See also

Arctic Basin Circulation. Current Systems in the Southern Ocean. Langmuir Circulation and Instability. Marine Mammal Migrations and Movement Patterns. Marine Mammal Overview. Marine Mammals, History of Exploitation. Okhotsk Sea Circulation. Open Ocean Convection. Satellite Passive Microwave Measurements of Sea Ice. Satellite Remote Sensing SAR. Sea Ice: Overview; Variations in Extent and Thickness. Sub Ice-shelf Circulation and Processes. Surface, Gravity and Capillary Waves. Weddell Sea Circulation.

Further Reading

Comiso JC and Gordon AL (1998) Interannual variability in summer sea ice minimum, coastal polynyas and bottom water formation in the Weddell Sea. In: Jeffries MO (ed.) *Antarctic Sea Ice, Physical Processes, Interactions and Variability*. Antarctic Research Series 74, pp. 293–315. Washington, DC: American Geophysical Union.

Gordon AL and Comiso JC (1988) Polynyas in the Southern Ocean. *Scientific American* 256(6): 90–97.

Martin S, Steffen K, Comiso JC *et al.* (1992) Microwave remote sensing of polynyas. In: Carsey F (ed.) *Microwave Remote Sensing of Sea Ice*. Geophysical Monograph 68, pp. 303–312. Washington, DC: American Geophysical Union.

Overland JE, Curtin TB and Smith WO (eds) (1995) Special Section: Leads and Polynyas. *Journal of Geophysical Research* 100: 4267–4843.

Smith SD, Muench RD and Pease CH (1990) Polynyas and leads: an overview of physical processes and environment. *Journal of Geophysical Research* 95 (C6): 9461–9479.

Stirling I (1997) The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems* 10: 9–21.

POPULATION DYNAMICS MODELS

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doi:10.1006/rwos.2001.0409

Introduction

The general purpose of population models of plankton species is to describe and eventually to predict the changes in abundance, distribution, and production of targeted populations under forcing of the abiotic environment, food conditions, and predation. Computer-based approaches in plankton ecology were introduced during the 1970s with the application of population models to investigate large-scale population phenomena by the use of mathematical models.

Today, virtually every major scientific research project of population ecology has a modeling component. Population models are built for three main objectives: (1) 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 that regulate their variability; (2) to estimate the flow of energy and matter through a given population; and (3) to study different aspects of behavioral ecology. The study of internal properties of a population, like the various effects of individual variability, and the study of interactions between populations and successions of population are also topics related to population models. The field of biological modeling has diversified and, at present, complex mathematical approaches such as neural networks, genetic algorithms, and dynamical optimization are coming into use, along with the application of supercomputers. However, the use of models in marine research should always be accompanied by extensive field data and laboratory experiments, for initialization, verification or falsification, or continuous updating.

Approach for Modelling Plankton Populations

Population Structure and Units

A population is defined as a group of living organisms all of one species restricted to a given area and with limited exchanges of individuals from other populations. The first step in building a population model is to identify state variables (components of the population) and to describe the interactions between these state variables and external variables of the system and among the components themselves. The components of a population can be (1) the entire population (one component); (2) groups of individuals identified by a certain state: developmental stages, weight or size classes, age classes (fixed numbers of components); or (3) all individuals (varying numbers of components).

The usual unit in population dynamics models is the number of individuals per volume of water, but the population biomass can also be used (in g biomass or carbon (C) or nitrogen (N)). When all individuals or groups of individuals are represented, the individual weight can be considered as a state variable. The forcing variables influencing the population dynamics are biological factors, mainly nutrients and predators, and physical factors, mainly temperature, light, advection, and diffusion.

Individual and Demographic Processes

Population models usually work with four major processes: individual growth, development, reproduction, and mortality. Growth is computed by the rate of individual weight change. Development is represented by the change of states (phases in phytoplankton and protozoan cell division, developmental stages in zooplankton) through which each individual progresses to reach maturity. Reproduction is represented by the production of new individuals. Mortality induces loss of individuals, and can be divided in two components: natural physiological mortality (due, for instance, to starvation) and mortality due to predation. Combination of the four processes permits one to stimulate (1) increase in terms of number of individuals in the population, (2) the body growth of these individuals, and (3) by combination of the two previously simulated values, the increase in total biomass of the population (which is usually termed ‘population growth’).

