



The Regulation of Interspecific Variations of Shell Shape in Bivalves: An Illustration with the Common “Clams” Fauna along French Coasts

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Author's contribution

The sole author designed, analyzed, interpreted and prepared the manuscript.

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ABSTRACT

I report an unexpected negative covariance occurring between two major parameters governing shell growth in marine bivalves, especially within the order Veneroida. This relationship is highlighted, here, considering a set of forty, rather common species of clams collected from French coasts. Interestingly, this negative covariance has two (geometrically related) consequences on the pattern of variation of shell shape at the inter-specific level:

- (i) An *extended* range of variation of shell elongation 'E' is made compatible with.
- (ii) A *severely restricted* range of variation of the ventral convexity 'K' of the shell contour.

I suggest that:

- (i) The *extended* range of interspecific variation of the shell elongation 'E' results from a trend towards larger differentiation between species according to this functionally important parameter E, while, in contrast,
- (ii) The *strongly restricted* range of variation of the ventral convexity 'K' of the shell contour might arguably result from a common need for improved shell resistance, face to mechanical solicitations from the environment, either biotic or abiotic.

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Accordingly, the negative covariance reported between these two growth parameters is understood as the indirect consequence of the selective pressures applying primarily upon the functionally-relevant shell shape parameters E and K.

Keywords: *Mollusc; Veneroida; shell contour; growth parameters; functional parameters; covariance; selective pressure; morphospace.*

1. INTRODUCTION

The shape of bivalves shells and, in particular the elongation E, ventral convexity K and dissymmetry D of the shell outline (Fig. 1 - right), are generally considered having significant functional implications regarding animal fitness (for *elongation*: [1-18]; for *ventral convexity*: [15]; for *dissymmetry*: [5,19]). Relevant criteria of animal fitness in this respect may include, in particular, the capacity of burrowing rapidly within seabed and the resistance of shell valves to mechanical crushing by predators. Accordingly, “*functionally-relevant*” parameters describing major aspects of the shell outline, such as elongation E, ventral convexity K and dissymmetry D, are likely being submitted to significant selective pressures.

Now, the animal has no direct control upon these “*functionally-relevant*” parameters, only an indirect influence, *via* the control of “*growth-related*” parameters (parameters α , ρ , δ ; Fig. 1 - left). This is because the shape of shell outline is not a geometrical figuration generated *per se*, defined at the outset, but the cumulative result of a progressive, accretionary growth process [20, 21]. The animal continuously controls the rate of peripheral accretion of new material at each location of the shell contour, all along the shell growth process [22,23], which, eventually, defines the shape of the shell outline. Thus, shell shape might relevantly be considered at two complementary points of view, namely *developmental* and *functional*:

- (i) Shell-shape considered as the *result* of the particular *process of shell-growth* for the animal under consideration and, in this respect, the shape is appropriately described by the set of *growth-related* parameters α , ρ , δ , or
- (ii) Shell-shape considered as the *subject* - and, eventually, the *result* - of *selective sorting*, according to the particular environmental conditions and, in this respect, the shape is appropriately described by the set of *functionally-relevant* parameters E, K, D.

Accordingly, if some specific constraint(s) happen to apply to the shape of the shell outline, they might be of either:

- *Developmental* origin, i.e. constraints applying *directly* to the growth-related parameters (α , ρ , δ), with induced consequences upon the pattern of functionally-relevant parameters (E, K, D);
- *Functional* origin, i.e. resulting from the selective sorting process applying directly to the functionally-relevant parameters (E, K, D) with induced, *indirect* impacts upon the pattern of growth-related parameters (α , ρ , δ).

Accordingly, defining the set of *reciprocal relationships* between the growth-related parameters α , ρ , δ and the functionally-relevant parameters E, K, D is a prerequisite to understand (i) how *developmental* constraints applying to shell-growth aspects may (directly) affect shell shape or, conversely, (ii) how *adaptive* constraints applying to functional aspects of shell shape may (indirectly) be selective upon shell growth parameters.

That said, such constraints, whatever their origins, will affect to some degree the *actually* occupied part of the shell morphospace, as compared to what would be the potentially occupied morphospace in the absence of these constraints [24].

Also, these constraints may conceivably concern either a limited group of taxonomically related species or apply to quite a larger taxonomic range.

