

Modelling the growth of *Tapes philippinarum* in Northern Adriatic lagoons

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ABSTRACT: The paper describes a bioenergetic individual-based model of the growth of *Tapes philippinarum*, a bivalve mollusc reared in the lagoons of the Northern Adriatic Sea. The model, which simulates the evolution of the size of an average individual, has been calibrated using different sets of experimental data collected in the lagoons of Venice and Goro, and has been validated against a 3 yr long, independent series of field measurements of the average size of a cohort. The formulations here proposed for describing the dependence of the gain and loss terms on water temperature and food ration have not been employed in relation to this species before, and allow one to apply the model also in eutrophic conditions. Possible applications of the model as a tool for site selection and management implementations are illustrated.

KEY WORDS: Model · Clam farming · *Tapes philippinarum* · Adriatic lagoons · Bioenergetic · Management

INTRODUCTION

Tapes philippinarum, a bivalve mollusc of the Indo-Pacific region, already reared in some European countries, was first introduced in Italy in 1983. As stocks of the endemic clam population of *Tapes decussatus* were decreasing rapidly, perhaps as a consequence of over-fishing and worsening water quality, a regional governmental organisation, CoSPAV, evaluated the potential growth of *T. philippinarum* by seeding small clams which were brought from Great Britain in the lagoon of Venice (Breber 1985). The clams showed a great capacity to adapt to the new environment, colonising the shallow areas of the lagoon of Venice, and almost entirely occupied the ecological niche of *T. decussatus*, which is now present only in very restricted areas of the northern lagoon. The environmental conditions were favourable not only for growth but also for the natural reproduction of the introduced bivalve (Pellizzato & Mattei 1986, Pellizzato 1990). As a result, starting from 1985, harvesting in the wild became a very

remunerative activity in the lagoon of Venice. From the beginning of 1985, very good results were achieved in the other lagoons of the Northern Adriatic Sea, such as Marano, Goro and Scardovari (Fig. 1), where coastal areas were exploited by local fishermen, organised in co-operative societies, for harvesting and rearing this species. In contrast, in the lagoon of Venice, since rearing was permitted only in very small areas, *T. philippinarum* were the subject of intensive and illegal fishery: due to the favourable environmental conditions, up to 4×10^7 kg were collected in 1995. As could be expected, prices rapidly fell from about 14 000 Italian Lire kg^{-1} to about 3000 Italian Lire kg^{-1} , as can be seen in Fig. 2 (1\$ \approx 1800 Italian Lire). Therefore, the costs related to the rearing of *T. philippinarum* in the other lagoons proved to be too high for many fishermen, who were forced to cease this activity.

The intensive and illegal fishery of *Tapes philippinarum* in the lagoon of Venice is not only a source of friction between 'professional' and 'occasional' fishermen, but also a source of environmental problems. In fact, due to the use of illegal high-impact fishing tools, such as the hydraulic dredge, this activity badly dam-

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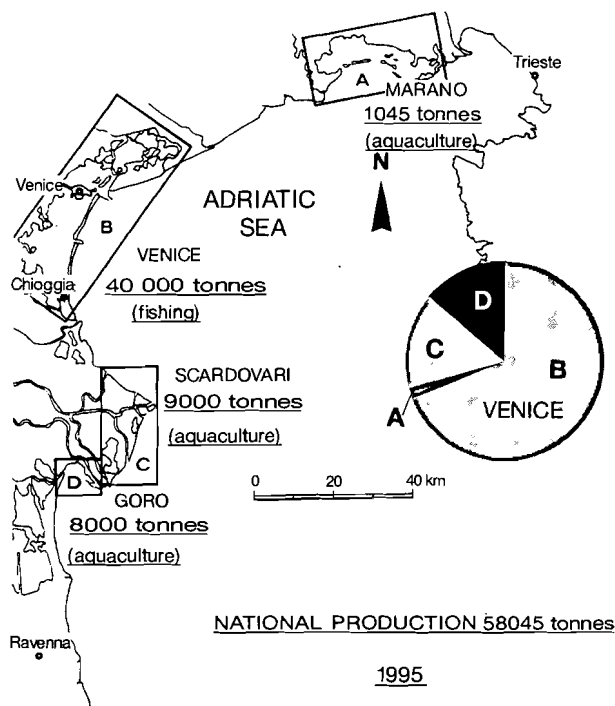


Fig. 1. Lagoons of the Northern Adriatic Sea where *Tapes philippinarum* is fished or reared

ages the benthic community, disrupts the compactness of bottom sediments, and causes the direct resuspension of a huge amount of small-sized particles. Furthermore, illegal fishery can also be a potential risk for the consumer, because the bivalve may not undergo the necessary sanitary controls before being introduced on the market (AECV 1996, Hall-Spencer et al. 1999). For these reasons, local authorities are now attempting to discipline the matter, with the introduction, also in the lagoon of Venice, of a regime of 'culture-based fishery'

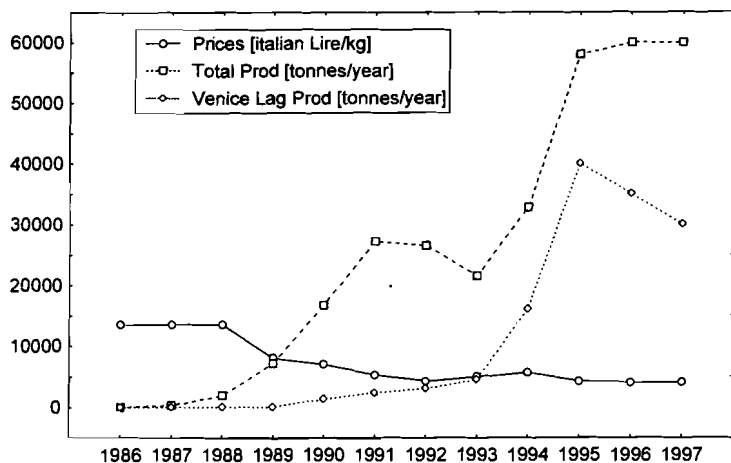


Fig. 2. Time evolution of total stocks and averaged prices for *Tapes philippinarum* in the Northern Adriatic lagoons and time evolution of the stock in the lagoon of Venice (1\$ = 1800 Italian Lire)

and/or proper rearing of *T. philippinarum* in given areas of the lagoon. To this regard, a model which relates the environmental conditions to the growth of this clam would be a useful tool.

