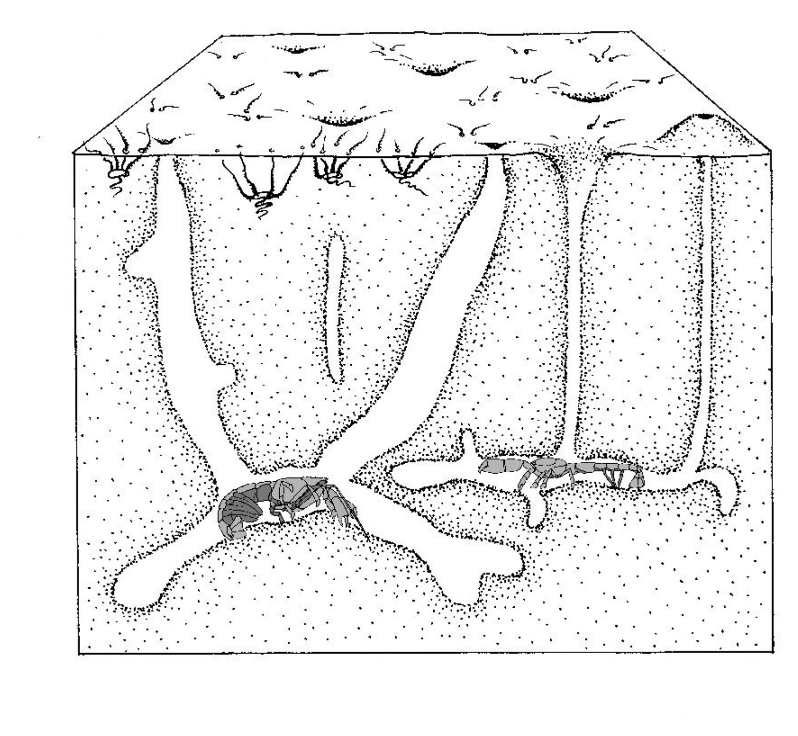
The benthic shift of the Frisian Front (Southern North Sea) ecosystem - Possible mechanisms



Teresa Amaro

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Teresa Paula Fernandes Amaro

Promotor: Prof.dr. M. Scheffer
Hoogleraar in de Aquatische Ecologie en Waterkwaliteitsbeheer,
Wageningen Universiteit

Co-promotor: Prof. Dr. Paulo Talhadas dos Santos
Hoogleraar in de Zoölogie en Antropologie, Porto Universiteit,
Portugal

Promotiecommissie: Prof .dr. J.A.J. Verreth, Wageningen Universiteit
Prof.dr. C.H.R. Heip, Rijksuniversiteit Groningen
Dr. C. J. M. Philippart, Royal Netherlands Institute for Sea Research (NIOZ), Den Burg
Prof. S. Stancyk, University of South Carolina, Columbia, USA
Dr. A. Rowden, Institute of Water & Atmospheric Research (NIWA), Wellington, New Zealand

Teresa Paula Fernandes Amaro

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– Possible mechanisms

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Contents

Part I

General Introduction

In recent years much attention has been directed to the identification and understanding of regime shifts in the ocean. Time series of fisheries catches, plankton abundance and other marine ecosystem properties indicate that ecosystems can switch abruptly from one dynamic regime to another (Scheffer, et al., 2001). The term regime shift was first used to describe the concurrent alteration between the abundance of sardines and anchovies in several parts of the world (Collie, et al., 2004). Later, the term was changed to describe abrupt changes in time of the abundance of a particular component of an ecosystem (Hare & Mantua, 2000). Such an event was proposed for the northern part of the Pacific Ocean during the mid 1970s. Here, a regime shift was described as the sudden increase of phytoplankton biomass as a consequence of a possible modification in the atmospheric circulation (Venrick, et al., 1987). According to Botsford and co-workers (1997), this resulted in a modification of the carrying capacity of the central North Pacific gyre and contributed to an increase in the abundance of fish and a decrease in the abundance of shrimps. More recently Reid and co-workers (2001), suggested that a similar shift might have occurred in the North Sea. After the mid 1980s, the pelagic ecosystem in the North Sea suffered dramatic changes observed in the phytoplankton (CPR phytoplankton colour index), zooplankton and fish (Gadoid species). So far the work done in this field has been mainly focused on the pelagic ecosystem. Especially at the North Sea, there is a strong pelagic-benthic coupling because the main food source for the benthic community is obtained through sedimentation of organic material. Therefore, benthic communites are expected to have changed along with the pelagic shifts. However, evidences for the latter are lacking due to the few studies done in this area.

The initial triggering mechanisms of regime shifts in marine ecosystems and subsequent positive feedbacks are still poorly understood. The oceanic circulation or climate can be expected to be the cause of regime shifts, but biological data are sometimes regarded as a more coherent explanation for regime shifts than the physical indices (Scheffer et al., 2001). For instance, a single change in the abundance of a key species might cause major shifts in the whole community composition (Hall et al., 1992). Fisheries are also regarded as a possible trigger of profound shifts in species abundances and composition at various trophic levels (Reid et al., 2000). As these three possible mechanisms are not mutually exclusive, it is still difficult to single out one dominant forcing and/or to predict the future evolution of marine ecosystems.

In this Thesis I investigate possible mechanisms that can be controlling the benthic ecosystem of an area located at the southern North Sea to provide a new and crucial insight in the functioning of marine ecosystems.

I first describe, in Part I, the occurrence of a benthic shift among the brittle star *A. filiformis*, the mud shrimp *Callianassa subterranea* and the macrobenthic fauna for the Frisian Front. For these purposes, several samples were collected with boxcores during a period from 1991 to 2002 and compared with the period from 1982 to 1991.

Part II contains six manuscripts. In the first of these manuscripts, the drastic decline in the *A. filiformis* population is hypothesized to be caused by a change in food supply, because *A. filiformis* is directly dependent on the vertical supply of food particles and thus primary production. However, long term data on the benthic food supply and on primary production at the Frisian Front is scarce and was not possible to obtain. One way to reconstruct whether the benthic food supply changed is to study the growth records deposited in the shells of suspension-feeding bivalves living at the

Frisian Front. Therefore, to investigate this, the widths of the internal growth bands in the chondrophore of the bivalve *Mya truncata* were analysed and assigned to calendar years. *Mya truncata* was selected because it can reach a maximum age of 40 years and because adults live deep in the sediment where they are protected from direct fishing disturbance. This study highlighted the absence of the 1987-2001 year classes in the bivalve *M. truncata* in the Southern North Sea. Comparisons with populations of these species from other areas indicate the absence of individuals <13 years of age as being atypical so it is hypothesized that infrequent recruitment might play a role for this situation. Causes for this are unknown but can be from a combination of factors. For example: (1) lack of actively reproductive adults, (2) lack of fertilization success because of low adult abundances or unbalanced sex ratios, (3) temporal/spatial mismatches in the timing of larval release and food supply (4) pre- and post-settlement mortality agents. In the second manuscript of Part II, preliminary information about the reproduction of *M. truncata* in Southern North Sea is given. Although this last study is not directly linked to resolve what actually triggered the benthic shift in the Frisian Front, it can give evidence for the reason of the shift, especially if other large long living bivalves display the same type of size distribution. The next manuscript has the objective to look for common inter-annual variations of the growth rate in the shells of three filter feeding bivalves (*Arctica islandica*, *Mya truncata* and *Chamelea gallina*) from the southeastern North Sea. To investigate this, their parallel growth trends were analysed. The second objective is to find the underlying mechanism if a parallel growth pattern is found. Environmental variables like food (phytoplankton colour), North Atlantic Oscilation (NAO) index, temperature and wind were tested.

Based on the last results, the next two manuscripts contain different hypotheses for two possible mechanisms (sediment resuspension and food competition) explaining the failure of the recovery of an adult *A. filiformis* population.

First, it is hypothesized that the increase of subsurface deposit feeder *C. subterranea* might play a role in the situation that exists now at the Frisian Front. *Callianassa subterranea* is known to construct a complex burrow consisting of several vertical shafts at a depth of up to 25 cm. It is also responsible for transporting a considerable amount of sediment from depth to the surface, being responsible for playing a significant role in modifying their environment and possibly causing a lot of resuspension by expelling sediment while creating their burrows. It is striking that this species showed an increase changing from 60 ind.m^{-2} in 1982 to 228 ind.m^{-2} in 1992 and to 319 ind.m^{-2} in 2000 whereas *A. filiformis* concomitantly decreased in the same area. Hence, the objective of this manuscript is to determine whether the increased densities of the deposit feeder *C. subterranea* in combination with the low densities of *A. filiformis* can be responsible for the change in the sediment erosion threshold and consequently for the failure of the recovery of an adult *A. filiformis* population. To test this hypothesis two experiments were performed on the effect of the changes in the abundance of *C. subterranea* and *A. filiformis* on the sediment erosion (threshold). As stated before, *C. subterranea* is likely to enhance erosion threshold of the sediment by increasing bottom roughness.

Amphiura filiformis, however, may either stabilize the sediment with its arms or destabilize it with its movements on the sediment seabed. To look for the actual role of this species on the sediment erosion threshold, another experiment was performed for when densities *A. filiformis* were high and for when they were low.

Another hypothesis for the failure of the recovery of the adult *A. filiformis* population involves food competition between *A. filiformis* and the thalassinid shrimps *Callianassa subterranea* and *Upogebia deltaura*. One method to establish whether the species belong to the same trophic level and are thus likely to compete for the same food source is by means of their stable isotope signatures i.e. $\delta^{13}C$ and $\delta^{15}N$. Carbon and nitrogen stable isotopic signatures ($\delta^{13}C$, $\delta^{15}N$) of *Amphiura filiformis*, thalassinid shrimps and of other common macro-organisms in the Frisian Front community are presented. Additionally stable isotopes in putative food sources such as sediment and suspended particulate matter were analysed and an attempt to estimate the number of trophic levels in the food chain of the Frisian Front community was also made. On the basis of the relative positions of the species of interest in the trophic chain, the likelihood of competition is discussed.

To explore whether the mechanisms mentioned above can be controlling the benthic Frisian Front ecosystem, a model was constructed and is presented at the end.

References

Botsford, L.W., Castilla, J.C. & Peterson, C.H., 1997. The management of fisheries and marine ecosystems. Science 277: 509-515.

Collie, J.S., Richardson, K. & Steele, J.H., 2004. Regime shifts: can ecological theory illuminate the mechanisms? Progress in Oceanography 60: 281-302.

Hare, S.R. & Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47: 103-145.

Reid, P.C., Borges, M.D. & Svendsen, E., 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fisheries Research 50: 163-171.

Reid, P.C., Battle, E.J.V., Batten, S.D. & Brander, K.M., 2000. Impacts of fisheries on plankton community structure. Ices Journal of Marine Science 57: 495-502.

Reid, P.C. & Edwards, M., 2001. Long term changes in the pelagos, benthos and fisheries of the North Sea. Senckenbergiana Maritima 31: 107-115.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413: 591-596.

Venrick, E.L., Mcgowan, J.A., Cayan, D.R. & Hayward, T.L., 1987. Climate and Chlorophyll-a - Long-Term Trends in the Central North Pacific-Ocean. Science 238:70-7.

Benthic shift of A*mphiura filiformis* and *Callianassa subterranea* populations in the period 1992-1997 at the Frisian Front (Southern North Sea)

by

Teresa Amaro, Gerard Duineveld

Royal Netherlands Institute for Sea Research

P.O. Box 59 1790 AB Den Burg

The Netherlands

Tel. ++ 31 222 369300

Fax ++ 31 222 319674

amaro@nioz.nl

(to be submitted)

Abstract

A possible shift in benthic dominance between the brittle star *Amphiura filiformis*, the mud shrimp *Callianassa subterranea,* as well as changes in the macrobenthic faunal community has been suggested in the Frisian Front area, southern North Sea during the period 1992-1997. To test this, several samples were collected between 1991 - 2002 and compared with samples from 1982 - 1989. A drastic decrease of the *A. filiformis* population and an increase of *C. subterranea* was observed in the southernmost locations of the Frisian Front. Moreover, analysis of the Non-metric multidimensional scale plot (MDS) also revealed a change in the entire macrobenthic faunal population of the Frisian Front.

Keywords: North Sea, Frisian Front, *Amphiura filifiormis*, *Callianassa subterranea*, Macrobenthos

Introduction

The Frisian Front is an area in the southern North Sea that has received increasing interest since work done by Creutzberg and co-workers (Creutzberg, 1985; Creutzberg et al., 1984; Creutzberg, 1983). It is positioned on the Dutch Continental Shelf at the transition between the permanently mixed waters of the Southern Bight (25 m depth) and the summer-stratified water masses of the Oyster Grounds (depth 50 m; figure 1).

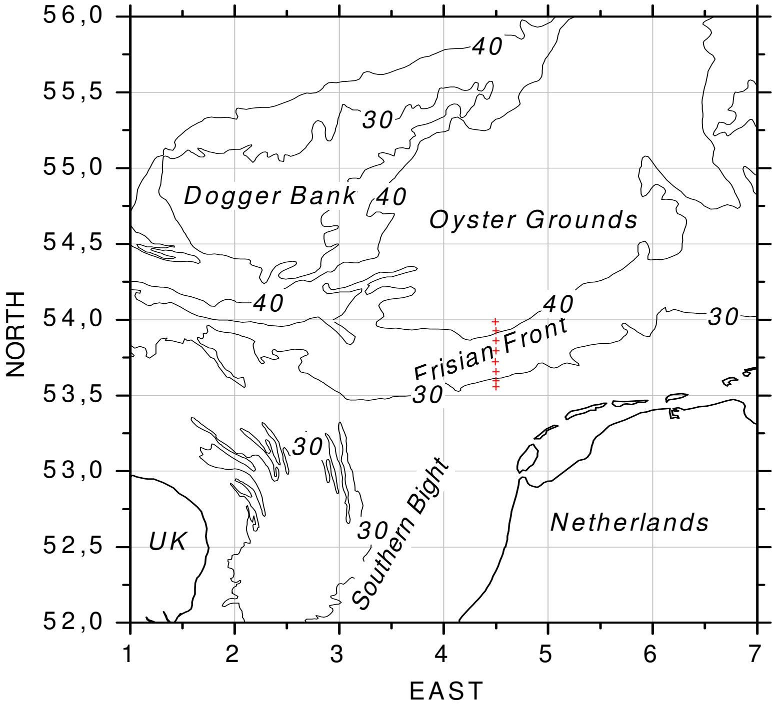

Figure 1 – map of the Southern North Sea with the main studied transect across the Frisian Front area. The stations are indicated as +.

Across a slope situated at approximately 53,50°N, the tidal current velocity drops below a critical value, resulting in the sedimentation of suspended particulate matter, both inorganic (silt) and organic (plankton) and causing a gradual south to north transition from coarser to finer sediment and mud in the northern part of the area

(Creutzberg & Postma, 1979). In spring, probably due to the import of turbid, nutrient rich waters from the British side of the Southern Bight, the water column is characterized by high chlorophyll concentrations and primary production (Creutzberg, 1985) that is deposited in the 30-40 meter depth transition zone. During the summer, lack of nutrients elsewhere in the North Sea limits the growth of algae. However, above this rich bottom zone the water can reside up to more than one month. When wind speeds are low, mineralization of organic material in the sediment causes an accumulation of nutrients in the water column, resulting in an additional algae bloom. In short, the benthic system will be fed by the pelagic input in spring and will feed the pelagic system in summer (Gee de, et al., 1991). Due to the deposition of particulate matter and fresh phytodetritus, this rich bottom area is characterized by high densities of macrobenthic species with a well defined north south zonation (Creutzberg et al., 1984). Where silt content was highest, high densities of *Amphiura filiformis* were found as well as a high benthic fauna biomass (25g AFDW. M^{-2}), of which half consisted of *A. filiformis* (Cadee, 1984; De Wilde et al., 1984). In 1984, in this area and particularly at the silty sand standard station (at 53,70°N, 4,50°E), this species reached a maximum density of 1433 ind./m^2. At that time, this population was dominated by high numbers of adults in most of the stations in the Frisian Front (Duineveld & Van Noort, 1986) while juveniles appeared to be scarce. In some northern stations, the highest numbers of juveniles occurred while adults were absent (Duineveld et al., 1987). Due to the fact that this species was known for its high numbers and stability for a long period (O'Connor et al., 1983) the study of this species ceased in this area in 1984. However as the North Sea is one of the most exploited seas in the world, the Dutch Ministry of Public Works and Transport decided to initiate a monitoring program, and macrofauna samples have been collected repeatedly since 1991 at several locations in the Dutch continental sector, including the standard station mentioned above (see references in Daan & Mulder, 2001). By looking at the results from this monitoring program and particularly from the standard station, a benthic shift in the macrobenthos was suggested, especially between the brittle star *A. filiformis* and the mud shrimp *Callianassa subterranea*. The present study had the objective of documenting the possible changes between the past and the present distributions and population structure of *A. filiformis* and *C. subterranea* along a south-north transect at 4,50°E (53,33°N to 54,15°N) through the Frisian Front. Special attention was given to the standard station (53,70°N and 4,50°E) due to the extensive data sets that exist from this site. Furthermore, we tried to evaluate whether together with the changes of these two species, the entire community changed.

Material and Methods

Amphiura filiformis and C. subterranea sampling

Amphiura filiformis and *C. subterranea* were collected during several cruises of *R.V. Pelagia* in June 1999, September 2000 and December 2001 and 2002 along the 1982 transect located across the Frisian Front (Figure 1). All samples were collected through a process of box coring (area= 0,068m^2 per boxcore) washed on board over a 1 mm sieve after which all visible *A. filiformis* and *C. subterranea* were counted and preserved in a buffered solution of 6% formaldehyde. To sample juvenile *A. filiformis*, the material passing through the sieve was also collected, preserved in a buffered solution of 6% formaldehyde, and sorted and counted in the lab (Duineveld & Van Noort, 1986). In 1999 and 2000, 4 boxcores were collected per station, while in 2001 and 2002 only three boxcores were collected. The densities of *A. filiformis* and *C. subterranea* were determined in each sample, and extrapolated to number.m^{-2}. The disc size of *A. filiformis* and the carapace length of *C. subterranea* were measured to the nearest 0,1 mm with an ocular binocular. The disc size was defined as the distance between alternating radial shields (Duineveld et al, 1987). *Amphiura filiformis* and *C. subterranea* densities from 1991 to 1994 were acquired from the monitoring program samples taken in early May at 53,70°N using the same methodology as explained above. *Amphiura filiformis* data before 1991 were taken partly from Duineveld et al. (1986), supplemented with unpublished data from the same author. From 1992 - 1998, all the samples were taken in May. In the year 1997, only one boxcore was taken but with a bigger area (area= 0,25m^2). The data from these years were extracted from reports done for the monitoring program mentioned in the introduction. In 1999 four boxcores with an area of 0,068m^2 each were pooled together in the same sieve.

Macrofauna Sampling

To determine whether there was a change in the macrobenthic fauna community across the Frisian Front transect between 1982 and 1999, two cruises were taken on the same transect following the same methodology (figure 1). At each station, 4 boxcores with an area of 0,068m^2 each were taken and pooled in the same sieve. They were washed through a 1mm sieve on board and preserved in a buffer solution of 6% formaldehyde. In the lab, all species were enumerated and identified to species, and densities were extrapoled to number.m^{-2}. Species composition along this transect from 1982 and 1999 was compared (see below).

Multivariate analysis

The macrofauna community comparison was analyzed with PRIMER v.5 – Plymouth Routines in Multivariate Ecological Research (Clarke & Warwick, 2001). Changes in the community composition of the Frisian Front between 1982 and 1999 have been visualized from non metric multidimensional scaling (MDS) plots based on triangular matrices of Bray Curtis similarities using 2nd root transformed species abundance data (Clarke & Warwick, 2001). Its purpose is to represent the samples as points such that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples. These kinds of plots have no axis scales. The results give a stress value that indicates how the points are placed in two dimensions in such a way as to satisfy the similarity raking exactly (Clarke & Warwick, 2001). A statistic, R, is also determined as a measure of the degree of separation between the years (1982 and 1999). This R-value ranges between –1 and 1 and is around zero if the null hypothesis of no differences in community composition is true. A value of R between zero and one indicates some degree of discrimination. The analysis of similarities hypothesis (1-way ANOSIM test) was applied to the Bray Curtis similarity matrix to look for differences between the stations in different years (defined a priori), using permutation/randomisation methods on this matrix. To learn how much each species contributes to the average sample dissimilarity between stations, a SIMPER test (similarity percentage) was applied to the data (Clarke & Warwick, 2001).

Results

The mean densities of the brittle star *A. filiformis* across the Frisian Front transect in (figure 1) in 1982 (Duineveld & Van Noort, 1986), 1999 and 2002 are plotted in Figure 2.

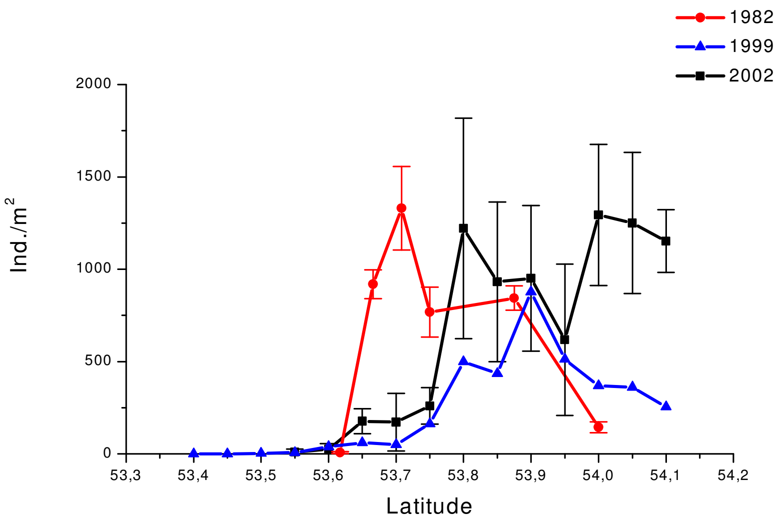

Figure 2 – Average densities of *A. filiformis* along the main transect in 1982, 1999 and 2002. Standard deviation is indicated by lines.

In 1982, *A. filiformis* appeared to have one main peak in densities at 53,70°N, with a mean of 1330 (stdev=226,2) individuals.m^{-2}. In 1999, the population was lower than 1982. Also, the maximum was located more to the north than in 1982, at 53,90°N with 877 individuals.m^{-2}and densities were low for the other locations in the studied transect. In 2002, the population increased, mostly in the northern parts of the Frisian Front transect, with a maximum of 1294 (stdev=382,3) individuals.m^{-2}, at 54,00°N.

Mean densities of *A. filiformis* at the standard station between 1982 to 2002 are plotted in figure 3.

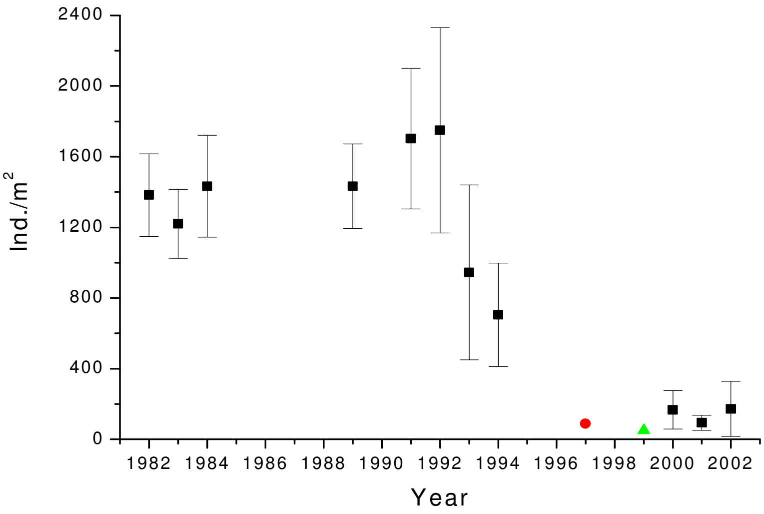

Figure 3 - Average densities of *A. filiformis* at the standard monitoring station (4,50°N and 53,70°N) between 1982 - 2002. Standard deviation is indicated by lines.

Legend: ■ 4 boxcores done separated, ● 1 big boxcore ▲ 4 boxcores together (check Material & Methods).

This figure shows that after a 10-year period with maximum densities around 1750 (stdev=581,6) individuals.m^{-2}, numbers declined from 1992 to 1997, and have remained constant at about 100 individuals.m^{-2} since. The size frequency distributions of *A. filiformis* along our study transect for 1982 and 2002 are plotted in figures 4 and 5, respectively. Figure 4 shows that in 1982 the four southernmost stations were dominated by large adults with disc sizes between 4 and 6,5 mm. Individuals with disc sizes smaller than 3 mm were scarce in all stations, except in the south of the Frisian Front, at 53,65°N, (a small peak between 1 and 2 mm) and at the north at 54,15°N (small peaks between 0,6 to 4 mm).

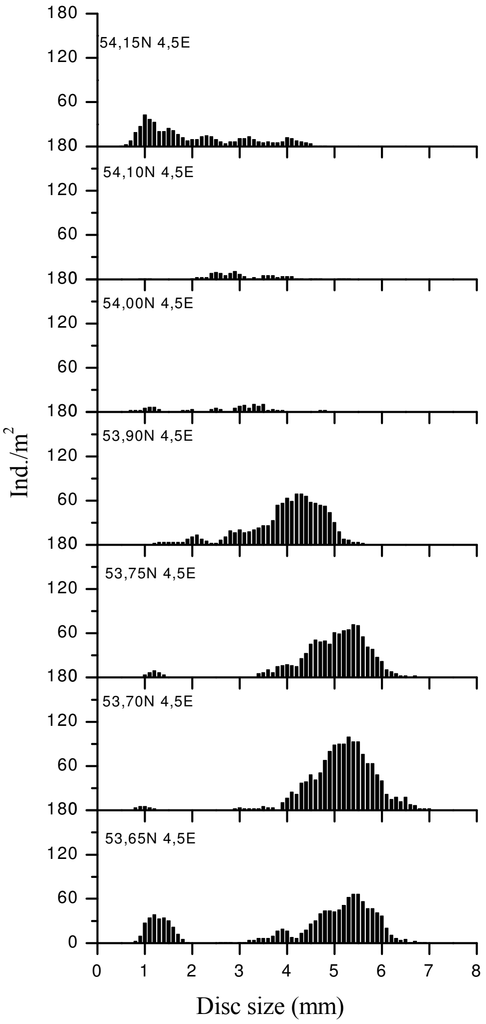

Figure 4 –Size frequency of *A. filiformis* (disc diameter, mm) along the main transect in September 1982.

All samples from 2002 were dominated by smaller individuals than in 1982 (figure 5). Three types of distribution patterns can be seen. In the south, the population seems to be dominated by a few adults; from 53,80°N to 53,90°N, all sizes between 2-6 mm are present; and to the north, from 53,95°N to 54,10°N, the populations are dominated by individuals between 1 - 3 mm.

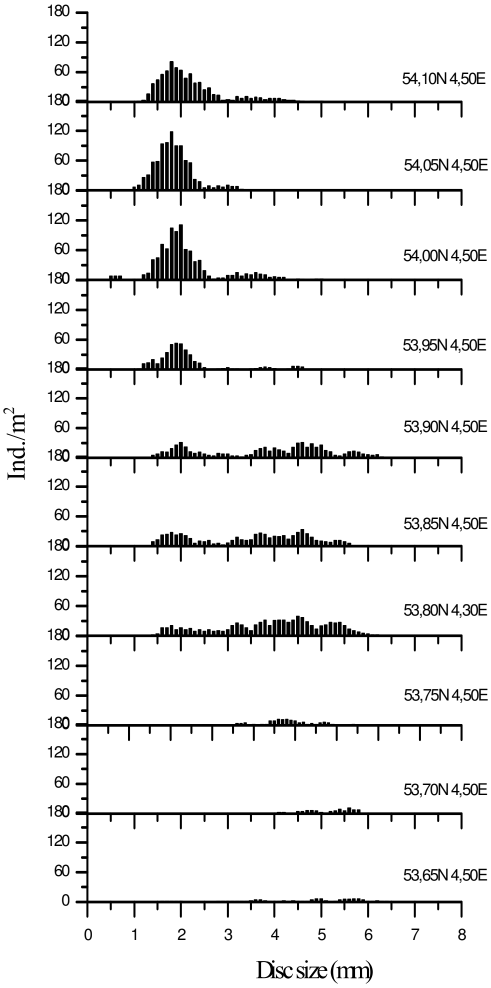

Figure 5 – Size frequency of *A. filiformis* (disc diameter, mm) along the main transect in December 2002.

Callianassa subterranea populations have also changed in the area. Figure 6 shows the mean densities of this species along the main transect for the years 1982, 1999 and 2002. In 1982, densities of *C. subterranea* were rather low along the entire transect, reaching a maximum of 62,4 (stdev=5,9) individuals.m^{-2} at 53,65°N. In 1999, the densities were up to 4 times higher than in 1982. Around the area located between the stations at 53,65°N and 53,70°N, the population reached its maximum with a mean of 176,8 individuals.m^{-2}. In 2002, *C. subterranea* densities were high again but only in the more northern areas like 53,80°N, 53,90°N and 53,95°N. Densities of *C. subterranea* at the standard station (53,70^{o}N - figure 7) showed an increase from 60 (stdev=25,2) individuals.m^{-2} in 1982, to 228 (stdev=86,7) individuals.m^{-2} in 1992, then, decreased to 160 (stdev=16) individuals.m^{-2} in 1994.

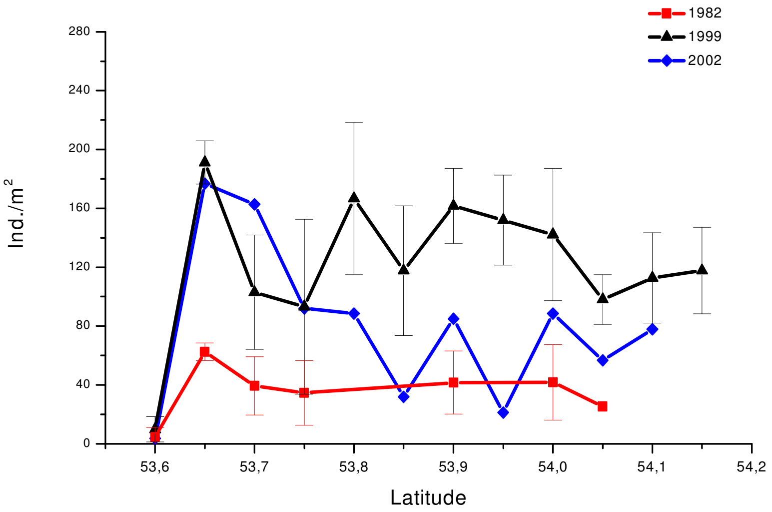

Figure 6 – Average densities of *C. subterranea* along the main transect in 1982, 1999 and 2002. Standard deviation is indicated by lines.

No data were collected between 1994 and 1996, but a high peak in density occurred in 1997, with 280 individuals.m$^{-2.}$ Another peak occurred in 2000 with the highest densities ever registered at 319 (stdev=69,3) individuals.m^{-2}. In 2001 and 2002 the densities were again lower in the entire area, with a maximum of 102 (stdev=38,9) individuals.m^{-2}.

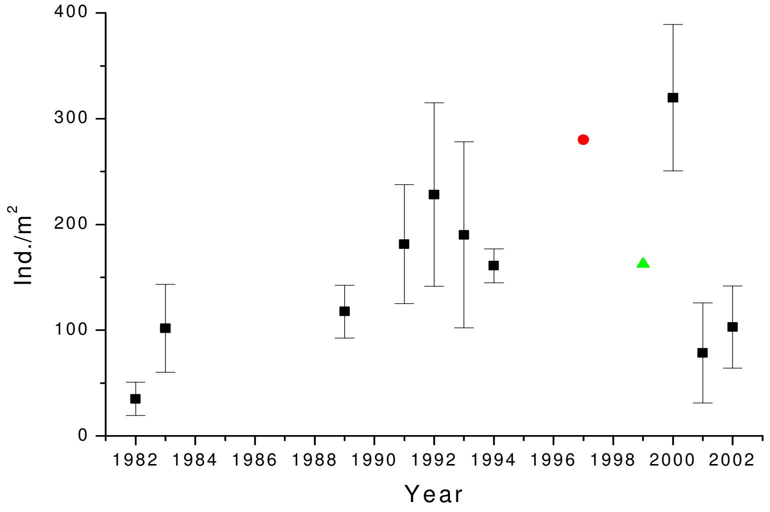

Figure 7 - Average densities of *C. subterranea* at the standard monitoring station (4,50°N and 53,70°N) since 1982 to 2002. Standard deviation is indicated by lines.

Legend: ■ 4 boxcores done separated, ● 1 big boxcore ▲ 4 boxcores together (check Material & Methods).

Concerning the population structure, the carapace length frequency distributions of this species were plotted for the year 1982 and 2000 (figures 8 and 9), since these years are from the same month (September).

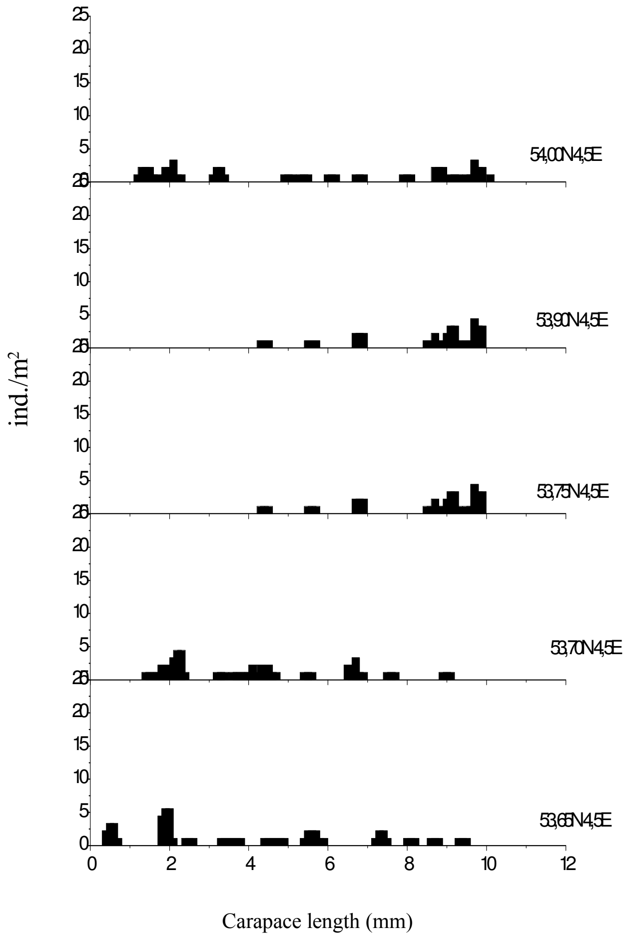

Figure 8 – Size frequency distribution plot (mm) of *C. subterranea* along the main studied transect in September 1982.

In September 1982, individuals with carapace lengths larger than 10 mm were absent at all the stations studied. Individuals smaller than 4 mm were absent in stations located at 53,75°N and 53,90°N. The stations 53,65°N and 53,70°N the individuals were between 0,4 and 9,5 mm in caparace length. In September 2000, there were no specimens larger than 12 mm and at the stations located at 53,65°N and 53,70°N individuals smaller than 2 mm were absent. At 53,90°N, 53,85°N and at 53,75°N all individuals were smaller than 6 mm. For the rest of the stations, individuals were distributed along all size classes.

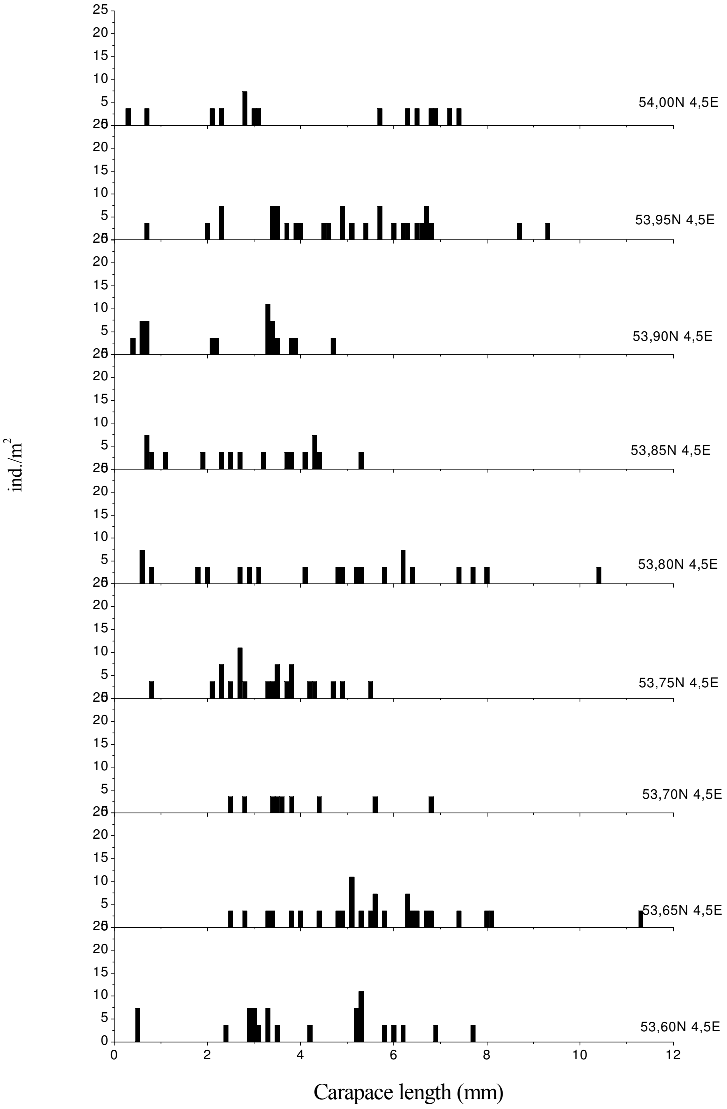

Figure 9 - Size frequency distribution plot (mm) of *C. subterranea* along the main studied transect in September 2000.

