Title

Normal versus gamma: stochastic models of copepod molting rate

Journal

Journal of Plankton Research, 29(11)

ISSN

0142-7873

Authors

Hu, Qiao
Petrik, Colleen M
Davis, Cabell S

Publication Date

2023-06-05

DOI

10.1093/plankt/fbm073

Peer reviewed

Normal versus Gamma: Stochastic models of copepod molting rate

Qiao Hu[1,*], Colleen M. Petrik[1] and Cabell S. Davis[1]

1 Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.

* Email: qhu@whoi.edu

Running Head: Stochastic copepod molting model

Key words: plankton, copepods, modeling, molting, normal, gamma

Abstract

Molting rate is a key life history parameter in copepods. Since copepod population growth is an inherently exponential process, accurate formulation of molting rate is of critical importance. Many experiments have been conducted to culture different copepod species under varying temperatures and food concentrations. Probability density functions (PDFs) then were used to estimate the median development time (MDT) of different copepod stages from the experimental data. These MDTs are used in copepod population models. Asymmetrical PDFs are widely used to model molting rate, because the shapes of these curves are similar to laboratory data on cohort development. In this paper, we developed an individual stochastic model (ISM) to simulate the molting rate with different PDFs. We showed that there was no connection between the asymmetry of cohorts and the asymmetry of the molting PDF. Although age-within-stage models have been widely used to simulate copepod population dynamics, we found that none had used the correct formulation of molting rate. The population model requires the probability of molting at each time step, whereas the laboratory-derived PDF is the frequency distribution of stage duration. Therefore, the PDF cannot be applied directly to the population model. We present here a corrected formula based on the PDF for use in copepod population models, termed the probability of molting for remaining individuals (PMR). Despite emphasis on use of the gamma function for copepod molting, we found simpler functions work equally well, but that prior use of incorrect molting rate functions in copepod models can seriously overestimate generation time.

Introduction

Development rate of copepods is a key factor regulating their population dynamics (Landry, 1978, 1983; Mclean, 1978; Aksnes and Magnesen, 1983, 1988; Vidal and Smith, 1986; Davis, 1987). Numerous laboratory experiments have been conducted under controlled conditions with different temperatures and food concentrations to examine the growth and development of individual species (Miller et al., 1977; Corkett and McLaren, 1978; Landry, 1978; Vidal, 1980; Thompson, 1982; Davis, 1983, 1984a; Davis and Alatalo, 1987, Carlotti and Nival, 1991, 1992; Ban, 1994; Klein Breteler et al., 1994, 1995; Lee et al., 2003; Dzierbicka-Glowacka, 2004; Jimenez-Melero et al., 2005). These experiments can be divided into two groups based on how the animals are raised. In the first group, copepods were reared in large containers with controlled temperature and food concentration. The experiment started with a cohort of eggs spawned over a short period of time (usually less than 24 hours). At each sampling time, a small portion of well-mixed sample was taken from each container. The sample was used to determine the stage composition of each culture and then was discarded. This method assumes the initial culture is large enough that the stage composition is not affected by sampling and that the sample size is large enough to reliably represent the culture. In the second group of experiments, copepods were reared individually in small containers under different temperature and food conditions. The experiment was also started with eggs spawned within 24 hours of each other. The stage of each animal was determined at each sample time. Due to the increased amount of labor inherent in this method, the total number of copepods being monitored was usually much smaller than the first method. However, since this method monitored the age and stage of each individual in the culture, it provided the median stage duration experimentally, without a probability model, as well as providing the stage composition of the cohort.

Different approaches have been proposed to estimate the median development time (MDT) from these experimental data (Landry, 1975, 1983; Uye, 1980, 1988; Vidal, 1980; Peterson and Painting, 1990; Trujillo-Ortiz, 1990; Klein Breteler et al., 1994; Souissi et al., 1997; Souissi and Ban, 2001; Lee et al., 2003; Jimenez-Melero et al., 2005). The curve describing the proportion of the cohort in a given life stage versus cohort age (termed “cohort shape”, e.g., Fig. 1A) had a distinctive

asymmetry, with the mode smaller than the mean. In addition, asymmetry was observed in the curve describing the frequency distribution for duration of a given life stage (termed "stage duration distribution", e.g., Fig. 1B). These two asymmetries have been attributed to individual variability in development time (e.g., Jimenez-Melero et al., 2005) and have often been confused with each other. In this paper, we present results from an individual stochastic model of copepod molting rate, which demonstrates that there is no direct connection between the asymmetries in cohort shape and stage duration distribution.

