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Growth of juvenile *Arctica islandica* under experimental conditions

R. Witbaard*, R. Franken & B. Visser

Netherlands Institute for Sea Research, PO Box 59 1790 AB Den Burg, The Netherlands

ABSTRACT: In two laboratory experiments, the effects of temperature and food availability on the growth of 10- to 23-mm high specimens of the bivalve *Arctica islandica* were estimated. Each experimental set-up consisted of 5 treatments in which either the food supply or the temperature differed. It was demonstrated that *Arctica* is able to grow at temperatures as low as 1 °C. A tenfold increase of shell growth was observed at temperatures between 1° and 12 °C. The greatest change in growth rate took place between 1° and 6 °C. Average instantaneous shell growth varies between 0.0003 at 1 °C to 0.0032/day at 12 °C. The results suggest that temperature hardly affects the time spent in filtration, whereas particle density strongly influences that response. Starved animals at 9 °C have their siphons open during only 12% of the time, whereas the siphons of optimally fed animals were open on average during 76% of the observations. Increased siphon activity corresponded to high shell and tissue growth. At 9 °C, average shell growth at the optimum cell density of 20×10^6 cell/l was 3.1 mm corresponding to an instantaneous rate of 0.0026/day. An algal cell density *(Isochrysis galbana, Dunaliella marina)* ranging between 5 and 7×10^6 cell/l is just enough to keep shells alive at 9 °C. Carbon conversion efficiency at 9 °C is estimated to vary between 11 and 14%.

INTRODUCTION

In recent years, attention has focused on the growth of *Arctica islandica* because of its commercial importance along the American east coast (Kennish et al., 1994). Knowledge about shell growth was obtained by applying the acetate peel method (Ropes, 1985; Ropes, 1988) which resulted in reliable estimates about longevity and annual growth rates. Murawski et al. (1982) estimated shell growth of 10-year old *Arctica* at 6.3% whereas in older animals growth rates as low as 0.2% were found. This low value for large animals corresponds to the results obtained by Forster (1981). He measured 0.1 mm growth (in-situ) over a one year period in *Arctica* with shell lengths between 82–108 mm. Estimates of growth rates for young *Arctica* were reported by Kennish et al. (1994). They transplanted artificially reared specimens with shell lengths between 9 and 20 mm to an offshore location in the Gulf of Maine (USA). Repeated measurements during the two following years demonstrated an enormous variability in shell growth. In some periods, average growth was ±1 µm/day, while in other periods the average growth was 25 µm/day. Kraus et al. (1992) transplanted specimens from an off-

* Addressee for all correspondence.

shore location to an estuarine location and demonstrated that growth can be increased considerably. In two years time, the experimental shells attained a size which would have taken 28 to 35 years in their natural off-shore habitat.

Quantitative relationships between growth and environmental factors are poorly known or speculative. Kraus et al. (1992), for instance, attributed the low growth rates in the offshore shells to disturbance or competition for food, but that supposition has never been substantiated by facts. While filtration rates in conjunction with temperature, animal size, or food concentration have been determined experimentally (Møhlenberg & Riisgård, 1979; Winter, 1969, 1978) virtually nothing is known about shell growth under controlled laboratory conditions.

The present paper describes the results of two growth experiments with juvenile *Arctica*. In the first experiment, the animals were kept under 5 different feeding regimes at a constant temperature. In the second experiment, the specimens were kept at 5 different temperature levels while food concentration was kept near optimum (Winter, 1969). The aim was to measure temperature dependent growth and to establish a relation between growth and food availability.

MATERIAL AND METHODS

Living specimens of juvenile *Arctica* were collected from the Süderfahrt site (see Brey et al., 1990) in Kiel Bay in the western Baltic Sea. Within 24 hours these animals were transferred under refrigeration to the Netherlands Institute of Sea Research (NIOZ). There they were placed in sand filled containers in a basin with aerated seawater until used. During the first four weeks, the animals were gradually acclimated to the experimental conditions. From this collection, a selection of animals to be used in the experiments was made on the basis of shell size.

Experiment I: food availability

The experimental set-up was comprised of 5 treatments (I–V) each with four replicates. Each replicate consisted of a container with a water volume of 10 l. These containers were placed in a thermostatically controlled basin in which the temperature was kept at 9.2 ± 1 °C. Two days a week the water in the replicates was flushed to avoid harmful concentrations of metabolites. Except for the replicates in treatment I, all replicates in the other treatments were continuously supplied with differing quantities of the same suspension of *Isochrysis galbana* and *Dunaliella marina* by a peristaltic pump. The ratio of food added to the treatments II : III : IV : V was 1 : 2.4 : 5.8 : 8.8 respectively. The specimens in treatment I received no food. In each replicate, the algae were held in suspension by gentle aeration. The evolving food conditions in each of the replicates was monitored twice a week by cell counts on an Elzone particle counter, and once a week by chlorophyll measurements on a Hitachi F2000 fluorescence meter following standard methods.

