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Research Article

Age and growth of a highly successful invasive species: the Manila clam *Ruditapes philippinarum* (Adams & Reeve, 1850) in the Tagus Estuary (Portugal)

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Abstract

The Manila clam *Ruditapes philippinarum* (Adams & Reeve, 1850) was introduced in several regions worldwide where it is permanently established. In Portuguese waters, the colonisation of the Tagus Estuary by this invasive species coincided with a significant decrease in abundance of the native *Ruditapes decussatus* (Linnaeus, 1758). This study aimed to estimate the age and growth of the Manila clam, to compare the growth performance between *R. philippinarum* and *R. decussatus* in several locations worldwide, and to ascertain whether the Manila clam's growth patterns contributed to the extensive distribution of this invasive bivalve in the Tagus Estuary. The growth of *R. philippinarum* in the Tagus Estuary was described through the von Bertalanffy equation $SL_t = 65.2[1 - e^{-0.34(t+0.93)}]$, corresponding to a phi-prime index (φ') of 3.160 and an overall growth performance of 4.974. This growth performance is the second highest recorded for *R. philippinarum* worldwide and was much higher than that of *R. decussatus* from Portugal. This study confirmed that the Tagus Estuary presents near-ideal environmental conditions for growth of the Manila clam. *R. philippinarum* displayed clearly invasive behaviour, spreading widely and growing faster than the native *R. decussatus*, which certainly contributed to the decline of its populations in the Tagus Estuary.

Key words: acetate peel technique, von Bertalanffy growth function, overall growth performance, phi-prime index, interspecific competition, *Ruditapes decussatus*

Introduction

Zoobenthos comprise the predominant group of non-indigenous species in marine ecosystems, representing approximately 57% of the introduced species, and molluscs are the most commonly introduced taxon (Streftaris et al. 2005). Bivalves are one of the most invasive groups because some rapidly attain very high densities, thereby accounting for most of the benthic faunal biomass (Carlton et al. 1990; Sousa et al. 2009). Although invasive bivalves have received less attention compared to other faunal groups, they are responsible for severe ecological and economic impacts (Sousa et al. 2009, 2011, 2014; Crespo et al. 2015). Because bivalves are filter feeders, they can consume huge quantities of particulate organic matter, thus causing starvation of the native species, and their settlement can also interfere with the respiration, reproduction and growth of native species (IUCN 2009; Sousa et al. 2009). Moreover, due to rapid growth, non-native species often become dominant in abundance and biomass in the invaded ecosystem, threatening and displacing native species (Pranovi et al. 2006). Finally, the proliferation and

accumulation of empty shells of invasive bivalves can change the bottom physical structure by decreasing the boundary layer current velocity and increasing the microhabitat complexity and heterogeneity (Sousa et al. 2009; Bódis et al. 2014).

The Manila clam or Asari clam *Ruditapes philippinarum* (Adams & Reeve, 1850) is native to the western Pacific Ocean (Rodríguez-Moscoso et al. 1992). It is native to the Philippines, south and east China Seas, Yellow Sea, Sea of Japan, Sea of Okhotsk, and around the southern Kuril Islands (Goulletquer 2015). Because of its considerable commercial value, *R. philippinarum* was intentionally introduced and became established in several regions worldwide including the Pacific coast of North America and along the shores of Europe from the United Kingdom to the Mediterranean basin (Jensen et al. 2004; Melià et al. 2004; Melià and Gatto 2005; Goulletquer 2015). This species was first introduced into the United States (Holland and Chew 1974) and Canada (Bourne 1982), and afterwards along the European coasts, entering from France through hatchery production (Parache 1982; Flassch and Leborgne 1992; de Montaudouin et al. 2016a; Cordero et al. 2017). Overfishing and irregular yields of the native grooved carpet shell *Ruditapes decussatus* (Linnaeus, 1758) encouraged the importation of *R. philippinarum* by European countries, which was followed by transfers within European waters for aquaculture purposes (Breber 2002; Savini et al. 2010; Goulletquer 2015). Briefly, in the early 1970's, French commercial hatcheries developed breeding techniques with Manila clams imported from North America and, by the early 1980's, spat production was sufficient to sustain a commercial production (Goulletquer and Heral 1997). This success was followed by several transfers within European waters for aquaculture purposes (e.g. to Ireland, Italy, Spain and Portugal) (Breber 2002; Savini et al. 2010; Goulletquer 2015). Subsequently, massive aquaculture production and natural reproduction resulted in further geographical expansion of *R. philippinarum*, whose populations became the target of intensive harvesting and fishing activities, becoming the major contributor to clam landings in Europe (Goulletquer 2015).

Although occurring in Portuguese waters for more than two decades, with a first record in 1984 (Ruano and Sobral 2000), and currently occurring at several estuaries and coastal lagoon systems (Campos and Cachola 2006; Gaspar 2010), it is unclear how the Manila clam was first introduced. Despite this species never having been licensed for shellfish production in Portugal, aquaculture remains the most likely vector of introduction. *R. philippinarum* was first introduced into clam farms in Ria Formosa Lagoon (southern Portugal), certainly transferred from Spain (Ruano and Sobral 2000), followed by introductions by shellfish harvesters into other estuarine systems during the last decade (Chainho et al. 2015; Chiesa et al. 2016). *R. philippinarum* presently is the dominant bivalve species in some areas of the Tagus Estuary (the focus of this study), particularly in shallow bays with extensive intertidal areas (Chainho et al. 2015). The colonisation of the Tagus Estuary by this invasive species coincided with a sharp decrease in abundance of the native *R. decussatus*, possibly due to interspecific competition for the same resources (Chainho 2014). For this reason, the local fishing community shifted the harvesting effort towards the Manila clam, and there now exists an important fishery targeting *R. philippinarum*, with an increased number of illegal harvesters operating in the Tagus Estuary due to easy access to the fishing areas and the current economic climate in Portugal (Ramajal et al. 2016).

