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**Growth-related life history traits of an invasive gammarid species:
evaluation with a Laird-Gompertz model.**

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C. Piscart, S. Devin, J.-N. Beisel and J.-C. Moreteau: Growth-related life history traits of an invasive gammarid species: evaluation with a Laird-Gompertz model.

Abstract: Although the invasive gammarid *Dikerogammarus villosus* (Crustacea, Amphipoda) is a recent successful invader of Western Europe's lakes and rivers, and a threat to North American aquatic ecosystems, its biology is scarcely known. Different growth models for each sex were established for the first time for a natural population of a freshwater gammarid. The Laird-Gompertz growth curve was used, on account it fit the best to our data, and was associated with an environmental forcing function to adjust the growth rate according to seasonal variations of environmental conditions. It was applied to a length decomposition obtained using the Bhattacharya's method, realised on data obtained from a one-year population dynamics study. The models allowed an assessment of biological traits such as life span, the age of sexual maturity, the potential number of generations per year and the growth rate depending on environmental conditions. Growth-rate differences between males and females were consistent with biological processes such as the allocation of energy for reproduction. *D. villosus* had higher rates of growth and earlier sexual maturity than all other taxa, demographics that perhaps explain its invasive tendencies and its ability to colonise numerous new ecosystems, thus to become a cosmopolitan freshwater species.

C. Piscart, S. Devin, J.-N. Beisel and J.-C. Moreteau: Growth-related life history traits of an invasive gammarid species: evaluation with a Laird-Gompertz model.

Résumé: Bien que le Gammaridae invasif *Dikerogammarus villosus* (Crustacea, Amphipoda) soit une espèce ayant récemment colonisé avec succès les hydrosystèmes d'Europe de l'Ouest, et qu'il constitue une menace pour les écosystèmes dulçaquicole d'Amérique du Nord, sa biologie reste méconnue. Des modèles de croissance ont été construits pour la première fois pour chaque sexe d'une population naturelle de gammare dulçaquicole. La courbe de croissance de Laird-Gompertz a été utilisée, associée à une fonction de forçage environnemental permettant d'ajuster la croissance aux variations saisonnières du milieu. Ces fonctions ont été appliquées à une décomposition de taille obtenue par la méthode de Bhattacharya obtenue sur des données provenant d'une étude de dynamique des populations menée sur un an. Ces modèles ont permis de déterminer des traits biologiques tels que l'espérance de vie, l'âge de maturité sexuelle, le nombre potentiel de générations par an et le taux de croissance en fonction des conditions environnementales. Les différences de taux de croissance entre mâles et femelles cadrent avec des processus biologiques tels que l'allocation d'énergie pour la reproduction. Une comparaison des caractéristiques biologiques de différents gammars d'eau douce ou saumâtre a souligné le caractère invasif de *D. villosus* (fort taux de croissance et maturité sexuelle précoce) et sa capacité à coloniser de nombreux nouveaux écosystèmes, donc de devenir une espèce cosmopolite en eau douce.

Introduction

The freshwater gammarid *Dikerogammarus villosus* Sowinsky is a Ponto-Caspian species first observed in the Rhine Basin in 1995 (bij de Vaate and Klink 1995) and in one of its main tributaries, the Moselle River, in 1999 (Devin et al. 2001). The ability of *D. villosus* to colonise new lakes and rivers easily after introduction has already been suggested by several studies (Nesemann et al. 1995; Kelleher et al. 1998). The consequence of its introduction into an ecosystem on the macroinvertebrate community can be significant, in particular because it is a competitive species exhibiting a large size and predatory behaviour (Dick and Platvoet 2000; Dick et al. 2002).

In spite of the importance of this species, its main biological, physiological and ecological traits are not well known. To date, results have been published about its reproduction (Ciolpan 1987; Muskó 1990; Kley and Maier 2003; Devin et al. *in press*), its geographical distribution (Devin et al. 2001; bij de Vaate et al. 2002) and its wide tolerance to salinity and temperature (Bruijs et al. 2001; Wijnhoven, 2003). However, no studies have been carried out to date on the growth of *D. villosus*, though growth-rate is generally assumed to play a central role in the biological invasion process (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001).

Growth models based on the length of individuals have not thus far been used to describe the population dynamics of freshwater gammarids in natural conditions. In the past, logistic models were used to describe weight increase for *Gammarus pulex* (L.) (Sutcliffe et al. 1981), *Gammarus roeselii* Gervais and *Gammarus fossarum* Koch (Pöckl 1992, 1995) under laboratory conditions. In the natural environment, two models are generally used to describe growth of a species (Gamito 1998): the Laird-Gompertz growth model and the Von Bertalanffy linear growth

equation. In this study, we innovate in modelling growth-at-length of natural populations of an invasive freshwater gammarid. The chosen model was associated with a temporal function to describe seasonal changes in *D. villosus* growth rates. The Cloern and Nichols (1978) is a function that could be integrated in a model to express time as a sinusoid. A lot of environmental parameters evolve with time, so we state that such a function integrates a whole range of ecological parameters such as temperature, chlorophyll-a concentration and dissolved oxygen levels. It has already been used successfully in several studies (Appeldoorn 1987; Le Gallo and Moreteau 1988).

A mathematical model could be a powerful tool in determining the mechanisms that underlie a biological invasion process. Moreover, associated with a traditional study of the life history of *D. villosus* (Devin et al. in press), growth modelling of a natural population allowed us to assess different biological life-history traits such as the reproduction period (by retro-calculation computing), age of sexual maturity, life-span and the potential number of generations per year, each parameter recognised as playing an important role during an invasion process (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001).

The results found with the growth model for *D. villosus* will be discussed in the light of similar modelling approach for other gammarid species.

