_a is specified as a constant velocity or as a function that varies in space and time. The coefficient K determines the rate of vertical diffusion and may be specified as either a constant or a variable value. The first two terms on the right hand side represent the biological processes that determine the rate of transfer to the next largest size. The number of larvae in a particular size class changes by growth of new individuals from the previous size class (growth$_{i-1}$), and the loss of individuals to the next largest size (loss$_i$) (see weight-structured models on page 600). Larval growth was modeled for the whole life cycle as a function of ambient temperature, salinity, turbidity and food, and the size range was partitioned into 271 size classes.

Vertical migration is represented by the last term on the right hand side of equation 12.113. Larval swimming ability w_b is parameterized using observed dependencies on temperature, salinity and larval size. Therefore, the total advective velocity, w, is composed of contributions from the vertical circulation w_a, and the size-dependent biologically produced vertical movement (sinking or swimming) w_b, with $w = w_a + w_b$.

The addition of biological terms makes equation 12.113 complex, and analytical solutions are difficult to extract without simplifications. As a consequence, such equations are solved numerically. Dekshenieks *et al.* (1996) used a Crank–Nicholson implicit finite difference scheme (see Sewell 1988) with a time step of 12 min, which was adequate to resolve the transfer of larvae between size classes.

A similar approach was used by Andersen and Nival (1991) and Richards *et al.* (1996) to simulate the vertical distribution of zooplankton (euphausiids and copepods respectively) that vary in space and time as a result of diel vertical migration. They studied the role of light intensity, the rate of change in light intensity, and the relative rate of change in light intensity. The equation they used is the same as equation 12.113, except that there are no biological processes affecting the biomass or the number of organisms; the vertical speed of the organisms, w_b, only depends on light. These authors present in detail in their papers the numerical methods that they used.

Studies of the distribution of organisms in regions where zooplankton may be aggregated (e.g. upwelling and downwelling regions, Langmuir circulations, internal waves) are usually undertaken with 2-D models. Wroblewski (1980, 1982) modeled population dynamics (with a stage-structured population model) of copepod species embedded in a circulation system simulating the upwelling off the Oregon coast. Simulations of the dynamics of *Calanus marshallae* (Wroblewski 1982) focused on the interaction between diel vertical migration and offshore surface transport.

The zonal distribution of the life-stage categories C_i of *C. marshallae* over the Oregon continental shelf was modeled by the two-dimensional (x, z, t) equation:

$$\frac{\partial C_i(x, z, t)}{\partial t} - \frac{\partial [u_a(x, z, t) C_i(x, z, t)]}{\partial x} - \frac{\partial [w_a(x, z, t) C_i(x, z, t)]}{\partial z}$$

$$- \frac{\partial}{\partial x}\left[K(x, t) \frac{\partial C_i(x, z, t)}{\partial x} \right] - \frac{\partial}{\partial z}\left[K(z, t) \frac{\partial C_i(x, z, t)}{\partial z} \right]$$

$$= \text{population dynamics} + \frac{\partial [w_{bi}(x, z, t) C_i(x, z, t)]}{\partial z} \qquad (12.114)$$

where w_{bi} is the vertical swimming speed of the *i*th stage, assumed to be a sinusoidal function of time:

$$w_{bi} = w_{si} \sin(2\pi t) \qquad (12.115)$$

with w_{si} the maximum vertical migration speed of the ith stage. The population dynamics model was presented on page 602.

The upwelling zone extended 50 km from the coast down to a depth of 50 m, and was divided into a grid with spacing 2.5 m in depth and 1 km in the horizontal. The author used a finite difference scheme with a time step of 1 h, which fell within the bounds for computational stability.

MODELING THE DISPERSION OF A POPULATION IN CIRCULATION MODELS WITH ADREs

An important development in zooplankton modeling is to make full use of the increased power of computers to simulate the dynamics of zooplankton (communities or populations) in site-specific situations by coupling biological and transport models, giving a high degree of realism. Structured population models and individual-based models allow detailed simulations of zooplankton populations in different environmental conditions.

