Original Research Article

Damping the impact of intraspecific variability of whorl growth-rate on the range of intraspecific variation of adult shell-size in gastropods with determinate growth: evidence of a finely-tuned regulating process

Abstract

Many species among shelled gastropods, either land snails or marine snails, exhibit determinate growth and, therefore, are expected to implement some regulating process aiming at limiting (damping) the impact on the final (adult) shell-size of the (possibly excessive) intraspecific variability in shell-development rate. Indeed, a usually more or less limited range of variation is allowed for adult shell-size, in those species having determinate growth. Mollusks are expected to be no exception in this respect and, up to now, the occurrence of such a regulating process has been systematically reported, despite a still too limited number of investigations. Yet, the question remained of the ability of this regulatory process to finely adjust the end of body and shell development (specifically in term of the final number of whorls), so as to limit the variations in adult shell-size, despite the amplitude of intraspecific variability in shell development rate.

I hereby provide preliminary empirical evidence for such a "finely tuned" regulating process – the strength of which mirrored by the degree of "Gouldian" negative covariance between whorl growth-rate and the number of whorls at adulthood. As expected, the strength of the regulating process reveals systematically increasing (i) with the amplitude of the intraspecific variability in shell development-rate and (ii) with the narrowness of the range of variation allowed for adult shell-size (narrowness which depends upon the identity of the particular species under consideration). In addition to the already reported usual occurrence of this regulating process among shelled gastropods, its "finely tuned" character provides here still further evidence as regards its major importance in controlling the species-specific adult body mass, and this even for typically soft-bodied animals.

Key-words: land snail, marine snail, growth regulation, size control

1. Introduction

Many kinds of animal species have determinate-growth; that is, their adult body-size/mass is constrained to remain within a more or less limited range of variation. As emphasized by TEXADA *et al.* [1], in those animals, the control of body-size and proportions is often important to favor their survival and reproduction. And, as adult body-size is determined by both the rate and the duration of juvenile growth, a negative covariance is expected to occur between growth-rate and growth-duration. At least, as far as the range of intraspecific variability in growth-rate and duration is likely to lead to excessive intraspecific variability in adult body size or mass, i.e., exceeding the species-specific allowed range of variation in adult body-size/mass.

Highlighting such a *negative covariance* thus bears witness of the involvement of some efficient *regulating process* efficiently controlling the adult body-size/mass at adult stage.

In the case of shelled gastropods, in particular land snails, the linear dimensions of the soft body are, of course, essentially undefined and it is therefore the adult body-volume which is expected to be under control, for those gastropod species having determinate growth. With, accordingly, straightforwardly implies a corresponding control of the size of adult shell itself, since shell volume usually tightly complies with soft body volume [2, 3].

In conispirally-coiled shells, approximately answering the ideal exponentially coiling model, the overall shell-size (i.e., shell-height for elongate shells or shell-width for globular or discoid shells) is directly dependent on (i) the whorl growth-rate (i.e. the expansion-rate per turn of the whorl section, from its initial size) and (ii) the number of whorls being reached. Accordingly, a *negative covariance* is expected to occur between the *whorl growth-rate* and the *number of whorls* reached at adulthood. Thus, highlighting a kind of "trade-off" between the respective intraspecific variations of (i) the whorl growth-rate and (ii) the number of whorls reached at adulthood. Thereby aiming at damping (buffering) more or less efficiently the variations of adult shell-size which characterized determinate-growth regulation. A trade-off quite similar indeed to that between body growth-rate and growth-duration, in non-molluscan animals.

Now, this expectation has been confirmed then empirically; at first in the land snail genus *Cerion* by S. J. GOULD and coworkers [4,5], and then, more recently, in a small series of species belonging to a variety of other shelled-gastropod genus, especially land snails [3,6-8]. With various strenght of the negative covariance, depending on species. But always reaching high statistical significance in all reported cases.

In accordance with the argument developed above, one can logically speculate that the level of negative covariance – appropriately measured by its coefficient of determination r^2 – will be all the *higher* that:

- the (species-specific) allowed range of variation in adult shell-size is *narrower*;
- the respective ranges of intraspecific variability of the whorl growth-rate and of the final number of whorls (both of them contributing to adult shell-size dispersion) are *larger*.

Since a *narrower* imposed variability in adult shell-size, as well as *larger* variabilities of the two contributors to shell-size, both require a stronger negative corrective covariance.