Materials and Methods

Sampling protocol

D. villosus was studied at Argancy, a sampling station on the Moselle River in France (49°12' N; 6°12' E). The population was sampled monthly from December 2000 to March 2001

and twice a month between March 2001 and December 2001. Two kinds of artificial substrates, with volumes of 2 and 5 liters and aperture surfaces ranging between 46 and 122 cm², were used. It allowed us to optimise the sorting of the individuals when very rich densities were reached in the substrates. For each date, both substrates were oriented vertical to the river bottom at approximately 0.5-2 m from the bank. The river temperature was recorded on each sampling occasion. Main physicochemical parameters for our study site were obtained from a regional freshwater database, the 'Banque de l'Eau Rhin-Meuse - Réseau National des Données sur l'Eau'.

Each *D. villosus* collected was measured to the nearest 0.1 mm from the tip of the rostrum to the base of the telson using a stereo-microscope fitted with an eyepiece micrometer. Adult individuals (longer than 6 mm) were sexed, the others were categorised as juveniles. The animals thus collected were used to adjust the growth-at-length model of *D. villosus*.

Analysis of monthly length-frequency structures

To separate a complex length-frequency distribution into cohorts, each cohort being defined as those individuals of the same age, a preliminary analysis indicated that the Bhattacharya method (Bhattacharya 1967) was particularly efficient with our data. The Bhattacharya graphical method consists of separating normal distributions, each representing a cohort of *D. villosus*, from the overall distribution, starting on the left-hand side of the total distribution. Once the first normal distribution has been determined, it is removed from the total distribution and the same procedure is repeated as many times as possible (Fig. 1). For each cohort, the mean size of the individuals, the corresponding standard deviation and the individual number were estimated.

Model choice

A preliminary analysis tested whether it is the Laird-Gompertz or the von Bertalanffy model that fit the best with the growth increment calculated. Coefficients of determination were respectively of 0.858 and 0.832. These values were not statistically different (t-test, $p=0.35$), thus this criteria is not sufficient to choose a model. However, the von Bertalanffy model provides a linear adjustment, so that the growth speed never decrease, while the growth increment of *D. villosus* is lower for large individuals. The only model that allow such a decrease in growth rate is the Laird-Gompertz model, thus we select this one.

Growth model equation

Growth of *D. villosus* was modelled by fitting a Laird-Gompertz curve to the length-at-date data using the Non-Linear module of the Statistica software (StatSoft 2000). According to Ricker (1979), the Gompertz equation used was:

$$[1] \quad L_t = L_0 \exp(k(1 - e^{-at}))$$

Where L_0 corresponds to length at $t=0$, k is the growth rate of the population, a is a dimensionless parameter such that ka is the growth rate at $t=0$ and L_t is the length at a given age t expressed in weeks.

The differences observed for each mean length of cohorts between two successive sampling dates were used to determinate the weekly growth rate. Growth rates were obtained by using the derived function of the Laird-Gompertz equation (Debouche 1979; Tanaka and Kikuchi 1980) :

$$[2] \quad \frac{dL}{dt} = k * L * \ln(L_\infty / L_t)$$

where L_{∞} is the asymptotic length of the population studied.

An efficient model had to take into account seasonal variations in environmental conditions, with suitable conditions for growth during spring and summer and slower growth during winter. To this end, a sinusoidal equation called the environmental forcing function (Ef) was used. The Ef must always be greater than or equal to zero because the growth cannot be negative. The selected environmental forcing function used, derived from the Cloern and Nichols (1978) equation (Le Gallo and Moreteau, 1988), is expressed as:

$$[3] \quad Ef = \exp(\alpha * \sin(2 * \pi / 52 * (WS - \beta)))$$

Where α and β are the adjusting constants of the model in time and WS is the time in weeks.

By combining equations 2 and 3, a general model for the *D. villosus* growth rate has been developed:

$$[4] \quad \frac{dL}{dt} = k * Lt * \ln(L_{\infty} / Lt) * \exp[\alpha * \sin(2 * \pi / 52 * (WS - \beta))]$$

The parameters of this model will be determined with the non-linear module of Statistica software (StatSoft 2000), using the quasi-Newton estimation method, which tends to minimise least squares during the process of adjustment of the model.

Results

Sexual differentiation and monthly length-frequency structures identified

A total of 2,710 males and 4,095 females were collected and measured during the sampling period. Distinct differences were found in the length distributions of males and females.

The mean length of males is higher than the mean length of females ($t = -27.03$, $df=6803$, $p < 0.0001$), this length difference being of $15 \pm 3 \%$.

The maximum length for males of *D. villosus* was 22.8 ± 0.1 mm (sampled in June 2001) and 18.6 ± 0.1 mm for females (sampled in March 2001). We chose to fix the asymptotic length at 23 mm for males. Females being 15 % shorter than males, we fixed female asymptotic length at 20 mm. For a full year survey, 19 cohorts for each sex were identified using the Bhattacharya method. The progression of the mean length considered for each cohort is reported in Fig. 2. The tracking of each cohort over time corresponds to compromises which follow four rules: (1) a cohort has a size which cannot decrease in the lapse of time considered, (2) the growth rate is not faster in winter than in summer, (3) the number of new cohorts observed after births should be the same for both sexes, (4) the variation in the growth rate over time must be biologically coherent (the size increase must fit with those classically encountered for freshwater gammarids and the growth rate variations shouldn't be too abrupt in regard to seasonal one).

Growth rates and environmental factors

The growth rates (G) were determined with $[(L_t - L_{t-1}) / (WS_t - WS_{t-1})]$ values for males and females. The values of growth per week ranged between 0.3 mm and 1.6 mm for males, this last value being observed for individuals measuring between 7 and 12 mm in spring. For females, the growth rates varied between 0.4 mm and 1.2 mm per week, the maximum value being observed in spring and summer (temperatures always above 12 °C) for individuals measuring between 7 and 13 mm. The minimum rates for males (0.3 mm per week) and females (0.4 mm per week) were observed for all sizes during the winter periods 2000 and 2001 when water temperatures fall below 12°C.

