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Tree of the sea

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1997

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Witbaard, R. (1997). *Tree of the sea: The use of the internal growth lines in the shell of Arctica islandica (Bivalvia, Mollusca) for the retrospective assessment of marine environmental change*. [Thesis fully internal (DIV), University of Groningen]. s.n.

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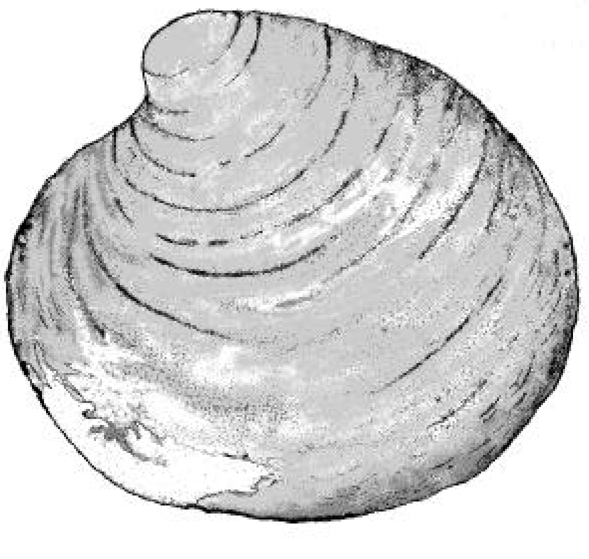
There is hardly any increase in shell height.
The shell has attained a height of approximately 8 cm. The periostracum starts to wear, often along the margin or at the most convex shell parts. Although the shell doesn't grow much in size, its weight increases considerably.

CHAPTER 5.

Geographical differences in growth rates of *Arctica islandica* from the North Sea and adjacent waters.



CHAPTER 5

Geographical differences in growth rates of *Arctica islandica* from the North Sea and adjacent waters

R. Witbaard

Part of this work has been published as; Witbaard, R. & G.C.A. Duineveld, 1990. Shell-growth of the bivalve *Arctica islandica* (L.), and its possible use for evaluating the status of the benthos in the subtidal North Sea. Basteria 54: 63-74.

ABSTRACT

Geographical differences in the shell growth rate of several populations of the bivalve *Arctica islandica* were estimated by using the growth lines laid down during their first 10 years of life. Attention was focused on populations from the North Sea, but for comparison small samples from adjacent waters were analysed as well. A four-fold difference in the average growth rate was found between the slowest and fastest growing specimens.

Principal component analysis was used to summarise the inter-relationships between environmental variables and growth rates. Shell growth correlated positively with primary production and temperature and inversely with depth and the silt content of the sediment. The North Sea specimens were found to have a strong positive correlation with grain size. Since sediment characteristics also depend on bottom currents, it is suggested that these increased rates reflect lateral seston flux as addiditonal food supply.

In a multiple regression model, average annual temperature, primary production and the interaction between production and water depth explained 50% of the variance. The derived standard coefficients for temperature, primary production and the interaction between depth and primary production were 0.90, 0.47 and -0.92. The results of this study suggest that the temperature effects on *in-situ* shell growth are easily over-ruled by other environmental factors.

If a similar model was calculated for the North Sea, 75% of the variance was explained by temperature, primary production and depth $*$ primary production. The standard coefficient for primary production was 1.26. The role of temperature in explaining the observed growth differences is negligible since the standard coefficient is -0.098.

INTRODUCTION

The bivalve *Arctica islandica,* which can be found in most shelf seas of the northern Atlantic (Nicol, 1951) is among the longest-lived bivalves known (Heller, 1990). Counts of the annual internal growth lines (Witbaard *et al*., 1994) suggest ages over

200 years (Ropes, 1985). While knowledge about geographical variability in growth rates of *Arctica* is well documented for the populations along the US and Canadian east coast (Ropes & Pyoas, 1982; Murawski *et al*., 1982) such knowledge is scarce for the populations from the north-west European shelf seas. This difference is caused by the fact that its commercial importance (Kennish *et al*., 1995) especially in America, stimulated research, while such stimuli remained absent in Europe.

There are, never-the-less, preliminary growth and longevity estimates for some European waters. Lovén (1929) arrived at an age of 11 years for shells from the Øresund but because he used externally visible growth lines he probably underestimated longevity. The results of Forster's (1981) *in-situ* growth experiment confirmed earlier views of low growth rates in adult shells. He found a growth rate of 0.1 mm/yr for 82-108 mm long shells.

Since 1990, the first papers on growth of *Arctica* from the North Sea (Witbaard & Duineveld, 1990), Baltic Sea (Brey *et al*., 1990) and Kattegat (Josefson *et al*., 1995) appeared. The results presented in these papers suggest large differences in the growth rates of *Arctica* in north-west European waters. Such growth differences are also indicated by the difference in shell size at the time at which the periostracum changed in colour. In juvenile shells the colour is yellowish brown, but as the shell grows older it turns black due to the deposition of iron complexes (Brey *et al*., 1990). Different populations often differ in the size at which this colour shift occurs. Because the shift is coupled to ageing, such difference suggests a geographical variation in growth rate. The existence of such geographical difference is confirmed by the results obtained by Witbaard & Duineveld (1990). They found growth rates 2 to 3 times higher in shells from the south-east North Sea as compared to the northern North Sea.

Because growth rate estimates for *Arctica* from other areas within the North Sea are still lacking, the present paper intends first to describe and secondly to explain the observed differences in growth rate. The latter is of special interest, since a better understanding of the growth determining factors might improve the use of *Arctica* as a retrospective, long-term indicator organism for productivity and benthic food availability as proposed by Witbaard & Duineveld (1990).

