Oecologia (2001) 128:56–61
DOI 10.1007/s004420100639

**David A. Lytle**

# Convergent growth regulation in arthropods: biological fact or statistical artifact?

Received: 17 May 2000 / Accepted: 21 November 2000 / Published online: 3 March 2001


**Abstract** Convergent growth regulation, where individuals adjust their growth trajectories to reach a targeted final body size, has been reported for many arthropod taxa. Divergent growth, where larger individuals grow proportionately more than smaller individuals, is seldom observed. Most studies based their conclusions on growth increment analysis: correlation or regression between body size at a particular molt and the increment grown during the next molt. These studies interpreted a negative relationship as evidence for convergent growth regulation, since smaller individuals appeared to grow more during the subsequent molt than larger individuals. Using random data simulations and an analysis of the statistics, I demonstrate that autocorrelation in these statistics generates false evidence for convergent growth, even when divergent growth actually occurred. I suggest model II geometric mean (GM) regression as an alternative method because it does not suffer from these statistical problems. A GM regression reanalysis of two published studies revealed evidence for divergent growth or no growth regulation in cases where the original studies reported convergent growth regulation, suggesting that the reported prevalence of convergent growth may be a statistical artifact.

**Keywords** Body size · Autocorrelation · Measurement error · Geometric mean regression · Model II regression

## Introduction

Body size is a key attribute of many organisms because it directly affects their survivorships, fecundities, competitive abilities, and other components of fitness. Because body size is determined by patterns of growth throughout an organism's ontogeny, body size is proximately a function of both endogenous mechanisms (hormones, physiological constraints, growth-reproduction tradeoffs) and environmental factors (temperature, resource availability, biotic interactions). Of particular interest is whether organisms regulate growth endogenously in order to reach a targeted final size that is neither too large nor too small relative to some optimal size (Tanner 1963; Riska et al. 1984; Klingenberg 1996; Twombly and Tisch 2000). Because many biological models make the assumption that body size is positively correlated with fitness (Roff 1992; Stearns 1992), it is important to know when an organism is inherently constrained to an intermediate body size.

The most commonly used method of testing for body size regulation in arthropods is to look for a significant relationship between pre-molt size and the amount grown during the subsequent molt stage, a method referred to here as "growth increment analysis". Plotted with molt increment on the *y*-axis and pre-molt size on the *x*-axis, the data can produce a significant (compared with 0) negative or positive correlation. Most studies have interpreted a significant negative correlation as evidence that convergent growth regulation (also called targeted growth, compensatory growth, negative feedback, or simply growth regulation) took place between the two molts, since smaller individuals appeared to grow more during the subsequent molt than larger individuals. Based largely on this method, convergent growth appears to be widespread among arthropods; it has been reported in decapods (Hartnoll and Dalley 1981), insects (Tanaka 1981), barnacles (West and Costlow 1987), crabs (Mohamedeen and Hartnoll 1989), shrimp (Freeman 1990), and copepods (Twombly and Tisch 2000). In these studies convergent growth occurred during some stages but not others: early stages only (West and Costlow 1987; Freeman 1990), late stages only (Tanaka 1981), or scattered throughout ontogeny (other studies). Non-regulated growth, where there was no significant relationship between pre-molt size and molt increment, oc-

D.A. Lytle (✉)
Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637, USA

*Present address:*
D.A. Lytle, Department of Entomology, University of Arizona, Tucson, AZ 85721, USA
e-mail: dalytle@ag.arizona.edu

curred in intervening stages. None of these studies reported any significant divergent growth, however, where larger individuals grew more during a given stage than smaller ones. This is surprising because studies employing different statistical methods have observed divergent growth in at least some stages (*Daphnia* studied with path analysis, Lynch 1988; mice studied with variance component analysis, Riska et al. 1984; water striders studied with common principal components, Klingenberg 1996).

