

Density and temperature-dependence of vital rates in the Manila clam *Tapes philippinarum*: a stochastic demographic model

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ABSTRACT: We developed a demographic and management model for the Manila clam *Tapes philippinarum* (one of the most important commercial mollusc species in Europe) from data collected in the Sacca di Goro lagoon, Italy. Herein, we describe growth and survival processes by 2 submodels incorporating temperature-driven fluctuations in vital parameters, density-dependent effects on survival, and sediment type as an indicator of the hydrodynamic regime. Nonlinear fitting and non-parametric statistics are used to calibrate the body growth and survival models from the available data and to associate a probability distribution to parameter estimates. The 2 models are stochastic in their formulation to account for environmental variability. We assess the suitability of our model to reproduce the life cycle of *T. philippinarum* at other sites by applying our model to data from the Bassin d'Arcachon (France) and the Eo estuary (Spain). We use Monte-Carlo simulations to forecast the expected biomass yield corresponding to different seeding and harvesting times along with its confidence intervals. The maximum obtainable yield is about 6 kg m⁻² and can be obtained by seeding in spring and harvesting in late fall of the following year. We show, however, that there is a trade-off between maximizing the average yield and minimizing yield variance.

KEY WORDS: Density-dependence · Survival · Body growth · Stochastic models · Manila clam · *Tapes philippinarum* · Aquaculture · Farming management

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INTRODUCTION

The Manila clam *Tapes philippinarum* Adams & Reeve is one of the mollusc species that, mainly driven by the shellfish market industry, has successfully spread throughout the world, far beyond the limits of its original habitat. This bivalve was first introduced to Italy in 1983, because of its higher productivity and resistance to anoxic conditions compared to the native species *T. decussatus*. In the last decade, Italy has become the leading European producer of clams, and one of the 3 major European producers of molluscs (25.7% of the European mollusc production in 1995), together with France (34.3%) and Spain (17.1%).

However, after the first expansion phase, a decreasing trend in *Tapes philippinarum* production was ob-

served during recent years (Rossi 1996, Solidoro et al. 2000). The major cause of this decline has long been identified as recurrent, extensive algal blooms of the seaweed *Ulva rigida*. However, the alteration in nutrient cycles caused by intensive mollusc farming also has an important impact on ecosystem productivity (Bartoli et al. 2001, Melià et al. 2003). A primary task in preserving lagoon ecosystems is to provide guidelines for a sustainable management of clam aquaculture. Understanding clam demography under different environmental conditions is an important step in this direction.

Herein, we present a demographic model for the Manila clam which provides a stochastic description of both growth in individual size and the survival dynamics of *Tapes philippinarum*, and quantifies the effect of the most important environmental variables on vital

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rates. It is calibrated with extensive data collected over several years in a eutrophic lagoon, Sacca di Goro (northern Italy), which is one of the major aquaculture areas in Italy (about 15% of the total Italian yield). However, the model structure is well suited to describing clam demography in other eutrophic lagoons.

Although previous studies have described body size growth of *Tapes philippinarum* under different environmental conditions (Mann 1979, Menesguen et al. 1984, Goulletquer & Bacher 1988, Bacher & Goulletquer 1989, Robert et al. 1993, Solidoro et al. 2000), survivorship has long been neglected. This is a major shortcoming, because mortality processes have a crucial importance in determining the overall biomass dynamics, and represent one of the most important factors affecting fishermen's harvests and profits (Cigaría & Fernández 2000). Moreover, the majority of models proposed so far to describe clam growth have necessitated estimation of a large number of parameters (e.g. the bioenergetic model proposed by Solidoro et al. 2000 and applied to *T. philippinarum* management in Pastres et al. 2001). Overparameterization will lead to large variances in the estimates, which can be overcome only by setting some parameters to literature values or by making *a priori* assumptions. Although this approach is reasonable if one wants to make preliminary explorations regarding the demography of a species, it becomes questionable when the purpose is to derive specific management policies for a given mollusc population. For this reason, we propose a purely phenomenological description of clam demography rather than a detailed interpretation of metabolic processes, considerably diminishing the model's complexity. As the resulting model has a reasonably small number of parameters, it can be calibrated on the basis of field data alone. Also, environmental variability can be estimated and a stochastic model of clam demography developed. This is fundamental to determining reliable management policies (Walters 1986), which are of paramount importance to the sustainability of clam farming.

MATERIALS AND METHODS

Field experiments and data analysis. Sacca di Goro (Fig. 1) is a shallow lagoon in the Po River Delta, with a mean depth of 1.5 m and an overall area of 26 km². It is characterized by strong anthropogenic eutrophication due to high nutrient inflow from the Po River, and is subject, especially in summer, to extensive seaweed blooms which lead to dystrophic events and high mortality rates of the benthic fauna (Viaroli et al. 1993).

Intensive farming of clams *Tapes philippinarum* and mussels *Mytilus galloprovincialis* has been the basis of

a local economy since the mid 1980s. The production of *T. philippinarum* reached 16 000 t in 1991 (Rossi & Pae-santi 1992), but a decline in productivity has become apparent in recent years, possibly due to extensive seaweed blooms.

The present work is based on data collected by the Dipartimento di Biologia Evolutiva, University of Ferrara (Rossi 1996) over 3 yr (1993 to 1995). The aim of the study was to measure clam growth and survival under different environmental and ecological conditions. Experimental sites, characterized by different sediment type and hydrodynamic regime, were seeded with clams of different sizes, at different densities and in different seasons; water temperature and salinity were recorded at seeding. In each experiment, chlorophyll *a* concentration, dissolved oxygen concentration and temperature of the water column were monitored. At the end of each experiment (the duration of which was usually 1 mo, but in some cases up to 1 yr), average length increment and percent mortality were estimated. The results of the 99 experiments conducted are summarized in Table 1.

To obtain preliminary information on the dependence of growth and mortality rates upon environmental and demographic variables, we carried out an extensive statistical analysis of the available data. The key variables regulating growth and survival processes were identified by means of multilinear stepwise regression. A summary of the results is shown in Table 2. Clam growth (expressed as average length increment d⁻¹) is significantly dependent upon initial clam size, mean water temperature and sediment type. Mortality (expressed as average instantaneous mortality rate) is significantly correlated to clam density and water temperature at seeding. The most important dependencies are summarized in Fig. 2.