In searching for the factors which could explain the observed differences in growth, attention focussed on bottom water temperature, depth and primary production because these are regarded as most relevant. Shell growth itself is likely to be modified directly by temperature and food supply (chapter 4). Combinations of these factors were used in multiple regression analyses to assess their relative importance in explaining shell growth.

MATERIAL AND METHODS

Growth rate

The specimens of *Arctica* dealt with in this study were collected during various (fishing) cruises, either with research vessels or commercial trawlers. Other samples were obtained from marine laboratories abroad. Most shells were gathered between September 1990 and December 1993. Sampling locations are given in figure 5.1 and details of these sites, together with environmental characteristics, are given in table 5.1 and table 5.2.

Table 5.1

Region	Station name	Site nr	Latitude	Longitude	Date of sampling	Nr. of shells
North Sea	F18/9	1	54°06'N	04°46'E	15-Mar-'91	6
North Sea	F14/6	2	54°12'N	04°32'E	June-'88	5
North Sea	Oyster Ground	3	54°22'N	05°40'E	13-Mar-'91	23
North Sea	Oyster Ground	4	53°52'N	04°59'E	13-Mar-'91	13
North Sea	Oyster Ground	5	54°18'N	05°45'E	04-Oct-'91	7
North Sea	Oyster Ground	6	54°22'N	04°53'E	15-Sept-'93	48
North Sea	Cleaver Bank	7	54°08'N	03°14'E	April-'90	3
North Sea	Silverpit north	8	54°08'N	02°12'E	16-Nov-'93	20
North Sea	Monkey Bank	9	56°30'N	06°00'E	18-Mar-'91	13
North Sea	Fladen Ground	10	59°24'N	00°31'E	May'83/Nov	20
North Sea	Fladen Ground	11	58°45'N	00°20'E	May '83	17
North Sea	Fisher Bank	12	57°00'N	03°30'E	02-May-'91	26
North Atlantic	Faroer I	13	61°35'N	06°02'W	May '88	3
North Atlantic	Faroer II	14	61°42'N	07°17'W	July'89	5
North Atlantic	Iceland	15	64°09'N	22°20'W	21-Nov-'91	2
North Atlantic	Iceland	16	66°20'N	22°52'W	02-Mar-'91	9
White Sea	Kandalaksha	17	66°18'N	33°38'E	12-Aug-'92	7
White Sea	Onega Bay	18	64°36'N	35°34'E	12-July-'50	19
White Sea	Kandalaksha	19	66°41'N	34°14'E	10-Aug-'49	5

Table 5.1. Sampling details of the *Arctica* specimens used in this study. Area and geographical names are given in the first two collumns. Station names and site numbers refer to those used in the text and figures 5.1a and 5.1b. Nr. of shells corresponds to the number of specimens for which the growth rate was determined.

