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Shell-growth of the bivalve Arctica islandica (L.), and its possible use for evaluating the status of the benthos in the subtidal North Sea

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Growth of *Arctica islandica* (Linné, 1767) was studied by means of acetate peels made of cross-sections of the hinge-tooth in the left valve. Both geographical and temporal growth differences exist. Specimens from the Oyster Grounds (southern North Sea) are growing faster than specimens from the Fladen Grounds (northern North Sea). In the beginning of this century Fladen Grounds animals grew faster than in the last decade. Furthermore the possible existence of long-term fluctuations in growth were investigated.

Key words: Bivalvia, Arcticidae, *Arctica islandica*, shell-growth, growth patterns, growth differences, North Sea.

INTRODUCTION

Growing concern about the possible adverse effects of increasing human impact on the benthic environment of the North Sea has resulted in a large quantity of recent data on the distribution and ecology of species and species-assemblages. For the evaluation of these data in terms of a negative or a positive development, it is necessary to have information on the variation of the parameters (temperature, food) involved. Yearly fluctuations in, for instance, the growth of subtidal North Sea benthos as related to the seasonal temperature cycle and food input are well known. However, growth fluctuations over longer periods have hardly been documented for subtidal species and yet, this type of data is imperative for assessing the present-day quality of the benthic environment.

In analogy with a tree, which contains a long record of its growth in the form of annual bands, one would like to have benthic animals with regular growth marks and a longer than usual life span. Suitable animals with skeletal growth marks, such as molluscs, generally have life spans of no more than ten years (Powell & Cummins, 1985); however, the bivalve *Arctica islandica* seems to be an exception.

For *A. islandica* from the east Atlantic coast, Thompson, Jones & Dreibelbis (1980) and Ropes (1985) have found evidence for the regular, in this case annual, formation of bands in the shell. They concluded that a maximum age of more than 150 years can be reached. For *A. islandica* living in the North Sea, estimates for age have not been made. Unraveling of growth patterns of *A. islandica* recorded in their shells during the past decades, may yield an indication for a general trend in their growth rates which subsequently can be related to one or more environmental variables. Moreover, comparison of growth patterns from different localities could throw some light on the historical and recent differences of the growth conditions.

In the present paper, growth rates of *A. islandica* of varying sizes (ages) from two localities in the North Sea are compared. Furthermore some preliminary attempts to detect general fluctuations in the growth rate are presented.

Biology of *A. islandica*

A. islandica is a large bivalve of approximately 13 cm maximum length with a thick heavy shell. In large specimens, the shell is covered by a black periostracum, but in juveniles it is light brown. Its distribution is boreo-atlantic and is limited by temperatures ranging between 0°C to 19°C (Nicol, 1951). In the North Sea the species is most common in the deeper parts north of Dogger Bank, but it is also regularly found in low numbers in the Oyster Grounds south of Dogger Bank. *A. islandica* seems to prefer fine, silty sediments, but has also been recorded from coarse sediments near Iceland (Madsen cited by Nicol, 1951).

A. islandica is a dioecious species with planktotrophic larvae. The reproductive season varies geographically (Von Oertzen, 1972). East Atlantic specimens seem to reproduce for the first time at about the age of ten years (Thompson, Jones & Ropes, 1980). According to Merrill et al. (1969) and Yonge & Thompson (1976) the species feeds on algae. Occasionally *A. islandica* buries itself in the sediment to a depth of several centimeters and assumes an anaerobic respiration (Taylor, 1976).

A. islandica is eaten by various fish species such as cod and haddock (Arntz, 1974; Cramer & Daan, 1986) and in shallower coastal areas (Baltic) also by eider ducks. Along the American east coast there is a commercial fishery for *A. islandica* (16000 tons meat in 1979) (Murawski et al., 1982).

MATERIAL AND METHODS

Origin of the material

The specimens were collected in the Fladen Grounds during the REFLEX program in 1983 (De Wilde et al., 1986) and from the Oyster Grounds during 1979 and 1980 (leg. F. Creutzberg). A beam trawl or a boxcore were used for collecting the animals. In the spring of 1988, additional material was collected in the Oyster Grounds area.

The Fladen Grounds, are situated in the northern North Sea (fig. 1). The local water depth is 100 m and the sediment consists mostly (> 80%) of silt and clay. The average water temperature near the bottom in the Fladen Grounds is 6.5°C with a yearly variation of only 1-2°C. Steele (1974) estimated the primary production in the Fladen Grounds to be 90 g $C/m^2/y$. Recent estimates by Fransz & Gieskes (1984) surpass 100 g $C/m^2/y$, but only a small part of this amount seems to reach the bottom (Cadée, 1986).

