

The clam siphon as indicator for growth indices in the soft-shell clam *Mya arenaria*

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Received: 1 July 2006 / Revised: 18 September 2006 / Accepted: 21 September 2006 / Published online: 24 October 2006
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Abstract Due to the species' deep burrowing behaviour, growth parameters of the soft-shell clam *Mya arenaria* L. 1758 are difficult to estimate, especially in deeper habitats which are not directly accessible. In this study, we analysed 192 specimens of *M. arenaria* and found, contrary to results of most other studies that the sigmoid Gompertz growth model (GGM) is appropriate to describe the growth. Predictions from this model confirm the finding of a life span up to 8 years and as a consequence of this, a maximum shell-length of 60 mm. Individual growth rates calculated from the first deviation indicate a nearly exponential growth in young individuals. The relationship between the clam siphon-width and age, shell-length and biomass conform to the GGM. This is a new approach to assess growth of *M. arenaria* and to solve practical problems that arise in field studies.

Keywords *M. arenaria* · Growth-indices · Siphon-width · Bertalanffy growth model · Gompertz growth model

Introduction

The soft-shell clam *Mya arenaria* Linnaeus, 1758, originates from the Northwest Atlantic and invaded European waters a few hundred years ago (Strasser 1999). In the Baltic Sea, it occurs frequently in high abundance and biomass on sandy substrates (Kube 1996; Forster and Zettler 2004). In both autochthonous and allochthonous populations, growth patterns, life span (4–28 years) and maximum shell-length (27–135 mm) vary considerably (e.g. Feder and Paul 1974; Newell and Hidu 1982; Brousseau 1978; Maximovich and Guerassimova 2003). Moreover, former investigations showed that growth of *M. arenaria* is influenced by several factors, e.g. salinity, predation, pollution and seasonal variation (Appeldoorn 1981; Newell and Hidu 1982; Beal et al. 2001; Beal and Kraus 2002; Strasser 2002; Weiss et al. 2002). In the Baltic Sea growth of *M. arenaria* has been less studied. While some papers reported a linear age-size relationship along with spatial variation in growth (Kube 1996; Kube et al. 1996), Munch-Petersen (1973) showed an exponential growth pattern in a Danish estuary, and for the White Sea Maximovich and Guerassimova (2003) described growth of *M. arenaria* by a von Bertalanffy growth curve. It seems to be difficult to generalize growth patterns in *M. arenaria* due to varying methods of data collection, spatial and temporal variations of growth, recruitment and settlement as well as different environmental conditions. Whatever method is used practical problems arise, especially for investigations in deeper habitats. Monitoring sampling is accomplished through van Veen grab and occasionally siphons are cut off while the respective shells are not retrieved (Forster and Zettler 2004). This causes problems in

Communicated by H.-D. Franke.

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estimating population structure, growth, biomass, production and filtration rates. In the present study we tested a new approach to estimate growth of *M. arenaria* in a typical brackish estuary and determined relationships, which allow for an estimation of body-mass and size of clams by using the size of the siphos.

Methods

A total of 192 individuals of *M. arenaria* were collected randomly from a brackish estuary in June 2003. The habitat called Schnatermann, is located at the Brei-ling, an estuary of the Warnow river, which flows into the Southern Baltic Sea near Rostock in Northeast Germany (Fig. 1). The salinity ranges between 8 and 12 PSU and the mean water depth from 0.1 to about 1 m except in the navigation channel. After treatment with magnesium chloride (MgCl) to prevent retraction of the clam siphos, the entire sample was fixed with 4% formaldehyde. Shell-length, -width and -height were measured to the nearest 0.01 mm with a digital calliper. The siphos-width was estimated approximately 1 mm below the siphos-opening to the nearest mm. Individual fresh-weight (FW) was determined immediately after taking the individual out of the fixative. Dry-weight (DW) was determined after heating treatment (60°C for 10–12 h) and ash-weight (AW) after ignition for 12 h at 550°C. Ash-free-dry-weight (AFDW = DW – AW) was calculated for each individual. All clams were weighed to the nearest 0.01 g. Age was determined by counting surface growth lines. We assumed an annual origin of growth line during winter periods at least for the sampling area. However, particularly in older specimens counting growth lines proved to be difficult. Specimens were divided into age classes (1-year steps) and for each class means ± standard