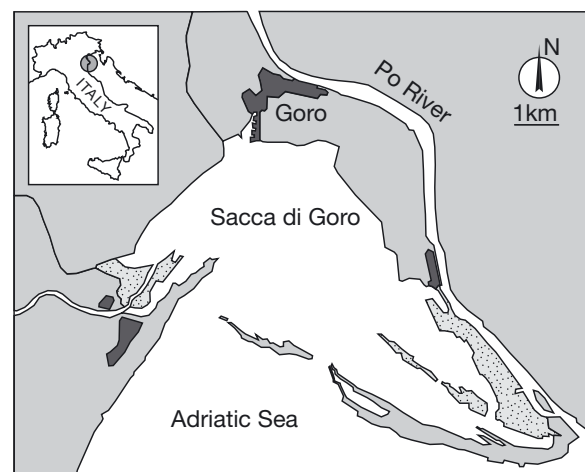


Fig. 1. Sacca di Goro lagoon (44° 47'–44° 50' N, 12° 15'–12° 20' E)

Table 1. Summary of data for Sacca di Goro experiments on *Tapes philippinarum* and used in preliminary statistical analysis and model calibration (after Rossi 1996). Subscript 0 identifies quantities measured at beginning of experiment, bar above symbol indicates average over whole duration of experiment. Sediment type and current speed were available only as categorized data. For sediment, categories were 1: muddy (sand content < 25%); 2: intermediate (25% ≤ sand content ≤ 75%); 3: sandy (sand content > 75%). Current speed was categorized as 1: slow (current speed < 5 cm s⁻¹); 2: intermediate (5 cm s⁻¹ ≤ current speed ≤ 15 cm s⁻¹); 3: fast (current speed > 15 cm s⁻¹)

Variable	Symbol	Units	Range	Mean ± SD
Seeding time	t_0	d	Dec 1993–Dec 1995	–
Experiment duration	Δt	d	25–351	67 ± 60
Temperature at seeding	T_0	°C	4.5–28.2	16.5 ± 7.1
Salinity at seeding	s_0	‰	18–35	30 ± 3
Sediment type	sed	–	1–3	–
Hydrodynamic regime	idr	–	1–3	–
Clam size at seeding	L_0	mm	1.47–44.42	22.70 ± 11.21
Avg. O ₂ saturation	\bar{O}	%	70.9–135.5	101.6 ± 16.9
Avg. chl a conc.	\bar{C}	µg l ⁻¹	0.57–8.64	3.87 ± 2.10
Avg. daily temperature	\bar{T}	°C	4.9–26.9	17.0 ± 6.5
Seeding density (n)	N_0	individuals m ⁻²	83–1982	662 ± 440
Seeding density (wt)	W_0	g m ⁻²	2–7452	1793 ± 1557
Mortality	m	%	1–65	17 ± 14
Length increment	ΔL	mm	0.19–18.45	3.40 ± 3.00

Model formulation. On the basis of our preliminary data analysis, we developed a demographic model consisting of 2 submodels describing body size growth and survival, respectively, and accounting for all the dependencies listed in the preceding subsection.

Temperature is the key environmental variable regulating both growth and survival of *Tapes philippinarum* (Mann 1979, Bernard 1983, Gouletquer et al. 1989). Menesguen et al. (1984) described seasonal fluctuations in *T. philippinarum* growth by modulating the growth constant of von Bertalanffy's (1938) model with a sine function.

We simulated seasonal temperature variations using the simple sinusoidal formulation proposed by Melià et al. (2003) for the Sacca di Goro lagoon. Temperature T (°C) at time t (in days, where $t = 0$ corresponds to 1 January) is then given by:

$$T(t) = f \cdot \sin\left(\frac{2\pi}{365}(t + e)\right) + g \quad (1)$$

where $e = -114.74$ (phase), $f = 9.76$ (maximum temperature variation), and $g = 16.35$ (mean annual temperature).

Body growth model: The von Bertalanffy (1938) model provides a simple, yet effective, description of the growth process of an organism. It can be written, in terms of the length L of the organism, as:

$$\frac{dL}{dt} = k \cdot (L_\infty - L) \quad (2)$$

where L_∞ is the asymptotic mean size and k is the so-called 'Brody growth constant'. Under the hypothesis that temperature influences only growth rate and not the maximum size an individual can reach, we consider the Brody growth constant as a linear function of water temperature, T :

$$k(t) = k_0 + k_T \cdot T(t) \quad (3)$$

where k_0 and k_T are parameters to be estimated and T is given by Eq. (1). A linear relationship provides a simplified, yet effective, representation of clam growth, at least within the annual temperature range of North Adriatic lagoons (between 5 and 25°C, Solidoro et al.

Table 2. *Tapes philippinarum*. Results of multiple regression of average instantaneous mortality rate μ and the average daily length increment $\Delta L/\Delta t$ versus environmental and demographic variables (see Table 1). Average instantaneous mortality rate was calculated as $\mu = (1/\Delta t) \cdot \ln(1 - m)$ where m is observed percent mortality throughout whole experiment. Only significant dependencies are shown. Regression performed with backward stepwise multiple regression routine of Statistica 5.1 (StatSoft). R^2_{adj} : adjusted coefficient of determination

Dependent variable	Coefficient estimate	SE	p-level	R^2_{adj}
μ (d⁻¹)				49.6%
(Intercept)	3.57×10^{-3}	0.63×10^{-3}	<<0.001	
N_0	4.70×10^{-6}	0.52×10^{-6}	<<0.001	
T_0	-1.75×10^{-4}	0.32×10^{-4}	<<0.001	
$\Delta L/\Delta t$ (mm d⁻¹)				83.8%
(Intercept)	-3.36×10^{-2}	0.89×10^{-2}	<<0.001	
L_0	-2.58×10^{-3}	0.18×10^{-3}	<<0.001	
\bar{T}	3.19×10^{-3}	0.31×10^{-3}	<<0.001	
sed	1.66×10^{-2}	0.24×10^{-2}	<<0.001	