Plankton Characteristics

Essential information to be built into models of plankton organisms are (1) the individual life duration (a few hours for bacteria; one to a few days for phytoplankton and unicellular animals; several weeks to years for zooplankton and ichthyoplankton organisms); (2) the range of change in size or weight between the beginning and the end of a life cycle; and (3) the number of individuals produced by a mother individual (from two individuals up to thousands of individuals). When developmental stages in the life cycle are identified, the stage durations are needed.

The observation time step has to be defined to adequately follow the timescale of the chosen variables, and thus should be smaller than the duration of the shortest phases.

Plankton Population Models

The most modeled component in marine planktonic ecosystems is phytoplankton production. Most of the phytoplankton models simulate the growth of phytoplankton as a whole, using only the process of photosynthesis. Few models deal with phytoplankton population growth dynamics at the species level. Existing models of other unicellular plankton organisms (bacterioplankton, species of microzooplankton) usually treat them as a single unit, except for a few models simulating phytoplankton and microbial cell cycles. In contrast, mesozooplanktonic organisms, including the planktonic larval stages of benthic species (meroplankton), and fish that have complex life cycles are extensively modeled at the population level.

Dynamics of Single Species

Population Models Described by the Total Density

When a population is observed at timescales much larger than the individual life span, and on a large number of generations, models with one variable (the total number of individuals or the total biomass in that population) are the simplest. These models postulate that the rate of change of the population number, N, is proportional to N (eqn [1], where r is the difference between birth and death rates).

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN \qquad [1]$$

The logistic equation (eqn [2]) represents limitation due to the resources or space (see **Figure 1**).

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) \qquad [2]$$

where K is the carrying capacity.

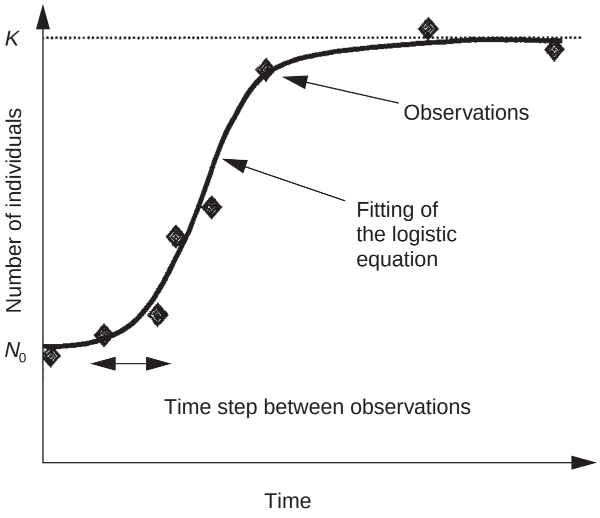

Figure 1 The growth of a plankton population with density regulation and its fitting by the logistic equation.

Population growth of bacteria, phytoplankton, or microzooplankton can be simulated adequately by the logistic equation. With addition of a time delay term into the logistic equation, oscillations of the population can be represented.

Population Models of Organisms with Description of the Life Cycle

If observations of a population are made with a time step shorter than the life cycle duration (**Figure 2**), the population development pattern is a succession of periods with decreasing abundance of individuals due to mortality, and increasing abundance due to recruitment of new individuals in periods of reproduction (cell division or egg production). Recruitment is defined as the input flux of individuals in a given state (stage, size class, etc.).

To represent such patterns, it is necessary to identify different phases in the life cycle, based on age, size, developmental stages, and so on. Two types of models can be developed:

- Structured population models, which consider the flux of individuals through different classes
- Individual-based models, which simulate birth, growth and development through stages and death of each individual