Chlorophyll concentration of the food source was regularly determined as described above. Carbon content of these suspensions was determined after wet oxidation on an Oceanography International MSA infrared analyser. Multiplying the aver-

Table 1. Overview of experimental conditions and main results per treatment in the food experiment at 9 °C. The values between parentheses indicate average when the deviant replicate is omitted

Treat.	Cell density (10^n cell/l)	Chloro-phyll (µg/l)	Siphon activity (%)	Δ Height (mm)	Δ Length (mm)	Δ Width (mm)	Δ Weight (mg)	Δ Index
I	0.49	0.04	12.6	0.06	0.03	−0.03	−5.59	−1.10
II	7.40	1.25	43.0	0.21	0.22	0.20	2.07	0.23
III	5.41	1.02	64.5	1.26	1.41	0.71	18.96	2.40
IV	14.74	2.66	64.1	2.05	2.34	1.11	42.78	4.74
	(9.80)	(1.88)	(73)	(2.25)	(2.58)	(1.22)	(42.83)	(4.69)
V	21.35	4.53	76.3	3.06	3.57	1.58	66.86	6.91

age carbon content/ml suspension with the quantity added per day to each container yielded an average supply of 62 µg POC/day per replicate in treatment II to 550 µg POC/day in the best fed replicates of treatment V.

Nine numbered glass jars were placed in each of the replicates, with one specimen in each jar. The average of triplicate measurements of shell height, shell length and shell width was used to describe actual shell size. These measurements were made with electronic callipers. Average standard deviation of the triplicate measurements was 0.06 mm. The size range of shells was kept as small as possible and varied between 12 and 20.5 mm (height). The specimens were divided among the replicates in such a way that at the start of the experiment average height and standard deviation in each of the replicates was approximately equal.

The relationship between size and ash-free dry weight (AFDW) was determined using 71 animals not involved in the experimental procedure. The shells were measured and soft tissue was removed and dried at 60 °C until constant weight was reached. After pre-weighing, the dried flesh was incinerated at 540 °C for three hours yielding the AFDW. The relation between shell height and weight was used to estimate the condition index (weight/height^3×1000) of each experimental *Arctica* at the start of the experiment.

When *Arctica* is buried in sediment, two modes of siphon activity were distinguished. In mode I the valves are closed, the mantle edge might be visible, but the siphons are closed. In mode II the mantle edge is extended and the siphons are fully open. According to Møhlenberg & Riisgård (1979) the mode with fully open siphons is associated with high filtration rates, while decreasing filtration rates are associated with partial closure of the valves, siphons, or mantle edges. Thus, the mode of siphon activity is an indication for the filtration activity and, therefore, probably for food uptake. In accordance, we recorded mode of siphon activity once a day for each individual specimen. At the end of the experiment, the number of days in which the specimen displayed open siphons (Mode II) was expressed in percentage of the total number of observations. This quantity is referred to as daily siphon activity.

Shells which died during the experiment were replaced by similar sized specimens to minimise the effects of differences in competition for food between replicates. These shells were not used in the final analyses.

After 68 days, the shells were remeasured, followed by the determination of their AFDW, as described above. The difference between the shell measurements at the start and end of the experiments was regarded as growth. Instantaneous growth rates (a) have been calculated for all shells as $a = (\mathrm{Ln}\ (y_t/y_0)/t)$, with y_0 equal to the initial shell size at the start of the experiment and y_t as the shell size at time t.

The differences between treatments were tested by analyses of variance (ANOVA), and the residuals were checked for normal distribution and departures from homoscedasticity by graphical methods. In all cases, the data satisfied the assumptions to justify ANOVA.

Experiment II: temperature

In the second experiment, an attempt was made to assess the effects of temperature on the growth of similar sized specimens as described for experiment I. The experimental set-up was essentially similar to that described above; five treatments (A, B, C, D, E) with four replicates each. Every replicate contained 6 labelled glass jars with one animal in each jar. The treatments differed in temperature with lowest average temperature set at 1.1° ± 0.2 °C for treatment A, and the highest average temperature set at 12° ± 0.8 °C for treatment E. The temperatures of treatments B, C and D were 3.2° ± 0.4 °C, 6.2° ± 0.5 °C and 9.2° ± 0.6 °C, respectively.

At the start of the experiment, the average shell height was 15.5 mm and ranged between 10.1 and 23.1 mm. Initial weight of the experimental specimens was estimated on the basis of an AFDW-height relationship determined from a reference group of 50 animals at the start of the experiment.