Hereafter, I report on a constraint upon shell shape recorded throughout a comprehensive group of “clams” species occurring along French Channel and Atlantic coasts (including in particular a series of species of the order Veneroida). This constraint has two (geometrically related) consequences at the *inter-specific* level: an unexpected negative covariance between two shell growth parameters (α and ρ) and a significant alteration of the

pattern of interspecific variations of shell shape. This alteration of the pattern of interspecific variations of shell shape consists of an increased extent in the interspecific variation of the shell elongation E coexisting with a severely decreased range in interspecific variation of the ventral convexity K of the shell outline, as compared to what would be these respective ranges of variation of E and K in the absence of this constraint.

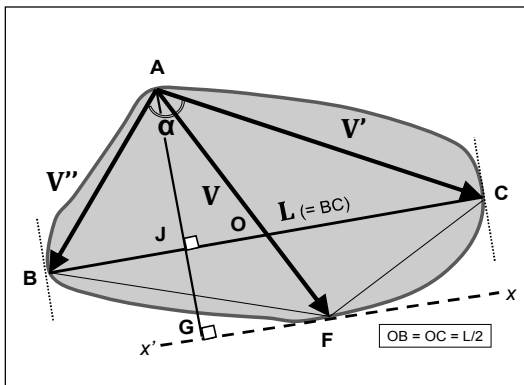
2. MATERIALS AND METHODS

2.1 Definitions of Growth-based Parameters and Functionally-relevant Parameters Characterising the Shape of the Shell Outline in Bivalves

In a *growth-based* approach of shell shape, the sagittal outline of shells may be appropriately parameterised synthetically using three indices associated to three “typical growth vectors” (Fig. 1 left), each of them extending from the valve umbo A. The umbo (or “apex”) being defined, here, as “the extreme dorsal side near the umbo itself”, as quoted by Galtsoff [25], see also Sokolowski et al. [9]. Let BC be the valve length L, then vectors V', V'' respectively join the apex A to the shell outline at the extremities B,C of the segment BC and vector V joins the apex A to the shell outline at point F via the middle O of segment BC. Finally, the segment AG is perpendicular to xx', the parallel through F to BC.

Three *growth-based* indices are defined as:

- * The *apical angle* 'α' (angle BÂC);



- * The *differential-growth index* 'ρ' identified to the ratio between axial (dorso-ventral) growth and mean lateral growth, $\rho = V / [\frac{1}{2}(V' + V'')]$;
- * The *dissymmetric-growth index* 'δ' identified to the ratio of the larger to the smaller lateral growth vectors, $\delta = V' / V''$.

These three parameters thus account, schematically, for the *growth pattern* of valves.

Alternatively, in a *functionally-relevant* approach, the main traits of the shape of shell outline may be synthetically characterised (Fig. 1 right) by (i) the shell elongation, i.e. the ratio of contour length to contour height, (ii) the valve dissymmetry, namely the degree of dissymmetry of the position of the umbo versus the anterior and posterior extremities of shell and (iii) the ventral convexity, that is the degree of prominence of the ventral side of the shell outline, opposite to umbo. Three indices are defined correspondingly (Fig. 1 right): the “shell elongation” index 'E' as the ratio $BC/AG = L/[V \cdot \cos(G\hat{A}F)]$, the “shell dissymmetry” index 'D' as the ratio CJ/BJ and the “ventral convexity” index 'K' as the ratio JG/AG .

The three growth-based parameters α, ρ, δ are *geometrically independent* factors, in the sense that no mutual dependence between α, ρ and δ is compelled by any purely geometric constraint: the direction and/or module of each vector may, indeed, freely be changed independently of the two others, in a purely geometric perspective. The same would hold true for the three

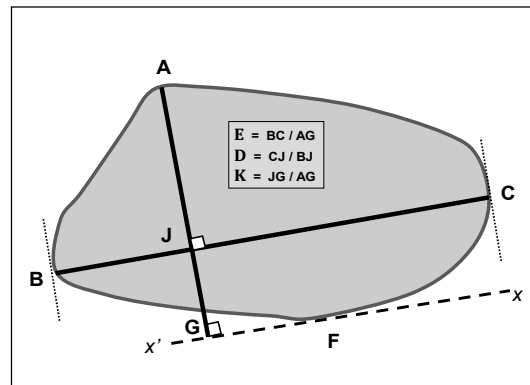


Fig. 1. The two alternative sets of descriptors accounting for the shape of the shell outline

* Left: The three growth-based parameters: apical angle $\alpha (= B\hat{A}C)$; differential growth index $\rho = V / [\frac{1}{2}(V' + V'')]$; dissymmetric growth index $\delta = V' / V''$;

* Right: The three functionally-relevant parameters: elongation E, dissymmetry D and ventral convexity K

functionally-relevant parameters E, D, K. Except that E,D,K on the one hand and α, ρ, δ , on the other hand, are *mutually linked* by a set of three geometrically-based equations:

$$E = f(\alpha, \rho, \delta) \tag{1}$$

$$D = g(\alpha, \delta) \tag{2}$$

$$K = h(\alpha, \rho, \delta) \tag{3}$$

(See Appendix 1 for the explicit expressions of these equations and their derivations).

