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Ecology and Bathymetry of the Late Quaternary Shelly Macrobenthos from Bathyal and Abyssal Areas of the Norwegian Sea.

With 16 Text-Figures and 2 Appendices.

WOLFGANG OSCHMANN.

Abstract.

[OSCHMANN, W. (1991): Ecology and bathymetry of the late Quaternary shelly macrobenthos from bathyal and abyssal areas of the Norwegian Sea. — Senckenbergiana marit., **21** (5/6): 155–189, 16 figs., 2 tabs.; Frankfurt a. M.]

The shelly macrobenthos (mainly molluscs) from continental slope to basin environments of the Norwegian Sea have been studied along a transect from the Norwegian Shelf Slope Break to Jan Mayen. The faunal diversity (36 taxa in total) is relatively high, but the average size of taxa is very small, with many taxa of meiobenthic dimensions. In general, the density and diversity of the macrobenthos decreases with increasing depth from 580 to 3222 m, but is also influenced by local factors. As no sample from <580 m could be collected, only maximum depth occurrence could be given. Due to isotherm conditions in the water column below 400 m hydrostatic pressure seems to be the main factor controlling depth range of species. Eurybathic taxa (10), ranging in depth from 580 to 3222 m, are remarkably abundant.

Using cluster analysis, five benthic associations have been determined, which are depth-related but exhibit some overlap as well as patchy distribution along the transect. Epifauna accounts for up to 40% and suspension-feeders up to 70% of the fauna. Both values are unusually high, and may be due to dropstones, which provide small hard substrates and cause environmental heterogeneity.

Kurzfassung.

[OSCHMANN, W. (1991): Ökologie und Bathymetrie des spätquartären schalentragenden Makrobenthos der bathyalen und abyssalen Bereiche des Europäischen Nordmeeres. — Senckenbergiana marit., **21** (5/6): 155–189, 16 Abb., 2 Tab.; Frankfurt a. M.]

Das schalentragende Makrobenthos (überwiegend Mollusken) am Kontinentalabhang und Becken des Europäischen Nordmeers wurde entlang eines Richtschnitts vom Norwegischen

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Schelfabhang bis Jan Mayen untersucht. Die Fauna zeigt eine hohe Diversität (36 Taxa). Die Durchschnittsgröße der Individuen ist sehr klein, viele Taxa erreichen lediglich die mesobenthische Größenklasse. Generell nimmt die Faunendichte und Diversität mit der Tiefe von 580 bis 3222 m ab, dieser Trend wird aber teilweise von lokalen Faktoren überprägt. Da keine flachen Bereiche beprobt werden konnten gibt die Tiefenverbreitung der meisten Taxa lediglich die Maximaltiefe an, nicht jedoch die Minimaltiefe. Die isothermen Bedingungen im europäischen Nordmeer unterhalb von 400 m Wassertiefe legen eine vom hydrostatischen Druck limitierte Tiefenverteilung nahe. Eurybathe Taxa (10), die von 580 bis 3222 m vorkommen, sind sehr häufig.

Mit Hilfe einer Cluster-Analyse wurden fünf Benthos-Assoziationen ermittelt, die eine Tiefenzonierung aufweisen, aber auch eine fleckenhafte Verteilung entlang der Probentraverse. Der Anteil von Epibenthos in den Assoziationen erreicht bis zu 40%, Filtrierer bis zu 70%. Beide Werte sind für Tiefseemilieus ungewöhnlich hoch, und stehen vermutlich mit dropstones im Zusammenhang. Als Hartsubstrate in Weichböden erzeugen sie ein heterogenes Milieu.

Introduction.

The Norwegian Sea is particularly suitable for studies of the (palaeo)ecology and bathymetry of shelly macrobenthos for two reasons, the morphology of the sea floor and the rather uniform temperature distribution. Normally the continental slope is a narrow area, dipping steeply compared to the shelf and abyssal plains. Sedimentary processes on continental slopes predominantly take place as gravitational transport (e.g. slides, slumps, debris or grain flows, and turbidity currents; cf. Stow 1986). On the slope and especially at its foot, where sediments are trapped, occur therefore harsh and inhospitable environments, particularly for the shelly macrobenthos (mainly molluscs). In the Norwegian Sea, however, the continental slope terminates already at a depth of about 1000 m and changes into a gently dipping plateau, the Vøring Plateau. Therefore bathyal environments are spread over a large area (Figs. 1, 3), and due to a much lower rate of terrigenous sedimentation provide more hospitable environments for shelly macrobenthos. The second reason is the rather uniform temperature distribution in the Norwegian Sea below 400 m (e.g. Dietrich et al 1975; Segschneider in: Gerlach et al. 1986; Peinert et al. 1987). These isotherm conditions rule out temperature as a critical factor governing distribution of the benthic fauna. Their depth ranges, therefore, must be controlled by other depth related parameters such as the hydrostatic pressure.

Material and Methods.

The samples were obtained during cruise II/2 of the German research vessel "METEOR" in the Norwegian Sea during July 1986. The sampling stations are arranged along a transect from the shelf edge of Norway to Jan Mayen Island near the mid oceanic ridge and cover a distance of about 1000 km. The material comes from 20 box core samples taken at 11 sampling stations with a depth between 580 and 3222 m (Fig. 1). Live shelly macrobenthos occurred in the samples only in rare numbers. In order to obtain reliable sample sizes with sufficient numbers of individuals of each box core about 15 kg of sediment was carefully washed through

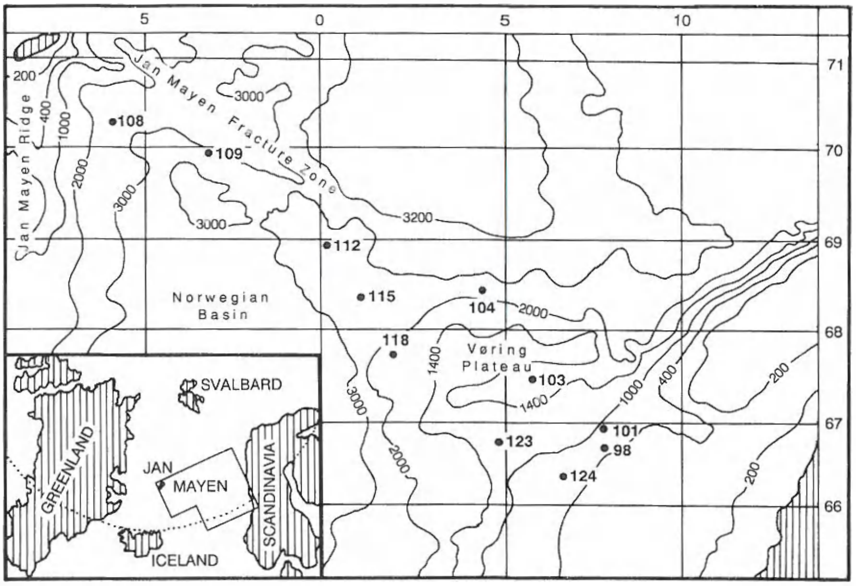

Fig. 1. Sketch map of the Norwegian Sea, with sampling stations of the box cores Nrs. 98–124.

Abb. 1. Lage der Probenstationen Nr. 98–124 im Europäischen Nordmeer.

a 0.5 mm sieve. This way the hardparts of most post-larval stages of the generally small and fragile shelly macrobenthos (mainly molluscs) were retrieved and served as the data base for studying the bathymetric distribution as well as the structure and relationship of the (palaeo)communities of the Norwegian Sea.

Applications of the community concept (association concept respectively) on shelly marine macrobenthos from shallow marine environments is an integral part of (actuo)-palaeontology (e.g. Dodd & Stanton 1981; Thomsen & Vorren 1986; Fürsich & Flessa 1987, 1991). Similar detailed investigations of bathyal and abyssal macrobenthos, however, are rare. Research is largely confined to taxonomy and autecology (e.g. Knudsen 1970, 1979; Allen & Sanders 1973; Sanders & Allen 1973, 1979; Clarke 1974; Bouchet & Warén 1979). Quantitative studies are rare (e.g. Gage 1977; Rowe et al. 1982; Grassle & Morse-Porteous 1987; Grassle 1989; Janssen 1989; Romero-Wetzel 1989; Rex et al. 1990; Hecker 1990) and usually include also taxa without hardparts which are far more common. In contrast, here only taxa with hardparts (mainly molluscs) are considered. This provides a data set comparable to others from modern and fossil shelf and deep sea environments.

Some biologists (e.g. Knudsen 1970) rejected hardparts as the sole data base for studies on ecology and bathymetry. Shells may have been disgorged by fishes or have lived attached to floating seaweed, and this way could have reached deep sea environments although originally living in shallow marine areas. The general small size of the taxa combined with a high number of growth bands (see below), the lack of dark colour pigments in the periostracum of shells, and the similarity to living macrobenthos from other deep sea environments exclude a major distortion of the data set in that way. Bulk sampling of dead shells is the accepted and appropriate way to obtain data in palaeoecology. In most cases they provide a good data base.

Population Structure.

As a first step of any faunal analysis the (par)autochthonous nature of the samples must be proved; transport and faunal mixing must be excluded. In the samples, few shells are fragmented and, apart from a few live individuals, bivalves occur disarticulated. Commonly size frequency histograms are used to estimate the autochthony of shells (e.g. DOTT & STANTON 1981; SØRENSEN 1984).

Here, size-frequency histograms of the bivalves *Astarte crenata* and *Yoldiella fraterna* are given (Fig. 2). These two species are, in some samples, abundant enough to produce reliable data. The size-frequency histograms correspond to a typical logarithmic curve and suggest therefore lack of transport. Such curves are typical of dead assemblages derived from populations with a high juvenile mortality and a decreasing mortality rate with age (e.g. DODD & STANTON 1981). Both the heterodont *Astarte crenata* (Fig. 2a, b) and the protobranch *Yoldiella fraterna* (Fig. 2c, d) exhibit similar patterns, despite their different larval development (planktotrophic versus lecitotrophic) and different life habit (endobenthic suspension-feeder versus mobile endobenthic deposit-feeder). SØRENSEN (1984) reports a bimodal size-frequency histogram for the bathyal protobranch bivalve *Phaseolus ovatus*, in his opinion related to growth cessation due to a protogynous (from female to male) sex change. Sex changes in bivalves are well known (e.g. MACKIE 1983), both prodandrous (from male to female, this is most common) and protogynous. Also rhythmic reversals are known. Thus, many bivalves are affected by growth cessations, but it is difficult to see how these influence the size-frequency pattern. Bimodal and polymodal size-frequency histograms are more likely related to sporadic larval settlement and/or certain stress factors within the ecosystem (e.g. ALLEN 1983).