Instantaneous or specific growth rates (G_s , % $Lt. day^{-1}$, an expression of growth) were determined and were correlated significantly for males and females with the mean length of animals (Fig. 3 and Table 1). As can be expected from these observations, specific growth rates were highest for young adults and G_s decreased with body size. The G_s -values ranged between 0.3 % and 3.1% for males and between 0.6 % and 2.5 % for females (Fig. 3). The mean growth-rate is $1.3 \% \pm 0.6 \% Lt. day^{-1}$ for males and $1.5 \% \pm 0.4 \% Lt. day^{-1}$ for females. Moreover, G_s -values depended on the temperature, the highest values being estimated for the highest temperatures (Fig. 3). A comparison of linear regression models corresponding to the three temperature levels chosen arbitrarily ($T \leq 12^\circ C$, $12 < T \leq 18^\circ C$ and $T > 18^\circ C$) show that the G_s -values of males are not significantly different from those of females when water temperatures exceed $18^\circ C$ (ANCOVA: slope comparison $F_{1,45}=0.423$, $p=0.519$ and intercept comparison $F_{1,46}=2.686$, $p=0.108$), corresponding to May-October 2001 period and for temperatures between $12^\circ C$ and $18^\circ C$ (ANCOVA: slope comparison $F_{1,15}=0.225$, $p=0.642$ and intercept comparison $F_{1,16}=0.152$, $p=0.702$). When water temperatures drop below $12^\circ C$, the female G_s -values are significantly higher than male G_s -values (ANCOVA: slope comparison $F_{1,23}=0.477$, $p=0.497$ and intercept comparison $F_{1,24}=4.481$, $p=0.045$ for intercept).

A seasonal variation in water temperature was considered, with the highest value during the summer (mid July, $24.4^\circ C$) and lowest during winter 2001 (mid-December 2001, $3.2^\circ C$). Optimal growth temperatures were found between June and August (Fig. 4), when water temperatures ranged between 20 and $22^\circ C$. In winter and early spring, when the temperatures were below $12^\circ C$, the absolute growth rates of females were higher than those of males (Fig. 4) agreeing with the results found with the specific growth rates (Fig. 3).

Several environmental factors, such as concentrations of Ca^{2+} ions ($mg.l^{-1}$) and dissolved oxygen ($mg.l^{-1}$), the seasonal pattern of Chlorophyll a concentration ($\mu g.l^{-1}$) and conductivity

($\mu\text{S}\cdot\text{cm}^{-1}$) were measured, but only Chlorophyll a concentration was correlated to the variations in the growth rate (Spearman rank correlation, $r_{\text{spearman}}=0.495$, $p < 0.0001$ for males and $r_{\text{spearman}}=0.319$, $p = 0.015$ for females).

Application of the Gompertz model with an environmental forcing function

Values of the parameters for males and females in equation 4 are presented in Table 2. The Laird-Gompertz model coupled with an environmental forcing function resulted in a good fit to length data, as shown by the determination coefficient ($r = 0.50$ for males and $r = 0.56$ for females) and p values ($p < 0.0001$) for the overall growth parameters (Table 2).

The variations in the growth rate $k(t)$ over the course of a year (Fig. 4) showed that the amplitude of the seasonal variation was lower for females than for males. The growth of females was higher in winter but fell below that of males when the water temperature exceeded $15\text{ }^{\circ}\text{C}$ in May 2001. After mid-October 2001, the water temperature dropped below $15\text{ }^{\circ}\text{C}$ and the growth of females again overtook the growth of males.

The curves calculated from observed sizes of cohorts obtained during the reproductive peak were plotted (Fig. 5). Newborn *D. villosus* measure approximately 1.8 mm (Devin et al. in press). The construction of an S-shaped model shows three phases: the exponential phase in the beginning, the linear phase around the inflection point and the satiation phase, when the final size is asymptotically approximated.

Our simulations for each cohort highlighted the regular arrival of new cohorts each 15 to 25 days from February to November (Fig. 2 and results not shown). However, the number of newborns at each date allowed us to consider that *D. villosus* presents three main reproductive periods, in mid-April, July, and in September-October (Fig. 5). During these three periods, reproduction increased and contributed to the large majority of individuals (Devin et al. in press).

The simulations with the Laird-Gompertz model were realised for these three reproduction peaks (Fig. 5), and highlighted seasonal growth differences.

Discussion

To our knowledge, the use of growth models to describe the growth of a freshwater gammarid in natural conditions has not been published to date. We have shown that the Laird-Gompertz growth model associated with an environmental forcing function efficiently described the growth at length of the invasive species *D. villosus*. This model can be used to determine certain biological traits such as the growth rate depending on environmental conditions, life span, age of sexual maturity and the potential number of generations per year.

The mean length observed in this study shows that males of *D. villosus* are longer than females. This difference has already been observed for *D. villosus* in the Danube river (Nesemann et al. 1995), for *Gammarus fossarum* and *Gammarus roeselii* (Pöckl 1995) and for *Gammarus pulex* (Sutcliffe et al. 1981; Gee 1988). In the literature, the maximum length of *D. villosus* cited was 30 mm (Nesemann et al. 1995) but the maximum lengths observed in the Moselle River were 22.8 ± 0.1 mm for males and 18.6 ± 0.1 mm for females.

Mean growth rates of each of the *D. villosus* cohorts were estimated and were found very important compared to that of other gammarid species. Logically, the rate changes according to the season and to body length, thus, the use of the environmental function in the model appears necessary. The maximum observed rates were 1.6 and 1.2 mm per week for males and females respectively. The maximum rate observed is associated with medium-sized individuals (between

7 and 13 mm), these sizes corresponding to the linear phase around the inflection point of the growth curve.