2.2 Relations between the Patterns of Covariation between α, ρ, δ and the Ranges of Variations of E, K, D

The way each of the three functionally-relevant parameters E, D, K depends upon each of the three growth-related parameters α, ρ, δ may be quantified by considering the signs of the corresponding partial derivatives ($\partial E/\partial\alpha, \partial E/\partial\rho, \partial E/\partial\delta, \partial D/\partial\alpha, \partial D/\partial\rho, \partial D/\partial\delta, \partial K/\partial\alpha, \partial K/\partial\rho, \partial K/\partial\delta$): Table 1, according to Béguinot [26,27].

Table 1. The signs of the dependence of each three functionally-relevant parameters E, D, K, upon each three growth-based parameters α, ρ, δ

	E	D	K
α	+	-	+
ρ	-	0	+
δ	+	+	-

Now, if a given functionally-relevant parameter has dependences of the *same* sign (either >0 or <0) upon two growth-based parameters then, a *positive covariance* between these two growth-based parameters will tend to *increase the range* of variation of the considered functionally-relevant parameter (as compared to what would be this range of variation if there was no covariance between these two growth-based parameters). And, conversely, a *negative covariance* between these two growth-based parameters will tend to *decrease the range* of variation of the considered functionally-relevant parameter.

Alternatively, if a given functionally-relevant parameter has dependences of *opposite* signs upon two growth-based parameters then, a *positive covariance* between these two growth-based parameters will tend to *decrease the range* of variation of the considered functionally-

relevant parameter. And, conversely, a *negative covariance* between these two growth-based parameters will tend to *increase the range* of variation of the considered functionally-relevant parameter.

Table 2. Evolution of the range of variations $\Delta E, \Delta K, \Delta D$ of the functionally relevant parameters E, K, D, according to the type of co-variation between growth-related parameters α, ρ, δ . Arrows pointing upward (resp. downward) stand for enlarged (resp. narrowed) ranges of variation while the sign ‘=’ stands for a non-affected range, as compared to what would be these ranges in case of mutual independence between α, ρ and δ

Patterns of co-variation of shell-growth parameters	ΔE	ΔK	ΔD
Covariance $\rho - \delta$ positive	↓	↓	=
Covariance $\rho - \delta$ negative	↑	↑	=
Covariance $\alpha - \rho$ positive	↓	↑	=
Covariance $\alpha - \rho$ negative	↑	↓	=
Covariance $\alpha - \delta$ positive	↑	↓	↓
Covariance $\alpha - \delta$ negative	↓	↑	↑

Based on the preceding arguments and information provided at Table 1 for the signs of the dependence of E, D, K upon α, ρ, δ , it is thus possible to predict how the range of variation of each of the three functionally-relevant parameters E, D, K, is either *enlarged, unchanged or restricted*, as compared to what would be these ranges in case of mutual independence between α, ρ and δ : Table 2. Accordingly, as already mentioned in Introduction, the ranges of variations of the functional parameters E, D, K depends not only upon the ranges of variations of the growth parameters α, ρ, δ , but depends also on the possible existence of covariances between the growth-based parameters α, ρ, δ .

Thus, as detailed in Table 2, each of the six types of covariances between the growth-based parameters α, ρ, δ is associated to one among six specific patterns of constraints upon the ranges of variations of E, K, D (and *vice-versa*). These patterns are characterised by the respective ranges of variations of E, K, D, each of them being either enlarged, restricted or unaffected - as compared to what would be the case if the variations of α, ρ, δ were mutually independent.

2.3 Origin and Treatment of Rough Data

The modules of growth vectors V , V' , V'' and the apical angle α between V' and V'' were measured for a series of forty, more or less common, bivalves species inhabiting seabed along French shores (Channel and Atlantic coasts) using iconographic data provided by Audibert & Deleamarre [28]. These forty species were selected according to the iconographic quality providing the better accuracy of measurements. Parameters α , ρ , δ and E , D , K , were then computed according to their definitions given above.

