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The faroese research vessel, Magnus Heinasson.
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Summary

A new map of benthic faunal associations and bottom types around the Faroes

Information was drawn from:

- nautical charts
- narratives of the many expeditions which since the mid - 1800's worked in or close to the area
- geological reports
- fishery ground surveys
- the station lists and field journals of the BIOFAR programs
- diaries and field notes by scientists who collected in the Faroes, kept in the Zoological Museum's archive.

The nautical charts give, based on casts of the lead, the very coarse pattern, with scattered indications of sediment types standardized into the official system of abbreviations. Most other sources present more detailed information on local areas. Because this was provided with different types of gear, and descriptions not only are given in different languages, but also cover a wide span of time representing the changing traditions within several fields, one must be cautious when extracting the information.

Bottom types

Calcareous sediments of various grades are widely distributed around the Faroes. The bottom of the upper plateau is dominated by sand, gravel and coarse shell gravel. A very fine-grained fragment sediment occurs on the top of the banks west of the Faroe Islands. It seems for a large part to origin from post-glacial times. The fauna here is very rich in meiofauna, but relatively poor in macrofauna compared to similar depth on the Faroe Plateau.

Sand, gravel and shell gravel is indicated by in Figure 1.

Fine sand is indicated by in Figure 1.

Gravel and stone mixed with sand and fine sand is the most common sediment type around the Faroes from about 300 m depth to about 1000 m. The gravel and stone originates partly from ice rafting during the time following the ice age, partly from the erosion of the islands.

Gravel and stone mixed with sand is indicated by in Figure 1.

At large depths (>1000 m) extensive areas are covered by silty substrate more or less mixed with fine sand. Samples have been taken in these areas, however, there is no complete knowledge of the biological communities living here. Most likely different species dominate depending on the depth and the water mass of the particular area. Shallow waters (< 400 m) have only few and small areas characterized predominantly by muddy substrate. Two such areas, at approximately 350 m depth, have been investigated during the BIOFAR program. Series of grab samples were taken in the areas indicated in 1987 through 1990. Each grab held 40 – 50 species, and more than 200 species in all have been identified from these samples. Infaunal polychaetes and bivalves dominate, but larger sized seapens, echinoderms and decapods occurred regularly.

Deep sea mud is indicated by in Figure 1.

The two investigated areas with muddy substrate is indicated by in Figure 1. See chapter 6.

Biocoenoses

Nautical charts include a few notions on "coral", but our sampling during the BIOFAR 1 program showed these areas to be dominated by stylasterids (Hydrozoa with a strong calcareous skeleton). Banks of *Lophelia*, the eye-coral, as well as "ostur" (accumulations of large sponges) around the edges of the Faroese plateau were not mentioned in the literature until 1988. During the BIOFAR programs, ostur, coral banks, octocoral- and stylasterid areas, and mussel beds were especially searched for and mapped in reports and scientific papers.

The following associations are treated in separate chapters of this report.

Accumulations of large-sized demosponges have been recorded in certain areas of the outer shelf around the Faroes. As it turned out, the phenomenon had gone unnoticed in earlier faunistic investigations, but was well known by local fishermen and the Faroese Fisheries Investigation (Fiskirannsóknarstovan) in Tórshavn. The local name for the sponge accumulation is "ostur" meaning "cheese bottom", a name that seems to refer to size, form and consistency of some of the sponges, and to the smell of broken specimens. Clearly dominant in terms of biomass, and quantity per catch, are four species of the family Geodiidae; *Geodia barretti* Bowerbank, 1858, *G. macandrewii* Bowerbank, 1858, *G.* sp. and *Isops phlegraei* Sollas, 1880, and the stellettid *Stryphnus ponderosus* (Bowerbank, 1866). These sponge species reach a considerable size, up to about 80 cm in maximum dimension and body weights of about 25 kg. A wide diversity of invertebrates has been shown to inhabit the sponges, thus, more than 242 associated species have been reported for the Faroe Islands.

Sponge accumulations indicated by in Figure 1. See chapter 2

Like the large sponges, banks of the cold water coral *Lophelia pertusa* L., 1758 have been recorded in certain areas of the outer shelf around the Faroes. More than 250 species of associated fauna were identified from coral blocks. *L. pertusa* is the dominant species on these banks, but other suspension-feeders are often seen as part of these associations as well. *L. pertusa* and other large branching corals are called "greinar" by the local fishermen. Other corals often associated with the *Lophelia* banks are *Paragorgia arborea* and *Primnoa resedaeformis*. *Lophelia* growth is slow and the large banks are very old, some of the Faroese banks reaching approximately 10.000 years of age.

Areas with *Lophelia pertusa* is indicated by in Figure 1. See chapter 3.

Paragorgia arborea is indicated by in Figure 1. See chapter 3.

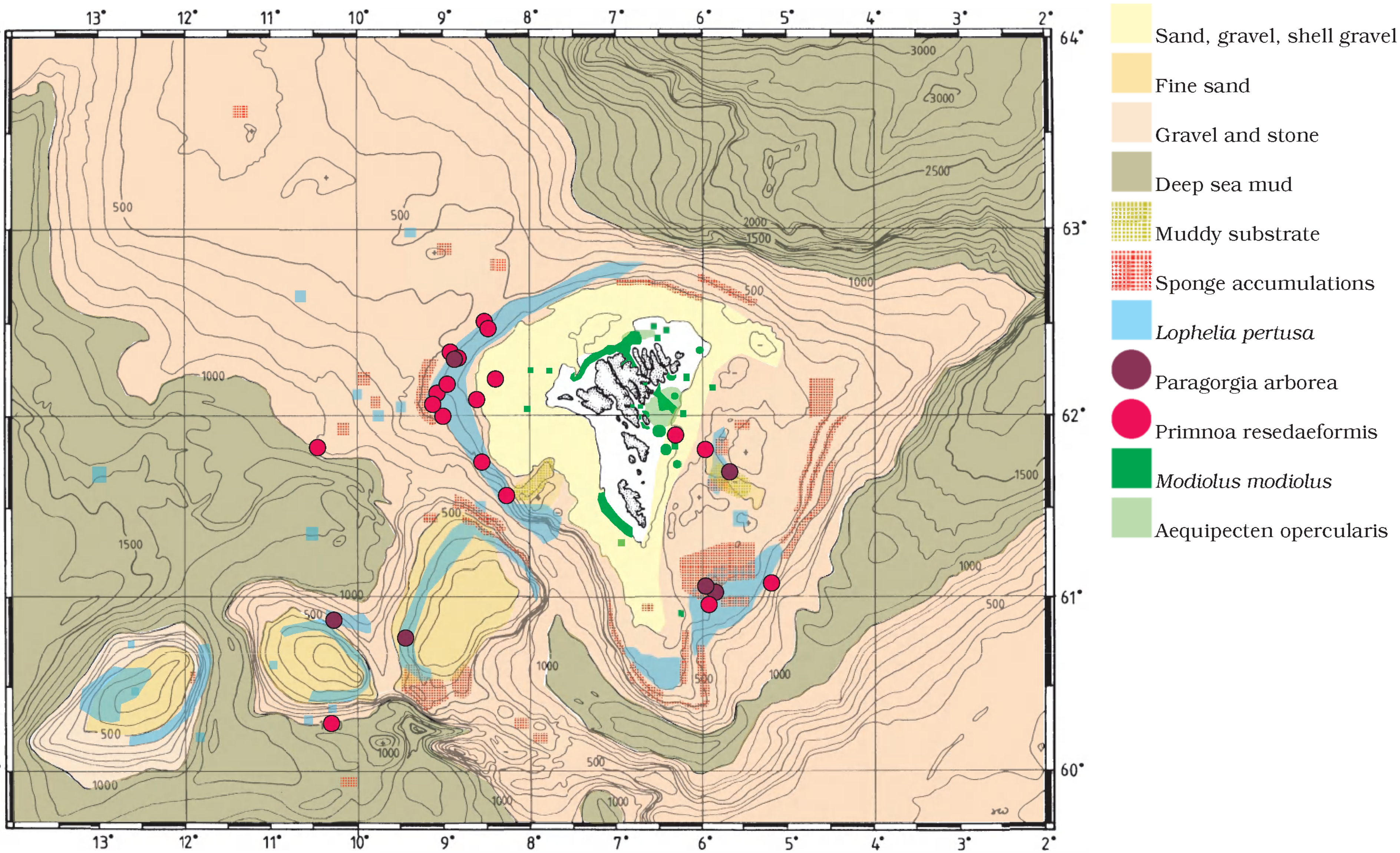
Primnoa resedaeformis is indicated by in Figure 1. See chapter 3.

The widespread beds of *Modiolus modiolus* (L., 1758), the horse-mussel, are mapped. The species is common around the Faroe Islands from beneath the low water mark to approximately 150 m depth. It is often found in large beds with densities up to 220 mussels per m^2. The epifauna was studied during the BIOFAR programme. Counting both sessile and motile epifauna, 143 species of metazoan invertebrates were identified and a total of 175 taxa found associated with these mussel-beds.

Areas with *Modiolus modiolus* beds is indicated by in Figure 1. See chapter 4.

Queen scallop fields (*Aequipecten opercularis* (L., 1758)) are found on the plateau at depths shallower than 100 m. Two fields are at present known of which the one east of the Faroe Islands is being harvested regularly. Identification of species associated with the queen scallop is currently done at the Faroese Fisheries Department. The horse mussel *M. modiolus* is a frequent bycatch, and galatheid crabs, echinoids (probably *Psammechinus milliaris*), and the buccinids are frequent epifauna. *Anomia* sp., serpulids, bryozoans and hydroids are often attached to the valves.

Areas with *Aequipecten opercularis* fields is indicated by in Figure 1. See chapter 5.


Sand, gravel, shell gravel
Fine sand
Gravel and stone
Deep sea mud
Muddy substrate
Sponge accumulations
Lophelia pertusa
Paragorgia arborea
Primnoa resedaeformis
Modiolus modiolus
Aequipecten opercularis
13°
12°
11°
10°
9°
8°
7°
6°
5°
4°
3°
2°
64°
63°
62°
61°
60°
500
1000
1500
2000
2500
3000

Contents

Introduction

Since the mid 1800's, the north-east Atlantic has been subject to numerous marine biological investigations and large expeditions. Most of them added to the knowledge of the seabed of the Faroes and of the invertebrates living there. Some particularly aimed at the Faroese area whereas others only took a few stations within the area on their way to more distant destinations. Generally, the studies aimed at the identification of species, and together these data provide invaluable information on the geographical distribution of the fauna. Only a few investigations aimed to describe assemblages of benthic invertebrates and their geographical extension within the area (Bruntse *et al.* 1999, Klitgaard 1995, Jensen & Frederiksen 1992).

The sea around the Faroe Islands is influenced by a number of water masses. These comprise cold water from the Norwegian Sea coming into the area through passages in the Scotland-Iceland Ridge, warm Atlantic water from the south and intermediate mixtures. The different water masses naturally influence the distribution of the species and the biological communities, as do variation in sediment type, water depth, temperature, organic input (food availability) and current regime.

The results from the comprehensive BIOFAR programs have not yet appeared in full. On the basis of the results found in the old series "The Zoology of the Faroes" and what have been published so far (ab. 80 scientific publications) together with unpublished records of the BIOFAR programs, it seems safe to conclude that the fauna and flora of the Faroe Islands are characteristic of the northern boreal Atlantic and that most biocoenoses have a wide geographical distribution. It should be pointed out, however, that in order to establish the exact type of communities present, their vulnerability etc., there is a need of further investigation in a few local areas. Such areas are above all the deeper parts of the Faroe-Shetland Channel, the southern flanks of the banks west of the Faroes, and the deep sea (>1000 m) west of the Faroes.

The key purpose of the present work is from the existing literature to describe the communities occurring in the Faroese area as defined by the economic exclusive zone, with some overlap into adjacent areas in some regions. The communities described are the large sponges (Chapter 2), the corals, particularly *Lophelia pertusa* (Chapter 3), *Modiolus modiolus* (Chapter 4), *Aequipecten opercularis* (Chapter 5) and soft substrate (Chapter 6).

As mentioned, a large part of the existing literature from the marine biological investigations in the Faroe area is split into papers and large cruise reports sectioned into taxonomic groups. Within this project it has not been possible to extract all of this information into communities or to areas of special interests, however, a full account of expeditions visiting the Faroe area is given in Chapter 7. It includes a brief survey of scientists, collectors and ships involved in gathering the information we have today about the marine life of the area. Also a bibliography of papers dealing with marine benthic invertebrates of the Faroes is provided in Chapter 8, including the first scientific investigation in the Faroes in the 1700's to papers dealing with the material collected during the resent BIOFAR program.

As a preparation for possible future oil drilling activity around the Faroes, oil companies have, for the first time in history, joined into a common network in order to gather existing data on an area. The present work is financed through this GEM network (Geological, Environmental and Meteorological/oceanographical workgroups).

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Klitgaard, A., 1995. The fauna associated with outer shelf sponges (Porifera, Demospongia) at the Faroe Islands, northeastern Atlantic. - Sarsia. 80: 1-22.

Jensen, A., R. Frederiksen, 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinia) on the Faroe shelf. - Sarsia. 77: 53-69.

"Ostur" - "cheese bottoms" - sponge dominated areas in Faroese shelf and slope areas

During the internordic BIOFAR I programme 1987-90 (Marine Benthic Fauna of the Faroe Islands (NE Atlantic); Nørrevang *et al.* 1994) intensive sampling of the macro-fauna around the Faroes was carried out at depths from about 100 m to 1200 m with different kinds of gear. Already during a pilot cruise in 1987, the occurrence of accumulations of large-sized sponges in certain areas of the outer shelf was noticed, and during the cruises of the following years particular attention was paid to these animals (Hougaard *et al.* 1991, Klitgaard *et al.* 1992, 1997) and to their associated fauna (Klitgaard 1991, 1995, Warén & Klitgaard 1991, Monniot & Klitgaard 1994). As it turned out, the phenomenon had gone unnoticed in earlier faunistic investigations (Brøndsted 1932), but was well known by local fishermen and the Faroes Fisheries Investigations (Fiskirannsóknarstovan) in Tórshavn.

Figure 1.
A trawl sample from an area with ostur west of the Faroes at 480 m (BIOFAR Stn. 540: Nørrevang *et al.* 1994). (© photo A.B. Klitgaard).

"Ostur"

The local name for the sponge accumulations is "ostur" meaning "cheese bottom", a name that seems to refer to the size, form and consistency of some of the sponges, and to the smell of broken specimens.

In areas with ostur, up to 50 species of sponges can occur and of these about 20 can reach sizes exceeding 5 cm in maximum diameter (Table 1).

Table 1. Regularly occurring sponge species that reach > 5 cm in maximum dimension in areas with ostur. (*) marks species that are dominating as to biomass. Besides the listed species, there is a number of smaller, lumpy or thickly encrusting species, some calcareous sponges, and about 20 thinly encrusting species, mainly belonging to the genus *Hymedesmia.*

Geodia barretti *
G. macandrewi *
G. sp. *
Isops phlegraei *
Stryphnus ponderosus *
Stelletta normani
Thenea valdiviae
T. levis
Tetilla cranium
Tethya aurantium
Polymastia mammillaris
Phakellia ventilabrum
P. robusta
P. rugosa
Axinella arctica
Tragosia infundibuliformis
Mycale lingua
Myxilla fimbriata
Melonanchora elliptica
Antho dichotoma
Petrosia crassa
Oceanapia robusta

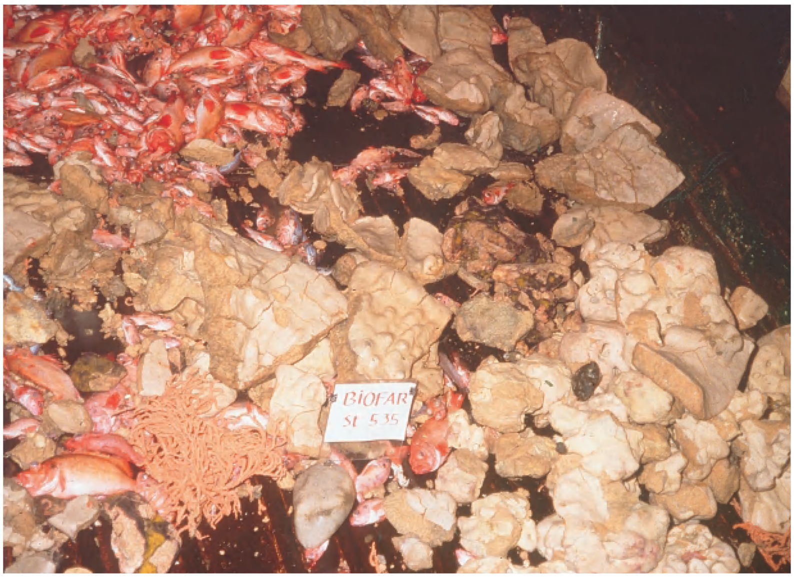


Figure 2.
Trawl haul from 370m depth dominated by *Geodia barretti* and *G.* sp. (BIOFAR Stn. 535; Nørrevang *et al.* 1994). Species of redfish (*Sebastes* spp.) are often caught when trawling in areas with ostur.
(© photo A. Nørrevang).