Figure 5.1

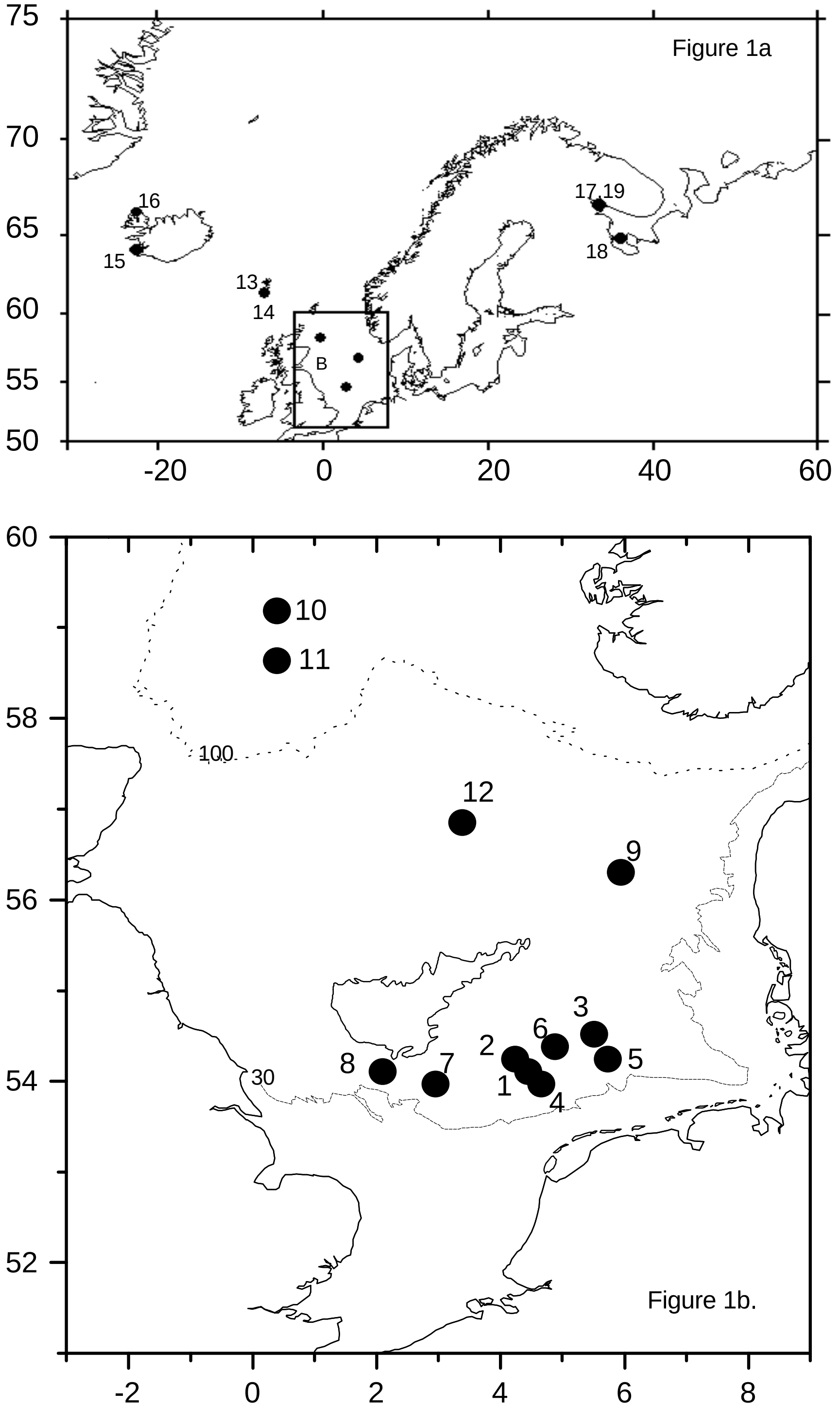


Figure 5.1. Geographical location of the sampling stations mentioned in the text. (a), Map of north-west Europe with sampling locations used in this study. The inset (B) refers to the North Sea and is given in more detail in figure (b), Numbers in both maps refer to the sites for which the details are given in table 5.1 and table 5.2.

Table 5.2.

Station name	Temp. °C ± stdev	Temp. Range	PrimProd gCm^{-2}yr^{-1}	Grainsize µm	% silt	Depth m.
F18/9	9.8±3.8 (1)	5.0-15.2	300 (6)	125-150 (14)	10-15*(14)	42
F14/6	9.6±3.6 (1)	4.9-15.0	270 (6)	<125 (14)	15-20*(14)	46
Oyster Ground I	9.4±3.8 (1)	4.7-15.2	270 (6)	150-200 (14)	5-10*(14)	40
Oyster Ground II	9.9±3.8 (1)	5.0-15.4	420 (6)	125-150 (14)	>20*(14)	37
Oyster Ground III	9.6±3.9 (1)	4.2-15.3	300 (6)	150-200 (14)	10-15*(14)	41
Oyster Ground IV	9.5±3.6 (1)	5.0-14.9	300 (6)	125-150 (14)	15-20*(14)	39
Cleaverbank	9.6±3.5 (1)	4.9-15.0	313 (7) **	200-250 (14)	2-5*(14)	35
Silverpit	9.8±3.3 (1)	5.3-14.5	422 (7) **	125-250 (14)	1-5(14)	40-68
Monkeybank	7.5±2.6 (1)	3.8-11.0	110 (8) **	125 (15)	5 (15)	52
Fladen Ground I	7.1±0.5 (1)	6.5-8.0	90 (9)	62-125 (16)	20-30 (16)	140
Fladen Ground II	7.1±0.5 (1)	6.5-8.0	90 (9)	31-62 (16)	50-90 (16)	140
Fisherbank	6.6±0.8 (1)	5.3-8.0	110 (8) **	125-250 (16)	5 (16)	61
Faroe Islands I	8.3±0.9 (2)		57 (10)	coarse shell sand (2)	-	177
Faroer IslandsII	7.5±1.1 (2)		57 (10)	gravel, cobbles (2)	-	134
Iceland Ísafjord	4.7±2.6 (3)	< 29.5	184 (11)	coarse sand. (†)	-	5-7
Iceland Faxaflói	6.2±3.1(4)	0.7-10.0	79 (12) **	Sand gravel (17)	-	30
Kandalaksha Bay I/II	4.3±5.6(5)	< 0-11.2	200 (13)	silt +stones (18)	-	6
Onega Bay	4.3 *		200 (13)	silty sand/clay (18)	-	17-20

Table 5.2. Sample locations with environmental variables. Numbers in brackets indicate literature source. 1=Tomczak & Goedecke, 1967; 2=Nørrevang *et al*., 1994; 3=Astthorsson, 1990; 4=Stefánsson & Jónsdóttir; 1974; 5=Babkov & Golikov, 1984; 6=Gee *et al*., 1991; 7=Riegman & Colijn, 1991; 8= Nielsen *et al*., 1993; 9=Steele, 1956; 1974; 10= Gaard & Mortensen, 1993; 11 Thordadottir, 1976; 12=Thordardottir, 1973; 13=Naletova *et al*., 1994; 14=Creutzberg & Postma, 1979; 15=Künitzer, 1990; 16=Basford & Eleftheriou, 1988; 17=Thors, 1978; 18=Personal communication N. Pantaleeva. †=estimate from contents in empty shells. * = temperature taken from Kandalaksha bay; ** estimated from daily production.

Standard measurements of height, length and width were made for each shell. The left hand valve of each pair was subsequently treated according to the method described by Ropes (1985) to obtain acetate peels from which the internal growth lines could be read and measured (Witbaard & Duineveld, 1990). Because the date of capture of each specimen is exactly known, the year in which a growth increment had been deposited and the age of the animal could be determined, by counting backwards, starting with the most recently deposited increments.