The bioenergetic individual-based model presented in this paper has been developed taking into account the existing literature. Nevertheless, we introduced some modifications in the formulations which relate the growth rate to the water temperature and food ration. In the calibration, we made use of a considerable body of field and laboratory data about the growth of *Tapes philippinarum* collected in the lagoons of the North Adriatic. This model thus represents the first attempt at relating this information to the set of parameters which characterize the growth of this species, such as its maximum specific growth rate, in this new environment.

The model has been validated against a 3 yr long, independent series of field measurements of the average size of a cohort. Therefore, it can be used for developing tools for the selection of rearing areas and for the management implementation where *Tapes philippinarum* has already been successfully reared.

STRUCTURE OF THE MODEL

In general, the growth of a bivalve, in relation to its age, can be described by means of the same class of equations proposed in Ursin (1967), for describing the growth of fish (Gouletquer et al. 1989, Raillard & Ménesguen 1994, Powell et al. 1995, Barillé et al. 1997):

$$\frac{dw_w}{dt} = A - C = G_{w\max} f_a(T, dR/dt) w_w^m - r_{w\max} f_c(T) w_w^n \quad (1)$$

where w_w represents the wet weight, T the water temperature, dR/dt the food ratio, i.e. the amount of food ingested per unity time, and $G_{w\max}$ and $r_{w\max}$, respectively, the maximum growth and respiration rates on a wet weight basis. The first term of Eq. (1), A , often called the anabolic term, quantifies the mass/energy income, which depends upon water temperature and food ration as described by the function f_a , while the second term, C , the catabolic one, describes the mass/energy loss, mainly due to respiration, influenced by temperature through f_c .

As pointed out in Ursin (1967), the 2 exponents m and n of Eq. (1) are, in fact, empirical coefficients, which relate the body size to the maximum possible absorption and to the rate of oxygen consumption, respectively. Nevertheless, their values are often taken as $m = 2/3$ and $n = 1$, because it is very difficult to dis-

criminate between 2 different model structures, that is, between 2 pairs of m and n , on the basis of the best-fit of experimental growth data. This choice has the additional advantage that Eq. (1) can be easily rewritten in terms of length, L , by introducing the isometric relation:

$$w_w = aL^3 \quad (2)$$

which holds true in most cases for fish and bivalves, thus obtaining:

$$\frac{dL}{dt} = G_{Lmax} f_a(T, dR/dt) - r_{Lmax} f_c(T)L \quad (3)$$

where the symbols are as before, but the maximum growth and respiration rates G_{Lmax} and r_{Lmax} are expressed on a length basis (Table 1; see Table 2 for an explanation of the variables).

If the temperature and food ratios are assumed to be constant in time, Eq. (3) simplifies to the well known Von Bertalanffy (1938) equation,

$$\frac{dL}{dt} = G_{Lmax} - r_{Lmax} L \quad (4)$$

which can be analytically solved

$$L = L_\infty \left\{ 1 - \left(1 - \frac{L_0}{L_\infty} \right) \exp[-r_{Lmax} (t - t_0)] \right\} \quad (5)$$

where $L_\infty = G_{Lmax}/r_{Lmax}$ is the maximum length a specimen can reach.

Eq. (5) is widely used, and it has also been adopted to describe the growth of *Tapes philippinarum* (Ménesguen et al. 1984). Nevertheless, Eq. (5) does not take into consideration the effects of seasonal fluctuations, which can be accounted for by the addition of a sinusoidal term:

$$L = L_\infty \left\{ 1 - \left(1 - \frac{L_0}{L_\infty} \right) \exp[r_{Lmax} (t - t_0) + k' \sin(\omega t + \varphi)] \right\} \quad (6)$$

where $\omega = 2\pi/365$, t is expressed in days and $L_0 = L(t_0)$.

In this case, the amplitude k' and phase φ of the sinusoidal term are purely descriptive parameters, which are not related to the physiology of the animal, as the rates of the metabolic processes are related to the temperature T and not to the season. In the model presented here, the water temperature T , as well as the food concentration in the water filtered by a clam, F , are introduced explicitly as external forcings. More precisely, the maximum growth rate and the respiration rates depend on the metabolism and therefore only on water temperature, while food scarcity may reduce the potential growth. Using a multiplicative assumption for the anabolic term, the model equation becomes:

$$\frac{dw_w}{dt} = G_{wmax} f_{gT}[T(t)] f_{gF}[F(t)] w_w^{2/3} - r_{wmax} f_{rT}[T(t)] w_w \quad (7)$$

or, on a length basis,

Table 1. Equations of the model

Isometric relation

$$W = aL^3$$

Allometric relation

$$w_d = b w_w^p$$

Growth equations

if $E > E^*$, which is equivalent to $F > F^*$

$$\frac{dL}{dt} = G_{Lmax} f_{gT}(T) f_{gF}(F) - r_{Lmax} f_{rT}(T)L$$

$$\frac{dw_w}{dt} = G_{wmax} f_{gT}(T) w_w^{2/3} - r_{wmax} f_{rT}(T) w_w$$

$$\frac{dw_d}{dt} = G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} - r_{dmax} f_{rT}(T) w_d$$

if $E \leq E^*$, which is equivalent to $F \leq F^*$

$$\frac{dL}{dt} = \frac{F}{F^*} G_{Lmax} f_{gT}(T) f_{gF}(F) - r_{Lmax} f_{rT}(T)L$$

$$\frac{dw_w}{dt} = \frac{F}{F^*} G_{wmax} f_{gT}(T) w_w^{2/3} - r_{wmax} f_{rT}(T) w_w$$

$$\begin{aligned} \frac{dw_d}{dt} &= \frac{E}{E^*} G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} - r_{dmax} f_{rT}(T) w_d \\ &= F V_f f_v(T) w_d^q \frac{E_F}{E_T} - r_{dmax} f_{rT}(T) w_d \end{aligned}$$

with

$$G_{dmax} = p G_{wmax} b^{(1/3p)} = p G_{lmax} 3a^{1/3} b^{(1/3p)}$$

$$r_{dmax} = p r_{wmax} = 3p r_{lmax}$$

Threshold below which growth is food limited

$$F^* = \frac{G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} E_T}{V_f f_v(T) w_d^q E_F}$$