The population status of this invasive species still remains largely unknown in the Tagus Estuary, and information on the growth of *R. phiplippinarum* in this estuarine ecosystem is non-existent. Consequently, the present study aimed to estimate the age and growth of the Manila clam in the Tagus Estuary and to compare the growth performance between *R. philippinarum* and *R. decussatus* in several locations worldwide. Several methods have been used to estimate age and growth of bivalves, including: mark and recovery experiments; size-frequency analysis, counting visible growth rings; and counting growth marks in the microstructure of the shell revealed through acetate peel replicas of polished and etched shells. Most of these methods have practical problems that are generally overcome by analysing internal shell micro-banding patterns revealed in acetate peels, which is a time-consuming technique that provides a reliable record of the age and growth of bivalves (see review by Richardson 2001).

A recent and straightforward explanation for the rapid establishment and successful proliferation of non-indigenous species is the enemy-release hypothesis, which postulates that the abundance or effects of some invasive species is related to the scarcity of, and reduced control by, natural enemies (pathogens, parasites and predators) in the introduced range compared to the native range (Colautti et al. 2004).

In this study, we hypothesised that growth performance of invasive populations of the Manila clam would be higher than growth performance of i) native populations of *R. philippinarum* (due to different environmental conditions) and ii) of native populations of *R. decussatus* (due to different characteristics of the species), thus contributing for
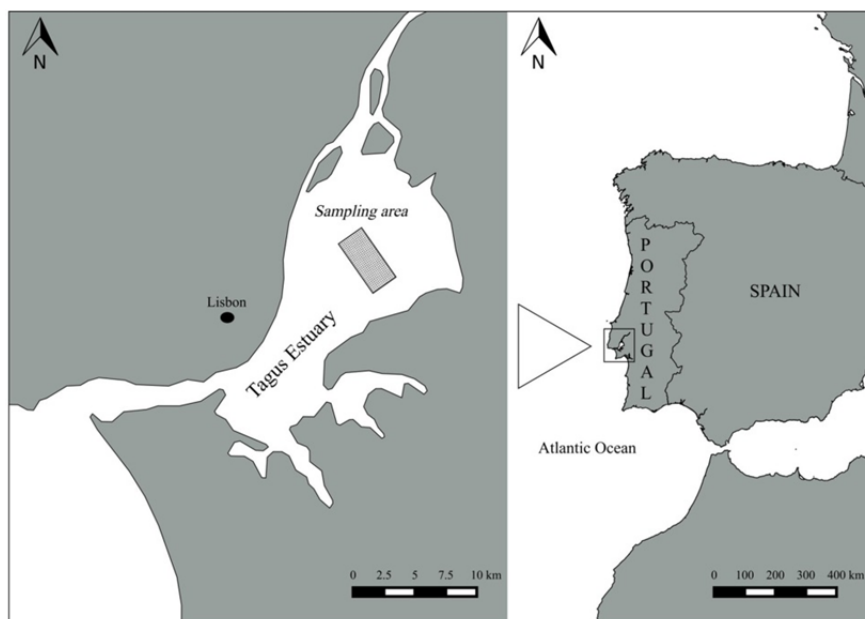
Figure 1. Map of the Tagus Estuary (central western Portugal) showing the area where the fishing surveys were performed for collecting the samples of the Manila clam (*Ruditapes philippinarum*).

the adaptiveness and competiveness that promoted the extensive colonisation and wide geographical expansion of the Manila clam. This study improves the current knowledge on the population dynamics of the invasive *R. philippinarum* and its potential harmful effects on the native *R. decussatus*. In addition, we provided valuable baseline information for supporting management measures for these populations and for predicting potential effects in other aquatic ecosystems recently colonised by the Manila clam.

Methods

Study area

The Tagus Estuary (38º44′N; 09º08′W), located in the central western coast of Portugal (Figure 1), covers an area of approximately 320 km² and is the largest estuary in Portugal, and among the largest estuaries in Europe (Cotter et al. 2013). The Tagus Estuary has a roughly linear structure in the initial and final stretches, although the main central water body is very wide, comprising several large bays along the southern bank (i.e. Montijo, Barreiro, and Seixal bays). This mesotidal estuary has an average tidal amplitude of 2.4 m, ranging from 0.9 m during neap tides and 4.1 m during spring tides (Dias et al. 2013). The estuary has an average depth <10 m, and approximately 40% of its area (138 km²) consists of intertidal mudflats (Cabral and Costa 1999) that have extensive salt marshes near the terrestrial margins (Caçador et al. 1996). Although the subtidal areas display heterogeneous bottom substrates, the upstream and intermediate zones are mainly composed by sandy-muddy sediments, while sandy sediments predominate in the downstream and adjacent coastal zones (Cabral and Costa 1999).

Although highly variable both inter-annually and seasonally, the average river flow is around 400 m³ s⁻¹. The water residence time is roughly 19 days (Braunschweig et al. 2003). The saline tide reaches about 50 km upstream from the mouth, near Vila Franca de Xira (Guerreiro et al. 2015), with salinity decreasing gradually from the lower to the upper zone of the estuary. Freshwater conditions occur in the vicinities of Vila Franca de Xira in typical hydrological years (Costa et al. 2007). Water temperature ranges between 8 °C during winter and 26 °C during summer (Cabral et al. 2001), representing conditions that are considerably cooler in winter and warmer in summer than the adjacent seawater (Bettencourt et al. 2003).

Integrated in the most populated region in Portugal (i.e., the Lisbon metropolitan area), the Tagus Estuary has long been subjected to intense anthropogenic pressures related to urban expansion, industrial development, agriculture, harbour infrastructures, and fishing activities – with the resultant problem of aquatic pollution (Caçador et al. 1996; França et al. 2005; Vasconcelos et al. 2007).

