RIJKSUNIVERSITEIT GRONINGEN

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.

Proefschrift

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. van der Woude,
in het openbaar te verdedigen op
vrijdag 30 mei 1997
des namiddags te 2.45 uur

door

Rob Witbaard
geboren op 25 augustus 1961
te Krommenie

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Referent:	Dr. H.J. Lindeboom

Tree of the sea

Het gebruik van interne groeilijnen in de schelp van *Arctica islandica* met het oog op het retrospectief inschatten van veranderingen in het mariene milieu

Het onderzoek waarop dit proefschrift berust werd uitgevoerd op het Nederlands instituut voor Onderzoek der Zee (NIOZ). De verwezelijking van het omslagontwerp werd mogelijk gemaakt door de assistentie van H. Hobbelink.

Contents

Voorwoord

Krom; niet recht, niet vlak, scheef. Die vorm ligt besloten in de naam "*Noordkromp*". De schelp van dit weekdier is sterk bolvormig ietwat getordeerd, en met geen mogelijkheid recht te noemen. Een treffender beschrijving is haast niet mogelijk. De overwegend noordelijke verspreiding verklaart eenvoudigweg het toevoegsel *noord* in zijn Nederlandse naam en ook de Duitse naam "*Island Muschel*" wijst hierop. Toch komt de noordkromp tot vrij ver in het zuiden van de Noordzee voor. De schelp spoelt echter zelden of nooit op de stranden van onze kust aan, uitgezonderd die van de oostelijke waddeneilanden. In de meeste gevallen betreft het dan nog losse afgesleten schelpen.

De zeldzame verschijning op het strand maakt de noordkromp tot een hoog gewaardeerd verzamelaarsobject; zelfs oude verweerde kleppen. Schelpenverzamelaars ervaren het ontbreken van een noordkromp in hun collectie doorgaans als een groot gemis. Dit wordt geïllustreerd door het korte verhaal van G.J. Zwier; "*Nummer 220: de noordkromp*". Drs. Bouke Daalder is voor een promotieonderzoek naar Schiermonnikoog gereisd, maar omdat het onderzoek niet wil vlotten, zoekt hij zijn toevlucht in het verzamelen van schelpen. De noorkromp is één van de laatste drie soorten die nog ontbreekt in zijn collectie. Bouke Daalder wil zijn verzameling compleet hebben voor hij Schiermonnikoog verlaat, om tenminste *iets* af te maken voordat zijn wetenschappelijk falen zijn ondergang in de wetenschap inluidt.

"*Op Schiermonnikoog zigzagde Bouke gejaagd tussen de hoog- en laagwaterlijnen. Als kind had hij geen interesse voor de lege kleppen op kunnen brengen. Om de tijd te doden had hij sinds zijn terugkeer naar het eiland besloten zich te verdiepen in de rijkdom van schelpesoorten. De tijdspassering was tot een obsessie uitgegroeid. Vóórdat zijn wetenschappelijke carrière volledig geruïneerd zou zijn, móést de collectie compleet worden.*"

Uiteindelijk lukt het,

" Met een van woede vertrokken gezicht trapt hij wild tegen een bult ringwier aan. Een grote, roestbruine schelp ligt half ondergedompeld in een plas zeewater. Bouke hurkt razendsnel neer en grijpt de noordkromp met beide handen uit het water. Nummer 220!......."

Als schooljongen kende ik ook dit gevoel van naarstig op zoek zijn naar die ene ontbrekende soort in mijn verzameling. Ook bij mij ontbrak de noordkromp. Jaren loop je over het strand, in de hoop die bijzondere vondst te doen. Toen ik regelmatig naar de visafslag in IJmuiden ging vond ik daar op een dag, verloren in een met rommel gevulde viskist, een enorme noordkromp, een intact doublet met het dier er nog in! Mijn dag kon niet meer stuk; in een euforische stemming keerde ik huiswaarts.

Wat ik toen niet wist was dat er jaren later honderden zouden volgen, van klein tot groot en van jong tot oud. Zo werd er in de periode tussen 1991 en 1994 waarin ik op NIOZ werkte, een collectie van bijna 3000 noordkrompen opgebouwd. Mijns inziens een unieke collectie met exemplaren die eind vorige eeuw of aan de absolute noordgrens van het verspreidingsgebied verzameld zijn.

De eerste grote aantallen noordkrompen verzamelde ik met het onderzoeksvaartuig *Aurelia* in maart 1991. De bedoeling was om dieren te bemachtigen voor het gebruik in groeiexperimenten. In de eerste week vingen we, op een enkel exemplaar na, niets en ook in het begin van de tweede week zag het er weinig rooskleurig uit. Al gauw ga je denken dat de noordkromp verdwenen is uit de zuidoostelijke Noordzee. Tegen het einde van de reis zette ik een slagroomtaart in als er meer dan 10 noorkrompen gevangen zouden worden. Er werd nog een laatste poging gedaan. Die avond was er een voetbalwedstrijd op TV die veel aandacht van de bemanning trok. Toen het net werd opgehaald en dit barstensvol noordkrompen zat, was het alsof de goudkoorts losbrak. Het fanatisme van de bemanning bij het uitzoeken van de vangst na anderhalve week vergeefs vissen, is onvergetelijk. Het kostte me dus een taart, maar ook de overpeinzing dat we misschien de laatste noordkrompen uit de Oestergronden hadden opgevist. Dat laatste was dus niet waar. Er volgden er meer, veel meer. Met name mijn buurman S. Boeyen, die beroepsvisser is, bracht enorme partijen levende dieren van zijn reizen mee.

Tijdens de diverse vaartochten op de Noordzee bleek wel dat noordkrompen zwaar te lijden hadden van de intensieve boomkorvisserij. Vaak bestond de vangst uit zwaar beschadigde schelpen; soms nog met een half verrotte inhoud. Dit onverwachte aspect kreeg en heeft nog steeds veel belangstelling. De interesse was zo groot dat met extra financiële middelen van BEWON, Richard Klein als dienstweigeraar aangesteld kon worden. De bestudering van de effecten van visserij op het bodemsysteem van de zuidoostelijke Noordzee groeide daardoor uit tot een complementaire studie met eigen vaartochten en extra personele inzet. In dit kader konden een videoprinter en een "polijstpan" worden aangeschaft waardoor de mogelijkheden maar vooral de capaciteit van het aantal te verwerken schelpen enorm verruimd werden. Eerst was het schuren en polijsten volledig handwerk en behalve dat dat stomvervelend was, was het vrijwel ondoenlijk om meer dan 5 schelpen op één dag te verwerken. In de polijstpan konden we 20 tot 30 schelpdoorsneden tegelijk aan.

Later in het voorjaar van 1991 reisde ik naar Nova Scotia (Canada), waar ik in contact kwam met Bob Baker, een commerciële "*Noordkromp visser*". Ik kon met hem meevaren en tot mijn verbazing werden er massa's levende noordkrompen met het grootste gemak boven water gehaald vanuit een 10 tot 15 meter lang bootje op slechts enkele mijlen uit de kust; heel wat eenvoudiger dan ik gewend was. De gevangen kleine noordkrompen, "*littlenecks*", waren bestemd voor menselijke consumptie. Ik heb ze daar dan ook voor het eerst geproefd, gekookt met een beetje azijn. De oudere en taaie dieren worden gebruikt in zg. "chowders". De populariteit van dat soort chowders is dan ook de belangrijkste reden van bevissing van oude volgroeide dieren langs de Canadese en Amerikaanse oostkust. Commerciële exploitatie van de Noordzee noordkrompen lijkt niet waarschijnlijk. De dichtheden zijn er, vergeleken met Canada of Amerika, erg laag. Dit laatste had ook zijn weerslag op de door mij geplande groeiexperimenten, omdat het niet mogelijk bleek om voldoende proefdieren uit de zuidoostelijke Noordzee te verzamelen. Hier kwamen vooral oude reeds volgroeide en dus traag groeiende dieren voor. De Oestergronden lijken wat dat betreft dan ook op een bejaardentehuis voor noordkrompen.

Aanvankelijk heb ik overwogen om voor de groeiexperimenten jonge dieren via Bob Baker te betrekken, maar uiteindelijk werd een logistiek eenvoudiger oplossing in de Kieler Bocht gevonden. Via Ulrich Fiedler en Heye Rumohr (Institut für Meereskunde Kiel) bleek het mogelijk om enkele malen op het onderzoeksvaartuig "*Littorina*" mee te varen en proefdieren te verzamelen. Zo konden in een tijdbestek van een middag enkele honderden dieren verzameld worden. In een koelbox nam ik deze dieren mee naar Nederland waar ze ingezet werden in de groeiexperimenten. De studenten Inge Slot, Rob Franken en Balder Visser verleenden hierbij zeer gewaardeerde assistentie.

Het zal duidelijk zijn dat deze studie nooit tot stand was gekomen zonder de hulp van talloze andere mensen. Op de eerste plaats zijn dat de bemanningsleden van de diverse onderzoeksschepen die mij in staat stelden noordkrompen te verzamelen. Ondanks de nodige ontberingen denk ik met plezier terug aan de vaartochten op de *Tridens*, *Aurelia*, *Pelagia*, *Littorina* en dat kleine Canadese bootje waarvan mij de naam ontschoten is.

Een heel bijzondere tocht was de reis naar de Shetlands in de winter van 1991. Met Bouwe Kuipers als expeditieleider overwonnen we ramp en tegenspoed. Nog op de rede van Texel kwam het anker van de *Pelagia* vast te zitten in oude vislijnen die daar op de bodem waren achtergelaten. Later trotseerden we de weergoden die op de noordelijke Noordzee de dienst uitmaken. Drie weken lang elke dag 2 of 3 maal vissen op noordkrompen. Behalve noordkrompen leverde het vissen in de Fladengronden ook een totaal verroeste zeemijn op. Dat hadden we niet direct door en omdat het monster met al die uitsteeksels in de mazen van het net bleef hangen, schudden en trokken we totdat het ding op het dek neerplofte. Pas toen zagen we wat het was. Behendig griste de bemanning twee grote zeewolven uit het inwendige van de mijn, legde deze apart, knoopten een touw om de mijn, en dumpten het gevaarte overboord. Deze onverwachte vangst toont op geheel eigen wijze het verrassende aspect van zeeonderzoek.

Behalve de bemanningen van de onderzoeksschepen ben ik veel dank verschuldigd aan Theo Kuip en Robert Lakeman, de technici van het experimenteel aquariumgebouw. Zij hielpen immer met het naar binnen takelen van containers zand, proefdieren en koelmachines. Voor het oplossen van problemen met het koelsysteem of vervangen van doorgeslagen stoppen kon ik bij hen terecht. Hun werkplaatsje stond altijd voor me open. Dat zelfde geldt voor de werkplaats van Herman Boekel. Ook wil ik Albert Kok en Eilke Berghuis, de beide vaste assistenten van de projectgroep bentische systemen, noemen. Albert zorgde ervoor dat allerlei standaard oplossingen gereed stonden, en samen met Ian Jenness stond hij aan de basis van het RNA/DNA werk dat nu zijn vruchten begint af te werpen. De ervaring en inzichten van Eilke voor het oplossen van experimentele problemen waren onmisbaar. Yvonne van de Waay, die ter afwisseling keek naar de groeilijnen in *Dosinia*, maakte voor mij duidelijk dat je een andere soort er niet even bij doet. Ook ontdekte ik dat begeleiden meer is dan iemand tewerk stellen.

Verder wil ik al de mensen memoreren die manuscripten lazen, becommentarieer-den maar bovenal suggesties gaven waardoor ze verbeterden. In het bijzonder wil ik mevr. I. Vosjan en Ian Jenness noemen, die mij hielpen met het Engels taalgebruik.

Natuurlijk is er veel werk blijven liggen. Ik heb de stille hoop dat ooit nog eens uit te kunnen werken en ik hoop dat het "groeilijnwerk" op de een of andere manier als onderzoeksrichting op het NIOZ blijft bestaan. De noordkromp heeft toch in al die jaren bij mij niet aan waarde ingeboet, nee sterker nog; de waarde is gestegen. Niet zozeer doordat we in drie noordkrompen een "parel" vonden, maar vooral door het feit dat een volgroeide noordkromp meer dan een eeuw oud kan zijn. Menige noordkromp heeft mijn grootouders overleefd en zal ook mij overleven. Ondanks dat ze niet zoveel te zeggen hebben, vertellen ze wel degelijk een verhaal. We kunnen niet naar dat verhaal luisteren, we moeten het lezen. Lezen vanuit de informatie die ze vastgelegd hebben in hun schelp.

1

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

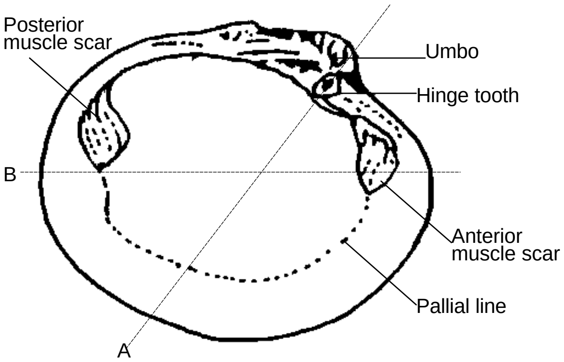


Figure 1.1. Inside view of the left-hand valve. The main morphological characteristics which are mentioned in the text are drawn. The dotted lines "A" and "B" respectively represent direction of maximum shell height and maximum shell length. Line A corresponds to the direction of sectioning. (Figure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

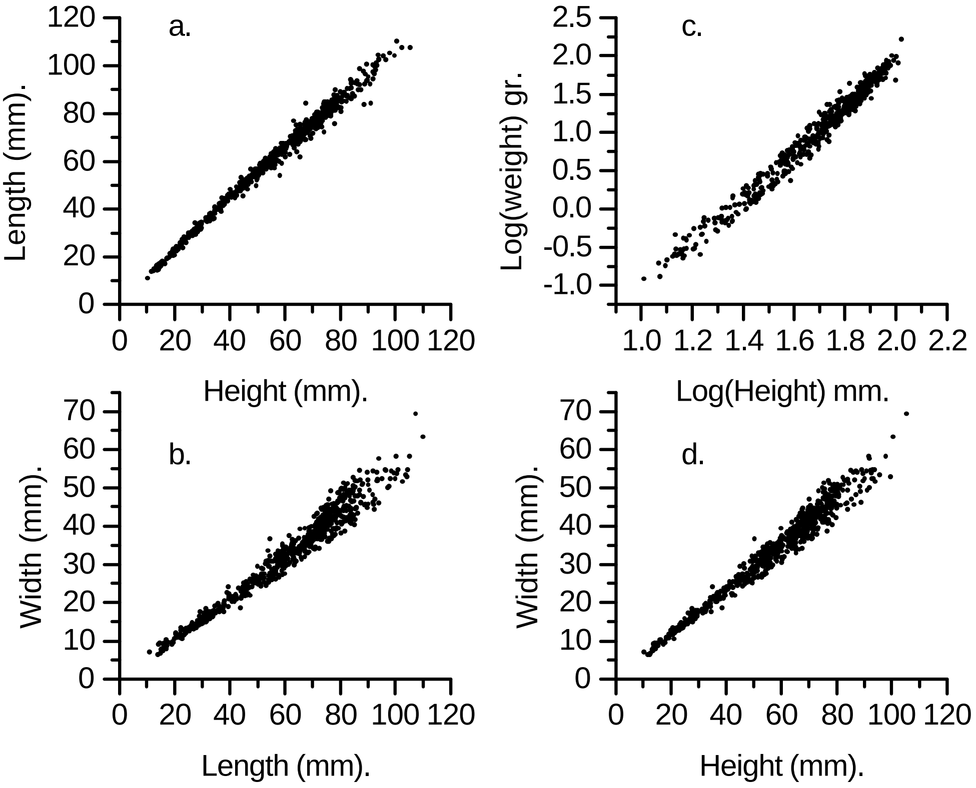


Figure 1.2. The morphological relationships of *Arctica* shells from the North Sea. (a), Shell height * shell length. (b), Shell length * doublet width. (c), Log(shell height) * Log(right hand valve weight). (d), Shell height * shell width. Width measured as maximum distance in umbonal region of shell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

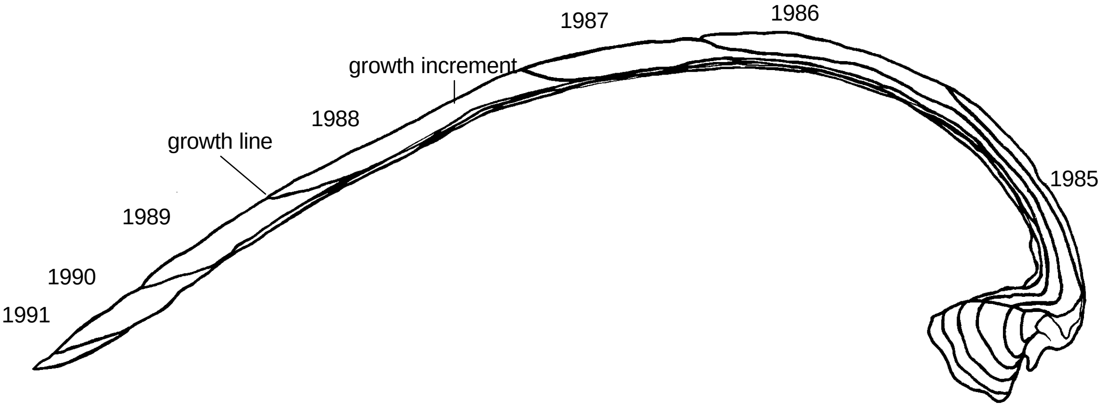


Figure 1.3. Shell cross-section along the line of maximum height (line A in figure 1.1) of an 8 year old specimen which was collected in March 1991. Growth lines are indicated by black lines. Most recently deposited increment is on the left side.

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

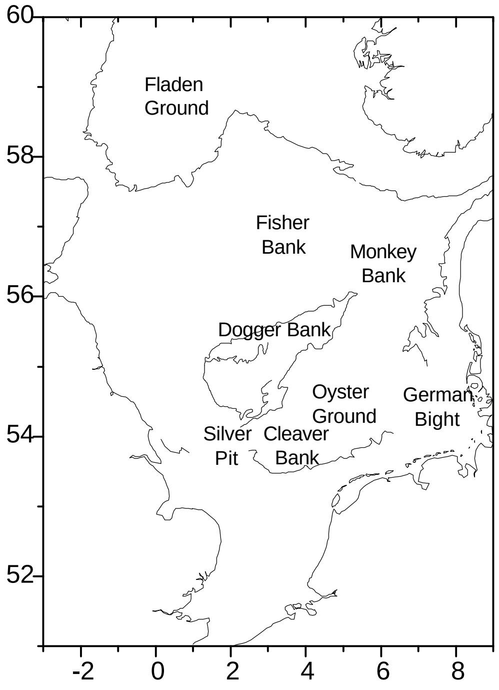


Figure 1.5. The North Sea with geographical names plotted at sites in the map which correspond to the areas frequently mentioned in this study.

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.

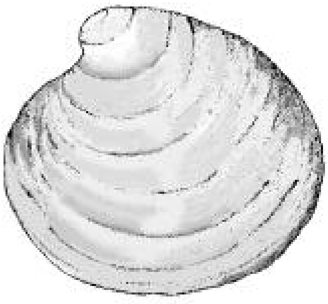
Chapter 7 deals with the use of the variable increment widths to construct a long-term chronology of (natural) growth variations which goes back to the beginning of this century. On basis of the results presented in chapter 4 and 5 a link with CPR phytoplankton data was expected. However, such a relation 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



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

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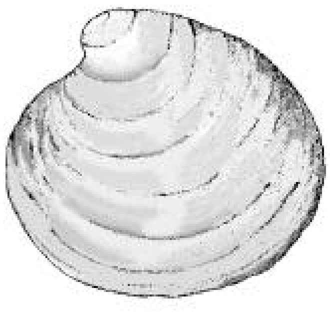

CHAPTER 2

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

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ABSTRACT

The present paper summarises new observations on the distribution, density, population structure and other topics of the ecology of the bivalve *Arctica islandica* in the North Sea. Where possible, a comparison with results reported in the literature is made.

Arctica is found over almost the entire North Sea north of 53°30'N. Here, its distribution seems to be limited to depths below that of the 30 meter depth contour. A comparison of density estimates made between 1970s and the early 1990s, suggest a decrease in abundance. In most areas of the North Sea the populations are dominated by full grown specimens exceeding 50 mm shell height. Smaller animals are rarely found. As a consequence the population P/B is low (0.03). Instantaneous mortality rates for full grown *Arctica* vary between 0.05 and 0.07. These values are much higher than reported for the western Atlantic. Mortality in the south-eastern North Sea is higher than in the northern North Sea.

About 31.5 % of the animals appeared to be infected by the commensal nemertean worm *Malacobdella grossa* but no significant effect of infection on the condition of the host was observed. Variation in shell morphology of different populations within the North Sea is discussed.

INTRODUCTION

Arctica islandica is the only living species of a bivalve genus which had its origin in the early Cretaceous (Nicol, 1951). *Arctica* is known under various common names such as "Iceland Cyprina", "Ocean Quahog" and "Mahogany Clam". The latter is derived from the golden brown colour of the periostracum present on the shells of young specimens. The periostracum becomes black when the animal grows older because of the deposition of iron complexes (Brey *et al.*, 1990).

Arctica has been studied for its anatomy (Salleudin, 1964; Palmer, 1979), behaviour (Taylor, 1976) and physiology (Bayne, 1971). Since the 1980s, ecological aspects of *Arctica* have become the subject of study because the species became commercially important along the American east coast (Kennish *et al.*, 1994). To arrive at acceptable levels of exploitation, information on distribution, population size and growth was urgently needed.

A significant result of these studies was the knowledge about growth rates and longevity. By counting the annually (chapter 3) deposited internal growth lines, Ropes (1985) estimated longevity to surpass 200 years, which has made *Arctica* the longest lived bivalve known (Heller, 1990).

Knowledge on growth production and population ecology in European waters remained scarce. At the Netherlands Institute for Sea Research (NIOZ) a project was initiated to fill this gap. Part of this study focussed on the use the of the internal growth lines to assess long-term variations in the benthic environment retrospectively. During this project, living *Arctica* were collected from all over the North Sea. This yielded new information about its distribution and ecology in the North Sea which is dealt with in the present paper.

DISTRIBUTION

Arctica is found in the shelf seas of the North European continent ranging from the Bay of Biscay in the south (Nicol, 1951) to the White Sea in the north (Zatsepin & Filatova, 1961). *Arctica* has been recorded from the North Sea in faunal studies throughout this century (Petersen, 1915, 1918; Davis, 1923, 1925; Holme, 1956; Hunt, 1925) but distributional maps reveal little detail (Seaward, 1990).

A map with higher spatial resolution (Witbaard *et al.*, 1994, chapter 3) was obtained in 1986, from the ICES Benthic Survey (IBS) (Duineveld *et al.*, 1991; Künitzer, 1990). However, this map was limited to the southern and central North Sea and was based on boxcore samples. While adult *Arctica* were found only sporadically, spat (zero age group) was quite abundant in these samples. Therefore, the map merely reflects the distribution and density of spat fall rather than the distribution of adults (Witbaard *et al.*, 1994). By plotting records collected since 1972 from commercial trawlers and from surveys with research vessels, a map has been constructed which more accurately reflects the distribution of adults (figure 2.1).

Arctica has been found over the entire North Sea north of 53°30'N. It is obvious that its southern limit of distribution closely follows the 30 meter depth contour up to the Danish coast where only a few specimens were found at shallower depths (56°00'N 08°02'E). Despite intensive sampling programs, *Arctica* has never been reported for the Dutch coastal waters or the Southern Bight (Noort et al., 1979-1986; Holtmann & Groenewold, 1992; 1994; Duineveld *et al.*, 1991).

Figure 2.1

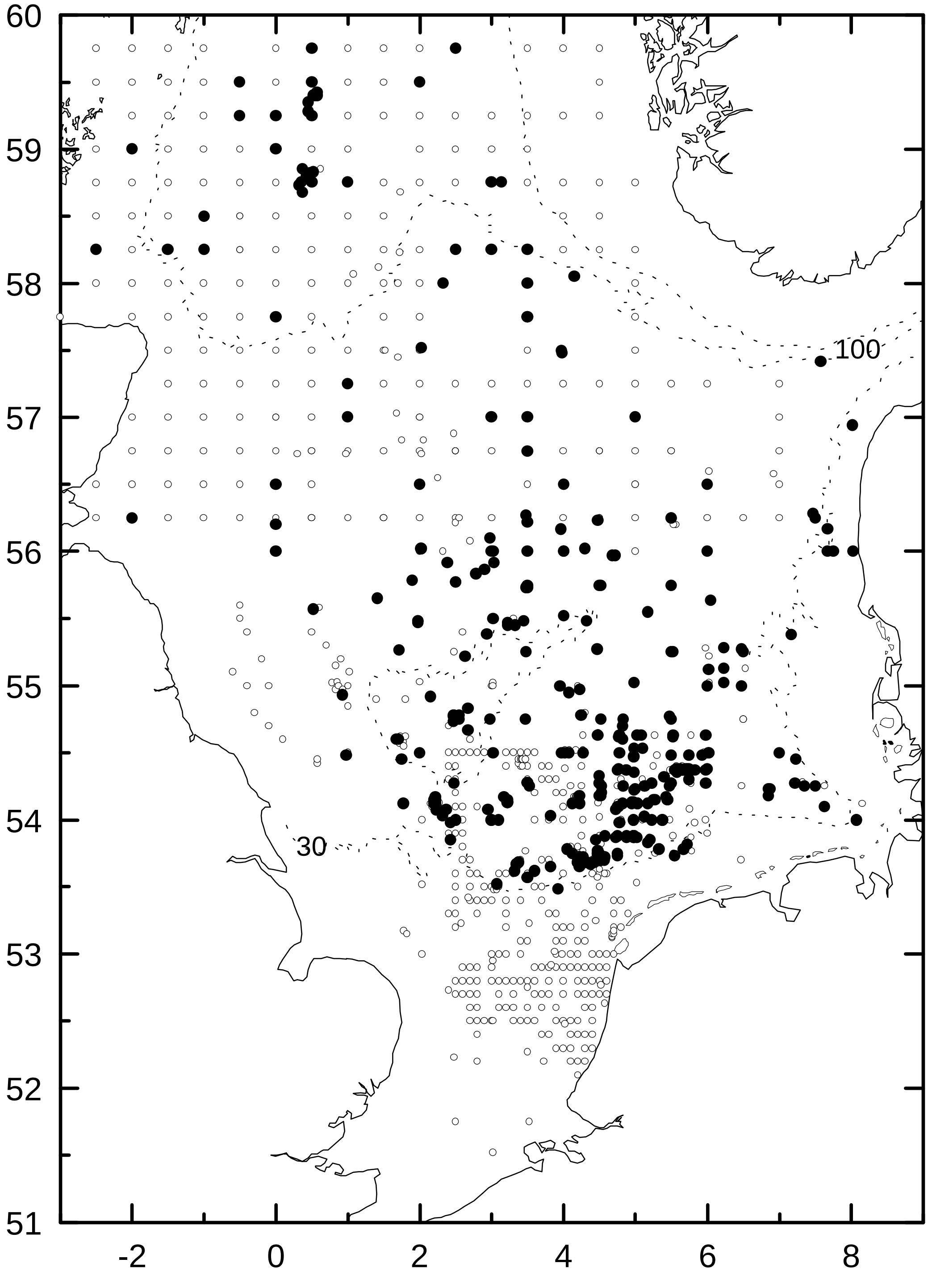


Figure 2.1. Distribution of *Arctica islandica* in the North Sea. Solid circles denote the occurrence of living *Arctica* while hollow circles indicate absence in the sample. Only the occurrence of full grown (non spat) animals is given. The map is composed of data collected between 1990 and 1995 by cruises with research vessels and commercial trawlers as well as data presented by Duineveld *et al.*, (1991); Künitzer (1990); Eleftheriou & Basford, (1989); Basford *et al.*, (1989); Heyman (unpublished); van Moorsel, (1993) and van Noort *et al.*, (1979-1986).

The 30 meter depth contour roughly follows the tidally mixed waters in the south and the deeper, summer stratified waters in the north. Across this boundary the sediment composition changes from coarse sand (median grain size 250-300 µm) in the south to mud (median grain size <125 µm) in the north (Creutzberg & Postma, 1985). Nevertheless a prominent role of sediment composition as distribution determining factor for adults seems unlikely. Although *Arctica* is most often found in fine grained sediments (Rowell & Chaisson, 1983; Thórarinsdóttir & Einarsson, 1994; Bearse, 1976) it has been recorded from coarse sand or gravel as well (Thórarinsdóttir & Einarsson, 1994; Zatsepin & Filatova, 1961). Locations within the North Sea where it occurs on relatively coarse sediments are the Monkey Bank, Cleaver Bank and the south-western part of Dogger Bank (see table 5.2).

It is possible that the southern limit of its distribution, coinciding with the 30 m depth contour, could be set by the maximum bottom water temperature of 16°C (Tomczak & Goedecke, 1964) which also approximately follows the 30 m depth contour. A similar temperature controlled limit has been observed along the American east coast. Here the distribution is confined to a body of cold bottom water in which the 16°C isotherm limits its inshore distribution (Mann, 1982). While mature *Arctica* can withstand temperatures up to 20°C (Loosanoff, 1953), such temperatures are detrimental to larvae since Lutz *et al*. (1989) observed optimum growth rates between 13 and 15°C. At higher temperatures larval growth decreases and ultimately stops. High tidal currents in the shallow waters are another possible reason for its absence. Sediment instability *i.e.* resuspension or sediment scour might inhibit larval settling or impair their survival.

DENSITY

In most areas of the North Sea, densities of *Arctica* are so low that they are rarely found in grab samples. It is only in the Fladen Ground that almost every boxcore yields one or more living specimens (Wilde *et al.*, 1986). Here, the estimated densities ranged from 10 to 16 individuals/m² (chapter 7). In the intensively sampled Oyster Ground area *Arctica* is rarely found in grab samples which suggests very low densities. Like for most other areas within the North Sea density estimates in de Oyster Ground are still semi-quantitative because they are based on beam trawl surveys. Experiments (Groot & Lindeboom, 1994) have shown that such trawl surveys give a poor quantitative estimate of the abundance of infaunal species. A twelve-fold fishing of the same area showed that the first trawl only contains 1 to 5% of the total number of *Arctica* caught (Fonds, 1994; Witbaard, 1995). Numbers of *Arctica* in the catch did not decrease until the 9th trawl passage and after the 12th passage it was estimated that about 100 % was caught. This repeated fishing of the same bottom area in the Oyster Ground (~54°32'N 05°05'E) yielded a density of 57 individuals/ha (0.006/m²). Using a deep digging dredge, Bergman & van Santbrink (1994) estimated the density of *Arctica* at 1800 quahogs/ha at 53°45'N 04°30'E. But even at such "high" (0.2 ind/m²) densities, elaborate boxcore sampling is needed to verify the actual density.

Despite the above mentioned difficulties to assess densities, a comparison has been made between abundance estimates made during the 1970s (Noort *et al.*, 1979-1986) and those made since 1990. In both periods an almost identical 5.5 m wide, fine meshed beam trawl was used. Only the number of tickler chains was higher during the surveys in the most recent period. The results are graphically displayed in figure 2.2.

Figure 2.2

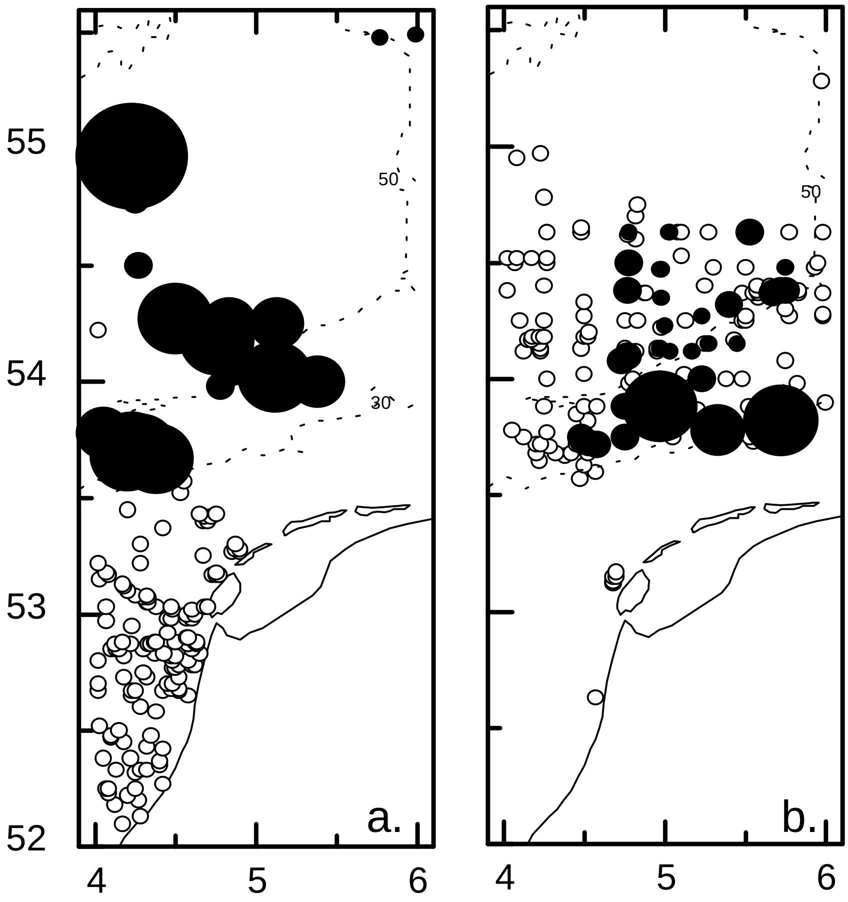


Figure 2.2. The comparison of relative densities of *Arctica islandica* in the south-eastern North Sea. The size of the circles corresponds to the relative abundance. Hollow circles indicate the absence despite sampling. (a), Abundance as estimated by Noort *et al.* (1979-1986) between 1972 and 1980. (b), Densities determined from cruises with RV "Aurelia" and RV "Pelagia" between 1990 and 1994.

