

Model of a shrimp population (*Philocheras trispinosus*) I. Simulation of the size structure

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ABSTRACT

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This study describes a stochastic model simulating the kinetics of the size structure of a shrimp population (*Philocheras trispinosus*). The model incorporates relationships which constitute the main functions of the population: growth, mortality and reproduction. The observed and simulated data are compared by multifactorial analysis. Two values are used for the adult mortality. The survival coefficient of the larvae is corrected to stabilise the simulated populations. The kinetics of size structure is followed with a good agreement between the simulations and the observations.

INTRODUCTION

Within the scope of an energetics study of a population, the use of a simulation model of the size structure allows the entry and exit flows to be followed over time. The crustacea, and notably the shrimps, are particularly suitable for this type of model, because there is a large amount of information available on the kinetics of the different stages (larvae, juveniles, females, males), on the size structure of the animals and on the parameters which regulate them (Georges and Grant, 1983; Staples, 1985).

Our simulation focuses on the dynamics of a population of the Caridae shrimp *Philocheras trispinosus* (Crangonidae), which lives in the infralittoral sand zones of the European coasts (Zariquey-Alvarez, 1968; Lagardère, 1971; Labat, 1980). Investigations relating to the role of epibenthic popula-

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tions have displayed how shrimps such as *P. trispinosus* occupy a key position in the food web of shallow soft bottoms (Kuipers and Dapper, 1981; Evans, 1984; Möller et al., 1985). The purposes of this model are, first, to simulate how the structure of the population varies, and second, to describe how energy flow is channeled through this population. The quantitative and qualitative information essential for the simulation of the population dynamics was provided by several studies (Labat, 1984, 1987). Information from similar species, especially *Crangon crangon*, was used in this study when data for the species in question were not available.

PRESENTATION OF THE MODEL

The model uses the individual as the basis of the simulated population. It follows the evolution over time of a theoretical group of animals, essentially as a function of growth, death and reproduction. It is based on an approach developed by Hampton and Majkowski (1985), to follow the evolution of the size structures of fish cohorts.

The future of each individual is followed in relation to its own characteristics: sex, growth parameters, mortality coefficient, and parameters connected with reproduction. The effect of temperature (the driving external variable) on the biological functions is also taken into account.

The succession of several generations is simulated by the recruitment of individuals which have resulted from reproduction by the previous generation, after they have passed through a larval phase, which is considered to be a compartment which the larvae enter when the eggs hatch, and which they leave on reaching adulthood. The duration of the stay in this compartment is dependent on the temperature. Their survival there is assumed to be independent of this duration.

The components and the biological functions of the system representing the population are presented in Fig. 1.

MATHEMATICAL FORMALIZATION OF THE FUNCTIONS OF THE MODEL

Temperature cycle: Function [TEMPERATURE]

The temperature cycle is represented by the function:

$$T(t) = T_{\text{moy}} - DT(\cos(\beta(t - t_{\text{min}})))$$

with $T(t)$ temperature at time t (Julian day): T_{moy} average annual temperature; DT half the range of the temperature variation; t_{min} time of minimum

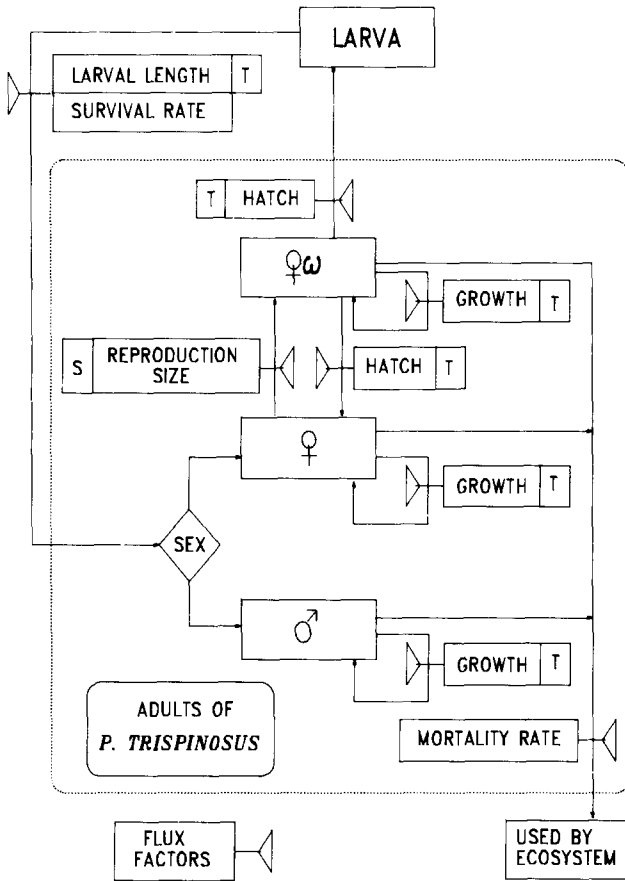


Fig. 1. Components and biological functions of the simulated population. T, temperature influence; S, seasonal influence.

temperature (Julian day): $\beta = 2\pi/365$. An adjustment from data collected over a 3-year period produces the following estimates:

$$T_{\text{moy}} = 15.77$$

$$DT = 5.46$$

$$t_{\text{min}} = 38.33$$

Figure 2A describes the adjusted function.