Macrofauna community of the Frisian Front studied transect

The non-metric multidimensional scale plot (Figure 10) shows a change in the community composition between 1982 and 1999. The analysis of similarity indicates that there are differences between the years with a global R value of 0,442 and a significance level of 0,001. Therefore, the null hypothesis (H_0=there are no differences in community composition) is rejected. The MDS stress is 0,09, which corresponds to a good ordination with no real prospect of a misleading interpretation (Clarke & Warwick, 2001).

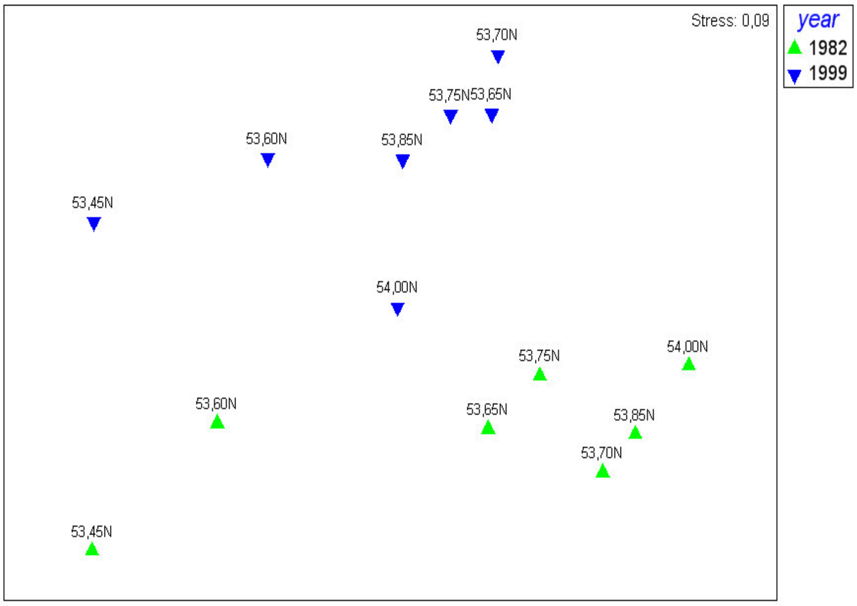

Figure 10 – Non-metric multidimensional scale plot (MDS) of the macrofauna assemblages on the main transect of the Frisian Front between 1982 and 1999. The symbols are based on the averaged abundance for each species overall the 7 stations, and then subjected to 2nd root transformation prior calculation of Bray-Curtis similarities. MDS stress=0,09.

To know which station(s) contributed the most to this change in community composition, a SIMPER test was performed. Table 1 represents the average percent dissimilarity between 1982 and 1999 at each station sampled. Stations located at 53,70N (the standard station) and 53,85°N changed the most in macrobenthic fauna composition, with 72,29 % and 72,02 % of dissimilarity respectively. Changes are smallest at the station 53,65°N; with 58,13% dissimilarity. The species *Scalibregma inflatum*, *Mysella bidentata* and *A. filiformis* contributed most to this change at 53,70°N and *Lanice conchilega*, *S. inflatum* and *A. filifiormis* were the species that contributed most at 53,85°N .

Table 1 – Average percent dissimilarity per station between 1982 and 1999 in the Frisian Front transect. The average percent that the main species contribute for the determination of the percent dissimilarity is also shown.

Station	Average % dissimilarity	Species	% dissimilarity
53,43 N	67,02	Spio filicornis Spiophanes bombyx	14,25 10,53
53,60 N	63,53	Scalibregma inflatum Lanice conchilega NEMERTEA	11,6 9,5 5,6
53,65 N	58,13	Scalibregma inflatum Mysela bidentada Amphiura filiformis	25,71 13,78 6,91
53,70 N	72,29	Scalibregma inflatum Mysela bidentada Amphiura filiformis	16,46 14,89 11,94
53,75 N	59,5	Scalibregma inflatum Amphiura filiformis Mysela bidentada	17,58 5,96 5,27
53,85 N	72,05	Lanice conchilega Scalibregma inflatum Amphiura filiformis	17,8 8,28 5,31
54,00 N	65,93	Lanice conchilega AMPHIPODA	12,52 5,67

Discussion

The main aim of this study is to evaluate the possible shift between not only *A. filiformis* and *C. subterranea*, but also the entire macrobenthic fauna composition of the Frisian Front in the Southern North Sea. *Amphiura filiformis* has decreased in abundance in the most southern areas of the Frisian Front and especially at the standard permanent station (53,70^{o}N). There, *A. filiformis* maintained population levels above 1000 individuals.m^{-2} between 1982-1992 (fig. 3), and most individuals were adults (fig. 4). After these 10 years of high densities, the population decreased in the southern stations (see figure 2), and currently remains constant at about 100 individuals per m^2. At the northern stations of the Frisian Front transect, *A. filiformis* seemed to have increased to high densities, suggesting a moving of the population to the north. However, juveniles dominate that population, and somehow are not able to survive (see figure 5). High densities of *A. filiformis* are known to be common in the NE Atlantic

Ocean and the North Sea. These aggregations have annual densities and population structures which vary very little from year to year. In Galway Bay, for example, the *A. filiformis* population was described as abundant and stable for at least 20 years. Adults accounted for 95% of the population and the annual recruits were found in low numbers (O'Connor et al., 1983). According to these authors, little could be said about the establishment of these high densities. Duineveld et al. (1987), however, when studying the *A. filiformis* population in the North Sea, suggested that this stability of high adult numbers could be explained by a long life span of *A. filiformis* (~20 years) (Muus, 1981) as a consequence of the older individuals, that are deeply buried in the sediment, being inaccessible to predators. This statement is supported by the constant small numbers of juveniles available to replace the adults. According to Muus (1981) & Duineveld & Van Noort (1986) the absence of the juveniles in the dense *A. filiformis* population and the high numbers of juveniles co-occurring with low numbers of adults is due to a possible interaction between adults and juveniles. Evidence for negative interactions between adults and juveniles in macrobenthic animals has been reported by David et al. (1997) Andreâ & Rosenberg (1991), Petersen (1982), Wodin (1976).

There are several hypotheses that can explain the drastic decline of the *A. filiformis* population in the southern part of the Frisian Front, especially at the standard station, including, lack of larval availability, a lack of food supply (see Part II) and predation (Duineveld et al., 1987). The two first factors, larval availability, and food supply can be related to changes in climatic conditions, such as wind and temperature. On the other hand, a change in sediment conditions can be another possible reason. The area of the standard station was characterized as the area with the highest level of organic carbon in the sediment due to the deposition and accumulation of fine material (Creutzberg, 1985). Benthic studies in the North Sea have shown that *A. filiformis* is a common inhabitant of these type of areas (Duineveld & Van Noort, 1986; Kingston & Rachor, 1982; Buchanan, 1963). The spatial pattern in the sediment composition was, however, quite similar to that found in the preceding years. The same holds both for median grain size as for silt contents of the sediments (Daan & Mulder, 2001). Given the stability of the population structure (at least 10 years), densities and low levels of juveniles, we can also speculate that this population could started to die off and the juveniles present in the area were not able to restore the population fast enough. In addition, anthropogenic causes, such as fishing gear could also have caused damage to the bottom fauna, especially to fragile species such as *A. filiformis*, which live within the penetration depth of a beam trawl. Nevertheless, the decrease in abundance of *A. filiformis* from ~1750 individuals.m^{-2} to ~100 individuals.m^{-2} took place over a period of 5 years (1992-1997). The Frisian Front has been fished for many years without a similar effect on *A. filiformis* population and this makes it an unlikely reason for the observed shift.

Conversely, *Callianassa subterranea* increased in abundance along the entire Frisian Front transect until 2000, especially in the southernmost locations. For example, at the standard station, this species went from about 40 individuals.m^{-2} in 1982 to 319 individuals.m^{-2} in 2000. In 2001 and 2002, however, densities decreased along the entire transect, to a maximum of 102 individuals.m^{-2}. We do not think this decrease is real, because samples were collected in late December for both years. Rowden et al. (1998) observed that *C. subterranea* burrow much deeper in cold months, and sampling methods will not reach them. Concerning the population structure, we observed no major changes at all sites between 1982 and 2000. In both years, the size-frequency distributions showed adults and juveniles in most of the stations studied. These results are supported by Rowden & Jones (1994) for the North Sea and are also found in other callianassids (Berkenbusch & Rowden, 1998; Berkenbusch, 2000).

The results from the MDS plot (figure 10) also indicate a change in the macrofauna community composition between 1982 and 1999 along the Frisian Front transect. This change was most profound at two main stations, 53,70N and 53,85N. Although the abundance of some species changed more than others, it seems that the entire community has changed. Changes in macrobenthic fauna communities have been intensively studied in the past and were considered a common event for several coastal and nearshore European regions Kroncke et al. (1998); Josefson et al. (1993); Rees & Eleftheriou (1989). Josefson et al. (1993) for example, suggested a transition in benthic community structure at two sites, one in the western and the other on the eastern part of the North Sea, in the late 1970s and early 1980’s. Kroncke, (1992) and Kroncke et al., (1998) also reported changes in the community densities in the Dogger Bank and in the East Frisian barrier islands located at the southern part of the North sea. The main factors responsible for changes in communities are often discussed in relation to environmental effects such temperature (Beukema, 1992; Ziegelmeier, 1970), anthropogenic impacts like eutrophication (Rosenberg et al., 1987) and fisheries (De Groot & Lindeboom, 1994). In the Frisian Front, the reason for the sudden change in the macrobenthic fauna community, as well as the decrease of *A. filiformis* and the increase of *C. subterranea* are still unexplainable. The reason for this change could have acted on the macrobenthic fauna community as a whole benefiting some species like *C. subterranea* and harming others like *A. filiformis*. Or, the shift from high to low densities in the *A. filiformis* population could have induced a change in the entire macrobenthic fauna community, implying that the *A. filiformis* population was crucial for maintaining the organization and diversity of the entire community. O’ Connor et al. (1983) also suggested that high densities aggregations of *A. filiformis* in Galway Bay, may control the overall community. On the other hand, *C. subterranea* could have also modified the community structure when its densities sudden increase. Berkenbusch et al. (2000), observed a change in space and time in the benthic community composition between sites of low and high *C. filholi* density. Posey (1986) also observed densities of several common macrofaunal species decreasing within a dense ghost shrimp bed in comparison to near areas of low shrimp density. Thus, it is possible from these statements to conclude that ghost shrimps like *C. subterranea* can change macrofauna composition in small areas.

In view of the generation time and growth rates of these brittle stars, the five years since the regime shift should have offered sufficient time for the brittle star populations to recover, but they have not. The persistence of the new community therefore suggests that there is a stabilizing mechanism that maintains the *C. subterranea* dominated situation and prevents *A. filiformis* from recovering to the original densities. To reveal this mechanism, we have to try to identify first the factors controlling the observed responses in the macrobenthic community. An understanding of the mechanism linking forcing and responding variables is needed in order to answer these questions.

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References

Andreâ C, Rosenberg R, 1991. Adult-larval interactions in the suspension-feeder bivalves *Cerastoderma edule* and *Mya arenaria* L. Mar Ecol Prog Ser 71: 227-234.

Berkenbusch, K., Rowden, A., 1998. Population dynamics of the burrowing ghost shrimp *Callianassa filholi* on an intertidal sandflat in New Zealand. Ophelia 49: 55-69.

Berkenbusch, K., Rowden, A. & Probert, P., 2000a. Temporal and spatial variation in macrofauna community composition imposed by ghost shrimp *Callianassa filholi* bioturbation. Mar Ecol Prog Ser 192: 249-257.

Berkenbusch, K., 2000b. Latitudinal variation in the reproductive biology of the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea). Mar Biol 136: 497-504.

Beukema, J., 1992. Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. Neth. J. Sea Res. 30: 73-79.

Buchanan J., Moore J., 1986. A broad review of variability and persistence in the Northumberland benthic fauna - 1971-85. J. Mar. Biol. Ass. U.K. 66: 641-657.

Cadee, G., 1984. Macrobenthos and macrobenthic remains on the Oyster Ground, North Sea. Neth. J Sea Res. 18 (1/2): 160-178.

Clarke, K., Warwick, R, 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar Ecol Prog Ser 216: 265-278.

Creutzberg, F., Postma, H., 1979. An experimental approach to the distribution of mud in the southern North Sea. Neth. J. Sea Res. 13 (1): 99-116.

Creutzberg, F., 1983. Biological activity in an area with a tidally-induced front. ICES C.M. 1983/L:4.

Creutzberg, F., Wapenaar, P., Duineveld, G., Lopez, N., 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. Rapp. P.-v. Reun. Cons. Int. Explor. Me 183: 101-110.

Creutzberg, F., 1985. A persistent chlorophyll a maximum coinciding with an enriched benthic zone. In: Gibbs, P.E. (Ed.). Proceedings of the 19th European Marine Biology Symposium Cambridge Univ. Press, 97-108 pp.

Daan R, Mulder M, 2001. The macrobenthic fauna in the Dutch sector of the North Sea in 2000 and a comparison with previous data. NIOZ-Rapport 2001-2, 93 pp.

David, P., Berthou, P., Noel, P. & Jarne, P.1997. Patchy recruitment patterns in marine invertebrates: a spatial test of the density-dependent hypothesis in the bivalve *Spisula ovalis*. Oecologia 111(3): 331-340.

De Groot, S., Lindeboom, H., 1994. IMPACT I - Environmental impact of bottom gears on benthic fauna in relation to natural resource management and protection of the North Sea. Netherlands Institute for Sea Research/Netherlands Institute for Fisheries Research, Den Burg, IJmuiden.

De Wilde, P., Berghuis, E.; Kok, A, 1984. Structure and energy demand of the benthic community of the Oyster Ground, Central North Sea. Neth. J. Sea Res. 18 (1-2): 143-159.

Duineveld, G., Noort, G., 1986. Observations on the population dynamics of *Amphiura filiformis* (Ophiuroidea Echinodermata) in the southern North Sea and its exploitation by the dab *Limanda limanda*. Neth. J. Sea Res. 20(1): 85-94.

Duineveld, G., Kunitzer, A., Heyman, R.P., 1987. *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. Neth. J. of Sea Res. 21: 317-329.

Gee de A, Baars M., van der Veer H., 1991. De Ecologie van het Friese Front. NIOZ-Rapport 1991-2, 96 pp.

Josefson, A., Jensen, J., Aertebjerg, G., 1993. The Benthos Community Structure Anomaly in the Late 1970s and Early 1980s - a Result of a Major Food Pulse. J. of Exp. Mar. Biol. and Ecol. 172: 31-45.

Kingston, P.& Rachor, E, 1982. North Sea level bottom communities. ICES Biological Oceanography Committee Report, CM1982/L.41.

Kroncke, I., 1992. Macrofauna standing stock of the Dogger Bank. A comparision: III. 1950-54 versus 1985-87. A final summary. helg. meers. 26 (2): 137-169.

Kroncke, I., Dippner, J., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar. Ecol. Prog. Ser. 167: 25-36.

Muus, K, 1981. Density and Growth of Juvenile Amphiura-Filiformis (Ophiuroidea) in the Oresund. Ophelia 20(2): 153-168.

O'Connor, B., Bowmer, T., Grehan, A., 1983. Long-Term Assessment of the Population-Dynamics of Amphiura-Filiformis (Echinodermata, Ophiuroidea) in Galway Bay (West-Coast of Ireland). Mar. Biol. 75: 279-286.

Peterson, C., 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecol Monogr. 52: 437-475.

Posey, M., 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, Callianassa californiensis. Mar. Ecol. Prog. Ser. 31:15-22.

Roads, D. & Young, D., 1970. The influence of Deposit-feeding Organisms on Sediment Stability and Community Trophic Structure. J. Mar. Res. 28: 150-178.

Rees, H., & Eleftheriou, A., 1989. North Sea benthos: A review of field investigations into the biological effects of man's activities. J. Cons. Int Explor. Mer. 45: 284-305.

Rosenberg, R., Gray, J., Josefson, A., Pearson, T., 1987. Petersen's stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? J. Exp. Mar. Biol. Ecol. 105: 219-251.

Rowden, A., Jones, M., 1994. A contribution to the biology of the burrowing mud shrimp, *Callianassa subterranea* (Decapoda, Thalassinidae). J. Mar. Biol. Ass. 74(3): 623-635.

Rowden, A., Jago, C., Jones, S., 1998. Influence of benthic macrofauna on the geotechnical and geophysical properties of surficial sediment, North Sea. Cont. Shelf Res. 18: 1347-1363.

Ziegelmeier, E., 1970. Über Massenvorkommen verschiedener makrobenthaler Wirbelloser während der Wiederbesiedlungsphase nach Schädigungen durch 'katastrophale' Umwelteinflüsse. Helg. Wiss Meeresunters 21: 9-20.

Part II

Growth variations in the bivalve *Mya truncata* : a tool to trace changes in the Frisian Front macrofauna (southern North Sea)?

by

Teresa Amaro[1], Gerard Duineveld, Magda Bergman, Rob Witbaard

[1] corresponding author

Royal Netherlands Institute for Sea Research

P.O. Box 59

1790 AB Den Burg

The Netherlands

Tel. ++ 31 222 369300

Fax ++ 31 222 319674

amaro@nioz.nl

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Abstract

Annual monitoring of the benthic fauna living at the Frisian Front (southern North Sea) has shown a tenfold decrease of the dominant brittlestar *Amphiura filiformis* in 1993-1995. In search of evidence that this decline was caused by a change in benthic food supply, we analysed variations in the shell growth of the bivalve *Mya truncata* from the Frisian Front during the period of interest. For this purpose the widths of the internal growth bands in the chondrophore of *Mya truncata* were standardised and assigned to calendar years. Averaging the yearly band width in the period 1985-2000 among 25 individuals revealed low growth rates in 1986 and 1992. Growth of *Mya truncata* quickly recovered after 1992 while *Amphiura filiformis* densities remained at low levels. Moreover, the 1986 dip in *Mya truncata* growth had no equivalent in *Amphiura filiformis* density. We conclude that there is no direct coupling between fluctuations in density of *Amphiura filiformis* and variations in growth of *Mya truncata*. The data we collected during this study on the size and spatial distribution of *Mya truncata* are discussed in the light of plans for the protection and conservation of long-lived benthic organisms in the North Sea.

Keywords: Growth, Bivalve, North Sea benthos

Introduction

The southern North Sea belongs to the world's most exploited shelf seas. A number of activities such as the intensive beam trawl fishery, oil and gas exploitation, and river inputs form potential threats to the ecosystem health and biodiversity. Because of concern about degradation and impoverishment of the benthic ecossystem**,** the Ministry of Public Works and Transport initiated a macrobenthos monitoring program in the Dutch continental sector, which started in the early 1990s. Results of this program have been published in a series of annual reports (references in Daan and Mulder 2001).

One of the monitoring stations is situated in the Frisian Front (Fig. 1) which separates the summer-stratified watermasses in the Oyster Ground and the permanently mixed waters in the Southern Bight (Tomczak and Goedecke 1964).

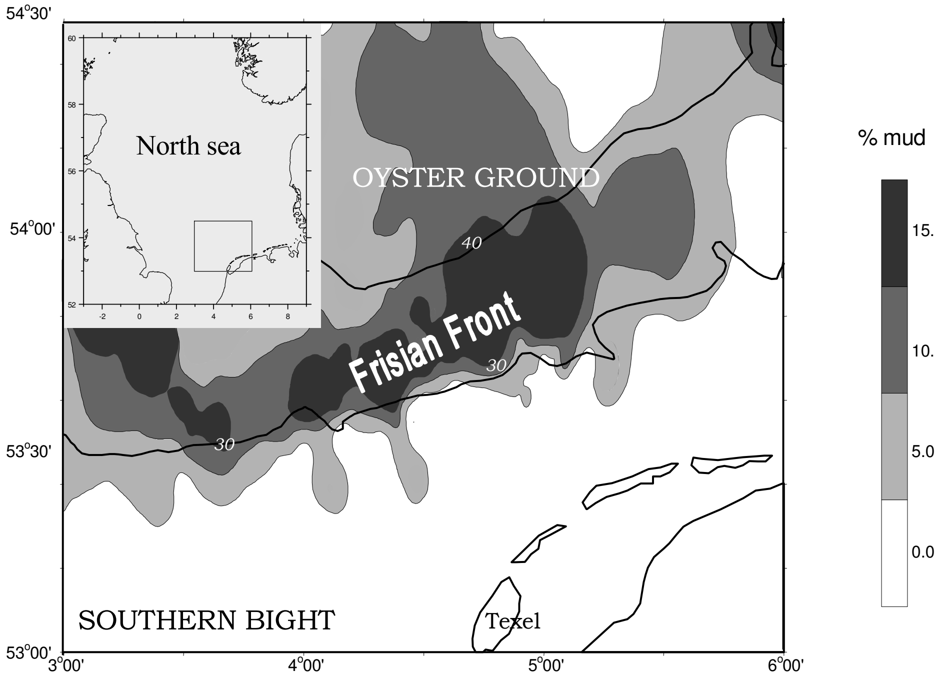

Figure 1. Map of the southern North Sea showing the 30 and 40 m isobaths, and the percentages of mud (particles < 64 μ) in grey scale. The mud patch marked Frisian Front is the area where the enriched benthic zone has been found (see text). Inset shows the study area in the North Sea.

Since the early 1980s this frontal zone has been subject of a series of studies, the earliest of which described the enrichment of benthic fauna in the vicinity of the front and the conspicuous zonation in feeding types (Creutzberg et al. 1984). Subsequent studies showed that during a large part of the year the water column over the enriched zone was characterised by elevated chlorophyll-a concentrations (Creutzberg 1985; Cramer 1991). The locally enhanced deposition of fresh phytodetritus was seen as explanation for the high biomass and high densities notably of interface-feeding organisms like the dominant brittle star *Amphiura filiformis*.

A recent comparison of the macrobenthic fauna living at the Frisian Front area between 1982 and 2002 showed that conspicuous numerical shifts have occurred among the key stone species in particular *A. filiformis* and *Callianassa subterranea*. *Amphiura filiformis* populations often can be stable for long periods (O'Connor et al. 1983). In the case of the Frisian Front population, a 10-year period with stable densities of levels above 100 ind.m^{-2} (Duineveld and Van Noort 1986) was followed by a period of decrease starting in 1993 and continuing till 1997 whereafter numbers have remained more or less constant at a level of one order of magnitude lower (details in Part I). One hypothesis for the observed shift is a change in food availability. As interface and suspension-feeder *A. filiformis* is directly dependent on vertical supply of food particles and thus primary production in contrast to subsurface feeders can sustain on more refractory carbon present in deeper sediment layers. However, we do not have long term data on the benthic food supply, neither on primary production at the Frisian Front.

One way to reconstruct whether the benthic food supply changed in the period when *A. filiformis* declined, is to study the growth records deposited in the shells of suspension-feeding bivalves living at the Frisian Front. By analogy with tree rings, various authors have used growth band patterns in skeletons of bivalves and corals to reconstruct chronological records of marine environmental changes (e.g. Lutz 1976; Brousseau 1987; Jones et al. 1989; Nakaoka 1994; Witbaard et al. 1997). We selected *Mya truncata* for this purpose because it can reach a maximum age of 40 years and because adults live deep in the sediment where they are protected from direct fishing disturbance (Hewitt et al. 1984). *Arctica islandica* which is also part of the local community has a more complicated growth band pattern because it can reach a much older age (> 100 y) and, moreover, is more exposed to damage and disturbance by beam trawl fishery (Witbaard and Klein 1994).

While analysing the growth of *M. truncata* from the Frisian Front we specifically searched for a common pattern among individuals during the period when *A. filiformis* densities drastically decreased. We discuss our findings on *M. truncata* in the light of available literature data on environmental changes in the southern North Sea during the period of interest. In addition to the growth data on *M. truncata* we report new information on its distribution in the Dutch sector.

Material & Methods

Site description

The study area is located in the southern North Sea which is characterised by a south to north increase of depth (20 – 50 m) and a decrease of maximum tidal velocity (1.8-0.7 knots). These factors contribute to a gradual south to north transition from coarse to fine sediment and to the occurrence of mud in the northern part of the area. At approximately 53,50°N, current velocities drop below a threshold value allowing (semi-) permanent deposition of mud and detritus, as well as the generation of summer stratification north of this latitude. A tidal front separates the mixed waters in the south from the summer-stratified waters in the north (Creutzberg 1984). Just north of this boundary, between the 30 m and 40 m isobaths there is a muddy zone (Frisian Front in Fig. 1) with high sediment concentrations of organic carbon (0.4 %), and algae pigments, and a high macrofauna biomass (~25g AFDW m^{-2}). This enrichment is probably related to the persistent chlorophyll-a maximum in the vicinity of the 30 m isobath (Creutzberg 1985).

Species description

Mya truncata has a wide, circumboreal distribution. It is a key species in food webs in arctic habitats (Welch et al. 1992). In Europe *M. truncata* is common along the entire coastline of the UK and Ireland down south to Biscay (Willmann 1989, Ballerstedt 2001). According to literature records, *M. truncata* does not have a special preference for sediment type. It has been found in sand, sandy mud or gravel from the lower shore down to about 70 m depth.

Sampling

Living specimens of *M. truncata* (n=96) were collected between June and December 2000 at the Frisian Front in a small area north of the 30 m isobath in the vicinity of position 53,80°N and 4,50°E. For collection we used the Triple-D dredge (Bergman and van Santbrink 1994) because the abundance of *M. truncata* is too low to allow efficient sampling with either boxcorer or van Veen grab. The Triple-D had a net with a mesh size of 1.4 cm (stretched), and its digging depth was 18 cm. The length of the hauls was 80 m, which is equivalent to a total surface of 16 m^2. Bivalves with a length > 10 mm are retained by the dredge. Intact specimens, damaged ones as well as cut-off siphons were counted for density estimates. A total of 25 intact shells from this collection were selected for age and growth analysis. These specimens were without any shell damage or visible growth disruption in the valve or chondrophore.

Chronology of growth variations

Internal growth bands were measured in acetate peels made of cross sections of the left valve. In accordance with MacDonald and Thomas (1980) and Hewitt and Dale (1984) who studied growth in the related *Mya arenaria* and the arctic *M. truncata*, respectively. We used the growth band pattern in the chondrophore since this part of the *Mya* shell yields the most distinct bands. Left–hand valves were embedded in epoxy resin (Polypox™, THV 500, harder 125) and sectioned with a diamond saw along a line through the hinge tooth to the point of maximum extension (Fig. 2).

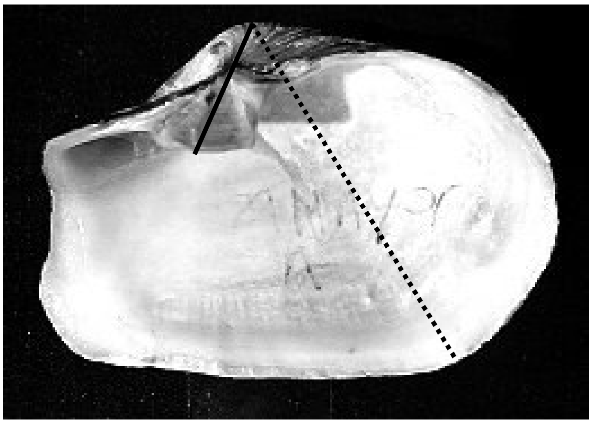

Figure 2. Photograph of the inside of a left valve of *M. truncata* with chondrophore. The solid line through the chondrophore is the direction along which the shell was sawed. The dotted line is the extension of this line along the exterior of the shell. The surface enclosed by these two lines is the actual plane of sectioning.

The cross sections were ground, polished and etched, and the micro-relief transferred to an acetate sheet (Ropes 1985). Each acetate peel was photographed in parts with a digital camera mounted on a microscope. A composite image of the peel was prepared in MS-PowerPoint and printed as hard copy. The widths of the growth bands were measured on the hard copy with a calliper and converted to actual shell dimensions. As all shells were collected alive in autumn 2000, each growth band could be assigned to the specific year in which it was formed by counting back from the shell margin. Band widths in the composite image were measured independently by two people. Disagreement between the two measurements was invariably due to 1) growth bands delimited by several closely grouped lines of which it was difficult to assess which one represented the annual growth stop; 2) progressively narrowing bands near the edge of the chondrophore making it difficult to distinguish one band from another. In such cases both readings were retained until later analysis (see below).

To be able to compare growth in a specific year in individuals of different ages, growth (band widths) had to be standardised because the growth rate of *M. truncata*, as most organisms, declines with age. This ontogenetic growth trend was removed by substituting absolute band widths by an index of relative growth viz. the log-transformed ratio between the observed and the expected band width (Cook et al 1990). The expected width in a particular year was derived from a fitted growth model. To determine which growth model was most efficient in removing the ontogenetic trend in *M. truncata*, we tried the following 5 commonly used growth functions (see Sager and Sammler 1983):

Gompertz: $L_t = L_\infty\, e^{-\exp(-k\,(t-\,t0))}$

von Bertalanffy: $L_t = L_\infty\,(1-e^{-k\,(t-t0)})$

Janoschek: $L_t = L_0 + (L_\infty - L_0)(1-e^{-k\,t^{\wedge}k^{*}})$

Logistic: $L_t = L_\infty + ((L_0-L_\infty) / (1+(t/t_0)^k)$

Boltzman: $L_t = L_\infty + (L_a-L_\infty) / (1+e^{(t-t0)/k})$

where L_t is the size at time t; L_0 is the size at t = 0; L_∞ is the maximum size; k and k^* determine the rate at which maximum size is approached; L_a is length at $t = t_0$. Our choice of a suitable growth function was only led by the best least squares fit and not by any inferences about the biological meaning of the models.

The series of index values were plotted with PAST32 software (SCIEM) in order to check the correspondence between replicate measurements of one shell and between different shells. Correspondence was calculated as “Gleichläufigkeit” (Schweingruber 1989) i.e. the number of similar growth rate changes in two measurement series expressed as a percentage of the total number of years that two series have in common. We used “Gleichläufigkeit” values to search for outliers and, in case of incongruous replicate readings, to decide which one fitted best to the overall pattern.

Results

Distribution and size of Mya truncata

The distribution of *M. truncata* in the Dutch Sector of the North Sea is shown in Figure 3. So far it has only been found in the Oyster Ground, i.e. north of 53,66 ^{o}N, which is the deeper part of the Dutch Sector (30-50 m water depth). The sediment in the Oyster Ground consists of muddy sand with percentages mud (< 64 μ) varying between 5 and 25. Highest densities of *M. truncata* in our samples, viz. > 50 ind.100 m^{-2}, appear to be concentrated in a narrow band running SW to NE along the Frisian Front. This band more or less coincides with highest percentages of mud (Pearson $r_{\text{mud-}Mya} = 0.71$, $p<0.001$). *Mya truncata* appears to be absent from the shallower (< 30 m) Southern Bight where clean sandy sediments (mud % < 5) and higher tidal current speeds prevail. Due to the combination of current speed and depth, the Southern Bight remains mixed throughout the year whereas in the Oyster Ground the water column becomes stratified during summer. As a consequence maximum bottom water temperatures in the Oyster Ground are lower than in the Southern Bight (Tomczak and Goedecke 1964).

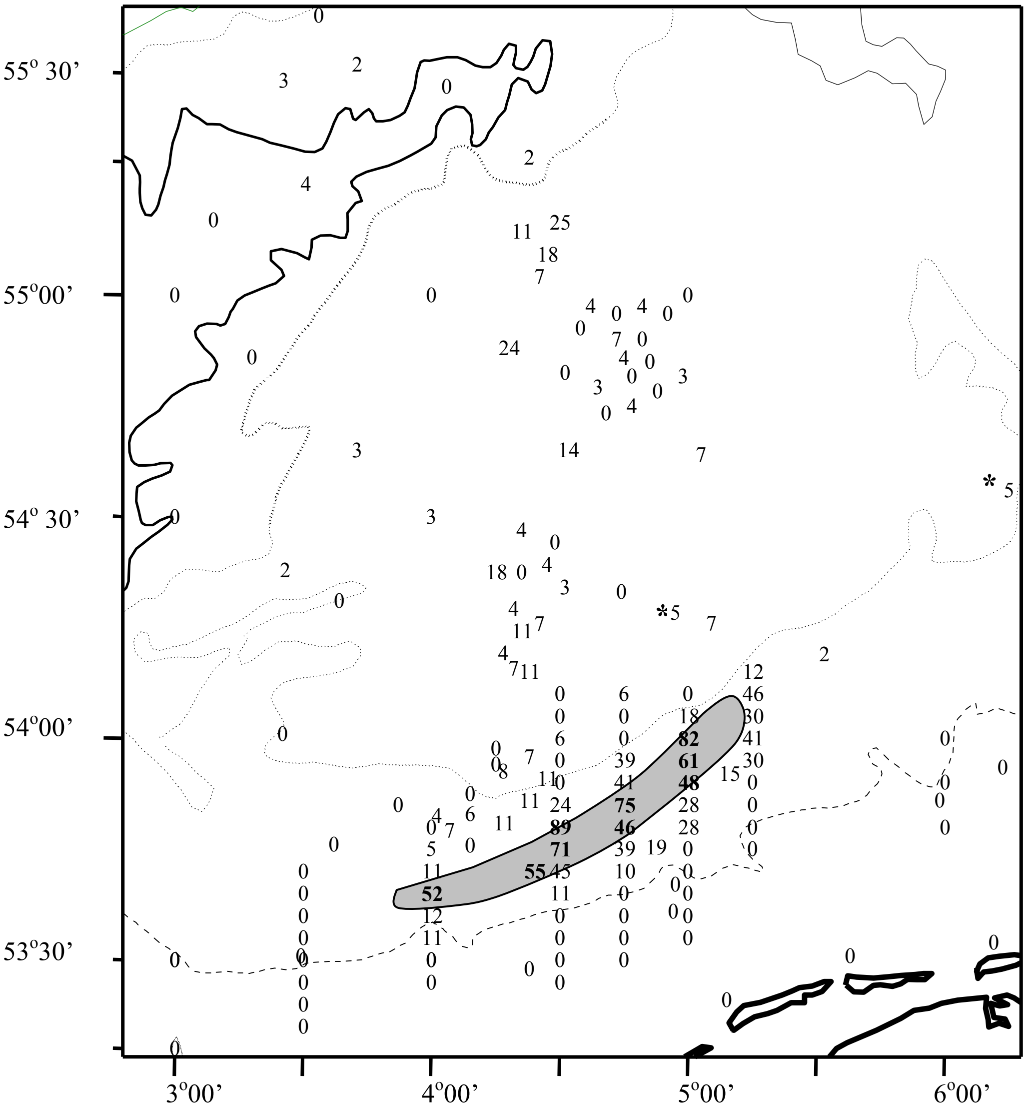

Figure 3. Distribution and densities (ind.100m^{-2}) of *M. truncata* in the Oyster Ground (southern North Sea). The shaded area comprises the stations where relatively high abundance (> 50 ind.100m^{-2}) of *M. truncata* were found.

* - Represents multiple samples in a small area.

Figure 4 shows the size frequency distribution of all *M. truncata* specimens caught (n=162) with the Triple-D dredge in the Dutch Sector over the period 1998 - 2000. Remarkably, individuals < 50 mm have almost not been caught with the Triple- -

D in spite of the fact that bivalves > 10 mm are retained in the dredge (Bergman and van Santbrink 1994). The yearly monitoring of the benthic fauna in the Dutch continental sector (Daan and Mulder 2001) using a boxcorer and 1 mm sieve has neither yielded any *M. truncata* between 0.5 and 4 cm (Dr. R. Daan, pers.comm).

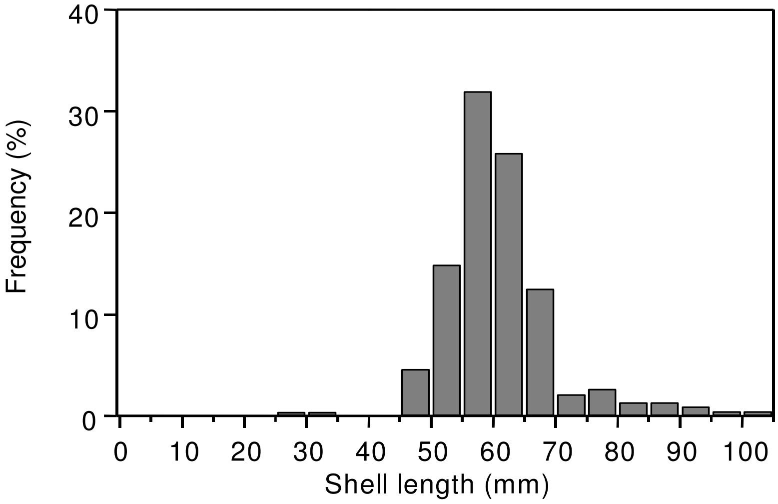

Figure 4. Length frequency distributions of *M. truncata* collected during the period 1998-2000.

Growth bands

Acetate peels of cross sections of the valve and chondrophore of *M. truncata* revealed distinct microgrowth bands composed of a dark line (growth stop) delimiting increments of variable width (Fig. 5).