The size of the circles indicates the relative abundance, with larger circles corresponding to higher densities. Noort *et al.* (1979-1986) did not sample very often in the Oyster Ground but they found *Arctica* at almost all of the stations they visited. At most stations the abundance was relatively high, while quahogs were either lacking or had a lower density in the most recent period. This difference is even more striking considering the higher sampling effort (denser sampling grid and the use of more tickler chains) in the most recent period.

Figure 2.3.

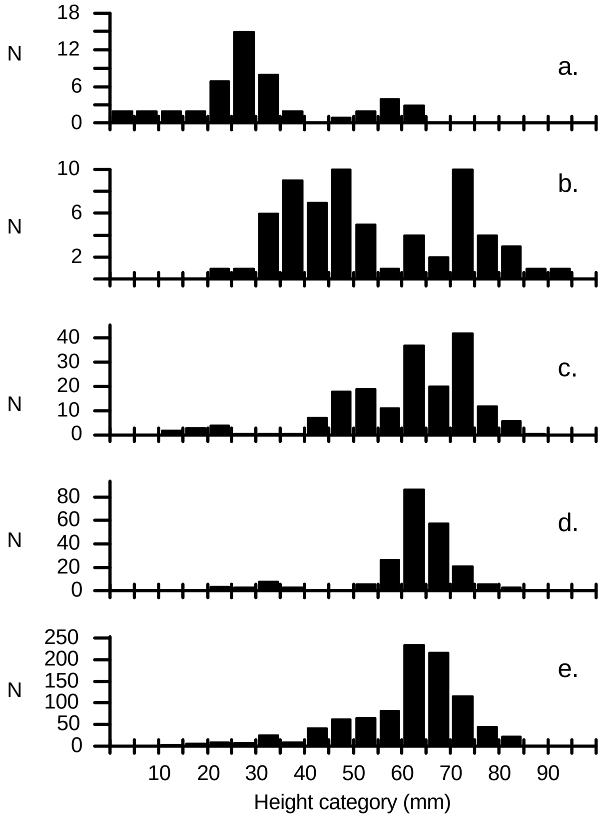


Figure 2.3. Size frequency distribution of four *Arctica islandica* populations within the North Sea. N= the number of *Arctica*. (a), Fladen Ground population (58°40'-59°20'N, 00°20'E) as sampled in 1983 by Wilde *et al*. (1986). (b), Population from the Silverpit (~54°08'N, 02°12' E) sampled in 1993. (c), Central Oyster Ground (Oyst I ~54°22'N, 05°40'E) sampled in 1991. (d), Southern Oyster Ground (Oyst II ~53°52'N, 04°59'E) sampled in 1991. (e), All animals collected from the Oyster Ground between 53°-55°N and 3°-6°E in the period 1990-1994.

For the North Sea, the estimated densities are low when compared to densities of full grown *Arctica* as reported for north-west Iceland, Nova Scotia or the White Sea, where up to 100 individuals/m² can be found (Rowell & Chaisson, 1983; Zatsepin & Filatova, 1961; Thórarinsdottir & Einarsson, 1994).

POPULATION STRUCTURE

In the North Sea, a few sites have been sampled intensely by boxcorers or have been trawled frequently with fine meshed nets (mesh size 2*2 cm). Size frequency distributions of the *Arctica* collected at these sites are depicted in figure 2.3.

In the samples from both the Fladen Ground (2.3a) and Silverpit (2.3b) a bimodal distribution was found. Such bimodality is less clear or even absent in all Oyster Ground samples (2.3c-2.3d). The latter are dominated by larger specimens with heights between 60 and 70 mm. A low abundance of small animals as compared to the abundance of large *Arctica* has also been observed for the populations along the American coast (Murawski & Serchuk, 1979a; Murawski *et al.,* 1982) and north-west Iceland (Thórarinsdottir & Einarsson, 1994). Murawski *et al.* (1982) suggested that this skewed size frequency distributions may have resulted from either irregular recruitment or low survival of recruits. Evidence for a low survival of recruits is supported by the disappearance of spat which was present in the spring of 1986 (Duineveld *et al*., 1991; see figure 3.1). This spatfall was never retraced as juvenile specimens in later years.

GROWTH & PRODUCTION

For the determination of a size weight relationship living animals were used which were collected between 1990 and 1994. First the shell height, shell length and shell width of each specimen were measured. Soft-tissue was subsequently removed, drained on paper and weighed, yielding the shell-free wet weight (sfww). Tissue was dried at 60°C until constant weight, yielding the shell-free dry weight (sfdw). For the determination of the ash contents the dried tissue was incinerated in a furnace at 540°C for three hours. The difference between sfdw and ash was taken as ash-free dry weight (afdw).

The ash-free dry weight was 13% of the shell-free wet weight and 80% of the shell-free dry weight. These results are very similar to those reported by Rumohr *et al.* (1987). The resulting relationship between height and afdw is depicted in figure 2.4.

When the size-weight relationship is combined with age-size regressions (chapter 5) and the age-frequency distributions (figure 2.3), an estimate for the population P/B ratio is obtained. When a growth season of one year without mortality or recruitment is assumed, the sum of weight increase of all animals corresponds to a minimal estimate of secondary production. These results are summarised in table 2.1 together with average shell size and average age of the animals in the population.

The average P/B for the Oyster Ground has the lowest value although the animals have growth rates which are 2 to 3 times higher than those from the Fladen Ground (Witbaard & Duineveld, 1990). As this discrepancy is caused by the different age structures of both populations, the P/B ratios were recalculated for separate age groups as well (table 2.2). This demonstrates a rapid decline in P/B with age. The youngest specimens have P/B ratios which exceed 1, but in animals older than 5 years the P/B ratio rapidly decreases to 0.02.

Figure 2.4

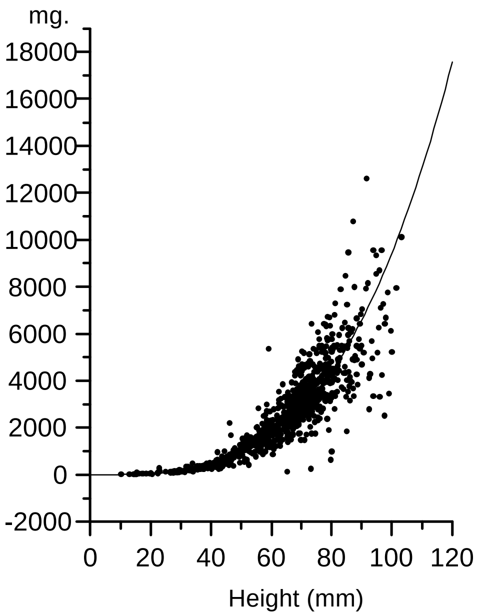


Figure 2.4. Relationship between shell height (mm) and ash-free dry weight (mg) for animals collected in the North Sea between 1990 and 1994. The equation for the best fitting regression line is $\mathrm{Weight}=0.0014*\mathrm{Height}^{3.14}$

Table 2.1

Area	Oyster Ground	Silver pit	Fladen Ground	Kiel Bay
Height	66.6	58.9	35.9	25
Avg. age	40.5	28.7	32.0	3-5
P/B pop.	0.02	0.04	0.03	0.34

Table 2.1. A comparison of P/B ratios of some *Arctica islandica* populations. Average P/B ratio together with average shell height and average age for specimens from populations in the Oyster Ground (~53°52'N, 04°59'E), Silverpit (~54°08'N, 02°12'E), Fladen Ground (58°40'-59°20'N, 00°20'E) and Kiel Bay (Brey *et al.*, 1990).

The population P/B for the North Sea is low compared to the Kiel Bay (Baltic Sea) population which is 0.34 (Brey *et al.*, 1990). This difference is mainly due to dominance of younger age classes in Kiel Bay. If similar age groups are considered, the average ratios compare well.

Table 2.2

Age (yr.)	Oyster Ground	Silver pit	Fladen Ground	Average
1-5	1.0		1.34	1.17
6-11	0.15	0.28	0.39	0.27
11-20	0.08	0.13	0.10	0.10
21-30	0.05	0.06	0.06	0.05
>30	0.02	0.02	0.01	0.02

Table 2.2. P/B ratios for different age groups in three areas of the North Sea. The last column gives the average P/B ratio for all areas. Geographical positions are as given in table 2.1.

MORTALITY

Among the predators which prey on *Arctica* are eider ducks (*Sommateria mollissima*), common scooter (*Melanitta nigra*) (Meissner & Brager, 1990), gulls (Zatsepin & Filatova, 1961), fishes (Schäfer, 1972; Arntz & Weber, 1970; Cramer & Daan, 1986), *Asterias rubens* (Anger, 1977; Hunt, 1925), *Natica* spp (Christensen, 1970) and *Buccinum undatum* (Nielsen, 1975). Spat are especially prone to predation by *Astropecten irregularis* (Christensen, 1970). In the south-eastern North Sea and in the Baltic Sea, bottom trawling is another significant source of mortality (Witbaard & Klein, 1994; Rumohr & Krost, 1990; Arntz & Weber, 1970).

From the size-frequency data (figure 2.3), instantaneous mortality rates were estimated by applying the method described by Brey *et al*. (1990). This was done for the populations from the Fladen Ground and the Oyster Ground. A comparison of both populations suggests higher mortality rates in the Oyster Ground. The instantaneous mortality rate for the Fladen Ground population is 0.32 during the first 10 years of life but decreases rapidly in older animals to less than 0.05. In the Oyster Ground mortality for *Arctica* exceeding 60 mm (>20 years) is estimated at 0.07.

The mortality rate for the North Sea populations is somewhat higher than those calculated for the American or Canadian east coast. Murawski & Serchuk (1979b) reported a value between 0.027 and 0.02 and Rowell *et al*. (1990) gave estimates which varied between 0.015 and 0.05. Brey *et al*. (1990) found a size dependence for the population in Kiel Bay (Baltic Sea). The mortality rate for *Arctica* less than 38 mm was 0.46, 0.06 for specimens with shells between 38 and 52 mm and finally 0.92 for animals larger than 52 mm. They ascribed this trend to the combined effects of size specific predation and bottom trawling (Brey *et al*., 1990). The higher mortality rates in the Oyster Ground (south-eastern North Sea) compared to the Fladen Ground points to a relation with the intense bottom trawling in the south-eastern North Sea as outlined in chapter 6. Therefore the decrease in abundance over the past two decades (figure 2.2) seems to be due to the effects of bottom trawling.

COMMENSALISM

Arctica islandica belongs to that group of bivalves which is used as a host by the nemertean worm *Malacobdella grossa* (Gibson, 1967, 1968). This worm is usually found between the mantel epithelium and the gills of its host. Sometimes two worms per *Arctica* are found and large shells are usually occupied by larger worms (Gibson, 1968; Gering 1911). The grade of infection differs among populations. Along the American east coast infected clams are rarely found (0-0.05%; Jones, 1979) while on average, 27 to 58% of the clams in Kiel Bay are infected (Gering, 1911; Arntz, 1972).

The analyses of 974 *Arctica* specimens from the North Sea, revealed an average infection percentage of 31.5. Larger *Arctica* were infected more frequently than smaller specimens (table 2.3b) which is consistent with the results of Gering (1911) and Arntz (1972). However, the differences in percentage of infection between different areas in the North Sea are small (table 2.3a).

Table 2.3a

Area	% infected	N.
North Sea (whole)	31.4	974
Oyster Ground	34.5	620
Fladen Ground	20.4	54
Central North Sea	26.0	68
German Bight	31.7	82
Western North Sea	25.7	105

Table 2.3b

Size class (mm)	% infected	N
<35	14.2	134
36-55	26.7	157
56-70	32.7	324
71-85	39.6	316
>85	34.6	81

Table 2.3. Percentage of *Arctica* infected with *Malacobdella grossa*. (a), Percentage of infection split per area in the North Sea. (b), Percentage of infection split per size group in the North Sea. N= the number of *Arctica* analysed.

Because commensals are thought to have either a positive or no effect on their host, the condition index (afdw/height^3) of infected and non infected *Arctica* (N=265) was compared. All clams used for this comparison were collected from one site in the Oyster Ground (54°22' N 05°40'E) within one week. The infected animals tended to have a slightly better condition index but the difference was insignificant. Still, Arntz (1972) observed a significant better condition of infected ***Arctica*.** This effect is thought to be the result of a stimulation of the filtering activity caused by the presence of the worm (Gibson, 1968).

PHENOTYPIC VARIATION

The maximum observed shell heights for the North Sea populations varied between 96.8 and 99.1 mm. Only for specimens from the Fladen Ground the maximum shell height was lower. It did not exceed 73.5 mm. The shape of the shell, *i.e.* the relationships between height, length, width and weight however appeared to differ. The shell shape of 7 North Sea populations was analysed in more detail, using measurements of height, length, width (chapter 1) and the weight of the right hand valve.

Figure 2.5

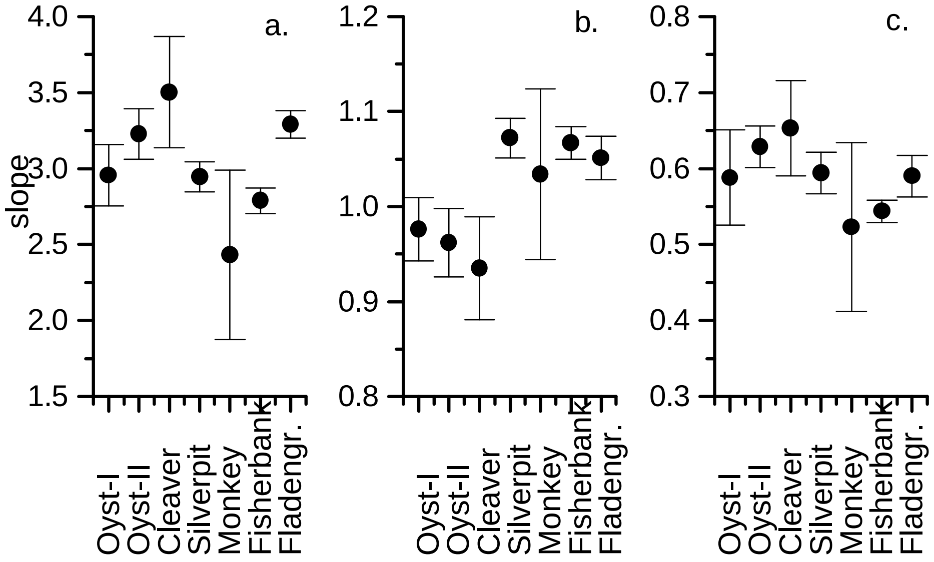


Figure 2.5. Morphological differences of 7 *Arctica* populations collected from the North Sea. Each graph gives the regression coefficient with the calculated comparison interval around it. If two intervals do not overlap, the coefficients differ significantly at $p<0.05$. (a), Regression coefficients between Log(shell height) and Log (shell weight). (b), Regression coefficients between shell height and shell length. (c), Regression coefficients between shell height and doublet width. Oyst-I (~54°22' N, 05°40'E), Oyst-II (~53°52'N, 04°59'E), Cleaver Bank (~54°10'N, 02-03'E), Silverpit (~54°08'N, 02°12' E), Monkey Bank (56°30'N, 06°00'E), Fisher Bank ~57°00'N, 03°30'E), Fladen Ground from between 58°40'-59°20'N, 00°20'E.

For each population these measurements were used for the establishment of a relationship between height & length, height & width and Log(height) & Log (weight). This relationship was determined by calculating the least square regression line and the difference between the regression coefficients was subsequently tested for significance by the calculation of T'-comparison intervals around them (Gabriel's approximate method; Sokal & Rohlf, 1982). In this way the steepness of the slope, describing the relationship between any of the measurements was tested. The coefficients are significantly different ($p<0.05$) if, when presented in a graphical display, the intervals do not overlap.

The results are depicted in figure 2.5. The populations collected from the southern North Sea (Oyster-I, Oyster-II, Cleaver) separate from those from the central and northern North Sea (Monkey Bank, Fisher Bank and Fladen Ground), while *Arctica* from the Silverpit have an intermediate position. The separation between northern and southern North Sea is less clear when the relations between Log(height) and Log(weight) are compared (figure 2.5a), *i.e.* the regression coefficient derived for the Fladen Ground specimens differs significantly from the other populations of the northern North Sea but not from those of the Oyster Ground. The relatively smaller length compared to shell height for the Oyster Ground population (figure 2.5b) may have resulted from frequent damage of the post-ventral shell margin by passing bottom trawls (see chapter 6). Frequent damage of this area may have resulted in a truncation of that shell side and thus explain the different regression coefficients.

However, it is unlikely that all differences are due to the effects of fisheries. Signs of truncation or other deformations are rarely found within the populations from Fladen Ground, Fisher Bank, Monkey Bank or Silverpit while these populations differ significantly in respect to their relation of shell weight and height. Whether these differences are phenotypic or genetically determined remains unknown. This surely needs attention because it could imply reproductive isolation of *Arctica* populations even within the North Sea.

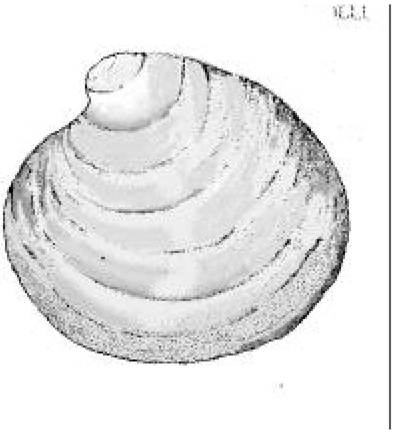
ACKNOWLEDGEMENTS

This paper could not have been presented without the assistance of colleagues, friends, and crews from both research vessels and commercial trawlers who collected living animals. I would especially like to thank A.R. Boeyen for the supply of many samples from the North Sea and the crew of RV Pelagia for their major contribution in collecting *Arctica*. Dr A. Eleftheriou and D. Basford deserve special thanks for their supply of distributional data of *Arctica* in the northern North Sea. The analyses of the data set of which the results are presented here have been made possible by the financial support of the Tidal Water Division of Rijkswaterstaat, the Hague (contract NZ 864).

The growth rate decreases drastically .
At this age the shell height is approximately 6 cm. The periostracum starts to change in colour. New growth increments deposited along the shell margin become so crowded that it is hardly possible to separate them externally from each other. The periostracum starts to turn black by the deposition of iron and manganese complexes.

CHAPTER 3

Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes



CHAPTER 3

Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes

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This chapter has been published in; Netherlands Journal of Sea Research 33(1): 91-101 (1994).

ABSTRACT

^{14}C analysis of material from the shells of *Arctica islandica* supports the hypothesis that the clear and definite banding of these shells are of annual origin. The pulse of ^{14}C around 1960, resulting from atmospheric nuclear bomb testing was recorded in the shells at a location in concurrence with that expected from band counting. The observed cyclic variation in stable isotopes of oxygen and carbon coincides with growth bands. This variation, at least for ^{18}O, agrees with annual temperature variations. This suggests that growth bands are a reflection of seasonally determined differential growth rates. The longevity of this species, coupled with variations in increment width, may provide important information regarding growth and productivity, as well as a record of past environmental conditions.

INTRODUCTION

The ocean quahog, *Arctica islandica* L. has a maximum shell length which can be as high as 10 cm and it is speculated that its longevity may be as long as 225 years (Ropes, 1985). *Arctica* is widely, but patchy, distributed in coastal waters of the North Atlantic. It is a sublittoral species, generally inhabiting sandy-mud to mud bottoms at depths as shallow as 4 m (Rowell *et al.*, 1990) to as deep as 482 m (Nicol, 1951). The species tolerates temperatures from 0° to 19°C (Nicol, 1951). Because of its inability to tolerate temperatures less than 0°C, *Arctica* is considered a boreal, but not an arctic genus (Nicol, 1951). The distribution of *Arctica* in the North Sea was first documented by Nicol (1951). A more detailed picture of this distribution resulted from the 1986 Synoptic Benthic Survey of the North Sea (Duineveld *et al.*, 1990, Duineveld *et al.*, 1991) (Figure 3.1). Since most of the individuals in this collection were juveniles, this distribution pattern may not accurately reflect the distribution of adults.

Figure 3.1

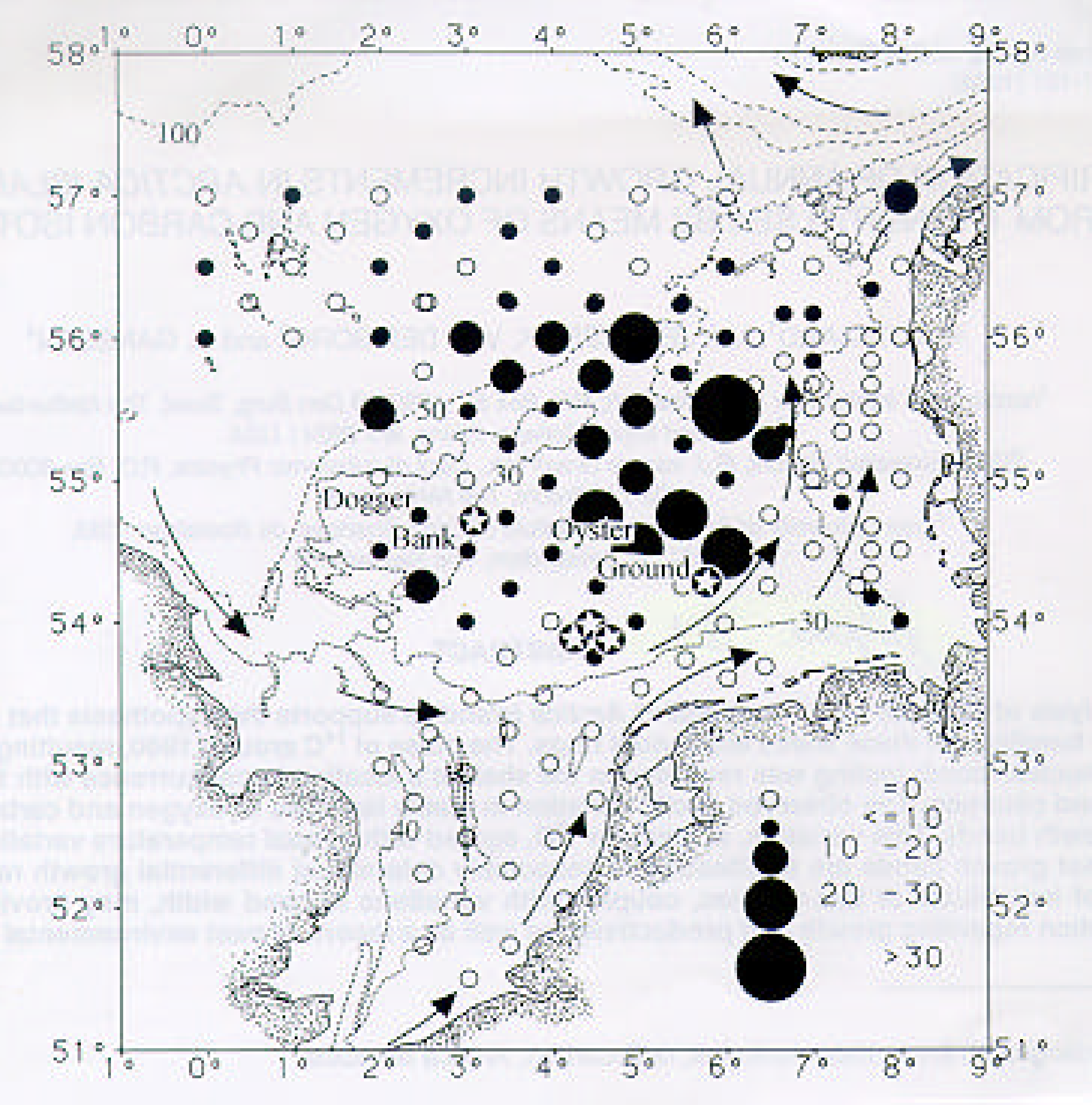

Figure 3.1. Map of central and southern North Sea showing distribution of *Arctica islandica*. Size of black circles reflects density in numbers/m² (After Duineveld *et al.*, 1991). Arrows indicate residual currents. Position from where the shells used in this study have been collected is indicated by ✪.

For a number of reasons, there is increased interest regarding growth and productivity measurements of *Arctica* (Brey *et al*., 1990). In American coastal regions, the ocean quahog has become commercially important for human consumption as a replacement for dwindling stocks of the surf clam (*Spisula solidissima*) (Thompson *et al*., 1980a). While *Arctica* is rarely fished commercially in Europe, it has been shown by Arntz (1974) that *Arctica* is an important food source for codfish in the Baltic Sea. Finally, because of its supposed longevity and the continuous record of its growth in variable width of growth bands, *Arctica* is now being seen as a potentially valuable tool for evaluating present environmental changes in terms of past events (Thompson & Jones, 1977; Jones, 1980; Witbaard & Duineveld, 1990).

Growth and productivity measurements depend on the reliability of the observed growth bands as accurate indicators of age. The earliest attempts to measure growth rates relied on external growth checks found on the shells of relatively small (<60 mm shell length) specimens of *Arctica* (Lovén, 1929). Larger specimens (>60 mm shell length) or those with more than 10 checks were difficult to evaluate because the rings near the margin of the valves were too tightly crowded or were partially obscured by the thick black periostracum or because of erosion of the earliest formed checks.

Recent investigations have relied on microscopic examination of internal banding patterns of *Arctica* shells. Because the bands in *Arctica* are narrow with little color contrast, they are not easily discerned. However, by cutting, polishing, and making acetate peels of the cross-section of *Arctica* shells, Thompson *et al*. (1980a; b), Jones (1980), and Ropes *et al*. (1988) were able to discern unambiguous growth bands, even in the most ancient individuals.

Evidence supporting the hypothesis that these are in fact annual bands, is given by Thompson *et al*. (1980a). This evidence includes: finding similar bands in surf clams (*S. solidissima*) which were proven to be annual; finding a low number of bands formed during the onset of sexual maturity that were not explained by less than an annual frequency; finding an expected number of bands formed sequentially in samples taken frequently during a 2-year period that reflected only an annual periodicity; finding a line deposited during the fall-winter, a period coinciding with spawning; and finding a consistent number of bands in a settlement and recovery experiment with young shells.

The results of a mark-release and recovery study (Murawski *et al*., 1982; Ropes *et al*., 1984a) provided more support of the hypothesis of annual band formation. Of 41816 specimens whose valve margins had been indelibly scored, 267 were re-covered and examined one and two years after release. In all cases, acetate peels made of the valves of the recaptured quahogs revealed the expected number of bands formed beyond the score-marks.

The age of deposited shell material can also be estimated using time-dependent signals from naturally occurring (Smith *et al.*, 1991) or anthropogenically produced radionuclides taken up by organisms from the surrounding water. Radionuclide measurements on *Arctica* growth rates have been reported by Turekian *et al.* (1982). Using both naturally occurring ^{228}Ra and ^{228}Th as well as bomb-produced ^{14}C, they concluded that the radiometrically determined growth rates for *Arctica*, at least for deep-water specimens, are compatible with those estimated from band counting.

While their ^{228}Ra and ^{228}Th studies returned expected results, the results from the ^{14}C studies were less definitive; *i.e.* they found a better fit of the data if a semi-annual banding was assumed, particularly for shallow living specimens. These results may be partly due to the method (Beta decay) used which required several shells representing different time windows to produce a composite ^{14}C chronology. This lack of confidence in shell deposition periodicity for shallow water specimens, coupled with the potential for differences due to geographical location were primary considerations for undertaking the present study. The relatively recent improve-ments in radionuclide measurement techniques were also a major factor.

To this end, sequential growth bands were examined by two independent procedures: 1) ^{14}C analysis and 2) analysis of stable oxygen and carbon isotopes.

Nydal & Lövseth (1983) and Nydal *et al.* (1984) reported that tropospheric radioactive carbon reached a peak in 1963. The Levels were twice their natural production rate (Berger, 1979). This increase was a direct result of atmospheric testing of nuclear weapons in the late 1950s and early 1960s. After 1963, input of ^{14}C from this source came to a virtual halt as a result of a partial test-ban treaty. Since that time, atmospheric levels of radioactive carbon have shown a continuous decline. A similar, but somewhat dampened pulse has also been reported for oceanic waters (Nydal *et al.*, 1979; Nydal *et al.*, 1984). The existence of this radioactive pulse provides an unequivocal chronological marker.

The stable oxygen isotope ratio (δ^{18}O) in carbonate shells has been shown (Krantz *et al.*, 1984; Wefer, 1985; Wefer & Berger, 1991; Kalish, 1991; Epstein *et al.*, 1953) to be a function of temperature and the δ^{18}O of the water. This latter is influenced by evaporation as well as the admixture of other water masses having different temperature and salinity characteristics. Since δ^{18}O values are inversely related to temperature, higher water temperatures correspond to lower δ^{18}O values of the carbonate deposited under such conditions.

Thus *Arctica* found in waters having an uniform salinity but a definite annual periodicity in bottom water temperature would be expected to show an annual periodicity in the $\delta^{18}O$ composition of its shell. Examples of this approach illustrating the periodicity of band deposition are given by Krantz *et al*. (1984) and Tan *et al*. (1988).

Because the stable carbon isotope ratios ($\delta^{13}C$) in carbonate shell materials are influenced by metabolic factors as well as by thermodynamic conditions (Fry & Sherr, 1988; Wefer, 1985; Kalish, 1991) the effect of temperature on $\delta^{13}C$ is less clear than for $\delta^{18}O$. Although Grossman & Ku (1986) found a small negative relationship between temperature and $\delta^{13}C$ for aragonitic mollusks, Romanek *et al*. (1992) did not find a temperature effect for abiogenic carbonates.

The role of metabolism is regarded as much more important (Wefer, 1985; Wefer & Berger, 1991; Kalish, 1991). Since metabolism is directly related to temperature and food supply, both of which vary in an annual cycle in the area under study, an annual periodicity for this isotope is to be expected.

Figure 3.2

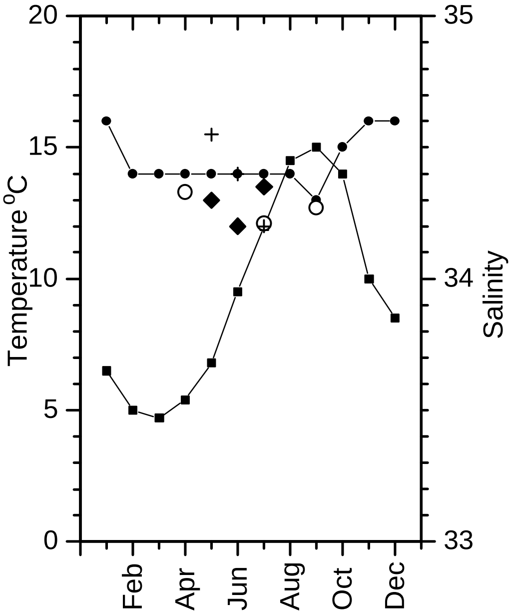

Figure 3.2. Long-term average seasonal variation in bottom water salinity (●) (Goedecke *et al*., 1976) and temperature (■) (Tomczack & Goedecke, 1964) for the southern Oyster Ground together with recent observations of salinities of Central North Sea bottom water (◆) and bottom frontal water (+) in 1986 (Li *et al*., 1989) and of Central North Sea bottom water in 1981 (❍) (Tijssen & Wetsteyn, 1983).

METHODS

Sample area and environmental setting

The animals used in this study were collected from the Oyster Ground, a 30-50 meter deep basin south-east of the Doggerbank. The area is covered with fine sandy sediments mixed with 10-20% clay (Creutzberg, 1984) and has an estimated annual primary production of 250 gC/m² (Gieskes & Kraay, 1984). The average bottom water temperature overlying the area varies between 5 and 15°C (figure 3.2) (Tomczack & Goedecke, 1964). Bottom water salinity variations are small, with the long-term average varying between 34.4 and 34.8 ‰ (Goedecke *et al*., 1967). In 1981, Tijssen & Wetsteyn (1983) found a bottom water salinity of 34.16 in July and 34.44 in May. More recently Li *et al*. (1989) found a similar range, *i.e.* 34.2 in June 1986 and 34.35 in July 1986 (figure 3.2).