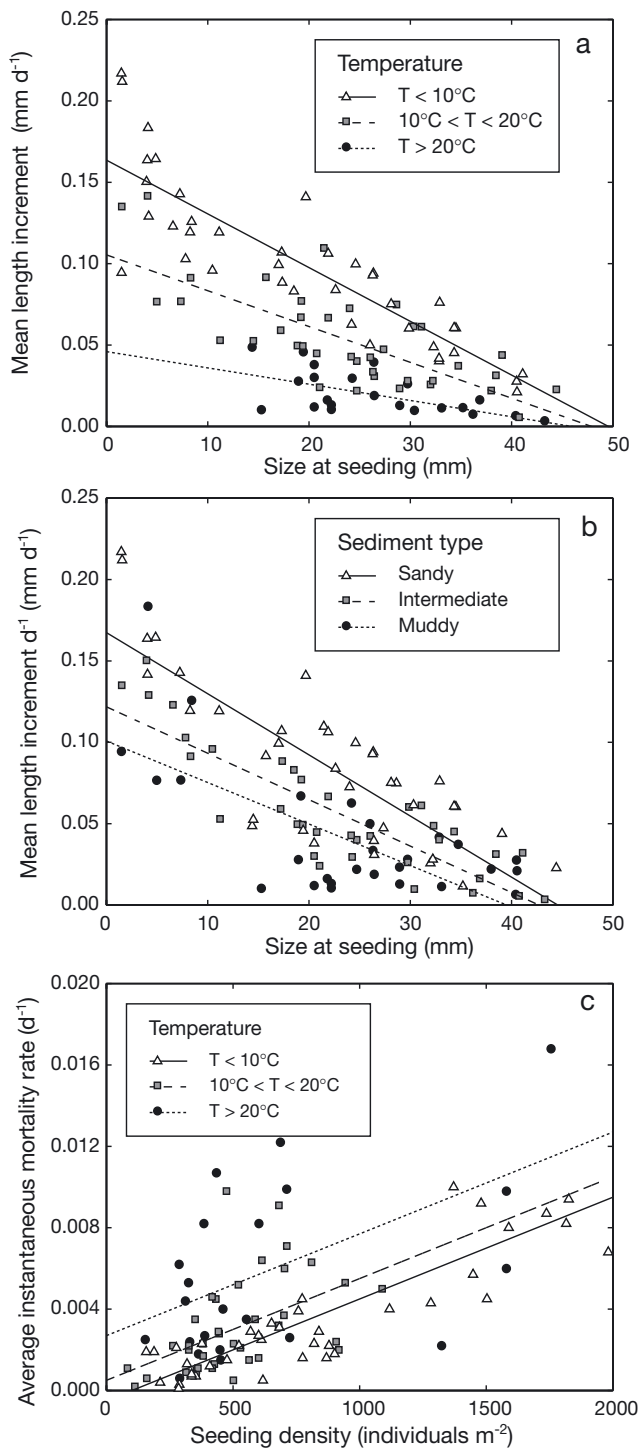


Fig. 2. *Tapes philippinarum*. Influence of temperature and sediment type on body growth and survival. Each symbol corresponds to 1 experiment; different symbols identify different classes of temperature or sediment type. Data for each class fitted by straight lines. (a) Mean length increment versus mean initial clam length (temperature categories); (b) mean length increment versus mean initial clam length (sediment type categories); (c) average instantaneous mortality rate versus initial clam density (temperature categories)

2000). The mean length increment of a clam population in a given time period (t_1, t_2) can be calculated by integrating Eq. (2) with k given by Eq. (3). We obtain:

$$\Delta L(t_1, t_2) = (L_\infty - L(t_1)) \cdot (1 - \psi(t_2)/\psi(t_1)) \quad (4)$$

where $\psi(t)$ is defined as:

$$\psi(t) = \exp\left[\frac{365}{2\pi} k_r f \cdot \cos\left(\frac{2\pi}{365}(t + e)\right) - (k_0 + k_r g) \cdot t\right] \quad (5)$$

and e, f and g are the parameters of the temperature model (Eq. 1). Eq. (4) can be interpreted as a modified, temperature-dependent form of Fabens' (1965) model, which is a reformulation of the von Bertalanffy model generally used when tag-recapture data are available for species that cannot be easily aged (Francis 1988).

In principle, the hydrodynamic regime has also a chief role in regulating the growth process of filter-feeders organisms, mainly by determining the availability of food and oxygen. Reliable flow data, however, are often difficult or expensive to collect. Coastal systems are indeed subject to frequent and rapid variations in the water regime, causing hydrological data to become obsolete after a very short time. The granulometry of the sediment is conditioned by the average hydrodynamic regime, and measuring the size distribution of sediment particles is much easier than determining flow profiles. For this reason, sediment type can provide a robust indicator of the suitability of a substratum for clam growth. The significance of the coupled effect of hydrodynamic regime and sediment roughness on filter-feeders' growth was stressed by Wildish & Kristmannson (1979), and the effectiveness of sediment type as an indicator of growth speed is confirmed by the results of our statistical analysis (see Table 2).

Sediment data provided by Rossi's (1996) study were only available as categorized data, classified according to 3 substratum categories (sandy, intermediate, and muddy; see Table 1). Therefore, we contemplated the use of 3 different parameter sets to describe clam growth on different substrata.

To further account for spatial and environmental variability of body growth, we adopted a stochastic formulation of the model. The uncertainty affecting population growth is described by introducing a multiplicative noise term into Eq. (4):

$$\Delta L(t_1, t_2) = (L_\infty - L(t_1)) \cdot (1 - \psi(t_2)/\psi(t_1)) \cdot \exp(\varepsilon_L(t_1, t_2)) \quad (6)$$

$\varepsilon_L(t_1, t_2)$ is assumed to be a Gaussian random factor, with mean zero and variance $\sigma_{\varepsilon_L}^2 \cdot (t_2 - t_1)$, proportional to the elapsed time between 2 measures; $\sigma_{\varepsilon_L}^2$ has to be estimated from data. This formulation assumes body size increments to be affected by a multiplicative log-normal noise process, with variance increasing with

time (i.e. logarithms of length increments in each elementary time unit follow a Brownian motion process). This choice avoids length increments from taking negative values.

Survival model: Let us consider a cohort of individuals being seeded in a unit area of a farming site. The number (N) of individuals of the cohort decreases through time, driven by mortality. Its variation can be described by the simple differential equation:

$$\frac{dN}{dt} = \mu(t) \cdot N(t) \quad (7)$$

where $\mu(t)$ is the instantaneous mortality rate of the population. We consider $\mu(t)$ to be a linear function of both clam density and temperature, i.e.

$$\mu(t) = \mu_0 + \mu_T \cdot T(t) + \mu_N \cdot N(t) \quad (8)$$

where μ_0 , μ_T and μ_N are parameters to be estimated, $T(t)$ is water temperature, given by Eq. (2), and $N(t)$ is population density. While the formulation of density-dependence is standard (a logistic term), the hypothesis of linearity between mortality and temperature can be quite strong. It provides, however, a good approximation of the phenomenon, at least within the temperature range of the Sacca di Goro, as confirmed by the statistical analysis (Table 2). Note that clam density is expressed as number of individuals (not as weight) per unit area for 2 reasons: (1) mortality shows a clearer correlation with the number of individuals than with their total biomass; (2) in this way we obtain 2 uncoupled equations for the description of body size growth and survivorship, considerably diminishing the complexity of the problem. Integrating Eq. (7) with μ given by Eq. (8) we obtain:

$$N(t) = \frac{\varphi(t) \cdot N_0}{\mu_N \cdot N_0 \cdot \int_{t_0}^t \varphi(\xi) d\xi + \varphi(t_0)} \quad (9)$$

where N_0 is the population size at time t_0 , $\varphi(t)$ is defined as:

$$\varphi(t) = \exp\left(\frac{365}{2\pi} \mu_T f \cdot \cos\left(\frac{2\pi}{365}(t + e)\right) - (\mu_0 + \mu_T g) \cdot t\right) \quad (10)$$

and e , f and g are the parameters of the temperature model (Eq. 2).

