Tree of the sea

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An one year old *Arctica* in de south-eastern North Sea.

It has a maximum shell height of 6.5 mm. The shell already has a pale yellow colour. Concentric ridges in the periostracum may be visible under magnification.

CHAPTER 1.

Introduction; setting the background and outline of this study

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DISTRIBUTION

Arctica islandica is the only extant species of a bivalve genus which has its roots in the early Cretaceous period. During this period, the genus only occurred in marine waters from temperate and boreal regions (Lutz *et al.*, 1982). However, fossils have been found at locations far more southern than its present day distribution. Thus, according to Zatsepin & Filatova (1961) the genus is a trace fossil, indicative for boreal transgressions in northern Eurasia.

Today *Arctica* is found on the continental shelves on both sides of the North Atlantic in Europe and North America. Along the American continent, its distribution stretches from Cape Hatteras in the south to New Foundland in the north (Rowell & Chaisson, 1983; Merrill & Ropes, 1969). Its occurrence at the southern tip of Greenland is disputed (Nicol, 1951). Dense populations are present on the north and north-west side of Iceland (Thórarinsdóttir & Einarsson, 1994) and more to the south it is found on the Faroese Shelf (pers. communication, A. Norrevang, Kaldbak Marine Laboratory, Faroer). Along the European continent its distribution encompasses the Bay of Biscay (Nicol, 1951), the English Channel, the Irish Sea (Mackie *et al.*, 1995, Seaward, 1990) and the North Sea (chapter 2). The Barentz Sea at 69°07'N, 36°05'E (N. Pantaleeva, pers. communication) belongs to the northernmost position from which *Arctica* has been recovered. It is found in the White Sea west of 39°E (Zatsepin & Filatova, 1961) where the bottom water temperature remains above 0°C. *Arctica* is also present in the straits between Denmark, Norway and Sweden (Petersen, 1913; 1915; 1918; Pearson *et al.*, 1985) as far south as Kiel Bay (Brey *et al*, 1990). Here its eastward extension is limited by the Arkona basin (Hagmeier, 1930).

The habitats occupied by *Arctica* are variable. The depth ranges from just below the low water line (S. Dahle, Aquaplan Niva, Tromsø; pers. communication) to 482 meters depth (Nicol, 1951). Fine grained sediments are preferred (Bearse, 1976; Rowell & Chaisson, 1983) but *Arctica* has been recorded from coarse sands and gravel (Thórarinsdóttir & Einarsson, 1994) as well. Normally it lives buried in the sediment with its short siphons just at the sediment-water interface (figure 6.1), but sometimes it may bury itself several cm beneath the surface (Taylor & Brand, 1976).

The salinity of the water at which *Arctica* is found can be as low as 16 ‰. Its temperature tolerance ranges roughly between 0 to 20°C (Nicol, 1951), but in many areas the 16°C summer isotherm coincides with its actual distribution limit (Mann, 1982; chapter 2).

Maximum densities occur in the northern parts of its distribution range which can be as high as 100 ind/m² (Zatsepin & Filatova, 1961; Thórarinsdóttir & Einarsson, 1994). In the North Sea maximum densities range from 0.18 ind/m² in the south-eastern part (Oyster Ground) to 16 ind/m² (chapter 2) in the Fladen Ground (northern North Sea). Like most bivalve species, its spatial distribution is very patchy. Arntz & Weber (1970) observed densities to vary between 4 and 13 ind/m² over a 6 km long transect in Kiel Bay.

TAXONOMY & MORPHOLOGY

The position of this species within the Phylum of the Mollusca is given in table 1.1. The taxonomy and nomenclature is well defined although the old name *Cyprina islandica* is sometimes still used in recent literature. In 1767, Linnaeus described the animal under the name "*Venus islandica*" but in 1817 Schumacher placed it within a new genus "*Arctica*". This name has precedence over "*Cyprina"* which was proposed in 1818 by Lamarck.