All replicates were fed with a phyto-plankton mixture as described for the experiment I. To ensure that growth took place under *ad libitum* food conditions, the availability in each replicate was kept in the optimum range of 10×10^6 to 20×10^6 cell/ltr (Winter, 1969). To maintain these levels, the peristaltic pumps which supplied each

Table 2. The results of a multiple regression analysis describing height growth (mm), being dependent on daily siphon activity expressed as % and average cell density in 10^6 cell/ltr. **2a:** The regression coefficients, the standardised coefficients and their significance for the model, growth = constant + a · cel/ml + b · activity. **2b:** ANOVA table describing the significance of the tested regression model

2a						
Variable	Coeff	Std Error	Std Coeff	Tolerance	T	P (2 Tail)
Constant	−0.839	0.279	0.000		−3.004	0.008
Cell density	0.0049	0.016	0.367 (a)	0.764	3.164	0.006
Activity	0.032	0.006	0.672 (b)	0.764	5.797	0.000
2b						
Source	SS	DF	MS	F	P	
Regression	22.179	2	11.090	40.219	0.000	
Residual	4.687	17	0.276			

replicate were adjusted when necessary. Every day the siphon activity for each individual animal was recorded. Twice a week the cell density and once a week the chlorophyll concentration were measured in each replicate. No POC measurements of the stock cultures were made, nor was the capacity of the pumps measured exactly. The experiment lasted 95 days and at the end the shells were treated as described for experiment I.

RESULTS

Experiment I: food availability

The average food conditions during the experiment and results per treatment are summarised in Table 1. Algal cell density ranged between virtually nothing (I) to 21×10^6 cell/l (V). As expected, the chlorophyll concentration followed the trend in cell density closely. One of the replicates in treatment IV strongly deviated from the norm in all measured parameters and we therefore recalculated the averages omitting these deviating values. The difference in siphon activity between the treatments (Figure 1) was most obvious. The shells in the non-fed containers (treatment I) had the lowest siphon activity with an average of 12.6% corresponding to 9 days. Shells in treatment V, which received the highest ration, were recorded with open siphons during 52 days, which is 76% of the experimental period. The shells in the replicates at intermediate food levels (treatments II–IV) were found with open siphons between 43 and 64% of the observations. The absence of a difference between treatment III and IV (Table 1) can be attributed to the deviating replicate of treatment IV. Shells in this replicate had open siphons during only 34% of the observations. The siphon activity of the deviant replicate differed significantly from the average values in the other replicates within the

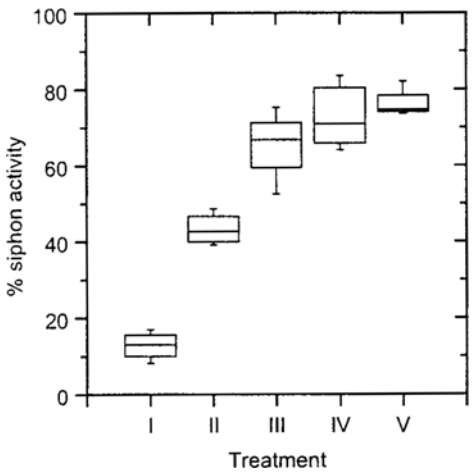


Fig. 1. Box and Whiskerplot of average daily siphon activity per treatment in experiment I. Treatments I–V correspond to an average POC supply of 0, 62, 150, 362, and 550 µg/day. The deviating replicate in treatment IV (see text) is omitted from the graph

treatment IV (Tukey HSD, pairwise comparison $p < 0.05$). This deviant replicate is therefore omitted from Figure 1 resulting in an average of 73% of observations at which the animals had open siphons.

Figure 1 illustrates that, within the range of foodsupplies used, average daily siphon activity reaches a maximum value of approximately 80%. The observed differences between treatments in average siphon activity appeared to be significant (Anova, $p < 0.05$). A Tukey HSD pairwise comparison demonstrated that the differences between the three best fed treatments (III to V) were insignificant but they all differed significantly ($p < 0.001$) from the starved and lowest fed treatment.

Notwithstanding the utmost precautions, the collection, transfer and adaptation of the animals caused the formation of a disturbance mark which was externally visible as a shallow groove on the external shell surface. In specimens which grew considerably, this mark was accompanied by a shift in colour of the periostracum from a yellowish hue to a darker brown colour. This mark facilitated the recognition of shell growth.

It appeared that high siphon activity corresponded to fast growth (Figure 2a). Not only did the differences between treatments show this relationship, but the same relationship exists for individual shells within treatments (Figure 2b), and it was absent in the food deprived treatment (I).

Animals with a siphon activity below 40% hardly grew, irrespective of the amount of food provided (Figure 2a). The average change for all shell dimensions is given in Table 1. The observed increase of 0.06 mm in the nonfed treatment (I) equals the measurement error and is therefore deemed insignificant. Maximum change in shell height was 4.7 mm for one shell in the best fed treatment (V). The average instantaneous

