Malacochronology, the application of dendrochronological methods on marine bivalve (shell) growth

R. Witbaard[1], E, Jansma[2,3] & U. Sass-Klaassen[3,4].

1. Royal Netherlands Institute for Sea Research, PO Box 59 1790 AB den Burg, Texel, The Netherlands;
e-mail: Witbaard@nioz.nl
2. National Service for Archaeological Heritage Management (ROB), PO BOX 1600 3800 BP, Amersfoort, The Netherlands;
3. Netherlands Centre for Dendrochronology (RING), PO BOX 1600 3600 BP, Amersfoort, The Netherlands;
4. Wageningen University, Environmental Sciences, Forest Ecology and Forest Management PO Box 342 6700 AH Wageningen, The Netherlands

Introduction

In the temperate marine environment the seasonality in water temperature and primary production results in a strong seasonality of biological processes, both in the water column and at the sea floor. For bivalves living at the seafloor and growing by accretion of calcium carbonate, this results in the deposition of annual growth layers (Jones, 1980; Witbaard *et al.*, 1994) comparable to those in trees (Fig. 1). Like for trees, it is assumed that environmental conditions during the period of shell growth manifest themselves in the deposited material, as a result of which both the compositional differences and the ring width itself contain information.

While for short-lived species the growth lines are often visible on the external shell surface, for long lived species the growth lines are - especially during the later phases of life - too narrow to be recognised on the external shell surface. By application of the acetate peel method (Kennish et al; 1980, Ropes, 1985) this problem can be overcome.

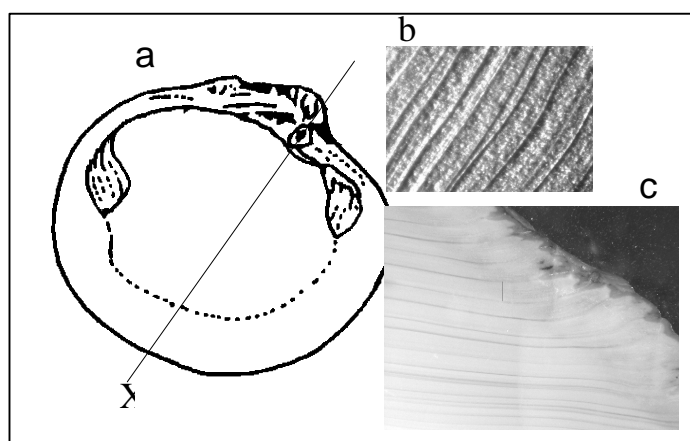*Figure 1: Schematic drawing of Arctica islandica. Line X indicates direction of sectioning and line of maximum growth. Photo insets show internal growth lines in the etched hinge section (b) as well as in a polished section of the valve (c).*

Application of this method to a number of bivalve species revealed that many of them have a longevity which surpasses earlier ideas (Heller, 1990). Various species can reach ages of decades rather than years. With maximum ages exceeding 200 years, *Arctica islandica* is the most illustrative and best known example (Jones, 1983). This approximately 10 cm high bivalve has a widespread distribution in the shelf seas of the North Atlantic. In the North Sea it can be found north of 53°30'N. Population densities may range from 0.1/m² to over 200/m² (Witbaard & Bergman, 2003). *Arctica* is a filter feeding species, i.e. it is dependent on small organic particles which are suspended just above the seafloor and which were produced in the illuminated surface waters.

Growth experiments with *Arctica islandica* demonstrated that shell growth of this species is mainly controlled by ambient seawater temperature and food supply (Witbaard *et al.*, 1997b; Kraus *et al.*, 1992). With this in mind the growth record is supposed to reflect rather basic ecosystem properties like water temperature and productivity. For many of the sites where *Arctica* can be found, no idea on long term variations of such environmental conditions exists. A study of *Arctica*'s shell growth could thus possibly reveal long-term trends in these variables retrospectively. In this paper we report on the shell growth of *Arctica* from the northern North Sea, with the aim to explore the relationship between biological functioning and climate in this area.

Material and methods

Shells of living specimens of *Arctica islandica* were collected in the Fladen Ground (northern North Sea), which is located about 100 miles North-East of Aberdeen (Scotland) and is 100 and 150 meter deep (Basford & Eleftheriou, 1988) (Fig. 2). The area is located just South of the major water inflows of Atlantic Water into the northern North Sea (Turrell, 1992a; Turrell, 1992b).