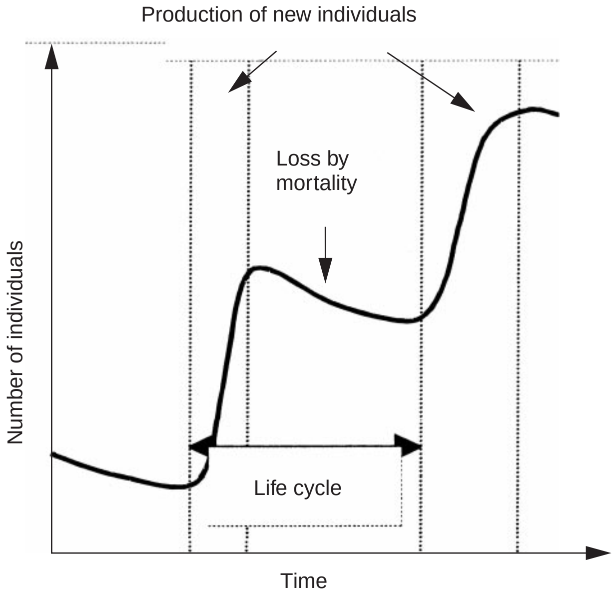

Figure 2 Total population abundance in controlled conditions. The population is initiated with newborn individuals, and decreases, first owing to mortality, until the maturation period, when a new generation is produced. At the end of the recruitment period of new individuals of second generation, the total abundance decreases, again owing to mortality. Owing to individual variability in development, loss of synchronism in population induces a broader recruitment period for the third generation. In nonlimiting food conditions, recruitment of new individuals is continued after few generations. The three generations correspond to the exponential phase presented in **Figure 1** (i.e., without density regulation).

The major distinction between physiologically structured population models and individual-based models in a stricter sense is that individual-based models track the fate of all individuals separately over time, while physiologically structured population models follow the density of individuals of a specific type (age or size classes, stages). These models are particularly used for representing the complex life cycles of zooplankton and ichthyoplankton, but have also been useful for studying the population growth of bacteria, phytoplankton, and microzooplankton, particularly division synchrony in controlled conditions (chemostat).

Structured Population Models

A population can be structured with respect to age (age-structured population models), stage (stage-structured population models), or size or weight (size or weight-structured population models). Two types of equations systems are usually used: matrix models, which are discrete-time difference equation models, and continuous-time structured population models.

Matrix models constitute a class of population models that incorporate some degree of individual variability. Matrix models 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.

The Leslie matrix is the simplest type of age-structured dynamic considering discrete classes. Suppose there are m age classes numbered 1, 2, …, 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 eqn [3] applies.

$$N_{j+1,t+1} = G_j N_{j,t} \qquad [3]$$

Individuals of the first age class are produced by mature individuals from older age classes and eqn [4] applies, where F_j is the number of age class

1 individuals produced per age class i individual during the time step τ.

$$N_{1,t+1} = \sum_{j=1}^{m} F_j N_{j,t} \qquad [4]$$

The system of eqns [3] and [4] can be written in matrix form (eqn [5]).

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{bmatrix}(t+1) = \begin{bmatrix} 0 & F_2 & F_3 & \dots & F_m \\ G_1 & 0 & 0 & \dots & 0 \\ 0 & G_2 & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & \dots & \vdots \\ 0 & 0 & & G_{m-1} & 0 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{bmatrix}(t) \qquad [5]$$

The Leslie matrix can easily be 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.

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

The earlier type of continuous-time structured model is usually referred to as the McKendrick–von Foerster equation, and uses the age distribution on a continuous-time basis in partial differential equations. This type of model has been developed to the extent that it can be used to describe population dynamics in fluctuating environments. In addition, it also applies 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 is eqn [6], where n is abundance of individuals of age a and mass m at time t.

$$\frac{\partial n(a,w,t)}{\partial t} + \frac{\partial n(a,w,t)}{\partial a} + \frac{\partial g(a,w,t)n(a,w,t)}{\partial w} = -\mu(a,w,t)\,n(a,w,t) \qquad [6]$$

where $\mu(a, w, t)$ is the death rate of the population of age a, weight w at time t.

The von Foerster equation describes population processes in terms of continuous age and time (age-structured models) according to eqn [7].

$$\frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} = -\mu(a,t)\,n(a,t) \qquad [7]$$

The equation has both an initial age structure φ at $t = 0$ (eqn [8]) and a boundary condition of egg production at $a = 0$ (eqn [9]).

$$n(a,0) = \varphi_0(a) \qquad [8]$$

$$n(0,t) = \int_0^{\infty} F(a, S_{\mathrm{R}})\,n(a,t)\,\mathrm{d}a \qquad [9]$$

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.

The same type of equation as [7] can be used where the age is replaced by the weight (weight-structured models (eqn [10]).

$$\frac{\partial n(w,t)}{\partial t} + \frac{\partial g(w,T,P)n(w,t)}{\partial w} = -\mu(w,t)\,n(w,t) \qquad [10]$$

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 $t = 0$ (eqn [11]) and a boundary condition of egg production at $w = w_0$ (eqn [12]).

$$n(w,0) = \varphi_0(w) \qquad [11]$$

$$N(0,t) = \int_0^{\infty} F(w, S_{\mathrm{R}})\,n(w,t)\,\mathrm{d}w \qquad [12]$$

F is the fecundity function, which depends on weight (w) and the sex ratio of the population S_{R}.