Compared with shallow water shelly macrobenthos the size of the bathyal and abyssal species in general is very small (e.g. ALLEN 1983). Out of approximately 2000 specimens from 30 taxa of molluscs the largest (*Buccinum* sp.) is only 2.7 cm high. The size-frequency histograms of *Astarte crenata* and *Yoldiella fraterna* show, that approximately 75% of the specimens are smaller than 5 mm, and more than 90% smaller than 1 cm (Fig. 2). This is also true of the other, less common taxa, and is in agreement with many other studies (e.g. KNUDSEN 1970, 1979; ALLEN & SANDERS 1973; GAGE 1977; ALLEN 1983). Deep sea bivalves, and less significantly also gastropods, have reduced energy expenditure for reproduction by a lower rate of fecundity with reduced numbers of eggs (e.g. SCHELTEMA 1972; SANDERS & ALLEN 1973; ALLEN 1983). Sexual maturity of both sexes, indicated by gonad development, starts already in individuals only two or three mm in size (e.g. SANDERS & ALLEN 1973; LIGHTFOOT et al. 1979). The most extreme cases reported

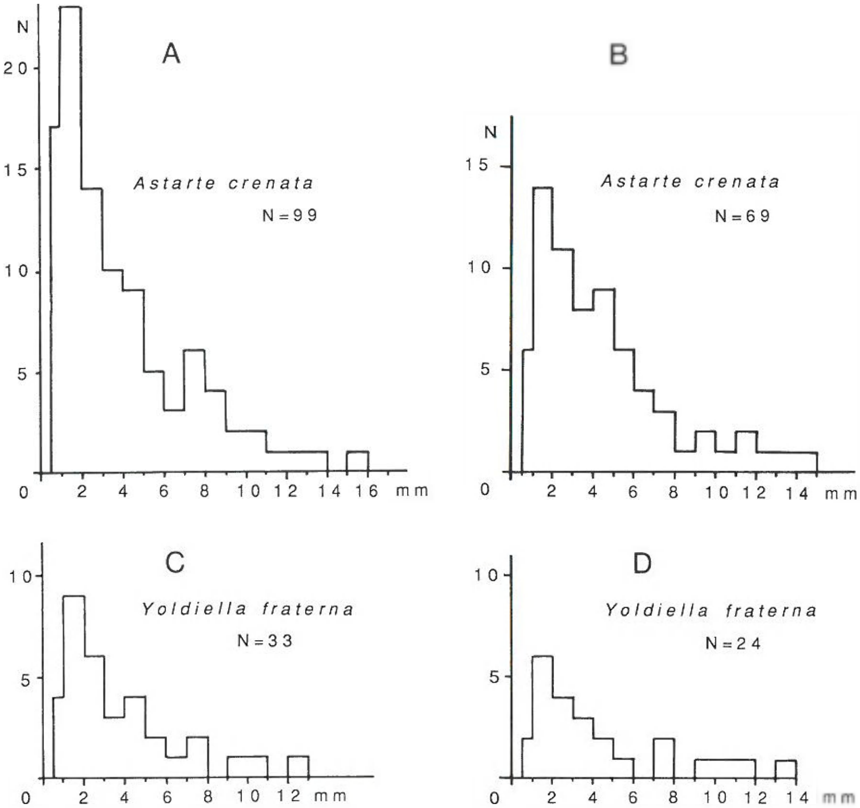

Fig. 2. Size-frequency histograms of the heterodont bivalve *Astarte crenata* and the protobranch bivalve *Yoldiella fraterna*. — A, C: sampling station 124; B, D: sampling station 98. — The histograms show a typical logarithmic shape and suggest high juvenile mortality and lack of transport. Both taxa are very small with up to almost 50% of specimens of meiobenthic dimensions (<2 mm).

Abb. 2. Die Größen-Häufigkeitsverteilungen der heterodonten Muschel *Astarte crenata* und der protobranchen Muschel *Yoldiella fraterna*. — A, C: Probenstation 124; B, D: Probenstation 98. — Die Histogramme zeigen eine typische logarithmische Verteilung, die eine hohe Sterberate der Juvenilformen und das Fehlen von Transport anzeigt. Beide Taxa sind sehr kleinwüchsig mit bis zu 50% der Individuen im Größenbereich des Mesobenthos (<2 mm).

are fertile *Microgloma yongei* and *M. turnerae*, both smaller than 1.1 mm (SANDERS & ALLEN 1977). These bivalves produce only one or two eggs at a time, compared to 100,000 or even millions of eggs of shallow water oysters (ANDREWS 1979). Seasonal scarcity of food due to strong seasonal variation in flux from surface waters in the high latitude Norwegian Sea (e.g. LIMPITT 1985; HONJO et al. 1988; GRAF

1989), the low water temperatures (approximately 0° C), and high hydrostatic pressure reduce substantially the metabolic rates, enzymatic activities and enzymatic reaction velocities (Georges 1979; Somero et al. 1983). The resulting very low growth rates (e.g. Grassle & Sanders 1973) cause micromorphy or miniaturisation of the deep sea taxa. Growth bands are numerous (Figs. 7–9), even in very small specimens. Turekian et al. (1975) reported an 8.4 mm long protobranch bivalve *(Tinaria callistiformis)* which was about 100 years old. Gonads appeared at a length of 4 mm and an age of 50 to 60 years. Gigantism, as has been reported from isopods, pantopods and polychaetes of deep sea and very cold antarctic deep shelf environments (e.g. Wolff 1962; Wägele & Schminke 1986) has not been found.

Density, Diversity and Composition of Macrobenthos versus Meiobenthos.

In neritic environments molluscs and foraminifera belong to separated size classes: macrobenthos (larger than 2 mm) and meiobenthos (0.2 to 2 mm; e.g. Mare 1942; Schaefer & Tischler 1983). In the present study the generally tiny molluscan-dominated macrobenthos (up to almost 50% of specimens are smaller than 2 mm; Fig. 2) overlaps remarkably with the meiobenthic size class. On the other hand, many foraminifera reach more than 2 mm in size. Some calcareous taxa, such as *Pyrgo murrhina* (Fig. 3) are up to 5 mm in diameter. The arenaceous *Rhabdamina abyssorum* reaches even more than two cm in length. The great overlap in size may enhance competition between foraminifera and mollusca or

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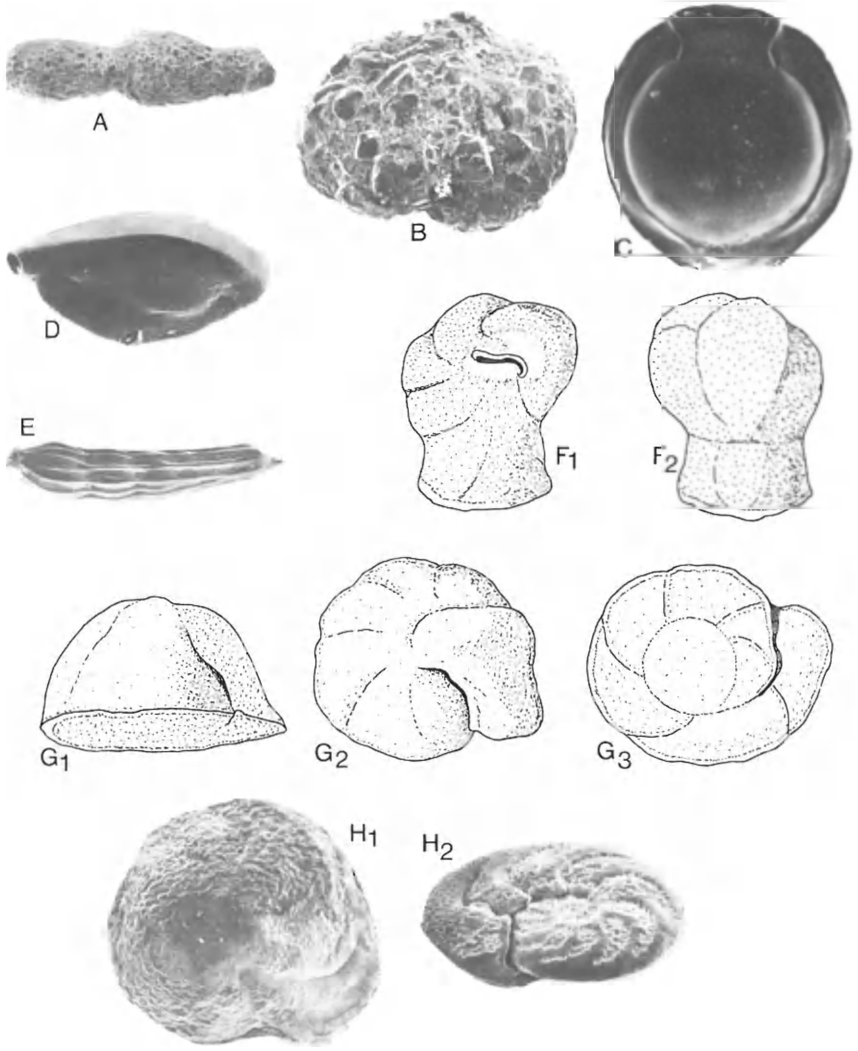
Fig. 3. Dominant taxa of foraminifera >0.5 mm. — A. *Reophax nodulosum;* side view, × 27. Sampling station 108. — B. *Cribrostomoides subglobosum;* oblique side view, × 27. — Sampling station 108. — C. *Pyrgo murrhina;* side view, × 22. Sampling station 108. — D. *Triloculina frigida;* side view, × 50. Sampling station 108. — E. *Dentalina cuvieri;* side view, × 20. Sampling station 108. — F. *Rupertina stabilis;* shells always attached to dropstones; side views, with aperture (F_1) and opposite side (F_2), × 16. Sampling station 98. — G. *Cibicides refulgensis;* shells always attached to dropstones; slightly oblique side view (G_1), convex umbilical side (G_2), and attached spiral side (G_3), × 23. Sampling station 98. — H. *Cibicidoides wuellersdorfi;* umbilical side (H_1), × 30, and spiral side (H_2), × 25. Sampling station 108.

Abb. 3. Häufige Foraminiferen-Taxa >0.5 mm. — A. *Reophax nodulosum;* Seitenansicht, × 27. Probenstation 108. — B. *Cribrostomoides subglobosum;* Ansicht schräg von der Seite, × 27. Probenstation 108. — C. *Pyrgo murrhina;* Seitenansicht, × 22. Probenstation 108. — D. *Triloculina frigida;* Seitenansicht, × 50. Probenstation 108. — E. *Dentalina cuvieri;* Seitenansicht, × 20. Probenstation 108. — F. *Rupertina stabilis;* Gehäuse auf Dropstones festgewachsen; Seitenansicht, mit Apertur (F_1) und gegenüberliegende Seite (F_2), × 16. Probenstation 98. — G. *Cibicides refulgensis;* Gehäuse auf Dropstones festgewachsen; Ansicht leicht schräg von der Seite (G_1), convexe Umbilicalseite (G_2), and festgeheftete Spiralseite (G_3), × 23. Probenstation 98. — H. *Cibicidoides wuellersdorfi;* Umbilicalseite (H_1), × 30, und Spiralseite (H_2), × 25. Probenstation 108.

meio- and macrobenthos respectively, which do not exist, or only at the earliest juvenile stages, in neritic environments. This is possibly one reason for the decreasing density and diversity of shelly macrobenthos with increasing water depth. In the last 20 years the limits of macro- and meiobenthic size categories progressively became smaller (at present: meiobenthos >0.06 mm, macrobenthos >0.12 mm; e.g. Rowe 1983) probably taking into consideration the great overlap between mollusca and other soft bodied metazoans and foraminifera. Unfortunately the progressive reduction of size classes has caused confusion. Presently no uniform standard for



deep sea benthos exists and the limits between shallow and deep marine benthos differ remarkably. Despite the terminological confusion it is appropriate to consider molluscan macrobenthos and foraminiferal meiobenthos together, although in the case of the latter it is done here only in a general way.

Along a transect from the shelf/slope break off Norway to Jan Mayen (Fig. 1) the density, diversity and general faunal composition of the molluscan dominated macrobenthos and the foraminiferal meiobenthos (list of taxa see appendix 1; most common taxa see Fig. 3) has been examined (Fig. 4).

The total faunal **density** (Fig. 4) varies from 1000 to 15000 specimens, (larger 0.5 mm/15 kg sediment), and in general increases with water depth. Sampling stations shallower than 1000 m (slope) contain between 1000 and 2000 specimens. At deeper stations the faunal density reaches up to 10 times that value. The reason for this remarkable increase is probably not due to a higher rate of productivity but a lower rate of sedimentation. Input of land-derived detritic material diminishes to the deeper and more offshore parts of the Norwegian Sea.