Laboratory results have been used in developing numerous models of copepod population dynamics（Wroblewski, 1980; Davis, 1984b,c; Sciandra, 1986; Jones and Henderson, 1987; Carlotti and Sciandra, 1989; Gaedke, 1990; Miller and Tande, 1993; Souissi and Nival, 1997; Plagányi et al., 1999; Souissi and Ban, 2001). These models can be divided into two categories, those with and those without age-classes in each stage (Souissi and Ban, 2001). Despite the existence of numerous models, we found that the molting rate has yet to be correctly formulated. The problem is that in the population model, difference equations are formulated on the population in a certain developmental stage at each time step, while the PDF for molting obtained from laboratory experiments is based on the whole initial cohort. For this reason, the laboratory-based PDF cannot be used directly in the population model. In this paper, we provide a corrected molting formula for population models, which can utilize the laboratory estimated PDFs. Use of the proper molting formulation is important, since it can have a substantial impact on population dynamics.

Methods

To find the correct molting rate formulation, we fit distribution functions to copepod data from published laboratory studies. We also developed an individual stochastic model (ISM), and used a 200 age-within-stage class model, to study the effect of underlying molting rate functions on cohort development.

We first fit probability functions to laboratory molting data for replicate cohorts of the copepod *Pseudocalanus elongatus* (Klein Breteler et al., 1994). Abundance data for each cohort first were converted to the proportion in each developmental stage. An accumulation sum was calculated for

every observation time to obtain the proportion of animals which had not passed each developmental stage. The resulting proportion in each stage was 1 minus the cumulative density function (CDF) of development time for that stage (Development time refers to cohort age, i.e. total age since birth, and is different from stage duration, which refers to the amount of time spent in a given stage). According to the law of probability, this resulting function should be monotonically decreasing, but due to sampling error inherent in the laboratory experiments, data for the first cohort did not strictly follow this rule. We made a minor modification by setting the trailing data point to zero when violation of this rule occurred. The PDF was obtained from the resulting CDF. Finally, we used the functions *normfit* and *gamfit* in the Matlab (MathWorks, 2006) statistics toolbox to fit the PDF. The resulting PDF can be used to calculate the MDT and probability of molting in population models.

Normal, Gamma, and Lognormal distributions

The PDF of the normal distribution with mean, μ, and standard deviation, σ, is the familiar Gaussian function of the following form:

$$f(x;\mu,\sigma) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right). \qquad (1)$$

The gamma distribution is also characterized by two parameters, called the shape parameter, k, and the scale parameter, θ. The gamma distribution represents the sum of *k* exponentially distributed random variables, each of which has mean θ. The PDF of the gamma distribution can be expressed in terms of the gamma function:

$$f(x;k,\theta) = x^{k-1}\frac{e^{-x/\theta}}{\theta^k \Gamma(k)} \quad \text{for } x>0,\ k>0 \text{ and } \theta>0. \qquad (2)$$

The gamma distribution is often written in terms of a shape parameter α=k and an inverse scale parameter β=1/θ, also called a rate parameter:

$$g(x;\alpha,\beta) = x^{\alpha-1}\frac{\beta^\alpha e^{-\beta x}}{\Gamma(\alpha)} \quad \text{for } x>0. \qquad (3)$$

Due to its asymmetric property, the gamma distribution has been widely used to model the molting rate function of copepods (Klein Breteler, 1994; Souissi et al. 1997; Souissi and Ban 2001; Lee et al. 2003; Jimenez-Melero et al. 2005).

The lognormal distribution is the probability distribution of any random variable whose logarithm is normally distributed. A variable might be modeled as lognormal if it is the multiplicative product of many small independent factors. The lognormal distribution can be written in the following form:

$$f(x;\mu,\sigma) = \frac{1}{x\sigma\sqrt{2\pi}} e^{-(\ln x-\mu)^2/2\sigma^2}, \qquad (4)$$

where μ and σ are the mean and standard deviation of the variable's logarithm. Carlotti and Nival (Carlotti and Nival, 1991) pointed out that the molting PDF of the copepod *Temora stylifera* follows a lognormal distribution (although they used a normal distribution to fit their data).

