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Growth of *Corophium volutator* Under Laboratory Conditions

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Abstract Temperature-dependent growth is an important factor in the population model of *Corophium volutator* that was developed to translate responses in a 10-day acute bioassay to ecological consequences for the population. The growth rate, however, was estimated from old data, based on a Swedish population. Therefore, new growth rates are estimated herein from two experiments using *Corophium volutator*. To save time, a tool was developed to use image analysis to measure *Corophium volutator*. The experiments show that *Corophium volutator* has a low growth rate at low temperatures (5–10°C). At higher temperatures no difference in growth rate between 15°C and 25°C was found. The growth rate from these experiments is comparable to data found in literature. A new relationship between temperature and individual growth was estimated, and incorporated into the *Corophium* population model. As the model also uses the same temperature relationship for reproduction, the modelled population growth rate at different temperatures changes as a result of the new data. The new growth rate and the updated temperature relationship result in reduced tolerance to external stressors, as previously predicted by the model.

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Introduction

The tube-dwelling amphipod *Corophium volutator* (Pallas, 1766) is an ecologically important representative of the infauna of marine sediments and is widely distributed along the northeastern American and western European coasts. It is an important prey for several migratory shorebirds (e.g. Gratto et al. 1984; Wilson 1989; Hamilton et al. 2003), demersal fish (Pihl 1985; Hawkins 1985) and a number of invertebrates (Pihl 1985; Sandberg 1994). *Corophium volutator* is widely used as bioassay tool for the assessment of contaminated sediments in countries like the Netherlands (Lourens et al. 1995), the United Kingdom (Thain et al. 2000), Germany (Peters et al. 2002) and Belgium (Heijerick et al. 2000). These are all 10-day acute tests that determine mortality. Although these acute bioassays have proven to be a useful tool in the assessment of sediment contamination, the ecological consequences for populations are not readily predicted from the bioassay response. One way of obtaining a better idea of ecological consequences of contaminated sediments is the use of chronic bioassays with reproduction endpoints (Peters and Ahlf 2005; Van den Heuvel et al. 2007; Scarlett et al. 2007). Another approach is to model the *Corophium volutator* population and to evaluate responses from acute tests using this model. Such a model, which gives more ecological meaning to acute bioassay tests results and helps reduce their uncertainty, was developed by Smit et al. (2006). One of the important factors in this model is the temperature-dependent growth rate of individual *Corophium*. The age and length of *Corophium volutator* are related by a growth curve describing the change of the length of an individual over time, based on an initial length, maximum length, food availability, and the growth rate. In the model of Smit et al. (2006), growth is described according to Kooijman (1993) by the Von Bertalanffy growth curve (Bertalanffy 1938):

$$L(t) = L_{max} \times \{1 - \exp[-\gamma \times t]\},$$

where
$L(t)$ = length of the individual at age t (mm),
L_{max} = maximum length of the individual (mm),
γ = growth parameter (month^{-1}),
t = time (d).

The Von Bertalanffy growth curve is often used in fisheries research (e.g. Chen et al. 1992; Lorenzen 1996; He and Stewart 2002), but also to study, for instance, the post-larval growth of the golden-striped salamander (Lima et al. 2000). Less often, the Von Bertalanffy growth model is used to describe the growth of evertebrata: Munch-Petersen and Kristensen (2001) used the Von Bertalanffy growth equitation to estimate the growth parameters for mussels in the Danish Wadden Sea, and Hernandez-Llamas and Ratkowsky (2004) used the Von Bertalanffy growth curve to estimate the growth of several crustaceans and molluscs.

The *Corophium volutator* model by Smit et al. (2006) was calibrated using literature data in order to describe a *Corophium volutator* population in Dutch coastal waters. The growth parameter is based on a study by Möller and Rosenberg (1982). They reported a length increase of 2 mm per month, which corresponds to an individual growth parameter, γ, of 0.33 month^{-1} at 20°C. This growth parameter is incorporated into the model, but it is based on old data and the population was Swedish, living under different climatic circumstances compared to Dutch populations.

The objective of this paper is to study the growth rate of *Corophium volutator*, originating from a Dutch population, at several temperatures. From this study the temperature-dependent growth parameter, γ, is estimated and compared to the growth parameter presently used in the model.

