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Tree of the sea

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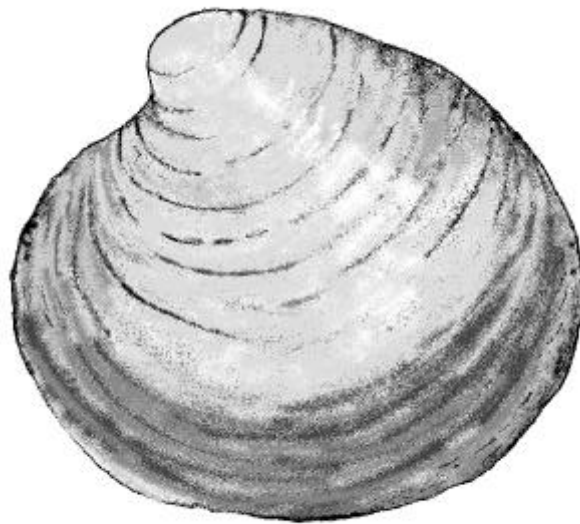
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At this age, the shell is almost entirely black. Only the outer margin of the periostracum has the yellow brown hue of younger *Arctica*. The growth lines along the shell margin can not be recognised anymore. At this age the animal has attained a shell height of approximately 7 cm.

CHAPTER 4

Growth of juvenile *Arctica islandica* under experimental conditions



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Growth of juvenile *Arctica islandica* under experimental conditions

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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. Both experimental set-ups consisted of 5 treatments; in the first the food supply differed, and in the second, the temperature was the controlled variable.

It was demonstrated that *Arctica* is able to grow at temperatures as low as 1°C. A ten-fold increase in shell growth was observed 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/day at 1°C to 0.0032/day at 12°C.

The results suggest that temperature barely 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 on average open during 76% of the observations. Increased siphon activity corresponded to high shell and tissue growth. At 9°C, average shell growth over the experimental period at the optimum phytoplankton cell density of $20 \cdot 10^6$ cell/l, was 3.1 mm. This corresponds to an instantaneous rate of 0.0026/day.

An algal cell density (*Isochrysis galbana*, *Dunaliella marina*) ranging between 5 and $7 \cdot 10^6$ cell/l is just enough to keep *Arctica* alive at 9°C. Carbon conversion efficiency at 9°C is estimated to vary between 11 and 14%.

INTRODUCTION

In recent years attention has focussed on the growth of *Arctica islandica* because of its commercial importance along the American east coast (Kennish *et al.*, 1994). Knowledge about shell growth has been obtained by applying the acetate peel method (Ropes, 1985; Ropes & Sheperd, 1988), resulting in reliable estimates about longevity and annual growth rates. Murawski *et al.* (1982) estimated shell growth of 10 year old

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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 over the following two years demonstrated an enormous variability in shell growth. In some periods, the average growth rate was ± 1 $\mu\text{m}/\text{day}$, while in other periods the average growth rate was 25 $\mu\text{m}/\text{day}$. Kraus *et al.* (1992) transplanted specimens from an off-shore location to an estuarine location and demonstrated that growth increased considerably in the richer environment. In two years time, the experimental shells attained a size which would have taken 27 to 35 years in their natural off-shore habitat.

Quantitative relationships between growth and environmental factors are either poorly known or speculative. Kraus *et al.* (1992), for instance, attributed the low growth rates in the off-shore shells to disturbance or competition for food but that supposition has never been substantiated. While filtration rates in conjunction with temperature, animal size or food concentration have been determined experimentally (Møhlenberg & Riisgard, 1979; Winter, 1978; Winter, 1969) 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 at 5 different food levels at a constant temperature. In the second experiment the specimens were kept at 5 different temperatures while food concentration was kept near optimum (Winter, 1969). The aim was to measure temperature dependent growth and to establish a relationship between growth and food availability.

MATERIAL & 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. The size range of shells was kept as small as possible and varied between 10 and 23 mm (height).