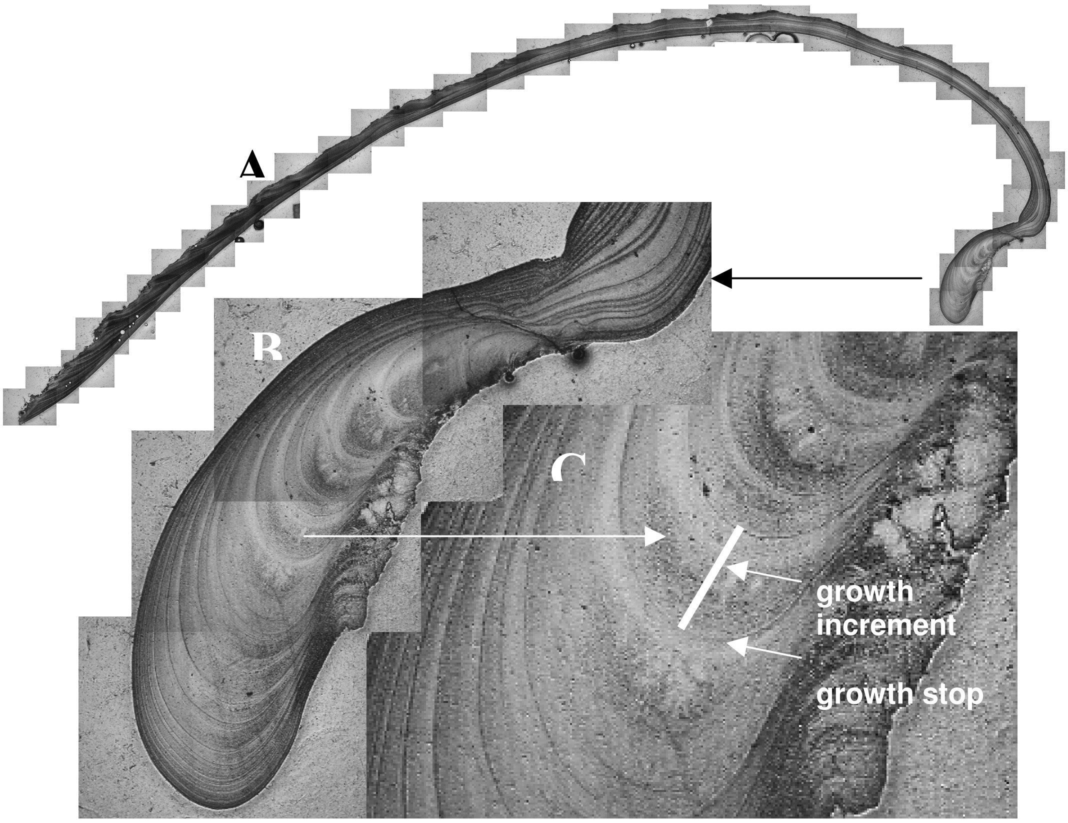

Figure 5. A) Composite image of an acetate peel of a cross section of a left valve of *M. truncata*. The distance from shell margin to chondrophore is 68.2 mm; B) Detail of chondrophore with growth band pattern; C) Example of a growth band consisting of increment and stop. The scale bar in the increment measures 360 µm.

Taking that the growth bands are formed annually, we estimated the ages of the 25 specimens studied to vary between 13 and 28 years (Fig. 6).

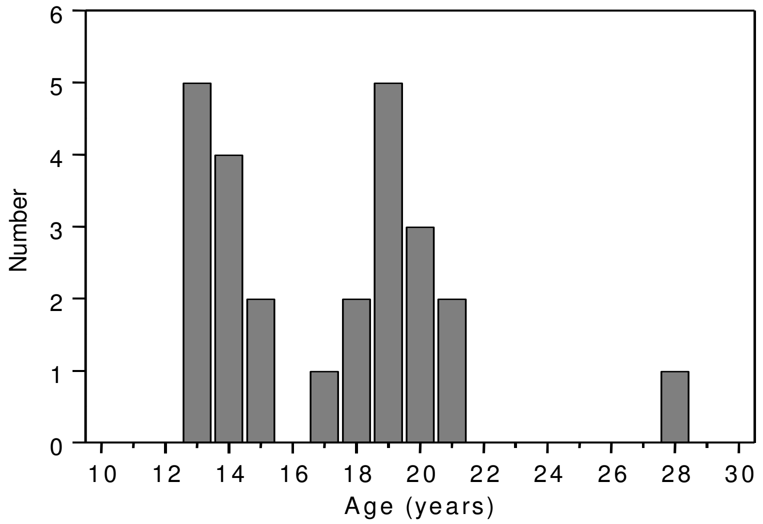

Figure 6. Age distribution of the 25 *M. truncata* used in this study.

After measuring the growth band widths in the chondrophore of each specimen, we made a plot of the cumulative chondrophore length vs age. By averaging the lengths at age we obtained the curve shown in Figure 7. One can see that there is a more or less smooth transition from rapid growth to a phase of slow growth as is also found in arctic *M. truncata* (Hewitt and Dales 1984). The increase of the standard deviations of the mean with age in Figure 7 is due to the decreasing number of data points and the increasing absolute size.

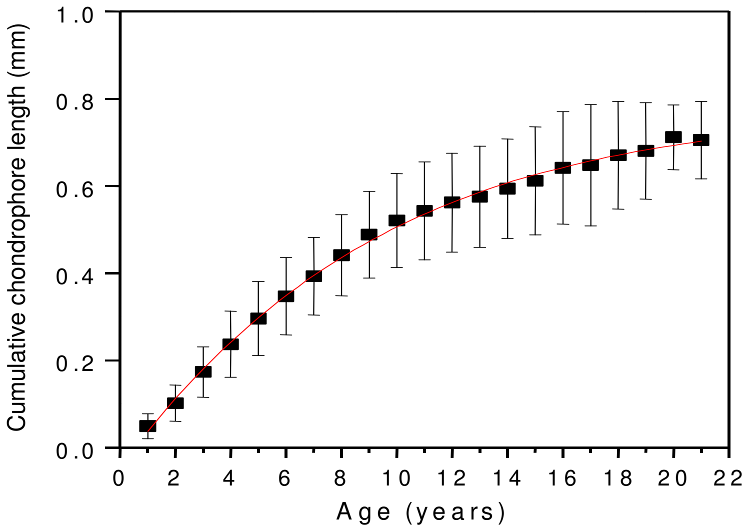

Figure 7. Chondrophore length vs age in *M. truncata.* Means (solid squares) and standard deviations (bars) are calculated from 25 series of cumulative band widths vs age. To illustrate the pattern, a line (Bolzman's function) was fitted through the means.

Of the five growth models used, Bolzman's growth function yielded the lowest sums of squares on average (Table 1) and, moreover, the residuals showed no consistent trend (Fig. 8).

Table 1. Mean (M) and standard deviation (SD) of the residual sum of squares obtained after fitting 5 different models to the cumulative hinge growth of *Mya truncata* (see Figure 8).

GROWTH MODEL	M Residuals	SD Residuals
Gompertz	0.00461	0.00391
Boltzman	**0.00322**	**0.00383**
Logistics	0.00402	0.00401
Bertalanffy	0.00705	0.00886
Janoschek	0.00794	0.00922

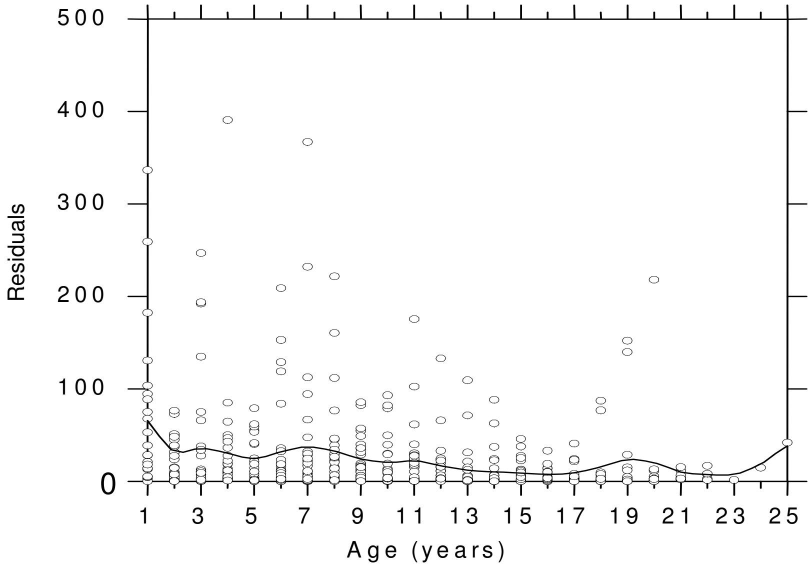

Figure 8. Plot of residuals vs age. The residuals represent the squared differences between the measured size at age and the size at age predicted by the Bolzman's model.

An example of Bolzman's function fitted to the cumulative chondrophore length of a *M. truncata* is given in Figure 7. Using the fitted values we calculated expected growth and subsequently the standardised index for each year. This ultimately gave 25 series of index values of variable length belonging to the 25 individuals. The ages in each series were then substituted by actual years, and averages and standard deviations of the index values were calculated for each particular year. We present these values for the years 1985-2000 since this period covers the years of the decline of *A. filiformis* and, moreover, values before 1985 were based only on a limited number of individuals (< 15).

Figure 9 shows a notched box plot (McGill et al. 1978) of the index values of the 25 *M. truncata* between 1985 and 2000. In 1988 and 1989 index values were positive i.e. growth was higher than expected with a tendency to decrease. In 1990 growth dropped below expected values and remained so until 1994. The largest negative deviation was found in 1992. The non-overlapping-notches around the box plots in

Figure 10 show that growth in 1992 was significantly lower than in 1988 which is confirmed by a t-test (t = -5.679, df = 54.9 p < 0.000). The same is true for the difference 1989 vs 1992 (t = -5.164 df = 48.7 p < 0.000). Noteworthy is that from 1992 onwards growth rates increased again attaining above expected values by the mid 90s. In subsequent years the variation became too large to allow any meaningful statistical comparison.

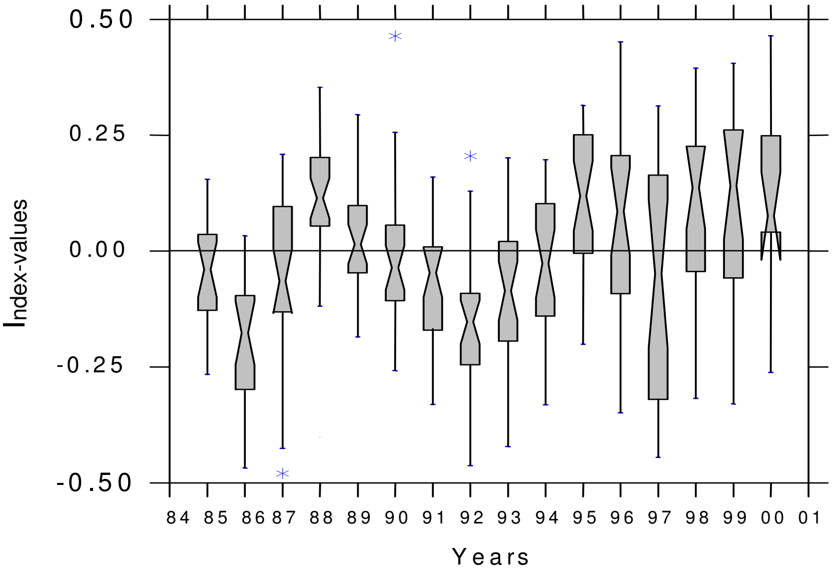

Figure 9. Notched Box plot of the index values over the period 1985-2000. Non- overlapping notches denote significant differences between means.

* - Represents outliers.

Discussion

The reason for undertaking this study on the growth of *M. truncata* at the Frisian Front was the dramatic decline of the dominant ophiuroid *A. filiformis* in 1993. The dense *A. filifornis* zone that was present throughout the period 1980-1992 was regarded as typical for - and coupled with - the organic enrichment of the Frisian Front. The enrichment of the frontal zone has been demonstrated in various studies in the form of high sediment respiration rates, elevated chlorophyll-a levels in the water column and sediment, and high biomass values of many taxa viz. invertebrates, demersal fish, pelagic organisms, hyperbenthos, seabirds (Creutzberg 1985; Cramer 1991; de Gee et al. 1991). A similar association between enhanced input from a pelagic front and the abundance of *A. filiformis* has been found in the Skagerrak (Josefson and Conley 1997), while on the west coast of Ireland high *A. filiformis* densities are associated with a gyre concentrating food (O'Connor et al. 1983).

In view of the close link between dense *A. filiformis* occurrences and enhanced food input, the first hypothesis to explain the *A. filiformis* crash at the Frisian front involved benthic food conditions. Direct measurement of benthic food supply at offshore turbulent sites requires scarce resources i.e. shiptime and special instruments (Duineveld and Boon 2002). Growth records deposited in bivalve shells like *M. truncata* can offer a simple alternative as the organisms integrate conditions over relevant time scales and, moreover, allow retrospective analyses (Richardson 2001).

The standardised growth record of *M. truncata* at the Frisian Front (Fig. 9) shows that during the period 1991-1993 growth was below expected values with 1992 being the year with the lowest average growth index. *Amphiura filiformis* densities were still at a normal high level in spring 1992 (~1500 ind.m^{-2}), but in the subsequent campaign of spring 1993 densities were below 1000 ind.m^{-2} for the first time in a decade (details Part I). *Amphiura filiformis* density continued to decrease in 1994 and remained at a low level in subsequent years whereas, the growth index of *M. truncata* showed an increase again from 1995 onwards (Fig. 10). So, at first sight, there seems to be no direct correlation between the two events. Hypothetically, however, enhanced mortality of *A. filiformis* in 1993 could have been caused by a depressed food supply in preceding year(s) deteriorating the condition of the brittlestars. Nilsson (1999) showed that arm regeneration in *A. filiformis* depends on food supply. With the many *A.*

filiformis in the Frisian Front population having one or more arms cropped by flatfish (Duineveld and Van Noort 1986), food shortage could lead to sustained loss of function and ultimately increased mortality. Assuming that the dip in *M. truncata* growth in 1992 represents a food shortage, it remains questionable whether the shortage would have been severe enough to have such a dramatic effect on *A. filiformis.* Figure 9 shows that the growth record of *M. truncata* contains another dip in 1986 which is as deep as the 1992 one. Still the *A. filiformis* numbers at the Frisian Front remained high throughout the 1980s. Given this somewhat inconclusive evidence from *M. truncata* we have looked for additional data which in one way or the other are indicative for the benthic food supply in the period of interest.

Long-term CPR data show that in the late 1980s phytoplankton biomass even increased above the long term mean and remained high since then, notably in winter (Edwards et al. 2002). Time-series on macrofauna biomass in the North Sea neither yield evidence of a marked drop in the early 1990s. Kröncke et al (1998) reported an increase of macrofauna biomass off the coast of Norderney in 1988 and persistently high levels in the following years. Daan and Mulder (2001) also did not find any marked change in macrofauna biomass in the major subregions of the southern North Sea in the period 1990-2000. In summary, the lack of compelling evidence for a large scale change in food availability in the southern North Sea, points at a local factor being responsible for the *A. filiformis* crash at the front. We do not rule out, however, that food shortage has played a role taking into account the steep gradient in environmental conditions at the Frisian Front. Forthcoming growth analysis of other suspension feeders e.g. *A. islandica* and *Dosina lupinus*, might produce more solid answers.

Besides a historical growth record of *M. truncata*, our study yielded new data on the spatial and size distribution of this bivalve species in the southern North Sea. The distribution of *M. truncata* in the southern North Sea appears to be concentrated round the Oyster Ground (Fig. 3). According to literature *M. truncata* is a boreal species without a distinct sediment preference. Hence we suppose that its distribution pattern in the southern North Sea is related to maximum temperatures which are lower in the Oyster Ground than in the Southern Bight due to stratification and depth. This does not explain the band of high densities at the muddiest sites of the Frisian Front in Figure 3. If sediment is not a relevant factor, the coincidence of highest *M. truncata* densities and mud percentages could point to a common hydrological factor, i.e. optimal conditions for deposition of both fine particles and of larvae, to locally favourable conditions for survival, or to a combination of both.

Another remarkable finding of our study is the skewed size distribution of the *M. truncata* that we have collected and specifically the lack of juveniles in the 1-4 cm size class. The cause for this skewness is unknown but could be infrequent larval supply and/or high juvenile mortality. Striking is that the other large and long-living bivalve in the southern North Sea, *A. islandica,* displays the same type of size distribution (Witbaard and Bergman, 2003). Comparing different North Sea *A. islandica* populations, these authors state that the skewed size distribution of *A. islandica* at the Frisian Front is atypical, and probably due to bottom trawling. They further argue that the Frisian Front stock will unlikely form a sustainable population if fishing pressure continues. We could not find data on *M. truncata* from less heavily fished regions to compare with, but we do point at the possibility of fishing being responsible for the peculiar size structure since juvenile *M. truncata* are likely more exposed to trawl damage than deeply buried older animals. In any case, the low adult density resulting from the presently poor recruitment rate may form an obstacle for successful fertilisation (Metaxas et al 2002) and thus self-sustenance. Then, the occurrence of *M.*

truncata and possibly *A. islandica* as well at the Frisian Front will, or has already, become dependent on the influx of pelagic larvae transported with UK coastal water.

Large and long-living benthic organisms, such as *A. islandica* and *M. truncata*, are frequently mentioned in the context of conservation of the southern North Sea biodiversity and as Ecological Quality Objectives - EcoQOs (Bisseling et al 2001). Success of measures to protect or restore these long lived benthic species depends on a proper insight into their population dynamics especially of its juvenile phase. The scarcity of relevant data on *M. truncata*, and also, on *A. islandica* (Witbaard and Bergman submitted) demonstrate that autoecological studies should receive the same support as monitoring studies.

Acknowledgments

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References

Ballerstedt, S., 2001. *Mya truncata*. Blunt gaper. Marine Life Information Network: <http://www.marlin.ac.uk>. Plymouth: Marine Biological Association of the United Kingdom.

Bergman, M. & van Santbrink, J., 1994. A new benthos Dredge (“Triple-D”) for quantitative sampling of infauna species of low abundance. Neth. J. Sea Res. 33: 129-133.

Bergman, M., & van Santbrink, J., 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J. Mar. Sci .57: 1321-1332.

Bisseling C., van Dam C., Schippers A., Van der Wielen, P. & Wiersinga W., 2001. Met de Natuur in zee. Rapport expertisecentrum LNV 48: 125 pp.

Brousseau, D. & Baglivo J.,1987. A comparative study of age and growth in *Mya arenaria* (soft-shell clam) from three populations in long island Sound. J. Shellfish Res. 6: 17-24.

Cook, E., Briffa, K., Shiyatov, S. & Mazepa, V., 1990. Tree ring standardisation and growth trend estimation. In: Cook E, Kairiukstis, L (Eds). Methods of dendrochronology. Applications in the environmental sciences. Kluwer Acadamic Publishers: 105-108.

Cramer, A., 1991. Benthic metabolic activity at frontal systems in the North Sea. PhD thesis, University of Amsterdam, 93 pp.

Creutzberg, F., Wapenaar, P., Duineveld, G. & Lopez, N., 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. Rapp. p.v. reun. cons. int explor. Mer., 183: 101-110.

Creutzberg, F., 1985. A persistent chlorophyll a maximum is coinciding with an enriched benthic zone. In: Gibbs PE (ed) Proceedings of the 19th European Marine Biology Symposium, Cambridge University Press: 97-108.

Daan, R. & Mulder, M., 2001. The macrobenthic fauna in the Dutch sector of the North Sea in 2000 and a comparison with previous data. NIOZ-Rapport 2001-2, 93 pp.

Duineveld, G. & Van Noort, G., 1986. Observations on the population dynamics of Amphiura filiformis, in the Southern North Sea and its exploitation by the dab, Limanda limanda. Neth. J. Sea Res. 20: 85-94.

Duineveld, G. & Boon, A., 2002. Short-term variations in the fluxes and composition of seston in near-bottom traps in the southern North Sea. Helgol. Mar. Res., 56: 140-148.

Edwards, M., Beaugrand, G., Reid, P., Rowden, A. & Jones, M., 2002. Ocean climate anomalies and the ecology of the North Sea. Mar Ecol Prog Ser 239: 1-10.

Gee de A, Baars, M. & van der Veer, H., 1991. De Ecologie van het Friese Front. NIOZ-Rapport 1991-2, 96 pp.

Hewitt, R. & Dale, J., 1984. Growth increments of modern *Mya truncata* L. from the Canadian Arctic, Greenland and Scotland. Curr. Res. Part B, geological Survey of Canada 84-1B: 179-186.

Jones, D., Arthur, M. & Allard, D., 1989. Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria* from Narragansett Bay, Rhode Island. Mar Biol 102: 225-234.

Josefson, A. & Conley, D., 1997. Benthic response to a pelagic front. Mar Ecol Prog Ser 147: 49-62.

Kröncke, I., Dippner, J., Heyen, H. & Zeiss, B., 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar. Ecol. Prog. Ser. 167: 25-36.

Lutz, R., 1976. Annual growth patterns in the inner shell layer of *Mytilus edulis* L. J Mar. Biol. Ass. U.K. 56: 723-731.

MacDonald B., Thomas, M., 1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. Mar Biol 58: 105-109.

Metaxas, A, Scheibling R. & Young, C., 2002. Estimating fertilization success in marine benthic invertebrates: a case study with the tropical sea star *Oreaster reticulatus*. Mar. Ecol. Prog. Ser. 226: 87-101.

Nakaoka, M., Matsui, S., 1994. Annual variation in the growth rate of *Yoldia notabilis* (Bivalvia: Nuculanidae) in Otsuchi Bay, northeastern Japan, analyzed using shell microgrowth patterns. Mar. Biol. 119: 397-404.

Nilsson, H., 1999. Effects of hypoxia and organic enrichment on growth of the brittle stars *Amphiura filiformis* (O.F. Mueller) and *Amphiura chiajei* Forbes. J. Exp. Mar. Biol. Ecol. 237: 11-30.

O'Connor, B., Brower, T. & Grehan, A., 1983. Long term assessment of the population dynamics of *Amphiura filiformis* in Galway bay. Mar. Biol. 75: 279-286.

Richardson, C., 2001. Molluscs as archives of environmental change. *In* Oceanography and Marine Biology: an annual review, vol. 39 (ed. R. N. Gibson, M. Barnes and R. J. A. Atkinson), 103-164 pp.

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

Sager, G. & Sammler, R., 1983. Mathematical Investigation into longevity of the Ocean Quahog *Arctica islandica* (Mollusca: Bivalvia). Int Rev ges Hydrobiol 68: 113-120.

Schweingruber, F., 1989. Tree rings. Basic and applications of dendrochronology. Kluwer Academic Publishers. 271 pp.

Tomczak, G. & Goedecke, E., 1964. Die thermische Schichtung der Nordsee auf Grund des mittleren Jahresganges der Temperatur in 1/2º- und 1º-Feldern gever: Hamburg. Deutsche hydrographische Zeitschrift, Ergänzungshefte, Reihe B 8: 182 pp.

Welch, H., Bergmann, M., Siferd, T., Martin, K., Curtis, M., Crawford, R., Conover, R., & Hop, H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, arctic Canada. Arctic 45: 343-357.

Willmann, R., 1989. Muscheln und Schnecken der Nord-und Ostsee. Neumann-Neudamm, Melsungen. 310 pp.

Witbaard, R. & Klein, R., 1994. Long term trends on the effect of the Southern North Sea beam trawl fishery on the bivalve mollusc *Artica islandica* L. ICES J. Mar. Sci. 51: 99-105.

Witbaard, R., Duineveld, G., & de Wilde, P., 1997. 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. & Bergman, M., 2003. The distribution of *Arctica islandica* in the North Sea. What possible factors are involved? J. Sea Res. 50: 11-25.

Does *Mya truncata* reproduce at it southern distribution limit? Preliminary information.

by

Teresa Amaro[1], Gerard Duineveld[1], Paul Tyler[2]

[1]Royal Netherlands Institute for Sea Research

P.O. Box 59

1790 AB Den Burg

The Netherlands

Fax ++ 31 222 319674

e-mail: amaro@nioz.nl

[2]School of Ocean and Earth Science,

University of Southampton SOC, Southampton SO14 3ZH,

United Kingdom

Fax:0044 2380 593059

e-mail: pat8@soc.soton.ac.uk

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Abstract

Previous investigations of the bivalve *Mya truncata* in the Southern North Sea revealed the absence of the 1987-2001 year classes. Since the species'southern-most distribution limit is the southern North Sea, at the Frisian Front, we examined if *M. truncata* was reproductively active in this region. Histological sections of reproductive tissues from individuals collected between June and April 2002 revealed synchronous gametogenesis with low numbers of vitellogenic oocytes. The low number of ripe oocytes may be one explanation for repeated recruitment failures of this species at this site.

Keywords: Reproduction, *Mya truncata*, North Sea benthos

Introduction

Monitoring of macrobenthos assemblages in the southern North Sea since 1991 has shown relatively constant species diversity and composition (Holtmann et al., 1999). Exceptions are the large bivalves *Arctica islandica* and *Mya truncata* that have recruitment patterns leading to populations composed of only a few year classes (Amaro et al., 2003; Witbaard & Bergman, 2003). For example, collections in the area during 2000-2001 revealed no individuals younger than 13 yr of age (Amaro et al. 2003). Comparisons with populations of these species from other areas indicate this age structure is atypical (e.g. Welch et al. 1992, Witbaard & Bergman, 2003). Causes for the infrequent recruitment in both species are unknown and require study if these species are to be protected in the framework of conservation of biodiversity in the North Sea (Berkel et al., 2002).

In this study we focus on bivalve *M. truncata* that is a characteristic but relatively rare species in the Oyster Ground (southern North Sea) with maximum densities of 1 ind. per m^{-2} (Amaro et al., 2003). The low densities are in contrast with arctic habitats where *M. truncata* is frequently a numerically dominant species reaching densities of >100 m^{-2} (Welch et al., 1992).

Causes for recruitment failures of this species in the southern North Sea can be from a combination of factors. For example: (1) lack of reproductively active adults, (2) lack of fertilization success because of low adult abundances (e.g., Levitan & Sewell, 1998, Metaxas et al., 2002) or unbalanced sex ratios, (3) temporal/spatial mismatches in the timing of larval release and food supply (e.g., Cushing, 1969) or (4) pre- and post-settlement mortality agents (e.g., Strasser & Günther, 2001). In this study, we determined if *M. truncata* has reproductively viable adults at the Frisian Front and if so the time of the year this takes place.

Material & Methods

Mya truncata were collected between June 2000 and April 2002 from a single locality centred at 53,48°N, 4,50°E (figure 1).

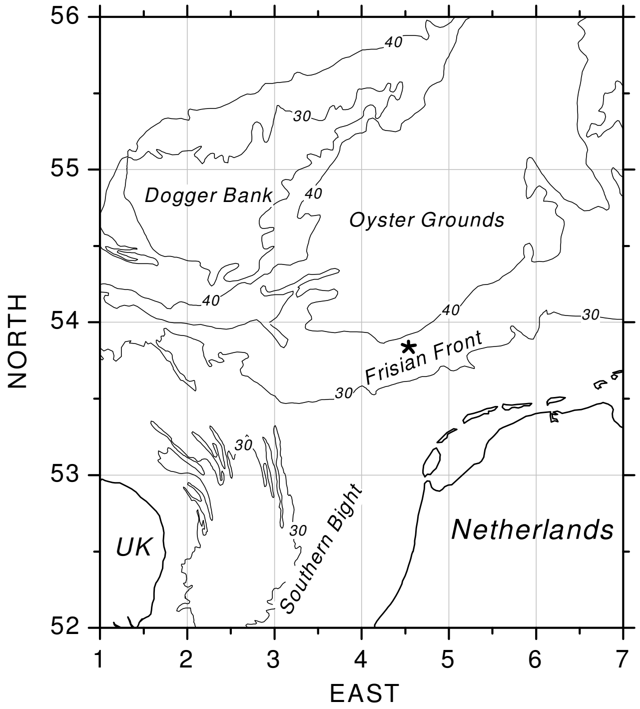

Figure 1. Map of the southern North Sea with Oyster Ground and the Frisian Front area. The * marks the station where *M. truncata* was caught.

Samples were collected using a Triple-D dredge (Bergman & van Santbrink 1994), and specimens were preserved in buffered sea-water formalin (4%) for transportation to the lab where they were transferred to 70% alcohol. Sex ratio and reproductive cycle (gametogenesis and oocyte-size distributions) was determined using standard histological techniques (Ramirez-Llodra, 2000). The sex of each specimen was determined microscopically. A classification scheme of five different gonadal stages was based on methods of Brousseau (1977, 1987) for *Mya arenaria*. Subsets of females were used to determine oocyte diameters using methods of Ramirez-Llodra (2002). A minimum of 100 oocytes was measured for each specimen in order to determine size-frequency distributions. Laruelle et al. (1994) have shown that measuring 50-200 oocytes per individual provides minimal statistical error at the intra-individual level. To avoid systemic errors, oocytes that showed processing artefacts were not measured.

Results

A total of 159 specimens were examined; shell lengths ranged from 47 mm to 78 mm (mean = 63 mm, S.D.= 6mm). Microscopic inspection of the histological sections of all specimens showed the species to be gonochoric with 85 of the specimens being males and 74 females (Table 1). The average sex ratio did not differ from unity (χ^2=0.022, df=1 p>0.05).

Table 1 – Numbers of *M. truncate* collected during the sampling survey.

Date	**Nr. of females**	**Nr. of males**
03rd June 2000	2	3
07th September 2000	27	31
12th December 2000	13	18
07th February 2002	17	17
01st April 2002	15	16

Figure 2 a, b shows the proportions of the males and females with gonads in each of the five developmental stages. In June 2000, all specimens were reproductively inactive (50 % - males and 67% - females were spent while remaining males and females were in an indifferent stage). In September 2000, females and males with developing gonads (55 % - males, 83 % - females) were present and in December 2000 fewer specimens had developing gonads (44.4 % -males, 27.3% - females). While samples were not collected in 2001, all specimens were ripening at the beginning of February 2002. By April 2002, 80 % of males and 72 % of females were in a spawned stage and the remaining males and females were in an indifferent reproductive stage.

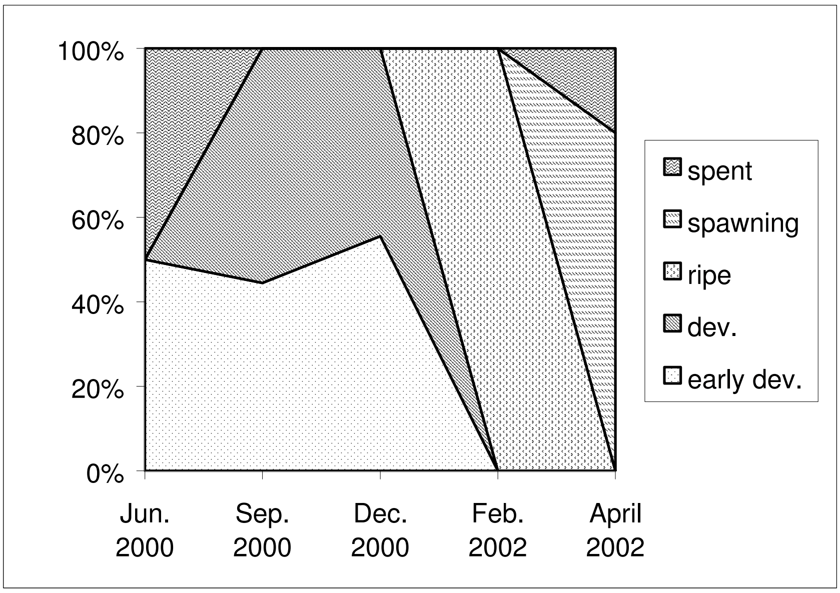

Figure 2. a) Percentages of the males with gonads in each development stage; **early development** - spermatogonia (indifferent cells) are the principal type of cells in the lumen; **development** - spermatogonia develop into spermatids that begin to arrange themselves into radial column; **ripe** – migration and prolifereration of the spermatids toward the centre. The differentiation of spermatozoa reaches its maximum; **spawning** - disorganisation of the radiating bands and only a few spermatozoa remain**, spent** - reduced lumen with the remains from what used to be a well developed male.

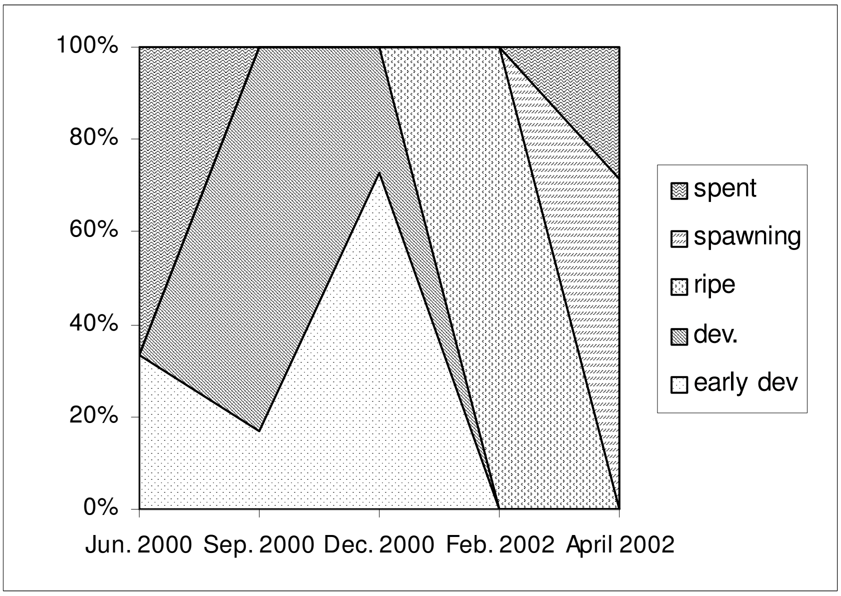

Figure 2b) Percentages of the females with gonads in each development stage; **early development** - oogonia (indifferent cells) are the principal type of cell present, **development** - developing of the oogonia into small primary oocytes that elongates on stalks. A central lumen becomes visible in each follicle; **ripe** - oocytes grow until they are spherical and occupy the entire lumen. **spawning** - a few oocytes are still present in each follicle; **spent** - remains of the oogenic cycle.

Size-frequency distributions of the oocytes were constructed to determine the timing of spawning (Figure 3).

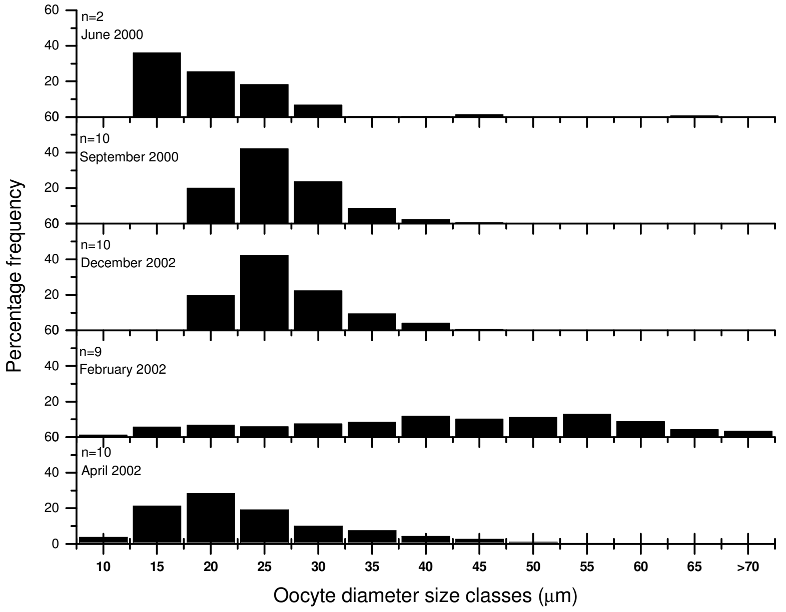

Figure 3. Oocyte size-frequency histograms of *M. truncata* for the months sampled. In each specimen, 100 oocytes were measured. n=number of specimens used.

In June 2000, most of oocytes were between 10 and 25 μm. Since there was no distinct change in the oocyte size between September and December 2000, spawning likely occurred before June. The oocyte size distribution in February 2002 was different from December 2000 (i.e. more uniform with sizes between 55 and 70 μm). However, there was considerable variation among the individuals (Figure 3). Only one female had an appreciable proportion (21 %) of oocytes > 70 μm while four females had much lower (~4-5%) percentages of oocytes of this size and four females (fig.4) had no oocytes larger than 55 μm. In the sample from April 2002 the average oocyte size had dropped considerably and large oocytes (55-70 μm) were almost absent (1%). Therefore in 2002, spawning events occurred between March-April.

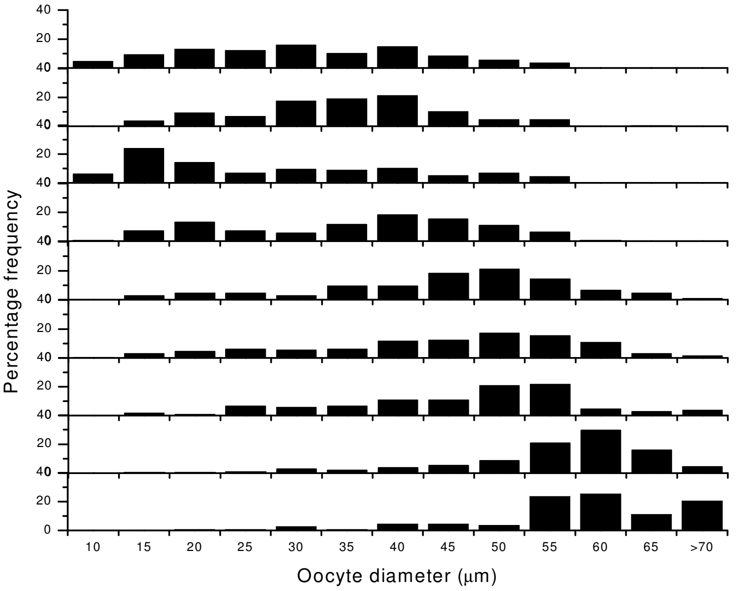

Figure 4. Oocyte size frequency distribution of *M. truncata* in February 2002. In each female analysed 100 oocytes were measured.

Discussion

Our observations, though based on a limited number of samples, suggest that male and female *M. truncta* display gametogenic synchrony at the study area. In 2000, all specimens collected in June were inactive or spent. In contrast, both females and males sampled in September and December were either in a developing stage, suggesting that ripening and further spawning occurred either before June or after December 2000. Gonads of males and females collected in February 2002 were ripening.

There were large female differences in oocyte sizes and percentages of large (> 70 µm) oocytes were low in number. While there is no published information on *M. truncata* oocyte size, in the related intertidal species (*Mya arenaria*) ripe oocytes are 65 - 70 µm diameter (Brousseau, 1987). If these dimensions are similar to *M. truncata*, 60 % (5 out of 9) of the February females had ripe oocytes though in low numbers. As no samples were collected in March, it is impossible to ascertain whether the low proportion of large oocytes were because 1) gonad ripening was still in progress and/or 2) the production of ripe oocytes is low altogether. However, in April 2002 most specimens of both sexes showed spawning characteristics, indicating gonad ripening was limited to February and spawning to March - April. If this is true, spawning events at the study were limited to the spring which coincides with lowest bottom water temperatures and low chlorophyll-a concentrations in surface waters (Boon & Duineveld, 1998).