deviations (SD) were calculated for shell-length (SL), -width (SW), -height (SH) and siphos-width (SWi). Individuals with values deviating from the mean of the respective age group by more than two fold SD were excluded from the statistical analyses (outliers). Tests of normality (Kolmogorov–Smirnov) and homogeneous variance (Levene’s test) were carried out for SL, SW, SH and SWi, but failed for all ($P < 0.05$). Standard error, F value, R^2 and significance ($P < 0.01$) have been given for the regression analyses. Because of allometric pattern in individual fresh-weight and shell-length relationship a specialised von Bertalanffy growth curve (sVBGF) with

$$L_t = L_\infty \cdot \left(1 - e^{-K \cdot (x - x_0)}\right)$$

was performed by the method of the weighed least squares, where L_t is the shell-length (mm), L_∞ the theoretical asymptotic length (mm), K the growth rate, x the age (years) and x_0 the age (years) of zero length. Because the residual variances were not constant around the independent (age) variable, weighed least squares estimate was applied (Neter et al. 1985). Thus, a Gompertz growth model (GGM) was performed with

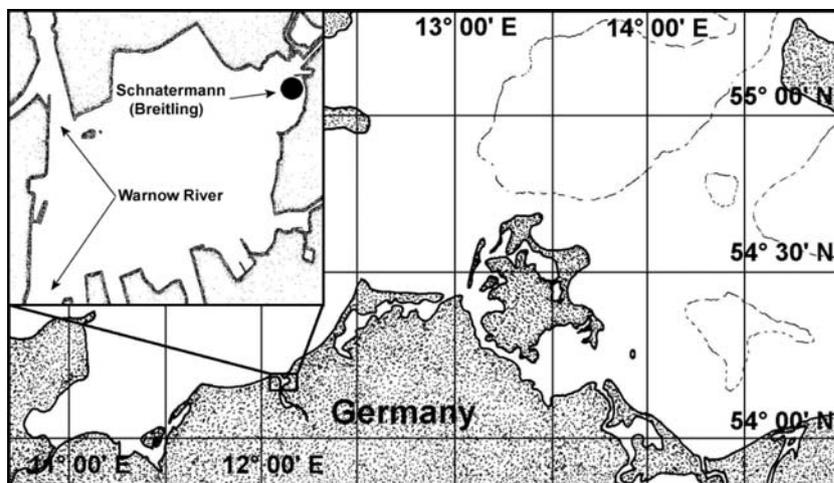
$$L_t = L_\infty \cdot e^{-e^{-K \cdot (x - x_0)}}$$

(unlike in the sVBGF, x_0 indicates the age at first inflexion point. All analyses were done using Statistica for Windows, Version 6, <http://www.statsoft.com>).

Results

The age structure of the individuals collected was relatively balanced (Fig. 2). Individuals with an age of 3 years were probably underrepresented; indicating

Fig. 1 Map of the study area with the “Schnatermann” location (inset above on the left); the black dot indicates the station where *M. arenaria* was collected in June 2003



unsuccessful reproduction or settlement, and only one individual of 8 years was found. About 55% of the specimens were 4–5 years old, the 5-years group comprising about 35% of the specimens. A decrease in frequency was observed for individuals older than 5 years. The shell-length ranged from 9.05 mm at first year to 60.08 mm at 8 years. It should be noted that clams called “ x year” had x annular rings. Both distribution and variances were not normal and homogeneous ($P < 0.05$), respectively for all tests. The age classes overlapped in shell-length (Fig. 3a) and the age–length relationship varied considerably within age groups, particularly in older individuals. Nevertheless, a Kruskal–Wallis ANOVA showed significant ($P < 0.01$) differences between age groups.