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 litre. These containers were placed in a thermostatically controlled basin in which the temperature was kept at $9.2 \pm 1^\circ\text{C}$. Twice a week the water in the replicates was flushed to avoid harmful concentrations of metabolites. All replicates except those in treatment I, 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 treatments II : III : IV and V was 1 : 2.4 : 5.8 : 8.8 respectively. Treatment I was the control and thus did not receive any food. In each replicate the algae were held in suspension by gentle aeration. 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 each suspension was determined after wet oxidation on an Oceanography International MSA infrared analyser. Multiplying the average carbon content/ml suspension with the quantity added per day to each container yielded an average supply of 62 $\mu\text{gPOC/day}$ per replicate in treatment II to 550 $\mu\text{gPOC/day}$ 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 an electronic callipers. Average standard deviation of the triplicate measurements was 0.06 mm. 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 (afdwt) 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 afdwt. The relationship between shell height and weight was used to estimate the condition index $((\text{weight}/\text{height}^3)*1000)$ of each experimental *Arctica* at the start of the experiment.

When *Arctica* is buried into the 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

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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 thus probably food uptake. We therefore recorded once a day for each individual specimen its mode of siphon activity and at the end of the experiment the number of days in which the specimen displayed open siphons (mode II) was expressed as 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, however, used in the final analyses.

After 68 days, the shells were remeasured, followed by the determination of the 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 $a = (\ln(y_t/y_0) / t)$, 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 the anova.

Table 4.1.

Treat.	Cell density (10 ⁶ cell/l)	Chlorophyll (µg/l)	Siphon act. (%)	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 (9.80)	2.66 (1.88)	64.1 (73)	2.05 (2.25)	2.34 (2.58)	1.11 (1.22)	42.78 (42.83)	4.74 (4.69)
V	21.35	4.53	76.3	3.06	3.57	1.58	66.86	6.91

Table 4.1. 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.

Experiment II: temperature

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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 the same as that described above; five treatments (A, B, C, D, E) with four replicates in each. Each replicate contained six labeled glass jars with one animal in each jar. The treatments differed in temperature with lowest average temperature set at $1.1 \pm 0.2^\circ\text{C}$ for treatment A and the highest average temperature set at $12 \pm 0.8^\circ\text{C}$ for treatment E. The temperatures of treatments B, C and D were $3.2 \pm 0.4^\circ\text{C}$; $6.2 \pm 0.5^\circ\text{C}$ and $9.2 \pm 0.6^\circ\text{C}$ 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 phytoplankton 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 $10 \cdot 10^6$ to $20 \cdot 10^6$ cell/l (Winter, 1969) by adjusting the peristaltic pumps which supplied each replicate when needed. The siphon activity for each individual animal was recorded once each day. 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 a precise measurement of the capacity of the pumps made. The experiment lasted 95 days and at the end the animals were treated as described for experiment I.

Figure 4.1

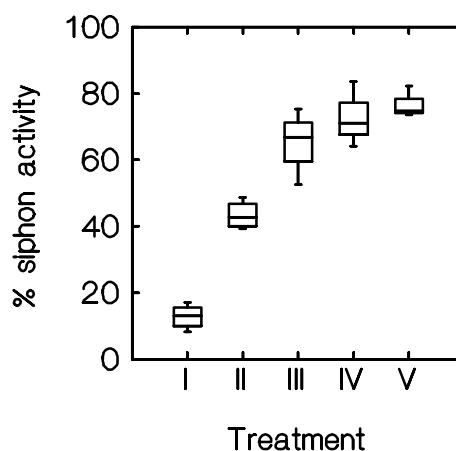


Figure 4.1. Box and Whiskerplot of average daily siphon activity per treatment in experiment I. Treatments I-V correspond to an average POC supply of 0, 62, 150, 362 and 550 $\mu\text{g}/\text{day}$. The deviating replicate in treatment IV (see text) is omitted from the graph.

RESULTS

Experiment I: food availability

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The average food conditions during the experiment and results per treatment are summarised in table 4.1. Algal cell density ranged between virtually nothing (I) to 21×10^6 cell/l (V). As would be expected, the chlorophyll concentration closely followed the trend in cell density. 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 4.1) 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, that 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 significant difference between treatment III and IV 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 treatment IV (Tukey HSD, pairwise comparison $p < 0.05$). This deviant replicate is therefore omitted from figure 4.1 resulting in an average of 73% of observations at which the animals had open siphons.