Various studies on the reproductive biology of bivalves have demonstrated temperature and food are the most important exogenous factors influencing the reproductive cycle (Thorson, 1946; Beer, 2000 Sastry, 1979;–Myint & Tyler, 1982). Generally, temperature needs to exceed a threshold value for vitellogenesis to proceed. Temperature also affects the transfer of nutrients needed for oocyte growth (Sastry, 1979; Rodriguez-Jaramillo et al., 2001). Long-term winter (January, February) sea water temperatures have risen in the North Sea between the early 1950s and late 1990s (Beare et al., 2002). Although there is no trend in the sea water winter temperature measured at the surface in the Oyster Ground (Anonymous, 2003), the temperature in the winter months have slightly increased. The low number of ripe oocytes found in our study combined with the possible increased of the temperature could be one explanation for the low number of ripe oocytes in February. Since there are no monthly samples throughout the year, it is not possible to assess definitive reproductive periodicity (Ramirez-Llodra et al., 2002, Tyler & Gage, 1984) in this species. According to Petersen (1978), more northerly locations *M. truncata* seems to spawn most of the year or mainly in the spring. Clearly, additional work is required to more fully understand causes of the repeated recruitment failures of this species at the southern limit of its distribution in the southern North Sea.

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References

Amaro, T., Duineveld, G., Bergman, M. & Witbaard, R., 2003. Growth variations in the bivalve *Mya truncata* : a tool to trace changes in the Frisian Front macrofauna (southern North Sea)? Helgol. Mar. Res. 57: 132-138.

Anonymous, 2003. Waterbase: www.waterbase.nl.

Beare, D., Batten, S., Edwards, M. & Reid, D., 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. J. Sea Res. 48: 29-49.

Beer, T., 2000. Pelagic larvae of bivalves in the Meroplankton of the Velikaya Salma Inlet, Kandalaksha Bay, the White Sea. Oceanology 40: 671-676.

Bergman, M. & van Santbrink J., 1994. A new benthos Dredge ("Triple-D") for quantitative sampling of infauna species of low abundance. Neth. J. Sea Res. 33: 129-133.

van Berkel, C, Boon, A. & Wiersinga, W., 2002. Natuurwaardenkaart Noordzee. Expertisecentrum LNV. Wageningen, 65 pp.

Brousseau, D., 1987. A comparative study of the reproductive cycle of the soft-shell clam, *Mya arenaria* in Long Island Sound. J. Shell. Res. 6: 7-15.

Boon, A. & Duineveld, G., 1998. Chlorophyll a as a marker for bioturbation and carbon flux in southern and central North Sea sediments. Mar. Ecol. Progr. Ser. 162: 33-43.

Brousseau, D., 1977. Spawning cycle, fecundity, and recruitment in a population of soft-shell clam *Mya arenaria*, from Cape Ann, Massachusetts. Fishery Bulletin. 76 (1): 155-166.

Cushing, D., 1969: The regularity of the spawning season of some fishes. J. Cons. int. Explor. Mer. 33: 81-97.

Holtmann, S., Duineveld, G. & Mulder M., 1999. The macrobenthic fauna in the Dutch sector of the North Sea in 1998 and a comparison with previous data. NIOZ Rapport 1999-5. Den Burg. 105 pp.

Laruelle, F., Guillou, J. & Paulet, Y., 1994. Reproductive pattern of the clams, *Ruditapes decussatus* and *R. philippinarum* on interdital flats in Brittany. J. Mar. Biol. Ass. U. K. 74: 351-366.

Levitan, D. & Sewell, M., 1998. Fertilization success in free-spawning marine invertebrates: review of the evidence and fisheries implications. *In*: Proceedings of the North Pacific Symposium on Invertebrate Stock assessment and Management.

(Jamieson, G.S. & Campbell A., Eds.). Can. Spec. Publ. Fish. Aquat. Sci. 125: 159-164.

Metaxas, A., Scheibling, R., & Young, C., 2002. Estimating fertilization success in marine benthic invertebrates: A case study with the tropical sea star Oreaster reticulatus. Mar. Ecol. Prog. Ser. 226: 87-101.

Myint, U. & Tyler, P., 1982. Effects of temperature, nutritive and metal stressors on the reproductive biology of *Mytilus edulis*. Mar. Biol. 67, 209-223.

Petersen, G., 1978. Life cycles and populations dynamics of marine benthic bivalves from the Disko Bugt are of West Greenland. Ophelia 17 (1): 95-120.

Ramirez-Llodra, E. 2002. Fecundity and life-history strategies in Marine Invertebrates. *In*: Advances in Marine Biology. Vol.43 (Southward, A.J., Tyler, P.A., Young, C.M., Fuiman, L.A, eds.). 88-154 pp. Academic Press, UK.

Ramirez-Llodra, 2000. Reproductive patterns of deep-sea invertebrates related to phylogeny and energy availability. Doctor of Philisophy Thesis. School of Ocean and Earth Science, University of Southampton. 164 pp.

Rodriguez-Jaramillo, C., Maeda-Martinez, A., Valdez M., Reynoso-Granados, T., Monsalvo-Spencer, P., Prado-Ancona, D., Cardoza-Velasco, F., Robles-Mungaray, M. & Sicard, M. , 2001. The effect of temperature of reproductive maturity of the penshell *Atrina maura* (Sowerby, 1835) (Bivalvia: Pinnidae). J. Shellfish Res. 20: 39-47.

Sastry, A., 1979. Pelecypoda (Excluding Ostreidae). *In*: Reproduction of marine invertebrates. Vol. 5. (Giese A.C. & Pearse J.S., eds), 113-292 pp. Academic Press; New York, NY (USA).

Strasser, M. & Günther, C-P., 2001. Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. J. Sea Res. 46: 57-67.

Thorson, G. & Jørgensen, C., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with specila reference to the planktonic larvae in the sound (Øresund) (with a section on Lamellibranch larvae by C. Barker Jørgensen). Meddelelser fra Kommissionen for Havundersøgelser. ; Serie. Plankton ; bd. 4, nr. 1. 523 pp.

Tyler, P., & Gage, J., 1984. The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea. Mar Biol 80, 63-74.

Welch, H., Bergmann, M.., Siferd, T., Martin, K., Curtis, M., Crawford, R., Conover, R. & Hop H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, arctic Canada. Arctic. 45: 343-357.

Witbaard, R. & Bergman, M., 2003. The distribution and population structure of the bivalve *Artica islandica* L. in the North Sea: what possible factors are involved? J. of Sea Res. 340: 1-15.

Parallel growth trends in three bivalve species indicate climate forcing on the benthic ecosystem in the southeastern North Sea

by

Rob Witbaard, Gerard Duineveld, Teresa Amaro, Magda Bergman

Royal Netherlands Institute for Sea Research

P.O. Box 59, 1790 AB Den Burg, Texel

The Netherlands

e-mail witbaard@nioz.nl

(Climatology Research, accepted)

Abstract

Internal growth lines in shells of three filter-feeding bivalves (*Arctica islandica*, *Mya truncata* and *Chamelea gallina*) from the southeastern North Sea were analysed in search of common inter-annual variations of their growth rate. The high similarity (69 - 80%) between the growth records in the three species points at a large scale (climatic) factor being responsible for an important part of the variation in shell growth. The common trend extracted from the individual growth records was correlated with monthly data on phytocolour, NAO index, temperature and wind. This showed that the strength and sign of the effect of latter three factors varies seasonally. Effects of wind strength and direction were analysed in detail as in-situ measurements showed that wind speeds above 10 m/s (Bft 6) cause resuspension of fine sediment at the site where the bivalves live. Resuspended sediment causes a drop in the quality of food for suspension feeders. During the bivalve growing season, NNW-ENE winds have a predominantly negative effect. The effects of other wind directions are less clear-cut. The highest proportion of variance in the common growth trend was explained by strong winds from a WNW direction in May. These WNW winds have the longest possible fetch in the study area and generate (high) long waves facilitating resuspension of fine sediment at relatively low wind strength. Moreover, WNW winds tend to delay the spring bloom thereby shortening the growing season.

Keywords: *Arctica islandica*, *M. truncata*, *C. gallina,* NAO index, temperature, wind, resuspension

Introduction

Recent studies have demonstrated the occurrences of Atlantic-wide temporal variations in the abundances of zoo- and phytoplankton (Reid et al. 1998, Reid et al. 2001) whereas Aebischer et al. (1990) showed that parallel trends occur across different trophic levels. These results indicate that large scale oceanic and climatic processes play a major role in the variability of the ecosystem structure and functioning in the North Atlantic. The unifying forcing factor that has been proposed to explain these parallel trends is the North Atlantic Oscillation (NAO) (Hurrell 1995, Reid et al. 2001, Ottersen et al. 2001, Drinkwater et al. 2003). The NAO index is the parameterisation of the pressure difference between Iceland and the Azores that largely controls the wind, temperature and precipitation over North Western Europe. Because of this influence it also affects the water circulation and stratification process in the North Sea.

Due to the close coupling between climate and hydrography, the attention on NAO-related changes focussed on abundances and distributions of planktonic organisms (algae, copepods, chaetognaths). Fishery economic interests have further contributed to this focus (Corten 2001, Beaugrand et al. 2003). A growing number of studies now also have shown that the variability in benthic communities is linked to the NAO (e.g. Kröncke et al. 1998, Hagberg & Tunberg 2000). This is not surprising as benthic organisms rely on organic matter derived from the pelagic system and thus on pelagic productivity. Moreover, climate steered hydrography (currents, stratification) might directly affect conditions for benthic organisms as well. One of the difficulties is that the effects of the NAO can differ between places (Ottersen et al. 2001) because its effect depends on ecosystem complexity and the degree and pathways by which the system is controlled. However, within a limited geographical area, ecosystem forcing by climate or hydrography is expected to result in congruent trends among related biotic components.

Though the NAO has been associated with changes in species composition and biomass of benthic communities (Wieking & Kröncke 2001), there are also more subtle effects of climatic variability such as on the growth rate of a species. Evidence for the latter comes from the analysis of the skeletal growth records of corals and bivalves. The correlation between climate and skeletal growth found so far pertain to selected single species with a suitable growth record. However, in order to verify that climatic variations have community-wide implications, these analyses should be done on several species from one community.

The objective of the present study was to determine whether such parallel growth patterns exist among three filter-feeding bivalves species (*Arctica islandica*, *Chamelea gallina* and *Mya truncata*) living near the Frisian Front in the south-eastern North Sea (Figure 1). Our second objective was to find the underlying mechanism if a parallel growth pattern is found. External (climatic) factors like bottom water temperature and primary production certainly affect the growth of filter-feeding bivalves (e.g. Dekker & Beukema 1999, Beukema et al. 2002). Food quality is probably another important factor that determines growth. Circumstantial evidence exists (Witbaard et al. 2001, Cranford et al. 1998, Grant et al. 1997) that in the southern North Sea resuspension of fine sediment causes a drop in the food quality of bivalves that leads to depressed shell growth. Resuspension of fine sediments is caused by the combination of tidal and wave currents (Van Haren et al., 2003). The latter is strongly controlled by wind. Pursuing this line of investigation we selected wind speed and direction as one of the additional key variables for shell growth and incorporated these in the statistical analysis. To validate the supposed link between wind and resuspension we used the data obtained by a benthic lander, which was deployed in the area of study in the summer of 2001.

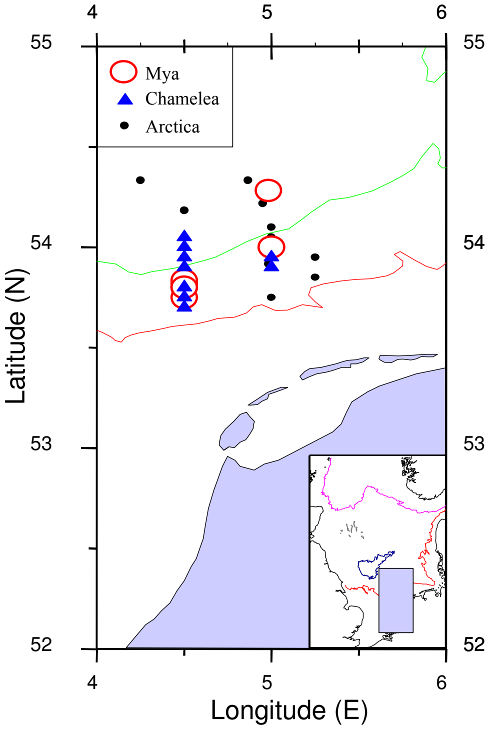


Figure 1. Origin of the bivalve specimens used in this study. For each species a separate symbol is given. Shaded area in the inset gives relative position of the area in the North Sea.

Material and Methods

Study site and sampling bivalves

Live specimens of the filter-feeding bivalves *A. islandica*, *C. gallina* and *M. truncata* were collected in and just north of the Frisian Front in the southern sector of the Oyster Grounds (south eastern North Sea). The sampling area is enclosed by corners 53,50^{o}N 4,50^{o}E and 54,50^{o}N 5,50^{o}E and is located about 30 nautical miles north off the isle of Texel (the Netherlands) (Figure 1). The depth in this area ranges from 30 m in the south to 45 m in the north. With the gradual deepening towards the north, the maximum tidal velocity decreases from 1.8 to 0.7 knots resulting in a south to north transition from coarse to fine sediments (Creutzberg et al. 1984, Creutzberg & Postma 1979). A tidal front at the southern border of the area separates the tidally mixed water mass in the south from the summer-stratified water that overlies the central Oyster Grounds (Creutzberg 1985). In the frontal zone a persistent chlorophyll-a maximum has been observed (Creutzberg 1985). The bottom water temperature ranges between approximately 4 ^{o}C in early spring to a maximum of 16 ^{o}C at the end of summer.

All three bivalve species live buried in the sediment and are typical filter feeders. *Chamelea gallina* is regarded as a lusitanic species while *A. islandica* and *M. truncata* are regarded as a boreal and boreal-arctic species respectively. The latter two species reach their southern distribution limit in the North Sea at the Frisian Front (Amaro et al. 2003, Witbaard & Bergman 2003). For *C. gallina* the Oyster Grounds belongs to the more northern parts of its distribution range (Witbaard et al. 2001). The specimens were collected during a series of cruises spread over the years 1998, 1999 and 2000. Collection took place with the Triple-D dredge (Bergman & van Santbrink 1994). Specimens of all three species were frozen for transport and storage. In the laboratory, their soft tissue was removed. In total 29 specimens of M. *truncata*, 21 specimens of *A. islandica*, and 27 specimens of *C. gallina* were used for this study.

Shell chronologies

The marked growth banding in shells of *A. islandica* and *C. gallina* is caused by the strong seasonal variation in temperature and production, and has been proven to have an annual origin (Witbaard et al. 1994, Ramon & Richardson 1992). Based on these results we assume that growth bands in *M. truncata* are annually formed as well although this periodicity has not been verified. On basis of band counts, the maximum ages of *M. truncata* and *C. gallina* are 27 and 21 years respectively (Amaro et al., 2003;

Witbaard et al., 2001). The maximum age of *A. islandica* is estimated to surpass 200 years (Jones 1983), although specimens with that longevity have never been found in this south eastern part of the North Sea.

Of each individual shell that we collected an acetate peel replica (Ropes 1985) of the etched shell cross-section was made to visualise and measure the growth increments in the hinge band. Because all specimens were caught alive, it was assumed that the year in which the outermost increment was deposited corresponded to the year of sampling. By counting backwards, each measured growth increment could be assigned to a particular calendar year. For each measured cross section this resulted in an absolutely dated time series of hinge band increment widths.

Because all specimens were relatively young, they showed an ontogenetic trend of decreasing growth ring widths with age. We removed this trend by fitting a 15-year cubic spline. This detrending procedure produced for each shell a time-index series that for each year reflected whether growth was below or above the expected rate. For each species, the dating of the individual time-series of growth variations was checked by cross-dating them with the dendrochronology computer programs COFECHA (Holmes 1983, Grissino-Mayer 2001) and PAST (http://www.sciem.com/). With the cross-dated and detrended time-series a species-specific standard chronology was constructed with the dendrochronology computer program ARSTAN (Cook 1985).

Environmental variables

A common trend from the bivalves's average chronologies of growth rate variations (check statistical section) was extracted and related to environmental variables. The environmental variables that were used for this analysis were phytoplankton standing stock, air and bottom water temperature, wind strength plus direction and NAO index. As a proxy for phytoplankton standing stock and primary production, we took the monthly CPR data on phytoplankton colour from the standard area D1 (SAHFOS, http://192.171.163.165/ standard_areas.htm). For the temperature, we used two temperature data sets. The first data set consists of air temperatures measured in De Bilt (Netherlands) by the KNMI (http://www.knmi.nl/onderzk/). Air temperatures can be regarded as a proxy for seawater temperatures in this part of the North Sea and the overall climate and weather in our area of investigation. The validity of this assumption was checked by using a second, much shorter data set on bottom water temperatures in the sampling area that were derived from model simulations by Pohlmann (1996). The wind data used in this paper refer to potential wind speed derived from wind measurements made by the Royal Netherlands Meteorological Institute (KNMI) at the offshore platform K13 located south of the area of investigation at (53,22N, 3,22E). Potential wind speed is the measured speed recalculated to the wind speed at a standardised height and roughness length to adjust for topographical differences at the location of measurement (see http://www.knmi.nl/samenw/hydra/). Since wind and temperature are related to the NAO index, this index was tested as unifying forcing factor representing large-scale climatic and oceanic processes.

Field observations on current speed and resuspension

As said before there are evidences (Witbaard et al. 2001, Cranford et al. 1998, Grant et al. 1997) that in the southern North Sea resuspension of fine sediment causes a drop in the food quality of bivalves which may depress growth in bivalves. To collect data on the resuspension, measurements were done from 29th May – 6th June and from 24th July – 12th September 2001 with a NIOZ custom-built tripod. This instrument was moored near the collection site of the bivalves at 53,70°N 4,50°E. The tripod was equipped with a current meter (Falmouth Scientific Instruments™ 3dACM) and an Optical Backscatter Sensor (Seapoint™). Both instruments were mounted 0.5 m above the sediment. A tilt sensor in the current meter could record movement of the tripod.

Statistics

A principal component analysis was used to extract the common trend from the species-specific average chronologies of growth rate variations. This common trend, being the first component extracted, was related to environmental variables by means of response function analysis (Fritts et al. 1971, Fritts & Shashkin 1995) and stepwise multiple regressions in SYSTAT v. 10. In this process, the standardised yearly common variations in shell growth are linked to monthly climatic variables. For the response function analysis we applied a four-month time lag between forcing factor and shell growth. This is based on the observed seasonal cycles of primary production and temperature in combination with the seasonal shell deposition in especially *Arctica islandica*. Data from the East coast of the US (Jones, 1980) plus empirical evidence from the northern North Sea (Witbaard et al. 2003) showed that *A. islandica* terminates its growth increment at the end of summer / autumn with a growth stop and starts depositing the new increment. The carbonate deposited between two growth stops thus partly represents autumn months of the year preceding the one in which the increment was terminated by the second growth stop. An increment thus actually covers the approximate period August-July, instead of January to December. As part of further analyses, a bootstrapped response function is calculated on basis of principal components of the monthly environmental variables, which resolves the problem of co-linearities of latter variables (Fritts et al. 1991).

Results

Analysis of growth variations

In the growth records of all three bivalve species, distinct growth rate variations can be seen over the last 20 to 40 years as illustrated by the Box-Whisker plots in Figure. 2a-c. The variation patterns show a great similarity between species (Figure. 2d). A sign-test yields a similarity of 69,4 and 78,6% between the *A. islandica* growth rate chronology and those of *M. truncata* and *C. gallina* respectively. *Mya truncata* and *C. gallina* have 69 % of their growth rate variations in common.

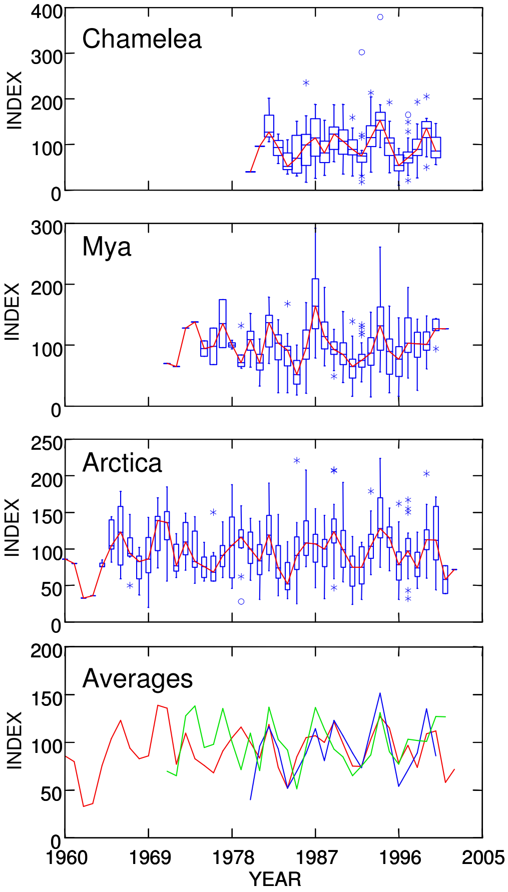


Figure 2. Box and whisker plots of annual growth variations in the three bivalve species collected from the south eastern North Sea. In the last panel the average curve of all three species is given. The index values along the y-axis represent standardized growth.

The common trend in the three species-specific chronologies was extracted by principal component analysis. The first principal component explained 69 % of the variance in all three species.

Environmental factors

Monthly CPR data (SAHFOS) on phytoplankton colour from area D1 were used as a proxy for primary production in the area. The correlation and response function analyses using the CPR data showed that except for December, the monthly phytoplankton colour is always positively related to shell growth.

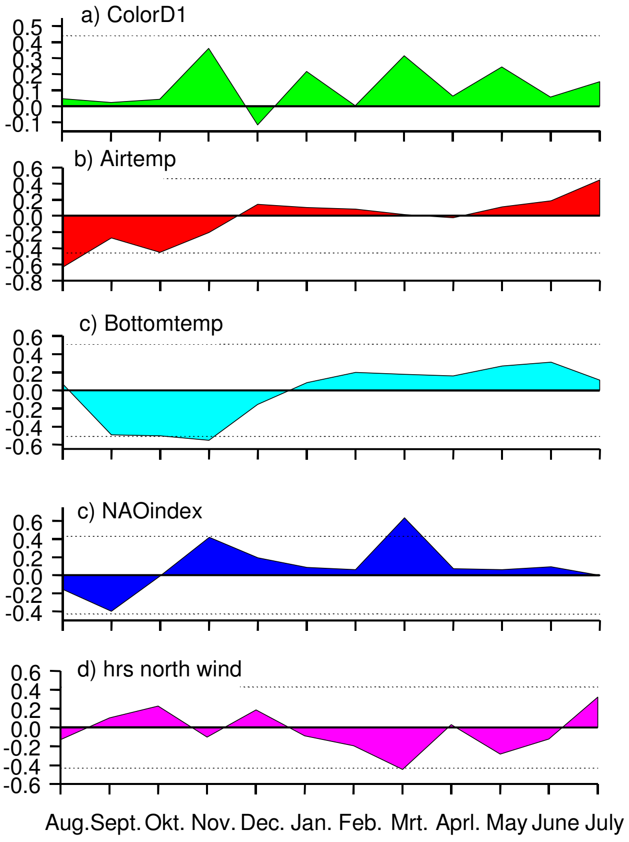


Figure 3. Correllograms between yearly shell growth and monthly averages of phytocolour (a), air temperature (b), bottom water temperature (c), the NAO index (d), and the duration of northerly winds (e). The dotted horizontal line denotes the significance level. The study period runs from 1980 to 2000.

However, none of the correlation coefficients (for the separate months) was significant (Figure 3a). Stepwise multiple regression neither yielded significant results for any of the months. Another variable that potentially affects shell growth directly is temperature. The outcome of the correlation analyses with the two sets of temperature data is given in Figure 3b-c. The comparison of these two graphs shows that the correlation between shell growth and bottom water temperature has a one-month time lag when compared to the correlation between shell growth and air temperature. It is furthermore evident from both graphs that whichever temperature data set is used, an inverse relationship exists between temperature during the end of summer and autumn and yearly shell growth. The results suggest that high temperatures between August and January depress shell growth. At the beginning of the new year the relationship between air temperature and shell growth reverses. During spring and early summer, higher temperatures tend to coincide with higher shell growth rates. The negative relationship between shell growth and the air temperature in August of the year preceding increment termination is highly significant. The correlation coefficients for the other months, i.e. September - January, are positive but non-significant. The response function model constructed on basis of the monthly air temperatures could explain 63 % of the variance in the growth rate variations. Figure 3d depicts the relationship between the shell growth time index series and the monthly NAO index values. In October the effect of NAO reverses from negative to positive and becomes highly significant in March. The corresponding response function model could explain 63% of the variation in shell growth. In Figure 4 the regression between shell growth and the NAO index is depicted and illustrates the significant positive relationship ($P<0.05$). From the above analyses it is still unclear what the underlying cause of the observed variations in shell growth is.

While the effect of temperature could be direct, an effect of wind might have indirectly affected shell growth by the generation of waves and resuspension of sediments.

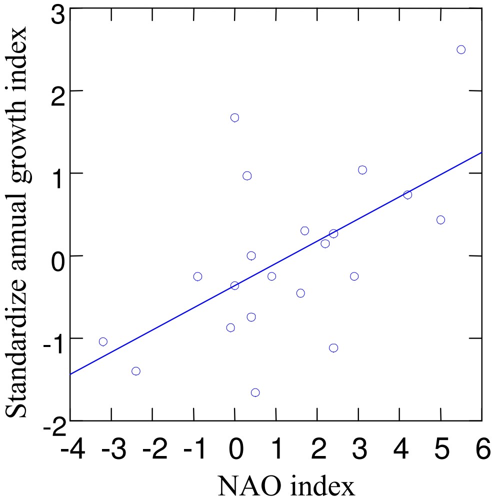
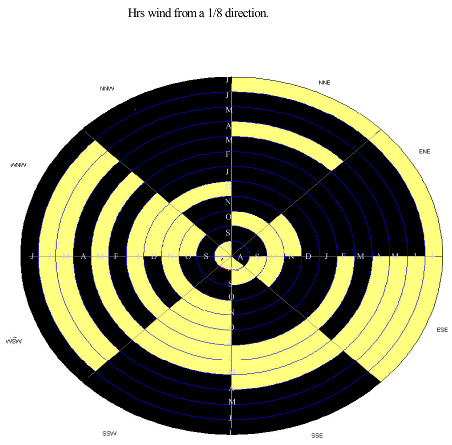


Figure 4. Regression between standardise annual shell growth and the NAO index in March. The regression is highly significant ($P<0.05$).

Wind thus may have altered the growth of the three bivalve species over the study period. We tested the effect of wind by using data that were collected at the offshore platform K13 (see above). The data set of hourly data on wind speed and direction was grouped into eight sectors each covering 45° of the compass (WNW, NNW, NNE, ENE, ESE, SSE, SSW, and WSW). For each sector, we calculated the monthly sum of hours that the wind came from that particular sector and correlated these monthly sums with the shell growth record. A second series of analyses was performed using the monthly sums of only those winds with a strength that, according to our in situ observations, surpassed the critical threshold for resuspension (10 m/s). The combined effect of wind direction and season on shell growth is depicted in Figure. 5a by means of a directogram. The circles are divided in 8 sectors representing the wind directions. Each concentric circle represents a month of the year starting with August in the centre of the graph. The shading in each sector displays the sign *i.e.* positive or negative, of the correlation between the annual shell growth index and the hours of wind coming from that sector in that particular month.



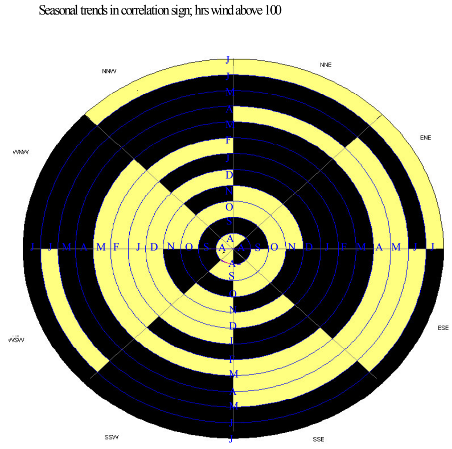


Figure 5. Directograms of the relationship between monthly wind data and shell growth. Wind directions have been subdivided into 8 sectors of 45°. Period in the year is given along the axis in the centre starting with August in the year before a growth band is terminated. A yellow sector denotes a positive relationship between growth and wind direction in that month while a black sector denotes a negative relationship. A) Directogram for the total hours of wind. The pattern is highly significant ($P<0.05$); B) Directogram for winds with a potential wind speed above 10 m/s.

The significance of the observed ordering (the pattern) of positive and negative relationships according to season and wind direction was tested by a series of run tests.

The generation of 1000 correlation matrices by bootstrapping was used to test the significance of the observed pattern. For each of the bootstrapped matrices the statistics for a runs test on columns (seasons) and rows (wind directions) was summed. The frequency distribution of this value was used to estimate the chance of finding a pattern as we observed in our study. This bootstrapping procedure showed that the probability to find a pattern as depicted in Figure 5a, was less then 5%. This finding suggests that the observed interaction between wind direction, hours wind, season and shell growth is not a merely random outcome. During most of the year especially winds with a north to northeasterly component appeared to depress growth. Winds with a westerly component tend to have a positive effect. In Figure 5b, a scheme is shown for the hours of wind with a speed, which causes the near bottom, current to surpass the critical erosion threshold. The pattern suggests that the effects of wind direction on shell growth vary seasonally. In spring and summer (outer circles), growth is positively correlated with strong winds from an easterly direction while in the same period strong winds from the westerly sectors tend to depress growth. However in the winter period (inner circles), strong easterly winds affect growth negatively. Strong northwesterly and westerly winds have negative effects in summer but have a positive effect in winter. The pattern in this case turned out to be non-significant ($P>0.05$) when tested with the procedure described above.

The analyses demonstrated that the effect of wind direction on shell growth was strongest for winds from a WNW direction. Strong winds (>10m/s) from this direction could explain 80 % of the variance in the time index series of shell growth. The percentage of variance explained by strong winds from other directions was on average 40% lower and except for winds from a NNE direction did not yield a significant response function model.

Relation wind speed and resuspension

The tripod with OBS and current meter was deployed twice near the collection site of the bivalves i.e. in late spring and late summer 2001. Due to a technical failure, we got no current meter data from the first period. In Figure. 6 we have combined the records of the current meter and OBS with the wind speed for the second period 24th July – 12th September. Spring tides in this period fell on 24th July, 6th and 21st August and 4th September.

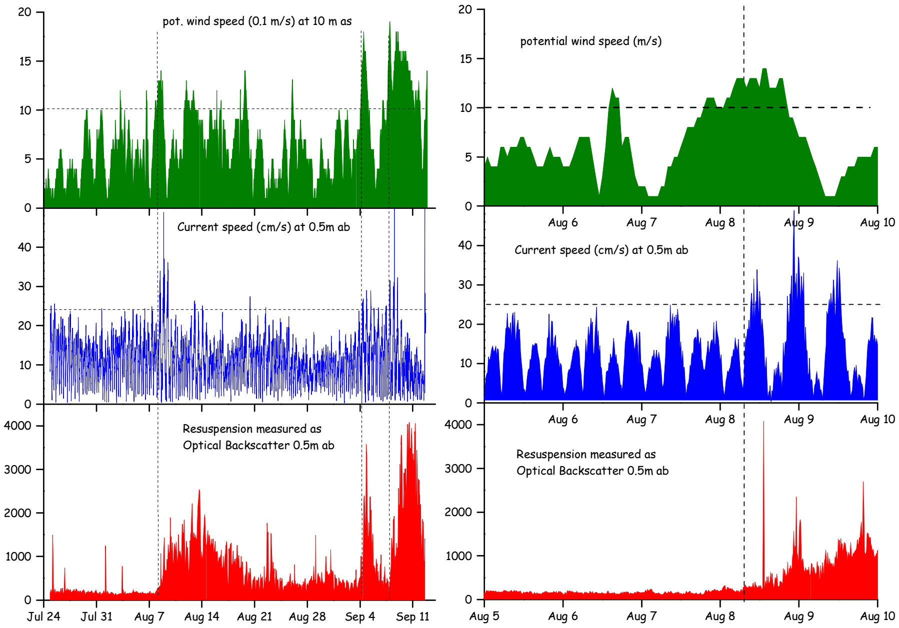


Figure 6. Combined plots of records of potential wind speed (in m/s at 10m above bottom) bottom current speed (cm/s) and turbidity measured as OBS at 0.5 m above the seabed. Left hand panel: recordings over entire period. Right hand panel: recordings over the period 5th to 10th August.

There are three major turbidity peaks visible in Figure. 2. The start of each peak (dotted lines Figure 6) coincides with enhanced current speed and wind strength. In the case of the first and second peak at 8th August and 5th September, currents related to the spring tide may have enhanced the wind (wave) effect. The third turbidity peak (8th

September) is due to wind alone. Spring tides alone do not evoke resuspension as can be seen around 24th July. This observation is in agreement with Williams et al. (1998).

Our data in Figure 6 show that current speeds over 25 cm/s (at 0.5 m height above bottom) give rise to resuspension of sediment. The empirical relation between turbidity, current (wave and tidal) and wind is illustrated in more detail in the right hand panels of Figure 6 covering the period 5th – 10th August. This interval began with a period of two quiet days with variable (S-SW) winds followed by a 24 h period with a strong breeze (10 m/s or Bft 6). After approximately half a day of strong SW breeze the maximum flood current speed in NE direction increased above 25 cm/s giving rise to an increase of the turbidity. A similar series of events can be shown for the peaks at 4th and 11th September. On basis of these observations, we took 10 m/s (~6 Bft) as the minimum wind speed required for resuspension of Frisian Front sediment.

Discussion

The various analyses all demonstrate that the common trend in shell growth of the three bivalve species is linked with climatic factors in the area of study. Determining the contribution of a combined effect of the factors to the growth trend is hampered by the length of the common growth index series in view of the great number of possible combinations of factors and months. There, however, exists a complex coupling between the separately tested factors. Winter air temperature in NW Europe is linked to the NAO index representing the air circulation pattern over the Atlantic. In positive NAO winters, strong westerly winds bring warm and wet air over NW Europe while in negative NAO winters low temperatures prevail and storm frequency is low (http://www.atmosphere.mpg.de/enid/1vs.html). Hence, a relationship between winter temperature and growth might be confounded by wind effects associated with the NAO index. Furthermore, effects of wind direction on shell growth can be confounded by the underlying seasonal coupling between wind direction and temperature. In winter, easterly winds in this part of the North Sea give rise to low temperatures whereas in summer similar winds are associated with high temperatures. The reverse is true for westerly winds.

Of all factors temperature is the most likely factor, which directly affects the metabolism and shell growth of bivalves as, found in laboratory experiments (e.g. Witbaard et al., 1997) and field studies (Witbaard et al., 1999). Shell growth in the three bivalve species indeed tends to be positively correlated with the bottom water temperature from early winter until the end of summer but the correlation is weak (Figure 3). From the end of summer (mainly August and September) throughout the autumn, temperature shows a stronger and above all a negative effect on shell growth. In the case of *Arctica islandica*, the bottom water temperature at the end of summer may approach or even surpass its upper temperature limit (Mann 1982, Lutz et al. 1982) and hence could affect shell growth negatively. Possibly, a similar temperature effect applies to the northern species *M. truncata* (Amaro et al., 2005). Furthermore, hypoxic conditions that are linked to high summer temperatures in the Oyster Grounds (de Wilde et al. 1984) could lead to a reduction of shell growth rates because the animals become temporally dormant (Abele 2002). The weak relation between growth and temperature in spring-summer as well as the stronger negative relation with fall-winter temperatures are in line with results of Schöne et al. (2003, 2004). They found a significant negative correlation between winter air temperature and shell growth in *Arctica islandica* from the Dogger Bank (central North Sea) and more recently showed that increment width in *A. islandica* shells from the SE North Sea does not correlate with temperatures in the growing season Feb - Sep. This strongly suggests that factors other than temperature might be more important for shell *in situ* shell growth.

The CPR phytoplankton colour is a measure of phytoplankton standing stock and probably food availability in the (upper) water column. Despite the almost continuous positive correlation between CPR phytoplankton colour (standing stock) and shell growth in Figure 3a, no significant coefficients were found. This suggests that either food production in the upper water layers has never been a limiting factor or that other factors overshadowed or modified the food supply to the seabed. It is indeed conceivable that shell growth is more likely determined by the amount and quality of food particles close to the seabed than to the standing stock in the upper water layers (Witbaard et al. 2003).

Previous studies showed that shell growth of *A. islandica* and *C. gallina* living in the fine sediments of the southern North Sea is suppressed when compared to specimens from coarse sediments (Witbaard et al., 2001). Field measurements show that regular resuspension of the fine sediment at the Frisian Front dilutes the food and lowers food quality for seston feeders (Duineveld & Boon 2002). This possibly explains the depressed growth rates. Various field and experimental studies have shown this to be the case in other areas with frequent resuspension (Grant et al. 1997, Cranford et al. 1998, Gremare et al. 1998, Urrutia et al. 1996, Emerson, 1990).

In the Northern North Sea, at 110 m, the extensive reworking of the bottom is attributed to be cause by the direct effect of surface waves (van Haren et al., 2003). Wave activity depends on wind direction and strength (van Haren, pers. communication). According to our measurements, we do think that the wind strengh has an indirect effect on the resuspension observed. Wave height would perhaps have been a better parameter to use instead of wind because it can be directly translated into a contribution to near bed shear velocity (Williams et al., 1998). Wave height data are however not available for our Frisian Front site while wind data being not as site specific, are amply available.

Our field observations in summer 2001 (Figure 6) showed that a current speed of 25 cm/s at a height of 50 cm above the seabed is required to resuspend the sediment. The comparison of the wind data with above lander measurements suggest that this critical erosion velocity is surpassed at potential wind speeds of 10 m/s (6 Bft). On basis of this comparison we took a minimum significant wind speed of 10 m/s to make an arbitrary separation between winds that do not and do evoke resuspension of fine sediments in the Oystergrounds. This threshold value is to some extent arbitrary because resuspension is caused by a combination of wind induced and tidally induced currents. The tidal period consequently affects the amount of wind necessary for resuspension i.e. at spring tide a smaller contribution from the wind (waves) is required than at neap tides. The correlation and response function analyses of shell growth and wind suggest that shell growth is particularly sensitive to winds from a northerly direction (Figure 3e). In autumn and early winter such winds tend to have a positive effect on shell growth but in spring the effect becomes significantly negative. This pattern becomes especially clear if strong winds from a WNW are studied.

