

## Model of a shrimp population (*Philocheras trispinosus*) II. Simulation of the energy fluxes

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(Accepted 21 February 1990)

### ABSTRACT

Labat, J.-Ph., 1991. Model of a shrimp population (*Philocheras trispinosus*). II. Simulation of the energy fluxes. *Ecol. Modelling*, 53: 95–107.

Using a model of the kinetics of the size structure of a shrimp population (*Philocheras trispinosus*), this work attempts to simulate the energy fluxes. It incorporates functions which take into account respiration, excretion, reproduction and energy loss by moulting. It calculates the biomasses and productions. The model describes these fluxes throughout the annual cycle for different values of the mortality coefficient. The simulations show how the evolution of the energy fluxes reflect the evolution of the demographic structure. For the simulated population, the mean of the  $K_2$  coefficient varies between 32 and 37% while the mean of the production/biomass ratio is between 7.19 and 9.01.

### INTRODUCTION

As the size structure of a population can be simulated at any time (Labat, 1991), the energy fluxes and the biomass can be defined from these elements and from the environmental temperature.

After Welch (1968), Crisp (1971), Bouché (1978) and Kerr (1982), the equation for the energetic balance of a crustacea population is written as:

$$A = M_e + E_x + M_u + P_r$$

where  $A$  is the assimilated energy,  $M_e$  the energy used by the general metabolism,  $E_x$  the excreted energy,  $M_u$  the energy contained in the moult, and  $P_r$  the energy contained in the increase in the organic material of the population.

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The general metabolism can be represented by:

$$M_e = M_{es} + M_{esda} + M_{eac}$$

where  $M_{es}$  is the standard metabolism,  $M_{esda}$  is that of the specific dynamic action, and  $M_{eac}$  is that connected with the animal's activity.

The production  $P_r$  is considered to be the total sum of the new body material created within a population in one time unit, whether or not this amount survives until the end of this period. It is production as defined by Ivlev (in Ricker, 1980). At the level of the population biomass, it represents the input.

From the point of view of the exchanges with the environment, 'environmental' production is the quantity of organic material which is lost at any moment by this population (loss of biomass through mortality; Banse and Mosher, 1980). In this case, if the mortality coefficient is constant, the ratio of production to biomass will be equal to this mortality (Allen, 1971; Brey, 1986).

The time-lag between these incoming and outgoing flows represents variations in the biomass stocked by the population.

#### FUNCTIONS AND SUB-ELEMENTS OF THE MODEL

Initially, the complementary functions will be considered which are necessary for the simulation of the biomass and of the fluxes from the size structure.

##### *Calculation of weight: Function [WEIGHT]*

The weight was estimated for each shrimp, as a function of its sex, its reproductive state (for females) and its size, using the relationship established for previous measurements:

$$P = aT^b$$

with  $P$  dry weight in mg, and  $T$  size in mm. The adjusted values of the parameters are the following:

	$a$	$b$
Males	0.01153	2.5176
Females	0.01253	2.5146
Females bearing eggs	0.00155	3.2334

*Metabolism: Function [METABOLISM]*

The metabolism was approached by defining respiration as a function of the weight and the temperature.

A general rule seems to exist in the animal kingdom, which connects respiration to the weight by a power function of the following type (Prosser, 1961; Dejours, 1975):

$$R = aP^b$$

with  $R$  respiration;  $P$  weight.

Biochemical reactions in general, and respiration in particular, are accelerated by temperature within a standard range of values. Several forms of the relationship can be used. In this case a linear function was used, which provides a good adjustment quality for this data set:

$$R = c(T + d)$$

with  $R$  respiration;  $T$  temperature.

The following relationships were used to connect respiration to the weight and to the temperature for each sex:

– For the females:

$$R = 0.20289(P^{0.9424})(T - 8.3301)$$

– For the males:

$$R = 0.13831(P^{0.6479})(T - 4.2594)$$

with  $R$  respiration expressed in  $\mu\text{g O}_2 \text{ h}^{-1}$  per animal;  $P$  weight in mg;  $T$  temperature in  $^{\circ}\text{C}$ .

*Energy equivalence of respiration*

In the experimental conditions used, when the animals were at rest and not fasting, the measurement of respiration corresponded to that of the standard metabolism plus that of the specific activity ( $M_{\text{es}} + M_{\text{esda}}$ ).