Figure 4.2

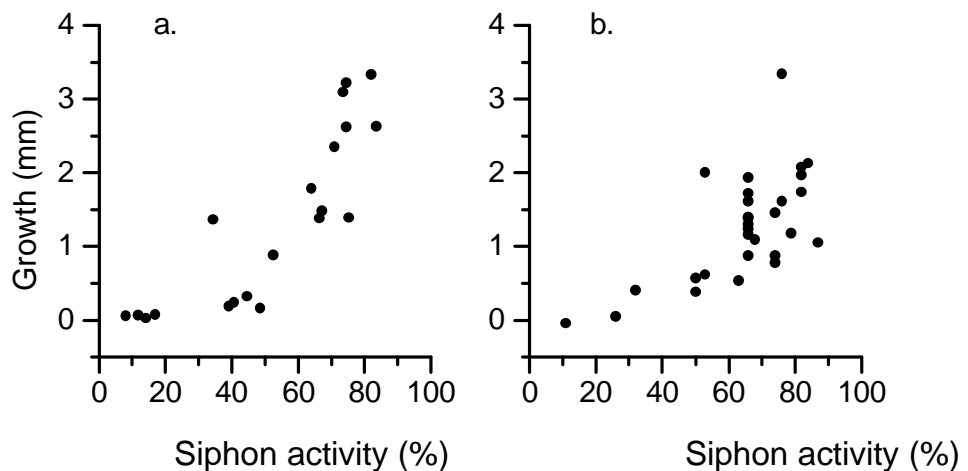


Figure 4.2. Relationship between average activity and average shell growth. (a), The dependence of average height growth per replicate in experiment I. Each symbol indicates a replicate average. (b), Similar relationship as in figure (a) for the siphon activity of individual shells within treatment III of the food experiment.

Figure 4.1 illustrates that, within the range of food supplied, 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,

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$p < 0.05$). 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.

Even though the utmost precautions were used, 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 displayed considerable growth, 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.

High siphon activity was observed to correspond to fast growth (figure 4.2a). Not only did the differences between treatments show this relationship, but the same relationship exists for individual shells within treatments (figure 4.2b), although it was absent in the food deprived treatment (I).

Figure 4.3

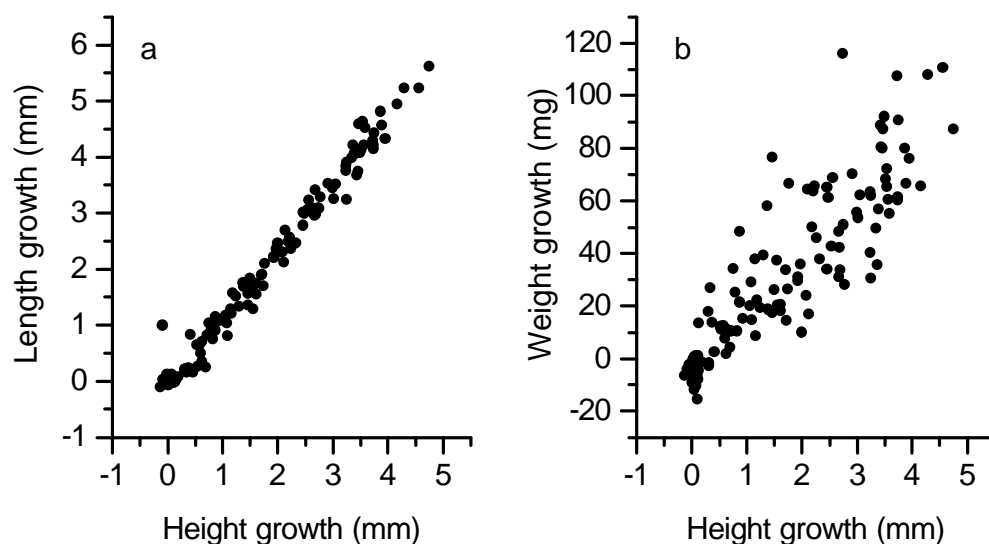


Figure 4.3. Relationship of measured height, length and tissue growth. (a) Linear relationship between height and length growth of the animals in experiment I. (b) The relationship between height and tissue growth of the animals in experiment I (food).