The relatively shallow (30-50 m depth) Oyster Grounds, south of Dogger Bank (fig. 1) are covered with fine sediment mixed with moderate amounts of silt and clay (10-20%). The yearly primary production is estimated to be 250 g C/m^2 (see De Wilde et al., 1984). Here the bottom water temperature varies between 4°C and 17°C.

The material from the Oyster Grounds consisted solely of medium-sized (7 cm) and large (> 9 cm) specimens, whereas the Fladen Grounds material also contained small (< 5 cm) specimens. Additonal specimens from the Baltic (don. C. Swennen, NIOZ) were retrieved from the stomachs of eider ducks. This material consisted of small to medium-sized specimens.

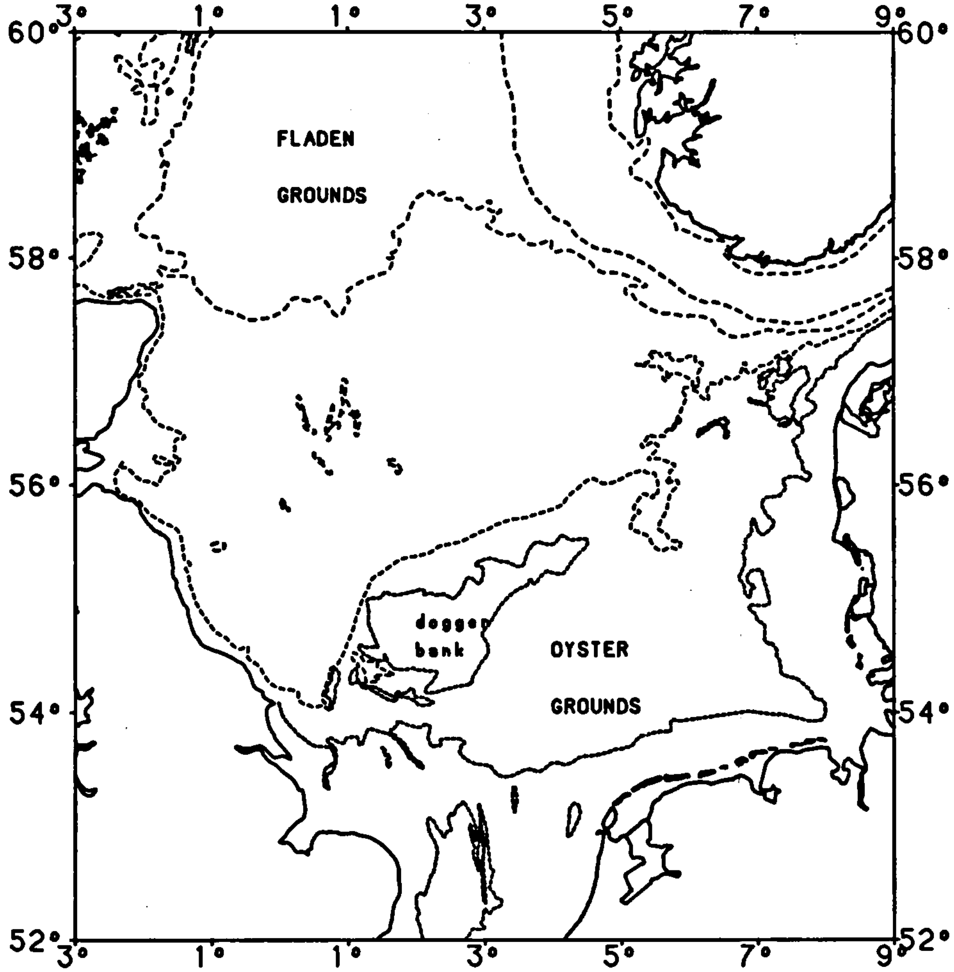

Fig. 1. The North Sea with the locations as mentioned in the text. Animals were collected in the Fladen Grounds during the Reflex program in 1983 (De Wilde et al., 1986) and in the Oyster Grounds in 1979/80 and in 1988.