It should be noted that reference [28] (the only one available that covers a sufficient taxonomic range of bivalve molluscs specific to French coasts) provides quantitative data for a typical shell specimen of each species *only*. As a consequence, the remarkable covariance highlighted hereafter may, *a priori*, results from the intermingled influences of both *intra*-specific and *inter*-specific variations, without the possibility of distinguishing between them on the only basis of the available rough data provided by [28]. Yet the range of *inter*-specific variations for important phenotypic traits, as those involved here, should normally substantially exceed the range of the corresponding *intra*-specific variations, so that the strong covariance highlighted below may arguably be attributed to *inter*-specific variations, at least predominantly. Now, in any case, whatever may be the respective true contributions of *intra*- and *inter*-specific variations to this recorded covariance, the advocated constraints involved would remain unchanged.

3. RESULTS

The values of the parameters α , ρ , δ and E , D , K , computed for each of the forty species studied are listed in Appendix 2.

Although no significant correlation exists between α and δ nor between ρ and δ , a highly significant negative covariance between α and ρ is observed within the series of forty species of clams studied here ($p < 0.0001$; Fig. 2).

Substantial modifications of the ranges of variations of the functionally-relevant parameters E and K are associated with this negative correlation between α and ρ , as depicted at Figs. 3 and 4. The recorded distribution of the couple of values of E and K , for the forty studied species, is compared to what it would be if the

interspecific variations of α , ρ , δ were mutually independent (simulated by artificially rebuilding forty new triplets $\{\alpha, \rho, \delta\}$ obtained by recombining at random the listed values of α , ρ , δ).

A slight enlargement of the range of variation of the shell elongation E (coefficient of variation of E multiplied by 1.39) coexists with a substantial reduction of the range of variation of the ventral convexity K (coefficient of variation of K divided by 2.4). These differences are significant for the elongation E (Bartlett test, $n = 40$, $\chi^2 = 4.45$, $p < 0.05$) and highly significant for the ventral convexity K (Bartlett test, $n = 40$, $\chi^2 = 25.0$, $p < 0.0001$).

4. DISCUSSION

As shown above on a theoretical basis (Tables 1 and 2), the respective ranges of variations of each functional parameters E , K , D , not only depends on the extent of variations of each of the growth parameters α , ρ , δ , but *depends also* (in a more subtle and insightful manner) on the occurrence of (*a priori* unexpected) covariances between these growth parameters (Table 2).

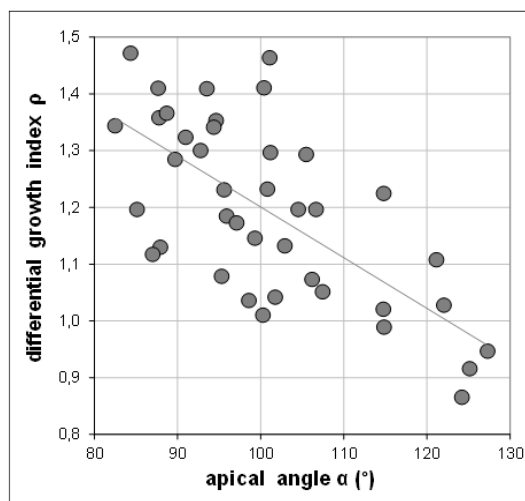


Fig. 2. The differential growth index ρ regressed against the apical angle α .

The negative correlation is highly significant: $r = 0.68$, $n = 40$, $p < 0.0001$

The negative covariance between α and ρ (instead of the expected mutual independence between α and ρ) may result from constraints having either:

- A *developmental* origin, as such operating *directly* upon the respective orientations

- and sizes of the “growth vectors” V, V', V'' , and, consequently, operating *directly* on α, ρ, δ , or;
- A *functional* origin, involving a selective sorting applying directly to one or several of the functionally-relevant parameter E, D, K and, thereby, influencing *indirectly* the growth-related parameters (via the relationships linking α, ρ, δ to E, K, D : equations (1), (2), (3)).