Animals with a siphon activity below 40% showed minimal growth, regardless of the amount of food provided (figure 4.2a). The average change for all shell dimensions is given in table 4.1. The observed increase of 0.06 mm in the non-fed 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 growth rates ranged between 0.0002- and 0.0026/day. Anova showed that shell growth rates differed significantly between treatments ($p < 0.05$). Growth in

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all three dimensions as well as growth of soft tissue were strongly related, with correlation coefficients ranging from 0.88 to 0.99 (figure 4.3). The ash-free dry weight of the non-fed treatment (I) showed an average decrease of 5.6 mg (table 4.1). Tissue weight in treatment II remained almost equal over the sample period with an average increase of only 2 mg. Although algal 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 4.1). 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 4.3b).

The combined effect of tissue growth and shell growth is given as the average condition index $((\text{weight}/\text{height}^3) \times 1000)$. 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 *Arctica* in treatment I decreased to 5.11. The average index values in all other treatments increased between 2 to 111% (figure 4.4).

Except for treatments 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.

Figure 4.4

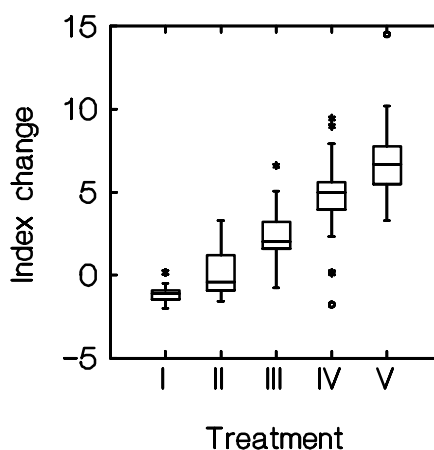


Figure 4.4. Box and Whisker plot of the change in condition index $(\Delta\text{weight}/\text{height}^3 \times 1000)$ of the experimental animals in the food experiment; * indicates outlier ($1.5 \times H$); ° outlier $3 \times H$.

A multiple regression model describing shell growth (height) as being dependent on average cell density and filtration activity, was fitted to the data (table 4.2). The regression was highly significant with a coefficient of determination of 0.68. The

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standardised regression coefficients (table 4.2a) illustrate the great importance of filtration activity (0.672), compared to the effect of algal density (0.367).

Table 4.2a

Variable	Coeff	Std Error	Std Coef	Tolerance	T	p(2 Tail)
Constant	-0.839	0.279	0.000	-	-3.004	0.008
Cell density	0.049	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

Table 4.2b

Source	SS	DF	MS	F	p
Regression	22.179	2	11.090	40.219	0.000
Residual	4.687	17	0.276		

Table 4.2. The results of a multiple regression analyses describing height growth (mm) being dependent on daily siphon activity expressed as % and average cell density in 10^6 cell/l. (a), The regression coefficients, the standardised coefficients and their significance for the model $\text{growth} = \text{constant} + a * \text{cel/ml} + b * \text{activity}$. (b), Anova table describing the significance of the tested regression model.

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, the amount of food provided needed to be adjusted based on differing consumption rates at the various temperature treatments 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 the algal cell density were observed between the treatments (figure 4.5a). 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 show the same trend since both are closely related (figure 4.5b).

The greatest possible effects of temperature on shell growth are best illustrated when the average maximum height growth per treatment is studied (figure 4.8a). 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 temperatures and the other group consisted of the treatments at the three highest temperatures. It

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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.

Figure 4.5.