The **diversity** (expressed by numbers of taxa; Fig. 4) is, compared with other deep sea environments, relatively high. Its values decrease with depth, but this general trend shows various modifications. Slightly below the shelf/slope break at 580 m 38 taxa were found, out of these 29 macrobenthos taxa (Fig. 4). These values remain constant at the next sampling station at 652 m. Going downslope off Norway, however, diversity values decrease rapidly. Only 17 taxa, out of these 12 belonging to the macrobenthos, are present near 1000 m depth. Station 101 is situated at the foot of the continental slope, where shelf-derived suspended matter and gravitationally transported sediments (e.g. turbidity currents) are trapped. Thus very presumably harsh environmental exists. On the Vøring Plateau itself, between 1000 and 1500 m depth (sampling stations 103 and 123), diversity values again increase to 21–22 taxa, with 15–16 belonging to the macrobenthos. The higher values here, compared to those at station 101 (near 1000 m) are presumably related to the more stable conditions of the physical environment. Going downslope from the plateau, the slope is even steeper than the shelf slope and the number of taxa again decreases. Stations 118 and 104 show diversity values of 17 and 20 taxa respectively, 12 of them macrobenthos. At station 115, which is situated at the foot of the plateau slope, minimum values are documented (14 taxa, out of these 8 macrobenthic ones). Gravitationally forced sedimentary processes (e.g. turbidity currents) presumably again form harsh and inhospitable environments particularly for the shelly macrobenthos. The diversity values at station 112 (16 taxa, out of these 9 macrobenthos) situated near to the Jan Mayen Fracture Zone and station 109 in the Norwegian Basin (20 taxa, out of these 12 macrobenthos) are still low. Station 108 is situated half way up slope to the Jan Mayen Ridge on a rounded hilltop and shows a significantly higher diversity (27 taxa, out of these 18 macrobenthos). Despite the much greater depth, this value is even slightly higher than that of the Vøring Plateau.

It should be also mentioned, that density and diversity of burrowing "wormlike" organisms (polychaetes, sipunculids and enteropneusts) in part differ remarkably from that of the shelly macrobenthos given (Romero-Wetzel 1989), which most likely refers to the great differences in life and feeding habits.

The **composition** of macro- versus meiobenthos also show a distinct pattern, with a remarkable decrease of macrobenthos with depth. At 580 m almost 30% of

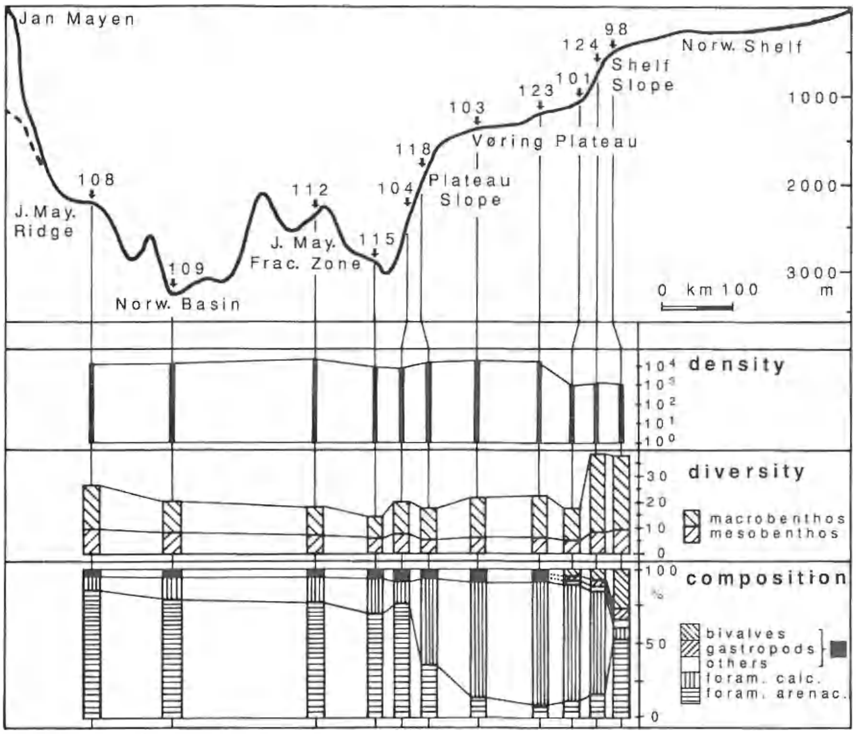


Fig. 4. Traverse from the Norwegian Schelf to Jan Mayen, showing the variation in faunal density (given as number of specimens >0.5 mm per 15 kg sediment), in diversity (numbers of taxa) and in composition of shelly benthic fauna (>0.5 mm).

Abb. 4. Traverse vom Norwegischen Schelf nach Jan Mayen und die Änderungen in der Faunendichte (Individuenanzahl >0.5 mm per 15 kg Sediment), in der Diversität (Anzahl der Taxa) und in der Zusammensetzung des hartteiltragenden Makrobenthos (>0.5 mm).

the individuals belong to the macrobenthos, with bivalves dominating (about 20%). The percentage of macrobenthos decreases rapidly with depth. At 1000 m only 14% of individuals belong to the macrobenthos. On the Vøring Plateau macrobenthos is only 8 to 10%. In basinal areas (Vøring Plateau slope, Norwegian Basin, Jan Mayen Fracture Zone and the slope of the Jan Mayen Ridge) macrobenthos does not reach more than 3%. This drastic decrease does not only reflect a reduction of macrobenthos in terms of absolute numbers, but also an increase (up to the factor 10) of meiobenthic foraminifera. The reason why meiobenthic foraminifera are that more successful in deep sea environments than macrobenthic molluscs is not understood. Probably the much simpler morphology and metabolic pathways of protozoan foraminifera are less affected by stress factors such as low temperature and high hydrostatic pressure than molluscs with their highly complex morphology and metabolism. The composition of meiobenthos also underlies significant changes. At 580 m calcareous foraminifera dominate with 80%. Already at 650 m arenaceous forms represent 90%. This relationship remains stable on the Vøring Plateau. Half downslope to the Norwegian Basin arenaceous and calcareous foraminifera are of equal abundance. In the Norwegian Basin with water depth below 2000 m calcareous foraminifera again dominate with about 80%. Apart from the shallowest sampling station, where *Rupertina stabilis* dominates, a form exhibiting special adaptations (e.g. LUTZE & ALTENBACH 1988), dominates, the distribution of foraminifera seems to be depth related.

Depth Range of Macrobenthic Taxa.

Apart from density, diversity and composition of the total fauna, also the depth range of 36 macrobenthic taxa have been studied (Fig. 5). Within the depth range studied (580 m – 3222 m), only one taxon, *Hyalopecten frigitus* seems to have its upper limit of range (cf. MENZIES & GEORGE 1972; BOUCHET & WARÉN 1979; although they give somewhat different ranges). For most taxa obviously their upper range limits, are shallower than 580 m and therefore are not reached. This is also supported by literature data (e.g. CLARKE 1974; HØISÆTER 1986; THOMSEN & VOREN 1986). In contrast, the lower range limit is well defined for most taxa (Fig. 5), although for rare taxa this may not be significant. It may also be that the taxa have somewhat different ranges in other areas (e.g. CLARKE 1962; KNUDSEN 1970, 1979; BOUCHET & WARÉN 1979), which probably reflects different oceanographic situations (e.g. with regard to temperatures and current regime).

The depth range of macrobenthic taxa in bathyal and abyssal depth is controlled by various physical factors. Apart from oxygen and nutrient supply, the hydrostatic pressure (one atm. increase for every 10 m depth), and the water temperature, which decreases drastically to values near 0° C at abyssal depth are most important. MADSEN (1961) postulated hydrostatic pressure as the dominant factor. Subsequently the strong influence of temperature was recognized (e.g. DAHL 1972; MENZIES & GEORGE 1972; CLARKE 1974; KNUDSEN 1979), and supported by the remarkable similarity of shallow water macrobenthos of the Arctic and deep water macrobenthos of the Norwegian Sea. KNUDSEN (1979) even defined the bathyal zone in terms of depth as ranging from 400 to 2000 m, and in terms of temperature as ranging from 10° to 4° C, and the abyssal zone as ranging from 2000 to 6000/7000 m with temperatures below 4° C. Obviously some taxa are rather sensitive to temperature changes (stenothermal), while others are tolerant (eurythermal). In the same way, some taxa are sensitive to, and others tolerant to changes in hydrostatic pressure (stenobathic versus eurybathic). Normally both variables change with depth and it is difficult to decide which factor is the overriding one. In the Norwegian Sea the surface water temperature changes from W to E from 4° to 10° C. The temperature of the intermediate water body (200 to 400 m depth) ranges from 0° to 6° C. From 400 m to the deep sea floor the temperature in the Norwegian Basin is rather uniform and varies from –0.5° to –0.9° C (DIETRICH 1975; SWIFT 1986; SEGSCHNEIDER in: GERLACH et al. 1986; PEINERT et al. 1987).

depth range of the macrobenthic taxa

	580	652	967	1157	1426	1895	2250	2283	2296	2808m	3222m
Hyalopecten frigidus						•		•		•	•
Bathyarca glacialis	•	•		•	•			•			•
Buccinum sp.	•	•				•		•		•	•
Hyalopecten cf. *graui*	•	•	•	•	•	•	•	•	•	•	•
Dacrydium ockelmanni	•	•		•	•	•	•	•	•	•	•
Kelliella miliaris	•	•				•		•	•	•	•
Parvicardium minimum	•	•						•			•
Policordia jeffreysi		•	•	•	•		•	•	•	•	•
Terebratula sp.	•	•			•		•	•			•
Thyasira sp.		•						•			•
Katadesmia cf. *colthoffi*	•	•	•	•	•	•	•	•	•	•	•
Sertella septentrionalis	•		•		•			•		•	
Limopsis aurita	•					•	•	•	•	•	
Hornera sp.	•	•	•	•	•		•	•	•		
Cuspidaria lamellosa	•	•				•	•		•		
Dentalium sp.	•	•		•				•	•		
"*Echinocardium*" sp.	•	•		•	•			•			
Astarte crenata	•	•	•		•		•	•			
Amauropsis sp.	•	•		•		•	•	•			
Leptochiton sp.	•	•				•	•				
Cyclopecten imbrifer	•	•	•	•	•		•				
Hiatella arctica	•	•	•	•	•	•					
Limatula louiseae	•	•		•	•	•					
Heteranomia sp.	•	•	•	•	•						
Yoldiella fraterna	•	•	•		•						
Crisia sp.	•	•	•	•							
Cylichna cf. *alba*		•		•							
Yoldiella sp.	•	•		•							
Crisiella cf. *producta*	•	•	•								
Bentharca sp.		•									
Entalina quinquangularis	•	•									
Epitonium sp.		•									
Pleurotomella sp.	•	•									
Poromya granulata		•									
Cylichnum cf. *africanum*	•										
Oenopotia sp.	•										

Fig. 5. Bathymetric distribution of the shelly macrobenthos of the Norwegian Sea. — Within the depth range of the study the various taxa show no upper limits, but well defined lower depth limits. Percentage of eurybathic taxa, ranging from 580 to 3222 m, is remarkably high.

Abb. 5. Tiefenverteilung des hartteiltragenden Makrobenthos im Europäischen Nordmeer. — Innerhalb des untersuchten Tiefenbereiches existiert keine Minimumtiefe, wohl aber eine maximal Tiefe für die verschiedenen Taxa. Der Anteil an eurybathen Taxa ist sehr hoch.