Three batches of living *Arctica* were collected and in total 103 shells were measured and used for the construction of a chronology of annual shell growth. The specimens originated from approximately 59° 20'N 00° 30' E. and were collected by boxcorer, trawl and dredge in 1983, 1991 and 2000.

To apply the acetate-peel method, shell cross-sections (Fig. 1a) were obtained by cutting the left hand valve along the axis of maximum growth. The surface of the exposed cross section was ground and polished (Fig. 1c) before it was being etched in a weak solution of HCl. The growth banding is based on a compositional difference of organic matrix and the size of the inorganic crystals. After etching this results in a relief in which the organic-rich and or larger crystals are visible as small ridges (Fig 1b). In the next step, this surface was transferred to a sheet of acetate by using a few drops of acetone. The "imaged growth bands" obtained in this way were counted and measured by means of a microscope.
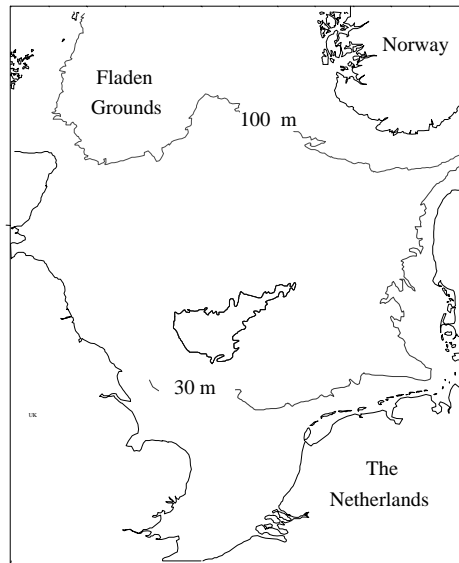
Figure 2: Location of the Fladen Grounds in the northern North Sea.

Because all specimens were caught alive, it was assumed that the outermost increment was formed in the year of sampling. By counting backwards, each measured growth increment could be assigned to a particular calendar year. For each specimen this resulted in an absolutely dated time series of 'shell-ring' widths. These time series were cross-dated with the programs COFECHA (Holmes, 1983; Grissino-Mayer, 2001) and PAST (http://www.sciem.com/main.html). The ontogenetic growth trend was removed by double detrending, using a negative exponential function in combination with a 66-year spline fit to remove the remaining low-frequency variation (Cook, 1985). For young specimens (~30 years old) we used a more flexible 15-year cubic spline to remove the ontogenetic trend. For each shell this detrending procedure resulted in an index series that for each year reflected whether growth was below or above the expected rate. From these detrended and cross-dated time series a standard chronology was constructed using the program ARSTAN (Cook, 1985) (http://www.ltrr.arizona.edu). Calibration of the standard chronology with environmental variables was done with principal component analyses and response function analyses (Fritts *et al.*, 1971; Fritts and Shashkin, 1995). We used monthly climatic data as well as monthly data on food availability, *i.e.* total phytoplankton, diatoms and copepod abundance from a sub-area enclosed by the corners at 57°30'N 02°00'E and 60°00'N 02°00'W obtained by the CPR survey (Colebrook *et al.*, 1991; SAHFOS, http://192.171.163.165/). The climatic indices tested were the North Atlantic Oscillation index (NAO) (Hurrell, 1995, (http://www.cgd.ucar.edu/ ~jhurrell/nao.html#monthly) and precipitation data for northern Scotland obtained from Jones and Conway (1997) (http://www.met-office.gov.uk/research/hadleycentre/ CR_data/Monthly/HadNSP_act.txt)
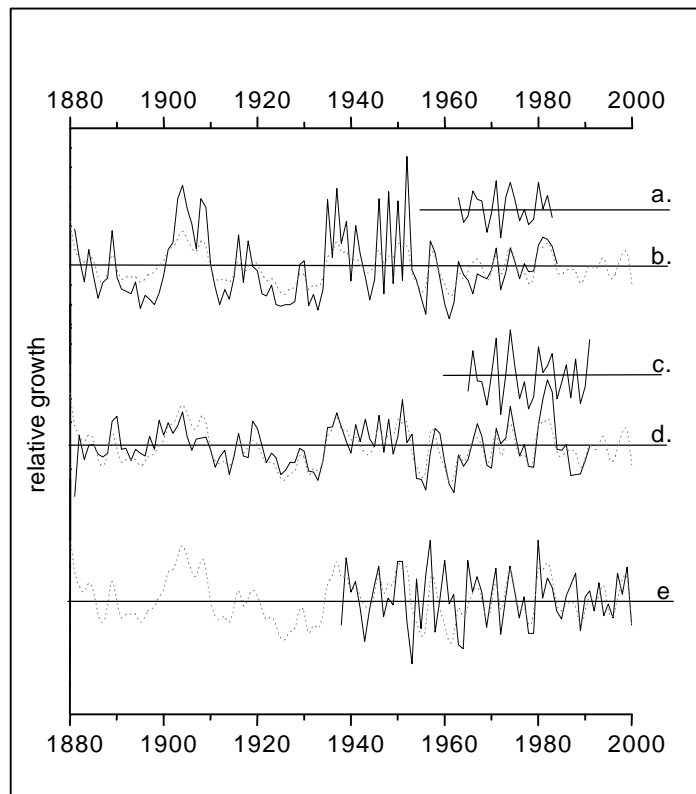
Figure 3: Chronologies of shell growth in Arctica islandica from the northern North Sea. Grey dotted line is the spline-fitted average chronology with superimposed the chronologies obtained from one of the subsamples. (a) young shells collected in 1983, (b) old shells collected in 1983, (c) young shells collected in 1991, (d) old shells collected in 1991, (e) young shells collected in 2000. Horizontal lines denote expected growth. Chronologies for young shells are displaced in upward direction for clarity.

