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Biogenic sediments, substrates and habitats of the Faroese shelf and slope

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Abstract

Based mainly on results obtained during the BIOFAR programmes 1987-1990 and 1995-1998 the present knowledge of biogenic substrates and habitats in Faroese waters are reviewed. Eleven categories are presented, viz. shell-sand and -gravel, coralline algae, *Laminaria* holdfasts and stipes, sponges, sponge spicule-mud and -mats, octocorals, *Lophelia* banks, horse mussel aggregations, scallops, pagurids and their gastropod shells, and brachiopods. The level of taxonomic identification in the original investigations varied according to aim and allocated resources, but all the results and observations indicate that the presence of stable biogenic structures adds significantly to the habitat heterogeneity within the given area.

Introduction

Sediments and substrates of biological origin are widely distributed in the sea. They are of many different kinds and provide habitats for an enormous variety of organisms. In the upper photic zone macroalgae and seagrass cover large areas with dense underwater forests and zooxanthellate corals form large and complex reef structures. At greater depths sponges and azooxanthellate corals form extensive aggregations or reefs, some of which are ancient

structures. At all depths, larger bivalves occur in patches of dense aggregations. Shell-sand and -gravel dominate about half of the world's shelf areas. Foraminiferan- (*Globigerina*), radiolarian- and diatom- mud cover millions of square-kilometres of abyssal plains (Dayton, 1985; Sebens, 1991; Seibold and Berger, 1993; Veron, 1995; Conway *et al.*, 2001; Rogers, 2004).

Biological units with certain characteristics, e.g. hydroid colonies, tubeforming polychaetes, bivalves and brachiopods, can form substrates measuring from a few square-centimeters and upwards. They are sometimes numerous and can be scattered regularly within a given area of otherwise low structural complexity, together forming a large albeit physically broken up habitat (Hughes, 1975; Sebens, 1991; Lohse, 1993). Large-sized species can accomodate numerous smaller species, and some of these can be very abundant (Bacescu, 1971; Klitgaard, 1995; Kunzmann, 1996). Large-sized species of sponges, corals and bivalves can be so abundant that the whole

populated area is influenced, physically by them, both hydrographically and biologically (Kay and Keogh, 1981; Sebens, 1991; Bett and Rice, 1992; Klitgaard *et al.*, 1997; Navarro and Thompson, 1997).

Numerous observations on biogenic sediments, substrates and habitats, and on the involved species have been made in the Northeast Atlantic waters around the Faroe Islands during the BIOFAR 1 programme (1987-1990) investigating depths from 100-1000 m (Nørrevang *et al.*, 1994; Tendal *et al.*, 2004), and the BIOFAR 2 programme (1995-1998) investigating the depth ranging from the tidal zone to 100 m depth (Sørensen *et al.*, 2000). They were obtained by a large number of people and reported at different levels of scientific acknowledgement.

The aim here is to give a survey of this knowledge, with foci on the different kinds and their distribution and on the biological role of biogenic sediments and of habitats that are formed or modified by certain abundant species. A substantial part of this information is available in regular publications. Other parts were extracted from various kinds of reports, ranging from students' supervised reports on smaller or larger training projects written in Danish, Norwegian or Swedish, over project status reports, annual reports and cruise reports in Danish, Faroese, German or English, to more substantial progress or environmental reports in English. Valuable were also charts, station lists, sea bottom photographs, cruise field sheets, personal field notes, and identification sheets from the specialists stored in the archives of the Kaldbak Laboratory

near Tórshavn. Finally, some personal observations have been included, both from the authors and from various colleagues.

Parasites and parasitism are not considered.

Terminology

Terms for animal and plant associations (or 'communities'), and for bottom types of mixed inorganic and organic or purely organic constituents are of both biological (ecological) and geological (sedimentological) origin. The terminology has been developed over a long period of time in research on widely different issues, and is highly inconsistent. Hence, the few terms used are outlined below.

Biogenic habitat: A habitat constituted solely or for the largest part formed by one or more abundant species or of their remains. In fact, it is often composed of a primary substrate (in the Faroes usually some grade of gravel) where the presence of an overlaying secondary substrate considerably increases the complexity of the habitat.