To perform this study a large amount of *Corophium volutator* individuals need to be measured. Measuring *Corophium volutator* by hand, as Ciarelli et al. (1994) did, is a time-consuming exercise. The time needed to measure individuals can be reduced by using image analysis. There are several examples of the use of image analysis in ecological studies. Johnson et al. (2001) used image analysis in the oyster embryo–larval test. Instead of counting malformed D-larvae by hand, they tried to automate the counting by using image analysis. González and Watling (2002) used image analysis to measure different specimens of *Hyallela* to describe new species. As a last example, Chen and Folt (2002) used image analysis to measure body lengths of zooplankton. The second objective of this study is to develop a tool to measure *Corophium volutator* using image analysis.

Materials and Methods

Corophium volutator

All amphipods used in this study were collected in the Oesterput. The Oesterput is an intertidal area in the Eastern Scheldt (The Netherlands). Animals were collected by sieving sediment from the intertidal zone with seawater over a 500-µm mesh. The remaining sediment fraction, containing the animals, was transported to the laboratory.

Length Measurement Using Image Analysis

In May, June and July 2000 *Corophium volutator* were collected in the Oesterput. In the laboratory a total of 492 *Corophium volutator* were preserved using 4% formalin solution. Formalin does not affect the length of the organisms.

For image analysis purposes, preserved *Corophium volutator* were taken out of the formalin solution, dried on a tissue and laid down on a blank sheet of paper. The animals were photographed using a digital camera. This resulted in pictures with a resolution of 1216×912 pixels. For calibration purposes a ruler was photographed together with the *Corophium volutator*. After photography, all *Corophium volutator* were measured individually (body length without antennae) under a binocular microscope.

The digital photographs were analysed using the software Image Pro Plus 5 (Media Cybernetics). Since *Corophium volutator* lie bent rather than straight without manipulation, straightforward measurement of length does not lead to the desired result. Two different options were used to obtain the best result: measuring the 'skeleton' after using a filter option, and measuring the surface area of the *Corophium volutator*.

A linear regression analysis ($y = ax + b$) between the length measured under a microscope and both the length of the 'skeleton' and the surface area resulted in an estimate of the parameters for a and b, and in a regression coefficient R^2.

In November 2003, the relationship between length measured under a microscope and length derived with image analysis was validated. Ninety-three *Corophium volutator* were collected in the field (Oesterput) and measured both by microscopy (measured length) and image analysis (calculated length).

The relationship between measured and calculated length was plotted, a trend line calculated and compared with the line $y = x$.

Corophium volutator for the Experiments

Parental stock amphipods used in this study were collected at the Oesterput, and kept in large aquaria at the standard temperature of 15°C. The water was refreshed every week by removing three-quarters of the overlying water and gently adding new seawater at 15°C. The overlying water was aerated continuously. *Corophium volutator* were fed with flake food for aquarium fish (Yadi).

The first newborn animals appeared after a period of three to four weeks when the sediment was carefully sieved over a 250-µm sieve.

Temperature Experiment

Four hundred and eighty one-month-old *Corophium volutator* (average length 3.1 mm) were randomly divided into 24 one-litre glass beakers, each containing 200 ml of sieved Oesterput sediment (250 µm) and 800 ml of filtered sea water. Subsequently these 24 glass beakers were randomly assigned to one of four temperatures: 5°C, 10°C, 15°C and 25°C. All glass beakers were placed in temperature-controlled rooms with a light regime of 24 hours of light. The *Corophium* were not fed; food was taken from the sediment. Twice a week, 400 ml of overlying water was refreshed. The experiment took place in May and June 2001. The confounding factors of salinity, oxygen saturation, pH and temperature were measured twice a week and checked using the criteria of Postma et al. (2002).

After two weeks, two glass beakers were randomly selected from each temperature experiment and the content was sieved through a 500-µm sieve. All living *Corophium volutator* were measured using image analysis. This was repeated after four and six weeks.

Time-dependent lengths were tested within each temperature using a Kruskall–Wallis test. Differences between the lengths in week six at the two highest temperatures were tested using a Mann–Whitney *U* test. Differences were deemed significant when $p < 0.05$.