Growth increment analysis differs from these other statistical methods in at least one important way. Because molt increment is the difference between post-molt and pre-molt size, correlations or regressions between pre-molt size and molt increment are implicitly autocorrelated. For this reason, the null hypothesis that the correlation coefficient $r$=0 or the slope coefficient $b$=0 may not be the appropriate one for testing whether a pattern is due to random chance versus growth regulation. Here, I present data suggesting that these tests suffer from autocorrelation in such a way that even strongly divergent growth patterns will often be mistaken for convergent growth. This occurs because small amounts of random measurement error can combine to produce a negative correlation or slope when there is actually none present. Thus, some of the evidence for convergent growth generated by growth increment analysis may be an artifact of small measurement errors propagating in a systematic way to produce pattern from noise.

## Methods and results

### Random data plots

To gain an intuitive understanding of how plots of pre-molt size versus molt increment behave statistically, plots from the literature were compared to plots generated from random data. Data were obtained from published plots for the barnacle *Balanus eburneus* (Fig. 3B in West and Costlow 1987, reproduced here as Fig. 1C) and the copepod *Boeckella triarticulata* (Fig. 2A in Twombly and Tisch 2000, reproduced here as Fig. 1A) using DataThief version 2.0 (Huyser and van der Laan 1994). Random data were generated by adding measurement error to the mean size at each molt, and these values were used to calculate molt increment (repeated 50