Functional response of temperature for growth, respiration and filtration

$$f_{gT}(T) = \left(\frac{T_{mG} - T}{T_{mG} - T_{oG}} \right)^{\beta_G (T_{mG} - T_{oG})} e^{\beta_G (T - T_{oG})}$$

$$f_{rT}(T) = \left(\frac{T_{mr} - T}{T_{mr} - T_{or}} \right)^{\beta_r (T_{mr} - T_{or})} e^{\beta_r (T - T_{or})}$$

$$f_v(T) = \left(\frac{T_{mv} - T}{T_{mv} - T_{ov}} \right)^{\beta_v (T_{mv} - T_{ov})} e^{\beta_v (T - T_{ov})}$$

$$\frac{dL}{dt} = G_{Lmax} f_{gT}[T(t)] f_{gF}[F(t)] - r_{Lmax} f_{rT}[T(t)]L \quad (8)$$

Eq. (7) can be written also on a dry weight basis, w_d , by using the allometric relation:

$$w_d = b w_w^p \quad (9)$$

with $p = 1.26$ and $b = 0.0234$ gdw/gww^p (g dry weight/g wet weight) as has already been identified by

Gouletquer & Wolowicz (1989) for *Tapes philippinarum*. In this way one finds:

$$\begin{aligned} \frac{dw_d}{dt} &= G_{dmax} f_{gT}(T) f_{gF}(F) w_d^{(1-1/3p)} - r_{dmax} f_{rT}(T) w_d \\ &= G_{dmax} f_{gT}(T) f_{gF}(F) w_d^{0.735} - r_{dmax} f_{rT}(T) w_d \end{aligned} \quad (10)$$

where the maximum growth and respiration rates on a dry weight basis, G_{dmax} and r_{dmax} , are related to the analogous parameters expressed on a different basis, in accordance with Table 1. Eq. (10) is used to assess the effects of food limitation on the growth rate.

MODELLING TEMPERATURE DEPENDENCE

The influence of the water temperature on the anabolic and catabolic terms has been investigated in several papers (e.g. Gouletquer et al. 1989, Maitre Allain 1982 and Bensch et al. 1992). All these authors express the gross growth rate and the respiration rate as a function of the dry weight and propose the following formulation:

$$f(T) = \alpha(T - \theta)^{\gamma} e^{-\delta(T - \theta)} \quad (11)$$

Eq. (11) presents a maximum value for $T = \gamma/\delta + \theta$. It depends on 4 parameters which are to be determined by means of a best-fit against experimental observations, but which cannot be easily interpreted in ecological terms. Furthermore, even though Eq. (11) provides a good fit for the experimental data presented in the papers quoted above, the values of the parameters proposed therein do not appear entirely satisfactory from the physiological point of view. In fact, at low temperatures the rate of metabolic processes in heterothermal organisms follows an exponential law, which is based on the fact that enzymatic activity increases in accordance with Arrhenius's law (Ursin 1967), but the parameters given in Bensch et al. (1992) do not yield this behaviour.

For this reason, we propose that the temperature dependence of the anabolic term is described by means of the formulation used by Lassiter & Kearns (1974) for modelling the growth rate of many phytoplanktonic species:

$$f(T) = G_{max} \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^{\beta(T_{max} - T_{opt})} e^{\beta(T - T_{opt})} \quad (12)$$

In this formulation, at low temperatures, the exponential factor determines the behaviour of the curve, while the importance of the rational factor increases as the temperature approaches its optimum, T_{opt} . After reaching its maximum, the curve decreases and the growth vanishes at $T = T_{max}$.

Eq. (12) has been used for modelling the temperature dependence of both the anabolic and catabolic terms. The 2 functions, $f_{gT}(T)$ and $f_{rT}(T)$, differ only by the values of the parameters:

$$f_{gT}(T) = \left(\frac{T_{mG} - T}{T_{mG} - T_{oG}} \right)^{\beta_G(T_{mG} - T_{oG})} e^{\beta_G(T - T_{oG})} \quad (13)$$

and

$$f_{rT}(T) = \left(\frac{T_{mr} - T}{T_{mr} - T_{or}} \right)^{\beta_r(T_{mr} - T_{or})} e^{\beta_r(T - T_{or})} \quad (14)$$

MODELLING FOOD AVAILABILITY DEPENDENCE

In order to grow at the maximum rate at a given temperature, any specimen of *Tapes philippinarum* must assimilate an amount of nutritive matter sufficient to satisfy the corresponding energetic demand. Since filter feeders, such as *T. philippinarum*, behave like predators which filter (that is 'search' and 'handle') and digest their prey at the same time, a Hollings Type I functional response appears appropriate in order to relate growth and energy assimilation (Hollings 1965). The growth rate is therefore assumed to increase linearly with the rate of energy assimilation up to a threshold E^* , and to remain constant above it. The threshold E^* can be seen either as the energy required for the maximum growth rate of a specimen at a given temperature, or as the maximum amount of energy the specimen can metabolise at that temperature. It is determined by the anabolic term of Eq. (10), and therefore it depends upon the size of the specimen and upon the water temperature as in:

$$E^* = \varepsilon_T G_{dmax} f_{gt}(T) w_d^{(1-1/3p)} \quad (15)$$

where ε_T is the energetic content of the clam.

