

GROWTH AND ENERGY BUDGET MODELS OF THE BIVALVE *ARCTICA ISLANDICA* AT SIX DIFFERENT SITES IN THE NORTHEAST ATLANTIC REALM

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ABSTRACT We compared lifetime and population energy budgets of the extraordinary long-lived ocean quahog *Arctica islandica* from 6 different sites—the Norwegian coast, Kattegat, Kiel Bay, White Sea, German Bight, and off northeast Iceland—covering a temperature and salinity gradient of 4–10°C (annual mean) and 25–34, respectively. Based on von Bertalanffy growth models and size–mass relationships, we computed organic matter production of body (P_{SB}) and of shell (P_{SS}), whereas gonad production (P_G) was estimated from the seasonal cycle in mass. Respiration (R) was computed by a model driven by body mass, temperature, and site. *A. islandica* populations differed distinctly in maximum life span (40 y in Kiel Bay to 197 y in Iceland), but less in growth performance (ϕ' ranged from 2.41 in the White Sea to 2.65 in Kattegat). Individual lifetime energy throughput, as approximated by assimilation, was highest in Iceland (43,730 kJ) and lowest in the White Sea (313 kJ). Net growth efficiency ranged between 0.251 and 0.348, whereas lifetime energy investment distinctly shifted from somatic to gonad production with increasing life span; P_S/P_G decreased from 0.362 (Kiel Bay, 40 y) to 0.031 (Iceland, 197 y). Population annual energy budgets were derived from individual budgets and estimates of population mortality rate (0.035/y in Iceland to 0.173/y in Kiel Bay). Relationships between budget ratios were similar on the population level, albeit with more emphasis on somatic production; P_S/P_G ranged from 0.196 (Iceland) to 2.728 (White Sea), and P/B ranged from 0.203–0.285/y. Life span is the principal determinant of the relationship between budget parameters, whereas temperature affects net growth efficiency only. In the White Sea population, both growth performance and net growth efficiency of *A. islandica* were lowest. We presume that low temperature combined with low salinity represent a particularly stressful environment for this species.

KEY WORDS: growth, production, energy budget, *Arctica islandica*

INTRODUCTION

The ocean quahog *Arctica islandica* is widely distributed on the continental shelves on both sides of the North Atlantic Ocean (Nicol 1951, Thompson et al. 1980a, Thompson et al. 1980b, Brey et al. 1990, Dahlgren et al. 2000). *A. islandica* is a long-lived bivalve species with a maximum age ranging from 40 y in the Baltic Sea (Zettler et al. 2001, Begum et al. 2009) to ~400 y off Iceland (Schöne et al. 2005b; see also Thompson et al. 1980b). *A. islandica* is a suitable archive of past environmental conditions that can be reconstructed from morphological and biogeochemical properties of the shell (e.g., Epple et al. 2006, Schöne et al. 2005b). Its wide geographical range of occurrence combined with its longevity makes *A. islandica* a prime candidate for monitoring and modeling long-term environmental and ecological dynamics (Harding et al. 2008). To understand better the ecological role of *A. islandica* in its environment and to be able to link the dynamics of *A. islandica* populations to environmental drivers, we need reliable models of energy metabolism at both the individual and population levels. Basic parameters of such models would be respiration, somatic growth, reproduction, and mortality. An extensive body of data on this species has already been published: Growth and/or production were investigated by Thompson et al. (1980a, 1980b) and Kennish et al. (1994), whereas Rowell et al. (1990) and Thorarinsdóttir (2000) provide information on maturation and reproduction. Particular aspects of *A. islandica* ecology (e.g., Appeldoorn 1983, Brey et al. 1990) and physiology (e.g., Taylor

& Brand 1975) have been described, but a systematic approach toward individual and population energetics is still lacking. Begum et al. (2009) made a first step by establishing a respiration model for *A. islandica*.

In the current study, our objectives were (1) to establish energy budget models for *A. islandica* populations from 6 different sites and (2) to evaluate the effects of temperature and salinity on the *A. islandica* energy budget.

MATERIALS AND METHODS

Sampling Sites

Ocean quahogs, *Arctica islandica* were collected in 2005 and 2006 from 6 sites: the Norwegian coast, Kattegat, Kiel Bay (Baltic Sea), White Sea, German Bight (North Sea), and Iceland (off northeast Iceland; Fig. 1 and Table 1). With the exception of Iceland, all animals were transported alive to the Alfred Wegener Institute for Polar and Marine Research (Bremerhaven, Germany), where they were maintained in aquaria with natural sediment at their respective annual mean habitat temperatures until further use in physiological experiments (for details see Begum et al. (2009)). Iceland animals were sacrificed after 7 days of acclimation at the Sandgerdi Marine Station (Iceland).

