Research Article

Shell Shape Analysis and Spatial Allometry Patterns of Manila Clam (*Ruditapes philippinarum*) in a Mesotidal Coastal Lagoon

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While gradual allometric changes of shells are intrinsically driven by genotype, morphometrical shifts can also be modulated by local environmental conditions. Consequently the common use of a unique dimension (usually length) to assess bivalves' growth may mask phenotypic differences in valve shape among populations. A morphometric exhaustive study was conducted on Manila clam, *Ruditapes philippinarum*, by acquiring data in the French Arcachon Bay (intrasite phenotypic variability) and by comparing with other sites in the literature (intersite phenotypic variability). 2070 shells were subsampled, weighted, and automatically measured using TNPC software. Some ratios' values indicate a relatively round and globular shape shell in comparison with other sites confirming poor conditions for some individuals. Among adult clams, three main morphological groups were identified and discussed according to spatial considerations. Allometric relations for pairs of shell descriptors were determined by testing classical linear and piecewise regression models on log-transformed relation of Huxley. A significant shape change correlated to size was observed; it corresponds to the second year of life of the clam. Relationships between density, disease, and shell shape are demonstrated and discussed related to other potential factors affecting shell shape. Finally, consequences on population regulation are addressed.

1. Introduction

Growth of individuals is commonly assessed by correlating the evolution of the largest dimension of the individuals along time. For bivalves, this dimension can be the valve's length as for cockle, clam, mussel, razor shell, the valve's height as for oyster, scallop [1]. The shape changes of the shell are induced by the differential growth vectors operating at distinct locations around the mantle edge [2], organ that plays a key role in the shell secretion. This highlights the need of taking into account several allometric ratios.

Those gradual allometric changes are clearly driven by genotype and occur during ontogeny; they are usually associated with the conservation concept of physiological favorable surface area to volume ratios [1]. At the same time, those morphometrical shifts can also be modulated by local environmental conditions [3–12].

So, the convenient approach which consists in considering growth through a unique dimension can mask phenotypic plasticity responses in valve shape. While bivalves allocate a significant portion of their total energy budget to shell growth [13], apparent disparities concerning length could occur among individuals even if they dedicate the same amount of energy to shell growth. Shell increments could indeed shift to other dimensions such as height, width, and thickness of the valve. This concern is important because it gives new arguments to suggest that deficient growth in length is not always due to problems of energy input deficit (e.g., phytoplankton) but could also be related to intrinsic considerations leading to specific morphological patterns.

In order to investigate the question of growth in the fullest possible way for ecological and commercial purposes, an exhaustive morphometric study is proposed by acquiring data in Arcachon Bay (intrasite phenotypic variability) and
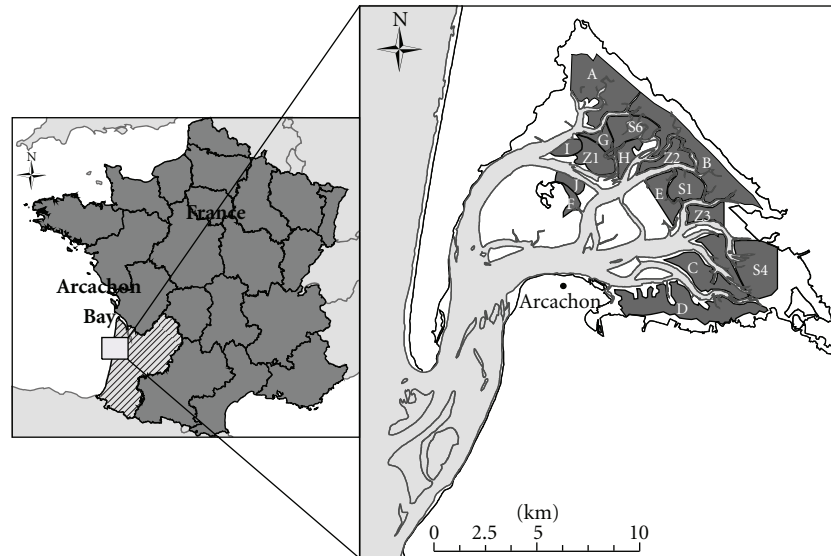
FIGURE 1: Maps showing the studied site Arcachon Bay (France) and localization of the sampled strata (Sources: ESRI, BD Carthage, Ifremer—M. Lissardy).

by comparing with other sites in the literature (intersite phenotypic variability). The chosen biological model is Manila clam, *Ruditapes philippinarum* (Adams and Reeve, 1850) which supports an important commercial fishing activity with around 550 to 1.000 tons per year for the Arcachon Bay located in the southwest coast of France, hoisting it at the first rank of French production sites.