With increasing age the shell-length increment decreased with a sigmoid pattern (Fig. 3a). Therefore, a specialised von Bertalanffy growth curve (sVBGF) was calculated. The curve best fitting the data was obtained for $L_{\infty} = 87.37 \pm 4.71$ (mm), $K = 0.16 \pm 0.01$ (mm) and $x_0 = 0.66 \pm 0.48$ (years). The model predicts that shell growth starts between 0.18 and 1.14 years (Fig. 3a). This was contrary to the information provided by rings. Furthermore, the curve partly runs beyond the range of measured values (Fig. 3a). Application of the GGM yielded a better fit (Fig. 3a). Therein L_{∞} was estimated at 62.56 ± 1.14 (mm) and was quite near to the observed maximum shell-length (60.03 mm). Table 1 gives detailed values of the estimated parameters. Moreover, the size specific growth curve (dx/dy) of the GGM showed a more reasonable progression (Fig. 3b). The sVBGF size specific growth rate decreased exponentially with age, whereas the GGM predicts an exponential increase of growth in shell-length up to an age of 2.5 years and a subsequent linear decrease

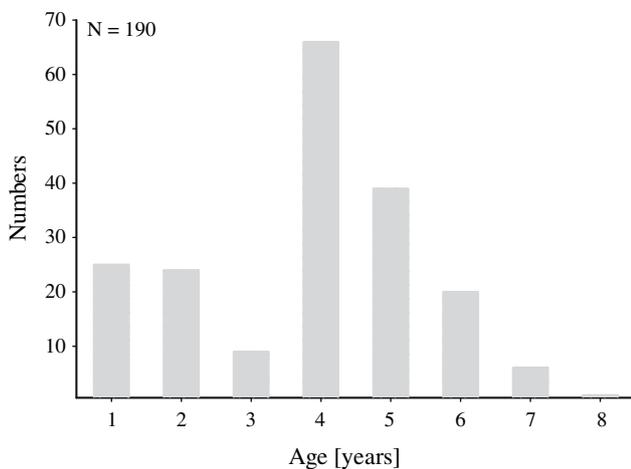


Fig. 2 Age structure of 190 specimens of *M. arenaria*

(Fig. 3b). With respect to the overall growth performance (for $OGP = \phi$ see Pauly (1979); Munro and Pauly (1983)), ϕ was determined at 3.1 (sVBGF) and 3.26 (GGM), respectively (Table 1). Compared to locations shown in Table 1, ϕ indicates suitable conditions for *M. arenaria* at the study site. The three-dimensional analysis of shell-length versus shell-height and shell-width indicates an isometric increase in both, volume and surface with $R^2 = 0.99$ (not shown by figure). Due to the relatively constant ratios between the different weight parameters (Fig. 6), shell-length (SL) shows an allometric relationship not only with fresh-weight (FW) (Fig. 4) but also with dry-weight (DW) as well as AFDW. Analogous relationships could be applied to shell-width (SW) vs. FW, DW and AFDW, and to shell-height (SH) versus FW, DW and AFDW, respectively. Consequently, a Gompertz growth curve could be calculated for body mass. As mentioned above there is an allometric relationship between shell-length and fresh-weight (Fig. 4) with

$$FW = a \cdot SL^b = 1.55 \times 10^{-4} \cdot L^{2.87}$$

Therein the standard error is ± 0.00 for a and ± 0.09 for b . From this equation we calculated the asymptotic fresh-weight (W_{∞}) by replacing SL with L_{∞} , obtained from the GGM (Table 1; Fig. 3a). Then we replaced L_t and L_{∞} with W_t and W_{∞} , respectively, from the GGM. Because of allometric relationship, we also had to use the condition factor $b = 2.87$ from the obtained relationship between FW and SL. This ultimately leads to