A multiplicative noise term can be introduced to account for the effect of environmental stochasticity, namely we assume:

$$N(t) = \hat{N}(t, t_0, N_0) \cdot \exp(\varepsilon_N(t_0, t)) \quad (11)$$

$\hat{N}(t, t_0, N_0)$ is the right-hand-side term of Eq. (9) and $\varepsilon_N(t_0, t)$ is assumed to be a Gaussian random factor, with mean zero and variance increasing with time, namely

$\sigma_{\varepsilon_N}^2 \cdot (t - t_0)$, where $\sigma_{\varepsilon_N}^2$ has to be estimated from data. A lognormal noise term affecting the survivorship process is considered a standard assumption when testing for density-dependence (see Royama 1992, Dennis & Taper 1994).

Although *Tapes philippinarum* has actively reproduced in Northern Adriatic lagoons since its introduction, the effect of spontaneous settlement in farming areas is negligible compared to that of artificial seeding (Rossi 1996). In fact, the settlement of naturally recruited juveniles generally takes place near the sand spit delimiting the lagoon on its SW side, in localized areas some distance from most farming areas. If natural recruitment is indeed negligible and dispersal of adult clams is small compared to displacements implemented by operators (moving clams from overcrowded areas to areas where clams have already been harvested is common practice), and if we hypothesize that no residual clams are present before seeding (i.e. the harvest is almost complete), the dynamics of clams in each farming site can be simply described by the dynamics of a single cohort given by Eq. (11), with N_0 being the initial seeded density.

Model calibration. The parameter estimates were obtained by fitting the models of body growth and survivorship to the data collected from 1993 to 1995. We minimized the following cost functions with reference to body size growth (Eqs. 4 & 5), and survivorship (Eqs. 9 & 10), respectively:

$$J_G(k_0, k_T, L_\infty) = \sum_i \frac{1}{\Delta t_i} [\ln(\Delta L_{i,obs}) - \ln(\Delta L_{i,est})]^2 \quad (12)$$

$$J_S(\mu_0, \mu_T, \mu_N) = \sum_i \frac{1}{\Delta t_i} [\ln(N_{f,i,obs}) - \ln(N_{f,i,est})]^2 \quad (13)$$

where ΔL_i and $N_{f,i}$ are mean length increment and population size at the end of the i th experiment, the subscript obs identifies directly measured quantities, the subscript est denotes the corresponding estimates obtained by model simulation, and Δt_i is the length (in days) of the i th experiment. Each cost function is the sum of squared residuals for the relevant model. The parameter values that minimize J_G and J_S were found by using the Nelder-Mead simplex algorithm (Nelder & Mead 1965).

To evaluate the uncertainty of parameter estimates, we used the most classical nonparametric method, the bootstrap (Efron 1979), which aims at mimicking the sampling process by random resampling (with replacement) of the original data set. Resampling is repeated a number of times (depending upon the desired accuracy) and each sample is used to calibrate the model again, obtaining a new parameter set. This provides a probability distribution for each parameter, from which the statistics of interest (mean, variance, estimate bias, confidence intervals) can be calculated. In this work

Table 3. *Tapes philippinarum*. Results of model calibration by bias-corrected bootstrapping. For each parameter we show the expected value of the estimate, the standard deviation and the percentiles. Parameters of the growth and survival submodels as from Eqs. (2), (3) & (8), respectively. σ_{ε_L} and σ_{ε_N} : standard deviations of residuals as from Eqs. (15) & (16)

Submodel Parameter	Unit	Exp. value	SD	Percentiles		SD of residuals
				5th	95th	
Growth (mud)						
k_T	$10^{-4} \text{ } ^\circ\text{C}^{-1} \text{ d}^{-1}$	0.89	0.14	0.66	1.10	
L_∞	mm	50.60	2.63	47.75	55.80	
σ_{ε_L}	$10^{-2} \text{ d}^{-0.5}$					4.59
Growth (intermediate)						
k_T	$10^{-4} \text{ } ^\circ\text{C}^{-1} \text{ d}^{-1}$	1.40	0.17	1.10	1.66	
L_∞	mm	46.94	3.09	44.55	53.86	
σ_{ε_L}	$10^{-2} \text{ d}^{-0.5}$					4.84
Growth (sand)						
k_T	$10^{-4} \text{ } ^\circ\text{C}^{-1} \text{ d}^{-1}$	1.45	0.16	1.19	1.71	
L_∞	mm	54.64	3.37	50.69	61.29	
σ_{ε_L}	$10^{-2} \text{ d}^{-0.5}$					2.76
Mortality						
μ_0	10^{-3} d^{-1}	3.55	0.83	2.72	5.63	
μ_N	$10^{-6} \text{ ind.}^{-1} \text{ d}^{-1}$	6.29	1.34	4.80	9.06	
μ_T	$10^{-4} \text{ } ^\circ\text{C}^{-1} \text{ d}^{-1}$	-2.17	-0.69	-4.30	-1.74	
σ_{ε_N}	$10^{-2} \text{ d}^{-0.5}$					1.58

the original data set of 99 experiments was resampled 1000 times. The bootstrapped parameter estimates were then calculated as:

$$\theta_B = \frac{1}{n} \sum_{j=1}^n \theta_j^* \quad (14)$$

where θ_j^* is the value of the generic parameter θ estimated from the j th bootstrap replicate ($j = 1 \dots n$, with $n = 1000$). A bias-corrected estimate for the parameter θ was then calculated as $\theta_{B, \text{b.c.}} = 2 \cdot \theta_0 - \theta_B$ (Efron 1982), where θ_0 is the value of the parameter obtained using the original data set. Confidence intervals for parameter estimates were calculated by using the bias-corrected percentile method (Efron 1982).

As for the noise terms of the stochastic models, if the error follows the assumption of the models given by Eqs. (6) & (11), the following quantities should be expected to have a Gaussian distribution with zero mean and variance equal to $\sigma_{\varepsilon_L}^2$ and $\sigma_{\varepsilon_N}^2$ respectively:

$$e_{L_i} = \frac{1}{\sqrt{\Delta t_i}} \cdot [\ln(\Delta L_{i, \text{obs}}) - \ln(\Delta L_{i, \text{est}})] \quad (15)$$

$$e_{N_i} = \frac{1}{\sqrt{\Delta t_i}} \cdot [\ln(N_{f, i, \text{obs}}) - \ln(N_{f, i, \text{est}})] \quad (16)$$

The estimate of the parameters $\sigma_{\varepsilon_L}^2$ and $\sigma_{\varepsilon_N}^2$ were therefore obtained as:

$$\sigma_{\varepsilon_L}^2 = \text{var}(e_L) \quad (17)$$

$$\sigma_{\varepsilon_N}^2 = \text{var}(e_N) \quad (18)$$

where var indicates sample variance.