Table 1.1

Taxon	
Phylum	Mollusca
Class	Bivalvia
Subclass	Heterodonta
Superfamily	Arcticacea
Family	Arcticidae
Genus	Arctica
species	islandica

Table 1.1. Taxonomy of *Arctica islandica* (from Høisæter, 1986).

The shell of this species is well described in most taxonomic works. The most striking characteristics are the almost circular shape, its heavy weight and the black periostracum. The umbo of the shell is positioned in the anterior part and often shows signs of dissolution when the periostracum has disappeared. The periostracum is yellowish brown in young animals but black in older specimens. The concentric ridges in the periostracum are not related to the internal growth lines. Maximum height is approximately 10 cm. Female shells tend to be bigger than males (Fritz, 1991). The morphological relations of the North Sea shells collected for the present study, are given in figure 1.2 and table 1.2. Height is approximately 90 (± 4) % of shell length and doublet width is 58 (± 4) % of shell height. Doublet width is on average 53 % of shell length. Log(shell height) and Log (weight of the right hand valve) were also found to be linearly related.

The two valves only differ in the structure of the hingeband. In this respect the most obvious difference is the large hinge tooth in the left hand valve. This tooth plays an essential role in this study. Anatomical peculiarities of the soft body parts are described by Salleudin (1964) and Palmer (1979), who described the histology of the intestines.

Figure 1.1

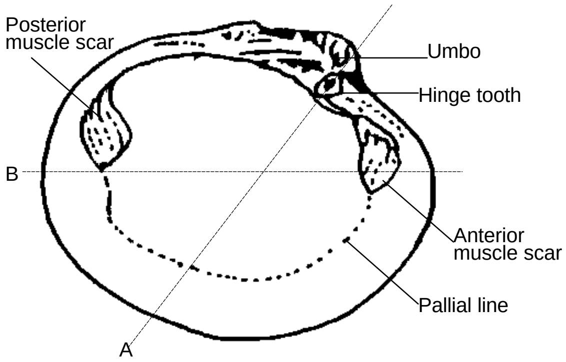

Figure 1.1. Inside view of the left-hand valve. The main morphological characteristics which are mentioned in the text are drawn. The dotted lines "A" and "B" respectively represent direction of maximum shell height and maximum shell length. Line A corresponds to the direction of sectioning. (Figure redrawn after Ropes, 1985)

SOME PHYSIOLOGICAL AND BEHAVIOURAL ASPECTS

The physiology of *Arctica* has been studied by many authors. Winter (1969; 1970; 1978) studied the relationships between combinations of filtration rate, filtration efficiency, animal size, temperature and particle density. The smallest animals he used (26 mm height) had a maximum filtration rate of 700 ml/hr. The largest animals (83 mm) had a filtration rate of about 7 litre/hr. Møhlenberg and Riisgård (1979) estimated filtration rates to be 3 to 6 times higher. The Q_{10} for the filtration rate varies between 2.05 (4-14°C) and 1.23 (10-20°C) (Winter, 1969). The filtration rate decreases with increasing particle size (Winter, 1969) and according to Møhlenberg and Riisgård

(1979) the filtration efficiency varies between 75 and 90 %. Winter (1969) found lower values which varied between 43-75%.