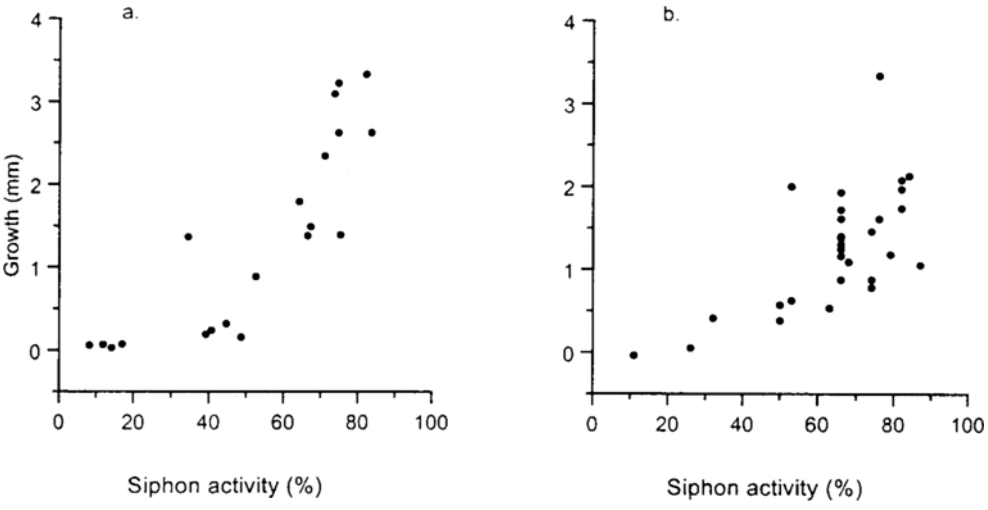


Fig. 2. Relationship between average siphon activity and average shell growth. **2a:** The dependence of average height growth per replicate in experiment I. Each symbol indicates a replicate average. **2b:** Similar relationship as in Figure 2a for the siphon activity of individual specimens within treatment III of the food experiment

growth rates ranged between 0.0002 and 0.0026/day. Analyses of variance showed that shell growth rates differed significantly between treatments ($p < 0.05$). Growth in all three dimensions, as well as growth of soft tissue, were strongly related with correlation coefficients ranging between 0.88 and 0.99 (Figure 3a/b).

The ash-free dry weight of the nonfed treatment (I) showed an average decrease of 5.6 mg (Table 1). Tissue weight in treatment II remained almost equal over the sample period with an average increase of only 2 mg. Although cell density in treatment III was lower than the density in treatment II, the average weight increase in treatment III (42.8 mg) was 2.3 times higher (Table 1). The shells in the best fed treatment increased 67 mg on average, but for some individual shells, growth of the soft tissue exceeded 100 mg (Figure 3b).

The combined effect of tissue growth and shell growth is given as the average condition index (weight/height^3×1000). For the reference group it was estimated to be 6.19 ± 0.05 at the start of the experiment. Compared to this value, the average index of the non-fed shells in treatment I decreased to 5.11. The average index values in all other treatments increased between 2 to 111% (Figure 4).

Except for treatment I and II, the changes in the condition index between all treatments were significant (Tukey HSD test, $P < 0.05$). The index changed at high food concentrations more rapidly than the corresponding siphon activity, suggesting that at high particle concentrations, minor increases in siphon activity lead to disproportionately high increases in tissue growth.

A multiple regression model describing shell growth (height) as being dependent on average cell density and filtration activity, has been fitted to the data. The regression

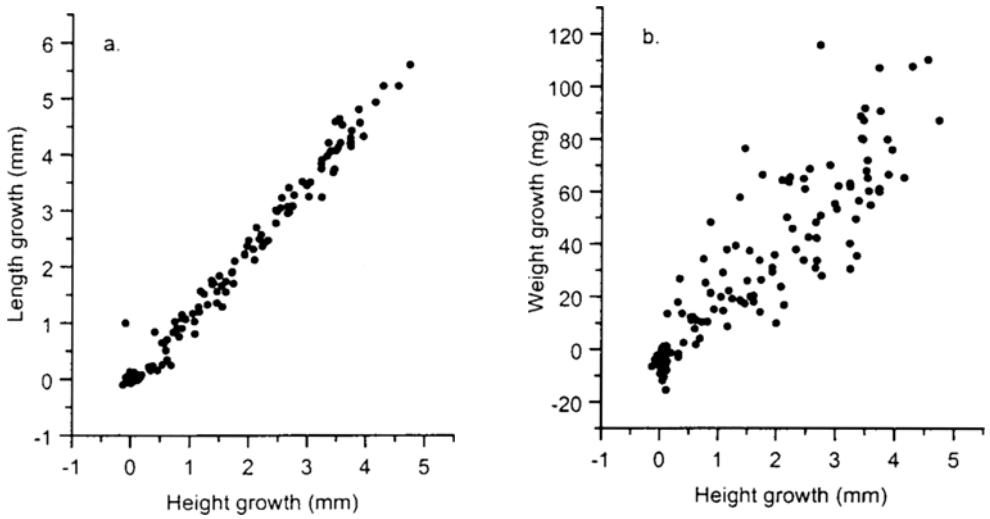
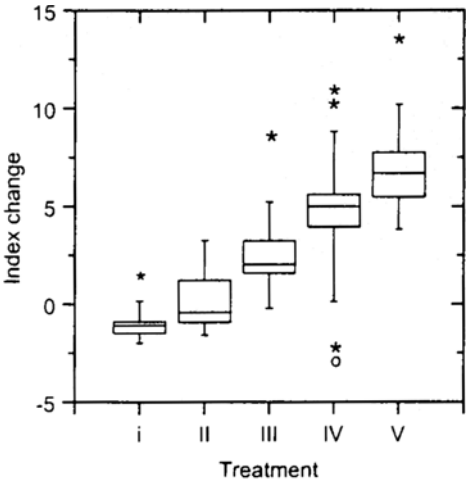