RESULTS

The results of the model calibration are given in Table 3. Note that, as the estimate of the growth parameter k_0 (Eq. 3) was not significantly different from zero, we re-calibrated the model eliminating k_0 . Also, the parameter set obtained for the survival model could generate slightly non-monotone survivorship curves, because the parameter μ_T is negative. Therefore, the model was re-calibrated by imposing $\mu(t)$ (Eq. 8) to be zero or positive at any instant t .

Fig. 3 compares observed versus predicted lengths and predicted versus observed densities respectively, supporting the good predictive performances of both submodels (body growth and survival).

There are 3 distinct growth models for the 3 classes of sediment type. We obtained increasing values of k_T for increasing proportions of sand in the substratum, indicating that clam growth is more rapid in sand than in mud. The values of L_∞ did not follow a clear trend, although sand was the most suitable substratum with respect to the asymptotic mean size L_∞ . The scatter plot in Fig. 4 (where the results of the bootstrap replicates are plotted in the $k_T - L_\infty$ plane) illustrates the clustered configuration of the parameter distributions for the 3 substrata.

The significance of using 3 distinct growth models instead of 1 unique model was tested by means of a nested model comparison. Residuals obtained with the model based on the 3 parameter sets were compared to those provided by a model with a single parameter

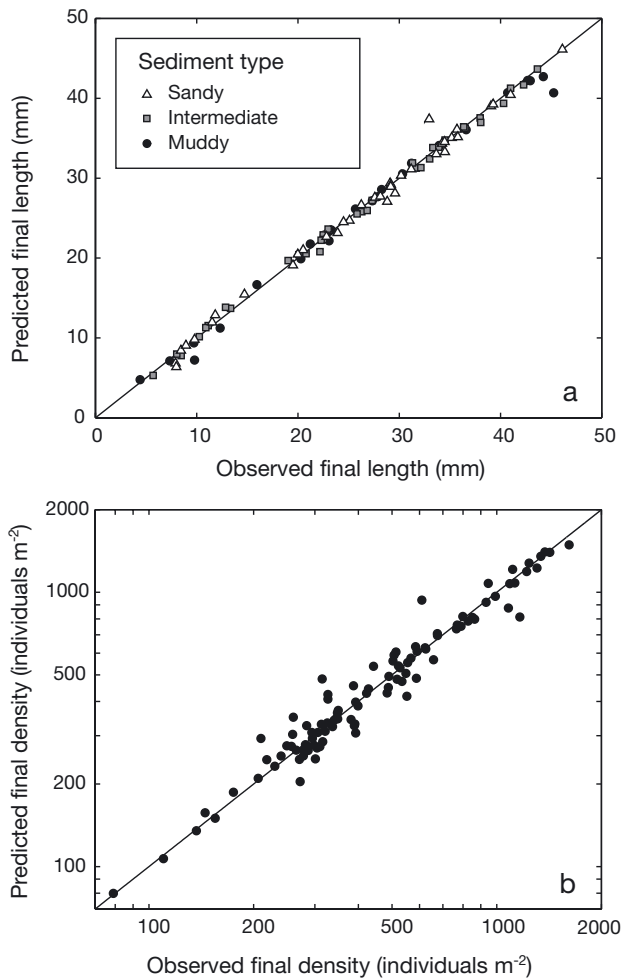


Fig. 3. *Tapes philippinarum*. Comparison between observed and predicted data. (a) Body-growth model: observed versus predicted final lengths as a function of sediment type. (b) Survival model: observed versus predicted final densities (log-scale)

pair, which was calibrated using the whole original data set with no distinction as to type of substratum. An F -test confirmed the significance of the difference between residual variances ($F = 18.87$, $p \ll 0.01$).

The normality of estimated residuals (Eqs. 15 & 16) was examined by means of a Kolmogorov-Smirnov test. It was confirmed for the growth models (muddy substratum: $d = 0.15$, $p > 0.2$; intermediate substratum: $d = 0.10$, $p > 0.2$; sandy substratum: $d = 0.14$, $p > 0.2$), while we obtained a borderline result for the survival model ($d = 0.12$, $0.1 < p < 0.15$). The parameters $\sigma_{\varepsilon_L}^2$ and $\sigma_{\varepsilon_N}^2$ were then estimated using Eqs. (17) & (18); their values are reported in Table 3.

By running the 2 stochastic models Eqs. (6) & (11) an adequate number of times over an adequate time horizon, we can generate not only the mean growth

and survival curves, but also the probability distribution of estimated clam size, density and biomass for a given set of initial conditions (initial length and density, seeding period and substratum). Fig. 5 shows the results of seeding 10 mm juveniles (10 mm is a common size for seed collected in natural nurseries) at a density of 1000 individuals m^{-2} on 1 May on a sandy substratum. The graphs highlight the effect of vital-rate fluctuations driven by temperature changes throughout the year. To calculate clam biomass from length, we used the allometric relationship reported by Solidoro et al. (2000) for *Tapes philippinarum* in Northern Adriatic lagoons:

$$W = 0.00026 L^3 \quad (19)$$

where W is the wet weight (in g) of a clam, and L its length (in mm). The total biomass B at a given time t is then calculated by multiplying W by the estimated clam density, i.e.

$$B(t) = 0.00026 L(t)^3 \cdot N(t) \quad (20)$$

Suitability of model for other lagoons

The question arises as to whether the model presented here can be effectively used to reproduce the demography of *Tapes philippinarum* at other sites. In fact, the model relies on some strong hypotheses, such as the linear dependence of vital rates upon temperature and the absence of food limitation. However, it should be noted that, at least in Europe, Manila clams have been intentionally introduced for commercial

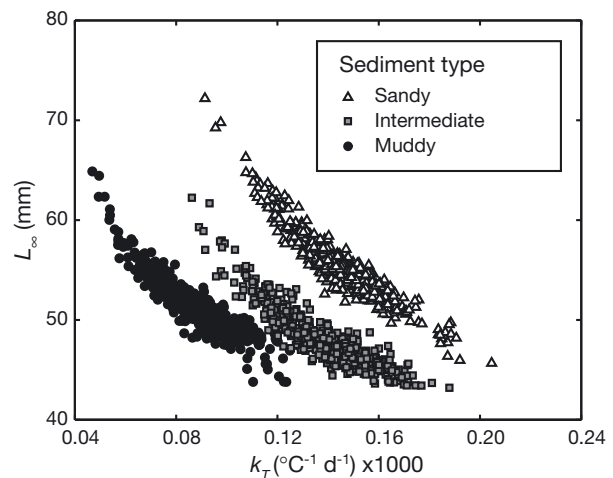


Fig. 4. *Tapes philippinarum*. Distribution of bootstrap replicates of L_{∞} (asymptotic mean size) and k_T (proportionality coefficient between Brody growth constant and temperature, see Eq. (3)) for the 3 growth models, corresponding to 3 different sediment types (sandy, intermediate and muddy)