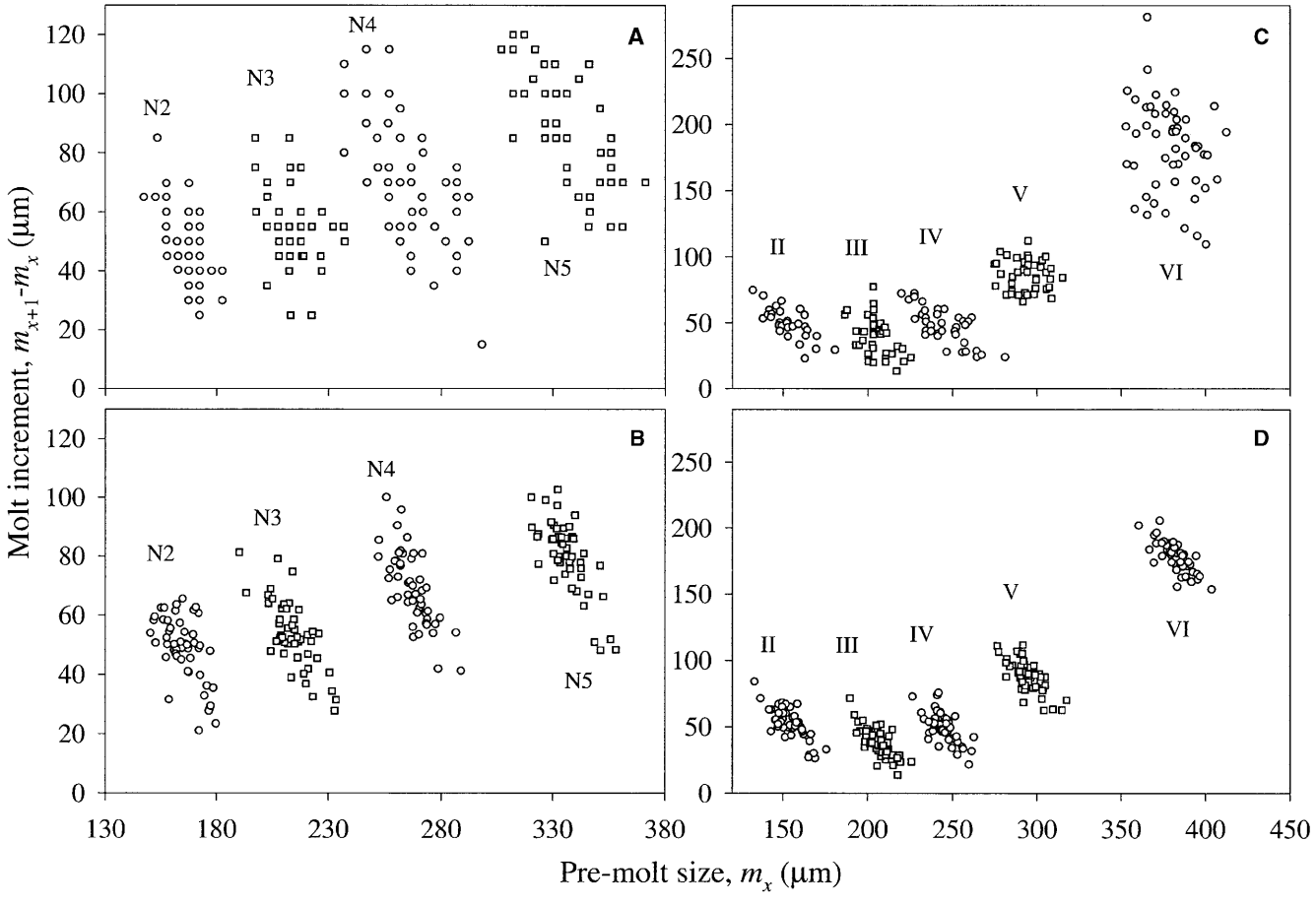


**Fig. 1A–D** Plots of pre-molt size versus molt increment using real and random data. **A** The copepod *Boeckella triarticulata*, reproduced from Twombly and Tisch (2000). Each correlation is significantly negative. **B** Random data based on means from the copepod data. Each correlation is significantly negative. **C** The barnacle *Balanus eburneus*, reproduced from West and Costlow (1987). Regressions for stages II–IV are significantly negative. **D** Random data based on means from the barnacle data. All regressions are significantly negative

**Table 1** *P*-values and interpretations of correlations between pre-molt size and molt increment ($H_0$: $r$=0) for the copepod *Boeckella triarticulata* (from Twombly and Tisch 2000), and a reanalysis using geometric mean regression on successive molt sizes ($H_0$: $v_{Y\cdot X}$=1). Sample sizes differ because not all data were retrievable from the original plots

| Stage | $r$ | $n$ | $P$ | Conclusion | $v_{Y\cdot X}$ | $n$ | $t$ | $P$ | Conclusion |
|---|---|---|---|---|---|---|---|---|---|
| N2 | –0.569 | 47 | 0.0001 | Convergent | 1.27 | 32 | 1.18 | 0.247 | No growth reg. |
| N3 | –0.311 | 47 | 0.033 | Convergent | 1.45 | 33 | 1.90 | 0.067 | No growth reg. |
| N4 | –0.664 | 47 | 0.0001 | Convergent | 1.02 | 44 | 0.13 | 0.897 | No growth reg. |
| N5 | –0.637 | 47 | 0.0001 | Convergent | 0.92 | 39 | –0.52 | 0.606 | No growth reg. |
| CI | –0.607 | 47 | 0.0001 | Convergent | 1.40 | 36 | 1.67 | 0.104 | No growth reg. |
| CII | –0.513 | 47 | 0.0002 | Convergent | 1.60 | 33 | 2.09 | 0.045 | Divergent |
| CIII | –0.181 | 47 | 0.223 | Weak conv | 1.51 | 40 | 2.56 | 0.015 | Divergent |
| CIV | –0.093 | 47 | 0.536 | Weak conv | 1.69 | 39 | 2.87 | 0.007 | Divergent |
| CV | –0.432 | 47 | 0.003 | Convergent | 0.99 | 43 | –0.11 | 0.913 | No growth reg. |