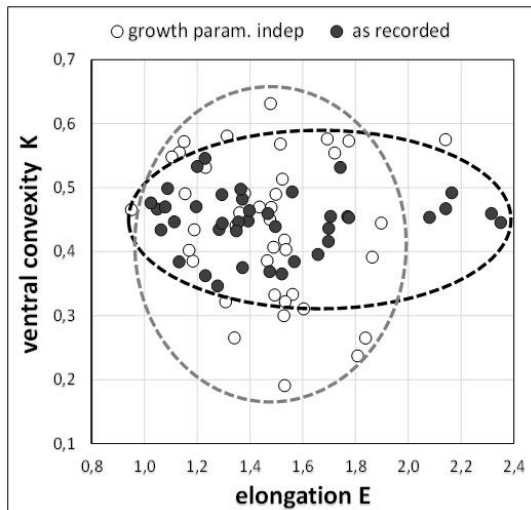
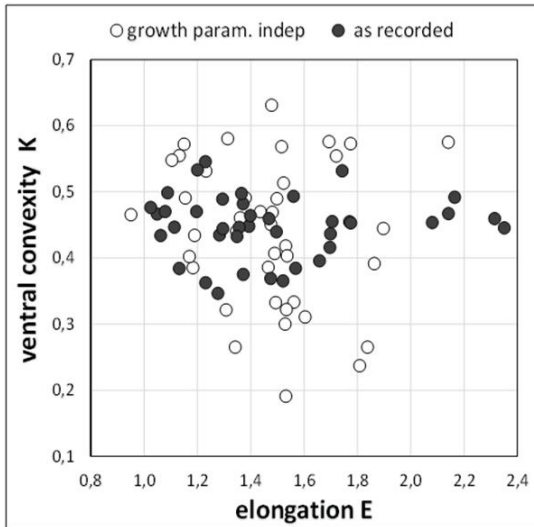


Fig. 3 & 3 bis. Comparison between the occupied morphospaces $\{E, K\}$:
 (i) *As recorded* for the 40 studied species (i.e. with the negative covariance between α & ρ);
 (ii) *Computed as it would be* if the growth parameters α, ρ, δ , were all varying independently from each other

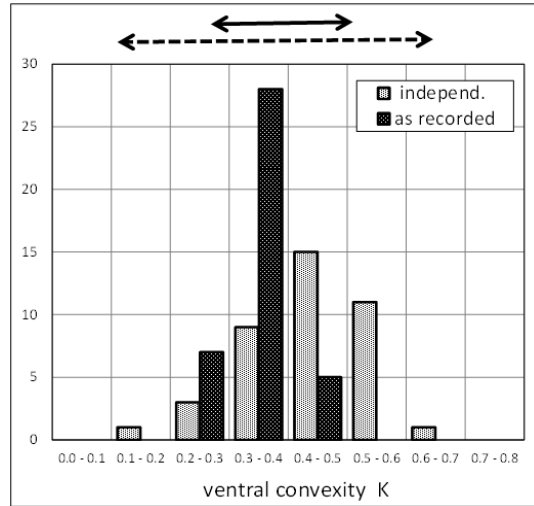


Fig. 4. Comparing the ranges of interspecific variations of the ventral convexity K , considering
 (i) The recorded data and
 (ii) The simulated situation if the variations of the growth-related parameters α, ρ, δ were mutually independent.
The difference between the ranges of interspecific variations of K is statistically highly significant: *Bartlett test*: $n = 40, S.D. = 0.047$ & $0.110 : \chi^2 = 25.0, ddl = 1, p < 0.0001$

Distinguishing between these two hypotheses, however, is generally considered far from being easy [29].

Yet, here, arguments seem rather in favour of the second hypothesis, namely a *selective process* applying directly to the functionally-relevant parameters E, K , of shell shape, with related, indirect consequences upon growth-related parameters α, ρ :

- 1) At first, it is to be noticed that the negative covariance between α and ρ , commonly reported among Veneroidae at the *inter-specific* level [27], is replaced by a positive covariance between ρ and δ at the *intra-specific* level, in Tellinoidae [26], as well as in Unionidae [27]. The interpretation of this contrasted pattern between the *intra-specific* and the *inter-specific* levels should likely make *more sense* in an “adaptive” perspective involving functional aspects of shell shape than according to a “developmental” point of view. It would, indeed, be difficult to understand a logic hypothetically supporting a *developmental*

constraint applying directly to growth-based parameters and which would change (quite arbitrarily) from a positive covariance between ρ and δ at the *intra*-specific level to a negative covariance between α and ρ at the *inter*-specific level.

Alternatively, a regulation applying directly to a given functionally-relevant phenotypic character, tending to reduce its range of variations at the *intra*-specific level and widen its range of variations at the *inter*-specific level – as recorded for the shell elongation E – would make more sense. And, indeed, the shell elongation E is repeatedly reported as one of the major shape parameter involved in selective adaptation to different habitat conditions (references provided above).