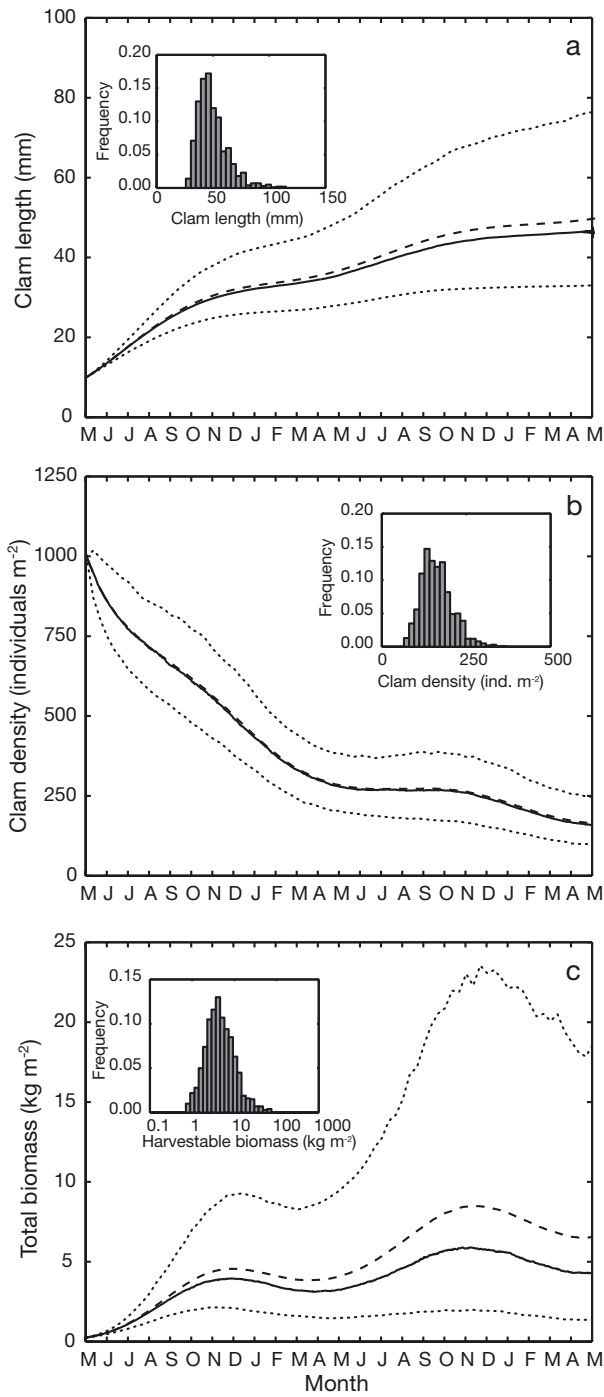


Fig. 5. *Tapes philippinarum*. Simulated body growth, survival and total biomass dynamics obtained by 1000 Monte-Carlo simulations of 2 yr duration with same initial conditions. —: median value; - - -: mean value;: 90% confidence intervals. Histograms in insets show empirical probability distributions for the 3 variables at end of simulations. (a) Body growth curve (seeding date 1 May, initial length 10 mm, sandy substratum); (b) survivorship curve (seeding date 1 May, seeding density 1000 individuals m^{-2}); (c) total clam biomass per unit area of rearing site (histogram in log-scale; initial conditions same as in a and b)

exploitation. As a consequence, the most suitable areas have been chosen for rearing, i.e. those characterized by relatively small temperature ranges and sufficient food supply. So, it is conceivable that our model can also perform efficiently for areas other than the Sacca di Goro lagoon. To assess the generality of the model we tested its performances against data from other European sites.

To validate the growth model, we used the experimental data of Robert et al. (1993) for 2 sites in the Bassin d'Arcachon (West France, Atlantic coast), Le Ferret and Les Jacquets. The Bassin d'Arcachon is a mesotidal system, characterized by the presence of large seagrass meadows and considerably lower eutrophication than Sacca di Goro. At both stations, hatchery spat of 10 mm length were seeded and their growth monitored over a 2 yr (1989 to 1990) period.

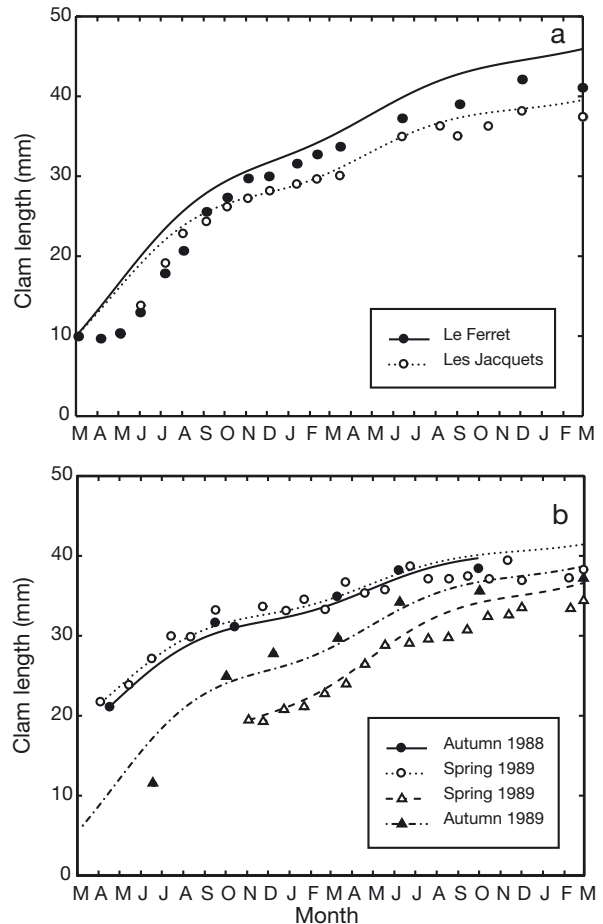


Fig. 6. *Tapes philippinarum*. Comparison between observed (●,○,△,▲) and simulated (—, , - - -, - - -) body growth at 2 sites in Bassin d'Arcachon (from Robert et al. 1993). (a) Growth of clams reared at Le Ferret and Les Jacquets; (b) growth of 4 commercial batches sown at different initial lengths and in different seasons at Les Jacquets

Additionally, at Les Jacquets, 4 commercial batches of clams, seeded in different seasons and at different sizes, were surveyed during the same period. A 2 yr temperature series was also recorded. No information was provided on sediment type at the 2 experimental sites. However, Le Ferret is strongly influenced by the Atlantic Ocean and its bottom can be expected to have a high sand content. Les Jacquets, in contrast, is likely to have a mixed (sand + clay) sediment composition, as have many sites in the bay interior.