Results

The average chronology of shell-growth variations in *Arctica islandica* is characterised by alternating periods in which growth is above or below expected growth. All different sub-samples, of both old and young shells as well as of the samples collected in the different years, show statistically similar patterns, which supports the idea that shell growth is the result of a common forcing factor (Fig. 3). Because the bottom water temperature in the area is almost constant, the attempts to explain the observed growth-rate variations focus on data indicative of food supply and food availability to the benthos community. These are the spring bloom production (diatom abundance), total algal production (phytoplankton colour) and copepod abundance, since the latter might compete for the same food source by intercepting food particles from the surface waters on their descent to the sea floor.

The response functions expressing the relationship between shell growth and the abundance of diatoms or total phytoplankton (expressed as phytoplankton colour units) explained only minor parts of the total variance in the average chronology (14% and 24%, respectively). The results, however, suggest the existence of a time lag between phytoplankton abundance and shell growth. The phytoplankton colour index of the autumn preceding growth correlated

higher with the chronology of growth rate variations than the spring phytoplankton colour values of the calendar year in which the growth increment was terminated.
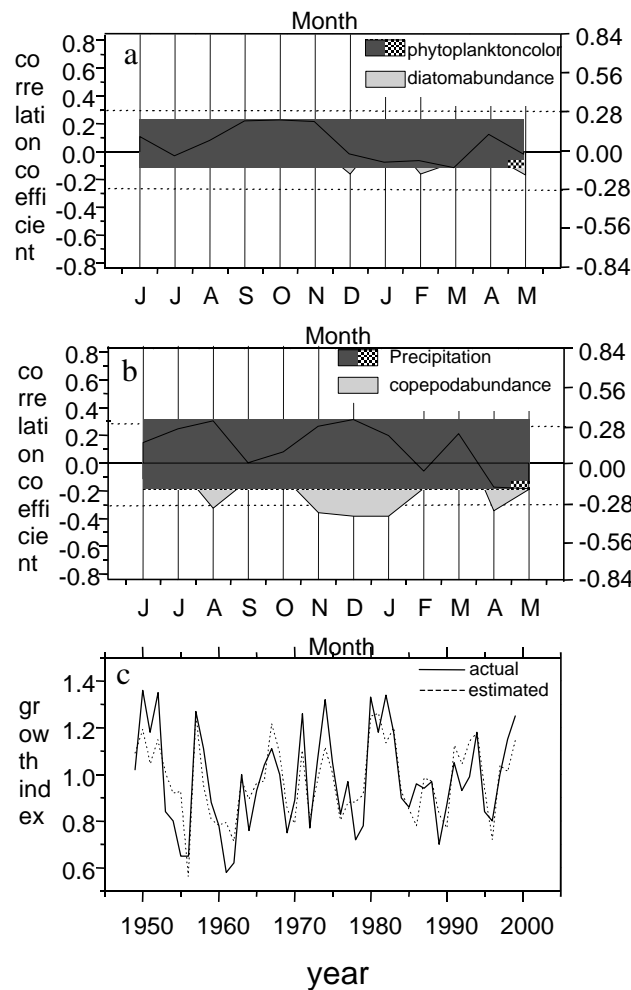