Study of major environmental factors shows that the growth rate was strongly correlated with the water temperature, which is an important parameter usually related to amphipod life history traits (Kinne 1961; Pöckl 1995; Rajagopal et al. 1999). Recently, Bruijs et al. (2001) showed the role of this factor for *D. villosus* populations and particularly for the colonisation process and species maintenance in new temperate areas.

An alternative form of analysis is the commonly used relative, specific growth rate, which is conveniently expressed as a percentage rate of growth, G_s . According to the temperature level, linear regressions of the G_s -values against Lt gave good fits for males and females. Thus, G_s declined with increasing Lt until the animals reached asymptotic maximum length. For *D. villosus*, the average growth rate is $1.3 \% \pm 0.5 \% Lt.day^{-1}$ for males and $1.5 \% \pm 0.4 \% Lt. day^{-1}$ for females. Above $12^\circ C$, no differences between the sexes being observed, the growth rate of *D. villosus* can be compared to that of other species. Specific growth rates were reported or calculated with length measures collected in the literature (Table 3). The comparison between the values cited in the literature and values in this study remains rather difficult because data concerning the G_s -values were generally obtained with fixed temperatures and under laboratory conditions. However, in comparing the same temperatures and the same sizes, the G_s -values of mature *D. villosus* are higher than those of others freshwater gammarids such as *G. fossarum* and *Gammarus duebeni* Lilljeborg as well as estuarine gammarids such as *Gammarus zaddachi* Sexton and *Gammarus salinus* Spooner (Table 3).

Under laboratory conditions, there are some contrasting results concerning the life spans of various gammarid species. For example, Welton and Clarke (1980) predict for *G. pulex* a lifespan of 17-23 months for females and up to 30 months for males at lower temperatures (4-17

°C) while Teichmann (1982) found lifespan between 14 and 18 months at 5-20 °C. Hynes (1955), in natural populations of *G. pulex*, found that at relatively high temperatures males and females normally live for 12-15 months. Starting from our model, with temperatures ranging between 3.2 °C and 22.2°C, we can estimate the *D. villosus* lifespan at 11-17 months for males and 10-11 months for females. Considering the river temperature regime and the specific growth rate in length, which increased with temperature, the predicted life spans appear rather long. Males would live longer than females, which explain the higher total number of cohort/date combinations for males compared to females (N=52 and 40 respectively). This difference has already been observed for *G. fossarum* (Pöckl 1992) and for *G. pulex* (Welton and Clark 1980) probably because males are less physiologically stressed than females. Furthermore, the disappearance of females after a reproductive period may limit overlap of generations (Fig. 5), reducing within-population competition and thus favouring the invasive ability of *D. villosus*. Such a lack of intraspecific competition has been shown to enhance species invasiveness (Holway et al. 1998).

With regard to the onset of sexual maturity, the smallest ovigerous females was observed at a size of 6 mm, which can be defined as the potential size of sexual maturity of *D. villosus*. This size corresponded to an age ranging between 33 and 55 days according to the date of birth. The age of sexual maturity for various freshwater gammarids was determined in several studies under laboratory conditions. For *G. pulex*, it is 87.5 days at 20 °C and 133 days at 15 °C (Welton and Clarke 1980; Sutcliffe et al., 1981). For *G. fossarum*, sexual maturity was reached in 115 days at 20.2°C and 250 days at 12°C and ranged between 80 days at 20.2°C and 210 days at 12 °C for *G. roeselii* (Pöckl 1995). For *Gammarus tigrinus* Sexton, sexual maturity was reached in 42 days at 25°C and 91 days at 16 °C (Hynes 1955), while Savage (1982) found it occurring in 39

days at 25°C and 61 days at 15°C. In comparison with other freshwater gammarids, *D. villosus* females are the most precocious in terms of reaching sexual maturity.

A total of 19 cohorts was observed between December 2000 and December 2001 with an appearance frequency generally ranging from 15 to 25 days (data obtained by retrocalculation, not shown). However, the number of juveniles sampled highlighted three main reproductive periods, though obviously the species reproduces all year long (Fig. 5). The growth model provided proof that each of these main generations could be traced to the reproduction of individuals recruited from the preceding main reproductive period. The size necessary for sexual maturity was quickly attained regardless of the season and allowed for egg development to produce a new generation that was observed in a peak of juveniles. Hence, *D. villosus* can be considered a multivoltine species. Two alternative hypotheses can be proposed to explain the significant number of cohorts. First, egg development can be very fast and the same female can reproduce twice within a short time period. Clemens (1950) has shown that the incubation period for *Gammarus fasciatus* Say ranged between 7 days at 24 °C and 21 days at 15 °C and Savage (1982) showed that for *G. tigrinus* the number of generations was approximately 50% greater at 25°C than at 15°C, results confirmed by Pöckl and Timischl (1990) for *G. fossarum* and *G. roeselii*. It is biologically possible that two successive reproductions could take place during the time observed between successive cohorts. Chambers (1977) has shown for example that theoretically, *G. tigrinus* could produce 16 broods during the breeding season between March and November. Pöckl (1992) reported that adult females of *G. fossarum* and *G. roeselii* released a brood approximately six to ten times. The second hypothesis supposes that females produced their broods in several waves one after another. According to Devin et al. (in press) the maximum relative abundance of ovigerous females observed was 32.6 % of the total number of females. Thus there are at least 67.4 % of females at each date that were not ovigerous. Those females can

became ovigerous and produce a brood at any time, explaining that there are a so high number of cohorts.