Method

The internal growth bands in shells of *A. islandica* were studied along cross sections of the unique hinge tooth in the left valve. To prevent splintering of the shell edge while sectioning (with a diamond saw), the valve was first immersed in epoxy resin (Polyservice THV 500). The valve was then cut along a line through the hinge tooth to the point of maximum shell extension (fig. 2). After polishing with carborundum powders, the cut edge was etched in a solution of HCl, creating a microrelief caused

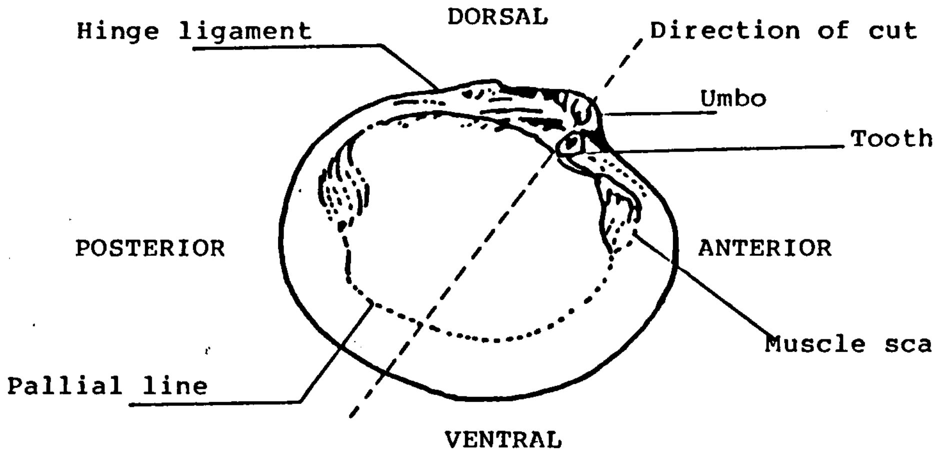

Fig. 2. Main morphological features of the left valve of *A. islandica*. The direction in which the cross-section was made is indicated by the dotted line (after Ropes, 1985).

by different effects of etching on growth-lines and growth-bands. Finally, the relief was transferred to a sheet of cellulose acetate ('acetate peel') (Kennish et al., 1980).

The width of the growth-bands represented in the acetate peels (fig. 3) were measured using an ocular micrometer mounted in a Zeiss compound microscope. Following the procedure of Ropes (1985), only the pattern in the hinge tooth was studied since the formation of this part of the shell is believed to be less susceptible to erratic environmental disturbance.

Statistical analysis of the growth patterns was performed by means of FORTRAN subroutines derived from the NAG library.

RESULTS

Regional and temporal differences in growth

The growth-bands along the first part of the axis of growth of the hinge tooth are easily distinguishable, but become progressively narrower along the distal portion of the axis of growth (fig. 4). This holds for all specimens collected in the North Sea and agrees with the high growth rate of juvenile and the reduced growth rate of adult specimens of molluscs in general [cf. *Spisula solidissima* (Dillwyn, 1817); Jones et al., 1978]. The specimens from the shallow Baltic habitat, however, had a much more erratic sequence of growth-band widths which showed little similarity to the North Sea specimens.

In order to model the growth, the width of successive bands was plotted cumulatively against the number of bands. Some examples are given in fig. 5. What is striking in this figure is the more or less abrupt transition from rapid growth to a phase of slow growth. Probably this change coincides with the onset of reproduction