We ran our model after setting the initial conditions (size at seeding and seeding period) to those reported for the different experiments by Robert et al. (1993). Clam growth in Le Ferret was simulated by choosing the parameter-set for sand, whereas for Les Jacquets we used the set calibrated with intermediate sediments (see Table 3). We calibrated 2 distinct temperature models with Robert et al.'s (1993) data. For Le Ferret we obtained $e = -64.07$, $f = 5.47$, and $g = 15.43$ (see Eq. 1). For Les Jacquets we used data from Gorp, an inner station near Les Jacquets, obtaining $e = -55.06$, $f = 8.08$, and $g = 15.85$.

Fig. 6 shows very good agreement between the observed data and the simulations. For the 2 simulations in Fig. 6a the determination coefficient R^2 was 0.89 (Le Ferret) and 0.95 (Les Jacquets), while for the simulations of Fig. 6b it ranged between 0.83 and 0.98.

For the survival model, we could find no data set as complete as that used for the growth model. Cigarría & Fernández (2000) do indeed show some mortality curves for *Tapes philippinarum* beds in the Eo estuary (NW Spain), but give only vague information about the seeding period, seeding densities and water temperature. In Fig. 7 we show 3 data sets from Cigarría & Fernández' (2000) experiments, together with 2 simulations obtained by running our model at 2 seeding densities (100 and 300 clams m^{-2}). We considered water temperature to follow the same pattern as at Le Ferret station (both sites are located in the Bay of Biscay).

Although a direct comparison cannot be made, the pattern followed by the experimental data and the simulations are quite similar, especially at the higher seeding density (300 clams m^{-2}), except for the first few months. In fact, Cigarría & Fernández (2000) separate the life history of the clams into 2 phases: a first phase characterized by high mortality (about 100 d), and a second phase of low mortality. Our data showed no evidence of this phenomenon, possibly due to the acclimation of hatchery clams (purchased from different countries) to the natural environment.

We can thus conclude that our model provides a fairly realistic description of *Tapes philippinarum*'s body growth and survival, despite uncertainty characterizing juvenile mortality.

Management implications

Combined, the growth and survival submodels can be used to forecast the yield associated with a given seeding policy. If the standing clam biomass of a given site is entirely harvested at the end of a rearing cycle, the curve in Fig. 5c can be interpreted as the harvestable biomass after a certain time has elapsed between seeding and harvesting. The biomass curve is characterized by annual peaks in the late fall, before the growth process slows down due to lower winter temperatures. This feature of biomass dynamics is generally valid, as it is essentially independent of a particular set of initial conditions (clam size and density at seeding and seeding season).

The biomass model provides a powerful tool for forecasting the total harvestable biomass of a farming site and for estimating the potential productivity of a farming area under given environmental and management conditions. A thorough bioeconomic analysis of clam-farming in a specific lagoon would require a description of its morphology, data on labor and fixed costs and on clam market prices, and a detailed description of seeding and harvesting activities. This would provide a realistic decision-support system for farming management, as the integration of economic and biological information would allow the optimization of seeding and harvesting cycles. This is beyond the scope of the present article. Nevertheless, useful information can be obtained by simply running model Eq. (20) to determine the production resulting from the

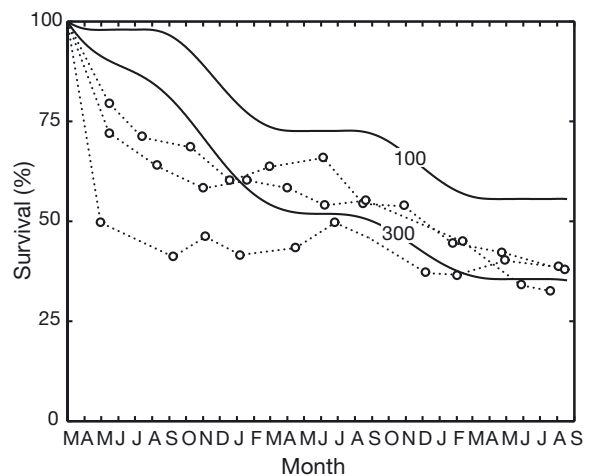


Fig. 7. *Tapes philippinarum*. Survival curves in the Eo estuary (from Cigarría & Fernández 2000). Observed data ($\cdots\circ\cdots$) compared with simulations at 2 seeding densities (100 and 300 clams m^{-2} , —). Note that original data represent predator-protected clam beds, while our model does not account for effects of predation

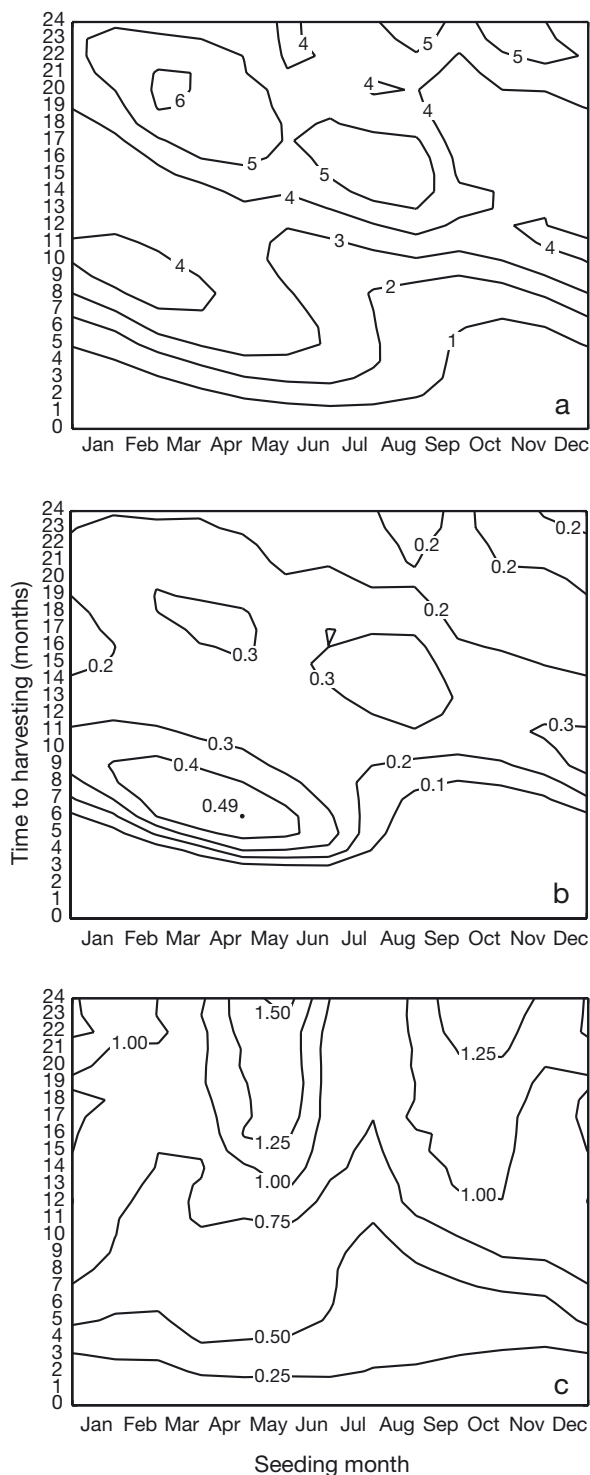


Fig. 8. *Tapes philippinarum*. Average production and associated uncertainty level as functions of seeding month and time to harvesting resulting from simulations of the stochastic model (initial length 10 mm, sandy substratum; seeding density 1000 individuals m^{-2}). (a) Standing clam biomass per unit area (kg m^{-2} , median values); (b) marketable yield per unit time ($\text{kg m}^{-2} \text{mo}^{-1}$, median values); (c) coefficients of variation

implementation of different seeding conditions and different harvesting times.