The approach for the animals' energy requirements should also take into account the activity of the animal throughout a daily cycle ( $M_{\text{eac}}$ ). Observations made by Sedgwick (1981) showed that the energy requirements of an active shrimp, *Crangon crangon*, were in the order of two times greater than those of the animal at rest. The nutritional rhythm of *Philocheiras trispinosus* indicates that its activity, like that of *Crangon crangon* (Van Donk and De Wilde, 1981), is essentially nocturnal. It therefore appeared that a maximum estimate of the metabolic demands for the animal's daily cycle could be calculated by multiplying the metabolic rate at rest by a factor of 1.5.

The energy equivalent of respiration depends on the kind of assimilated nutrients used at the time of the oxidation reactions. In accordance with Elliott and Davison (1975), the value  $3.2 \text{ cal mg}^{-1} \text{ O}_2$  was used.

These data resulted in the following relationship:

$$M_e = (R \times 3.2 \times 24 \times 1.5) / 1000 \\ = 0.1152R$$

with  $M_e$  total metabolic demand of a daily cycle, expressed in calories per animal per day;  $R$  respiration at rest in  $\mu\text{g O}_2 \text{ h}^{-1}$  per animal. The energy flux represented by excretion ( $E_x$ ), has been related to the function [METABOLISM]. In effect, excretion is the result of oxidation of proteins. The ratio O/N is linked to the type of animal nutrition, and in particular to the size of the protein fraction. The fraction of the excreted energy as a function of the respiratory metabolism can be identified if this ratio is known. From the available data on this species (Labat, 1987) and the comparable data from *Crangon crangon* (Regnault, 1981; Regnault and Lagardère, 1983), the average value for this ratio can be estimated at 35; this represents an excreted energy value in the order of 5% of the respired energy:

$$E_x = 0.05M_e$$

where  $E_x$  and  $M_e$  are the values in calories of the excretion and the metabolism, respectively, over 24 h.

#### *Losses by moulting: Function [MOULT]*

As the simulation of the growth was decided to be of a continuous nature, it was not possible to determine directly the losses connected with moulting. However, by comparison with the literature data for *Crangon crangon*, it was possible to identify the order of size of this element. From the size/growth relationship at the moult, size/duration of the intermoult (Mauchline, 1977), size/weight ratio (Szaniawska, 1980), moult-weight/body-weight ratio [Nelson et al. (1977) with *Macrobrachium rosenbergii*] and the equivalents in calories of the moulting ( $2.50 \text{ cal mg}^{-1}$  dry weight) and of the whole shrimps ( $4.11\text{--}4.20 \text{ cal mg}^{-1}$  dry weight) (Szaniawska, 1980; Evans, 1984), the ratio of the amount of calories lost in the form of moulting to the amount of calories produced by growth was determined. From these data, and from the assumption that *P. trispinosus* follows the same rules during its growth, the ratio 0.2 was used as a rough but realistic estimate:

$$M_u = 0.2P_r$$

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In agreement with Jobling (1983), we have used the thermochemical calorie ( $\text{cal}_{\text{th}}$ ) as the unit of measurement which, even if it is not the official unit, is the most frequently used (1 cal = 4.184 J).

where  $M_u$  was the loss by moulting in calories, and  $P_r$  was the production in calories, as defined by Ivlev. This estimate introduced a slight bias into the simulation, as it did not take into account the variations of this relationship with the size structure of the population.

#### FUNCTIONING OF THE MODEL

At each time step ( $t$ ), the biomass was computed by summing the weight calculated from the size and the sex of each theoretical individual which constituted the population. Such an operation was also carried out for all the individuals that died. The first biomass was that of the living population, the second represented the production of the population for the ecosystem. The equivalence energy/weight used was  $3.81 \text{ cal mg}^{-1}$  (Villiers, 1979).

Two kinds of productions are computed: production as defined by Ivlev, and the environmental production. For the calculation of the production as defined by Ivlev, the formula proposed by Crisp (1971) was used:

$$P_r = (B_1 - B_0) + M$$

where  $B_0$  was the biomass at the beginning,  $B_1$  the biomass after time  $t$ , and  $M$  the total mortality expressed as the sum of the weights of the animals which died during time  $t$ .

The 'environmental production',  $M$ , is the sum of biomass lost through mortality. Simulated productions were calculated for each time-step (1 day) and added up during the time-lag between two outputs of the model.