The main objective of the report below is to provide the results of *empirically testing* the *double hypothesis* stated above.

2. Materials and Methods

2.1-Materials

Eight *land snail* species and one *marine snail* species were considered in this study, all of them collected from France (Burgundy for land snails and Normandy for the marine snail). Four species have globular shells, one has discoidal shell and four have more or less elongate shells. For each species, a local population was sampled bringing together a sufficient number of adult shells to identify statistically significant trends (if any).

As regards the eight *land snail* species:

* *Cepaea nemoralis* (Linneaus 1758) : 103 sampled adult individuals, located at Saint Vallerin (Saône & Loire department, south Burgundy);

* *Cornu aspersum* (O.F. Müller 1774) : 33 sampled adult individuals, located at Salins-les-Bains (Jura department, Franche-Comté);

* *Monacha cartusiana* (O.F. Müller 1774) : 115 sampled adult individuals, located at Saint Vallerin (Saône & Loire department, south Burgundy);

* *Helicodonta obvoluta* (O.F. Müller 1774) : 83 sampled adult individuals, located at Blois-sur-Seille (Jura department, Franche-Comté);

* *Pomatias elegans* (O.F. Müller 1774) : 110 sampled adult individuals, located at Saint Vallerin (Saône & Loire department, south Burgundy);

* *Chondrula tridens* (O.F. Müller 1774) : 51 sampled adult individuals, located at Germagny (Saône & Loire department, south Burgundy);

* *Ena montana* (Draparnaud 1801) : 28 sampled adult individuals, located at Val-Suzon (Côte d'Or department, central Burgundy);

* *Zebrina detrita* (O.F. Müller 1774) : 43 sampled adult individuals, located at Le Parrotier (Vaucluse department, Provence).

For the *marine snail* species:

* *Euspira catena* (da Costa 1778) : 70 sampled adult individuals, located at Villers-sur-Mer (Normandy)

Additional details are provided for land snails populations in references [3,6] and for the marine snail in references [7,8].

2.2-Method

For each individual shell, both the number of whorls n_a reached at adulthood and the shell-size Δ_a (i.e. diameter D_a for globular and discoidal shells or height H_a for elongate shells) were measured:

- the shell size by using a numeric calliper (to the precision of 1/10 mm);
- the number n_a of whorls at adult stage by careful examining the shell from the apex, according to the procedure prescribed in [9,10], using a stereo-microscope at moderate magnification, a procedure which allows reaching a precision at the level of 1/10 whorl revolution.

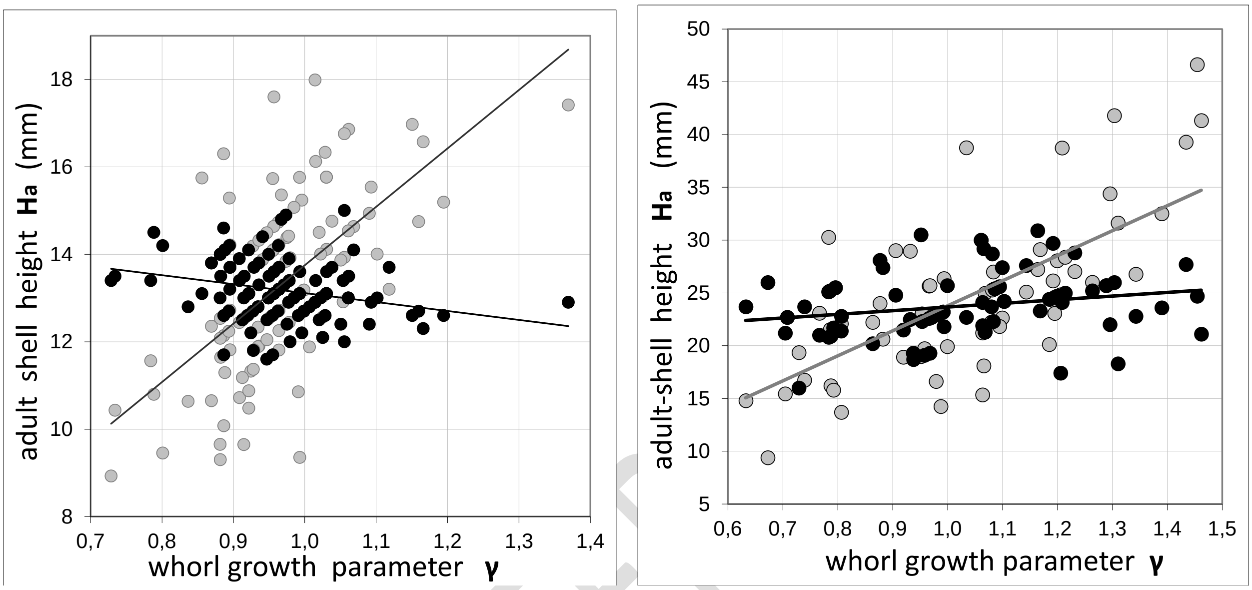
Subsequently, the progressive development of whorl-section (involving the contributions of both the first whorl-size and the exponential-like expansion of the whorl section along successive turns) is computed, according to the procedure described in [3,6-8] (procedure briefly recalled in Appendix), thus providing the "whorl-growth parameter" 'γ', quantifying the contribution of progressive whorl growth to the shell-size reached at adulthood.