Sampling design

Fishing surveys were performed during February and March 2011, within a sampling area of approximately 10 km^2 in the zone with highest abundances of Manila clam in the Tagus Estuary (Figure 1). Samples were collected on-board a commercial fishing boat using bivalve dredges towed for approximately 30 seconds at a constant speed of 2 knots in each sampling station. These dredges consist basically of a metallic frame, a toothed lower bar and a rectangular metallic grid box opening posteriorly (for details, see Gaspar et al. 2014).

Samples were sorted on-board immediately after each tow, and specimens of *R. philippinarum* were separated from the other species. In the laboratory, shell length (SL – maximum distance on the anterior-posterior axis) and shell height (SH – maximum distance on the dorsal-ventral axis) were measured for each bivalve using a digital calipers (precision of 0.01 mm).

Age and growth

A total of 30 individuals with broad size range (28.4–62.0 mm SL) were analysed to estimate the age and growth of *R. philippinarum*. Using a wide size range (and thus different age-groups) allows attenuation of inter-annual variability in bivalve growth. Two complementary ageing techniques, based on the growth rings on the external surface of the shell and based on the growth marks in the internal structure of the shell revealed in the acetate peel replicas, were employed. Counting and measuring of growth rings were made by two independent observers, and independently for each ageing technique (shell surface rings and internal growth marks), and additional readings were performed whenever a pair of values did not match.

Initially, the rings deposited on the external surface of one valve were counted and measured with the digital calipers. Subsequently, the internal structure of the shell was analysed through acetate peel replicas of resin-embedded, polished and etched sections of the other valve, following the standard technique for ageing commercially-exploited bivalve species along the Portuguese coast (Gaspar et al. 1995, 1999, 2004; Moura et al. 2009, 2013). Cut surfaces were etched in 0.01M HCl for 3 min and acetate-peel replicas were prepared using the technique described by Richardson et al. (1979), and mounted between a slide and a cover slip. The acetate replicas of the shells were observed under a binocular microscope and visible growth rings were marked on the glass slide. The entire acetate peel and the respective marks were digitized and distances between the umbo and each growth ring were measured to the nearest 0.01 mm using the image processing and analysis software Image J (version 1.50b, NIH, Bethesda, Maryland).

Because measurements in acetate peels are relative to shell height (SH), data were converted into shell length (SL) by using regression analysis (Gaspar et al. 2002). The SL vs. SH relationship for *R. philippinarum* collected in the Tagus Estuary (n = 2995, range = 15.2–62.0 mm SL; $r = 0.966$, $P < 0.001$) was:

$$SL = 1.644 \times SH^{0.941}$$

A von Bertalanffy growth function (VBGF) was fitted to the age–length data obtained for *R. philippinarum*, through an iterative curve fitting procedure employing non-linear least-squares regression (Gauss-Newton method). This procedure provided estimates of the growth coefficient (K), asymptotic shell length (SL$_\infty$) and theoretical age at shell length zero (t_0), through the following equation (von Bertalanffy 1938):

$$SL_t = SL_\infty [1 - e^{-K(t-t_0)}]$$

Growth performance

Since growth often is described by multi-parameter non-linear models (such as VBGF), it is difficult to compare growth among different taxa in a statistically robust manner (Brey 1999), which prompted the development of growth performance indices to overcome this difficulty. To make individual growth estimates comparable, the growth performance index (phi-prime index, φ') (Munro and Pauly 1983) and the overall growth performance (OGP, P) (Pauly 1979) were calculated through the following equations:

$$\varphi' = Log_{10}K + 2Log_{10}SL_\infty$$

$$P = Log_{10}\left(K \times SL_\infty^3\right)$$

As a first approach for comparing the growth performances of *R. philippinarum* and *R. decussatus* worldwide, analyses of variance (ANOVA) were performed using each population as a replicate within the respective geographical area (*R. philippinarum* in Europe, Asia and North America; *R. decussatus* in Europe). The parameters analysed included K, L$_\infty$, φ', P, and the estimated ages at 35 mm SL (minimum landing size – MLS in the Mediterranean) and at 40 mm SL (MLS in the Atlantic). Each time significant differences between groups were detected, pairwise multiple comparisons were made using the Tukey *a posteriori* test. The analyses were performed using the software package SigmaStat$^©$ (version 3.5, Systat

Software, San Jose, CA) with statistical significance level of $P < 0.05$.

In the present study, φ' was employed to illustrate the variation in the growth performance index of *R. philippinarum* throughout its distributional range, either as a native species in Asian waters or as an introduced species along the North American and European coasts. For this purpose, the φ' value of each population was plotted as a function of the geographical coordinates (latitude and longitude) of the respective study areas, thus providing an illustration of the variation in the growth performance as a function of the geographic distribution. In addition, an auximetric grid was produced to graphically compare the variation in the overall growth performance (P) between *R. philippinarum* and *R. decussatus* from several locations worldwide.

A stepwise linear regression was performed to ascertain the main factors related to variation in the growth performance between native and invasive populations of the Manila clam. This stepwise linear regression was performed using the growth performance index (φ') as dependent variable, and the geographical coordinates (latitude and longitude), ocean (Pacific *vs.* Atlantic + Mediterranean), aquatic system (estuary *vs.* non-estuarine system) and species status (native *vs.* introduced) as independent or predictor variables. The analysis was performed using the software package SPSS© (version 21, IBM Corp., Armonk, NY) with statistical significance level of $P < 0.05$.

Results

In the present study, counting of shell-surface growth rings proved unreliable, resulting in systematic overestimation of the age of *R. philippinarum* and poor between-reader agreement (17.2%); therefore, these data was excluded from further analysis. In contrast, acetate peel replicas of the shells proved adequate for estimating the age and growth of the Manila clam from the Tagus Estuary, allowing to clearly discriminating the phases of slow and fast shell growth.

As expected, the acetate peels detected both the outer composite prismatic layer and the inner homogeneous layer (Figure 2A), with the outer prismatic layer displaying distinct growth patterns. Bands of rapid growth appeared as wide transparent regions and slow growth was recognisable by narrow dark lines (Figure 2B) usually associated with a cleft on the shell surface (Figure 2C). False rings were discernible as a sudden interruption of the natural growth pattern and also could show a surface cleft (Figures 2 D–E).