Morphometry

We measured shell height (H; greatest distance from umbo to ventral shell margin) to the nearest 0.1 mm and determined

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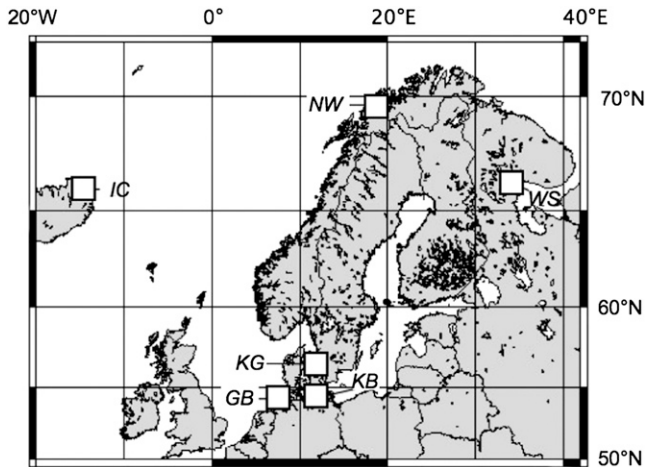


Figure 1. Sample locations of *A. islandica*. GB, German Bight; IC, Iceland; KB, Kiel Bay; KG, Kattegat; NW, Norwegian coast; WS, White Sea. Map redrawn from www.aquarius.geomar.de.

shell dry mass (SDM; 48 h drying at 60°C), tissue wet mass (soft tissue drained on paper), and tissue dry mass (48 h at 60°C) with 0.01-g precision. Tissue ash-free dry mass (AFDM = DM – ash) was calculated from tissue ash content (24 h incineration at 500°C (Brey & Hain 1992)), and shell ash free dry mass (SAFDM) was determined accordingly after incineration for 36 h at 480°C (Shumway & Newell 1984, Gouletquer & Wolowicz 1989). Shell ash after incineration was assumed to represent shell carbonate.

Mass was related to shell height by allometric equations of the type

$$M = a \times H^b$$

(measured in milligrams and millimeters), which were established by linear regression of $\ln(M)$ on $\ln(H)$. We used analysis of covariance (ANCOVA, $\ln(\text{mass})$ versus $\ln(\text{shell height})$ and site) to determine whether specific relationships differed between sites, and established site-specific models when necessary.

Growth

Left shell valves were used to determine the individual age following the protocol of Begum et al. (2009). A von Bertalanffy growth function model was fitted to the resulting size-at-age

data pairs by means of the nonlinear iterative Newton algorithm (Brey 2001)

$$H_t = H_\infty \times (1 - e^{-k(t-t_0)})$$

(measured in millimeters and years) where H_∞ is asymptotic shell height, k is the Brody growth coefficient, t is age, and t_0 is the theoretical age at which height equals 0. We tested the residuals of the common growth model (data from all sites) for between-site differences in growth by means of analysis of variance (ANOVA) and established site-specific models when necessary. Size at age H_t could be converted into mass at age M_t by means of the size–mass relationships just described. The growth performance index ϕ' was calculated according to Pauly and Munro (1984):

$$\phi' = \log(k) + 2 \times \log(H_\infty)$$

Individual Somatic Production

AFDM and SAFDM were converted into energy content by the factor 20.45 J/mg AFDM (Brey 2001). Individual somatic body production (P_{SB}) and somatic shell production (P_{SS}) were calculated from the increment in mass with age (measured in Joules per time interval):

$$P_{SB,t} = M_{SB,t} - M_{SB,t-x}$$

where P_{SB} is somatic body production, $M_{SB,t}$ and $M_{SB,t-x}$ are body mass at age t and $t-x$, and x is the increment in age (calculations for P_{SS} accordingly).

Individual Calcium Carbonate Production

Individual calcium carbonate production (P_{CC}) was calculated the same way:

$$P_{CC,t} = M_{CC,t} - M_{CC,t-x}$$

(measured in grams per time interval), where P_{CC} is calcium carbonate production, $M_{CC,t}$ and $M_{CC,t-x}$ are calcium carbonate mass at age t and $t-x$, and x is the increment in age.

Individual Gonad Production

Individual gonad production was inferred from the difference between pre- and postspawning body mass in *A. islandica*. Personal observations (K.B.) and unpublished data of G.

TABLE 1.

Geographical location, water depth, and mean annual habitat temperature of sampling sites, and number of animals used to establish basic models.

Site	Location	Salinity (‰)	Depth (m)	Temperature (°C)	Sample Size (N)			
					BM	SDM	Size at Age	Respiration
Kattegat	56°10'N 11°48'E	31	33	8	45	44	130	45
White Sea	66°18'N 33°38'E	25	10	4	39	52	54	22
Kiel Bight	54°32'N 10°42'E	25	25	10	51	273	170	51
Iceland	66°02.6'N 14°48.8'W	35	14–22	5	96	239	229	96
Norwegian coast	69°39'N 18°57'E	33	10–30	4	58	68	153	57
German Bight	54°09'N 07°47'E	31	40	10	18	267	139	18

BM, body mass; SDM, shell dry mass.

TABLE 2.

Site-specific morphometric relationships of the type
 $\ln(\text{mass}) = a + b \times \ln(\text{height})$ in *A. islandica*.