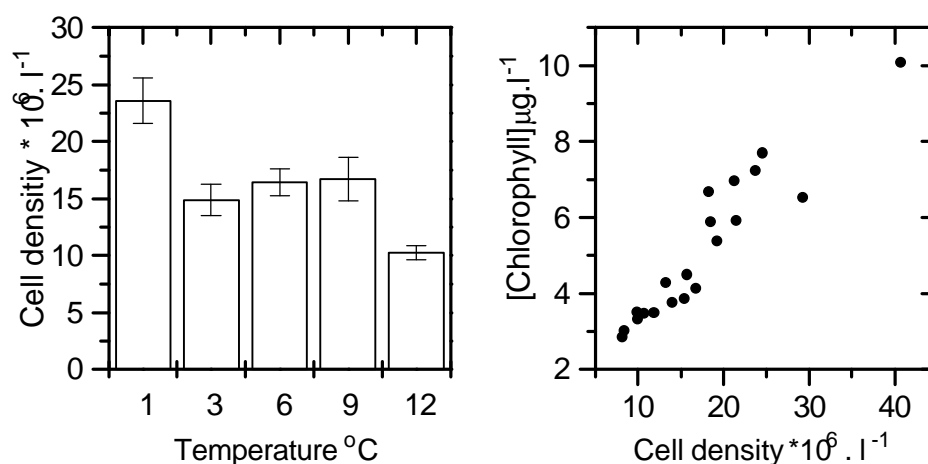


Figure 4.5. Relationship between average algal cell density, temperature (°C) and chlorophyll concentration (µg/l). (a), Average cell density per treatment in the temperature experiment. Bars indicate standard errors. (b), Relationship between cell density and chlorophyll concentration in µg/l.

Table 4.3

Treatm.	Temp. °C	[chl a] µg/l	cell/l *10 ⁶ .	ΔHeight (mm)	ΔWeight (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	2.08±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	12.0	3.5	11.9	5.44±0.99	106.1±46.4	6.18±0.58	68±9

Table 4.3. Overview of the results per treatment obtained in experiment II. Growth measurements in mm or mg + or - standard deviation. A to E refer to treatments of which the average conditions are given in the three columns on the left.

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 only marginally significant ($p=0.046$) (figure 4.6).

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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 4.7a).

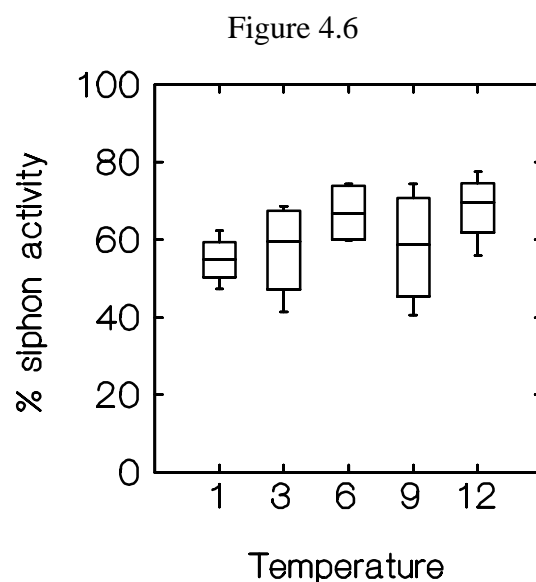


Figure 4.6. Box and Whiskerplot of average daily siphon activity per treatment in experiment II (Temperature °C). Only a slight increase in siphon activity is visible between 1 and 12°C.

Shell growth occurs at all temperatures, even at 1°C, although the average increase at that temperature was small (0.40 mm). The average growth between 3 and 12°C ranged between 1.34 to 5.4 mm (table 4.3). The difference in growth between 6 and 9°C was small whereas the increase was relatively large between 9 and 12°C. Corresponding instantaneous daily growth rates range from 0.0003 to 0.0032/day, thus a ten-fold increase in shell growth takes place between 1.1 and 12°C.