**Table 2** *P*-values and interpretations of regressions between pre-molt size and molt increment ($H_0$: $b$=0) for the barnacle *Balanus eburneus* (from West and Costlow 1987), and a reanalysis using geometric mean regression on successive molt sizes ($H_0$: $v_{Y\cdot X}$=1)

| Stage | $b$ | $n$ | $t$ | $P$ | Conclusion | $v_{Y\cdot X}$ | $t$ | $P$ | Conclusion |
|---|---|---|---|---|---|---|---|---|---|
| II | –0.89 | 31 | –6.43 | <0.05 | Convergent | 0.76 | –1.77 | 0.089 | No growth reg. |
| III | –0.72 | 37 | –2.46 | <0.05 | Convergent | 1.49 | 1.91 | 0.065 | No growth reg. |
| IV | –0.74 | 42 | –6.44 | <0.05 | Convergent | 0.73 | –2.43 | 0.020 | Convergent |
| V | –0.06 | 42 | –1.08 | ns | No growth reg. | 1.44 | 2.39 | 0.022 | Divergent |
| VI | –0.35 | 51 | –1.08 | ns | No growth reg. | 2.20 | 3.88 | <0.001 | Divergent |

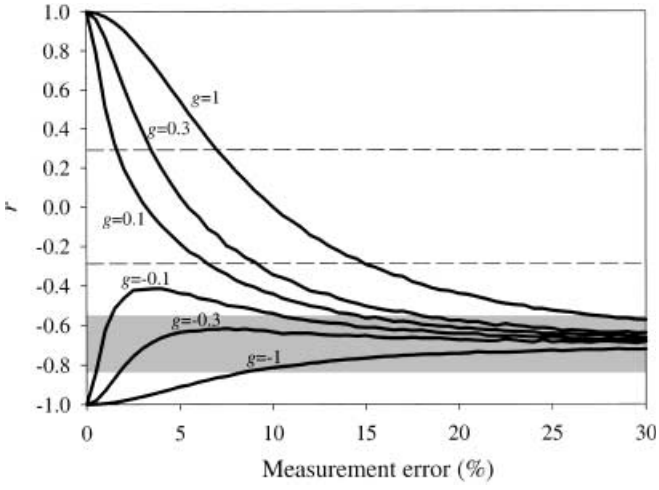


**Fig. 2** Effect of measurement error on the correlation ($r$) between pre-molt size $m_1$ and molt increment. Values of $g$ denote actual growth patterns excluding measurement error: $g$>0 represents divergent growth and $g$<0 is convergent growth. Values of $r$ outside (–0.279, 0.279, *dashed lines*), are significantly different from 0; values of $r$ outside (–0.533, –0.824, *shaded area*), are significantly different from –0.7071 ($df$=48, $\alpha$=0.05). Under the null hypothesis that $r$=0, measurement error tends to generate significantly negative values of $r$ which lead to the false conclusion that convergent growth occurred

times for each plot). Measurement errors were drawn at random from a normal distribution with mean=0 and standard deviation equal to 5% of the mean size of the smallest molt. This simulates absolute measurement error, where the amount of error is fixed and does not change relative to the size of the object being measured (e.g., the same microscope objective is used to measure size at all molts). Measurement error of 5% was used for the copepod data because this value was reported for similar-sized nauplii of another copepod species (Twombly 1995) and because this is near the accuracy of the actual data (measurements were taken to the nearest 5 µm); 5% error was also used for the barnacle data.

Figure 1 compares the random and actual data. For the copepods the graphs are similar although the actual data (Fig. 1A) are slightly more dispersed than the random data (Fig. 1B). This could be due to natural size variation in the actual data or to an underestimation of measurement error in the simulations. Random data using 8% measurement error produced plots nearly indistinguishable from the actual data. Correlations for the actual data had been reported as significantly negative, leading to the conclusion that convergent growth regulation occurred in all stages (Table 1). Correlations for the random data were also significantly negative ($t$-test, $df$=48, $P$<0.0001). The actual barnacle data (Fig. 1C) were qualitatively similar to the random data (Fig. 1D), although the relationship was more dispersed in later stages relative to the random data. Significant negative slopes had been reported for stages II-IV only, leading to the conclusion that convergent growth occurred during these stages (Table 2). All five random data slopes were significantly negative ($t$-test, $df$=48, $P$<0.0001).