Sex determination of the recruited animals: Function [SEX]

The shrimp are assumed to be either male or female as soon as they are recruited, with an equal proportion of each sex; this is in accordance with

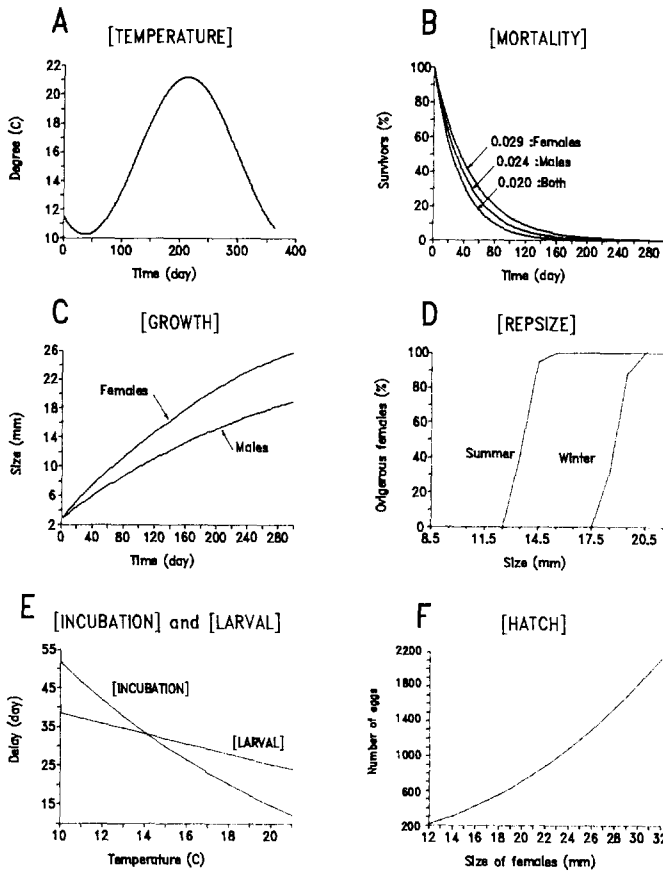


Fig. 2. (A) Simulation of the temperature cycle. (B) Simulation of the mortality. (C) Simulation of the growth. (D) Simulation of the reproduction size. Oviparous females frequency against size. (E) Simulation of the development length of eggs and larval stages as a function of the temperature. (F) Simulation of the eggs number as a function of the female size.

the 'expected sex ratio' (Wenner, 1972), and the results of the determination of the sex of post-larvae of *Crangon crangon*, which all originated from the same spawn (Dalley, 1980):

$$P(\text{male}) = P(\text{female}) = 0.5$$

with $P(\)$ = probability of either sex.

Survival: Function [MORTALITY]

Survival is described by:

$$N_2 = N_1 \exp(-Z(t_1 - t_2))$$

with N_1, N_2 number of animals at times t_1 and t_2 ; Z mortality coefficient. The probability of mortality, PM, over an interval (t_1, t_2) is given by:

$$PM = 1 - \exp(-Z*(t_1 - t_2))$$

When the product $Z(t_1 - t_2)$ is small, PM is only slightly different from this product. This approximation is used in the model in order to simplify the simulations.

The data obtained for the studied species (Labat, 1987), indicate two alternatives for the mortality value: either 0.024 for males and 0.029 for females, or a value of 0.02 for both sexes (Fig. 2B). The former pair of values represents estimates obtained through numerical analysis, and the latter is value-corrected to take into account possible emigration, which would cause an overestimation of the mortality.

Growth: Function [GROWTH]

A function derived from the growth expression proposed by von Bertalanffy (1957) was used, but with the incorporation of a periodic term (Buestel and Laurec, 1975; Cloern and Nichols, 1978). Thus the expression becomes:

$$L(t) = L_{inf} - (L_{inf} - L_{min}) \exp(-K(t - t_0)) - K'/\beta \cos(\beta(t_0 - \theta)) - \cos(\beta(t + \theta))$$

where $L(t)$ is size at time t ; L_{inf} asymptotic size; L_{min} recruitment size (3 mm); K Brody coefficient; K' periodic growth coefficient ($K' \leq K$); $\beta = 2\pi/365$; θ date in Julian days of the highest temperature in the cycle ($\theta = 220$), t_0 time of recruitment.