Individual stochastic model

A simple stochastic model was constructed with S developmental stages and N individual animals. The mean and standard deviation of stage duration were obtained from laboratory experiments (Carlotti and Nival, 1991). Normal, gamma, and lognormal distributions were used to simulate the molting probability for each stage. The desired PDF and CDF were computed from these means and standard deviations of each developmental stage at the resolution of the model time step. The time step of 0.1 day was selected so that there were more than 10 time steps before an animal could molt to the next stage. The model was initialized such that all the animals were in the first developmental stage with age of 0. In every time step, each individual animal, n_i, was evolved according to the following rules:

1) *generate a uniform random variable v between 0 and 1;*
2) *if* $v < p_m(n_i(t).stage, n_i(t).age)$ *and* $n_i(t).stage < S$, *then*

$$n_i(t+1).stage = n_i(t).stage + 1 \qquad (5a)$$

$$n_i(t+1).age = 0 \qquad (5b)$$

else

$$n_i(t+1).stage = n_i(t).stage \qquad (5c)$$

$$n_i(t+1).age = n_i(t+1).age + 1 \qquad (5d)$$

3) *repeat steps 1) and 2) until a total of T steps was reached.*

Here i is the index of individuals, t is time, $p_m(s, a)$ is the molting probability of the individuals in stage s and age of a. Each animal n_i has two attributes: its development stage and its age in that

stage. Thus, in the above notation, $n_i(t).stage$ and $n_i(t).age$ are the stage and age-within-stage, respectively, of an individual animal n_i at time t.

Age-within-stage model

We used an age-within-stage model developed by Davis (Davis, 1984b, c) for the copepod *Pseudocalanus* to verify our findings. The model includes 13 life stages: 1 egg stage, 6 naupliar stages, 6 copepodite stages, and the last stage being adult. The state variables ($N_{i,k}$) are the number of individuals which have been in stage i for k days. It evolves according to:

Molting,

$$N_{i+1,0}(t+1) = \sum_{k=0}^{Ki} N_{i,k}(t) S_i P_{i,k} \qquad (6)$$

Not molting,

$$N_{i,k+1}(t+1) = N_{i,k}(t) S_i (1 - P_{i,k}). \qquad (7)$$

Where t is time in days, and $P_{i,k}$ is the probability of molting from stage i age k to stage $i+1$ age 0. The probability is calculated according to the formula described below, which is different from the normal CDF used (incorrectly) in Davis (Davis, 1984b, c). Different PDFs (normal, gamma, lognormal) are used for comparison. K_i, the number of age classes in stage i, was 10 for stages 0-11 and 80 for the adult stage, giving a total of 200 age-stage classes. For simplicity, we chose the survival rate, S_i, to be 1 for all the stage classes in order to examine only the effects of molting. We only compared the populations within 1 life-cycle, thus reproduction was not included in the model.

Derivation of corrected formulation for molting rate

The PDFs discussed above are all in terms of the proportion of the *original* population in a given life stage that will be molting at time t. However, copepod population dynamics models are often formulated in terms of the *remaining* population that is still in stage s. A number of modelers used a within-stage CDF as the probability of molting in their models (Davis, 1984b, c; Soussi and Ban, 2001). In Davis (Davis, 984b,c), this CDF had a mean equal to the mean stage duration and a standard deviation of 0.1 times the mean, which with adjustment gave a reasonable generation time and spread of the cohort across life stages over time. The CDF, however, tells us what proportion of the original population *has molted* by time t, while, in the model, we need the proportion of

individuals remaining in a certain stage that *will molt* at time *t*. It turns out there is a simple relationship between the PDF in terms of the original population *($f_o(t)$)* and the PDF in terms of the remaining population *($f_r(t)$)*. To be clear, we define "original population" as the total number of individuals passing through stage *i*, and the "remaining population" as the number of individuals remaining in stage *i* at time *t*. The CDF, $F_o(t)$, can be obtained from $f_o(t)$ according to the following relationship:

$$F_o(t) = \int_{-\infty}^{t} f_o(x)dx. \qquad (8)$$

Then $f_r(t)$ can be calculated as,

$$f_r(t) = f_o(t)/(1 - F_o(t)). \qquad (9)$$

This corrected PDF, $f_r(t)$, then gives us the desired molting function for the model, and is the probability of molting for remaining individuals. We will call this corrected molting function the Probability of Molting for Remaining animals (PMR) {explain}.

Results

We fit Klein Breteler's (Klein Breteler, 1994) data set with both a normal PDF and a gamma PDF (Fig. 2) and found very little difference between the two curves. This finding was very interesting because the normal distribution was symmetric and the gamma distribution asymmetric. The gamma distribution has been the dominant model used to fit laboratory experimental data, with a number of studies emphasizing the importance of using the gamma distribution rather than other distributions (Soussi and Ban, 2001; Jimenez-Melero et al., 2005).