It seems strange that random data could produce such a clear and significantly negative pattern, but this occurs because the $y$-axis ($m_{x+1}$-$m_x$) implicitly contains the $x$-axis ($m_x$). Due to this part-whole relationship, random independent measurement errors propagate in such a way that they produce negative correlations. To visualize this, imagine that because of chance measurement error an individual at stage 1 was measured as smaller than its true size. Even if the subsequent measurement at stage 2 is close to the true size, the difference $m_2$–$m_1$ will appear unusually large because it contains the increment actu-ally grown plus the error in $m_1$. Conversely, $m_1$s that are by chance measured as larger than the true values will tend to produce smaller molt increments. Thus, there is an inherent asymmetry in plots of pre-molt size and molt increment that tends to generate negative correlations or negative slopes.

How much measurement error is tolerable?

The probability that measurement error will generate false evidence for regulated growth depends on the strength of the actual growth pattern relative to the degree of measurement error. Strength of the underlying growth pattern consists of two parts: the amount of within-stage size variation (measurement error of a given magnitude will have a smaller effect if there is a lot of "spread" in size) and the amount of growth regulation that occurs (strong growth regulation, whether divergent or convergent, will be easier to detect than weak regulation). Growth regulation, as it is interpreted in studies that used growth increment analysis, can be formalized by the following equation:

$$inc_i = (\bar{m}_2 - \bar{m}_1) + g(m_{i1} - \bar{m}_1). \quad (1)$$

Eq. 1 describes how the molt increment for an individual $i$ depends on its pre-molt size $m_{i1}$. Body size regulation occurs relative to the mean molt increment $\bar{m}_2$–$\bar{m}_1$, and the parameter $g$ controls the sign and strength of body size regulation. When $g$=0 no growth regulation occurs because individuals grow a fixed amount regardless of pre-molt size. Molt increment and pre-molt size will be uncorrelated in this case. When $g$<0 convergent growth regulation occurs because smaller individuals grow more than larger individuals, producing a negative correlation between molt increment and pre-molt size. Perfect convergent growth occurs when $g$=–1 because all individuals reach the same size at molt 2 regardless of size at molt 1. When $g$>0 divergent growth occurs because individuals that are large at molt 1 grow more than smaller individuals, resulting in a positive correlation.

Figure 2 simulates how measurement error affects the correlation between pre-molt size and molt increment when the true growth pattern is known. Each simulation was produced as follows. Pre-molt body sizes ($m_{i1}$s) were generated for 50 individuals by drawing them at random from a normal distribution with mean body size $\bar{m}_1$=100 units and standard deviation of 10 units. This represents the initial within-stage size variation. Individuals then grew an increment determined by Eq. 1, with $\bar{m}_2$=150 and values of $g$ representing strong (±1), intermediate (±0.3), or weak (±0.1) growth regulation. These pre-molt body sizes and growth increments represent the underlying values measured without error. Random measurement error (normally distributed with mean=0 and standard deviation equal to a specified percentage of $\bar{m}_1$) was added to the actual $m_{i1}$ and $m_{i2}$ values to produce observed values. The correlation between observed values of pre-molt size and molt increment was then calculated. This was repeated 1000 times at each level of measurement error, and the average value of $r$ was graphed. Levels of measurement error ranged from 0 to 30% of $\bar{m}_1$ in 0.5% increments.

The case where $r$ is significantly different from zero corresponds to the regions outside the dashed lines in Fig. 2. It is readily apparent that measurement error often leads to the erroneous conclusion that no growth regulation, or even convergent growth, occurred when in fact divergent growth occurred ($g$>0 lines). This type II error was worse when growth regulation was weakly divergent; less than 3% error caused the $g$=0.1 line to become nonsignificant. Measurement error also caused divergent growth patterns to appear significantly convergent. Remarkably, even when actual growth was strongly divergent ($g$=1), only 15% measurement error produced significant negative values of $r$, suggesting that growth was convergent. On the other hand, when growth was in fact convergent ($g$<0 lines), measurement error did not cause values of $r$ to deviate from being significantly negative. Thus, the greatest peril of using the null hypothesis that $r$=0 to test for growth regulation is the chance of mistaking divergent growth for convergent growth, not vice versa.