The respective degrees of *intra-specific variability* of the whorl-growth parameter γ, of the number of whorls reached at adult stage n_a and, finally of the adult shell-size Δ_a are quantified by means of the corresponding coefficients of variation (C.V.) – ratio of standard deviation to the mean. The strength of the negative covariance between the whorl-growth parameter γ and the number of whorls at adult stage n_a is quantified by the coefficient of determination r^2 of the covariance. The selection of those shells having reached the adult stage is classically recognized according to aperture morphology [2, 11-13].

3. Results: *testing the double hypothesis*

3.1 – A reminder: the efficiency of the process of regulating the adult shell-size, highlighted in two examples

At first, the negative covariance between shell-development parameters γ and n_a (up to now systematically reported in marine and land snails [2-8]) indirectly highlights the involvement of a process of more or less drastic regulation of the degree of intra-specific variability of the body-volume reached at the adult stage. Which is reflected, in turn, by the corresponding regulation of the degree of intra-specific variability of adult shell-size Δ_a. As an example, Figures 1 and 2 provide empirical evidence of the efficiency of this regulation process. Indeed, while the adult shell-size (here shell-height H_a) remains substantially independent of the intraspecific variations of the whorl growth parameter γ, the *artificial cancellation* of the regulation process (computed by redistributing the values of n_a *independently of* the values of γ, thus cancelling their actual negative covariance) leads, as expected, to a strong (of course positive) dependence of the adult shell-size upon the whorl growth parameter γ. And, thus, a marked increase in the dispersion of adult shell-size, likely exceeding the allowed range of variation of adult shell-size, specific to the species under consideration.



Figures 1 & 2 – Adult shell height H_a versus the whorl growth parameter γ. Left: *Pomatias elegans* (110 shells). Right: *Euspira catena* (70 shells). *Black points*: as recorded; *grey points*: after random redistribution of values of the number of whorls n_a independently of the whorl growth parameter γ, i.e. without any covariance between n_a and γ. After references [7,8].

3.2 – empirically testing the double hypothesis addressed in Introduction

Now, the question specifically addressed in Introduction, was: does the regulation process, which already seems widespread (up to now) among gastropods species, proves, *moreover*, being also rather finely-tuned (narrowly "adapted") to the amplitude of the intraspecific variability of shell growth in each particular species? Since one may speculate that a *larger* intraspecific variability in shell growth (and/or a *narrower* allowed variability in adult shell-size) would call for a *stronger* regulating process (that is a stronger trade-off between γ and n_a).

That is, more precisely: does the coefficient of determination r^2 of the negative covariance between γ and n_a (which mirrors the strength of the regulation process) actually *increases* with either (i) a *narrower* range allowed for the intraspecific variations of adult shell-size in the species under study, or (ii) *larger* ranges of intraspecific variability of both the whorl growth-rate and the final number of whorls?

Table 1 provides, for each of the nine studied species, the *degrees of intra-specific variability* (in terms of the corresponding coefficients of variation):

(i) for the two main parameters – γ and n_a – characterizing the shell development up to its stabilisation at the adult stage;

(ii) for the resulting adult shell-size Δ_a.

Table 1 also provides, for each of the nine studied species, the coefficient of determination of the negative covariance observed (systematically) between γ and n_a.