Since growth during the first phase of life is almost linear (Witbaard & Duineveld, 1990) the coefficient of regression, which expresses the steepness of the regression line, was used as the parameter for growth rate. Therefore, the best fitting least squares linear regression line over the first 10 cumulative increment widths was calculated. For shells younger than 10 years, the regression was calculated over the maximum available number of increments and in shells where the growth record was incomplete, due to erosion of the umbonal region, the number of missing rings was determined by comparing the number of growth increments in the valve with the number of increments in the hinge band. In these cases the regression was subsequently calculated over the number of available increments remaining of the first 10 ontogenetic years. These regression based estimates for shell growth during the juvenile phase have been compared by drawing notched Box and Whisker plots (McGill *et al*., 1978) (figure 5.2).

Figure 5.2

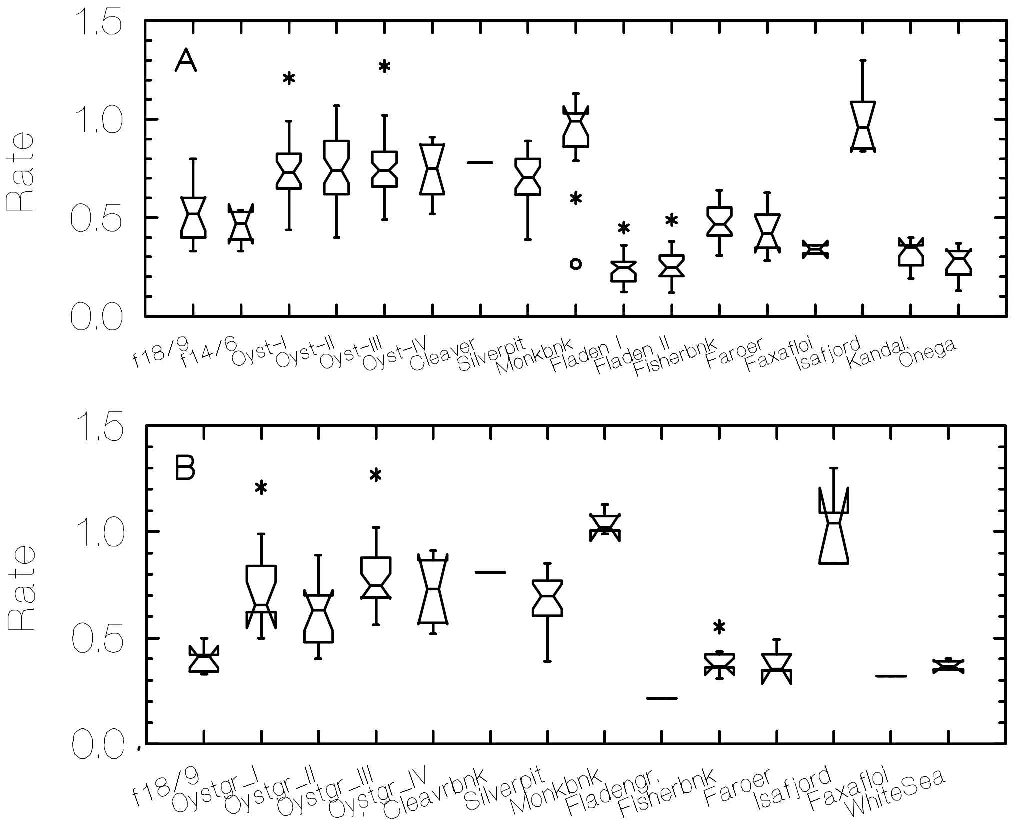


Figure 5.2. Notched Box and Whisker plot of juvenile growth rates of *Arctica islandica*. (a), Growth rates irrespective of the period in which the shells settled on the sea floor. The horizontal bar in each box represents median growth rate. Notches indicate 95% confidence limits. ∗=Outlier (1.5xH); o=far outside value (3xH). A horizontal bar without a notched box (-) represents an average value because 3 or fewer animals were available. (b), Growth rates of juvenile specimens which settled on the sea floor between 1980 and 1990. Legend otherwise as in figure (a).

All individual growth rate estimates during the juvenile phase from each site were averaged to obtain a population average growth rate. These average values were then used in a multiple regression analysis to assess the relative importance of depth, temperature and primary productivity in the determination of shell growth rates. For this purpose it was assumed that growth increases with increasing temperature and food supply (chapter 4). Data on these environmental variables were retrieved from the literature and are listed in table 5.2. The growth rate data were also examined for the possibility of a relationship with geographical latitude. For shell samples which contained both old and young shells, estimated age and shell height were used to construct age-height relationships.

RESULTS

In figure 5.2a the median growth rate of each population is drawn irespective of the year in which the shells settled on the sea-floor. The average rates range from 0.20 to 1.0. The lowest average rates were found for shells from the Fladen Ground (sites 10, 11; northern North Sea) and for shells from the White Sea (sites 17-19 Onega Bay and Kandalaksha Bay); highest rates were found for shells collected from the Ísafjord in north-west Iceland (site 16) and the Monkey Bank (site 9) in the central eastern North Sea. Thus both the fastest and the slowest growth rates were observed at the most northern locations. This suggests that the relationships between growth rate and temperature or geographical latitude might be of less importance than shown in figure 5.4.