At the southern border of the Oyster Ground, a hydrographic tidal front is present which separates the well mixed waters in the south from the summer stratified waters in the north. The position of this front roughly follows the 30 meter depth contour. Associated with this front, a chlorophyll maximum is found (Creutzberg, 1985) together with a rich benthic fauna (Creutzberg, 1984).

Three of the shells used for ^{14}C analysis came from this frontal area. A fourth shell used for ^{14}C was collected from the northwestern part of the Oyster Ground just south of the Doggerbank. The shell which was used for stable isotope analyses was collected north-east of the frontal area.

Analysis of ^{14}C

Sample Preparation

For the ^{14}C analyses 31 samples were taken from four shells which were collected from the southern North Sea. Sampling details are given in table 3.1.

Table 3.1

Shell nr.	Height (cm)	Latitude	Longitude	Date dd/mm/yr	Number of bands	Number of samples
RWL7	8.2	53°41' N	04°25' E	14/03/88	66	12
140	7.2	54°06' N	04°45' E	06/09/88	47	13
RW4C	6.9	53°41' N	04°19' E	14/03/88	27	5
BH40C	9.4	54°45' N	02°59' E	06/05/80	155	1

Table 3.1. Sampling details for the shells used in ^{14}C analyses.

The internal growth bands were made visible by making acetate peels (Ropes, 1985) of epoxy embedded cross-sections. Based on these peels sampling location from the shell cross-section was determined and $CaCO_3$ cores were extracted by using a diamond tipped hollow coring bit (Ø 3x1.8 mm). Thus the samples were taken parallel to the shell surface thereby minimizing contamination with carbonate from the inner nacrous layer. Every sample was assigned to a band count, starting with band 1 at the distal shell margin, *i.e.* the most recently deposited increment. When possible individual bands were sampled but most samples taken refer to a group of bands. This because it was not possible to sample bands from the later growth phases separately due to their narrow width.

From shell RWL7 each of the opposing cross-sections was sampled. The first series consisted of four samples (UtC 1013-1016) representing growth band 1 to 10, band 33 to 38, band 50 to 55 and band 60 to 63. The second batch was taken from the other half of the cross-sectioned shell and consisted of 8 samples of 5 band width intervals (UtC 1070-1077) covering the 40 most recently deposited increments.

Shell 140 contained 47 growth bands of which 13 samples were taken covering the 37 most recently deposited increments.

Five cores were taken from shell RW4C representing 5 * 5 band intervals for the 25 most recently formed growth bands.

From the very large specimen BH40C a single core was taken from 5 bands which represented juvenile growth which was located 150 to 155 bands from the distal shell margin.

Measurement

The samples of 10 to 30 mg carbonate were dissolved in 4 % HCl. The emerging CO_2 was trapped and converted into graphite targets by reduction in an excess of hydrogen with iron powder as a catalyst (Vogel *et al.*, 1984). The graphite targets containing 0.5 to 3 mg carbon were used for analysis with the Utrecht tandem accelerator (Borg *et al.*, 1987). The $\Delta^{14}C$ values were calculated from the ^{14}C-activity (A_{sn}) normalized to $\delta^{13}C$ =-25 per mil with $\Delta^{14}C = (A_{sn}/A_{abs} - 1) * 1000$ per mil, where A_{abs} is the absolute activity of the international standard (Stuiver & Polach, 1977).

Analysis of ^{18}O and ^{13}C

Sample preparation

Shell material from a relatively small specimen of *Arctica* (shell no. 195; shell height = 2.6 cm) was used for the analysis of oxygen and carbon isotopes. This specimen was collected on March 6th 1991, at 54°22'N, 05°40'E. An acetate peel of the cross-section of the left-hand valve was prepared as described by Ropes *et al.* (1984a; 1984b). From this peel both internal growth bands and external growth checks were easily discerned. This information was used to determine where to take samples from the right hand valve. To do this, the concave side of the right-hand valve was first filled with epoxy to reinforce it. Then, using a scalpel and dental drills, the periostracum and irregularities in the shell material were removed from the convex surface.

Table 3.2

Shell nr.	growth band (1)	Estimated year (2)	UtC nr (3)	δ^{13}C (4)	Δ^{14}C (5)	error (6)
RWL7	1-5	1984-1988	1070	1.5	147	± 8
RWL7	1-10	1979-1988	1013	1.46	157	± 7
RWL7	10-15	1974-1979	1071	1.5	136	± 10
RWL7	15-20	1969-1974	1072	1.07	168	± 14
RWL7	20-25	1964-1969	1073	1.67	180	± 13
RWL7	25-30	1959-1964	1074	1.85	-16	± 7
RWL7	30-35	1954-1959	1075	1.8	-45	± 8
RWL7	33-38	1951-1956	1014	1.29	-25	± 8
RWL7	35-40	1949-1954	1076	1.3	-64	± 8
RWL7	40-45	1944-1949	1077	1.77	-58	± 7
RWL7	50-55	1939-1934	1015	2.55	-15	± 9
RWL7	60-63	1926-1929	1016	2.03	-39	± 6
140	1-6	1983-1988	2712	2	129	± 7
140	7-13	1976-1982	2711	2	105	± 10
140	14-17	1972-1975	2710	2	203	± 7
140	18-24	1965-1971	2709	2	201	± 7
140	25-26	1963-1964	2708	2	213	± 7
140	26-27	1962-1963	2707	2	138	± 9
140	27	1962	2706	2	171	± 12
140	28-30	1959-1961	2705	2	40	± 10
140	31-32	1957-1958	2704	2	-44	± 14
140	33-34	1955-1956	2703	2	-45	± 8
140	35	1954	2702	2	-44	± 7
140	36	1953	2701	2	-64	± 12
140	37	1952	2700	2	-51	± 15
RW4C	1-5	1984-1988	1078	.18	114	± 22
RW4C	5-10	1979-1984	1079	1.5	142	± 13
RW4C	10-15	1974-1979	1080	1.5	166	± 17
RW4C	15-20	1969-1974	1081	2.81	139	± 20
RW4C	20-25	1964-1969	1082	1.83	206	± 6
BH40C	150-155	1826-1831	1017	2.93	-33	± 6

Table 3.2. Results of the ^{14}C analyses from sequential cores from four shells from the North Sea. (1), reference to growth bands sampled, counting backwards from most recent deposited. (2), Estimated absolute time scale. (3), Laboratory number UtC. (4), δ^{13}C with respect to PDB measured at Utrecht geology department, the "2" values are estimates. (5), Δ^{14}C with respect to 100 % modern (after normalization to delta 13=-25 per mil; age corrected). (6), Standard error of Δ^{14}C.

In total, six growth increments were sampled. Within each individual growth increment, shell material was sampled by cutting concentric grooves on the convex surface parallel to the growth checks and the outer shell margin. In this way, 2 to 14 sample points were collected from each growth increment, which allowed chronological growth sequence to be established. From the most recently deposited increment VI, only one sample could be taken. Collected material was stored in small glass jars until analysed for stable-isotope composition. After collection of the samples a cross-section of the right hand valve was made to check the depth of sampling (figure 3.4).

Measurement

Samples were dissolved for approximately 10 minutes at 50°C with 100% phosphoric acid (H_3PO_4 in vacuum) by adding droplets of the acid to the samples. The evolved CO_2 gas was frozen at -180°C in glass bottles after being purified from water at -80°C. The isotope composition of the gas was analyzed with a Finnigan MAT 251 mass-spectrometer. The results are expressed as deviations in per mil from the PDB standard, where:

$$\delta^{18}O = \frac{(46 / 44\text{sample} - 46 / 44\text{standard })}{(46 / 44\text{standard})} \text{ x } 1000$$

and

$$\delta^{13}C = \frac{(45 / 44\text{sample}- 45 / 44\text{standard})}{(45 / 44\text{standard})} \text{ x}1000$$

Analytical precision from a working standard was 0.04 ‰ for $\delta^{13}C$ and 0.08 ‰ for $\delta^{18}O$ during the period of measurement.

RESULTS

^{14}C

Table 3.2 lists the results of the ^{14}C analysis on the sequential cores taken from various shells. The ^{14}C values of the growth bands from all shells are also illustrated in figure 3.3. The time intervals indicated on the horizontal axis of this plot represent the periodic growth increments revealed in the cross sections made of the shells.

$\Delta^{14}C$ levels from the oldest bands vary from -64 per mil to -15 per mil for shell RWL7. An abrupt increase in $\Delta^{14}C$ to about +180 per mil occurs at the 25th growth band prior to the most recently deposited. Thereafter, a gradual reduction in $\Delta^{14}C$ values occurs, reaching a level of about 148 per mil in the youngest growth bands. Shell 140 showed essentially the same pattern. Maximum $\Delta^{14}C$ was 213 per mil for the sample taken from band 25-26 prior to most recently deposited.

Figure 3.3

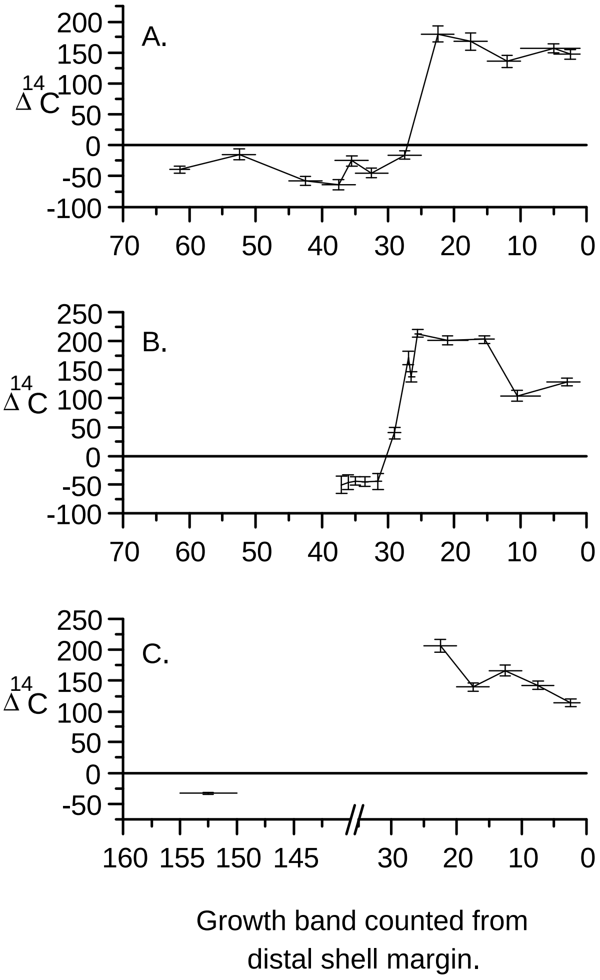

Figure 3.3. Graph of $\Delta^{14}C$ values (per mil) found in sequential cores of four shells of *Arctica islandica*. Horizontal axis represents number of increments with most recently formed (1988) on right. Abrupt increase in $\Delta^{14}C$ occurs about 25 increments before time of collection. (a), Shell RWL7. (b), Shell 140. (c), Shells RW4C and BH40C.

The cores taken from shell RW4C included the 25 growth increments deposited prior to 1988. Only high $\Delta^{14}C$ values were observed from this shell, similar to those found in the 25 most recently deposited growth increments of the other shells, with an equal decrease over time. The single measurement from growth bands 150-155 in shell BH40C gave a ^{14}C value of -33 per mil. This is somewhat more enriched than the values found in the older (prebomb) growth increments of shells RWL7 and 140.

^{18}O and ^{13}C

Both $\delta^{18}O$ and $\delta^{13}C$ values show cyclic variations (figure 3.4). And for both isotopes, a break in the pattern occurs between increments III and IV. The $\delta^{18}O$ values found over all sampled increments varied from a minimum of 1.15 to a maximum of 3.99 per mil. Intra-incremental $\delta^{18}O$ ranges varied from 0.67 to 1.5 per mil. The pattern within all individual increments is essentially the same: a sharp increase between the termination of one band and the beginning of the next followed by a gradual decrease through the major portion of the band. The higher values are thus found in the earliest deposited portion of a given increment while the lowest values are found in those parts deposited just before the observed growth stops. Further, an overall trend of decreasing values with time, superimposed on the cyclic variations, can be observed. For $\delta^{13}C$, a gradual increase in values with time was found with values ranging from 0.58 per mil for the oldest increment formed to 2.39 for increment V. Within individual increments differences ranged from 0.56 to 1.06 per mil. Minimal values are for all increments found in the first deposited parts.

DISCUSSION

^{14}C

The abrupt increase in ^{14}C values observed in figure 3.3 almost certainly resulted of the bomb-produced pulse which peaked in the troposphere in 1963. The time difference between this peak and the collection date of the shells (1988) was 25 years which coincided closely with the number of growth increments represented between the peak signal in the shells and the collection date. The difference in both the exact position of the peak and the absolute values for shell RWL7 and shell 140 is probably due to the precision of sampling. The growth increments are so narrowly spaced in the later growth phase that it was not possible to extract samples from all individual years. Thus most of the ^{14}C values represent an average for a number of years.

However, these data are direct evidence that the growth bands in the shell represent an annual event. Results similar to those described above have been reported by Weidman & Jones (1993a) using a specimen from Georges Bank. Their record of ^{14}C for a North Sea specimen (Weidman & Jones, 1993b) was incomplete but shows a trend very similar to that presented here.

The close coincidence between the number of growth bands counted backwards and the occurrence of the rapid increase in $\Delta^{14}C$ was not necessarily expected; it would not have been unreasonable to expect a time-lag between finding this peak in the atmosphere and its appearance in the North Sea.

Figure 3.4

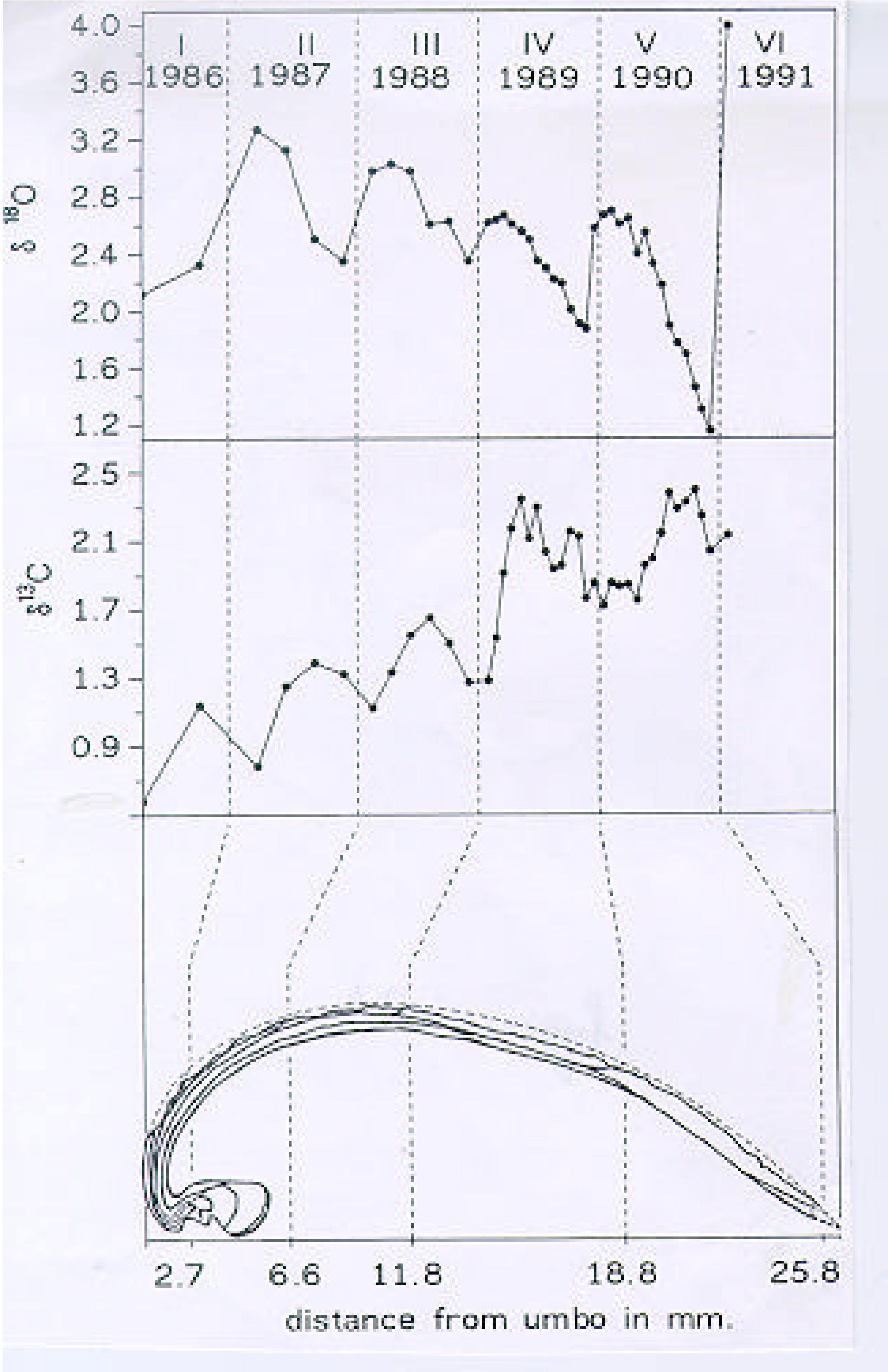

Figure 3.4. Cross-section of shell no. 195 after being sampled. Dotted vertical lines indicate increment boundaries, curved dotted line approximates the presampled outer shell surface. Obtained δ ^{18}O ‰ (PDB) and δ^{13}C ‰ (PDB) results of sequential samples are given for corresponding shell segments. Six increments were sampled with most recent increment shown on right. Increment number (I,II,III,IV,V,VI) together with the represented year is given in the upper part of the figure.

Model estimations of Broecker *et al*. (1985) for instance, demonstrated that peak height, and the date and time interval in which the maximum $\Delta^{14}C$ is reached differs among oceans and with latitude within an ocean basin. They noted that the rise towards maximum values in the northern temperate Atlantic Ocean surface waters is far steeper than for other latitudinal zones. Unfortunately the measure-ments for the northern North Atlantic (45°N-75°N) are only available from 1965 until 1967 (Nydal *et al.*, 1984). Consequently, the effect of the nuclear bomb testing on the northern North Atlantic Ocean surface has to be assessed from data collected from more southern areas, *i.e.* from a latitude between 25° and 39°N.

It seems likely from these data that for the northern North Atlantic Ocean surface waters the ^{14}C pulse mainly peaked in the period 1967-1969 (Nydal *et al.*, 1979), some four years after the occurrence of the peak in the troposhere. Since that time, ^{14}C levels in the ocean surface waters have declined gradually (Nydal & Löveseth, 1983).

Because the southern North Sea is so shallow and well mixed, it might be expected that interchange with the atmosphere would be more rapid here, with the maximum ^{14}C values occurring somewhat earlier than in the surface waters of the large ocean basins. This may especially be true for the region from where the shells for this study were collected. It is a region where a tidal front generates vertical water transport which is accompanied by an increased primary production. Hence, the $\Delta^{14}C$ signal might be expected to be more rapidly transferred to the benthic fauna when compared to deeper sites where such vertical transport with increased production is lacking.

In this regard, it is interesting to note that the results of the Georges Bank specimen from Weidman & Jones (1993a) shows maximum peak in $\Delta^{14}C$ somewhat later compared to both their own North Sea specimen and the results presented here. Hence they have suggested that *Arctica* could well be used as an indicator to measure the arrival time of the ^{14}C pulse to the different regions of their extensive range and to use it in studies on watermass transport.

The pre-bomb values for the period 1944 -1952 are on average -53 per mil, a value comparable to those given by Tanaka *et al*. (1990) and Weidman & Jones, (1993a; 1993b). The pre-bomb value obtained from shell BH40C is, however, less depleted (-33 ± 6 per mil). This difference can be explained by the effect of the combustion of fossil fuels (Suess, 1958). The sample represents the pre-industrial time period of the early 19th century (1826-1831). Since the later part of the 19th century the industrial revolution caused a massive release of CO_2 (^{14}C free) leading to a depletion of the atmospheric $\Delta^{14}C$. This effect was overshadowed since the onset of nuclear bomb testing in the late 1950s.

Stable isotopes

The cyclic periodicity shown by both the $\delta^{18}O$ and $\delta^{13}C$ data closely follows the increment band patterns (figure 3.4), providing further evidence that these bands are annual in nature.

The geographical region from which shell 195 was collected is characterized by a distinct annual temperature cycle as well as an annual cycle of phytoplankton abundance. Variation in salinity within any given year are minimal, usually not exceeding 0.4 ‰. The expected variation in $\delta^{18}O$ values due to these small variations in salinity would be around 0.2 per mil as calculated using the empirical relationship developed for North Atlantic waters (Ganssen, unpublished):

$$\delta^{18}O = -14.555 + 0.417 * \text{salinity}$$

The long-term average bottom water temperature for this area fluctuates annually between 4 and 15°C (figure 3.2). The expected maximum annual variation in $\delta^{18}O$ due to these temperature differences would be 2.5 per mil. The observed differences within any given increment of shell deposition, however, did not exceed 1.65 per mil (figure 3.4).

The most rapid observed changes are almost invariably found at the inter-incremental boundaries with the largest occurring between increments V & VI. The magnitude of this change (2.84 per mil.) closely resembles the expected value of 2.5 based on an annual temperature variation of 11°C. These observations suggest that carbonate is deposited during only a fraction of the annual temperature cycle, with the initiation and termination of growth occurring at different bottom water temperatures.

To explain these observations, we propose a mechanism in which the steep inter-incremental changes reflect a "winter stop" in which growth stops at the end of summer and does not resume again until the following spring. Thompson *et al.* (1982b) have suggested that the formation of the growth line for *Arctica* found in North American waters takes place in fall or at the end of summer in close coincidence with reproduction, and that most growth takes place during the spring and early summer. *Arctica* seems to have a similar reproductive cycle in European waters (Oertzen, 1972), which would imply that growth line formation in this region also occurs at a time with maximum bottom water temperatures, resulting in minimum $\delta^{18}O$ values just prior to increment termination. This, together with the expectation that significant shell growth is probably not resumed before the following spring, is illustrated by the narrow band width of the sixth increment in the specimen we studied. This narrow increment must have been deposited between the autumn prior to the sampling date and the time of sampling, *viz.* March. During this period, bottom water temperatures are low and would have yielded maximum $\delta^{18}O$ values in juxtaposition to the depleted $\delta^{18}O$ carbonate deposited during the end of the previous growing season. This would result in a rapid change in carbonate composition at the increment boundary as observed. A complete winter stop in growth is proposed because the main food supply (the spring phytoplankton bloom) is not present before the month of March (Creutzberg, 1985; Reid *et al.*, 1990).

During the development of the spring bloom, the bottom water temperature increases slowly, a pattern which seems to be mirrored in the slowly decreasing $\delta^{18}O$ values for the earliest deposited materials within each band. This is especially noticeable in increments III, IV and V.

Thus, the mean seasonal temperature cycle can explain most of the observed variation in $\delta^{18}O$ levels. The gradual decrease within each increment reflects the gradual warming of the bottom water between spring and autumn. The rapid $\delta^{18}O$ increases at the increment boundaries mark a winter stop in growth beginning at the end of summer (high temperatures) and ending the following spring (low temperatures). The slowly decreasing $\delta^{18}O$ values for the earliest parts of each increment thereby reflects the period during spring in which the phytoplankton bloom develops but increases in temperature are still small.

The difference in magnitude between inter- and intra-annual $\delta^{18}O$ variations might also be an effect of the sampling technique. Because growth increments tend to be overlapping, sampling too deeply near the outer incremental boundary would result in contamination of the sample with shell material from the deeper internal nacrous layer, material which had been deposited more recently. Analysis of such contaminated material would result in less depleted $\delta^{18}O$ values than would be expected for so late in the growing season. Since the most recently deposited increment would have no deposits underlying it, it would be minimally contaminated and thus would more accurately reflect the complete seasonal temperature change. From the cross-section made (figure 3.4) it can be seen that this might indeed have influenced the stable isotope values for the first three increments sampled.

Another explanation for the differences observed in intra- and inter-incremental variation as proposed by Weidman *et al.* (1994) might be due to a shutdown temperature below which growth stops. This mechanism also implies a growth season shorter than an entire year. Weidman *et al.* (1994) concluded from their results that this temperature was approximately 8°C, at least for the specimen they studied.

Absolute temperatures cannot be derived from our data as we did not measure the $\delta^{18}O$ values of the bottom water. However, if one assumes a maximum bottom water temperature of 15°C coinciding with band termination, growth must have started at a temperature of approximately 4°C (March, see figure 3.2) based on the $\delta^{18}O$ difference between increment V and VI. This indicates that growth can take place at a much lower temperature than proposed by Weidman *et al.* (1994). This is corroborated by experiments where an average shell growth of 1.3 mm/3 months for ~15 mm high shells was achieved at a temperature of 3°C (chapter 4).

We therefore suggest that the onset of growth is mainly determined by food availability which in turn is closely regulated by the seasonal cycle. The start of growth is thereby triggered by the development of the spring bloom (Graf *et al.*, 1984; Davies & Payne, 1984; Smetacek, 1984) which will begin each year at approximately the same time and temperature. This might suggest a "shutdown" temperature, but more likely reflect the temperature at which the food supply to the benthos starts. If so, different populations of *Arctica* from different environmental settings could appear to have different "shutdown" temperatures.

The interpretation of $\delta^{13}C$ is much more difficult than for $\delta^{18}O$. First of all there is no agreement on the effect of temperature on $\delta^{13}C$ values of aragonitic carbonate. Based on literature Kalish (1991) concluded that the temperature effect would be small and may even be uncertain. Latter supposition has been confirmed by the observations of Romanek *et al.* (1992) who did not find an effect of temperature on $\delta^{13}C$ values for abiogenic carbonates.

Metabolism is generally regarded as much more important (Wefer, 1985; Wefer & Berger, 1991) in determining variation in $\delta^{13}C$ values, but because metabolism is directly controlled by both temperature and food supply a cyclic variation in the ^{13}C composition of the increments could be expected. However, Erlenkeuser (1976) found that the shell carbonate was deposited in isotopic equilibrium with the bicarbonate of the surrounding bottom water which thus suggests that a vital effect is likely to be absent.

Local watermass variations may also influence $\delta^{13}C$ ratios and there might also be a seasonality in the local DIC (Dissolved Inorganic Carbon) composition of the bottom water. A phytoplankton bloom may result in a relative enrichment of the water. And if *Arctica* indeed deposits its carbonate shell in equilibrium with surrounding DIC a gradual enrichment in the carbonate during the phytoplankton bloom may be seen. After the bloom collapse local DIC values come back to normal values resulting in a gradual decrease before band termination. Again a cyclic pattern will be the result.

Between increment III and IV there is a sharp transition in both $\delta^{13}C$ and $\delta^{18}O$ which might be related to the effects of ontogenetic development. Because such effects involve major metabolic changes, e.g. changes in weight specific metabolism, the onset of reproduction and changes in age specific growth, it is likely that they may well effect $\delta^{13}C$ ratios. These effects may, however, be spread over several growing seasons and thus would tend to change gradually rather than enhance cyclic patterns.

An environmental change to explain the observed transition can however not be excluded. Indications for such an environmental change was first given by Lindley *et al*. (1990) who observed a massive occurrence of Doliolids in the German Bight. This planktonic organism is regarded as an indicator of oceanic waters. They also noted that the sea surface temperature (SST) in June was 2 to 3°C higher than normal. Later Becker & Wegner (1993) reported that the mean annual SST for 1990 was 0.7 °C higher than the decadal mean. In 1992 Becker *et al*. also reported an anomalous high salinity in the southern North Sea and the Channel. There are thus indications of abnormal hydrographic conditions in the early 1990s so it is reasonable to suppose that these abnormal hydrographic conditions also affected the bottom water and consequently its isotopic compositon. The observed transition might also have been an indirect effect in terms of a prolonged food supply, which caused growth under warmer conditions, hence more depleted $\delta^{18}O$ values.

Despite the uncertainties in the interpretation of the stable isotope data, we conlude on the basis of the $\Delta^{14}C$ results together with the repeating cyclic variation in stable isotopes, which are in close coincidence with the growth bands, that these bands, are indeed annual.

Additional evidence for an annual deposition pattern for North Sea specimens comes from our observations of a population found at 140 m in the northern North Sea (59°20'N 0°30'E) (see chapter 7). This population was sampled twice; first in 1983 and again in 1991. The earlier sample consisted of 6 young shells and the later sample of 18 shells. From acetate peels (Ropes, 1985) prepared of the hinge part of these shells, measurements of the internal growth increments were made. Because the date of sampling was known for each group, a known year could be assigned to each of the growth increments. For those shells from which the period of overlap was long enough, the % similarity of growth variations or "Gleichläufigkeit" (Schweingruber, 1989) was calculated. The average value found for all possible pairs was 73%, indicating that both groups of shells showed similar growth variations for the pre-1983 period. This implies an annual deposition periodicity because the number of deposited increments in the 1991 sample was equal to the number of years since 1983.

While we recognize that this study is based on only a limited number of shells, it is deemed significant that the complementary results of the different methods employed all support the conclusion that the observed growth rings are annual.

ACKNOWLEDGEMENTS

The authors would like to thank G. Berger, G.C.A. Duineveld and especially W. Mook and the referees for critically reading the manuscript and suggesting major improvements. We also wish to thank A.F.M. de Jong for his help in preparation of the ^{14}C samples.

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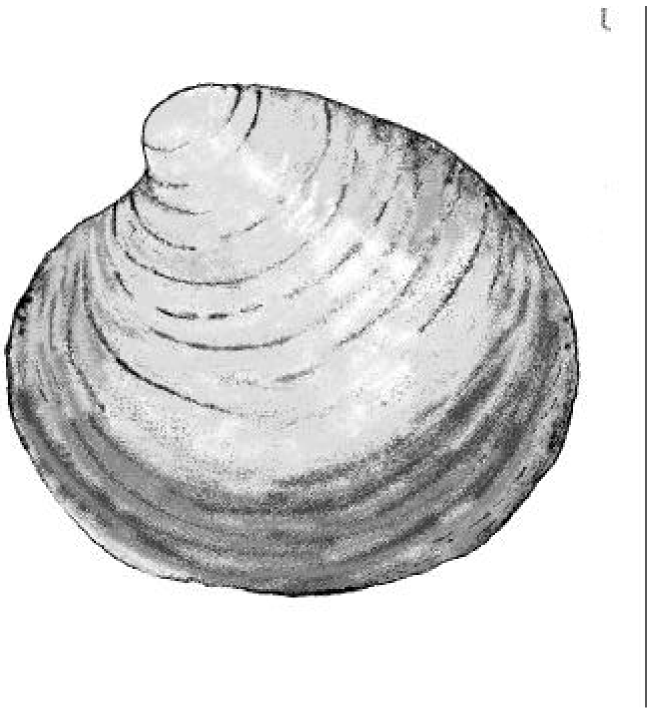
At this age, the shell is almost entirely black.
Only the outer margin of the periostracum has the yellow brown
hue of younger *Arctica*. The growth lines along the shell margin
can not be recognised anymore. At this age the animal has
attained a shell height of approximately 7 cm.

CHAPTER 4

Growth of juvenile *Arctica islandica* under experimental conditions



CHAPTER 4

Growth of juvenile *Arctica islandica* under experimental conditions

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Submitted to: Helgoländer Meeresuntersuchungen.

ABSTRACT

In two laboratory experiments the effects of temperature and food availability on the growth of 10 to 23 mm high specimens of the bivalve *Arctica islandica* were estimated. Both experimental set-ups consisted of 5 treatments; in the first the food supply differed, and in the second, the temperature was the controlled variable.

It was demonstrated that *Arctica* is able to grow at temperatures as low as 1°C. A ten-fold increase in shell growth was observed between 1 and 12°C. The greatest change in growth rate took place between 1 and 6°C. Average instantaneous shell growth varies between 0.0003/day at 1°C to 0.0032/day at 12°C.

The results suggest that temperature barely affects the time spent in filtration whereas particle density strongly influences that response. Starved animals at 9°C have their siphons open during only 12% of the time, whereas the siphons of optimally fed animals were on average open during 76% of the observations. Increased siphon activity corresponded to high shell and tissue growth. At 9°C, average shell growth over the experimental period at the optimum phytoplankton cell density of $20*10^{6}$ cell/l, was 3.1 mm. This corresponds to an instantaneous rate of 0.0026/day.

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

INTRODUCTION

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

Arctica at 6.3% whereas in older animals growth rates as low as 0.2% were found. This low value for large animals corresponds to the results obtained by Forster (1981). He measured 0.1 mm growth (in-situ) over a one-year period in *Arctica* with shell lengths between 82-108 mm. Estimates of growth rates for young *Arctica* were reported by Kennish *et al*. (1994). They transplanted artificially reared specimens with shell lengths between 9 and 20 mm to an offshore location in the Gulf of Maine (USA). Repeated measurements over the following two years demonstrated an enormous variability in shell growth. In some periods, the average growth rate was ±1 µm/day, while in other periods the average growth rate was 25 µm/day. Kraus *et al*. (1992) transplanted specimens from an off-shore location to an estuarine location and demonstrated that growth increased considerably in the richer environment. In two years time, the experimental shells attained a size which would have taken 27 to 35 years in their natural off-shore habitat.