Various ecological factors are identified for their effect on bivalve shell shape: wave impact, trophic conditions, water depth, density... [2, 14]. In this study, we decided to focus on two factors integrating a populational dimension and be susceptible to influence the growth and the shell shape: density and brown muscle disease—emerging pathology. Several studies have already been conducted on density dependence of the Manila clam's shell shape but without consensus [15–18]. One of the supposed effects is that the dorso-ventral shell axis (height) should be the most affected by space competition since buried clams present their anteroposterior axis (length) almost perpendicular to the substrat [18]. Concerning pathology, we considered it challenging to study relationships between the prevalence of BMD affection which is known for having negative impact on the functioning of the adductor muscles involved in the shell's closure [19] and shell shape. Those features were preferred to other potential factors such as perkinsosis or brown ring disease since their low impacts on the Arcachon Bay population were demonstrated [20]. For other environmental modulators, (such as type of sediment, shore level, etc) data at sufficient fine scale are not currently defined.

2. Materials and Methods

2.1. Study Site. Arcachon Bay is a $156 \, \text{km}^2$ semi sheltered lagoon in the southwest coast of France (Figure 1). Mostly composed of tidal flats ($110 \, \text{km}^2$ within the inner lagoon);

this mesotidal system is characterized by a sediment composition ranging from mud to muddy sands and colonized by vast *Zostera noltii* seagrass meadows. Both influenced by external neritic waters and by continental inputs [20], this bay presents a semidiurnal macrotidal rhythm. Temperature and salinity gradients within the bay are controlled by the characteristics of these water masses as well as the slow renewal of water by tides [21]. With an average salinity of 30 (source Archyd network) which is higher than freshwater salinity and lower than seawater one's, the investigated area is considered as brackish water [22].

2.2. Origin of the Data. *R. philippinarum* shells were collected in Arcachon Bay during the last biomass survey in 2010. Henceforth biennial, this field survey is carried out with a standardised protocol (stratified random sampling) with 14 strata located at intertidal level (excluding channels) investigated for a total of 490 sampling stations. Sediments, core of $0.25 \, \text{m}^2$ ($0.5 \, \text{m} \times 0.5 \, \text{m}$) on a $0.2 \, \text{m}$ depth, were sampled with a Hamon grab at the high tide and filtered onboard with running water over a set of three sieves with 2, 1, and 0.5 cm mesh sizes. On the whole collected shells, 2070 shells were randomly subsampled.

2.3. Shells Preparation and Morphology Descriptors of Individuals. In laboratory, all the shells were first cleaned and dried at 38°C for 48 h. Then, the valves were separated and analyses on two high-resolution pictures (lateral and ventral views) were performed with the TNPC software (Digital Processing for Calcified Structures, http://www.TNPC.fr) on left valve. To describe the morphology of the individuals, seven classical parameters were retained:

(i) length (*L*), defined as the longest distance from front edge to back edge (mm). It is the reference length obtained from lateral view;

Table 1: Morphometric variables for arcachon bay.

Descriptor	Formulae	Minimum	Maximum	Mean	Ecart-type
Elongation index	$= H/L$	0.66	0.86	0.75	0.02
Compacity index	$= W/L$	0.19	0.38	0.28	0.02
Convexity index	$= W/H$	0.35	0.51	0.37	0.03
Circle index lateral view	$= AL/0.25 \times L^2 \times \pi$	0.65	0.85	0.73	0.02
Circle index ventral view	$= 2 \times AV/0.25 \times LVent^2 \times \pi$	0.36	0.70	0.48	0.04
Reference Ellipse index lateral view	$= AL/0.25 \times L^2 \times \pi$	2.63	3.43	2.94	0.10
Reference Ellipse index ventral view	$= 2 \times AV/0.25 \times LVent^2 \times \pi$	0.73	1.40	0.95	0.08
Weight ratio 1	$= SM/L$	0.06	1.76	0.57	0.27
Weight ratio 2	$= SM/H$	0.08	2.17	0.76	0.35
Weight ratio 3	$= SM/W$	0.23	5.80	2.02	0.88

(ii) ventral length ($LVent$), as the longest distance from front edge to back edge (mm). It is the reference length obtained from ventral view;

(iii) height (H), as distance from the umbo to edge (mm). It is obtained from lateral view;

(iv) width (W), as the longest distance of the valve in a lateral plane across the valve (mm). It is obtained from ventral view;

(v) weight or shell mass (SM), as dry mass of the left valve (mg);

(vi) area lateral (AL), as area of the left valve projection (mm^2) from lateral view;

(vii) area ventral (AV), as area of the left valve projection (mm^2) from ventral view.