Figure 4: Lagged correlations of monthly variables and the average annual shell growth indices for the period 1949-1999. Dotted lines indicate the significance level (p<0.05). (a) Correlation with monthly average phytoplankton colour and total diatoms, (b) correlation with monthly precipitation over northern Scotland and total copepod abundance in the northern North Sea, (c) comparison of the actual shell growth rate variations and predicted variations on the basis of a response function model with copepod abundance and precipitation as predictor variables.

While the correlations between shell growth and phytoplankton data were insignificant, shell growth was significant negatively correlated with the lagged copepod abundance (Fig. 4b). The response function based on copepod abundance in the prior autumn and the following spring period could explain about 48% of the variance of the inter-annual variation in shell growth. Copepod abundance in the northern and central North Sea has been shown to be related to the NAO index (Fromentin and Planque, 1996). During the wintermonths of studied period (1949-1999) the shell growth showed a positive correlation to the NAO index altough that correlation never reached significance. Alternatively, we used the average

monthly precipitation over northern Scotland as a descriptor for more local hydrographical conditions in the Fladen Ground because it most likely reflects factors that are important in the determination of benthic food supply such as wind stress, stratification, river run-off and the start and length of the spring-bloom. We found a positive relationship between shell-growth and the amount of rainfall in the preceding winter and an negative correlation with precipitation during spring (April-May) (Fig. 4b).

The combination of copepod abundance and the precipitation over Scotland for a 12 month period explained 66% of the variance in the growth rate chronology of *Arctica* (Fig. 4c). A reduction of the number of months to the winter period exclusively, did not lead to a great loss of explained variance in the response function. The combination of precipitation and copepod abundance for the period between November and May still explains 61% of the total variance, suggesting that conditions during autumn and following spring are important for shell growth.

Discussion

With the exception of temperature, climate will affect shell growth indirectly by changing ecosystem properties like primary production, sedimentation and the length of the period in which primary production takes place. The documented inter-annual variations in bottom-water temperature in the Fladen Ground (Ellet and Blindheim, 1992) as well as the recently reported anomalies in Sea Surface Temperature (SST) for the northern North Sea (Reid *et al.*, 1998) seem to be too small to explain the observed *in situ* shell growth variations in view of the results obtained from experiments (Witbaard *et al.*, 1997b). Therefore, the most likely remaining factor to explain these growth rate differences would be the supply of food.

A significant relationship between shell growth and phytoplankton colour or diatom abundance was however absent (see also; Witbaard, 1996; Witbaard *et al.*, 1997a). Apparently there is only a weak direct link between primary production in the surface waters and shell growth 140 meters below. One possible reason could be the rapid development of a dense copepod population in early spring.

Particle-flux measurements in the Fladen Ground indeed show that in spring only small amounts (10–25%) of the primary production sink to the seafloor (Davies & Payne, 1984). Cadee (1986) even estimated that most of the primary produced material ended up in the pool of dissolved organic matter. Hence benthic food availability seems to be depressed.
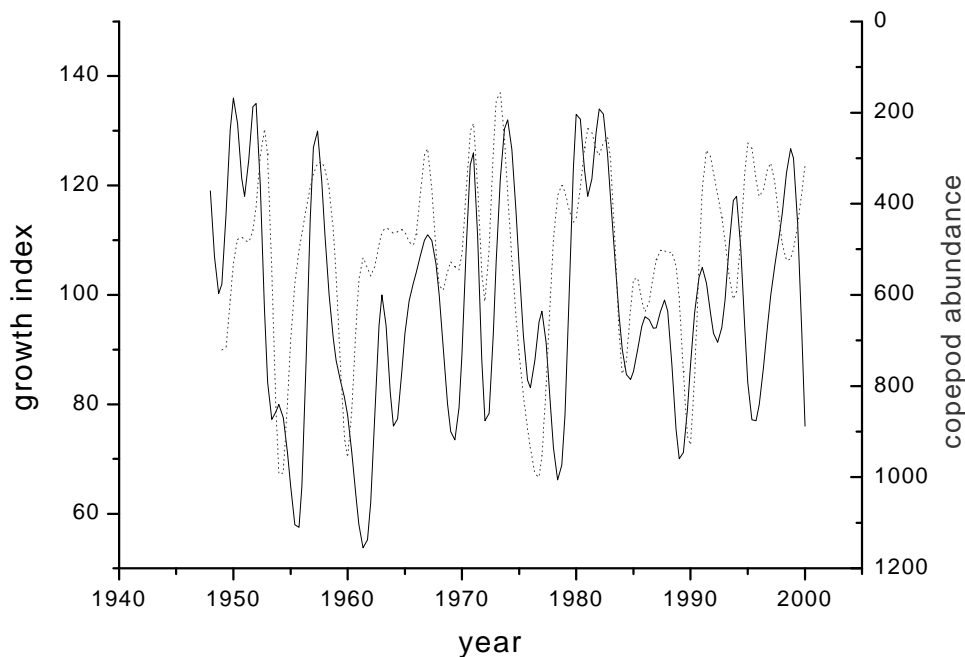
Figure 5: Observed correspondence between shell-growth indices (continue line) and 6-month lagged copepod abundance (dotted line) as obtained from the CPR data base. Copepod abundance scale (righ side) is reversed.