$$W_t = W_{\infty} \cdot \left(e^{-e^{-K(x-x_0)}} \right)^b$$

This equation indicates an only slight increase in fresh-weight during the first 2 years which was less than that of shell-length (compare Figs. 4, 5). As with individual shell-length, the values of individual fresh-weight overlapped widely between age groups. The mean ratios of FW/DW, FW/AFDW and DW/AFDW were largely homogeneous ($P > 0.01$ for all) over shell-length classes (Fig. 6a, b). The overall means of these ratios can be used as conversion factors (Fig. 6b): 1:2.5 for FW/DW; 1:2.9 for FW/AFDW; and 1:1.2 for DW/AFDW.

The mean meat yield of individual shell-length ranged between 59 and 68% and thus proved to be relatively independent of shell-length. The siphon itself is a component of the soft tissue in bivalves and we found a relationship ($R^2 = 0.70$) between siphon-width (SWi) and fresh-weight (FW) (Fig. 7a, b). The regression analysis based on siphon-widths centralized to

Fig. 3 a Modelled growth curves (Gompertz and von Bertalanffy), and **b** size species growth rate curves of *M. arenaria*. Note Regression was weighed by age because of non-constant residual variance around the independent variable

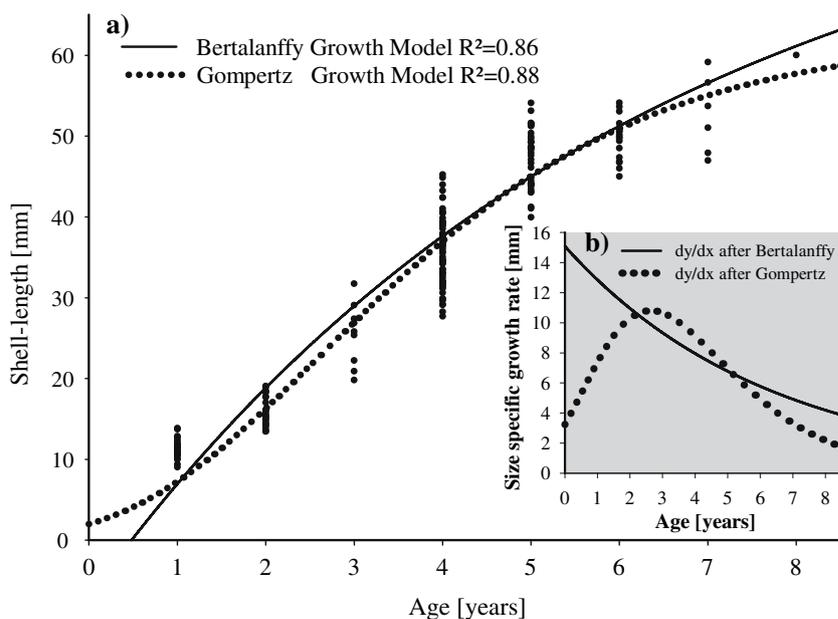


Table 1 Growth indices for *M. arenaria* from different locations

Location (author) (used model)	K	L_{∞}	OGP [ϕ]
Sugatuck River, USA (Brousseau and Bagivlo 1987) (sVBGF)	0.05	81.10	2.52
Roskilde Fjord, Denmark (Munch-Peterson 1973) (sVBGF)	0.30	60.10	3.03
Kandalasksha Bay (Site A), Russia (Maximovich and Guerassimova 2003) (sVBGF)	0.20	49.40	2.68
Inner Oslo fjord, Norway (Winther and Gray 1985) (sVBGF)	0.10	109.38	3.08
Potato Island, Nova Scotia, USA (Appeldoorn 1983) (sVBGF)	0.10	81.55	2.81
Breitling, Baltic Sea, Germany (present study) (sVBGF)	0.16	87.37	3.09
Breitling, Baltic Sea, Germany (present study) (Gompertz)	0.47	62.56	3.26