The losses by moulting were deduced from the production values using [MOULT]. The model computed the energy demand connected to the respiratory metabolism of the population, by summing the demands of each individual using [METABOLISM].

Finally, loss by reproduction (in the form of spawning by the adult population per day) was calculated as a function of the number of eggs reaching hatching and of their calorific value; by analogy with *Crangon crangon*, this value was taken to be 0.053 calories for an egg at the end of development.

Two simulations (1 and 2) were run using two alternative mortality coefficients (see Labat, 1991).

*Energy aspects of Simulation 1.* Figure 1 represents the different components of the energy budget of the population over time, in the form of a cumulative histogram. The cycles are well pronounced. There is an important difference between the lowest (winter) and the highest (summer/autumn) levels:  $4.02$  to  $42.13 \text{ cal m}^{-2} \text{ day}^{-1}$ . The proportion of energy used for growth (production) in relation to the assimilated energy

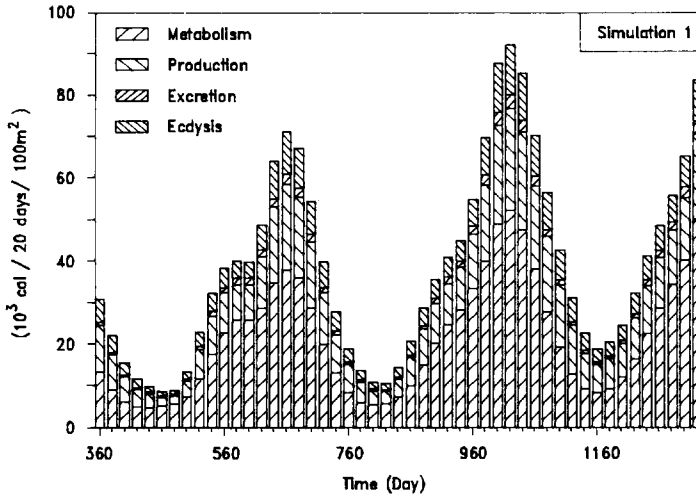


Fig. 1. Energy balance components of the simulated population. Cumulated histograms. Simulation 1.

also varies greatly, as it can be seen in Fig. 2 which shows the evolution of the production/assimilation coefficient ( $K_2$  as defined by Ivlev). The factors responsible for this effect are the increase of production which follows recruitment, and the increase in the proportion of respiratory metabolism which is positively connected to the temperature. The periods of low yield occur mainly during the summer, between the two principal peaks of

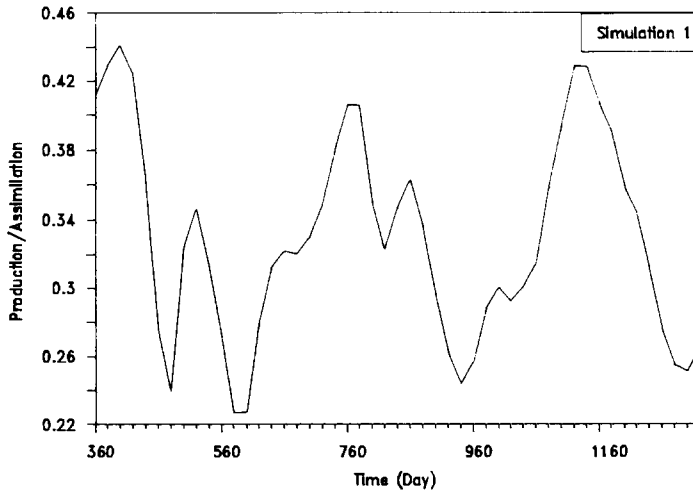


Fig. 2. Production/assimilation ratio. Simulation 1.