Due to the individual variability of the coefficients L_{inf} , K and t_0 in the growth equation (Sainsbury, 1980; Fréon, 1984; Hampton and Majkowski, 1985; Rosenberg and Beddington, 1985), each simulated individual was assumed to possess its own parameter set. We assume that the parameters

TABLE 1
Means and standard deviations of the growth parameters (from Labat, 1987)

	Males		Females	
	M	STD	M	STD
L_{inf}	28.236	8.0	32.044	3.0
K	0.00338	0.0005	0.00514	0.0005
t_0	277.71	10.0	280.36	10.0
K'	0.000106		0.000934	

follow a normal distribution law, $N(M, \text{STD})$. In view of the difficulties of the numerical estimation of these parameters (Burr, 1988), their values were obtained by adjustment of the winter cohort data (Labat, 1987) for the mean (M), and empirically from the size range of these cohorts for the standard deviation (STD) (Table 1). The parameter K' (the effect of temperature on growth) is assumed to be constant for individuals of the same sex. Figure 2C represents the growth of males and females.

Determination of the transition of a female to a female bearing eggs: Function [REPSIZE]

The increase with size in the frequency of females bearing eggs indicates that, with growth, more females are able to reproduce and nearly all the females in the larger size range bear eggs. A gamma distribution law, $G(N, B)$, was used to define this relationship. Parameters of the distribution are defined by: Mean = NB , and variance = NB^2 . It represents the probability for a female to bear eggs as a function of her size. This law was chosen because of: (1) the existence of an origin where the probability is equal to 0 (corresponding to the minimum reproductive size); (2) its asymmetric form (when $N = 2$). A biological phenomenon such as reproduction with respect to a given size is well represented by this kind of law.

According to the population cycle, there is one size/reproduction ratio for the winter cohort, and one for the summer. The parameter B and the origins of the two ratios are calculated in such a way that the averages and the standard deviation of the sizes of the females bearing eggs correspond to the observations. The parameter B is equal to 1.79, and the origins are at 17.8 mm (winter) and 12.5 mm (summer). Simulations of the two gamma-distribution functions used one plotter in Fig. 2D.

Duration of incubation of the eggs: Function [INCUBATION]

Only the cumulative duration of the development of the eggs and larvae is known for *P. trispinosus* (Labat, 1984, 1987). To quantify the part concerning only the egg development, *Crangon crangon* data were used. The temperature was assumed to be responsible for the regulation of the duration of this development; a polynomial relationship is used in accordance with Havinga (1930) and Tiews (1970):

$$D_1 = d_1(T^{d_2}) + d_3$$

with D_1 duration in days; T ambient temperature in °C. From the data of

Havinga (1930), Tiews (1954, 1970), and von Meixner (1967), the parameters have been computed as follows (Fig. 2E):

$$d_1 = 730.934$$

$$d_2 = -0.09462$$

$$d_3 = -535.89$$

Number of liberated larvae: Function [HATCH]

The number of larvae introduced into the 'larval compartment' is equal to the number of eggs reaching the end of the incubation period. This is connected to the size of the shrimp by a *power* relationship (Campillo, 1979; Gros, 1979; Boddeke, 1982):

$$NL = n_1 L^{n_2}$$

with NL number of larvae released to the environment; L size in mm of the shrimp bearing eggs. The parameters deduced from the *P. trispinosus* data (Labat, 1987) are (Fig. 2F):

$$n_1 = 0.658$$

$$n_2 = 2.331$$

Duration of larval development: Function [LARVAL]

The duration of larval development allows the delay to be determined, after which a contingent of liberated larvae are going to be recruited by the simulated population, as either males or females. We have assumed a linear function of the temperature.

