Shell growth of *Astarte elliptica* (Bivalvia) from Kiel Bay (Western Baltic Sea)

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ABSTRACT: Information on growth and age of *Astarte elliptica* (Brown, 1827), a common bivalve in muddy sand sediments in Kiel Bay below 15 m water depth, is scattered and inconclusive. Unchanged size-frequency distributions from October 1984 to September 1985 at the 'Süderfahrt' sampling station, 21 m water depth, suggest very slow growth. There was no linear correlation between the distinct concentric external shell ridges and internal shell growth bands. Internal growth bands were counted from acetate peels of sections of the tooth region examined by scanning electron microscopy. Evidence for an annual periodicity of growth band formation is discussed. A life span of about 20 yr is deduced for *A. elliptica* in Kiel Bay.

INTRODUCTION

Growth and production of benthic invertebrates have been studied as part of the energy flow through the ecosystem and with regard to their influence on the demersal fish stocks of Kiel Bay (e.g. Arntz 1970, 1971, 1977, 1980, Arntz & Brunswig 1975, Samtleben 1977, Brey 1984, 1986, Schaefer et al. 1985). To calculate production of benthic invertebrates it is necessary to know their growth rates and age compositions.

Astarte elliptica (Brown, 1827) is a common bivalve in Kiel Bay in muddy sand sediments below 15 m water depth (Kühlmorgen-Hille 1963), which reachs high biomass values. There is a lack of well-founded knowledge about its growth rates and longevity; available information is scattered and inconclusive.

Jaeckel (1952) assumed a maximum age of more than 2 yr. The quantitative investigation carried out by Kühlmorgen-Hille (1963) showed that no conclusions about growth and age of *Astarte* species could be derived from size-frequency distributions, because the size composition of the populations seemed to remain unchanged during the whole year of study. Such constant size-frequency distributions point to a very slow growth of the species. Erlenkeuser et al. (1975) sug-

gested a possible life span of more than 10 yr for *A. elliptica* in Kiel Bay, based on determination of shell ^{14}C-activity in some larger specimens.

The aim of the present paper is to determine the maximum age and thereby to obtain information on growth of *Astarte elliptica* in Kiel Bay.

As the hydrography of Kiel Bay shows distinct seasonal variations (e.g. in temperature, oxygen content, salinity: Rumohr 1979; sedimentating phytoplankton blooms: Smetacek 1985, Graf 1987) one may also expect seasonal variations in the growth pattern of *Astarte elliptica*. The seasonal growth variations may result in visible growth marks on the external shell surface as has been shown for various bivalves, e.g. Orton (1926), Haskin (1954), Craig & Hallam (1963), Theisen (1973). Such external patterns are present in *A. elliptica* in form of very distinct concentric ridges on the external shell surface (Fig. 1). It is however not clear whether these ridges are formed periodically and thus can be used for age determinations. Internal growth bands previously have been used for age determination of pluriannual organisms and for the reconstruction of the time course of past events, once their periodicity was established (Lutz 1976, Jones et al. 1978, Jones et al. 1983) and are here described for *A. elliptica*, together with results of a laboratory growth experiment. We define growth bands as zones of different structure alternating with shell increments and corresponding to periods of reduced growth (Dillon & Clark 1980).

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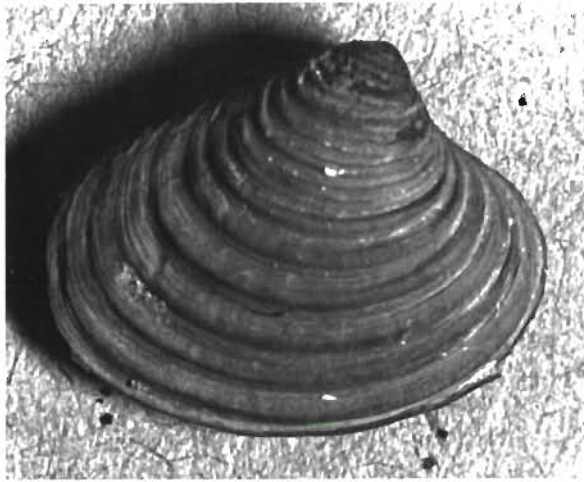
Fig. 1. *Astarte elliptica*. External shell ridges of a 12.8 mm long individual collected on 24 Apr 1985 at 'Süderfahrt'

valve, where growth bands tend to fan out and additional bands can appear (Ropes 1982).