The seasonal changes in the study of the theoretical growth of males and females shows that the differences between the sexes are strongly correlated with water temperature. An important threshold in *D. villosus* growth appeared at 15°C, the growth of females dropping below that of males above this temperature. This result can be explained by the reproductive cycle during which female resources are, for the most part, allocated to egg production. A study of *Dikerogammarus haemobaphes* Eichwald reproduction showed that females began egg production when the water temperature exceeded 17°C (Muskó 1993) and another Ponto-Caspian amphipod, *Corophium curvispinum* Sars, was found to extend egg production when water temperature exceeded 10°C (Rajagopal et al. 1999) or 12°C (Muskó 1993), depending on the ecosystem.

The general conclusion from the analysis of growth at length presented is that a mathematical model can be useful in order to check certain hypotheses formulated during classical analyses of population dynamics. However, the choice of an appropriate growth model is important as it may have a decisive effect on the simulation results of a dynamic ecological model. The use of a model allowed us to describe the growth of immature individuals, showing that mature *D. villosus* females were much younger than other freshwater gammarids. Moreover, we have shown that *D. villosus* has a short generation time and a rapid growth rate (particularly among the younger animals). These three attributes are very important in the biological invasion process (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001). Bruijs et al.(2001) highlighted a wide environmental tolerance and finally Devin et al. (in press) show that this abundant and widely distributed species also has a high reproductive capacity. Our contribution confirms the

invasive potential of *D. villosus* and suggests its ability to maintain itself in newly colonised areas, becoming a cosmopolitan species in freshwater ecosystems.

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Table 1 : Regression equations for the relationship between specific growth rates, G_s . ($\% Lt.day^{-1}$) and mean size of cohorts. The G_s -values were separated into 3 categories according to water temperature T : $T < 12^\circ C$; $12 \leq T < 18^\circ C$; $T \geq 18^\circ C$. n is the number of cohort, constants a and b are obtained with $G_s = b .Lt + a$, and r is the coefficient of determination.

	T (°C)	<i>n</i>	<i>b</i> estimate	<i>a</i> estimate	<i>r</i>	<i>p</i>
Males	T < 12	14	-0.071	1.488	0.57	0.0175
	$12 \leq T < 18$	11	-0.116	2.479	0.61	0.0235
	$T \geq 18$	27	-0.153	3.228	0.71	<0.0001
Females	T < 12	7	-0.104	2.017	0.71	0.0357
	$12 \leq T < 18$	12	-0.167	3.004	0.80	0.0005
	$T \geq 18$	21	-0.187	3.382	0.76	<0.0001

Table 2 : Estimates of growth parameters of the equation 4. L_{∞} was fixed to 23 mm for males and 20 mm for females. n is the number of observed growth rates. The coefficients of determination r for males ($r = 0.50$) and females ($r = 0.56$) are highly significant ($p < 0.0001$).

		Parameter Estimate	Std. dev.	<i>t</i>-values	df	<i>p</i>
Males	k	0.0999	0.0051	19.51	49	<0.0001
$n = 52$	α	-0.4216	0.0663	-6.35	49	<0.0001
$L_{\infty} = 23 \text{ mm}$	β	-11.4318	1.1061	-10.34	49	<0.0001
Females	k	0.1189	0.0036	32.65	37	<0.0001
$n = 40$	α	0.2781	0.0399	6.96	37	<0.0001
$L_{\infty} = 20 \text{ mm}$	β	12.8432	1.1518	11.15	37	<0.0001

Table 3 : Mean G_s -values (G_s % $Lt.day^{-1}$) observed in experimental conditions

Species	G_s-values	ages	temperatures	Sex	Literature sources
<i>G. duebeni</i>	1.6 - 2.4%	Juveniles	19-20°C	Juveniles	Kinne, 1959
<i>G. duebeni</i>	0.3 - 0.7%	Young adults	19-20°C	Males/Females	Kinne, 1959
<i>G. fossarum</i>	0.8 %	Young adults	20°C	Males/Females	Teckelmann, 1974
<i>G. fossarum</i>	1.3 %	Young adults	20°C	Males	Pöckl, 1995
<i>G. fossarum</i>	1.1 %	Young adults	20°C	Females	Pöckl, 1995
<i>G. fossarum</i>	0.9 %	Young adults	15°C	Males/Females	Teckelmann, 1974
<i>G. fossarum</i>	1.1 %	Young adults	15°C	Males	Pöckl, 1995
<i>G. fossarum</i>	0.9 %	Young adults	15°C	Females	Pöckl, 1995
<i>G. fossarum</i>	0.9 %	Young adults	12°C	Males	Pöckl, 1995
<i>G. fossarum</i>	0.7 %	Young adults	12°C	Females	Pöckl, 1995
<i>G. fossarum</i>	0.6 %	Young adults	10°C	Males/Females	Teckelmann, 1974
<i>G. fossarum</i>	0.7 %	Young adults	8°C	Males	Pöckl, 1995
<i>G. fossarum</i>	0.6 %	Young adults	8°C	Females	Pöckl, 1995
<i>G. fossarum</i>	0.2 %	Young adults	5°C	Males/Females	Teckelmann, 1974
<i>G. salinus</i>	9.9 %	Young juveniles	19-20°C	Juveniles	Kinne, 1960
<i>G. salinus</i>	6 %	Juveniles	19-20°C	Juveniles	Kinne, 1960
<i>G. zaddachi</i>	9.4 %	Young juveniles	19-20°C	Juveniles	Kinne, 1961
<i>G. zaddachi</i>	5 %	Juveniles	19-20°C	Juveniles	Kinne, 1961
<i>G. salinus</i>	1 %	Adults	19-20°C	Males/Females	Kinne, 1960
<i>G. zaddachi</i>	1 %	Adults	19-20°C	Males/Females	Kinne, 1961
<i>D. villosus</i>	0.5 - 1.5%	Young adults	7-8°C	Males	This study
<i>D. villosus</i>	1.1 - 1.3%	Young adults	7-8°C	Females	This study
<i>D. villosus</i>	1 - 2.4%	Young adults	13-16°C	Males	This study
<i>D. villosus</i>	1.6 - 1.8%	Young adults	13-16°C	Females	This study
<i>D. villosus</i>	1.6 - 2.6%	Young adults	18-22°C	Males	This study
<i>D. villosus</i>	1.7 - 2.3%	Young adults	18-22°C	Females	This study

Fig. 1: Example of a decomposition of a size-frequency distribution into several normal distributions with the Battacharya method. The distribution provided is that of males, the first of September.