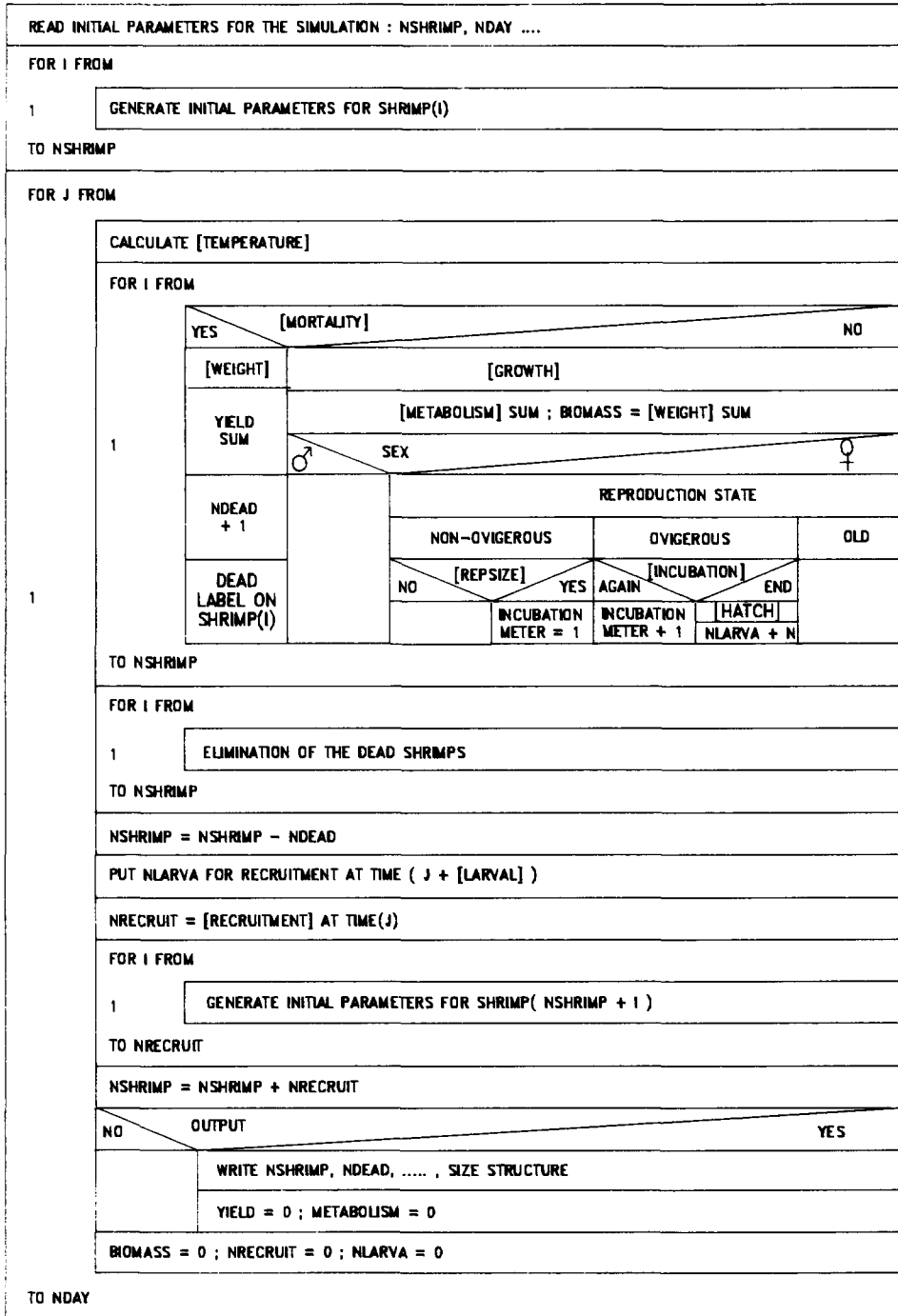
$$DL = l_1 T + l_2$$

with DL the duration of larval development in days; T temperature in °C. There are no data for *P. trispinosus*, so those of *C. crangon* and *C. septemspinosa* were used. From the data of Ehrenbaum (1890), Thorson (1946), Regnault and Costlow (1970), and Dalley (1980) the following parameters were computed (Fig. 2E):

$$l_1 = -1.327$$

$$l_2 = 51.88$$

An estimation of the duration of the egg + larval development observed during the winter period lies between 60 and 100 days, with a probability maximum at 90 days (Labat, 1987). The simulation functions ([INCUBATION])



+ [LARVAL]) produced a value of 80 days with equivalent thermal conditions.

Number of recruited shrimps: Function [RECRUITMENT]

The number of recruited adult shrimps was computed from the number of larvae remaining at the end of the development period [LARVAL], and from the survival coefficient. The latter was adjusted by successive simulations to maintain the relative stability of the population. The linear stock/recruitment relationship used here expresses a density-independent hypothesis, without any compensatory mechanism for recruitment. It assumes the predominance of physical environmental factors over the biological factors (Sissenwine, 1984).

FUNCTIONING OF THE MODEL

The diagram in Fig. 3 describes the algorithm followed by the program, to simulate the kinetics of the size structure of the population.

Initial steps

For the initial time, the cohort recruited in the autumn was simulated. The mean sizes for males and females were computed from the growth function and the parameters of the individual variability chosen as described in function [GROWTH]. From it, the initial characteristics of each original individual (sex, growth parameters, and mortality coefficient) either stemmed from their estimated averages, or were randomly derived from their own probability functions. It is important to ensure that, at the beginning of the simulation ($t = 0$), the recruitment must have ended and that reproduction is not yet started; a date between the 330th and the 360th day of the annual cycle complied with these conditions.