Model	Site	a	b	N	R ²
BM vs. size	Kattegat	-5.481	3.217	45	0.864
	Norwegian coast and German Bight	-5.290	3.228	76	0.987
	White Sea and Kiel Bay	-6.012	3.330	90	0.976
SDM vs. size	Iceland	-4.123	3.091	96	0.988
	Kattegat and White Sea	-1.464	2.819	96	0.987
	Norwegian coast and German Bight	-2.347	3.144	335	0.949
	Kiel Bay	0.157	2.580	273	0.994
	Iceland	-2.780	3.121	239	0.995

Common models were fitted for sites that did not differ significantly (as indicated by ANCOVA of $\ln(M)$ versus $\ln(H)$ and site). BM, body mass (measured in milligrams ash-free dry mass); SDM, shell dry mass (measured in milligrams dry mass).

Thorarinsdóttir (northwest Iceland) indicate a $\pm 30\%$ decrease in body mass during spawning:

$$P_{G,t} = M_{SB,t} \times 0.3$$

(measured in Joules per year), which is in the range of values reported for other bivalves (e.g., *Patinopecten yessoensis*, 0.27 (Fuji & Hashizume 1974); *Tellina tenuis*, 0.39 (Trevallion 1971)). Ropes et al. (1984) and Rowell et al. (1990) indicate that in *A. islandica*, minimum age at maturity is 6 y, whereas at age 22 y all animals are mature. In the Iceland population, the corresponding ages are 9 y and 32 y, respectively (Thorarinsdóttir 2000). We incorporated this pattern into the individual gonad production calculation by assuming a linear increase in production from 0 at minimum age to 100% (equal to one third the body mass) at age at full maturity.

Individual Respiration

Respiration (R) was computed by a model driven by body mass (M ; AFDM) temperature (T) and site (derived from the respiration model published by Begum et al. 2009):

$$\ln(R) = 14.701 + 0.552 \times \ln(M) - 3748.232/T + D \times [\ln(M) - 0.418]$$

with $N = 193$ and $R^2 = 0.894$ (measured in micromoles of oxygen per hour, grams AFDM, and degrees Kelvin), where $D = -0.211$ for the White Sea and $D = +0.211$ for all other sites. Note that $\ln(\text{body mass})$ is centered to mean = 0 in the interaction term. Respiration was converted from $\mu\text{mol O}_2\text{h}^{-1}$ to J d^{-1} by multiplying by 11.2320 (see Brey 2001).

Population Mortality Rate

Because our limited samples did not provide reliable information on population size or age structure, we inferred mortality rate from maximum age, assuming that mortality follows the single negative model, as is common in most bivalve populations (e.g., Brey 1999):

$$N_t = N_0 \times e^{-Z \times t}$$

where N_0 is the number of animals in an age class at recruitment, N_t is the number at age t , and Z is the instantaneous rate of mortality. If we set $N_0 = 1$ and $N_{t_{max}} = X$ at t_{max} = age of oldest animal, than mortality rate amounts to

$$Z = -\ln(1/X)/t_{max}$$

(measured in rate per year).

Kilada et al. (2007) computed mortality rates from age frequency data of *A. islandica* at 2 different sites at the Canadian coast: St. Mary's Bay ($Z = 0.10/\text{y}$) and Sable Island (0.03/y). Using their maximum age at both sites, 72 y and 210 y, respectively, we find that the reported mortality rates are approximated quite accurately with $X = 0.001$ ($Z = 0.033/\text{y}$ and 0.096/y, respectively). We applied this approach to our populations using t_{max} = average age of the 3 oldest animals found.

Individual Lifetime Energy Budget Model

We computed the individual lifetime energy budget for *A. islandica* at each site by combining the corresponding relationships and models for growth, production, and respiration into a numerical integration scheme. All calculations, except for gonad production, were carried out incrementally with step size x = maximum age $t_{max}/1,000$. Thus, actual as well as cumulative values of production (P_{SB} , P_{SS} , P_G) and respiration (R) could be computed for any age and age interval.

We computed the corresponding assimilation A by

$$A = P_T + R$$

(measured in Joules per individual per time interval) where $P_T = P_{SB} + P_{SS} + P_G$, and estimated consumption C by

$$C = A/0.4$$

(measured in Joules per individual per time interval), using an average assimilation efficiency of 0.4 for suspension-feeding bivalves (Bayne & Newell 1983, Crisp 1984, Shumway 1991). Gross production efficiency (Ivlev's K_1 (Ivlev 1961)) and net production efficiency (Ivlev's K_2) were calculated by

$$K_1 = P_T/C \text{ and } K_2 = P_T/A.$$

Population Energy Budget Model

The population annual energy budget is based on the same data as the individual lifetime budget, but with mortality rate included (i.e., the "number" of animals in the individual model decreases exponentially with age from 1 to 0.001 according to mortality rate Z). If we assume the population to be in steady state, than individual lifetime production equals population annual production (see Allen (1971), for example). Because we do not know the true abundance of *A. islandica* at the different sites, we only computed ratios between budget parameters (growth efficiencies) and population biomass.