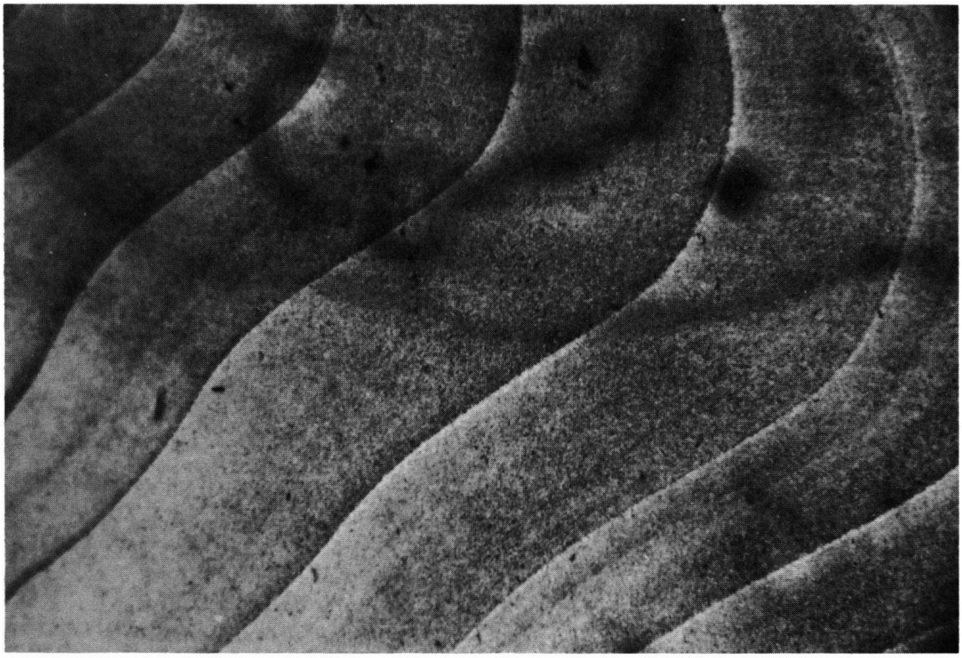

Fig. 3. Micrograph of growth bands as visible in an acetate peel of the hinge tooth. Magnification 6.3 x.

(Thompson, Jones & Ropes, 1980) resulting in a slowing down of shell growth. The exact position of this inflection point varies among individuals, but seems to be roughly situated between band 10 and 15 in all North Sea specimens.

Several generalized models are available to describe the growth of invertebrates over their entire lifespan (see, e.g. Gage, 1987). Analysis of the present material, however, showed that in the case of *A. islandica*, growth could be best described by combining two models. A similar approach has been followed by Murawski et al. (1982).

In a regression analysis a simple linear model $Y = a + bX$ showed the best fit for the first ten years in the North Sea material. In this model "b" denotes the estimated growth rate; "a" the width of the first measured growth-band; "X" the band number and "Y" the cumulative band width. Since not all specimens contained ten growth-bands, only the first eight bands have been taken into account. The estimated growth rates (b in the regression model) with calculated comparison intervals (see Sokal & Rohlf, 1981) have been plotted in fig. 6a for all North Sea individuals sampled. This figure shows that the growth-rates of Fladen Grounds animals are much lower than those of the Oyster Grounds animals. It is also clear that presently young Fladen Grounds animals are growing slower than the now old ones did in their youth.

For the second phase of (slow) growth in adult specimens, the best fit was found using the model $Y = a + b(\log X)$. For this phase estimated growth-rates (b) and comparison intervals are shown in fig. 6b. In this case the slowest growth was also found

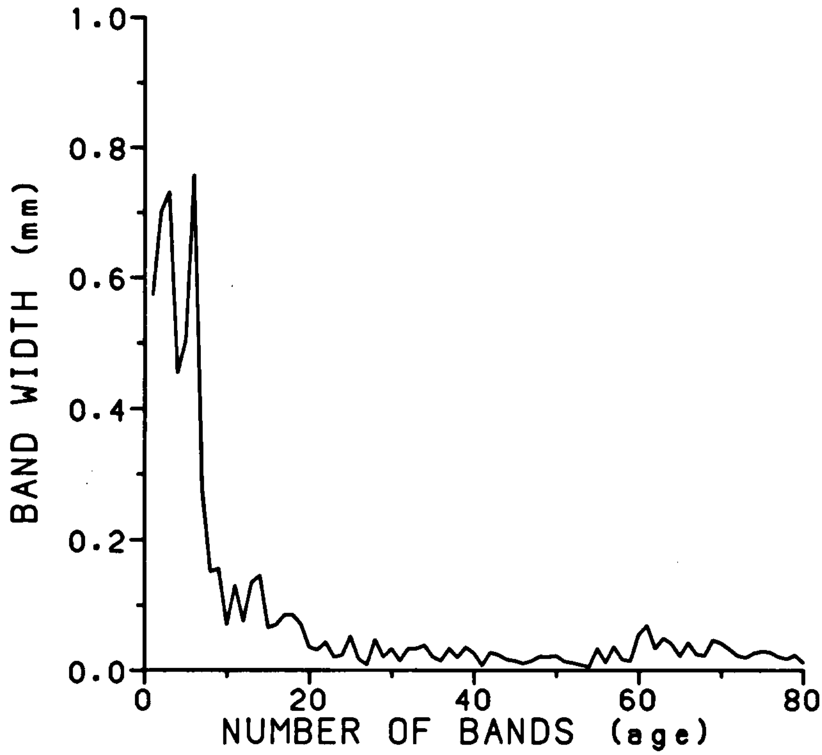

Fig. 4. Plot of the width of succesive bands in the hinge tooth of *A. islandica*. Noticable is the abrupt decline in growth band width at an age of about ten years.

in the Fladen Grounds material. From this it can be concluded that during the past 100-150 years, conditions for growth of *A. islandica* have been better in the Oyster Grounds as compared to the Fladen Grounds. This implies that the recently established gross differences in primary production and temperature in these areas, which directly influence the scope for growth of the suspension-feeding *A. islandica*, have probably existed throughout this period.