As mentioned above, the influence of food availability on the growth of the bivalve is assessed by comparing this term with the amount of energy actually ingested per unit time, which can be expressed as

$$E = VF\varepsilon_F \quad (16)$$

where V is the filtering rate, F is the concentration of food particles in filtered water, and ε_F is the energetic content of the food. If the energy ingested (E) is higher than, or equal to, E^* there is no food limitation, and $f_{gF}(F) = 1$. Conversely, when E is lower than E^* the growth is proportionally reduced. The influence of energy availability is therefore:

$$f_{gF}(F) = f(E) = \min\left(1, \frac{E}{E^*}\right) \quad (17)$$

Finally, if one knows the average caloric content of the food particles, the ratio E/E^* can be restated as F/F^* , by defining the threshold value of the nutrient concentration in water, F^* , which depends on the caloric content of the particles and can be identified with the minimum concentration of food particles which assures the maximum growth rate:

$$F^* = \frac{E^*}{V\epsilon_F} \quad (18)$$

Taking this into account, Eq. (17) can be restated in terms of the concentration of food particles in the filtered water:

$$f_{gF}(F) = \min\left(1, \frac{F}{F^*}\right) \quad (19)$$

The filtration rate V depends, in general (Lehman 1976), on the maximum filtration rate V_f , on the size of the animal, on the temperature, on the concentration of food particles, and on the presence of inorganic seston, which can obstruct the filter. This last factor is very difficult to quantify for a cohort of bivalves reared in a natural medium, and, therefore, it has not been included in our model:

$$V = V_f f_v(T) f_v(w_d) f_v(F) \quad (20)$$

The influence of temperature on filtration rate has been modelled by means of the same function used for the anabolic term, which provided a good fit to the experimental data collected in the lagoon of Venice:

$$f_v(T) = \left(\frac{T_{mv} - T}{T_{mv} - T_{ov}}\right)^{\beta_v(T_{mv} - T_{ov})} e^{\beta_v(T - T_{ov})} \quad (21)$$

Size dependence has been described by means of the allometric equation given in Bensch et al. (1992):

$$f_v(w_d) = c w_d^q \quad (22)$$

If one assumes that the concentration of food particles does not affect the filtration rate, $f_v(F)$, until the animal has satisfied its energetic demand, E^* , and incorporates c in V_f , the filtration rate can therefore be expressed as

$$V = V_f f_v(T) w_d^q \quad \text{if } E \leq E^* \quad (23)$$

Now, by combining Eqs. (18) & (23) it is possible to calculate the threshold value of the nutrient concentration F^* , which indeed can also be computed by the energetic balance between energetic demand and supply at the threshold point $E(F^*) = E^*$,

$$E^* = \epsilon_T G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} = V F^* \epsilon_F \quad (24)$$

$$F^* = \frac{G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} \epsilon_T}{V_f f_v(T) w_d^q \epsilon_F} \quad (25)$$

Finally, it can be noticed that when the food concentration in the water, or the energetic contents of the food, is sufficiently high to yield a rate of energy income which exceeds E^* , the efficiency of the filtration-digestion processes must decrease. Such a decrease might be described by reducing the filtration rate in accordance with a hyperbolic law (Lehman 1976):

$$V = V_f \frac{E^*}{E} f_v(T) w_d^q \quad \text{if } E > E^* \quad (26)$$

The influence of food concentration and of size on growth rate, Eq. (19), is shown in Fig. 3. The bold lines show the dependence of the threshold F^* on body size. The Holling Type I functional responses for each size are obtained by taking cross-sections of Fig. 3 in the phytoplankton-limitation plane.

The model equation then becomes:

$$\frac{dw_d}{dt} = G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} - r_{dmax} f_{rT}(T) w_d \quad \text{if } E > E^*, \text{ which is equivalent to } F > F^* \quad (27)$$

and

$$\begin{aligned} \frac{dw_d}{dt} &= \frac{E}{E^*} G_{dmax} f_{gT}(T) w_d^{(1-1/3p)} - r_{dmax} f_{rT}(T) w_d \\ &= F V_f f_v(T) w_d^q \frac{\epsilon_F}{\epsilon_T} - r_{dmax} f_{rT}(T) w_d \end{aligned} \quad \text{if } E \leq E^*, \text{ which is equivalent to } F \leq F^* \quad (28)$$

Eqs. (27) & (28) can also be rewritten on a wet weight basis, see Table 1.

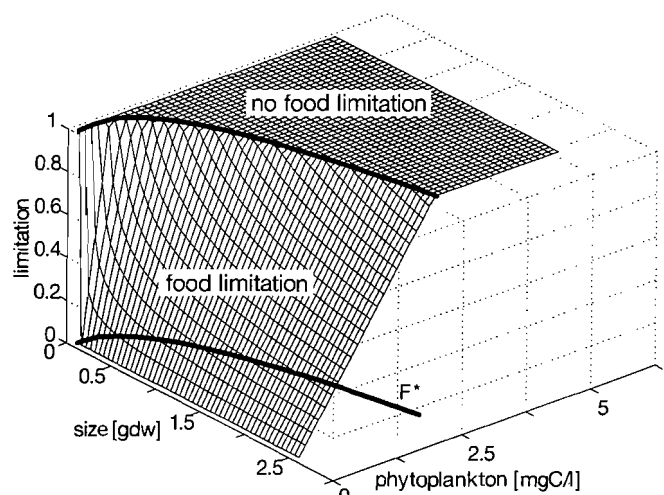


Fig. 3. Relationship between growth of *Tapes philippinarum*, food availability and size of the clam. The energetic threshold F^* is computed on the basis of an energetic balance and depends on temperature and size of the clam

EXPERIMENTAL DATA

As far as the Northern Adriatic lagoons are concerned, we were able to calibrate the model by using 3 different sets of data:

(1) Laboratory measurements of the respiration rates of single specimens of *Tapes philippinarum*, collected at 2 sites in the lagoon of Venice at different times of the year (Nesto 1997). This set of data was then pooled with another set of oxygen consumption measurements, published in Gouletquer et al. (1989), which were obtained from samples from the estuary of Marennes-Oléron (France). In both cases, the average value and its standard deviations were given. In spite of the different origins of the samples, the oxygen consumption measured in the lagoon of Venice and in the French estuary, normalised to the average weight of the sample, could not be discriminated on the basis of a *t*-test. By combining the 2 data sets one obtains a good coverage of the interval of water temperatures between 5 and 25°C (see Fig. 4a). This range is representative of the annual range of temperatures encountered at the latitude of the North Adriatic.