Remarks: As to scale the biogenic habitat can range from cm-sized patches to km-wide areas. To give meaning as a habitat there must be species living in it, either the ones that created it or others who take some kind of advantage of it.

Biogenic sediment: Sediment mainly (by rough judgement >90%) of protist, algae or animal origin. It is derived from the hard parts left behind when living organisms die or shed some of their skeleton constituents.

A main distinction is between calcareous and siliceous sediments.

Habitat-forming species: The living species physically 'being' the habitat or producing the material constituting it, or a combination thereof.

Remarks: In case all individuals die, the structure and other characteristics of the habitat may change considerably and within a short period of time. Also, a number of other species may occur in the habitat simply because the specific locality is suitable for them to sustain life rather than due to the presence of the habitat forming species.

Habitat-modifying species: Species which by their presence, activity or their products modify a habitat such as to create more room for other species, or space for more species so diversity and abundance become higher than in surrounding areas.

Faroese biogenic habitats

The categories treated here are: Shell-sand and -gravel, coralline algae, *Laminaria* holdfasts and stipes, sponges, sponge spicule-mud and -mats, octocorals, *Lophelia* banks, horse mussels, scallop, pagurids and their gastropod shells, and brachio-pods. The reason they have been selected is either that some results from investigations during BIOFAR are available, or that investigations in other areas indicate that further research in the Faroe area might be rewarding.

Shell-sand and -gravel

The outer shelf of the Faroes, between 100

and 200 m depth comprises about 15000 km² (Hansen, 2000a). The sediment is shell-gravel mixed with sand and stone over a considerable part of this area, with the main shell component being large fragments (often cm-size) of *Modiolus*, although other molluscs, cirripedia and echinoderms are represented as well. The top of the Faroe Bank down to 200 m depth covers an area of about 2900 km² and about half of this is covered by shell-sand, with grains of the mm-size, similar to other holocene biogene carbonate sediments in areas off Shetland and the Hebrides (Wilson, 1979; Hansen, 2000b; Magnussen, 2002). In both cases the degradation seems to be caused mainly by boring sponges, and to a minor degree of other boring organisms (Young and Nelson, 1985; Tendal, unpubl.obs.).

It is believed that large triangle dredge and epibenthic sledge samples, in combination with bottom photographs, field sheets and preliminary identification lists, give a fairly reliable impression of the amount of macrofauna. In most shelf samples the number and abundance of macrofauna is low. The species that constitute this fauna are common, and of wide northern boreal shelf distribution.

Low species numbers and abundance are also seen in the benthic macrofauna of the finer sediment on the Faroe Bank. However, this fauna is remarkable due to the large size of some of the species, and to the presence of a number of southerly distributed species not known from the Faroese shelf and slope (Nørrevang, 1993; 1997; Schmidt *et al.*, 2002). In contrast, the hy-

perbenthic macrofauna is diverse, as illustrated by the mysids, the cumaceans and the shrimps, so far the only groups of this fauna that have been comprehensively worked up (Brattegard and Meland, 1997; Brattegard and Rømer, 1998; Gerken and Watling, 1999). The presence of a rich fauna of hyperbenthic crustaceans may be part of the explanation for the Faroe Bank housing a comparatively rich fish fauna (Magnussen, 2002). The diversity of the meiofauna on the Faroe Bank is one of the highest known in the sea, comprising many unusual forms and quite a number of species new to science (Hansen, 2000b; 2004; Heiner, 2003; 2004; Clausen, 2004; Kristensen, 2004).

Coralline algae

Coral weed, *Corallina officinalis*, L., forms small, erect bushes up to 12 cm high, but generally less than 10 cm. They attach by calcified disc-shaped holdfasts. The calcareous, segmented branches form a turf-like canopy that covers patches up to several meters across. This species is distributed worldwide, and common in the North Atlantic. It is known from investigations in Norway, New Zealand and the UK that such patches house a diverse fauna of small animals (Hedley *et al.*, 1967; Dommasnes, 1968; 1969; Hagerman, 1968; Hicks, 1980; Crisp and Mwaiseje, 1989; Grahame and Hanna, 1989).