Statistical Analysis

Effects of habitat temperature, maximum age, and growth performance on energy budget parameters and ratios were

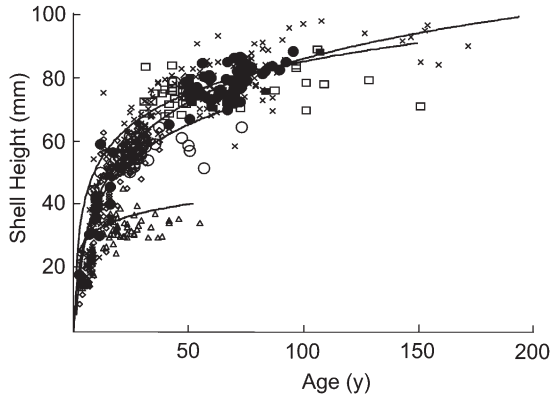


Figure 2. von Bertalanffy growth curves and corresponding size-at-age data in *A. islandica* from the 6 sites. ANOVA of the residuals of the common growth model indicated a significant difference between sites except for the Norwegian coast and the German Bight, and for Iceland and Kiel Bay. Δ , White Sea; \diamond , Kiel Bay; \circ , Kattegat; \bullet , Norwegian coast; \square , German Bight; \times , Iceland.

analyzed by nonparametric correlation (Spearman's ρ) and by multiple linear regressions. We used ANOVA and ANCOVA to explore the relationships between individual and annual budget ratios.

RESULTS

Morphometry

The initial full factorial ANCOVA model of body and shell mass $\ln(\text{AFDM})$ and $\ln(\text{SDM})$ versus $\ln(\text{shell height})$ and site indicated all sites differ significantly with the exceptions of the Norwegian coast and German Bight, and White Sea and Kiel Bay in AFDM, and Norwegian coast and the German Bight and the White Sea and Kattegat in SDM, respectively (Table 2).

Growth and Mortality

We found growth to differ significantly between all sites except between the Norwegian coast and the German Bight and between Iceland and Kiel Bay (Fig. 2 and Table 3). Growth performance (index ϕ') ranged between 2.41 in the White Sea and 2.65 in Kattegat, and was found to be independent of annual mean habitat temperature and salinity (Spearman's rank correlation, $P > 0.050$). Maximum age t_{max} in our samples ranged from 40 y in Kiel Bay to 197 y in Iceland, and our

estimate of mortality rate varied accordingly between 0.035/y (Iceland) and 0.173/y (Kiel Bay, Table 5).

Energy Budgets

Individual somatic production P_S increases steadily until a maximum is reached, and decreases again thereafter, whereas gonad production P_G , respiration R , and assimilation A continue to increase over the lifetime, albeit at diminishing rates (Fig. 3). The cumulative values (Table 4) indicate differences in the individual lifetime budget between sites. Lifetime energy throughput, as approximated by assimilation, is lowest at the White Sea (313 kJ) and highest at Iceland (43,730 kJ). The fraction of energy allocated to somatic production P_S is lowest in the long-lived Iceland animals (0.011) and increases with decreasing life span to 0.069 in Kiel Bay. The share of gonad production P_G in assimilation shows just the opposite trend, but is generally higher (0.191–0.337). Accordingly, the P_S -to- P_G ratio decreases distinctly with increasing life span. Lifetime net growth efficiency is rather similar at all sites; it ranges between 0.251 (White Sea) and 0.348 (Iceland), whereas the respiration-to-assimilation ratio shows a corresponding inverse pattern. Lifetime shell carbonate deposition is between 5 g (White Sea) and 107 g (Iceland).

At the population level (i.e., accounting for the effect of mortality), the ranking of sites according to production and net growth efficiency remains about the same, but the balance between somatic production, gonad production, and respiration shifts (Table 5). In the annual population budget, the share of somatic production in assimilation increases to values between 0.054 (Iceland) and 0.167 (White Sea). The share of gonad production decreases accordingly, to values between 0.061 (White Sea) and 0.277 (Iceland). Matched-pair tests indicate that P_S/A is significantly higher (average 0.104 compared with 0.034, $P < 0.001$) and P_G/A is significantly lower (0.184 compared with 0.263, $P < 0.001$) in the population budget compared with the individual budget. Population production-to-biomass ratio is estimated between 0.203 (German Bight) and 0.285 (Kiel Bay).

Spearman's rank correlation indicates significant ($\alpha = 0.10$) effects of maximum age t_{max} on the budget parameter ratios R/A , P_T/A , P_S/A , P_G/A , and P_S/P_G on both the individual and the population levels, whereas temperature and growth performance had no significant effects. When age effects are accounted for (2-way analysis) and the outlier White Sea is excluded, however, net growth efficiency P_T/A decreases and R/A increases significantly ($P < 0.05$) with temperature in both lifetime and population budget (Fig. 4, Tables 4 and 5).

TABLE 3.

von Bertalanffy growth parameters and corresponding growth performance index (ϕ') of *A. islandica*.