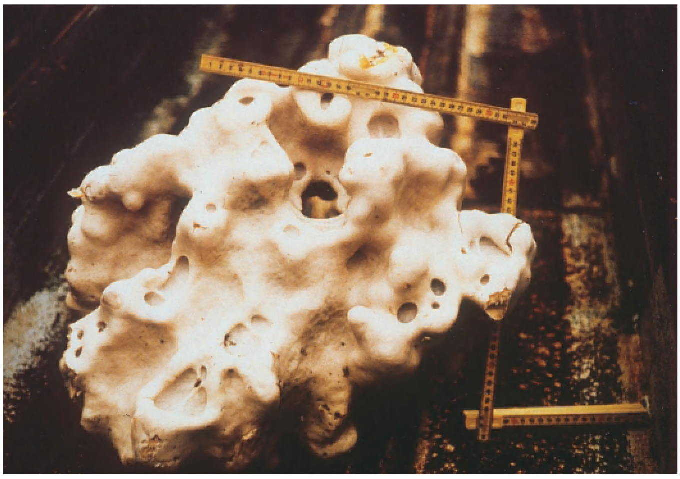
Figure 3.
The authors examining some of the large-sized specimens of *Geodia barretti* and *G.* sp. from a trawl haul from 364 m depth on BIOFAR Stn. 531 (Nørrevang *et al.* 1994). (© photo A. Nørrevang).

Clearly dominant in terms of biomass, and quantity per catch, are four species of the family Geodiidae; *Geodia barretti* Bowerbank, 1858, *G. macandrewi* Bowerbank, 1858, *G.* sp. and *Isops phlegraei* Sollas, 1880, and the stellettid *Stryphnus ponderosus* (Bowerbank, 1866).

These sponge species are all widely distributed in the Northeast Atlantic and reach considerable sizes. We have encountered specimens measuring about 80 cm in maximum dimension and with body weights of about 25 kg (Tendal & Klitgaard in prep.). Faroese fishermen have told us about single sponges that are more than 1 meter in diameter and sometimes almost too heavy for a man to lift. In some areas up to 20 tons of sponges can be caught in a single trawling, the net being virtually filled up and so loaded that there is a danger of damage during the on board hauling.

How do the ostur species look?

Species of the genera *Geodia* and *Isops* can either be more or less irregular lumpy, or funnel-shaped, or they can be round and regular. All species of Geodiidae are characterized by the possession of a cortex composed of a special kind of small, round, siliceous spicules (sterrasters).



Figur 4 A, B
Two specimens of *Geodia barretti* being irregular lumpy to very different degrees but both having numerous openings (osculae) of varying dimensions, each being covered by a sieve-like structure. (© photo O.S. Tendal).

Figure 5.
Specimens of *Geodia macandrewi* generally have a regular, spherical body-form with a diameter larger than the height so the specimens appear somewhat flattened.
(© photo O.S. Tendal)

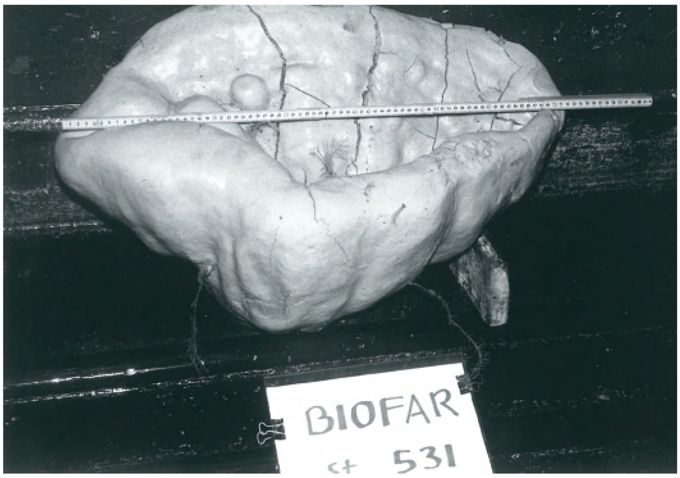


Figure 6.
Large specimens of *Geodia* sp. are often funnel-shaped with a deep cavity.
(© photo O.S. Tendal)

Figure 7.
Specimen of *Isops phlegraei* normally become more and more funnel-shaped when growing bigger. The cortex is sometimes covered by a thick "fur" of spicules. (From BIOFAR Stn. 043 Nørrevang *et al.* 1994).
(© photo G. Brovad)

There is only one species of the genus *Stryphnus* in the Northeast Atlantic, *S. ponderosus*. This is a massive, lumpy sponge characterized by a thick "fur" of vertically oriented siliceous spicules. Often a very deep, narrow excurrent cavity is present making the sponge look like a "chimney".

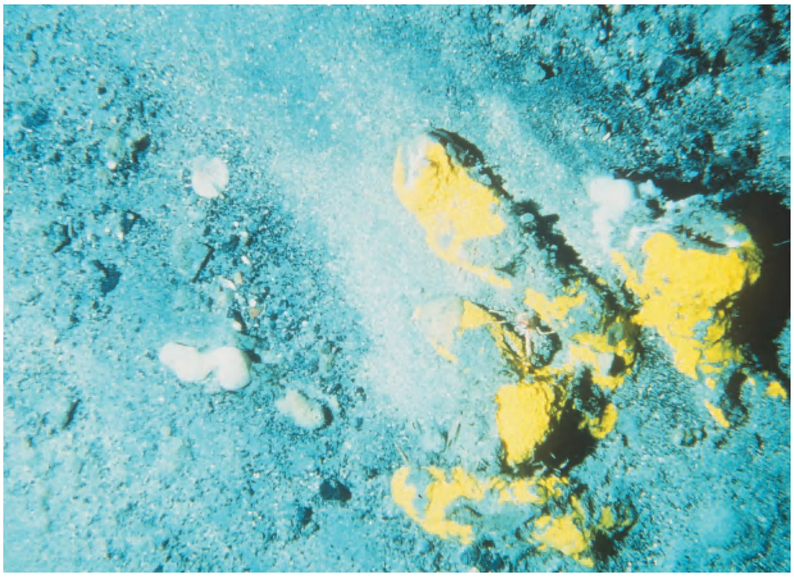


Figure 8.
Underwater photograph from an area with ostur at 400 m depth west of the Faroe Islands (BIOFAR Stn. 664; Nørrevang *et al.* 1994). The sulfur yellow colour of the specimens of *Stryphnus ponderosus* is due to an encrusting sponge species, *Aplysilla sulphurea* Schulze, 1878, which often covers most of the surface of *S. ponderosus*. (© photo J. Gutt).

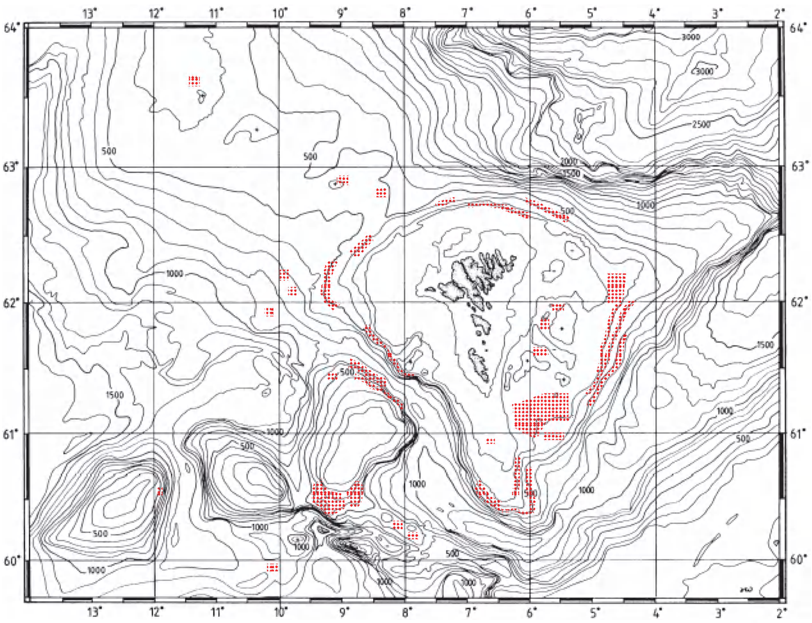


Figure 9.
All known occurrences of ostur at the Faroe Islands. (Redrawn from Klitgaard *et al.* 1997).

The distribution of ostur

We made a special effort during the BIOFAR I program to map in detail the geographic distribution and the bathymetric range of the ostur areas around the Faroe Islands. This included either one or both of us taking part in all 9 cruises and compiling a variety of relevant information (Klitgaard *et al.* 1997).

Ostur was found at 76 BIOFAR I stations at depths between 233 and 833 m, located around the Faroes and the banks to the west. In addition eleven hundred underwater photographs were taken during the BIOFAR cruise in May 1990 at depths between 60 and 1050 m (J. Gutt, Alfred-Wegener-Institut für Polar- und Meeresforshung, Bremerhaven). Some series of these photographs were utilized to supply additional information on the distribution of the sponges and the nature of the bottom in various sections of the shelf and slope.

During BIOFAR cruises in 1987 and '88 with the Faroese R/V *Magnus Heinason* crew members pointed to the widespread experience accumulated among fishermen concerning bottom conditions around the Faroe Islands. Traditionally when trawling, fishermen avoid areas with ostur because of the risk of catching several tons of sponges, overfilling the gear and damaging the catch. Accordingly, trawler captains often mark such areas on their charts and in their log books. Thus, in 1989 and '90, in cooperation with Rune Frederiksen and Andreas Jensen (Zoological Museum, Copenhagen), inquiry schemes with questions on coral banks and sponge accumulations were sent to Faroese trawler captains. A number of informative answers were received, and the information on corals was published in Frederiksen *et al.* (1992) while that on the sponges was used in Klitgaard *et al.* (1997), supplementing or supporting the BIOFAR data.

In addition the Fiskirannsóknarstovan (Fisheries Research Institute) has included some areas with ostur in a book of charts showing the distribution of areas where the bottom is unsuitable for trawling in Faroese waters ("Tóv", Anonymous 1988).

In Figure 9 the above mentioned different types of information are combined into a detailed map of the sponge accumulations around the Faroe Islands.

In view of the very extensive information provided by commercial trawling we find it safe to conclude that areas with ostur are present in long, narrow zones close to and parallel to the shelf break (in depths from about 250 to 500 meters) in various places all around the Faroes, and north-east and south-east on the Faroe Bank. The trawling mostly follow depth contours, but judged both from them, and from the dredge series and photographic transects of the BIOFAR I program, it seems that the depth interval of a zone is often less than 100 m, while the width may in some cases be 1-2 km. Southeast to the Faroes, south of Suðuroy Bank, there is a larger field with ostur, on a plateau-like area which seems to have no topographical relation to the shelf break.

How common is ostur ?

A broad definition of ostur is "a restricted area where large sponges are strikingly common". In the areas described as ostur at the Faroe Islands, sponges are estimated to constitute more than 90 % of the biomass, excluding benthic fish. We have no quantitative samples and the characterization "strikingly common" is based on the fishermen and our own experience. A conservative estimate, based on triangle dredgings taken during BIOFAR 1 cruises, suggests that there is 1 large sponge per 10-50 m^2. Likewise, estimation based on series of underwater photos from areas indicated as ostur at the Faroe Islands suggests a density of 1 specimen per 10-30 m^2 (Klitgaard *et al.* 1997).

What characterizes the distribution of ostur ?

Substratum

The geodiid sponges sampled during the BIOFAR I program often appeared on deck with stones of different sizes incorporated in the cortex (Figure 10). Also, sponges of this family are most often seen in underwater photographs from areas with a gravelly substratum.

Figure 10.
A *Geodia barretti* specimen with several stilt-like projections each attached to a piece of gravel. (Specimen sampled on BIOFAR Stn. 352; Nørrevang *et al.* 1994). (© photo G. Brovad).

Most sampled specimens of *Stryphnus ponderosus* had deposits of sand incorporated in the tissues and specimens seen in photographs sit on sand, sometimes partly covered by the sand (Fig. 8).

The experience from the BIOFAR sampling, the bottom photographs and the limited information in the literature (Spärck 1929) gives the general impression that the sediments in the Faroese shelf and slope areas consist mostly of sand and gravel with cobbles and stones, or even scattered boulders. Accordingly, accessibility of suitable substratum seems not to be a limiting factor in the occurrence of ostur. Current-produced features seen on photographs from ostur areas such as sand fans on the lee side of stones and ripples demonstrate sediment mobility and we suggest that the sponges live in a current-swept environment with a variable current direction.

Hydrography

The sponge aggregations are predominantly found in warm, Atlantic water. The distribution follows broadly those regions on the shelf break where the bottom slope matches the slope of propagation of the internal tidal waves, that is regions with a critical slope. An intensification of the bottom currents is often observed in such areas.

A tendency to aggregate in the vicinity of regions with critical slope seems to be a general phenomenon for large suspension feeders. The BIOFAR results show this for the scleractinian coral *Lophelia pertusa* (L., 1758) (Frederiksen *et al.* 1992) as well as for large octocorals, stylasterids and some brachiopods (pers.obs.).
The elevated bottom current speed at the critical slope is probably as such not beneficial to the suspension feeders. The causal link is thought to be an increased food supply, produced indirectly by processes that are associated with the internal waves. Two mechanisms have been proposed (Frederiksen *et al.* 1992, Klitgaard *et al.* 1997) (Figure 11):

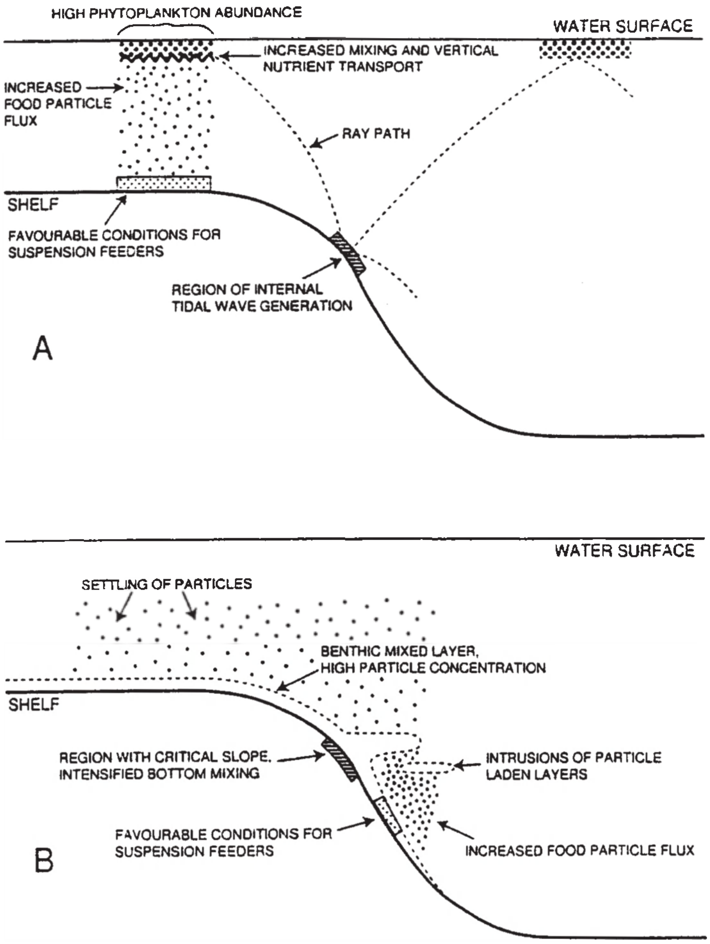


Figure 11.
Two scenarios (A, B) for a connection between internal tidal mixing and an increased food particle flux to the benthos. The thickness of the bottom mixed layer is greatly exaggerated. (From Klitgaard *et al.* 1997).