K = growth factor, L_{∞} = asymptotic shell-length (mm), and OGP [ϕ] = overall growth performance after Munro and Pauly (1983)

1 mm classes, showed for the range between 5 and 13 mm a pronounced relationship for FW vs. SWi, while adjacent ranges had to be omitted from the analyses (Fig. 7a). As FW is related to SL (Fig. 4), there is also a correlation between SWi and SL (Fig. 7b). The condition coefficient for SL versus SWi was close to one ($b = 0.8$), and this suggests a linear relationship between these parameters for SWi values ranging from 5 to 13 mm (Fig. 7b). The FW/SWi- and the SL/SWi-relationships are equivalent as indicated by $R^2 = 0.70$ for both.

Discussion

Many authors used external growth rings for estimating age of *M. arenaria* (Newcombe 1935; Brousseau 1979; Munch-Petersen 1973; Appeldoorn 1983; Kube 1996; Kube et al. 1996), though for some habitats no external growth rings for *M. arenaria* were found (e.g. Mead and Barnes 1903). But even though external growth

rings are present, a relationship between age and growth rings is not mandatory as demonstrated by MacDonald and Thomas (1980) for the Prince Edward Island. Instead, they advise to use internal growth patterns of *M. arenaria* (MacDonald and Thomas 1980). In most cases growth rings were present and usable for estimating age (e.g. Brousseau and Bagivlo 1988; Maximovich and Guerassimova 2003), but in Kandalashka Bay (White Sea) the first ring was not present in clams older than 2-years (Maximovich and Guerassimova 2003). In this study growth rings were present and assumed to be formed during the winter season. If the findings of Maximovich and Guerassimova (2003) also apply to the investigated area, we have to concede that the age of specimens may be underestimated. If this is the case, the given age structure (Fig. 2) may be affected. However, for the determination of growth curves this is negligible because only the parameter x_0 is changed as long as always clear growth rings were used. Nevertheless, we found small numbers of juvenile clams and a markedly decreasing

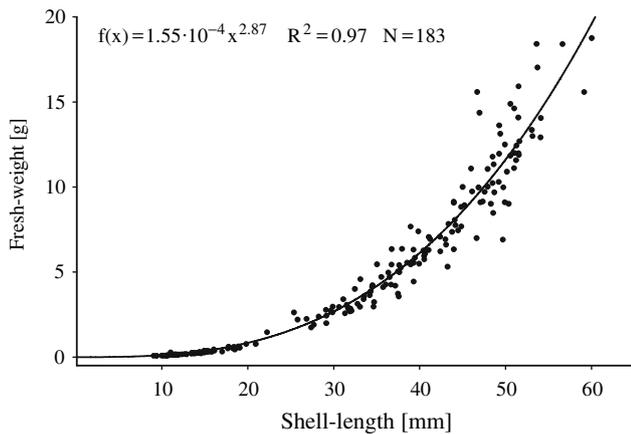


Fig. 4 Scatterplot with regression of individual fresh-weight versus shell-length for *M. arenaria*

abundance of individuals older than 4-years (Fig. 2). Probably a decline of recruitment, settlement and survival occurred either in the last season or the season before.