- 2) Moreover, there are relevant reasons – in terms of selective advantages – for a strict restriction of the range of variation of the ventral convexity K , equally maintained at both the *intra*- and the *inter*-specific levels. The ventral portion of valves is often the weakest part of the shell and, thus, more at risks [20], since the ventral part of the shell, especially the postero-ventral sector, is ordinarily less thick and thus less resistant than the dorsal part. Increasing ventral convexity, that is ventral prominence, would thus still enlarge the corresponding weakened zone.

Also, a larger convexity would tend to reduce the sealing pressure along the ventral margin (at given unchanged positions of insertions of the adductor muscles) and thus would make easier the shell opening by predators. Accordingly, a sufficient level of shell mechanical resistance to various kinds of environmentally induced stresses might preclude too high values of ventral convexity. Conversely, a sufficient value of ventral convexity might well be dictated by the avoidance of excessively acute profiles of valves contour at the anterior and posterior extremities (i.e. around C and B, Fig. 1) which would inevitably result from too weak a convexity. Such acute portions would be at still greater risks and more prone to suffer local breakage. Accordingly, an optimally centred and size-limited range of values for the ventral convexity K of shell outline would thus arguably be selected, as is actually observed.

5. CONCLUSION

In Bivalves mollusks, the range of variations of shell-shape and, specifically the range of variations of shell-dimensions ratios, may be regulated by either geometrical or biological constraints. *Geometrical* constraints, if any, are usually easily detected as the trivial consequences of topological incompatibilities. In contrast, *biological* constraints that affect shell traits are generally rather difficult to demonstrate directly but may be uncovered indirectly by the occurrence of unexpected (i.e. non-trivially explained topologically) covariance(s) between shell traits or dimensional parameters. Such a significant (and negative) covariance has been demonstrated here between shell elongation E and shell contour convexity K , considering a large taxonomical range of Bivalves (order Veneroida) that inhabit French coasts.

Beyond the demonstration of their actual efficiency (in terms of the resulting covariance), likely hypotheses relative to the nature of these biological constraints has been discussed as a first step, but still remain to be tested directly.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX 1

The equations relating the valve-shape parameters E, D, K to the valve-growth parameters α , ρ , δ

Note that choosing, in both approaches (valve-shape and valve-growth), a limited number of parameters to describe the shell outline, rather than implementing more refined approaches, such as Fourier analysis of shell contour, is deliberate. As the shell outline in bivalves is generally relatively simple, the main traits of shell outline may be fairly well captured by even a limited number of appropriately chosen parameters [30].

Moreover, a major advantage of limiting the number of parameters is that the equations linking growth-based shape parameters and functionally-relevant shape parameters may be derived under an explicit *analytical* form, as such more appropriate to readily bring out and highlight the rationale behind the equations.

$$E = [(\delta^2 - 2\delta \cdot \cos(\alpha) + 1) \cdot (4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2)]^{0.5} / (\rho \cdot (\delta + 1) \cdot \delta \cdot \sin(\alpha)) \quad (1)$$

$$D = (\delta^2 - \delta \cdot \cos(\alpha)) / (1 - \delta \cdot \cos(\alpha)) \quad (2)$$

$$K = 1 - E \cdot \{(X/(E \cdot \cos(\theta)))^2 - 0,25 \cdot [1 + (X/(E \cdot \cos(\theta)))^2] - (X/(\delta \cdot E \cdot \cos(\theta)))^2\}^{0.5} \quad (3)$$

with $X = 2\delta / (\rho \cdot (\delta + 1))$; $\cos(\theta) = 2\delta \cdot \sin(\alpha) / (4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2)^{0.5}$ and E defined above.

NB: for the specific case where shell are (sub-) symmetric ($\delta = 1$), the three equations simplify as:

$$E = [2(1 - \cos(\alpha))]^{0.5} / \rho; \quad D = 1; \quad K = 1 - [1/2 (1 + \cos(\alpha))]^{0.5} / \rho$$

Demonstration of equations (1), (2) and (3)

The following, classical relationships between angles, sides and height in triangles are applied here within the triangle ABC (see Fig. 1):

$$BC = L = (V'^2 + V''^2 - 2V'V''\cos(\alpha))^{0.5} \quad (A1)$$

$$JC = (L^2 + V'^2 - V''^2) / (2L) \quad (A2)$$

$$AJ = [V'^2 - ((L^2 + V'^2 - V''^2) / (2L))^2]^{0.5} \quad (A3)$$

► valve-elongation

$E = BC/AG = L/AG = L/(AF \cdot \cos(\theta)) = L/(V \cdot \cos(\theta))$, with $\theta = \text{angle } G\hat{A}F$.