- An increased primary production where internal wave mixing promotes nutrient flux to the surface (Fig. 11 A)
- A leakage of food-particle rich water from the bottom mixed layer to the stratified ocean interior (Fig. 11 B).

The prominent sponge field southeast of Suðuroy differs from most other aggregations by a large extent and relatively shallow depth. A special case of the first mechanism may explain the presence of this ostur area, which otherwise seems hard to connect to any particular feature of the area.

An important question in this connection is what the exact nature of the diet of the sponges is. Demosponges are generally regarded as unselective suspension feeders, filtering particles from bacterial size to about 6 µm in diameter (Reiswig 1975, Wolfrath & Barthel 1989). Whether this also apply for the geodiid species and *Stryphnus ponderosus* is however presently not known.

Causes of changes in the distribution of ostur

The experience of fishery biologists and fishermen is that although ostur is found in the same general area over long periods of time, the localities where there are the highest concentrations may change; in fact, some fishermen say that "the ostur is wandering".

The large size, low organic content and predominance of large specimens in the catches from ostur areas have lead us to the assumption that the dominant species are slow growing and probably take at least several decades to reach the sizes commonly encountered. The lack of small specimens is remarkable and indicates that reproduction must be an infrequent event. Being suspension feeders the ostur species depend on a constant water current through their system of internal incurrent and excurrent canals to maintain their metabolic activities of respiration, filtering of particles and growth. Thus, it seems reasonable to assume that the sponges are dependent on a certain stability with respect to water mass characteristics and kinds and amount of particles in the water. This makes the ostur species vulnerable both to changes in the local hydrographic regime, and to physical disturbance.

A special kind of physical disturbance occurs when water near the bottom become more heavily loaded with suspended material which sediments out covering the surface of the sponge, and clogging the filtration system. Intense resuspension can occur due to natural causes like sediment slides, violent storms or unusually high internal waves, but additional causes, introduced in modern times, are nearby trawling and oil drilling. Some degree of self-cleaning of the canal system is possible for the sponges. However, if the resuspension event happens too often the sponge may no longer be able to do this and its metabolic activity may be depressed to a level at which the specimens can no longer survive; the sponge is smothered.

A very direct kind of physical disturbance is trawling. Intensive trawling probably rapidly leads to severe depletion of ostur areas. During our investigations around the Faroes, areas indicated as ostur in "Tóv" (Anonymous 1988) were sampled, but we found no sign of the ostur species and Faroese fishermen told us that trawling had recently begun in these areas. Modern trawlers are working deeper than trawlers did before, extending the fishing grounds and so are destroying areas of ostur. Fishermen have told us that certain bottom areas are being "improved" by repeatedly towing the large bobbins gear over the bottom crushing the sponges that would otherwise fill up the trawl, so that gradually the area is "improved" into a reasonable trawling ground.

Biological importance of ostur

The exact nature of the biological importance of the ostur areas is difficult to outline in more detail, and the need of *in situ* investigations is obvious. Nevertheless, on the basis of our experience gathered from the examination of numerous ostur catches and series of underwater photographs from the Faroe Islands, we feel capable of making some suggestions.

The physical heterogeneity of the local area and the number of available microhabitats are clearly increased by the presence of the large-sized ostur sponges. Thus, a very rich fauna (> 242 species) has been shown to be associated with the dominant sponges in ostur areas at the Faroe Islands (Klitgaard 1991, 1995, Warén & Klitgaard 1991). The majority of the associated species are facultative being found also as members of the local fauna outside ostur areas; this seems to be a general phenomenon in temperate/cold waters for sponges (Klitgaard 1995) as well as for *Lophelia pertusa* (Jensen & Frederiksen 1992).

The heterogeneous nature of the ostur areas and the presence of a rich mixed fauna of invertebrates, probably makes them recruitment areas for certain species of fish. Thus, we observed large numbers of redfish (*Sebastes* spp.) in trawl hauls from ostur areas around the Faroe Islands during the BIOFAR program (Figure 2).

Another feature of ostur is that when the sponges die, large amounts of spicules are released. These can either form a local spicule mat on the bottom, or be transported by bottom currents to other localities. A number of such localities with spicule mats were found around the Faroe Islands. The occurrence of large quantities of spicules changes both the composition and structure of the local sediment and this might in turn influence the composition of the local benthic fauna as has been reported for hexactinellid dominated areas in the Porcupine Seabight (Bett & Rice 1992) and from many other areas in the NE Atlantic (Barthel & Tendal 1993).

It seems logical to direct future research towards the potential for designating ostur regions as refuges from which the dispersal of invertebrates as well as fish could replenish the surrounding trawled areas, such as has been proposed already for other types of marine habitats (Dugan & Davis 1993).

Other parts of the North Atlantic

Dense aggregations of sponges are not strictly a Faroese phenomenon but are known to occur in many other places in the northeast Atlantic. Thus, investigations have been performed in the Porcupine Seabight (Rice *et al.* 1990), and off Bjørnoya and West Spitzbergen (Blacker 1957, Dyer *et al.* 1984, Barthel *et al.* 1991). In addition charts and the reports of fishermen and biologists as well as actual samples show that ostur areas also exist in the Barents Sea, along the Norwegian coast and south of Iceland and Greenland (Klitgaard & Tendal in press).

Conclusions

The general results given above, and our other information and experience allow us to draw some conclusions and to state some points of importance:

- ostur, viz. sponge dominated areas, are widely distributed around the Faroes, and in parts of the northeast Atlantic, dominated by warm, Atlantic water.

- such dense aggregations of sponges have always been found close to the shelf break or on places with similar high-energy water movement conditions.

- although dominated by sponges, ostur areas house a rich fauna of other kinds of animals, especially large numbers of filter- and suspensionfeeders, for example corals.

- ostur areas are presumably important recruitment areas for certain stock of fish as food seems abundant and the environment is undisturbed (no trawling or oil drilling activity).

- large amounts of silicious sponge spicules are produced and scattered after the death of the sponges. They are often transported to other localities, and become part of the sediment. Sometimes they are even concentrated in certain local areas forming a kind of loose felt.

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Lophelia pertusa and other cold water corals in the Faroe area

The scleractinian (stone coral) cold water coral *Lophelia pertusa* (L., 1758) is well known from the north-east Atlantic. In the Faroe area it was observed for the first time at the eastern part of the Wyville Thomson Ridge at 969 m depth by the expedition of HMS 'Lightning' in 1868 (Wyville Thomson 1873) (Figure 1). *L. pertusa* builds large banks, structures that can extend to several hundred meters in diameter and rise several tens of meters above the sea floor. In contrast to tropical corals *L. pertusa* is lacking symbiotic algae.

The geographical distribution of *Lophelia pertusa* within the area

Lophelia pertusa is widely distributed and has been recorded from most seas (Jungersen 1917, Zibrowius 1980, Cairns 1994, Copley *et al.* 1996, Mortensen 1999, Hovland & Mortensen 1999). In the north-east Atlantic it is often to be found on the upper slope of off shore banks and near the continental shelf break at depth of generally 200 – 400 m, in temperature of 4 – 8°C and at a salinity of 33.5-35.2 S (Wilson 1979a, Frederiksen *et al.* 1992).

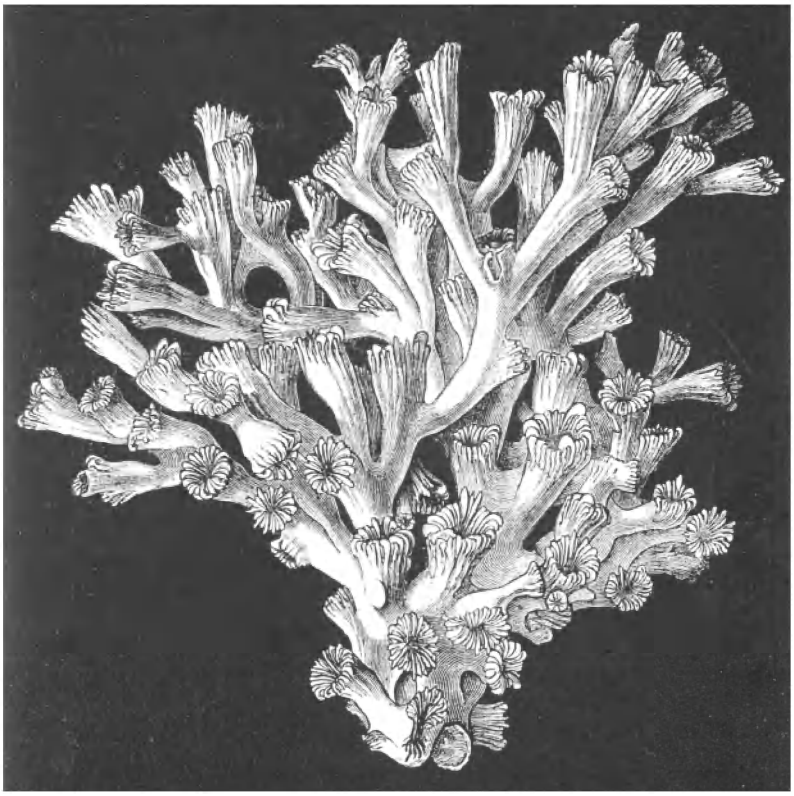

Figure 1.
Lophelia pertusa (from Wyville Thomson 1873).

In 1979 Wilson published a map of the occurrence of *Lophelia pertusa* within the north-east Atlantic (Wilson 1979a). He gathered the information from published records and also included sites known by local fishermen. The corals make up a risk of getting the fishing nets caught and ripped, and the fishermen have for years marked coral areas on their maps, whenever they came across any. Some of the banks were destroyed in the attempt to turn the areas into good fishing grounds. As the knowledge about the *Lophelia* banks and their inhabitants has grown, public interest has increased. In some countries attempts have been made to protect *Lophelia* banks, as for example in Norway, where trawling was recently regulated and in some areas even stopped.

During the BIOFAR program (1987-1991) a special effort was made to further register the *Lophelia* banks in the Faroe area and to test some of the stations within the Faroe area listed by Wilson (1979a) and pointed out by Faroese fishermen (Nørrevang *et al.* 1994, Frederiksen *et al.* 1992). A map of areas where *Lophelia pertusa* occurred was compiled from all existing knowledge. (Figure 2).

In the Faroes *Lophelia pertusa* is the most abundant coral. It occurs in single colonies as well as banks of considerable dimensions. *Lophelia* was always found deeper than 200 m by Frederiksen *et al.* (1992), with the largest occurrence on the shelf and upper slope of the banks at 250 – 450 m. The 200 m upper limit is general for the offshore distribution in the North Atlantic (Zibrowius 1980) and probably relates to maximum current speeds generated by extreme wave conditions met during long periods (Frederiksen *et al.* 1992). In some Norwegian fjords *Lophelia* has been recorded as shallow as 39 m depth (Rapp & Sneli 1999).

Growth and morphology

The *Lophelia* colony is assumed to develop from a planula, which settles on the surface of rocks, stones, pebbles or old coral branches. As the colony grows and becomes larger the network of intertwined branches forms attractive microhabitats and shelter for other invertebrates. With age the living tissue withdraws from the lowest part of the colony and only the outer approximately 1 m of the coral bank supports living polyps (Wilson 1979b). The degradation of coral banks is carried out by a few very abundant species that actually bore in the coral. They are mainly boring sponges such as species of *Cliona* and *Alectona*, but also boring polychaetes are important excavators (Frederiksen *et al.* 1992). When the inner and lower dead parts are attacked, the basal support of the colony is weakened which can lead to a physical collapse of the colony. However, even after the collapse, the living outer branches of the colony will continue to grow (Wilson 1979b).

Branches broken off from the living coral, which fall onto the sediment, may continue growth, or become substrate for new planulae, thus providing substrate for a new colony. Some of the broken branches frequently fall into the colony where they are caught and trapped amongst the intricate branching and in time become cemented to the structure (Wilson 1979b). As the colonies and branchlets in the ring surrounding the original colony grow, they in turn generate debris around them that will provide further colonies. When the surrounding ring becomes larger, difficulties in feeding and long term stagnation of water movements may cause the death of the inner portion of the large *Lophelia* colonies (Chamberlain & Graus 1975).

The limitation in size of the colonies is, as also summarized by Wilson (1979b), determined by such factors as: the mechanical strength of the living, growing branches of coral (Stetson *et al.* 1962), the dynamics of water flow through the colony in relation to feeding (Chamberlain & Graus 1975), and the rate of weakening of the dead portions of the colonies by activities of boring

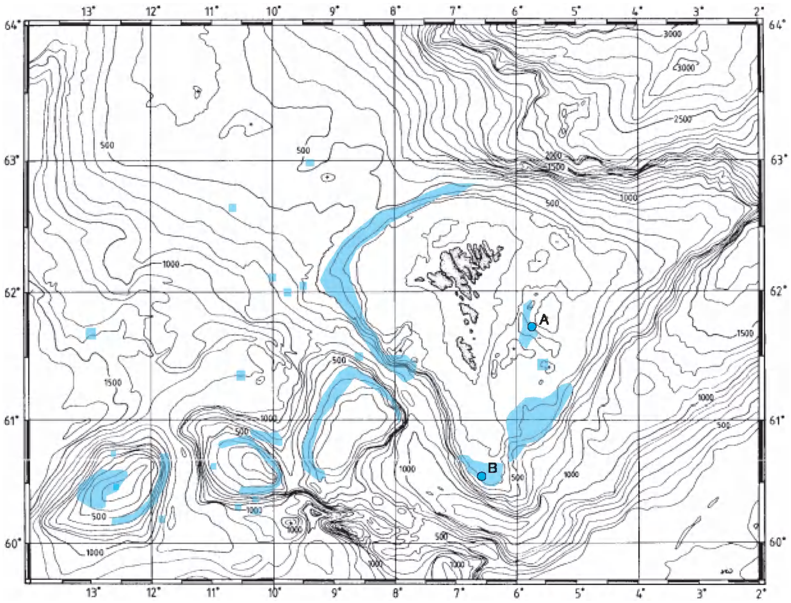

Figure 2.
Distribution of *Lophelia pertusa* in Faroe waters. A and B are localities where coral associated fauna was investigated (see Jensen & Frederiksen 1992).

sponges and polychaetes etc. Consequently, the banks reach an equilibrium of formation and degradation.

Feeding

The knowledge about *Lophelia's* feeding strategy is limited, but from aquarium experiments lasting for three years in Trondhjem Biological Station, Norwegian University of Science and Technology, it has been found highly variable (Rapp & Sneli 1999). They suggested zooplankton and "marine snow" to be the main food sources. They also found that the well known mucus production, formerly regarded as a mechanism to cope with stress, sedimentation and "fouling" organisms, was important in enabling large prey and large numbers of prey to be captured and ingested. In situ studies on a bank off Norway showed the food to be planktonic crustaceans (Heinrich *et al.* 1997)

Unpublished results from aquarium experiments show that when fed different types of prey Crustacea, with a size up to at least 35 mm together with Chaetognatha was the preferred food source. Ctenophora, medusa and pure gelatine pellets were rejected, indicating that *Lophelia* use both tactile and chemosensitive receptors in discrimination and selection of prey. High concentrations of prey induced high capture rates (Rapp *et al.*, submitted).