Fig. 3. Algorithm of the simulation model

N SHRIMP	Number of simulated shrimps
N DAYS	Number of simulation days
N DEAD	Number of dead shrimps
N LARVA	Number of larva
N RECRUIT	Number of recruited shrimps
SHRIMP(i)	Ith shrimps
TIME(j)	Jth day
[FUNCTION]	Function of the model (see text).

The simulated number of shrimps has to be sufficient to prevent the disappearance of the population during periods of low density, and also to be not too costly in computation time. We chose 2000 shrimps, a number corresponding to a population found over an area of about 100 m² in reality.

Progress followed by the simulation

After the initial phase, a daily time-step was used in this simulation. The future of each shrimp was envisaged: death [MORTALITY], growth [GROWTH], reproduction [REPSIZE] [HATCH], egg hatching [INCUBATION]. A set of random numbers allowed the timing of the stochastic events (death, reproduction) to be decided. Larvae liberated on a certain day entered the larval compartment; after a delay, which was a function of the temperature [HATCH], they were recruited as adult shrimps, and their number was a function of the larval survival coefficient [RECRUITMENT]. These individual parameters were defined as before, except the initial time, t_0 , of the growth function. This sequence was repeated for each time step, until the end of the simulation. The total duration of the simulation was chosen to allow the evaluation of the temporal evolution of the population: approximately 1000 days were sufficient for two annual cycles to be followed, starting from the first simulated recruitment.

Output from the model

The output from the model is recorded with a prefixed time-step. Basically, its value was determined by counterbalancing the level of accuracy of the process with the number of simulations; 20 days were adequate.

Two types of results were thus produced:

- a histogram of the sizes of the males and/or females
- a summary of the model's parameters (date, temperature, number of individuals living and dead, male and female; female bearing eggs, larvae etc...).

USE OF THE CORRESPONDENCE ANALYSIS TO STUDY AND EVALUATE THE SIMULATION OF THE KINETIC OF THE SIZE STRUCTURES

Correspondence analysis, or the CA (Benzecri et al., 1973), is an ordination method (so-called inertia method) which has been widely used in the analysis of ecological data (Gower, 1987). Its aim is to describe parsimoniously the total variance, or so-called inertia, of a multidimensional data set in a sample of few dimensions (or axes). These few dimensions are the best abstraction of the information contained in the data. Among the inertia

methods, correspondence analysis is concerned with contingency tables and uses a Chi-square metric. Correspondence analysis can be used to describe size structures (Badia and Do-Chi, 1976). Starting from the cloud of samples within the size-classes space, and the cloud of classes in the samples space, this factorial analysis provides the best possible summary of the kinetics of the size structure of a population over time, in a new space of reduced dimensions. Using the Chi-square distance, the CA compares the shape of the strength of the samples and of the size classes.

A sample position will be defined using all the size classes: the closeness is related to the abundance and the distance to the scarcity. Picard (1982) has shown, using the topology in the 1-2 plane of cyclical biological data, how it is possible to demonstrate not only the growth but also the scattering of the observations within the classes.

Growth causes individuals from small size-classes to move into bigger size-classes; the correspondence between the size classes and the sampling dates will be an indicator of this kinetic, and their distances from the center of the cloud will represent the relative scattering of the occurrences within the classes.

This approach allows observed data to be compared with computed or simulated data (Badia and Do-Chi, 1976). In this case, the evolution of observed and simulated size structures in the main factorial plans allows the quality of the method to be appreciated.

SIMULATION EXAMPLES

Several simulations were carried out using the two alternative mortality coefficients. Several values for the larvae survival coefficient were considered, in order to stabilize the population numbers. Two 'stable' simulations are analysed here.

Simulation 1. For this simulation, the daily adult mortality coefficient was 0.02. Several simulations were carried out with different rates of survival for the larval phase. A survival of 0.07 produced a population that was nearly stable during approximately 3 years.

During the simulation, the variations of the computed densities are near to the observed variations (Fig. 4) (Labat, 1984, 1987). A three-dimensional representation of the evolution of the female size structure over time is given in Fig. 5. A large winter reduction in the population, and two periods of recruitment, one in the spring and the other in the autumn, were observed. The second simulated peak was greater than the first. This is due to the faster growth and the smaller size of summer-reproductive females. These characteristics, linked with a constant mortality, resulted in a larger number

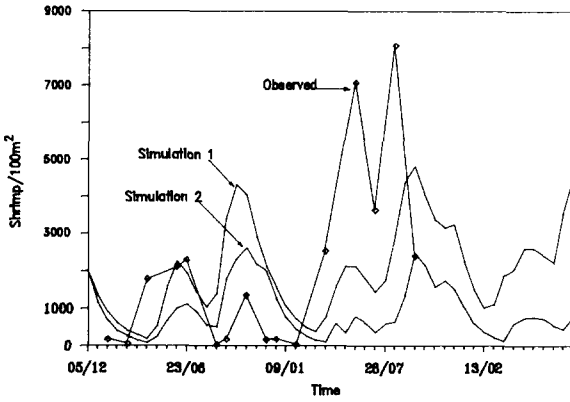


Fig. 4. Development of the simulated strength (simulation 1 and 2) and the observed strength for a standard area of 100 m².