In order to further confirm our findings, we used a simple ISM with 4 life stages to determine the difference between gamma and normal molting PDFs on cohort development (with both PDFs having the same stage-specific mean and variance). The 4 stages included eggs, nauplii, copepodites CI-V, and adults (ENCA). Cohort shapes produced by the two models are very close to each other (Fig. 3), indicating little difference between the gamma and normal distribution as the molting PDF. The modeling result is consistent with our finding on data fitting. In addition, both models yield asymmetrical cohort shapes (Fig. 3). This asymmetry is more evident in the later

225 stages (copepodites) than the earlier stages (nauplii), which is consistent with the laboratory results.
226 The asymmetric cohort shapes seen in copepodites from both models appear very similar to the
227 gamma distribution.
228
229 Not only have asymmetrical cohort shapes been observed in laboratory experiments, but
230 asymmetrical molting rates have also been observed. In order to explore the effect of the
231 asymmetrical molting probability on population dynamics, we used experimental data from Carlotti
232 and Nival (Carlotti and Nival, 1991). First, we fit normal, gamma, and lognormal distributions to
233 data on *Temora stylifera* copepodites CIII-CV (from Fig. 2 in Carlotti and Nival, 1991) (Figs. 4A-
234 C). We found that none of the probability models fit the data very well. We used Pearson's chi-
235 square test (Chernoff and Lehmann, 1954) to find the goodness of fit of these three probability
236 models to the observed histogram data. The null hypothesis is that the observed histogram data
237 come from the tested distributions. We found no significant fit for any of the models to the CIII (p
238 $<< 0.01$ for all the models) or CV data ($p << 0.01$ for all the models). The gamma and lognormal
239 distributions fit the CIV data significantly ($\alpha=0.05$; $p=0.57$, 0.73 for gamma and lognormal
240 respectively), while the normal distribution did not ($\alpha=0.05$; $p=0.03$).
241
242 We again used our ISM with the mean stage durations and standard deviations for *Temora stylifera*,
243 stages CII-CV, taken from Table I of Carlotti and Nival (Carlotti and Nival, 1991), and used
244 normal, gamma and lognormal distributions as molting PDFs (Fig. 5). We chose a time step of 0.1
245 day and initialized the model with 1000 CII at age 0. The stage cohorts from the three statistical
246 models were not as close as in the hypothetical (ENCA ISM) case in Fig. 3, however, the
247 differences among the three models were rather small compared to the standard deviations of the
248 mean duration time from the laboratory experiments. In order to evaluate the results of different
249 simulations, we compared the MDT predicted from the models to that from the laboratory
250 experiment (Table I). The difference between the models and the laboratory data were well below
251 1 standard deviation of the laboratory experiment. It is interesting to note that the normal
252 distribution was better at predicting the development time of CIV than the gamma and lognormal
253 distributions (Table I).
254

The difference between the CDF and PMR as molting rate functions with normal versus gamma distributions is illustrated in Fig. 6. The CDFs were generated by Matlab functions *normcdf* and *gamcdf*. The PDFs were calculated as the difference between consecutive values of CDFs. The PMRs were calculated according to Equation 9. The mean and standard deviation for *Eurytemora affinis* were from Table I (N1-N3 group, EXP1) of Souissi and Ban (2001). With this mean and standard deviation, using the CDF as the molting rate depressed the early molting rate (for both normal and gamma distributions) compared to the PMR (Fig. 6)

In order to investigate how much delay was introduced by this treatment, we used the age-within-stage model for *Pseudocalanus* developed by Davis (Davis, 1984b, c). The parameter values in Davis (Davis, 1984b, c) were used except we used the PMR as well as the CDF. The model used a total of 200 age-stage-classes. We grouped them into 4 developmental stages for plotting (Fig. 7). As expected from Fig. 6A, the CDF molting rate tended to delay each developmental rate compared to that of PMR. In order to quantify such delay, we compared the MDTs from the two models to experimental values (i.e. those from the laboratory experiments) (Table II). Our simulation showed that using the CDF as the molting rate could delay the MDT of *Pseudocalanus* more than 12 days.