Figure 5.3

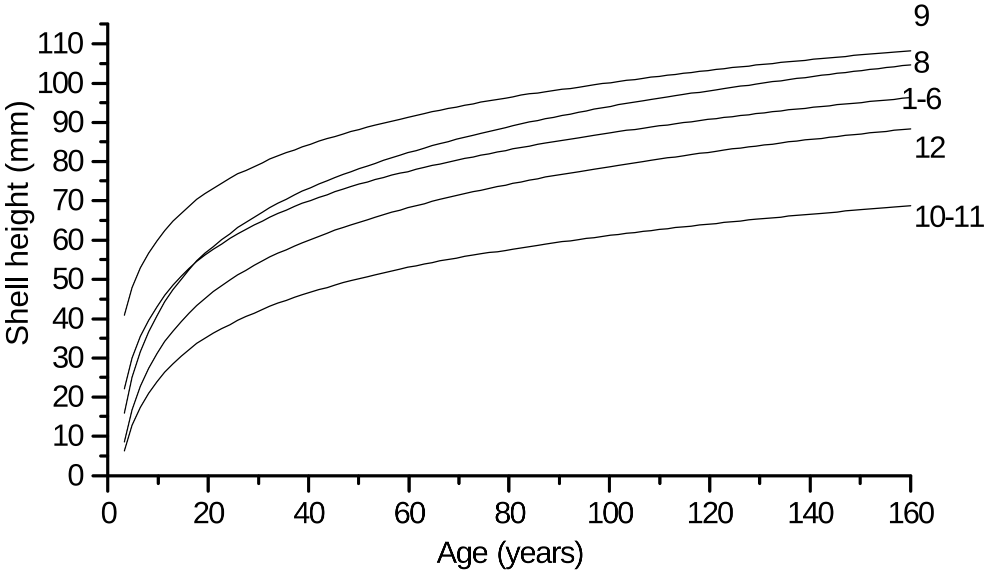


Figure 5.3. Growth curves estimated by least squares regression for all populations from the North Sea for which an almost complete size spectrum of shells was available. Numbers correspond to sites as given in table 5.1 and figure 5.1. 1-6 = Oyster Ground; 8 = Silverpit; 9 = Monkey Bank; 10-11 = Fladen Ground; 12= Fisher Bank. Regression equations are given in table 5.3.

Except for shells from sites 1 and 2 in the Oyster Ground, the average growth rates for shells from the southern North Sea (sites 1-8) are nearly equal and ranged from between 0.69 (site 8, Silverpit) to 0.78 (site 7, Cleaver Bank). The shells sampled from the Oyster Ground (sites 1-6) all have a very similar average growth rate of ~0.75. Shells from both locations in the Fladen Ground (sites 10 & 11) did not differ from one another. Shells from the southern location in the Fladen Ground (site 11) have an average growth rate of 0.26 ± 0.02 and from the northern site 0.24 ± 0.02. Growth rates at the Fisher Bank (site 12) (0.47 ± 0.03) are significantly lower, while shells collected from the Monkey Bank (site 9) had significantly higher growth rates (0.90 ± 0.04) than all of the southern North Sea populations (3-8).

The two shell samples collected from the Faroe Islands (sites 13 & 14) have been pooled and the average growth rate (0.43 ± 0.05) is comparable to the intermediate growth rate of shells from the Fisher Bank. The shells collected from two bays (Onega Bay and Kandalaksha Bay) in the White Sea (sites 17 & 18), have low growth rates of 0.27 ± 0.04 and 0.32 ± 0.04 respectively, while the shells collected from Ísafjord (site 15) in north-west Iceland have significantly higher growth rates (0.99 ± 0.05). Two shells collected from Faxaflói (south-west Iceland) (site 16) were found to have a growth rate of 0.32 and 0.36.

Part of the observed differences in figure 5.2a might reflect temporal variation, since no distinction was made for the period in which the shells settled on the seafloor. Therefore an additional Box and Whisker plot (figure 5.2b) was made which included only specimens which had settled between 1980 and 1990. The figure shows that growth rates for the most recent decade are almost equal to those given in figure 5.2a. The relative differences between populations remain similar. Some populations are not included in this comparison because no individuals were found which had settled after 1980.

Table 5.3

Location (site nr)	Size range	Regression	R	p
Fladen Ground (10-11)	22-73 mm	$H=-12.39+15.98*Ln(A)$.	0.96	<0.001
Oyster Ground (1-6)	15-99 mm	$H=-0.048+18.96*Ln(A)$	0.85	<0.001
Monkey Bank (9)	56-100 mm	$H=20.57+17.28*Ln(A)$	0.93	<0.001
Silverpit (8)	20-93 mm	$H=-10.93+22.78*Ln(A)$	0.89	<0.001
Fisher Bank (12).	21-93 mm	$H=-15.45+20.45*Ln(A)$	0.57	ns.

Table 5.3. Equations for the best fitting regression lines for 5 populations from the North Sea depicted in figure 5.3. Size range denotes shell height (H) in mm. A=age in years; ns= not significant.

All shells from the North Sea originating south of Doggerbank (1-8) have similar growth rates with an average value of 0.69 ± 0.19. Again their growth rate can be contrasted to the lower growth rates of shells from the Fisher Bank (0.40 ± 0.06) and the higher growth rates for Monkey Bank specimens (1.05 ± 0.09). Average growth rates of shells from the locations in the Oyster Ground (1-6) was 0.70 ± 0.19 and varied by location between 0.61 and 0.78. Except for the growth rates of shells from location F18/9 (0.40 ±0.06) neither of these populations differed significantly.

Although the clam sample from the Cleaver Bank was represented by only 2 specimens which had settled in the eighties, it indicates a somewhat higher average growth rate (0.80) compared to the rest of the southern North Sea. The single specimen of this age group from the Fladen Ground again indicated a much lower growth rate of 0.21 for the deep northern North Sea.