(2) Estimation of the average monthly increase in length of samples taken from the Sacca di Goro, where the species is reared (Rossi 1996) (see Fig. 4b). These data were collected in the frame of a monitoring and research program aimed at assessing the effects of different factors on the growth of this species: specimens of different average initial lengths were seeded in selected areas and the length distribution within each area was then determined after approximately 1 mo. The program also included the monitoring of chlorophyll *a* and temperature. The standard deviation for the average value was not available.

(3) Laboratory measurements of the filtration rate of specimens of *Tapes philippinarum*, which were collected at the above-mentioned 2 sites in the lagoon of Venice (Fig. 4c) (Nesto 1997).

The corroboration of the model was carried out on the basis of a set of data collected in the lagoon of Marano (Zentilin & M.P. unpubl. data). The average wet weight of a cohort, water temperature and chlorophyll *a* concentrations were collected on a monthly basis for 3 yr. Standard deviations were not available.

RESULTS

The estimation of the 15 parameters of the model cannot be done by means of a single best-fit against a collection of data which describe the growth of a cohort, because the problem of non-identifiability arises. In other words, the variation of 2 or more parameters

may affect the output of the model, that is the weight, roughly in the same way.

For this reason, we decided to carry out a stepwise estimation, using, in sequence, the 3 different sets of data described in the previous section. In the first step, the respiration rate as a function of water temperature was estimated from the oxygen consumption data. The parameters were determined by using weighted least squares, with weights proportional to the reciprocal of the standard deviation of each sample. The minimum of the cost function was found by using a simplex method (Press et al. 1986). The parameters, given in Table 2, are in agreement with the general knowledge of the tolerance of bivalves in high temperatures (Bodoy et al. 1986, Sobral & Widdows 1997) and with the findings of other studies; for example, the optimal temperature estimated by Gouletquer et al. (1989) is around 20°C, while r_{\max} is 0.4 ml O₂ h⁻¹ gdw⁻¹, which is equivalent to 195 J h⁻¹ gdw⁻¹, which is equivalent to a specific rate of fasting catabolism, $R_{d\max}$, of 0.010 d⁻¹ (Gouletquer et al. 1989).

The maximum anabolism $G_{L\max}$ and the effect of temperature on the anabolic term $f_{gT}(T)$ were estimated on the basis of the set of length measurements taken in the Sacca di Goro. In this eutrophic area, the chlorophyll concentration is always rather high, and therefore it is possible to assume that growth is mainly affected by the temperature. From each length difference, ΔL , one can compute and estimate the anabolic term at a given temperature by using Eq. (8):

$$G_{L\max} f_{gT}[T(t)] f_{gF}[F(t)] \cong \frac{\Delta L}{\Delta t} + r_{L\max} f_{rT}[T(t)] L \quad (29)$$

In this way, one obtains the data shown in Fig. 4b, which were fitted using Eq. (13). The results of the best-fit are reported in Table 2. The minimum of the cost function was again found by using a simplex algorithm.

The data collected in the lagoon of Venice (Nesto 1997) regarding the influence of the temperature on the filtration rate were not sufficient to attempt the calibration of the 4 parameters of Eq. (16). Therefore it has been assumed that the responses of the assimilation and filtration rates to the variation in water temperature is the same. Accordingly, this data set was only used to estimate the filtration rate at the optimal temperature. The value obtained is comparable with the experimental findings of Sorokin & Giovanardi (1995).

Table 2 also includes the confidence interval for the parameters calibrated in this study. The filtration, anabolic and respiration rates as a function of the temperature thus obtained are plotted in Fig. 4.

Other parameters, such as the allometric coefficients and caloric conversion coefficients, were taken from the literature, as indicated in Table 2. It should be