These seven parameters consist in linear or surface measures directly obtained from the shape analysis (lateral or ventral views) and weight measure of each left valve. Respective accuracies of almost 1.10^{-3} millimeter and 0.1 mg are associated to linear and weight measures. Taken separately, those parameters do not allow describing the shell morphology because of a size effect. So not only to characterize the general morphology tendencies at the bay and at the strata scales, but also to examine allometric patterns for this population, 10 shape descriptors were defined from these parameters (Table 1). Such indices are supposed to give synthetic information on growth [23].

(i) Elongation index, Compactness index, and Convexity index to consider the coupled ratios between the 3 dimensions of the valve: a compact and convex bivalve has its width greater than 50% of its height which means a Convexity index greater than 0.5 [24];

(ii) Circle index lateral view (CIL) and Circle index ventral view (CIV) to compare the valves' forms to circular ones: the first one is the area of the valve (lateral view) related to the surface of a circle with L as

diameter. The second one is twice the area of the valve (ventral view) related to the surface of a circle with $LVent$ as diameter. Those two indices are complementary, respectively, to Elongation and Compactness index. For both of them, if the value is close to 1, it means that the shape tends to be circular.

(iii) Ellipse index lateral view (EIL) and Ellipse index ventral view (EIV) are also considered to compare the valves' forms with elliptical ones. The first one is the area of the valve (lateral view) related to the surface of an ellipse with L and 0.5 L as diagonals. The second one is twice the area of the valve (ventral view) related to the surface of an ellipse with $LVent$ and 0.5 $LVent$ as diagonals. Those indices are also complementary to Elongation and Compactness indices since they provide information on the more or less flattened form of the shell.

(iv) Three descriptors involving the weight and successively the 3 dimensions (L, H, and W) with weight ratio 1, weight ratio 2, and weight ratio 3.

For *Ruditapes philippinarum*, globularity is described as a result of a faster increase of width related to length [7]. In terms of indices retained above, this character can be defined for clams presenting high Compactness, CIV, and EIV indices.

According to Hamai [25], Ohba [3], and Eagar et al. [9], morphometric characteristics could reveal more or less favorable environmental conditions. For Manila clam, a low Elongation index is observed to localities presenting clams with high condition index [23] meaning favorable environmental conditions. Consequently, CIL index close to 1 and EIL index greater than 1 could indicate unfavorable environmental conditions.

Moreover, Watanabe and Katayama [23] linked those morphometrics characteristics to commercial considerations for *Ruditapes philippinarum*: the less palatable individuals are

the ones with fatter and rounder shell shape that is, high value of Elongation index and CIL index close to 1.

In other words, the best shape for ecological and economical purposes needs to be considered as a combination of several characteristics: at least low H/L ratio combined with low values of CIL and EIL.

2.4. Multivariate Analysis

2.4.1. Shell Shape Analysis. In this subsection, all samples were considered. After brief descriptive statistics, linear regressions were performed on the logarithmically transformed data on parameters and shape descriptors versus size. It allows to account for significant shape changes correlated to size and is based on the classical equations for allometry ($Y = aX^k$) proposed by Huxley [26]. Focusing on the coefficient named k (allometric exponent) provides information about differences of growth rates between the two considered descriptors, in particular when it concerns width versus length it can reflect globularity as defined above. This parameter allows summarizing the growth rate and so it is compared to other areas.

When problems of "bad fitting" (presence of a shift between observed and predicted data) were detected using for example the corresponding residuals of this classical model, an alternative model built on piecewise regressions [27] was tested. It is also called segmented regressions model. It provides regression analysis on both sides of an automatically determined breakpoint. This methodology was used by Katsanevakis et al. [28] for bivalves' species. The choice of the "best" model was undertaken by using the AIC (Akaike Information Criterion; [29]) score; the lowest AIC score gives the one to select. The breakpoint is a parameter which can be viewed as an indicator of fast ecological changes or linked to marked events [28]. The regression equations before and after this breakpoint illustrate the shift of the shell growth to different morphological patterns during ontogeny.

2.4.2. Spatial Allometry Patterns. In this part, clams longer than 30 mm (i.e., 661 clams) were retained to consider spatial variability of allometric descriptors. This choice was decided in order to avoid size effect and to consider whether a link with two of the shape potential drivers (density or the brown muscle disease—coded BMD) could be detectable (since the smallest clam presenting this pathology was 26 mm long). To interpret the allometric variability in terms of density, two classes were defined: below 100 clams m^{-2} ("low density"); above 100 clams m^{-2} ("high density"). Concerning pathology, proportion of clams infected by BMD within the sample was coded into 3 classes: no clams infected ("No BMD"); below 3.7% of infected clams ("Low BMD"); above 3.7% of infected clams ("High BMD"). Normalized principal components analysis (NPCA) was conducted in order to consider the relations between the synthetic shape descriptors and spatial considerations (strata encoded by letters, see Figure 1), density and proportion of clams infected by BMD (added as supplementary factors). This methodology is widely used for such investigations [30, 31].