Growth rates and age of coral banks

Growth is slow. Possible growth rates of 4.1 – 7.5 mm/year were reported in a more than 100 year old investigation (Duncan 1877). These rates were direct measurements of *Lophelia* colonies settled on cables laid out and recovered after 6 years. Recent studies suggest, based on oxygen and carbon ratio measurements related to growth line patterns in the skeleton, an average growth of 4.3 mm/year in shelf corals and 7.0 mm/year in corals from the Trondheim fjord (Mortensen & Rapp 1998). These growth-rates give an estimated age of minimum 300 years for a colony of 1.5 m height. 15 m large banks might then be at least 2000 years old, but accounting for fragmentation and decomposition, the banks are undoubtedly much older. Age determination by isotope techniques allows by comparison with similar Norwegian investigations (Hovland *et al.* 1998) to estimate the age of *Lophelia* in the Faroe area to be approximately 9000-10.000 years (Unpublished information, Israelson and Tendal). Mikkelsen *et al.* (1982) found that data derived from stable isotope ratio analysis of corals from the Trondheim fjord indicated a growth rate of 2.5 cm/year, however, Mortensen & Rapp (1998) found it to be surprisingly high and suggested the reason to be bulk-sampling of more than one growth layer.

Figure 3.
Blocks of live and dead *Lophelia pertusa*. The intricate branching provides space and shelter for a variety of species. (© section of photo by O.S. Tendal)

Lophelia banks as a habitat

In the mature coppice, only the outer 1 – 2 m is alive. Beneath this, dead coral and fragments are found in a compact core. The banks function as sediment traps by reducing the bottom current speed, and often fine mud, sand and particles are trapped within the branches of the banks (Stetson *et al.* 1962).

Compared to the surrounding seabed, the network of intertwined branches forms a variety of habitats and shelter for many different organisms, like for example the free space between the coral branches, the smooth surface of the living *Lophelia*, the detritus laden surface of dead *Lophelia* and the cavities inside dead *Lophelia* made by boring sponges (Mortensen *et al.* 1995) (Figure 3). The dead coral debris and trapped sediment supports a rich fauna of sponges, anemones, bryozoans, calcareous tube building polychaetes, brachiopods, bivalves, asteroids and echinoids, and also provide shelter for several scavengers (Wilson 1979b).

During the BIOFAR project, a thorough investigation of the fauna associated with *Lophelia pertusa* banks was carried through at two sites indicated in Figure 2. This is the only investigation on the fauna associated with *Lophelia* within the Faroe area; however, investigations of Norwegian coral banks (Burdon-Jones & Tambs-Lyche 1960) and blocks from the Bay of Biscay (LeDanois 1948) suggested a rich associated fauna. In the Faroe area 11 blocks from site A and 14 blocks from site B of 0.2 – 2.0 kg were examined. An echogram of site A showed the bank to be 10 m high and 110 m wide. The area is exposed to tidal currents with an average speed of 50 cm/s. Site B has an average speed of 35 cm/s. (Jensen & Frederiksen 1992). At both sites the average temperature is 6 – 8°C with a standard deviation of 0.5 – 1.0°C (Westerberg 1990). Clay and silt were found between the coral branches at both sites.

As expected a highly diverse and rich fauna was shown to be associated with the *Lophelia* banks. In the BIOFAR study 300 species were identified, of which 256 species were found on the blocks examined and 42 species were identified from loose coral rubble. A list of species occurring at minimum half of the 25 blocks is provided in Table 1.

The most species rich groups were Polychaeta (67 species), Bryozoa (45 species) and Porifera (29 morphological types) and in number of individuals, not counting the colonial species, the dominant groups were Polychaeta, Bivalvia, Echinodermata and Brachiopoda (Jensen & Frederiksen 1992).

Jensen & Fredriksen (1992) found that most individuals occurred in the dead coral blocks from the inner part of the bank or colony, and only 20 species, represented by more than 1 individual, were found exclusively on the living part of the corals. The coral polyps are not interconnected, as epithelium does not cover the entire surface of the skeleton and fauna associated with the live coral blocks were found between calices rather than on or in the living tissue of *Lophelia*. Polychaeta and Gastropoda occurred in twice as many individuals on dead as on live coral. Crustacea, Sipuncula, Bivalvia, and Nematoda were found in 4 - 8 times as many individuals on dead as on live coral. Ascidia, Anthozoa and Echinodermata were found in more than 10 times as many individuals on dead as on live coral and Brachiopoda were found to be more than 50 times as frequent on dead than on live coral.

Of the 20 most abundant species only four showed a correlation between the number of individuals and coral weight. For live coral blocks these were the polychaete *Eunice norvegica*, the bivalve *Modiolula phaseolina* and nemertea sp. A., and on dead coral only the polychaete family Paraonidae.

Many juveniles were found in the corals by Jensen & Frederiksen (1992) and the corals may provide a good nursery area with protection from predators like it is known from the holdfasts of the large brown algae *Laminaria* in shallower water (Christie *et al.* 1994, Worsaae 1998).

The associated fauna is facultative as none of the species occurring in the samples were exclusively found in *Lophelia pertusa* banks and obligatory associated to it. Many of the species are common in the Faroese area, and the corals may thus act as an important habitat for recruitment of species to the more barren surrounding deep water areas. This is contrary to Dons (1944) who for a Norwegian bank mentioned about 50 species to be obligate *Lophelia* associated fauna and nearly always found on the stone-coral banks he investigated. How-

Figure 4.
Trawl catch from 375 m depth west of the Faroe Islands. BIOFAR Stn. 535 (Nørrevang *et al.* 1994). The characteristic animals are, in addition to *Lophelia*, large branches of the octocoral *Paragorgia*, the bivalve *Acesta*, the brittle star *Gorgonocephalus*, and large sponges of the genus *Geodia* (© photo by A. Klitgaard).

ever, Burdon-Jones and Tambs-Lyche (1960) only found a limited overlap of species when comparing Dons species list with what they found on a coral bank in a Norwegian fjord near Bergen, and suggested as Jensen & Frederiksen (1992) for the Faroes that no such obligate fauna exists.

The coral banks in the north-east Atlantic are built by *Lophelia pertusa* alone, whereas other cold water corals like *Madrepora oculata* (L., 1758) and *Solenosmilia variabilis* Duncan, 1873 are found scattered and sometimes use *Lophelia* as substrate The associated fauna consists mainly of suspension and particle feeders like the coral itself (Figure 4). *Lophelia* banks are found in areas with considerable water movement and abundant suspended material (Jensen & Frederiksen 1992).

The study by Jensen & Fredriksen (1992) only included the closely associated fauna. The main part of the mobile species are not obtained with the type of gear used (triangle dredge) and free-living species could be lost during haul up. Video investigations with ROV (Remote Operated Vehicle) on Norwegian banks showed the presence of several fish species at the banks. Especially redfish and saithe dominated the fish fauna (Mortensen *et al.* 1995).

Large numbers of *Eunice norvegicus* (L., 1767) were found associated with the banks. This large polychaete can grow up to 20 cm in length. It lives in parchment-like tubes in the living part of the coral where the coral strengthens the tubes by overgrowing and encapsulating them. Another very common species was the brittlestar *Ophiactis balli* (Thompson, 1840) which lives in the dead skeletons of the polyps or other cavities, with the body hidden and protected and arms extended to feed. Such cavities are also often occupied by the bivalves *Hiatella arctica* (L., 1767) or *Acar nodulosa* (Müller, 1776) (Jensen & Frederiksen 1990).

The importance of food supply on the distribution of *Lophelia pertusa* banks

Lophelia pertusa is a suspension-feeder and as such is dependent on food being brought to it. Studies on the distribution of corals in Norwegian fjords suggest areas of strong current as a preferred habitat (Dons 1944). This was not supported by Frederiksen *et al.* (1992) for the distribution of *Lophelia pertusa* in the Faroes. They found the densest concentrations to occur close to areas where the conditions allow internal tidal waves to break at the sloping bottom. They argued that the food supply to passive suspension feeders like corals not necessarily increases with increasing current speed but that the crucial factor is the particle flux to the bottom mixed layer. Two different types of possible increases in sedimentation rates were discussed (Frederiksen *et al.* 1992).

One is by internal waves generated by the advection of stratified water across bottom contours by the barometric tide. This generates rays of energy, that enhance the vertical mixing and results in nutrient rich bands parallel to the shelf break contour, which in turn enhances phytoplankton production within the bands. The increased production would at least seasonally lead to a higher vertical detritus flux and thereby higher food availability for the suspension feeders at the bottom. However, the horizontal advection is much larger than the downward flux of small particles, and these would be transported away from the production sites before reaching the bottom. Only faecal pellets and marine snow have a sinking rate large enough to enable the surface production to reach the bottom mixed layer close to the production site. As the water depth increases the vertical detritus flux to the bottom becomes weaker and the spatial separation between production site and the area where the surplus is deposited increases. Another explanation could be that when the bottom slope equals the rays, called the critical slope, the local increase in mixing intensity will lead to a thickening of the bottom mixed layer and to a resuspension of organic particles that may have been deposited, thereby increasing the availability of food (Frederiksen *et al.* 1992, Klitgaard & Tendal, this volume).

This could explain the known distribution

Table 1.
Invertebrates associated to *Lophelia pertusa* occurring at a minimum half of the 25 blocks are shown. Number shows frequency of occurrence.

NEMATODA	
Deotostoma sp.	14
POLYCHAETA	
Eusyllis blomstrandi Malmgren 1867	13
Sphaerosyllis spp.	17
Typosyllis armillaris (O.F. Müller, 1776)	19
Paraonidae indt.	14
Lanassa cf. *venusta* (Malm, 1874)	14
Polycirrus cf. *norvegicus* Wollebæk, 1912	16
Perkinsiana socialis (Langerhans, 1884)	14
Placostegus tridentata (Fabricius, 1779)	19
Protula tubularia (Montagu, 1903)	14
MOLLUSCA, Bivalvia	
* *Modiolula phaseolina* (Philippi, 1844)	19
Heteranomia squamula (smooth) (L., 1758)	17
H. squamula (scaly) (L., 1758)	16
Hiatella arctica (L., 1767)	20
CRUSTACEA	
Gnathia sp. juvenile	19
G. abyssorum G.O. Sars 1872	13
G. dentata G.O. Sars, 1871	14
SIPUNCULA	
Golfingia minuta (Keeferstein, 1862)	19
BRYOZOA	
Crisia eburnea (L., 1758)	18
C. aculeata Hassall, 1841	13
Idmidronea atlantica (Forbes in Johnston, 1847)	18
Cabarea ellisii (Fleming, 1814)	13
Porelloides laevis (Fleming, 1828)	13
Sertella beaniana (King, 1846)	14
BRACHIOPODA	
Crania anomala (O.F. Müller, 1776)	14
Terebratulina retusa (L., 1758)	15
Macandrevia cranium (O.F. Müller, 1776)	15
ECHINODERMATA	
Ophiactis abyssicola M. Sars, 1861	17
O. balli (Thompson, 1840)	14

* By wrong identification the species is given as *M. modiolus* in Jensen & Frederiksen (1992).

of *Lophelia pertusa* in the area of the upper shelf and in the vicinity of critical slope areas in the Faroes. Such conditions would not only be a benefit for growth of *Lophelia* but also for other suspension feeders (Frederiksen *et al.* 1992), such as the large sponges as is indicated by their distribution (Klitgaard & Tendal, this volume).

Others have suggested that the *Lophelia* banks off Mid Norway are linked to areas of hydrocarbon seeps (Hovland *et al.* 1998, Hovland & Thomsen 1997). The reason for this kind of distribution is again suggested to be an enhancement in food supply in relation to surrounding more barren areas. At hydrocarbon seeps the water becomes enriched with inorganic and organic carbon components that might be utilized by micro-organisms which again can be used as food by filter feeders and so forth. If the chemical and micro-organic condition is stable over prolonged periods, and the substrate and current regime is favorable, particle feeders including *Lophelia* find optimum conditions for settling and growth (Hovland *et al.* 1998).

Variation in morphology

Variation in morphology of *Lophelia* might be correlated with differences in the energy levels at the place of growth. From bottom contours, it is assumed that slender, tall forms are from low energy environments compared to the compact forms that might be found in high-energy environments. The difference in tall and compact forms is also reflected in the internal structure of the corals as the compact forms have a denser skeleton (Mikkelsen *et al.* 1982). Compact and extended growth forms may occur in different parts of the same colony indicating differences in the rate of budding, probably correlated with the availability of food. The spacing and orientation of the polyps certainly suggest that the growth attempt to maximize the exploitation of the food supply (Freiwald *et al.* 1997).

Reproduction and recolonization

Wilson (1979b) did not find evidence of successful settlement of planulae from the submarine dive on the Rockall Bank and he concluded that almost all growth in *L. pertusa* was by asexual budding. Accordingly death of *L. pertusa* will leave the given area barren for a long time. Even when recolonized, it will take many years for the newly settled *Lophelia* planulas to grow into banks of considerable size, due to the slow growth rate, and for the rich associated fauna to develop. Of course recolonization will only take place if the disturbance that killed the former *Lophelia* banks has ceased.

Lophelia pertusa and most sessile suspension feeders are effected and physically disturbed when the water becomes loaded with suspended inorganic particles as an effect of nearby trawling or by the discharge of cuttings from the oil industry. We do not know the long-term effect of drilling activities on neighbouring *Lophelia pertusa* banks or other hard bottom communities. However, the effect from a rise in sediment influx could be a partial or total burial of coral colonies. The sediment covers the surface and all the hollows of the colony, and in time the corals and their associated fauna may be smothered and totally buried if the sediment load continues.

Concluding remarks

Lophelia banks are widely distributed within the Faroese EEZ, and are particularly found close to the shelf break or on places with similar high-energy water movement conditions.

Lophelia banks get very old and the estimated age of *Lophelia* in the Faroe area is approximately 10,000 years. Growth is slow, and if destroyed either by physical damage or by smothering, the banks are only very slowly rebuilt, if at all.

Although no obligate associated *Lophelia* fauna exists, the banks are very rich in associated species and in number of individuals, and may function as nursery and recruitment area for the more barren surroundings.

Primnoa resedaeformis

The octocoral *Primnoa resedaeformis* (Gunnerus 1763), 'sea corn' or 'rice coral' has been found many times at the Faroes (Figure 5). It was first recorded by Thomson (1906) in the Faroe-Shetland Channel, later by Madsen (1944) from two localities west of the Faroes, by Grasshoff and Zibrowius (1983) from Bill Bailey Bank, and finally during the BIOFAR project at 18 localities all around the Faroes (Nørrevang *et al.* 1994, Tendal in prep.).

It has been taken at 90-1020 m depth, with most records between 200 and 500 m. The two localities shallower than 200 m are on the western and eastern side of the Faroese plateau, while the only two deeper than 500 m, both at around 1000 m, are on the northern and southern flanks of the Bill Bailey Bank, respectively. All records, except the northernmost of the deepest and one in the Faroe-Shetland Channel are from areas dominated by North Atlantic water, with temperatures of 6-8°C. The remaining two are from water of 2-4°C (Westerberg 1990).

Most samples are fragments, but a number of whole specimens, about 1 m high were taken by the trawls. According to literature this is the normal maximum size for the species all over its North Atlantic distribution area (Broch 1912, Carlgren 1945, Breeze *et al.* 1997). Specimens of that size are supposed to be of considerable age, at least 500 years old (Strömgren 1970, Risk *et al.* 1998). *P. resedaeformis* has been reported to be viviparous but nothing is known of the reproduction frequency (Thomson 1906; the remark by Breeze *et al.* 1997 that the development is pelagic seems unconfirmed).

The species is to be considered very vulnerable to physical damage.