Long-term fluctuations in growth

Considering the resemblance of growth fluctuations within young Fladen Grounds specimens given in fig. 7 it seems reasonable to assume that such simultaneous fluctuations have been induced by one or more external factor(s). It is expected that such environmentally induced patterns are also apparent in the long phase of slow growth in adult *A. islandica*.

The fluctuations in actual growth can be regarded as deviations from the expected value. For the present case the expected growth has been calculated on the basis of

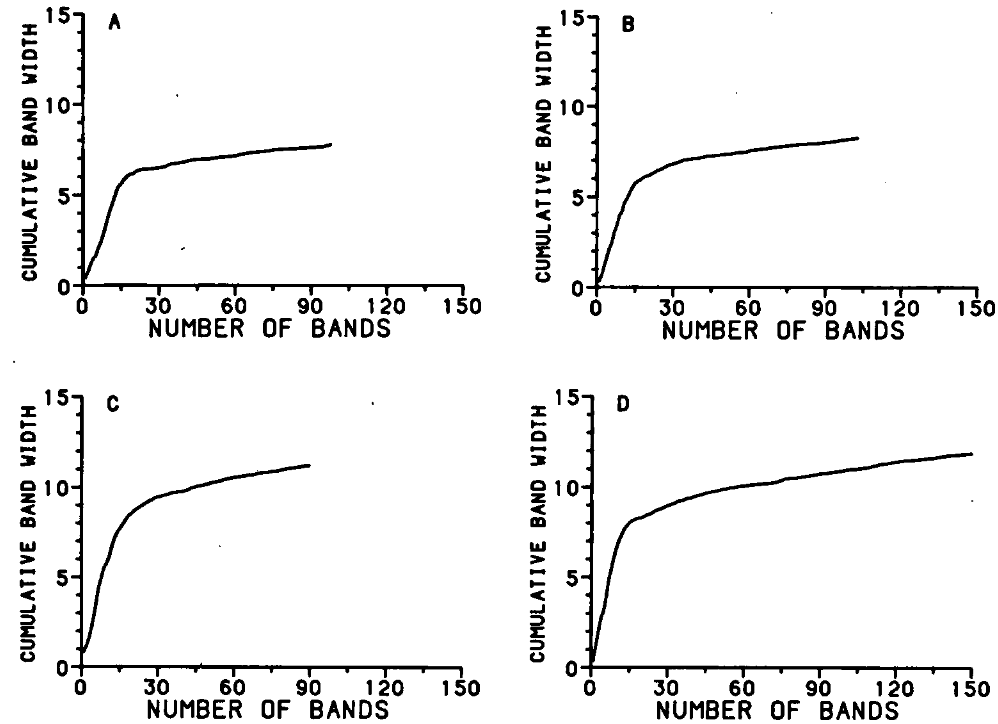

Fig. 5. Growth curves for two Fladen Grounds (A & B) and two Oyster Grounds specimens (C & D). The vertical axes show the cumulative hingeband width in µm. The horizontal axes show the number of growth bands.

the regression model Y = a + b(logX), whereas deviations from the expected growth were calculated as the ratio between expected and actual growth. For studying trends, only fluctuations with a long period are of interest. Therefore a moving average (five years) was calculated through the data-points. Some preliminary results for adult animals from both the Fladen and Oyster Grounds are shown in fig. 8. In five out of seven Fladen Grounds specimens investigated, there are indications of the existence of three periods of relatively fast growth. In the remaining two specimens the pattern is less pronounced. The peaks and troughs, however, do not coincide in all individuals which impedes the interpretation of the patterns. There is no definite explanation for these shifting peaks. They could be artefacts as well as for example endogenous growth cycles.

Within the Oyster Grounds material there is some resemblance between the long term growth patterns of the studied specimens. However, the degree of similarity is smaller than in Fladen Grounds specimens.