Fig. 3. Relationship of measured height, length, and tissue growth in experiment I (food).
3a: Linear relationship between height and length growth of the animals.
3b: The relationship between height and tissue growth of the animals



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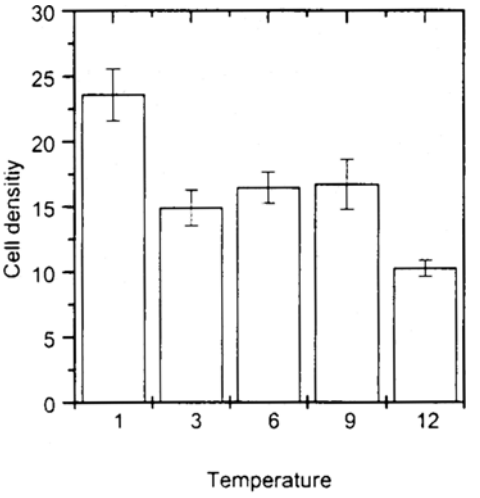

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Fig. 4. Box and Whisker plot of the change in condition index (Δ Weight/height³×1000) of the experimental animals in the food experiment; * indicates outlier (1.5×I I); ° outlier 3×I I

Fig. 5. Relationship between average cell density, temperature (°C), and chlorophyll. Average cell density per treatment in the temperature experiment. Bars indicate standard errors

was highly significant (Table 2b) with a coefficient of determination of 0.68. The standardised regression coefficients (Table 2a) illustrate the great importance of filtration activity (0.672), compared to the effect of algal density (0.367) (Table 2).

Experiment II: Temperature

In experiment II it was essential to ensure that growth was not limited by a shortage of food, but rather that it was entirely controlled by temperature. Thus, all treatments received differing quantities of food to compensate for the observed differences between treatments in the loss of particles. This implied that the supply rates of the peristaltic pumps needed to be regularly adjusted, in an attempt to keep cell density as close as possible to the optimum value as reported by Winter (1969).

Nevertheless, significant differences in algal cell density were observed between the treatments (Figure 5). Cell density at 12 °C was significantly lower when compared to 3°, 6°, or 9 °C, while the cell density in treatment A (1 °C) was significantly higher (Tukey HSD pairwise comparison, $p < 0.01$). The differences in the average chlorophyll concentrations shows the same trend since both are closely related.

The greatest possible effects of temperature on shell growth are best illustrated when the average maximum height growth per treatment is studied (Figure 6a). A Tukey HSD test showed that two groups could be distinguished which differed significantly ($p < 0.01$). The first group consisted of the replicates at the two lowest tempera-

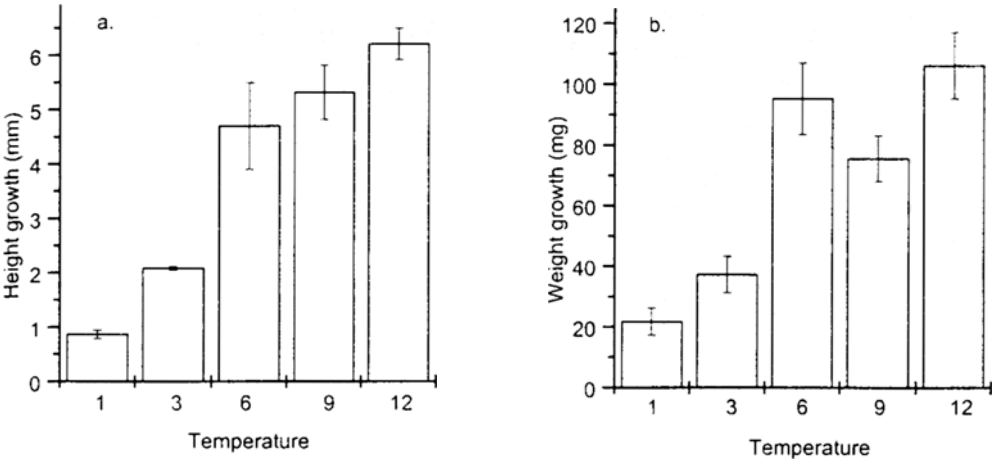

Fig. 6. Growth of the experimental animals under the five different temperature conditions, but with food concentration kept near optimum. **6a:** Average maximum shell growth per treatment. Height growth in mm. **6b:** Average weight growth per treatment in mg. Bars indicate standard error

tures and the other group consisted of the treatments at the three highest temperatures. It appeared that the effect of increasing temperature on the change of the shell height is greatest below 6.2 °C. Between 1.1° and 3.2 °C height increases with 0.58 mm/°C, and between 3.2° and 6.2 °C maximum height increases with 0.87 mm/°C. Above 6.2 °C the increase is half to one third of that, i.e. 0.2–0.3 mm/°C.