Obviously all samples in this study have been taken from an isotherm environment. The depth range of the taxa therefore should be controlled by the hydrostatic pressure. The majority of the taxa here seem to reach their maximum tolerance of hydrostatic pressure, and thus their maximum depth of occurrence. However, out of 36 taxa of macrobenthos 10 are tolerant to pressure changes between 58 and 322 atm., representing a depth range from 580 to 3222 m. This proportion is remarkably high compared to results of MENZIES & GEORGES (1972), according to whom eurybathic taxa constitute only a small percentage (normally less than 1%) of the deep sea fauna. This is even more surprising when considering, that the great majority of deep sea bivalves have lecitotrophic larvae or direct development and thus lack a planktonic dispersal stage (KNUDSEN 1970, 1979; SCHELTEMA 1972; ALLEN & SANDERS 1973; BOUCHET & WARÈN 1979; LIGHTFOOD et al. 1979). Nonetheless planktonic larval development also exists, mainly among gastropods, but also in bivalves (KNUDSEN 1970, 1979; BOUCHET & WARÈN 1979; LIGHTFOOD et al. 1979; ALLEN 1983). Veliger larvae of deep sea bivalves and gastropods have been recorded from the surface waters of the oceans (BOUCHET & WARÉN 1979; LUTZ et al. 1980; ALLEN 1983), and also in several hundreds to even 2000 m depth (e.g. SCHELTEMA 1972; THIEDE 1974), although it is still today largely unknown, how larvae move some thousand meters upwards and sink down again. SCHELTEMA (1972) assumes that deep sea currents may help to distribute lecitotrophic larvae horizontally and perhaps also vertically during their short (lasting some hours to at most a few days) non-feeding pelagic stage. KNUDSEN (1970, 1979) reports of so-called "guest species" which normally are restricted to abyssal depth, but may occur locally also in shallower water. This "abnormal" vertical distribution is in his opinion due to upwelling. The inverse process probably produces shallow water guest species in bathyal and abyssal areas of the Norwegian Sea. The bottom water of the Norwegian Sea derives from very cold (–0.5° C) and thus very dense surface water of the Greenland Sea (e.g. DIEDRICH 1975; SWIFT 1986). The high density causes a turnover of the water masses within the water column and may bring larvae of shallow water guest species down to deep sea environments. Unfortunately, the type of larval development for most of the taxa occurring there is not yet known. It is therefore still speculative to link the broad depth range of the eurybathic taxa to planktotrophic larval development, which would those larvae allow to disperse over wide horizontal and vertical areas.

Benthic Faunal Analysis.

Most ecological and palaeoecological studies are concerned with single taxa and individuals (autecology). The contrasting approach focuses on describing and interpreting organisms in context with other coexisting organisms. These synecological studies have become an integral part of biology since the end of the last century (e.g MÖBIUS 1877). Unfortunately, the comprehensive study of the total biotic component of an ecosystem, the biocoenosis, is in general too expensive. Therefore, the analysis of only part of the taxonomic groups, for example of those belonging to the same size classes, is more practical. NEWELL et al. (1959) named these partial representations of the biocoenosis organism communities. Apart from the much easier handling and retrieval of the data, this concept permits the comparison of ecological and palaeoecological studies, provided, both use the preservable part of a biocoenosis, such as in our case the shelly macrobenthos. Nevertheless, there are remarkable differences between data sets of living and fossil taxa. The latter underwent additional information loss by various taphonomic processes (e.g. transport, diagenetic solution, time-averaging; LAWRENCE 1968; STANTON 1976; FÜRSICH 1978; FÜRSICH & ABERHAN 1990). This should be referred to terminologically by differentiating between the living community in ecology and the dead association in palaeoecology (e.g. FÜRSICH 1984; OSCHMANN 1988).

Taphonomy.

In the present study taphonomic biases are in general of minor importance. Biostratinomic distortion by transport and faunal mixing can be excluded as has already been demonstrated above. The age of the shell material reaches from present-day to several thousand years. However, it does not go beyond the last deglaciation period (approximately 9,500 years BP; JANSEN & VEUM 1990), which is indicated by a dark layer of sediment and an increased amount of sand and pebble-sized dropstones. The percentage of carbonate hardparts in this horizon is generally very low, due to reduced carbonate production by organisms and/or increased carbonate dissolution. Diagenetic solution starts already in the Recent to subrecent topmost layer of sediment. Traces of chemical corrosion are already visible on specimens lying on sediment surface, probably due to the much higher amount of CO_2 in the bottom water compared to shelf environments. The presence of aragonitic taxa which generally dominate, as well as of calcitic taxa indicate, that diagenetic distortion has not (jet) taken place. Time-averaging, as far as it results from the analysis of bulk samples, is indeed a conceptual limitation, and in general, an inherent problem of palaeontological studies. Fortunately environmental conditions did not alter much in the last few thousand years since the latest deglaciation period. Therefore, major changes in the faunal composition, which after time-averaging would result in major misinterpretations, can be excluded.

Procedure.

The characteristic attribute of communities and associations is their recurrence in space and time (PETERSEN 1924; conceptual limitations see OSCHMANN 1988). Identification of recurrence needs statistical approach. In this study 20 box core samples from 11 stations have been available. Out of these 15 had been rich enough (in number of taxa and number of specimens) to apply computer-aided sorting. A Q-mode cluster analysis, the hierarchical agglomerative WARD method from SPSS (advanced statistic package) has been used to create a dendrogram (Fig. 6; further details regarding the procedure see OSCHMANN 1988).

To define the associations from the dendrogram (Fig. 6) the samples within a particular cluster were combined, by adding up and grouping all individuals of the particular species according to their relative abundances (App. 2). An association is characterised by the relative abundance and frequency percentage of the different species and by the trophic group composition and the life-habit structures (WALKER

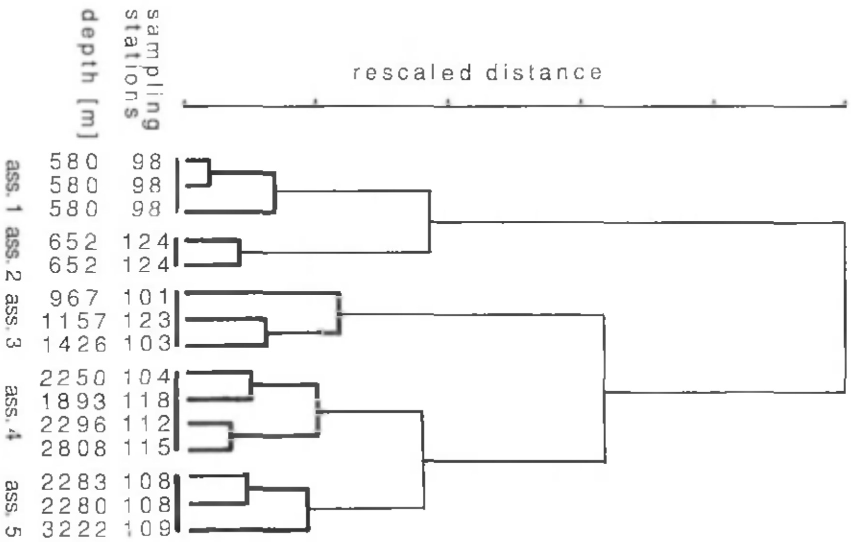


Fig. 6. Dendrogram of a Q-mode cluster analysis (hierarchical agglomerative Ward method from SPSS advanced statistics).

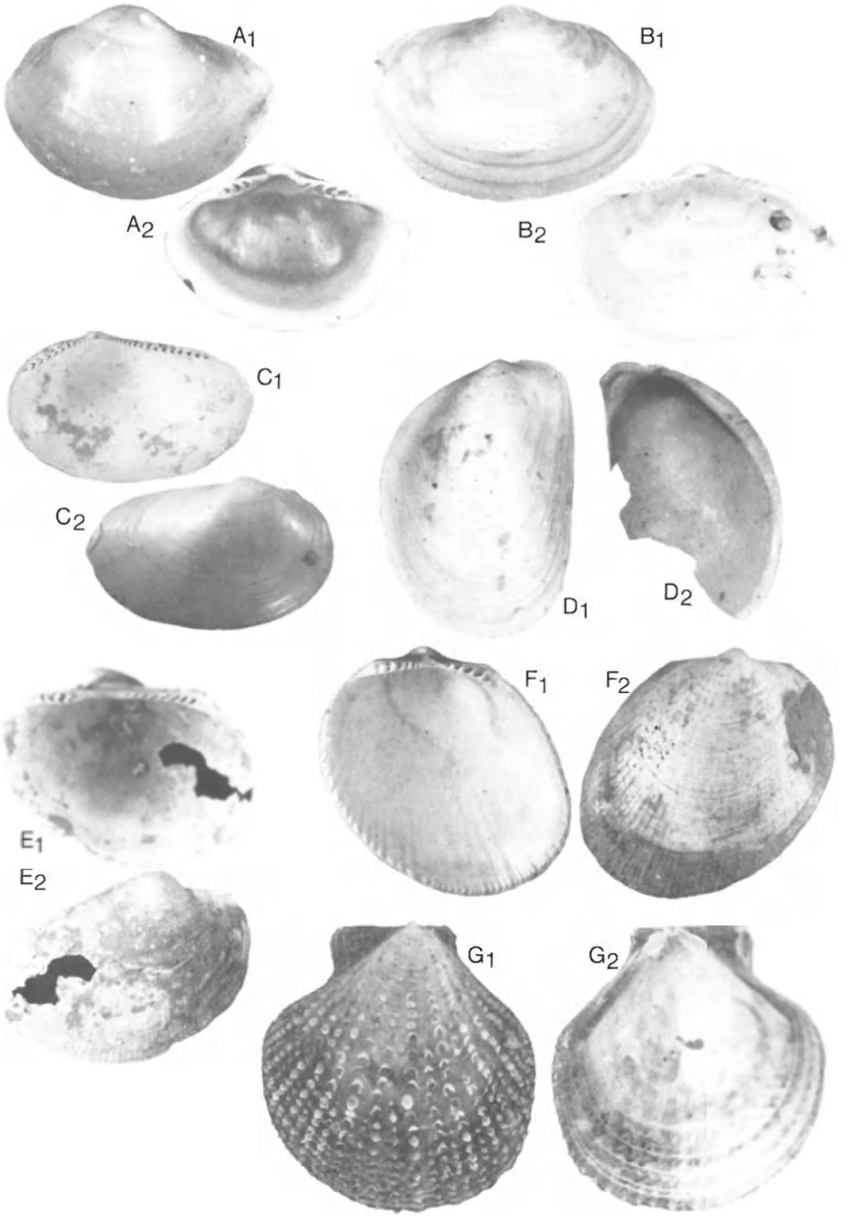
Abb. 6. Dendrogram einer Q-Clusteranalyse (hierarchisches agglomeratives Verfahren nach Ward des SPSS Advanced Statistics Programms).

▶

Fig. 7. Taxa of the trophic nuclei of the associations (see also Figs. 8–9). — A. *Yoldiella fraterna;* left valve exterior (A$_1$), right valve interior (A$_2$); × 13. Sampling station 98. — B. *Yoldiella* sp. paired valves; right valve exterior (B$_1$), left valve interior (B$_2$); × 13. Sampling station 98. — C. *Katadesmia* cf. *colthoffi;* right valve exterior (C$_1$) and interior (C$_2$); × 5.5. Sampling station 109. — D. *Dacrydium ockelmanni;* right valve exterior (D$_1$), fragmented right valve interior (D$_2$); × 11. Sampling station 98. E. *Bathyarca glacialis;* right valve interior (E$_1$) and exterior (E$_2$); × 4.5. Sampling station 98. — F. *Limopsis aurita;* right valve interior (F$_1$) and exterior (F$_2$); × 3.5. Sampling station 98. — G. *Cyclopecten imbrifer;* left valve exterior (G1$_1$ and interior (G$_2$); × 3.5. Sampling station 98.

Abb. 7. Taxa der trophischen Kerne der Assoziationen (siehe auch Abb. 8 und 9). — A. *Yoldiella fraterna;* linke Klappe von außen (A$_1$), rechte Klappe von innen (A$_2$); × 13. Probenstation 98. — B. *Yoldiella* sp.; zweiklappig; rechte Klappe von außen (B$_1$), linke Klappe von innen (B$_2$); × 13. Probenstation 98. — C. *Katadesmia* cf. *colthoffi;* rechte Klappe von außen (C$_1$) und von innen (C$_2$); × 5.5. Probenstation 109. — D. *Dacrydium ockelmanni;* rechte Klappe von außen (D$_1$), fragmentierte rechte Klappe von innen (D$_2$); × 11. Probenstation 98. — E. *Bathyarca glacialis;* rechte Klappe von innen (E$_1$) und außen (E$_2$); × 4.5. Probenstation 98. — F. *Limopsis aurita;* rechte Klappe von innen (F$_1$) und außen (F$_2$); × 3.5. Probenstation 98. — G. *Cyclopecten imbrifer;* linke Klappe von außen (G$_1$) und von innen (G$_2$); × 3.5. Probenstation 98.