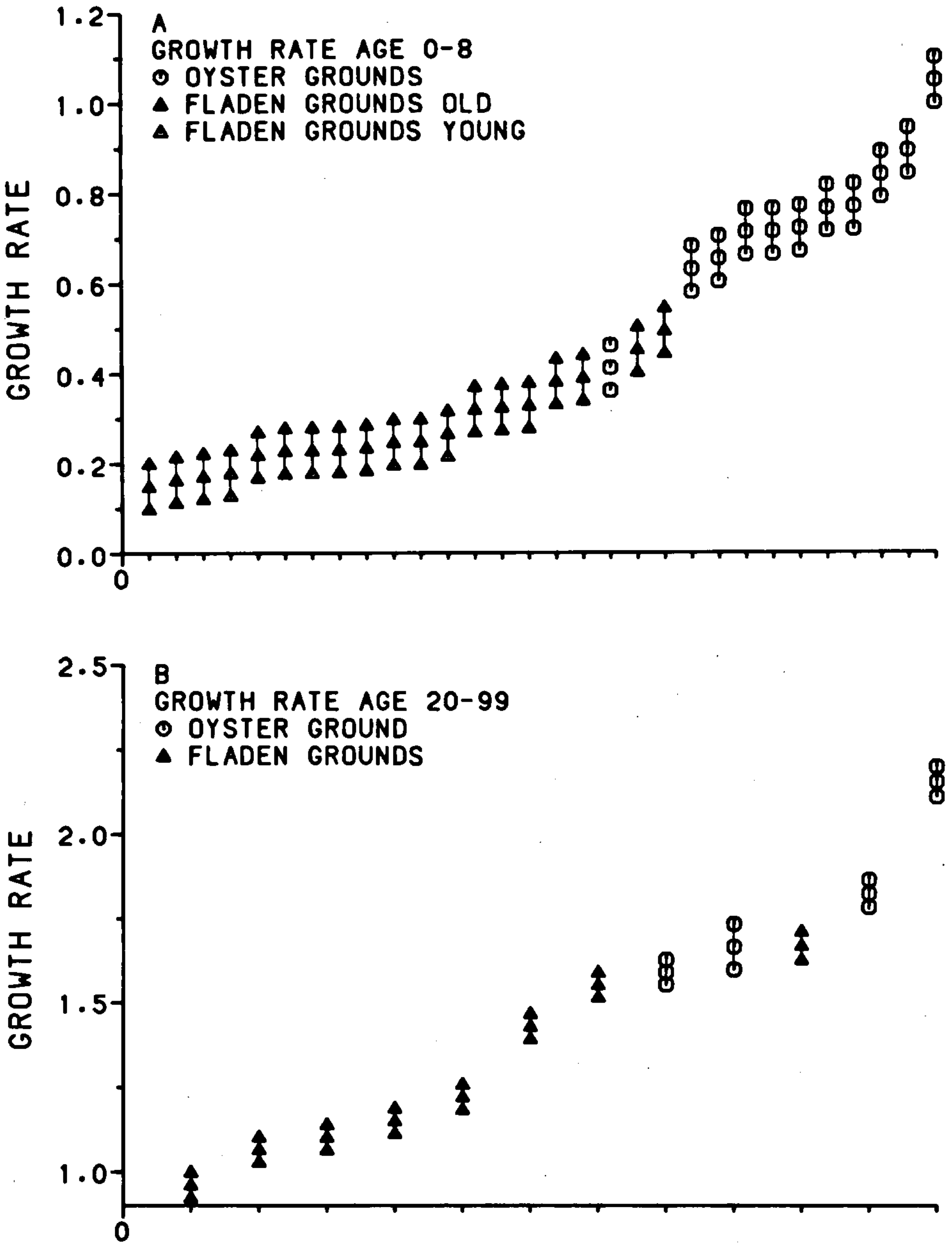

Fig. 6. Comparison of growth-rate estimates (b) of *A. islandica* specimens from different geographical regions. On the vertical axes the estimated growth-rate is given. Around the growth-rate (b) a comparison interval was calculated, denoted by the vertical line. A. Shows the growth rate (b) during the first eight years of life calculated on basis of the model Y = a + bX. B. Shows growth-rate (b) during years 20 to 99 calculated on basis of the model Y = a + b(logX). Non-overlapping comparison intervals denote a significant difference between the respective growth-rates.