The right valves were first embedded in resin for stabilisation and each valve was cut from the umbo to the ventral margin (Fig. 2) along the axis of maximum
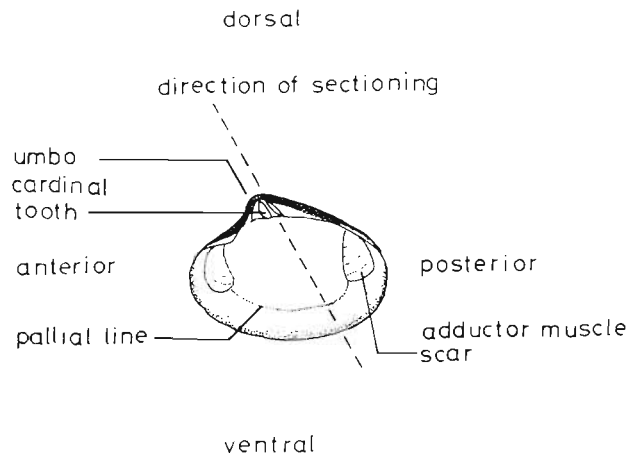

Fig. 2. *Astarte elliptica*. Internal features of the right valve with the direction of sectioning (broken line)

MATERIALS AND METHODS

Sampling took place at about monthly intervals from October 1984 to September 1985 at the 'Süderfahrt' station in the eastern part of Kiel Bay, where muddy sand sediment prevails, in 21 m water depth. At each sampling date ten 0.1 m^2 Van-Veen grab samples were taken. Additional shell material from this station was dredged in April 1985. Grab and dredge material was passed through 1 mm sieves and fixed in 4 % borax-buffered formaldehyde. Shell length of *Astarte elliptica* was measured to the lower 0.1 mm with a sliding gauge.

In order to define the relationship between external shell ridges and shell growth, the ridges of 79 individuals collected in April 1985 were counted and plotted against shell length. The distances between successive ridges were determined by making imprints of the external shell surface of 3 individuals. The distances were measured with a stereo-microscope at 64-fold magnification.

From the 79 *Astarte elliptica* individuals investigated for shell ridges, 49 individuals of different sizes were used for study of internal growth bands in the shell. Shell length ranged from 3.0 to 28.6 mm. The prominent cardinal tooth of the right valve was chosen for examination. Previous investigations have shown that growth structures are also clearly visible in parts other than the valve, i.e. the chondrophore of *Spisula solidissima* (Jones et al. 1978), the teeth of *Venus striatula* (Guillou & Sauriau 1985) and the hinge plate of *Arctica islandica* (Thompson et al. 1980). Destructive environmental impacts have a less pronounced influence on the more protected hinge region than on the exposed

growth as described by Kennish et al. (1980) and Ropes (1982). After grinding and polishing, the shell sections were studied for growth patterns under a stereo-microscope. The preparation of acetate peels followed the procedure described by Kennish et al. (1980), but with the modification of etching with a 1 % HCl solution for 15 s.

For examination of the ultrastructure, acetate peels were made of the shell sections from 2 individuals of 20.5 mm shell length collected in April 1985. The polished and etched shell slices were coated with carbon and gold/palladium under vacuum and examined under a Cambridge S-150-scanning electron microscope (SEM) operated at 20 kV. Growth bands visible on photographs of the acetate peels of both individuals were counted and the corresponding crystal arrangements identified on scanning electron micrographs of the coated shell sections. The distances between identified successive growth bands were measured from scanning electron micrographs at 500-fold magnification.