Fig. 8a shows the median standing biomass (equal to the total harvestable biomass) resulting from Monte-Carlo simulations as a function of seeding and harvesting times. The best results in terms of yield can be obtained by seeding in spring (February to April) and harvesting in late fall (20 mo later). This is in agreement with fishermen's experience and previous work based on data for both Sacca di Goro and other lagoons (Menesguen et al. 1984, Rossi 1996, Solidoro et al. 2000). Actually, a first biomass peak, about 4.5 kg m^{-2} , is reached after 8 to 9 mo (i.e. in the late fall of the same year), while the maximum harvestable yield (about 6 kg m^{-2} , a figure that is consistent with Rossi's [1996] estimates) is reached after 20 mo. However, the choice of a sound rearing policy cannot rely on the maximization of the total yield alone. In fact, more biomass could be harvested at the second than at the first peak (with an increase of 33%), but this would require a 120 to 150% increase in the time between seeding and harvesting. A more effective indicator of productivity can therefore be obtained by dividing the harvestable biomass by the time to harvesting. On the other hand, the actually marketable yield depends upon the probability that clams have reached the minimum commercial size (25 mm in the Sacca di Goro lagoon). Computing the marketable yield is indeed possible thanks to the Monte-Carlo approach, which provides not only the average size of clams, but also their length distribution. Fig. 8b shows the marketable yield per unit time. The maximum marketable yield per unit time (about $0.49 \text{ kg m}^{-2} \text{mo}^{-1}$) can be obtained by seeding in spring (between April and May) and harvesting 6 mo later (between October and November). Therefore, from this point of view, a rapid turnover of seeding and harvesting cycles would be more convenient.

These results refer to the average yield, but an important component of decision-making is variance in the yield. Fig. 8c shows the uncertainty level associated with biomass estimates (measured as coefficient of variation, ratio of standard deviation to mean): firstly, second biomass peak is associated with a much higher degree of uncertainty; secondly, there is an apparent trade-off between the maximizing total harvestable biomass and minimizing yield variability.

DISCUSSION

We have provided a novel and robust approach to describing growth and survival of *Tapes philippinarum* in eutrophic lagoons. The results of our study in Sacca di Goro demonstrate the existence of density-

dependent effects and the influence of temperature fluctuations on the vital rates of this species, 2 aspects of crucial importance for management purposes.

Density-dependent survival has a fundamental role in determining the major features of the dynamics of many aquatic populations, and sets the upper limits of productivity for farmed species. Despite this, the description of survival has usually been neglected; this is a weak point, because the negative consequences of 'overseeding' become apparent only when considering the negative correlation of survival with density. In fact, fishermen often seed great quantities of juveniles, a practice which can have a severe impact on the environment, having noxious effects on the benthic fauna, altering the structure of the biocoenosis, and resulting in high mortality rates and low productivity of clam beds (Sorokin et al. 1999, Bartoli et al. 2001, Melià et al. 2003).

By describing the dependence of growth and mortality rates upon seasonal temperature fluctuations, we have revealed the importance of temperature as a key variable in vital processes and underlined the alternation of favorable and unfavorable periods for seeding and harvesting. Spring is confirmed to be the most suitable seeding season if fishermen aim at maximizing the harvestable biomass, whereas late fall appears to be the optimal harvesting period.

The calibration of different growth models for different sediment types allows us to account for another important environmental factor. Our results show, in agreement with the literature (see e.g. Rossi 1996), that rearing sites with high sand content are preferable in terms of both growth speed and maximum attainable size. In fact, sandy bottoms indicate good water circulation and higher oxygen availability.

Our data give no evidence for size- or age-dependence of the mortality rate, although size-dependent mortality processes are common features in many aquatic species and have been reported also for molluscs (see e.g. Barbeau & Caswell 1999). Note, however, that predator losses, which are typically size-dependent (Cigarría & Fernández 2000), are almost negligible in the Sacca di Goro lagoon population.

Also, no significant dependence of growth and mortality rates upon chlorophyll *a* concentration (an indicator of phytoplankton density) was found. Food supply may not represent a limiting factor for clams in the study area (Rossi 1996), because the Sacca di Goro lagoon is a eutrophic water body. Although food supply could have a significant effect in oligotrophic systems, our model seems to work very well also when applied to sites with lower levels of eutrophication (e.g. the Bassin d'Arcachon).

The absence of density-dependent effects on body-size growth, which can have a significant impact on

the dynamics of bivalve populations in other environmental conditions (see e.g. Weinberg 1998), suggests that intraspecific competition does not chronically affect this bivalve community. Competition might indeed occur only during brief periods, possibly related to dystrophic events, therefore affecting survival rather than body growth. Quite likely, in this eutrophic environment oxygen rather than food availability is the limiting resource. The impact of hypoxic conditions on clam survival is still poorly known and deserves further investigation.

Compared to existing models for *Tapes philippinarum*, ours offers the advantage of relative simplicity combined with a good predictive power for a specific location; as the number of parameters is reasonably small, calibration can be carried out on the basis of field data that are easily available, and statistical significance of the model can be established. The application of a nonparametric calibration technique, such as the bootstrap, allows us to measure the uncertainty associated with parameter estimates.

The stochastic formulation accounts for inter-individual variability in vital rates and provides useful information about the uncertainty of production forecasts. This information can be quite valuable for management purposes, as it permits the association of a risk level with yield estimates. Deterministic models, such as those proposed previously to describe *Tapes philippinarum* life history (e.g. Meneguen et al. 1984, Solidoro et al. 2000), can indeed provide only an approximation of the average yield when applied to the management of clam farming. With a stochastic model we can not only evaluate the expected performance of a given management policy, but also the uncertainty of the forecasts. This approach can therefore be effective for the development of risk-averse management policies, a choice that can be attractive when planning the exploitation of biological resources (Walters 1986) whose dynamics are intrinsically affected by a high level of uncertainty. For these reasons, we believe that the demographic model presented here, properly integrated with bio- and socio-economic information, can be a powerful tool in the management of clam-farming. It could provide useful guidelines for an efficient and sustainable exploitation of *T. philippinarum* in the future.

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