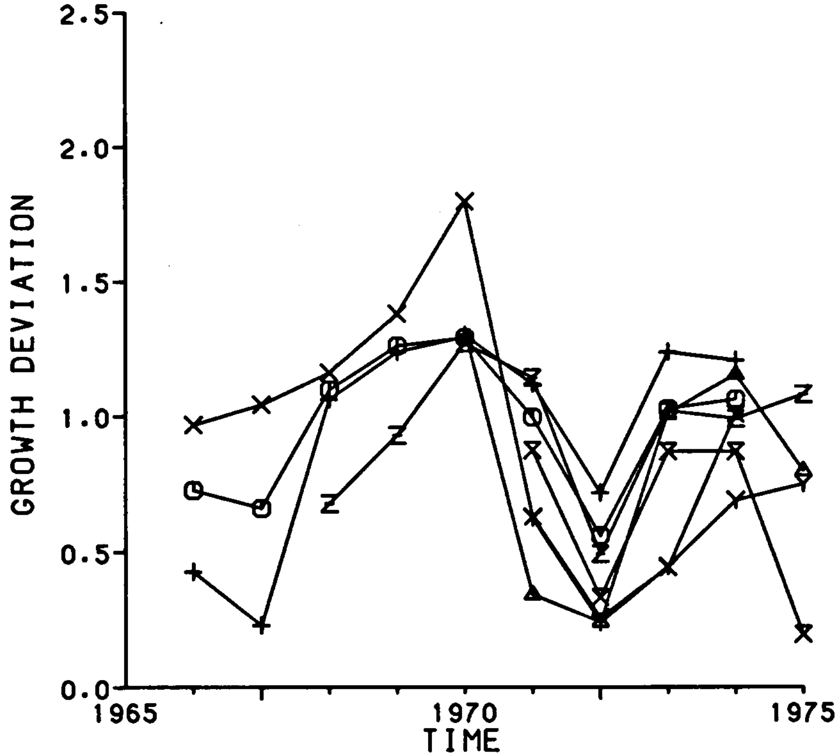

Fig. 7. Growth deviations from expected growth of young Fladen Grounds animals of *A. islandica*. This figure illustrates that external factors exert influence on the population and that growth deviations are not inherent to the individual.

DISCUSSION

An essential prerequisite for drawing conclusions from the measurements shown in this paper, is knowledge about the frequency with which growth-bands are deposited in the shell. Experiments with marked and recaptured *A. islandica* shells along the U.S. east coast showed the formation of one band per year (Murawski et al., 1982). Additional evidence for the annual formation of growth-bands is obtained from measurements on man introduced and natural radio-isotopes (see Turekian et al., 1982; Bennet et al., 1982). However, Turekian et al. (1982) stated that on the basis of the ^{14}C content, shallow-living *A. islandica* may have a biannual periodicity whereas deep-living (55 m depth) *A. islandica* probably have an annual periodicity in the formation of growth-bands.

Since several of the afore-mentioned measurements were done on only a few animals, and since quite young animals were used, more definite proof for the annual periodicity in *A. islandica* is required. This applies especially to the densely aligned bands in the outer part of large shells. The frequently abrupt transition in the width