C. officinalis is widely distributed and abundant around the Faroes. It occurs from the littoral, where it is often found in rock pools, and over a wide range of wave exposures, down to 20 m depth (Bruntse *et al.*,

1999; Wegeberg *et al.*, 2001).

Preliminary investigations of both the macro- and meiofauna were carried though from the tidal zone down to 5 m depth just off the Kaldbak Laboratory in September 1995 and in May and July 2001 (Kristensen, 1995; 1996; Trygvadóttir, 2001). The results showed the living algae to house a diverse and abundant fauna of foraminiferans, sponges, hydrozoans, turbellarians, kinorhynchs, nematodes, polychaetes, oligochaetes, ostracods, harpacticoids, pycnogonids, halacarids, tardigrades, sipunculids, gastropods, bivalves, bryozoans, asteroids, ophiuroids and ascidians. In this fauna, by necessity consisting of small animals, the border between macro- and meiofauna is blurred, as also shown by a considerable overlap between the two investigations. The taxa fall into size-based arbitrary categories of species, permanently small-sized species of classical meiofauna and small-sized macrofauna on one side, and into temporary meiofauna, viz. newly settled and young specimens of larger-sized species on the other.

Considering the rather extensive area covered by *C. officinalis*, the association is bound to interact with the surroundings. One interaction is the function as nursery ground as indicated by the large numbers of newly settled postlarvae and juveniles of large-sized species, of for example asteroids and mussels (Dinesen and Ockelmann, 2004; Dinesen, unpubl. obs.). If not eaten by predators or just dying because of unsuitable conditions when growing larger, they may migrate and colonize other habitats at greater depths nearby (Snæli, 1968;

Dinesen and Ockelmann, 2004). Another interplay that also influences the coralline algae association profoundly is that the turfs act as hunting grounds for larger mobile predators in the area (Choat and Kingett, 1982).

Other red algae, such as species of *Lithothamnion* have elsewhere been found to house a rich fauna as well (Snæli, 1968).

Laminaria holdfasts, stipes and fronds

In the coastal waters of Denmark, Germany, Great Britain, Ireland and Norway several species of *Laminaria* accommodate a species rich flora and fauna that is different in time and space according to the position on the algae and the conditions of the physical factors offered by the habitats (Jones, 1969; 1971; Edwards, 1980; Hayward, 1988; Schulze *et al.*, 1990; Christie *et al.*, 1994; Dahl and Dahl, 2002).

Extensive areas with *Laminaria digitata* (Huds.), *L. hyperborea* (Gunnerus) and *L. saccharina* (L.) are found in various places around the Faroes, from the littoral to about 20 m depth (Nielsen and Gunnarsson, 2001). Detailed studies have been carried out on the epiphytes of holdfasts and stipes of *L. hyperborea* (Worsaae, 1996; 1998; Bruntse *et al.*, 1999; Kongsrud, 2000). Associated with the stipes were about 20 species of algae and about 100 macrofauna species. The number of species were highest at exposed localities, but they were only slightly lower at moderately exposed and sheltered sites. Over the entire exposure range, 12 algae and 74 invertebrates were common. The biota associated with holdfasts is less studied than those with stipes.

The Faroese fauna appears as rich in species and individuals as comparable investigations in Norway. Both diversity and abundance of species are higher in larger (older) holdfasts than in smaller (Worsaae, 1996; Bruntse *et al.*, 1999).

The majority species are small-sized or sessile, especially in the holdfasts that may represent a small 'island-ecosystem'. For those which grow larger the habitat rather functions as a nursery ground from which they migrate after reaching a certain stage or size (Snæli 1968).

Stipes and holdfasts play a significant role as feeding grounds for some larger animals such as crabs (*Cancer pagurus*), urchins (*Strongylocentrotus droebachiensis*) and even fish (Hilddén, 1978 (the example is *Ctenolabrus rupestris*, but it should be noted that the species has not (yet) been recorded from the Faroes); Christie *et al.*, 1994).