1972). Data regarding autecology (App. 1) derive from Knudsen (1967, 1970, 1979), Allen & Sanders 1973), Allen & Morgan (1979), Oliver & Allen (1980 a, b), Sanders & Allen (1973, 1977), Allen (1983), Kohn (1983), Morton 1983, and



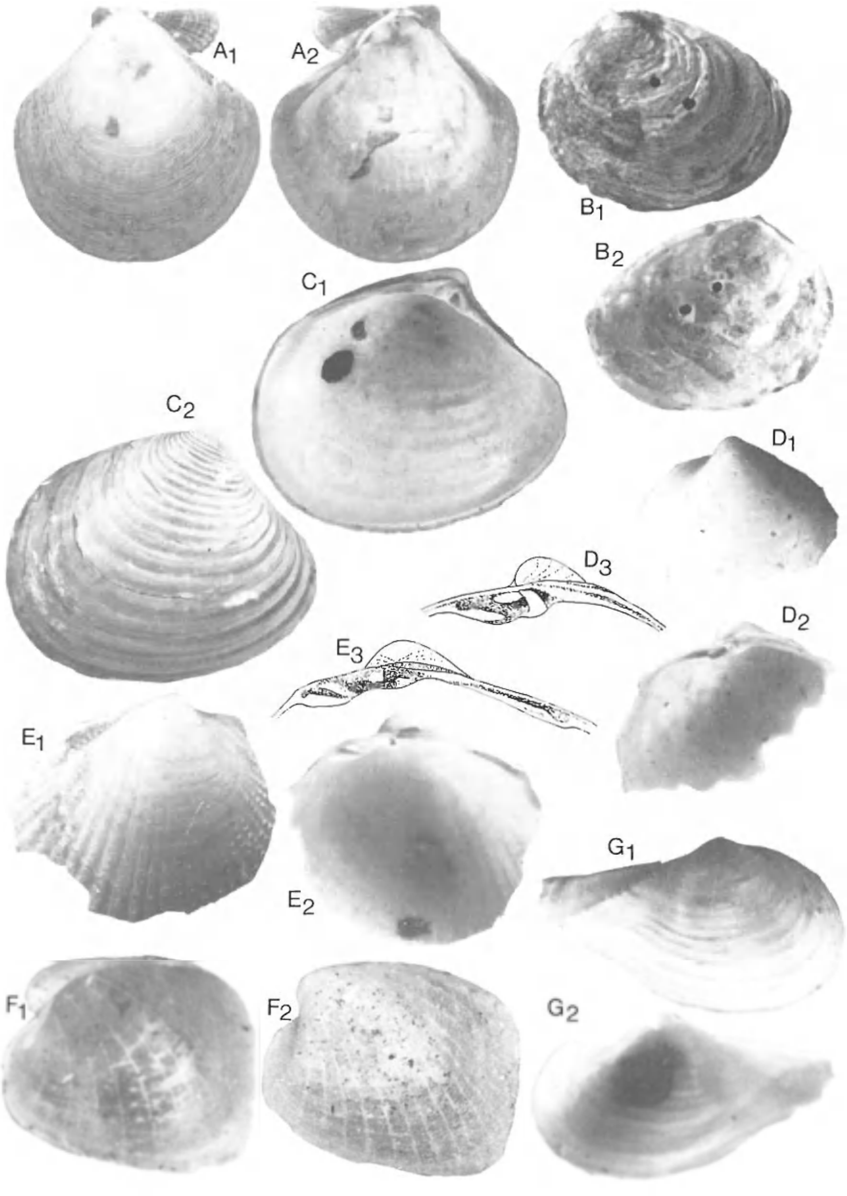


Fig. 8. Taxa of the trophic nuclei of the associations (continuation of Fig. 7, see also Fig. 9). — A. *Hyalopecten* cf. *graui;* right valve exterior (A_1) and interior (A_2); × 3.5. Sampling station 98. — B. *Heteranomia* sp.; left valve bored, exterior (B_1) and interior (B_2); × 4. Sampling station 98. — C. *Astarte crenata;* left valve interior with drill hole (C_1), right valve exterior (C_2); × 3.5. Sampling station 98. — D. *Kelliella miliaris;* left valve exterior (D_1) and

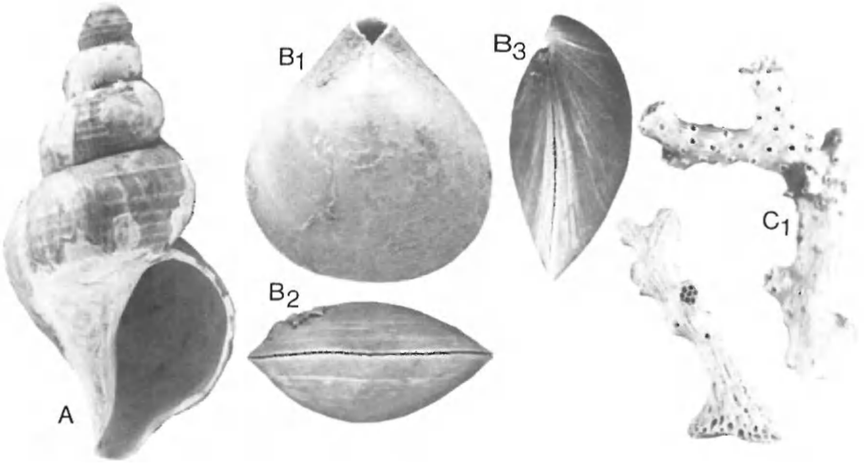


Fig. 9. Taxa of the trophic nuclei of the associations (continuation of Figs. 7–8). — A. *Buccinum* sp.; largest specimen found in the Norwegian Sea; × 2. Sampling station 108. — B. "*Terebratula*" sp.; dorsal view (B_1), anterior view (B_2) and lateral view (B_3); × 3.5. Sampling station 124. — C. *Hornera* sp.; two fragmented colonies; × 7.5. Orifices of the zooids are almost exclusively oriented to one side of the colonies (C_1) and probably result from a preferentially unidirectional bottom current. Sampling station 101.

Abb. 9. Taxa der trophischen Kerne der Assoziationen (Fortsetzung von Abb. 7–8). — A. *Buccinum* sp.; größtes gefundenes Individuum im Europäischen Nordmeer; × 2. Probenstation 108. — B. „*Terebratula*" sp.; von dorsal (B_1), von vorne (B_2) und von lateral (B_3); × 3.5. Probenstation 124. — C. *Hornera* sp.; zwei fragmentierte Kolonien; × 17.5. Vermutlich durch gerichtete Bodenströmungen bedingt sind die Orofícien der Zooide nahezu alle an einer Seite der Kolonie angeordnet (C_1). Probenstation 101.

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interior (D_2), × 22; sketch of hinge of left valve (D_3), × 31. Sampling station 98. — E. *Parvicardium minimum;* right valve exterior (E_1) and interior (E_2), × 16; sketch of hinge of right valve (E_3), × 24. Sampling station 124. — F. *Policordia jeffreysi;* right valve interior (F_1), left valve exterior (F_2); × 13. Sampling station 124. — G. *Cuspidaria lamellosa;* right valve exterior (G_1) and left valve interior (G_2); × 16. Sampling station 124.

Abb. 8. Taxa der trophischen Kerne der Assoziationen (Fortsetzung von Abb. 7, siehe auch Abb. 9). — A. *Hyalopecten* cf. *grayi;* rechte Klappe von außen (A_1) und von innen (A_2); × 3.5. Probenstation 98. — B. *Heteranomia* sp.; linke Klappe mit Bohrlöchern, von außen (B_1) und von innen (B_2); × 4. Probenstation 98. — C. *Astarte crenata;* linke Klappe von innen mit Bohrloch (C_1), rechte Klappe von außen (C_2); × 3.5. Probenstation 98. — D. *Kelliella miliaris;* linke Klappe von außen (D_1) und von innen (D_2), × 22; Schloßskizze der linken Klappe (D_3), × 31. Probenstation 98. — E. *Parvicardium minimum;* rechte Klappe von außen (E_1) und von innen (E_2), × 16; Schloßskizze der rechten Klappe (E_3), × 24. Probenstation 124. — F. *Policordia jeffreysi;* rechte Klappe von innen (F_1), linke Klappe von außen (F_2); × 13. Probenstation 124. — G. *Cuspidaria lamellosa;* rechte Klappe von außen (G_1) and linke Klappe von innen (G_2); × 16. Probenstation 124.

Thomsen & Vorren (1986). To obtain adequate results and to be able to compare trophic and life-habit structures of different associations it is practical to take only the more common taxa (80% of the total number of specimens). They form the trophic nucleus of an association (Walker 1972). Taxa which occur in the trophic nucleus of one or more associations are illustrated by photographs (Figs. 7–9) and by sketches (Figs. 10–14).

Description of Associations.

Astarte crenata/Heteranomia sp. Association.

(Fig. 10; App. 2).

The association is represented by three samples, all from sampling station 98, and consist of 29 taxa and 226 specimens. The depositional environment of this association is the upper slope near the shelf slope break in 580 m depth. Eleven

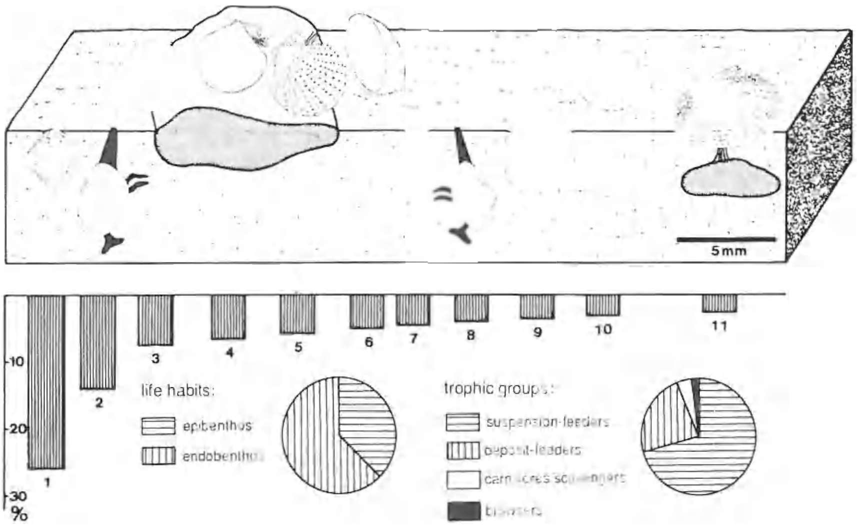

Fig. 10. Trophic nucleus of the *Astarte crenata/Heteranomia* sp. association. — 1. *Astarte crenata;* 2. *Yoldiella fraterna;* 3. *Heteranomia* sp.; 4. *Hyalopecten* cf. *graui;* 5. *Cyclopecten imbrifer;* 6. „*Terebratula*“ sp.; 7. *Parvicardium minimum;* 8. *Yoldiella* sp.; 9. *Dacrydium ockelmanni;* 10. *Kelliella miliaris;* 11. *Bathyarca glacialis.*

Abb. 10. Trophischer Kern der *Astarte crenata/Heteranomia* sp. Assoziation. — 1. *Astarte crenata;* 2. *Yoldiella fraterna;* 3. *Heteranomia* sp.; 4. *Hyalopecten* cf. *graui;* 5. *Cyclopecten imbrifer;* 6. „*Terebratula*“ sp.; 7. *Parvicardium minimum;* 8. *Yoldiella* sp.; 9. *Dacrydium ockelmanni;* 10. *Kelliella miliaris;* 11. *Bathyarca glacialis.*

taxa are within the trophic nucleus: *Astarte crenata* (21.6%), *Yoldiella fraterna* (13.7%), *Heteranomia* sp. (7.5%), *Hyalopecten* cf. *graui* (6.6%), *Cyclopecten imbrifer* (5.7%), *"Terebratula"* sp. (4.9%), *Parvicardium minimum* (4.4%), *Yoldiella* sp. (4.0%), *Dacrydium ockelmanni* (3.5%), *Kelliella miliaris* (3.1%), *Bathyarca glacialis* (2.6%). Apart from the brachiopod *"Terebratula"* sp., all taxa are bivalves.