In figure 5.3, the age-height curves are given for 5 populations from the North Sea for which the entire size-spectrum of shells was available. The corresponding equations for the calculated best fitting regression lines are given in table 5.3. Comparison of these curves with both the uncorrected and the time-corrected (settled between 1980 and 1990) growth rate estimates for the first 10 years of life, indicates very similar relative differences between populations. This implies that the growth rates reflect a long-term systematic difference in one or more of the basic environmental site characteristics such as temperature, water column productivity, sedimentation or food supply.

The inter-relationship between standardized growth rates and environmental variables was analysed by principal component analyses (PCA) and is summarized as biplot in figure 5.4. The cosine between two vectors equals the correlation between two variables. Thus an angle of about 90° means no correlation and an angle of 180° means that two variables are negatively correlated. About 60% of the total variance is explained by both components. It can readily be seen from the figure that the average growth rates are negatively correlated with depth but positively correlated with primary production and temperature. The relationships with grain size or silt is less strong. The inverse relationship between growth rate and latitude is almost certainly due to the effects of temperature since both have a strong but negative correlation ($R=-0.90$, $p<0.001$).

The data from the North Sea tend to split from the other data as indicated by the separation of filled and hollow symbols. The North Sea data were therefore analysed separately as well. This demonstrated that although most relations remained very similar the correlation with primary production became less strong. The correlation with grain size was highly significant (figure 5.5). For the North Sea the first two principal axis explain 90% of the variance.

Figure 5.4

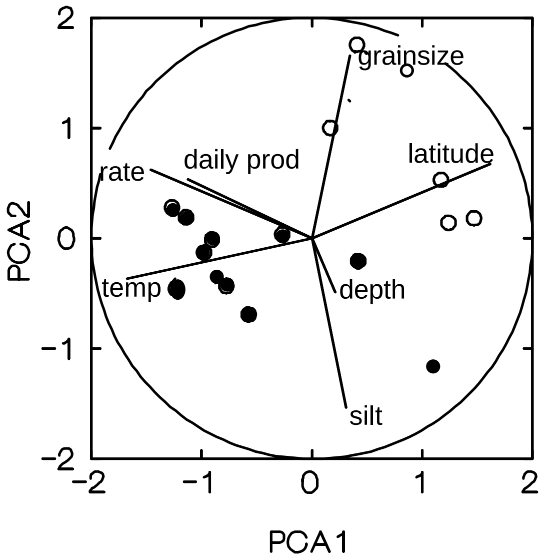


Figure 5.4. Covariance biplot of growth rate and environmental data. Dots indicate sample scores on the first and second PCA axis. Open symbols represent stations outside the North Sea (13-19), filled symbols represent stations within the North Sea (1-12).

The environmental data were used to construct a multiple regression model which at best describes the observed growth rates within the constraints of increasing growth with increasing temperature and increasing food supply (see chapter 4). Simultaneously, an inverse interaction between food supply and depth is believed to exist; *i.e.* the amount of the primary production which reaches the seafloor depends on depth. The model tested had the general form of:

*Rate=constant+ a*primary production+b*average temperature+c*(depth∗ primary production).*

The standardised regression coefficients calculated for such a model then give the relative contribution of each factor in explaining the total variance. The results of the fit of this model are given in table 5.4a. This table illustrates that the probabilities for all individual factors are below or close to significance level and the combination of these three factors could effectively explain ~50% of the total variance (table 5.4b). The interaction between depth and primary production has the highest effect (standard coefficient = -0.92), followed by the effects of temperature (0.90) and primary production itself (0.47). Introduction of other parameters in the model led to spurious and often insignificant results without any ecological meaning.

Table 5.4a

Variable	Coefficient	Std Error	Std Coef	Tolerance	T	p (2 Tail)
Constant	-0.051	0.231	0.000	-	-0.221	0.828
Average temp.	0.107	0.048	0.897	0.235	2.236	0.042
Primary production	0.001	0.000	0.468	0.646	1.933	0.074
Depth*prim. prod.	-0.00005	0.000	-0.922	0.253	-2.386	0.032

Table 5.4b

Source	Sum-Squares	DF	Mean-Square	F-Ratio	p
Regression	0.448	3	0.149	4.155	0.027
Residual	0.504	14	0.036		

Table 5.4a. Results of the multiple regression fit of the model, *Rate=constant+ a*primary production+b*average temperature+c*(depth∗ primary production)* for all data. (a), Standard coefficients give relative contribution of each factor in explaining the total variance. (b), Analysis of variance for the multiple regression model for which the parameters are given in table (a), The fit is significant at $p<0.05$.

When the same methods were applied to only the North Sea populations, the same three factors explained 75% of the total variance (table 5.5). While the effect of temperature for the model applied to all data is large, its relative influence for the North Sea subset is negligible (standard coefficient= -0.098). Instead, the primary production is the most important determinant of growth rate with a standard coefficient of 1.26. The combined effect of depth and primary production is comparable in both cases (-0.922 and -0.851). The "-" sign illustrates that growth decreases with increasing depth which is presumably due to a reduced flux of material towards the bottom.

Introduction of grain size, as additional term indicative of lateral transport, does not improve the model significantly. If depth itself is introduced as an additional factor, 10% more of the variance is explained.