The numerical realization of this equation 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 eqn [13], where $\mu_i(t)$ replaces $\mu(w_i,t)$

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \left[\frac{g_{i-1}}{\Delta w_{i-1}}\right]N_{i-1} - \left[\frac{g_i}{\Delta w_i}\right]N_i - \mu_i N_i \qquad [13]$$

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 dynamic of the weight class covering the range Δw_1 is described by eqn [14].

$$\frac{dN_1}{dt} = R - \left[\frac{g_1}{\Delta w_1}\right]N_1 - \mu_1 N_1 \qquad [14]$$

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 eqn [15].

$$\frac{dN_Q}{dt} = \left[\frac{g_{Q-1}}{\Delta w_{Q-1}}\right]N_{Q-1} - \mu_Q N_Q \qquad [15]$$

The rate of recruitment of newborns to the population is given by eqn [16] where $\beta(t)$ represents the per capita fecundity of an average adult at time t.

$$R(t) = \beta(t)N_Q(t) \qquad [16]$$

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.

Stage-structured Population Models

Plankton 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 term of developmental stage, using ordinary differential equations (ODEs).

A single ODE can be used to model each development stage or group of stages: for instance, a copepod population can be subdivided into four groups: eggs, nauplii, copepodites, and adults. The equation system is eqns [17]–[20], where R is recruitment, α is the transfer rate to next stage, and μ is the mortality rate.

$$\text{Eggs} \quad \frac{dN_1}{dt} = R - \alpha_1 N_1 - \mu_1 N_1 \qquad [17]$$

$$\text{Nauplii} \quad \frac{dN_2}{dt} = \alpha_1 N_1 - \alpha_2 N_2 - \mu_2 N_2 \qquad [18]$$

$$\text{Copepodids} \quad \frac{dN_3}{dt} = \alpha_2 N_2 - \alpha_3 N_3 - \mu_3 N_3 \qquad [19]$$

$$\text{adults} \quad \frac{dN_4}{dt} = \alpha_3 N_3 - \mu_4 N_4 \qquad [20]$$

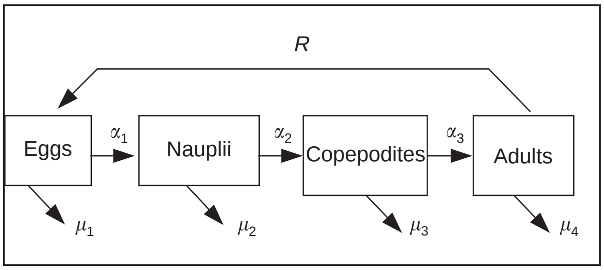

Figure 3 Schematic representation of the population dynamics mathematically represented by eqns [17]–[20]. α_i = transfer rate of stage i to stage $i + 1$; μ_i = mortality rate in stage i; R = recruitment: number of eggs produced by females per day.

The system of ODEs is solved by Euler or Runge–Kutta numerical integration methods, usually with a short time step (approximately 1 hour).

In the model presented in **Figure 3**, the transfer rate of animals from stage to stage and the mortality at each stage are expressed as simple linear functions, which induce a rapidly stable stage distribution. To represent the delay of growth within a stage, more refined models consider age-classes within each stage, or systems of delay differential equations. They have a high degree of similarity with observed cohort development in mesocosms or closed areas (**Figure 4**).

Individual-based Models of a Population

Individual-based models (IBMs) describe population dynamics by simulating the birth, development, and eventual death of a large number of individuals in the population. IBMs have been developed for phytoplankton, zooplankton, meroplanktonic larvae, and early life history of fish populations. Object-oriented programming (OOP) and cellular automata techniques have been applied to IBMs.

As powerful computers become more accessible, numerous IBMs of plankton populations have been developed, mainly to couple them with 1D-mixed layer models (phyto- and zooplankton) and circulation models (zooplankton).