Clams living in experimental protected areas showed a higher survival compared to exposed areas (Beal and Kraus 2002) and reduced epibenthic predation could also positively affect the recruitment of bivalves (Strasser 2002). Generally, predation is a regulator for survival and settlement of juvenile clams, especially for *M. arenaria* (Günther 1992). In the Pomeranian Bay predation by fishes and sea ducks occur, especially on juvenile or small clams, because they are living in the dynamic surface of the sediment (Kube 1996). In dynamic sediments juvenile clams are moved to the sediment surface and thus are frequently exposed to predators. At the Schnatermann mainly epibenthic predators such as *Crangon crangon* and *Hediste diversicolor* occur (for clams < 2 mm) as well as sea ducks which may be responsible for cropping on small clams and therefore reduce the abundance of juvenile *M. arenaria*. Furthermore, settlement on soft bottoms is determinate by the local hydrodynamic and topographic conditions (Günther 1992, and references therein), which are documented by bed load sediment transport and erosion for the Pomeranian Bay (Kube 1996). It cannot be ruled out that these unmeasured factors affect *M. arenaria* in the observed area. A constant mortality rate as assumed by Munch-Petersen (1973) as well as size- or age-dependent decrease of mortality with constant survival after maturation (Brousseau 1978) may not be evidenced due to the fact that age frequencies do not decrease at a constant rate in the observed area (Fig. 2). Indeed, decreasing number of individuals with increasing age may be interpreted as a constant mortality rate, but within the

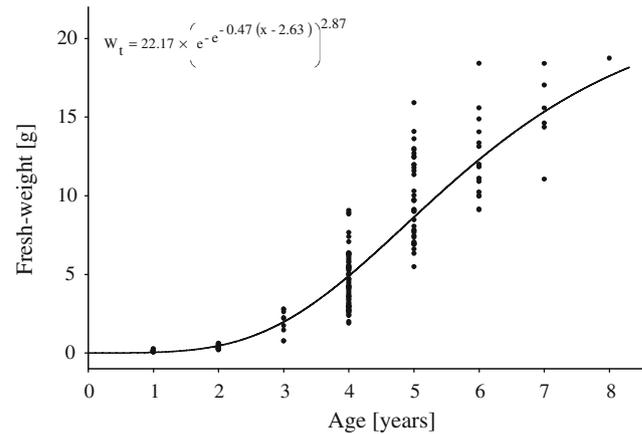


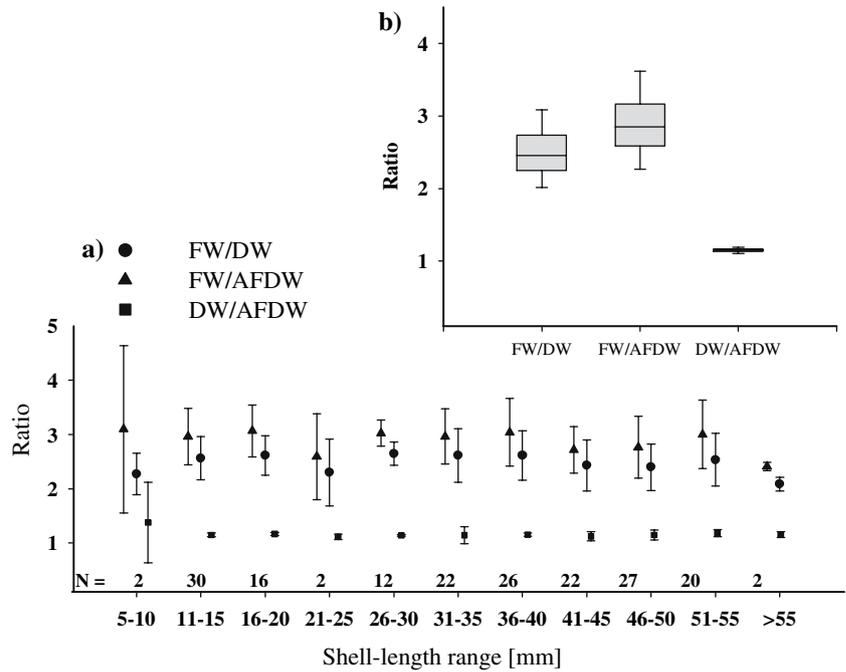
Fig. 5 Gompertz growth model (GGM) for fresh-weight of *M. arenaria*. The parameters were estimated by computer regression (Statistica 6.0) as well as from data obtained from Figs. 3a and 5. Both estimates were equal. For details, see text

total age-range this is not proved. Rather we assume an age-dependent mortality rate after maturation as described by Günther (1992) and Maximovich and Guerassimova (2003).