Full Growth Experiment

Eight hundred two-week-old animals were randomly divided into 40 one-litre glass beakers, each filled with 200 ml sieved Oesterput sediment (250 µm) and 800 ml filtered sea water, so each glass beaker contained 20 *Corophium*. The experiment was conducted at a temperature of 15°C. Three times a week, animals were fed with suspended flake food for aquarium fish (Yadi) at a dosage of 30 mg for each beaker glass, added to the overlying water. This amount of food is enough to feed the *Corophium*, without the risk of decaying materials on the sediment. Twice a week, 400 ml of overlying water was refreshed. The confounding factors of salinity, oxygen saturation, pH and temperature were measured twice a week and checked using the criteria of Postma et al. (2002).

For a period of three to eight weeks after the start of the experiment, every four or five days, four randomly selected beaker glasses were sieved and the surviving *Corophium volutator* were measured by image analysis. This experiment was conducted between September and November 2003.

Updated Temperature Dependence of the Growth Parameter γ

Based on the data collected in the temperature experiment, and the procedures as described by Smit et al. (2006), a new Arrhenius temperature relationship was defined. From the results of the full growth experiment, a growth parameter, γ, was estimated using the software programme SYSTAT version 8.0, including the standard error on this estimate and the 95% confidence interval.

Model Calculation

To evaluate the effects of the updated temperature relationship and the new individual growth parameter on the results of the population model, calculations of the population growth rate were performed after the new figures were incorporated into the *Corophium volutator* model developed by Smit et al. (2006). Calculations were performed using the temperature regime between May 1994 and April 1995 to calculate a new yearly population growth rate for this year. Also, the maximum mortality measured in a bioassay was calculated to reduce this yearly population growth rate to one.

Results

Image Analysis

In total, 452 *Corophium volutator* were sampled in the Oesterput (May: 75, June: 239, July: 138) for image

Table 1 Results of the regression analysis ($y = ax+b$)

	a	Standard error of *a*	*b*	Standard error of *b*	R^2
'Skeleton'	0.57	0.016	1.8	0.080	0.74
Surface area	0.35	0.0062	2.6	0.039	0.88

analysis purposes. Both the regression analysis between measured length and 'skeleton' length, and between measured length and surface area, resulted in a significant regression. Table 1 shows the results. Because of the higher R^2, the surface area was used to estimate lengths in the experiments.

In November 2003, the derived model was validated using 93 *Corophium volutator*. The measured and calculated lengths are plotted in Fig. 1, together with the $x = y$ line. This line shows the optimal situation, measured and calculated lengths are equal. Next to the $x = y$ line, the trend line is added ($y = 0.8645x + 0.604$; $R^2 = 0.7807$). The figure shows an overall good estimate of the lengths. Only the lengths of the smaller (< 3 mm) *Corophium volutator* are underestimated when Image Pro plus is used. For the other length classes, calculated lengths are approximately equal to the measured lengths.

Temperature Experiment

In this experiment *Corophium volutator* were kept at several temperatures. All confounding factors met the criteria stated by Postma et al. (2002). Figure 2 shows the average length and standard error of *Corophium volutator* in this

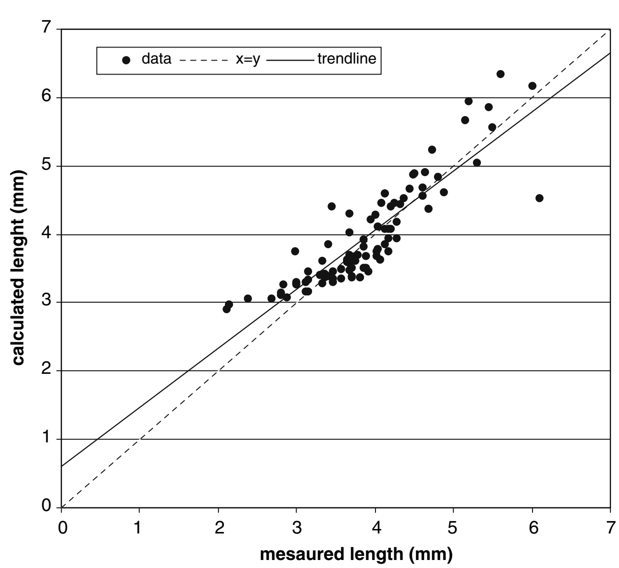

Fig. 1 Relation between measured length and calculated length of *Corophium volutator*, including the line $x = y$ and trend line