Discussion

We started with data on stage frequency collected from cultured cohorts of *Pseudocalanus elongatus* by Klein Breteler et al. (Klein Breteler et al., 1994) and found that symmetrical and asymmetrical density functions fit the data equally well (they were nearly identical, Fig. 2). In order to explain asymmetrical cohort shapes found by Sciandra (Sciandra, 1986) for cultured copepods, we developed the ISM and simulated the molting rate. We found that the asymmetry in the cultured cohorts was due to the difference in variance of the stage duration for consecutive development stages. For example, the smaller variance in stage duration for nauplii than copepodites caused asymmetry in the cohort shape for copepodites (Fig. 3). This ISM demonstrated that both symmetrical and asymmetrical PDFs can produce asymmetrical cohort shapes (Fig. 3). The model also revealed that the asymmetry of the underlying molting function made little difference to the cohort shapes or the MDTs (Fig. 3).

In order to explore the effect of the asymmetrical molting probability observed by Carlotti and Nival (Carlotti and Nival, 1991), we fit their histograms with normal, gamma and lognormal PDFs (Fig. 4). We found that the difference in median development time estimated from different probability models is less than 0.5 day, which is well below experimental error. We further used the simple ISM with the above normal, gamma, and lognormal PMRs and found that the three models yielded similar cohort shapes (Fig. 5). Furthermore, the normal PMR model had a closer agreement to the MDT for copepodite stages from laboratory data than the gamma and lognormal PMR models.

The mean of the molting rate function determines when molting will happen, while variance controls how fast molting will proceed. For developing stages which are well separated, using an asymmetrical molting rate function only yields asymmetry on the rising curve of cohorts (i.e. the rising slope is different than the asymptotic slope). The nature of asymmetry of cohorts is a result of the unequal variance between two consecutive stages. For developing stages which are not well separated, the variances of two or more consecutive stages determine the cohort shape for a given stage.

Neither symmetrical nor asymmetrical distributions fit very well the data on molting rates from the laboratory experiments in which copepods were reared individually. We think there are several causes for this disagreement. First, due to the extensive amount of labor involved in an individual-based experiment, the number of individuals raised was generally small and the sample errors for each time bin therefore were relatively large. Thus there is a large amount of uncertainty in the histogram data (Fig. 4). Second, the observation intervals were too large, which might have resulted in many animals molting within same time interval, making it almost impossible for a smooth PDF to fit the histogram data well. Third, the molting rate histogram suggested that there might be two populations in each developmental stage, indicating that we need to use a mixture model to fit the molting histogram data instead of a unimodal density function.

In summary, with the corrected formula of the molting PDF, what we have termed the PMR, we found that the specific shape of the molting density function was not as important as previous

studies of copepod models have emphasized. Both our data fitting and modeling results suggest that only the mean and standard deviation of the molting function were important in modeling copepod molting. Using the same mean and standard deviation, a simple probability distribution is able to do as well as a complicated one in modeling copepod population dynamics. Our finding suggests we can use a simpler statistical model for the probability function without sacrificing the quality of the model. This correction is applicable to age-dependent copepod models, such as age-within-stage models, individual stochastic models, and individual based models.

Acknowledgements

We are grateful to W. C. M. Klein Breteler for providing us his raw data of his early paper. Funding for this research was provided by NOAA (GLOBEC) grant NA17RJ1223.

References

Aksnes, D. L. and Magnesen, T. (1983) Distribution, development, and production of *Calanus finmarchicus* (Gunnerus)in Lindåspollene, western Norway, 1979. *Sarsia* **68**, 195-208

Aksnes, D. L. and Magnesen, T. (1988) A population dynamics approach to the estimation of production of four calanoid copepods in Lindåspollene, western Norway. *Mar. Ecol. Prog. Ser.*, **45**, 57–68.

Ban, S. (1994) Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of calanoid copepod *Eurytemora affinis*. *J. Plankton Res*., **16**, 721-735

Carlotti, F. and Sciandra, A. (1989) Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) coupling individual growth and larval development. *Mar. Ecol. Prog. Ser.*, **56**, 225–242.

Carlotti, F. and Nival, S. (1991) Individual variability of development in laboratory-reared *Temora stylifera* copepodites: consequences for the population dynamics and interpretation in the scope of growth and development rules. *J. Plankton Res.*, **13**, 801–813.

347 Carlotti, F. and Nival, S. (1992) Moulting and mortality rates of copepods related to age within
348 stage: experimental results. *Mar. Ecol. Prog. Ser.*, **84**, 235–243.