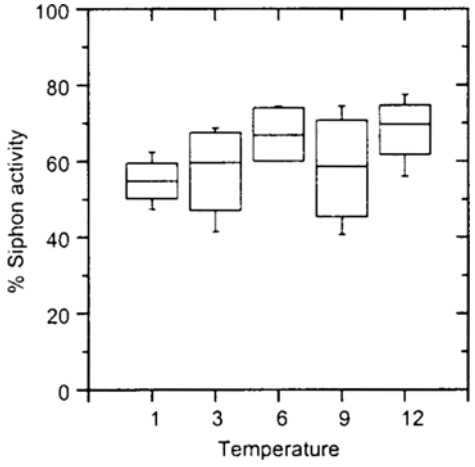

Fig. 7. Box and Whiskerplot of average daily siphon activity per treatment in experiment II. Only a slight increase in siphon activity is visible between 1° and 12 °C

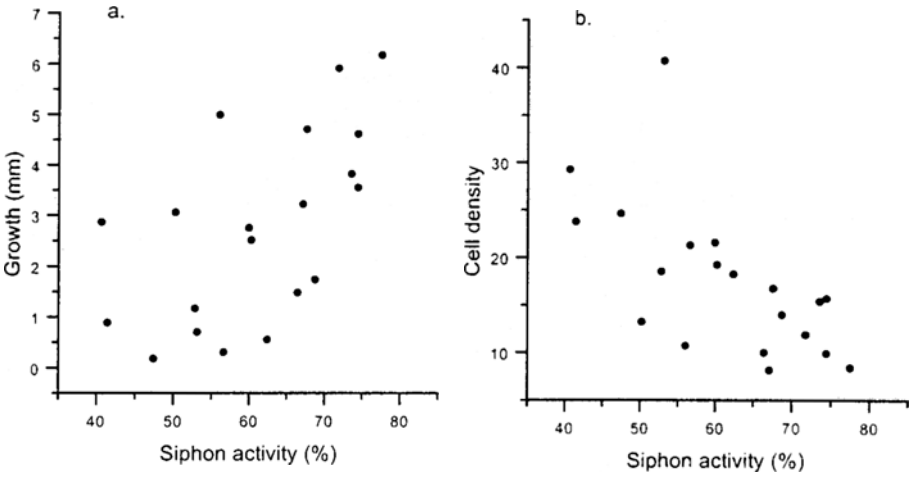

Fig. 8. Relationship between growth, daily siphon activity, and cell-density in the temperature experiment. **8a:** Average height growth (mm) versus average siphon activity per treatment. **8b:** Relationship between average cell density and average siphon activity per replicate

While in experiment I, great differences in siphon activity were observed between the poorly fed and best fed treatments, the change in siphon activity with increasing temperature was marginally significant ($p = 0.046$) (Figure 7).

None of the treatments differed from each other in their average daily siphon activity, although a weak relation between shell growth and siphon activity existed (Figure 8a).

Shell growth occurs at all temperatures, even at 1°C, although the average increase at this temperature was small (0.40 mm). The average growth between 3° and 12 °C ranged between 1.34 to 5.4 mm (Table 3). The difference in growth between 6 ° and 9 °C was small, whereas, the increase was relatively great between 9° and 12 °C. Corresponding instantaneous daily growth rates range from 0.0003/day to 0.0032/day, thus a tenfold increase in shell growth takes place between 1.1° and 1.2 °C.

Table 3. Overview of the results per treatment obtained in experiment II. Growth measurements in mm or mg ± standard deviation. A to E refer to treatments of which the average conditions are given in the three columns on the left

Treatment	Temp. (°C)	[chl a] (µg/ltr)	cell/ltr ×10⁶	Δ Height (mm)	Δ Weight (mg)	max Δ height (mm)	Activity (%)
A	1.1	7.9	26.2	0.40 ± 0.36	21.7 ± 20.1	0.68 ± 0.16	55 ± 6
B	3.2	5.1	16.5	1.34 ± 0.75	37.3 ± 26.8	2.09 ± 0.07	57 ± 13
C	6.2	4.9	18.0	3.2 ± 1.5	95.3 ± 49.9	4.69 ± 1.6	67 ± 8
D	9.2	4.2	15.1	3.43 ± 1.8	75.5 ± 33.7	5.3 ± 0.99	58 ± 15
E	12	3.5	11.9	5.44 ± 0.99	106.1 ± 46.4	6.18 ± 0.58	68 ± 9