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 (age, size, weight, nutrient or reserve pool, etc.). These variables may be grouped together in some data structure that represents a single individual, or they may be collected into arrays (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

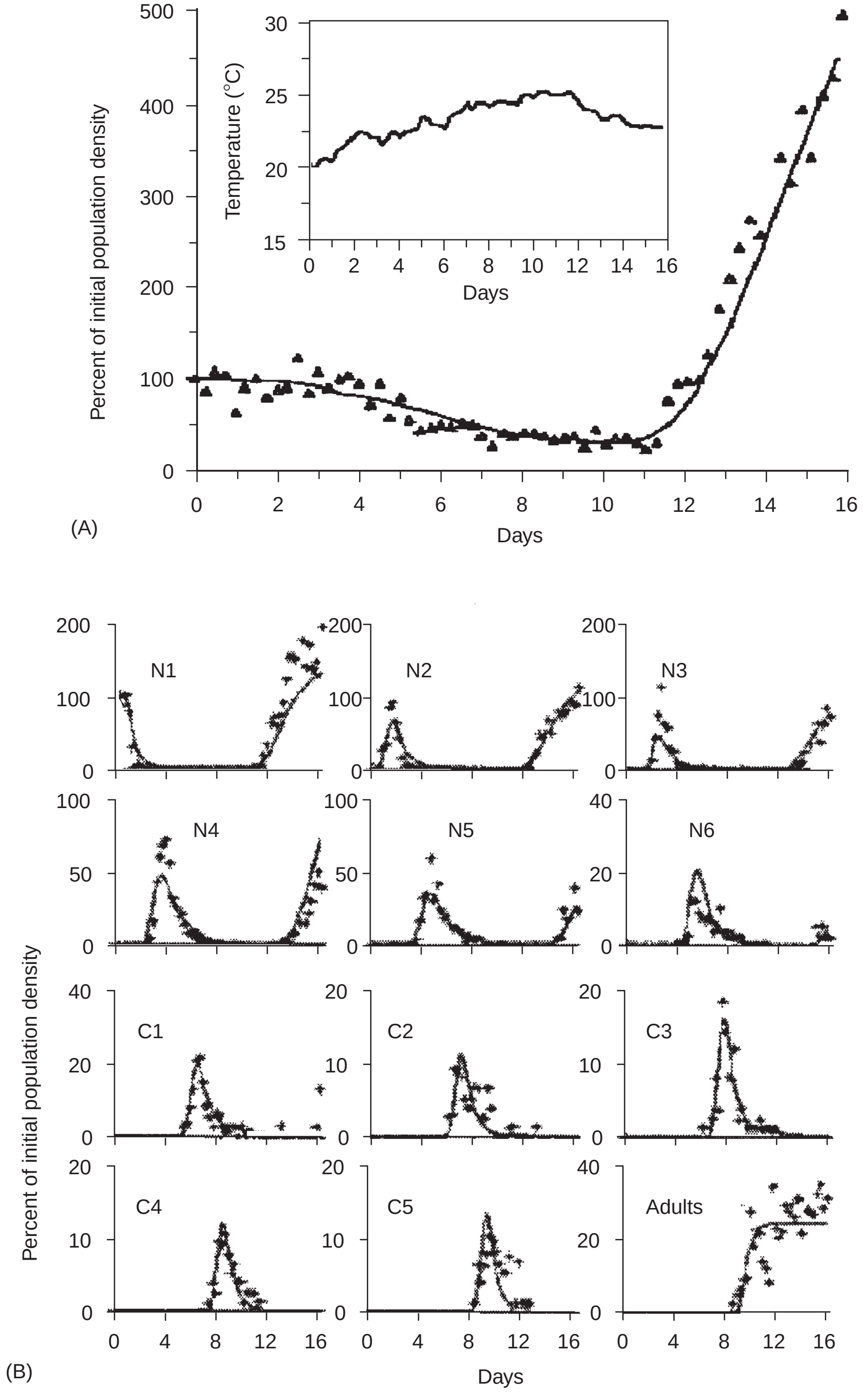

Figure 4 Simulation of the cohort development of the copepod *Euterpina acutifrons* in mesocosms with a structured stage and age-within-stage model. (A) Total population during development, with variable temperature and constant food supply (points = experimental data; line = simulation). The initial density decreases owing to mortality and then increases to newborn individuals (as the first part in **Figure 2**). (B) Naupliar stages (N1 to N6), copepodite stages (C1 to C5), and adults during development (points = experimental data; line = simulation). The simulation start with similar N1 of same age. Reproduced from Carlotti F and Sciandra A, 1989. Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) coupling individual growth and larval development. *Mar. Ecol. Prog. Ser.*, 56, 3, 225–242.

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 eqn [21].

$$X_{i,j}(t) = X_{i,j}(t - \mathrm{d}t) + f(X_{1,j}(t - \mathrm{d}t), \ldots, X_{i,j}(t - \mathrm{d}t)) \qquad [21]$$

$X_{i,j}(t)$ 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. When the fate of all individuals during the time-step $\mathrm{d}t$ has been calculated, the changes to the environment under the effects of individuals can be updated. Any stochastic process can be added to eqn [21].