Quantitative relationships between growth and environmental factors are either poorly known or speculative. Kraus *et al*. (1992), for instance, attributed the low growth rates in the off-shore shells to disturbance or competition for food but that supposition has never been substantiated. While filtration rates in conjunction with temperature, animal size or food concentration have been determined experimentally (Møhlenberg & Riisgard, 1979; Winter, 1978; Winter, 1969) virtually nothing is known about shell growth under controlled laboratory conditions.

The present paper describes the results of two growth experiments with juvenile *Arctica*. In the first experiment the animals were kept at 5 different food levels at a constant temperature. In the second experiment the specimens were kept at 5 different temperatures while food concentration was kept near optimum (Winter, 1969). The aim was to measure temperature dependent growth and to establish a relationship between growth and food availability.

MATERIAL & METHODS

Living specimens of juvenile *Arctica* were collected from the Süderfahrt site (See Brey *et al*., 1990) in Kiel Bay in the western Baltic Sea. Within 24 hours these animals were transferred under refrigeration to the Netherlands Institute of Sea Research (NIOZ). There they were placed in sand filled containers in a basin with aerated seawater until used. During the first four weeks the animals were gradually acclimated to the experimental conditions. From this collection a selection of animals to be used in the experiments was made on the basis of shell size. The size range of shells was kept as small as possible and varied between 10 and 23 mm (height).

Experiment I: food availability

The experimental set-up was comprised of 5 treatments (I-V), each with four replicates. Each replicate consisted of a container with a water volume of 10 litre. These containers were placed in a thermostatically controlled basin in which the temperature was kept at 9.2 ± 1°C. Twice a week the water in the replicates was flushed to avoid harmful concentrations of metabolites. All replicates except those in treatment I, were continuously supplied with differing quantities of the same suspension of *Isochrysis galbana* and *Dunaliella marina* by a peristaltic pump. The ratio of food added to treatments II : III : IV and V was 1 : 2.4 : 5.8 : 8.8 respectively. Treatment I was the control and thus did not receive any food. In each replicate the algae were held in suspension by gentle aeration. Food conditions in each of the replicates was monitored twice a week by cell counts on an Elzone particle counter and once a week by chlorophyll measurements on a Hitachi F2000 fluorescence meter following standard methods.

Chlorophyll concentration of the food source was regularly determined as described above. Carbon content of each suspension was determined after wet oxidation on an Oceanography International MSA infrared analyser. Multiplying the average carbon content/ml suspension with the quantity added per day to each container yielded an average supply of 62 µgPOC/day per replicate in treatment II to 550 µgPOC/day in the best fed replicates of treatment V.

Nine numbered glass jars were placed in each of the replicates, with one specimen in each jar. The average of triplicate measurements of shell height, shell length and shell width was used to describe actual shell size. These measurements were made with an electronic callipers. Average standard deviation of the triplicate measurements was 0.06 mm. The specimens were divided among the replicates in such a way that at the start of the experiment average height and standard deviation in each of the replicates was approximately equal.

The relationship between size and ash-free dry weight (afdw) was determined using 71 animals not involved in the experimental procedure. The shells were measured and soft tissue was removed and dried at 60°C until constant weight was reached. After pre-weighing, the dried flesh was incinerated at 540°C for three hours yielding the afdw. The relationship between shell height and weight was used to estimate the condition index ($(\text{weight}/\text{height}^3) * 1000$) of each experimental *Arctica* at the start of the experiment.

When *Arctica* is buried into the sediment, two modes of siphon activity were distinguished. In mode I the valves are closed; the mantle edge might be visible but the siphons are closed. In mode II; the mantle edge is extended and the siphons are fully open. According to Møhlenberg & Riisgård (1979), the mode with fully open siphons is associated with high filtration rates, while decreasing filtration rates are associated with partial closure of the valves, siphons, or mantle edges. Thus the mode of siphon activity is an indication for the filtration activity and thus probably food uptake. We therefore recorded once a day for each individual specimen its mode of siphon activity and at the end of the experiment the number of days in which the specimen displayed open siphons (mode II) was expressed as percentage of the total number of observations. This quantity is referred to as daily siphon activity.

Shells which died during the experiment were replaced by similar sized specimens to minimise the effects of differences in competition for food between replicates. These shells were not, however, used in the final analyses.

After 68 days, the shells were remeasured, followed by the determination of the afdw as described above. The difference between the shell measurements at the start and end of the experiments was regarded as growth. Instantaneous growth rates (a) have been calculated for all shells as $a=(\text{Ln } (y_t/y_o) / t)$, with y_o equal to the initial shell size at the start of the experiment and y_t as the shell size at time t.

The differences between treatments were tested by analyses of variance (anova) and the residuals were checked for normal distribution and departures from homoscedasticity by graphical methods. In all cases, the data satisfied the assumptions to justify the anova.

Table 4.1.

Treat.	Cell density (10^6 cell/l)	Chlorophyll (µg/l)	Siphon act. (%)	Δ Height (mm)	Δ Length (mm)	ΔWidth (mm)	Δ Weight (mg)	Δ Index
I	0.49	0.04	12.6	0.06	0.03	-0.03	-5.59	-1.10
II	7.40	1.25	43.0	0.21	0.22	0.20	2.07	0.23
III	5.41	1.02	64.5	1.26	1.41	0.71	18.96	2.40
IV	14.74	2.66	64.1	2.05	2.34	1.11	42.78	4.74
	(9.80)	(1.88)	(73)	(2.25)	(2.58)	(1.22)	(42.83)	(4.69)
V	21.35	4.53	76.3	3.06	3.57	1.58	66.86	6.91

Table 4.1. Overview of experimental conditions and main results per treatment in the food experiment at 9°C. The values between parentheses indicate average when the deviant replicate is omitted.

Experiment II: temperature

In the second experiment an attempt was made to assess the effects of temperature on the growth of similar sized specimens as described for experiment I. The experimental set-up was essentially the same as that described above; five treatments (A, B, C, D, E) with four replicates in each. Each replicate contained six labeled glass jars with one animal in each jar. The treatments differed in temperature with lowest average temperature set at 1.1 ± 0.2°C for treatment A and the highest average temperature set at 12 ± 0.8°C for treatment E. The temperatures of treatments B, C and D were 3.2 ± 0.4°C; 6.2 ± 0.5°C and 9.2 ± 0.6°C respectively.

At the start of the experiment, the average shell height was 15.5 mm and ranged between 10.1 and 23.1 mm. Initial weight of the experimental specimens was estimated on the basis of an afdw-height relationship determined from a reference group of 50 animals at the start of the experiment.

All replicates were fed with a phytoplankton mixture as described for the experiment I. To ensure that growth took place under *ad libitum* food conditions, the availability in each replicate was kept in the optimum range of $10*10^6$ to $20*10^6$ cell/l (Winter, 1969) by adjusting the peristaltic pumps which supplied each replicate when needed. The siphon activity for each individual animal was recorded once each day. Twice a week the cell density and once a week the chlorophyll concentration were measured in each replicate. No POC measurements of the stock cultures were made nor was a precise measurement of the capacity of the pumps made. The experiment lasted 95 days and at the end the animals were treated as described for experiment I.

Figure 4.1

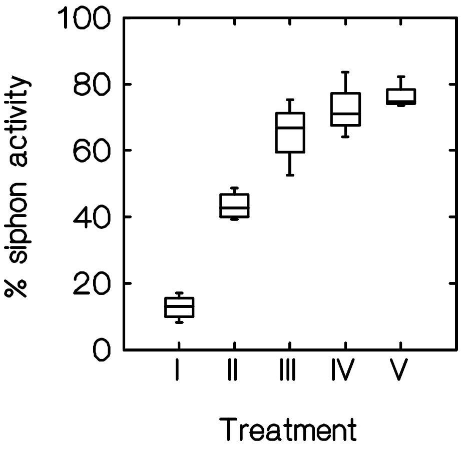


Figure 4.1. Box and Whiskerplot of average daily siphon activity per treatment in experiment I. Treatments I-V correspond to an average POC supply of 0, 62, 150, 362 and 550 µg/day. The deviating replicate in treatment IV (see text) is omitted from the graph.

RESULTS

Experiment I: food availability

The average food conditions during the experiment and results per treatment are summarised in table 4.1. Algal cell density ranged between virtually nothing (I) to $21*10^6$ cell/l (V). As would be expected, the chlorophyll concentration closely followed the trend in cell density. One of the replicates in treatment IV strongly deviated from the norm in all measured parameters and we therefore recalculated the averages omitting these deviating values.

The difference in siphon activity between the treatments (figure 4.1) was most obvious. The shells in the non-fed containers (treatment I) had the lowest siphon activity with an average of 12.6% corresponding to 9 days. Shells in treatment V, that received the highest ration, were recorded with open siphons during 52 days, which is 76% of the experimental period. The shells in the replicates at intermediate food levels (treatments II-IV) were found with open siphons between 43 and 64% of the observations. The absence of a significant difference between treatment III and IV can be attributed to the deviating replicate of treatment IV. Shells in this replicate had open siphons during only 34% of the observations. The siphon activity of the deviant replicate differed significantly from the average values in the other replicates within the treatment IV (Tukey HSD, pairwise comparison $p<0.05$). This deviant replicate is therefore omitted from figure 4.1 resulting in an average of 73% of observations at which the animals had open siphons.

Figure 4.2

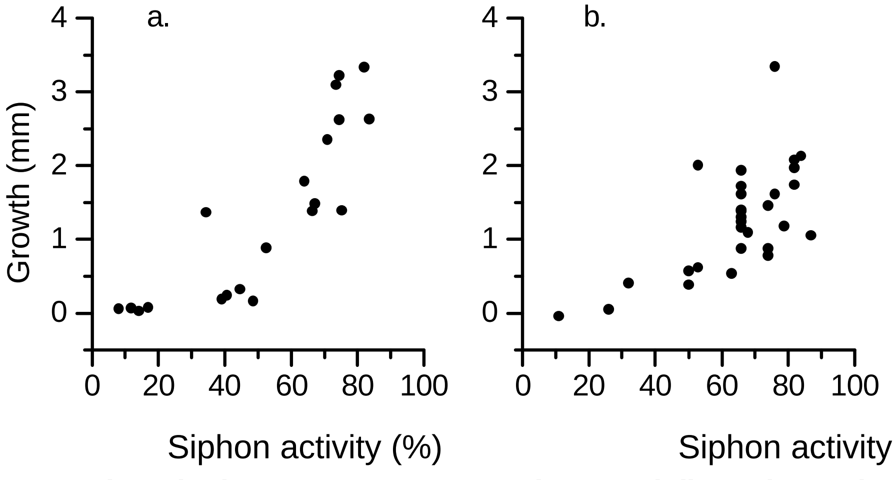


Figure 4.2. Relationship between average activity and average shell growth. (a), The dependence of average height growth per replicate in experiment I. Each symbol indicates a replicate average. (b), Similar relationship as in figure (a) for the siphon activity of individual shells within treatment III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

Figure 4.1 illustrates that, within the range of food supplied, average daily siphon activity reaches a maximum value of approximately 80%. The observed differences between treatments in average siphon activity appeared to be significant (anova, p<0.05). A Tukey HSD pairwise comparison demonstrated that the differences between the three best fed treatments (III to V) were insignificant but they all differed significantly (p<0.001) from the starved and lowest fed treatment.

Even though the utmost precautions were used, the collection, transfer and adaptation of the animals caused the formation of a disturbance mark which was externally visible as a shallow groove on the external shell surface. In specimens which displayed considerable growth, this mark was accompanied by a shift in colour of the periostracum from a yellowish hue to a darker brown colour. This mark facilitated the recognition of shell growth.

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

Figure 4.3

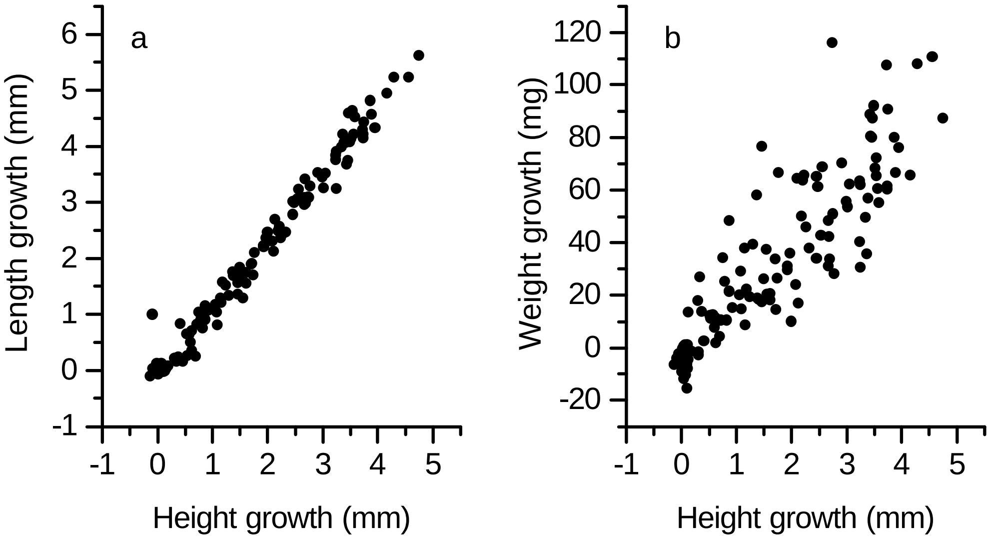


Figure 4.3. Relationship of measured height, length and tissue growth. (a) Linear relationship between height and length growth of the animals in experiment I. (b) The relationship between height and tissue growth of the animals in experiment I (food).

Animals with a siphon activity below 40% showed minimal growth, regardless of the amount of food provided (figure 4.2a). The average change for all shell dimensions is given in table 4.1. The observed increase of 0.06 mm in the non-fed treatment (I) equals the measurement error and is therefore deemed insignificant. Maximum change in shell height was 4.7 mm for one shell in the best fed treatment (V). The average instantaneous growth rates ranged between 0.0002- and 0.0026/day. Anova showed that shell growth rates differed significantly between treatments (p<0.05). Growth in all three dimensions as well as growth of soft tissue were strongly related, with correlation coefficients ranging from 0.88 to 0.99 (figure 4.3). The ash-free dry weight of the non-fed treatment (I) showed an average decrease of 5.6 mg (table 4.1). Tissue weight in treatment II remained almost equal over the sample period with an average increase of only 2 mg. Although algal cell density in treatment III was lower than the density in treatment II, the average weight increase in treatment III (42.8 mg) was 2.3 times higher (table 4.1). The shells in the best fed treatment increased 67 mg on average but for some individual shells, growth of the soft tissue exceeded 100 mg (figure 4.3b).

The combined effect of tissue growth and shell growth is given as the average condition index ((weight/height^3)$*$1000). For the reference group it was estimated to be 6.19 ± 0.05 at the start of the experiment. Compared to this value, the average index of the non-fed *Arctica* in treatment I decreased to 5.11. The average index values in all other treatments increased between 2 to 111% (figure 4.4).

Except for treatments I and II, the changes in the condition index between all treatments were significant (Tukey HSD test, $p<0.05$). The index changed at high food concentrations more rapidly than the corresponding siphon activity, suggesting that at high particle concentrations minor increases in siphon activity lead to disproportionately high increases in tissue growth.

Figure 4.4

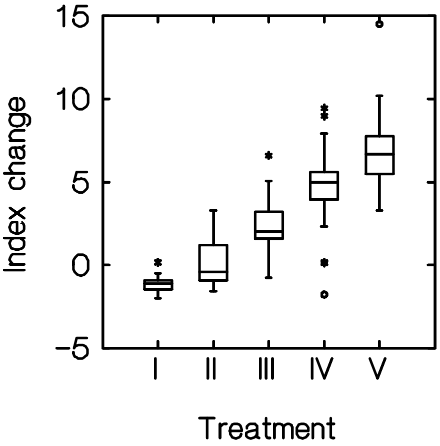


Figure 4.4. Box and Whisker plot of the change in condition index (Δweight/height^3*1000) of the experimental animals in the food experiment; * indicates outlier (1.5*H); ° outlier 3*H.

A multiple regression model describing shell growth (height) as being dependent on average cell density and filtration activity, was fitted to the data (table 4.2). The regression was highly significant with a coefficient of determination of 0.68. The standardised regression coefficients (table 4.2a) illustrate the great importance of filtration activity (0.672), compared to the effect of algal density (0.367).

Table 4.2a

Variable	Coeff	Std Error	Std Coef	Tolerance	T	p(2 Tail)
Constant	-0.839	0.279	0.000	-	-3.004	0.008
Cell density	0.049	0.016	0.367 (a)	0.764	3.164	0.006
Activity	0.032	0.006	0.672 (b)	0.764	5.797	0.000

Table 4.2b

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

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

Experiment II: Temperature

In experiment II it was essential to ensure that growth was not limited by a shortage of food but rather that it was entirely controlled by temperature. Thus, the amount of food provided needed to be adjusted based on differing consumption rates at the various temperature treatments to compensate for the observed differences between treatments in the loss of particles. This implied that the supply rates of the peristaltic pumps needed to be regularly adjusted, in an attempt to keep cell density as close as possible to the optimum value as reported by Winter (1969).

Nevertheless significant differences in the algal cell density were observed between the treatments (figure 4.5a). Cell density at 12°C was significantly lower when compared to 3, 6 or 9°C, while the cell density in treatment A (1°C) was significantly higher (Tukey HSD pairwise comparison, $p<0.01$). The differences in the average chlorophyll concentrations show the same trend since both are closely related (figure 4.5b).

The greatest possible effects of temperature on shell growth are best illustrated when the average maximum height growth per treatment is studied (figure 4.8a). A Tukey HSD test showed that two groups could be distinguished which differed significantly ($p<0.01$). The first group consisted of the replicates at the two lowest temperatures and the other group consisted of the treatments at the three highest temperatures. It appeared that the effect of increasing temperature on the change of the shell height is greatest below 6.2°C. Between 1.1 and 3.2°C height increases with 0.58 mm/°C and between 3.2 and 6.2 °C maximum height increases with 0.87 mm/°C. Above 6.2°C the increase is half to one third of that, i.e. 0.2-0.3 mm/°C.

Figure 4.5.

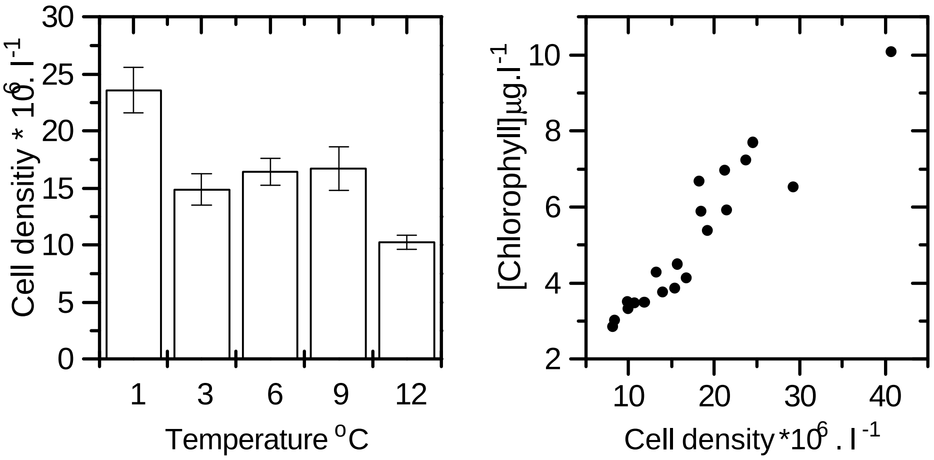


Figure 4.5. Relationship between average algal cell density, temperature (°C) and chlorophyll concentration (µg/l). (a), Average cell density per treatment in the temperature experiment. Bars indicate standard errors. (b), Relationship between cell density and chlorophyll concentration in µg/l.

Table 4.3

Treatm.	Temp. °C	[chl a] µg/l	cell/l $*10^6$.	ΔHeight (mm)	ΔWeight (mg)	max Δ height (mm).	Activity %
A	1.1	7.9	26.2	0.40±0.36	21.7±20.1	0.68±0.16	55±6
B	3.2	5.1	16.5	1.34±0.75	37.3±26.8	2.08±0.07	57±13
C	6.2	4.9	18.0	3.2±1.5	95.3±49.9	4.69±1.6	67±8
D	9.2	4.2	15.1	3.43±1.8	75.5±33.7	5.3±0.99	58±15
E	12.0	3.5	11.9	5.44±0.99	106.1±46.4	6.18±0.58	68±9

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

While in experiment I great differences in siphon activity were observed between the poorly fed and best fed treatments, the change in siphon activity with increasing temperature was only marginally significant (p=0.046) (figure 4.6).

None of the treatments differed from each other in their average daily siphon activity although a weak relation between shell growth and siphon activity existed (figure 4.7a).

Figure 4.6

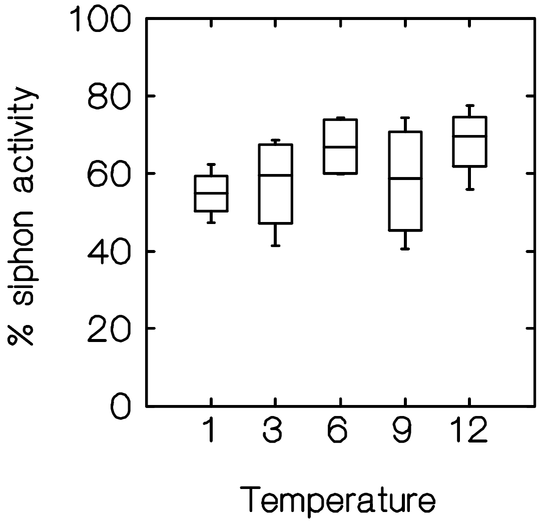


Figure 4.6. Box and Whiskerplot of average daily siphon activity per treatment in experiment II (Temperature °C). Only a slight increase in siphon activity is visible between 1 and 12°C.

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

In all treatments, the average weights increased. As with shell growth, average tissue growth at 1.1 and 3.2°C was significantly different from tissue growth at 6.2, 9.2 or 12°C. The greatest increase (207 mg) for an individual animal was found at a temperature of 6.2°C. Average values for all treatments are given in table 4.3. Height and weight growth were strongly correlated (figure 4.3) but the greatest change in condition index took place at 6.2°C (figure 4.9), indicating that the tissue weight increased more rapidly than shell volume during the experimental period at that temperature.

DISCUSSION

In short-term experiments, Winter (1969) determined the effects of temperature and particle density on filtration rate and food utilisation by *Arctica*. Between 4 and 14°C, both the filtration rate and phagocytosis increased by a factor of ~2. Winter (1969) observed that at increasing particle densities the filtration rate decreases but differences in the utilisation of the ingested food keeps the assimilation efficiency at approximately 67%. Based on this, higher growth rates can be expected at higher temperatures. Because growth is dependent on the equilibrium of food uptake as well as the amount needed for maintenance, growth tends to increase at higher temperatures given the premise that the availability of food is high enough. The direct effect of temperature on the metabolic rate may limit growth as well, even when food availability is high enough. The border-line conditions at which *Arctica* ceases to grow are poorly known, but because the (shell) growth record of *Arctica* is seen as a valuable tool to reconstruct environmental change, a good understanding of such conditions would be of high value.

Figure 4.7

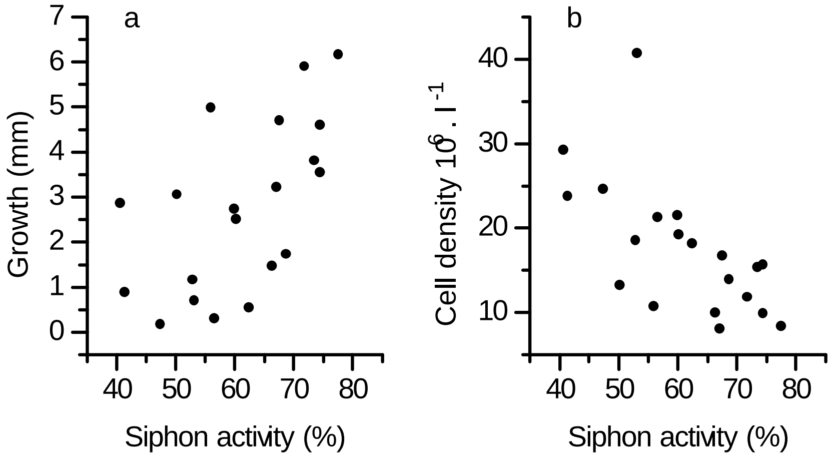


Figure 4.7; Relationship between growth, daily siphon activity and cell-density in the temperature experiment. (a), Average height growth (mm) versus average siphon activity per treatment. (b), Relationship between average cell density and average siphon activity per replicate.

Mortality of experimental animals gives the first indication of marginal conditions for growth. In experiment II, 19% of the experimental animals died. They were equally divided over all temperatures and replicates. Thus none of the temperatures caused higher mortality, which was expected on basis of the natural temperature range at which *Arctica* occurs (Merrill *et al*., 1969). Although total mortality (17%) in the food experiment (I) was similar, most animals died in treatments II and III. In the non-fed treatment (I) only 8% died. These starved animals became quiescent for long periods and were found only now and then with open siphons to "sample" the food conditions. The fact that the animals in treatments II and III were more frequently active, suggests that the continuous low cell densities in these treatments promoted high filtration rates (Winter 1969). Their energy expenditure would have been higher than that of the starved *Arctica*. The increased energy need was not covered by the energy uptake from the amount of ingested food. As a consequence the animals died. We therefore assume that the food conditions in treatments II and III were marginal for survival and growth. At 9°C this corresponds to an algal cell density of 5 to $7*10^6$ cell/l or a supply rate of 6.2 -15.0 µgPOC/day*l.

The above mentioned cell densities should be treated with some caution because we observed an inverse relationship between siphon activity and particle density (figure 4.7b). This suggests that the animals effected particle density, but also illustrates that siphon activity is related to food uptake. This relation is substantiated by the positive correlation between this activity and growth (figure 4.2; figure 4.7a). Thus although the daily siphon activity is a rather crude measure it appears to give a valid measure of the feeding activity of each individual animal.

The control of particle density was not a problem in the food experiment (I) because the aim was to limit the shell growth by the food availability. For the temperature experiment, however, it could have implied food limitation. There were, however, no indications that food-limited growth occurred since the highest rate was found at 12°C although particle density was lowest at that temperature.

The inverse relationship between temperature and particle concentration (figure 4.5a) agrees with the results of Winter (1969) who found a doubling of filtration rate between 4 and 14°C. While temperature has a minimal effect on the daily siphon activity, the results of the food experiments do suggest that *Arctica* adjusts decreasing filtration rates at increasing cell densities by increasing the time spent to filtration. This result does not contradict Winter's (1969) findings of decreasing filtration rates with increasing cell densities because daily siphon activity does not say anything about the filtration rate. Rather, it should be seen as a measure for the time spent to filtration. The results suggest that within the range of particle densities used, the uptake of food is optimised by maximisation of the food uptake by prolonged periods of filtration at low rates.

The rapid change in shell growth between 1 and 12°C under optimum food conditions results from the combination of changing filtration rates (Q_{10}=2.05; Winter, 1969) and increased phagocytes (Q_{10}=2.15; Winter 1969). The results of this study suggest that the greatest change in the growth rate takes place in the lower part of the temperature range (1-6°C). This implies that small differences in the bottom water temperature during spring may have a rather large impact on shell growth. The results obtained in the food experiment furthermore suggest that at high particle densities minimal changes in the time spent to filtration may lead to a disproportionately large change in shell growth. The combination of these results therefore suggest that the bottom water temperature at the time when the sedimenting spring bloom reaches the bottom is a main determinant of shell growth.

Figure 4.8

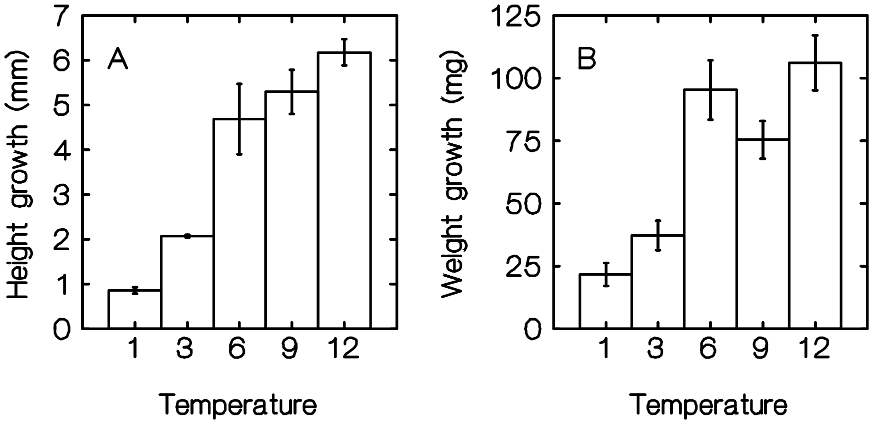


Figure 4.8. Growth of the experimental animals under the five different temperature conditions but with food concentration kept near optimum. (a), Average maximum shell growth per treatment. Height growth in mm. (b), Average weight growth per treatment in mg. Bars indicate standard error.

A quantitative inter-relationship between temperature and food availability and growth can not however, be determined on the basis of the data presented in this study. The results of chapter 5 indicate, however, that the effect of temperature on *in-situ* growth is small. The spatial differences in growth rates of natural North Sea populations could not be explained by temperature. Neither could temperature explain the huge temporal variation in shell growth of specimens from the Fladen Ground (chapter 7). While the growth rate itself might be limited by temperature, the results of the temperature experiment demonstrate that growth is possible at temperatures below 6°C. These results therefore contradict the conclusion of Weidman *et al.* (1994) who proposed the existence of a shutdown temperature at ± 6°C below which growth stops (chapter 3).

The absence of such lower temperature limit is also suggested by field data on growth of shells which started as early as March (chapter 3) or the extremely high growth rates of shells from north-west Iceland (chapter 4). In fact, many authors discuss the uncoupling between the onset of growth and temperature (Broom & Mason, 1978; Kristensen & Kanneworf, 1986). Their results tend to confirm the idea that food availibilty triggers the start of growth.

Winter (1969) estimated the assimilation efficiency between 4 and 12°C to be 67%. However, since the absorbed food is partly utilised for maintenance, it is difficult to estimate tissue and shell growth from such a value. We therefore use an estimate of the carbon conversion efficiency (ΔBiomass/Consumption; *sensu* Crisp, 1984) from the results of experiment I. The results of experiment II were not examined, as the lack of knowledge about the effect of small stepped changes in temperature on filtration rates make it difficult to estimate a detailed effect on the assimilation efficiency.

Figure 4.9

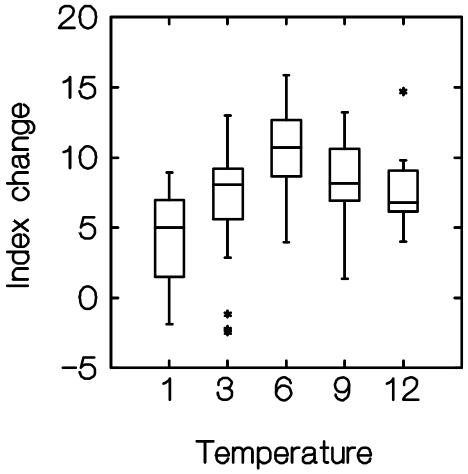


Figure 4.9. A Box and Whisker plot of the change in condition index (Δ(weight/height^3)$*$1000) of the animals at five different temperatures. * indicates outlier (1.5*H).

The conversion efficiency was estimated from the change in afdw of the animals and their estimated uptake of carbon. Gonadal production, as a part of ΔBiomass, could be omitted since all shells were below the size at which they become sexual mature (Rowell *et al.*, 1990; Ropes *et al.*, 1984b; Thompson *et al.*, 1980b). Because we did not quantify the carbon losses (Dissolved Organic Carbon, faeces, etc.) from our experimental system, the carbon consumption for each specimen was estimated from their calculated filtration rate by subsequent multiplication with the average cell density, daily siphon activity and average carbon content per ml. This then yields an estimate for carbon consumption during the experimental period. Filtration rate (FR l/hr) was estimated from tissue dry weight (W, g) by applying the equation derived from Møhlenberg & Riisgård (1979) (FR=5.55*W^0.62). This equation was preferred over that of Winter (1978), since Møhlenberg & Riisgård (1979) worked with shell sizes very similar to those we used. Afdw is assumed to be 80% of the dry weight (Witbaard, 1995) and the carbon content is assumed to be 40% of that. The retention efficiency at which particles are withheld by the gills of *Arctica* varies between 75 and 90% (Møhlenberg & Riisgård, 1978). The evolving average conversion efficiency for the three best fed treatments (III-V) then varies between 9.2 and 11.7% when 90% of the algal material is retained. When 75% of the particles are retained the average conversion efficiency varies between 11.1 and 14.1%. If one accounts for the organic matter deposited as periostracum and shell matrix the efficiencies are on average 2% higher.