Individuals of *Astarte elliptica* dredged in May 1985 from the 'Mittelgrund' station (16 m water depth) in the western part of Kiel Bay were first measured and then transplanted into boxes with macrofauna-free habitat sediment and kept at 10 °C in the laboratory. Cultures of the green alga *Nannochloris* sp., which tolerates brackish water conditions (Witt et al. 1981), were used as food. The aquarium was kept dark to establish conditions as natural as possible. Water was exchanged monthly. Control of pH, nitrite and ammonia concen-

trations exhibited only minor deviations from natural conditions. The experiment was started on 24 May 1985 and lasted until 3 Oct 1985. At the end of the experiment the final shell length of the individuals was measured.

RESULTS

Size structure

A total of 1720 *Astarte elliptica* individuals were caught on 10 occasions between October 1984 and September 1985. The abundance varied between 54 ind m^{-2} in September 1985 and 350 ind m^{-2} in April 1985, with a mean value of 172 ind m^{-2} (Fig. 3). With
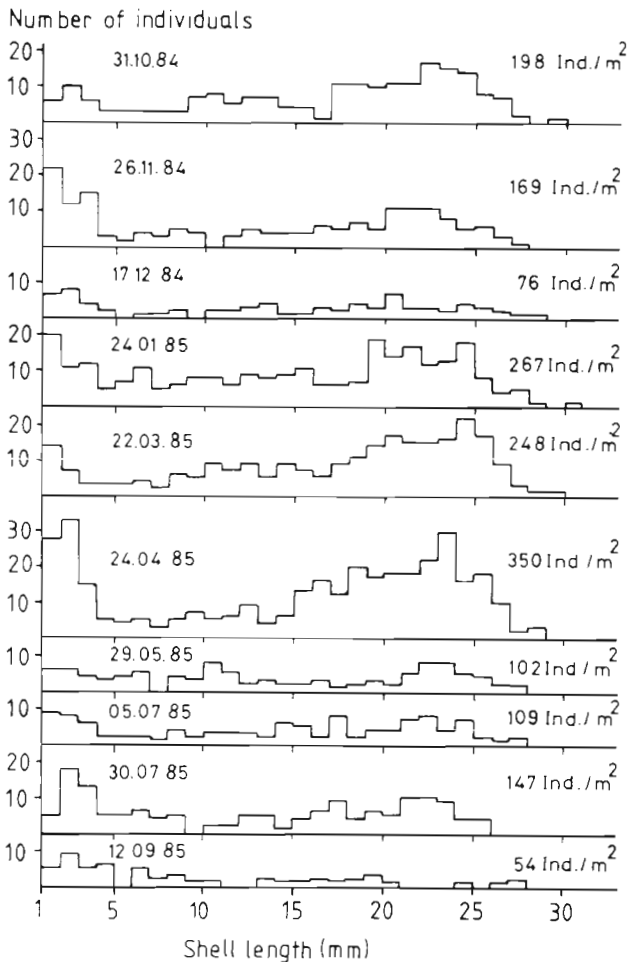

Fig. 3. *Astarte elliptica.* Size-frequency histograms of shell length from grab samples at 'Süderfahrt'

the exception of September 1985 the samples show nearly identical bimodal size-frequency distributions characterized by a high number of 1 to 4 mm long individuals and a considerably larger group of 16 to 25 mm long individuals. The maximum shell length meas-

ured in the samples was 31.4 mm. The nearly constant size-frequency distributions suggest very slow shell growth of the species during the time of investigation. If recruitment is annual, the larger individuals making up the right-hand mode are likely to include several age groups of the population.

Growth experiment

Increase in shell length during the laboratory growth experiment from May to October was very low for all individuals. A maximum increase of 1.4 mm yr^{-1} was calculated for small individuals with a shell length up to 5 mm, and of 0.6 mm yr^{-1} for large individuals with a shell length >15 mm, on the basis of a 132 d experiment (Table 1).

Table 1. *Astarte elliptica.* Maximum shell growth in aquaria at 10 °C. Food was *Nannochloris* sp.