DISCUSSION

Both the age-height curves and the steepness of the regression lines over the first 10 increments resulted in similar relative growth differences between populations. Shells from the Monkey Bank grow the fastest and shells from the Fladen Ground have the lowest growth rates. The very similar estimates by both methods was not unexpected since there is a good relation between the increment widths measured in the hinge band and in the valve (Thompson *et al.*, 1980a). Furthermore, it appeared that shells from the Oyster Ground all had very similar growth rates. This is counter to the expectation that shells from the southern border (Oyster Ground II) would have grown faster than shells from the other locations within the area. This is because that population originates from a frontal area with enhanced production (Gee *et al.*, 1991) and increased bottom chlorophyll concentrations (Creutzberg, 1985). In fact, the samples in the more eastern parts of this area (sites 3, 5 & 6) had the highest rates. A possible explanation for this pattern might be related to the hydrography of the area. Residual currents flowing in a north-east direction may transport material to these downstream locations. Here *Arctica*, as a filter feeder, could benefit from this increased supply.

Table 5.5a

Variable	Coefficient	Std Error	Std Coef	Tolerance	T	p (2 Tail)
Constant	0.957	0.551	0.000	-	1.736	0.121
Average temp.	-0.016	0.081	-0.098	0.132	-0.202	0.845
Primary production	0.002	0.001	1.259	0.108	2.352	0.047
Depth *Prim. prod	-0.00007	0.000	-0.945	0.525	-3.890	0.005

Table 5.5b

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Regression	0.381	3	0.127	8.086	0.008
Residual	0.126	8	0.016		

Table 5.5. Results of multiple regression analyses for the North Sea data. (a), Standard coefficients give the relative contribution of each factor in explaining the total variance. (b), Analysis of variance for the multiple regression model of which the parameters are given in table (a).

The observed growth rates fit well within the ranges reported for other areas. Ropes & Pyoas (1982), Murawski *et al.* (1982), and Rowell *et al.* (1990) used age-length relations to describe growth for the populations off the American and Canadian east coast. Following the procedure of Thompson *et al.* (1980a), shell height was used in this study as measure for shell size, since it corresponds to the direction in which the shells were sectioned for the preparation of the acetate peels (chapter 1). For the purpose of conversion, an average ratio of height : length = 0.91 (± 0.03 n=771) can be used.

If a comparison is made with the American populations, it appears that shells from the Monkey Bank (site 9) have growth rates which are very similar to those from the

Georges Bank (north-west Atlantic). Shells from the Silverpit (8) and Oyster Ground (1-6) have growth rates similar to those from Long Island (Mid-Atlantic Bight) (table 5.6). The regression coefficient of approximately 0.70 (estimated from Thompson's (1980a) figure 5.6 of cumulative hingeband width against age) also suggests very similar growth rates for shells from the southern North Sea and the Mid-Atlantic Bight. Rowell *et al*. (1990) studied shells of two near-shore populations from Nova Scotia (Canada) and found that 10 year old shells varied in length from 40 to 50 mm. At an age of 20 years shell length is approximately 55 mm implying that the growth rate is also comparable to those of shells from the southern North Sea. Fritz (1991) studied age and growth of large specimens (>70 mm length) only. These were collected off New Jersey and belong to those with the highest growth rates, comparable to those from Georges Bank, Monkey Bank or Ísafjord (table 5.6). Thus, most size-at-age data obtained from this study compare well to the ranges reported earlier for the American and Canadian east coast. However, it is evident that the growth rates of shells from the Fladen Ground and the White Sea have the lowest rates recorded to date.

Table 5.6.

Age	North Sea					N. Atlantic			Western Atlantic				
year	Oyster	Fladen	Monk	Silver	Fisher	White Sea	Ísa fjord		Nova Scotia	Nw Jersey	Nw Jersey	Georges Bank	Long Island
10	43.6	24.4	60.4	41.5	31.6	17.3	51.1		≅45	-	-	60.9	41.4
20	56.8	35.5	72.3	57.3	45.8	30.1	62.5		≅55	-	-	69.9	58.7
50	74.2	50.1	88.2	78.2	64.6	-	-	-	-	82.8	80.7	83.8	-
100	87.3	61.2	100.1	94.0	78.7	-	-	-	-	90.5	87.2	96.1	-

Table 5.6. Shell height (mm) at a given age (years) for populations in the north-west European waters and along the American and Canadian coast. Data are derived from this study as well as from literature sources which are mentioned in the text.

Such data do not, however, explain the causative factors for the observed variation in growth rates. As a filter feeder, *Arctica* is directly dependent on the amount of suspended phytodetritus in the bottom water. This benthic food availability is determined by the quantity of sedimenting material which arrives at the bottom water. This in turn will depend on primary production, water column processes and water depth. Once the material has settled on the sea floor, it is no longer available to suspension feeders, unless it becomes resuspended by bottom currents. Such resuspended material may be an important (additional) food source (Grizzle & Morin, 1989; Wildish & Kristmanson, 1985) but could not be used as a variable in this study because too few data were available. Instead, sediment grain size was used as a measure for such additional food supply because it might be an indication for resuspension by bottom water currents, at least in shallow areas. If true, higher growth rates can be expected in coarse grained sediments because of higher bottom seston fluxes. This relation is evident for North Sea specimens (figure 5.5).

The most likely factors responsible for the observed population differences in growth rates are primary production and temperature (table 5.2). The role of temperature, however, is less clear than would be expected based on theoretical grounds as indicated by the results in chapter 4 or on the Q_{10} values given by Winter (1969).