Site	Age t_{max} (y)	H_∞ (mm)	K (/y)	t_0 (y)	N	R^2	ϕ'
Kattegat	58	89.544	0.055	-0.254	130	0.530	2.65
Norwegian coast and German Bight	90 and 125	79.837	0.066	-3.858	292	0.870	2.62
Iceland and Kiel Bay	197 and 40	86.150	0.045	-2.556	399	0.900	2.53
White Sea	44	35.637	0.200	0.234	54	0.410	2.41

ANOVA of the residuals of the common growth models indicate that all sites differ significantly except for the Norwegian coast and the German Bight, and Iceland and Kiel Bay. H_∞ , asymptotic height; K , Brody growth coefficient; N , number of data; t_0 , age at which height would equal 0.

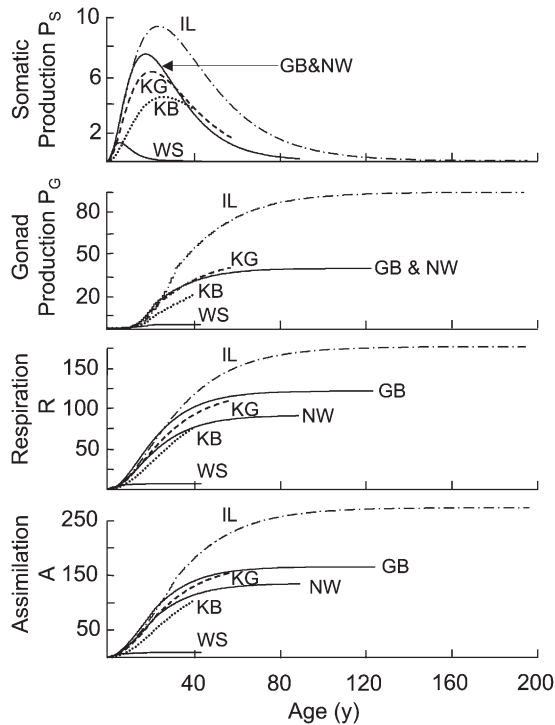


Figure 3. Actual individual somatic production P_S (body + shell), gonad production P_G , respiration R , and assimilation A ($A = P_S + P_G + R$) as a function of age in *A. islandica* from 6 different sites (measured in kilojoules per year). Please note that all values are adjusted to a time interval of 1 y. GB, German Bight; IL, Iceland; KB, Kiel Bay; KG, Kattegat; NW, Norwegian coast; WS, White Sea.

DISCUSSION

Methodology

Our energy budget model of *A. islandica* comprises approaches with different levels of reliability. The determination of individual age from shell growth bands is a proven standard procedure in *A. islandica* (Thompson et al. 1980a, Turekian et al. 1982, Schöne et al. 2005a). Modeling of individual growth and computation of somatic production use established standard routines in population dynamics (Brey 2001). Individual respiration is estimated from a tested multifactorial model

(Begum et al. 2009). Our estimates of gonad production and of consumption, however, may be less reliable. Gonad production is of particular concern, because there are several sources of potential bias. We inferred P_G from the annual cycle in total soft body mass, which indicates a spawning-related 30% loss in body mass (own observations, Kiel Bay; G. Thorarinsdóttir, unpublished, northwest Iceland). It remains unknown whether this ratio is valid for all populations and throughout lifetime beyond maturity. Estimates of (somatic) body mass are reliable, because they are based on animals collected in presumably spent condition (February and October). Our definition of size at maturity suffers from similar shortcomings. We use an average value with uncertain validity for all populations. This is of less concern, however, because gonad production is comparatively low in small clams. To estimate consumption, we use an average assimilation efficiency of 0.4. Measured values for filter-feeding bivalves range between 0.25 and 0.70 (Hibbert 1977, Warwick et al. 1979, Bayne & Newell 1983). In other words, we can expect that the “true” assimilation efficiency of *A. islandica* is (1) anywhere within this range and (2) not necessarily the same at all 6 sites, because it might be affected by differing food composition (MacDonald & Thompson 1985a, MacDonald & Thompson 1985b, MacDonald & Thompson 1986, Vakily 1992). Our approach toward mortality rate requires that the single negative model describe the decrease in numbers with time appropriately, which may not hold true for all populations (see Brey et al. (1990), for example).

Growth and Longevity of *A. islandica*

A. islandica is the longest lived mollusc species known to science, with a reported maximum age close to 400 y (Schöne et al. 2005b). Phases of metabolic rate depression combined with extraordinarily high antioxidant capacities may be one key factor for this extended life span (Taylor & Brand 1975, Abele et al. 2008). Our study indicates distinct differences in life span between populations (Table 2). We can confirm the extraordinary high ages attained in populations around Iceland, where animals close to 200 y old are regularly encountered (Schöne et al. 2004, Schöne et al. 2005a, Strahl et al. 2007). In the southern North Sea, maximum age appears to be about 150 y (Witbaard et al. 1994, Witbaard et al. 1999, Epple et al. 2006), and our value of 125 y for the German Bight fits well in this picture. No information on age of *A. islandica* from the Norwegian coast or Kattegat has been available so far, but our estimate for the

TABLE 4.