Expected correlation when no growth regulation occurs

As measurement error increased in the simulations, $r$ converged on –0.7071. The reason for this is shown by an examination of the correlation between pre-molt size and molt increment. The general formula for the correlation between two variables $X$ and $Y$ is

$$r_{XY} = \frac{\mathrm{COV}(X,Y)}{\mathrm{SD}(X)\mathrm{SD}(Y)}. \quad (2)$$

Because pre-molt size $m_1$ and molt increment $m_2$–$m_1$ are implicitly related, their correlation is

$$= \frac{\mathrm{COV}(m_2 - m_1, m_1)}{\mathrm{SD}(m_1)\mathrm{SD}(m_2 - m_1)} \quad (3)$$

$$= \frac{\mathrm{COV}(m_1, m_2) - \mathrm{VAR}(m_1)}{\sqrt{\mathrm{VAR}(m_1)}\sqrt{\mathrm{VAR}(m_1) + \mathrm{VAR}(m_2) - 2\mathrm{COV}(m_1, m_2)}}. \quad (4)$$

Assuming measurement errors in $m_2$ and $m_1$ are independent and equally variable, as measurement error becomes large relative to the actual pattern in the data $\mathrm{COV}(m_2,m_1)\rightarrow 0$ and Eq. 4 collapses to $-1/\sqrt{2}$. This demonstrates that when random measurement error is high relative to the underlying pattern in the data, the expected value of the correlation between pre-molt size and molt increment approaches –0.7071. It can be shown by an analogous argument that under the same conditions the value of a simple linear regression slope coefficient is –1. This result calls into question the use of the null model that $r$ or $b$=0 to test whether a correlation is due to random chance (versus the alternative hypothesis of being attributable to growth regulation). Under this null hypothesis, the noisier the data are the lower the resulting $P$-value will be – an undesirable property of any test statistic.

It is important to note that real biological variability can cause the same problems as measurement error. Because of this, there is no reliable way to "factor out" the influence of measurement error from that due to real bio-

logical processes. This can be seen by partitioning the observed variances and covariances into components due to actual biological variability (subscripted *a*) and to measurement error (subscripted *e*):

$$\mathrm{VAR}(m_1)=\mathrm{VAR}(m_{a1})+\mathrm{VAR}(m_{e1})+2\mathrm{COV}(m_{a1},m_{e1}) \quad (5a)$$

$$\mathrm{VAR}(m_2)=\mathrm{VAR}(m_{a2})+\mathrm{VAR}(m_{e2})+2\mathrm{COV}(m_{a2},m_{e2}) \quad (5b)$$

$$\mathrm{COV}(m_1,m_2)=\mathrm{COV}(m_{a1},m_{a2})+\mathrm{COV}(m_{e1},m_{e2}) +\mathrm{COV}(m_{a2},m_{e1})+\mathrm{COV}(m_{a1},m_{e2}). \quad (5c)$$

When measurement errors are independent, which will typically be the case, the covariance terms containing errors become zero. Substituting actual variances for observed ones into Eq. 4,

$$= \frac{\mathrm{COV}(m_1,m_2)-\mathrm{VAR}(m_1)+\mathrm{VAR}(m_{e1})}{\sqrt{\mathrm{VAR}(m_1)+\mathrm{VAR}(m_{e1})}\sqrt{\mathrm{VAR}(m_1)-\mathrm{VAR}(m_{e1})+\mathrm{VAR}(m_2)-\mathrm{VAR}(m_{e2})-2\mathrm{COV}(m_1,m_2)}}. \quad (6)$$

Eq. 6 shows that either biological variance or error variance will produce a highly negative correlation in the absence of any correlation between $m_1$ and $m_2$. Even without measurement error, if $m_1$ is uncorrelated with $m_2$ and their variances are equal (e.g., when no growth regulation occurred) Eq. 6 still converges on –0.7071. As with Eq. 4, this convergence also occurs when measurement errors predominate. Thus, accounting for measurement error can only solve some of the autocorrelation problems associated with correlations between pre-molt size and molt increment.