Figure 5.5

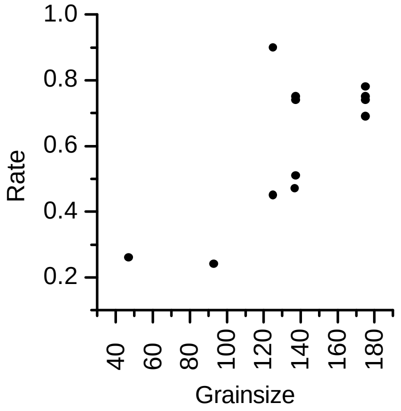


Figure 5.5. Growth rate of North Sea *Arctica* plotted against median grainsize in µm.

While the standard-coefficient for temperature in the multiple regression model (applied to the entire dataset) is significant, such significance could not be demonstrated when the model was applied only to the North Sea data. Hence, the difference in growth rates between shells from Monkey Bank, Fisher Bank and Fladen Ground could not be explained by a difference in average temperature. Similarly, the comparison of size at a given age for shells from the New York Bight and the Oyster Ground (table 5.6) suggests the importance of factors other than temperature alone. Size at a given age is comparable in both areas, although the average temperature in the New York Bight is 2.5°C lower and the maximum temperature almost 5°C lower. The fastest growing shells from Ísafjord, living at an average temperature of 4.7°C, also illustrate that temperature is easily over-ruled by other factors. Primary productivity, with its associated supply to the benthos, seems to be most relevant of these. The results of this study, as well as data from the literature suggest such a link.

Growth rates in areas with higher water column productivity are generally higher. In the Oyster Ground, with an estimated primary production of 270-420 gCyr^{-1}m^{-2} (Gee *et al*., 1991) shell growth is 3 times as fast as in shells from the Fladen Ground, for which the primary production is estimated at 90-100 gCyr^{-1}m^{-2} (Steele, 1974; Steele, 1956). Similar trends can be observed along the American east coast. Shells from the highly productive Georges Bank (249-423 gCyr^{-1}m^{-2}; O'Reilly & Busch, 1984) grow faster than shells from the less productive New York Bight (230-270 gCyr^{-1}m^{-2}; O'Reilly & Busch, 1984) or Sable Bank (102-128 gCyr^{-1}m^{-2}; Mills & Fournier, 1979). The significant relation of growth rate to primary production as found in this study, was nevertheless surprising. This is because earlier attempts to relate interannual variations in shell growth of *Arctica* to variations in the phytoplankton community, as recorded by the CPR data (Witbaard, 1996, chapter 7) were unsuccesfull. Josefson *et al*. (1995) was also unable to demonstrate a relationship between the growth of shells at the pycnocline and the locally increased food availability.

High primary production is likely to lead to increased benthic supply although the amount of phytodetritus which ultimately reaches the bottom is dependent on processes taking place in the water column as well as on water depth. The inverse relation between shell growth and depth is nicely illustrated by the fast growing but shallow living (5-7 meter) shells from Ísajord. The short water column enables these shells to almost utilise directly the material which has been produced in the upper water layers. Besides higher quantities of food, these shells probably also receive material of better quality. On its short way down, very little decompositon of the phytodetritus will occur. Deep living shells will not only receive only a portion of what has been produced in the upper water layers (25 to 30%, Davies & Payne, 1984), but will in addition receive material of lower quality because decomposition already has started during its way down.

While production and sedimentation in relation to water depth strongly influence benthic food supply, the actual utilisation and availabiltiy is also dependent on animal responses (Grizzle *et al*., 1992), benthic boundary layer processes (Frechette *et al*., 1993), sediment topography (Yager *et al*., 1993), and advective transport (Grizzle & Lutz, 1989; Wildish & Kristmanson, 1985). Additional supply by lateral advection may indeed be an important food source for *Arctica* in the North Sea. This is suggested by the strong correlation between shell growth and sediment grain size (figure 5.5). Increased growth rates in coarse sediments were also reported by Duineveld &

Jenness (1984) for the echinoid *Echinocardium cordatum*. They also attributed this trend to the increased food availability in the southern North Sea due to resuspension. Thus, the results of the present study show that observed latitudinal differences could be best explained by the effects of temperature, primary production and food supply, the latter expressed as an interaction between production and depth. The extremely high growth rates of shells from north-west Iceland and the insignificance of the temperature effects for North Sea populations suggest however, that temperature is easily overruled by other factors. This is especially evident for the North Sea data where the high correlation between growth and grain size suggest that food supply by lateral advection may be an important food source. Such a mechanism might then explain the poor relationship between phytoplankton abundance and inter-annual growth variations as reported by Witbaard (1996) or Josefson *et al*. (1995). It poses interesting questions on the availability, quality and utilisation of suspended material by benthic filter feeding macrofauna and stresses the importance of measuring food availability and quality at a scale which is relevant to macrobenthos. Only then a better understanding of the structure and functioning of the benthic ecosystem can be achieved.

ACKNOWLEDGEMENTS

This study would not have been possible without the enormous supply of *Arctica* provided by colleagues and friends. Therefore I would like to thank A.R. Boeyen for the supply of many shell samples from the North Sea as well as the many colleagues from NIOZ with especially the crew of RV Pelagia for their major contribution and enthusiasm in collecting *Arctica*. Thanks are also given to Dr. G.W.M. van Moorsel from Bureau Waardenburg for the supply of *Arctica* from the Cleaver Bank, Dr. Steingrímsson from the Marine Biological Institute in Reykjavík who collected the *Arctica* from north-west Iceland, Dr. A. Norrevang and Dr J.A. Sneli for the shells from Faroe Islands and Dr. N. Panteleeva (Dalnie Zelentsy, Russia) for the shells from the White Sea.