Shell length (mm)	n	Maximum increase (mm in 132 d)
below 5.0	11	0.5
5.0– 9.9	8	0.3
10.0–14.9	1	0.3
15.0–19.9	3	0.2
20.0–24.9	1	0.2

External shell ridges

The number of external shell ridges of 79 *Astarte elliptica* individuals sampled in April 1985 was counted and plotted against shell length (Fig. 4). A significant linear relation represented by the equation $y = 10.63 + 0.72\ x$ ($r = 0.913$, $n = 79$, $p \leq 0.001$) was obtained. Deviations from the calculated regression line are spread over the whole range of measurements more or less equally. They are probably caused by difficulties in discerning the initial ridges in the umbonal area. In most specimens this area was covered with a manganese concretion. Removing this concretion generally resulted in the destruction of some ridges so that they could not be counted.

In spite of this uncertainty, ridges are numbered from the umbo to the ventral margin. In 3 individuals (20.7 to 26.4 mm shell length) the distance between successive ridges was measured. The distances increase in the first set of about 12 ridges, with a strong linear relation (Fig. 5). The coefficients of slope were not significantly different ($p \leq 0.05$, tested after Sachs 1984) in the 3 individuals. Peripherally, ridges are more prominent; their distances are equal between the 5th and 7th

Number of external ridges

$y = 10.632 + 0.719x$
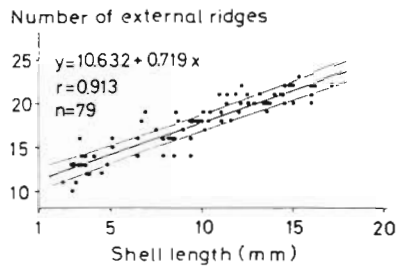$r = 0.913$
$n = 79$

Shell length (mm)

Fig. 4. *Astarte elliptica*. Correlation of shell length with number of external shell ridges of 79 individuals from 'Süderfahrt'; 24 Apr 1985. Calculated regression line and corresponding 95 % confidence limits

Distance between successive ridges (mm)

a

$y = 0.138 + 0.098x$
$r = 0.984$

b

$y = 0.160 + 0.100x$
$r = 0.967$

c

$y = 0.151 + 0.080x$
$r = 0.987$

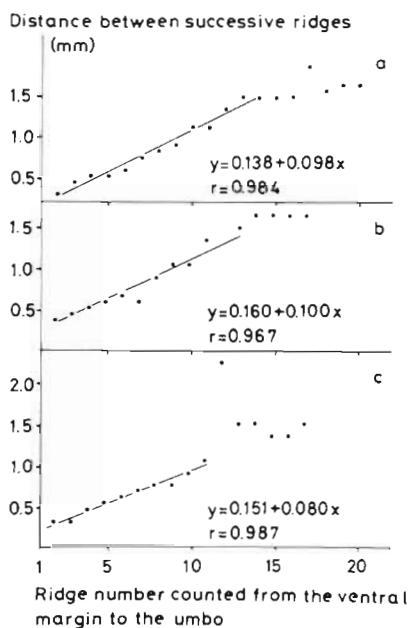Ridge number counted from the ventral margin to the umbo

Fig. 5. *Astarte elliptica*. Plot of external ridges against the distance between successive ridges of 3 individuals with shell lengths (a) 26.4 mm, (b) 20.9 mm, and (c) 20.7 mm, from 'Süderfahrt', 24 Apr 1985. Calculated regression lines

peripheral ridges. This means that in older individuals the concentric external shell ridges are formed according to the pattern of the shell sculpture characteristic for the species *Astarte elliptica* (Fig. 1), independent of allometric growth.

Internal growth bands

A further argument supporting the idea that external shell ridges, at least the peripheral ones, are not strictly related to age is provided by the investigation of internal growth bands within the shell. It was not possible to trace the growth bands from the tooth region to the outer shell surface in shell sections (Fig. 6) because the