Calculations were carried out under R (http://cran.r-project.org/web/packages/Rcmdr/index.html) and the following packages: factomineR for NPCA, stats for linear regressions, and SiZer for piecewise regressions (http://cran.r-project.org/web/packages/SiZer/index.html; [32]).

3. Results

3.1. Shell Shape in Arcachon Bay. The range of studied population length was between 10.4 and 45.0 mm (mean: 27.4 mm; standard deviation: 5.21 mm). Other statistics on the morphometric variables are summarized in Table 1. The mean shell pattern (average values) was described by an Elongation index of 0.75, a Compactness index of 0.28, and a Convexity index of 0.37. By comparison with traditional forms (circular or elliptical), valve shape was better described as circular when it was seen from the side view and elliptical when seen from ventral view. For the three weight ratios, the values were ranging between 0.57 and 2.02 and presented higher variability within the considered population than the other morphometric variables (relative standard deviations around 45%).

3.2. Allometric Patterns. Classical linear regressions (Figures 2(a)–2(g); see also Supplementary Materials available online at doi: 10.1155/2012/281206) revealed isometry for pattern such H related to L (called H to L allometric relation), characterized by an allometric exponent (k) equal to 1.00 indicating that an increase of the length did not induce changes of growth rate of the height. For other (W versus L, H versus L, SM versus L, SM versus H, and SM versus W) allometric relations, k exceeded 1.00 which means a positive allometry for these pairs of variables. Higher k values were obtained for relation involving the weight. No significant relations were obtained for the circle or ellipse indices in relation to the length. For H to L allometric relation, classical and piecewise regressions had similar goodness of fit (AIC scores close to −2360). For SM to L allometric relation, AIC score with classical model amounted to 859, whereas it is established to 854 with piecewise regression, this second modeling was considered to be better adjusted to our data for this ratio. The results of these two piecewise regressions (H to L, SM to L) showed breakpoints corresponding, respectively, to $L = 15.7$ mm and $L = 19.6$ mm.

3.3. Spatial Allometry Patterns, Density, and Disease Effects. For clams longer than 30 mm, the shape was correctly summarized by the first three dimensions of the NPCA (93.8% of the variance) described in Table 2, hereafter called Character 1, Character 2, and Character 3.

Heavy shells (regarding classical linear dimensions) with high values of width related to length were found in strata A, C, and S1. Those globular shells were associated with low-density levels (average 48 clams m^{-2}) and high proportions of clams infected by BMD (average 12% of the sample) (see Figures 3 and 4). Besides, those two factors were significantly discriminated on the first axis which was characterized by the variables SM/L, SM/H, W/L ratios, circle and reference ellipse lateral indices.
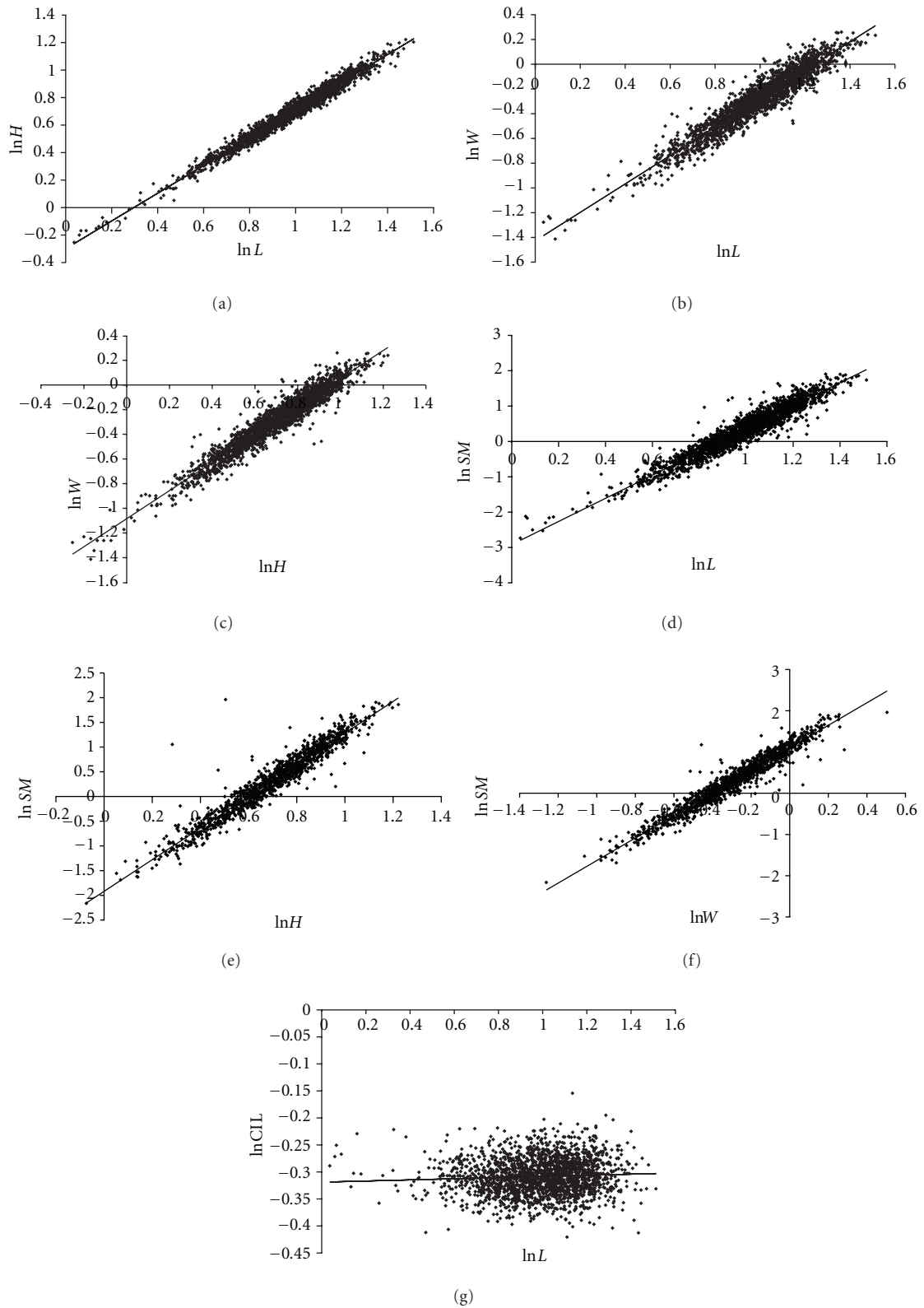
(a)