Let first consider the subset of those seven species (*Ena montana, Helicodonta obvoluta, Chondrula tridens, Cepaea nemoralis, Zebrina detrita, Pomatias elegans, Cornu aspersum*) having relatively similar allowed ranges of intraspecific variations of adult shell-size (C.V.(Δ_a) ≈ 5% $\pm$ 1%, see Table 1).

Table 1 – The reported coefficients of variations (C.V.) for the intraspecific variability of (i) the whorl growth parameter γ, (ii) the adult number of whorls n_a, (iii) the adult shell-size Δ_a and the coefficient of determination (C.D.) for the negative covariance between γ and n_a (all results reported in references [3-6-8]).

	Ena m.	**Helico**	**Chondr**	**Cepaea**	**Zebrin**	**Pomat**	**Cornu**	**Monac**	**Euspir**
C.V. γ	4.9%	5.6%	6.4%	7.6%	9.4%	9.4%	11.4%	9.8%	19.6%
C.V. n_a	2.6%	2.8%	4.1%	3.1%	3.6%	3.7%	3.2%	4.6%	6.7%
C.V. Δ_a	5.1%	3.9%	6.4%	4.7%	6.3%	5.3%	4.9%	11.2%	13.3%
C.D. covar	62%	66%	76%	67%	81%	81%	81%	28%	63%

Figure 3 highlights a clear trend for the coefficient of determination r^2 of the negative covariance between γ and n_a to regularly increase with the sum of the coefficients of variations of γ and of n_a. Thus, highlighting the “fine-tuned” adaptation of the strength of the negative covariance between shell parameters γ and n_a. The latter bearing indirect witness of the efficient control applying to the adult body volume, through the associated shell volume.

Now let consider, in addition, the eighth land snail species, *Monacha cartusiana*, which stands out by a markedly *wider* range of allowed variability in adult shell-size (11%). Figure 4 shows that, for this species, the coefficient of determination of the negative covariance between γ and n_a is (as expected) substantially lower than for the seven other land snail species with more restricted allowed variability for adult shell-size, around 5% (and this even at a same level of intraspecific variability of shell development parameters).

Similarly, the marine snail species, *Euspira catena*, which also singularizes by a *wide* range of allowed variability in adult shell-size (13%), still provides additional confirmation of the preceding trend, as shown in Figure 5.

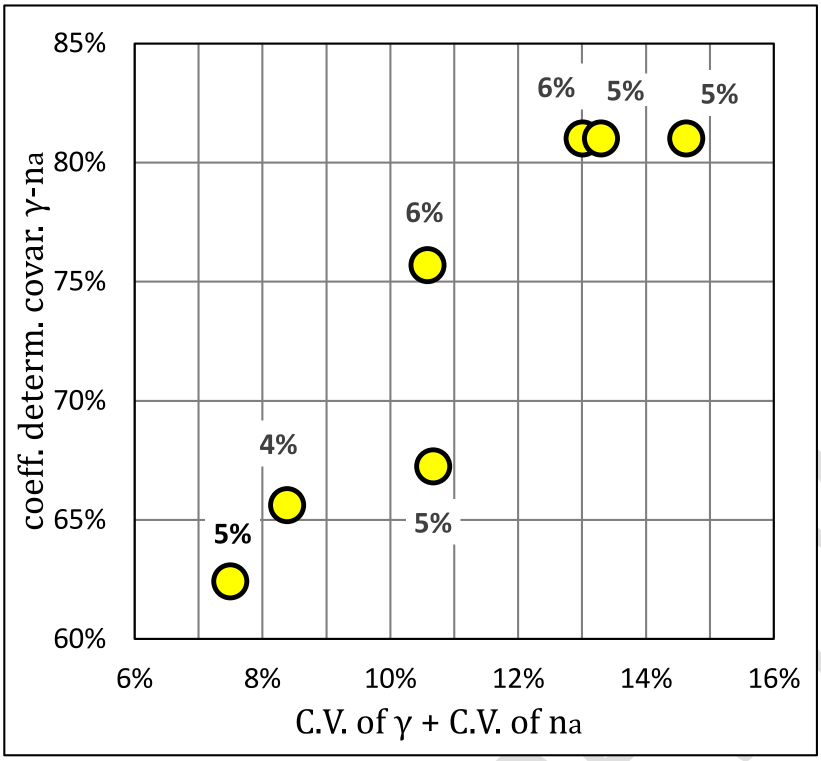


Figure 3 – The coefficient of determination r^2 of the negative covariance between γ and n_a, plotted against the sum of the coefficients of variations of γ and of n_a, for the seven land snail species having similar allowed ranges of intraspecific variations of adult shell size (C.V.(Δ_a) ≈ 5% ± 1%). Data from Table 1. *As hypothesized*, the coefficient of determination of the covariance strongly increases with C.V.(γ) + C.V.(n_a).