The VBG equation describing growth of the invasive *R. philippinarum* in the Tagus Estuary was:

$$SL_t = 65.2[1 - e^{-0.34(t+0.93)}]$$

In recent surveys to assess the status of the Manila clam populations in the Tagus Estuary, 55% of individuals caught were below the MLS (individuals smaller than 13 mm SL were absent from the samples due to the dredge size-selectivity) (authors own data). The oldest *R. philippinarum* examined was age-6 but the sample size (n = 30) was small. According to this equation, *R. philippinarum* reaches the MLS for Portuguese waters (MLS = 40 mm SL) slightly before age-2. The estimated asymptotic shell length (SL_∞ = 65.2 mm SL) was slightly larger than the largest shell (62 mm SL) sampled in the present study.

The ANOVA's for comparing the growth parameters and performances (K, L_∞, φ', P and estimated ages at 35 and 40 mm SL) detected differences between *R. philippinarum* and *R. decussatus* from different geographical areas (Table 1). For *R. philippinarum* from different geographic areas, statistically significant differences were found for K ($P = 0.013$), φ' ($P = 0.003$), estimated ages at 35 mm SL ($P = 0.021$) and estimated ages at 40 mm SL ($P = 0.027$). The phi-prime index (φ') for growth performance was higher in the non-native populations of *R. philippinarum* in Europe compared to the native populations from Asia ($P < 0.05$) but not significantly different from the non-native populations in North America ($P > 0.05$). In contrast, the ANOVA's comparing the growth parameters and performances did not detect any statistically significant differences between European populations of the invasive *R. philippinarum* and the native *R. decussatus* ($P > 0.05$) (Table 1).

The growth performance index (phi-prime) of the Manila clam in the Tagus Estuary (φ' = 3.160) revealed a clear separation of the Asian (western Pacific Ocean), North-American (eastern Pacific Ocean) and European (Atlantic Ocean and Mediterranean Sea) populations of the Manila clam (Figure 3). The value φ' = 3.050 completely separates the populations introduced in Europe, with considerably higher growth performance indices, from all remaining populations of *R. philippinarum* (either native from Asia or introduced in North America). The highest phi-prime values (φ' > 3.150) were recorded in introduced populations located at intermediate latitudes and longitudes (Tagus Estuary in Portugal and Bandirma Bay in Turkey), with quadratic relationships in both cases (latitude: $r^2 = 0.49$; d.f. = 12; $P < 0.05$. longitude: $r^2 = 0.50$; d.f. = 12; $P < 0.05$).
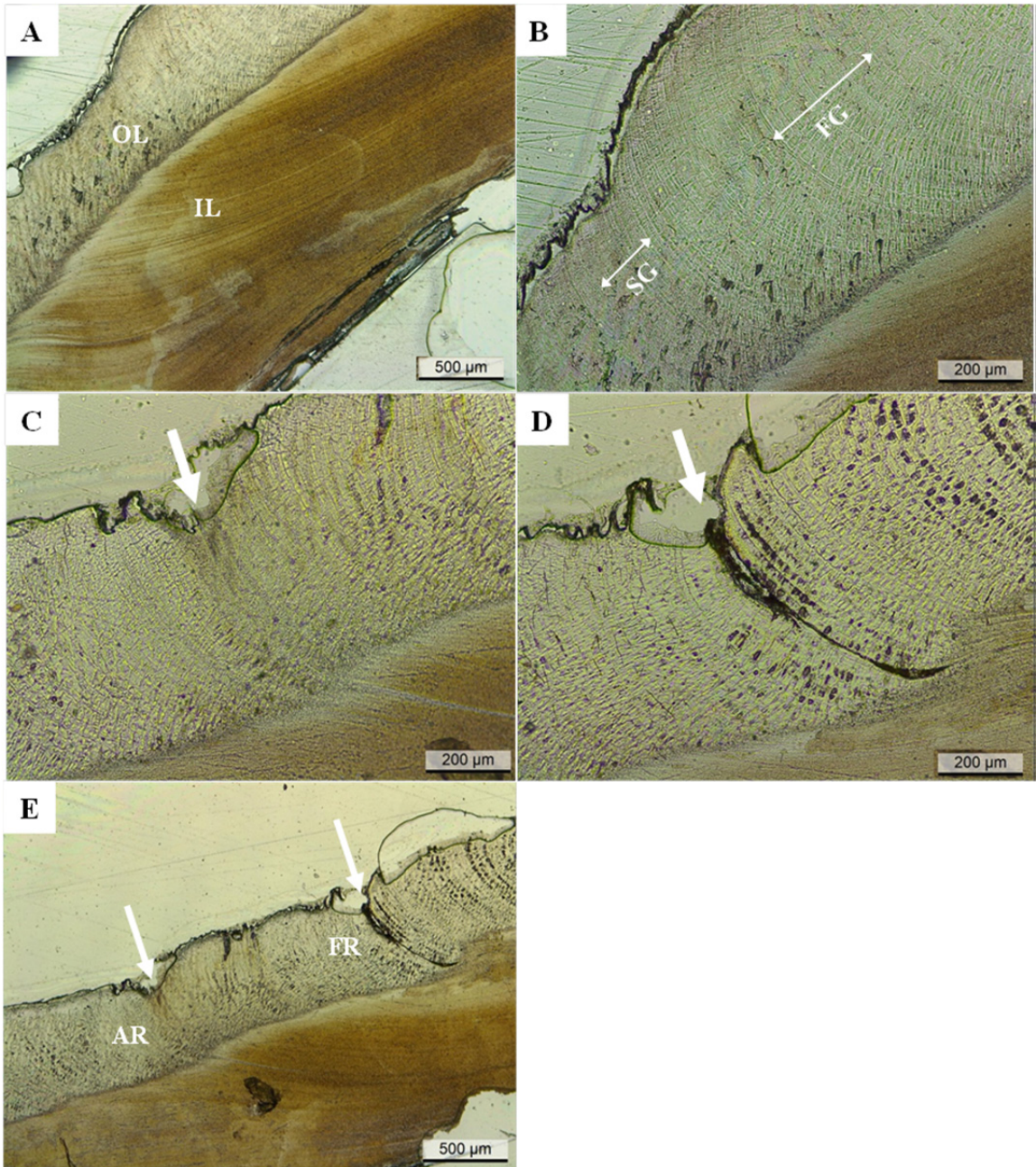
Figure 2. Photographs of acetate peel sections of *Ruditapes philippinarum*. A) acetate peel of sectioned shell illustrating the two layers; B) outer prismatic layer exhibiting two distinct growth patterns; C) annual growth ring associated with a cleft on the shell surface; D) false growth ring associated with a cleft on the shell surface; E) acetate peel illustrating the distinction of annual growth rings (progressive narrowing of growth bands) from false rings (sudden interruption of the natural growth pattern). OL, outer composite prismatic layer; IL, inner homogeneous layer; SG, slow growth, FG, fast growth; AR, annual ring; FR, false ring. Photo by P. Moura.