### Geometric mean regression

An alternative method is to remove autocorrelation by directly examining the relationship between $m_1$ and $m_2$. In a regression of $m_2$ on $m_1$, a slope of 1 indicates no growth regulation, slope >1 indicates divergent growth, and slope <1 is convergent growth. Although model I regression is clearly not appropriate because it assumes $m_1$ is measured without error (and errors in $m_1$ would cause the slope to appear less than it actually is), model II regression requires only that the ratio of error variances in $m_1$ and $m_2$ remain constant – an assumption that will be met for absolute measurement error. In model II geometric mean (GM) regression, the variables are standardized and the slope of their principal axis is computed (Ricker 1973; Sokal and Rohlf 1995). In practice this slope, $v_{Y\cdot X}$, is simply the ratio of the standard deviations, $s_y/s_x$. This ratio makes biological sense, because if convergent growth is occurring the variance in $m_2$ should be reduced relative to the variance in $m_1$. The null hypothesis that $v_{Y\cdot X}=1$ can be used to test for growth regulation. GM regression has the advantage that as measurement errors become large relative to the actual pattern, $v_{Y\cdot X}$ converges on 1 and the null hypothesis is not rejected.

Tables 1, 2 show a reanalysis of the copepod and barnacle data using GM regression. GM regression suggests no evidence for growth regulation in all but three copepod molt stages, and these are cases of divergent rather than convergent growth. Similarly, no growth regulation was detected in early barnacle stages, but both convergent and divergent growth occurred in later stages. The conclusions reached using GM regression are almost exactly opposite those reached using molt increment statistics, and suggest that at least for these taxa convergent growth is the exception rather than the rule.

## Discussion

The findings presented here suggest that negative relationships between pre-molt size and molt increment do not provide reliable evidence for convergent growth regulation. This was demonstrated in three ways. First, simulations using random data consistently produced significant negative correlations and regressions very similar to patterns reported in the literature. Second, simulations demonstrated that even modest degrees of measurement error can generate a significant negative correlation when the actual correlation is positive. Third, an analysis of the correlation and regression coefficients used in these tests showed that highly negative values are expected a priori when the pattern-to-noise ratio in the data is low.

Given these properties it is no surprise that studies using growth increment analysis consistently found convergent growth. Conversely, the lack of evidence for divergent growth is suspicious since even strongly divergent growth patterns often appeared convergent when the $r$ or $b$=0 null hypothesis was employed. Because a reanalysis of the copepod and barnacle data using geometric mean regression suggested that convergent growth was rare, it is possible that similar results might emerge from reanalysis of other studies.

Other studies have demonstrated that the expected correlation between two variables related by a part-whole relationship is non-zero. The study of allometric growth relationships has received the most attention (Pearson 1897; Atchley et al. 1976, and the ensuing debate in *Systematic Zoology* 27(1); Packard and Boardman 1988), but the problem has also come up in hydrology (Yalin and Kamphuis 1971), limnology (Kenney 1982), and community ecology (Weller 1987; Prairie and Bird 1989; Jackson 1997). Although some authors recognize that the study of these part-whole relationships can be useful so long as the autocorrelation is explicitly recognized, it is generally agreed that measurement error poses an especially serious problem for these statistics (Prairie and Bird 1989; Rayner 1985).

Aside from GM regression, other related statistical methods may be useful for analyzing growth increment data. When measurement errors are correlated, a more general form of GM regression may be used (the general

structural relation, Rayner 1985). Klingenberg (1996) used common principal components (Klingenberg et al. 1996) to analyze individual growth data in water striders. Although this study did not account for measurement error, the method did account explicitly for patterns generated by the part-whole relationships inherent to ontogenetic data. As a result, the study found some evidence for convergent growth in early stages and divergent growth in later stages. The path analysis method developed by Lynch (1988) deals with measurement error directly. The method partitions variance within each molt increment into biological and measurement error components. When measurement errors are known (i.e., when multiple measurements are taken for each observation) they can be factored out of the analysis. Applying this technique to *Daphnia* growth data, Lynch found that even though measurement error was very low (around 1%), when not accounted for it greatly affected values of path coefficients, although the qualitative conclusions of the study were not altered. The analysis found evidence for both convergent and divergent growth.