A. islandica individual lifetime energy budget parameters.

Site	Life Span		P_S (kJ)	P_G (kJ)	P_T (kJ)	R (kJ)	A (kJ)	P_{CC} (g)	P_S/A	P_G/A	P_T/A	R/A
	(y)	(y)										
Kattegat	58		224	1,251	1,475	3,626	5,101	61	0.044	0.245	0.289	0.711
Norwegian coast	90		255	2,552	2,807	5,917	8,724	85	0.029	0.292	0.322	0.678
German Bight	125		257	4,087	4,344	12,139	16,483	86	0.016	0.248	0.264	0.736
White Sea	44		14	64	79	234	313	5	0.045	0.206	0.251	0.749
Kiel Bay	40		126	347	472	1,341	1,814	37	0.069	0.191	0.261	0.739
Iceland	197		462	14,754	15,215	28,514	43,730	108	0.011	0.337	0.348	0.652

A , assimilation ($A = P_S + P_G + R$); P_{CC} , calcium carbonate production; P_G , gonad production; P_S , somatic production; P_T , total production ($P_T = P_S + P_G$); R , respiration.

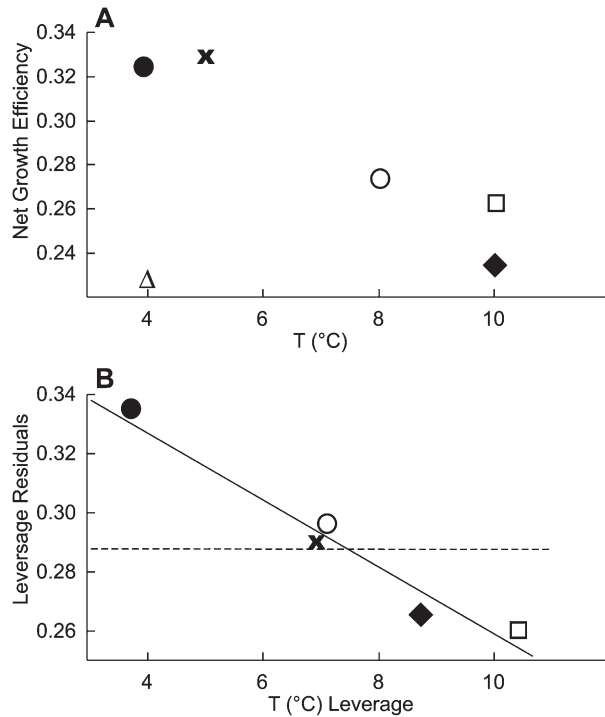


Figure 4. Relationship between population net growth efficiency (P_T/A) and mean annual habitat temperature in *A. islandica*. (A) Plot of P_T/A versus temperature. (B) Partial leverage plot of the corresponding multiple linear model $P_T/A = 0.3547 + 0.0002 \times t_{max} - 0.0117 \times \text{temperature}$. $n = 5$ (White Sea excluded), $P = 0.018$. This plot shows the residual of each data point both with (distance from solid line) and without (distance from horizontal stippled line) the temperature effect in the model. Δ , White Sea; \blacklozenge , Kiel Bay; \circ , Kattegat; \bullet , Norwegian coast; \square , German Bight; \times , Iceland.

Kattegat population (58 y) already points toward a decrease in longevity with decreasing salinity. This becomes clearly evident at the low-salinity sites of the White Sea and Kiel Bay, where life span is less than 50 y (compare also Brey et al. (1990) and Zettler et al. (2001)). Low salinity can act as a stress factor for marine bivalves that increases the energetic “costs” for physiological functioning under conditions close to the tolerance limits and thus limits maximum attainable age and size (Davis & Calabrese 1964, Shurova 2001, Sukhotin et al. 2007), depending on how

well a species is adapted to low and/or fluctuating salinity regimes (e.g., Gilbert 1973).

When comparing the overall size–growth pattern between sites, the most striking observation is the distinctly different growth pattern in White Sea animals (Fig. 2). The early phase of rapid growth takes about 10 y only, and subsequently growth levels out at comparatively small size ($H_\infty = 35.6$ mm). We presume that low temperature combined with low salinity represent a particularly stressful environment for *A. islandica*, as observed in other marine bivalve species (e.g., Davis & Calabrese 1964, Saxby 2002, Arun 2009). The growth curves for Kattegat, the German Bight, and the Norwegian coast, and Iceland and Kiel Bay, albeit significantly different (Fig. 2), are similarly shaped. During the first 25 y of life the animals attain more than two thirds of infinite height, whereas growth slows down rapidly during the remaining lifetime (Fig. 2). We are uncertain, however, how to interpret the significant differences in growth between these site groups, because the unequal distribution of size-at-age data may have introduced some undetectable bias (Fig. 2). Nevertheless, quite the same growth pattern has been observed in other populations of *A. islandica* (see, for example, Thompson et al. (1980a), Thompson et al (1980b), Lewis et al. (2001), Thorarinsdóttir and Jacobson (2005), and Kilada et al. (2007)). Accordingly, our growth model parameters (except for the White Sea) fall well into the range of published values: $k = 0.022\text{--}0.060/\text{y}$ and $H_\infty = 80.00\text{--}101.23$ mm. So far, we cannot identify the likely temperature effect on growth rate; a geographically more extensive data set might be required here (described later).