The stepwise linear regression indicated that the growth performance of *R. philippinarum* throughout its range was mainly influenced by the predictor variables "introduced" and "longitude" (which is highly correlated with "latitude": $r = -0.82$; n = 15; $P < 0.001$), as expressed by the following linear function:

$$\varphi' = 2.665 + 0.467 \, Introduced + 0.002 \, Longitude$$

Table 1. Analyses of variance (ANOVA) for comparing mean values of the von Bertalanffy growth coefficient (K), asymptotic shell length (SL$_\infty$), growth performance indices (φ' and OGP) and estimated ages at 35 and 40 mm SL (MLS in Mediterranean and Atlantic waters, respectively) between *Ruditapes philippinarum* and *Ruditapes decussatus* from different geographical areas (Europe, Asia and North America). *Rp*, *R. philippinarum*; *Rd*, *R. decussatus*; EUR, Europe; ASI, Asia; AME, North America; MLS, minimum landing size; [ns], not significant. Statistically significant differences ($P < 0.05$) detected by the ANOVA's and Tukey tests are highlighted in bold.

| Parameter | ANOVA | | Post-hoc pairwise multiple comparisons (Tukey test) | | | | | |
	F	P	q	P	Comparisons *Rp*	q	P	Comparisons *Rp* vs *Rd*
K	4.757	**0.013**	4.031	**0.048**	***Rp*-EUR > *Rp*-ASI**	1.378	0.766 [ns]	*Rp*-EUR = *Rd*-EUR
			4.327	**0.031**	***Rp*-EUR > *Rp*-AME**			
			0.850	0.930 [ns]	*Rp*-ASI = *Rp*-AME			
SL$_\infty$	0.853	0.483 [ns]						
φ'	6.777	**0.003**	5.346	**0.007**	***Rp*-EUR > *Rp*-ASI**	1.295	0.797 [ns]	*Rp*-EUR = *Rd*-EUR
			3.969	0.052 [ns]	*Rp*-EUR = *Rp*-AME			
			0.869	0.926 [ns]	*Rp*-ASI = *Rp*-AME			
OGP	2.471	0.095 [ns]						
Age (MLS = 35 mm SL)	4.172	**0.021**	4.177	**0.039**	***Rp*-EUR < *Rp*-ASI**	1.053	0.878 [ns]	*Rp*-EUR = *Rd*-EUR
			3.214	0.142 [ns]	*Rp*-EUR = *Rp*-AME			
			0.552	0.979 [ns]	*Rp*-ASI = *Rp*-AME			
Age (MLS = 40 mm SL)	3.937	**0.027**	3.425	0.111 [ns]	*Rp*-EUR = *Rp*-ASI	0.402	0.992 [ns]	*Rp*-EUR = *Rd*-EUR
			2.125	0.458 [ns]	*Rp*-EUR = *Rp*-AME			
			1.027	0.885 [ns]	*Rp*-ASI = *Rp*-AME			