According to Dickson et al. (1988) northern winds have a delaying effect on primary production and thus potentially could affect benthic food availability. We however could not demonstrate a relationship between shell growth and the CPR data, which makes it likely that other factors related to wind are important. Our in situ measurements suggests that the effect of wind on sediment resuspension plays a key role and could supply us with a mechanism which could explain the observed variations in shell growth. Rhoads & Young (1970) observed that increased turbidity in the water column had a significant negative effect on the growth of the suspension feeding bivalve *Mercenaria mercenaria*. In another experiment it was found that shell growth of bivalves decreased by a maximum of 38% during storm at high levels of phytoplankton and by 18% when phytoplankton levels were low (Turner & Miller, 1991).

Winds from a North Westerly direction have the longest possible fetch in the southeastern North Sea and result in long wave lengths. They will thus have a relatively large contribution to the near bottom currents and thus to the resuspension of fine bottom material in the southeastern North Sea. For *A. islandica* the spring period is the supposed main growing season (Jones 1980, Witbaard et al. 1994) and wind mediated resuspension in this period is likely to depress shell growth due to its negative effects on food quality.

Most likely this resuspension will not be limited to bivalves alone but will also apply to all interface feeders that need to sort nutritious particles from the near bed suspension (see next manuscript).

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REFERENCES

Abele, D., 2002. The radical life giver. Nature 420: 27

Aebischer, N., Coulson, J. & Colebrook, J., 1990. Parallel long-term trends across four marine trophic levels and weather. Nature 347: 753-754.

Amaro T., Duineveld, G. & Tyler, P., 2005. Does *Mya truncata* reproduce at it southern distribution limit? Preliminary information. Jour. Shellfish Res 24(1) (in press).

Amaro, T., Duineveld, G., Bergman, M., & Witbaard, R., 2003. Growth variations in the bivalve *Mya truncata*: a tool to trace changes in the Frisian Front macrofauna (southern North Sea)? Helgol Mar Res 57: 132-138.

Beaugrand, G., Brander, K., Lindley, J., Souissi, S. & Reid, P., 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664.

Bergman, M. & van Santbrink, J., 1994. A new benthos dredge (Triple D) for quantitative sampling of infauna species of low abundance. Neth J Sea Res 33: 129-133.

Beukema, J., Cadee, G., Dekker, R., 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. J. Sea Res. 48: 111-125.

Cook, E., 1985. A time series analysis approach to tree ring standardization: Tuscon University of Arizona, 171 pp.

Corten, A., 2001. Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. Fish Res. 50: 189-204.

Cranford, P., Emerson, C., Hargrave, B. & Milligan, T., 1998. In situ feeding and absorption responses of sea scallops *Placopecten magellanicus* (Gmelin) to storm induce changes in the quantity and composition of seston. J. Exp. Mar. Biol. Ecol. 219: 45-70.

Creutzberg, F., Wapenaar, P., Duineveld, G. & Lopez-Lopez, N., 1984. Distribution and density of the bentic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. Rapp p-v Reun cons Int. Explor. Mer. 183: 101-110.

Creutzberg, F., 1985. A persistent chlorphyll a maximum coinciding with an enriched benthic zone. In: Gibbs PE (ed) Proceedings of the 19th EMBS. Cambridge University press, Cambridge UK: 97-107.

Creutzberg, F. & Postma, H., 1979. An experimental approach to the distribution of mud in the southern North Sea. Neth. J. Sea Res. 13: 99-116.

Dekker, R. & Beukema, J., 1999. Relations of summer and winter temperatures with dynamics and growth of two bivalves *Tellina tenuis* and *Abra tenuis* on the northern edge of their intertidal distribution . J. Sea Res. 42: 207-220.

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

Drinkwater, K., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C., Ottersen, G., Pershing, A. & Walker, H., 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic Oscillation: climatic significance and environmental impact. Geophysical Monographs American Geophysical Union 134: 211-234.

Duineveld, G. & Boon, A., 2002. Short-term variations in the fluxes and composition of seston in near-bottom traps in the southern North Sea. Helgol. Mar. Res. 56: 140-148.

Emerson, C., 1990. Influence of sediment disturbance an water flow on the growth of the soft-shell clam *Mya arenaria* L. Can J Fish Aq Sci 47: 1655-1663.

Fritts, H., Blasing, T., Hayden, B. & Kutzbach, J., 1971. Multivariate techniques for specifing tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. J. Appl. Meterol. 10: 845-864.

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

Fritts, H., Vaganov, E., Sviderkaya, I. & Sashkin, A., 1991. Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width number of cells cell size cell wall thickness and wood density. Climate Res 1: 97-116.

Grant, J., Cranford, P. & Emerson, C., 1997. Sediment resuspension rates organic matter quality and food utilization by sea scallops (*Placopecten magellanicus*) on Georges Bank. J. Mar. Res. 55: 965-994.

Gremare, A., Amouroux, J., Chaabeni, Y. & Charles, F., 1998. Experimental study of the effect of kaolinite on the ingestion and the absorption of monospecific suspensions of *Pavlova lutheri* by the filter-feeding bivalve *Venus verrucosa*. Vie Milieu 48: 295-307.

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

Hagberg, J. & Tunberg, B., 2000. Studies on the covariation between physical factors and the long-term variation of the marine soft bottom macrofauna in western Sweden. Est Coast Shelf Sci 50: 373-385.

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

Hurrell, J., 1995. Decadel trends in the north Atlantic Oscillation: Regional temperatures and precipitation. Science 269: 676-679.

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

Jones, D., 1983. Sclerochronology: reading the record of the molluscan shell. Am. Sci. 71: 384-391.

Kröncke, I., Dippner, J., Heyen, H. & Zeiss, B., 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar. Ecol. Prog. Ser. 167: 25-36.

Lutz, R., Mann, R., Goodsell, J. & Castagna, M., 1982. Larval and early post larval development of *Arctica islandica*. J. Mar. Biol. Ass. U.K. 62: 745-769.

Mann, R., 1982. The seasonal cycle of gonadal development in *Arctica islandica* from the southern New England shelf. Fish. Bull. 80: 315-326.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. & Stenseth, N., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128: 1-14.

Pohlmann, T., 1996. Predicting the thermocline in a circulation model of the North Sea-Part I: model description calibration and verification. Cont. Shelf Res. 16: 131-146.

Ramon, M. & Richardson, C., 1992. Age determination and shell growth of *Chamelea gallina* (Bivalvia: Veneridae) in the western Mediterranean. Mar. Ecol. Prog. Ser. 89: 15-23.

Reid, P., Edwards, M., Hunt, H. & Warner, A., 1998. Phytoplankton change in the North Atlantic. Nature 391: 546.

Reid, P., Holiday, N. & Smyth, T., 2001. Pulses in the eastern margin current and warmer water off the north west European shelf linked to North Sea ecosystem changes. Mar. Ecol. Prog. Ser. 215: 283-287.

Roads, D. & Young, D., 1970. The influence of Deposit-feeding Organisms on Sediment Stability and Community Trophic Structure. J. of Mar. Res. 28: 150-178.

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

Schöne, B., Kröncke, I., Houk, S., Freyre Castro, A. & Oschmann, W., 2003. The cornucopia of chilly winters: ocean quahog (*Arctica islandica* L. Mollusca) master chronology reveals bottom water nutrient enrichment during colder winters (North Sea). Senck. Mar. 32: 165-175.

Schöne, B., Freyre Castro, A., Fiebig, J., Houk, S., Oschmann, W. & Kröncke, I., 2004. Sea surface water temperatures over the period 1884-1983 reconstructed from oxygen isotope ratios of a bivalve mollusk shell (*Arctica islandica*, southern North Sea). Paleo. 212: 215-232.

Turner, E. & Miller, D., 1991. Behaviour and growth of Mercenaria mercenaria during simulated storm events. Mar. Biol. 111: 55-69.

Urrutia, M., Iglesias, J., Navarro, E. & Prou, J., 1996. Feeding and absorption in *Cerastoderma edule* under environmental conditions in the Bay of Marennes-Oleron (western France) J. Mar. Biol. Ass. U.K. 76: 431-450.

Van Haren, H., Howarth, M., Jones, K. & Exxi, I., 2003. Autumnal reduction of stratification in the northern North Sea and its impact. Cont. Shelf Res. 23: 177-191.

Wieking, G. & Kröncke, I., 2001. Decadal changes in macrofauna communities on the Dogger Bank caused by Large-Scale climate variability. Senck. Mar. 31: 125-141.

Wilde, P., Berghuis, E. & Kok, A., 1984. Structure and energy demand of the benthic community of the Oyster Ground central North Sea. Neth. J. Sea Res. 18: 143-159.

Williams, J., Humphery, J., Hardcastle, P. & Wilson, D., 1998. Field observations of hydrodynamic conditions and suspended particulate matter in the southern North Sea. Cont. Shelf Res. 18: 1215-1234.

Witbaard, R., Jenness, M., Borg, K., van der Ganssen, G., 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., Franken, R. & Visser, B., 1997. Growth of juvenile *Arctica islandica* under experimental conditions. Helg. Meer. 51: 417-431.

Witbaard, R., Duineveld, G. & Wilde, P., 1999. Geographic differences in growth rates of *Arctica islandica* (mollusca: Bivalvia) from the North Sea and adjacent waters. J. Mar. Biol. Ass. U.K: 79 907-915.

Witbaard, R., Duineveld, G. & Bergman, M., 2001. The effect of tidal resuspension on benthic food quality in the southern North Sea. Senck. Mar. 31: 225-234.

Witbaard, R., Jansma, E. & Sass-Klaassen, U., 2003. Copepods link quahog growth to climate. J. Sea Res. 50: 77-83.

Witbaard, R. & Bergman, M., 2003. The distribution of *Arctica islandica* in the North Sea. What possible factors are involved? J. Sea Res. 50: 11-25.

The consequences of the changes in the abundance of *Callianassa subterranea* and *Amphiura filiformis* on the sediment erosion threshold at the Frisian Front (SE North Sea)

by

Teresa Amaro[1,] Gerard Duineveld, Magda Bergman, Marten Scheffer[2],

[1] Royal Netherlands Institute for Sea Research

P.O. Box 59 1790 AB Den Burg

The Netherlands

Tel. ++ 31 222 369300

Fax ++ 31 222 319674

amaro@nioz.nl

[2]Aquatic Ecology and Water quality management Group

Postbus 8080

6700 DD Wageningen

The Netherlands

Marten.Scheffer@wur.nl

(to be submitted)

Abstract

To study the effects of the changes in abundance of both *Amphiura filiformis* and *Callianassa subterranea* on sediment resuspension in the Frisian Front, we performed two laboratory experiments. Firstly we compared the impact of the distinctive species densities of *C. subterranea* and *A. filiformis* in the early eighties and the late nineties on the erosion threshold of sediment from the Frisian Front. The results indicated that the resistance of the sediment to erosion was on average lower with high densities of *C. subterranea* and low densities of *A. filiformis*, representing the situation in the late 1990's. A second experiment focusing on the effect of specifically *A. filiformis* densities on the erosion threshold showed that low densities of *A. filiformis* as found in the late nineties lowered the resistance to erosion. The experimental results indicate that the present-day species composition with high densities of *C. subterranea* and low densities of *A. filiformis* leads to a more frequent and enhanced resuspension of bottom materials which most likely hampers the recovery of the *A. filiformis* adult population.

Key Words: Resuspension threshold, *A. filiformis*, *C. subterranea*, suspension feeder, deposit feeder, Frisian Front.

Introduction

Benthic studies in the 1980's have shown that the passive suspension feeder *Amphiura filiformis* (Loo et al, 1996) had a widespread occurrence in the North Sea. Its major densities were mainly confined in fine grained and silty sediments at the Frisian Front (southern border of the Oyster Ground), and along the southern slope of the Dogger Bank. Their size distribution showed that juveniles were generally scarce at the stations with high densities of adults, whereas highest numbers of juveniles occurred at the stations with low adult abundances (Duineveld et al., 1987, O'Connor et al., 1983). For practical reasons, this species was monitored along the Frisian Front and especially at a single station, situated precisely at 53,70^{o}N, and 4,50^{o}E (see Part I). In here, densities were monitored annually since 1982. *Amphiura filiformis* was dense and dominated by adults and over a 10 years period (1982-1992) slowly raised with densities ranging from 1383 (stedv=233,8) ind./m^2 in 1982 to 1750 (stdev=581,5) ind./m^{-2} in 1992 (Part I). In 1993, however, a steep decline in numbers started and lasted till 1997 after which the *A. filiformis*, now being dominated by juveniles, reached another stable period but at a level of one magnitude lower than before the decrease (~100 ind.m^{-2}) (Part I).

Several hypotheses can be considered to explain why *A. filiformis* has not yet restored its high densities dominated by adults that used to exist in the Frisian Front before 1993. Studies have shown that variations in large-scale patterns of species' abundances are often correlated with changes in the physical environment, such as temperature (Ottersen et al., 2001), oxygen (Loo et al., 1996) and sediment grain size (Posey, 1986). Biotic interactions such as food competition and physical interference may also play a role. Concerning physical interference, it has become clear that resident animals can influence the local physical characteristics, by bio-stabilisation or biodestabilisation. Bio-stabilizers can either influence the hydrodynamics by protection the seabed (e.g. mussel beds, macroalgae, salt marsh macrophytes), or enlarging the critical erosion threshold by enhancing cohesiveness (e.g. microphytobenthos). In contrast, the feeding activity of mysids (Roast et al., 2004**)** and bottom fish (Sheffer et al., 2003), or the burrowing activity of dense populations of the amphipod *Corophium volutator* (de Deckere et al, 2000), act as destabilizers by increasing the surface roughness and so reducing the critical sediment erosion threshold leading to an enhance erodability (Widdows & Brinsley, 2002). Erosion of the sediment or resuspension occurs when the shear stress (friction of the water against the bottom) surpasses a minimum value (critical shear stress) and thus exceeds the strength of the sediment (the shear strength) (Tengberg *et al.,* 2003). The expulsion mounds produced by certain benthonic species have also the capacity to alter the seabed properties and erosinal processes (Rowden *et al*., 1998b). In the North Sea, for instance, the burrowing deposit feeder, *Callianassa subterranea* is known to construct a complex burrow consisting of several vertical shafts at a depth of up to 25 cm. According to several studies this species is responsible for transporting a considerable amount of sediment from depth to the surface and deposited as mounds around the exhalent opening. The annual production is estimated between 3,5 kg (Witbaard & Duineveld, 1989) to 11 kg dry expelled particles/m^2 (Rowden *et al*., 1998b). Both the expulsion mounds and the expelled particles contribute to lower the erosion threshold of the sediment by increasing bottom roughness (Rowden *et al*., 1998a). Striking is that this species showed an increased of its densities in the same area and at the same time that *A.filiformis* decreased, changing from 60 ind.m^{-2} in 1982 to 228 ind.m^{-2} in 1992 and to 319 ind.m^{-2} in 2000 (Part I).

The objective of this study is to determine whether the increased densities of the deposit feeder *C. subterranea* in combination with the low densities of *A. filiformis* can be responsible for the change in the sediment erosion threshold of the Frisian Front. To test this hypothesis a laboratory experiment was performed to measure the effect of the distinctive combinations in abundances of *C. subterranea* and *A. filiformis* as observed in the early 1980's and late 1990's on the sediment erosion threshold. To elucidate the role of *A. filiformis* that may either stabilize the sediment with its arms (Buchanan, 1964; Loo et al., 1996; Solan & Kennedy, 2002) or destabilize the seabed with its movements (Rowden *et al.*, 1998b), the effect of its specific densities in the early 1980's and late 1990's on the sediment threshold was determined in a second experiment. The impact of a lower sediment erosion threshold on the unsuccessful recovery of the adult *A. filiformis* population in the Frisian Front is discussed.

Material and methods

Collection and maintenance of sediment and species

Before the start of the laboratory experiments, we collected sediment at the standard station (53,70°N, and 4,5°E) located at the Frisian Front (figure 1).

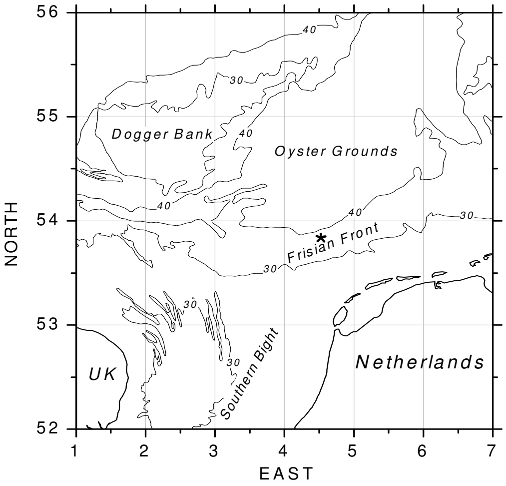

Figure 1 - Map of the southern North Sea showing the Frisian Front and the vicinity of the sampling station (53,70°N and 4,5°E).

In order to provide a suitable environment for both species to live in, eight barrels (diameter of 74 cm and a height of 130 cm) were filled with sediment (50 cm deep layer to create an environment as natural as possible for *C. subterranea*) collected with several boxcores in June 2003. In the laboratory, the sediment was defaunated by exposing the barrels to hot fresh water for two weeks. After all the organisms had died, the aerated barrels were placed in a climate room and supplied with running sea water with a salinity of ~34 mg/l and a temperature of ~11 °C to resemble the field situation (figure 2). A small cylinder (45cm diameter; 100 cm high) was placed in the center of each barrel to create a circular channel of water (0,28 m^2), in which the experiments were performed.

Prior the first experiment, the barrels were stoked with *A. filiformis* and *C. subterranea* in densities representative of the eighties and the nineties. Living specimens *A. filiformis* (total nr = 1800 individuals) and *C. subterranea* (total nr = 318 individuals) were collected with boxcores at the Frisian Front in in the vicinity of position 53,80^{o}N and 4,50^{o}E (figure1) in December 2003. To stock the barrels for the second experiment another 1800 specimens of *A. filiformis* were collected at the same site in February 2004. At sea, each *C. subterranea* was placed in a 10 cm box filled with sediment, whereas each 10 adult *A. filiformis* were kept in small plastic boxes filled with sediment. All boxes were placed in survival tanks with running seawater. After the cruise, both species were kept in a climate room (figure 2) with seawater temperature (11 °C) and salinity (34 mg/l) similar to the field situation.

Figure 2 - Barrels used in the experiment.

The set up of the experiments

After two weeks of acclimatization, *C. subterranea* (carapace length: 5,5 +/-1 mm) and *A. filiformis* (disc size: 5,1 +/- 0,8 mm) were evenly distributed with adhering sediment (to avoid extra stress) over the circular channels of the barrels. Only the largest sized specimen*s* from our samples were used to assure sufficient burrowing activity. During three weeks period, the specimens were fed with 1 ml of *Isochrysis* (Duineveld, pers. comm.) per day. Running seawater flowed constantly over the barrels to prevent the accumulation of food and depletion of oxygen.

For the first experiment four barrels were stocked with high densities of *A. filiformis* (1500 ind./m^2) and low densities of *C. subterranea* (36 ind./m^2), representing the situation at the standard station in the early eighties (exp. 1.1). These barrels were tested against four barrels with low densities of *A. filiformis* (107 ind./m^2) and high densities of *C. subterranea* (229 ind./m^2), representing the situation in the nineties after the collapse (exp. 1.2). The density of 319 ind./m^2 observed in later nineties was not possible to be provided for the experiment because not all *C. subterranea* had survived during the period of acclimatisation.

Prior to the second experiment the barrels were defaunated again and repopulated with *A. filiformis*, which had one week to acclimatise. Three barrels with high densities of *A. filiformis* (1464 ind./m^2) representing the densities in the eighties (exp. 2.1) were tested against three barrels with low densities of *A. filiformis*(107 ind/m^2) representing the late nineties (exp. 2.2). To measure the effects of species composition on the erosion threshold of the sediment a water current was generated with a stepwise increased velocity. To avoid that selective settlement of previously resuspended particles should influence the sediment characteristics, each experiment was executed as a single observation.

Measurements of sediment erosion resistance in the lab

The resistance of the sediment to erosion was measured by exposing it to a water flow of gradually increasing velocity. This was done with an instrument used by Scheffer et al. (2003) called hydrocopter. This instrument was placed over in the circular channel between the two cylinders of each barrel. Suspended from the rotor, four blades with an average distance of 30 cm above the sediment caused a water current of adjustable velocity. Tests revealed that the rotor speed had to be kept constant during 5 minutes to generate a stable level of turbidity in the channel. During the experiments the speed ranging from 2 till 19 Rounds Per Minutes (RPM) was stepwise increased with 1 rpm. Before starting the experiment the relationship of the rotor RPM and the actual water velocity was checked using a velocity meter (RC2 by Aqua Data, UK, accurancy 0,5 cm.s^{-1}) mounted 35 cm above the bottom. During the experiments the relative amount of resuspended particles sediment in the water was continuously measured with an OBS sensor (Seapoint^{TM}) situated below the paddles at 20 cm above the sediment. The instrument detects light (880 nm) scattered by particles suspended in water and generates an output voltage proportional to the turbidity or suspended solids.

This output is a measure of the relative turbidity, and thus indicative for the erosion threshold of the sediment. A data logger (Signatrol SL707) was used to record the rotor speed and associated turbidity every 8 seconds. Using current velocity (cm.sec-1) as converted from rotor speed and relative turbidity derived from the OBS, turbidity curves were constructed.

Measurements of turbidity, current velocity and wind speed at the Frisian Front

To collect data on the turbidity and current velocities, a NIOZ Lander was used. This instrument was equipped with a current meter (Falmouth Scientific Instruments™ 3dACM) and an Optical Backscatter Sensor (Seapoint™) and was deployed at 53,70^{o}N and 4,5^{o}E (our monitoring station). Both instruments were mounted 50 cm above the sediment, from which current speed and the resistance of the sediment to erosion were measured. After retrieval, the data on water current speed and turbidity were analysed in combination with the associated data on wind speed derived from the web (www.knmi.nl/hydra). The correlation between the wind, current speed and turbidity as quantified in the field was used to examine whether the V_{T50} values derived from the laboratory experiments were realistic for the field situation (see statiscical section for determination of V_{T50}).

For an adequate comparison between the field measurements and the laboratory experiment, we converted the current speed measured at 50 cm in the field to a recording height of 35 cm as used in the laboratory experiments. The conversion was based on a logarithmic velocity profile for the bottom boundary layer (Chriss & Caldwell, 1984) and the estimates for the seabed roughness of the Frisian Front were based on the estimations done by Rowden et al. (1998b).

Statistical analyses

To compare turbidity between treatments we used the half saturation speed V_{T50}, which approximates the water velocity at which erosion increases most steeply. This parameter was used as indicator of the resistance of the sediment to erosion by Scheffer *et al.* (2003). For each replicate in the experiment, the half saturation speed V_{T50} was estimated graphically. Within experiment 1 and 2, these V_{T50}'s were tested for statistically significant differences using a non-paramatic statistical test, the Kruskal Wallis test for 2 groups:

$$KW = \frac{12}{N(N+1)}\sum_{i=1}^{k} n_i \left(R_i - \frac{N+1}{2} \right)^2$$ with: n_i = sample size for each of the k groups

R_i = sum of ranks for group I

I = 1,2,….,k)

To get insight whether the differences in these V_{T50}'s are realistic for the field situation and can contribute to the explanation of the population shift of *A. filiformis* in the field, average of the half saturation speeds V_{T50} were compared with current regimes measured in the field.

Results

Measurements of turbidity, current velocity and wind speed at the Frisian Front

Results of the *in situ* measurements of current velocity and turbidity in the Frisian Front are depicted with their associated wind data in fig. 3. The start of the three major turbidity peaks (dotted lines) in the 6 weeks recording period coincided with wind speeds exceeding 10 $m.s^{-1}$ and current velocities beyond 25 $cm.s^{-1}$. At current speeds over 25 cm.s^{-1} (measured at 0.5 m height above the seabed) the critical shear stress exceeds the shear strength of the seabed at the Frisian Front.

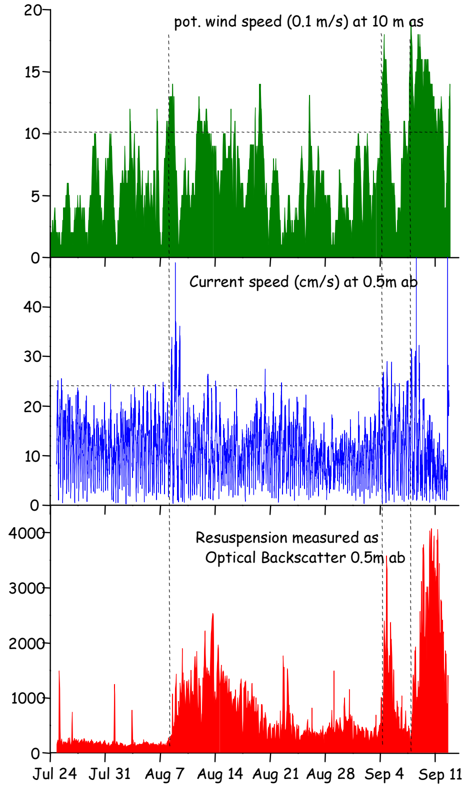

Figure 3 - Ambient current speed, resuspension and wind data measured during the period between 24th July and 12th September 2001 at the Frisian Front. Dotted line indicates an increase of the wind speed, current velocity and resuspension for the 7th July 2001 (for more explanation of this figure check previous manuscript).

We used this minimum *in situ* current speed to evaluate the significance of the sediment erosion threshold as observed in the laboratory experiments. The conversion of this current speed (25 cm.s^{-1}) to 35 cm above the seabed gives a critical current speed at the Frisian Front between ~18 - 22 cm.s^{-1} depending on the estimate of bed roughness.

Experiment 1

The aim of this experiment was to measure the effects of the changes from the different proportions of *C. subterranea* and *A. filiformis* that occurred in the 1980's and in the 1990's on the sediment erosion (threshold). In figure 4 the mean turbidity curves derived from single measurements in three (exp 1.1) and four (exp.1.2) replicate barrels are depicted.

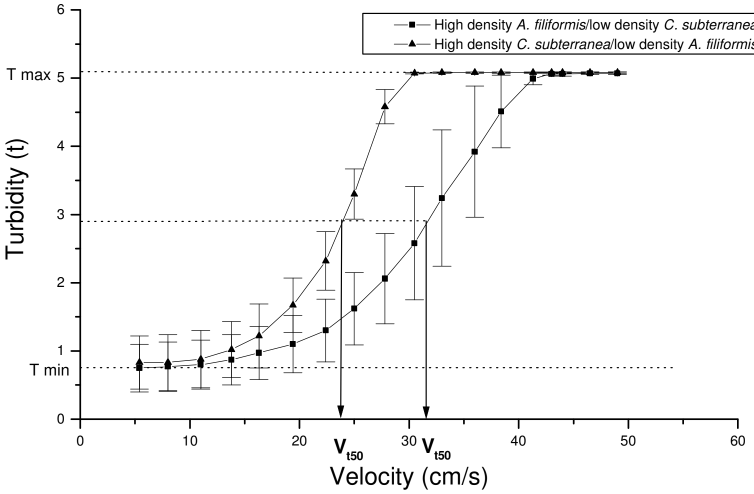

Figure 4 - Turbidity curves at different current velocity in experiment 1 (exp. 1.1 low densities of *C. subterranea* and high densities of *A. filiformis*; exp. 1.2 high densities of *C. subterranea* and low densities of *A. filiformis*). Mean V_{T50} of experiments 1.1 and 1.2 are depicted.

A failure of the OBS recording led to the attainment of only three replicates in experiment 1.1. The differences between the half saturation velocities V_{T50} of exp.1.1 and exp. 1.2 were statistically significant (χ^2: 4.5 (df 1), $p< 0.034$). This indicates that the sediment erosion threshold was lower with high densities of *C. subterranea* and low densities of *A. filiformis* (exp.1.2) representing the situation in the late 1990's. At a minimum current velocity of 22 $cm.s^{-1}$, where the critical shear stress in the field gave rise to resuspension of sediment, a statistically significant difference in the level of turbidity was found between exp 1.1 and exp. 1.2 ($\chi 2$: 4.50 (df 1), $p< 0.034$).

Experiment 2

The aim of this experiment was to measure the effects of the changes from the different proportions of *A. filiformis* on the sediment erosion (threshold). Figure 5 shows the mean turbidity curves for experiment 2.1 and experiment 2.2 from single measurements in the three replicate barrels.

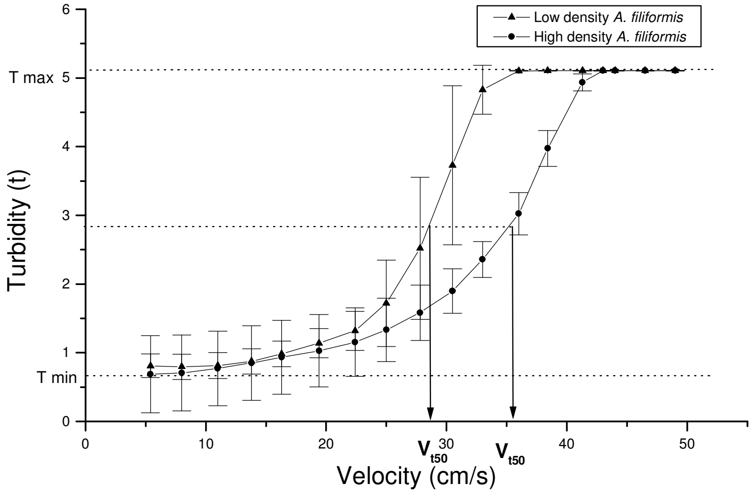

Figure 5 – Turbidity curves at different current speeds in experiment 2 (exp. 2.1 high densities of *A. filiformis*; exp. 2.2 low densities of *A. filiformis*). Mean V_{T50} of experiments 2.1 and 2.2 are depicted.

The differences in the half saturation velocities V_{T50} of exp.2.1. and exp. 2.2 were statistically significant (χ^2: 3.86 (df 1), $p< 0.049$), indicating that the sediment erosion threshold was lower with low densities of *A. filiformis* (exp.2.2) representing the situation in late nineties. At a minimum current velocity of 22 cm.s^{-1}, where the critical shear stress in the field gave rise to resuspension of sediment there was no statistically significant difference in the level of turbidity between exp.2.1 and exp. 2.2 (χ^2: 1.190 (df 1), $p< 0.275$)

Discussion

The reason to undertake this study was to find indications whether the steady increase in *C. subterranea* along with the collapsed densities of *A. filiformis* in he early nineties could have lowered the sediment erosion threshold of the Frisian Front. A next question was whether a lowered threshold could have been the reason for the failure of the adult *A. filiformis* population.

Results of experiment 1 (figure 4) indicated that the differences in the half saturation velocity V_{T50} obtained from both density combinations were statistically significant. High densities of *C. subterranea* and low densities of *A. filiformis*, representing the situation after the collapse of *A. filiformis* in the early nineties, led to a lower erosion threshold of the sediment than the inversed density composition in the early eighties. The high variance in both experiments can be explained due to the patchy distribution of the species in the circular channels that led to different contributions of bare sediment. This might have influenced the critical erosion strength and thus the level of turbidity measured. Since both species buried themselves in the sediment, we could not see the distribution and record the degree of patchiness in the experimental sets.

The question arises whether the conditions of the experiments can be comparable to the field situation. In other words if the current speed and critical shear stress at which turbidity starts in the laboratory experiments is realistic in the present field situation. In the laboratory, the critical erosion speed in experiment 1.2 (situation 1990) lies between 15 and 20 cm.s^{-1} when measured at 35 cm above the bottom (figure 4). In 2001, current speeds over 25 cm.s^{-1} (measured at 50 cm) above the seabed (fig.3) gave rise to resuspension of sediment in the Frisian Front (figure 3). After conversion (see results), the critical current speed was determined to be between ~18 - 22 $cm.s^{-1}$. This range is somewhat above the values measured in the laboratory, but still very close to the values measured in the laboratory experiments. This might be due to the fact that various species common at the Frisian Front like tube-building polychaetes have a stabilising effect, but were absent in the experimental setting. So we think that the experimental results provide a realistic minimum current speed that generates the critical shear stress and thus applicable to the field situation at the Frisian Front.

The impact of characteristic densities of exclusively *A. filiformis* in the early 1980's and 1990's on the sediment erosion threshold was clarified in a second experiment. Results of experiment 2 indicated that the differences in the half saturation velocity V_{T50} obtained from the distinctive *A. filiformis* densities were statistically significant. High densities as in the early 1980's contribute to a significant higher erosion threshold. Thus, it seems that *A. filiformis* is improving the habitat conditions by stabilizing the sediment at least in comparison to the effect of *C. subterranea* has on the conditions of the sediment. This is in contradiction with earlier suggestions on the de-stabilising effect of high densities of *A. filiformis* assumed by Rowden et al. (1998b). However, Rowden *et al.* (1998b), did not measured the actual erosion threshold and the outcome of the second experiment clearly shows the opposite. In this experiment, the critical erosion speed at which turbidity starts was also compared to the field situation. Here, however, no significant difference in turbidity was found at the minimum current speed (22 $cm.s^{-1}$) generating the critical shear stress, suggesting that the significantly increased turbidity at this current speed in experiment 1.2 was mainly due to the high abundance of *C. subterranea*. *Callianassa subterranea* is known to construct a complex burrow being responsible for transporting a considerable amount of sediment from depth to the surface consisting of several vertical shafts at a depth of up to 25 cm

(Witbaard et Duineveld, 1989) and possibly causing a lot of resuspension by expelling sediment while creating their burrows (Rowden *et al.*, 1998a). Thus, when in high densities the bed roughness will be enhanced which will lead to a lower critical shear stress. This can be illustrated by calculations of the role of *C. subterranea* in the sediment resuspension in the North Sea by means of Z_0 (bottom boundary roughness) done by Rowden et al. (1998b). Values of Z_0 increased from 0,0007 cm in January, when the activity of these shrimps is low, to 0,79 cm in September, when this shrimp expulsion activity was at its peak. Higher bed roughness tends to lower the erosion threshold of the sediment, i.e. the sediment is resuspended at lower current speeds. An increase of *C. subterranea* densities as took place in the 1990's would thus mean that resuspension begins at lower current velocities than previously in the 1980's when densities were relatively low. This implies that at present resuspension will happen more frequently at the Frisian Front, since this lower current speed of ~25 $cm.s^{-1}$ at 50 cm above the seabed needed to generate the critical shear stress (fig.2) will occur more regularly than the higher speed that was necessary to initiate resuspension in the early 1980's.

The minimum current speed is induced by a combination of tide and surface waves (Van Haren, pers. communication). The latter is controlled by wind. According to figure 2, the minimum speed to induce resuspension is only reached in case of wind forces higher than Bft 5 (>10 m.sec-1; fig.2). According to series of high resolution wind data such wind forces occurred about 20% of the year at the Frisian Front in 2001 (www.knmi.nl/hydra). Since such wind speeds do occur in the offshore North Sea in the last decade (See manuscript page 88) and particles settle down very slowly (fig 2), the Frisian Front fauna is exposed more frequently to longer periods of high turbidity than in the eighties.

At present, resuspension at the Frisian Front might be further facilitated by the increase of other engineering species like *Upogebia* spp. (Duineveld, non published data). *Upogebia* burrows to a depths of 40 cm (Duineveld ea prep) and expels settled material during digging activities. This bioturbator also showed a steep increase in numbers between 1982 (5 ind.m^{-1}) and 1997-‘99 (100 ind.m^{-1}), along a transect up to 10 km north and south of the standard station (53,70^{o}N and 4,50^{o}E). At this standard station densities steadily increased from 1982 (3 ind.m^{-1}) to 1997 (50 ind.m^{-1}), since then followed by a period of mean densities of *circa* 20 ind.m^{-1}. The impact of such a density increase on the erosion threshold of the sediment is not measured, but it seems plausible that this threshold is lowered by higher abundances generating a higher bottom boundary roughness.

Although the reason for the collapse of *A. filiformis* lies beyond the scope of this paper it is striking that this break down of numbers is not a local phenomenon. Schroder (2003) describes a similar collapse of *A. filiformis* 85 miles to the northeast at the White Bank in a fine-grained (median grain size 150µm) and silty (5-10%) sediment. From 3000 ind.m^{-2} in 1992, the population decreases up to 116 ind.m^{-2} in 1996. In contrast to the Frisian Front, here the population recovered and in 1998 the *A filiformis* population was normalized again. In this area no signs were observed of growing populations of engineering species like *C. subterranea* and *Upogebia* spp. over the last 2 decades. This might underline the role of enhanced densities of burrowing species in the non-recovery of an adult *A. filiformis* population at the Frisian Front, possibly mediated by enhanced resuspension.

More frequent and longer periods of enhanced resuspension might work adversely on the recovery of an adult population of the interface suspension feeding *A. filiformis*, since it causes dilution of the suspended food particles. Rhoads & Young

(1970) observed that increased turbidity in the water column had a significant negative effect on the growth of the suspension feeding bivalve *Mercenaria mercenaria*. In another experiment it was found that shell growth of bivalves decreased by a maximum of 38% during storm at high levels of phytoplankton and by 18% when phytoplankton levels were low (Turner & Miller, 1991). Duineveld & Boon (2002) showed that resuspension of the fine sediment at the Frisian Front causes dilution of the organic fraction in the seston and thus lower the food quality for seston feeders. Comparison of growth in the interface feeding bivalves *Chamelea gallina* and *Arctica islandica* and the sea urchin *Echinocardium cordatum* showed that the skeletal growth was faster in organically poor sediments than in the food rich, fine-grained Frisian Front (Witbaard et al, 2001). The authors point to the fact that in the silty frontal zone the food quality was poor as it was mixed with large amounts of resuspended silt that remain long in suspension, whereas in the coastal areas the coarser sand grains quickly settle at slack tide. This difference is believed to be an important mechanism behind the low growth in the frontal area. Since *A. filiformis* is also an interface suspension feeder, more frequent and longer periods with higher load of suspended solids caused by increased numbers of *C. subterranea* and other engineering species may interfere with its feeding efficiency. This may keep its population from optimizing its growth and reproduction.