It should be noted that also species of other brown macroalgae, such as *Ascophyllum* and *Fucus*, house a rich flora and fauna (Hayward, 1988; Davis *et al.*, 1999).

Sponges

Experience and numerous reports from all over of the world show that large sponges form habitats for other species of sponges as well as for members of other phyla (Bacescu, 1971; Klitgaard, 1995 (numerous references herein); Kunzmann, 1996). In the NE Atlantic, prior to the BIOFAR projects, there were only scattered reports and observations mainly on any one kind of sponge and a few associated species from different areas (references in Klitgaard,

1995).

During BIOFAR 1 a special investigation aimed at a survey of the associated fauna of the large-sized species of *Geodia*, *Isops*, *Stryphnus*, *Phakellia* and *Thenia* occurring around the Faroes. The effort resulted in 250 species being found associated with 11 species of sponges, in various combinations and abundances (Klitgaard, 1995). A preliminary study of the meiofauna and small macrofauna in *Thenia* might indicate a richer fauna in specimens from soft bottom than from gravel (Hansen *et al.*, 1989). The 11 sponge species constitute the main part of the biomass of sponge dominated areas, ostur ('cheese bottoms') both at the Faroes and in other parts of the northern boreal region (Klitgaard *et al.*, 1997; Klitgaard and Tendal, 2001; 2004). Ostur are loosely defined as 'a restricted area where large sponges are strikingly common'. This kind of habitat occurs all around the Faroes, generally on coarse gravel bottom with some current. It appears to be particularly well developed as narrow bands along the shelf break, at depths of about 250 to 500 m, in areas where the energy from internal waves is the basis for, at least tide-wise, increased water movements, resuspension and perhaps also convection of fine particulate matter. Originally it probably covered several thousands of km² but trawling seems to have reduced the size of the distribution areas.

Only a few of the associated species utilize the sponges as a food source (Klitgaard, 1995; Warén and Klitgaard, 1991). Instead the presence of the large sponges enhances the number and complexity of

microhabitats in the area. The majority of species find good positions and currents for their filtering activity either inside the sponge or outside on the top or side of it, pockets with accumulations of particles for detritus feeders, or a hunting ground for smaller carnivores. The sponges also provide places for hiding egg masses during their development, and function as nursery grounds, or as regular shelter against larger predators. So far no fish species eating the sponges have been found, but some juveniles sometimes utilise the hollows and crevices as shelter.

A preliminary investigation, based on station lists, bottom photographs, field journals and identification sheets from the archive of the Kaldbak Laboratory indicates that the ostur are 5-10 times richer in species than a similar, nearby gravel bottom without the sponges (Tendal, unpubl. obs.).

Sponge spicules

When sponges die their skeletons disintegrate and the spicules are scattered on the bottom by currents, slides, bioturbation, etc. It takes a long time for silicious spicules to dissolve, at least for the larger ones and, accordingly, a certain accumulation can take place. This means that in any given sediment sample one nearly always find some sponge spicules (Barthel and Tendal, 1993). Spicules may remain at the locality where the sponges live, or they may be transported in suspension by currents to some other place, where they sink down and accumulate. The accumulations of the first kind are by far the largest, as is best

known from Antarctica, but also from certain parts of the NE Atlantic, and they have been shown to accomodate a rich fauna of smaller invertebrates (Barthel, 1992a; b; Bett *et al.*, 1992; Bett and Rice, 1992; Barthel *et al.*, 1996).

In Faroese waters sponge spicules have been found in the sediments from various sponge habitats (Klitgaard and Tendal, 2001). They are scattered and few in sand from gravelly-sandy bottoms, but they can be so numerous on more silty locations that washing the sediment for macrobenthos is difficult and sometimes almost impossible (Josefson, 2001; Tendal, unpubl. obs.).

Due to the current regime around the Faroe Islands coherent spicule mats of the later kind are seemingly found only locally, covering maybe some hundreds of m². In some such places east of the Faroes the spicule component of the sediment is obviously allochthonous. In other localities, especially those with numerous specimens of the demosponge genus *Thenea* the mats are autochthonous.