Tooth region with growth bands close to each other

Inner layer with myostracal-type prisms
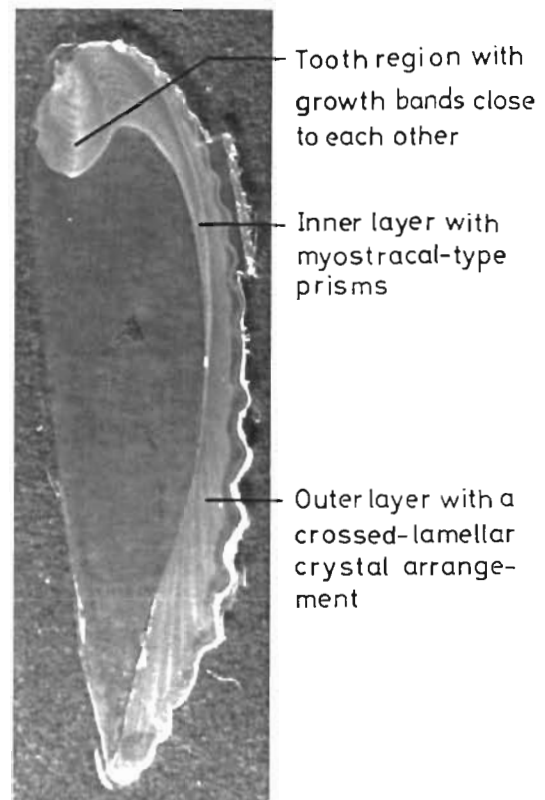
Outer layer with a crossed-lamellar crystal arrangement

Fig. 6. *Astarte elliptica*. Acetate peel of the radial shell section of the right valve of an individual with a shell length of 25.3 mm, collected on 24 Apr 1985 at 'Süderfahrt'

inner layer is built up of myostracal prisms (Taylor et al. 1973). However, in acetate peels of the valves of larger individuals (>20 mm shell length), it was possible to discern assemblages of darker bands which should correspond to growth bands. Only in the middle part of the valve do these darker bands seem to terminate in the external ridges, otherwise they terminate irregularly either in a ridge or between 2 ridges. Close to the ventral margin, it sometimes appears that more than one band terminates in a ridge. Assuming annual formation of growth bands, this means that it takes several years to form a peripheral external shell ridge.

Under the stereo-microscope all of the studied polished and etched shell sections of *Astarte elliptica* showed a pattern of banding. Opaque bands alternate with somewhat darker translucent bands that are clearly visible in the tooth region (Fig. 7). Discriminating the bands in the tooth region became more difficult as the number of bands increased in larger valves. This problem was overcome by using acetate peels of the shell sections. Bright growth bands were recognizable contrasting with the darker colour of the growth increments as shown in Fig. 8.

The enumeration of growth bands was complicated by the varying strength and structure of the bands;

Fig. 7. *Astarte elliptica*. Polished and etched shell section with growth pattern visible in the tooth region of a 14.0 mm long individual collected on 24 Apr 1985 at 'Süderfahrt'
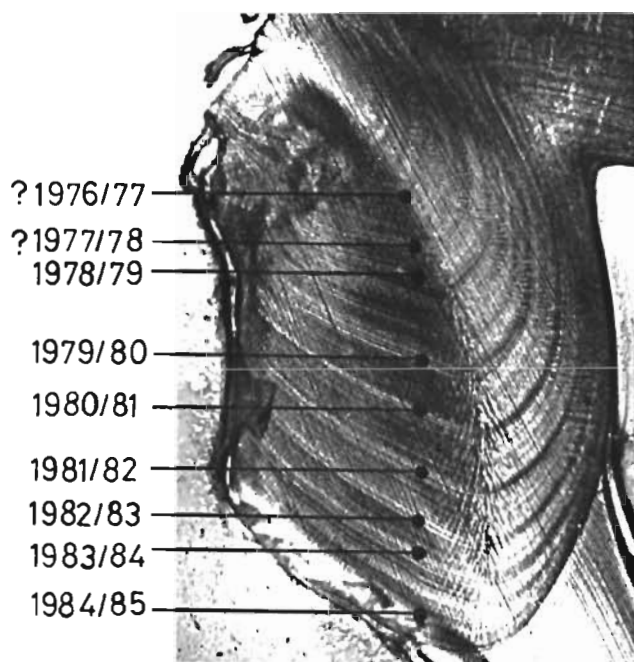

Fig. 8. *Astarte elliptica*. Acetate peel of the tooth region (right valve) of a 20.5 mm long individual collected on 24 Apr 1985 from 'Süderfahrt'. The growth bands are numbered with the year when they were probably secreted, assuming annual formation

some being bold and prominent in between finer bands. Fig. 8 shows 11 growth bands and the hypothetical years of secretion under the assumption that they are formed annually. The black and white print of the acetate peel was taken with crossed nicols, which results in a better contrast between growth bands and increments, facilitating counting procedures.