To compare the experimental growth rates with rates reported in the literature, we transformed all values to instantaneous rates. This demonstrates that the results in experiments I and II yield similar estimates. At 9°C in the temperature experiment (II) the instantaneous growth rate was 0.0032/day and in treatment V of the *food* experiment it was 0.0026/day. These experimentally obtained rates compare well to values reported for animals grown under natural conditions. The average instantaneous daily rates for 12 to 20 mm long shells from Kiel Bay (Brey *et al.*, 1990) range between 0.0011 and 0.0024 when an 8 month growing season is assumed, starting with the spring bloom in March and ending in October (Trustler & Samtleben, 1988). The same was done with the absolute rates reported by Kennish *et al.* (1994). They re-measured transplanted animals with a shell length between 9.2 and 19.9 mm 5 times. Absolute growth ranged between 0.16 and 5.28 mm. Expressed as daily instantaneous rates over the full 485 day period it varied between 0.0023 and 0.0013. The maximum observed *in-situ* instantaneous growth rate in that study is estimated at 0.0025/day for the smallest animals. Thus the *in-situ* growth rates in both Baltic and the Gulf of Maine are very similar to the average rates obtained in the experiments and illustrates that reliable growth rate estimates for juvenile *Arctica* can be obtained from laboratory experiments.

ACKNOWLEDGEMENTS

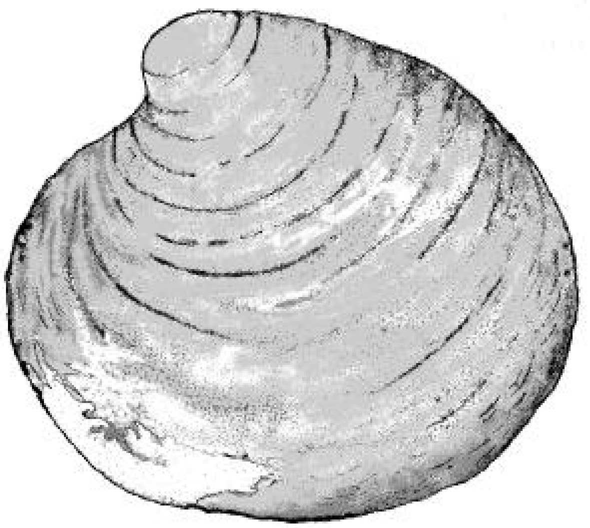
Many people contributed to this study. We would like to thank J. Hegeman for this help with the carbon measurements and A. Noordeloos for her help with the chlorophyll measurements. N. Schogt and W. Kleinbreteler are thanked for their assistence with the particle counts and for their advise concerning the culturing of the algae. The technical assistance and maintenance of the experimental systems by T. Kuip and R. Lakeman is especially acknowledged. Dr H. Rumohr, U. Fiedler and the crew of R.V. Littorina (Institut für Meereskunde, Kiel) are thanked for providing the opportunity to collect juvenile *Arctica* from Kiel Bay.

65

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

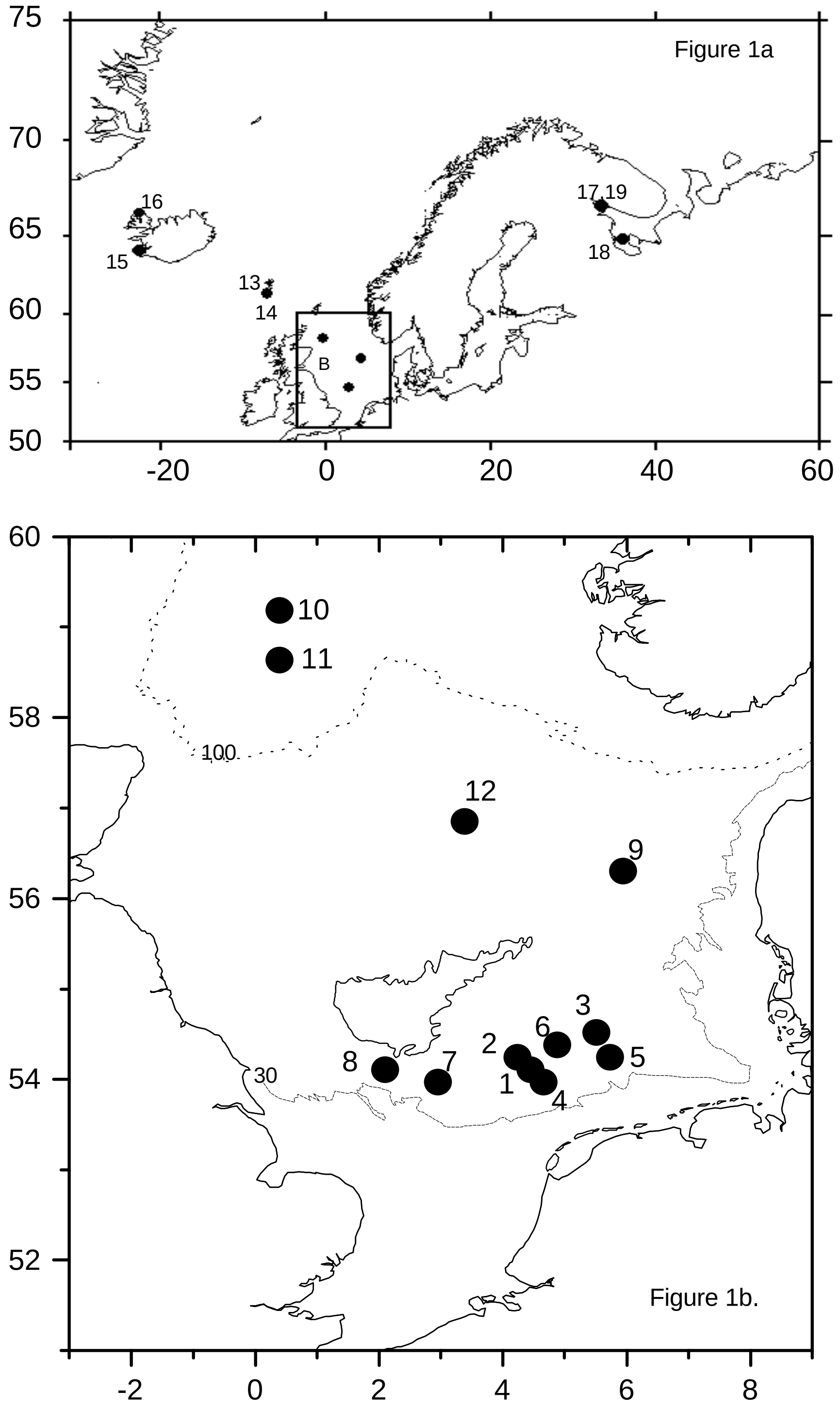


Figure 5.1. Geographical location of the sampling stations mentioned in the text. (a), Map of north-west Europe with sampling locations used in this study. The inset (B) refers to the North Sea and is given in more detail in figure (b), Numbers in both maps refer to the sites for which the details are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

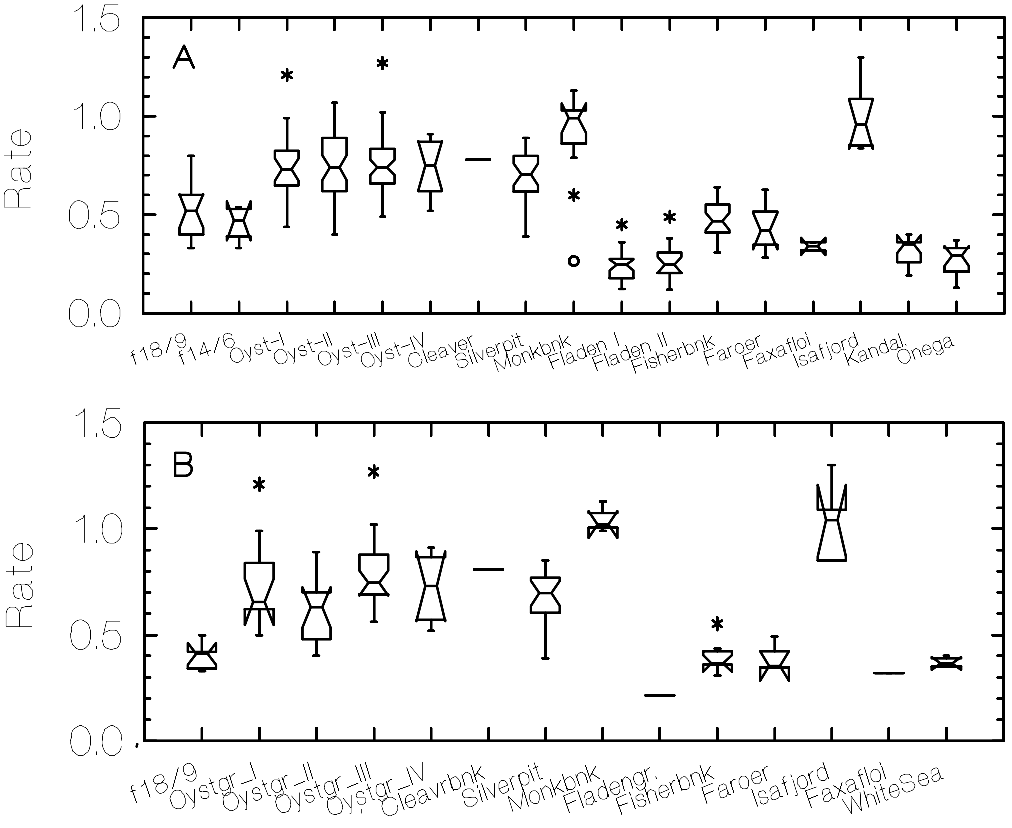


Figure 5.2. Notched Box and Whisker plot of juvenile growth rates of *Arctica islandica*. (a), Growth rates irrespective of the period in which the shells settled on the sea floor. The horizontal bar in each box represents median growth rate. Notches indicate 95% confidence limits. $*$=Outlier (1.5xH); 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

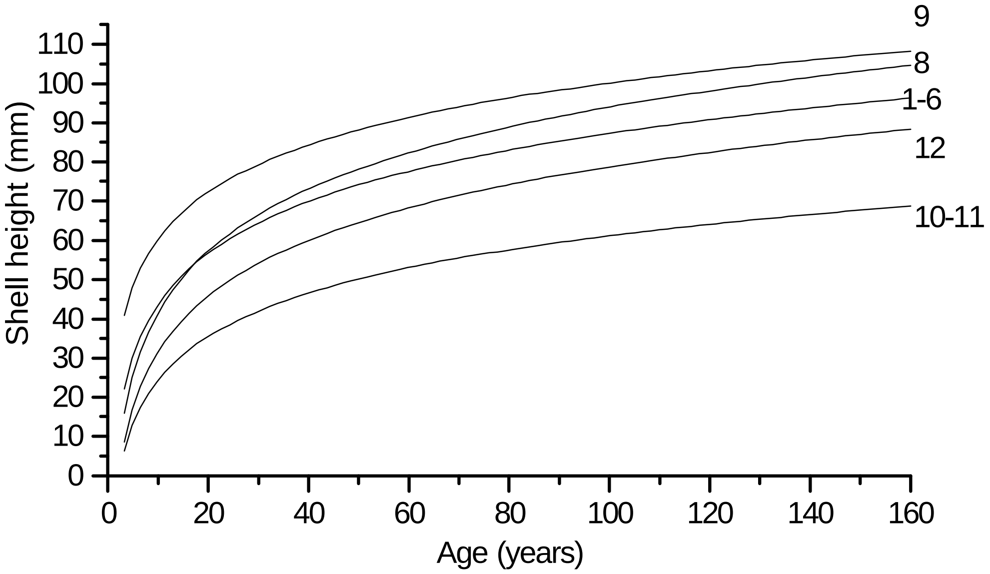


Figure 5.3. Growth curves estimated by least squares regression for all populations from the North Sea for which an almost complete size spectrum of shells was available. Numbers correspond to sites as given in table 5.1 and figure 5.1. 1-6 = Oyster Ground; 8 = Silverpit; 9 = Monkey Bank; 10-11 = Fladen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

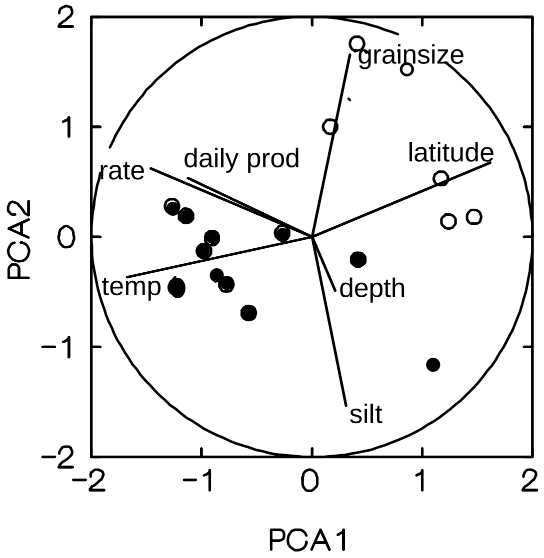


Figure 5.4. Covariance biplot of growth rate and environmental data. Dots indicate sample scores on the first and second PCA axis. Open symbols represent stations outside the North Sea (13-19), filled symbols represent stations within the North Sea (1-12).

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

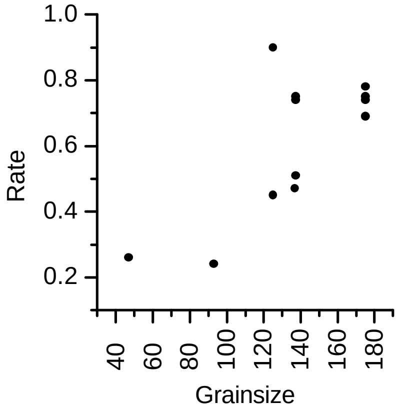


Figure 5.5. Growth rate of North Sea *Arctica* plotted against median grainsize in µm.

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.

CHAPTER 6*

The effects of southern North Sea beam trawl fishery on the bivalve mollusc *Arctica islandica* L. (Mollusca, Bivalvia)

R. Witbaard & R. Klein

This chapter is based on;

Witbaard R. & R. Klein, 1993. A new a approach in studying the long-term effects of bottom trawling. ICES CM 1993/K16: 8pp.; Witbaard, R. & R. Klein, 1994. Long-term trends on the effects of southern North Sea beam trawl fishery on the bivalve mollusc *Arctica islandica* L. (Mollusca, Bivalvia). ICES J. Mar. Sci., 51: 99-105; Klein, R. & R. Witbaard, 1995. Long-term trends in the effects of beam trawl fishery on the shells of *Arctica islandica.* NIOZ rapport 1995-3: 15pp.

ABSTRACT

Arctica islandica has been used as an indicator organism for the intensity of bottom trawl fishery in the southern North Sea. That this species is affected by beam trawl fisheries is illustrated by the high incidence of damage found on shells from heavily fished areas whereas these numbers are lower in less intensively fished areas.

The inventory of damage patterns demonstrated that damage and scars were evenly distributed over both valves.

Between 80 and 90% of the damage and scars were found at the posterior ventral side of the shell. This can be explained by the orientation of the living animal in the upper sediment layer and the horizontal movement of the tickler chains on the bottom.

According to literature the percentage of damaged North Sea shells was above what could be expected on basis of natural scar frequencies. A comparison of the average number of scars per shell was made between samples from the south-eastern North Sea and samples collected off Nova Scotia (Canada). Whereas only 2% of the North Sea shells was without scars about 40% of the Canadian shells was without damage.

Scars on the external shell surface were dated by internal growth lines, revealing that all sampling sites had been disturbed at least once a year since 1970.

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Logit regression showed that the observed trends could be the effect of fishing. The average number of scars for all samples show s a striking coincidence with the change in capacity of the Dutch fishing fleet over the last 20 years.

INTRODUCTION

In the southern North Sea the most important fishing gear used is the beam trawl (de Groot, 1973; Welleman, 1989). This gear consists of two sledges held apart by a beam to which the net is attached. In front of the net a variable number of tickler chains is present in order to increase the catch (de Groot, 1984; Creutzberg *et al*., 1987; Fonds, 1991). A detailed description of the gear is given by Blom (1990).

Welleman (1989) gives a brief review of research carried out in the 1970s, to describe the effects of trawling on the sea bed qualitatively. However, since then the Dutch fishing fleet has changed considerably. For example engine power, beam width, gear weight, fishing speed and the number of vessels (>300 HP) have increased (Welleman, 1989). These changes initiated a renewed interest in research on the effects of fishing gear on the seabed and benthos of the North Sea. Most of this present-day research focusses on short-term or direct effects, such as penetration depth of the tickler chains (Bergman & Hup, 1992), survival of by-catch (Bergman *et al.*, 1990; Bergman, 1992; Fonds *et al.*, 1992) or the change in sediment characteristics (Laban & Lindeboom, 1991).

Recent attempts to study long-term effects by comparing the fauna of "unfished" and fished areas are frustrated by the fact that even in these "unfished" areas trawl marks were found (Bergman, 1992). It can furthermore be argued that present day benthic communities already are impoverished by the repeated disturbance associated with the fishing activities. These communities will already have reached a new equilibrium state from which the fragile and sensitive species have disappeared. Thus it can be questioned if such approach could reveal the effects of fisheries. Therefore a method was developed (Witbaard & Klein, 1993) in which above-mentioned problems are avoided. The long-term trends of the effects of beam trawling on *Arctica islandica* were assessed by using the internal growth lines. *Arctica islandica* is a large bivalve mollusc which is widely distributed over the North Sea and northern Atlantic (chapter 2). The animal lives buried in the sediment with its short siphons protruding from the sediment surface (figure 6.1).

It produces annual internal growth marks (chapter 2) which can be made visible and used for age determinations (Ropes, 1985). Because the growth of an increment is related to environmental conditions, successive increments can reflect environmental change in time. Witbaard & Duineveld (1990) for instance discussed such application of the annual growth marks of *Arctica* to evaluate the status of the benthic environment in the North Sea.

In the same way repetitive non-lethal shell damage, due to beam trawl fishery, could lead to a scar-record that reflects the distribution of the beam trawl fishery through time and space. The use of *Arctica* in such way is especially interesting since longevity surpasses 100 years and thus may offer possibilities to assess man's impact during the last century. The present study deals with this aspect. It was questioned whether *Arctica islandica* could be used as an indicator species to study the long-term effects of beam trawling on the benthic environment. The following aspects were considered:

- Description of damage and damage patterns in *Arctica* shells, to see if there is any systematic pattern possibly caused by fisheries.
- Dating of externally visible scars by using the internal growth lines with the aim to estimate the frequency of the bottom disturbance.
- Relate the observed trends to any trend in fishing intensity.

Figure 6.1

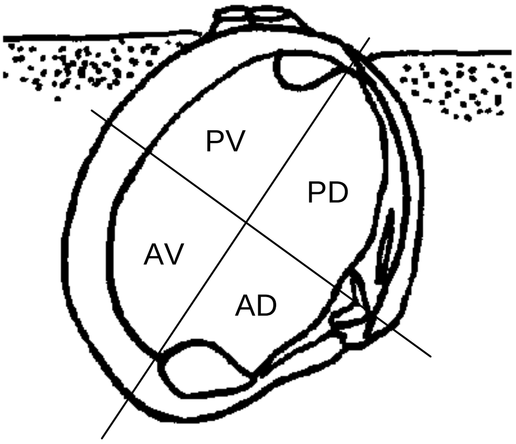

Figure 6.1. Normal orientation of *Arctica* buried in the sediment. Subdivision of a left-hand valve into four equally sized areas indicated by crossing lines. Abbreviations; AD = anterior dorsal, AV = anterior ventral, PV = posterior ventral and PD = posterior dorsal.

MATERIAL AND METHODS

Damage patterns in empty shells

Between March and December 1991 over 1700 empty shells, both single valves and doublets ("doublet" meaning that of each shell at least the hinge part of both valves was present), were collected from 146 stations in the North Sea. These shells were analyzed for the presence, degree and position of damage. The stations were clustered into three areas, north-west North Sea, mid-west North Sea and the south-east North

Sea (table 6.1), to see whether regional differences in damage and damage patterns existed. For this analysis only "doublets" were used. Stations where no "doublets" were found were excluded from the analyses.

To study the position of the injuries the shell was divided into four areas of equal size; anterior dorsal (AD), anterior ventral (AV), posterior ventral (PV) and posterior dorsal (PD). The posterior ventral side is where the siphons are located (figure 6.1). Damage was assigned to one of these four categories according to the position of the major area of damage. Shells of which more than 50% was missing, were treated as a separate group because the location of the damage could not be determined.

Table 6.1

		Border positions		No. of	No. of
Area	No. of stations	Longitude	Latitude	damaged doublets	undamaged doublets.
North-west North Sea	8	1°44'-3°59'E	58°41'-59°24'N	97	35
Mid-west North Sea	8	1°45'-3°00'E	56°06'-57°31'N	127	96
South-east North Sea	66	3°16'-6°00'E	52°59'-54°59'N	429	48

Table 6.1. Number of undamaged and damaged doublets for the three areas described in the text. For each area the position of the outermost stations is given. The last two collumns give the number of recently damaged empty doublets and the number of complete empty doublets. Scars were not seen as recent damage.

The relative size of damage of each shell (in percentage) was estimated to classify it into categories ranging from shells of which more than 50% was missing to undamaged. Scars originating from previous encounters were recorded separately. Main categories distinguished here were: *repaired cracks* and a *bulbous grayish* thickening of the internal shell layers caused by the enclosure of sediment within the calcium carbonate.

Shell strength

Small *Arctica* are almost lacking in the populations from the south-east North Sea (chapter 2). Such population structure may be related to a size specific difference in sensitivity to bottom trawling. Therefore the size dependence of shell strength was tested. The sample used was collected from the south-east North Sea at 53°52'N, 04°59'E (sample 3, table 6.2). Four groups were formed according to shell height. The shell heights within these groups were approximately 20, 40, 60 and 80 mm. After removal of the soft tissue, the shells were dried at room temperature for one week.

Shell strength was measured as the maximum force needed to crush a shell and was recorded with an automated material testing system (INSTRON corp. series IX 1.04). The force was applied on a maximum of 0.8 mm^2 shell surface at the point of maximum valve convexity. The shell was kept in place by a piece of plasticine.

Scar Trend Determination

Four samples from the North Sea (table 6.2) were used for Scar Trend Determination (STD). In September 1993 sample 1 and 2 were collected during the IMPACT I program (EC FAR MA 2-549) from two different locations in the south-east North Sea. During this cruise the R.V. "Tridens" was equipped with a commercial 12 m beam trawl. Sample 3 was collected with R.V. "Aurelia" in March 1991 by using a fine meshed 5.5 m beam trawl. Sample 4 was collected with a commercial trawler on 4 October 1991. Shell samples were frozen on board.

Of each sample approximately 50 of the smallest specimens were selected for STD since larger *Arctica* are more difficult to analyze. After thawing, soft tissue was carefully removed and the shells were dried at room temperature.

Table 6.2

Area	Sample	No. of stations	No. of shells	Latitude	Longitude
North Sea	1	1	42	54°22'N	04°51'E
North Sea	2	1	42	54°42'N	04°49'E
North Sea	3	4	50	53°52'N	04°59'E
North Sea	4	1	48	54°03'N	06°18'E
Canada	5	1	10	43°29'N	61°44'W
Canada	6	1	12	43°30'N	65°30'W
Canada	7	1	20	43°29'N	65°28'W

Table 6.2. Sampling details of the shells used in STD. Sample 3 is a composite sample of specimens collected at four locations around the position given.

Of each shell a drawing was made in which the position and size of scars was recorded. Observed scars were arranged into categories according to their position (AD, AV, PD, PV) as mentioned above. Then the left-hand valves were embedded in epoxy resin (polypox, THV 500, harder 125) to facilitate further processing, *i.e.* sawing along mapped scars. If the scars were not symmetrically distributed over both valves the right-hand valve was also included in the analyses. This procedure resulted in the preparation of several sections per shell.

Each section was ground, polished and etched in order to make acetate peels (Kennish *et al.*, 1980). These peels were photographed by means of light microscopy. Recognition of the scars was done by comparing the drawings, photos and original shell sections. Because the shell grows by annual accretion of an increment, it was possible to assign a year to each increment. Each damaged increment was subsequently marked with the year in which it was found. In this way a chronology of the occurrence of scars for each shell was obtained. The long-term trend in scar frequency was determined by counting the scars for every year in all shells of the entire sample. For comparison, these frequencies were expressed as percentage of the total number of shells that accounted for that year.

In addition to these four North Sea samples, three samples collected from Nova Scotia at the Canadian east coast (sample 5-7; table 6.2) were analyzed on the presence of externally visible scars. Scars were not dated as described above. These samples served as a reference to estimate natural scar frequencies, since there is, except for some scalloping, no commercial fishing in the area from where they were collected (D. Gordon, pers. communication).

Statistical analyses

The scar frequencies are obtained by summing scar/year occurrences of all individuals in each sample. In these summations different aged animals are equally judged. If the occurrence of a scar is exclusively related to bottom fisheries and not to the size of the animal, the observed long-term trend in the occurrence of scars in a sample would be a direct reflection of the fishing effort. In this context one can speak of a *year* related effect. If there is a size or age dependent difference in survival or repair of the damage, the observed time trends can be influenced by the age composition of the samples. Such effects are referred to as an *age* related effect. It neither can be excluded that an interaction between such *age* and *year* related effect exists.

Logit regression (Jongman *et al.*, 1987; Crawley, 1993) was used to decide which of above factors most likely caused the observed long-term trend in scar frequencies. In logit regression a response model is fitted which describes the probability of occurrence of, in this case, a scar being dependent on *age*, *year* or both factors. The model fits are made according to the maximum likelihood principle in which the residual deviance is used to evaluate the model fit. It is tried to minimize this deviance. For the application here, four models have been fitted. The null model describes a common probability of all observations and is based on one parameter. The other models include either the effects of *year*, *age* or both. The difference in deviance between the null model and any of the other models is used to test its significance, *i.e.*

to determine which of the variables (*age*, *year* or both) resulted in a better fit, expressed as a decrease in deviance.

RESULTS

Damage patterns in empty shells

The regional differences in the ratio of undamaged to damaged doublets is given in table 6.1. Only 10% of the empty doublets from the south-east North Sea were undamaged. In samples from the northern North Sea and mid-west North Sea about 40% were undamaged.

A similar trend was found when the amount of damage was expressed as a percentage of the missing shell material. The samples from the mid-west and northern North Sea showed lower percentages of damage in the categories 5-25%, 25 - 50% and >50% missing. The category <5% did not differ between areas studied.

Comparison of the left and right hand valves showed that damage was equally divided over both valves. In all three geographical areas, most damage was situated on the posterior ventral side of the shell. In the northern and mid-west North Sea this accounted for about 50% while in the south-east North Sea 82% of the damage was found on the posterior ventral side (figure 6.2). Other shell parts were less frequently damaged. Within the south-east North Sea only 13% of the damage was found at the anterior ventral side. Similarly is in both groups of shells (caught empty and living) about 90% of the scars positioned on the posterior shell side.

Figure 6.2

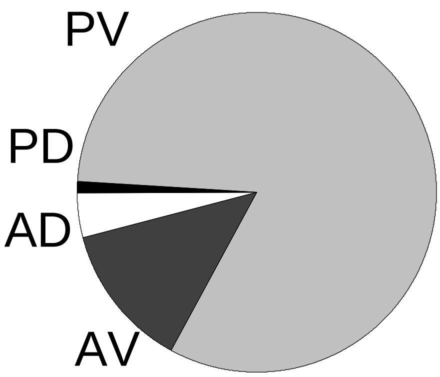

Figure 6.2. Relative proportion of positioned damage in dead shells collected from the south-east North Sea. Abbreviations explained in text and figure 6.1.

Shell strength

Figure 6.3 shows that shell strength increases with size. Mean forces to crush shells from the smallest and largest categories was 300 (±64) N ($Kg.m.s^{-2}$) and 800 (±345) N ($Kg.m.s^{-2}$), respectively. Only the category with the smallest shells (20 mm) differed significantly from the other categories. The other categories did not differ from each other (H-test, $p< 0.05$).

Figure 6.3

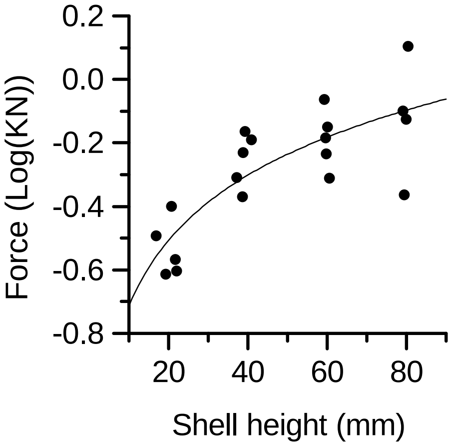

Figure 6.3. The relation between shell height and the force needed to crush it. Through the points a logarithmic regression is fitted; y=-1.4+0.7Log(x). r=0.8 ($p<0.05$). Force in Log(kN) and shell height in mm.

Scar trend determination

A total of 182 shells, almost equally divided over the four samples, was analyzed in STD. Size distribution and number of scars per shell for these samples and the samples from the Canadian east coast is given in figure 6.4. The low number of large shells shows that small shells were preferred in the analyses and does not represent the population size distribution. The figure illustrates that the number of scars/shell does not bear a relation with shell height. The maximum number of scars found on one specimen was 15 (sample 2) and only 3 shells from sample 2 did not have recognizable scars. The average number of scars per shell for the North Sea samples was 4.4 (±0.7). The Canadian shells have a much lower scar frequency of 1.2 (± 0.9). The percentage of shells without scars in the Canadian samples is about 42% whereas only 2% of the North Sea shells were without scars.

The oldest animal used for STD originated from sample 3 and had an age of 80 years, hence offering the possibility to backdate to 1912. Specimens in the other samples were much younger, not extending any further than 1960 or 1950.

Figure 6.4

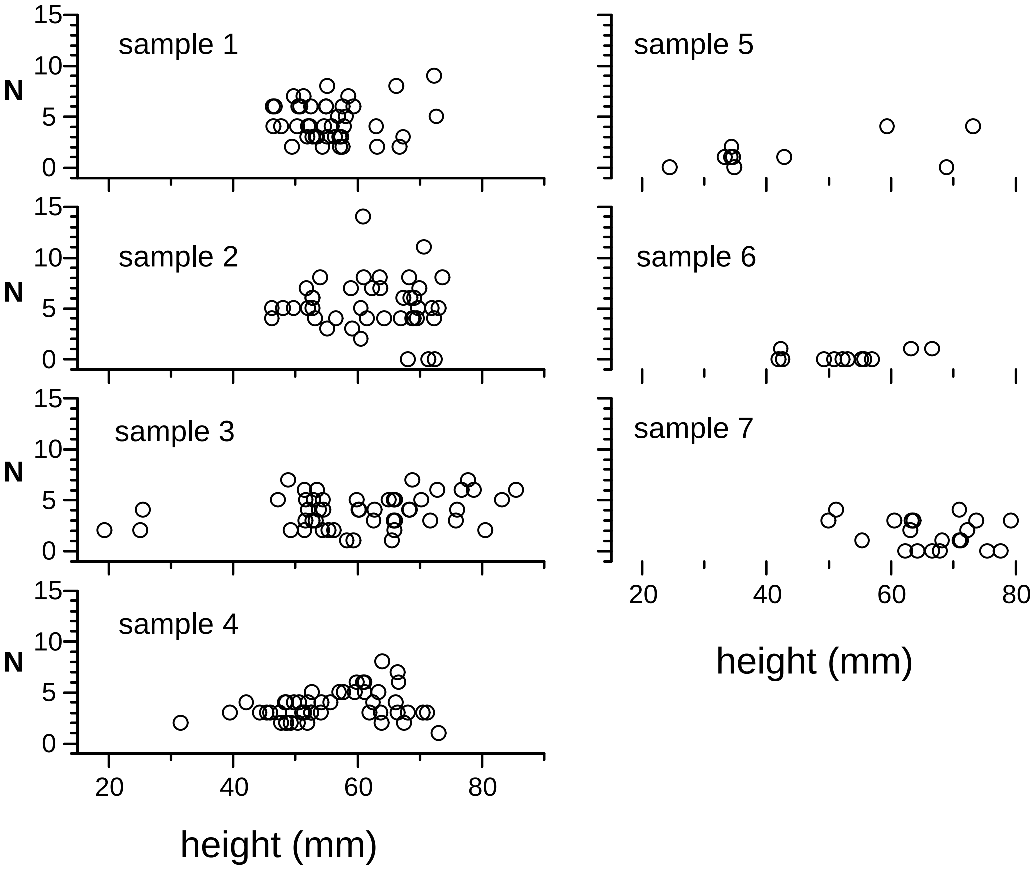

Figure 6.4. Number of scars per shell. For each shell of a certain size (horizontal axis) the total number of scars (N) is given on the vertical axis. Samples 1 to 4 were used in STD and originated from the North Sea. Samples 5, 6 and 7 originated from the east Canadian coast.