Figure 1.2

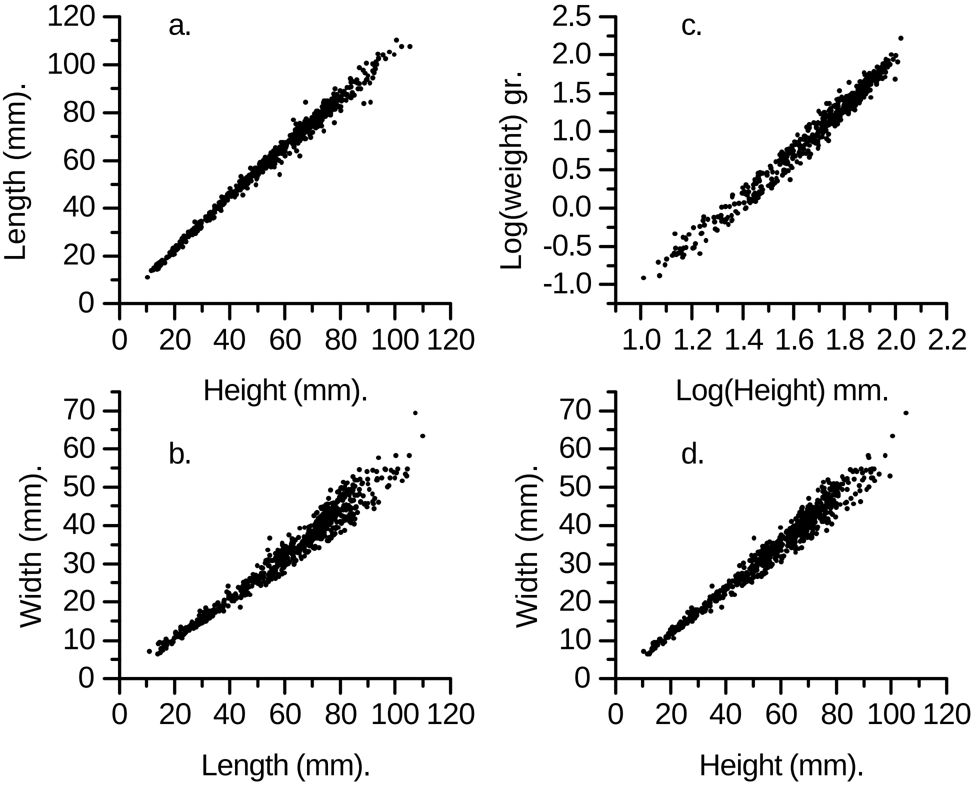

Figure 1.2. The morphological relationships of *Arctica* shells from the North Sea. (a), Shell height * shell length. (b), Shell length * doublet width. (c), Log(shell height) * Log(right hand valve weight). (d), Shell height * shell width. Width measured as maximum distance in umbonal region of shell doublet. Other measurements as depicted in figure 1.1.

Table 1.2

Relationship	a	b	n	r
Height*Length	2.59	1.04	711	0.995
Height*Width	-0.58	0.59	711	0.984
Length*Width	-1.69	0.56	711	0.980
Log(H)*Log(W)	-4.07	3.00	589	0.989

Table 1.2. Regression parameters which were calculated for the morphological relationships between two shell measurements. All regressions had the general form Y=a+b*X., n= number of shells measured, r = correlation coefficient. All regressions were highly significant ($p<0.001$). Data points have been plotted in figure 1.2.

The irregular burrowing behaviour of *Arctica* drew the attention of Taylor (1976). He observed that *Arctica* may bury itself several cm beneath the sediment surface for periods as long as 24 days. During such periods the animal shifts to an anaerobic metabolism (Oescher, 1990; Taylor, 1976). According to Dries & Theede (1974) *Arctica* may survive anaerobic periods exceeding 40 days but the resistance to anoxic conditions is dependent on ambient temperature (von Oertzen & Schlungbaum, 1969), animal size (Schultz, 1969), and probably also the H_2S concentration of the environment although *Arctica* is known to be very resistant to this compound, *i.e.* *Arctica* has been found in bottoms with interstitial H_2S concentrations of 200 μmolair (Oescher & Storey, 1993). Despite the above observations, a mass mortality, due to anoxic conditions, was recorded along the New Jersey coast (USA) in 1976 (Murawski *et al.*, 1976). The gradual decrease of *Arctica* in the southern parts of the Baltic Sea is also thought to be the result of short but repeated anoxic periods (Gosselck, 1987).

Aerobic respiration has been studied by Bayne (1971). The respiratory responses of *Arctica* under varying conditions was studied in detail by Taylor & Brand (1975a; 1975b).

GROWTH

Arctica is a very long-lived species. Ages exceeding 200 years have been reported by Ropes (1985). His estimates have been based on counts of annually deposited growth increments (chapter 3).