The von Bertalanffy growth curve is a common tool to analyse growth data and growth rates. This model was copiously discussed before, and recently Urban (2002) pointed out that the generalised von Bertalanffy model (VBGF developed by Pauly (1979)) yields the best fit for data corresponding to his study. Using of the VBGF implicates the knowledge of the so-called surface factor D , which comprises net effects of anabolism and catabolism (e.g. Pauly 1979). Alternatively D could theoretically be estimated from the shape of the shell but due to the irregular shape of the shell of *M. arenaria* difficulties arise and for this reason we did not test the VBGF in this study.

While past investigations in the Baltic Sea have shown linear growth of *M. arenaria* (Kube 1996), many researchers demonstrated isometric relationships between shell-length and fresh-weight (Feder and Paul 1974; Munch-Petersen 1973; Winther and Gray 1985). For cases of isometric relationships the specialised von Bertalanffy growth model (sVBGF) is recommended. It generates an asymptotic growth curve while the VBGF as well as the GGM reflect a sigmoid curve. The sVBGF suggests that most available energy is spent on producing new tissue or shell material during early lifetimes while with increasing age the available energy is dislocated to life-sustaining activities as indicated by the exponential decaying of the growth curve (Fig. 3). The raw data given in this study indicate a sigmoid growth-curve. Additionally, we found an isometric relationship ($b = 2.87$) between shell-length and fresh-

Fig. 6 Different weight ratios of 182 specimens of *M. arenaria*. **a** Means (\pm SD) for different shell-length ranges, and **b** box plots over all shell-length ranges

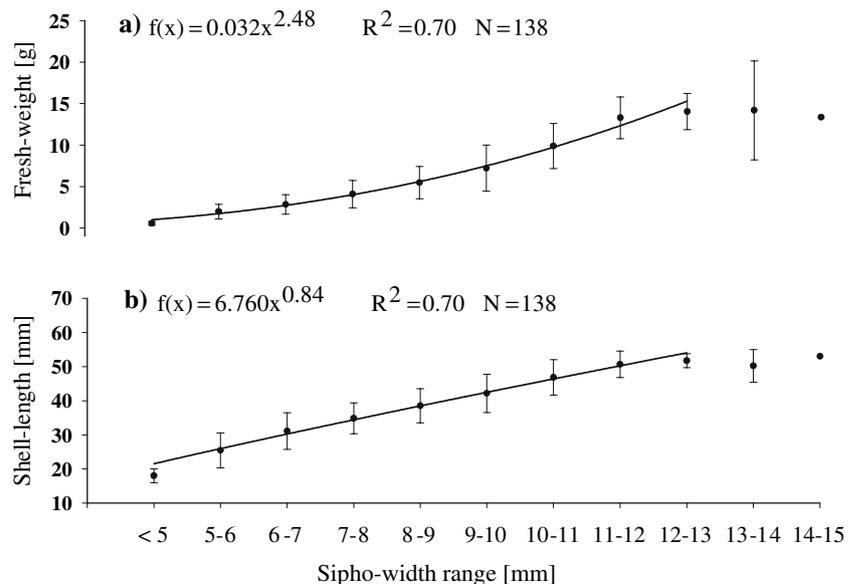


weight whereas the condition factor *b* corresponds to values which were found at several locations (Feder and Paul 1974; Munch-Petersen 1973; Winther and Gray 1985). Hence, we tested the sVBGF as well as the GGM by means of analysing the residuals. However, the GGM predicts the asymptotic shell-length more reliably than the sVBGF does.