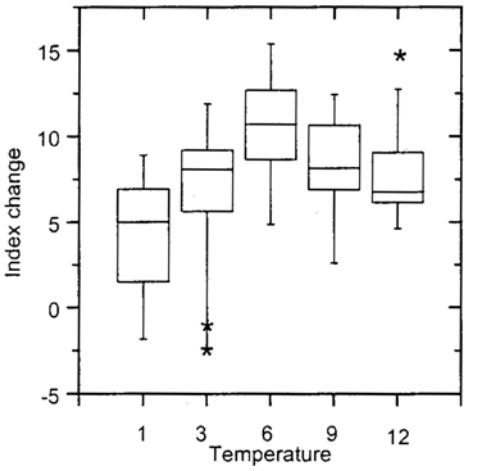

Fig. 9. Box and Whisker plot of the change in condition index (Δ Weight/height³×1000) of the animals at five different temperatures; * indicates outlier (1.5×II)

In all treatments, the average weights increased. As with shell growth, average tissue growth at 1.1° and 3.2 °C was significantly different from tissue growth at 6.2°, 9.2°, or 12 °C. The greatest increase (207 mg) for an individual animal was found at a temperature of 6.2 °C. Average values for all treatments are given in Table 3. Height and weight growth were strongly correlated (Figure 3) but the greatest change in condition index took place at 6.2 °C (Figure 9), indicating that the tissue weight increased more rapidly than shell volume during the experimental period at that temperature.

DISCUSSION

In short-term experiments, Winter (1969) determined the effects of temperature and particle density of filtration rate and food utilisation by *Arctica*. Between 4° and 14 °C, both the filtration rate and phagocytosis increased by a factor ~2. Winter (1969) observed that at increasing particle densities, the filtration rate decreases but differences in the utilisation of the ingested food keeps assimilation efficiency at approximately 67%. Based on this, higher growth rates can be expected at higher temperatures. Because growth is dependent on the equilibrium of food uptake and the amount needed for maintenance, growth tends to increase at higher temperatures, given the premise that food availability is high enough. The direct effect of temperature itself on the metabolic rate may limit growth as well, even when food availability is high enough. The border-line conditions at which *Arctica* ceases to grow are poorly known, but because the (shell) growth record of *Arctica* is seen as a valuable tool to reconstruct environmental change (Witbaard & Duineveld, 1990; Witbaard, 1996), a good understanding of such conditions would be of high value.

Mortality of experimental animals gives the first indication to marginal conditions for growth. In experiment II, 19% of the experimental animals died. They were equally divided over all temperatures and replicates. Thus, none of the temperatures caused higher mortality, which is in accordance with the natural temperature range of 0° and 19 °C as reported by Merrill et al. (1969). Although total mortality (17%) in the food experiment (I) was similar, most animals died in treatments II and III. In the non-fed treatment (I) only 8% died. These starved animals became quiescent for long periods and were found only now and then with open siphons to "sample" the food conditions. Besides the fact that the animals in treatments II and III were more frequently active, the continuous low cell densities in these treatments promoted high filtration rates (Winter, 1969). Their energy expenditure would have been higher than that of the starved *Arctica*. The increased energy need was not covered by the energy uptake from the amount of ingested food. As a consequence, the animals died. We therefore assume that the food conditions in treatments II and III were marginal for survival and growth. At 9 °C this corresponds to an algal cell density of 5 to 7×10^6 cell/ltr or a supply rate of 6.2–15.0 µg POC/day · ltr.

The above mentioned cell-densities should be treated with some caution, because we observed an inverse relationship between siphon activity and particle density (Figure 8b). This suggests that the animals controlled particle density, but also illustrates that siphon activity is related to food uptake. This relation is substantiated by the positive correlation between this activity and growth (Figure 2; Figure 8a). Thus, although the daily siphon activity is a rather crude measure, it appears to give a valid measure of the feeding activity of each individual animal.

The control of particle density was not a problem in the food experiment I, because the aim was to limit the shell growth by the food availability. For the temperature experiment, however, it could have implied food limitation. There were, however, no indications that food-limited growth occurred since the highest rate was found at 12 °C, although particle density was lowest at that temperature.

The inverse relationship between temperature and particle concentration (Figure 5) agrees with the results of Winter (1969) who found a doubling of filtration rate between 4° and 14 °C. While temperature hardly affects the daily siphon activity, the results of the food experiments do suggest that *Arctica* adjusts decreasing filtration rates at increasing cell densities by increasing the time spent in filtration. This result does not contradict Winter's (1969) findings of decreasing filtration rates with increasing cell densities, because daily siphon activity says nothing about the filtration rate. It should be seen as a measure for the time spent in filtration. The results, therefore, suggest that within the range of particle densities used, the uptake of food is optimised by maximisation of the food uptake by prolonged periods of filtration at low rates.

This means that the rapid change in shell growth between 1° and 12 °C under optimum food conditions results from the combination of changing filtration rates (Q_{10} = 2.05; Winter, 1969) and increased phagocytes (Q_{10} = 2.15; Winter, 1969). The results of this study suggest that the greatest change in the growth rate takes place in the lower temperature range (1–6 °C). This implies that small differences in the bottom water temperature during spring may have a rather large impact on shell growth. The results obtained in the food experiment furthermore suggest that at high particle densities, minimal changes in the time spent in filtration, may lead to a disproportionately large

change in shell growth. The combination of these results, therefore, suggest that the bottom water temperature at which the sedimenting spring bloom reaches the bottom is a main determinant of shell growth.