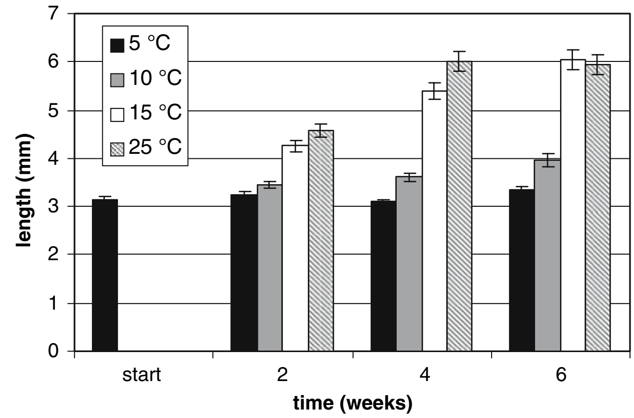

Fig. 2 Average lengths, including standard error, of *Corophium volutator* after two, four and six weeks at several temperatures

experiment. At a temperature of 5°C the *Corophium volutator* grew from 3.14 to 3.34 mm (average). Although this was no large increase, the Kruskall–Wallis test showed that there were at least two moments in time where the lengths differed significantly ($p = 0.005$). The average growth rate at this temperature was 0.0048 mm/d. At a temperature of 10°C, the lengths also differed significantly ($p < 0.001$) at at least two time points. The average growth rate was 0.019 mm/d. *Corophium volutator* kept at a temperature of 15°C also show a significant growth ($p < 0.001$) between at least two time points, but a higher rate compared with 10°C. At a temperature of 15°C an average growth rate of 0.069 mm/d was achieved. At 25°C, finally, growth was also significant ($p < 0.001$) between a minimum of two time points. The rate was comparable to the rate at 15°C, namely 0.067 mm/d. A Mann–Whitney *U* test shows that there is no significant difference in length at week six between *Corophium volutator* at 15°C and 25°C ($p = 0.692$). Based on the results, an updated Arrhenius temperature relationship was constructed. As the new data only refers to temperatures between 5°C and 25°C, the parameters describing the higher temperature ranges (>25°C) were not changed. Figure 3 shows the best-fit (minimum log likelihood) temperature relationship based on the new data. The parameters that were changed are the lower tolerance temperature level T_L, the Arrhenius temperature constant (T_A), the Arrhenius temperature constant for the lower tolerance temperature (T_{AL}). See Smit et al. (2006) for a description of the different parameters. The updated values for T_L, T_A and T_{AL} are 283, 10 and 50,000 K, respectively.

Full Growth Experiment (15°C)

The temperature experiment showed an optimum growth rate at 15°C. Therefore, the full growth experiment was

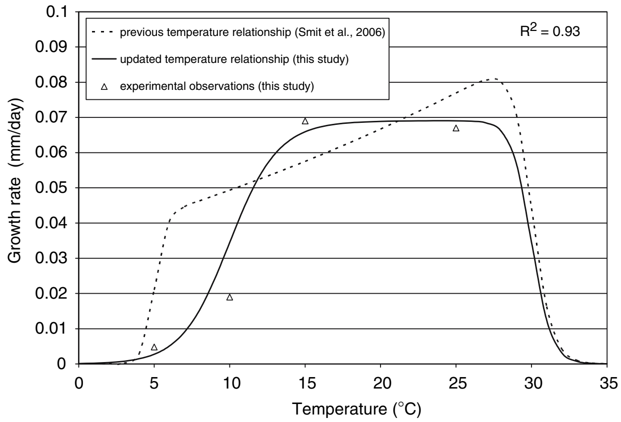

Fig. 3 Previous and updated Arrhenius temperature relationship between growth rate (mm/day) and temperature as a result of the new available data from this study. (Pearson $R^2 = 0.93$)

conducted at a temperature of 15°C. All confounding factors measured during this experiment met the criteria stated by Postma et al. (2002). In this experiment *Corophium volutator* grew from an average length of 3.1 to 5.7 mm in 31 days, yielding a daily growth rate of 0.084 mm/d. Figure 4 shows the average length, including the standard error, at each age.