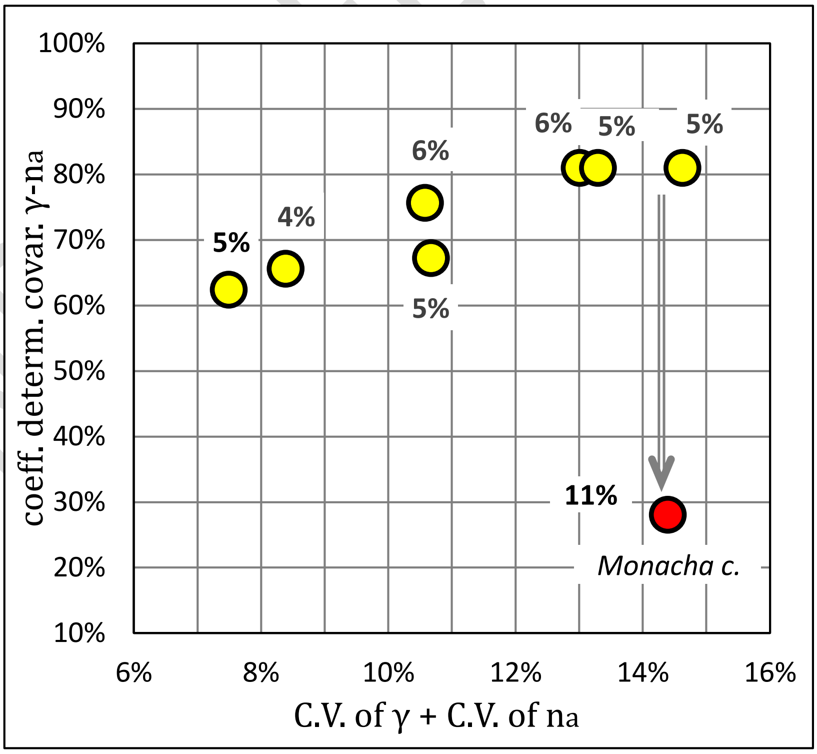


Figure 4 – The same as Figure 3 with, in addition, *Monacha cartusiana*. *As hypothesized*, the coefficient of determination of the covariance strongly decreases for this species which allows a markedly wider range of variability in adult shell-size (C.V.(Δ_a) ≈ 11% instead of 5% ± 1%).