In the association the epibenthos to endobenthos ratio is 38.7% to 61.4%. The trophic groups are dominated by suspension-feeders (70%), deposit-feeders are represented by 22.6%. Carnivores/scavengers (4.8%) and browsers (2.2%) are of minor importance.

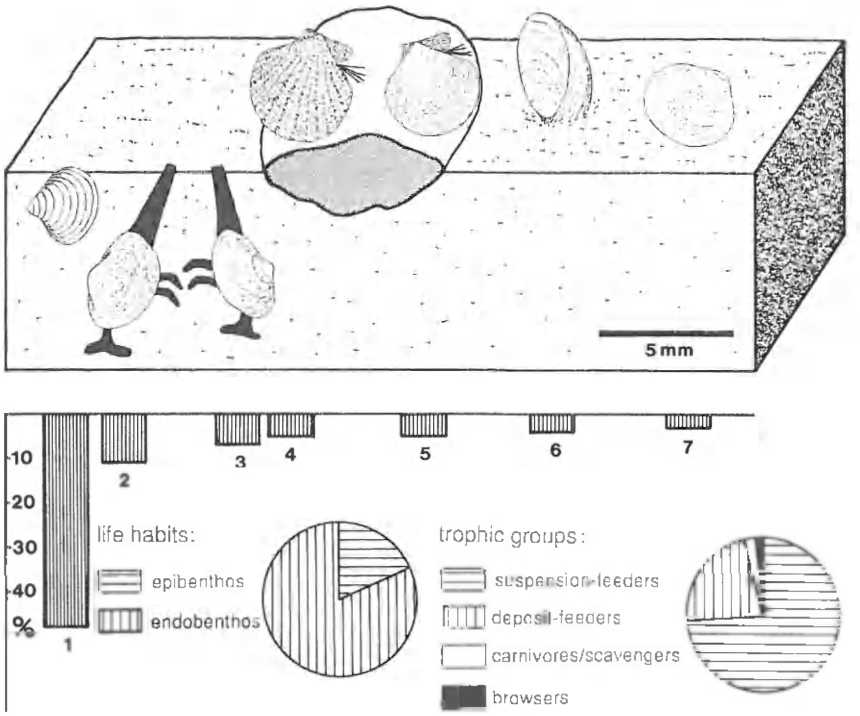

Fig. 11. Trophic nucleus of the *Astarte crenata/Yoldiella fraterna* association. — 1. *Astarte crenata;* 2. *Yoldiella fraterna;* 3. *Yoldiella* sp.; 4. *Cyclopecten imbrifer;* 5. *Hyalopecten* cf. *graui;* 6. „*Terebratula*" sp.; 7. *Kelliella miliaris.*

Abb. 11. Trophischer Kern der *Astarte crenata/Yoldiella fraterna* Assoziation. — 1. *Astarte crenata;* 2. *Yoldiella fraterna;* 3. *Yoldiella* sp.; 4. *Cyclopecten imbrifer;* 5. *Hyalopecten* cf. *graui;* 6. „*Terebratula*" sp.; 7. *Kelliella miliaris.*

Astarte crenata / Yoldiella fraterna Association.

(Fig. 11; App. 2).

Two samples, both from sampling station 124, are grouped in this association which consists of 31 taxa and 401 specimens. The samples come from a mid slope environment at a depth of 652 m. Six taxa form the trophic nucleus: *Astarte crenata, Yoldiella fraterna, Yoldiella* sp., *Cyclopecten imbrifer, Hyalopecten* cf. *graui, "Terebratula"* sp., and *Kelliella miliaris.* Apart from the brachiopod *"Terebratula"* sp., all specimens are bivalves.

The percentage of epibenthos is 19.3%, that of endobenthos 79.6 %. Suspension-feeders are represented by 73.8%, and clearly dominate the deposit-feeders (22.4%), carnivores/scavengers (2.3%), and browsers (1%).

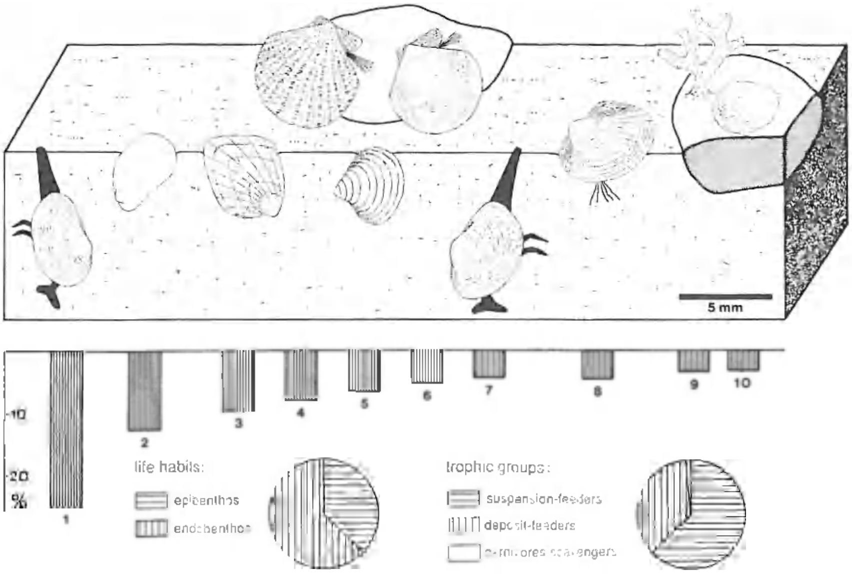

Fig. 12. Trophic nucleus of the *Katadesmia* cf. *colthoffi/Dacrydium ockelmanni* association. — 1. *Katadesmia* cf. *colthoffi;* 2. *Dacrydium ockelmanni;* 3. *Policordia jeffreysi;* 4. *Cyclopecten imbrifer;* 5. *Astarte crenata;* 6. *Hyalopecten* cf. *graui;* 7. *Yoldiella fraterna;* 8. *Bathyarca glacialis;* 9. *Hornera* sp.; 10. *Heteranomia* sp..

Abb. 12. Trophischer Kern der *Katadesmia* cf. *colthoffi/Dacrydium ockelmanni* Assoziation. — 1. *Katadesmia* cf. *colthoffi;* 2. *Dacrydium ockelmanni;* 3. *Policordia jeffreysi;* 4. *Cyclopecten imbrifer;* 5. *Astarte crenata;* 6. *Hyalopecten* cf. *graui;* 7. *Yoldiella fraterna;* 8. *Bathyarca glacialis;* 9. *Hornera* sp.; 10. *Heteranomia* sp..

Katadesmia cf. *colthoffi* / *Dacrydium ockelmanni* Association.

(Fig. 12; App. 2).

The association consists of three samples from stations 101, 103 and 123. 21 taxa and 138 specimens from environments at the foot of the slope (967 m) and the mid (1127 m) and outer Vøring Plateau (1426 m) are grouped together. The trophic nucleus consists of ten taxa: *Katadesmia* cf. *colthoffi* (24.8%), *Dacrydium ockelmanni* (12.2%), *Policordia jeffreysi* (9.4%), *Cyclopecten imbrifer*, (7.9%), *Astarte crenata* (6.3 %), *Hyalopecten* cf. *graui* (5.1%), *Bathyarca glacialis* (4.3%), *Yoldiella fraterna*, (4.3%), *Hornera* sp. (3.6%), and *Heteranomia* sp. (3.6%). Apart from the bryozoan Hornera sp., all taxa are bivalves.

Endobenthos (62.4%) is nearly twice as common as epibenthos (37.8%). The trophic composition is dominated by suspension-feeders (63.4%). Deposit-feeders represent 35.4%, whereas carnivores/scavengers are rare (1.4%).

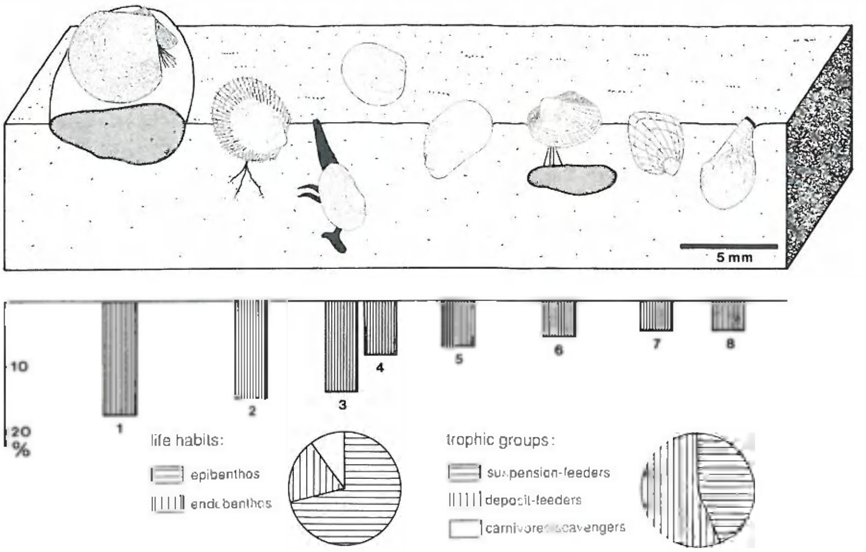

Fig. 13. Trophic nucleus of the *Hyalopecten* cf. *graui/Limopsis aurita* association. — 1. *Hyalopecten* cf. *graui*; 2. *Limopsis aurita*; 3. *Katadesmia* cf. *colthoffi*; 4. *Kelliella miliaris*; 5. *Dacrydium ockelmanni*; 6. *Bathyarca glacialis*; 7. *Policordia jeffreysi*; 8. *Cuspidaria lamellosa*.

Abb. 13. Trophischer Kern der *Hyalopecten* cf. *graui/Limopsis aurita* Assoziation. — 1. *Hyalopecten* cf. *graui*; 2. *Limopsis aurita*; 3. *Katadesmia* cf. *colthoffi*; 4. *Kelliella miliaris*; 5. *Dacrydium ockelmanni*; 6. *Bathyarca glacialis*; 7. *Policordia jeffreysi*; 8. *Cuspidaria lamellosa*.

Hyalopecten cf. *graui* / *Limopsis aurita* Association.

(Fig. 13; App. 2).

The association is represented by four samples from the stations 104, 112, 115 and 118, and consists of 18 taxa and 109 specimens. The samples come from the Vøring Plateau-slope down to the foot of the slope (1893 to 2808 m) and from a seamount near the Jan Mayen Fracture Zone (2296 m). There are seven taxa, all bivalves, within the trophic nucleus: *Hyalopecten* cf. *graui*, (19.3%), *Limopsis aurita* (17.4%), *Katadesmia* cf. *colthoffi* (16.5%), *Kelliella miliaris* (8.3%), *Dacrydium ockelmanni* (7.3%), *Bathyarca glacialis* (5.5%), *Policordia jeffreysi* (4.6%), and *Cuspidaria lamellosa* (4.6%).

Epibenthos is nearly as abundant (43.9%) as endobenthos (55.8%). Suspension-feeders are represented by 72.3%, deposit-feeders by 17.4%, and carnivores / scavengers by 10%.

Katadesmia cf. *colthoffi* / *Hyalopecten* cf. *graui* Association.

(Fig. 14; App. 2).

The association consists of three samples from stations 108 and 109 which are situated in the Norwegian Basin (3222 m) and at the slope of the Jan Mayen Ridge (2283). 18 taxa and 92 specimens are grouped together. The trophic nucleus consists of seven taxa: *Katadesmia* cf. *colthoffi* (29.6%), *Hyalopecten* cf. *graui* (15.3%), *Bathyarca glacialis* (13.2%), *Kelliella miliaris* (8.7%), *Buccinum* sp. (6.5%), *Policordia jeffreysi* (5.4%), and *Parvicardium minimum* (4.3%). All taxa, except the gastropod *Buccinum* sp., are bivalves.

In the association the epibenthos to endobenthos ratio is 2:3. The trophic groups are dominated by suspension-feeders (60.5%). Deposit-feeders represent 22.6%, and carnivores/scavengers 7.7%.

Discussion of Associations.