In the northern North Sea the downward particle flux seems to be controlled by the cold water copepod *Calanus finmarchicus.* In early spring, a seed population of this species is advected into the northern North Sea from its deep overwintering sites in the neighbouring Atlantic (Bryant *et al.*, 1998; Gallego *et al.*, 1999; Madden *et al.*, 1999). The population develops rapidly in March and peaks in April-May (Planque and Fromentin, 1996) i.e. the period of the spring bloom. This timing together with a grazing capacity of 40-90% of the daily primary production (Radach et al, 1984), not only controls the magnitude of the spring phytoplankton bloom but also the subsequent export flux towards the bottom. Therefore the observed negative correlation between shell growth and copepod abundance reflects a competition for the same food source which is depicted in Figure 6.

Weather conditions have a large influence on the advection and population development of *C. finmarchicus* in the northern North Sea (Gallego *et al.*, 1999; Harms *et al.*, 2000; Madden *et al.*, 1999). To explain the interannual variations in the abundance of *C. finmarchicus,* Fromentin and Planque (1996) summarised a possible climate-foodweb structure which explains the interannual variation in shell-growth rates of *Arctica* as well.
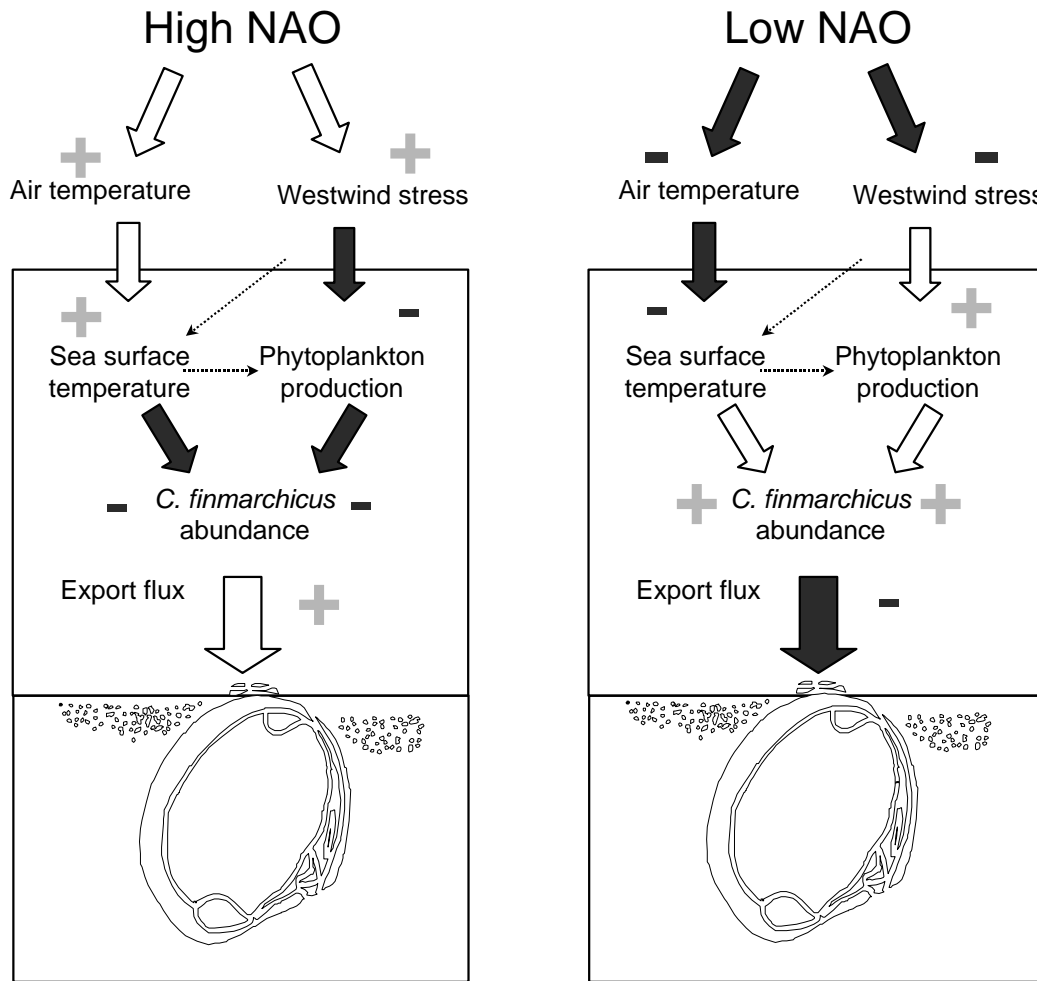
Figure 6: Graphical representation of the model as proposed by Fromentin and Planque (1996). The two extreme states of the NAO are given. "+" sign indicates a positive and "-" indicates a negative feedback to the controlling factor.