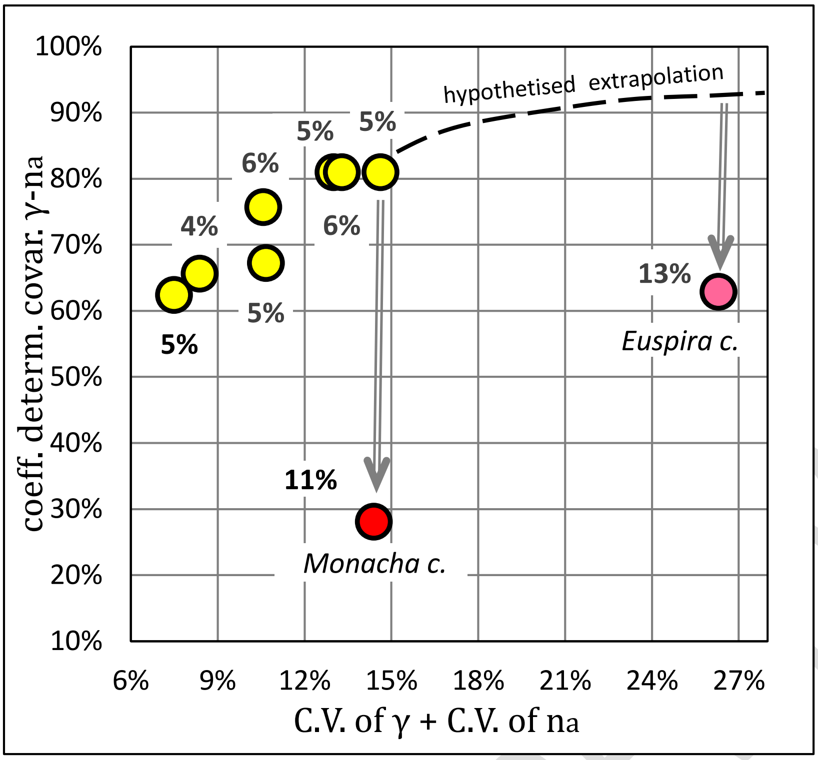


Figure 5 – The same as Figure 4 with, in addition, *Euspira catena*. A second *confirmation* that the coefficient of determination of the covariance strongly decreases when a markedly wider range of variability in adult shell-size is allowed (here C.V.(Δ_a) ≈ 13% instead of 5% $\pm$ 1%).

4. Discussion: *assessing the likelihood of the tested double-hypothesis*

Beyond the seemingly widespread involvement of a regulating process aiming at buffering the consequences of (excessive) intraspecific variability in body and shell progressive development in shelled gastropods, the question addressed by this study was to check whether this regulating process is, moreover, more or less finely tuned (i.e. "self-adaptative") to the degree of intraspecific variability in shell development parameters (namely, γ and n_a). That is to check whether the regulation proves being all the *stronger* than:

(i) *larger* is the intraspecific variability in shell development parameters γ and n_a and/or

(ii) *narrower* is the range of intraspecific variability allowed for the adult shell-size (as species-specifically prescribed).

The results presented in Figure 3 on the one hand and Figures 4 and 5 on the other hand, respectively addressed the two parts of this double hypothesis and provides positive evidence in favour of both – was logically expected.

Thus, for those seven species which show a rather severe limitation of the intraspecific variability of shell-size Δ_a (and body-volume) at adult stage (with coefficients of variation C.V.(Δ_a) all remaining around 5%, cf. Figure 3), the strength of the regulating process – as mirrored by the coefficient of determination of the negative covariance between γ and n_a – clearly "adapts" to the degree of variability in the shell development factors (γ and n_a): the larger is {C.V.(γ) + C.V.(n_a)}, the higher is the determination r^2 of the negative covariance between γ and n_a, with seemingly a proportionate (sublinear) answer. This applies to the first part of the double hypothesis.

As for the second part of the hypothesis – the relaxation of the regulation (at given degree of variability of shell development factors) for those species less demanding upon a limited dispersion of adult shell-size, the evidence from Figures 4 and 5 provide clear confirmations of the second part of the double hypothesis.

Additional evidence for a severe control of adult shell-size Δ_a (also with C.V.(Δ_a) ≈ 5%) have been reported elsewhere [11,12,14] in land snails. And it is likely that a similarly strong regulating process was involved here as well, although, regrettably, no testing in this regard has been carried out in any of these three studies.

Now, as convincing as all these preliminary results may appear, in support of the double hypothesis invoked, the still rather limited number of case studies (nine) upon which they are based calls for still further investigation.

In particular, although a severe control of adult shell-size Δ_a (C.V.(Δ_a) ≈ 5%), involving strong regulation process, seems somewhat more common (7 + 3 case studies) than is medium control (11% - 13% for C.V.(Δ_a)) (2 case studies), this figure yet deserves further attention.

But, at least one case has been reported of a very relaxed control of the intraspecific variability in adult shell-size, regarding a species, *Notodiscus hookeri* Reeve 1864, yet exhibiting determinate growth [13]: a series of populations of this species from different localizations in Kerguelen and Crozet Archipelago (some of them even rather close to each other) show strikingly different degrees in the control of adult shell-size, ranging from 5% up to no less than 27% in C.V.(Δ_a)! Once again, no further analysis of the existence and strength of a negative covariance between γ and n_a – correlative of the involvement of a regulation process – was regrettably carried out.

It is worth noting, however, that *Notodiscus hookeri* is substantially smaller (Δ_a = 3.9 – 5.1 mm) than all the preceding species. And I have the suspicion (unfortunately very badly substantiated for the moment) that adult shell-size might perhaps be more or less poorly controlled in such tiny species, despite their having determinate growth.