Figure 1.3

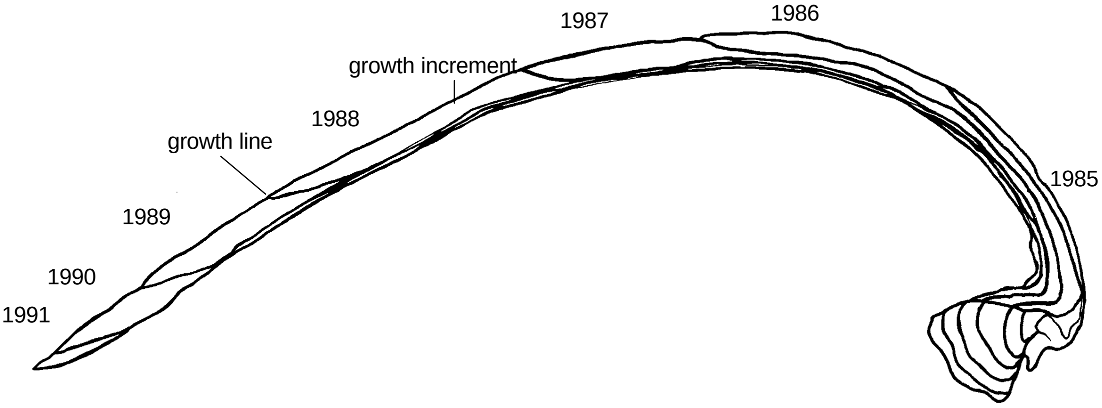

Figure 1.3. Shell cross-section along the line of maximum height (line A in figure 1.1) of an 8 year old specimen which was collected in March 1991. Growth lines are indicated by black lines. Most recently deposited increment is on the left side.

The terminology regarding these growth increments and growth lines is somewhat confusing. In this study, the description given in Ropes *et al*. (1984) is adopted. The term *increment* represents the amount of calcium carbonate which has been deposited during one year. It is also sometimes called the *growth band*, GI II layer or in a descriptive way as wide or light band. Each increment is delimited by a *growth line* (figure 1.3) sometimes called narrow band, dark band or GI I.

The aragonitic shell of *Arctica* consists of three layers, the outer prismatic layer is separated from the inner layer by a thin myostracum. The increment, myostracum and growth line have different microtextural elements. The growth line is composed of irregular simple prisms and the increment has a homogenous structure, which consists of irregular complex crossed lamellar and crossed acicular-crossed lamellar microstructures (Jones, 1980). A more detailed description and the spatial distribution of crystal morphotypes in a shell cross-section is given in Ropes *et al*. (1984).

In small animals the growth lines can be seen on the external shell surface, but in older specimens they become so crowded that individual recognition becomes difficult. Therefore Ropes (1985) adopted the acetate peel technique from palaeontology (Kummel & Raup, 1965), to visualise the internal growth lines in shell cross-sections of *Arctica*. In this technique the difference in shell micro-structure between a growth line and increment is utilised. After sectioning of the shell (figure 1.1), the surface of the cross-section is polished and subsequently etched in a 1% solution of HCl. The *organic* parts of the carbonate matrix are thereby conserved, while the *carbonate* parts are dissolved. Thus the etching procedure results in a cross-section in which the structural difference between increment and growth line is transformed into a micro-relief. This micro-relief is subsequently transferred to a 0.1 mm thick piece of cellulose acetate (Agar scientific LTD; Stansted, Essex, U.K.) which is "melted" on the etched section by a few drops of acetone. After evaporation of the acetone, the sheet acetate can be removed from the cross-section, fitted between object glasses and studied by light microscopy. The structural differences are now visible as gradations in opaqueness of the acetate peel (figure 1.4).

In this study, the preparation of acetate peels is used as a standard technique to examine shell growth. Earlier studies demonstrated that growth variations in the hinge and valve correspond closely. However, the growth record in the hinge band is nicely condensed, well defined and less susceptible to short term environmental disturbance because growth in that area takes place under maximum conditions of shielding (Thompson *et al*., 1980a). Therefore attention was focussed on the measurement of hinge band increments of the left hand valve. The left hand valve was used because it contains the large hinge tooth which is oriented in the direction of maximum shell height along a line which crosses the umbo. Sectioning along this line guarantees that all growth increments can be traced back and each increment is crossed at a square angle.