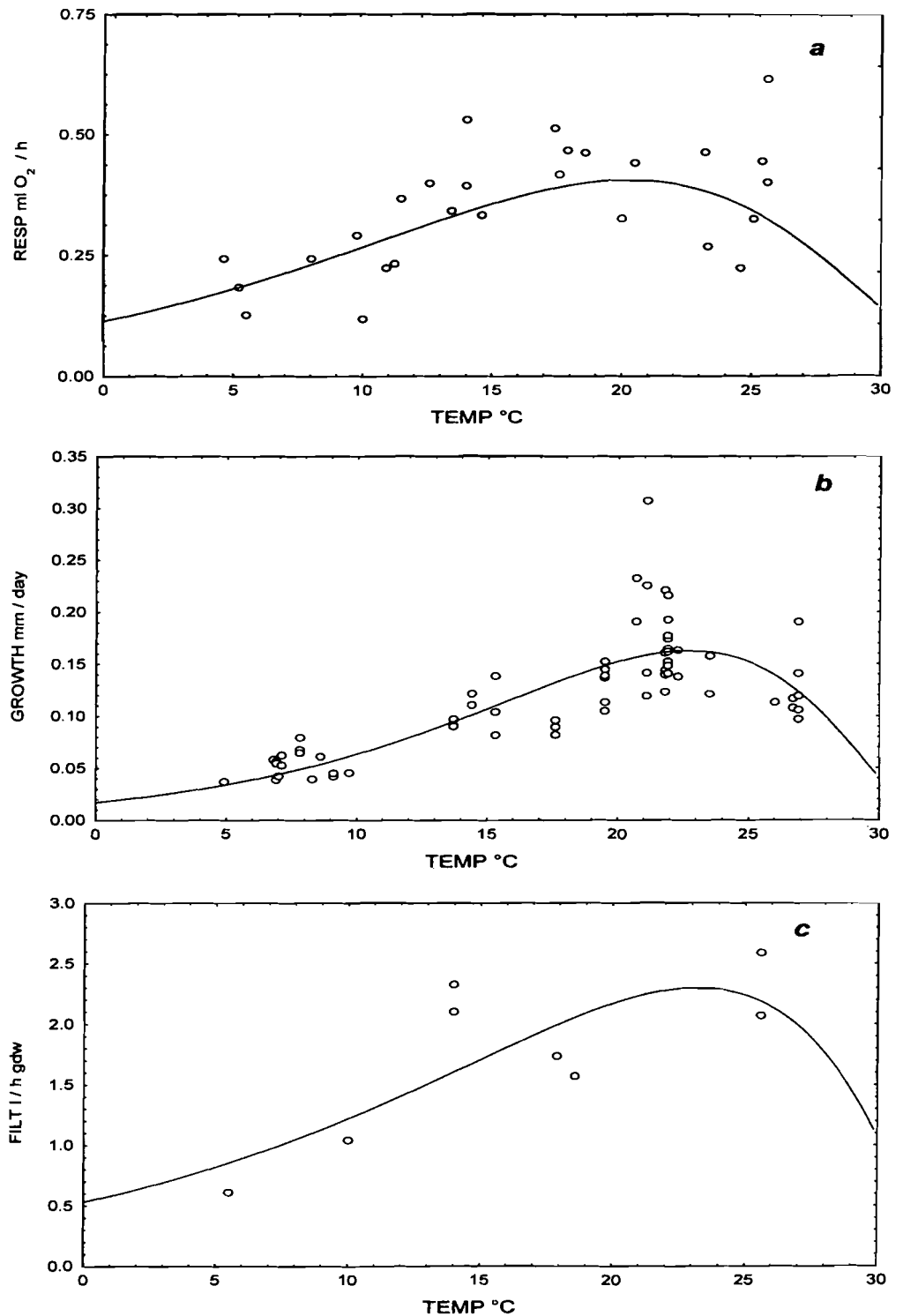


Fig. 4. Influence of temperature on (a) the respiration rate of single specimens collected in the lagoon of Venice and in the estuary of Marennes-Oléron; (b) average monthly increase in length of sample taken in the Sacca di Goro; (c) filtration rate of single specimens collected in the lagoon of Venice. The lines represent the functional forms used in the model

stressed that F^* is the threshold computed on the basis of the dry weight, Eq. (25), because the energetic conversion coefficients are usually measured in this unit. On the other hand, large sets of dry weight data do not exist for the Northern Adriatic lagoons, and, therefore, the dry weight equation could not be straightforwardly

applied to our case-study. However, both equations are mathematically equivalent, if one assumes that the allometric relation (Eq. 9) holds true, and they can be used for the calibration of the model.

A first corroboration of the parameterisation proposed here is obtained by computing the ratio between

Table 2. Variables and value (\pm SE) of parameters used in the model

Variable	Explanation	Value	Error (%)	Unit	Source
w_w	Wet weight				
w_d	Dry weight				
L	Length				
T	Water temperature				
dR/dt	Food ratio				
F	Food concentration in water				
G_{wmax}	Max. growth rate on a wet weight basis	0.031	(± 9)	$gww^{1/3} d^{-1}$	This study
r_{wmax}	Max. respiration rate on a wet weight basis	0.0081	(± 6)	d^{-1}	This study
G_{dmax}	Max. growth rate on a dry weight basis	0.014	(± 9)	$gdw^{0.265} d^{-1}$	This study
R_{dmax}	Max. respiration rate on a dry weight basis	0.010	(± 6)	d^{-1}	This study
G_{Lmax}	Max. growth rate on a length basis	0.16	(± 4)	$mm d^{-1}$	This study
R_{Lmax}	Max. respiration rate on a length basis	0.0027	(± 6)	d^{-1}	This study
m	Coeff. of Ursin equation	2/3			Ursin (1967)
n	Coeff. of Ursin equation	1			Ursin (1967)
a	Coeff. of allometric equation relating w_w to L	0.00026	(± 9)	$gdw mm^{-3}$	This study
b	Coeff. of allometric equation relating w_d to w_w	0.0234			Gouletquer (1989)
p	Coeff. of allometric equation relating w_d to w_w	1.26			Gouletquer (1989)
q	Coeff. of allometric filter velocity	0.32			Bensch et al. (1992)
T_{mG}	Max. temperature for growth	32		$^{\circ}C$	Pellizzato (1990)
T_{oG}	Optimal temperature for growth	22.7	(± 2)	$^{\circ}C$	This study
β_G	Coeff. of temperature growth	0.2	(± 14)	$^{\circ}C^{-1}$	This study
T_{mr}	Max. temperature for respiration	35		$^{\circ}C$	Pellizzato (1990)
T_{or}	Optimal temperature for respiration	20.5		$^{\circ}C$	Bensch et al. (1992)
β_r	Coeff. of temperature respiration	0.17	(± 8)	$^{\circ}C^{-1}$	This study
T_{mv}	Max. temperature for filtration	32		$^{\circ}C$	Pellizzato (1990)
T_{ov}	Optimal temperature for filtration	22.7	(± 2)	$^{\circ}C$	This study
β_v	Coeff. of temperature filtration	0.2	(± 14)	$^{\circ}C^{-1}$	This study
ϵ_F	Energetic content food	4.7		$J \mu g^{-1} chl a$	Platt & Irwin (1973)
ϵ_T	Energetic content of <i>Tapes philippinarum</i>	19200		$J gdw^{-1}$	Gouletquer (1989)
V_f	Max. filtration rate	2.3	(± 13)	$l d^{-1}(gdw^q)^{-1}$	This study

G_{wmax} and r_{wmax} , which represents an estimation of the maximum length L_{∞} : our estimate of 60.3 mm is consistent with the observations collected in the Northern Adriatic lagoons (Rossi 1996).

The model presented in the previous paragraphs was then tested against the independent set of wet weight data collected in the lagoon of Marano, where the evolution of a cohort of *Tapes philippinarum* had been studied for 3 yr, by collecting monthly samples of the wet weight, temperature and chlorophyll *a*. In order to relate the chlorophyll *a* concentration to the caloric content of the planktonic pool, one should know the composition of the phytoplanktonic pool, and the energetic content of each species. As this kind of information was not available for the lagoon of Marano, we used the ratio energy: mg C given in Platt & Irwin (1973) and the ratio carbon: chlorophyll given in Sakshaug et al. (1989) to estimate the ratio energy:chlorophyll ($4.7 J \mu g^{-1} chl a$).