Various studies point at the fact that next to the impact on food quality high densities of bioturbators like *C. subterranea*. may alter the seabed dynamics and may inhibit settlement and survival of recruits. Settlers in an unstable silty seabed inhabited by burrowing shrimps may suffer mass juvenile mortality (Roads & Young, 1970). Frequent erosion may also alter biogeochemical characteristics of sediments making them less attractive to settlers. Experiments showed that sediments when disturbed by biotic or physical disturbance were rejected by new recruits of *M. mercenaria* during the interval of biogeochemical disturbance and recovery (Marinelli & Woodin 2002, Woodin et al., 1998). Given the high numbers of juvenile *A. filiformis* in the Frisian Front area in the late nineties, however, negative impacts of enhanced erodability on larval settlement do not seem very relevant. Moreover, adverse relations between burrowing shrimps and a variety of other species are mentioned in literature. Spionid polychaetes (*Streblospio benedicti, Pseudopolydora kempi*), the amphipod *Corophium acherusicum*, and the tanaid *Leptochelia dubia* were significantly more abundant when *C. californiensis* was excluded as compared to when the latter were present (Posey, 1986). Posey (1991) also proposed that dense aggregations of *U. pugettensis* could be responsible for the local community composition In New Zealand tidal flats. *Callianassa filholi* is held to be related to dissimilarities in benthic community structure between sites of low and high shrimp density (Berkenbusch et al., 2000).

Based on the experiments described in this paper it can be concluded that resuspension and subsequent turbidity at the Frisian Front is probably intensified by the increase in density of *C. subterranea* plus the concomitant drop in *A. filiformis* numbers. This more frequent and enhanced resuspension most likely inhibits the recovery of the adult *A. filiformis* population. The detailed effects of this exaggerated resuspension on the settlement, growth, mortality and reproduction of *A. filiformis* need to be studied. Given the negative impacts of resuspension and turbidity on seston feeders in general, it seems unlikely that the *A. filiformis* population is able to restore itself.

Acknowledgments

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References

Berkenbusch, K., Rowden, A., Probert, P., 2000. Temporal and spatial variation in macrofauna community composition imposed by ghost shrimp *Callianassa filholi* bioturbation. Mar. Ecol. Prog. Ser., 192: 249-257.

Buchanan, J. & Moore, J., 1986. A broad review of variability and persistence in the Northumberland benthic fauna - 1971-85. J. Mar. Biol. Ass. U.K. 66: 641-657.

Chriss,T. & Caldwell, D., 1984. Universal similarity and the thickness of the viscous sublayer at the ocean floor. J. Geoph. Res. 89: 52-69.

De Deckere, E., 2003. Faunal influence on sediment stability in intertidal mudfats. Ph.D.Thesis. Groningen University. 112 pp.

Duineveld, G.. &. Noort, G., 1986. Observations on the population dynamics of *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the Southern North Sea and its exploitation by the dab, L*imanda limanda*. Neth. J. of Sea Res. 20(1): 85-94.

Duineveld, G., Kunitzer, A. & Heyman, R., 1987. *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. Neth. J. of Sea Res. 21(4): 317-329.

Duineveld, G. & Boon, A., 2002. Short-term variations in fluxes and composition of seston in near-bottom traps in the southern North Sea. Helg. Mar. Res., 56: 140-148.

Loo, L.-Ove., Jonsson, P., Skold, M & Oarlsson, O., 1996. "Passive suspension feeding in *Amphiura filiformis* (Echinodermata: Ophiuroidea): feeding behaviour in flume flow and potential feeding rate of field populations. Mar. Ecol. Prog. Ser. 139: 143-155.

Marinelli, R. & Woodin, S., 2002. Experimental evidence for linkages between infaunal recruitment, disturbance, and sediment surface chemistry. Limnol. Oceanogr., 47(1): 221-229.

O'connor, B., Bowmer, T. & Grehan, A., 1983. Long-Term Assessment of the Population-Dynamics of *Amphiura-Filiformis* (Echinodermata, Ophiuroidea) in Galway Bay (West-Coast of Ireland). Mar. Biol., 75 (2-3): 279-286.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P., Stenseth, N., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128: 1-14.

Posey, M., 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. Mar. Ecol. Prog. Ser. 31:15-22.

Posey, M., Dumbauld, B. & Armstrong, D., 1991. Effects of a burrowing shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. J. of Exp. Biol. and Ecol. 148: 283-294.

Roads, D. & Young, D., 1970. The influence of Deposit-feeding Organisms on Sediment Stability and Community Trophic Structure. J. of Mar. Res. 28:150-178.

Roast, S., Widdows, J., Pope, N. & Jones, M., 2004. Sediment-biota interactions: mysid feeding activity enhances water turbidity and sediment erodability. Mar. Ecol. Prog. Ser. 281: 145-154.

Rowden, A., Jago, C., & Jones, M., 1998a. Influence of benthic macrofauna on the geotechnical and geophysical properties of surperficial sediment, North Sea. Cont. Shelf Res. 18: 1347-1363.

Rowden, A., Jones, M. & Morris, A., 1998b. The role of *Callianassa subterranea* (Montagu) (Thalaasinidea) in sediment resuspension in the North Sea. Cont. Shelf Res. 18: 1365-1380.

Scheffer, M., Portielje, R. & Zambrano, L., 2003. Fish facilitate wave resuspension of sediments. Limn. and Ocean. 48(5): 1920-1926.

Schroeder, A., 2003. Community dynamics and development of soft bottom macrozoobenthos in the German Bight (North Sea) 1969-2000. PhD thesis, Univ. Bremen, 265 pp.

Solan, M. & Kennedy, R., 2002. Observation and quantification of in situ animal-sediment relations using time-lapse sediment profile imagery (t-SPI). Mar. Ecol. Prog. Ser., 228:179-191.

Tengberg, A., Almroth, E. & Hall, P., 2003. Resuspension and its effects on organic carbon recycling and nutrient exchange in coastal sediments: in situ measurements using new experimental technology. J. of Exp. Mar. Biol. and Ecol. 285-286: 119-142.

Turner, E. & Miller, D., 1991. Behaviour and growth of *Mercenaria mercenaria* during simulated storm events. Mar. Biol., 111 55-69.

Widdows, J., Brinsley, M., 2002. Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. J. of Sea Res. 48, 143-156.

Witbaard, R. & Duineveld, G., 1989. Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu) (Thalassinidae) from the southern North Sea. Sarsia 74: 209-219.

Witbaard, R., Duineveld, G. & Bergman, M., 2001. The effect of tidal resuspension on bethic food quality in the southern North Sea. Senck. Marit. 31 (2): 225-234.

Woodin, S., Marinelli, R. & Lindsay, S., 1998. Process-specific cues for recruitment in sedimentary environments: Geochemical signals? J. Mar. Res., 56: 535-558.

Trophic relations in a macrobenthic community at the Frisian Front (S north sea) based on δ ^{13}C, δ ^{15}N isotopes with special emphasis on *Amphiura filiformis* (ECHINODERMATA, OPHIUROIDEA) and thallassinid shrimps

by

Gerard Duineveld*, Magda Bergman, Teresa Amaro

Royal Netherlands Institute for Sea Research

P.O. Box 59

1790 AB Den Burg

The Netherlands

Fax ++ 31 222 319674

* corresponding author

e-mail: duin@nioz.nl

(submitted)

Abstract

The possibility of trophic interactions between interface suspension-feeding brittlestar *Amphiura filiformis* and two burrow-dwelling mud shrimps *Callianassa subterranea* and *Upogebia deltaura* living in a silty sand community in the North Sea was investigated using their stable isotope signatures δ^{13}C and δ^{15}N. In an attempt to determine their trophic positions, isotopic signatures were analyzed of the most common species in the community, ranging from invertebrates to fish, and of bulk sediment and suspended particulate matter (SPM). The species were grouped according to feeding guild and the mean δ^{13}C and δ^{15}N of the groups were compared. Only carnivorous invertebrates and demersal fish had a δ^{15}N different, i.e. higher, from the other groups. No significant difference was found between δ^{15}N of suspension-feeders, interface deposit-feeders and deep deposit-feeders. With respect to δ^{13}C only fish were different. The δ^{13}C and δ^{15}N values of the sediment (0-15 cm) were invariably low and indicative of fresh organic matter. Values for SPM were higher and more variable. The maximum difference between δ^{15}N at the base (suspension feeders) and top (fish) of the food web was ~8 ‰ pointing to 3 trophic levels. However, the large variance of δ^{15}N within groups of suspension- and deposit-feeders did not permit assigning trophic levels to our species of interest *A. filiformis*, *C. subterranea* and *U. deltaura*. A statistical test of δ^{15}N of the three species showed no differences. Hence we cannot exclude that the three species compete for the same quality of organic matter. Such competition may contribute to the lack of recovery of the *A. filiformis* population after a dramatic decline in the early 1990's in the Frisian Front.

Keywords: Stable isotopes, *Amphiura filiformis*, thalassinid mud shrimps, North Sea, trophic levels

Introduction

Benthic assemblages dominated by the brittlestar *Amphiura filiformis* are common in fine sand throughout the North Sea and adjacent areas (Künitzer et al. 1992). High densities of *A. filiformis* are indicative for areas with enriched benthic food supply (Buchanan & Moore 1986, Josefson & Jensen 1992, Rosenberg 1995, Josefson & Conley 1997, O'Connor et al. 1983, Göransson 2002). In the southern North Sea, *A. filiformis* used to be particularly abundant at the Frisian Front along the southern border of the Oyster Grounds (Figure 1) where local gradients in depth and current speed give rise to enhanced deposition of fine (organic) particles (Creutzberg & Postma, 1979).

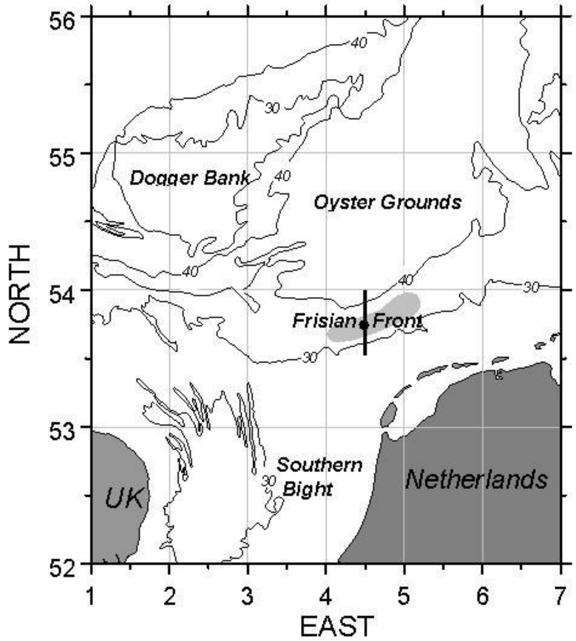

Figure 1 – Map of the Southern North Sea and the mud patch at the Frisian Front (shaded area). The vertical line represents a transect of 14 stations across the Frisian Front at 4,50°E (see Figure 4) and the • indicates the approximate position of the monitoring station (53,70°N).

Samples taken at a monitoring station in the Frisian Front since 1982 showed a drop in the density of *A. filiformis* in 1993 in concert with an increase of burrowing mud shrimps *Callianassa subterranea* and *Upogebia deltaura* (Part I, Duineveld, unpublished data). This shift followed a decade (1982-1992) with stable and high densities of adult *A. filiformis*. After the shift occurred, adult *Amphiura* numbers have remained more or less constant at a level of one order of magnitude lower (Part I). Causes of the actual shift are obscure (see Amaro et al. 2003). It is even more puzzling why the annually reproducing *Amphiura filiformis* is not able to regain dominance in their habitat. For instance on the White Bank (SE North Sea), *Amphiura filiformis* re-appeared with high densities within 5 years after a dramatic drop in the early 1990's (Schroeder 2003).

Hypothesis explaining the lack of recovery of *A. filifiormis* have been reviewed (previous manuscripts). One hypothesis involves food competition between *A. filiformis* and the burrowing shrimps. This may seem unlikely considering that *A. filiformis* is an interface suspension-feeder (Loo et al. 1996) whereas deep-dwelling *C. subterranea* and *U. deltaura* (see Figure 2) are recorded as deposit-feeder and suspension-feeder, respectively (Nickell & Atkinson 1995, Astall et al. 1997, Stamhuis et al. 1998).

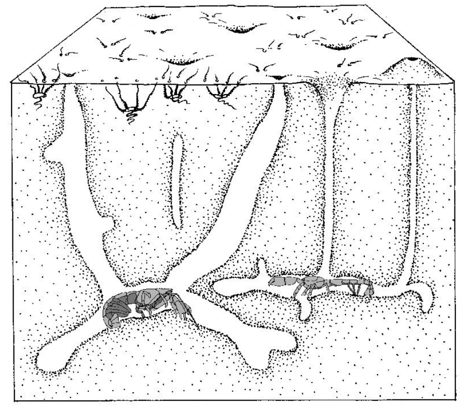

Figure 2 – Sketch of the position of *Amphiura filiformis*, *Callianassa subterranea* and *Upogebia deltaura* in the sediment. Burrow outlines are based on resin casts. Horizontal and vertical scale is 15 x 15 cm (not exact).

Judging from their feeding behaviour, *A. filiformis* presumably accesses fresh and thus high quality organic material while the deep-living shrimps, especially deposit-feeding *C. subterranea*, collect older and more refractory organic matter. If above assumptions are correct, competition between *A. filiformis* and the mud shrimps for seasonally fresh input will be limited since the fine sediment of the Frisian Front contains a relatively large buffer of refractory organic material (C_{org} 0.2 %). Competition, however, will become more intense if deep-living shrimps also require fresh material. This could consist of particles that either escape through the sieve of *A. filiformis* arms and are mixed deeper in the sediment or particles that passively or actively directly enter the vertical funnel-shaped openings of the shrimp burrows (Allanson et al. 1992, Nickell & Atkinson 1995). To determine if competiton for fresh food can play a role in the species shift precise information on food sources is needed. Thusfar all inferences are based on morphology and behavioral observations in the laboratory.

One method to establish whether the species belong to the same trophic level and thus likely compete for the same food source, is by means of their stable isotope signatures i.e. $\delta^{13}C$ and $\delta^{15}N$ (Fry & Sherr 1984, Michener & Schell 1994, Post 2002). Especially $\delta^{15}N$ is a useful tool to estimate trophic position because the heavier nitrogen isotope accumulates in the consumer with each successive trophic transfer by approximately 3-4 ‰ relative to its diet (DeNiro & Epstein 1978, Minagawa & Wada 1984, Post 2002). The ratio of carbon isotopes, in contrast, changes little (1 ‰ or less) as carbon moves through food webs and therefore can be typically used to evaluate the ultimate carbon source for an organism when sources differ in $\delta^{13}C$ signature, e.g. terrestrial vs marine C (Fry & Sherr 1984, Davenport & Baxter 2002, Post 2002).

Moreover δ^{13}C is sensitive to variation of the lipid content of animal tissue (Monteiro et al. 1991, Iken et al. 2001, Lorrain et al. 2002).

In this study we present carbon and nitrogen stable isotopic signatures (δ^{13}C, δ^{15}N) of *Amphiura filiformis*, thalassinid shrimps and of other common macro-organisms in the Frisian Front community. We additionally analysed stable isotopes in putative food sources such as sediment and suspended particulate matter. Measurements were made in different periods of the year to compensate for seasonal variation in isotopes (Vizzini & Mazzola 2003) though study of seasonal variation was outside the scope of this study. With the isotope data we make an attempt to estimate the number of trophic levels in the food chain of the Frisian Front community. On the basis of the relative positions of the species of interest in the trophic chain, we discuss the likelihood of competition.

Material & Methods

Study site

The Frisian Front is an area in the southern North Sea lying just north of the 30 m isobath between the permanently mixed shallow Southern Bight and the (summer) stratified, deeper Oyster Grounds (Figure1). The water depth across the Frisian Front area gradually increases from 25 to 40 m while maximum tidal current velocities decrease from 1.8 to 0.7 knots in south to north direction. These gradients are responsible for a transition from clean medium sand to muddy sand in the north (Creutzberg & Postma 1979). North of the 30 m isobath there is a narrow zone where the mud content peaks (25% particles <64 μm). This muddy zone is characterized by relatively high concentrations of sediment Corg (0.5 %) and a local maximum in macrofauna biomass (~25g AFDW m^{-2}). The brittle star *A. filiformis* used to account for a large proportion (~45%) of this biomass (Cramer 1991).

Sampling

Samples for this study were collected from at 53,80N, 4,50E in the zone with highest mud content (Figure 1). Samples were collected in three different periods viz. April 2002, August 2002 and June 2003. In April and August 2002, organisms were collected with a Triple-D dredge which excavates a surface area of 20 m^2 down to 18 cm depth (Bergman & van Santbrink 1994). In June 2003, specimens were collected with a 30 cm diameter boxcorer. Dredge and boxcore samples were washed on a 5 or 1 mm sieve, respectively, and residues were sorted on board for species of interest. Of the larger organisms, parts of muscle tissue (fish) or specific body parts (e.g. abdomen of crustaceans) were saved for isotopic analysis. Whole animals were used in case of small species. With bivalves, the soft tissue was always removed from the shells. All samples were stored at -80 oC directly on board of the ship. Isotopic analysis was performed on at least 2 samples composed of pooled whole or parts of organisms. The number of items in a pooled sample varied between 5 and 10.

In each cruise, two boxcore samples for sediment were taken which were subsampled with an acrylic corer of 4 cm diameter and 20 cm length. At selected depths (see Table 4) samples (10 cc) were taken out of the subcore, homogenized and frozen (-80 ^{o}C). In all three cruises 20 l of near-bottom water was collected with a CTD rosette-sampler for suspended particulate matter. The water samples were first sieved over 100µm netting in order to exclude zooplankton samples and then filtered over a glassfiber GF/F filter (0.7 µ).

Analytical technique

Before isotopic analysis all samples (sediment, animal or SPM filter) were freeze-dried, grinded in a mill mortar and homogenized. The technique used for the isotope analysis was elemental analyzer - isotope ratio mass spectrometry (EA-IRMS). The analyses were performed by Iso-Analytical Ltd. (Cheshire, UK). The δ^{13}C and δ^{15}N values reported here are defined as: δX=[(Rsample - Rstd)/Rstd] x 1000, where X=^{13}C or ^{15}N, and R=^{13}C/^{12}C or ^{15}N/^{14}N. Results are referred to Vienna PDB for C and to atmospheric nitrogen for N and expressed in units of ‰. At least 20% of the samples were analysed in duplicate for quality control. The reference material used in the analysis of tissue samples was NBS 1577a (bovine liver) with a δ^{13}C value of –21.68 ‰ vs. V-PDB and a δ^{15}N value of 7.25 ‰ vs air. NBS 1577a is traceable to IAEA-CH-6 (Sucrose) with an accepted δ^{13}C value of –10.40 ‰ vs V-PDB and IAEA-N-1 (Ammonium Sulfate) with an accepted δ^{15}N value of 0.40 ‰ vs air. For sediment samples, the reference used was Iso-Analytical flour with a δ^{15}N value of 2.55 ‰ vs air. The flour is traceable to IAEA-N-1 (Ammonium Sulfate) with an accepted δ^{15}N value of 0.40 ‰ vs air.

Statistical comparisons

Differences in mean isotopic signatures between groups of data were tested with a one-way anova using SPSS 11.7. Values from different periods of the year were pooled. When groups had unequal variances, as determined by the Levene statistic, the Brown-Forsythe statistic was used to test for the equality of group means instead of the F-statistic. To determine which group means were different from each other, a Tukey's HSD or Tamhane’s T2 post hoc test was applied in case of equal or unequal variances, respectively.

Results

A total of 72 taxa were identified in the samples taken during the 3 cruises of which 35 species were caught in sufficient numbers to be analysed for their isotopic signature (Table 1).

Table 1. Average δ^{13}C and δ^{15}N of the species in this study. Second column denotes the feeding group to which the species was assigned: isf - interface suspension-feeders, idf - interface deposit-feeders, sdf – subsurface deposit-feeder, ci - carnivorous invertebrates, cf - carnivorous fish. Species in each group are ranked according to δ^{15}N.

SPECIES	Group	δ^{13}C	δ^{15}N
Turitella communis	isf	-18.1 ± 0.9	8.5 ± 0.7
Nucula nitidosa	isf	-17.4 ± 0.0	9.1 ± 0.5
Spisula subtruncata	isf	-18.6	9.4
Corbula gibba	isf	-18.4 ± 2.0	9.7 ± 0.4
Arctica islandica	isf	-18.0	9.9
Chaetopterus spec.	isf	-18.8 ± 0.1	10.0 ± 0.3
Thracia convexa	isf	-19.7	10.4
Dosinia lupinus	isf	-18.3 ± 0.1	10.5 ± 1.8
Mya truncata	isf	-17.6 ± 0.2	10.8 ± 0.1
Chamelea gallina	isf	-19.2	11.3
Amphiura filiformis	isf	-20.6 ± 1.9	12.0 ± 0.6
Upogebia deltaura	idf	-19.6 ± 0.5	10.8 ± 0.3
Golfingia spp.	idf	-17.0 ± 0.3	11.0 ± 0.8
Cucumaria elongata	idf	-16.7 ± 0.7	12.5 ± 0.4
Owenia fusiformis	idf	-19.0	12.5
Callianass subterranea	sdf	-19.4 ± 0.4	10.9 ± 0.5
Notomastus latericeus	sdf	-15.9 ± 0.4	10.6 ± 0.4
Nephtys hombergi	ci	-15.7 ± 0.4	11.6 ± 0.9
Nereis longissima	ci	-15.8 ± 0.2	11.8 ± 0.6
Corystus cassivelaunus	ci	-18.2 ± 1.2	11.8 ± 1.2
Glycera spp.	ci	-17.5 ± 0.2	12.6 ± 3.0
Ophiura texturata	ci	-19.6	13.0
Ophiura albida	ci	-19.0 ± 1.2	13.1 ± 0.7
Liocarcinus holsatus	ci	-14.8 ± 0.8	13.8 ± 0.7
Astropecten irregularis	ci	-17.9 ± 0.8	14.3 ± 1.1
Pagurus bernhardus	ci	-16.1	14.8
Nephtys caeca	ci	-14.8	14.9
Sagartiocheton	ci	-18.4	14.9
Asteria rubens	ci	-14.9 ± 1.6	15.1 ± 0.1
Pleuronectes platessa	cf	-15.8	14.7
Buglossidium luteum	cf	-16.6 ± 1.2	14.8 ± 0.7
Limanda limanda	cf	-16.5 ± 0.5	15.3 ± 0.9
Arnoglossus laterna	cf	-17.7	15.4
Merlangius merlangus	cf	-16.2 ± 0.6	15.8 ± 0.3
Enchelyopus cimbrius	cf	-17.1	16.3

To give a comprehensive overview of the isotopic signatures belonging to the different trophic levels in the community which *A. filiformis*, *C. subterranea* and *U. deltaura* are part of, we classified the species according to their isotopic signature and feeding guild. For the latter we distinguished 4 groups on basis of published data on their feeding mode (cf. Flach et al. 1998) viz. 1) interface suspension feeders i.e. species collecting suspended particles with appendages or siphons, 2) interface depositfeeders taking deposited particles with appendages or siphons; 3) subsurface deposit-feeders feeding on particulate organic matter buried below the surface, 4) carnivorous invertebrates feeding on dead organisms. Demersal fish were treated as separate group because they can migrate between, and feed in different communities. Classification of *U. deltaura* remains ambiguous. This species is reported as suspension-feeder but lives in tunnels beneath the sediment surface. We provisionally assigned the species to the interface deposit-feeders as its food source possibly resembles the material lying at the surface of the sediment.

The outcome of this classification is shown in Figure 3.

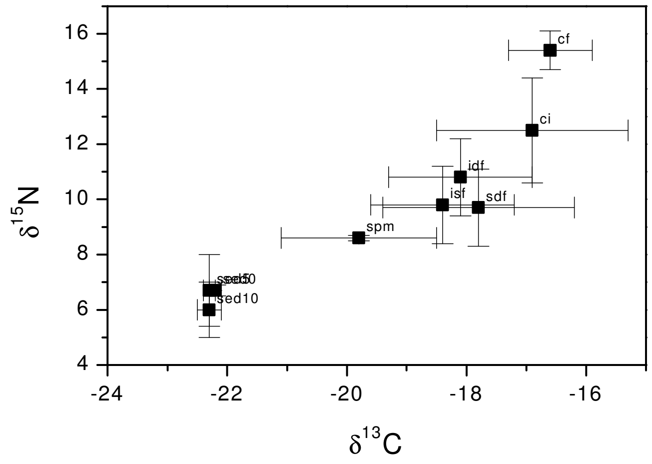

Figure 3 – Plot of δ^{13}C and δ^{15}N of the mean of the interface feeders, deposit feeders, predators, sediment and SPM for all the months sampled. The bars represent +/- st.dev.

The assumption underlying Figure 3 is that fresh organic matter i.e. the isotopically lightest fraction is consumed by interface feeders, and primarily by suspension feeders, while subsurface deposit feeders assimilate on average more recycled, older material which is isotopically more enriched (Kikuchi & Wada 1996, Iken et al. 2001). Predators consume representatives of above groups and therefore should have relatively heavy signatures. Since the $\delta^{15}N$ increases ~3 ‰ with each trophic level as opposed to 1 ‰ or less in $\delta^{13}C$, the largest differences between feeding groups were expected to concern $\delta^{15}N$ and we therefore primarily focus on $\delta^{15}N$.

Some of these assumptions are validated by the stable isotope signatures shown in Figure 3 despite the variation and overlap between groups. Lowest $\delta^{15}N$ signatures among the species that we caught consistently belong to interface suspension feeders in accordance with the above presumptions (Table 1). However, interface suspension feeders as a group do not differ in $\delta^{15}N$ from the group of organisms collecting deposited food from the sediment surface i.e. the interface deposit-feeders (Table 2).

Table 2. Post hoc test (Tukey/Tamhane's T2) between mean $\delta^{15}N$ and $\delta^{13}C$ of the feeding groups. Underlined comparisons are significantly different at $P < 0.05$.

$\delta^{15}N$	**isf**	**idf**	**sdf**	**ci**	**cf**
isf					
idf	.276				
sdf	.767	.723			
ci	.000	.180	.000		
cf	.000	.012	.000	.007	

$\delta^{13}C$	**isf**	**idf**	**sdf**	**ci**	**cf**
isf					
idf	1.000				
sdf	1.000	1.000			
ci	.078	.912	1.000		
cf	.002	.766	1.000	1.000	

Since the δ^{15}N ranges of the two groups are overlapping (see Table 1) there is most likely a gradual variation in the age of the organic matter assimilated by interface feeders rather than strictly separated sources.

Assuming that subsurface deposit-feeders assimilate more refractory (isotopically enriched) organic matter than organisms feeding at the sediment-water interface, δ^{15}N signatures of *C. subterranea* and *Notomastus latericeus* appear unexpectedly light in comparison to those of interface deposit- and suspension-feeders (Figure 3). The post-hoc test in Table 2 shows that mean δ^{15}N signature of pooled subsurface deposit-feeders does not differ from that of interface suspension- or deposit-feeders. In the context of this study it is important whether this conclusion also holds for our three target species viz. *A. filiformis, C. subterranea* and *U. deltaura*. The outcome of the post-hoc test in Table 3 shows that isotopic signatures of the three species are neither significantly different.

Table 3. Post hoc test (Tukey/Tamhane's T2) between mean δ^{15}N and δ^{13}C of three species of interest (see text). Underlined comparison are significantly different at $P< 0.05$.

δ^{15}N	**Amphiura filiformis**	**Callianassa subterranea**	**Upogebia deltaura**
Amphiura filiformis			
Callianassa subterranea	0.188		
Upogebia deltaura	0.158	1.00	

δ^{13}C	**Amphiura filiformis**	**Callianassa subterranea**	**Upogebia deltaura**
Amphiura filiformis			
Callianassa subterranea	0.905		
Upogebia deltaura	0.940	0.914	

Carnivorous invertebrates appear on average more enriched (heavier) in δ^{15}N than any of the forementioned groups (13.5 mean ± 1.3 sd.). This is in accordance with the premise that carnivorous invertebrates (partly) feed on members of forementioned groups. The mean δ^{15}N of carnivorous invertebrates is significantly different from most other groups at the 5 % level except in the case of interface deposit-feeders where the difference is marginally significant (Table 2). Carnivorous fish species had the highest δ^{15}N signatures (15.4 mean ± 0.6 sd.) in line with their assumed trophic position. The δ^{15}N of fish are significantly different from all the other groups (Table 2). Highest δ^{15}N values belong to the whiting *Merlangius merlangus* and the fourbearded rockling *Enchelyopus cimbrius* (Table 1). The difference in mean δ^{15}N between the fish and interface suspension-feeders is 5.6 ‰. The maximum difference between any two species in these two groups is 7.8 ‰.

The variation in δ^{13}C among the species within feeding groups was equal or sometimes even larger than with δ^{15}N (see Figure 3). This is unexpected given the conservative character δ^{13}C during transfer in the food web. Significant differences between δ^{13}C of feeding groups (Table 2) are limited to the groups at the base and the top of the food web i.e. interface suspension-feeders (-18.4 mean ± 0.7 sd.) and fish (-16.6 mean ± 0.7 sd.). The difference between mean δ^{13}C of the two groups is 1.8 ‰ and the maximum difference between any two species is 4.8 ‰.

The mean isotopic values of near-bottom SPM (suspended particulate matter) and sediment are shown in Table 4. The downcore differences of the sediment δ^{15}N and δ^{13}C are not significant (one-way Anova, p=0.309). The pooled δ^{15}N values of the sediment were significantly lower than all the organism groups. The same is true for the δ^{13}C of the sediment except for the difference with the group of subsurface deposit-feeders which has a particularly large variance in δ^{13}C. The differences between δ^{15}N and δ^{13}C of sediment and SPM are not significant which is due to the high values for the April SPM sample. Otherwise sediment and SPM differ significantly in terms of δ^{15}N but not in δ^{13}C.

Table 4. Mean δ^{13}C and δ^{15}N (+/- s.d.) of near-bottom suspended particle matter (SPM) and sediment collected in April, June and August.

	δ^{13}C	**δ^{15}N**
SPM bottom	-19.4 ± 1.2	10.0 ± 2.6
Sed 0 - 1cm	-22.1 ± 0.1	6.7 ± 0.3
Sed 4 - 5cm	-22.3 ± 0.2	6.9 ± 1.4
Sed 10 – 15 cm	-22.3 ± 0.1	6.0 ± 0.7

Discussion

Trophic levels background community

The objective of this study was to verify whether there is a potential trophic competition between the interface feeding *A. filiformis* and the burrowing shrimps *C. subterranea* and *U. deltaura*. The trophic position of species can only be properly evaluated having information on the range of δ^{13}C and δ^{15}N in the community and the trophic levels (Post, 2002). For this we plotted the isotopic signatures of the species of interest among the range of signatures in the background community including those of potential food sources (cf. Davenport & Bax 2002). The plot in Figure 3 shows a trend in δ^{15}N enrichment coinciding with a change in the presumed trophic position. Most prominently carnivorous invertebrates (crustaceans, polychaetes) and fish have higher δ^{15}N signatures compared to groups of deposit-and suspension feeders assimilating particles closer to the base of the food chain the community. Due to the wide variation in δ^{15}N in the latter groups, no differences could be established between the group means (Table 2). Causes for this wide variation could be of two types. Firstly group classification of the species on basis of literature could be incorrect and/or species show flexibility in feeding mode. Secondly potential food sources i.e. suspended, surface and buried organic particles, are isotopically not distinct enough. The latter appears true for surface and buried C and N since there was no signifiant downcore variation in $\delta^{15}N$ and $\delta^{13}C$ and values are moreover very close (Table 4). Also the difference between SPM and sediment is ambiguous.

Nevertheless, in spite of the variation within groups and lack of distinction between potential sources, some species seem to be consistently 'lighter' in N than others. One of these species is the gastropod *Turritella communis* having an average $\delta^{15}N$ of 8.5 ‰ (s.d. +/- 0.7). Assuming that *Turritella* assimilates the isotopically lightest fraction of organic material (N) available to the macrobenthic community, and *Enchelyopus cimbrius* represent the top trophic level (Table 1), the maximum range of $\delta^{15}N$ in the community becomes 8.5 – 16.3 ‰. The ~ 8 ‰ difference that we found in $\delta^{15}N$ between the supposed base of the food chain and demersal fish is within the range of values reported by Jennings & Warr (2003) for a much wider part of the North Sea. It also conforms to the value by Das et al. (2003) for the southern North Sea. Moreover our values for base $\delta^{15}N$ (suspension feeding bivalves) matches values reported by Jennings & Warr (2003) and Das et al. (2003).

With the lowest trophic level having a $\delta^{15}N$ of 8.5 ‰, the corresponding basic food source would have a $\delta^{15}N$ ~ 5 ‰ if a mean enrichment of 3.4 ‰ per trophic transfer (Minagawa & Wada 1984, Post 2002) is adopted. Clearly our $\delta^{15}N$ values for SPM are not that low (Table 1) taken that SPM is their food source. Mismatch between assumed base food and lowest trophic level in benthic food webs is often explained by selective assimilation (e.g. Riera et al. 2002) though the process starts with selective ingestion (e.g. Savina & Pouvreau 2004, Ward & Shumway 2004). Davenport & Baxter (2002) report $\delta^{15}N$ enrichment between 0.8 and 1.4 ‰ for uptake of SPM by marine filter-feeding molluscs while Lorrain et al. (2002) found values above 3.4 ‰ in scallops compared to near bottom SPM. More in general, Post (2002) depicts the wide variation in enrichment at single trophic transfers underlying the overall mean value of 3.4 ‰. Besides species variability in particle selection, assimilation and excretion, any spatial variation in particle composition within bulk sediment and SPM (e.g. Buscail et al. 1995, Grant et al. 1997, Zimmerman & Canuel 2001) further contributes to the variance in δ^{15}N among organisms near the base of the food web (Table 1). Variance in δ^{15}N at the base is likely propagated higher up the food chain. This may partly explain the wide range in δ^{15}N of invertebrate carnivores as in Table 1.

The difference in δ^{15}N between base and top of the Frisian Front food web i.e. ~8 ‰ points to 3 trophic levels taking a 3.4 ‰ enrichment. The ~8 ‰ corresponds with other North Sea data (see above) but the estimated number of trophic levels is tentative for several reasons. One is doubt about general applicability of 3.4 ‰ (Post 2002). The wide variation in δ^{15}N among species supposedly all feeding at the base of the food web is significant in this respect (Table 2). Another reason is that in our samples we missed the smallest interface feeders like spionid polychaetes and phoronids which may alter the δ^{15}N range of the community. For similar reasons, Jennings et al. (2001) refrained from assigning the epifauna benthos they caught in the North Sea to specific trophic levels. They instead used presumed linearity between trophic level and δ^{15}N to assess changes in trophic position within and between communities. Following Jennings et al. (2001) we will use statistical differences in δ^{15}N between species of interest to determine whether there is potential trophic competition.

Species of interest

The burrowing brittlestar *A. filiformis* is a passive suspension feeder that holds its arms up in the flow and traps both non-living particulate suspension matter and phytoplankton (Buchanan 1964, Loo et al. 1996, Solan & Kennedy 2002). *Callianassa subterranea* is a subsurface deposit-feeder digging up and sorting sediment in its burrow (Stamhuis et al. 1998). According to Nickell & Atkinson (1995), *C. subterranea* could supplement its diet by suspension feeding but no visual records of this activity have been reported as far as we know. The other shrimp *U. deltaura* is reported to be primarily a suspension-feeder filtering particles from the irrigation flow through its burrow (Lindahl & Baden 1997, Astall et al. 1997, Pinn et al. 1998). Based on their feeding mode and the principal particles source i.e. near bottom water or sediment, we assume that *A. filfiormis* is able to access the freshest particles, followed by *U. deltaura* while *C. subterranea* would be supplied with more recycled i.e. decomposed material. We therefore hypothesised that the three species differed in δ^{15}N reflecting the age of particles they ingested. This hypothesis is based on earlier studies showing that older i.e. more decomposed sedimentary organic matter is isotopically enriched in comparison to POM (Mishima et al. 1999, Davenport & Baxter 2002, Riera et al. 2002). On basis of the results Table 3 our hypothesis must be rejected. Hence despite the fact that *A. filiformis* is an interface-feeder while *U. deltaura* and *C. subterranea* are feeding inside burrows, all three seem to feed at the same trophic level. Some additional support for the contention that the three species ingest the same quality organic material is the occurrence of chlorophyll-a in Frisian Front cores down to 15 cm depth (Figure 4) (see also Boon & Duineveld 1998). Because of chlorophyll-a is a highly labile compound (Wakeham et al. 1997) its presence deep in the sediment points to rapid as well as deep mixing. These observations are in line with those of Dauwe et al. (1999) who found relatively high concentrations of highly degradable enzymatically hydrolysable amino acids (EHAA) deep in the Frisian Front sediment.

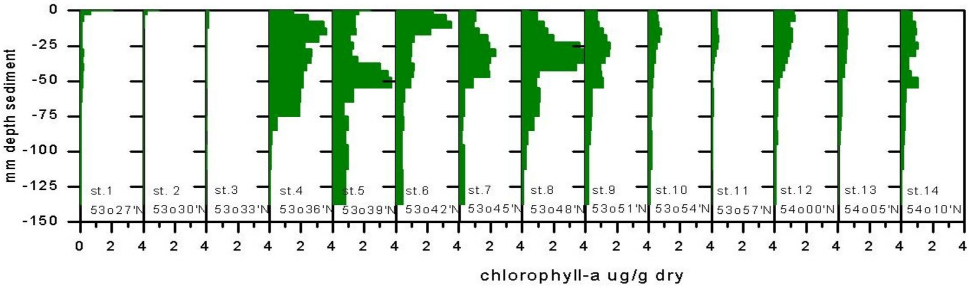

Figure 4 – Downcore profiles of chlorophyll-a along a transect across the Frisian Front (see Figure 1) sampled in June 2000 (Duineveld unpubl.). Station 6 is the monitoring station.

There are alternative explanations for the light δ^{15}N signature of the Frisian Front sediment that do not involve fresh OM. Mineralisation of the organic matter pool in the sediment may result in an increased proportion of ^{15}N-depleted inorganic nitrogen. Further fixation of 'light' ammonium produced during mineralisation to clay particles may decrease the δ^{15}N ratio as well (Freudenthal et al. 2001, Schubert & Calvert 2001). Also the relative importance of denitrification in the many suboxic burrows at the Frisian Front (Howe et al. 2004) could contribute to a low δ^{15}N signature. Sedimentary denitrification has little effect on N-isotope fractionation (Lehmann et al. 2004) and thus does not lead to an increase of δ^{15}N. Most likely, however, fresh OM does play a role in the light δ^{15}N signature since δ^{13}C values that were relatively low as well (Figure 2, Table 4) and in the range reported for pelagic phytoplankton carbon (Lorrain et al. 2002).