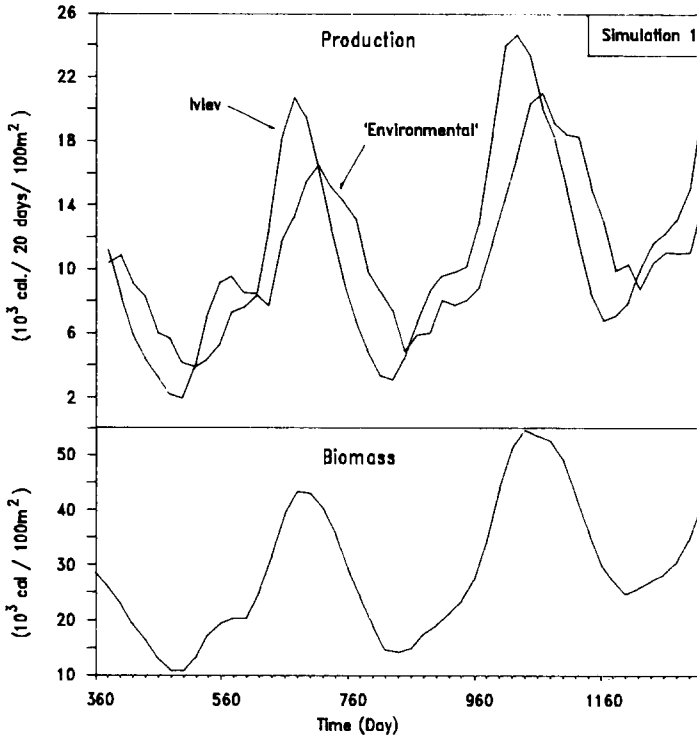


Fig. 3. Production as defined by Ivlev and 'environmental' production and resulting biomass. Simulation 1.

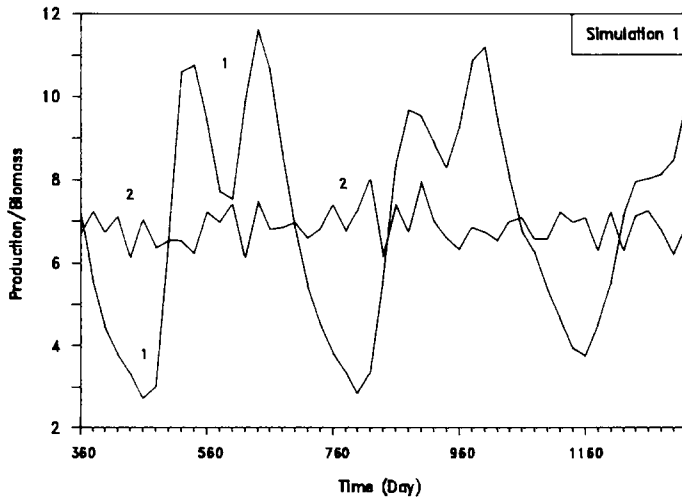


Fig. 4. Production and biomass ratio. 1. Ivlev production. 2. 'Environmental' production. (Productions are extrapolated over a year). Simulation 1.

recruitment and when the temperature is maximum; inversely, the high yields occur at the period when the young individuals with high growth arrive at times when the water is not yet heated up or when it is already sufficiently cooled down.

Estimates of the production as defined by Ivlev, and of the 'environmental' production, are described in Fig. 3. These two fluxes represent the input and the output of the biomass, respectively, which increase or decrease as a function of the sign of their differences (Fig. 3). The variations in the ratio of production (Ivlev) to biomass also reflect the changes in the population structure (Fig. 4): the highest values correspond to the youngest populations (recruitment periods), the lowest to the oldest populations (in order to be comparable to literature values, the production is here extrapolated over a year). The 'environmental' production shows random variations around a constant mean, because it depends on the mortality coefficient, which is expected to be constant.

*Energy aspects of Simulation 2.* The cycles of the different components of the simulated energy balance alternate between high and low production phases. In Fig. 5, the cumulated histograms of the different components of the assimilated energy are shown, while Fig. 6 displays the ratio production/assimilation,  $K_2$ . These phases reflect the evolution of the energy variations of the population as a function of its demographic structure, and of the thermal cycle. The populations composed largely of young

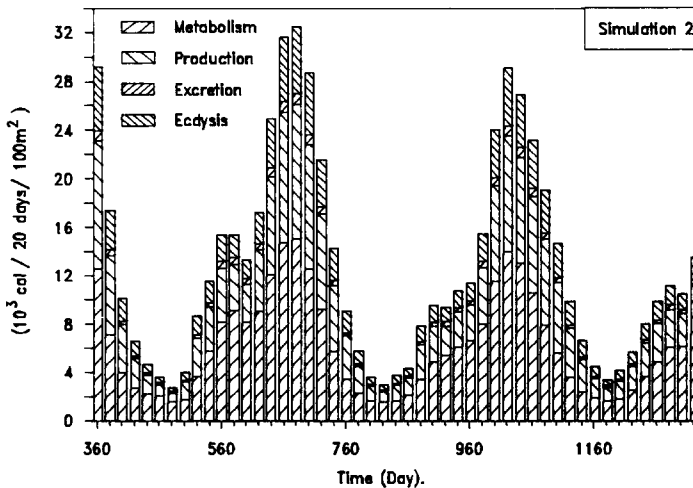


Fig. 5. Energy balance components of the simulated population. Cumulated histograms. Simulation 2.