Octocorals

In samples it is commonplace to see some fauna regularly associated with the large upright octocorals of the order Gorgonaria (Tendal, unpubl. obs. from the NE Atlantic). Apart from casual reference to single species there are, however, only few published accounts. In an *in situ* study performed with manned submersible on *Primnoa* specimens in the Gulf of Alaska it was found that these serve both as habitat and prey for 9 megafauna invertebrate groups and for a number of fish (Krieger and Wing,

2002). Off Nova Scotia foraminifers, hydroids and crustaceans were found to be well represented on the large octocorals, especially *Primnoa resedaeformis* (Gunnerus, 1763) (Henry, 2001; Hawkes, 2004; Buhl-Mortensen and Mortensen, 2004). Other groups of animals seem not to have been investigated in detail.

The largest gorgonarians in the Faroese fauna are *Paragorgia arborea* Linné, 1758 and *Primnoa resedaeformis*. Both are found scattered along the shelf edge and the edge of banks, and while the first mentioned never seems to be preserved in large numbers, the latter has in some localities been found in abundance (Tendal, 1992; Bruntse and Tendal, 2001a; b; Tendal and Jensen, in prep.). The BIOFAR material has not been analysed for fauna living on and of these corals, and because the samples were taken with towed gear, only the sessile species can be recognized.

Both species are slow-growing and reach old age, *Paragorgia* at more than 1000 years (Tendal and Carstenson unpubl.) and *Primnoa* at 100-500 years (Strømngren, 1970; Andrews *et al.*, 2002; Risk *et al.*, 1998; 2002). In places where they are abundant they provide for other species a 3-dimensional, high (1 m or more) relief habitat. This is very stable over time, but also most vulnerable to kinds of disturbance that modify or destroy parts of the area, such as commercial trawling (Breeze *et al.*, 1997; Nelson and Gordon, 1997; Risk *et al.*, 1998; Fosså *et al.*, 2002). Although rather poorly investigated in other parts of the world also, experience nevertheless shows that the thickets of these corals

house a distinct fauna of invertebrates and fish, dependant on the corals as polyp feeders, suspension feeders and as protection sites for small species and small specimens of larger-seized species. To what extent this is also the case for the Faroese corals is not known, but it should be investigated, both because these areas may be useful high-diversity spots, and because destruction seems irreparable, at least at a normal human scale.

Coral banks

The azooxanthellate scleractinian coral *Lophelia pertusa* (Linne, 1758) forms banks (or 'bioherms', 'reefs') all along the North Atlantic continental margin, mainly at 200-500 m depth. On the European side it has been found from northern Norway to off Spain, and on the American side from Nova Scotia to Gulf of Mexico (Moore and Bullis, 1960; Mortensen, 2000). In the early literature on *Lophelia* banks two opinions are often met with, one is that the banks house a rich animal life, the other that they are rare. The first view is correct; on Norwegian banks 614 species have been registered and in the whole NE Atlantic more than 1300 (Garcia *et al.*, in prep.). The second notion is wrong, investigations in selected areas have demonstrate the presence of hundreds of large and small banks scattered over the outer shelf and upper slope (Fosså *et al.*, 2002; Map produced by the British Geological Survey). Although the whole distribution area of the species has not been investigated in sufficient detail, it is obvious that there exist thousands of *Lophelia* banks. Such a strong represen-

tation shows that instead of being an exotic touch in some local faunas, mostly of interest to a small group of biologists interested in rare species, strange life forms, diversity problems, etc, the banks play a central role in the benthic ecosystems all along the North Atlantic continental margin.

During BIOFAR *Lophelia* was found to be widely distributed around the Faroes and on the banks to the west of the islands (Frederiksen *et al.* 1992; Bruntse and Tendal 2001a; b). A calculation, based on reports from Faroese fishermen, of the size of the area where living coral banks are found comes to 11,000 km². To this should be added that there are a further 8,000 km² where corals lived earlier (J. Sørensen, pers. com.). The associated fauna has been investigated in detail in two localities (Jensen and Frederiksen, 1992), and a total of 298 taxa were found, representing nearly all marine macrofauna phyla.