The relationship between age and length was fitted using the Von Bertalanffy growth curve, using 469 data points in total and the value of the growth rate parameter γ estimated. Table 2 shows an overview of the results.

The value of 0.359 for γ at a temperature of 15°C was incorporated into the *Corophium volutator* model developed by Smit et al. (2006).

Model Calculations

As a result of the updated growth rate and temperature relationship, the resulting temperature relationship with the population growth rate, as derived with the model, also

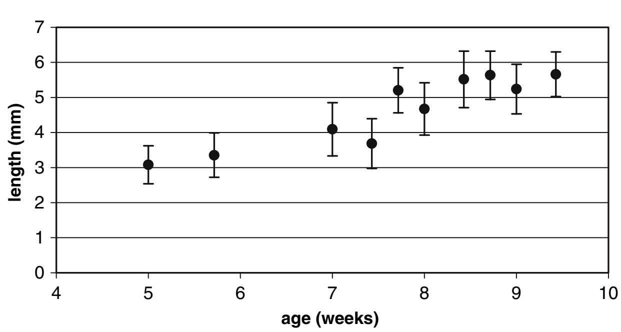

Fig. 4 Average length of *Corophium volutator*, including standard error, at each age

Table 2 Estimated parameters of the Von Bertalanffy growth curve.

Parameter	Value
Growth parameter γ (month^{-1})	0.359
Standard error	0.00643
Confidence interval (95%)	0.347–0.372
N	469

changed. Figure 5 presents the new temperature dependency of the population growth rate.

Based on the temperature profile between May 1994 and April 1995, the model predicts an average population growth rate of a *C. volutator* population of 1.015 month^{-1}. With the model, it is predicted that bioassay mortality of 10.9% will reduce this value to 1 month^{-1}.

Discussion

The Oesterput, where the amphipods used for this study were collected, is situated in a temperate climate zone. From December to March the average water temperature is approximately 5°C. In April, October and November, the average temperature is approximately 10°C. May, June and September have an average temperature around 15°C, and in July and August the average temperature is around 20°C (www.waterbase.nl).

Temperatures (or temperature-dependent resources) are known to determine the life history of *Corophium volutator* (Wilson and Parker 1996). Peer et al. (1986) showed that the growth rate of *Corophium volutator* slowed considerably after the end of September and remained low until April. Cunha et al. (2000) showed lower growth rates of *Corophium multisetosum* in the period December to April compared to the period September to November.

The temperature experiment shows that at 5°C the *Corophium volutator* in the laboratory show a small amount of growth, which is in agreement with the months in which this temperature occurs in the field and with the growth rates according to Peer et al. (1986) and Wilson and Parker (1996). In this study *Corophium volutator* starts to grow slightly at an experimental temperature of 10°C. Looking at the months in which this temperature occurs, the growth rates are lower according to the results of the study of Peer et al. (1986), but for October and November there is disagreement with the results of Cunha et al. (2000). This difference could be caused by the difference in subspecies, as this study was performed with *Corophium volutator*, not with *Corophium multisetosum*.

In the temperature experiment *Corophium volutator* showed high growth rates at temperatures of 15°C and

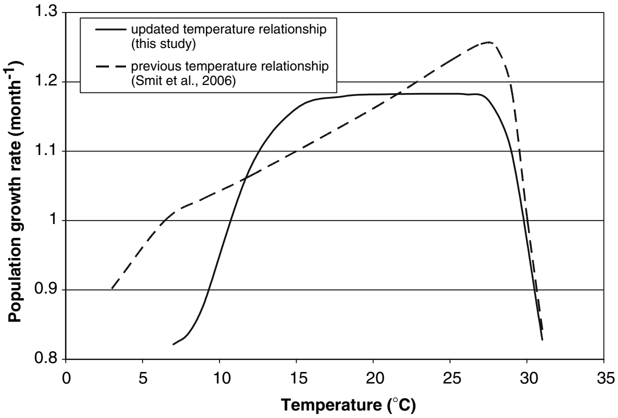

Fig. 5 Temperature dependency of the population growth rate for a *Corophium volutator* population derived from the Leslie matrix model described by Smit et al. (2006)