Accounting for the definitions of $\rho = V'/1/2 (V' + V'')$ and $\delta = V'/V''$, it comes:

$$V'' = 2V/(\rho \cdot (\delta + 1)) \quad (A4)$$

Equation (A1) yields then:

$$L/V'' = (\delta^2 - 2\delta \cdot \cos(\alpha) + 1)^{0.5} \quad (A5)$$

From (A4) and (A5):

$$(L/V) = 2(\delta^2 - 2\delta \cdot \cos(\alpha) + 1)^{0.5} / (\rho \cdot (\delta + 1)) \quad (A6)$$

Now, $JO = JC - L/2$ and from (A2) and (A3) , it follows:

$$\text{tg}(\theta) = JO/AJ = (V'^2 - V''^2)/(4L^2.V'^2 - (L^2 + V'^2 - V''^2)^2)^{0.5}$$

and as $\delta = V'/V''$,

$$\text{tg}(\theta) = (\delta^2-1)/(4\delta^2(L/V'')^2 - ((L/V'')^2 + \delta^2 - 1)^2)^{0.5}$$

Substituting L/V'' by its expression in (A5) yields:

$$\text{tg}(\theta) = (\delta^2-1)/(2\delta.\sin(\alpha)) \text{ and then:}$$

$$\cos(\theta) = (1/(1 + \text{tg}^2(\theta)))^{0.5} = 2\delta.\sin(\alpha)/(4\delta^2 \sin^2(\alpha) + (\delta^2-1)^2)^{0.5} \quad (\text{A7})$$

Finally, equations (A6) and (A7) yield for the elongation $E = L/(V.\cos(\theta))$:

$$E = [(\delta^2 - 2\delta.\cos(\alpha) + 1).(4\delta^2 \sin^2(\alpha) + (\delta^2-1)^2)]^{0.5}/(\rho.(\delta + 1).\delta.\sin(\alpha)) \quad (\text{A8})$$

► **valve-dissymetry**

$D = JC/JB = JC/(L - JC)$ and, according to (A1) and (A2):

$D = (\delta^2 - 1 + (L/V'')^2)/(1 - \delta^2 + (L/V'')^2)$. With (L/V'') defined at equation (A5), it comes:

$$D = (\delta^2 - \delta.\cos(\alpha))/(1 - \delta.\cos(\alpha)) \quad (\text{A9})$$

► **convexity K of the ventral contour of valve**

The convexity K of the ventral contour of valve is defined by the ratio $K = JG/AG = 1 - AJ/AG$

From equation (A3) and accounting for $E = L/AG$, it comes:

$$K = 1 - [V'^2 - ((L^2 + V'^2 - V''^2)/(2L))^2]^{0.5} (E/L)$$

$$K = 1 - E.\{(V'/L)^2 - 0.25[1 + (V'/L)^2 - (V''/L)^2]\}^{0.5}$$

According to equation (A4), $V''/L = 2/(E.\rho.(\delta + 1))$ and $V'/L = 2\delta/(E.\rho.(\delta + 1))$

Substitution of V'/L and V''/L by their expressions above yields finally:

$$K = 1 - E.\{(X/(E.\cos(\theta)))^2 - 0.25[1 + (X/(E.\cos(\theta)))^2 - (X/(\delta.E.\cos(\theta)))^2]\}^{0.5} \quad (\text{A10})$$

with $X = 2\delta/(\rho.(\delta + 1))$; $\cos(\theta) = 2\delta.\sin(\alpha)/(4\delta^2 \sin^2(\alpha) + (\delta^2-1)^2)^{0.5}$ according to equation (A7) and E defined by equation (A8).