Fig. 2: Evolution of the mean length of the cohorts of males (a) and females (b) identified between December 2000 and December 2001 using the Bhattacharya method. The isolated points were estimated using the Bhattacharya method, but could not be connected.

Fig. 3: Specific growth rates (G_s % $Lt.day^{-1}$) plotted against mean length of cohort for *D. villosus* males (a) and females (b). The curves for specific growth rates are drawn from the constants of the linear equations in Table 1. The G_s -values were separated into 3 categories according to water temperature T .

Fig. 4: Seasonal changes of the theoretical $k(t)$ -values found with the Gompertz growth model for males and females along one year according to the temperatures.

Fig. 5: Simulation of growth for the three reproduction peaks for males (a) and females (b) using the Laird-Gompertz model associated with the environmental function. The dotted line represents the frequency of juveniles in the population.

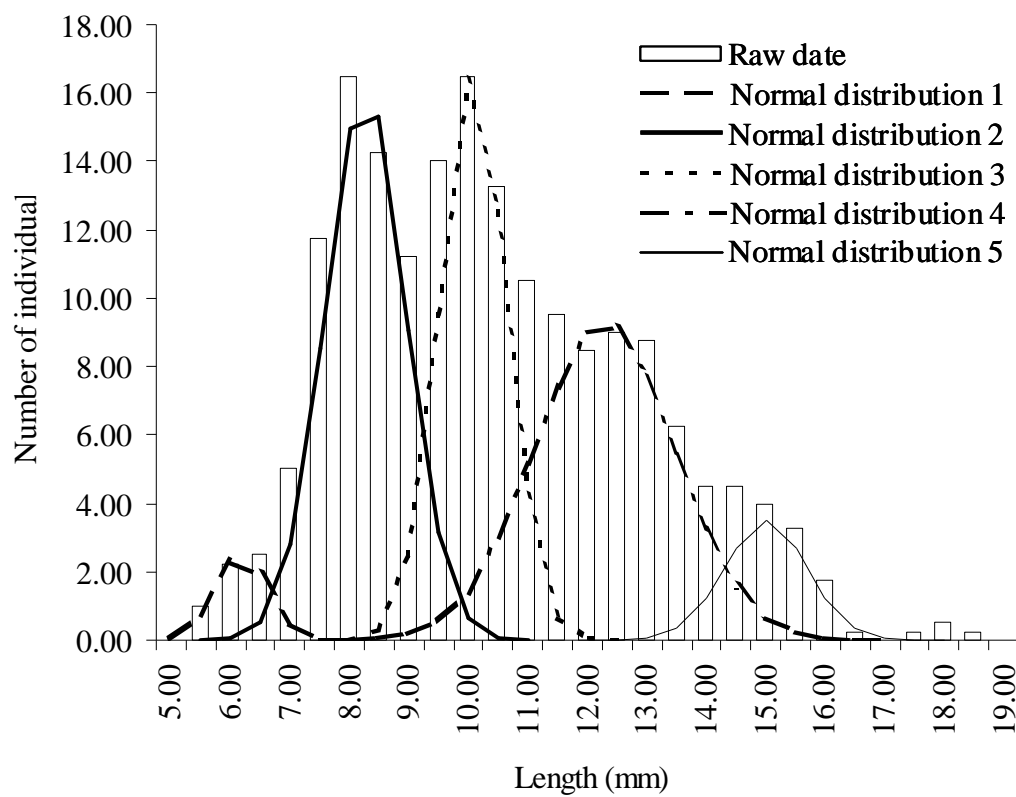


Figure 1. Piscart et al.