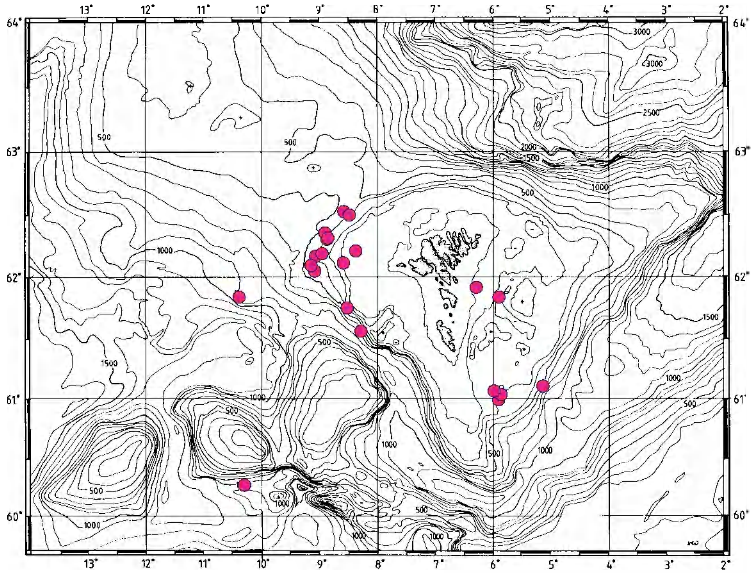

Figure 5.
Distribution of *Primnoa resedaeformis* in the Faroe area.

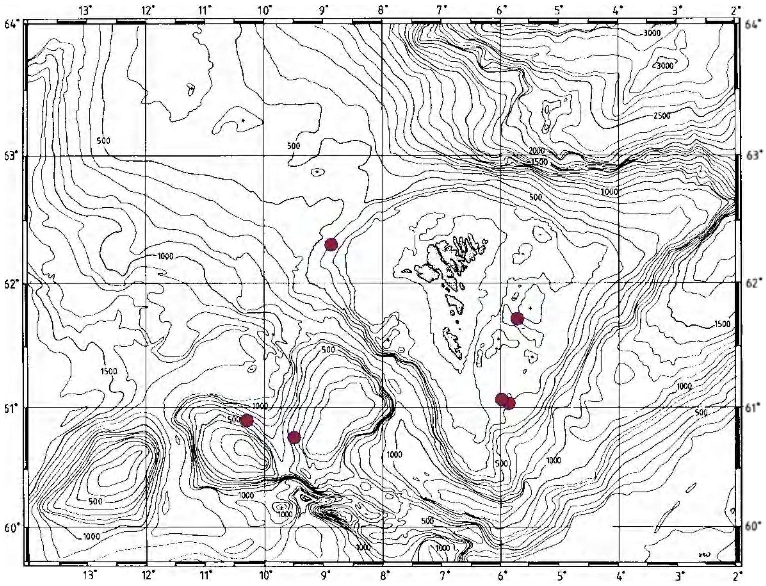

Figure 6.
Distribution of *Paragorgia arborea* in the Faroe area.

Paragorgia arborea

The octocoral *Paragorgia arborea* (Linné 1758), 'sea tree' or 'bubble gum coral' is known from several locations in the Faroes (Figure 6). It was first mentioned by Madsen (1944; the same specimen mentioned and shown on a photograph in Vedel Thåning 1958), and during the BIOFAR project 6 other records turned up (Tendal 1992, Nørrevang *et al.* 1994, Tendal in prep.).

It has been taken at 260-649 m depth, with 6 of the records shallower than 500 m. All records are from the southern part of the area, from North Atlantic water with a temperature of 6-9°C, and with calculated current velocities of 45-60 cm/sec (Westerberg 1990).

The largest fragment found during the BIOFAR project was a branch 12 cm thick, about 150 cm long and with a branching part 50 cm wide. Fishermen have told about colonies of about 2.5 m height. The species grows very slowly, and specimens of that size are at least 1500 years old (Tendal & Israelson, unpublished). The reproduction pattern is unknown (the remark by Breeze *et al.* 1997 that the development is pelagic seems unconfirmed).

Tendal (1992) believed the species to be more widespread, as the gear used during the BIOFAR project in many cases was too small. Of the 7 samples, 5 were obtained by trawl.

The species must be considered very vulnerable to physical damage.

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Modiolus modiolus beds

The horse mussel *Modiolus modiolus* (L., 1758) occurs in small patches or forms extensive beds with large densities in sublittoral hard bottom habitats, where it attaches to the hard substrate by the byssus threads. The horse mussels can grow to a shell length of more than 200 mm (Wiborg 1946), and can reach an age of up to 48 years (Anwar *et al.* 1990). *Modiolus modiolus* beds can be considered rather stable habitats, taking into account the adult size, the immobility and the longevity of the species.

Large aggregations of the horse mussels may in cause of time change the original substrate considerably, as increased biodeposition due to faeces, pseudofaeces, byssus, shell debris from dead horse mussels and accretion of silt and detritus adds to the existing hard bottom substrate (Dinesen 1999).

The two main investigations from the Faroes on *Modiolus modiolus* beds and their associated fauna are by Spärck (1929) early in this century and later by G. Dinesen, Zoological Museum, Copenhagen, as part of the BIOFAR program in 1988-1991 (Dinesen 1996). A minor investigation was briefly reported on by Zaptsepin and Rittkh (1977). They all found *M. modiolus* to be widely distributed within the Faroese area, Figure 1, with beds both on open coasts and in the fjords and sounds between the islands.

The horse mussel beds occur over widely different depths from the lower shore inside the fjords to approximately 210 m depth on the Faroe plateau (Dinesen 1999). In the Faroes, horse mussels from the fjords grow considerably larger, up to 150 mm, than horse mussels from the plateau that as a maximum reach a shell length of 120 mm (Dinesen 1999). Spärck often found a density of as many as 50 mussels per m^2, however, Dinesen recorded 220 *Modiolus* per m^2 on BIOFAR Stn. 662 (Nørrevang *et al.* 1994), probably the highest density ever recorded (Dinesen 1999).

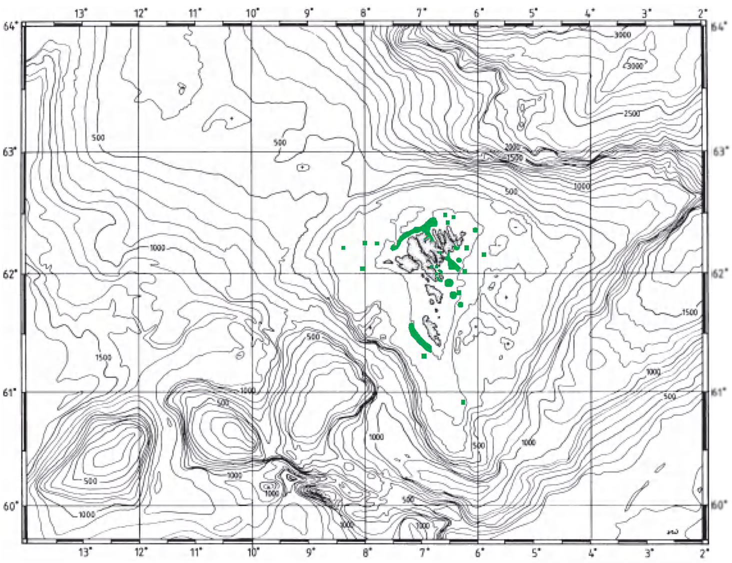

Figure 1.
A map of the Faroes with the occurrence of *Modiolus modiolus* indicated (based on Spärck (1929) and Dinesen/BIOFAR database).

The *Modiolus* association consists of the horse mussels with fauna attached to the valves, fauna living within the sediment between the horse mussels, and motile fauna moving about the horse mussels in search for food. Spärck (1929) listed 26 different taxa of invertebrates (including *M. modiolus*) from the beds (Table 1). During the BIOFAR program Dinesen investigated both sessile and motile epifauna of *M. modiolus* within the Faroe Islands and the surrounding waters. She identified 143 species among a total of 175 taxa of metazoan invertebrates. She found the same species as listed by Spärck apart from one, the cirripedia *Chirona hameri*. A short summary has been published (Dinesen 1999).

Spärck suggested a strong dependence on hydrographical conditions and in particular a constant and effective water renewal to be the main factors influencing the distribution of *Modiolus* beds as he found the weight of the epifauna to be large (17 kg per m^2).

The *Modiolus* beds and their association are important because of their extension and from a fisheries point of view. The fauna associated to the *Modiolus* beds contains a number of organisms that are eaten

Table 1.
Invertebrates commonly living among *M. modiolus* (Spärck, 1929).

Nemertes	Nemertes indet.
Polychaeta	Polychaeta indet.
	Polyonidae indet.
	Harmothoe imbricata (L., 1767)
	Lepidonotus squamatus (L., 1758)
	Pherusa plumosa (O.F. Müller, 1776)
Mollusca	Polyplachophora indet.
	Gastropoda indet.
	Bivalvia indet.
Crustacea	Crustacea indet.
Decapoda	*Galatea nexa* Embleton, 1835
	Eualus pusiola (Krøyer, 1841)
	Eupagurus sp.
	Hyas coarctatus Leach, 1815
Echinodermata	Echinodermata indet.
	Henricia cf. *sanguinolenta* (O.F. Müller, 1776)
	Ophiopholis aculeata (L., 1767)
	Ophiotrix fragilis (Abildgaard, 1789)
	Strongylocentrotus droebachiensis (O.F. Müller, 1776)
Ascidiacea	Ascidiacea indet.

Table 2.
Invertebrates commonly living on *M. modiolus* (Spärck 1929).

Porifera	Porifera indet.
Hydrozoa	Hydrozoa indet.
	Hydrallmannia falcata (L., 1758)
Cirripedia	*Chirona hameri* (Ascanius, 1767)
Bryozoa	Bryozoa indet.

by the cod, especially *Galatea nexa* and *Ophiopholis aculeata*. *Hyas* sp. and the annelids are also of importance.

Modiolus beds are also known from other regions in the North East Atlantic; Sweden (Petersen 1918, Gislén 1930), Iceland (Spärck 1937, Einarsson 1941), Norway (Wiborg 1946), Denmark (Thorson 1950), Isle of Man (Bruce *et al.* 1963), England (Warvick & Davies 1977), North Ireland (Brown & Seed 1977), Scotland (Comely 1978). The resulting number of identified associated taxa and species from these investigations vary as different collecting gear have been used, and also different levels of determination have been reached. However, all the investigations show that there is a rich fauna associated to the Modiola beds in the North East Atlantic.

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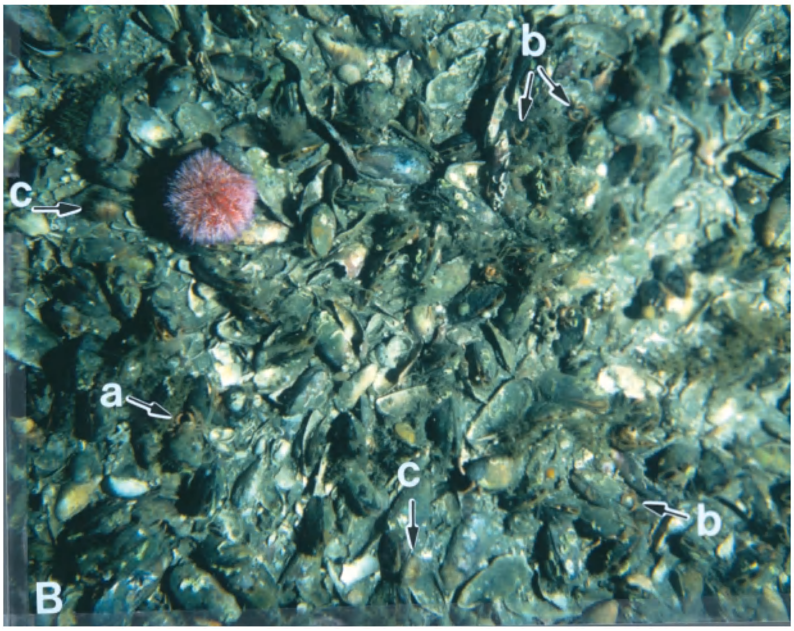

Figure 2.
The under-water photograph shows a section of a *M. modiolus* bed from the Faroe plateau at a depth of 77 m (BIOFAR stn. 662: Nørrevang *et al.* 1994). The pink sea urchin is *Echinus esculentus* L., 1758. a. *Hyas coarctatus* Leach, 1815. b. *Galatheidae*, probably *Galatea nexa* Embleton, 1835. c. *Strongylocentrotus* spp. The photo covers 0.87 m² (© photo J. Gutt, Alfred-Wegener-Institut, Bremerhaven).

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Aequipecten opercularis grounds

The queen scallop *Aequipecten opercularis* (L., 1758) is common all over the Faroe area, in waters outside the islands at depth of 50 – 200 m, and occasionally in the fjords (Høpner Petersen 1968) (Figure 1). Most of the information on the distribution of queen scallop in the Faroes is available from about 100 stations worked in 1903-1954 (Ursin 1956). Finds were concentrated at moderate depth in the shore region off the northern islands at 57 – 128 m. Queen scallops were most often caught in the interval 75-99 m, although a single find occurred at 173 m on the Faroe Bank (Ursin 1956).

Two areas of particularly large concentrations occur on the Faroe plateau, one to the north of the northern islands and the other east of the central islands. Together these two areas make up a total of about 400 km^2 (Figure 1). The beds are found at 60 – 110 m on sandy, rocky or soft bottom (Nicolajsen 1997).

The southernmost ground has been fished regularly for approximately 30 years. The northern ground was fished for several months in 1989 and 1990, but has not been fished by scallop trawlers since late 1990 when the factory trawler fishing the area was sold. Due to protests from longline fishermen the exploitation of scallops in the area was never restarted even though many vessels applied for the fishing rights (Nicolajsen 1997).

In recent years the question has been opened again whether to fish scallops in the northern area, and finances were granted to investigate how much change the scallop fishing does to the area, as longliners argue that their fishing grounds are destroyed. This investigation is currently going on at the Fisheries Research Institute in Tórshavn, the Faroe Islands.

The area inhabited by the queen scallops is much the same as that covered by the horse mussel *Modiolus*. Rapid water renewal seems to be advantageous, particularly for the development of dense beds. The bottom slope off the southern island is steeper than farther northwards and *Modiolus* is restricted to a narrow zone and queen scallops have not been found in this area (Ursin 1956).

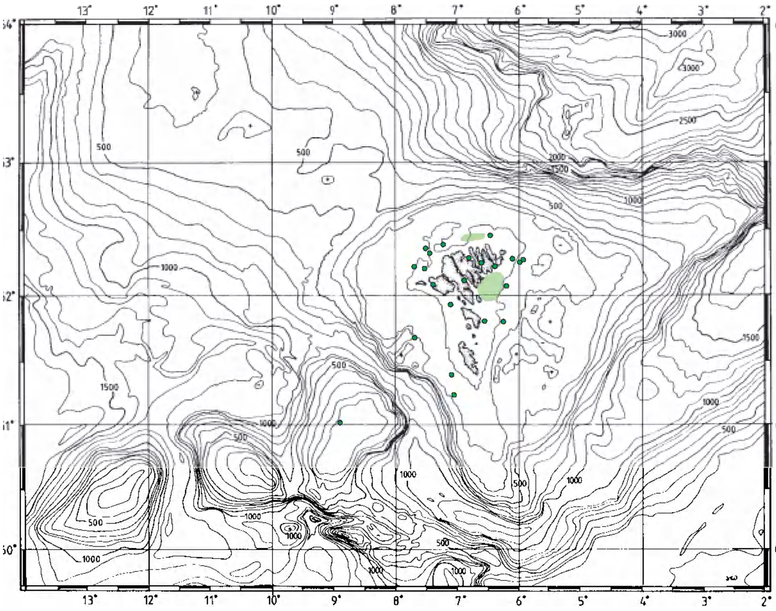

Figure 1.
Distribution of the queen scallop, *Aequipecten opercularis* in Faroese waters. Dots indicate single stations. Hatched areas indicate large quantities.

The dominant cohabitants in the scallop field north-east of Nolsoy are all common species such as the whelks *Buccinum undatum* L., 1758 and *Neptunea despecta* (L., 1758), the mussels *Tridonta elliptica* (Brown, 1827), *Clausinella fasciata* (da Costa, 1778), *Acanthocardium echinata* (L., 1758), *Modiolus modiolus* (L., 1758), *Arctica islandica* (L., 1767), and *Venerupis rhomboides* (Pennant, 1777), the starfish *Asterias rubens* L., 1758, *Henricia* sp. and *Hippasterias phrygiana* (Parelius, 1768), the brittlestar *Ophiothrix fragilis* (Abildgaard, 1789), the seaurchins *Strongylocentrotus droebachiensis* (O. F. Müller, 1776) and *Echinus esculentus* L., 1758, the seaanemone *Urticina felina* (L., 1761), the hydroids *Abietinaria abietina* (L., 1758) and *Hydrallmannia falcata* (L., 1758) and the hermit crab *Pagurus bernhardus* (L., 1758) (Nicolajsen 1997). The associated species from the northern ground are being worked up, and data are at this moment not available.