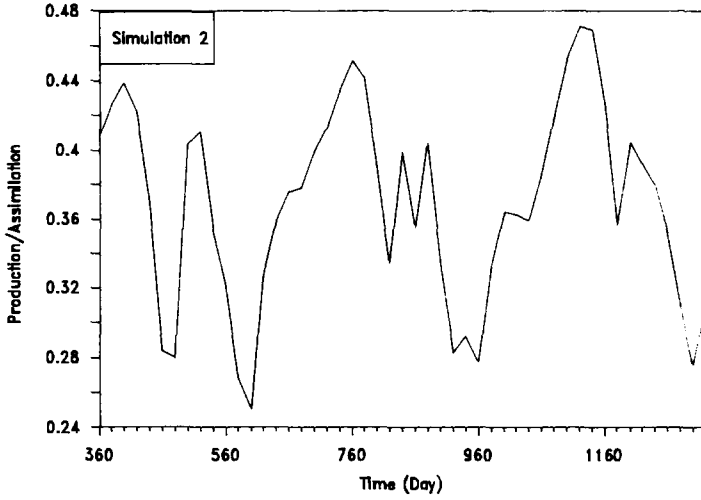


Fig. 6. Production/assimilation ratio. Simulation 2.

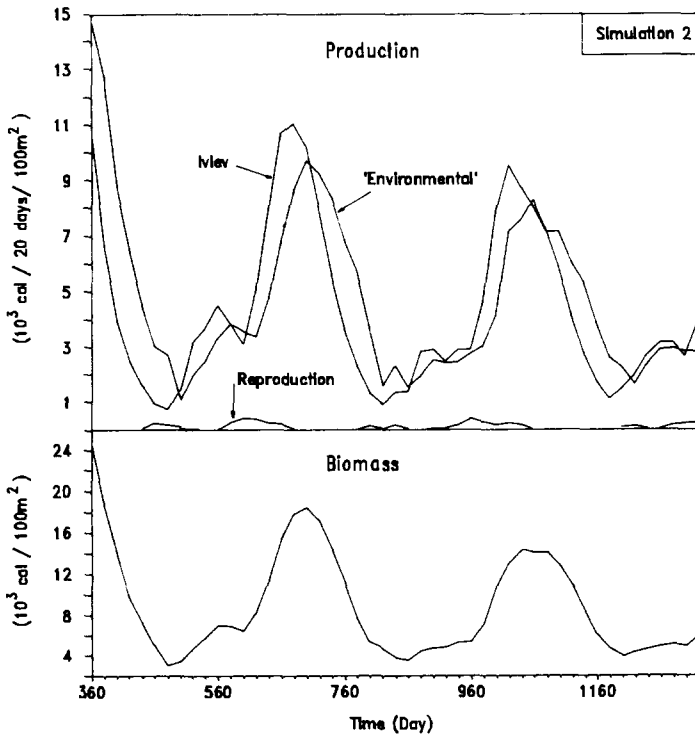


Fig. 7. Production as defined by Ivlev and 'environmental' production and resulting biomass. Simulation 2.

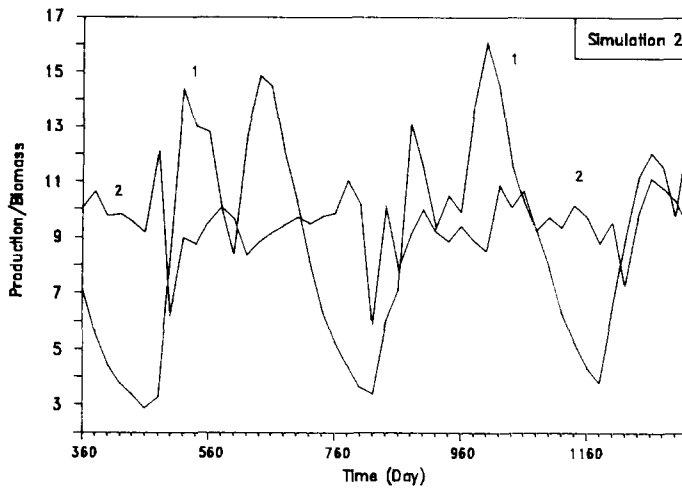


Fig. 8. Production and biomass ratio. 1. Ivlev production. 2. 'Environmental' production. (Productions are extrapolated over a year). Simulation 2.

individuals have a much higher  $K_2$  ratio than those composed of older individuals.