In the last decade, some efforts have been made to develop such physical–biological models. The current development of advanced circulation models will strongly increase the number of such studies.

Davis (1984b) developed a species-specific model for *Pseudocalanus* sp. incorporating 13 stages in an idealized steady gyre around the Georges Bank. Equation 12.110 was written as:

$$\frac{\partial N_{i,j}}{\partial t} + \frac{2\pi}{T_r}\frac{\partial N_{i,j}}{\partial \theta} - \frac{K}{r^2}\frac{\partial^2 N_{i,j}}{\partial \theta^2} = \text{population dynamics} \qquad (12.115)$$

where $i = 1$ to 13 for all developmental stages, K is the horizontal coefficient of eddy diffusivity, r is the radial distance from the center of the bank, and θ is the angular coordinate.

The equation can be solved analytically without biological terms, but the addition of the biological term (see Continuous-time structured population methods, section 12.4.2) makes the analytical solution intractable, and a numerical solution of the complete biological–physical model was required. Advection and diffusion were approximated as centered difference terms and were solved numerically using the improved Euler method.

Recent progress has been made in the representation of the physical part of Davis's (1984b) model. Lewis *et al.* (1994) investigated the role of wind variability on the dispersion of a copepod population, using an advanced 3-D physical model of Georges Bank without tides. Currently the simulations presented by Lynch *et al.* (1998) are probably the most sophisticated example of the dispersion and dynamics of a zooplankton population in a site-specific study (Georges Bank). Equation 12.110 was reduced to the horizontal dimension making assumptions about the vertical distribution of organisms. Fluid velocities in the horizontal plane were derived from a hydrodynamical model (Lynch *et al.* 1996). The transport equations were solved using a Galerkin method (Sewell 1988). The population dynamics were represented by a stage- and age-structured population dynamics model similar to the model presented by Davis (1984a; see page 600 for details) with biological parameters relevant for *Calanus finmarchicus*. Lynch *et al.*'s (1998) model results gave a credible scenario for the initiation of the spring *Calanus* bloom by simulating the emergence of copepodites at the right time and place in comparison to observations.

12.6.5 Spatial distribution of zooplankton in ecosystem models coupled with ADREs

Physical–biological models of various levels of sophistication have been developed recently for different regions of the ocean. An overview of many marine interdisciplinary models is given in Wroblewski and Hofmann (1989), Hofmann (1993) and Hofmann and Lascara (1998).

Biological models were configured first as compartmental ecosystem models in an upper ocean mixed-layer (e.g. Fasham *et al.* 1990). Zooplankton can be represented by one variable (as in NPZ models) or more (e.g. by distinguishing mesozooplankton and microzooplankton). In this second case, the model generally takes into account several size classes of phytoplankton. This class of ecosystem model has been coupled to one-dimensional physical models (McGillicuddy *et al.* 1995a; Prunet *et al.* 1996a, 1996b; Oguz *et al.* 1996), and embedded into two-dimensional (Klein and Steele 1985) and three-dimensional circulation models (Fasham *et al.* 1993; Sarmiento *et al.* 1993; McGillicuddy *et al.* 1995b; Moisan *et al.* 1996; Levy *et al.* 1998).

As emphasized by Spitz *et al.* (1998), one of the difficulties with these models is obtaining an estimate of parameters. A systematic and non-subjective technique of adjusting the model parameters consists of using observations in conjunction with a data assimilation technique (Armstrong *et al.* 1995; Matear 1995; Lawson *et al.* 1995, 1996; Prunet *et al.* 1996b). A second difficulty is the presentation and interpretation of results. Ecosystem models are complex, and when biological effects are combined with physical effects in a 3-D environment, a large amount of information is produced. This information results from non-trivial interactions and dynamics, and there is much scope for developing innovative ways to summarize or integrate this information into a meaningful form.

12.6.6 Further reading

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