Growth lines

Figures 6.5 and 6.6 illustrate the appearance of damage in shell cross sections. Two types were distinguished:

- Type I. The former shell margin does not show any sign of breakage. Only soft tissue has been damaged which causes a depression in the shell surface that delineates pre- and post-damage growth (figure 6.5c).
- Type II. The former shell margin was demolished. Sometimes shell fragments clinging onto the shell were still present. Because the shell margin which supported the mantle was removed, post-damage growth is resumed at a lower level causing a dip in the shell. This dip may be visible over a prolonged growth interval (figure 6.5d).

Both types of injury often occur in combination with the enclosure of sand grains within the shell material (figure 6.6). Sometimes complete aggregations of sand are present. The periostracum may or may not be present over the injury.

Figure 6.5

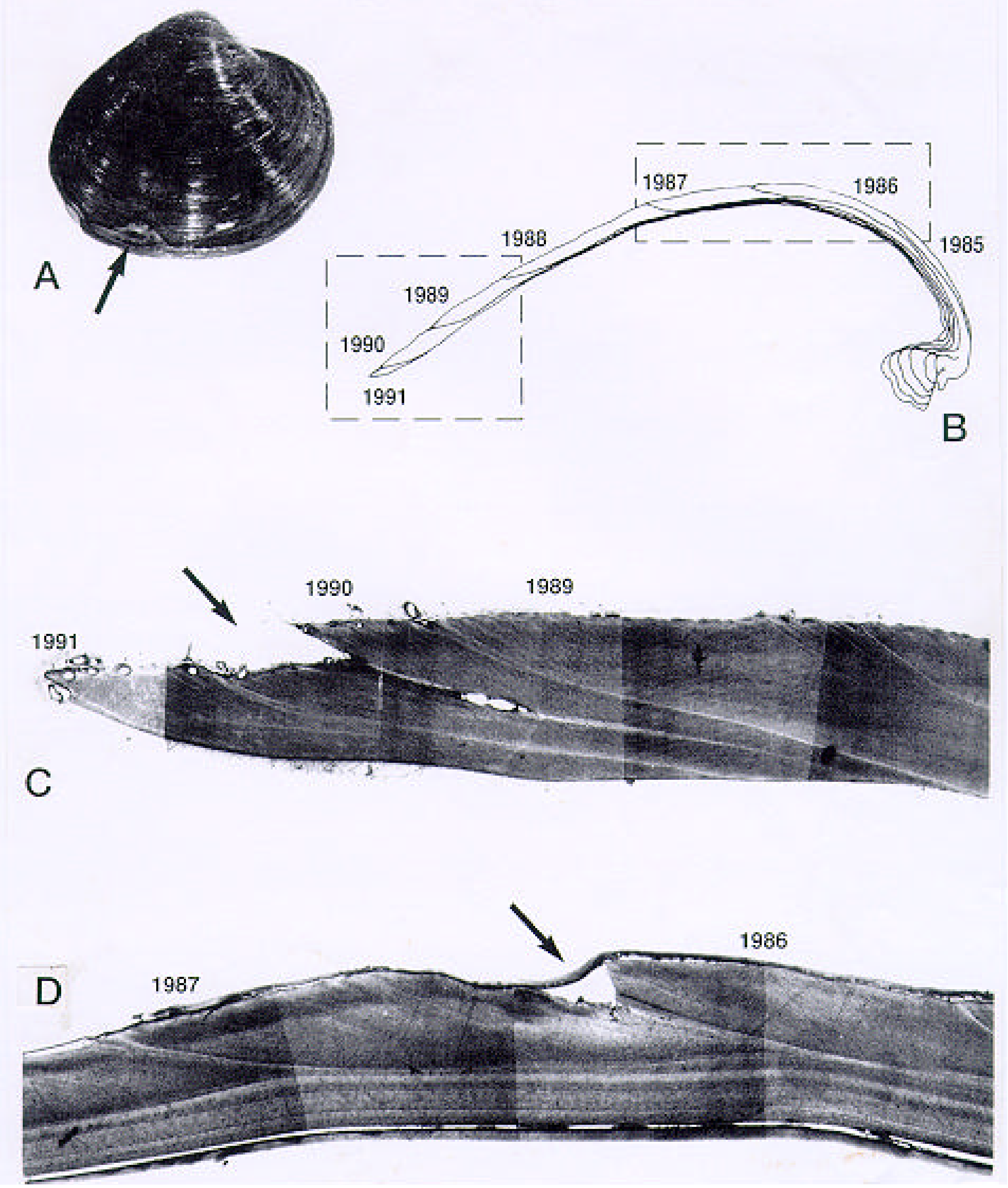

Figure 6.5. The appearance of scars on the external shell surface and in cross-section. (A), The arrow indicates an old, but repaired injury. (B), Schematic drawing of a cross section showing the outline of photos C and D. (C), A clear dip in the shell is found, but no definite signs of a broken margin are visible. (D), A clear dip in the shell surface is visible.

Figure 6.6

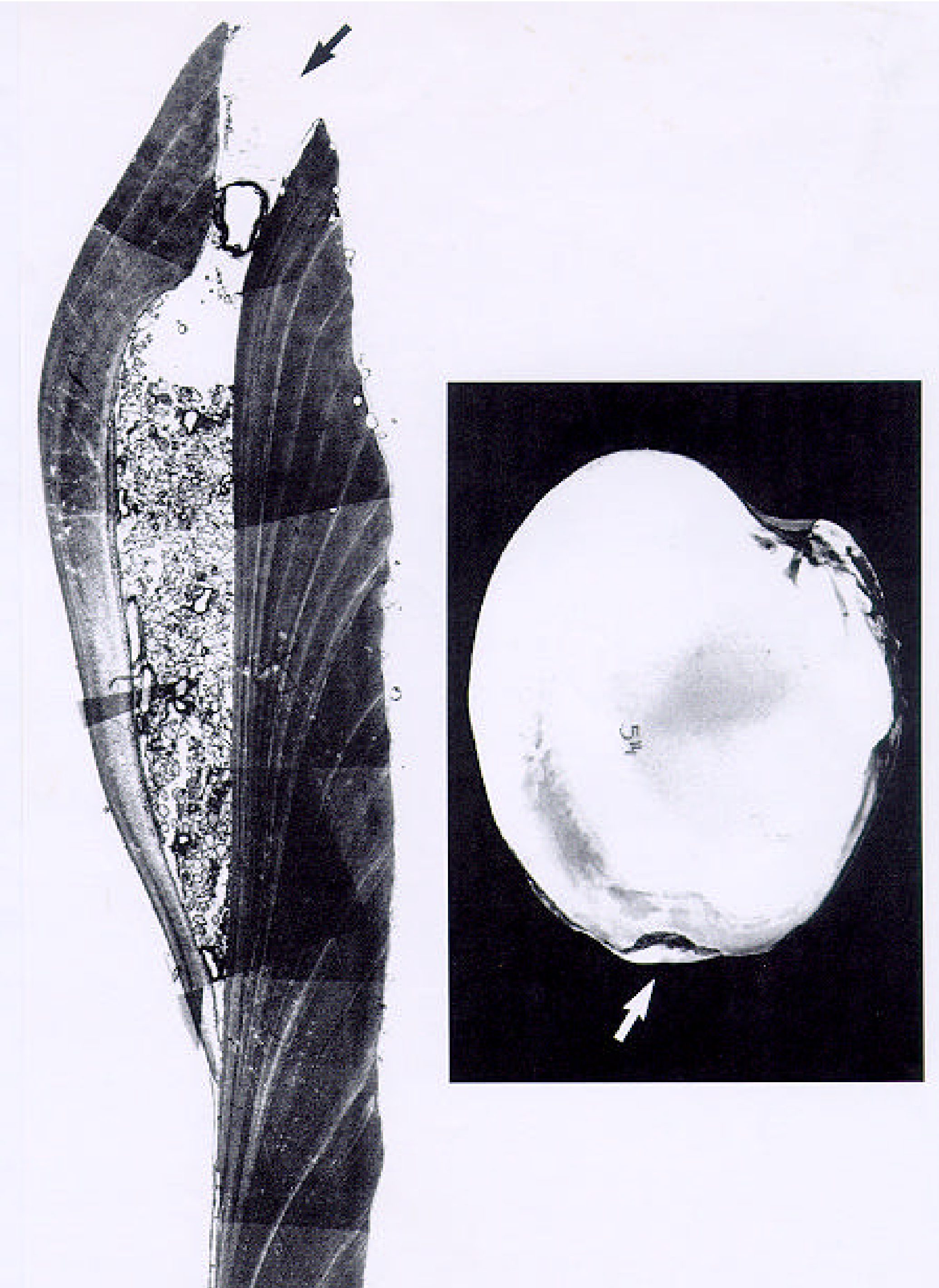

Figure 6.6. Inside view of a right hand valve with cross-section of the posterior part. The greyish thickening of the post ventral margin is caused by the enclosure of sand grains within the calcium carbonate. This is clearly illustrated in the cross-section.

Figure 6.7

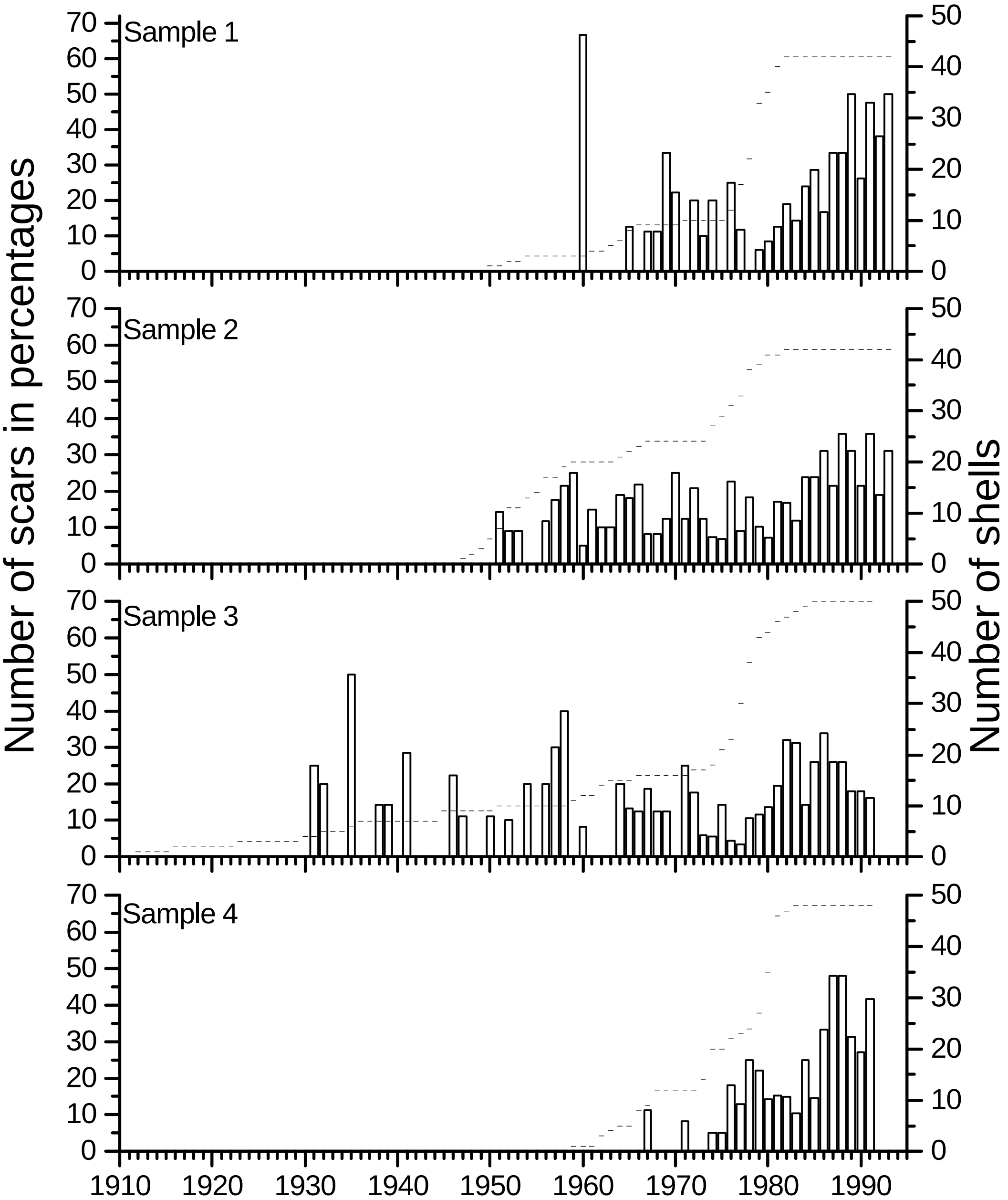

Figure 6.7. Frequency of scars on *Arctica* shells from the samples from the North Sea (Sample 1-4). Each bar represents the relative occurrence of scars (damaged and repaired increments) per year. The number of shells with a scar in a certain year is given as a percentage of all shells studies. The total number of shells studied for every year is illustrated by the horizontal dashed line.

Figure 6.7 illustrates for the four North Sea samples the frequency of scars (damaged increments) present in each year relative to the total number of shells studied for that year. It is obvious that scars are present throughout the time series back to 1931. In all samples at least one scar in every year was found since the late 1970s. Maximum scar/shell ratios in the most recent period for samples 1, 2, 3 and 4 are 0.50, 0.36, 0.34 and 0.48 respectively. Except for sample 2 do all collections suggest more frequent damage since the mid 1970s. Before that period certain years were without scars. All samples show roughly the same trend of a rapid increase in damage in the 1980s with a slight decrease in most recent years. The similarity of the observed trends in each of the samples has been compared in table 6.3 for the period since 1977. Except for sample 3 are all other combinations positively correlated with each other.

Table 6.3

	Sample 1	Sample 2	Sample 3	Sample 4	Engine power
Sample 1	16	16	14	14	15
Sample 2	* 0.757	16	14	14	15
Sample 3	0.190	0.297	14	14	14
Sample 4	* 0.592	** 0.692	0.084	14	14
Engine power	**0.763	** 0.712	* 0.612	* 0.515	15

Table 6.3. Correlation of the average scar-trends in the four samples since 1977 (≥ 20 shells/year). For each correlated pair the number of overlapping years and the correlation coefficients are given. In the last row the correlation coefficients between the annual average number of scars and the capacity of the fishing fleet (in HP) is made. * indicates significant at $p<0.05$; ** indicates significant at $p<0.01$.

In sample 4 a more or less abrupt increase in the percentage damaged shells can be recognized for the years 1976 and 1986. Mean values were calculated for the periods delimited by those years. For the period 1959-1975, 1976-1985 and 1986-1991, the means were 2.0% (± 4.1), 17.3% (± 5.1) and 38.2% (± 8.9) respectively. All differences observed were significant (H-test, $P \leq 0.001$).

The statistical analyses to decide upon the most likely cause (*age*, *year* or both) of the observed trends is summarized in table 6.4. For each of the samples a comparison is made between the *age*-, *year*- and the combined model with the null model. All three models appeared to have a good fit and led to a significant reduction of the scaled deviance when compared to the null model. For samples 2, 3 and 4, the reduction in deviance for the *age* model is slightly larger than for the *year* model. Only in sample 1 this trend is opposite. The combination model (*age* + *year*) gives in all cases the greatest reduction in deviance. Presented results suggest that both *age* and *year* effectively explain the observed trends. The slightly larger *age* effect in three of the samples may indicate a size dependent effect on either survival, repair or recognition of the scars. The observation that the combined model gives the highest reduction in scaled deviance may illustrate that both the age of the animal at the moment the scars were formed as well as the year in which the scars were formed could have had its effect on the observed frequencies.

Table 6.4

Sample	Number (n)	Model type	Scaled Deviance(sD)	Degrees freedom	$^{**}G^2$ (sDa-sDb)	v (dfa-dfb)	p
1	42	null model	876.0	797	-	-	-
		age model	770.2	754	105.8	43.0	<0.001
		year model	754.2	754	121.8	43.0	<0.001
		combined	685.6	711	190.4	86.0	<0.001
2	42	null model	1166.1	1233	-	-	-
		age model	1052.7	1187	113.4	46.0	<0.001
		year model	1092.3	1187	73.8	46.0	<0.01
		combined	973.6	1141	192.5	92.0	<0.001
3	50	null model	1096.0	1269	-	-	-
		age model	913.1	1190	182.9	79.0	<0.001
		year model	956.4	1190	139.6	79.0	<0.001
		combined	794.8	1111	301.2	158.0	«0.01*
4	48	null model	837.0	787	-	-	-
		age model	727.3	755	109.8	32.0	<0.001
		year model	736.7	755	100.3	32.0	<0.001
		combined	665.9	723	171.1	64.0	<0.001

Table 6.4. Summary of the results of the logit regression. For each sample the number of shells, the tested models, the scaled deviance of the tested model and its difference to the deviance of the null model is given. The significance of the decrease in deviance by the addition of a *year, age* or *year + age* effect is summarized in the last column (p).

DISCUSSION

There are several observations which suggest that *Arctica* is negatively affected by bottom trawling. A comparison of relative densities during the seventies compared to such estimates made between 1990 and 1993 suggest a decrease in abundance (chapter 2). The mortality rate in the south-east North Sea (Oyster Ground) also seems to be higher than that in the northern North Sea or western Atlantic (chapter 2). The destructive effect of bottom trawling is also illustrated by the low numbers of undamaged shells found in the heavily fished south-east North Sea whereas in more northern areas about four times as many undamaged shells are found (table 6.1). Direct evidence that *Arctica islandica* is indeed influenced by fisheries came from Fonds (1991), Fonds *et al.* (1992) and our own observations. Fonds (1991) reported that up to 90% of *Arctica* caught by a commercial trawler were severely damaged. His estimate for mortality of these shells ranged from 74 to 90%. He demonstrated that shells are damaged on board as well as during the process of fishing. Both the number of damaged shells and the total number of shells caught increases when tickler chains are used. The mean number of damaged shells was 74% with ticklers versus 27% without (Fonds, 1991).

Estimates for the penetration depth of the tickler chains vary depending on bottom type (Welleman, 1989). Such estimates have been based on direct experimental evidence (Margetts & Bridger, 1971; Bridger, 1972) as well as on the occurrence of certain infaunal species in the catch. Bergman & Hup (1992) estimated in this way a penetration depth of 6 cm in hard sand. Stones can be dug out by ticker chains (Bridger, 1970; Margetts, 1971), so *Arctica* may be dug out in a similar way.

Such observations illustrate the vulnerability of *Arctica* to bottom trawling. Even ticklers only moving over the sediment surface can explain the damage pattern of a high percentage of posterior ventral damage (siphon side). The cumulative long-term effect of damage on that shell side might explain the relative shorter shell length to shell height in the shells from the Oyster Ground as reported in chapter 2.

Caddy (1968) observed that sand was forced into the shell of *Placopecten magelanicus* by the passage of a dredge. The grayish thickening (figure 6.6), caused by sand enclosures within the calcium carbonate, found in *Arctica* shells may be explained by similar process; in this case, possibly caused by the passage of a trawl.

Abrupt physical disturbances, for instance temperature, may cause damage patterns comparable to those caused by fisheries (Ropes *et al.*, 1984). There is, however, very little current research on this topic (Anon., 1992a), and therefore it is difficult to estimate its significance. It is furthermore unlikely that such abrupt events occur in the subtidal environment sampled. The physical disturbances mentioned above cause growth interruptions over the whole shell (Kennish, 1980), while damage caused by fisheries can be distinguished by its local character and mainly posterior position.

Predators may also damage *Arctica* shells but the question is raised which predator in the south-east North Sea utilizes full grown *Arctica* shells. It is unrealistic to assume that damage by for instance lobsters can explain the mass occurrence of damaged shells in the south-east North Sea. Despite its near absence in this area a lobster (*Homarus americanus*) could only open a 7 cm-high *Arctica* shell after series of repeated trials (own observation). If the lobster succeeded the fractures made were differently positioned and shaped, compared to those found in dead shells from the Oyster Ground. Arntz & Weber (1970) also demonstrated that cod (from the Baltic) was not able to crush *Arctica* shells larger than 4 cm. Because *Arctica* from the North

Sea have thicker shells than those from the Baltic a great impact by cod in the North Sea is not expected.

The average number of scars in the Canadian shells compare well with the literature value for natural scar frequencies of 1.6. A maximum of 4 scars per individual is considered to be high and the number of damaged shells scarcely exceed 50% (Miller, 1983; Vermeij *et al*., 1981; Vermeij, 1983; Schmidt, 1988; Vale & Rex, 1988). The average frequency of scars in North Sea shells is much higher compared to these figures or to the Canadian samples, underlining that the North Sea specimens have a higher damage frequency than can be expected on basis of natural causes.

The age-frequency distribution of the *Arctica* population may be a reflection of a size dependent effect of bottom trawling. In the south-east North Sea juvenile shells (1-3 cm high) are rarely found, while spat (zero age group; 1-7.5 mm high) and full-grown shells (>5 cm high) are more regularly found (chapter 2). This odd size distribution can be explained by the difference in shell strength as presented in figure 6.3. The figure shows that large shells can resist higher forces than small shells; thus fishing mortality for juvenile shells is probably higher. The results found by Rumohr & Krost (1992), however, suggest a contradictory effect of an otter trawl. They found higher percentages of damaged shells with increasing shell size. It is unknown whether this has to do with any specific action of the otter trawl.

What actually happens in the field is hard to estimate. Factors like sediment type, total shell surface, surface of impact, burrowing depth, and tickler-chain penetration into the sediment, all play a role.

Link with fisheries

The observed increase in the occurrence of scars can be explained by developments in the fishing fleet which were initiated by the European policy on fisheries. This policy aimed at the improvement of the economic position of the fisheries. Despite measures that have been taken since the early 1980s to limit the overall fishing capacity, the result has been a net increase of this capacity (Anon., 1992b). This was caused by both structural changes within the fishing fleet and the gear used. In the period 1972-1990 total engine power increased from approximately 250.10^3 to 600.10^3 HP (Anon., 1991), which was mainly caused by the increase of the number of vessels larger than 1500 HP. These changes have led to higher fishing speeds, a wider range of action and qualitative changes of the fishing gear. The resulting change in temporal and spatial distribution of the Dutch beam trawl fleet is however poorly documented, *i.e.* in variable units, irregularly and until recently for whole ICES rectangles only. Because the results of this study represent disturbance on a much smaller scale, it is difficult to relate the observed long-term trends in scar occurrence exactly to changes of fishing intensity at sea.

The composition of the Dutch fleet in terms of engine power is, however, well documented (Anon., 1992b) and this measure was therefore used in a preliminary comparison with the results presented here. It is likely that the fishing intensity at any site somehow reflects the developments in the total capacity of the fleet. Increased engine power which resulted in heavier gears, wider beams and higher fishing speeds will have led to a greater destructive action and an increased bottom surface being fished. Thus even at a constant number of trawlers in a certain area this will result in a net increase in fishing intensity.

Figure 6.8

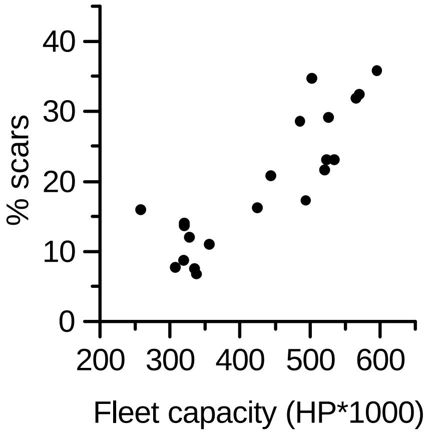

Figure 6.8. Graphical display of the correlation between the average scar incidence (all four samples) and the developments in the Dutch beam trawl fleet expressed as engine power.

The statistical analyses demonstrated that the STD patterns (figure 6.6) indeed may be the result of a *year* c.q. fishery related effect and the scar trends for all four stations were significantly correlated with the overall increase of fishing capacity (table 6.3). Figure 6.8 illustrates this relationship and suggests that the average number of scars is a reflection of the fishing effort. Whether the observed patterns in STD are a reflection of the change in qualitative characteristics or a redistribution of the fishing fleet in space and time, cannot be said. Known estimates for the above mentioned redistribution concern ICES quadrants (areas of approximately 3400 km^2), while the results presented in figure 6.3 concern processes at a local scale.

Not until recently, knowledge about fishing intensity on such local scales was lacking. However, in 1991 Rijnsdorp *et al*. demonstrated that within an ICES quadrant the distribution of the fishing fleet may be very heterogeneous. Such detailed information is lacking for the period in which greatest changes within the Dutch fishing fleet took place. Dating the scars in the shells of *Arctica islandica* may however, give insight in small-scaled spatial distribution of the fishing fleet in the past.

ACKNOWLEDGEMENTS

We thank Prof. Dr. P.A.W.J. de Wilde , G.C.A. Duineveld, M. Bergman, Dr. H.J. Lindeboom and B. Bak for critically reading the manuscript, the crew of R.V. "Pelagia", R.V. "Tridens" and the commercial trawler for their assistance in collecting the material. M. Fonds is acknowledged for both reading the manuscript and collecting material and Dr. Ir. A. Bakker of the Technical University Delft for his assistance and the use of the equipment to measure shell strength. Dr. T. Rowell of Bedford Oceanographic Institute (Halifax, Canada) is thanked for the provision of the Canadian samples. Dr. J. van der Meer is acknowledged for his help with the statistical analyses. This study was made possible by the financial support of BEON (contract DG-474) and the European Community (contract PEM/9307).

CHAPTER 7[*]

A long-term growth record derived from *Arctica islandica* (Mollusca, Bivalvia) from the Fladen Ground (northern North Sea)

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The manuscript of this chapter has been accepted for publication in the J. Mar. Biol. Ass. UK. Those parts dealing with juvenile shells have been published as: Growth variations in *Arctica islandica* L. (Bivalvia, Mollusca); A reflection of hydrography related food supply. ICES Journal of Marine Science, 53; 981-987 (1996).

ABSTRACT

Long-term variations in shell growth of the mollusc *Arctica islandica* (Mollusca, Bivalvia) from the northern North Sea have been assessed retrospectively by using the annually deposited internal growth lines. Relatively young specimens yielded a detailed year-to-year chronology while the growth record of specimens older than 30 years yielded time series with a length exceeding 100 years. The long-term growth trends demonstrated a marked alternating sequence of periods in which growth was below and above expectation. A 33-year long cycle could be discerned. Since the 1960s the growth patterns in *Arctica* from two nearby locations were opposite, while they resembled each other in the period before 1960.

Although expected, no significant correlations were found between shell growth and local bottom water temperature or CPR phytoplankton variables. The alternative hypothesis to explain the variations in shell growth is the existence of a link between local hydrographical phenomena and the occurrence of the *Arctica* beds. The stations from where the specimens were collected were discovered when a drogue was caught by a local eddy. It is speculated that this distribution pattern is the consequence of import and accumulation of organic matter by the eddy system. This idea is supported by the correlation between the variations in the influx of North Atlantic water into the North Sea which determines the existence of the eddy.

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[*] **This chapter will be published in the J. Mar. Biol. Ass. (77) 1997 and is reprinted with permission of the Marine Biological Association of the United Kingdom. Those parts dealing with the juvenile specimens has been published as “Growth variations in Arctica islandica L. (Bivalvia, Mollusca): A reflection of hydrography related food supply” and is reprinted with the permission of the copyright holder (ICES).**

INTRODUCTION

The scarcity of long-term data on offshore marine benthos is regrettable since the benthic community can be seen as a time-integrated response to the ambient environmental conditions. Changes in these conditions are likely to affect both the community structure and certain attributes of their members, such as reproduction and growth. In species with skeletal parts, annual growth can often be recognised by the rhythmic deposition of the hard structures. This feature enables a retrospective analysis of growth variations of the organisms in question, analogous to trees (Jones, 1983). However, the lifespan of most subtidal invertebrates (<10 years) in combination with the inaccuracy in ageing sub-fossil material hamper in most cases the construction of reliable long-term series covering the past century.

In this respect, the bivalve mollusc *Arctica islandica* is of special interest because it complies with four criteria proposed by Thompson & Jones (1977) that should be met in order to make a species useful:

1: Specimens from one population demonstrate synchronised growth variations (Thompson *et al*., 1980; Witbaard & Duineveld, 1990).
2: The species has a consistent annual formation of growth lines, even in the oldest individuals (Turekian *et al*., 1982; Thompson *et al*., 1980; Ropes, 1988; Witbaard *et al*., 1994).
3: It has a great longevity. Ages of 100 years are common in most populations (Ropes, 1985; Witbaard & Duineveld, 1990).
4: Growth is continuous throughout life which can be concluded from the fact that the oldest animals still deposit annual growth lines (Thompson *et al*., 1980; Ropes *et al*., 1984).

In the present study, temporal growth variations in two dense patches of *Arctica islandica* in the Fladen Ground (northern North Sea) are described by methods originating from dendrochronology and adopted by sclerochronology (Jones, 1983). We focussed on this particular population because it originates from an area which is under direct influence of the Atlantic Ocean. The water depth in the Fladen Ground shelters the population from erratic short-term disturbances like storms or abrupt temperature changes. Hence, growth variations in the local *Arctica islandica* population are assumed to reflect important changes in the water column processes (*e.g.* primary production or sedimentation rates). In order to test this hypothesis, the ensuing growth patterns were correlated with environmental data such as CPR phytocolour and annual and monthly abundance of diatoms and dinoflagellates.

METHODS

Site description

The Fladen Ground is located about 100 miles north-east off Aberdeen (Scotland). The bottom consists of an irregular pattern of glacial depressions between 100 and 150 meter depth (Basford & Eleftheriou, 1988). The area is located just south of the major water inflows from the Atlantic Ocean into the northern North Sea (figure 7.1). The central and deeper parts of the area lie in the centre of an only recently recognised, semi-permanent, topographically steered cyclonic eddy formed by the "Fair Isle Current" and the "East Shetland Atlantic Inflow" (Turrell, 1992a; 1992b; Svendsen *et al.*, 1991).

Figure 7.1

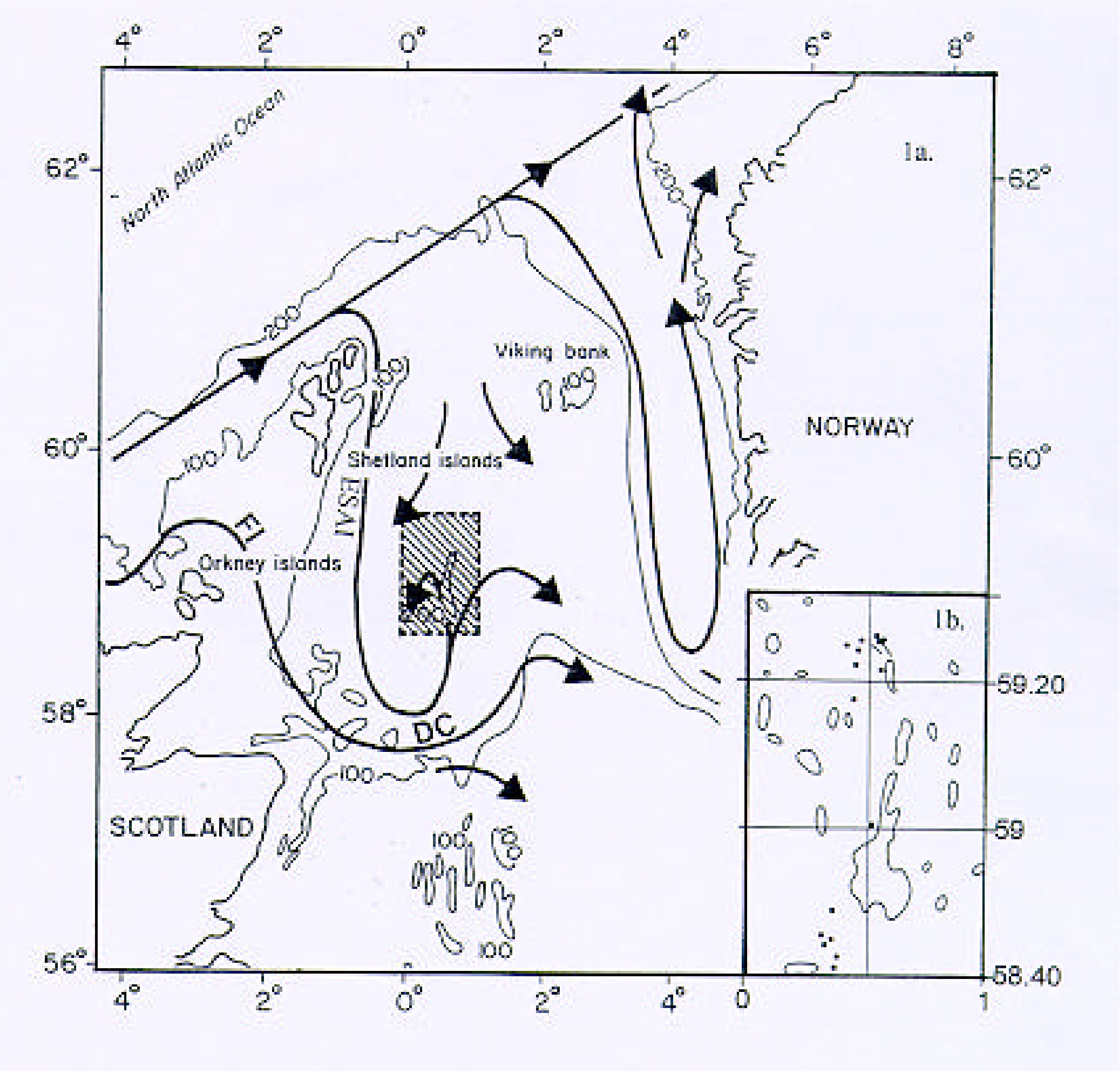


Figure 7.1. Map showing the northern North Sea with main circulation patterns (after Turrell, 1992a, 1992b). FI, Fair isle current; DC, Dooley current; ESAI, East Shetland Atlantic Inflow. The hatched area represents the REFLEX box as studied by Wilde *et al*. (1986). The inset gives the sampling locations within the REFLEX box. •, stations sampled by Wilde *et al*. (1986); \ = trawl tracks taken in December 1991.