A quantitative interrelationship between temperature and food availability and growth cannot, however, be determined on the basis of the data presented in this study. The comparison of growth rates of field populations (Witbaard, in prep.) indicate that the effect of temperature on *in-situ* growth is small and is easily overruled by other factors. The spatial differences in growth rates of natural North Sea populations could not be explained by temperature. Neither could temperature explain the huge temporal variation in shell growth of specimens from the Fladen Ground (Witbaard, 1996; Witbaard & Duineveld, 1990). While the growth rate itself might be limited by temperature, the results of the temperature experiment demonstrate that growth is possible at temperatures below 6 °C. These results therefore contradict the conclusion of Weidman et al. (1994) who proposed the existence of a shutdown temperature at ±6 °C under which growth stops (Witbaard et al., 1994). The absence of such a lower temperature limit is also suggested by field data on growth of shells which started as early as March (Witbaard et al., 1994) or the extremely high growth rates of shells from north-west Iceland (Witbaard, in prep.). Many authors indeed point to the uncoupling between the onset of growth and temperature (Broom & Mason, 1978; Christensen & Kanneworff, 1985), and their results as such confirm the idea that food availability triggers the start of growth. Although *Arctica* can survive temperatures of ±20 °C, the distributional border in many populations is set by the 16 °C isotherm (Mann, 1982). Because larvae tend to grow optimally between 13 and 15 °C (Mann & Wolf, 1983) that temperature range might be the optimum for post larval specimens as well. Indeed, preliminary growth rate estimates at temperatures above 12 °C suggest an optimum temperature somewhere between 12° and 18 °C (Witbaard, 1995).

Winter (1969) estimated the assimilation efficiency between 4° and 12 °C at 67%, but since the absorbed amount is partly utilised for maintenance it is hard to estimate tissue and shell growth from such a value. We therefore estimated the carbon conversion efficiency (ΔBiomass/Consumption; sensu Crisp, 1984) from the results of experiment I. The lack of knowledge about the effect of temperature on filtration rates, impaired the estimation of a temperature effect on assimilation efficiency.

The conversion efficiency was estimated from the change in AFDW of the animals and their estimated uptake of carbon. Gonadal production, as a part of ΔB, could be omitted since all shells were below the size at which they become sexually mature (Rowell et al., 1990; Ropes et al., 1984; Thompson et al., 1980). Because we did not quantify the carbon losses (Dissolved Organic Carbon, faeces, etc.) from our experimental system, the carbon consumption for each specimen was estimated from their calculated filtration rate by subsequent multiplication with the average cell density, daily siphon activity, and average carbon content per ml. This then yields an estimate for carbon consumption during the experimental period. Filtration rate (FR l/hr) was estimated from tissue dry weight (W, g) by applying the equation derived from Møhlenberg & Riisgård (1979) (FR = 5.55×W^0.62). This equation was preferred over that of Winter (1978), since Møhlenberg & Riisgård (1979) worked with shells very similar in size to those we used. AFDW is assumed to be 80% of the dry weight (Witbaard, 1995) and the carbon content is assumed to be 40% of that. The retention efficiency at which

particles are withheld by the gills of *Arctica* varies between 75 and 90% (Møhlenberg & Riisgård, 1979). The evolving average conversion efficiency for the three best fed treatments (III–V) then varies between 9.2 and 11.7% when 90% of the algal material is retained, and when 75% of the particles is retained, the average conversion efficiency varies between 11.1 and 14.1%. If one accounts for the organic matter deposited as periostracum and shell matrix the efficiencies are on average 2% higher.

To compare the experimental growth rates with rates reported in literature, we transformed all values to instantaneous rates. This demonstrates that the results in experiment I and II yield similar estimates. At 9 °C in the temperature experiment II the instantaneous rate was 0.0032/day and in treatment V of the *food* experiment it was 0.0026/day. These experimentally obtained rates also compare well to values reported for animals which grew under natural conditions. The average instantaneous daily rates for 12- to 20-mm long shells from Kiel Bay (Brey et al., 1990) range between 0.0011 and 0.0024 when an 8-month growing season is assumed (starting with the spring bloom in March and ending in October) (Trutschler & Samtleben, 1988). The same was done with the absolute rates reported by Kennish et al. (1995). They re-measured transplanted animals with a shell length between 9.2 and 19.9 mm 5 times. Absolute growth ranged between 0.16 and 5.28 mm. Expressed as daily instantaneous rates over the full 485-day incubation period it varied between 0.0023 and 0.0013. The maximum *in-situ* instantaneous growth rate observed in that study is estimated at 0.0025/day for the smallest animals. Thus both the *in-situ* growth rates in the Baltic and Gulf of Maine are very similar to the average rates obtained in the experiments, illustrating that reliable growth rate estimates for juvenile *Arctica* can be obtained from laboratory experiments.

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