The maximum shell-length of *M. arenaria* varies considerably within its geographical distribution and ranged from 27 to 135 mm (Munch-Petersen 1973; Feder and Paul 1974; Brousseau 1979; Appeldoorn 1981, 1983; Winther and Gray 1985; Brousseau and

Baglivo 1987; Emerson et al. 1988; Maximovich and Guerassimova 2003). In this study the maximum shell-length was 60.03 mm and the asymptotic shell-length ranged from 62.56 mm for the GGM to 87.37 mm for the sVBGF. In dependence on the used model the theoretical age at which the asymptotic shell-length is achieved, is 8 (GGM) or 23 years (sVBGF). With respect to the possibility of underestimating age, the asymptotic shell-length arise at about 10 years in the GGM and is confirmed by the raw data. For the purpose of comparison we recalculated the asymptotic shell-length from data for the Pomeranian Bay ob-

Fig. 7 Relationships between siphon-width and **a** fresh-weight and **b** shell-length, respectively, of 138 specimens of *M. arenaria* (means \pm SD)



tained by Kube (1996) and computed a range from 24 to 50 mm for the maximum shell-length. This variability emphasises the influence of environmental factors on growth rates and maximal body size. Low salinity is identified as a main environmental factor related to growth, but recently the Chlorophyll a content in seston, stimulated by *N*-enrichment, was identified as main factor that influence growth rates of *M. arenaria* rather than low salinity (<20 PSU) (Carmichael et al. 2004). However, the results of growth rates in form of both, the *K* value and ϕ , were relatively high compared to more marine habitats (Table 1) whereas the asymptotic shell-length was reached at lower values and at a minor age. Both, the *K* value and ϕ may indicate the availability of better food supply and quality in the observed area.

With respect to growth analyses we present here a new method to estimate growth indices from the siphon-width of *M. arenaria*. To our knowledge, literature has never dealt with this approach before. The burrowing depth of siphon-exhibiting organism depends on the length of the siphon (Zwarts and Wanik 1989) and in general, larger infaunal species tend to bury deeper than smaller conspecifics. This has been shown for *M. arenaria* as well (Zaklan and Ydenberg 1997). Furthermore, the filtration rates of *M. arenaria* increased with both, increasing weight and shell-length (Riisgård and Seerup 2003). Consequently it is necessary that the rate of food intake is positively correlated to the rate of inflow. According to Poiseuille's equation of flow through a tube, increased rates of inflow are only possible through either enlarging the pressure differential or enlarging the diameter of the tube. Enlarging the pressure differential is for *M. arenaria* only to a certain extent possible (Jørgensen and Riisgård 1988). Because of the physical exigency *M. arenaria* must be able to enlarge the diameter of the siphon. For this purpose the diameter of the siphon can be assumed to be proportional to the siphon-width of *M. arenaria* and hence we found a relationship between siphon-width and fresh-weight as well as shell-length.

Relationships between shell-length and fresh-weight may be usable to calculate production and biomass (Brey 2001) and our results are in agreement with this (Figs. 4, 5). If we succeed in establishing, for example, the relationship between siphon-width and shell-length to the relationship between shell-length and fresh-weight, we can estimate age, biomass etc. of the clam. This is important particularly for sites which are not directly accessible and whereby the use of a van Veen grab may cut off the clam siphons (Forster and Zettler 2004). Consequently and due to the deep burrowing behaviour of *M. arenaria* (up to 35 cm) large and thus

older individuals may be under-represented in samples. The present study has demonstrated how to alleviate the problem described above. Furthermore, a direct linkage between siphon-width and filtration rates of *M. arenaria* could be obtained through this method.

Acknowledgment The authors would like to express their gratitude to Jacob O'Mahony, University of Edinburgh, Scotland for correction and valuable comments on this manuscript. Also we would like to thank the editor-in-chief for time and effort he has spent on this paper. And we are indebted to Dr. Stefan Forster, University of Rostock, Germany for reviewing the last draft and his valuable comments on this manuscript.

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