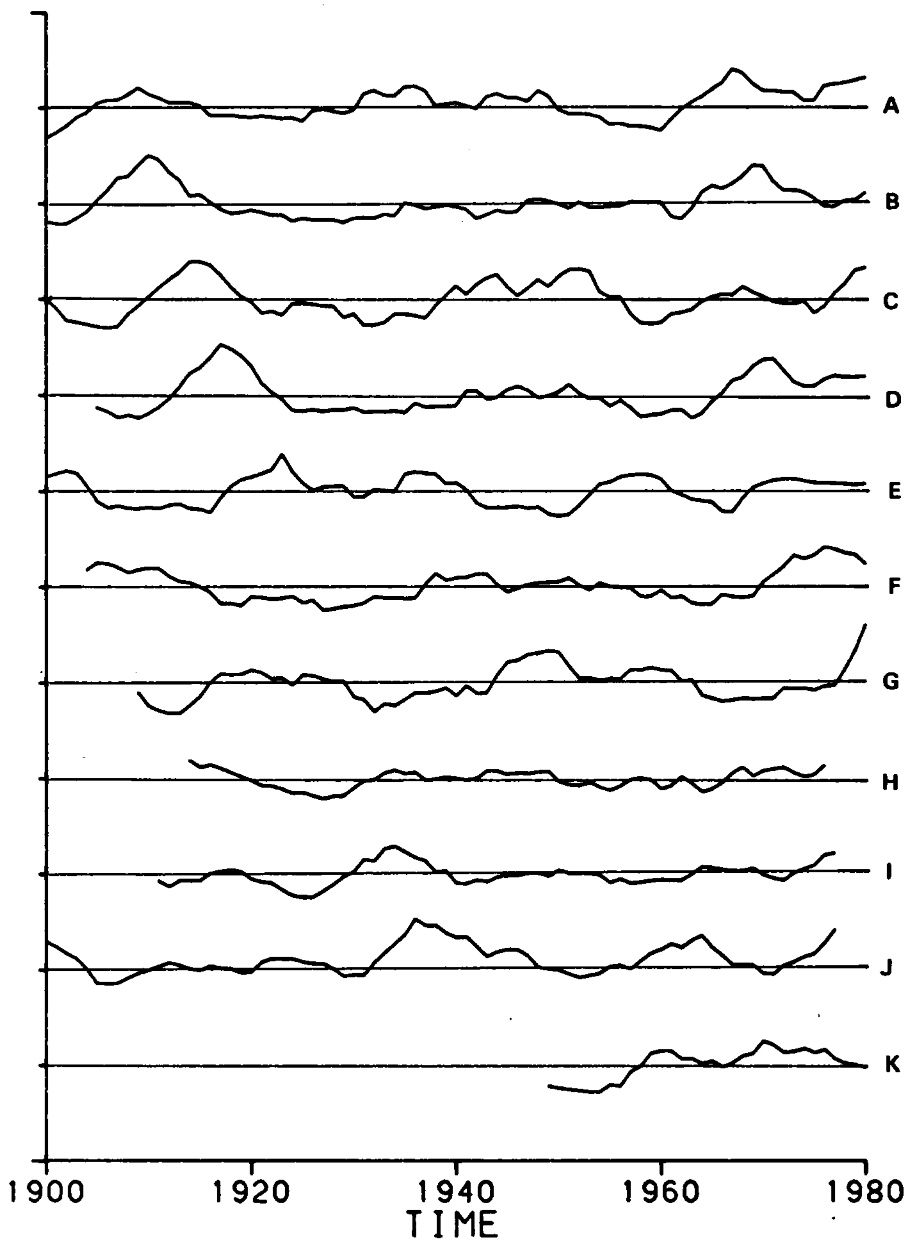

Fig. 8. Long-term fluctuations in the growth of Fladen Grounds (a to g) and Oyster Grounds (h to k) animals of *A. islandica*. The straight horizontal line represents the mean growth. The fluctuating line represents the five year moving average of the quotient of measured and expected growth. The latter is based on the calculated regression model Y = a + b(logX) for the age of 20 to 99.

of successive bands (see fig. 5) may indicate a change in periodicity, possibly in conjunction with sexual maturity. Before being amenable to analysis of growth fluctuations, an exact dating should be performed on one or several growth bands in the shell of *A. islandica.* Bomb deposited ^{14}C would perhaps be a means for calibrating the growth bands. More research on this subject is presently being carried out by the authors.

Despite this lack of information, we have tentatively tried to elucidate growth fluctuations, assuming that every band observed in North Sea *A. islandica* represents a one-year period. One of the first problems we faced was how to define the 'normal' growth in order to detect any deviations. There are to our knowledge no data on the growth of *A. islandica* under constant conditions. The 'normal' growth therefore has to be inferred from the growth, including all fluctuations, observed in the field. Our analysis has shown that in all North Sea *A. islandica*, the entire adult growth-phase can be adequately described by one (and the same) function. This implies that growth in any one year bears a fixed relationship, not only to the growth in prior years, but also in the years thereafter. The magnitude of this relationship varies individually as shown by the different values for the coefficients in the regression model. These observations persuaded us to use the deviations from the average individual growth, predicted by the regression over the entire adult lifespan for detecting growth fluctuations. If, instead, we had used the mean growth averaged over all specimens from a population, we would have found that some specimens grew faster than others at all times.

Although the peaks shown in fig. 8 are not completely congruent, they suggest the occurrence of long term fluctuations in the growth rate of *A. islandica.* From other sources (Dickson et al., 1975; Corten, 1986) it is known that large-scale climatic variations have taken place in the North Sea during this century. However, using a Spearman rank correlation, no significant relationship was found between growth variations of the young Fladen Grounds specimens and summer or winter temperatures or temperature anomalies in the Fladen Grounds area or adjacent area (Smed, 1975, 1981). It can be stated now that more research is needed to discover the factors influencing the above mentioned longterm trends.

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