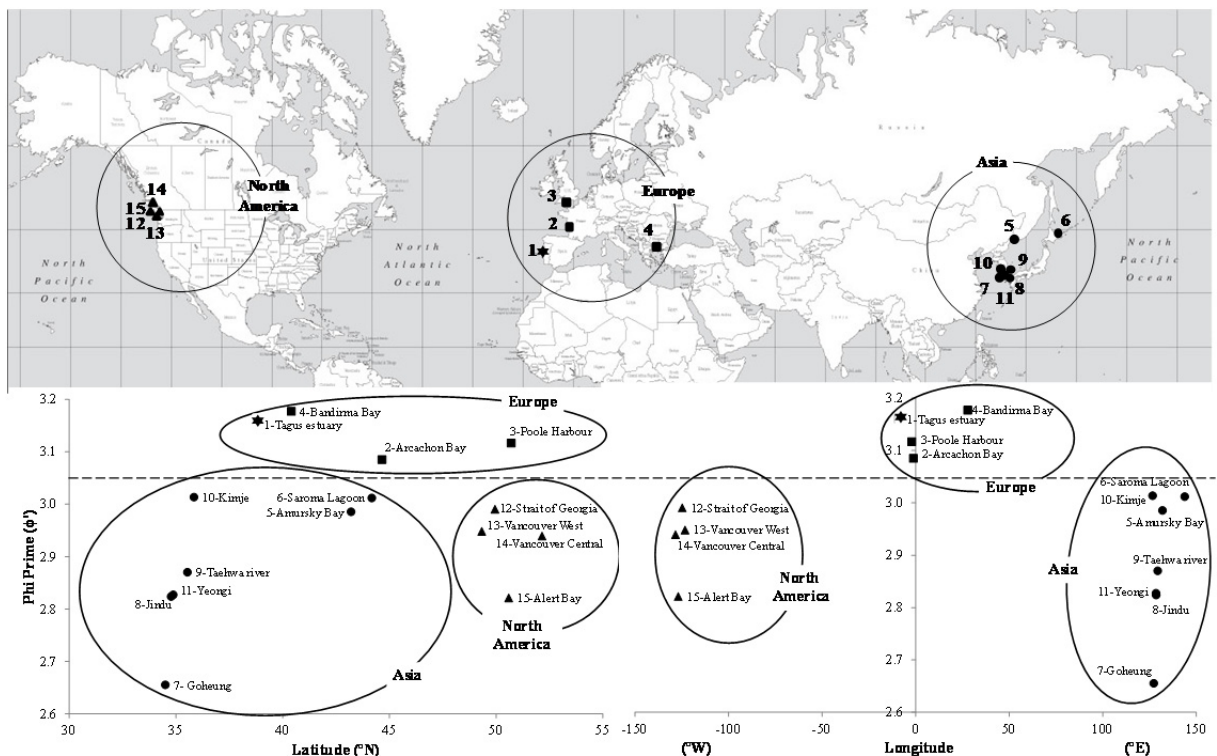
Figure 3. Variation of the growth performance index (phi-prime, φ') according to the geographical location (latitudinal and longitudinal coordinates) of the populations of *Ruditapes philippinarum* distributed worldwide. Circles delimit the groups of populations from different continents (Tagus Estuary - star; Europe - squares; Asia - circles; North America - triangles) and the interrupted line (φ' = 3.050) separates the populations introduced in Europe from the remaining populations (introduced in North America and native from Asia). Further details on those populations of the Manila clam (numbers, locations and references) are compiled in Table 2.
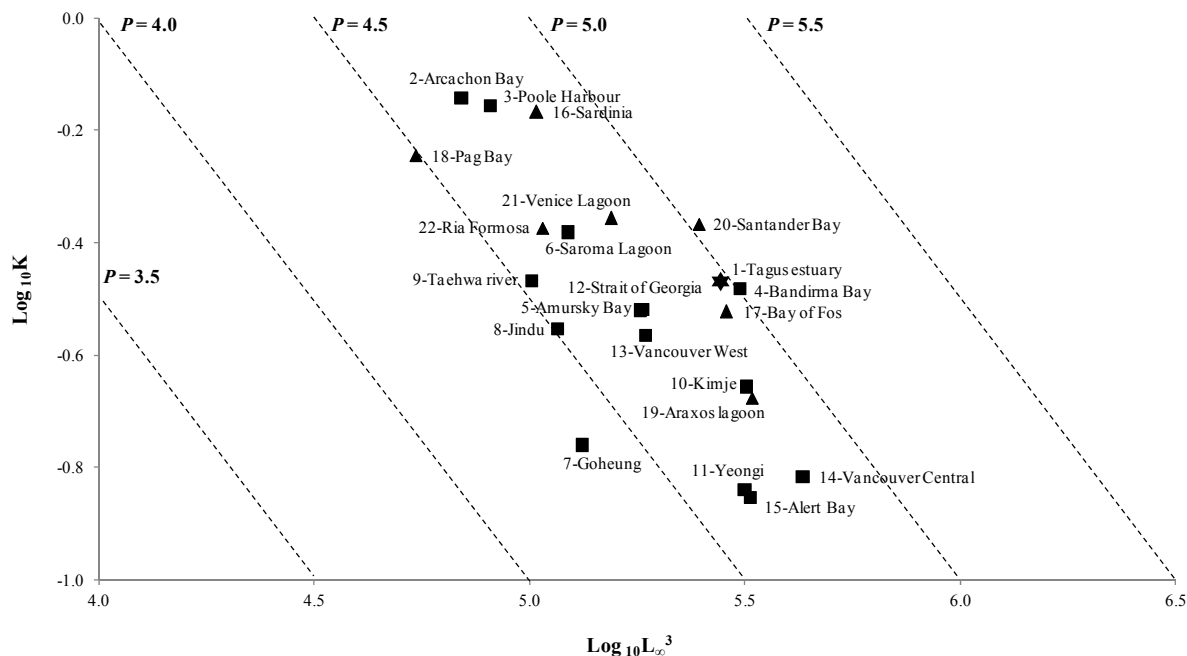
Figure 4. Auximetric grid for comparison of the overall growth performance (OGP, P) between populations of *Ruditapes philippinarum* (Tagus Estuary - star; other populations - squares) and *Ruditapes decussatus* (triangles) distributed worldwide. Diagonal lines indicate equal OGP values. Further details on those populations of the Manila clam (numbers, locations and references) are compiled in Table 2.

This model ($F = 9.189$; d.f. = 12; $P = 0.004$) for the growth performance index (φ') of *R. philippinarum* explained > 60% of the variation ($r^2 = 0.605$). In practice, this means that the growth performance of the Manila clam is higher in introduced populations of this species ("*Introduced*": $t = 4.133$; $P = 0.001$), being also favoured by increasing longitude ("*Longitude*": $t = 3.181$; $P = 0.008$).

The overall growth performance (OGP) of the Manila clam population introduced in the Tagus Estuary (OGP = 4.974) was among the highest growth performances recorded for this species throughout its vast distributional range, being only lower than the OGP displayed by *R. philippinarum* in Bandirma Bay (Turkey). In addition, OGP of the invasive Manila clam in the Tagus Estuary was only surpassed by the native population of *R. decussatus* from Santander Bay, Spain (Figure 4).