In summer the area is thermally stratified with a thermocline between 30 and 70 meter (McIntyre, 1961). This thermocline traps a bell of cold water in the central parts of the area, resulting in a seasonal temperature variation of the bottom water between 5.7 and 7.8°C (Faubel *et al.*, 1983). Year to year variations of the bottom temperature in summer are even smaller and cover the range between 5.9-7.3°C (Ellet & Blindheim, 1992). Stratification lasts until the end of summer. A major part of the primary production takes place in April and May and the net annual primary production ranges between 57 and 100 gr.C.m^{-2} (Steele, 1956; 1974; Fransz & Gieskes, 1984). The benthic fauna of the area has been described in a series of papers (McIntyre, 1961; Faubel *et al.*, 1983; Hartwig *et al.*, 1983; Wilde *et al.*, 1986; Eleftheriou & Basford, 1989; Basford & Eleftheriou, 1988 and Basford *et al.*, 1989). Wilde *et al.* (1986) was, however, the first who reported high numbers of *Arctica islandica* in the area, *viz.* 16 ind.m^{-2} accounting for up to 75% to the total ash-free dry weight biomass. Trawl surveys in the northern North Sea by Basford *et al.* (1989) substantiated that these high densities are restricted to a few small patches, which explains why they were not found in other studies (Hartwig *et al.*, 1983; McIntyre, 1961).

Collecting and ageing

Three batches of living *Arctica* were collected in the Fladen Ground on two occasions. The first two batches were recovered during the REFLEX expedition in spring 1983 by Wilde *et al.* (1986). The positions of the benthic stations sampled during this expedition were determined by the position of a drogue buoy which was followed (Mulder & Manuels, 1982). This resulted in two station clusters, one to the south (58°45'N 0°20'E) and the other to the north (59°25'N 0°30'E) (see inset in figure 7.1). The third batch of *Arctica* was collected in December 1991 when the northern location was resampled with a beam trawl during a cruise with RV. Pelagia. Table 7.1 summarises the origin and date of collection of all 62 shells used for this study.

Acetate peel replica of *Arctica* shell cross-sections were used to make growth line measurements. All acetate peels were made of left-hand valves in accordance with Ropes (1985, 1988). Of each individual shell two or three different, but parallel cross-sections and peels were made. The widths of the growth increments in the peels were measured under 30-125 X magnification with a Zeiss compound microscope equipped with ocular micrometer and a Sony CCD video camera (XC77CE) plus video printer (Sony, UP860CE). In young specimens, measurements were made of the hinge-band, while in older specimens, they were made of the valve proper. Each growth increment was assigned to a particular year starting from the edge of the shell resulting in a time series of increment widths.

Table 7.1

Station	Lat.	Long.	Depth (m)	Young	Old
South 1983	58°45'N	0°20'E	120-140	11	4
North 1983	59°25'N	0°30'E	120-180	6	5
North 1991	59°25'N	0°30'E	120-180	18	18
Total				35	27

Table 7.1. Summary of sampling details. Location, depth and the number of young and old shells from each location is given. Young shells have shell heights between 20 and 50 mm. The age of the young shells varies between 10 and 30 years.

Chronologies of growth variations

Because of the bimodal age distribution of the *Arctica* samples and the non-linear ontogenetic growth of the species (Witbaard & Duineveld, 1990), groups of young clams ($\leq$ 30 years; shell height $\leq$ 50 mm) and old clams (> 30 years) were treated separately.

The synchrony of year-to-year variations in young shells was estimated by calculating the "Gleichläufigkeit" (Schweingruber, 1989) which is actually a sign-test. This test examines the number of similar growth rate changes (acceleration or deceleration) in two shells. It expresses the similarity as percentage of the total number of years that the two shells have in common. These percentages were averaged to obtain a measure of the similarity within and between any of the three clam samples.

A standardised growth index for young shells was obtained by comparing observed and expected growth for a certain year. Estimated expected growth in a particular year was defined as the average growth in 6 surrounding years. Measured growth was subtracted from estimated growth and the difference between expected and observed growth was then divided by the standard deviation of the (6-years) average (Witbaard, 1996). The resulting index value, which can be positive or negative, expresses the magnitude of the deviation. In this way a time series of index values was obtained for each shell. The index time series of the specimens in a sample of clams were averaged to obtain a mean chronology for the sample in question. These mean chronologies were correlated with each other to determine the level of synchrony between the separate samples. For a comparison between growth deviations and environmental data both the mean chronologies and individual index time series were used.

Growth increments in old shells, as in young shells, were transformed into a time series of index values expressing the deviation between observed and expected growth. In order to do so, first the strong correlation ($R_{average}$=0.86) between the (moving) average increment widths and the corresponding standard deviations was eliminated by a logarithmic transformation of the increment widths. Because of the remaining ontogenetic trend of decreasing widths with age, expected growth was defined by a best-fitting (least squares) curve through the transformed increment widths. In all cases, a logarithmic curve turned out to be the most appropriate one. The required index (I_t) was obtained by $\mathrm{Log}(I_t) = \mathrm{Log}(R_t)\text{-}\mathrm{Log}(G_t)$, and is zero when observed growth (R_t) equals expected growth (G_t), while it is positive or negative with an unbound maximum in case of a difference. For each of the separate measurements (27 old shells; 62 peels) a time series of index values was composed. These time series were subsequently averaged per sample giving rise to a mean chronology in which the common signal is enhanced and the noise cancelled out. The mean chronologies of the samples were correlated with each other to assess the synchrony. The coherence among the index time series was calculated with the mean correlation technique and in accordance with Cook & Kariukstis (1990) the following statistics were calculated:

- Average correlation between corresponding time intervals of all combinations of time series (R_{total}).
- Average correlation between corresponding time intervals of index series from different cross-sections of the same shell (R_{within}).
- Average correlation between corresponding time intervals of cross-sections of different shells ($R_{between}$).
- Effective correlation coefficient which incorporates the within and between cross-section signal. It takes the number of cross-sections per shell into account ($R_{effective}$).

The change in chronology coherence with increasing interval length was determined by recalculating the R-statistics after successive 10-year extensions of the time interval, *i.e.* 1991-1972, 1991-1962, 1991-1952 etc. All parameters have been calculated separately for each of the samples collected in 1983 (north and south) and the sample collected in 1991. On the basis of the correlation statistics the following quantities were derived (Cook & Kariukstis 1990):

- Expressed Population Signal (EPS). It expresses the variance which is explained by the common signal as fraction of the total variance in the chronology and is defined as; $EPS=R_{between}/(R_{between}+(1\text{-}R_{between})/n)$ with n= total number of shells and $R_{between}$ is substituted with $R_{effective}$ since more than one cross-section per shell was used.
- Signal to Noise Ratio (SNR). The SNR is a measure of the strength of the signal common in all shells and is calculated as $N^*R_{between}/(1\text{-}R_{between})$.
- Chronology Standard Error (SE) is calculated as $1\text{-}R_{effective}/n$.
- Subsample Signal Strength (SSS). It is a measure which describes how well a subset of index time series describes the chronology of a larger set of index time series. It is

calculated as the quotient of EPS values of the subset and reference sample. The sample collected in 1983 was chosen as the subset of the chronology of north 1983+1991.

Figure 7.2

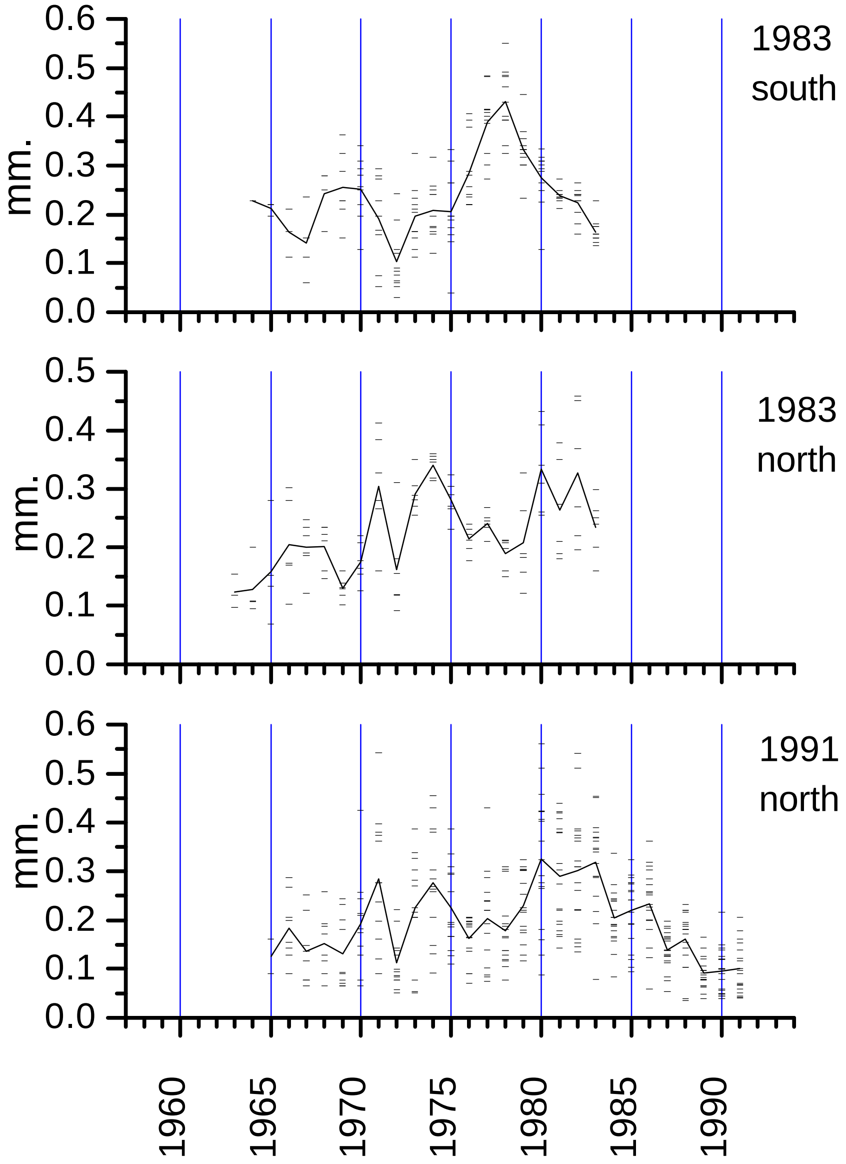


Figure 7.2. Temporal growth variations of young *Arctica* collected at the northern and southern locations in the Fladen Ground in 1983 and 1991. Each bar represents the increment width (mm) of one *Arctica* specimen. The lines connect the average increment width values of all clams in one sample.

RESULTS

Young shells

Figure 7.2 illustrates the variable widths of the hinge-band increments of young shells from both locations. Shells collected at the northern location (1983 and 1991) are characterised by a period of slow growth between 1976 and 1979 and a period of enhanced growth between 1980 and 1983. Shells from the southern site show the opposite trend of increasing widths since the early-1970s until 1978.

The percentage of shells with similar signed deviations for each year and the averaged individual index time series (mean chronology) of these young shells is depicted in figure 7.3a-c and in figure 7.3d-e. In some years (1966, 1969, 1975, 1976, 1978) 100% of the shells had equally signed deviations but these years are not always necessarily the ones with the largest deviation. Despite the opposite growth variations between north and south, growth was strongly depressed at both locations in 1972. Both the magnitude of deviation and percentage of shells was high.

Table 7.2

sample	South 1983	North 1983	North 1991
South 1983	0.78		
North 1983	0.53	0.79	
North 1991	0.50	0.67	0.60

Table 7.2. Average "Gleichläufigkeit" of the young shells sampled in 1983 and 1991. The values indicate the average fraction of synchronous growth variations.

The average similarity of growth variations between two shells, expressed as "Gleichläufigkeit", is given in table 7.2 and ranges between 0.50 and 0.79. The table illustrates that the similarity within a sample is much higher than that between different samples. A maximum "Gleichläufigkeit" value of 94% was found for two shells from the same boxcore collected in 1983.

The coefficient of correlation between the average index series (figure 7.3d-e) describes their similarity. For the 1983 and 1991 sample from the northern site a correlation of 0.83 ($n=13$; $p < 0.01$) was found. The correlation between north 1991 and south 1983 was almost zero whereas north 1983 and south 1983 were negatively correlated with a coefficient of -0.43.

Old shells

The mean chronologies (averaged index time series per sample) for the old shells in the samples south 1983, north 1983, north 1991 are given in figure 7.4a-c. In all samples one can discern an alternation of periods in which growth is either above or below the predicted values. In the chronologies from the northern site (figure 7.4b-c) the periods 1900-1915, 1937-1954 and 1979-1987 have predominantly positive (average) index values, while the intermediate periods have negative values. Except for the opposite trends since 1960, the long-term patterns of the northern and southern chronologies are very similar. Auto correlation indicates a 33-year-long cycle.

figure 7.3

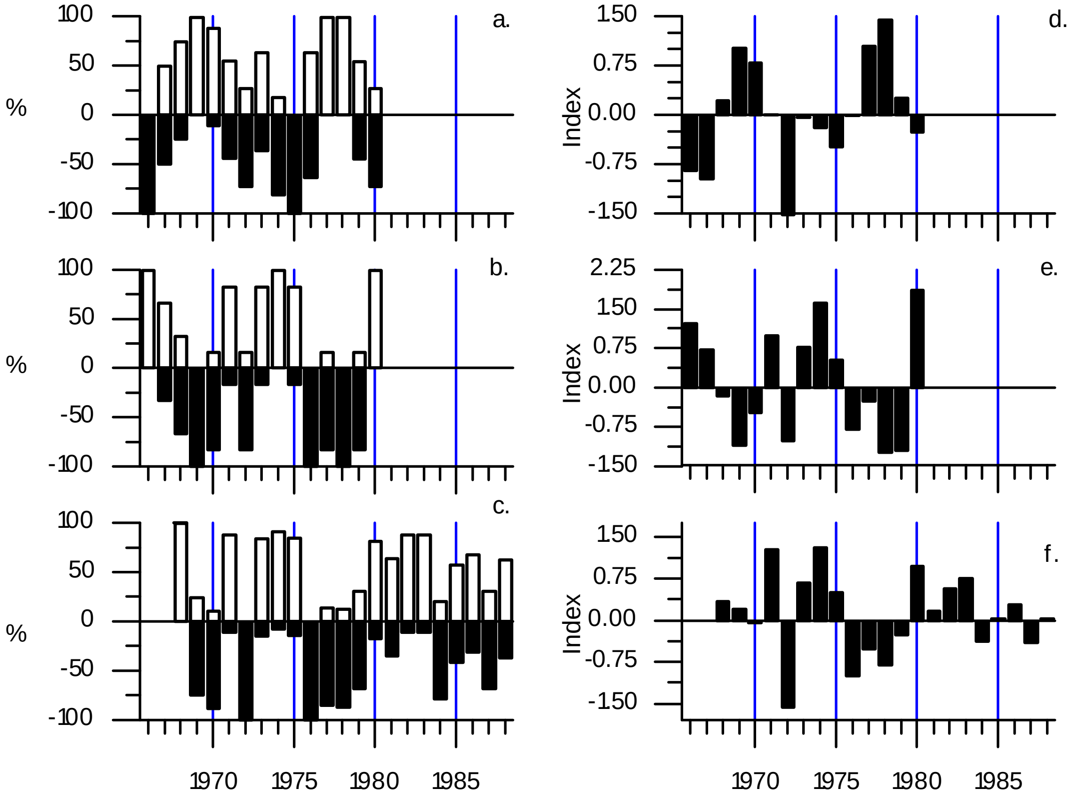


Figure 7.3. Event diagrams and magnitude of positive and negative growth deviations of young *Arctica* collected at south 1983 (a, d), north 1983 (b, e) and north 1991 (c, f). Figure (a-c), The percentage of specimens with similar signed growth deviations for subsequent years. (d-f), Mean index values calculated as deviation from 6 year mean.

The correlation between mean chronologies of north 1983 and north 1991 was 0.54. The coefficient of correlation between the northern chronology (1983+1991) and the southern one is 0.57. The correlation over the last 30 years is negative (R=-0.47), which is similar to that observed in the growth patterns of young shells.

There is also a good relation between the mean chronologies of young and old shells. The best correlation (R=0.79) was found for the shells from the southern site. The coefficient of correlation between mean chronologies derived from the young and old shells from the northern location varied between 0.42 and 0.64.

Figure 7.4

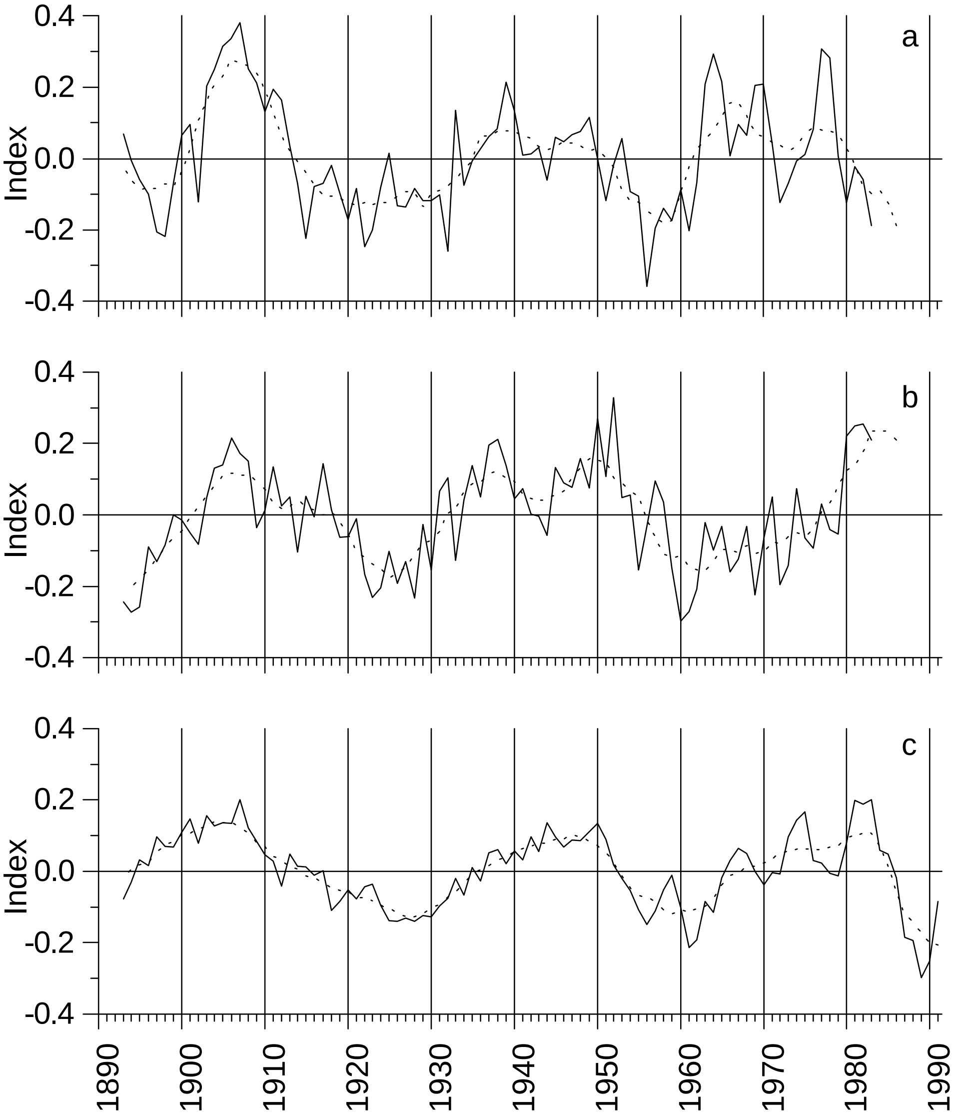


Figure 7.4. Mean chronologies of standardized growth variations in old shells from the Fladen Ground. Shown are the unsmoothed mean chronologies. The dotted lines represent the 3 year adjacent average. (a), South 1983, (b) North 1983 and (c) North 1991. Growth index on vertical axis.

Figure 7.5 illustrates the change of the Expressed Population Signal (EPS) and summarises the correlation statistics (table 7.3) which describe the coherence of the chronology, back in time. All samples except north 1983 have EPS values which exceed the value of 0.85 which is an arbitrate value indicating an acceptable level of coherence in dendrochronology (Cook & Kariukstis, 1990). EPS of north 1991 stays close to this value for the complete length of the chronology while EPS of south 1983 drops below that value when the oldest section is included.

Figure 7.5

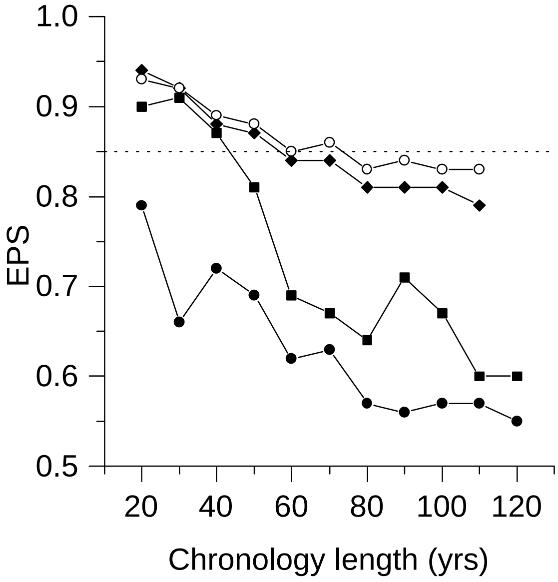


Figure 7.5. The dependence of the Expressed Population Signal (EPS) of chronology length for old shells. EPS values for unsmoothed chronologies. The dotted horizontal lined indicates an EPS value which is regarded as acceptable in dendrochronology. ■ south 1983; ● north 1983; ◆; north 1991; ❍ north 1983+1991.

SNR shows the same tendency with high values of SNR for the most recent sections and low values when the oldest sections are included (see table 7.3). The chronology of north 1991 has the highest SNR values, mainly due to the high number of shells. The Subsample Signal Strength (SSS) of north 1983, when considered as subset of the combined northern sample (1983+1991), is 0.69 for the period 1991-1892. This implies that by studying only 5 shells approximately 70% of the common signal of the entire chronology is found.

Correlation between chronologies and CPR-data

We correlated the individual time index series as well as the mean chronologies with both monthly and annual CPR phytoplankton data (area B2) *i.e.* the relative abundance of individual species of large dinoflagellates, large diatoms and the phytocolour index as well as their annual totals. Neither the mean chronologies of old nor young shells were significantly correlated with either annual phytocolour, annual diatom abundance or annual dinoflagellate abundance or resulted in negative correlations (table 7.4). Only some combinations of the monthly abundance of certain diatoms or dinoflagellate species with some of the individual index time series were significantly correlated, but this might be due to chance. A pattern with high correlations in spring could not be discerned.

Period	R_{tot}	R_{with}	R_{betw}	R_{eff}	SNR	EPS	SE
				South 1983.			
1991-72	0.6	0.73	0.58	0.69	5.52	0.90	0.28
1991-62	0.59	0.67	0.57	0.71	5.3	0.91	0.27
1991-52	0.49	0.58	0.47	0.62	3.55	0.87	0.31
1991-42	0.35	0.42	0.34	0.51	2.06	0.81	0.35
1991-32	0.27	0.42	0.24	0.36	1.26	0.69	0.4
1991-22	0.25	0.40	0.22	0.34	1.13	0.67	0.41
1991-12	0.22	0.35	0.19	0.31	0.94	0.64	0.42
1991-02	0.26	0.37	0.24	0.38	1.26	0.71	0.39
1991-1892	0.22	0.30	0.20	0.34	1	0.67	0.41
1991-1882	0.17	0.23	0.15	0.27	0.71	0.6	0.43
				North 1983			
1991-72	0.42	0.74	0.38	0.43	3.06	0.79	0.34
1991-62	0.3	0.66	0.24	0.28	1.58	0.66	0.38
1991-52	0.31	0.54	0.27	0.34	1.85	0.72	0.36
1991-42	0.26	0.40	0.23	0.31	1.49	0.69	0.37
1991-32	0.21	0.39	0.18	0.25	1.1	0.62	0.39
1991-22	0.22	0.43	0.19	0.25	1.17	0.63	0.39
1991-12	0.18	0.37	0.15	0.21	0.88	0.57	0.40
1991-02	0.16	0.29	0.14	0.20	0.81	0.56	0.40
1991-1892	0.15	0.26	0.14	0.21	0.81	0.57	0.40
1991-1882	0.15	0.25	0.14	0.21	0.81	0.57	0.40
				North 1991			
1991-72	0.35	0.56	0.34	0.45	9.37	0.94	0.17
1991-62	0.3	0.53	0.29	0.39	7.41	0.92	0.18
1991-52	0.2	0.43	0.19	0.28	4.27	0.88	0.20
1991-42	0.19	0.39	0.18	0.28	4.03	0.87	0.20
1991-32	0.15	0.32	0.14	0.23	3.02	0.84	0.21
1991-22	0.14	0.30	0.13	0.22	2.79	0.84	0.21
1991-12	0.12	0.27	0.11	0.19	2.33	0.81	0.21
1991-02	0.12	0.27	0.11	0.19	2.33	0.81	0.21
1991-1892	0.12	0.27	0.11	0.19	2.33	0.81	0.21
1991-1882	0.11	0.27	0.10	0.18	2.09	0.79	0.21

Table 7.3. R-statistics and derived quantities describing the coherence between the individual time index series which were used to calculate the mean chronologies for the samples collected in 1991 and 1983

The results appeared to be better when the seventies were studied exclusively. During that period the mean chronologies showed some striking similarities with the CPR data. For the years 1971 to 1979 the mean chronology derived from young shells from north 1991 yielded marginally significant correlations of 0.49 and 0.51 with phytocolour and total annual total diatom abundance, respectively.

DISCUSSION

Methodology

The high similarity of growth patterns in young shells, with 1972 as a recognisable year with strongly depressed growth, can be used to align or cross-date the chronologies from north 1983 and 1991. Results of this effort show that the excess number of growth increments in shells from 1991 as compared to those from 1983 equals the number of years which had passed since 1983 (figure 7.2). These data support the earlier findings of Witbaard *et al*. (1994) which indicate that growth increments in clams from both shallow and deeper waters are deposited annually. Furthermore, the high synchrony of growth variations in the shells from one locality suggests that a common environmental factor influenced the growth rate of different individuals in a similar way.

Table 7.4

Sample	Period	Diatoms	Dinoflag.	Phytocolour
young shells south 1983	1966-1980	0.16	0.16	0.26
young shells north 1983	1966-1980	-0.02	-0.17	-0.10
young shells north 1991	1968-1988	0.07	-0.21	0.05
old shells south 1983	1960-1983	-0.15	0.19	-0.23
old shells north 1983	1960-1983	-0.28	0.17	0.37
old shells north 1991	1960-1991	-0.33	-0.16	-0.35

Table 7.4. Correlation coefficients between the mean chronologies and indices of annual total abundance of large diatoms, dinoflagelates and phytocolour.

We checked the robustness of the time series that we obtained in two ways. Firstly, we applied alternative standardisation methods, *e.g.* the corridor-method (Cook & Kariukstis, 1990), which resulted in chronologies similar to the ones presented in this paper. Secondly, we constructed a large number of time series composed of randomly generated index values from which we calculated the statistical parameters listed in table 7.3. As these parameters were statistically insignificant for these randomly generated series, we concluded that our measured time series are unlikely a result of chance.

The lower correlation between old shells and the gradual deterioration of the chronology parameters (SNR, EPS; table 7.3) back in time, reflects the difficulty in achieving an exact alignment of the yearly variations in old shells. This deficiency is ascribed to measurement errors due to the misinterpretation of rings or the presence of disturbance rings.

Our data, moreover, show the effect of sampling with a high spatial resolution. The 1983 boxcore samples show a high coherence compared to the 1991 sample which was collected with a beam trawl (see table 7.3). Compared to replicate boxcore samples from one position, a beam trawl covers a much larger area. This enhances the chance of including clams from sites with locally different sediment type or topography being factors which could affect food availability and growth (see Yager *et al*., 1993).

Environmental factors

The strong coherence among the index time series at one location and the spatial differences in growth between the two locations suggests the existence of a common environmental factor controlling shell growth, which varies over small spatial scales within the Fladen Ground.

As in many bivalves (Broom & Mason, 1978; Jones, *et al*., 1989), laboratory experiments with *Arctica* (chapter 4) reveal a clear correlation between temperature and growth. However, the year-to-year variations of the bottom water temperature in the Fladen Ground (Ellet & Blindheim, 1992) are so small that they can not explain the observed growth differences in young shells. This observation is supported by the lack of a positive correlation between local bottom water temperature and shell growth.

Another factor which directly affects growth rate is food availability. Its effect on *Arctica* growth can be easily demonstrated under experimental conditions (chapter 4), but determining the in-situ food availability, its variations and the effect on in-situ clam growth is more difficult. For this reason, we examined the relation between shell growth and phytoplankton standing stock derived from the CPR data (dinoflagellates, diatoms, phytocolour index; see table 7.4). However, few significant correlations were found.

One explanation for these poor correlations is the large difference in spatial resolution of both data sets (see Evans & Edwards, 1993). In the present study, we assessed the variability of food supply in the benthic boundary layer over an area of only a few km², while the CPR data consist of phytoplankton variables averaged over an area of thousands km². In view of the difference we found between growth variations of *Arctica* from the northern and southern locations, a strong correlation is not expected between the CPR data and local deviations in *Arctica* growth. This will only be the case with a drastic alteration of the food web over the whole area, which can overshadow small-scale differences. In this respect, it is interesting to note some striking similarities between the mean chronologies of young shells and the CPR data during the 1970s. The extremely low growth in 1972 coincided with minimum diatom abundance, while the period with depressed growth between 1975 and 1980 was characterised by low diatom abundance and less intense phytoplankton blooms (Dickson *et al*., 1988b; Reid *et al*., 1990). During the 1970s marked changes in both weather and hydrographic conditions occurred in the northern North Sea. At this time, the "great salinity anomaly" (Dickson *et al*., 1988a; Turrell, 1992b) and a drastic reduction in the inflow of Atlantic water (Svendsen & Magnusson, 1992) took place in the northern North Sea. Corten & v.d Kamp (1992) regarded these changes as the most likely explanation for the concurrent changes in the stocks of several pelagic fish species (herring, sand eel, mackerel). Such large-scale events may also have caused the observed changes in the growth rate of *Arctica* at both sampling locations.

In view of recent hydrographical data published by Turrell (1992b) and Svendsen *et al*. (1991), it is likely that there exists a link between the growth of *Arctica* and the hydrographical regime in the Fladen Ground. The dense *Arctica* beds in the Fladen Ground lie in an area under the influence of a topographically steered eddy (Turrell, 1992a, b). The water circulation within this current system concentrates particles at its centre (Svendsen *et al*., 1991) and, consequently, affects the benthic food supply. Turrell (1992b) summarised evidence for the existence of the eddy in the area, *e.g.* the accumulation of fine sediments and the high chlorophyll content of these sediments. The final stationary positions of the drogue followed by Wilde *et al*. (1986) which led to the discovery of the two *Arctica* patches also points to the eddy system described by Turrell (1992a, b). According to Svendsen *et al*. (1991) the circulation over the Fladen Ground is coupled to the Atlantic inflow because parts of the Dooley Current (DC) and East Shetland Atlantic Inflow (ESAI) contribute to it (figure 7.1). Therefore, variations in these two currents may influence the strength of the eddy and, consequently, the accumulation of material in its centre. Hence annual variations in growth of *Arctica,* being the result of the eddy-mediated food supply, may reflect the variable inflow of Atlantic water into the northern North Sea.

We examined this hypothesis by comparing the growth variations of *Arctica* with data on the Atlantic inflow as estimated by Turrell (1992b) (*i.e.* on basis of wind direction and wind stress). The year-to-year variation in the wind driven component of the ESAI explains a significant part ($R=0.56$ $p<0.05$) of the growth variations observed in young animals from the northern location (figure 7.6).