The SPM as we sampled in this study had a more decomposed signature than bulk sediment though differences in δ^{15}N and δ^{13}C were marginally (in)significant due to variance in SPM values. Nevertheless we had expected SPM to be the primary food source for the suspension feeders at the Frisian front like *A. filiformis*. One explanation for our SPM values would be that the finest SPM fraction that is in long-term suspension (Jago et al. 1993) and thus advected over long distances, contains more decomposed OM than the sediment. Resuspension of locally produced OM from the sedimentary matrix by tidal currents may temporarily lower the bulk SPM isotopic signature but never below that of the sediment. Moreover, fresh and isotopically light detrital aggregates deposited during algae blooms have high settling velocities (Jago et al. 1993) thus tend to remain on the seabed or only for short periods in suspension. Tidal resuspension is a cause for short term temporal variation in SPM quality and we should have accounted for this variation if logistics would have allowed. Apart from above temporal variation, SPM quality also varies with height above the seabed due to hydrodynamic sorting. Profiles of organic compounds (e.g. pigments) typically show enhanced concentrations in close proximity (cm's) of the seabed (e.g. Thomsen & van Weering 1998, Jähmlich et al. 1999). Conventional methods like the rosette sampler we used do not allow samples to be taken at heights that are relevant for infaunal organisms (Duineveld & Boon 2002). This nutritious near bead flow is shared by *Amphiura* and *Upogebia* when the latter irrigates its burrow. If passive irrigation occurs (see Allanson et al. 1992) this would directly be of benefit to *Callianassa* living deep down in the sediment. Otherwise *Callianassa* is dependent on particles trapped by the funnel shaped burrow opening or particles rapidly mixed below the surface after they are deposited during decreasing currents (Duineveld & Boon 2002).

In summary, isotopic evidence in this study supplemented by other observations strongly indicate that the food sources of the three species in question are much closer in origin than would be anticipated from their feeding mode. Hence we do not exclude competitive effects between the species.

Acknowledgements

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References

Allanson, B., Skinner, D. & Imberger, J., 1992: Flow in prawn burrows. Estuarine, Coastal and Shelf Science, 35: 253-266.

Amaro, T., Duineveld, G., Bergman, M. & Witbaard, R., 2003: Growth variations in the bivalve *Mya truncata*: a tool to trace changes in the Frisian Front macrofauna (southern North Sea)? Helgoland Marine Research, 57: 132-138.

Astall, C., Taylor, A. & Atkinson, R., 1997: Behavioural and physiological implications of a burrow-dwelling lifestyle for two species of Upogebiid mud-shrimp (Crustacea: Thalassinidae). Est. Coast. and Shelf Sci., 44: 155-168.

Bergman, M. & van Santbrink, J., 1994: A new benthos Dredge ("Triple-D") for quantitative sampling of infauna species of low abundance. Neth. J. Sea Res., 33: 129-133.

Boon, A. & Duineveld, G., 1998: Chlorophyll a as a marker for bioturbation and carbon flux in southern and cenral North Sea sediments. Mar Ecol Prog Ser, 162: 33-43.

Buchanan, J., 1964. A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution. J. of the Mar. Biol. Ass. of the U. K., 44: 565-576.

Buchanan, J. & Moore, J., 1986: A broad review of variability and persistence in the Northumberland benthic fauna - 1971-85. J. of the Mar. Biol. Ass. of the U. K., 66: 641-657.

Buscail, R., Pocklington, R. & Germain, C., 1995. Seasonal Variability of the Organic-matter in a medimentary moastal environment - sources, degradation and accumulation (Continental-Shelf of the Gulf-of-Lions, Northwestern Mediterranean-Sea). Cont. Shelf Res., 15: 843-869.

Cramer, A., 1991. Benthic metabolic activity at frontal systems in the North Sea. PhD Thesis, University Amsterdam, 92 pp.

Creutzberg, F. & Postma, H., 1979. An experimental approach to the distribution of mud in the Southern North Sea. Neth. J. of Sea Res., 13: 99-116.

DeNiro, M. & Epstein, S., 1978. The influence of diet on the distribution of carbon isotopes in animals. Geoch. et Cosmo. Acta, 45: 341-351.

Das, K., Lepoint, G., Leroy, Y. & Bouquegneau, J., 2003. Marine mammals from the southern North Sea: feeding ecology data from δ^{13}C and δ^{15}N measurements. Mar. Ecol. Prog. Ser., 263: 287-298.

Davenport, S. & Baxter, N., 2002. A trophic study of a marine ecosystem of southeastern Australia using stable isotopes of carbon and nitrogen. Can. J. of Fish. and Aqu. Sci. 9: 514-530.

Dauwe, B., Middelburg, J., Van Rijswijk, P., Sinke, J., Herman, P. & Heip, C., 1999. Enzymatically hydrolyzable amino acids in North Sea sediments and their possible implication for sediment nutritional values. J. of Mar. Res.. 57: 109-134.

Duineveld, G. & Boon, A., 2002. Short-term variations in the fluxes and composition of seston in near-bottom traps in the southern North Sea. Helg. Mar. Res., 56: 140-148.

Flach, E., Lavaleye, M., de Stigter, H. & Thomsen, L., 1998. Feeding types of the benthic community and particle transport across the slope of the N.W. European continental margin (Goban Spur). Prog. in Ocean., 42: 209-231.

Freudenthal, T., Wagner, T., Wenzhofer, F., Zabel, M., Wefer, G., 2001. Early diagenesis of organic matter from sediments of the eastern subtropical Atlantic: Evidence from stable nitrogen and carbon isotopes. Geoch. Et Cosmo. Acta 65: 1795-1808.

Fry, B. & Sherr, E., 1984. δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. Cont. in Mar. Sc., 27: 13-47.

Grant, J., Cranford, P. & Emerson, C., 1997. Sediment resuspension rates, organic matter quality and food utilization by sea scallops (Placopecten magellanicus) on Georges Bank. J. of Mar. Res., 55: 965-994.

Göransson, P., 2002. Petersen's benthic macrofauna stations revisited in the Öresund area (southern Sweden) and species composition in the 1990s - signs of decreased biological variation. Sarsia 87: 263-280.

Howe, R., Rees, A. & Widdicombe, S., 2004. The impact of two species of bioturbating shrimp (*Callianassa subterranea* and *Upogebia deltaura*) on sediment denitrification. J. of the Mar. Biol. Ass. of the U. K., 84: 629-632.

Iken, K., Brey, T., Wand, U., Voigt, J. & Junghans, P, 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Prog. in Ocean., 50: 383-405.

Jago, C., Bale, A., Green, M., Howarth, M., Jones, S., McCave, I., Millward, G., Morris, A., Rowden, A. & Williams, J., 1993. Resuspension processes and seston dynamics, southern North-Sea. Philosophical Transactions of the Royal Society of London. Series A. Physical Sciences and Engineering, 343: 475-491.

Jähmlich, S., Thomsen, L. & Graf, G., 1999. Factors controlling aggregate formation in the benthic boundary layer of the Mecklenburg Bight (western Baltic Sea). J.of Sea Res. 41: 245-254.

Jennings, S., Pinnegar, J., Polunin, N. & Warr, K., 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Mar. Ecol. Prog. Ser., 213: 127-142.

Jennings, S. & Warr, K.J., 2002. Environmental correlates of large-scale spatial variation in the δ^{15}N of marine animals. Mar. Biol., 142:1131-1140.

Josefson, A. & Jensen, J., 1992. Growth patterns of *Amphiura filiformis* support the hypothesis of organic enrichment in the Skagerak-Kattegat area. Mar. Biol., 112: 615-624.

Josefson, A. & Conley, D., 1997. Benthic response to a pelagic front. Mar. Ecol. Prog. Ser., 147: 49-62.

Kikuchi, E. & Wada, E., 1996. Carbon and nitrogen stable isotope ratios of deposit-feeding polychaetes in the Nanakita River Estuary, Japan. Hydro. 321: 69-75.

Künitzer, A., Basford, D., Craeymeersch, J., Dewarumez, J.-M., Dörjes, J., Duineveld, G., Eleftheriou, A., Heip, C., Herman, P., Kingston, P., Rachor, E., Rumohr, H. & de Wilde, P., 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES J. of Mar. Sci., 49: 127-143.

Lehmann, M., Sigman, D. & Berelson, W., 2004. Coupling the N-15/N-14 and O-18/O-16 of nitrate as a constraint on benthic nitrogen cycling. Mar. Chem., 88: 1-20.

Lindahl, U. & Baden, S., 1997. Type three functional response in filter feeding of the burrowing shrimp *Upogebia deltaura* (Leach). Ophelia, 47: 33-41.

Loo, L.-O., Jonsson, P., Skold, M. & Karlsson, O., 1996. Passive suspension feeding in *Amphiura filiformis* (Echinodermata: Ophiuroidea): feeding behaviour in flume flow and potential feeding rate of field populations. Mar. Ecol. Prog. Ser., 139: 143-155.

Lorrain, A., Paulet, Y.-M., Chauvaud, L., Savoye, N., Donval, A. & Saout, C., 2002. Differential δ^{13}C and δ^{15}N signatures among scallop tissues: implications for ecology and physiology. J. of Exp. Mar. Biol. and Ecol., 275: 47-61.

Michener, R. & Schell, D., 1994. Stable isotopes ratios as tracers in marine aquatic food webs. In: Lajtha K. & Michener, R.H. (Eds.): Stable isotopes in ecology and environmental science: 138-157; Blackwell Scientific.

Mishima, Y., Hoshika, A. & Tanimoto, T., 1999. Deposition rates of terrestrial and marine organic carbon in the Osaka Bay, Seto Inland Sea, Japan, determined using carbon and nitrogen stable isotope ratios in the sediment. J. of Oceanog. 55: 1-11.

Minagawa, M. & Wada, E., 1984. Stepwise enrichment of δ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geoch. et Cosmoch. Acta, 48: 1135-1140.

Monteiro, P., James, A., Sholto-Douglas, A. & Field, J., 1991. The δ^{13}C trophic isotope spectrum as a tool to define carbon pathways in marine food webs. Mar. Ecol. Prog. Ser., 78: 33-40.

Nickell, L. & Atkinson, R., 1995. Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. Mar. Ecol. Prog. Ser., 128: 181-197.

O'Connor, B., Bowmer, T. & Grehan, A., 1983. Long-term assessment of the population dynamics of *Amphiura filiformis* (Echinodermata: Ophiuroidea) in Galway Bay (west coast of Ireland). Mar. Biol. 75: 279-286.

Pinn, E., James, R., Atkinson, A. & Rogerson, A., 1998. Particle size selectivity and resource partitioning in five species of Thalassinidea (Crustacea: Decapoda). Mar. Ecol. Prog. Ser., 169: 243-250.

Post, D., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecol. 83: 703-718.

Riera, P., Stal, L., Nieuwenhuize, J, 2002. δ^{13}C versus δ^{15}N of co-occurring molluscs within a community dominated by *Crassostrea gigas* and *Crepidula fornicata* (Oosterschelde, The Netherlands). Mar. Ecol. Prog. Ser. 240:291-295.

Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. Neth. J. Sea Res. 34, 303-317.

Savina, M. & Pouvreau, M., 2004. A comparative ecophysiological study of two infaunal filter-feeding bivalves: *Paphia rhomboides* and *Glycymeris glycymeris*. Aquac. 239: 1-4.

Schroeder, A., 2003. Community dynamics and development of soft bottom macrozoobenthos in the German Bight (North Sea) 1969-2000. PhD thesis University of Bremen, 265 pp.

Schubert, C., Calvert, S., 2001. Nitrogen and carbon isotopic composition of marine and terrestrial organic matter in Arctic Ocean sediments: implications for nutrient utilization and organic matter composition. Deep-Sea Res Part I 48, 789-810.

Solan, M. & Kennedy, R., 2002. Observation and quantification of in situ animal-sediment relations using time-lapse sediment profile imagery (t-SPI). Mar. Ecol. Prog. Ser., 228:179-191.

Stamhuis, E., Dauwe, B. & Videler, J., 1998. How to bite the dust: Morphology, motion pattern and function of the feeding appendages of the deposit-feeding thalassinid shrimp *Callianassa subterranea*. Mar. Biol., 132: 43-58.

Thomsen, L. & van Weering, T., 1998. Spatial and temporal variability of particulate matter in the benthic boundary layer at the N.W. European Continental margin (Goban Spur). Prog. in Oceanog., 42: 61-76.

Vizzini, S. & Mazolla, A., 2003. Seasonal variations in the stable carbon and nitrogen isotope ratios (13C/12C and 15N/14N) of primary producers and consumers in a western Mediterranean coastal lagoon. Mar. Biol., 142: 1009-1018.

Wakeham, S., Lee, C., Hedges, J., Hernes, P. & Peterson, M., 1997. Molecul indicators of diagenetic status in marine organic matter. Geochim. et Cosmoch. Acta, 61: 5363-5368.

Ward, E. & Shumway, S., 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. J. of Exp. Mar. Biol. and Ecol., 300: 83-130.

Zimmerman, A. & Canuel, E., 2001. Bulk organic matter and lipid biomarker composition of Chesapeake Bay surficial sediments as indicators of environmental processes. Estu. Coast. and Shelf Sci., 53: 319-341.

A possible mechanism for a marine benthic regime shift in the North Sea

Egbert H. van Nes[1], Teresa Amaro[2], Marten Scheffer[1], Duineveld, G.C.A.

[1]Departement of Aquatic Ecology and Water Quality management
Wageningen University
P.O. Box 8080, NL-6700 DD Wageningen
The Netherlands
Tel.: +31 317 483898
Fax: +31 317 484411
E-mail: Egbert.vanNes@wur.nl

[2]Royal Netherlands Institute for Sea Research
P.O. Box 59
1790 AB Den Burg
The Netherlands
Fax ++ 31 222 319674
E-mail: amaro@nioz.nl

(to be submitted)

Abstract

A sharp shift from a brittle star (*Amphiura filiformis*) dominated state to a burrowing shrimp (*Calianassa subterranea)* dominated situation was observed in a region of the North Sea known as The Frisian Front. There are no indications that food levels or other relevant conditions in this part of the North Sea are different than before. Yet, the new state has persisted until today. This suggests that this regime shift represents a transition between alternative stable community states. Here we propose an explanation for such bistability, which is well in line with experimental and field observations. We experimentally demonstrated that sediments inhabited by *C. subterranea* are more susceptible to sediment resuspension by tidal currents and wave forces than sediments inhabited by *A. filiformis*. Although the burrowing *C. subterranea* apparently thrive under these conditions, recruitment of *A. filiformis* may be hampered seems on such unstable frequently resuspended sediments. We use a model to demonstrate that the resulting feedback between the benthic community and sediment stability may cause the new shrimp dominated state to be stable.

Key-words: regime shift; *Amphiura filiformis*; *Calianassa subterranea*; catastrophic shift; alternative stable state; bioturbation; resuspension; competition

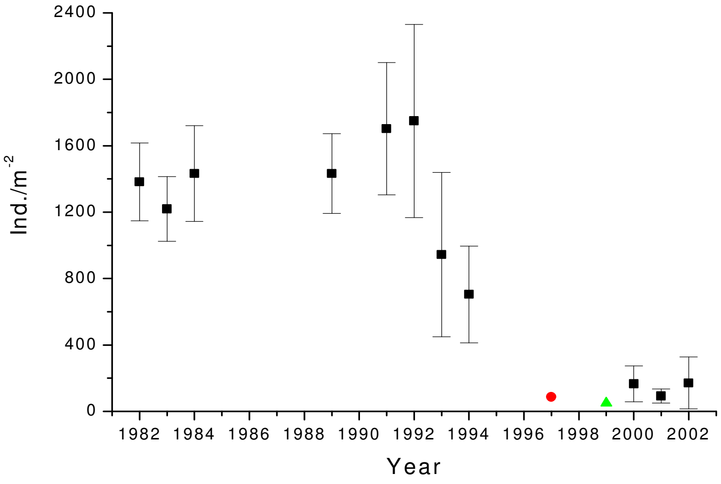
Introduction

Sharp shifts to a contrasting state have been observed in marine communities at scales varying from individual kelp beds (Steneck et al., 2002) and coral reefs (Done, 1991; Knowlton, 1992; Nystrom et al., 2000) to the entire North Sea (Beaugrand, 2004) and even the Pacific Ocean (Hare et al., 2000). Although it has been hypothesized that some of these regime shifts represent catastrophic transformations between alternative self-stabilizing states (Collie et al., 2004; Scheffer et al., 2004), few studies provide compelling evidence or suggest mechanisms that could explain such dynamics (Beamish et al., 2004; Van de Koppel et al., 2001).

Here we analyze a benthic shift in the southern part of the Frisian Front, a part of the North Sea. The Frisian Front is positioned on the Dutch Continental Shelf at the transition between the permanently mixed waters of the Southern Bight (25 m of depth) and the summer-stratified water masses of the Oyster Grounds (depth 50 m) (Creutzberg, 1983). Due to the local deposition of particulate matter and fresh phytodetritus, this area is characterized by high densities and high biomass of interface-feeding species with a well defined north south zonation (Creutzberg et al., 1984). Moreover, during a large part of the year the water column over the enriched zone is characterized by elevated chlorophyll-a concentrations (Cramer, 1991; Creutzberg, 1985). The brittle star *Amphiura filiformis*, used to be extremely dominant and stable in this area. In the period between 1984 and 1992, its densities ranged from 1433 to 1750 ind. m^{-2} (Duineveld et al., 1986). However, in the years after 1992 the population collapsed to less than 10% of its original densities (Figure 1a). Associated with this sharp shift, the entire macrobenthic fauna community changed and the mud shrimp *Calianassa subterranea* became a dominant species (Part I) (Figure 1b). In this article, we outline and scrutinize a potential positive feedback that may have triggered this shift.

We use a model to indicate whether this positive feedback could indeed have triggered the shift.

a)



b)

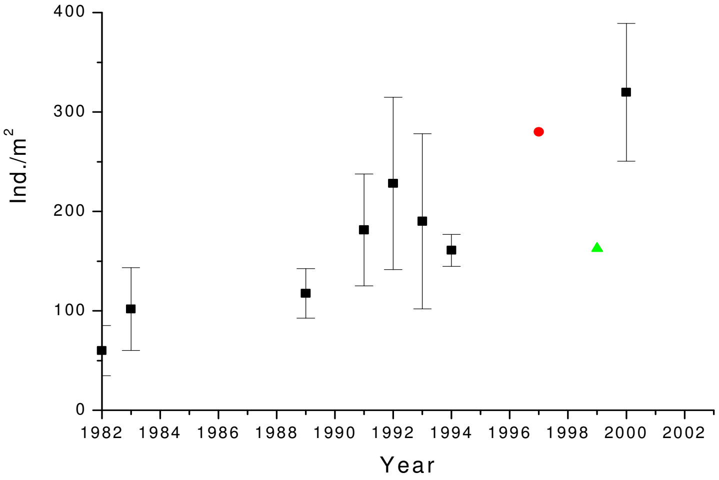


Figure 1. Average densities of *A. filiformis* (a) and *C. subterranea* (b) at the standard monitoring station (4º30'N and 53º70'N) since 1982 to 2002 (after 2000 we don't have reliable data for *C. subterranean*). Legend: ■ 4 boxcores done separated, ● 1 big boxcore (area= 0.25 m^2) ▲ 4 boxcores together (area=0.272 m^2).

A potential mechanism for the shift

Field measurements reveal high concentrations of suspended sediments in the Frisian Front region. This indicates that sediment erosion and resuspension are important features of the current ecosystem state. In the manuscript of page 120, it is experimentally demonstrated that *A. filiformis* reduces the susceptibility of sediments to erosion by water movement, whereas by contrast, *C. subterranea* makes sediments more susceptible to resuspension. This implies that a shift from *A. filiformis to C. subterranea* may effectively promote sediment erosion. At the same time, *A. filiformis* and *C. subterranea* (or other mud shrimps like *Upogebia deltaura*) are likely to compete for same food source (see previous manuscript). This could imply a positive feedback loop as the mud shrimps apparently thrive under conditions with high resuspension and successful recruitment of its competitor *A. filiformis* seems less likely on such unstable frequently resuspended sediments. Thus, as soon as *C. subterranea* becomes dominant, they create conditions that reduce the chances for their competitors. By contrast, dominance of *A. filiformis* could prevent sediment resuspension and therefore this species also improves its own conditions.

Material & Methods

A model

To explore whether the mechanisms that are described before can cause alternative equilibria, we formulated a simple competition model of the brittlestars *A. filiformis* (*A*) and mud shrimps *C. subterranea* (*C*) based on the models of Armstrong and McGehee (1980). We assumed that both species are competing for one resource *F* (for instance space or food). The growth rate of both species (r_A and r_C) is assumed to be limited by this resource in a Monod fashion (with half-saturation coefficients $H_{F,A}$

and $H_{F,C}$). The species have a fixed loss factor (m_A and m_C). The resource is not renewable and both species use or occupy a fixed fraction (a_A or a_C) of the total available resource (F_0).

$$\begin{aligned} \frac{dA}{dt} &= r_A\,A\frac{F}{F+H_{F,A}} - m_A\ \mathrm{A} \\ \frac{dC}{dt} &= r_C\,C\frac{F}{F+H_{F,C}} - m_C\,C \qquad (1) \\ F &= F_0 - a_A A - a_C C \quad (F \geq 0) \end{aligned}$$

To this basic competition model, we added the effect that both species have on the sediment erosion threshold (*R*). These effects were shown experimentally by Amaro et al., in prep.-a (see manuscript about sediment erosion within this Thesis). *Amphiura filiformis* has a stabilizing effect on the sediment stability, whereas the burrowing activities of *C. subterranea* make the sediment more susceptible to erosion:

$$R = R_0 + R_A\frac{A}{h_A + A} + R_C\frac{C}{h_C + C} \qquad (2)$$

R_0 represents the erosion threshold of the sediment, whereas the second and the third terms represent the effect of *A. filiformis* and *C. subterranea* on the sediment erosion threshold, respectively (R_C is a negative value). Both species have a maximum effect (R_A or R_C) and the relation between the biomass and the erosion threshold is modeled with a Monod function (h_A and h_C). The increased susceptibility of the sediment to erosion makes that there is more resuspension if the water movement (*w*) exceeds the threshold *R* (Figure 2). Assumed is that the losses of A. *filiformis* increase with increasing resuspension, whereas the suspended material does not harm *C. subterranea*.

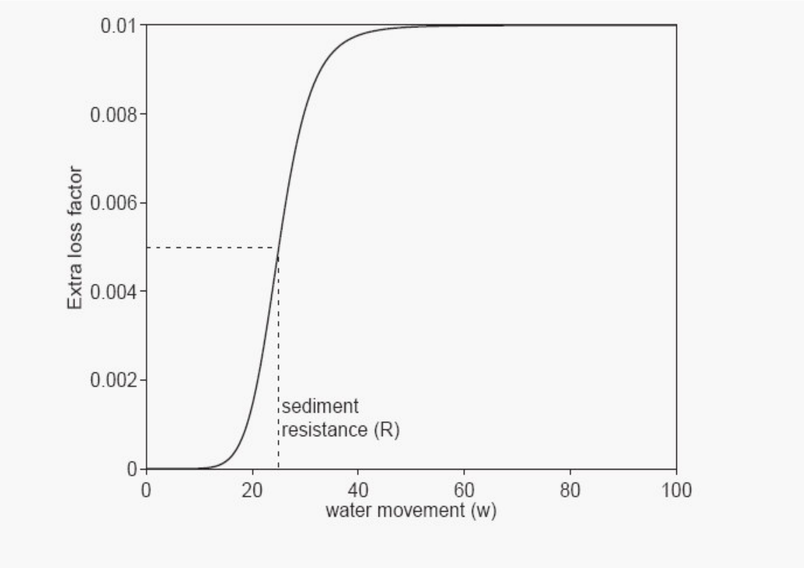


Figure 2. The assumed relation between water movement and mortality of *A. filiformis.*

The model thus becomes:

$$
\begin{aligned}
&\frac{dA}{dt} = r_A\, A \frac{F}{F + H_{F,A}} - m_A\, A - m_{re\mathrm{sup}}(R,w)\, A \\
&\frac{dB}{dt} = r_B\, C \frac{F}{F + H_{F,C}} - m_C\, C \\
&m_{resusp}(R,w) = m_E\, \frac{w^p}{w^p + R^p}
\end{aligned}
\qquad (3)
$$

The interpretation and dimensions of variables and parameters as well as the default values used are summarized in Table 1. The values relatively to the erosion threshold and wind effect were estimated from the results of laboratory experiments and field samples, whereas growth rates were taken from literature (Josefson et al., 1995; Muus, 1981; Rowden et al., 1994).

In the equations (4), water movement is a fixed parameter. As this is not realistic, we generated a noisy water movement for some analyses. We used the recurrent relation of Hasselmann (1976) on a daily basis to generate red noise (i.e. noise with autocorrelation) with an approximate period of λ days (λ>1 = red noise):

$$w_{(t)} = \left(1 - \frac{1}{\lambda}\right)\left(w_{(t-1)} - \overline{w}\right) + \overline{w} + \beta\varepsilon \qquad (4)$$

In which ε is number drawn from a standard normal distribution and β is determining the amount of noise and $\overline{w}$ is the average water movement.

Table 1. The default parameters of the model. 1 calibrated to get realistic biomass values of both species. 2 *A. filiformis* is assumed more efficient. 3 based on experiments of Amaro (in prep.-a) 4 reasonable value 5 assumption 6 (Josefson et al., 1995; Muus, 1981) 7 (Rowden et al., 1994) 8 dependent on wind, arbitrary default value. * Arbitrary resource units.

Parameter	Description	Default value	Unit	Ref.
a_A	Resource occupation by *A. filiformis*	0.15	-	1
a_C	Resource occupation by *C. subterranea*	0.05	-	1
F_0	Total available resources	1	*	1
h_A	Effect of *A. filiformis* on resistance of sediment	2.5	g m^{-2}	3
$H_{F,A}$	Half-saturation coefficient of resource for *A. filiformis*	0.5	*	2
$H_{F,C}$	Half-saturation coefficient of resource for *C. subterranea*	1	*	2
h_C	Effect of *C. subterranea* on resistance of sediment	5	g m^{-2}	3
m_A	Mortality rate of *A. filiformis*	0.01	d^{-1}	4
m_E	Extra mortality of *A. filiformis* due to resuspension	0.01	d^{-1}	4
m_C	Mortality rate of *C. subterranea*	0.01	d^{-1}	4
p	Power of a Hill function	8	-	5
R_0	Resistance of sediment for resuspension	0.25	m s^{-1}	3
r_A	Growth rate of *A. filiformis*	0.04	d^{-1}	6
R_A	Maximum effect of *A. filiformis* on resuspension	0.05	m s^{-1}	3
r_C	Growth rate of *C. subterranea*	0.04	d^{-1}	7
R_C	Maximum effect of *C. subterranea* on resuspension	-0.05	m s^{-1}	3
w	Water movement	0.25	m s^{-1}	8

The simulations were done using a fourth order Runga-Kutta procedure as implemented in MATLAB. The two-dimensional bifurcation plots were created with bifurcation analyzing software (LOCBIF Khibnik et al., 1992).

Results

It can be shown that the simple competition model (equation 1) has no alternative equilibria (Appendix 1) because the slope of the nullclines is always the same for both species. The species that is able to grow with lower resource levels or that have a smaller mortality rate is simply superior (Appendix 1). This is in line with the competitive exclusion principle (Hardin, 1960), which predicts that the maximum number of coexisting species equals the number of resources (Armstrong et al., 1980). We further assume that *A. filiformis* is superior to C. *subterranea* with respect to resource competition.

Both species are ecological engineers (Jones et al., 1994) and change the sediment susceptibility to resuspension (Amaro et al., in prep.-a - see manuscript about sediment erosion within this Thesis). If we assume that *A. filiformis* is negatively affected by increased suspended solids, the model indeed can have alternative equilibria for realistic parameter values (corresponding to our experimental data). This can be understood graphically as the suspended solids effect causes the nullcline of *A. filiformis* to bend down at higher biomasses of *C. subterranea* (Figure 3), making it possible that the nullclines cross.

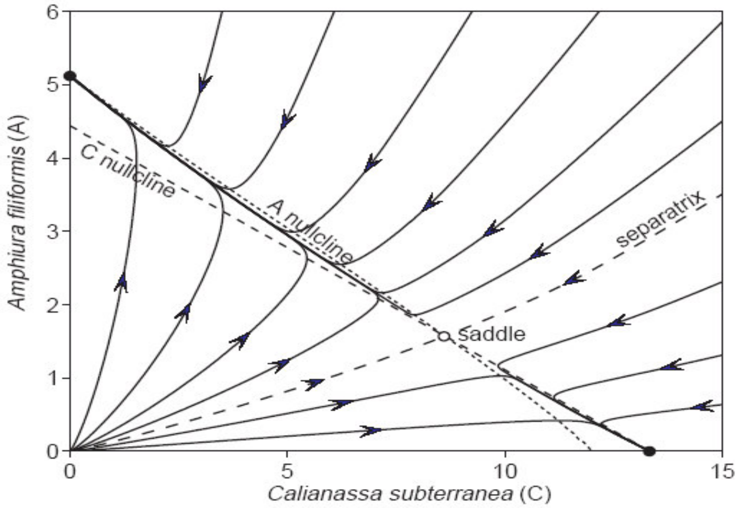


Figure 3. The phase plane with some trajectories at a moderate water movement (w=25). The nullcline of *A. filiformis* is bend down due to the increased resuspension caused by *C. subterranea*. There are two alternative equilibria (dominance of either species). For parameters see: Table 1.

The model can now have two stable states with dominance of either *A. filiformis* or *C. subterranea*. Between both stable nodes, there is an unstable saddle, which is part of the separatrix that represents the border between the two basins of attraction.

To check the robustness of this result, we analyzed the effect of different parameters on the result. The existence of alternative equilibria is highly dependent on the water movement (Figure 4).

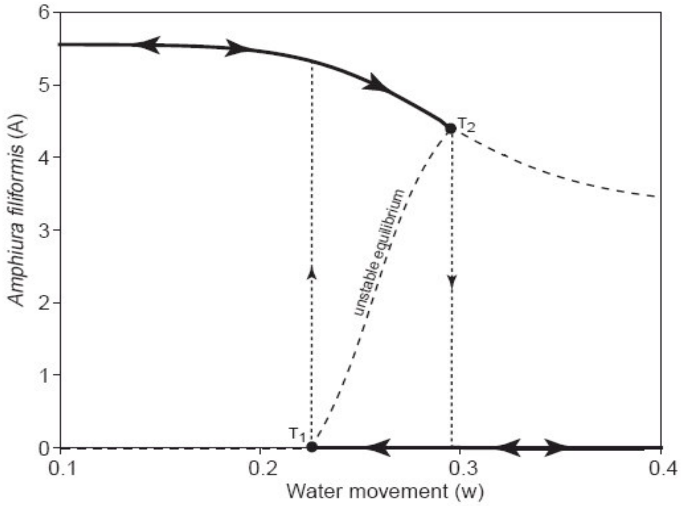


Figure 4. One dimensional bifurcation diagram of the effect of water movement (w in m s^{-1}). Between both transcritical bifurcations (T_1 and T_2), there are alternative equilibria.

At a water movement of 0.22 and 0.29 m s^{-1} there are two thresholds, corresponding to transcritical bifurcations (T_1 and T_2 in Figure 4). Between both bifurcations, alternative equilibria exist. A simulation of the behavior of the system in response to stochastic fluctuations in the water movement demonstrates that this bistability in a fluctuating environment can easily lead to incidental regime shifts such as the one observed at the Frisian Front (Figure5). Note that it is not enough that water movement crosses the 'bifurcation value' briefly. Only after the water movement is for longer periods above the critical value, a regime shift occurs. Note also the long periods in which both species can coexist in a variable environment.

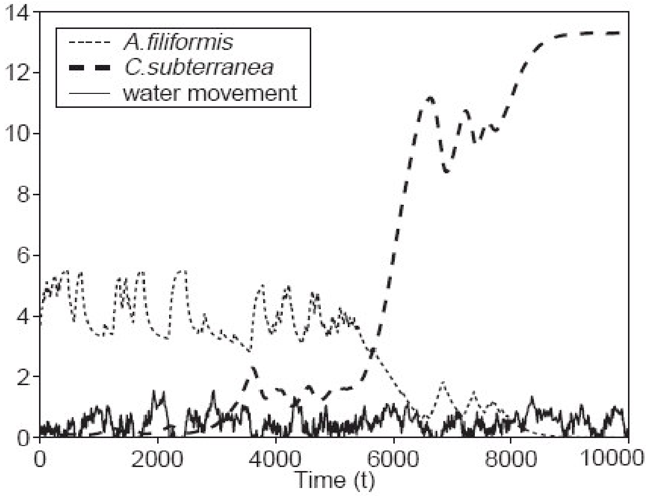


Figure 5. Simulation the effect of noise on the water movement on the shift to the other state. The mean water movement $\overline{W}$ was 0.45 m s^{-1}. Though this value is well above the transcritical bifurcation (T_2) the variations can postpone the regime shift for a long period (β= 0.05 m s^{-1}, λ= 80 d., $w_{(t)}$ was forced to positive values).

We also checked the effects of some other parameters on the range of water movements where alternative equilibria occur. The extra loss of *A. filiformis* due to erosion (m_E) is an important parameter as it determines how strong the *A. filiformis* nullcline is bended down. There is a certain minimum effect needed to bend the nullcline strong enough (ca. 0.005). Above this value, the zone of alternative equilibria rapidly increases, and further increase of the parameter has little effect (Figure 6a). The parameter m_A (loss of *A. filiform*is) must be between 0.016 and 0.005 for alternative equilibria (Figure 6b). From the equations in the appendix it can be deducted that if m_A increases 0.016, *A. filiformis* is simply the inferior competitor, so *C. subterranea* will always become dominant. On the other hand, if *A. filiformis* becomes a very strong competitor (mortality loss <0.005), the effect of increased resuspension is never strong enough to let *A. filiformis* disappear. Similarly, the half-saturation coefficient of resource for resource limitation of *A. filiformis* ($H_{F,A}$) needs to be between two boundaries (Figure 6c). If $H_{F,A}$ exceeds 1, *A. filiformis* is not superior, else if $H_{F,A}$ is below ca. 0.4, the sediment effect is not strong enough.

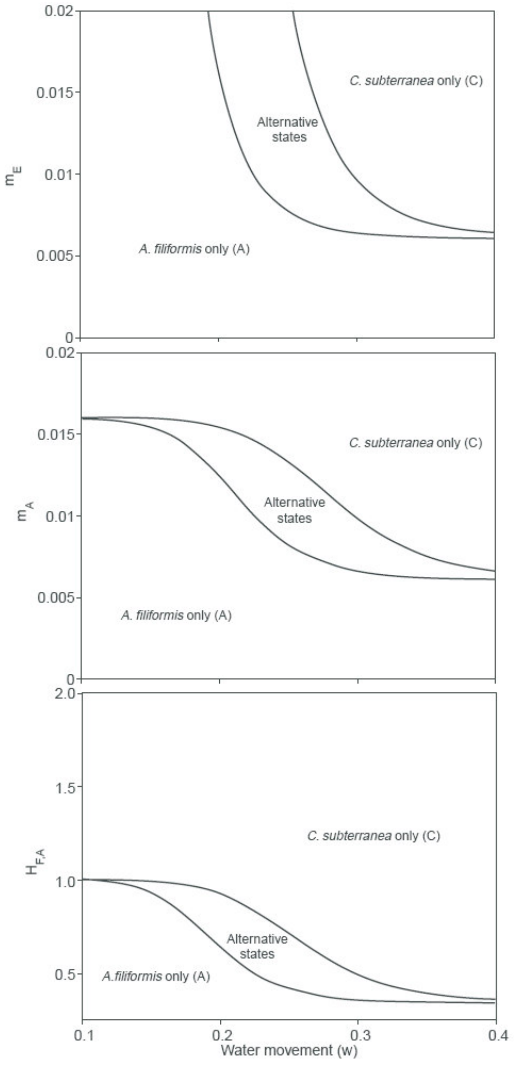


Figure 6. Two dimensional bifurcation diagrams of a. Half-saturation coefficient of resource for *A. filiformis* ($H_{F,A}$) versus water movement (w); b. Extra loss due to erosion (m_E) versus water movement (w) and c Loss of *A. filiformis* (m_A) versus water movement (w). The bifurcations were continued using Locbif (Khibnik et al., 1992).

Finally, it should be noted that in a qualitative sense shrimps are not essential to let the model produce alternative stable states. As *A. filiformis* stabilizes the sediment, and is thus promoting its own conditions. Therefore, even without suppressing *C. subterranea* the stabilizing of the sediment is a positive feedback. However, simulations show that the measured effect of brittle stars on sediment stability (R_C) and the assumed extra mortality due to suspended matter (m_E) are both not strong enough to let alternative stable states arise (results not shown).

Discussion

Shifts between alternative states are usually induced by some disturbance, but the likelihood of such a shift depends also on the resilience of a state, i.e. the disturbance it can take and still return to the same state (Holling, 1973). Importantly, the observation of a sudden shift in a community is not necessarily related to alternative stable states (Scheffer et al., 2003a). Two obvious alternative explanations would be that 1) there has been a permanent shift in an important controlling factor (e.g. temperature), or 2) the system has been hit by a severe disturbance from which it is simply slow to recover. Let us first consider these two alternatives to the alternative stable states explanation.

With respect to the first option, we have no evidence that external control factors such as food of the North Sea or the state of the North Atlantic oscillation are systematically different in the new state from what was observed during the brittle star state. Amaro et al. (2003) tried to link the decline in densities of *A. filiformis* to a food shortage by analyzing variations in the shell growth of the filter feeder bivalve *Mya truncata* from the Frisian Front during the period of interest. The authors concluded that there was no direct coupling between fluctuations in density of *A. filiformis* and variations in growth of *M. truncata*. It therefore seems unlikely that a change in food conditions would have caused the dramatic collapse of *A. filiformis*.