Discussion

The growth coefficient (K) of *R. philippinarum* introduced in Europe was considerably higher at higher latitudes (Arcachon Bay and Poole Harbour) than at lower latitudes (Tagus Estuary and Bandirma Bay) (Table 2). Consistent with K, the shell asymptotic

length (SL$_\infty$) in Arcachon Bay and Poole Harbour was considerably smaller than in the Tagus Estuary and in Bandirma Bay (Table 2). This apparently contradicts Bergmann's rule where there is a trend of increasing body size with latitude within broadly distributed species (Bergmann 1847). Although size–latitude trends are common in bivalves, generalizable patterns may not exist because mechanisms differ among lineages and/or regions and vary between hemispheres and coastlines (Berke et al. 2013). Indeed, some marine bivalves lacked correlation between mean size and latitude (e.g. Roy and Martien 2001; Roy et al. 2001; Berke et al. 2013). In addition, studies comprising native and invasive species reported that successful invasive bivalves tend to be large-bodied (Roy et al. 2001), which is supported by evidence that introductions shift body size trends related to abiotic factors (e.g. water temperature), changing latitudinal patterns, and reshaping eco-geographical patterns of body size (Blanchet et al. 2010).

Differences in the growth parameters (K and SL$_\infty$) of *R. philippinarum* introduced in Europe might be due to specificities of the locations and to variation in the quantity and quality of food (Dang et al. 2010). The duration of the invasion might also influence the adaptive capacity, with mature populations already

Table 2. Values of the von Bertalanffy growth coefficient (K), asymptotic shell length (SL_∞) and growth performance indices (φ' and OGP) of *Ruditapes philippinarum* and *Ruditapes decussatus*. Ageing method: AP, acetate peels; MR, mark and recapture; SR, surface rings; LF, length-frequency distribution; SEM, scanning electron microscopy. [A], alien; [N], native.

No.	Species	K (yr^{-1})	SL_∞ (mm)	φ'	OGP	Ageing method	Study area	Reference
1	*Ruditapes philippinarum*	0.34	65.2	3.160	4.974	AP	Tagus Estuary, Portugal (Atlantic Ocean) [A]	present study
2	*Ruditapes philippinarum*	0.72	41.1	3.085	4.699	MR	Arcachon Bay, France (Atlantic Ocean) [A]	Dang et al. (2010)
3	*Ruditapes philippinarum*	0.70	43.3	3.117	4.753	SR	Poole Harbour, England (Atlantic Ocean) [A]	Humphreys et al. (2007)
4	*Ruditapes philippinarum*	0.33	67.5	3.177	5.006	LF	Bandirma Bay, Turkey (Marmara Sea) [A]	Çolakoğlu and Palaz (2014)
5	*Ruditapes philippinarum*	0.30	56.6	2.986	4.738	SR	Amursky Bay, Peter the Great Bay. Russia (Sea of Japan – East Sea) [N]	Ponurovskii (2008)
6	*Ruditapes philippinarum*	0.42	49.7	3.012	4.708	SR	Saroma Lagoon, Hokkaido. Japan (Sea of Okhotsk) [N]	Goshima et al. (1996)
7	*Ruditapes philippinarum*	0.17	51.0	2.655	4.363	–	Goheung coast, Korea (Southern Sea of Korea) [N]	Yoon et al. (2011)
8	*Ruditapes philippinarum*	0.28	48.8	2.824	4.512	–	Jindu coast, Hansan Island. Korea (Southern Sea of Korea) [N]	Cho and Jeong (2007)
9	*Ruditapes philippinarum*	0.34	46.6	2.870	4.539	SR	Taehwa River, Ulsan, Korea (Eastern Sea of Korea) [N]	Choi et al. (2011)
10	*Ruditapes philippinarum*	0.22	68.3	3.014	4.848	SR	Kimje coast, Korea (Western Sea of Korea) [N]	Chung et al. (1994)
11	*Ruditapes philippinarum*	0.15	68.1	2.827	4.660	SR	Yeongi coast, Tongyeong, Korea (Southern Sea of Korea) [N]	Cho et al. (2008)
12	*Ruditapes philippinarum*	0.30	56.8	2.991	4.745	SR	Strait of Georgia, BC, Canada (Pacific Ocean) [A]	Bourne (1982)
13	*Ruditapes philippinarum*	0.27	57.1	2.948	4.705	SR	Vancouver West coast, BC, Canada (Pacific Ocean) [A]	Bourne (1982)
14	*Ruditapes philippinarum*	0.15	75.5	2.939	4.818	SR	Vancouver Central coast, BC, Canada (Pacific Ocean) [A]	Bourne (1982)
15	*Ruditapes philippinarum*	0.14	68.8	2.821	4.659	SR	Alert Bay, BC, Canada (Pacific Ocean) [A]	Bourne (1982)
16	*Ruditapes decussatus*	0.68	47.0	3.177	4.849	SR	Sardinia, Italy (Mediterranean Sea) [N]	Cannas (2010)
17	*Ruditapes decussatus*	0.30	65.9	3.115	4.934	SEM	Bay of Fos, Marseille, France (Mediterranean Sea) [N]	Garcia (1993)
18	*Ruditapes decussatus*	0.57	37.9	2.913	4.492	AP	Pag Bay, Croatia (Adriatic Sea) [N]	Jurić et al. (2012)
19	*Ruditapes decussatus*	0.21	69.0	3.002	4.841	SR	Araxos Lagoon, Greece (Ionian Sea) [N]	Chryssanthakopoulou and Kaspiris (2005)
20	*Ruditapes decussatus*	0.43	62.8	3.229	5.027	LF	Santander Bay, Spain (Atlantic Ocean) [N]	Pato (1979)
21	*Ruditapes decussatus*	0.44	53.7	3.103	4.833	–	Venice Lagoon, Italy (Adriatic Sea) [N]	Breber (1985)
22	*Ruditapes decussatus*	0.42	47.5	2.979	4.656	SR	Ria Formosa Lagoon, Portugal (Atlantic Ocean) [N]	Banha (1984)

adapted to local environmental conditions displaying more competitive growth features. Although the growth of farmed Manila clam depends on water temperature (Melià et al. 2004), the present comparisons showed that this species grows fast even at higher latitudes, confirming its adaptive capacity to a wide range of water temperatures. These trends in the growth parameters might also be influenced by the harvesting effort and management measures to which those populations have been subjected. The Manila clam was introduced into British waters in the 1980's, with the fishery in Poole Harbour regulated

by a MLS of 40 mm SL (Humphreys et al. 2007). Similarly, it was introduced in Arcachon Bay in 1980, being subjected to a MLS of 40 mm SL until 2007 and then decreased to 35 mm SL (Dang et al. 2010). The size distributions in both populations reflect the harvesting activity and fishing regulations, either through smaller SL_∞ (Humphreys et al. 2007) or size-frequency distributions lacking specimens > 40 mm SL (Dang et al. 2010).