Bivalves are by far the most important group of the shelly macrobenthos. This is in agreement with other studies of deep sea environments (e.g. HESSLER & JUMARS 1974; GAGE 1977; GRASSLE & MORSE-PORTEOUS 1987; ROMERO-WETZEL 1989), which considered both soft bodied and shelly macrobenthos and discovered that bivalves are second in abundance after polychaetes, or at least the most abundant group with hardparts. The percentage of epibenthos is remarkably high and ranges from almost 20 to more than 40% (Fig. 15). Slope and basin environments elsewhere consist of homogenous soft substrate environments, which almost exclusively are colonized by endobenthos (e.g. ALLEN 1983). Norwegian Sea slope and basin environments differ from low latitude deep sea environments by the occurrence of ice rafted material, i.e. dropstones. These sand-to-pebble-sized hard substrates produce an environmental heterogeneity, which due to new niches results in a distinct increase of epibenthos (cf. OSCHMANN 1990).

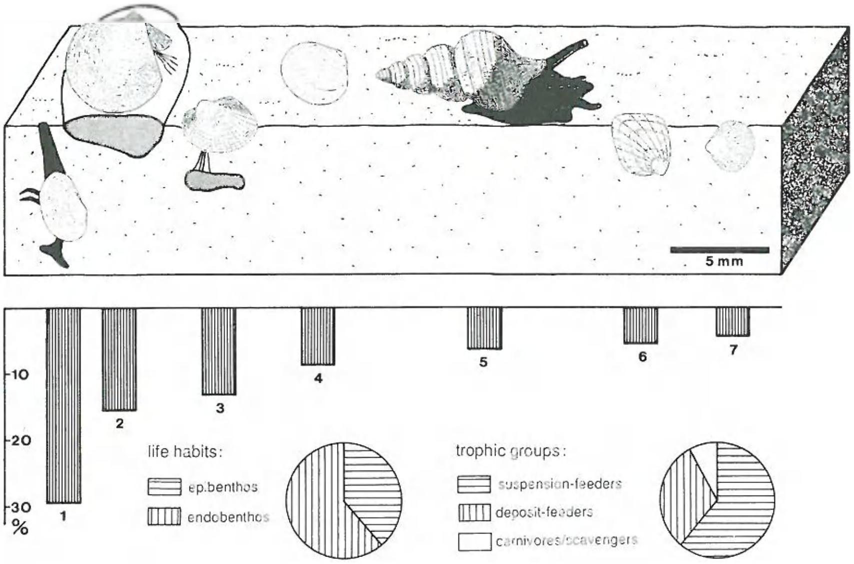

Fig. 14. Trophic nucleus of the *Katadesmia* cf. *colthoffi/Hyalopecten* cf. *graui* association. — 1. *Katadesmia* cf. *colthoffi;* 2. *Hyalopecten* cf. *graui;* 3. *Bathyarca glacialis;* 4. *Kelliella miliaris;* 5. *Buccinum* sp.; 6. *Policordia jeffreysi;* 7. *Parvicardium minimum.*

Abb. 14. Trophischer Kern der *Katadesmia* cf. *colthoffi/Hyalopecten* cf. *graui* Assoziation. — 1. *Katadesmia* cf. *colthoffi;* 2. *Hyalopecten* cf. *graui;* 3. *Bathyarca glacialis;* 4. *Kelliella miliaris;* 5. *Buccinum* sp.; 6. *Policordia jeffreysi;* 7. *Parvicardium minimum.*

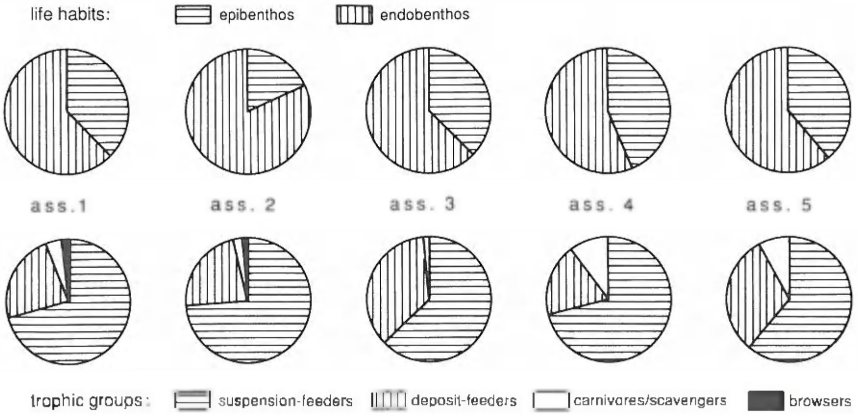

Fig. 15. Distribution and variation of the life habits and the trophic groups of the associations.

Abb. 15. Verteilung und Variation der Lebensweise und der trophischen Gruppen in den Assoziationen.

The trophic structures (Fig. 15) of the associations differ also from other deep sea environments. Normally deposit-feeders, especially protobranch bivalves, dominate with 70 to 90%. Protobranch bivalves are able to convert scleroproteins, which are available throughout the year in and on the surface of substrate to metabolic energy (e.g. ALLEN 1978, 1983). Therefore deposit-feeders should be less strictly bound to the seasonal plankton flux from surface waters than suspension-feeders. Nevertheless, suspension-feeders dominate throughout the associations, ranging from 60 to 70% (Fig. 15). Most epibenthic bivalves living attached to dropstones are suspension-feeders and thus increase the percentage of this trophic group. Some taxa such as *Bathyarca* and *Limopsis* show a progressive change in life habit from epibyssate, attached to firm substrate, to endobyssate, partially buried in soft substrate (e.g. OLIVER & ALLEN 1980 a, b; ALLEN 1983). Additionally, suspension-feeding heterodont cardiid and venerid bivalves occur in large numbers. Most of them have an endobenthic mode of life, but some (e.g. *Kelliella miliaris*) have been observed crawling along the sediment water interface (e.g. THOMSEN & VOREN 1986). High hydrostatic pressure and the low temperatures in deep sea environments are thought to be responsible for the reduced metabolic rates (e.g. GEORGES 1979; SOMERO et al. 1983; GRASSLE & MORSE-PORTEOUS 1987) and thus cause the very low growth-rate and the small size of taxa (see above). The low metabolic rates probably enable the fauna to endure periods of starvation more easily than shallow water taxa, no matter whether they are deposit-feeders or suspension-feeders. An additional adaptive pathway is storing energy during the summer abundance period, which then can be used by catabolism during winter starvation period (e.g. BAYNE 1985). The peak of primary production in the Norwegian Sea takes place within a few months during summer, but on an annual scale it is almost as high as in upwelling areas (GRAF, Institut für Meereskunde Kiel, personal communication 1990). Suspension-feeders directly use the plankton flux and probably receive within the short period more food than the deposit-feeders during the whole year. Resuspension of the phytodetritus on the sea floor, due to weak bottom currents, may elongate the period during which suspended food is available (e.g. LAMPIT 1985). Like in other deep sea environments the proportion of carnivores and scavengers increases with depth, reaching up to 10%, whereas the few browsers occur only in the association of the upper shelf slope.

It has been shown (see above) that the diversity of the macrobenthos, in terms of numbers of taxa, decreases distinctly with depth. Expressed by rarefaction curves, the diversity of all associations of this area (Fig. 16; cf. SANDERS 1968; HESSLER & JUMARS 1974) is high, compared to other deepsea evironments. In general, there is a decrease with depth, but not very pronounced. The Associations 1 and 2 from the upper shelf slope show the highest values. Slightly reduced values signify the Vøring Plateau (Ass. 3). Again slightly lower are the values of Associations 4 and 5 from the Plateau Slope, the Jan Mayen Fracture Zone, the Norwegian Basin and the Jan Mayen Ridge.

More significant than the reduction of diversity with depth is the spatial distribution of the associations along the transect from the Norwegian shelf to Jan Mayen (Figs. 2–3). Associations 1 and 2 occur only on the upper to middle shelf slope. Association 3 is restricted to the Vøring Plateau. The samples from the Plateau Slope and the Jan Mayen Fracture Zone belong all to Association 4, and the samples from the Norwegian Basin and the Jan Mayen Ridge form Association

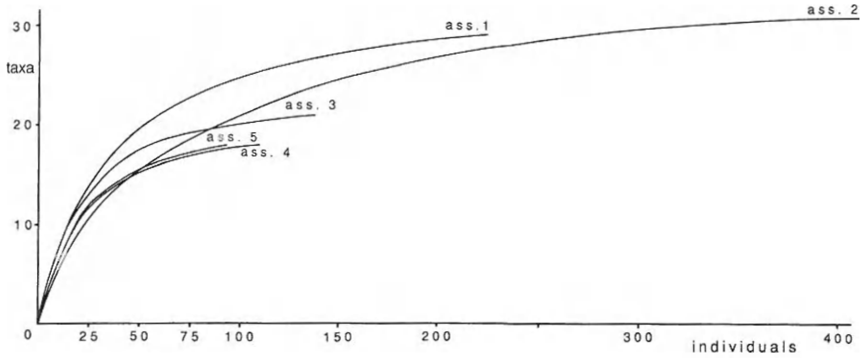

Fig. 16. Faunal diversity expresed by rarefaction curves show in general high diversity values which decrease only slightly with depth.

Abb. 16 Faunendiversität, ausgedrückt durch Rarefaction-Kurven. Die Diversität ist generell hoch und nimmt nur gering mit der Tiefe ab.

5. Water depth and spatial vicinity seems to be equal important for grouping of the samples in Associations 1 to 3. In the case of Associations 4 and 5 spatial vicinity seems more important then the water depth. This lateral variability most probably reflects regional variations of physical factors, e.g. terrigenous sediment input, plankton flux from surface waters and currents. Input of terrigenous sedimentation from the large area of the Norwegian Shelf and Vøring Plateau is much higher in comparison to input from the small area of the Jan Mayen Ridge and Jan Mayen Shelf and Island. Surface water temperatures decrease from 10° C off Norway to 4° C at Jan Mayen (e.g. Dietrich et al 1975; Swift 1986), and concomitantly the plankton productivity. This results in a lower rate of flux to the benthic environments, which is further diminished by the much greater water depth of the basinal environments.

Conclusions.

1. Dead shelly macrobenthos (mainly molluscs) taken as bulk samples from box cores occurs throughout at the Norwegian Sea floor from 580 m to 3222 m depth.

2. Size-frequency distributions of some taxa show a logarithmic relationship and favour autochthony of the fauna. The taxa are very small (50% <2 mm) but show a high number of growth bands and are therefore thought to be relatively old.

3. Faunal density and species diversity decrease remarkably with depth. The macrobenthos (mainly molluscs) – meiobenthos (benthic foraminifers) ratio shifts from 40/60 at 580 m to 10/90 and even lower at 1000 m and greater depth.

4. Uniform temperatures (–0.5° to –0.9° C) below 400 m suggest that hydrostatic pressure as the dominating physical factor controlls the depth range

of taxa. The upper range limits of most taxa are shallower than 580 m; the lower range limits, however, are well defined. Out of 36 taxa, 10 are eurybathic occurring from 580 m to 3222 m.

5. Five largely depth related associations of shelly macrobenthos have been determined by cluster analysis. They also occur consecutively along the sampling traverse from the Norwegian shelfbreak to Jan Mayen.

6. The life habit and trophic structure of associations are rather uniform, but differ from other deep sea environments by their high percentage of epibenthos (partly more than 40%), and suspension feeders (up to 70%). This may be due to a short, but very pronounced nutrient flux from surface waters in summer, and due to environmental heterogeneity, caused by dropstones, which serve as small islands of hard substrate.

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Appendix 1. List of the bathyal and abyssal taxa of the Norwegian Sea, and there life habit and trophic character adapted from literature.

Anhang 1. Bathyale und abyssale Taxa des Europäischen Nordmeeres und ihre Lebens- und Ernährungsweise nach Literaturdaten.