The all-important ecological role of the living corals is that they form over a long time a complex 3-dimensional bank structure. Very few, if any, of the associated species are able to utilize them as food, and it is obvious from samples and *in situ* photographs that even in a large bank only a thin outer layer, at maximum 1 meter thick, but normally much less, comprises living corals. Thus, by far the largest part of a bank is a framework of dead coral branches at various stages of degradation. This is caused by boring animals and fungi, especially sponges of the genera *Aka* and *Alectona*, by the weight of overlying parts, by physical forces like currents and by chemical dissolution of the calcarous matter.

Near the basis of the bank the coral branches are highly fragmented, partly dissolved and often embedded in silty sediment. In the middle part multiple sizes of interstices and different stages of degradation are present as well as pockets filled with various grades of sediment, and it comprises a very large number of small habitats very different kind. It is here that majority of the associated species find their living place, shelter for egg deposition or protection against larger predators, hunting grounds, and nursery areas (Mortensen *et al.*, 1995; Husebø *et al.*, 2002; Tendal, pers. obs.). Some large longlived species, like the octocorals *Paragorgia arborea* and *Primnoa resedaeformis* and sponges of the genus *Geodia* also live on the bank, underlining the slow growth of this habitat. Over time a variety of growth rates has been suggested for the corals, from 4.1 mm to 2.5 cm per year, but the best estimate seems to be 4.3 to 7.0 mm per year, depending on shelf or fjord conditions (Mortensen and Rapp, 1998). Considering the slow growth and the degradation it is clear that banks several meters high must be thousands of years old, as it has been shown for banks in Norway (Hovland *et al.*, 2002). Thus, the habitat comprising a bank or a group of banks and the associated fauna is a long since established ecosystem, even if the involved species also live in other habitats in the area.

Horse mussel aggregations

Modiolus modiolus (L., 1758) is well known from throughout the NE and NW Atlantic subtidal as a living substrate for

many other species (e.g. Spärck, 1929; Einarsson, 1941; Brown and Seed, 1977; Sebens 1985; Ojeda and Dearborn, 1989; Dinesen, 1996), a hardbottom association even being named after it (Petersen, 1913). The horse mussel can grow to be older than 45 years (Anwar *et al.*, 1990), and large, up to 23 cm in shell length (Wiborg, 1946). Specimens attach to each other by their byssus, thereby forming a 3-dimensional structure of dead shells, byssus and live mussels (Suchanek, 1985; Witman, 1985). The mussel patches are of different density and range and when compact and extensive these habitats are often referred to as beds, banks or reefs.

M. modiolus is distributed all around most of the Faroes at a depth range of 0-210 m (Dinesen and Ockelmann, 2004; Snæli *et al.*, 2004). In some areas at depths of 65-95 m, it forms dense aggregations, covering up to 100% of the sea floor, and housing more than 188 animal species representing most higher taxa of the marine macrofauna (Dinesen and Bruntse, 2001; Dinesen and Tendal, in prep.). Few of these species feed on *Modiolus*. Many are suspension or filter feeders that use the live mussels and shell debris as a substrate, some are detritus feeders finding particles of different origin in the crevices between and under the living and dead shells and byssus, and others again are carnivores preying on other members of the associated fauna.

So far no species are known to be obligate in association with *M. modiolus*. However, on the eastern Faroe shelf, pyramidelid gastropods that feed on the mussels' body fluid are common (Schander, 1995).