This type of model can add a lot of detail in the representation of physiological functions. Individual growth can be calculated as assimilation less metabolic loss, and the interindividual variation in physiology can be represented by adding stochastic processes or parameters describing the characteristics of each individual (growth and development parameters, mortality coefficient, and parameters connected with reproduction). The end results are unique life histories, which when considered as a whole give rise to growth/size distributions that provide a measure of the state of the population.

Calibration of Parameters

Parametrization of a model can range from very simplistic to extremely complex depending upon the amount of information known about the population under consideration. Bioenergetic processes (ingestion, egestion, excretion, respiration, and egg production) are usually modeled from experimental results, whereas biometrics (size, weight, …) and demographic (development rate, mortality rate, …) parameters are estimated by combining data from life tables collected in the field or from laboratory studies.

To solve for the unknown parameters, new techniques have been developed such as inverse methods and data assimilation by fitting simulations to data.

Spatial Distribution of Single Plankton Populations

An important development in plankton population modeling is to make full use of the increased power of computers to simulate the dynamics of plankton (communities or populations) in site-specific situations by coupling biological and transport models, giving high degrees of realism for interpreting plankton population growth, transport, spatial distribution, dispersion, and patchiness. Structured population models and individual-based models allow detailed simulations of zooplankton populations in different environmental conditions. Physical–biological models of various levels of sophistication have been developed for different regions of the ocean.

Spatial Plankton Dynamics with Advection–Diffusion–Reaction Equations

Equation [22] is the general physical–biological model equation used to describe the interaction between physical mixing and biology.

$$\frac{\partial C}{\partial t} + \nabla \cdot (v_{\mathrm{a}} C) - \nabla \cdot (K \nabla C) = \text{‘biological terms’} \qquad [22]$$

$C(x, y, z, t)$ is the concentration of the biological variable, which is a functional group (phytoplankton, microzooplankton, or zooplankton), a species or a developmental stage, or a size class (in which case the number of equations would equal the number of stages or size classes) at position x, y, z at time t. The concentration can be expressed as numbers of organisms or biomass of organisms per unit volume. $v_{\mathrm{a}}\,(u_{\mathrm{a}}, v_{\mathrm{a}}, w_{\mathrm{a}})$ represents the advective fluid velocities in x, y, z directions. $K_{\mathrm{x}}, K_{\mathrm{y}}, K_{\mathrm{z}}$ 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 eqn [22], 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 eqn [22] 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 (the concentration of a cohort) to detailed population dynamics. Physical–biological models of various levels of sophistication have been developed recently for different regions of the ocean.

Biological models can be configured as compartmental ecosystem models in an upper-ocean mixed layer, where phyto-, microzoo-, and mesozooplankton are represented by one variable. In extended cases, the model takes into account several size classes of phyto-, microzoo-, and zooplankton. Such types of ecosystem model have been coupled to one-dimensional physical, and embedded into two-dimensional and three-dimensional circulation.

Studies of plankton population distribution in regions where plankton may be aggregated (e.g., upwelling and downwelling regions, Langmuir circulations, eddies) can be undertaken with populations described by equations of the McKendrick–von Foester type coupled with 2D or 3D hydrodynamical models.

In 1982, Wroblewski presented a clear example with a stage-structured population model of *Calanus marshallae*, a copepod species, embedded in a circulation system simulating the upwelling off the Oregon coast. Simulations of the dynamics 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 [23], where w_{bi} is the vertical swimming speed of the ith stage, assumed to be a sinusoidal function of time: $w_{bi} = w_{si}\sin(2\pi t)$, with w_{si} the maximum vertical migration speed of the ith stage.

$$\frac{\partial C_i(x,z,t)}{\partial t} + \frac{\partial\,[u_a(x,z,t)C_i(x,z,t)]}{\partial x} + \frac{\partial[w_a(x,z,t)C_i(x,z,t)]}{\partial z} - \frac{\partial}{\partial x}\left[K(x,t)\frac{\partial C_i(x,z,t)}{\partial x}\right] - \frac{\partial}{\partial z}\left[K(z,t)\frac{\partial C_i(x,z,t)}{\partial z}\right] = \text{population dynamics} + \frac{\partial[w_{bi}(x,z,t)C_i(x,z,t)]}{\partial z} \quad [23]$$

The population dynamics model was presented in eqns [17]–[20].