20°C, with no significant difference between these temperatures. This is in agreement with the months in which both Peer et al. (1986) and Cunha et al. (2000) found high growth rates. Looking at the temperatures of the sea water during the period between May and September, which is the growth season, it is not surprising that no significant difference between 15°C and 25°C was found. Peters and Ahlf (2005) showed that even higher temperatures can have a negative effect: the breeding success of *Corophium volutator* was significantly better at 15°C than at 23°C.

Considering the amount of sediment (200 ml), the number of animals (20), the permanent light availability for algal growth and the duration of the experiment (six weeks), it was not likely that food became limited during the temperature experiment.

In the full growth experiment a growth rate of 0.084 mm/d was found, which is comparable to data found in literature for young *Corophium volutator*. Van den Heuvel et al. (2007) found a mean growth rate of 0.08–0.10 mm/d, using *Corophium volutator* from the same population as this study. Peters and Ahlf (2005) found an average growth of 0.07 mm/d in laboratory experiments, and Conradi and Depledge (1998) observed a growth rate of around 0.06 mm/d over the first seven weeks.

Peer et al. (1986) plotted the relation between total body length and daily length specific growth rate, and showed a linear relationship between both parameters. This means that older animals have lower growth rates. This is confirmed by the study of Brown et al. (1999), who reported growth rates of around 0.03–0.04 mm/d based on length measurements up to 100 days, and the results of Peer et al. (1986) who estimated a growth rate of 0.019–0.029 mm/d for the whole population.

In the full growth experiment there is no possibility of food limitation, because the sediments were saturated with food due to feeding with fish food.

The results of the development of a tool to automate measuring the length of *Corophium volutator* seem to be successful. A significant relationship was found between the surface area calculated by the image analysis software and the measured lengths. This validation several years later shows that this model remained valid. With the presented recalculation model there will always be an error around the measured lengths, especially for the smaller and larger animals. This study, and also a study by González and Watling (2002), shows that it is possible to develop such tools for measuring lengths of amphipods.

From the full growth experiment the growth parameter γ was estimated to be 0.395 month^{-1}. This value is comparable to the growth parameter estimated from the Von Bertalanffy model for the blue shrimp *Litopenaeus stylirostris* (0.41) (Hernandez-Llamas and Ratkowsky 2004), Catarina scallop *Argopecten ventricosus* (0.37) (Hernandez-Llamas and Ratkowsky 2004) and the blue mussel *Mytilus edulis* (0.20) (Munch-Petersen and Kristensen 2001). On the other hand, it differs somewhat from that of the rainbow mother-of-pearl mollusc *Pteria sterna* (1.71) (Hernandez-Llamas and Ratkowsky 2004).

Although the growth parameter estimated from this study is slightly higher compared to the growth rate (γ) of 0.33 original used in the model (Smit et al. 2006), the resulting average population growth rate calculate by the model is lower. This is a result of the updated temperature relationship based on the growth results from this study. This temperature relationship is also applied to describe the temperature dependency of reproduction (Smit et al. 2006). As the average population growth rate under a realistic temperature regime, as obtained in this study (1.015 month^{-1}), is lower than the original calculated average population growth rate (1.055 month^{-1}), the population is predicted to be less tolerant to additional stress (predation, food limitation or toxic stress).

Although an increased population is predicted by the model (1.015 month^{-1}), a declining population density over the period May 1994 and April 1995 is observed in the Oesterput. When a combination of food limitation and predation is included in the model a population growth rate of 0.909 is calculated for this period (Smit et al. 2006).

It is recommended to calculate maximum bioassay mortality, reducing the intrinsic population growth rate to one, for more than just one year. Based on a representative yearly temperature regime, the average bioassay mortality that is required to reduce the average population growth rate to one can be predicted.

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