349 Chernoff, H. and Lehmann, E.L.(1954) The use of maximum likelihood estimates in χ^2 tests for
350 goodness-of-fit. *The Annals of Mathematical Statistics* **25**:579-586
351
352 Corkett, C. J. and McLaren, I. A. (1978) Biology of *Pseudocalanus*. *Adv. Mar. Biol*. **15**, 1-233.
353
354 Davis, C. S. 1983. Laboratory rearing of marine calanoid copepods. *J. Exp. Mar. Biol. Ecol.*, 71,
355 119-133.
356 Davis, C. S. 1984a. Food concentrations on Georges Bank: Non-limiting effect on growth and
357 survival of laboratory reared *Pseudocalanus* sp and *Paracalanus parvus*. *Mar. Biol.*, 82,
358 42-46.
359 Davis, C. S. (1984b) Predatory control of copepod seasonal cycles on Georges Bank. *Mar. Biol.* **82**,
360 31-40
361
362 Davis, C. S. (1984c) Interaction of copepod population with the mean circulation on Georges Bank
363 *J. Mar. Res.*, **42**, 573-590
364
365 Davis, C.S. and P. Alatalo. 1992. Effects of constant and intermittent food supply on life history
366 parameters in a marine copepod. *Limnol. Oceanogr.*, 37, 1618–1639.
367
368 Davis, C. S. (1987) Components of the zooplankton production cycle in the temperate ocean. *J.*
369 *Mar. Res.*, **45**, 947-903
370
371 Dzierbicka-Glowacka, L. (2004) Growth and development of copepodite stages of *Pseudocalanus*
372 sp. *J. Plankton Res.*, **26**, 49-60.
373
374 Gaedke, U. (1990) Population dynamics of the calanoid copepods *Eurytemora affinis* and *Acartia*
375 *tonsa* in the Ems-Dollart-Estuary: A numerical simulation. *Arch. Hydrobiol.*, **118**, 185–226.

376
377 Jimenez-melero, R., Santer, B. and Guerrero, F. (2005) Embryonic and naupliar development of
378 *Eudiaptomus gracilis* and *Eudiaptomus graciloides* at different temperatures: comments on
379 individual variability. *J. Plankton Res.*, 27, 1175-1187.
380
381 Jones, R. and Henderson, E. W. (1987) The dynamics of energy transfer in marine food chains. *S.*
382 *Afr. J. Mar. Sci.*, **5**, 447–465.
383
384 Klein Breteler, W. C. M., Schogt, N. and van der Meer, J. (1994) The duration of copepod life
385 stages estimated from stage-frequency data. *J. Plankton Res.*, 16, 1039-1057.
386
387 Klein Breteler, W. C. M., Gonzalez, S. R. and Schogt, N. (1995) Development of *Pseudocalanus*
388 *elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar. Ecol.*
389 *Prog. Ser.*, **119**, 99–110.
390
391 Landry, M. R. (1975) The relationship between temperature and the development of life stages of
392 the marine copepod *Acartia clausi* Gisbr. *Limnol. Oceanogr.*, **20**, 854–858.
393 Landry, M. R. (1978) Population dynamics of the planktonic marine copepod *Acartia clausi*
394 Giesbrecht in a small temperate lagoon. *Int. Rev. Gesamten Hydrobiol.* **63**, 77-119
395
396 Landry, M. R. (1983) The development of marine calanoid copepods with comment on the
397 isochronal rule, *Limnol. Oceanogr.* **28**, 614-624
398 Lee, H., Ban, S. Ikeda, T. and Matsuishi, T. (2003) Effect of temperature on development, growth
399 and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. *J.*
400 *Plankton Res.*, 25, 261-271.
401
402 McLaren, I. A. (1978) Generation lengths of some temperate marine copepods: estimation,
403 production and implication. *J. Fish. Res. Bd Can.*, 345, 1330-1342
404
405 Miller, C. B., Johnson, J. K. and Heinle, D. R. (1977) Growth rules in the marine copepod genus
406 *Acartia*. *Limnol. Oceanogr.*, **22**, 326-335

Miller, C. B. and Tande, K. S. (1993) Stage duration estimation for *Calanus* populations, a modelling study. *Mar. Ecol. Prog. Ser.*, **102**, 15–34.

Peterson, W. T. and Painting, S. J. (1990) Developmental rates of the copepods *Calanus australis* and *Calanoides carinatus* in the laboratory, with discussion of methods used for calculation of development time. *J. Plankton Res.*, **12**, 283–293.