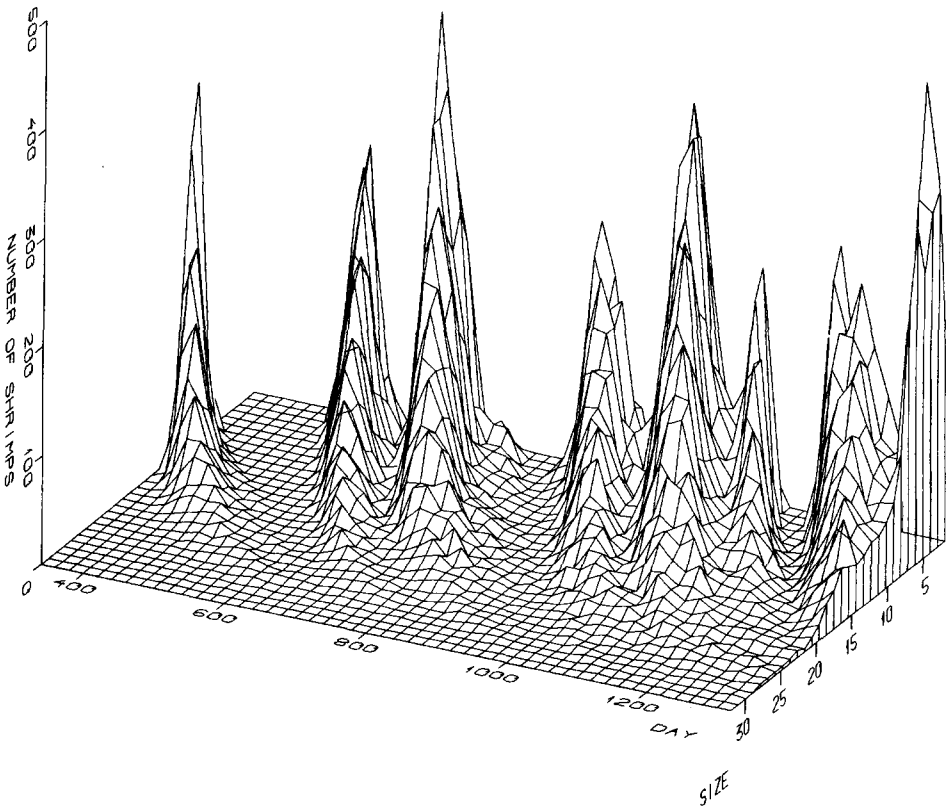


Fig. 5. Tridimensional view of the females size/structures kinetic of the simulation 1. The number of simulated shrimps is plotted against size and time.

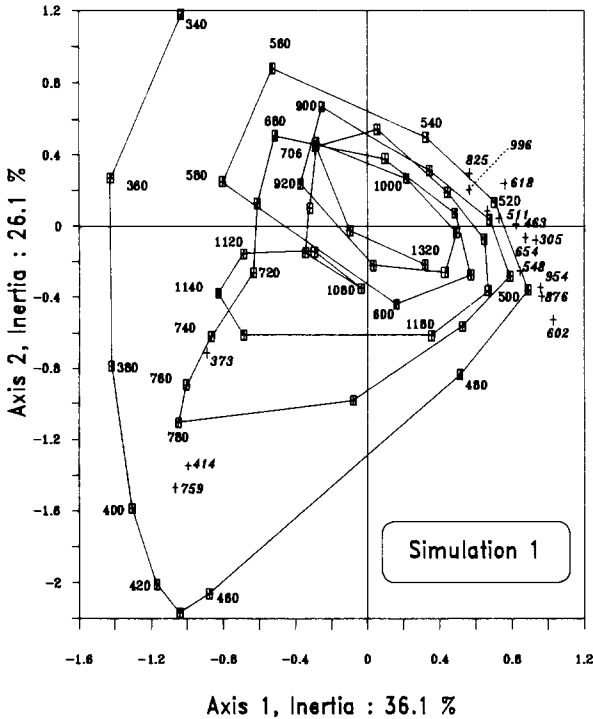


Fig. 6. Simulation 1. View of the 1-2 plane of the Correspondence Analysis applied to size/structures. The observed size/structures are taken as supplementary elements (in italics).

of females bearing eggs, and therefore a larger recruitment. With time, there is a tendency towards an extension of the recruitment peaks; this is particularly evident with the ‘bimodalisation’ of the summer/autumn recruitment.