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 4.3. Height and weight growth were strongly correlated (figure 4.3) but the greatest change in condition index took place at 6.2°C (figure 4.9), 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 on filtration rate and food utilisation by *Arctica*. Between 4 and 14°C,

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both the filtration rate and phagocytosis increased by a factor of ~2. Winter (1969) observed that at increasing particle densities the filtration rate decreases but differences in the utilisation of the ingested food keeps the 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 as well as the amount needed for maintenance, growth tends to increase at higher temperatures given the premise that the availability of food is high enough. The direct effect of temperature 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, a good understanding of such conditions would be of high value.

Figure 4.7

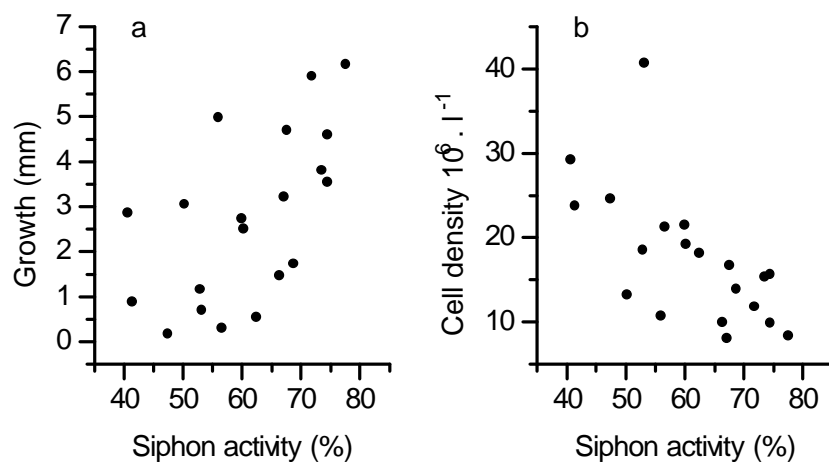


Figure 4.7; Relationship between growth, daily siphon activity and cell-density in the temperature experiment. (a), Average height growth (mm) versus average siphon activity per treatment. (b), Relationship between average cell density and average siphon activity per replicate.

Mortality of experimental animals gives the first indication of 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 was expected on basis of the natural temperature range at which *Arctica* occurs (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. The fact that the animals in treatments II and III were more frequently active, suggests

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that 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*10⁶ cell/l or a supply rate of 6.2 -15.0 µgPOC/day*1.

The above mentioned cell densities should be treated with some caution because we observed an inverse relationship between siphon activity and particle density (figure 4.7b). This suggests that the animals effected 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 4.2; figure 4.7a). 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 4.5a) agrees with the results of Winter (1969) who found a doubling of filtration rate between 4 and 14°C. While temperature has a minimal effect on 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 to filtration. This result does not contradict Winter's (1969) findings of decreasing filtration rates with increasing cell densities because daily siphon activity does not say anything about the filtration rate. Rather, it should be seen as a measure for the time spent to filtration. The results 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.

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 part of the 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 to filtration may lead to a disproportionately large change in shell growth. The combination of these results therefore suggest that the bottom water temperature at the time when the sedimenting spring bloom reaches the bottom is a main determinant of shell growth.

Figure 4.8

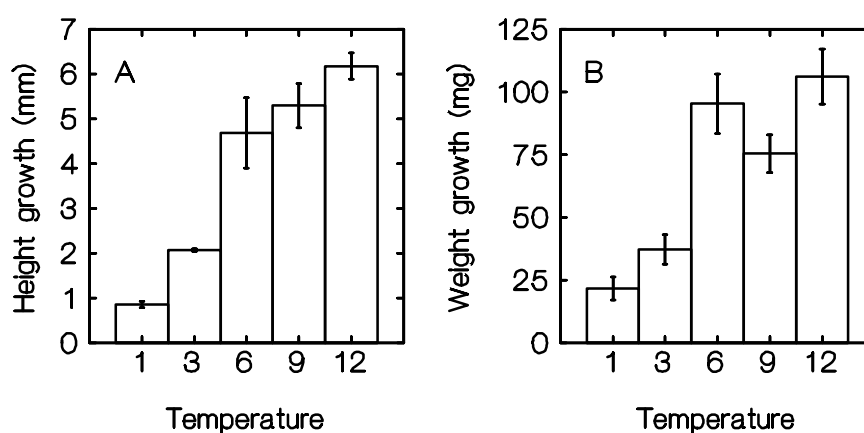


Figure 4.8. Growth of the experimental animals under the five different temperature conditions but with food concentration kept near optimum. (a), Average maximum shell growth per treatment. Height growth in mm. (b), Average weight growth per treatment in mg. Bars indicate standard error.