Two major points emerge from the findings in this study. First, statistics that relate growth increments to size at a particular stage should be used with extreme caution, or avoided entirely when other methods can be used instead. Second, a careful accounting of measurement error should be part of any study that examines growth patterns throughout ontogeny. Until these issues are addressed, the prevalence and direction of growth regulation in arthropods will remain obscure.

**Acknowledgements** I thank Anna Jolles and two anonymous reviewers for comments on an earlier version of this manuscript. I also thank Steve Pacala, Stuart Sandin, and Alan Tessier for insightful discussions on the statistical methods.

## References

Atchley RA, Gaskins CT, Anderson D (1976) Statistical properties of ratios. I. Empirical results. Syst Zool 25:137–148

Freeman JA (1990) Molt increment, molt cycle duration, and tissue growth in *Palaemonetes pugio* Holthuis larvae. J Exp Mar Biol Ecol 143:47–61

Hartnoll RG, Dalley R (1981) The control of size variation within instars of a crustacean. J Exp Mar Biol Ecol 53:235–239

Huyser K, Laan J van der (1994) DataThief v2.0b. Available from http://archives.math.utk.edu/software/mac/graphingAids/DataThief/

Jackson DA (1997) Compositional data in community ecology: the paradigm or peril of proportions? Ecology 78:929–940

Kenney BC (1982) Beware of spurious self-correlations. Water Resour Res 18:1041–1048

Klingenberg CP (1996) Individual variation of ontogenies: a longitudinal study of growth and timing. Evolution 50:2412–2428

Klingenberg CP, Neuenschwander BE, Flury BD (1996) Ontogeny and individual variation: analysis of patterned covariance matrices with common principal components. Syst Biol 45:135–150

Lynch M (1988) Path analysis of ontogenetic data. In: Ebenman B, Persson L (eds) Size-structured populations: ecology and evolution. Springer, Berlin Heidelberg New York, pp 29–46

Mohamedeen H, Hartnoll RG (1989) Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenus* (L). J Exp Mar Biol Ecol 134:1–24

Packard GC, Boardman TJ (1988) The misuse of ratios, indices, and percentages in ecophysiological research. Physiol Zool 61:1–9

Pearson K (1897) Mathematical contributions to the theory of evolution. On a form of spurious correlation which may arise when indices are used in the measurement of organs. Proc R Soc Lond 60:489–498

Prairie YT, Bird DF (1989) Some misconceptions about the spurious correlation problem in the ecological literature. Oecologia 81:285–288

Rayner JMV (1985) Linear relations in biomechanics: the statistics of scaling functions. J Zool Lond A 206:415–439

Ricker WE (1973) Linear regression in fishery research. J Fish Res Bd Can 30:409–434

Riska B, Atchley WR, Rutledge JJ (1984) A genetic analysis of targeted growth in mice. Genetics 107:79–101

Roff DA (1992) The evolution of life histories. Chapman and Hall, New York

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Tanaka A (1981) Regulation of body size during larval development in the German cockroach, *Blattella germanica*. J Insect Physiol 27:587–592

Tanner JM (1963) Regulation of growth size in mammals. Nature 199:845–850

Twombly S (1995) Phenotypic variation in metamorphosis in four species of freshwater copepods. Freshwater Biol 34:29–38

Twombly S, Tisch N (2000) Body size regulation in copepod crustaceans. Oecologia 122:318–326

Weller DE (1987) A reevaluation of the –3/2 power rule of plant self-thinning. Ecol Monogr 578:23–42

West TL, Costlow JD (1987) Size regulation in larvae of the crustacean *Balanus eburneus* (Cirripedia: Thoracica). Mar Biol 96:47–58

Yalin MS, Kamphuis JW (1971) Theory of dimensions and spurious correlation. J Hydrol 9:249–265