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 (**Figure 5**).

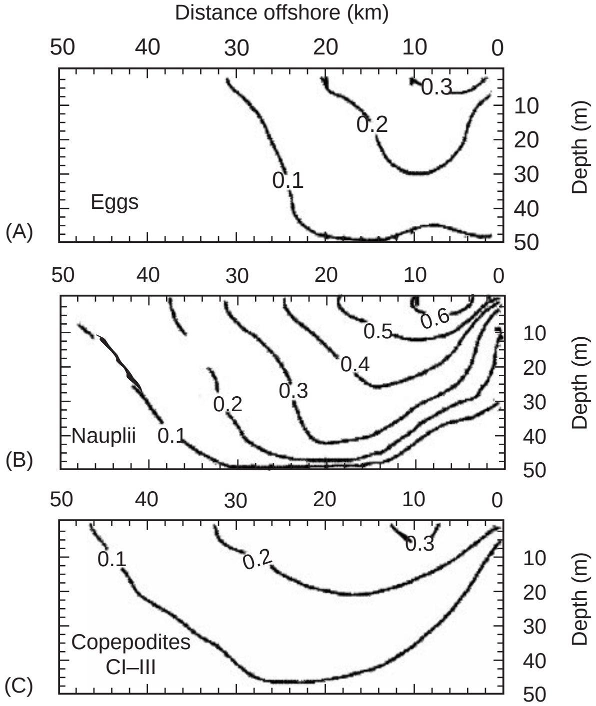

Figure 5 Model of *Calanus marshallae* in the Oregon upwelling zone. The figure shows the simulated zonal distribution of (A) eggs, (B) nauplii, and (C) early copepodites at noon on 15 August. Concentrations of each stage are expressed as a fraction of the total population (all stages m^{-3}). (Reproduced with permission from Wroblewski JS, 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. *Deep Sea Research* 29: 665–686.

Coupling IBMs and Spatially Explicit Models

Individual-based models are more and more frequently used to assess the influence of space on the population dynamics, namely on the time course of population abundances and the pattern formation of populations in their habitats. This approach uses simulated currents from sophisticated 3D 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. 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 provide the velocity vector $\mathbf{v} = (u, v, w)$ as a function of location $\mathbf{x} = (x, y, z)$ and time t, and the particle trajectories are obtained from the integration of eqn [24].

$$\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{v}(x, y, z, t) \qquad [24]$$

The simplest model of dispersion is a random walk model in which individuals move along a line from the same starting position. These trajectories could be modified by turbulent dispersion as described in the section below. Once the larval/particle position is known, additional local physical variables can be estimated along the particle's path: e.g., temperature, turbulence, light, etc., and input to the IBM. The physical quantities are then included in biological (physiological or behavioural) formulations of IBMs (see below).

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.

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's development and growth. The simulated plankton distributions from these models tend to compare better with observed distributions than do models that use passive particles. Sensitivity studies show that behavior is an important factor in determining larval transport and/or retention.

The coupling of IBMs of zooplankton and fish populations and 3D circulation models is a recent field of study, even for fish models. Generally, models that describe the spatial heterogeneity of the habitat have been designed to answer questions about the spatial and temporal distribution of a population rather than questions about the numbers and characteristics of surviving individuals. They 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.

Modeling Behavioral Mechanisms, Aggregation and Schooling, and Patches

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. The Lagrangian approach can take into account the behavior of individual organisms and the effects of the physical environment upon them. Although Eulerian approaches are mathematically tractable, the methods do not explicitly address the density dependence of aggregating individual behavior within a patch.

Dynamic optimization allows descriptions of the internal state of individuals, which may lead to both variable and fluctuating motivations among individuals over short time periods.

Interactions between Populations

Models with Plankton Populations in Interaction

Simple models of two species interactions take the form of eqns [25] and [26].

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 - k_1 N_1 N_2 \qquad [25]$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 - k_2 N_1 N_2 \qquad [26]$$

These population models represent some special experimental situations or typical field situations. Interactions between two species have been rarely treated by population models with description of the life cycle, although structured population models as well as IBM models can represent interactions between species such as predation, parasitism, or even cannibalism.

As an example, Gaedke and Ebenhöh presented in 1991 a study on the interaction between two estuarine species of copepods, *Acartia tonsa* and *Eurytemora affinis*. They first used a simple model based on eqns [25] and [26] including (a) predation (including self-predation of immature stages) by *Acartia* on the two, (b) a term of biomass gain of *Acartia* by this predation, and (c) a density-dependent loss term caused by predation by invertebrates or by 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.