Figure 1.4

Figure 1.4. Photographed acetate peel of the hingeband section

Although there is still some debate about the exact environmental factors which lead to the deposition of a growth line, most studies suggest that the depostition is related to reproduction which normally takes place in late summer or autumn (Jones, 1980). However, like the exact reason for growth line deposition, the stimulus for spawning is poorly understood (Landers, 1976). Some authors consider a minimum temperature of 13.5 °C as the critical factor (Loosanoff, 1953), while according to others the *change* in temperature in autumn (loss of stratification) is the key factor (Mann & Wolf, 1983). A firm link between growth line deposition and reproduction is not clear because immature *Arctica* also deposit distinct growth lines (Thompson *et al.*, 1980). Most likely a combination of factors (Mann, 1982) determines spawning and growth line deposition.

There is a strong ontogenetic decrease in growth rate with age which is probably related to maturation. The age at which the first signs of reproduction are visible is variable (3-7 year) and depends on location and sex (Jones, 1980; Ropes *et al*, 1984b; Rowell *et al*, 1990). The minimal size for fully mature shells varies between 40 and 55 mm. Most knowledge about reproduction however, is confined to the populations along the American and Canadian east coast and there is virtually nothing known about maturation and reproduction of North Sea specimens.

The larval period is relatively long; it varies between 32 (Lutz *et al.*, 1980) and 60 days (Landers, 1976). The larval stages have very different responses to temperature and pressure. These responses strongly determine place and time of settlement (Mann & Wolf, 1983; Mann, 1986). At settlement the larvae have an average size of 230-290 µm. At an age of 7.5 months the shell has attained a size between 1 and 6.5 mm (Lutz *et al.*, 1982; Muus, 1973).

OUTLINE OF THE CHAPTERS

The strong need to assess marine benthic environmental change was the main reason to initiate this study. In 1977 Thompson & Jones speculated about the use of *Arctica* as being the *"tree of the North Atlantic"*, *i.e.* using the growth record laid down in the shell in a way similar to growth lines in trees. Much research has been carried out since the original idea was proposed. However, most studies focussed on growth and meat yield to arrive at a sustainable commercial exploitation of *Arctica* to replace the dwindling stocks of other commercial bivalve species. The original idea was not pursued until the 1990s. At that time the present project was initiated at NIOZ. Similarly a project at Woods Hole Oceanic Institute (USA), to use the isotopic constitution of the growth increments to reconstruct watermass transport and bottom water temperature along the American Shelf (Weidman *et al.*, 1993; Weidman *et al.*, 1994), started.

There are several reasons for choosing *Arctica* for these studies. The first is because of its high longevity. The extremely high ages which these animals attain implies that environmental change can be assessed, at least for the 20th century. Secondly; *Arctica* is widely distributed over the boreal North Atlantic with the consequence that a consistent data set can be obtained for a large geographical area.

Much knowledge about the ecology of *Arctica* from the American east coast has been gathered, but virtually nothing was known about the ecology of North Sea *Arctica*. Growth differences between the various North Sea populations have been recorded before (Witbaard & Duineveld, 1990), but the mechanisms which determine these differences are still poorly understood. This lack of knowledge impairs the translation of observed growth variations to environmental change. Therefore, this study has a two-fold approach. Firstly to find quantitative relationships between environmental variables and growth and secondly to illustrate the use of the internal growth lines to assess environmental change in the benthic environment.