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Macrofauna in soft sediments on the Faroe shelf

Background

The Faroe Shelf is highly influenced by water currents from the Atlantic Ocean and the distance to industrialized and densely populated areas is long. It may therefore be anticipated that influence of pollution is relatively small compared to, for instance, parts of the North Sea and the Scandinavian Seas, Skagerrak, Kattegat and the Baltic Sea. Since benthic macrofauna in soft sediments often is used as an indicator of environmental quality, sampling of this faunal category on the Faroe shelf would constitute a reference to more polluted areas. This was the background for sampling sediment macrofauna on the Faroe shelf in the period 1987 - 1990 within the BIOFAR program. The area is relatively exposed (high energy environment) and the inputs of organic matter as well as fine grained inorganic matter from land is small which has the consequence that fine grained deposits are scarce on the shelf. The pilot survey in 1987 revealed two areas on the shelf with fine grained deposits suitable for quantitative macrofaunal sampling, one on the west side (Skeivibanka) and one on the east side (East Suðuroy) of the shelf, both at 300-350 m water depth (Figure 1, Table 1). The areas were sampled once a year in the period 1987 - 1990, and sampling was made in May except for 1987 when samples were taken in July.

Methods

Methods used were quantitative sampling with a modified Smith-McIntyre grab which covers a surface area of 0.1 m^2 and has a maximum penetration depth of 20 cm. Sampling was performed while the ship was drifting. At each time and station a number of replicate samples (3 – 6) were taken and in 1988 a large spatial grid of stations were sampled in each of the two areas, with one grab sample per station. Subsamples, one per grab sample, was taken of the surface (0-2 cm) sediment for analysis of grain size and content of organic matter. Sediment samples were deep-frozen (at minimum -20°C) for later analysis. Grab samples were sieved through a 1 mm square metal mesh and the retained

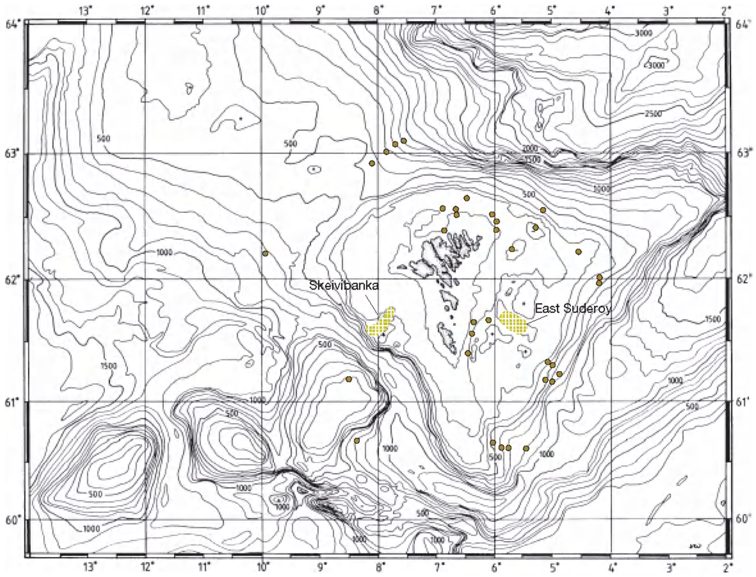

Figure 1.
Map of the Faroes with soft bottom areas indicated. Dots show Smith-MacIntyre grab samples from the BIOFAR program.

material preserved in 5% buffered formalin. In the laboratory the individuals of each species were enumerated, and the formalin wet weight of all individuals for each species (or rather taxon) were determined. After determination and weighing all material was stored in 80% ethanol.

Investigated localities

A description of surface sediment composition is shown in Table 1. The ignition loss, a measure of the organic content, is low at both localities and varies between 2.5 and 4.5. Water content and the percentage silt-clay (percent fines) are similar in the two areas and typical for sandy silt bottoms. In the eastern area (East Suðuroy) the bottoms may contain great amounts of sponge spicules.

Fauna

The total abundance, which was relatively low at both sites with 1000 - 2000 ind./m^2, was dominated by polychaetes (40-50%) followed by molluscs and the category 'remaining'. Dominating species among polychaetes were *Paramphinome jeffreysi* at both sites and *Paradiopatra quadricuspis* at the eastern site. Molluscs were dominated by bivalves of the genus *Thyasira* at both sites, and 'remaining' was dominated

Table 1.
Approximate positions, depths and sediment characteristics at the two areas on the Faroe shelf sampled for sediment macrofauna. Locality W: Skeivibanka, Locality E: east Suðuroy. For detailed positions see Nørrevang *et al.* 1994.

Locality and year	Latit. N	Longit. W	Depth (m)	Number samples	Ignition loss (%)	Water content (%)	Percent fines (< 50 micr)
W 87	61° 40'	07° 50'	329-350	3	2.8-3.3	37-39	34-46
W 88	61° 41'	07° 47'	317-367	15	2.7-3.9	35-40	-
E 87	61° 42'	05° 50'	350	1	4.3	47	47
E 88	61° 43'	05° 50'	349-351	2	3.3-4.1	42-48	-

by sipunculids notably *Onchnesoma steenstrupi.*

The biomass was dominated by echinoderms, in particular the sea urchin *Brisaster fragilis* at the western site, and molluscs where the bivalve *Tridonta elliptica* was the dominant at both sites. *Brisaster fragilis* was not included in Table 2 as only few specimen occurred in the samples. Total biomass in wet weight including shells was somewhat less than 50 g/m^2, which using published conversion factors corresponds to ca 2.5 g AFDW/m^2. This is a low figure relative to many coastal shallow areas, and probably reflects a small input of degradable organic matter to the benthic environment in these areas.

The species composition in terms of abundance is characterized by a high evenness and the number of taxa per areal unit is similar to the northern part of the North Sea and parts of the Skagerrak (Eleftheriou & Basford 1989). For instance, the number of taxa of the 4 major groups (Polychaeta, Mollusca, Echinodermata and Crustacea) on a 1/2 m^2 ranges from 60-90. The total number of taxa found at the two sites in the 4 years was above 200. The most frequently occurring taxa in the total samples on each of the two sites, 31 grabs from Skeivibanka and 15 grabs from Eastern Suðuroy, are listed in Tables 2 and 3 respectively.

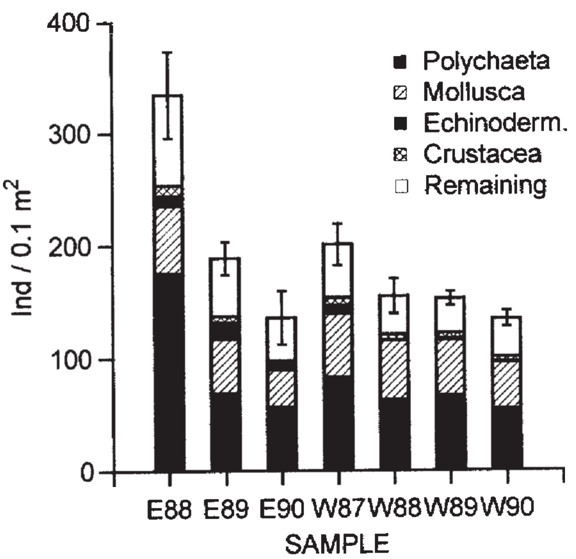

Figure 2.
Distribution of abundance on major taxonomic groups at the two sites (E and W) from the period 1987-1990. Error bars denote 2 x SE (Standard Error) of the total. Each sample based on 3-5 replicate grabs.

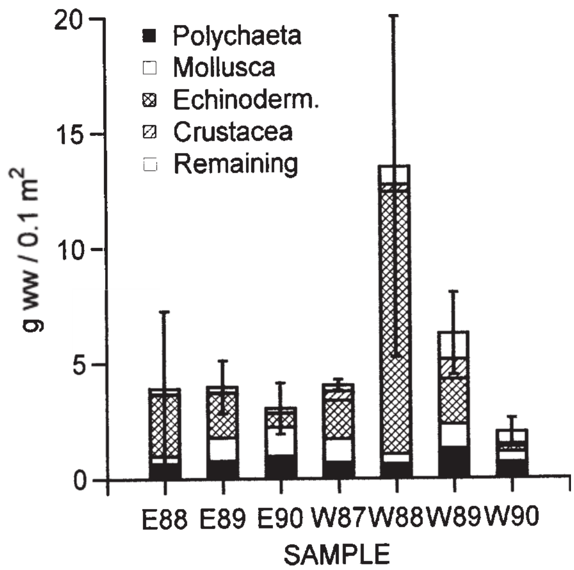

Figure 3.
Distribution of biomass on major taxonomic groups at the two sites (E and W) from the period 1987-1990. Error bars denote 2 x SE (Standard Error) of the total. Each sample based on 3-5 replicate grabs.

Table 2.
List of taxa at the western site of the Faroe Islands, Skeivibanka, occurring in more than 50 % of the total 31 grab samples (1987-1990) ranked by frequency.

Taxon	Group	No of individuals	No of samples
Onchnesoma steenstrupi Koren & Danielssen, 1875	Sipuncula	698	30
Caudofoveata		254	30
Thyasira ferruginea (Forbes, 1851)	Bivalvia	303	30
Thyasira obsoleta (Verrill & Bush, 1898)	Bivalvia	246	30
Paramphinome jeffreysi (McIntosh, 1868	Polychaeta	324	29
Paraonis gracilis (Tauber, 1879)	Polychaeta	136	29
Yoldiella lucida (Lovén, 1846)	Bivalvia	154	29
Polydora sp.	Polychaeta	74	28
Prionospio sp.	Polychaeta	83	28
Amaeana trilobata (M. Sars, 1863)	Polychaeta	92	27
Diplocirrus glaucus (Malmgren, 1867)	Polychaeta	95	27
Nemertea		74	26
Notomastus latericeus M. Sars, 1851	Polychaeta	84	26
Chaetozone setosa Malmgren, 1867	Polychaeta	72	24
Yoldiella nana (M. Sars, 1865)	Bivalvia	59	24
Amphipoda		74	23
Tridonta elliptica (Brown, 1827)	Bivalvia	58	23
Thyasira croulinensis (Jeffreys, 1847)	Bivalvia	136	22
Lumbrineris gracilis (Ehlers, 1868)	Polychaeta	60	21
Cirratulidae	Polychaeta	55	20
Ophelina abranchiata Støp-Bowitz, 1948	Polychaeta	36	20
Spiophanes sp.	Polychaeta	49	20
Aricidea jeffreysi (McIntosh, 1879)	Polychaeta	63	19
Euclymeninae	Polychaeta	36	19
Lumbrineris impatiens Claparède, 1868	Polychaeta	44	19
Onchnesoma squamatum (Koren & Danielssen, 1875)	Sipuncula	40	18
Aglaophamus malmgreni Théel, 1879	Polychaeta	39	17
Thyasira sp.	Bivalvia	43	17
Pectinaria auricoma (O.F. Müller, 1776)	Polychaeta	19	16

Table 3.
List of taxa at the eastern site, E. Suðuroy, occurring in more than 50 % of the total 15 grab samples (1987-1990) ranked by frequency.

Taxon	Group	No of individuals	No of samples
Onchnesoma steenstrupi Koren & Danielssen, 1875	Sipuncula	398	15
Golfingia sp.	Sipuncula	149	15
Lumbrineris sp.	Polychaeta	79	15
Paradiopatra quadricuspis (M. Sars in G.O. Sars, 1872)	Polychaeta	157	15
Paramphinome jeffreysi (McIntosh, 1868)	Polychaeta	177	15
Caudofoevata		132	15
Yoldiella lucida (Lovén, 1846)	Bivalvia	144	15
Nemertea		58	14
Onchnesoma squamatum (Koren & Danielssen, 1875)	Sipuncula	52	14
Amphipoda		62	14
Yoldiella nana (M. Sars, 1865)	Bivalvia	45	14
Maldanidae	Polychaeta	114	13
Thyasira ferruginea (Forbes, 1851)	Bivalvia	170	13
Ophiura sp.	Ophiuroidea	77	13
Aglaophamus sp.	Polychaeta	60	12
Chaetozone setosa Malmgren, 1867	Polychaeta	23	12
Prionospio sp.	Polychaeta	37	12
Amaeana trilobata (M. Sars, 1863)	Polychaeta	28	11
Antalis sp.	Scaphopoda	17	11
Thyasira obsoleta (Verrill & Bush, 1898)	Bivalvia	25	10
Cirratulidae	Polychaeta	40	9
Thyasira croulinensis (Jeffreys, 1847)	Bivalvia	22	9
Ampharetidae	Polychaeta	42	8
Myriochele sp.	Polychaeta	15	8
Thyasira granulosa (Monterosato, 1875)	Bivalvia	10	8
Ophiura sarsii Lütken, 1858	Ophiuroidea	12	8

In the comprehensive macrobenthic survey west of the Shetland Islands (CORDAH 1998) species composition and biomass was studies in relation to depth. In the present study samples were taken within the same depth range and water mass. The species frequently found here are all known from west of Shetland survey, however, whereas polychaetes and bivalves dominate the Faorese samples, polychaetes and crustaceans were the most dominant species in the area west of Shetland. The species in the Faroe samples seem to fit best in the CORDAH Group 1. This group consists of samples from a water depth below 617 m. This is considerably deeper than the Faroe samples which were taken at 317-367 m. The sediment is probably more important as the percent fines are higher in the Faroe samples (34-47% < 50 micr.) than in the other 3 Groups described from west of Shetland, whereas Group 1 has 3.99-69.58% proportion of mud (< 63 micr.).

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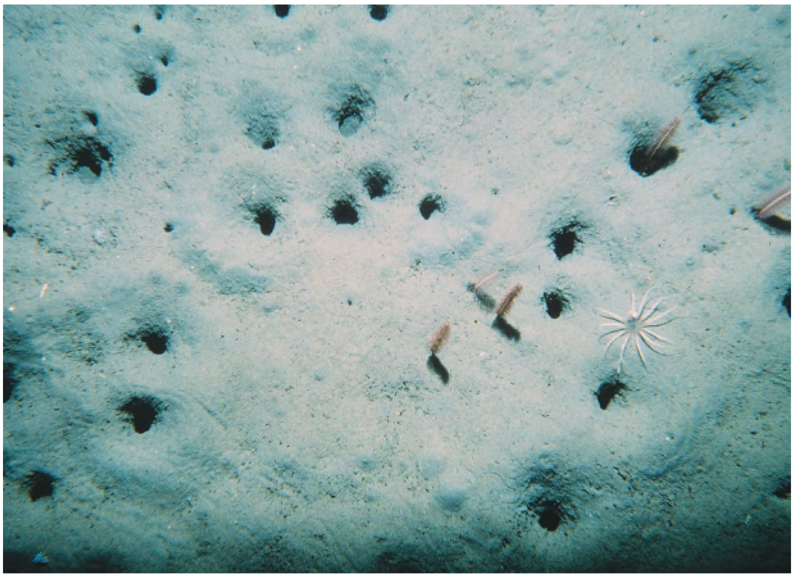

Figure 4.
Under-water photograph from a soft bottom area at 345 m depth at the western side of the Faroes showing *Virgularia* sp. and brisingid asteroid (BIOFAR Stn. 645: Nørrevang *et al.* 1994). (© photo J. Gutt).

A brief history of investigations on the benthic fauna of the sea around the Faroe Islands, with emphasis on the expeditions and research vessels

Introduction

Information on the benthic fauna of the Faroes is very scattered in the literature, and when extracting details, one must remember that the extent of "the Faroese area" has changed over time in accordance with the international agreements on fishery limits. A 3 nautical miles limit was agreed upon with Great Britain in 1901 and maintained until 1955, when a provisional arrangement extended it to 6 miles. In 1959 a 12 nautical miles limit was introduced, with some fishing rights for British trawlers as close to the coast as 6 miles. However, Faroese fishermen demanded new negotiations, and when these did not lead to agreement, Denmark declared the 12 miles to be in force from 1964. Finally, from 1978 a Faroese Exclusive Economic Zone (EEZ) was set at 200 nautical miles (Madsen 1990).