In almost all of the studied shell sections parts of the umbo were lacking, which was probably caused by

mechanical forces or by dissolution removing one or more of the earliest lines.

Ultrastructure of growth bands

The crystal arrangements which compose the growth bands visible on the acetate peel of a 20.5 mm long individual (see Fig. 8) were also examined by SEM. Micrographs of a section of the etched tooth region show the crossed-lamellar arrangement of the crystals which is interrupted by lines of somewhat larger granular prisms (Fig. 9a) and lines of larger prisms which are oriented with their long axis parallel to the growth direction in the tooth region (Fig. 9b).

Fig. 10 shows the sequence of crystal arrangements in a profile through the tooth. The hypothetical years of secretion 1974/75 to 1984/85 are given. Each year from 1975 onwards encloses several lines which together form the growth bands distinguishable on the acetate peels (see Fig. 8). The corresponding bands on the SEM-micrograph of the whole tooth region are indicated in Fig. 11.

Growth band discrimination

Erosion of the shell in the umbonal area affects the hinge region, too, so that bands in the oldest parts of the tooth are difficult to discriminate. The question marks regarding the years of secretion shown in Fig. 10 reflect this uncertainty. Bands with larger prisms, oriented with their long axis parallel to the growth direction in the tooth appear only in the middle of the tooth profile (VP in Fig. 10: 1979/80, 1980/81, 1981/82, 1982/83). Bands of smaller and granular prisms, some of them (GP_H in Fig. 10) more evident than others (GP) form the remaining growth bands identified on the acetate peel.

In the tooth region of the second 20.5 mm long individual, which was studied by SEM, 11 growth bands could be enumerated as in the individual of Figs. 8 to 11. The identification of growth bands in the proximal part of the tooth was also difficult, because of erosion of this area. The tooth region of this specimen showed only slight deviations in the crystal arrangements of the growth bands in comparison to the tooth profile documented in Fig. 10.

The distances between successive growth bands in the tooth regions of both individuals showed a slight decrease from the umbo toward the distal part of the tooth. However, there was some variation especially between those bands marked with question marks (bands that were difficult to identify) in the umbonal areas (Fig. 12).
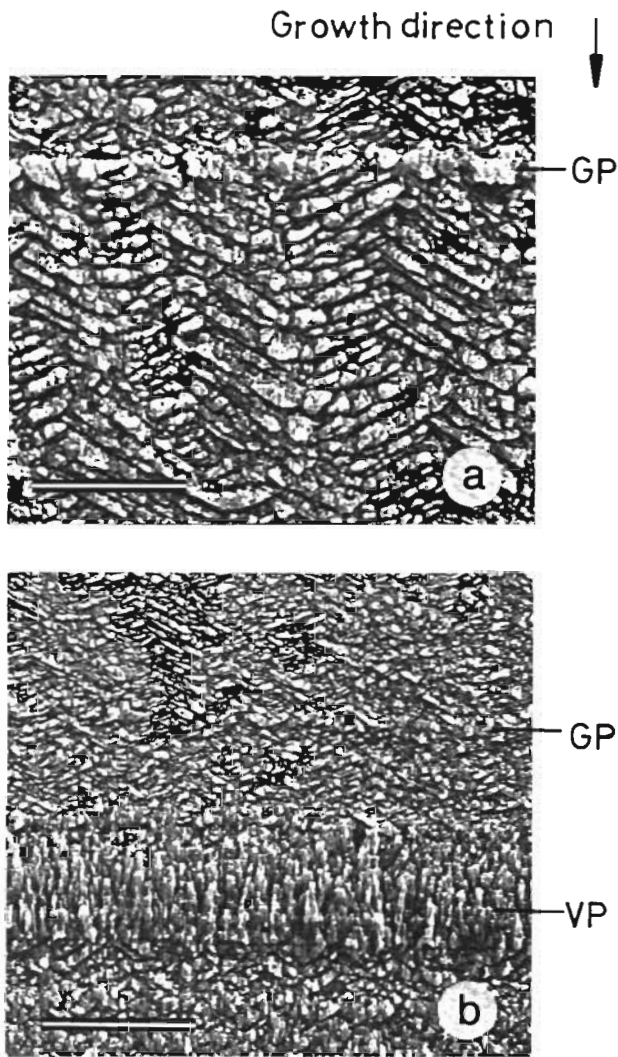
Growth direction ↓