(b)

(c)

(d)

(e)

(f)

(g)

Figure 2: Allometric relations for pairs of parameters and shape descriptors (logarithmically transformed data).

TABLE 2: NPCA synthetic descriptors.

Selected principal components	Description	Shape tendency
Character1	Individuals presenting high values for *SM/L*, *SM/H*, *W/L* ratios, high indices related to ventral circle and reference ellipse	Heavy shells regarding linear measures and high values of width related to length-globular individuals
Character2	*L*, *H/L*, EIL, CIL and two of the weight ratios (*SM/H* and *SM/W*): the higher the indices of related mass and length, the less the clam presents a round form (lateral view)	Heavy shells regarding linear dimensions but associated to high values of lengths
Character3	Shells with high *H/L* ratio and lateral indices, by opposition to low *W/L* and *W/H* ratios	Round shells (lateral view) and little width related to length and height
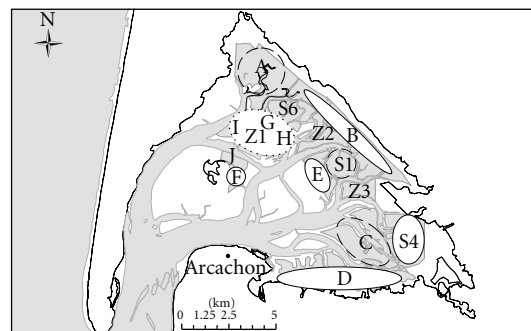
FIGURE 3: Spatial vizualisation of the allometry patterns related to density and disease.
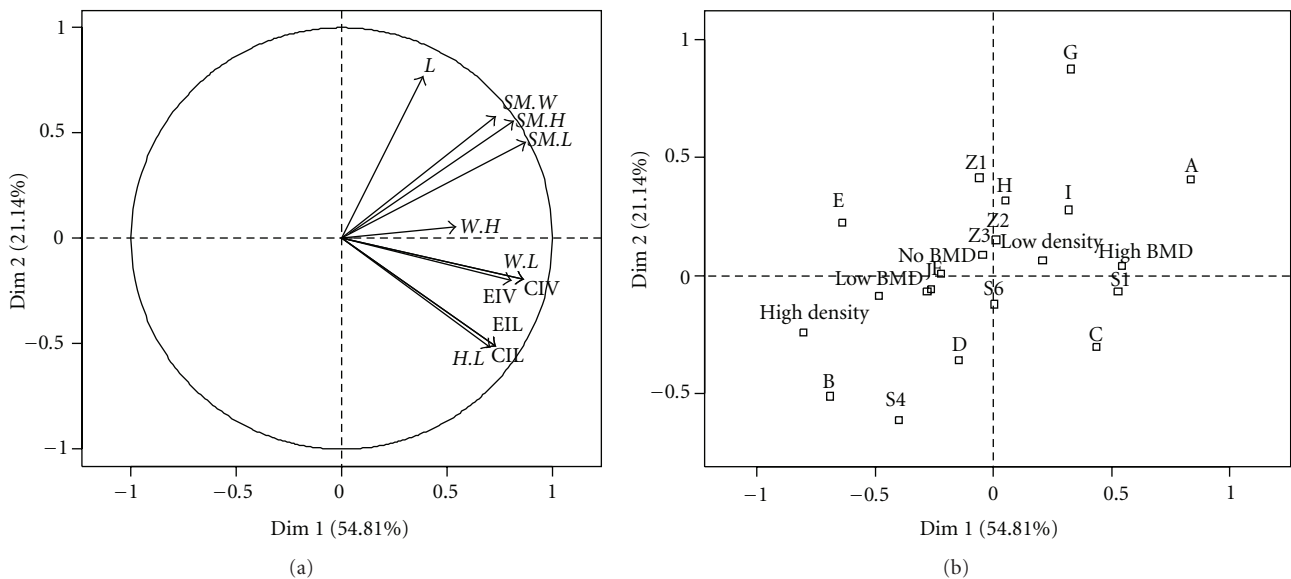