5. Conclusion

A small series of reports (initiated by the seminal report by S.J. GOULD), have already highlighted the (up-to-now systematic) occurrence of a more or less strong negative covariance between the two main factors of shell development (whorl-growth and number of whorls at adult stage) among shelled gastropod species having determinate growth. This covariance witnessing in turn, the involvement of a more or less severe regulating process aiming at limiting the intraspecific variability of the adult shell-size (and adult soft-body volume), despite the direct influence of the intraspecific variability of the two main factors of shell development which together rule the adult shell-size.

Here, we have further tested empirically the speculative, yet likely, hypothesis that the strength of the regulating process is "adaptative". That is, this regulating process actually proves being all the *stronger* than (i) the intraspecific variability of the two main factors of shell development is *larger* and (ii) the allowed range of intraspecific variation of the adult shell-size is *narrower*. This thus finely-tuned answer of the regulating process provides additional impetus to the major importance of some minimal level of "dimensional homeostasis" – yet depending upon species – at the time of reaching adult stage in those species exhibiting determinate growth. We provide evidence, here, that this likely stands, as well, for animals with soft bodies – the shell playing the role of a particular kind of exoskeleton.

However, as convincing as it may seem, the evidence provided here remains based upon a still too limited number of case studies and therefore requires further investigations to be carried out on this subject.

Appendix

Quantifying the respective contributions of shell-development parameters to the adult shell-size in conispirally-coiled shells

For those gastropod species with shell coiling geometry fairly approaching a conispiral profile and approximately answering the ideal exponential model (i.e. logarithmic spiral coiling), the *contribution*, δ_i, of whorl number 'i' to the overall shell dimensions Δ (shell height or shell width) is, according to [15-22]:

$$\Delta_i = \delta_1.\varepsilon^{(i-1)}$$

where:

- δ_1 is the contribution of whorl number one ;
- ε is the rate of whorl expansion (and, as well, the ratio between the contributions of two successive whorls: $\varepsilon = \delta_{i+1}/\delta_i$).

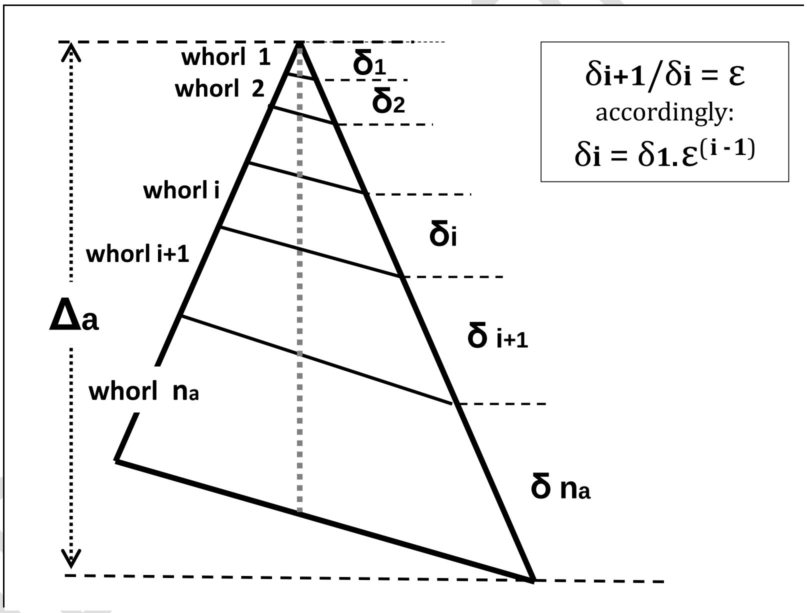


Figure A1 – Schematic sketch of the section of an ideally conispirally coiled shell, showing the morphometric parameters involved in this study: n_a the number of whorls at adult stage; δ_i the contribution to shell-height of the i^{th} whorl ; ε the ratio of expansion of whorl section per revolution ; Δ_a the final, adult shell size. Here, for an elongated shell shape, the overall shell size is identified to shell height. But alternatively, a globular or discoidal shell shape would answer a similar schematic sketch with, accordingly, the overall shell size taken as the shell diameter.