Figure 1.5

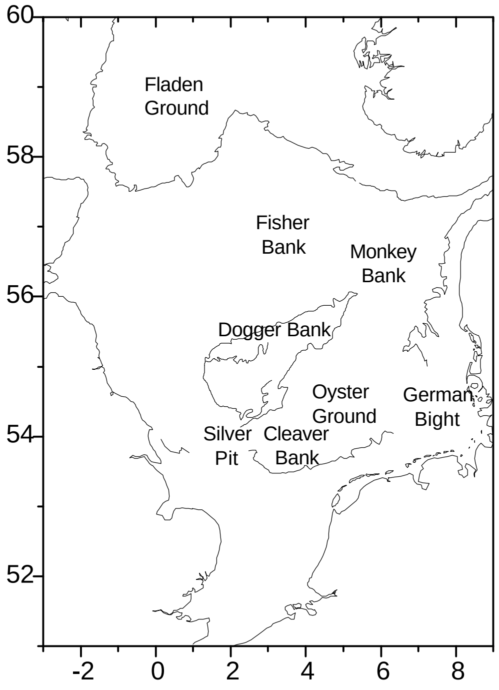

Figure 1.5. The North Sea with geographical names plotted at sites in the map which correspond to the areas frequently mentioned in this study.

The collection of *Arctica* from many sampling points in the North Sea (figure 1.5) has yielded much information about the ecology of *Arctica* in the North Sea. These general aspects are dealt with in **chapter 2**. Relevant topics such as distribution, population-structure, spatial differences in shell morphology and the degree of infection with the nemertean worm *Mallacobdella grossa* are presented and compared with the background of existing knowledge obtained from other areas.

In **chapter 3** the annual deposition of growth increments in *Arctica* from the North Sea is discussed. The periodicity of increment deposition was questioned because animals from shallow living populations along the American coast yielded contradictory results. This problem was deemed significant because most parts of the southern North Sea are rather shallow in comparison with the American locations. Radiocarbon ($\Delta^{14}C$) and stable isotopes of oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) were used to verify the annual deposition.

Chapter 4 and 5 deal with the factors which determine growth. **Chapter 4** describes the results of two experiments in which the growth response of ± 15 mm high *Arctica* was studied in relation to experimentally manipulated conditions. In the first experiment the temperature was held constant at 9°C, but food supply varied. In the other experiment the experimental animals were fed *ad-libitum* at 5 different temperatures, ranging between 1 and 12°C. In both experiments siphon activity, tissue growth and shell growth were measured.

Chapter 5 deals with an inventory of geographical differences in the growth rates of juvenile specimens originating from populations from the North Sea, Faroe Islands, Iceland and the White Sea. A comparison between growth rates, local primary production, bottom water temperature, water depth and sediment type has been made. The aim of the comparison was to find the factors which underlay the observed differences and are likely to influence *in-situ* shell growth.

From the collection of *Arctica* for the study described in chapter 5, it became evident that almost all shells in the south-eastern part of the North Sea were damaged. The shell side where the siphons are located was often marked by scars or missing fragments. High numbers of *Arctica* which had recently died, were caught in the vicinity of active commercial trawl fishing. This observation in combination with the location of damage on these shells suggested that the damage was related to the effects of tickler chains used in beam trawl fishing. In **chapter 6**, damage and damage patterns are described which support these assumptions. Subsequently, scars were used in combination with the internal growth lines to estimate the long-term trend in the effect of bottom fisheries.

Chapter 7 deals with the use of the variable increment widths to construct a long-term chronology of (natural) growth variations which goes back to the beginning of this century. On basis of the results presented in chapter 4 and 5 a link with CPR phytoplankton data was expected. However, such a relation could not be proved. Neither could a relationship with the long-term trend in bottom water temperature be proved. These negative results led to an alternative hypothesis in which the variable influx of Atlantic water into the northern North Sea explains the variations shell growth.

In **chapter 8** the results of the preceding chapters are summarised and general conclusions are drawn.

Then, a growth spurt takes place.
In ten years of time the specimens may attain a size of approximately 4.5 cm height. The periostracum has a yellow to brown colour. Among the superficial striations of the periostracum, annual growth lines which are recognisable as a shallow groove, can be discerned.

CHAPTER 2

Notes on the biology and ecology of the bivalve *Arctica islandica* L. from the North Sea