During winters with a predominant high NAO index, west-wind stress and precipitation increases over north-west Europe and Scotland. As a consequence, stratification of the water column is delayed and phytoplankton production will start late and is low (see Dickson et al, 1988 for a discussion of the mechanism). The subsequent development of the copepod population is depressed which leads to high fluxes of phytoplankton to the seafloor resulting in high shell growth rates. In winters with a low NAO index; lower temperatures, less wind and early stratification promotes the rapid development of *C. finmarchicus* populations which matches the onset of the spring bloom and therefore depresses the downward flux of phytoplankton material which ultimately results in low rates of shell growth. This is in line with our observations which show a significant positive relationship between shell growth and rainfall amounts and the NAO index. However, although precipitation rates in northern Europe strongly depend on the NAO index, thepositive relationship between the NAO index and growth record remained statistically weak. This does not exclude the NAO as

an underlying mechanism but demonstrates that local conditions have a larger impact on shell growth and modify the NAO signal to such an extent that it cannot always be recognised clearly.

Acknowledgements

References

Basford, D. & A. Eleftheriou (1988): The benthic environment of the North Sea (56° to 61°N). J. Mar. Biol. Ass. U.K. 68: 125-141

Bryant, A. D., Hainbucher, D. & M. Heath (1998): Basin-scale advection an population persitence of *Calanus finmarchicus*. Fish. Oceanogr. 7: 235-244

Cadee, G.C. (1986): Organic carbon in the water column and its sedimentation, Fladen Ground (North Sea), May 1983. Neth. J. Sea Res. 20: 347-358

Colebrook, J.M., Warner, A.J., Proctor, C.A., Hunt, H.G., Pritchard, P., John, A.W.G., Joyce, D. & R. Barnard (1991): 60 years of the continuous plankton recorder survey: a celebration. Sir Alistar Hardy foundation for Ocean Science. Plymouth: 24 p.

Cook, E.R. (1985): A time series analysis approach to tree ring standardization. Thesis of the University of Arizona: 171 p.

Davies, J.M. & R. Payne (1984): Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. Mar. Biol. 78: 315-324

Dickson, R.R., Kelly, P.M., Colebrook, J.M., Wooster, W.S. & D.H. Cushing (1988): North winds and production in the eastern North Atlantic. J. Plankton Res. 10: 151-169

Ellet, D.J. & J. Blindheim (1992): Climate and hydrogrpahic variability in the ICES area during the 1980s. ICES Mar. Sci. Symp.195 : 11-31

Fritts, H.C., Blasing, T.J., Hayden, B.P. & J.E. Kutzbach (1971): Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. J. Applied Meteor.10: 845-864

Fritts, H.C. & A.V. Shashkin (1995): Modelling tree-ring structure as related to temperature, precipitation, and day length. In: Lewes, T.E. (ed), Tree rings as indicators of ecosystem health. CRC Press London: 17-57