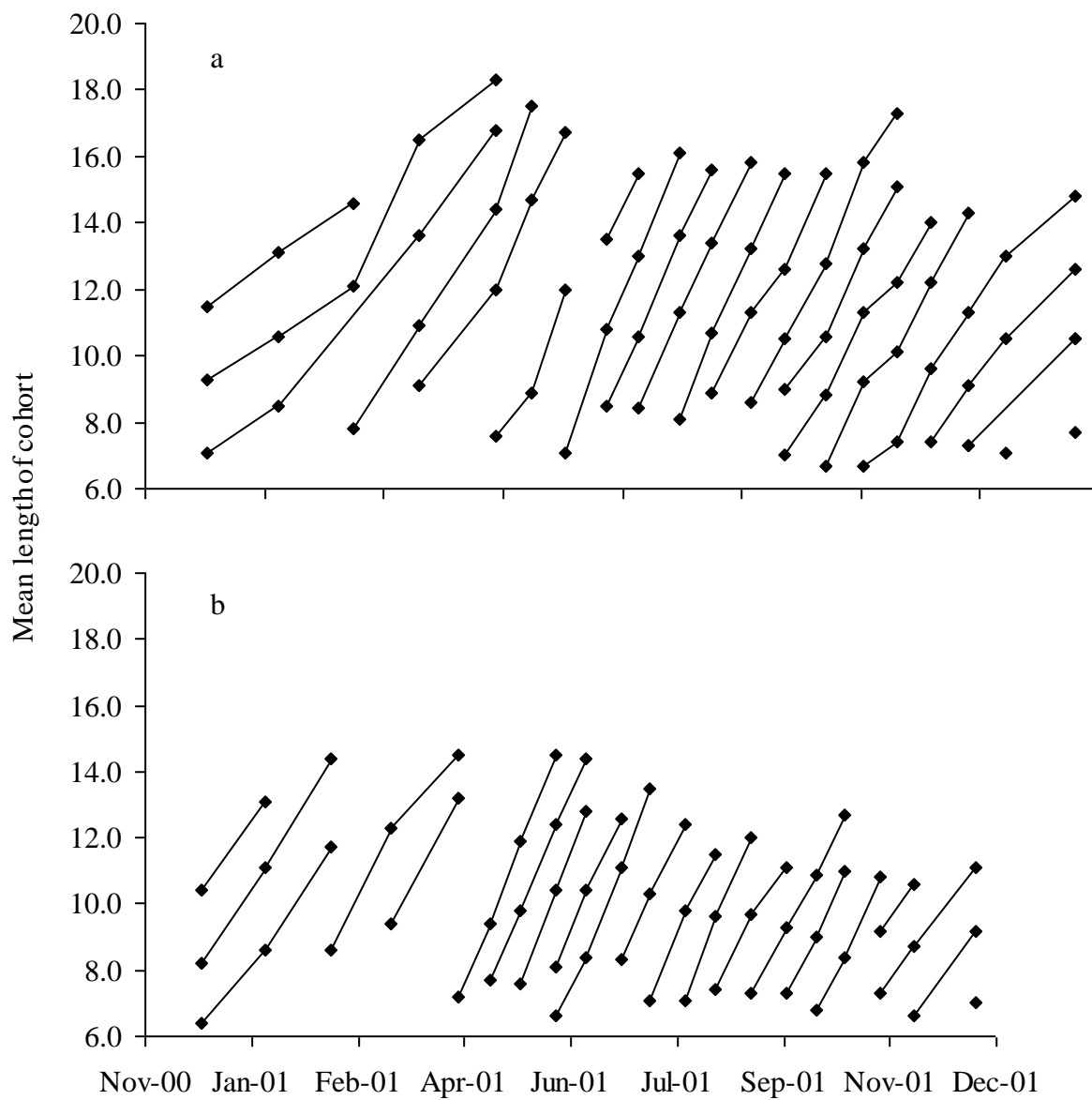


Figure 2. Piscart et al.

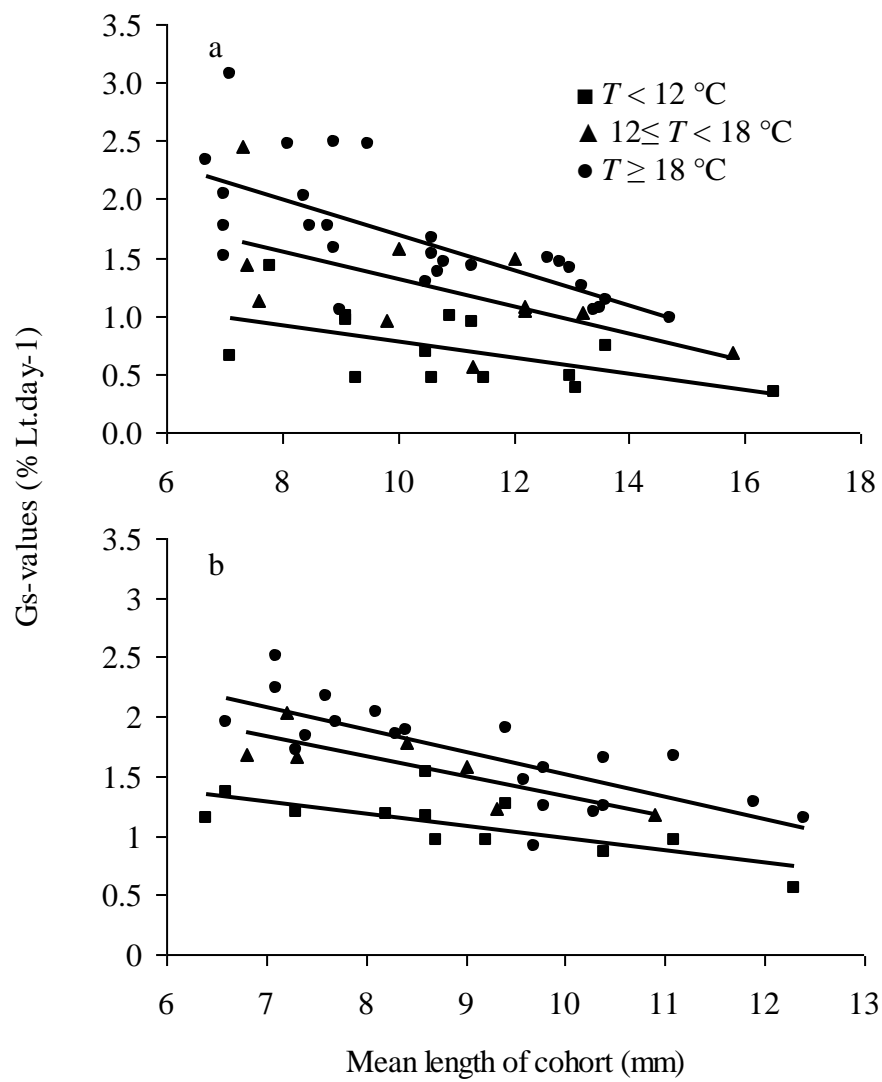


Figure 3. Piscart et al.