The evolution of the size structures with time can be studied using a CA. The data table is formed by the number of simulated females per size-class, for each time step (20 days) (Fig. 5). Observed values of size structure (Labat, 1987), are entered as supplementary individuals.

The projections of the dates in the 1-2 factorial plane are represented in Fig. 6. This plane represents 62% of the inertia of the cloud. A good agreement between the kinetics of the simulated and observed structures can be deduced from their topological similarities in the 1-2 plane of the CA, especially in the winter periods. The recruitment periods are characterized by a less accurate agreement; this is due to the rapidly changing aspect of the size structure during these periods. Small time-differences are represented by large modifications in the size structure.

Several observations can be made:

- The sizes follow a continuous cyclical progression; the larger sizes, greater than 22-23 mm, play a less important role.

- The simulations are characterized by a double annual cycle.
- The study of the stability in time of the structure of the simulated population demonstrates a small delay in the first year, which gets blurred in the following years.
- The size dispersion of the population increases during the simulation. This is signified by a progressive closing towards the centre of the cloud, for identical periods of the annual cycle.
- On comparing the topology of the winter and summer cohorts' cycles, there appears to be a greater size dispersion in the summer cohort.

Simulation 2. For this simulation, the adult daily mortality coefficient was 0.024 for the males and 0.029 for the females.

After preliminary trials, the larval development cycle has been extended by 10 days. Because of the parameters from simulation 1 and the mortality values used here, we have witnessed a succession that is too fast for the recruitment. This extension of the cycle corresponds to comparisons made between the observed durations and those simulated from literature data.

The use of several different survival coefficients for the larval stage in the simulations, led to the use of a larval survival figure of 0.24 which resulted in a nearly stable population.

The evolution of the whole population is represented in Fig. 4, and the evolution of the size structures with time in Fig. 7.

The periodicity of the characteristic events, comparable maximums and minimums, is about 1 year. The spring peak in recruitment is less than that at the end of the summer/beginning of autumn. Some size dispersion develops with time. These results are similar to those obtained in the simulation 1, but the final number of shrimps is generally smaller. This last observation is explained by the dual effects of a higher adult mortality, and the necessity for a smaller number of females to reproduce due to the greater larval survival rate.

The stability of the size structure is again evident from the results of a CA on the female size classes. From the topology of the simulation dates on the 1-2 plane of the CA (Fig. 8), a strong compatibility with simulation 1 was demonstrated. This plane represents 57% of the inertia. The decreases of the distance in the centre of the cloud of the cycle dates indicates that the dispersion of sizes is going to increase.

The closeness with the observed size structures is described as before through a projection of the data from supplementary individuals in the 1-2 plane (Fig. 8). The conclusions are again similar to those of simulation 1: a good winter compatibility, and greater variability during the recruitment period. Generally, for the inertia explained by the very similar 1-2 plane (62% and 57%), the average correlation of the observed data (from supple-