(a)

(b)

FIGURE 4: NPCA on morphometric variables (individuals and variables graphs) with strata, density, and BMD as supplementary factors.

TABLE 3: Comparison of morphometric results with other sites including Europe.

Site/Area	Mean morphometrics results	Length (S. D.) indications of the studied population (mm)	Sources
Japan	$\overline{H/L}$ from 0.70 to 0.75 $\overline{W/L}$ from 0.40 to 0.45	Range 10.8 (0.60) to 11.5 (0.63)	Deduced from Watanabe and Katayama [23]—Figure 3
China	$\overline{H/L}$ = 0.69 $\overline{W/L}$ = 0.44	Mean Length 20.35 (1.35)	Deduced from Fan et al. [33]—Table 1
Spain (bottom culture)	$\overline{H/L}$ from 0.58 to 0.73 $\overline{W/L}$ from 0.41 to 0.48	Range 13.7 (0.26) to 26.6 (0.43)	Deduced from Cigarría and Fernández [18]—Table 1
Tunisia	$\overline{H/L}$ = 0.69 $\overline{W/L}$ = 0.44	Mean Length 35.0 (3.82)	Deduced from Ben Ouada et al. [30]—Table 1
Italy	$\overline{H/L}$ = 0.71 $\overline{W/L}$ = 0.50	Mean Length 39.2 (5.7)	Deduced from Geri et al. [34]—Table 1
France (Barfleur)	$\overline{H/L}$ from 0.68 to 0.71 $\overline{W/L}$ from 0.40 to 0.48	Range 19 to 33	Deduced from Gérard [7]—Figures 32 and 36

Note: after having checked for valves symmetry on a subsample, the W/L ratio (obtained by TNPC system) for Arcachon was multiplied by two in order to allow for realistic comparison with published ratios.

Heavy shells (regarding classical linear dimensions) but associated to high values of lengths were found in strata G, H, Z1, and Z3.

Those two types of strata differ from strata B, E, and S4 for which individuals presented low weight related to length, height, or width.

Stratum D was illustrated by circular shells (lateral view) and little width related to length and height by opposition to strata F, S1, and Z3.

Spatial visualization of those results revealed a typology defined by 3 main areas which differ in particular by their distance to the ocean connection (Figure 3).

4. Discussion

4.1. Shell Shape: Profile and Main Characteristics according to Some Populational Descriptors. This current study investigates the morphometric traits of *Ruditapes philippinarum* within Arcachon Bay using ratios classically employed for calcified structures. Observed values for those ratios (Table 1) establish that this population is characterized by relatively round ($H/L = 0.75$, CIL = 0.73) and globular shells ($W/L = 0.28$, EIV = 0.95). Those results confirm the professional observations on the existence of a peculiar morphological pattern (so-called globular or "*boudeuses*" clams by French fishermen) which is described by a more compact form as usually observed.

Those conventional morphometric variables allow for comparison between the Arcachon Bay population and other ones from remote sites (deduced from [7, 18, 23, 30, 33, 34]). It emphasizes that shells are characterized by a much less elongated and more globular form than in other sites including Europe (Table 3) highlighting so a less favorable environment for the development of the clam and also individuals less attractive for economical point of view. These results are still consistent if we consider only the smallest individuals as Cigarría and Fernández [18], Watanabe and Katayama [23] did (data not shown).

Dependence of shell morphology on local environmental conditions has been indicated by Costa et al. [12] reminding inter alia the phenotypic plasticity in valve shape with a reference to the work of Kwon et al. [11] on transplantation results. They correspond more globally to the concept proposed by Lucas [8] in which ecological conditions seem to strongly influence both bivalves' morphology and physiology. The spatial patterns observed at the bay scale advocate for the existence of specific local environmental conditions that could be related for example to the hypsometric level or to continental input. Unfortunately in this present study, we couldn't take into account those kinds of factors.