The aim is here to give a survey, as complete as possible, of the expeditions by research vessel and nationality during which samples of invertebrate benthos were collected within the nowadays Faroese EEZ, or very close to its borderlines. It should be noted that quite a number of other expeditions have visited Faroese waters. Their purpose was fishery research, plankton investigations or hydrographic observation, or they were just passing by on their way to other destinations.

Summaries in part covering the theme are given by Spärck (1928) and Vedel Thåning (1943).

The early period: travelers and laymen

In order to collect the material for a comprehensive description of the Faroes, the Danish government had the Faroese born economist and naturalist Jens Christian Svabo travelling all over the islands in 1781-1782. His observations are to be found in a large hand-written manuscript which, however, was not printed until 1959. It includes a list of about 20 marine invertebrate species, mostly molluscs and crustaceans (Svabo 1959).

Jørgen Landt, who was a priest in the Faroes 1791-1799, also worked out a description of the Islands, published in 1800. He gave a list of close to 60 marine invertebrate species, about half of them molluscs, the rest being sponges, cnidarians, polychaetes, crustaceans, bryozoans and echinoderms (Landt 1800). Some specimens were sent to Copenhagen to be included in what later became the collections of the Zoological Museum (Fabricius 1797).

The later professor of zoology at the University of Copenhagen, Japetus Steenstrup, was the first trained zoologist sampling Faroese marine fauna. In 1844 he was appointed part of the company attending the crown prince, the later King Frederik VII, during travel to Scotland and the Faroes. This gave Steenstrup the opportunity to dredge from rowing boats around some of the Islands, and also to establish useful contacts to officials and private persons (Steenstrup 1914). Strange enough, Steenstrup never published any results from his sampling efforts, but it seems from the comments in a list accompanying the collection that it comprised mostly molluscs of which 43 species were recorded (Mörch 1868).

Oscar Schmidt, professor of zoology in Jena, lived for several months in the Faroes in the spring of 1848. He collected turbellarians around Tórshavn (Schmidt 1848a,b).

When investigating the possibilities for laying a telegraph cable from Europe to America via the Faroes and Iceland, the Brittish 'Fox' in 1860 took a few bottom samples east and west of the Faroes (Zeilau 1861).

When investigating the possibilities for laying a telephone cable from Europe to America via the Faroes and Iceland, the British 'Fox' took a few bottom samples east and west of the Faroes in 1860 (Zeilau 1861). The Same year and for the same purpose another British ship 'Bulldog' visited the Faroes, and some few samples were taken in Vestmanna Sound (Willich 1862)

In 1872 the Danish government supported an expedition to the Faroes in order to explore the possibilities of mining the coal-layers. The German zoologist Rudolph von Willemoes-Suhm took part in order to describe the fauna. He seems mostly to have been interested in the vertebrates, but also collected annelids around Tórshavn (Kortum 1996, Willemoes-Suhm 1872a,b, 1873).

At this time the tradition had developed that interested officials, priests, officers and doctors collected specimens and sent them to the Zoological Museum in Copenhagen. These collections were not systematically made, rather they comprised specimens which somehow seemed remarkable. A fine example of this is chief administrator Müller, who most years between 1847 and 1892 sent mainly crustaceans and fishes, but also a few hydroids, "Worms" and bryozoans.

Thus, until the last part of the 1800-years there were only scattered efforts to provide surveys of the Faroese benthic fauna, with exception of the molluscs, which at the time attracted the interest of many educated persons. A detailed account of collectors and collections of molluscs from this period is given by Mörch (1868).

The era of British expeditions: topography, hydrography and fauna of the Scottish-Faroese deep-sea area

During the 1860'ies it became, on the basis of work of Norwegian, British and French colleagues, increasingly clear to the British marine zoologists W.B. Carter and C. Wyville Thomson, that the deep-sea probably housed a rich, undescribed fauna. They succeeded in 1868 in getting at their disposal the paddle steamer 'Lightning' for cruises between Scotland and the Faroes, also visiting Tórshavn in August 1868 (Carpenter 1868, Rice 1986). The 'Lightning' was old, almost falling apart and poorly suitable for the purpose, but nevertheless these two months of sounding, dredging and hydrographic observation were breaking the ground for the immense efforts that during the next 100 years were to be displayed all over the world by many nations on numerous ships, whose names are now the milestones in the history of exploration of the deep oceans.

The demonstration by 'Lightning' of the existence of a diverse life at great depths and of unexpected strong temperature variations from south to north in the area led, in the following decades, to the British expeditions with 'Porcupine', 'Knight Errant', 'Triton', 'Goldseeker', and 'Silver Belle' (Carpenter *et al.* 1870, Deacon 1977, Wyville Thomson 1880, Tizard 1883, Tizard & Murray 1882, Wolfenden 1909, Rice 1986, Damkaer 2000). The results were, in brief, that along what is today the southern border area of the Faroese EEZ, the Wyville Thomson Ridge was discovered and mapped, the hydrographic pattern of the area was explained and a new and rich fauna described. Some of the data have been published in separate papers, but the main part was included in the large material collected and worked up from the Challenger Expedition, and appears in some of the volumes in this large series.

Figure 1.
Drawing by Madame Holten, wife of the Faroese Governor M. Holten, probably of the paddle steamer 'Lightning' with Tórshavn in the foreground (Wyville Thomson 1873).

It should be mentioned here that in 1898 a few samples were taken in the Wyville Thomson Ridge area by the German steamer 'Valdivia' while this deep-sea expedition was on its way to the main working area around Africa and in the Indian Ocean (Schulze 1904).

International efforts: the fauna of the eastern, northern and western deep-sea areas of the Faroese EEZ

On the basis of a well-argued recommendation from the professors H. Mohn and G.O. Sars, it was decided by the Norwegian government to hire and fit out the steamer 'Vøringen' for deep-sea investigations in the Norwegian Sea during the summers of 1876-1878 (Wille 1882). The expedition visited the Faroes in July 1876 and took a number of samples east and north of the islands, thereby delivering the first insight into the fauna of that area (Hansen 1885).

In 1900, 1902, 1904, 1905 and 1910 the Norwegian fishery research vessel 'Michael Sars' during cruises led by professor J. Hjort in the Norwegian sea and the North Atlantic visited the Faroes and took some samples at depths larger than 1000 m (Friele 1902, Grieg 1927, Murray & Hjort 1910, Wollebæk 1909). In the expeditions in 1900 and 1902 Danish scientists were onboard the 'Michael Sars' and sampled in a number of places, mostly on the Faroe plateau. Another Norwegian research vessel, 'Armauer Hansen', worked near the Faroes in 1914 (Helland Hansen 1913, 1914).

The French oceanographic vessel 'Pourqois pas?' took a few samples when having short stays in the Faroes in 1913 and 1930.

The next research vessel from which work was done at large depths seems to have been the German fisheries research ship 'Anton Dohrn' on a cruise led by professor H. Thiel in 1966; numerous samples were taken in the area of the Faroe-Iceland Ridge, mainly for the purpose of meiofauna investigations (Reinke-Kunze 1986, Thiel 1971).

The German fishery research ship 'Walther Herwig" worked briefly in 1974 and 1981 on the banks west of the Faroes (Reinke-Kunze 1986).

A joined French-Swedish project, NORBI, carried out onboard the French oceanographic research vessel 'Jean Charcot' successfully investigated the deep basins of the Norwegian and Greenland Seas in 1975 and came close to the north-east corner of the Faroese EEZ (Dahl *et al.* 1977).

Since 1981 the Norwegian research vessel 'Håkon Mosby' from the University in Bergen has, under the leadership of the marine zoologist T. Brattegard, made numerous benthos investigations all over the Norwegian sea, especially in deep water. During cruises in 1983, 1986 and 1987 samples were taken inside the Faroese EEZ (Brattegard & Rømer 1998). These samples were later included in the station list of the BIOFAR programme (Nørrevang *et al.* 1994).

The Dutch research vessel 'Pelagia' worked in the Faroe-Shetland Channel in 1997 securing a small number of benthos samples (Raaphorst 1997).

Danish investigations around the Faroes and on the outer shelf

The role of naval ships.

There is a long tradition for the Danish Navy to support marine research with sampling opportunities and logistics. While commander of the mail-ship to Iceland and the Faroese, C.F. Wandel did some dredging in 1878 (Steenstrup 1880). At the Faroes, the ship's doctor Halberg dredged bottom animals from the surveying scooner 'Diana' under Commander C. Irminger in1884, and one of the ship officers, lieutenant commander Jensen, did the same in 1886 (Steenstrup 1887, Levinsen 1889). Some samples were provided by commander C.F. Wandel on the cruiser 'Fylla' in 1890, 1891 and 1892 (Levinsen 1893, 1894). In 1895 and 1896 the cruiser 'Ingolf', under commander Wandel, carried through comprehensive investigations west of the Faroes (Wandel 1899, Wolff 1967, 1997).

On numerous occasions fishery inspection and surveying vessels working in the Faroese, Icelandic and Greenland waters have given space and time for scientists' work for periods up to several months. In some cases young biologists being onboard as conscripts got a special permission to take samples. The opportunity was used for the first time in the Faroes in 1898, when the zoologist R. Hørring collected with the 'Diana' (Vedel Tåning 1943/44). This vessel was used again in 1899 and 1901, and in 1902, the last year of her function (Larsen 1932). In 1899 the most comprehensive sampling hitherto carried through in the Faroes was done by the zoologist T. Mortensen from the inspection vessel 'Guldborgsund'. The survey and fishery inspection ship 'Beskytteren' was used for investigations during the summers of 1902, 1904, 1905, 1907 and 1909, and again 1926, 1927 and 1933. In 1931 'Hvidbjørnen' gave time for sampling as did 'Thetis' in 1946 and next generation fishery inspection ships, also called 'Hvidbjørnen' and 'Thesis', in 1979 and 1991 respectively (Olsen & Storgaard 1998).

Fishery research vessels.
Bought in 1902, the steam trawler 'Thor' started work in the Faroes and Iceland the following year. Simultaneously with fishery and plankton research, samples of bottom invertebrates were provided in the years 1903 through 1906, and again in 1913 (Schmidt 1909).

During the onset of a plankton investigation expedition across the Atlantic, the hired, privately owned schooner 'Margrethe' in 1913 spent some time on the Faroes, and quite a number of benthic samples were collected by the fishery biologist P. Jespersen (Vedel Thåning 1952).

In 1920 the Danish government bought a British steam trawler, somewhat larger than 'Thor', and equipped it for fishery investigation work. It was named 'Dana' and was, until it sunk in 1935 after a collision, used both for longer expeditions and local work. Bottom invertebrate samples were taken in the Faroes in 1925, 1926 and 1927. A replacement, also named 'Dana'

Figure 2.
The Danish fishery inspection ship 'Beskytteren' in Tórshavn on King Christian X's birthday, September 1926 (Photo by P.L. Kramp, archive of the Zoological Museum, Copenhagen).

was not built and ready until 1938; meanwhile other ships were chartered to carry through the fishery investigations (Vedel Thåning 1943). The new 'Dana' took some samples in 1938 and 1939, when the 2nd World War broke the communication between Denmark and the Faroes. After the war, 'Dana' provided scattered bottom invertebrate samples in 1946, 1954 and 1961.

In 1964 the Faroese government bought the trawler 'Jens Christian Svabo' for local fishery investigation, thereby providing a year-round basis for scientific marine work. With a major rebuilding in 1967, it functioned until 1980, when it was replaced by the larger 'Magnus Heinasson'. The last-mentioned was used for intensive bottom invertebrate sampling in 1987 through 1991 and again in 1998.

Major benthic investigations in the Faroese EEZ

"The Ingolf Expedition"
In 1880 a plan for a Danish deep-sea expedition west and north of the Faroes and around Iceland and southern Greenland was developed by the zoologist C. Lütken and the naval officer C.F. Wandel. Various preparations were made, among them that

Figure 3.
The Faroese research vessel 'Magnus Heinason' (Photo, G. Bruntse)

Wandel in 1880 was sent to USA to take part in a cruise, led by professor A. Agassiz and commander J.R. Bartlett onboard the survey-vessel 'Blake' (Wandel 1881). It was, however, not until 1895-1896 that the naval cruiser 'Ingolf' could set out and carry through its investigations, comprising 24 stations west of the Faroes (Wandel 1899, Wolff 1967, 1997). The results are published in the series "The Danish Ingolf Expedition" at the Zoological Museum, Copenhagen.

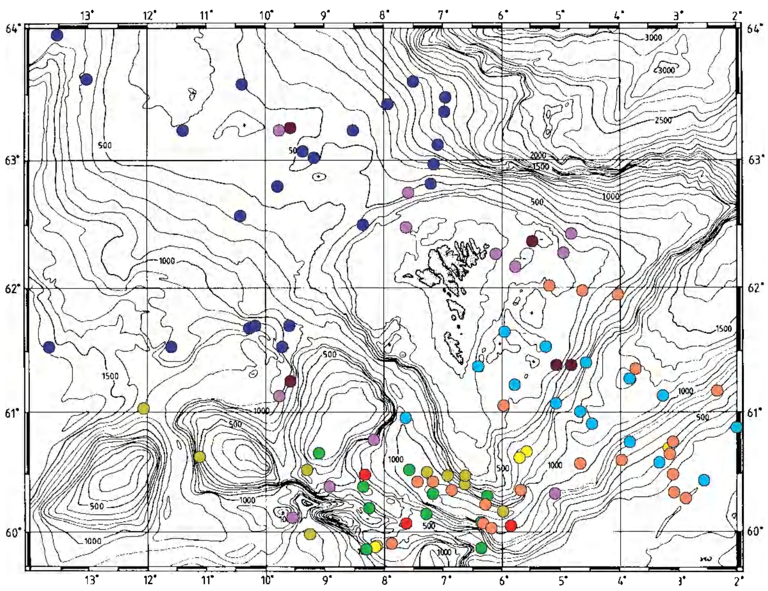

Figure 4.
Sampling stations of the older expeditions compiled from various sources. The Danish Ingolf expedition: ● The Michael Sars 1910 expedition: ●, The Michael Sars 1902 expedition: ●, Deutsche Tiefsee Expedition: ●, Triton: ●, Lightning: ●, Porcupine: ●, Knight Errant: ●, 2 stations by Fylla, 1 by the Norwegian North Atlantic Sea Expedition and a few other single stations ●.

"The Zoology of the Faroes"

In the beginning of the 1920'ties Danish zoologists realized that while the vertebrate fauna of the Faroes was fairly well investigated, the knowledge of the invertebrates was very scattered and insufficient. An organizing committee was appointed and a generous grant was obtained from The Carlsberg Foundation for a zoological investigation of the islands (Spärck 1928). Intensive collection efforts were displayed during 5 years, beginning in 1924, both at sea and on land. The marine sampling was carried out from the inspection vessel 'Beskytteren' in 1926, and the fishery research vessel 'Dana' in 1925, 1926 and 1927. The largest part of the samples were from between the islands and inside the 3 nautical miles fishery limit; accordingly, very few samples came from depths larger than 200 m. The results are to be found in the series "The Zoology of the Faroes", 1928 through 1971, in which 59 of the 68 chapters were published before 1940.

"The BIOFAR Program"

With the erection of the EEZ in 1977, the Faroes got the scientific responsibility for a much larger area than before. At the same time there was among marine biologists in the Nordic countries a growing anxiety over the decreasing marine taxonomic expertise. As it was, no single country was any more able to handle its own fauna, not even all the largest groups to full extent. It was felt that the Nordic traditions for cowork in marine sciences should be reinforced, and moreover, it seemed that the resources for a larger project were available. The result was the creation of the Internordic BIOFAR Program in 1987, with the aim of investigating the Faroese marine bottom fauna between 100 m and 1000 m depth. The limits were chosen, because it was felt that "The Zoology of the Faroes" had covered the shallower parts sufficiently, and the larger depths were to a great extent already worked over by previous expeditions. Also, local fishery interests, who were going to support the project with an appreciable amount of ship-time, did not reach beyond about 1000 m.