The observation of the evolutions of the Ivlev and 'environmental' productions (Fig. 7) demonstrates that their relative importances alternate several times during the annual cycle, a fact linked to the fluctuations in the demographic structures that have already been described; in this simulation, a higher mortality makes this feature particularly clear. These alternating predominances of the two fluxes are the cause of the variation in the biomass (Fig. 7).

The outgoing flux, represented by the release of larvae, can be equivalent to 10% of the production during the reproductive periods (Fig. 7); on average it represents 2.5% of the annual production.

The examination of the relationship between production (Ivlev) and biomass (Fig. 8) is another illustration of the effect of changes in the demographic structure of the simulated population. The periodicity and the way in which it varies, are identical to those of simulation 1; the only differences are the mean level and the amplitude, which are directly linked to the mortality coefficient value.

## DISCUSSION

Several approximations were made during this study. When specific data were not available on the species in question, an analogy was made with *Crangon crangon*. The continuous representation of growth introduced an

error in the estimation of losses by moulting. This problem could have been avoided by taking into account the duration of the intermoult, and the growth at the moult. Only the effects of temperature, sex and weight of the animal were used in the estimation of the metabolism. Potential changes connected with food, physiological state, etc. were not considered.

A comparison of the two simulations demonstrates that there is a good similarity between the flux cycles, the yields and the biomasses. This is also the case for the similarity between the kinetics of the size structures, which have already been established (Labat, 1991). The two annual generations are characterized by a large production of young individuals; this addition of organic material is basically stocked by the population. With the demographic evolution of the population, this 'stock' is given up to the environment, because production is reduced and is exceeded by mortality. In effect, when production, as defined by Ivlev, is greater than the loss by mortality, organic material is stocked. There is more material gained than lost in the compartment. In contrast, the reverse situation reflects a reduction in the biomass. The former situation is observed in populations consisting of young individuals with rapid growth; the latter is observed in groups where the number of older individuals exceeds the number of younger ones.

The differences observed between the results of the two simulations can be linked to the differences in the mortality coefficient. A high mortality coefficient results in a generally younger and therefore smaller population structure. From this, the production/biomass ratio as well as the production/assimilation ratio are going to be greater:

- Simulation 1:  $P_r/B = 7.19$ ,  $P_r/A = 32\%$  and  $P_r/M_e = 57.89\%$  for a mortality coefficient of 0.020.
- Simulation 2:  $P_r/B = 9.01$ ,  $P_r/A = 37\%$  and  $P_r/M_e = 67.62\%$  for mortality coefficients of 0.024 and 0.029;

The mean level of the absolute values of the biomasses and of the fluxes is going to be lower in a simulation with high mortality because the density of the simulated population is weaker.

In conclusion, the simulation of the abundance and of the kinetics of the size structure, allows the essential fluxes which regulate the population of *Philocheras trispinosus* to be followed, through the use of functions which represent the size/weight ratios and the metabolism. Therefore, this approach allows us to follow the fluxes, the stocking and the ecosystem's potential use of the trophic level that this species represents. It describes the variations between the different yields of the use of the assimilated energy ( $K_2$  as defined by Ivlev, ratio of production to metabolism). The ratios of production/biomass are characterized throughout the annual cycle from the estimates which take into account the 'environmental' production and the production as defined by Ivlev. The effect of energy stocking, represented by

the biomass and due to the flux difference between the production as defined by Ivlev and 'environmental' production, is particularly evident. The simulation process ensures, as precisely as possible, a quantitative dynamic representation of the different fluxes and accumulations.

#### ACKNOWLEDGMENTS

I greatly appreciated the constructive comments of A. Laurec. I thank H. Woodward for his help in English translation and M. Panouse for his useful advice and language corrections.