Our study focuses on two factors that may affect the observed shape descriptors within the bay: i/density and ii/presence of an emergent disease, the BMD. Relationships among low density (below 100 clams m^{-2}), absence or low presence of BMD (proportion of clams infected by BMD within the sample ranging from 0 to 3.7%) and clams presenting high SM/L, SM/H, and W/L ratios are highlighted using the observed values in Arcachon Bay.

The question of density dependence of the Manila clam's shell shape appears to have been considered in the literature but with no consensus. In our study, concomitance between high densities and propensity to be elongated is depicted. This is comparable to the results obtained by Cigarría and Fernández [18] in Eo Estuary (Spain) for this same species but under lowest densities conditions for Arcachon Bay (maximal density in the present work: 358 clams m^{-2}; 1000 clams m^{-2} for Eo estuary). For the Spanish site, this height's density dependence was interpreted as a consequence of space competition since the height corresponds to the horizontal occupation in the sediment (because of the position of the buried clam). Space competition issue was also reported for *Cerastoderma edule* [35, 36]. Alumno-Bruscia et al. [37] describe as well an elongation of the shell for high population

density for *Mytilus edulis*, while it is interesting to note that they raised the question of a consequence of a real physical interference, food depletion, or a combination of both. With respect to Manila clam, different observations have been made. Clam density was identified among other factors to impact the suitability of lagoon's areas (at local scale) for clam cultivation through a model-based approach [38]. For high densities conditions, Ohba [15] observed an increase of length proportionately less important than the ones in height and width. Bourne and Adkins [16] reported a common happening of stunted clams for wild populations and Mitchell [17] stated for Manila clam that density in the Canadian beach determines the maximum size they will grow before stunting occurs. Otherwise, a competition for space was also suggested between *Ruditapes philippinarum* and three species (*Mactra veneriformis, Nihonotrypaea japonica, and Upogebia major*) by Tamaki et al. [39]. For the Arcachon population, low density levels are associated with heavy and globular character. A common unfavorable environmental factor (see below) could be considered to explain these observations. Because the densities remain much lower than other studied sites, we can address in the same time the question of an environmental reason going beyond density strictly seen as spatial interference as suggested by some authors. A possible limitation of the maximum carrying capacity due to all the filter feeding species and not only within the Manila clam's population could be a hypothesis. On intraspecific competition issues to explain growth deficit, it would also have been interesting to consider the biomass. Insofar as we selected here the individuals above 30 mm, we consider that the biomass and density are well correlated.

To the best of our knowledge, correlation between disease and morphology had not been studied. For the Arcachon population, relationships between high proportion of clams affected by BMD and globular form (associated to heavy clams regarding length and height) have been described. Recently highlighted by Dang et al. [19], this pathology affects the posterior adductor muscle and leads to a progressive calcification of this organ. Valve activity and clam mobility appear to be affected, including valves hermetic ability. Because causal relationship between the globular form and BMD has not been demonstrated, we can wonder if the disease could have impacted the globular form or if unfavorable environmental condition leading to specific shape patterns could have favored the affection development in specific site. The first hypothesis is supported by a significant discrimination of the BMD modalities on the first axe which is characterized by the variables *SM/L*, *SM/H*, *W/L* ratios, circle and reference ellipse lateral indices. It implies that the disease would develop a sufficiently long time to modify the shell shape. So far, the only available information is that the smaller infected recorded clam is 26 mm long (de Montaudouin, personal communication). For the second hypothesis, no argument is available up to now. Both of them are in accordance with the description of a decrease of the condition index (for Arcachon Bay) associated to the BMD pathology [40]. It is also consistent with the highlighted correlation between *H/L* and to a less extent *W/L* with nutritional condition indices described by

Watanabe and Katayama [23]. More generally, the observed globularity is in accordance with phenotypic changes under "unfavorable" conditions described by several authors [3, 9, 25].

Apart from density and disease effects, other factors have been proposed or demonstrated to impact the shell morphology. From an evolutionary point of view, defense against predator is considered as the most important function of the shell as reminded by Tokeshi et al. [41]. Considering different species of bivalves including a related species *Ruditapes variegatus*, these authors pointed out that the larger the shell, the more resistant the shell is regarding breakage by predators. For *M. balthica* in the North Sea, the hypothesis of a selective predation of the more globular shells has been proposed by Luttikhuizen et al. [42]. For avian predators, this form may mean a harder prey to swallow but also promotes a higher salt content which is according to Visser et al. [43] research, energetically costly to excrete. Those biological interpretations are applicable for fast predators but for slower ones, the capacity of moving away and burrowing deeper is considered as prevailing and is easier for flatter shells [42].