Shelly Macrobenthos
Schalentragendes Makrobenthos

Bivalvia	life habit	trophic group
Astarte crenata	end.	sus.
Bathyarca glacialis	end.	sus.
Bentharca sp.	epi.	sus.
Cuspidaria lamellosa	end.	car/sca.
Cyclopecten imbrifer	epi.	sus.
Dacrydium ockelmanni	end.	sus.
Heteranomia sp.	epi.	sus.
Hiatella arctica	end.	sus.
Hyalopecten frigidus	epi.	sus.
Hyalopecten cf. *graui*	epi.	sus.
Katadesmia cf. *colthoffi*	end.	dep.
Kelliella miliaris	epi.	sus.
Limatula louiseae	end.	sus.
Limopsis aurita	end.	sus.
Parvicardium minimum	end.	sus.
Policordia jeffreysi	end.	sus.
Poromya granulata	end.	car/sca.
Thyasira sp.	end.	sus.
Yoldiella fraterna	end.	dep.
Yoldiella sp.	end.	dep.
Polyplacophora		
Leptochiton sp.	epi.	browser

Gastropoda	life habit	trophic group
Amauropsis sp.	end.	car/sca.
Buccinum sp.	epi.	car/sca.
Cylichna cf. *alba*	end.	dep.
Cylichnum cf. *africanum*	end.	dep.
Epitonium sp.	epi.	car/sca.
Oenopotia sp.	epi.	car/sca.
Pleurotomella sp.	epi.	car/sca.
Scaphopoda		
Siphonodentalium sp.	end.	dep.
Entalina quinquangularis	end.	dep.
Brachiopoda		
"*Terebratula*" sp.	epi.	sus.
Bryozoa		
Crisia sp.	epi.	sus.
Crisiella cf. *producta*	epi.	sus.
Sertella sp.	epi.	sus.
Hornera sp.	epi.	sus.
Echinodermata		
"*Echinocardium*" sp.	end.	dep.

key: epi. = epibenthos; end. = endobenthos; sus. = suspension-feeder; dep. = deposit-feeder; car/sca. = carnivore/scavenger; browser

Foraminifera (only taxa larger 0.5 mm listed)

arenaceous:

Cribrostomoides subglobosum
Eggerella sp.
Hyperammina sp.
Reophax nodulosum
Rhabdammina abyssorum
Rhizammina sp.
Saccammina sp.
Saccorhiza ramosa

calcareous:

Cibicides refulgensis
Cibicidoides wüllerstorfi
Dentalina cuvieri
Globobulimina sp.
Melonis sp.
Nodosaria subsoluta
Pyrgo murrhina
Quinqueloculina sp.
Robulus sp.
Rupertina stabilis
Triloculina frigida
Uvigerina sp.

Appendix 2. Composition of the associations (* denotes members of the trophic nucleus)

Anhang 2. Zusammensetzung der Assoziationen (* Taxa der trophischen Kerne)

Astarte crenata/*Heteranomia* sp. Association

	N	%	presence %	mode of life	mode of feeding
**Astarte crenata*	61	26.1	100	end.	sus.
**Yoldiella fraterna*	31	13.7	100	end.	dep.
**Heteranomia* sp.	17	7.5	100	epi.	sus.
**Hyalopecten* cf. *graui*	15	6.6	100	epi.	sus.
**Cyclopecten imbrifer*	13	5.7	66	epi.	sus.
*"*Terebratula*" sp.	11	4.9	100	epi.	sus.
**Parvicardium minimum*	10	4.4	66	end.	sus.
**Yoldiella sp.*	9	4.0	66	end.	dep.
**Dacrydium ockelmanni*	8	3.5	66	epi.	sus.
**Kelliella miliaris*	7	3.1	100	epi	sus
**Bathyarca glacialis*	6	2.6	100	end.	sus.
Leptochiton sp.	5	2.2	100	epi.	browser
Amauropsis sp.	4	1.8	66	end.	car/sca.
Siphonodentalium sp.	4	1.8	66	end.	dep.
Buccinum sp.	3	1.3	33	epi.	car/sca.
Limopsis aurita	3	1.3	66	end.	sus.
Pleurotomella sp.	2	0.9	33	epi.	car/sca.
Cylichnum cf *africanum*	2	0.9	33	end.	dep.
Entalina quinquangularis	2	0.9	33	end.	dep.
Sertella septentrionalis	2	0.9	66	epi.	sus.
Crisiella cf. *producta*	2	0.9	66	epi.	sus.
Hiatella arctica	2	0.9	33	end.	sus.
Katadesmia cf. *colthoffi*	2	0.9	33	end.	dep.
Oenopotia sp.	1	0.4	33	epi.	car/sca.
Cuspidaria lamellosa	1	0.4	33	end.	car/sca.
"*Echinocardium*" sp.	1	0.4	33	end.	dep.

Hornera sp.	1	0.4	33	epi.	sus.
Limatula louiseae	1	0.4	33	end.	sus.
Crisia sp.	1	0.4	33	epi.	sus.
	226	100.1			

epibenthos 38.7%; endobenthos 61.4%; suspension-feeders 70.5%; deposit-feeders 22.6%; carnivors/scavengers 4.8%; browsers 2.2%

Astarte crenata/Yoldiella fraterna Association

	N	%	presence %	mode of life	mode of feeding
**Astarte crenata*	194	48.4	100	end.	sus.
**Yoldiella fraterna*	44	11	100	end.	dep.
**Yoldiella sp.*	28	6.9	100	end.	dep.
**Cyclopecten imbrifer*	19	4.7	100	epi.	sus.
**Hyalopecten* cf. *graui*	19	4.7	100	epi.	sus.
**"Terebratula"* sp.	15	3.7	100	epi.	sus.
**Kelliella miliaris*	12	2.9	50	epi.	sus.
Siphonodentalium sp.	9	2.4	100	end.	dep.
Thyasira sp.	8	2	50	end.	sus.
Bathyarca glacialis	7	1.7	100	end.	sus.
Parvicardium minimum	7	1.7	50	end.	sus.
Leptochiton sp.	4	1	100	epi.	browser
Katadesmia cf. *colthoffi*	4	1	50	end.	dep.
Cuspidaria lamellosa	3	0.7	50	end.	car/sca.
Entalina quinquangularis	3	0.7	50	end.	dep.
Dacrydium ockelmanni	3	0.7	50	epi.	sus.
Policordia jeffreysi	3	0.7	50	end.	sus.
Amauropsis sp.	2	0.5	50	end.	car/sca.
Crisiella cf. *producta*	2	0.5	100	epi.	sus.
Poromya granulata	2	0.5	50	end.	car/sca.
Bentharca sp.	2	0.5	50	epi.	sus.
Hiatella arctica	2	0.5	50	end.	sus.
Limatula louiseae	2	0.5	50	end.	sus.
Epitonium sp.	1	0.2	50	epi.	car/sca.
Pleurotomella sp.	1	0.2	50	epi.	car/sca.
Buccinum sp.	1	0.2	50	epi.	car/sca.
"Echinocardium" sp.	1	0.2	50	end.	dep.
Cylichna cf. *alba*	1	0.2	50	end.	dep.
Heteranomia sp.	1	0.2	50	epi.	sus.
Hornera sp.	1	0.2	50	epi.	sus.
Crisia sp.	1	0.2	50	epi.	sus.
	401	99.5			

epibenthos 19.3%; endobenthos 79.6%; suspension-feeders 73.8%; deposit-feeders 22.4%; carnivors/scavengers 2.3%; browsers 1%

Katadesmia cf. *colthoffi*/*Dacrydium ockelmanni* Association

	N	%	presence %	mode of life	mode of feeding
**Katadesmia* cf. *colthoffi*	34	24.9	100	end.	dep.
**Dacrydium ockelmanni*	17	12.3	66	epi.	sus.
**Policordia jeffreysi*	13	9.5	100	end.	sus.
**Cyclopecten imbrifer*	11	7.9	100	epi.	sus.
**Astarte crenata*	9	6.4	66	end.	sus.
**Hyalopecten* cf. *graui*	7	5.2	100	epi.	sus.
**Yoldiella fraterna*	6	4.4	66	end.	dep.
**Bathyarca glacialis*	6	4.4	66	end.	sus.
**Hornera* sp.	5	3.6	100	epi.	sus.
**Heteranomia* sp.	5	3.6	100	epi.	sus.
Limatula louiseae	4	2.8	66	end.	sus.
Hiatella arctica	4	2.8	100	end.	sus.
Siphonodentalium sp.	3	2.1	33	end.	dep.
Echinocardium sp.	3	2.1	66	end.	dep.
Sertella septentrionalis	3	2.1	66	epi.	sus.
Crisia sp.	2	1.4	66	epi.	sus.
Crisiella cf. *producta*	2	1.4	66	epi.	sus.
Amauropsis sp.	1	0.7	33	end.	car/sca.
Yoldiella sp.	1	0.7	33	end.	dep.
Cylichna cf. *alba*	1	0.7	33	end.	dep.
"*Terebratula*" sp.	1	0.7	33	epi.	sus.
	138	99.7			

epibenthos 38.2%; endobenthos 61.5%; suspension-feeders 64.1%; deposit-feeders 34.9%; carnivors/scavengers 0.7%

Hyalopecten cf. *graui*/*Limopsis aurita* Association

	N	%	presence %	mode of life	mode of feeding
**Hyalopecten* cf. *graui*	21	19.3	100	epi.	sus.
**Limopsis aurita*	19	17.4	100	end.	sus.
**Katadesmia* cf. *colthoffi*	18	16.5	100	end.	dep.
**Kelliella miliaris*	9	8.3	75	epi.	sus.
**Dacrydium ockelmanni*	8	7.3	100	epi.	sus.
**Bathyarca glacialis*	6	5.5	75	end.	sus.
**Policordia jeffreysi*	5	4.6	50	end.	sus.
**Cuspidaria lamellosa*	5	4.6	75	end.	car/sca.
Amauropsis sp.	4	3.6	50	end.	car/sca.
Hornera sp.	2	1.8	50	epi.	sus.
Hyalopecten frigidus	2	1.8	50	epi.	sus.
Cyclopecten imbrifer	2	1.8	25	epi.	sus.

"Terabratula" sp.	2	1.8	25	epi.	sus.
Leptochiton sp.	2	1.8	50	epi.	car/sca.
Astarte crenata	1	0.9	25	end.	sus.
Hiatella arctica	1	0.9	25	end.	sus.
Limatula louiseae	1	0.9	25	end.	sus.
Dentalium sp.	1	0.9	25	end.	dep.
	109	99.7			

epibenthos 43.9%; endobenthos 55.8%; suspension-feeders 72.3%; deposit-feeders 17.4%; carnivors/scavengers 10%

Katadesmia cf. *colthoffi*/*Hyalopecten* cf. *graui* Association

	N	%	presence %	mode of life	mode of feeding
**Katadesmia* cf. *colthoffi*	27	29.6	100	end.	dep.
**Hyalopecten* cf. *graui*	14	15.3	100	epi.	sus.
**Bathyarca glacialis*	12	13.2	100	end.	sus.
**Kelliella miliaris*	8	8.7	66	epi.	sus.
**Buccinum* sp.	6	6.5	100	epi.	car/sca.
**Policordia jeffreysi*	5	5.4	100	end.	sus.
**Parvicardium minimum*	4	4.3	100	end.	sus.
Hyalopecten frigidus	3	3.3	66	epi.	sus.
Thyasira sp.	2	2.2	66	end.	sus.
Sertella septentrionalis	2	2.2	66	epi.	sus.
"Terebratula" sp.	2	2.2	33	epi.	sus.
Dacrydium ockelmanni	1	1.1	33	end.	sus.
Astarte crenata sp.	1	1.1	33	end.	sus.
Limopsis aurita	1	1.1	33	end.	sus.
Hornera sp.	1	1.1	33	epi.	sus.
Echinocardium sp.	1	1.1	33	end.	dep.
Siphonodentalium sp.	1	1.1	33	end.	dep.
Amauropsis sp.	1	1.1	33	end.	car/sca.
	92	100.6			

epibenthos 39.6%; endobenthos 60.5%; suspension-feeders 60.9%; deposit-feeders 31.9%; carnivors/scavengers 7.7%