Plagányi, É., Hutchings, L., Field, J. G. and Verheye, H. M. (1999) A model of copepod population dynamics in the Southern Benguela upwelling region. *J. Plankton Res.*, **21**, 1691–1724.

Sciandra, A. (1986) Study and modelling of development of *Euterpina acutifrons* (Copepoda, Harpacticoida). *J. Plankton Res.*, **8**, 1149–1162.

Souissi, S. and Ban, S. (2001) The consequences of individual variability in moulting probability and the aggregation of stages for modelling copepod population dynamics. *J. Plankton Res.*, **23**, 1279–1296.

Souissi, S. and Nival, P. (1997) Modeling of population dynamics of interacting species: effect of exploitation. *Environ. Model. Assess.*, **2**, 55–63.

Souissi, S., Carlotti, F. and Nival, P. (1997) Food- and temperature-dependent function of moulting rate in copepods: an example of parameterization for population dynamics models. *J. Plankton Res.*, **19**, 1331-1346

Thompson, B. M. (1982) Growth and development of *Pseudocalanus elongatus* and *Calanus* sp. in the laboratory. *J. Mar. Biol. Assoc. UK*, **62**, 359-372

Trujillo-Ortiz, A. (1990) Hatching success, egg production and development time of *Acartia californiensis* Trinast (Copepoda: Calanoida) under laboratory conditions. *Cienc. Mar.*, **16**, 1–22

438 Uye, S. (1980) Development of neritic copepods *Acartia clausi* and *A. steueri*. II. Isochronal larval
439 development at various temperatures. *Bull. Plankton Soc. Japan*, **27**, 11–18.
440
441 Uye, S. (1988) Temperature-dependent development and growth of *Calanus sinicus* (Copepoda:
442 Calanoida) in the laboratory. *Hydrobiologia*, **167**/**168**, 285–293.
443
444 Vidal, J. (1980) Physioecology of zooplankton. II. Effects of phytoplankton concentration,
445 temperature and body size on the development and molting rates of *calanus pacificus* and
446 *Pseudocalanus*. *Mar. Biol*., **56**, 134-146
447
448 Vidal, J. and Smith, S. L. (1986) A simulation of the distribution of *Acartia claus*i during the
449 Oregon upwelling. August 1973. J. Plankton Res. **2**, 46-68
450
451 Wroblewski, J. S. (1980) A simulation of the distribution of *Acartia clausi* during Oregon
452 Upwelling, August 1973. *J. Plankton Res.*, **2**, 43–68.
453

Appendix A Derivation of corrected formulation of molting rate

Suppose we have a molting probability density function $f_o(t)$, and its corresponding cumulative density function $F_o(t) = \int_{-\infty}^{t} f_o(s)ds$. At time t_0, none of the animals has molted from stage *k* to stage *k+1*, and in *n* time steps, all the animals have molted from stage *k* to stage *k+1*. From the definition, $f_o(t_0), f_o(t_0 + dt), \cdots, f_o(t_0 + (n-1) \times dt)$ corresponds to the proportion of the original population that will molt from stage *k* to stage *k+1* from time $t_0, t_0 + dt, \cdots, t_0 + (n-1) \times dt$ to time $t_0 + dt, t_0 + 2 \times dt, \cdots, n \times dt$, and $F_o(t_0), F_o(t_0 + dt), \cdots, F_o(t_0 + n \times dt)$ corresponds to the proportion of the original population that has ALREADY molted to the next stage at time $t_0, t_0 + dt, \cdots, t_0 + n \times dt$. From our definition, $F_o(t_0) = 0$. At any time interval $t_0 + j \times dt$ to $t_0 + (j+1) \times dt$, the proportion of remaining animals are $1 - F_o(t_0 + j)$, and there is $f_o(t_0 + j \times dt)$ percentage of the original animals that will molt to next stage. Let the molting rate of the remaining animals be $f_r(t_0 + j \times dt)$, then

$f_o(t_0 + j \times dt) = (1 - F_o(t_0 + j \times dt)) \times f_r(t_0 + j \times dt)$, i.e.

$f_r(t_0 + j \times dt) = f_o(t_0 + j \times dt) / (1 - F_o(t_0 + j \times dt))$. More generally, we have

$f_r(t) = f_o(t) / (1 - F_o(t))$.