The adaptation of the Manila clam to the environmental conditions in European waters was reflected in the high growth performance indices ($\varphi' > 3.050$)

displayed by those populations. The highest φ' worldwide was recorded in Bandirma Bay, followed by the Tagus Estuary, with populations from Poole Harbour and Arcachon Bay also displaying higher φ' than those introduced in North America and native in Asia (Table 2). Concerning the comparison of the overall growth performances, *R. philippinarum* introduced in Turkey and Portugal presented similar OGP to those of the native *R. decussatus* from Santander Bay and from Bay of Fos, with the population in the Ria Formosa Lagoon displaying one of the lowest OGP (Table 2).

The growth performance index of *R. philippinarum* did not exhibit a clear latitudinal trend throughout its distributional range, possibly because variation is more related to local environmental characteristics than to latitude. Ideally, the comparison of φ' between three very different ecoregions (Europe, North America and Asia) should include cumulative degree-days above a threshold, an often overlooked but well-known parameter influencing bivalve growth (e.g. Incze et al. 1980; MacDonald and Thompson 1985). Still, high growth performances confirmed that European estuaries and bays provide favourable environmental conditions (more empty niches, fewer diseases and parasites, fewer native competitors) for the Manila clam. The fact that North American and Asian populations of *R. philippinarum* displayed comparable and overlapping φ', possibly reflects the earlier introduction along North American coasts and more similar environmental conditions among these regions.

Water temperature does not seem the main factor for the colonisation by *R. philippinarum*. Lower temperatures did not prevent the naturalisation in British waters (Jensen et al. 2004; Humphreys et al. 2015), and it reproduced successfully and rapidly naturalised in Arcachon Bay (Goulletquer et al. 1987). In North America, this species became established and shares an ecological niche with native bivalves, without affecting biodiversity (Becker et al. 2008). In other locations, low recruitment was reported (Dang et al. 2010) and *R. philippinarum* did not show invasive behaviour (Humphreys et al. 2015). In contrast, some European estuaries and bays provided suitable conditions, namely the Tagus Estuary, for this species to show invasive behaviour: spreading quickly and growing fast, competing for resources, and causing the decline of native bivalves (Chainho 2014; Chainho et al. 2015; Ramajal et al. 2016). Recent surveys in the Tagus Estuary collected 2,953 specimens of *Ruditapes* spp., of which 99.5% were *R. philippinarum* and only 0.5% were *R. decussatus* (authors own data). Additionally, a study on macrobenthic biodiversity patterns in the Tagus Estuary further confirmed the extreme rarity of *R. decussatus* compared to *R. philippinarum* (Piló et al. 2015).

In several European estuaries and lagoons, *R. philippinarum* supplanted *R. decussatus* by occupying its ecological niche and relegating the native species to restricted areas (Bidegain and Juanes 2013). For instance, the invasion of the Venice Lagoon by the Manila clam decreased the distribution and density of all other bivalve species (Pranovi et al. 2006). This species colonised most embayments along the French Atlantic coast and replaced the native European clam (Flye-Sainte-Marie et al. 2007), which is supported by the high OGP achieved by *R. philippinarum* in Arcachon Bay (Table 2). Likewise, the establishment of the Manila clam in the Marmara Sea poses a serious threat for *R. decussatus* (Tunçer et al. 2004; Genez et al. 2015), with the highest OGP registered by *R. philippinarum* in Bandirma Bay (Table 2) further strengthening the risk of invasion in Turkish waters.

In contrast, in Poole Harbour (Humphreys et al. 2015) and in Santander Bay (Juanes et al. 2012), these congeneric species co-exist and their relative abundances do not display negative correlation. In these cases, interspecific competition for space or resources is not intense (Juanes et al. 2012) and predation rather than competition limits their densities (Bidegain and Juanes 2013). Moreover, recent studies reported population decline of the Manila clam in Arcachon Bay, suggesting that low condition and fitness might be due to poor trophic condition, high prevalence and intensity of disease, pollution, and low efficiency of the immune system (de Montaudouin et al. 2016b). The high OGP of *R. decussatus* in those Spanish and French bays (Table 2) indicate that *R. philippinarum* may not pose a dangerous threat, as the introduced species has not yet supplanted the native species (Juanes et al. 2012).

The Manila clam appears to be larger, faster growing, more resistant to parasites (Breber 1985), with wider feeding spectrum, and higher food-conversion efficiency than *R. decussatus* (Bodoy et al. 1980; Sorokin and Giovanardi 1995). In addition, *R. philippinarum* reaches the size at sexual maturation (29.4 mm SL) before one year-old and has a long spawning season in the Tagus Estuary (authors own data). Unfortunately, there is no information on the growth of *R. decussatus* in the Tagus Estuary to compare the growth performance between native and invader populations. The only data available was reported for *R. decussatus* from the Ria Formosa Lagoon, which displayed much lower growth performance than *R. philippinarum* in the Tagus Estuary (Table 2), although such comparison should be interpreted cautiously because of the distinct environmental conditions prevailing in these aquatic systems.

This study should be strengthened by increasing the sampling effort and analysing the growth of the Manila clam from a wider area, to improve its representativeness towards the whole population in the Tagus Estuary. Additional studies are required, namely on the population status and dynamics, reproductive cycle, spawning season, and size at sexual maturity of *R. philippinarum*. This information would provide baseline information for management strategies to minimise the negative impacts caused by this invasive species on the native biodiversity, particularly on autochthonous bivalves.

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