These authors then used two-stage-structured population models with stage-specific interactions (with similar equations to [17]–[20]) allowing the predation of large individuals of *A. tonsa* (copepodites 4 to adults) on nauplii of both species to be represented. The results of this detailed numerical model were compared with results obtained using the simpler model with two variables. The predation on nauplii by *Acartia tonsa* appears to be key factor in the interaction of the two copepod populations.

Food Webs with Population Models

Structured models should be chosen to stimulate the dynamics of several interacting species. The stage-based approach will be acceptable with few species, but quickly become intractable with increasing numbers of species. In this case, a community model based on size structure and using prey–predator size ratio is the alternative approach. There is a continuum of models from detailed size spectrum structure up to large size classes representing functional (trophic) groups in food web models. The detailed size spectrum approach is particularly useful when simulating the predation of a fish cohort on its prey, whereas large functional groups are required for large-scale ecosystem models. Numerous examples include models with size structure of herbivorous zooplankton populations and their prey, and their interactions, in a nutrient–phytoplankton–herbivore–carnivore dynamics model. Size-based plankton model with large entities consider the size range 0.2–2000 μm, picophytoplankton, bacterioplankton, nanophytoplankton, heterotrophic flagellates, phytoplankton, microzooplankton, and mesozooplankton.

See also

Biogeochemical Data Assimilation. Carbon Cycle. Fish Larvae. Fish Migration, Vertical. Fish Predation and Mortality. Gelatinous Zooplankton. Krill. Lagrangian Biological Models. Large Marine Ecosystems. Marine Mesocosms. Microbial Loops. Network Analysis of Food Webs. Nitrogen Cycle. Ocean Gyre Ecosystems. Patch Dynamics. Phosphorus Cycle. Plankton. Polar Ecosystems. Small-scale Patchiness, Models of. Small-scale Physical Processes and Plankton Biology. Upwelling Ecosystems.

Further Reading

Carlotti F, Giske J and Werner F (2000) Modelling zooplankton dynamics. In: Harris RP, Wiebe P, Lenz J, Skjoldal HR and Huntley M (eds) *Zooplankton Methodology Manual*, pp. 571–667. New York: Academic Press.

Caswell H (1989) *Matrix Population Models: Construction, Analysis and Interpretation*. Sunderland, MA: Sinauer Associates.

Coombs S, Harris R, Perry I and Alheit J (1998) *GLOBEC* special issue, vol. 7 (3/4).

DeAngelis DL and Gross LJ (1992) *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems*. New York: Chapman and Hall.

Hofmann EE and Lascara C (1998) Overview of interdisciplinary modeling for marine ecosystems. In: KH Brink and AR Robinson (eds) *The Sea*, vol. 10, Ch. 19, pp. 507–540. New York: Wiley.

Levin SA, Powell TM and Steele JH (1993) *Patch Dynamics*. Lecture Notes in Biomathematics 96. Berlin: Springer-Verlag.

Mangel M and Clark CW (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton, NJ: Princeton University Press.

Nisbet RM and Gurney WSC (1982) *Modelling Fluctuating Populations*. Chichester: Wiley.

Renshaw E (1991) *Modelling Biological Populations in Space and Time*. Cambridge Studies in Mathematical Biology. Cambridge: Cambridge University Press.

Tuljapurkar S and Caswell H (1997) *Structured-population Models in Marine, Terrestrial, and Freshwater Systems*. Population and Community Biology Series 18. New York: Chapman and Hall.

Wood SN and Nisbet RM (1991) *Estimation of Mortality Rates in Stage-structured Populations*. Lecture Notes in Biomathematics 90. Berlin: Springer-Verlag.

Wroblewski JS (1982) Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone – a simulation. *Deep Sea Research* 29: 665–686.

POPULATION GENETICS OF MARINE ORGANISMS

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doi:10.1006/rwos.2001.0298

Introduction

This article provides a brief overview of the principles of population genetics and applications in ocean science. The specialized vocabulary of genetics is defined, and central concepts and approaches are summarized in an abbreviated historical context. Finally, specific topics that have been addressed in the marine biological literature illustrate major areas of application of population genetics in ocean science.

Definitions and Historical Approaches

Population genetics is the branch of genetics that explores the consequences of Mendelian inheritance