The current growth rate measurements confirmed our previous observation (Strahl et al. 2007) that, compared with other bivalve species, growth rate of *A. islandica* is very low. The growth constant of k less than $0.06/\text{y}$ (Fig. 5) is among the lowest values observed in bivalves (Vakily 1992). Growth performance, on the other hand, is about average for bivalves. The average ϕ' of 2.5 ($n = 12$, all published growth models) for *A. islandica* does not differ significantly from the average ϕ' of 157 bivalve populations (Fig. 5, ANOVA, $P = 0.060$, unpublished data collection).

Characteristics and Constraints of the *A. islandica* Energy Budget

Our *A. islandica* energy budget model combines the standard features of bivalve biology—in other words, asymptotic individual growth, gonad production directly proportional to

TABLE 5.
A. islandica population annual energy budget ratios from 6 different geographical sites.

Site	Life Span		$Z(\text{y})$	P_S/A	P_G/A	P_T/A	R/A	P_T/C	P_T/B_T
	(y)								
Kattegat	58		0.119	0.132	0.146	0.277	0.723	0.111	0.251
Norwegian coast	90		0.077	0.117	0.210	0.327	0.673	0.131	0.214
German Bight	125		0.055	0.073	0.194	0.267	0.733	0.107	0.203
White Sea	44		0.157	0.167	0.061	0.229	0.771	0.092	0.213
Kiel Bay	40		0.173	0.146	0.092	0.238	0.762	0.095	0.285
Iceland	197		0.035	0.054	0.277	0.331	0.669	0.132	0.214

A , assimilation ($A = P_S + P_G + R$); B_T , annual average total biomass; C , consumption ($C = A/0.4$); P_G , gonad production; P_S , somatic production; P_T , total production ($P_T = P_S + P_G$); R , respiration; Z , total mortality.

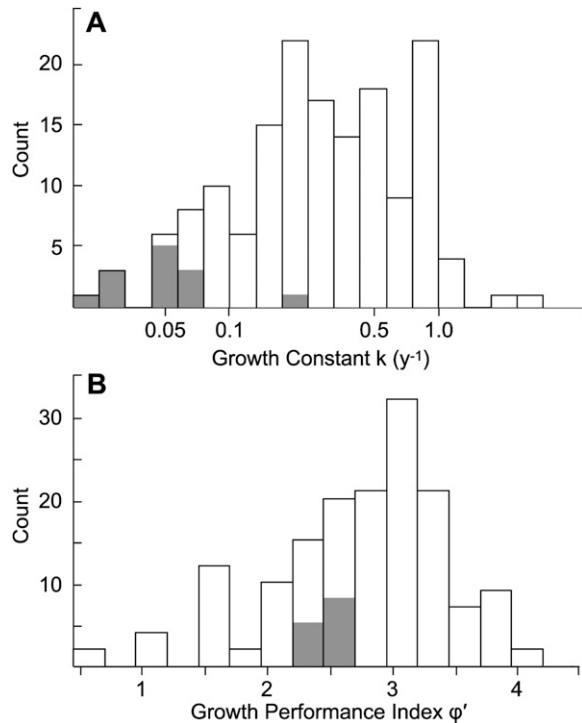


Figure 5. (A, B) Distribution of growth constant k (A) and growth performance index ϕ' (B) of the von Bertalanffy growth function of 157 different bivalve populations, including 12 populations of *A. islandica* (gray bars, current study; Thompson et al. 1980a, Thompson et al. 1980b, Anonymous 1995, Lewis et al. 2001, Thorarinsdóttir & Jacobson 2005, Kilada et al. 2007). Other data collected by Brey (1999, 2001). Growth constant k is significantly ($P < 0.001$) lower in *A. islandica*.

body mass, and respiration related to body mass by a power function (see, for example, Vakily (1992), Mathieu and Lubet (1993) Brey (1999), and Begum et al. (2009)). Hence, with increasing age the relationships between different parts of the individual energy budget change in a predictable way—for example, P_S/A will decrease, whereas P_G/A will increase (see Table 4 and Fig. 3).