The second alternative explanation would be that the system has been slow in recovering from a disturbance such as a trawling activity or an extreme shear stress due to storm and tidal current action. However, in view of the generation time and growth rates of these *A. filiformis*, the five years since the regime shift should have offered sufficient time for the brittle star populations to recover. The persistence of the new community state therefore suggests that there is a stabilizing mechanism that maintains *C. subterranea* dominated situation and prevents the *A. filiformis* from recovering to the original densities.

Our model suggests that the interaction between sediment stability and the benthic community is a plausible mechanism that could cause alternative stable states in this system. Although our observations of suspended solids in the field, and the measured differential effect of the two key-species on sediment stability are well in line with the model, we obviously do not have a 'proof' that the proposed mechanism is indeed responsible for the apparent stability of the two contrasting states.

In fact, there are many aspects of the biology of the species that are poorly known, and many potentially important features that we left out of consideration. For instance, age structure dynamics may have been important, and synchronous die-off of the adult brittle star population combined with long-term lack of recruitment could have caused the crash. Indeed, for ten years juveniles have been scarce, particularly in the southernmost areas of the Frisian Front (Part I). Moreover, we have no data on the negative effect of sediment erosion on the brittle stars, even though it seems quite reasonable to assume that sediment resuspension may prevent the larvae to settle. It has been shown that changes in sediment surface chemistry caused by disturbance of sediments, may affect settlement affect recruitment infauna's decisions (Marinelli et al., 2002; Woodin et al., 1998). Given the high numbers of *A. filiformis* in the Frisian front are in late nineties, negative impactes of enhanced erodability on larval settlement do not seem to be very relevant. Another uncertainty is the nature of the resource competition between shrimps and brittle stars. Stable isotope analyses suggest that on our site they have essentially the same diet. However, *A. filiformis* is a passive suspension feeder (Buchanan et al., 1986; Loo et al., 1996; Solan et al., 2002), whereas *C. subterranea* is basically a subsurface deposit-feeder (Stamhuis et al., 1998; Stamhuis et al., 1996).This would suggest that the brittle stars have 'primacy' in the food competition as they trap the food particles before they settle and become available to the shrimps. On the other hand, other aspects of the interaction between the species could contribute to bi-stability. For instance, shrimps could cause juvenile mortality of the recruits (Roads & Young, 1970). Direct competition for space could be another important aspect in the interaction between both species (Wilson, 1990).

Importantly, although we have stressed the competition between C. subterranean and A. filiformis, C. subterranean are not essencial to obtain the bistability in the model. Our analyses showed that a simpler mechanism, i.e. the more positive feedback between brittle stars and sediment stability might potentially lead to alternative stable states. However, in this case we need a stronger effect of brittle stars on sediment stability than measured in the experimental set-up. Therefore, it may well be that the essence of the mechanism is the interaction between brittle stars and sediment stability. This would be analogous to the positive feedback between sediment stability and benthic microbial communities that has been shown to cause alternative stable states on tidal flats (Van de Koppel et al., 2001) and lake sediments (Scheffer et al., 2003b).

A major unresolved aspect is the question what actually triggered the regime shift. One possibility is an episode of intense local trawl fishery. This could tip the balance, as fragile species such as *A. filiformis* live within the penetration depth of a beam trawl. On the other hand, fluctuations in factors such as water movement, temperature and food availability may have had an impact. Our simulations illustrate that the system with alternative attractors can show a striking regime shift in response to a randomly fluctuating environment, even if no obvious anomaly in the environmental fluctuations that could be 'the trigger' seems present (Figure 5). This illustrates just how illusive the search for causes of regime shifts can be if one focuses merely on the analysis of field patterns.

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Appendix 1

The simple competition model (equation 1) has the following nullclines for *A. filiformis* (A^*):

$$\begin{aligned} &\frac{dA}{dt} = r_A\, A \frac{F_0 - a_A A - a_C C}{F_0 - a_A A - a_C C + H_{F,A}} - m_A\, A = 0 \\ &\Rightarrow A^* = -\frac{a_C}{a_A} C^* + \frac{F_0}{a_A} - \frac{m_A H_{F,A}}{(r_A - m_A) a_A} \vee A^* = 0 \end{aligned} \qquad (5)$$

Similarly the nullclines for *C. subterranea* (C^*) are:

$$\begin{aligned} &\frac{dC}{dt} = r_C\, C \frac{F_0 - a_A A - a_C C}{F_0 - a_A A - a_C C + H_{F,C}} - m_C\, C = 0 \\ &\Rightarrow A^* = -\frac{a_C}{a_A} C^* + \frac{F_0}{a_A} - \frac{m_C H_{F,C}}{(r_C - m_C) a_A} \vee C^* = 0 \end{aligned} \qquad (6)$$

These nullclines are linear with the same slope ($-a_C/a_A$), so there cannot be stable coexistence nor alternative equilibria, as it is then required that both nullclines cross. The equilibrium with only A. *filiformis* becomes stable if the intercept of the *A. filiformis* nullcline is larger than the intercept of the *C. subterranea* nullcline:

$$\frac{F_0}{a_A} - \frac{m_A H_{F,A}}{(r_A - m_A)a_A} > \frac{F_0}{a_A} - \frac{m_C H_{F,C}}{(r_C - m_C)a_A} \qquad (7)$$

Thus:

$$\frac{m_A}{(r_A - m_A)} H_{F,A} < \frac{m_C}{(r_C - m_C)} H_{F,C} \qquad (8)$$

This means that the superior species can deplete the resource better or that has a smaller ratio between losses and maximum net growth rate.

References

Amaro T, Duineveld G, Bergman M & Witbaard, R., 2003. Growth variations in the bivalve *Mya truncata*: a tool to trace changes in the Frisian Front macrofauna (southern North Sea)? Helgol. Mar. Res. 57: 132-138.

Armstrong, R., McGehee, R., 1980. Competitive exclusion. Am Nat 115: 151-169.

Beamish, R., Benson, A., Sweeting, R. & Neville, C., 2004. Regimes and the history of the major fisheries off Canada's west coast. Prog. Oceanogr. 60: 355-385.

Beaugrand, G., 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. Prog. Oceanogr. 60: 245-262.

Buchanan J. & Moore, J.,1986. A broad review of variability and persistence in the Northumberland benthic fauna - 1971-85. J Mar. Biol. Ass. U.K. 66: 641-657.

Collie, J., Richardson, K. & Steele, J., 2004. Regime shifts: Can ecological theory illuminate the mechanisms? Prog. Oceanogr. 60: 281-302.

Cramer, A., 1991. Benthic metabolic activity at frontal systems in the North Sea. In: PhD thesis, University of Amsterdam, 93 pp.

Creutzberg, F., 1983. Biological activity in an area with a tidally-induced front. ICES CM 1983/L: 1-13.

Creutzberg, F., 1985. A persistent chlorophyll a maximum coinciding with an enriched benthic zone. In: Gibbs PE (ed) Proc. 19th Europ. Mar. Biol. Symp. Cambridge University Press, Cambridge, 97-108 pp.

Creutzberg, F., Wapenaar, P., Duineveld, G. & Lopez, N., 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. Rapports et proces verbaux des reunions / Commission Internationale pour l' Exploration Scientifique de la Mer Mediterranee 183: 101-110.

Done, T., 1991. Phase shifts in coral reef communities and their ecological significance. Hydrobiol. 247: 121-132.

Duineveld, G. & van Noort, G., 1986. Observations on the population dynamics of *Amphiura filiformis* (Ophiuroidea Echinodermata) in the southern North Sea and its exploitation by the dab *Limanda limanda*. Neth. J. Sea Res. 20(1): 85-94.

Hardin, G., 1960. The competitive exclusion principle. Sci. 131: 1292-1297.

Hare, S. & Mantua, N., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr. 47: 103-145.

Hasselmann, K., 1976. Stochastic climate models, Part I: Theory. Tellus 28: 473-485.

Holling, C., 1973. Resilience and stability of ecological systems. Annu Rev Ecol Syst 4: 1-23

Jones, C., Lawton, J. & Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.

Josefson, A., Jensen, J., Nielsen, T. & Rasmussen, B., 1995. Parameters of a benthic suspension feeder along a depth gradient across the Pycnocline in the Southern Kattegat, Denmark. Mar. Ecol. Prog. Ser. 125: 107-115.

Khibnik, A., Kuznetsov, Y., Levitin, V., Nikolaev, E., 1992. Continuation techniques and interactive software for bifurcation analysis of ODE's and iterative maps. Physica D 62: 360-370.

Knowlton, N., 1992. Thresholds and multiple stable states in coral reef community dynamics. Am Zool 32: 674-682.

Loo., L., Jonsson, P., Skold, M. & Karlsson, I., 1996. Passive suspension feeding in *Amphiura filiformis* (Echinodermata: Ophiuroidea): Feeding behaviour in flume flow and potential feeding rate of field populations. Mar. Ecol. Prog. Ser. 139: 143-155.

Marinelli, R. & Woodin, S., 2002. Experimental evidence for linkages between infaunal recruitment, disturbance, and sediment surface chemistry. Limnol Oceanogr 47: 221-229.

Muus, K., 1981. Density and growth of juvenile *Amphiura filiformis* (Ophiuroidea) in the Oresund. Ophelia 20: 153-168.

Nystrom, M., Folke, C. & Moberg, F., 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol. Evol. 15: 413-417.

Rowden, A. & Jones, M., 1994. A contribution to the biology of the burrowing mud shrimp, *Callianassa subterranea* (Decapoda, Thalassinidea). J Mar. Biol. Ass. U.K. 74: 623-635.

Scheffer, M. & Carpenter, S., 2003a. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18: 648-656.

Scheffer, M., Portielje, R. & Zambrano, L., 2003b. Fish facilitate wave erosion. Limnol Oceanogr. 48: 1920-1926.

Scheffer, M. & van Nes, E., 2004. Mechanisms for marine regime shifts: Can we use lakes as microcosms for oceans? Prog. Oceanogr. 60: 303-319.

Solan, M. & Kennedy, R., 2002. Observation and quantification of in situ animal-sediment relations using time-lapse sediment profile imagery (t-SPI). Mar. Ecol. Prog. Ser. 228: 179-191.

Stamhuis, E., Dauwe, B. & Videler, J., 1998. How to bite the dust: morphology, motion pattern and function of the feeding appendages of the deposit-feeding thalassinid shrimp *Callianassa subterranea*. Mar. Bio. 132: 43-58.

Stamhuis, E., ReedeDekker, T., vanEtten, Y., deWiljes, J., Videler, J., 1996. Behaviour and time allocation of the burrowing shrimp *Callianassa subterranea* (Decapoda, Thalassinidea). J. Exp. Mar. Biol. Ecol. 204: 225-239.

Steneck, R., Graham, M., Bourque, B., Corbett, D., Erlandson, J., Estes, J.& Tegner, M. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Envir. Conserv. 29: 436-459.

Van de Koppel, J., Herman, P., Thoolen, P. & Heip, C., 2001. Do multiple stable states occur in natural ecosystems? Evidence from tidal flats. Ecol. 82: 3449-3461.

Wilson, W., 1990. Competition and predation in marine soft-sediment communities. Ann. Rev. Ecol. Syst. 21: 221-241.

Woodin, S., Marinelli, R. & Lindsay, S., 1998. Process-specific cues for recruitment in sedimentary environments: Geochemical signals? J. Mar. Res. 56: 535-558.

Summary

The North Sea is the world's most productive shelf sea despite its relatively small surface area (575 000 km^2). For a number of years there is growing concern about the degradation and impoverishment of the subtidal North Sea benthic ecosystem due to its increased exploitation, in particular by beam trawling. This concern is fuelled by reports stating that annual fishing mortality of *e.g.* bivalve populations is up to 35% and that the density and age structure of some of the larger invertebrate species have decreased in the southern North Sea. In the mid 1980s Reid and co-workers suggested that a regime shift may have happened in the North Sea. Using biological indicators, they showed that the pelagic ecosystem of the North Sea underwent dramatic changes observed from phytoplankton to fish. It has been hypothesized that this regime shift resulted from the combination of three main factors: a change in the local hydro-meteorological forcing (wind intensity and sea surface temperature), a displacement of oceanic biogeographical boundaries to the west of the European Continental shelf, and an increase in the oceanic inflow into the North Sea. It was suggested that these features were linked to each other and that they have been influenced by common and large scale climatological forcing. Generally warmer water species have increased whereas colder water species have decreased in the North Sea.

In the southern areas of the Frisian Front (southern North Sea), a drastic shift in the abundance of most of the macrobenthic fauna during 1992-1997has also been revealed. Especially a shift in abundances from the brittle star *Amphiura filiformis* and the mud shrimp *Callianassa subterranea* was recorded. *Amphiura filiformis* had a main peak in densities of ~1330.individuals per m^2 in 1982 and was at its maximum in 1992 with ~1750 individuals per m^2. At this time, the population was mainly composed of adults and few juveniles. After this 10-year period of high densities, the population

decreased and nowadays it remains constant with 100 individuals per m^2. In contrast to this decrease, *C. subterranea* has been increasing in abundance since 1982, from ~40 to ~319 individuals per m^2 in 2000. Nowadays, there are no signs of recovery towards the former situation in which *A. filiformis* dominated the community. This suggests a shift from one stable dominated state to another.

In this Thesis I investigate possible mechanisms that can be contolling the benthic ecosystem of an area located in the southern North Sea to provide new and crucial insight in the functioning of marine ecosystems.

Initially it was hypothesized that changes in food availability could be related to shifts in dominant species. One way to reconstruct whether the benthic food supply changed in the period when *A. filiformis* declined was to study the growth records deposited in the shells of suspension-feeding bivalves living at the Frisian Front. For this purpose I selected *Mya truncata* because it can reach a maximum age of 40 years and because adults live deep in the sediment where they are protected from direct fishing disturbance. While analysing the growth of *M. truncata* from the Frisian Front I specifically searched for a common pattern among individuals during the period when *A. filiformis* densities drastically decreased. The results showed no direct coupling between fluctuations in density of *A. filiformis* and variations in the growth of *M. truncata*. Moreover, when looking to the distribution of this bivalve, a skewed size distribution was found due to a lack of juveniles in the 1-4 cm size class. Strikingly, other large and long-living bivalves in the Frisian Front, like *Artica islandica*, displayed the same type of size distribution. Beside its skewed age composition, the distribution of *M. truncata* in the southern North Sea displays an abrupt limit at the 30m isobath at the southern border of the Oyster ground. This isobath not only marks the transition from sandy sediment in the Southern Bight to silty sand in the Oyster Ground but also from the permanently mixed warmer water in the south to the relatively cold summer-stratified water in the north. *Mya truncata* is known to have no substrate preference and hence we assumed that the temperature difference of the bottom water (4 °C between spring-and summer) limits its distribution. The occurrence of poor recruitment at a location near the border of an apparently temperature limited distribution led to the hypothesis that the poor recruitment might also be temperature related. In this study we restricted ourselves to the gametogenesis, which is known to be negatively affected by high temperatures to test if *M. truncata* is reproductively active in this region and whether the lack of individuals in the smaller size classes was related to the shift in the macrobenthic fauna. Although, there were no samples to cover a complete annual cycle, histological sections of reproductive tissues from the individuals collected between June 20001 and April 2002 revealed synchronous gametogenesis with low numbers of vitelogenic oocytes. This low number of ripe oocytes combined with the possible increase in temperature by the time food is scarce may explain the repeated recruitment failures of *M. truncata* in the Frisian Front. Since it was not possible to have samples for each month of the year, the definitive reproductive periodicity of this bivalve was not possible to assess. Clearly, additional work is required for a better understanding of the causes for repeated recruitment failure of *M. truncata*.

To investigate whether variations in annual growth of bivalves indicate climatic forcing on the benthic ecosystem in the Southern North Sea, environmental variables like food availability (indicated by phytoplankton colour), the North Atlantic Oscillation (NAO) index, seawater temperature and wind strength were tested. By looking at the inter-annual variations of three bivalves from the Frisian Front *A. islandica, M. truncata and Chamelea gallina*, a high similarity (69-80%) between their growth records was shown. This common trend extracted from individual growth records was correlated

with monthly data on phytoplankton colour, NAO index, seawater temperature and windstrength and direction. It was shown that the last three factors varied seasonally. Concerning wind, field measurements in the summer at the Frisian Front indicated that northerly and westerly wind speeds above 10 m/s (Bft 6) lead to resuspension of fine sediments and negative effects on shell growth during some months in the year were observed. Also, fine sediments at water depths above 40 m in the Frisian Front were observed that could easily be resuspended by wind induced waves, whereas tidal current speeds are just below the critical threshold value for resuspension in this area. It was concluded, therefore, that annual growth could mainly be explained by seasonal effects of wind. If this is true resuspension can be the underlying mechanism that might have contributed to the failure of the adult *A. filiformis* population. But how? *Callianassa subterranea*, is responsible for transporting a considerable amount of sediment from depth to the surface, playing a significant role in modifying their environment and possibly causing a lot of resuspension by expelling sediment while creating their burrows. What is striking is that this species showed an increase in its densities in the same area at the same time that *A.filiformis* decreased. In part II, it is shown that the erosion threshold of the sediment was on average lower, with high densities of *C. subterranea* and low densities of *A. filiformis* representing the situation in the 1990's in direct contrast to the 1980s (with low densities of *C. subterranea* and high densities of *A. filiformis*). This leads us to conclude that the increase of *C. subterranea* enhanced the instability of the sediment and caused a higher resuspension of finer particles. High abundance of *A. filiformis* had the opposite effect of stabilizing the sediment. The shift from a benthos community dominated by *A. filiformis* to *C. subterranea* might have aggravated the resuspension and turbidity at the Frisian Front. It has further been shown that the effect of *C. subterranea* is even more pronounced when northerly and westerly

winds are above 10 m/s (Bft 6). Erosion might also prevent planktonic larvae of *A. filiformis* to settle and might cause settled stages to be transported away. And when they settle, their chances to survive are small due to the unstable mud. On the other hand, *C. subterranea* lives deep in the sediment and is hardly affected by high resuspension. Furthermore, it is thought that resuspension of bottom material affects both quality and quantity of food for benthic suspension and filterfeeders like *A. filiformis*. This affects their condition and survival chances and leads to a reduced reproductive output and to lower numbers of viable larvae. The change in sediment conditions keeps the benthic community in its present state and prevents the recovery towards the former situation where *A. filiformis* dominated the community. Once initiated, the shift in the abundance of the two species might have developed a persistent character independent of climatic forcing. Given the negative impact of resuspension and turbidity on seston feeders in general, it appears unlikely that the *A. filiformis* population will be restored. However, the exact effect of more frequent and enhanced resuspension on the growth and reproduction of *A. filiformis* needs further investigation. Moreover, an experiment exposing *A. filiformis* recruits to different levels of turbidity is needed to test how sediment disturbance affects larval settlement

Using the stable isotope approach I have also shown that during summer months, *A. filiformis* and other Thalassinid shrimps like *C. subterranea* and *Upogebia* spp., are likely to compete for the same food source. This makes it even more difficult to maintain the *A. filiformis* population.

To explore whether or not the above mentioned mechanisms could indeed lead to alternative stable states, a model was constructed. The model suggested that the interaction between sediment stability and the benthic community is a plausible mechanism that could cause alternative stable states in this system.

Although I identified possible reasons for the apparent stability of the two contrasting states, it was not possible to clarify what factors initially caused the decrease and increase of *A. filiformis* and *C. subterranea* populations, respectively. Natural fluctuations in environmental conditions have altered and regulated ecosystems throughout their evolutionary history. More recent, anthropogenic impacts can act in the ecosystem and cause major environmental changes. In the southern North Sea, for example, beam trawling is economically the most important and widely used fishing method. The effects of this fishing activity are not easily detectable because effects can be masked by other co-acting regulators, such as eutrophication, fluctuations in population dynamics and climatic variation. The IMPACT programme (1998) had the objective to decipher the effects of different fishery types of on the North Sea and Irish Sea ecosystems. In general the passage of demersal fishing gear flattens the contours of the sediment surface and can severely damage the burrows or tube systems of epi- and infauna like *A. filiformis*. Moreover, the movement of the trawl over the seabed can cause suspension of lighter sediment fractions and this can lead to more pronounced changes in areas with substantially finer sediments. Hence, mortality due to trawling activities mainly occurs directly as a result of physical damage by the passage of the trawl or indirectly by disturbance of the seabed macrofauna and subsequent predation. It is very likely that commercial bottom trawling affects the composition of the benthic community. Populations of vulnerable species with more sensitive life history strategies may decrease to low levels and/or to a locally more restricted distribution. Nevertheless, the decrease in abundance of *A. filiformis* from ~1750 individuals per m^2 to ~100 individuals per m^2 took place over a period of 5 years (1992-1997). The Frisian Front has been fished for many years without a similar effect on the *A. filiformis* population. This makes fishing an unlikely trigger for the observed shift. Another explanation for triggering this shift may be found in the population structure of *A. filiformis* itself. During the time that this species was abundant (between 1982 and 1992) the population was mainly composed of adults with very few juveniles present. So, it could also be that the population started to die off and that the few juveniles were not able to restore the population fast enough. Once this happened a shift occurred from a stable *A. filiformis* dominated state to a stable *C. subterranea* dominated state. Especially at the southern places of the Frisian Front (like the standard station), 72% of the macrobenthic species has changed in numbers due to a number of species that disappeared together with *A. filiformis.* Whether *A. filiformis* or *C. subterranea* plays a key role in the control of the other benthic fauna in the area remains unknown.

This Thesis revealed that still little is understood about the complex dynamic system of benthic communities. However, by studying the mechanisms that are controlling this system, we will get a better understanding of how climate change may affect these benthic communities. This highlights the importance of maintaining long term monitoring programmes of benthic fauna or even extend research.

Samenvatting

De Noordzee is ondanks het relatief kleine oppervlak van 575.000 km^2 's werelds meest productieve zee op een continentaal plat. Sinds een aantal jaren bestaat er een groeiende bezorgdheid omtrent de achteruitgang en verandering van het benthische ecosysteem ten gevolge van de toegenomen exploitatie, met name door boomkorvisserij Deze bezorgdheid wordt gevoed door rapporten over de jaarlijkse sterfte door visserij, die bijvoorbeeld in populaties tweekleppigen tot 35% bedraagt en door rapporten over de afname van de dichtheids- en leeftijdsstructuur van sommige populaties van grotere ongewervelde soorten in de zuidelijke Noordzee.

In het midden van de jaren-80 hebben Reid en medewerkers gesuggereerd dat een verschuiving van het regime in de Noordzee heeft plaatsgevonden. Aan de hand van biologische indicatoren lieten zij zien dat het pelagische ecosysteem van de Noordzee een dramatische verandering heeft ondergaan. Parallelle veranderingen werden waargenomen in fytoplankton , zooplanten en vispopulaties. De h ypothese die door hen werd opgeworpen was dat deze regime verandering het resultaat was van de combinatie van drie factoren: een verandering in de lokale hydro-meteorologische aandrijving (wind energie en oppervlakte zeewater temperatuur), een verplaatsing van de oceanisch-biogeografische grenzen naar het westen van het Europese continentaal plat en een toename van de instroom van oceaanwater naar de Noordzee. Er werd gesuggereerd dat deze drie factoren met elkaar in verband staan en werden beïnvloed door algemene en grootschalige klimatologische krachten. Sinds de tachtiger jaren zijn soorten die indicatief zijn voor warm water, toegenomen terwijl soorten indicatief voor koud water juist zijn afgenomen in de Noordzee.

Op het Friese Front, de zuidelijke rand van de Oestergronden, in de zuidelijke Noordzee werd ook een dramatische verandering in de aanwezigheid van enkele macrobenthische soorten vastgesteld. Gedurende de periode 1992-1997 veranderden metname de aantallen van de slangster (*Amphiura filiformis),* en de moddergarnaal (*Callianassa subterranea)*. In 1982 kwam *A. filiformis* in dichtheden met piekwaarden van ongeveer 1330 individuen per m^2 voor. In 1992 waren de dichtheden maximaal en bedroegen ongeveer 1750 individuen per $m^{2.}$ Op dat moment bestond de populatie voornamelijk uit volwassen exemplaren en weinig jongen. Na deze 10-jarige periode met hoge dichtheden nam de populatie af. Tegenwoordig is deze vrij stabiel met een dichtheid van 100 individuen per m^2. De aanwezigheid van *C. subterranea* is juist toegenomen van ongeveer 40 exemplaren per m^2 in 1982 tot 319 individuen per m^2 in 2000. Tot 2002 zijn er geen aanwijzingen voor herstel van de oude situatie, waarin *A. filiformis* de gemeenschap domineerde en dichtheden van *C. subterranea* veel lager waren. Deze persistentie van de gemeenschapsstructuur suggereert dat het bentisch ecosysteem van de ene stabiele, dominante toestand naar een andere stabiele toestand is overgegaan.

In dit proefschrift onderzoek ik de mechanismen die de benthisch levensgemeenschap in de zuidelijke Oestergronden zouden kunnen controleren om daarmee te komen tot nieuwe en cruciale inzichten over het functioneren van mariene ecosystemen in het algemeen en de mogelijke processen die aan de bentische “shift” ten grondslag liggen.

In eerste instantie werd verondersteld dat veranderingen van de dominante soort (*A. filliformis*) gerelateerd zou kunnen zijn aan een gewijzigde voedselbeschikbaarheid. Om dit voor bovenstaande periode en gebied te testen, werd de groei geregistreerd in de schelpen van *Mya truncata,* bepaald. *Mya truncata* werd geselecteerd omdat deze soort een leeftijd tot 40 jaar kan bereiken en net als *A. filiformis* leeft van gesuspendeerd organisch materiaal. Daarnaast leven volwassen exemplaren diep in het sediment waardoor ze beschermd zijn tegen directe verstoring ten gevolge van bodemvisserij. Bij de analyse van de groei van *M. truncata* heb ik gekeken of het gemeenschappelijk patroon van schelpgroei tussen individuen gelijkenis vertoonde met de populatieontwikkeling *c.q.* de drastische dichtheids afname van *A. filiformis*. De resultaten lieten geen direct verband zien. (zie part 2)

De grootteverdeling van *M. truncata* laat zien dat er een gebrek aan juvenielen in de 1 tot 4 cm klasse is. Opvallend was dat andere grote en langlevende tweekleppigen in het Friese Front, zoals *Artica islandica*, eenzelfde verdeling laat zien. Naast de scheve leeftijdssamenstelling laat de distributie van *M. truncata* in de zuidelijke Noordzee een abrupte grens zien ter hoogte van de 30 meter dieptelijn aan de zuidelijke rand van de Oestergronden. Deze grens markeert zowel de transitie van zandig sediment in de Zuidelijke Bocht naar silt bevattend zand in de Oestergronden maar ook de transitie van permanent gemengd, relatief warm, water in het zuiden naar relatief koud, in de zomer gestratificeerd, water in het noorden. *Mya truncata* heeft geen specifieke voorkeur voor een bepaald type substraat. Daarom hebben we aangenomen dat het temperatuursverschil van het bodemwater (4°C van voorjaar naar zomer) de verspreidingslimiet bepaald. De slechte populatie aanwas op een locatie vlakbij de grens van een ogenschijnlijk temperatuur-gelimiteerde distributie heeft geleid tot de hypothese dat de slechte rekrutering eveneens aan temperatuur gerelateerd zou kunnen zijn. Daarom heb ik gekeken of de voorplantingscapaciteit van *M. truncata* misschien beperkend was. In deze studie heb ik mijzelf beperkt tot bestudering van de gametogenese omdat het bekend is dat deze negatief beïnvloed wordt door hoge temperaturen. Dit om te testen of *M. truncata* actief reproduceert in het Friese Front gebied en of het gebrek aan kleinere (jongere) dieren eventueel ook te relateren is aan de bovenbeschreven verandering binnen de macrobenthische fauna. Uit histologische secties op weefsel afkomstig van de voortplantingsorganen van individuen verzamelt tussen juni 2001 en april 2002 bleek dat er sprake was van een synchrone gametogenese met lage aantallen van vitelogene oöcyten. Deze lage aantallen van rijpe oöcyten in combinatie met de mogelijke temperatuurstijging ten tijde van voedselschaarste zou het herhaalde mislukken van de rekrutering van *M. truncata* in het Friese Front kunnen verklaren. Vanwege het ontbreken van monster materiaal voor enkele maanden van een jaar, was het niet mogelijk om de definitieve reproductieve periodiciteit voor deze tweekleppige vast te stellen. Aanvullend onderzoek is nodig om de oorzaken voor het bij herhaling mislukken van de voortplanting binnen *M. truncata* populaties volledig te begrijpen.

Om te onderzoeken of variaties in de jaarlijkse groei van *M. truncata* een mogelijke klimatologische invloed op het benthische ecosysteem in de zuidelijke Noordzee indiceert, werd ook een vergelijking gemaakt met de jaarlijkse groeivariaties in twee andere schelpsoorten. Ook werd de relatie met omgevingsvariabelen zoals voedselrijkdom (fytoplankton kleur), de Noord Atlantisch Oscillatie (NAO) Index, temperatuur en wind onderzocht. Bij drie schelpsoorten, *A. islandica, M. truncata* en *Chamelea gallina* werd een grote gelijkenis (69-80%) tussen hun interjaarlijkse groeivariaties vastgesteld. Hieruit werd een algemene groeitrend afgeleid die werd gecorreleerd met de omgevingsvariabelen. Er werd geconcludeerd dat jaarlijkse groei voornamelijk zou kunnen worden verklaard door seizoensgebonden wind effecten.

Zomermetingen op het Friese Front gaven aan dat noordelijke en westelijke winden met snelheden boven de 10 m/s (Bft 6) leiden tot resuspensie van de fijne sedimentfractie.

In de Oestergronden, op diepten groter dan 40 meter, werd fijn sediment waargenomen dat gemakkelijk opnieuw in suspensie gebracht kan worden door golven veroorzaakt door wind terwijl de getijdenstroomsnelheden in dit gebied net onder de kritische drempelwaarde voor re-suspensie ligt.

Geresuspendeerde fijne sedimentdeeltjes verlagen de kwaliteit van eveneens gesuspendeerd organisch materiaal dat als voedsel voor tweekleppigen dient. Deze lagere voedsel kwaliteit zal tot verminderde groei leiden. Er wordt daarom geconcludeerd dat jaarlijkse groei voornamelijk zou kunnen worden verklaard door seizoensgebonden wind effecten. Als dit effect van re-suspensie het onderliggende mechanisme is, zou dat dan ook hebben kunnen bijgedragen aan de achteruitgang van de volwassen *A. filiformis* populatie. Maar hoe? Deze vraag werd met een serie experimenten benaderd.

Tijdens het graven van zijn gangenstelsel in de bodem transporteert *C. subterranea* behoorlijke hoeveelheden fijn sediment van grote diepte naar het oppervlakte. Daardoor speelt hij een belangrijke rol bij het veranderen van zijn omgeving en daarmee ook een cruciale rol bij het ontaan van re-suspensie van het sediment. Wat opvallend is, is dat deze soort een dichtheidstoename liet zien in hetzelfde gebied en gedurende dezelfde tijd als waarop *A. filiformis* in aantal afnam. In deel II van dit proefschrift laat ik zien dat de drempelwaarde voor het optreden van sediment erosie gemiddeld lager lag bij hoge *C. subterranea* dichtheden en lage dichtheden van *A. filiformis* zoals gedurende de jaren-90 dan in de omgekeerde situatie met hoge dichtheden *A. filiformis* en lage dichtheden *C. subterranea* zoals die in de jaren-80 werden gevonden. De toename van *C. subterranea* leidt tot een vergroting van de instabiliteit van het sediment en daarmee tot een toename van de gevoeligheid van de bodem voor re-suspensie van fijne sediment deeltjes. Hoge dichtheden van *A. filiformis* had het tegenovergestelde effect en verhoogde de stabiliteit van het sediment. De verandering van een benthos gemeenschap gedomineerd door *A. filiformis* naar een gemeenschap gedomineerd door *C.subterranea* zou re-suspensie en troebelheid hebben kunnen doen verergeren in het Friese Front. Erosie zou kunnen verhinderen dat planktonische *A. filiformis* larven zich permanent kunnen vestigen. Reeds gevestigde stadia zouden met het sediment geresuspendeerd en vervolgens met de waterstroom weggevoerd kunnen worden. *C. subterranea,* echter, leeft diep in het sediment en wordt nauwelijks beïnvloed door verhoogde sediment re-suspensie. Verder wordt er gedacht dat re-suspensie van bodemmateriaal zowel de kwantiteit als de kwaliteit beïnvloed van het voedsel voor metname benthische suspensie- en filterraars zoals *A. filiformis*. Dit is van invloed op de conditie en overlevingskansen en kan leiden tot een afname van reproductie en tot lagere aantallen van levensvatbare larven. Het is aannemelijk dat de veranderde erosie gevoeligheid van het sediment de huidige gemeenschap in stand houdt en herstel of terugkeer van de geemeenschap naar de oude situatie, waar *A. filiformis* de gemeenschap domineerde, verhindert. De shift in de aanwezigheid van de twee soorten zou, wanneer eenmaal opgang gekomen, wel eens een blijvend karakter kunnen hebben en onafhankelijk van klimatologische factoren zijn. Omdat de negatieve impact die re-suspensie en water vertroebeling heeft op seston-voeders in het algemeen, lijkt het onwaarschijnlijk dat de *A. filiformis* populatie zich zal kunnen herstellen. Er zal echter meer onderzoek gedaan moeten worden naar het exacte effect van toegenomen re-suspensie gebeurtenissen. Metname het effect daarvan op de groei en reproductie van *A. filiformis*. Bijvoorbeeld een experiment waarin *A. filiformis* rekruten worden blootgesteld aan verschillende gradaties van vertroebeling van het water. Dit zou inzicht kunnen geven omtrent de rol van resuspensie op de vestiging en overleving van larven.

Door gebruik te maken van stabiele isotopen heb ik laten zien dat gedurende de zomermaanden *A. filiformis* met o.a. Thalassinide garnalen zoals *C. subterranea* en *Upogebia spp.* concurreert om dezelfde voedselbron. Gezien de enorme aantals toename van deze crustaceen valt te verwachten dat het momenteel nog moeilijker voor een *A. filiformis* populatie is om stand te houden.

Om te onderzoeken of de bovengenoemde mechanismen inderdaad zouden kunnen leiden tot een alternatieve stabiele toestand werd er een model geconstrueerd. De verkregen resultaten zijn consistent met de voorgestelde mechanismen.

Hoewel ik mogelijke redenen heb geïdentificeerd voor de schijnbare stabiliteit van de twee contrasterende toestanden, bleek het niet mogelijk om te achterhalen welke factoren ten grondslag lagen aan de aanvankelijke afname van *A. filiformis* en toename van *C. subterranea* populaties. De waargenomen populatie veranderingen kunnen een effect zijn van menselijk handelen. In de zuidelijke Noordzee bijvoorbeeld is boomkorvisserij de meest voorkomende vismethode. Het IMPACT programma uit 1998 had als doel om inzicht te verschaffen in de effecten van verschillende visserijtypen op de ecosystemen van de Noordzee en Ierse Zee. In het algemeen vlakt de passage van demersal vistuig de contouren van het sedimentoppervlak af en kan het de graaf- en leefgangen van epi- en infauna zoals van *A. filiformis* beschadigen. Bovendien kan de beweging van de korover de zeebodem leiden tot het in suspensie gaan van de fijnere sediment fractie. Dit kan weer leiden tot een sterkere verandering in de sediment karakteristiek van met name gebieden die voor een groot deel bestaan uit zulk fijn sediment bestaan en daarmee de soorten die daar leven. Sterfte door boomkor activiteiten wordt vooral direct veroorzaakt door de fysieke schade als gevolg van de passage van de kor of indirect door verstoring van de macrofauna op de zeebodem en de daarmee samenhangende predatie. Het is daarom erg waarschijnlijk dat commerciële boomkor visserij de samenstelling van de benthische levensgemeenschap beïnvloedt waardoor populaties van kwetsbare soorten kunnen afnemen tot lage aantallen en / of tot een lokaal beperkter voorkomen. Niettemin voltrok de afname in *A. filiformis* van ongeveer 1750 individuen per m^2 naar rond de 100 exemplaren per m^2 zich over een periode van slechts 5 jaar, tussen 1992 en 1997 terwijl het Friese Front al sinds vele jaren bevist wordt zonder dat er een vergelijkbaar effect op de *A. filiformis* populatie werd waargenomen. Dit maakt bodemvisserij dan ook een onwaarschijnlijke 'trigger' voor de waargenomen afname. Een andere verklaring voor wat de verandering in de *A. filiformis* populatie initieerde zou de populatie structuur van *A. filiformis* zelf kunnen zijn. In de periode dat deze soort rijkelijk aanwezig was (tussen 1982 en 1992) bestond de populatie voornamelijk uit volwassen exemplaren en weinig jongen. Het zou dus ook nog zo kunnen zijn dat de populatie aan het afsterven was en dat het aantal overlevende juvenielen onvoldoende was om de populatie in stand te houden of zich te laten herstellen. Dit had dan tot gevolg dat een verandering optrad van een stabiele, door *A. filiformis* gedomineerde toestand, naar de stabiele toestand gedomineerd door *C.subterranea*. Voornamelijk in de zuidelijke delen van het Friese Front (zoals het standaard station) is de macrobenthische faunaveranderd doordat 72% van het een aantal soorten tegelijkertijd met *A. filiformis* een veranderende populatie liet zien. Het blijft een vraag in hoeverre *C. subterranea* of *A. filiformis* een sleutelrol hebben in het controleren van de populaties van de andere macrobentische soorten.

In dit proefschrift laat ik zien dat er heden ten dage nog weinig begrepen wordt van het complexe, dynamische systeem van benthische gemeenschappen. Dit benadrukt het belang van het handhaven van langdurige monitor programma's van bentische fauna.

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Curriculum Vitae

Teresa Paula Fernandes Amaro was born on the 15th February 1975 in Porto, Portugal. She was educated at Rodrigues de Freitas High School, after which she went to the Sciences Faculty of Porto University where she studied Biology. As part of her degree, she decided to go to the Royal Netherlands For Sea Research to be specialized in marine Sciences. There, she did a practical period of 9 months and when back in Porto, she received her Licenciate degree. At the end of 1999 she decided to do volunteer work at the Royal Netherlands For Sea Research and in September of 2000 she started her PhD with a grant from Fundação Para a Ciência e Tecnologia.