#### REFERENCES

- Allen, K.R., 1971. Relation between production and biomass. *J. Fish. Res. Board Can.*, 28: 1573–1581.
- Banse, K. and Mosher, S., 1980. Adult body mass and animal production/biomass relationships of field populations. *Ecol. Monogr.*, 50: 355–379.
- Bouché, M.B., 1978. Discussions d'écologie. III – Remarques sur les transferts entre maillons trophiques. *Bull. Ecol.*, 9: 289–299.
- Brey, T., 1986. Estimation of annual P/B-ratio and production of marine benthic invertebrates from length-frequency data. *Ophelia, Suppl.*, 4: 45–54.
- Crisp, D.J., 1971. Energy flow measurements. In: N.A. Holme and A.D. McIntyre (Editors), *Methods for the Study of Marine Benthos*. IBP Handbook 16, Blackwell, Oxford, pp. 197–279.
- Dejours, P., 1975. *Principles of comparative respiratory physiology*. North-Holland, Amsterdam, 253 pp.
- Elliott, J.M. and Davison, W., 1975. Energy equivalent of oxygen consumption in animals energetics. *Oecologia Berlin*, 19: 195–201.
- Evans, S., 1984. Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish west coast. *Estuarine Coastal Shelf Sci.*, 18: 651–672.
- Jobling, M., 1983. Growth studies with fish – overcoming the problems of size variation. *J. Fish Biol.*, 22: 153–157.
- Kerr, S.R., 1982. Estimating the energy budgets of actively predatory fishes. *Can. J. Fish. Aquat. Sci.*, 39: 371–379.
- Labat, J.-Ph., 1987. Dynamique et modélisation d'un échelon trophique de l'épibenthos des sables de l'infralittoral, *Philocheras trispinosus* (Caridea: Decapoda), Région de Banyuls-sur-mer. Thèse de Doctorat d'État, Univ. P. et M. Curie, Paris, 120 pp.
- Labat, J.-Ph., 1991. Model of a shrimp population. I. Simulation of the size structure. *Ecol. Modelling*, 53: 75–93.
- Mauchline, J., 1977. Growth of shrimps, crabs and lobsters – an assessment. *J. Cons. Int. Explor. Mer.*, 37: 162–169.
- Nelson, S.G., Li, H.W. and Knight, A.W., 1977. Caloric, carbon and nitrogen metabolism of juvenile *Macrobrachium rosenbergii* (De Man) (Crustacea, Palaemonidae) with regard to trophic position. *Comp. Biochem. Physiol.*, 58: 319–327.
- Pandian, T.J., 1967. Changes in chemical composition and caloric content of developing eggs of the shrimp *Crangon crangon*. *Helgol. Wiss. Meeresunters.*, 16: 193–283.

- Prosser, C.L., 1961. In: Prosser and Brown (Editors), *Comparative Animal Physiology*, 688 pp.
- Regnault, M., 1981. L'excrétion azotée chez les crustacés et les facteurs l'influençant. *Oceanis*, 7: 769-786.
- Regnault, M. and Lagardère, J.-P., 1983. Effects of ambient noise on the metabolic level of *Crangon crangon* (Decapoda, Natantia). *Mar. Ecol. Progr. Ser.*, 11: 71-78.
- Ricker, W.E., 1980. Calcul et interprétation des statistiques biologiques des populations de poissons. *Bull. Fish. Res. Board Can.* 191F, 409 pp.
- Sedgwick, R.W., 1981. The survival, behaviour and respiratory physiology of *Crangon vulgaris* (Fabr.) in the polluted Thames estuary. *Mar. Sci.*, 15: 123-133.
- Szaniawska, A., 1980. Element of ecological energetics of *Crangon crangon* (L.1758) (Crustacea, Decapoda) in Gdansk Bay. *ICES/C.M.* 1980/L:6, 9 pp.
- Van Donk, E. and De Wilde, P.A.W.J., 1981. Oxygen consumption and motile activity of the brown shrimp to temperature and body size. *Neth. J. Sea Res.*, 15: 54-64.
- Villiers, L., 1979. Contribution à l'étude de la nutrition et de ses aspects énergétiques chez des formes juvéniles de *Deltentosteus quadrimaculatus* (Valenciennes) (Pisces: Gobiidae). Thèse 3e cycle, Univ. P. et M. Curie, Paris, 139 pp.
- Welsh, H.E., 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology*, 49: 755-759.