Fig. 9. *Astarte elliptica*. Scanning electron micrographs of a section of the tooth region representing the crossed-lamellar crystal arrangement. (a) In the upper part note line of granular prisms (GP); scale bar = 10 μm. (b) Note line of granular prisms and a layer of larger prisms, oriented with their long axis parallel to the growth direction in the tooth; scale bar = 20 μm. Direction of growth is shown by the arrow. Same shell as in Fig. 8
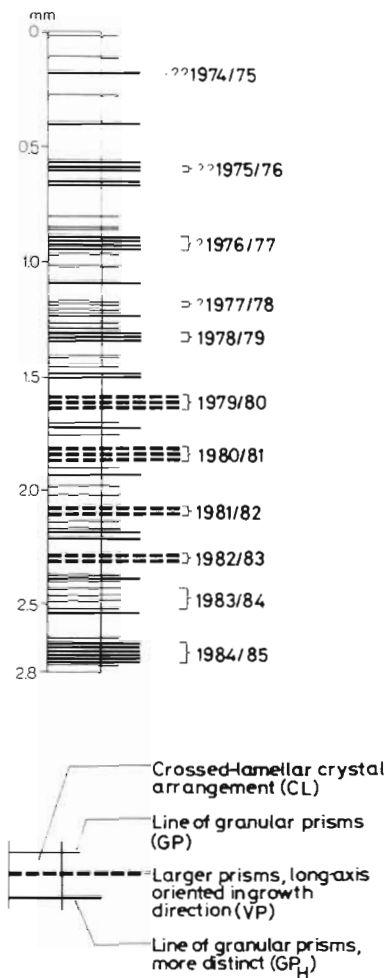

Fig. 10. *Astarte elliptica*. Sequence of crystal arrangements identified from SEM-micrographs of the tooth region of a 20.5 mm long individual (the same as in Fig. 8) represented in form of a diagram. The groups of lines of prisms which compose the growth bands visible on the acetate peel (see Fig. 8) are numbered by the hypothetical years of secretion. The question marks indicate the uncertainties in relating crystal arrangements to growth bands in the oldest (upper) part of the tooth

DISCUSSION

The size-frequency histograms, the growth experiment, and the ^{14}C-analysis of some shells up to a length of about 28 mm by Erlenkeuser et al. (1975, p. 286: 'must be attributed to long life span of the bivalves that should markedly exceed 10 years'), suggest that *Astarte elliptica* is a very slow-growing species. Therefore we assume that the internal marks in the shells are annually secreted growth bands. The conclusion is that *A. elliptica* can attain a maximum age of about 20 yr.

According to Wada (1961) larger crystals are formed during periods of slow growth. In the present study

larger crystals were observed in the internal growth bands, whereas the increments consisted of small crystals. These findings lead to the conclusion that internal growth bands were formed during periods of slow growth and the increments represent periods of normal growth. The distances between the bands decrease from the umbo towards the distal part of the tooth. However, the decrease is not very distinct. Nevertheless it can be inferred that shell growth in the first years of life was faster than in later years. This conclusion is supported by the larger growth increments measured after 132 d of growth under laboratory conditions in small than in large individuals, indicating that growth is asymptotic.