A comparison between the observed wet weight data and the simulation is presented in

Fig. 5. The computed values are in agreement ($R^2 = 0.95$) with the observations, with a difference of less than 10% for the prediction of the wet weight reached after 3 yr, even though, in this lagoon, the concentra-

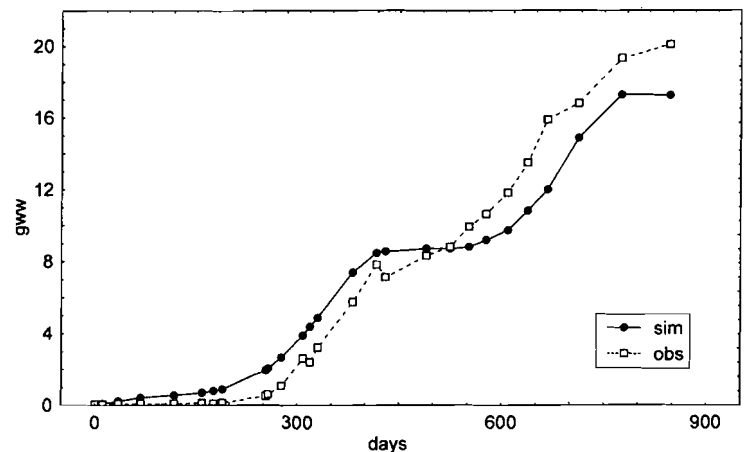


Fig. 5. Comparison between an independent set of observed wet weight data and the simulation. Computed values are in good agreement with the observations ($R^2 = 0.95$)

tion of chlorophyll *a* is not as high as in the Sacca di Goro, and the growth of *Tapes philippinarum* can be limited by the availability of food, in particular with regard to the older specimens.

DISCUSSION

The growth rate of *Tapes philippinarum*, in relation to its age and to external forcings, is described in the literature by using 3 different approaches, which are the regression models (Gouletquer & Bacher 1988), the 'best-fit' of empirical curves against cohort data (Bodoy et al. 1980, Ménesguen et al. 1984), and the 'energetic budget' approach (Bensch et al. 1992).

Of the 3 approaches, the latter is certainly the most appealing, because it is based on the physiology of the bivalve and is, therefore, of more general applicability. Nevertheless, its use as a management tool could be limited by the fact that the 'natural' state variable in this case is the dry weight, which is much more difficult to measure than the wet weight or the length.

The model presented here combines the last 2 approaches in an attempt to retain the advantages of the energetic budget approach, while expressing the growth in respect to the wet weight and/or length. In this way, the model could be calibrated and corroborated with the large body of experimental field information already collected on the Northern Adriatic lagoons.

Accordingly, the model was developed in 3 stages:

(1) An 'empirical' equation, of the Von Bertalanffy-type in differential form, was used to describe the growth of *Tapes philippinarum*, in terms of the wet weight as a function of temperature.

(2) The parameters were calibrated against the respiration rates measured in the lagoon of Venice and the net growth of the wet weight data collected in the Sacca di Goro. The gross growth rate thus obtained represents the maximum potential growth of the species in the actual trophic conditions of the Northern Adriatic lagoons.

(3) By using an allometric relation, the equation was restated in terms of the dry weight, which can be converted into energetic units. In this way, the maximum potential growth estimated on a wet weight basis can be expressed in energetic units, thus finding the energetic demand of a specimen of a given wet weight at a given temperature. Once one knows the caloric content and the density of the phytoplanktonic pool which constitute the diet of *Tapes philippinarum* in a given environment, one is

able to assess whether their growth is limited by food availability.

Therefore, the model assumes the validity of the same allometric relationship between the wet weight and the dry weight for the whole period of simulation; this can be questioned if one wishes to investigate in detail the energetic aspects of growth, because, in this way, the energy loss due to spawning is not taken into account. However, considering the accuracy of the prediction of the model, and therefore its applicability, one is more concerned with an estimation of the uncertainty of the model output, due to the variability of the allometric coefficients. Fig. 6 shows the comparison between the simulations obtained from the values assumed by the exponent p in Eq. (9) before and after spawning, as given in (Bensch et al. 1992). As one can see, there is very little difference at the end of the first year, while after 2 yr the uncertainties of the wet weight and length, estimated as half of the difference between the 2 cases, are around 10 and 5%. These uncertainties are comparable with the ones induced by other sources, such as those associated with the estimates of the other parameters.

On the other hand, the use of the allometric relation (Eq. 9) allows one to estimate the energetic demand of a specimen from *in situ* wet weight measurements, and therefore to identify the functional response of the growth rate with respect to food availability. This represents an improvement when compared with the model described in Bensch et al. (1992), where the growth is taken as simply proportional to the concentration of food particles in the medium. In fact, the absence of a physiological threshold, F^* , would lead to an overestimation of the growth at phytoplankton densities as high as those typical for the Northern

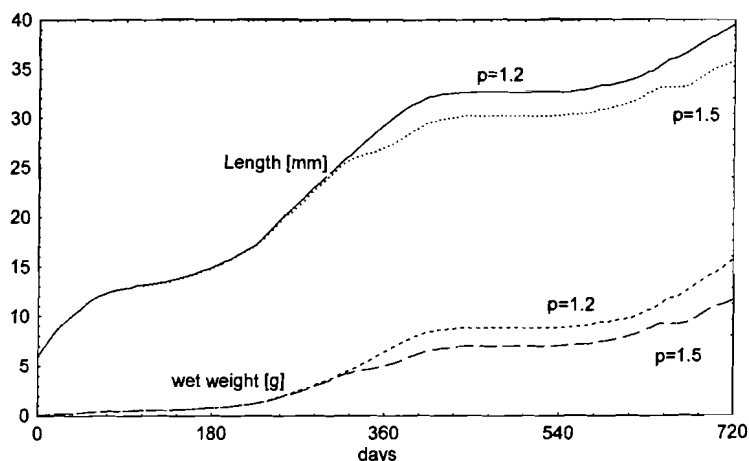


Fig. 6. Comparison of simulations obtained by using the best-fitted values of the exponent p of the allometric relation between wet weight and dry weight given before and after spawning

Adriatic lagoons. The link between the wet weight, which is easily measurable, the growth rate and the energetic demand can also be used to assess indirectly the energetic content of the particulate matter ingested by the clam.