Appendix B MATLAB code for generating corrected molting rate from stage frequency data

Note parameters may vary with different experiment settings. For experiment with error, data may need clean up before use following code.

```
kdata =importdata('copepod.txt'); % load the frequency data
age =kdata.p241(:,1); %  sampling time
stage =size(kdata.p241,1) % number of stages
t=0:.1:25;  % sampling interval of probability density function
offset =5;  % initial age of animals before experiment
for k=1:stage,
```

```
482         rv=[]; histogram of stage duration time
483         pdf=kdata.p241(:,1+k)/sum(kdata.p241(:,1+k)); probability density function
484         for j=1:length(age), rv=[rv;age(j)*ones(round(1000*pdf(j)),1)]; end
485         [t1, t2] =gamfit(rv); % fit the histogram data with gamma distribution
486         fo(k, :)=gampdf(x,t1,t2); % probability density function of Gamma distribution for original
487 population
488         Fo(k, :)=gamcdf(x,t1,t2); % cumulative density function of Gamma distribution
489         Fr(k, :)=fo(k, :))./(1-Fo(k,:)); % corrected molting probability density function
490 end
491
492
```

Table and Figure legends

Table I Differences in the expected and simulated MDT of copepodite *Temora stylifera* were below experimental error. The expected values were taken from Table I in Carlotti and Nival (Carlotti and Nival, 1991). The ISMs with normal, gamma and lognormal distribution, mean and standard deviation from Table I (Carlotti and Nival, 1991), were simulated. The MDTs were estimated as the time when 50% of the cohort had passed a given stage. PMR — Probability of Molting for Remaining animals (Eqn. 8).

Table II MDT of *Pseudocalanus* The expected values were obtained from Davis (Davis, 1984b, c). The age-within-stage model with normal distribution was simulated with the PMR (PDF) and the CDF (CDF) as molting rates. A delay in the MDT from the expected occurs when using the CDF, but not with the PDF. The MDTs were estimated as the time when 50% of the cumulative population had past a given stage.

Fig. 1 Diagram of a typical cohort shape (A) and a stage duration distribution (B)

Fig. 2 Similarity between normal (dash lines) and gamma (dots) distributions fitted to *Pseudocalanus elongatus* data from Fig. 4 in Klein Breteler et al. (Klein Breteler et al., 1994). Data in his Fig. 4a and 4b are from replicate cultures. The data points are plotted with different symbols for each developmental stage. Corresponding figures in Klein Breteler et al. (Klein Breteler et al., 1994): A) Fig. 4a female; B) Fig. 4a male; C) Fig. 4b female; D) Fig. 4b male.

Fig. 3 Similarity between the results from simple ENCA ISMs with a normal (solid lines) and a gamma (circles) PMR molting functions. The mean and variance in the stage durations were the same for both normal and gamma distributions. The four curves from left to right correspond to eggs, nauplii, copepodites CI-CV, and adults.

Fig. 4 The poor fit of normal (circles), gamma (dashed), and lognormal (solid) distributions to laboratory data on *Temora stylifera* from Fig. 2A-C of Carlotti and Nival (Carlotti and Nival, 1991). A) stage CIII; B) stage CIV; C) stage CV

Fig. 5 Comparison of results from ISMs with a normal (solid lines), a gamma (circles), and a lognormal (dots) distribution as the PMR molting function. The means and standard deviations for the stage durations (CII-CV) were taken from Table I in Carlotti and Nival (Carlotti and Nival, 1991). The ISMs were initialized with 1000 individuals in stage CII. The five stages are, from left to right, CII, CIII, CIV, CV, and adults respectively.

Fig. 6 Comparison of CDF (solid), PDF (dot-dashed), and PMR (dashed) molting rate functions using normal (A) and gamma (B) distributions.

Fig. 7 Simulated populations using a 200 age-within-stage class model. Normal CDF (solid lines), gamma CDF (dots), normal PMR (dashed lines), and gamma PMR (diamonds). Both normal and gamma CDF models overestimated the MDT significantly (cf. Table II).

538 Table I

Life Stage	MDT (Days)			
	Expected	Normal PMR	Gamma PMR	Lognormal PMR
CII	2.25	2.25	2.17	2.20
CIII	4.31	4.37	4.01	4.02
CIV	6.82	6.90	6.48	6.42
CV	9.95	10.01	9.60	9.55

539

540

541 Table II

Life Stage	MDT (Days)		
	Expected	PMR	CDF
Egg	4.34	4.77	5.76
N1-N6	20.99	21.73	28.70
C1-C5	42.71	43.49	55.39

542

543