The main influence of predation on molluscan shell morphology has also been indicated by Watanabe and Katayama [23], but they attributed preferentially significant local differences in elongation and compactness indices to differences of nutritional conditions as explained above.

Other factors such as current velocity, water depth, or nature of the sediment have also been proposed for their influence on Venerids' shape [7, 44–46]. For Gérard [7], the nature of the sediment is of a great influence on the sharpness of the shell. For *Tapes rhomboides*, a related species, globular character was depicted in the Plymouth region (Great Brittany). Originally attributed by Holme [44] to an effect of pressure (related to water depth), this conclusion was challenged by Eagar [45] who focused on other physical conditions (muddy substrates and sheltered localizations). He made the physiological assumption that "obesity" could prevent the shell from sinking within the sediment and could provide stability. On other bivalves species (*Tellina tenuis, Donax vittatus, Macoma balthica,* and *Cerastoderma edule*), Trueman et al. [47] reported an effect of substrate of particle size and shell shape on the penetration of the bivalves' shells.

Up to now, those environmental factors are incompletely known for Arcachon Bay by comparison with other sites and should require further investigations.

4.2. Allometric Patterns: Synthetic Descriptors of Main Interest of Growth. For the first time, our study provides allometric data for the main exploited stock in France (see Table 1 and Figure 2). Allometric coefficient (k) is ranging between 1 (isometry for H to L) and 3 (positive allometry with higher coefficient for ratios taking into account the weight). Those values are consistent with other allometric patterns described for *Ruditapes philippinarum* and related species such as *Ruditapes decussatus, Ruditapes variegatus,* and *Tapes rhomboides* [7, 41, 48, 49]. In particular, considering that age is in turn reflected by the length like Eagar et al. [9] did, our results confirm that the globular character is more pronounced in ageing individuals.

Both linear and piecewise regressions models fit correctly the data for H to L and SM to L relationships, despite the fact that the piecewise model appears to be better in the case of SM to L. Both of them highlight discontinuities in the relative growth curves with marked breakpoints at length 15.7 mm and 19.6 mm. After the growth becomes faster for directions other than length and clams tend to be globular. Katsanevakis et al. [28] estimated that those changes in growth trajectories during ontogeny were worth being taking into account since they can be linked to marked events in the life history or fast ecological changes. For Manila clam, the identified breakpoints correspond to the second year of life of the clam; they match with the supposed size of maturity for this species. According to Holland and Chew [50], sexual maturation begins at 5 mm and spawning at 20 mm for Manila clam.

For *Venerupis senegalensis*, it is interesting to note that Eagar [45] observed a second breakpoint interpreted as a shell-limiting process for H to L and W to L for length class plotted against length of shell. The physiological explanation proposed by this author was a weaker efficacy of muscles when respiratory and food-collecting capacity per unit tissue decrease while the length increases. Those results were obtained with mean ratios per length classes, ignoring the individual variability information.

Spatial variability is shown and three main morphological groups of adult clams are identified. For those clams, similar shell shape appears to be grouped in the proximate strata G, H, and Z1; they could be seen as clams living in optimal conditions compared to the rest of the bay. The shape tendencies also appear to differ by their distance to the ocean connection (Figure 3). A high intertidal localization (involved in particular in the access time to food supply) could intervene but the necessary data were not considered in this work to address this point. This would be consistent with the observations of stunted clams especially in high intertidal areas and at higher clam densities done by Bourne and Adkins [16].

Morphometric investigations led by Ben Ouada et al. [30] on *Ruditapes decussatus* for sites along the Tunisian coast identified the existence of three phenotypes (globular, slender, truncated) and established a high polymorphism not only at between-population but also at within-population scales. This high variability within population was also genetically demonstrated [51, 52]. Nevertheless, Luttikhuizen et al. [42] established that shell shape variation was not randomly distributed over sites for *Macoma balthica,* and Costa et al. [12] indicated that "contribution of local adaptation to the morphological differentiation of population of clam is still poorly studied phenomenon."

4.3. Regulation Considerations. Currently four conservation measures are applied to regulate the fishing activity (number of licenses, minimum legal harvest size, fishing period, and no-take zones). Among those, the minimum legal harvest size is the only measure defined by European legislation; in practice applicable to the whole catches in Europe. Manila clam in Arcachon Bay presents a growth deficiency above 32 mm [20] and the present study reveals a different morphology for the shell shape compared to other sites with a propensity to be globular. These characteristics are both driven by environmental factors and exploitation; do they reflect a situation of stress for this species or adaptation? Can they challenge the minimum legal harvest size for the benefit of a local one more adapted to this situation?

Conflict of Interests

All authors declare no conflict of interests.

Acknowledgments

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