During the years from 1987 to 1991 a large number of Nordic scientists, students and technicians took part in 9 cruises onboard the Faroese 'Magnus Heinason' and the Norwegian 'Håkon Mosby'. Besides, visiting cruises were carried through onboard the British 'Challenger' and the German 'Valdivia'. An important local support came from the Faroese Coastguard, who put their ships at disposal for a number of shorter cruises with the purpose of special investigations. After sorting at the locally erected Kaldbak Laboratory, the material was sent out internationally to a large number of specialists for identification and further work. Publications are now appearing in English in the Faroese journal "Fróðskaparrit" and in various international journals, among which especially the Norwegian "Sarsia" should be mentioned.

Because the older shallow-water investigations turned out nevertheless to be somewhat insufficient, a shallow-water BIOFAR 2 was run from 1995 through 1998, including also the flora.

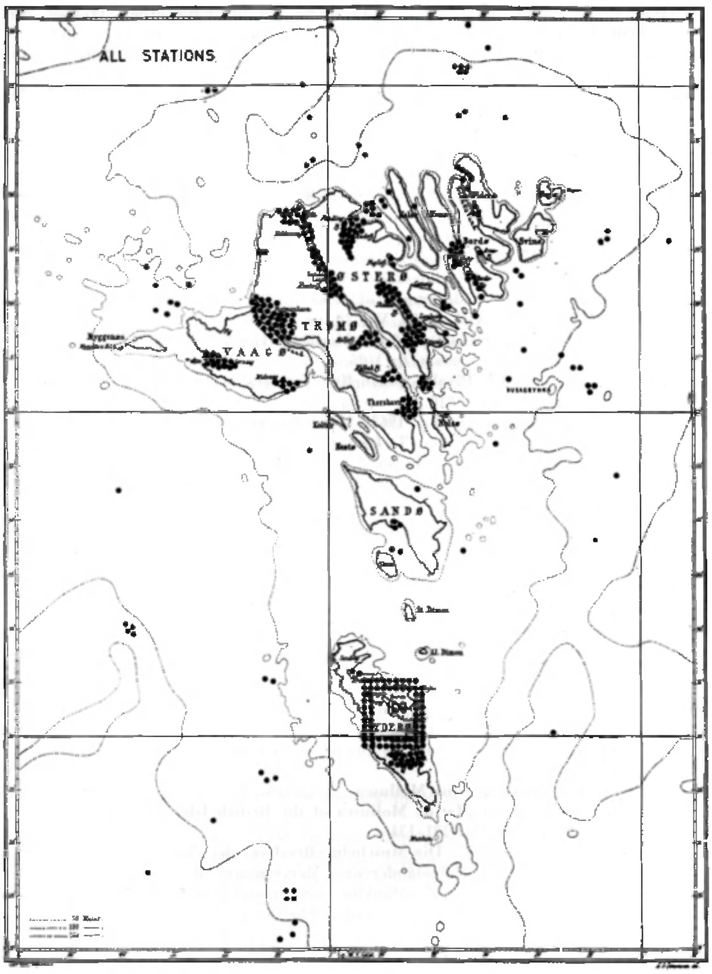

Figure 5.
The sampling stations of "The Zoology of the Faroes" program. After G. Høpner Petersen 1968.

Maps of benthos sampling sites

When the First World War broke out, and for a number of years stopped all seagoing research, a large part of the Faroese area had been sampled. The sampling activity had been rather high on and around the Wyville Thomson Ridge, lower in the other parts (Figure 4). Quite accidentally, most samples were taken in deep water, and relatively few lower than 500 m (they are not all shown in the map). The material was scattered in the collections of many institutions in different countries, and the results were to be found in numerous publications in a large number of journals and series. As it was, the effort to gather all this information was, in a way, already done for a number of groups treated in the monographs of the comprehensive 'Ingolf' report. Since there had been no need for a fauna survey of that particular area, it was, however, even in those reports troublesome to extract the information from the multitude of

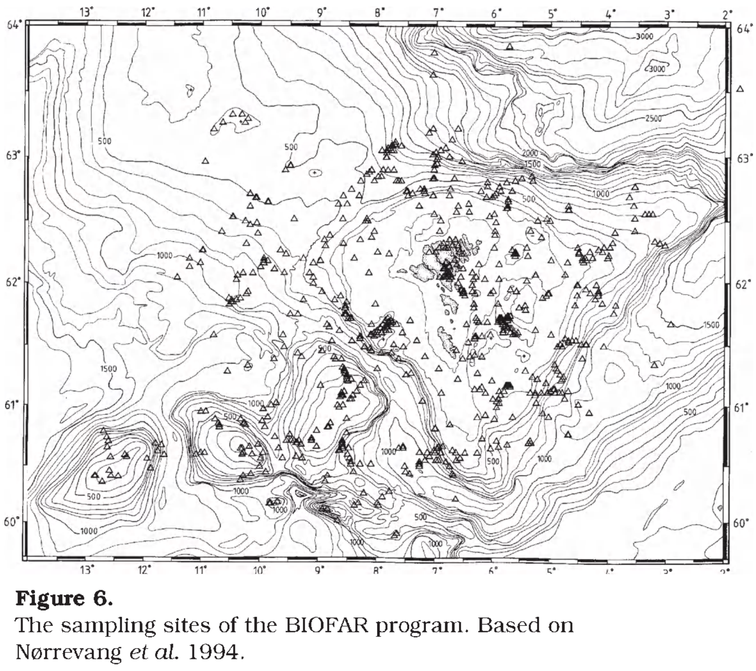

Figure 6.
The sampling sites of the BIOFAR program. Based on Nørrevang *et al.* 1994.

results from many parts of the Northeast Atlantic.

The obvious lack of knowledge about the shallow water fauna was realized by zoologists from the Zoological Museum of the University of Copenhagen, who managed to create a program "The Zoology of the Faroes" during which sampling was done in the later part of the 20'ties. Sampling efforts were restricted to between the islands and parts of the plateau largely within the 3-miles fishery limit (Figure 5); about 400 localities were sampled (Høpner Petersen 1968). The outer shelf and upper slope were still left unsampled.

During the BIOFAR program the effort was directed towards closing the gaps between 100 and 1000 m depth (Figure 6). Because new kinds of gear (Smith-McIntyre grab, Sneli detritus sledge (Sneli 1998), Rothlisberg-Pearcy hyperbenthic sledge (Buhl-Jensen 1986, Brattegard & Fosså 1991), and photography) were used it was decided as far as possible to cover the area without too much consideration of earlier sampling. Close to 600 localities were sampled with about 800 deployments of gear (Nørrevang *et al.* 1994).

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A bibliography of benthic marine invertebrates of the Faroese Economic Exclusive Zone

Our aim has been to compile a list, as complete as possible, of the scientific literature in which records of bottom invertebrates from the Faroese Economic Exclusive Zone are mentioned. As given, the list is an print from a newly erected literature database later to be found and constantly updated in the Kaldbak Marine Biological Laboratory, The Faroe Islands, and the Zoological Museum, Copenhagen.

There are some delimitation problems. Although the island group of The Faroes has been the target of some fauna projects it has, in a wider sense, only been at the periphery of the working areas of a number of expeditions from several countries. Some stations were taken within what is today the Faroese EEZ, others were on the borderline or close outside. Reports on stations inside the limit are all included; in borderline cases as well as regarding stations outside but close, we have taken a pragmatic view and included the reference in question where the results can be expected to be valid within the EEZ as well. We also have listed revisions and fauna surveys, where Faroese information is included even if they do not treat new material; in our opinion this gives an easier access to the relevant literature for the users of the bibliography. In a number of cases articles of a more popular nature has been included, mostly selected from the point of view that they bring information not given elsewhere. Some are in Faroese or Danish, but it is obviously of local interest to list them.

The bibliography is in four parts. The first lists the publications alphabetically. The second groups the publications under taxonomic headings. The third and fourth are lecture and poster abstracts, respectively.

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Associated: Dinesen 1994 (horse mussel); Jensen & Frederiksen 1990; 1992 (corals); Frederiksen 1992 (corals); Klitgaard 1990; 1991a; 1991b; 1995 (sponges); Kristensen 1996 (Corallina); Svavarsson & Davidsdóttir 1994 (Isopoda); Worsaae 1998 (Laminaria holdfasts).

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Brady 1882; 1884; Cedhagen 1994; Hofker 1929; Kiær 1899; Svavarsson & Davidsdóttir 1994.

PORIFERA

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CNIDARIA

Hydrozoa: Allman 1874; 1883; Broch 1914; 1916; 1918; Kramp 1929; Leloup 1954; Thorson 1992; 1993; Winter 1883.

Anthozoa: Anonymous 1988; Carlgren 1912; 1913; 1921; 1930; 1942; Danielsen 1887; 1890; Duncan 1874; 1878; Fabricius 1797; Frederiksen 1992; Frederiksen *et al.* 1992; Frederiksen & Jensen 1992; Grasshoff & Zibrowius 1983; Jensen & Frederiksen 1990, 1992; Jungersen 1904, 1917; Kramp 1930; Madsen 1944; Marshall 1883; Marshall & Fowler 1887; Nørrevang & Tendal 1992; Sclater 1886; Tendal & Nørrevang 1990; Tendal 1992a; 1992b; 1996; Thomson 1906; 1931; Wilson 1975; 1979; Zibrowius 1980.

PLATYHELMINTHES

Ax 1993a; 1993b; 1994; Bock 1913; Schmidt 1848a; 1848 b; 1852; Steinböck 1930; Örsted 1844.

NEMERTEA

Bürger 1907; Overgaard Nielsen 1968.

NEMATODA

Ditlevsen 1926; Højgaard 1995; Køie 1993.

PRIAPULIDA

Wesenberg-Lund 1928; 1930.

ANNELIDA

Polychaeta: Boysen-Bennike 1968; Brattström & Thorsen 1941; Danielsen & Koren 1881; Ditlevsen 1917; 1929; Ehlers 1908; Graff 1884; Hansen 1879; 1882; Heiner 1911; Holthe 1978; 1986; Kirkegaard 1998; Knight-Jones 1994a; 1994b; Levinsen 1883; M'Intosh 1882; 1885; Mackie & Pleijel 1995; Malmgren 1867; Pleijel 1991, 1993a; 1993b; 1993c; Selenka 1885; Støp-Bowitz 1948; Sæmundsson 1918; Wesenberg-Lund 1928; 1950; Willemoes-Suhm 1873.

Oligochaeta: Ditlevsen 1936;

Hirudinea: Bruun 1928;

CRUSTACEA

General: Norman 1882; Sars 1877; 1879; 1885; 1886.

Ostracoda: Brady & Norman 1889; Stephensen 1929; 1935.

Copepoda: Hansen 1923; Norman 1903; Schellenberg 1922; Stephensen 1929.

Cirripedia: Boschma 1928a; 1928b; Broch 1924; 1953; Høeg & Lütken 1985; Nilsson-Cantell 1978; Pilsbury 1916; Spengler 1790; Steenstrup 1852; Stephensen 1929, 1935; Weltner 1917.

Nebaliacea: Hansen 1920; Stephensen 1929.

Mysidacea: Brattegard & Meland 1997; Me-

land & Brattegard 1995; Stephensen 1929.
Cumacea: Gerken & Watling 1999; Hansen 1920; Norman 1879; Stephensen 1929.
Isopoda: Hansen 1916, Johansen & Brattegard 1998; Klitgaard 1991a; Negaescu & Svavarsson 1997; Norman 1886; Stephensen 1929; Svavarsson 1982; 1984; 1987a; 1987b; 1988a; 1988b; Svavarsson *et al.* 1990; 1993; Svavarsson & Davidsdóttir 1994.
Tanaidacea: Hansen 1913; Stephensen 1929.
Amphipoda: Berge & Vader 1997a; 1997b; Brandt 1872; Larsen 1996; 1998; Lütken 1873; Mayer 1890; 1903; Norman 1900; Myers 1998; Palerud & Vader 1991; Schellenberg 1926; Stebbing 1908; Stephensen 1923; 1925; 1928; 1931; 1944; Tesch 1911; Wagler 1926.
Decapoda: Appelöff 1906; Balss 1911; 1925a; 1925b; Berggren 1990; 1993; Brattegard & Rømer 1998; Christiansen 1969; Doflein 1902; 1913; Grieg 1926; Hansen 1908; Nicolajsen 1989; Sandberg & McLaughlin 1998; Sivertsen & Holthuis 1956; Stephensen 1928; Sund 1920; Wollebæk 1909.

PYCNOGONIDA

Hansen 1886; Hoeck 1882; Meinert 1899; Olsen 1913; Sars 1877; 1879; 1891.

MOLLUSCA

General: Bouchet & Warén 1979; Friele 1886; 1901; 1903; Högg 1905; Jeffreys 1863; 1869; 1878; 1879; 1881a; 1881b; 1882a; 1882b; 1883a; 1883b; 1884a; 1884b; 1885; Lyell 1842; Montcervelle & Favonne 1780; Mørch 1868; Posselt 1898; Seaward 1990; Simpson 1910; Sneli 1992; Warén 1991; 1993.
Amphineura: Knudsen 1970; Muus 1959; Salvini-Plaven 1975; Sneli 1992; Warén & Klitgaard 1991.
Gastropoda: Bergh 1900; Bouchet & Warén 1993; Chemniz 1788; 1795; 1874; Fabricius 1797; Grieg 1920; Lemche 1929; Martens 1904; Schander 1995; Schiøtte 1998; Spärck & Thorsen 1933; Warén *et al.* 1993.
Bivalvia: Dinesen 1994; Grieg 1920; Høpner Petersen 1968; Jensen 1912; Jensen & Spärck 1934; Madsen 1949; Nicolajsen 1997; Ockelmann 1958; Thiele & Jaeckel 1931; Ursin 1956.
Scaphopoda: Grieg 1920; Jaeckel 1932; Muus 1959; Thorsen & Spärck 1929.
Cephalopoda: Hoyle 1886; Lönnberg 1891; Muus 1959; Nielsen 1930; Posselt 1889; Russel 1921; Spärck 1923; Steenstrup 1861.

ENTOPROCTA

Kramp 1934.

SIPUNCULA

Danielsen & Koren 1881; Wesenberg-Lund 1928; 1930.

BRYOZOA

Busk 1882; Hasenbak 1932; Hayward 1994; Kramp 1934; Nordgaard 1907; Selenka 1885.

BRACHIOPODA

Davidson 1896; Grieg 1920; Helmcke 1939; 1940; Hägg 1905; Posselt 1898; Paknevich 1997; Thomsen 1990; Wesenberg-Lund 1940; 1941.

ECHINODERMATA

General: Bell 1883; 1892; Danielsen & Koren 1879; Grieg 1921; Levinsen 1886; Lieberkind 1929; Lütken 1856; Mortensen 1927.
Crinoidea: Carpenter 1888; Clark 1923; 1970; Danielsen 1892; Wyville Thomsen 1871.
Asteroidea: Danielsen & Koren 1884; Lieberkind 1935; Ludwig 1897; Madsen 1987; Sibuet 1979; Sladen 1882, 1889; Sneli 1999.
Echinoidea: Agassiz 1882; Danielsen 1892; Döderlein 1906; Mortensen 1903; 1907; Wyville Thomson 1874.
Ophiuroidea: Emson *et al.* 1994; Grieg 1893; Hoyle 1884; Lyman 1882; Mortensen 1933; Tyler & Fenaux 1994.
Holothuroidea: Danielsen 1882; Heding 1935; 1942; Ludwig & Heding 1935; Madsen & Hansen 1994; Théel 1882.

ASCIDIACEA

Bjerkan 1905; Hartmeyer 1911; 1912; 1923; 1924; Herman 1884a; 1884b; 1886; 1888; Michaelsen 1904; 1921; Millar 1966; Monniot & Monniot 1979; Monniot & Klitgaard 1994; Thompson 1930; 1931; Traustedt 1880; Ärnbäck-Christie-Linde 1934; 1952.

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