The food particle concentration in filtered water does not necessarily coincide with food particle concentration in the water column. Several models have been proposed to describe how the presence of a bed of filter-feeder organisms might affect the vertical distribution of plankton concentration (Frechette et al. 1983, O'Riordan et al. 1995), by inducing a boundary concentration layer. The thickness of the layer depends mainly on the hydrodynamic regime of the water body itself and on a number of physiological details, such as height and orientation of the siphons of the bivalves. The application of these conclusions, no doubt important when using a 1-dimensional model, would however be premature at the present stage, given that our paper focuses on a 0-dimensional bio-energetic individual-based model of a specific clam, *Tapes philippinarum*. Moreover, the practical implementation of these findings would imply the existence of experimental information not yet available in our case study. Therefore, the simplification of assuming that the water body is well mixed, and the food particle concentration homogeneous, is presently maintained. On the other hand, such an assumption is also adopted in many studies addressing the coupling between the planktonic community and filter-feeder population (Cloern 1982, Powell et al. 1995).

The model proposed here represents a basis for developing more sophisticated tools for optimizing the rearing activity of *Tapes philippinarum*. However, in its present form, it can already provide some indications, for example with regard to the identification of the optimal month for seeding. By forcing the model with the temperature and chlorophyll data recorded in the lagoon of Venice in 1996, one can compute how long it takes for specimens of a given size, seeded in different months, to reach the market weights. The continuous and dashed lines in Fig. 7 show the number of months required for a specimen, initially 3 mm long, to grow to, respectively, the marketable sizes 'medium' (37 mm) and 'large' (40 mm). The results indicate that if one plans to harvest medium-sized clams, the optimal months for seeding 3 mm long individuals are from January to May, while if one plans to harvest large-

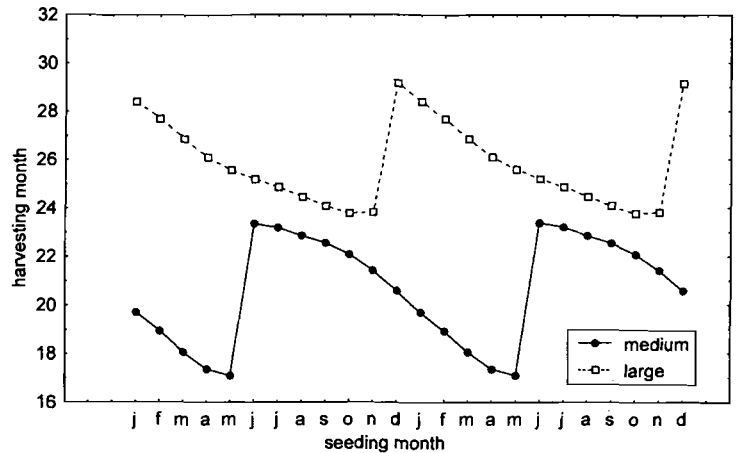


Fig. 7. Continuous and dashed lines show the number of months required for an individual (initially 3 mm long) to grow to, respectively, the marketable sizes 'medium' (37 mm) and 'large' (40 mm)

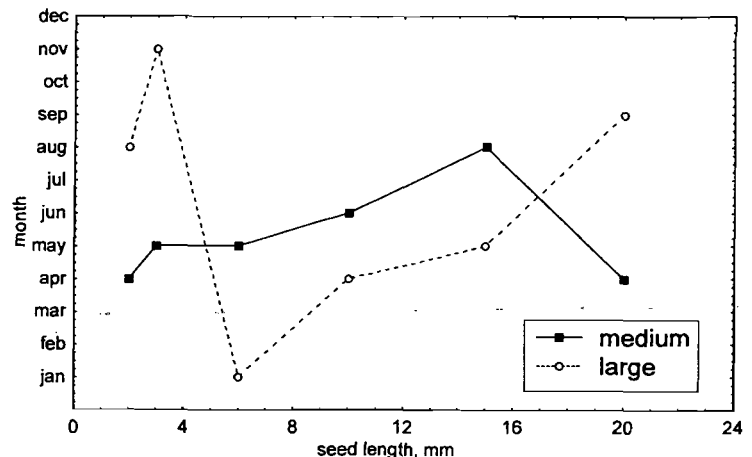


Fig. 8. Optimal month of seeding for individuals to be harvested at the 'medium' size (continuous line) and for individuals to be harvested at the 'large' size (dashed line)

sized individuals, the optimal months are from July to October. Furthermore, it can be noted that the amount of time required for an individual to grow from medium to large size ranges from 8 mo for specimens seeded in December to May, to 2 mo for specimens seeded in June to November. These computations allow one to evaluate the optimal seeding months in relation to the initial size of the seeds. Fig. 8 illustrates this result, by showing the optimal month for seeding specimens to be harvested at the medium (continuous line) and large market weight (dashed line).

CONCLUSION

The model presented in this paper retains the advantages of the energetic budget approach, but since

growth is expressed with respect to the wet weight and/or length, the calibration and validation of the model could be based on the large body of experimental field information. This paper represents a first attempt at interpreting such information by means of a dynamic model and of relating it to the set of parameters which characterize the growth of this species in this new environment. Since the basic parameters of the anabolism and catabolism are related to environmental conditions, this approach presents some advantages with respect to regression models, where the parameters can be less clearly interpreted in physiological terms. On the other hand, the model does not require sophisticated measurements and, therefore, it has a wider applicability than models which describe the *Tapes philippinarum* physiology in greater detail.

The model accurately reproduces the growth of *Tapes philippinarum* in the Northern Adriatic lagoons, and gives the possibility of evaluating the time evolution and yield of a cohort, based on plausible scenarios of temperature and chlorophyll *a*. The predictions of the model could be improved by the acquisition of more information on the energetic coefficient of the particulate matter which constitutes the diet of the clams in a given environment.

The model can be used as a tool for research, since it enables one to use field data for estimating parameters seldom directly measured. It can also be used as a basis for developing a Decisional Support System, and, as was shown in the 'Discussion' section, it can already give some useful indications about the optimal seeding month and the optimal size of the seeds.

Further improvements should include the estimation of a site-specific mortality rate also in relation to the seeding density. The model could then be used for the selection of the areas which will be devoted to the rearing of this species, and for the management of this activity where *Tapes philippinarum* has already been successfully reared.

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