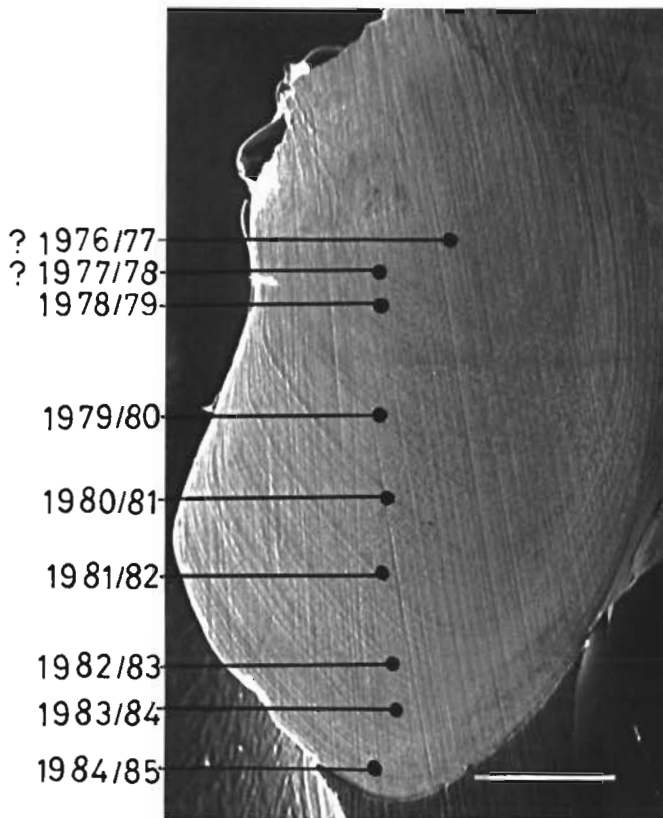In Kiel Bay, bottom water temperatures show a dis-

Fig. 11. *Astarte elliptica*. SEM-micrograph of the whole tooth region of a 20.5 mm long individual (same as in Figs. 8 to 10). The growth bands are numbered with the hypothetical year of secretion. Scale bar = 0.5 mm

Both these factors suggest that growth should be high in summer and low in winter. Thus it can be assumed that annual seasons trigger growth band formation in the shell of *Astarte elliptica* in Kiel Bay.

Situations of extreme oxygen depletion below the summer halocline in Kiel Bay (Ehrhardt & Wenck 1984, Weigelt & Rumohr 1986) last only up to several weeks, and are probably not responsible for the secretion of growth bands in *Astarte elliptica*. This species, occurring in poorly oxygenated soft sediments, exhibits especially high tolerance to temporary oxygen deficiency (Dries & Theede 1974). Another possibility is that spawning could trigger the secretion of growth bands in the shell, as shown for e.g. *Spisula solidissima* (Jones et al. 1978) and *Arctica islandica* (Thompson et al. 1980). However *Astarte*-populations in the Baltic, as shown by Oertzen (1972), do not have a defined spawning season, so that it seems improbable that spawning has a great influence on growth band formation, although we cannot exclude that individuals of *Astarte* have distinct spawning events which influence growth. Further research is necesssary to corroborate our assumption that growth band formation is annual, but at present it seems that this is the most probable assumption.
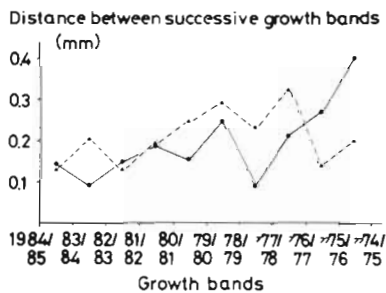
Fig. 12. *Astarte elliptica*. Plot of number of growth bands (hypothetical year of formation) against the distance between every 2 growth bands in the tooth region of 2 individuals from 'Süderfahrt', 24 Apr 1985, both with a shell length of 20.5 mm

tinct seasonality at 20 m depth with maximum temperatures of about 14 °C in September decreasing to about 1 °C in March (Rumohr 1979). Low winter temperatures are an important periodical factor in slowing down growth (Craig & Hallam 1963, Clark 1974). Food supply too, has annual seasonality: it is high from April (settlement of the spring phytoplankton bloom) to the end of October (autumn blooms), and low in winter.

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