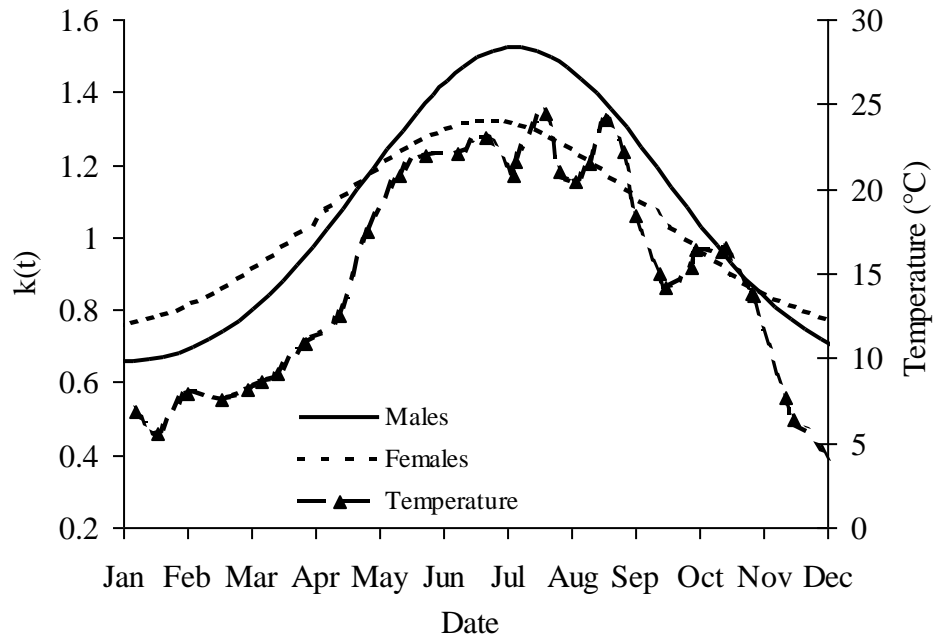


Figure 4. Piscart et al.

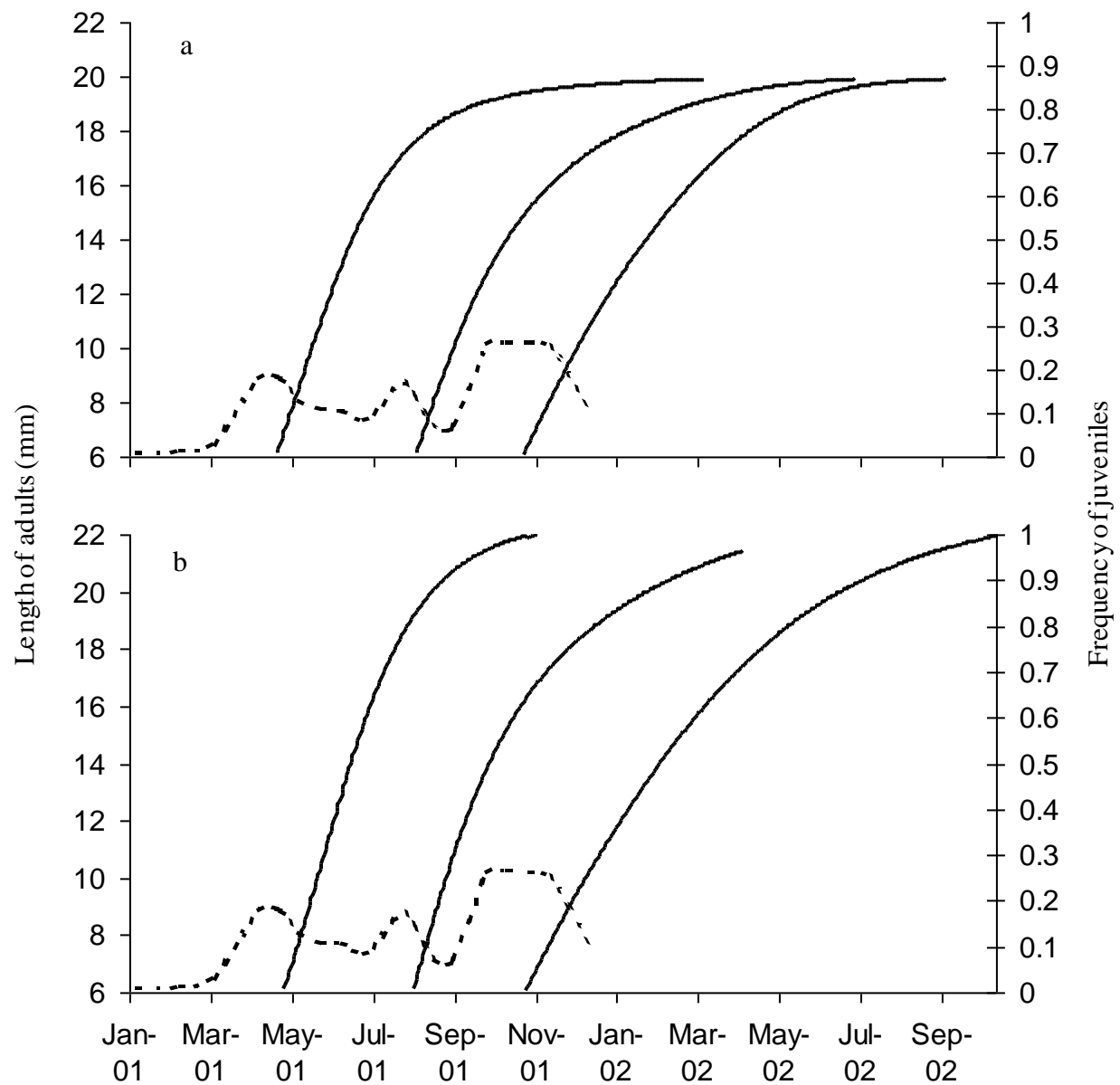


Figure 5. Piscart et al.