Fromentin, J.-M. & B. Planque (1996): Calanus and environment in the eastern North Atlantic. II. Influence fo the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser.134: 111-118

Gallego, A., Mardaljevic, J., Heath, M.R., Hainbucher, D. & D. Slagstad (1999): A model of the spring migration into the North Sea by *Calanus finmarchicus* overwintering off the Scottish continental shelf. Fish. Oceanogr. 8: 107-125

Grissino-Mayer, H.D. (2001): Evaluating cross-dating accuracy: a manual and tutorial for the computer program COFECHA. Tree-ring Res. 57: 205-221

Harms, I.H., Heath, M.R., Bryant, A.D., Backhaus, J.O. & D.A. Hainbucher (2000): Modelling the Northeast Atlantic circulation: implications for the spring invasion of shelf regions by *Calanus finmarchicus*. ICES J. Mar. Sci. 57: 1694-1707

Heller, J. (1990): Longevity in molluscs. Malacologia 31: 259-295

Holmes, R.L. (1983): Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull. 43: 69-78

Hurrell, J.W. (1995): Decadal trends in the north Atlantic Occilation: Regional temperatures and precipitation. Science 269: 676-679

Jones, D.S. (1983): Sclerochronology: Reading the record of the molluscan shell. American Scientist 71: 384-391

Jones, D.S. (1980): Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. Paleobiology 6(3): 331-340

Jones, P.D. & D. Conway (1997): Precipitation in the British Isles: an Analysis of area-average data updated to 1995. Int. J. Climatol. 17: 427-438

Kennish, M. J., Lutz, R.A. & D.C. Rhoads (1980): Preparation of acetate peels and fractured sections for observation of grwoth patterns within the bivalve shell. In Skeletal growth of aquatic organisms. Biological records of environmental change. (eds. D. C. Rhoads and R. A. Lutz), pp. 597-601. New York / London: Plenum Press.

Kraus, M.G., Beal, B.F., Chapman, S.R. & L. McMartin (1992): A comparison of growth rates in *Arctica islandica* (Linnaeus, 1767) between field and laboratory populations. *Journal of shellfish research* 11: 289-294

Madden, H., Beare, D., Heath, M.R., Fraser, J.G. & A. Gallego (1999): The spring/early summer distribution of *Calanus* spp. in the northern North Sea and adjacent waters. Fish. Oceanogr. 8: 138-152

Planque, B. & J.-M. Fromentin (1996): Calanus and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser.134: 101-109

Radach, G., Berg, J., Heinemann, B. & M. Krause (1984): On the relation of primary production to grazing during the Fladen Ground Experiment 1976 (Flex'76). In: Fasham, M.J.R., (ed). Flows of energy and material in marine ecosystems. Theory and practice. NATO conference series, Plenum Press, New York: 597-628

Reid, P.C., Planque, B. & M. Edwards (1998): Is observed variability in the long-term results of the continuous plankton recorder survey a response to climate change? Fish. Oceanogr. 7: 282-288

Ropes, J.W. (1985): Modern methods used to age oceanic bivalves. The Nautilus 99: 53-57

Turrell, W.R. (1992a): The east Shetland Atlanctic Inflow. ICES Mar. Sci. Symp 195: 127-143

Turrell, W.R. (1992b): New hypotheses concerning the circulation of the northern North Sea and its relation to North Sea fish stock recruitment. ICES J. Mar. Sci. 49: 107-123

Witbaard, R., Jenness, M.I., Van der Borg, K. & G. Ganssen (1994): Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes. Neth. J. Sea Res. 33: 91-101

Witbaard, R. (1996): Growth variation in *Arctica islandica* L. (Mollusca): a reflection of hydrography-related food supply. ICES J. Mar. Sci. 53: 891-987

Witbaard, R. & M. Bergman (2003): The distribution of *Arctica islandica* in the North Sea. What possible factors are involved? Neth. J Sea . Res. accepted.

Witbaard, R., Duineveld, G.C.A. & P.A.W.J. deWilde (1997a): A long-term growth record derived from *Arctica islandica* (Mollusca, Bivalvia) from the Fladen Ground (northern North Sea). J. Mar. Biol. Ass. U.K. 77: 801-816

Witbaard, R., Franken, R. & B. Visser (1997b): Growth of juvenile *Arctica islandica* under experimental conditions. Helgoländer meeresunters. 51: 417-431