APPENDIX 2

Valve-shape parameters E, D, K and the corresponding valve-growth parameters α , ρ , δ , for forty common species of clams along French shores (Typical values from reference [28])

	α °	ρ	δ	E	D	K	
V	<i>Abra alba</i>	105	1,20	1,28	1,37	1,48	0,48
V	<i>Abra tenuis</i>	103	1,13	1,12	1,39	1,20	0,45
V	<i>Acanthocardia aculeata</i>	101	1,46	1,67	1,23	2,37	0,55
V	<i>Acanthocardia echinata</i>	82	1,34	1,42	1,06	2,23	0,43
V	<i>Acanthocardia tuberculata</i>	88	1,41	1,77	1,20	3,31	0,47
V	<i>Arcopagia crassa</i>	90	1,28	1,16	1,11	1,34	0,45
V	<i>Arctica islandica</i>	94	1,41	1,87	1,29	3,24	0,49
V	<i>Callista chione</i>	93	1,30	1,79	1,36	3,03	0,45
V	<i>Capsella variegata</i>	125	0,92	1,44	2,14	1,59	0,47
M	<i>Corbula gibba</i>	88	1,13	1,04	1,23	1,08	0,36
V	<i>Diplodonta rotundata</i>	100	1,41	1,50	1,20	1,99	0,53
V	<i>Donacilla cornea</i>	102	1,04	1,34	1,57	1,63	0,38
V	<i>Donax trunculus</i>	107	1,05	1,51	1,70	1,88	0,42
V	<i>Dosinia exoleta</i>	95	1,35	1,03	1,09	1,06	0,50
V	<i>Dosinia luopinus</i>	88	1,36	1,22	1,05	1,53	0,47
V	<i>Gari fervensis</i>	124	0,87	1,17	2,08	1,22	0,45
A	<i>Glycymeris glycymeris</i>	89	1,37	1,02	1,02	1,03	0,48
V	<i>Laevicardium crassum</i>	84	1,47	2,50	1,47	7,97	0,46
V	<i>Loripes lacteus</i>	91	1,32	1,03	1,08	1,06	0,47
V	<i>Lutraria angustior</i>	127	0,95	1,52	2,16	1,68	0,49
V	<i>Lutraria lutraria</i>	121	1,11	1,47	1,74	1,66	0,53
V	<i>Lutraria magna</i>	122	1,03	2,04	2,35	2,52	0,45
V	<i>Macoma balthica</i>	85	1,20	1,00	1,13	1,00	0,38
V	<i>Macra glauca</i>	99	1,15	1,16	1,35	1,29	0,43
V	<i>Macra stultorum</i>	107	1,20	1,18	1,36	1,30	0,50
M	<i>Mya arenaria</i>	106	1,07	1,08	1,50	1,12	0,44
V	<i>Petricola pholadiformis</i>	115	1,22	2,68	2,31	3,90	0,46
V	<i>Pseudopythina macandrewi</i>	100	1,01	1,02	1,52	1,04	0,37
V	<i>Ruditapes decussatus</i>	96	1,18	2,03	1,66	3,58	0,40
V	<i>Ruditapes philippinarum</i>	105	1,29	1,91	1,56	2,76	0,49
V	<i>Scrobicularia plana</i>	97	1,17	1,07	1,28	1,13	0,44
V	<i>Spisula elliptica</i>	99	1,04	1,11	1,47	1,21	0,37
V	<i>Spisula solida</i>	95	1,08	1,02	1,37	1,03	0,38
V	<i>Spisula subtruncata</i>	87	1,12	1,27	1,28	1,65	0,35
V	<i>Tapes rhomboides</i>	101	1,23	2,11	1,70	3,48	0,44
V	<i>Tellina donacina</i>	115	1,02	1,39	1,77	1,59	0,45
V	<i>Tellina incarnata</i>	115	0,99	1,02	1,71	1,03	0,46
V	<i>Timoclea ovata</i>	96	1,23	1,42	1,29	1,89	0,44
V	<i>Venerupis corrugata</i>	101	1,30	2,38	1,77	4,18	0,45
V	<i>Venus verrucosa</i>	94	1,34	1,93	1,40	3,38	0,46
	<i>as recorded</i>	α °	ρ	δ	E	D	K
	average	101	1,19	1,47	1,48	2,07	0,45
	standard deviation	12,05	0,158	0,45	0,351	1,334	0,047
	coefficient of variation	0,119	0,133	0,307	0,237	0,645	0,106
	<i>mutually independent growth parameters</i>	α °	ρ	δ	E	D	K
	average	101	1,19	1,47	1,47	2,10	0,44
	standard deviation	12,05	0,158	0,45	0,282	1,338	0,109
	coefficient of variation	0,119	0,133	0,307	0,191	0,638	0,246

Orders: V = Veneroidea; M = Myoidea; A = Arcoida; V: 37, M: 2, A: 1

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