Consequently, life span (measured as maximum age t_{max}) exerts a distinct effect on budget parameters and their relationships (Fig. 3 and Tables 4 and 5). A 5-fold increase in maximum age (44 y (White Sea) to 197 y (Iceland)) translates into a 100-fold increase in lifetime energy throughput (313–43,730-kJ assimilation). This effect is even more pronounced in those parts of the energy budget that increase in relative significance with age, such as gonad production P_G . The Q_{10} for *A. islandica* respiration is about 2.5 (Begum et al. 2009), and thus temperature should exert a corresponding effect on somatic production (i.e., growth). We cannot detect this effect within the 6°C range (4–10°C) in ambient temperature of the populations studied here, most likely because of methodological shortcomings. Apparently the high variability in individual size-at-age data together with other site-specific effects (e.g., salinity) obscure the temperature effects on growth and thus on somatic production. This problem may be overcome either with a more thorough analysis of growth (more samples, analysis of individual growth history) or with the direct measurement of somatic production in controlled experiments.

The mortality rates estimated for *A. islandica* ($Z = 0.035$ – $0.175/y$) are at the lower end of the range observed in bivalves from cold–temperate regions (Brey 1999), but still they cause a distinct shift of energy throughput from gonad to somatic production (Tables 4 and 5). This is particularly visible in the average (over all populations) P_S -to- P_G ratio that increases from 0.147–0.743 with increasing Z .

We can interpret maximum age and mortality as interacting endogenous (physiological) and exogenous (ecological) determinants of population age and size structure, which in turn determines population reproductive output. Apparently, *A. islandica* is capable of maintaining persistent populations across a wide range of population age structures. This may be one key to the wide distribution of this species throughout the North Atlantic shelf areas. Nevertheless, *A. islandica* might be prone to recent environmental change. Apparently, abundances decreased substantially in the southern North Sea, where the clam became rare in once densely populated areas such as the Oyster Ground (Witbaard & Bergman 2003) and the German Bight (own observations). This might be a consequence of enhanced temperature in the southern North Sea (e.g., Wiltshire & Manly 2004), but also of the extraordinary high intensity of bottom trawling in this area (e.g., Rijnsdorp et al. 1998).

Population productivity of *A. islandica* is low compared with other bivalves. Both somatic (P_S/B) and total (P_T/B) production-to-biomass ratios are significantly below average for bivalve populations when the effect of average body mass on P/B is taken into account (ANCOVA, Fig. 6), whereas in P_G/B , *A.*

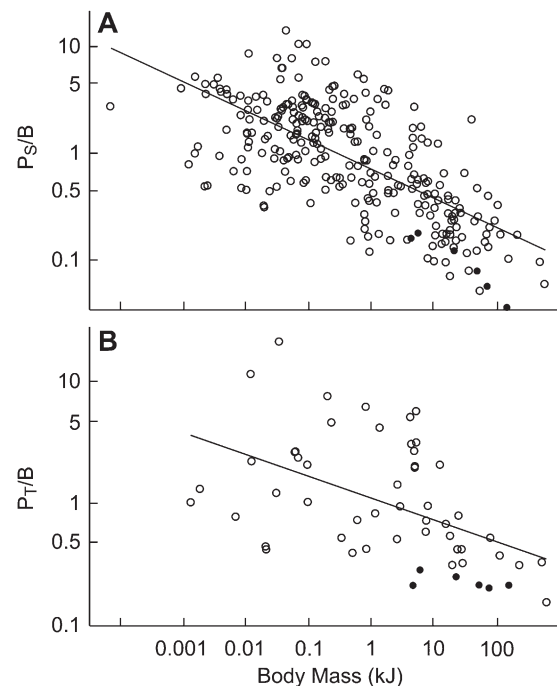


Figure 6. (A, B) Relationship between average body mass and (A) annual somatic production-to-biomass ratio P_S/B and (B) annual total production-to-biomass ratio P_T/B in 279 (P_S/B) and 55 (P_T/B) different bivalve populations, including the 6 *A. islandica* populations of this study (●). Data collected by Brey (1999, 2001). Both P_S/B and P_T/B are significantly lower in *A. islandica* (ANCOVA, $P < 0.001$ and $P = 0.006$, respectively).

islandica is just indistinctive of other bivalves ($P = 0.051$). The low somatic productivity comes to no surprise, because P_S/B equals mortality rate Z in steady-state populations. Judging from the extraordinary life span of *A. islandica*, we would have expected a more pronounced difference in gonad productivity. As a result of our more empirical approach toward gonad production, however, this finding should be interpreted with some caution.

Our estimates of net growth efficiency P_T/A (average, 0.11) and of gross growth efficiency P_T/C (average, 0.28) fall well in the range of published values for bivalve populations (e.g., Trevallion 1971, Fuji & Hashizume 1974, Thompson 1974, Bayne & Newell 1983). Thus, we are confident that our budget models are valid representatives of *A. islandica* individual and population energy flow dynamics, and that they will be of use in further studies of *A. islandica* population dynamics under changing environmental conditions. There is, however, always

room for improvement, particularly regarding measurements of site-specific growth rates, of gonad production, and of assimilation efficiency. This will help to understand better the observed differences in life span and populations dynamics of *A. islandica*, especially regarding the White Sea population, which cannot yet be explained by environmental differences. Further investigations of intrinsic and extrinsic factors influencing animals physiology and performance should show to what extent the environment and population genetics control life span.

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