Then, for a shell with n whorls, the shell size is the sum of these n successive contributions:

$$\Delta(n) = \Sigma_{i=1\ \text{to}\ n}(\delta_i) = \Sigma_{i=1\ \text{to}\ n}(\delta_1.\ \varepsilon^{(i-1)}) = [\delta_1/(\varepsilon - 1)].(\varepsilon^n - 1) \qquad \text{(A1)}$$

$$\Delta(n) = c.(\varepsilon^n - 1) \qquad \text{(A1 bis)}$$

with $\Sigma_{i=1\ \text{to}\ n}$ designing the summation extended to the n whorls of the shell and $c = [\delta_1/(\varepsilon - 1)]$

The size of a shell reaching its adult stage, with a corresponding number n_a of whorls, is thus Δ_a (= $\Delta(n_a)$) defined as follows:

$$\Delta_a = c.(\varepsilon^{na} - 1) = [\delta_1/(\varepsilon - 1)].(\varepsilon^{na} - 1) \qquad (A2)$$

Some more or less limited discrepancies may exist, of course, between the specific reality and the idealised, classical coni-spiral model involving whorls contributions *regularly increasing exponentially* with the whorl numbering label. Yet, here, focus is placed on the inter-individual *variability* and we are dealing with *variations* of shell size, rather than with the estimates of size itself. As *first order* discrepancy regarding the *absolute* values taken by a parameter have only *second-order* influence upon the interindividual *variations* of this parameter, using the idealised classical model features appropriate to the subject under study.

Defining a synthetic parameter 'γ' accounting for the combined contributions of growth parameters δ_1 and ε

The parameters δ_1 and ε govern together the *geometry of progressive shell development* (equation A2). Either or both parameters are subjected to intra-specific variability, inducing in turn, an inter-individual variability of the shell size reached at any *given* number of whorls. As for any other phenotypic character, the intra-specific variability of shell growth parameters may conveniently be considered by reference to a conventionally defined "type specimen" (characterised by the referential values δ_1* and ε* of parameters δ_1 and ε respectively).

The consequence on the adult-shell size of the intra-specific variability of growth parameters δ_1 and/or ε may then be quantified by the variations of the ratio:

$$\gamma = \Delta_a/\Delta_a^* \qquad (A3)$$

where:

- Δ_a is the adult size of the shell under consideration;
- Δ_a^* is the size that the type specimen (or any specimen having the same parameters δ_1* and ε*) would take for a number of whorls *equal* to the number of whorls n_a of the adult-shell under consideration. The value of Δ_a^* is provided by equation (A2) with $\delta_1 = \delta_1^*$ and $\varepsilon = \varepsilon^*$:

$$\Delta_a^* = c^*.(\varepsilon^{*na} - 1), \text{ with } c^* = \delta_1^*/(\varepsilon^* - 1) \qquad (A4)$$

Thus defined, the parameter γ *integrates* the influence of δ_1 and ε on the geometrical development of the shell *all along* its ontogeny (*via* ε) and since its very beginning (*via* δ_1). Although there is, of course, no possibility of disentangling the respective contributions to γ of parameters δ_1 and ε, it remains that γ conveniently accounts for the *combined* contributions of δ_1 and ε to the overall shell size Δ, at any given value of the number of whorls, by reference to a freely chosen type specimen of the corresponding species.

Parameter γ may thus be aptly designed as a comprehensive "*whorl-growth parameter*". Moreover, *from a practical point of view*, this parameter γ benefits by its *particularly easy evaluation*, only requiring the simple measurement of the adult-shell size Δ_a, subsequently introduced in equation (A3), while the more delicate measurements of δ_1 and of ε pertaining to the type specimen had to be carried out *only once and for all*, and then introduced in equation (A4).

Practical procedure

Consider a population of adult individuals (belonging to a same species having been previously typified with a referential "type specimen", in terms of the values of δ_1* and ε*) submitted to a morphometric study. For each individual, both the number of whorls n_a and the shell size Δ_a are measured, the later by using a numeric calliper and the former by careful examination from shell apex (according to procedure described in [9,10]) under stereo-microscope at moderate magnification, typically allowing a precision at a level of 1/10 whorl revolution. Now, introducing the measured values δ_1* and ε* in equation (4) provides the value of Δ_a*. Then, introducing the measured value of Δ_a in equation (3) provides the values of the whorl-growth parameter γ for each of the individual shells under study. Thus, the growth components n_a and γ (that have together determined the adult shell size Δ_a) are thus *conveniently and easily made available for each member individual* of the population under study.

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