Figure 7.6

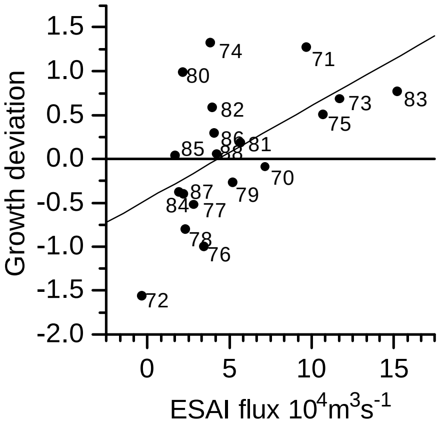


Figure 7.6. The correlation between the estimated East Shetland Atlantic Inflow (ESAI flux in $10^4 m^3 s^{-1}$; Turrell, 1992) and the magnitude of growth deviations (vertical axis) observed in young shells collected at the northern locations in 1991. (R=0.56, n=19, $p<0.05$). Numbers in graph indicate years.

Inflow into the northern North Sea is linked to the outflow along the Norwegian Trench (Dooley & Furnes, 1981; Reid *et al.*, 1992). A stronger outflow is compensated by an increased inflow. Growth variations of *Arctica* should, according to our hypothesis, also correspond to the outflow along the trench. The relation between changes in the outflow (Furnes, 1992) and the mean chronology of *Arctica* growth from the northern location (1991+1983) is depicted in figure 7.7. The two datasets differ in details, *i.e.* maxima or minima do not coincide but the periodic alternation in both datasets have similar tendencies *i.e.* faster growth during periods of increased outflow and depressed growth during periods of reduced outflow along the Norwegian Trench. The estimated fluxes of Atlantic water into and out of the northern North Sea explain a significant part of both the long- and short-term growth variations of *Arctica*. It is therefore hypothesised that the underlying mechanism causing the variations in *Arctica* growth is the temporal variation in the strength of the topographically steered eddy.

A further extension of our hypotheses is that the (partly) opposing trends result from shifts in the position of the eddy. While the southern border of the eddy is determined by the 100 meter-depth contour its northward extension may be variable. As a result the bottom area, which is influenced by the eddy, might have had a variable position or dimension and consequently have favoured either the *Arctica* at the southern location, the *Arctica* from the northern location or both locations. Thus, a north-south movement of the area with increased deposition may explain the opposing growth variations between north and south in recent years. The absence of opposing growth variations in the older chronology sections suggests that such conditions are exceptional and indicate that the Fladen Ground is, at least temporarily, less homogeneous than assumed previously.

Figure 7.7

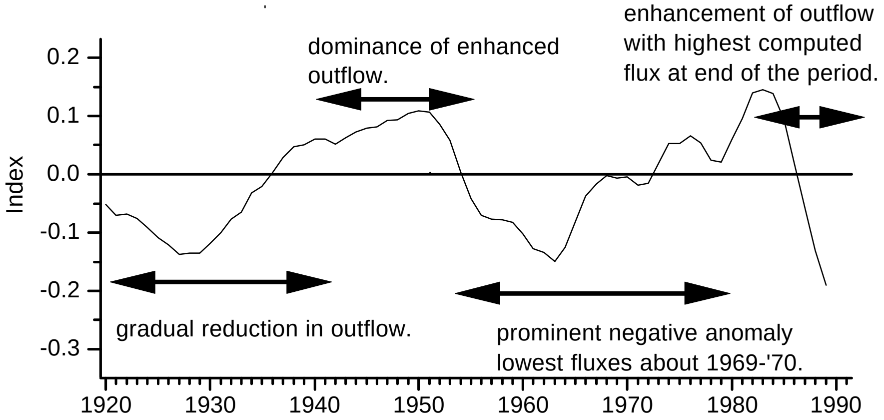


Figure 7.7. The tentative relation between the long-term mean chronology (north 1983+1991) with the estimated outflow along the Norwegian trench (Furnes, 1992).

The corresponding trends in the older chronology sections and changes reported for other regions suggest that the observed variations in shell growth of *Arctica* may be related to changes of a geographical scale larger than the Fladen Ground and which were not limited to most recent decades. Changing climatic conditions are often mentioned in such context (Aebisher *et al.*, 1990; Dickson *et al.*, 1988b).

The minimum index values in the early 1960s with their subsequent recovery concurred with the so called "gadoid outburst", the birth of exceptionally strong year classes of gadoid fishes (Cushing 1982), and coincided with a renewed and successful settlement of young *Arctica* in the Fladen Ground. Such successful settlement and recruitment were absent during the preceding 60 years as revealed by age structure analyses of the population. Conditions for juvenile survival or adult reproduction apparently improved since 1960.

There are other datasets as well which either demonstrate similar long-term trends or are characterised by obvious changes during similar periods. Austen *et al.* (1991) and Evans & Edwards (1993) observed changes in community structure of benthos and plankton respectively in the North Sea between 1979 and 1980, and our data likewise show such abrupt changes.

Similarities with other datasets are not limited to the most recent period. The increasing index values (figure 7.4) since the mid 1920s coincide with faunal changes in the English Channel which is known as the "Russell cycle" (Cushing, 1982). Its main feature is the replacement of *Sagitta elegans* by *Sagitta setosa*, but also comprises the northward expansion of fish species with a southern origin between 1922 and 1950. During this period a predominance of Atlantic conditions in Arctic waters has also been observed (Blacker, 1957).

First signs of a reversal to the original fauna-composition in the English Channel were observed in the early 1960s and consisted of the reappearance of low densities of *S. elegans*, the changing abundance of non-clupeid fish larvae and the appearance of mackerel off Cornwall. In this period, shell growth indices also returned to their 1930 values. The more rapid return of the growth indice values of *Arctica* compared with the abundance change of the indicator species in the Channel is probably caused by the time it takes for these species to build a population with densities high enough to be sampled properly. These observations suggest that the underlying mechanism might have a North Sea wide extension and we assume hydrographical changes to be responsible. We thereby distinguish two periods in the chronology of growth variations of *Arctica*, a period comprising the years before 1960 during which the northern and the southern population have corresponding growth variations and a period after 1960 when the two populations have opposing growth trends. Thus even in putative stable regions like the Fladen Ground, the benthic environment can endure changes that generate heterogeneity on small spatial and temporal scales. Our observations stress the value of long-term growth studies for getting on track of events or mechanisms which control the functioning of the benthic community. Of course, studies like the present ones can only generate correlative evidence, actual multi disciplinary field studies are necessary to resolve the exact processes.

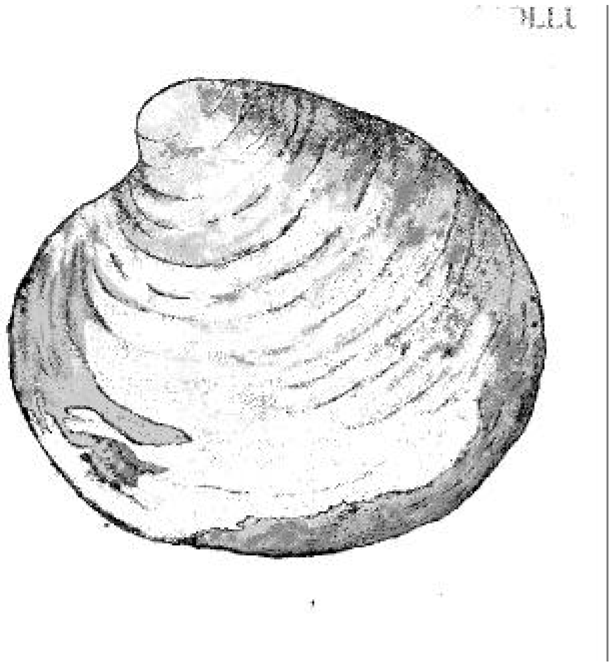
ACKNOWLEDGEMENTS

We would like to thank the Sir Allistar Hardy Foundation for allowing use of its CPR data as well as Dr. W.R. Turrell, Marine Laboratory Aberdeen, for the use of his data on the hydrography of the northern North Sea. We are also very grateful to the crew of R.V. "Pelagia" for their assistance in the collection of the *Arctica* specimens.

The animal almost reached the maximum size.
Shell height is a little over 9 cm. Large parts of the valves are without periostracum.
The shell is extremely heavy because each year it has deposited a small increment
along its margin, but also deposited a carbonate layer along the entire internal surface
of the valve.

CHAPTER 8.

Summary and conclusions



CHAPTER 8.

Summary and conclusions

SUMMARY

Within the North Sea the southernmost distribution limit of *Arctica* follows the 30 m depth contour. This border is most likely set by the maximum bottom water temperature of 16°C.

Densities of 16 individuals/m² were found in the northern North Sea. In the south-eastern North Sea the maximum density of 0.1ind/m² is low, especially compared to those around Iceland or the western Atlantic. In the south-eastern North Sea the densities decreased between the 1970s and the early 1990s. Both the percentage of sampling stations and the corresponding densities decreased. The mortality rate in the south-eastern North Sea is twice as high as that in the northern North Sea. The results of chapter 6 suggest that this difference is related to the difference in the intensity of beam trawling. In the south-eastern North Sea undamaged *Arctica* are rarely found. About 80% of the injuries on the shells were found on the post ventral shell side. The passage of tickler chains are held responsible for these injuries. Small injuries may result in a scar and the subsequent time trend analyses in their occurrence did show an increase since ± 1970. This time trend corresponded with the increase in the total engine capacity of the Dutch beam trawl fleet. The temporal changes in the occurrence of scars on the shells of *Arctica* may therefore yield information about the frequency of fishing disturbance on benthic communities with a high spatial resolution.

Most populations in the North Sea consist of specimens with ages exceeding 30 years and shell heights larger than ~50 mm. Secondary production for these populations was estimated on basis of the corresponding size frequency distribution and size weight relationships. This yielded an average population P/B of 0.03. The age specific P/B ratio decreased from 1.2 in 1 to 5-year-old specimens to 0.02 for animals older than 30 years.

About 31.5% of the *Arctica* from the North Sea is infected with the commensal nemertean worm *Mallacobdella grossa* but no geographical difference in the percentage of infection was found. There was however a strong size-dependence. The infection increased from 14% in shells smaller than 35 mm height to 37 % in animals larger than 71 mm. Infected animals had a better condition index than uninfected specimens but the difference was insignificant.

Some of the North Sea populations differed in their shell morphology. These differences could originate from a genetic difference but the relatively shorter length to height in the Oyster Ground specimens can be caused by frequent damage by fisheries as well.

^{14}C analysis of material sequentially sampled from three different shells of *Arctica islandica* supports the hypothesis of an annual growth increment deposition. The ~1960 pulse of ^{14}C which resulted from the atmospheric nuclear bomb tests was recorded in each of the shells at a location in concurrence with that expected from band counting. The observed cyclic variation in stable isotopes of oxygen and carbon also coincides with growth bands *i.e.* the variation in δ^{18}O and δ^{13}C within each growth increment agrees with the expected variation on the basis of the seasonal variation in temperature and primary production. Thus all isotopic data confirm the hypothesis of annual increment deposition and took away the doubts about a sub-annual deposition for shallow living specimens. Later, additional evidence for annual growth line deposition of deep living *Arctica* from the northern North Sea was found as well. The alignment of the variable increment widths measured from shells originating from two samples which were collected at the same location but 8 years apart, showed that the excess number of growth increments in the most recent sample equals the number of years which had passed since the first sampling date. Thus both deep and shallow living *Arctica* deposit growth increments annually which justifies the use of the internal growth lines for the construction of biochronicles on basis of the shells of *Arctica islandica* as presented in chapter 6 and 7.

The δ^{18}O data suggested that shell growth starts early in the year even at low temperatures. This observation was supported by the results of growth experiments which demonstrated that shells can grow at temperatures below 6°C and thus contradict the suggestions made in literature that growth stops below that temperature. At optimal food conditions instantaneous shell growth increases from 0.0003/day at 1°C to 0.0032/day at 12°C. Thus a tenfold increase in growth was found. At higher temperatures the increased growth could not be attributed to the daily siphon activity but will have resulted from increasing filtration rates and phagocystosis (Winter, 1969). Greatest change in growth rate was found at temperatures below 6°C. This suggests that small differences in bottom water temperature during the period that the springbloom sediments towards the bottom might strongly influence shell growth.

The daily siphon activity is strongly influenced by the availability of food. Starved specimens were active during 12.5% of the observational days. Fed animals were active between 40 and 80% of the observations. At high particle densities the animals compensate for the lower filtration rates (Winter, 1969) with prolonged periods of activity. The good relation between the average percentage of activity and growth illustrates that daily siphon activity is a good measure for filtration activity and food uptake. The growth of shell and tissue at 9°C suggest that a particle density between 5 and 7* 10^6 cell/ltr is just high enough to keep juvenile *Arctica* alive. The carbon conversion efficiency for *Arctica* with 10-23 mm high shells at 9°C is estimated to vary between 11 and 14%.

The geographical differences (chapter 5) in growth rates subscribe the results of the experiments described in chapter 4. Shell growth measured over the first 10 years of life showed a fourfold difference between slowest and fastest (average) rate. Both rates were found at the northern edge of its distribution (64-66°N) and illustrate that temperature might be overruled as growth determing factor. Principal component analyses demonstrated that the average growth rates correlated better with primary production than with average bottom water temperature. Temperature has a significant effect on growth when seen over the entire latitudinal range (52°-66°N) but the effect on animals from the North Sea is small. Their growth was negatively correlated with water depth and sediment silt content. These results suggest that within the North Sea the difference in shell growth mainly originates from the difference in primary production and the associated sedimentation of phytodetritus towards the bottom. The major role of food supply in the determination of the shell growth rates for the northern North Sea is supported by the results presented in chapter 7. The great inter-annual variations in growth of animals (<30 years) from the Fladen Ground could not be explained by inter-annual temperature variations. A relation between shell growth and phytoplankton standing stock could neither be demonstrated, although there were some striking similarities with some of the major events described for the northern North Sea. The most obvious one was the similarity between shell growth rates and the inflow of Atlantic water along the eastern side of the Shetlands. That inflow determines the existence of a topographically steered eddy overlying the area. The central parts of the eddy coincide with the area where high densities of *Arctica* were found. It is hypothetised that these *Arctica* beds are linked to the eddy because the water circulation within the eddy leads to enhanced deposition of phytodetritus in these central areas. This implies that the shell growth variations of specimens of this population may reflect variations in the influx of Atlantic water into the North Sea.

Long-term chronologies of growth variations were constructed on the basis of growth line patterns in shells of specimens older than 30 years. These chronologies showed a marked alternating sequence of periods in which growth was below or above the expected values. The comparison of the growth line patterns of these old shells with the outflow along the Norwegian Trench also suggests a link between shell growth and the inflow of Atlantic water into the North Sea.

CONCLUSIONS

In marine benthic biology it has often been tried to assess cause-effect relationships by studying changes in the benthic community. Although such an approach can be fruitful it is often hampered by the high variability in benthic community structure or by the lack of relevant reference data. Sub-lethal effects for individual species remain unrecognised in the community structure approach although studying such sub-lethal effects may be very promising, especially when *Arctica islandica* is used. *Arctica* is a valuable indicator organism because it combines the following characteristics;

- There is an overwhelming amount of knowledge on physiology, anatomy and behaviour. Many scientists used *Arctica* in experiments because of its attractive size and easiness to handle.
- *Arctica* is a slow growing, long living species with an irregular recruitment. These aspects make it sensitive to disturbance. Changes in survival or recruitment may strongly affect population structure (Rees & Dare, 1993).
- Its geographical range as well as the habitats in which *Arctica* lives, vary widely. This implies that for different areas a congruent data-set can be obtained.
- *Arctica* fulfils the requirements to construct a biochronicle (Thompson & Jones, 1977).
- *Arctica* is immobile. Once it has settled on the sea floor it remains stationary. It can not escape from adverse conditions. Changes in the environment will control survival, reproduction and growth. During shell growth, information from the environment is incorporated into the annually deposited carbonate increments and the growth record of *Arctica* therefore forms an environmental archive. The disclosure of this archive enables the retrospective assessment of environmental change.

Being a slow growing organism with high longevity *Arctica* is a promising indicator organism. Changes in the population structure and abundance (chapter 2) are likely to reflect environmental change. However, the study of changes in its population structure is impaired by the low densities in combination with the difficulties to sample *Arctica* quantitatively. The lack of knowledge on reproduction and settlement in the North Sea makes it furthermore difficult to interpret the observed changes. Are they natural or man induced ?

As outlined above the annually deposited growth increments are a valuable archive in which environmental information is stored year after year. Until recently this archive was under-utilised. Some of the possible applications have been illustrated in this study;

- The incremental width itself gives information about both temporal and spatial differences in growth rate (chapter 4, 5 and 7). Consistent geographical differences in in-situ growth rates point to structural differences between areas. For the North Sea the differences appear to reflect differences in benthic food availability.
- Temporal differences in the growth rates might point to both local changes and wide ranging changes in the structure or functioning of the marine ecosystem. This topic has partly been covered in chapter 7. It gives the possibility to judge man induced changes against changes with a natural cause.
- The increment appearance itself (chapter 6) enables the assessment of man's impact *e.g.* physical disturbance by bottom fisheries on the marine benthic ecosystem .
- The chemical constitution of each increment is another valuable source of information. The isotopic constitution of the carbonate was used to prove the annual deposition periodicity in shallow living *Arctica*. The reverse can be done as well *e.g.* the chemical constitution of successive increments can be utilised to construct time series on for example the input of ^{14}C or micro-pollutants like heavy metals. Especially the development of high precision sampling and analyses methods (nuclear techniques like PIXE or INAA) may yield an overwhelming amount of information even on a seasonal time scale (Nyström, 1995).

It was impossible to deal with all these topics in this thesis but still the results presented in chapters 6 and 7 illustrate some of the great advances of using the internal growth lines in *Arctica* to assess changes in the marine environment retrospectively.

Samenvatting & conclusies

SAMENVATTING

De zuidelijkste verspreiding van *Arctica islandica* binnen de Noordzee volgt ongeveer de 30 meter dieptelijn. Deze grens is waarschijnlijk gerelateerd aan de maximale bodemwater temperatuur van 16°C die samenvalt met deze dieptelijn. Maximale dichtheden in de zuidoostelijke Noordzee van gemiddeld 0.1dier/m² zijn laag vergeleken met dichtheden in meer noordelijke delen van het verspreidingsgebied of de westelijke Atlantische Oceaan. Binnen de Noordzee werden de hoogste dichtheden van adulte dieren van 16 individuen/m² in de Fladengronden (noordelijke Noordzee) aangetroffen. Een vergelijking van de tussen 1972 en 1982 en in de 90er jaren geschatte dichtheden suggereert een abundantie afname. Zowel het aantal stations waarop *Arctica* werd aangetroffen als de dichtheden op die stations waren gedaald.

In de Oestergronden is het sterftecijfer twee maal zo hoog als dat in de Fladengronden. De resultaten zoals beschreven in hoofdstuk 6 maken aannemelijk dat dit verschil te wijten is aan de intensieve boomkorvisserij in de zuidoostelijke Noordzee. Ongeveer 80% van de recente schade en littekens op de schelp van *Arctica* wordt aangetroffen op de posterio-ventrale schelpzijde. Deze schade wordt veroorzaakt door de wekkerkettingen welke deel uitmaken van het boomkorvistuig. Bij het passeren van een boomkor worden fragmenten van de schelp afgebroken. Sommige van deze beschadigingen herstellen, maar blijven als litteken zichtbaar. De analyse van de tijdtrend in het voorkomen van deze herstelde beschadigingen levert een tijdserie op die de frequentie van verstoring door de boomkorvisserij op zeer lokale schaal weerspiegelt. Het unieke is dat deze trend wordt samengesteld op grond van een van de visserij onafhankelijke methode. De trend vertoont een sterke correlatie met de ontwikkelingen in het motorvermogen van de Nederlandse boomkorvisserijvloot.

De meeste populaties in de Noordzee zijn opgebouwd uit schelpen die ouder zijn dan 30 jaar met een schelphoogte van 50 mm of meer. De gemiddelde productie-biomassa verhouding, *z.g.* P/B ratio, van deze populaties wordt geschat op 0.03. Er is een sterke leeftijdsafhankelijkheid. In 1 tot 5 jaar oude dieren is de ratio gemiddeld 1.2. Deze neemt af tot 0.02 voor dieren ouder dan 30 jaar.

Van de in de Noordzee gevangen *Arcticas* bleek 31.5% besmet te zijn met de commensale nemertijne worm *Mallacobdella grossa.* Binnen de Noordzee werden echter geen geografische verschillen in besmettingsgraad gevonden. Wel was er een sterke afhankelijkheid van lichaamsgroote. Van dieren kleiner dan 35 mm was gemiddeld 14% besmet, terwijl van dieren groter dan 71 mm, 37% besmet was.

Geïnfecteerde dieren bleken een iets betere conditieindex te hebben, maar het verschil met niet-geïnfecteerde dieren was niet significant.

Vergelijking van de schelpmorfologie bracht kleine verschillen tussen diverse Noordzee populaties aan het licht. Deze verschillen kunnen op een genetische verschil berusten maar de relatief kortere schelplengte t.o.v. de schelphoogte voor Oestergrond dieren in combinatie met het frequent beschadigen van de posteriore schelpzijde door bodemvisserij kan ook een oorzaak zijn.

De ^{14}C analyse van schelpmateriaal dat sequentieel van drie schelpen was bemonsterd ondersteunt de hypothese dat in de Noordzee ook de ondiep levende noordkrompen jaarlijks 1 groeiincrement vormen. De "1960"-piek in de atmosferische ^{14}C concentratie, die het gevolg was van bovengrondse kernproeven op metname Nova Zembla, kon in de schelp terug worden gevonden op een plaats die verwacht werd op grond van het tellen van de inwendige groeilijnen. Ook bleek de cyclische variatie van ^{18}O en ^{13}C binnen elk der afzonderlijke incrementen overéén te komen met de verwachting op grond van de jaarlijkse variatie in temperatuur en primaire produktie. Dus alle isotoop data bevestigen de hypothese van een jaarlijkse incrementvorming. In een later stadium werd een extra bewijs voor jaarlijkse incrementvorming gevonden voor diep levende noordkrompen uit de noordelijke Noordzee. De sterke overeenkomst van groeiïncrementbreedtes maakte het mogelijke de groeipatronen in schelpen die met een tussentijd van 8 jaar waren verzameld, over elkaar heen te leggen. In het meest recent verzamelde monster bleken evenveel incrementen bijgevormd als dat er jaren waren verstreken sinds het eerste monster verzameld werd. Dus zowel diep als ondiep levende noordkrompen in de Noordzee zetten groeilijn en increment af met een jaarlijkse periodiciteit. Deze resultaten rechtvaardigen dus het gebruik van de interne groeilijnen voor het construeren van zogenaamde biochronologieën, zoals geïllustreerd in hoofdstuk 6 en 7. Uit de ^{18}O data blijkt ondermeer dat schelpgroei vroeg in het voorjaar start, zelfs bij lage temperaturen. Deze observatie werd later in groeiexperimenten bevestigd. Die experimenten lieten zien dat de groei van juveniele schelpen bij een toename van temperatuur en voedselaanbod, stijgt. Onder optimale voedselcondities neemt de instantane groeisnelheid toe van 0.0003/dag bij 1°C tot 0.0032 bij 12°C. Dus tussen 1 en 12°C neemt schelpgroei toe met een factor 10.

Het bleek ook dat *Arctica* heel goed in staat is bij temperaturen lager dan 6°C te groeien. Deze resultaten spreken daarbij de in de literatuur gemaakte beweringen, dat schelpgroei beneden 6°C stopt, tegen. De toename van de groei met toenemende temperatuur kon niet verklaard worden uit een toename in siphonactiviteit.

Waarschijnlijk hangt dit samen met een toename van de filtratiesnelheid en fagocytose (Winter 1969).

De grootste *verandering* van de groeisnelheid vindt plaats bij temperaturen beneden 6°C. Dus kleine verschillen in de bodemwatertemperatuur tijdens de periode dat de voorjaarsbloei uitzakt, kunnen grote consequenties hebben voor de schelpgroei. Hoewel een toename van de temperatuur geen invloed heeft op de siphonactiviteit van de proefdieren, bleek de voedselbeschikbaarheid dat wel te hebben. Niet gevoerde dieren waren gemiddeld gedurende 12.5% van de experimentele periode actief; de best gevoerde dieren waren gedurende 80% van de tijd actief. Dieren die weinig of geen siphonactiviteit vertoonden bleken niet gegroeid te zijn. Siphonactiviteit is dus een goede maat voor filtratieactiviteit en voedselopname. Hoewel het vleesgewicht van niet-gevoerde dieren daalde, trad geen verandering in de schelpdimensies op. De geringe schelp- en weefselgroei bij 9°C bij een gemiddelde partikeldichtheid tussen de 5 en 7 miljoen cellen/l maakt het aannemelijk dat deze dichtheden net voldoende zijn om de dieren in leven te houden of geringe schelpgroei te bewerkstelligen. De conversie van koolstof door de proefdieren varieert tussen 11 en 14%.

De verschillen in gemiddelde groeisnelheid tussen natuurlijke populaties binnen en buiten de Noordzee (hoofdstuk 5) onderschrijven de experimentele resultaten. De gemiddelde groeisnelheden gemeten over de eerste 10 levensjaren voor deze natuurlijke populaties verschilden met een factor vier. Opvallend was dat de populaties waarbij deze extremen werden gevonden beiden afkomstig waren van de noordrand van het verspreidingsgebied. Deze observatie laat zien dat temperatuur als groeifactor, overschaduwd kan worden door andere factoren. Voedseltoevoer is daarbij de meest waarschijnlijke. Een principale component analyse liet inderdaad zien dat primaire productiviteit beter correleerde met gemiddelde groeisnelheid dan temperatuur. Temperatuur had wel een significant effect wanneer beschouwd over de gehele geografische range (52°-66°N), maar voor de gemiddelde groeisnelheden binnen de Noordzee was het effect niet aantoonbaar. Schelpgroei van dieren uit de Noordzee was bovenal negatief gecorreleerd met waterdiepte en slibgehalte van het sediment. Dit betekent dat de groeiverschillen binnen de Noordzee vooral zijn toe te schrijven aan lokale verschillen in primaire produktie en de daarop volgende sedimentatie van phytodetritus.

De complexiteit en interacties tussen groeibepalende factoren blijkt ook uit de resultaten beschreven in hoofdstuk 7. De groeivariaties van relatief jonge dieren (<30 jaar) uit de Fladengronden kon niet worden verklaard aan de hand van bekende variaties in de temperatuur van het bodemwater. Er bestond echter ook geen goede relatie met de jaarlijkse variatie in fytoplankton abundantie. Wel waren er treffende overeenkomsten met enkele zeer markante gebeurtenissen in de noordelijke Noordzee. De meest opvallende is de overeenkomst tussen de groeivariaties en de jaarlijkse variaties in de instroom van Atlantisch water ten oosten van de Shetland eilanden. Deze instroom beïnvloedt de aanwezigheid van een door de bodemtopografie gestuurde ronddraaiende watermassa. Het centrale deel van deze "eddy" valt samen met de locaties waar hoge dichtheden noordkrompen zijn gevonden. Verondersteld wordt daarom dat beide gekoppeld zijn, omdat de watercirculatie binnen de eddy kan leiden tot een verhoogde depositie van fytodetritus in het centrum. De instroom van Atlantisch water bepaalt in sterke mate de aanwezigheid van deze eddy en depositie van materiaal. Dit betekent dat de variabele groeisnelheden van de alhier levende dieren een indirecte reflectie zijn van de variatie in de instroom van Atlantisch water.

Op basis van de groeilijnpatronen van dieren uit de Fladengronden die ouder dan 30 jaar waren, werden chronologieën geconstrueerd die terug gaan tot het eind van de vorige eeuw. Deze chronologieën bleken een opvallende afwisseling te vertonen van perioden waarin de groei hoger was dan verwacht en periodes waarin deze lager was dan verwacht. Vergelijking met hydrografische data laat zien dat deze variaties waarschijnlijk gekoppeld zijn aan de instroom van Atlantisch water.

CONCLUSIE EN NABESCHOUWING

Om beter inzicht te krijgen in het functioneren van mariene bentische ecosystemen heeft men dikwijls geprobeerd om aan de hand van veranderingen in de gemeenschapsstructuur, ingreep-effect relaties te bestuderen. Een dergelijke benadering kan veelbelovend kan zijn, maar wordt veelal gehinderd door een gebrek aan historische gegevens of is de natuurlijke variabiliteit binnen een gemeenschap te groot om met zekerheid zulke relaties aan te tonen. Bij de "gemeenschapsbenadering" blijven sublethale effecten zoals verminderde conditie, reproduktie of groei veelal onopgemerkt. De resultaten van het hier gepresenteerde onderzoek illustreren dit in het bijzonder; *Arctica islandica* leent zich uitstekend voor een autoecologische benadering omdat deze soort een aantal specifieke eigenschappen combineert.

- Door zijn aantrekkelijke grootte en het gemak waarmee met het dier kan worden omgegaan, hebben veel onderzoekers *Arctica islandica* als onderzoeksobject gebruikt. Er is derhalve veel bekend met betrekking tot zijn fysiologie, gedrag en anatomie, hetgeen dus een enorme hoeveelheid achtergrond informatie verschaft.
- *Arctica* is een traag groeiende, lang levende soort met een onregelmatige broedval . De soort is daardoor extra gevoelig voor verstoring. Veranderingen in overleving en aanwas van juvenielen kunnen in sterke mate de populatie structuur beïnvloeden (Rees & Dare, 1993).

- Zijn geografische verspreiding, maar ook de uiteenlopende habitats waarin hij voorkomt, maken het mogelijk, een vergelijkbare dataset voor milieu veranderingen voor zeer uiteenlopende gebieden samen te stellen.
- *Arctica* voldoet aan alle eisen die aan een organisme gesteld worden voor het opstellen van zg. "biochronologieën" (Thompson & Jones, 1977).
- De soort is nauwelijks mobiel. Wanneer het dier zich eenmaal op de zeebodem gevestigd heeft, zal het niet noemenswaardig van plaats veranderen. Dit impliceert dat omgevingsomstandigheden in sterke mate het functioneren en overleven bepalen. Omdat schelpgroei in belangrijke mate bepaald wordt door de omgeving bevat ieder in de schelp aangelegd increment informatie over de milieucondities waaronder het increment werd gevormd. Juist hierin ligt de kracht van *Arctica*. Door deze informatie te ontsluiten, kunnen jaar-tot-jaar veranderingen in het milieu retrospectief bestudeerd worden. Zelfs voor perioden of plaatsen waarvoor geen andere datasets bekend zijn.

In eerste instantie lijken vooral de populatie ecologische aspecten van *Arctica* van groot belang voor het gebruik van deze soort als indicatororganisme. Het bestuderen van veranderingen in bijvoorbeeld de populatiestructuur wordt echter bemoeilijkt doordat de dichtheden in de Noordzee over het algemeen laag zijn en een kwantitatieve bemonstering moeilijk is. Ook is het gebrek aan kennis over de voortplanting van de in de Noordzee aanwezige populaties een gemis.

De aanleg van de jaarlijkse incrementen biedt echter perspectieven. Zoals eerder genoemd vormen zij een archief. Dit archief is tot nu toe vrijwel onbenut gebleven. Diverse voorbeelden, zoals gepresenteerd in deze studie, illustreren dit:

- De incrementbreedte zelf, geeft informatie over zowel temporele als ruimtelijke groeiverschillen (hoofdstuk 4, 5 en 7). Consistente geografische verschillen wijzen daarbij op structurele verschillen tussen zeegebieden en lijken voor de Noordzee goede graadmeters voor bentische voedselbeschikbaarheid te zijn.
- De temporele groeiverschillen kunnen aanwijzingen leveren over veranderingen die gelijktijdig plaats vinden in wijd uit elkaar gelegen zeegebieden en kunnen daarbij aanwijzingen geven voor de onderliggende grootschalige processen. Dit onderwerp werd gedeeltelijk behandeld in hoofdstuk 7. Inzicht in de aard van de groeiverschillen maakt het ook mogelijk de effecten van menselijk handelen af te wegen t.o.v. natuurlijke invloeden.
- De veranderingen in de uiterlijke verschijningsvorm van een increment kan ook informatie geven over de frequentie waarin fysische verstoringen van het bentische milieu optreden, bijvoorbeeld bodemvisserij (hoofdstuk 6).

- De chemische samenstelling van ieder increment is een andere waardevolle bron van informatie. Hoewel de isotoop samenstelling van de incrementen werd gebruikt om de jaarlijkse vorming daarvan vast te stellen kan het omgekeerde ook. De chemische samenstelling van elk increment kan gebruikt worden voor het samenstellen van tijdseries van bijvoorbeeld vervuilende stoffen. Met name moderne bemonsterings- en (nucleaire) analysetechnieken zoals PIXE (Proton Induced X-ray Emittance) en INAA (Induced Neutron Activation Analyses) kunnen tot een zeer hoge, zelfs seizoenale, resolutie leiden (Nyström, 1995).

In dit proefschrift zijn slechts een aantal van de bovengenoemde aspecten aangestipt. Deze illustreren voldoende dat *Arctica islandica* met zijn jaarlijkse groeilijnen en groeiincrementen een volwaardig indicatororganisme is, waarmee milieuveranderingen retrospectief bestudeerd kunnen worden.

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