A quantitative inter-relationship between temperature and food availability and growth can not however, be determined on the basis of the data presented in this study. The results of chapter 5 indicate, however, that the effect of temperature on *in-situ* growth is small. 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 (chapter 7). 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 $\pm 6^\circ\text{C}$ below which growth stops (chapter 3). The absence of such lower temperature limit is also suggested by field data on growth of shells which started as early as March (chapter 3) or the extremely high growth rates of shells from north-west Iceland (chapter 4). In fact, many authors discuss the uncoupling between the onset of growth and temperature (Broom & Mason, 1978; Kristensen & Kanneworf, 1986). Their results tend to confirm the idea that food availability triggers the start of growth.

Winter (1969) estimated the assimilation efficiency between 4 and 12°C to be 67%. However, since the absorbed food is partly utilised for maintenance, it is difficult to

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estimate tissue and shell growth from such a value. We therefore use an estimate of the carbon conversion efficiency ($\Delta\text{Biomass}/\text{Consumption}$; *sensu* Crisp, 1984) from the results of experiment I. The results of experiment II were not examined, as the lack of knowledge about the effect of small stepped changes in temperature on filtration rates make it difficult to estimate a detailed effect on the assimilation efficiency.

Figure 4.9

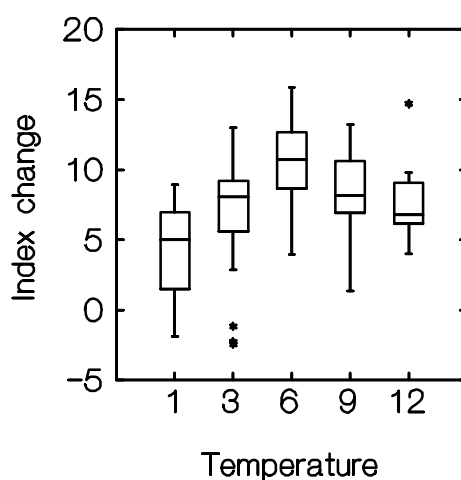


Figure 4.9. A Box and Whisker plot of the change in condition index ($\Delta(\text{weight}/\text{height}^3) \cdot 1000$) of the animals at five different temperatures. * indicates outlier ($1.5 \cdot H$).

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 $\Delta\text{Biomass}$, could be omitted since all shells were below the size at which they become sexual mature (Rowell *et al.*, 1990; Ropes *et al.*, 1984b; Thompson *et al.*, 1980b). 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) ($\text{FR} = 5.55 \cdot W^{0.62}$). This equation was preferred over that of Winter (1978), since Møhlenberg & Riisgård (1979) worked with shell sizes very similar 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, 1978). The evolving average conversion efficiency for the three best fed treatments (III-V) then varies between 9.2 and 11.7% when 90% of

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the algal material is retained. When 75% of the particles are 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 the literature, we transformed all values to instantaneous rates. This demonstrates that the results in experiments I and II yield similar estimates. At 9°C in the temperature experiment (II) the instantaneous growth rate was 0.0032/day and in treatment V of the *food* experiment it was 0.0026/day. These experimentally obtained rates compare well to values reported for animals grown 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 (Trustler & Samtleben, 1988). The same was done with the absolute rates reported by Kennish *et al.* (1994). 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 period it varied between 0.0023 and 0.0013. The maximum observed *in-situ* instantaneous growth rate in that study is estimated at 0.0025/day for the smallest animals. Thus the *in-situ* growth rates in both Baltic and the Gulf of Maine are very similar to the average rates obtained in the experiments and illustrates that reliable growth rate estimates for juvenile *Arctica* can be obtained from laboratory experiments.

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