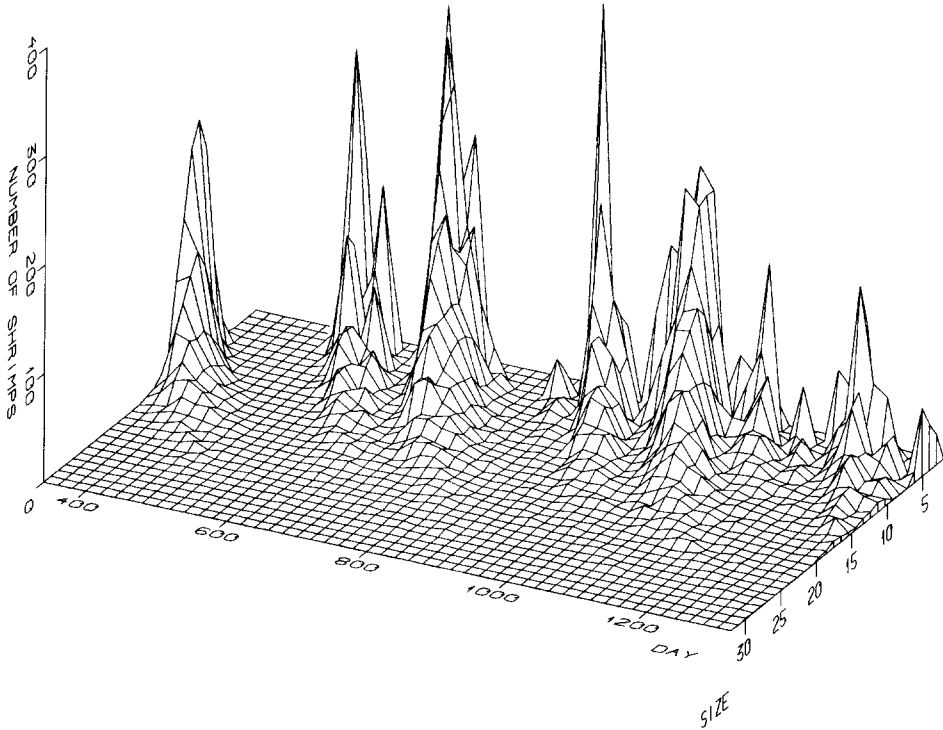


Fig. 7. Tridimensional view of the female size/structures kinetic of the simulation 2. The number of simulated shrimps is plotted against size and time.

mentary individuals) is almost identical for the two simulations: 0.469 for the first and 0.458 for the second.

DISCUSSION

This approach to the simulation of a population's size structure allows complex biological phenomena to be represented: qualitatively, quantitatively, continuously and discontinuously. It takes into account individual variability, which exists for certain biological functions and, at the same time, the differences existing between the sexes at the level of their biological parameters and of their futures. It requires not only an estimate of the parameter's average values, but also their variabilities. These estimates are often difficult to obtain and also to link with non-verifiable distributional hypotheses. It is a tool to observe if an overall likelihood exists of the different biological functions described: mortality, growth and reproduction. However, a good agreement between simulation and observation does not

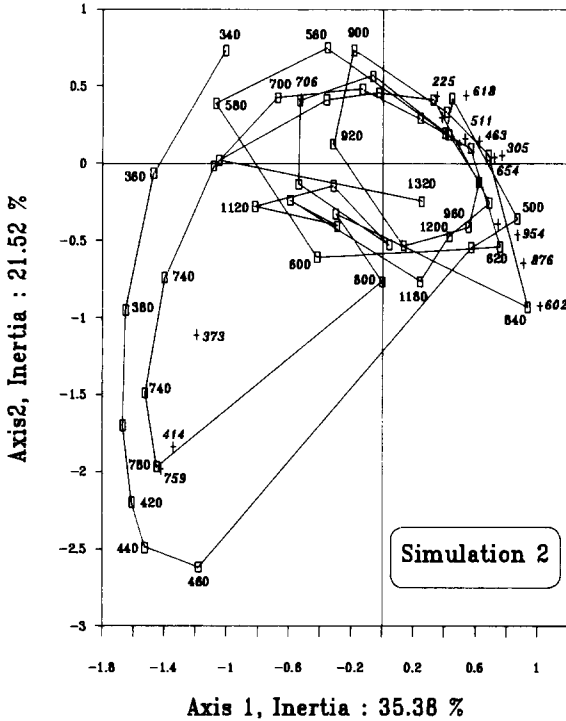


Fig. 8. Simulation 2. View of the 1-2 plane of the Correspondence Analysis applied to the simulated size/structures. The observed size/structures are taken as supplementary elements (in italics).

necessarily imply the validity of the parameters used, as the existence of colinearities leads to multiple solutions.

This model possesses a stochastic character, as the characteristics (growth and sex) and the fate (mortality and reproduction) of each individual are picked at random. However, when the number of simulated shrimps is large, the different states of several simulations at a given time, t , are very close to each other. The repetition several times of the simulation with the same parameters shows that the variation in the simulations is linked to the existence of periods of small population numbers.

Several approximations are made:

- Growth is considered to be continuous. Other formulae could have been used (Mauchline, 1977; Conan and Gundersen, 1979), but, in the population considered here, the short duration of the intermoultings and the asynchronous moultings allow the growth to be considered as continuous.
- The females bear eggs as a function of their size. The number and the size structure of the males play no role in the reproduction.

- The females bearing eggs continue to grow during the period when they carry their eggs. This approximation is necessary due to the assumption that growth is continuous. The error introduced is considered to be small; it results in an overestimate of the number of eggs of less than 10%.
- In the model described here, the females only reproduce once. A simple modification could simulate the ability to reproduce several times, but an estimate of the length of the period between reproductions would then be necessary.

The simulations have shown that the size structure tends to disperse with time. This may reflect the fact that regulating factors within the same cohort, such as mortality or differential growth, were not taken into account.

In this model, an absence of a stock/recruitment regulation causes an instability in the strength over time. Therefore, in the long run a simulation could not be stable in strength.

In conclusion, the simulation approach presented here allows the kinetics of the size structure of a population to be followed with a good agreement between the simulations and the observations. As in all mode approaches, it is necessary to make certain approximations and simplifications. Using these simulations it is possible to simulate the energetic fluxes and the biomass fluctuations; this is carried out by incorporating the functions which represent the essential elements of the energetic balance into the model, as a function of the sex, the individual's size and the temperature.

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