The shell of the live mussels is being excavated by boring sponges of the genus *Cliona* and spionid polychaetes. External on the shell of live mussels, the gastropod *Capulus ungaricus* (L., 1758) live often attached to the posterior part; elsewhere this species seems to benefit directly from the filter feeding currents of the mussels (Shaman, 1956). Hydroids and octocorals are often abundant on the shells. The erect colonies of carnivorous suspension feeders like the cnidarians *Hydrallmania falcata* (L., 1758), *Abietinaria abietina* (L., 1758), *Thuiaria thuja* (L., 1758) and *Alcyonium digitatum* L., 1758, and species of the bryozoan genus *Dendrobaenia* may benefit from the feeding activity of the mussels. The hydroid colonies themselves house a number of species but this fauna is little known in Faroese waters. Among these epibionts are other hydroids (Thorsen, 1992), calcareous tubeworms, and crustaceans including cirripeds and caprellids (Larsen, 1998) and several bryozoans. Whelks and other species deposit their eggs on the mussel shells and many mobile species, such as decapods and brittle stars, probably take advantage of the mussel matrix as a hide out from predation. The *Modiolus* aggregation appears to take the ecological role of forming more microhabitats than are available nearby and, accordingly, the diversity of the associated invertebrate fauna is expected to be higher within this habitat.

A few species are found only as newly metamorphosed or juveniles, and in these cases the bank may serve as a nursing ground. The hyperbenthic fauna and fish

associated with *Modiolus* aggregations are little known. Research on juvenile cod (*Gadus morhua*) from Nova Scotia has shown that some cottid predators are less successful in rocky reef and cobble habitats than on open sand bottoms and that the young cod utilises rocks, empty scallop shells and other debris in seagrass beds as shelter (Tupper and Boutilier, 1995). When exposed to an active predator, juvenile cod from New Foundland preferentially hide among cobble (7-12 cm in diameter) but also artificial kelp, and thereby significantly reduces the risk of predation by older conspecifics (Gotceitas *et al.*, 1995). Considering the common abundance of *Modiolus* in the subtidal, the adult size of the mussels (usually 8-16 cm in shell length), and the 5-15 cm high, sessile biota on the living shells (in the Faroes mainly red algae in the photic zone and erect, colonial animals in deeper water), as well as the species richness of the associated fauna, these mussel aggregations may be important nursing grounds for juvenile fish finding both shelter and food here.

Scallops

In other areas of the NE Atlantic a rich fauna has been found encrusting the shells of the queen scallop, *Aequipecten opercularis* (L., 1758). It comprises foraminiferans, ciliates, sponges, hydrozoans, anthozoans, entoprocts, bivalves, barnacles and bryozoans (Haward and Haynes, 1976; Ward and Thorpe, 1991).

The queen scallop is widely distributed all over the Faroese shelf, at depths from about 20 to 450 m (Snæli *et al.*, 2004). Fish-

able beds covering an area about 400 km² are found in the north eastern part, at depths of 60-120 m, on soft, sandy and stony bottoms (Nicolajsen, 1997).

On the eastern shelf, the shells of live *A. opercularis* from the deeper part of the *Modiolus* aggregation belt, are heavily overgrown by a variety of organisms, including sponges, hydrozoans, tube worms (serpulids and spirorbids), saddle oysters, barnacles, as well as encrusting and erect bryozoans (Dinesen, unpubl. obs.) So far the epizoans on the mobile substrate represented by the shells of the queen scallop have not been studied in detail in the Faroes.

Pagurid shells

One of the remarkable habitats of biological origin is the movable one of pagurids and the gastropod shells in which they live. Several investigations show that numerous species use the shell as a hard substrate, taking advantage of avoiding siltation and constantly being kept above the bottom in the water column. Some probably also having benefit from the hermit crabs' eating activities (Samuelsen, 1970; Jensen and Bender, 1973; Stachowitsch, 1977). Young hermit crabs are fast growing, often changing their "house" to a larger one, resulting in a relatively short time for an epibiotic fauna to develop. As they grow older and larger the pagurids grow more slowly, and have increasing difficulties finding suitable shells. The epibiotic fauna gets more time for growth and recruitment, and the number of species increase. In some cases a single

species over time dominates and cover the whole shell surface, viz. species of the sponge genus *Suberites* or of the hydroid genus *Hydractinia* (Jensen, 1970; Mills, 1976; Van Soest, 1993).

No investigation of the epiphytes of hermit crab shells has been made in the Faroes. In a preliminary study of the pagurids in the area, three species, *Pagurus bernhardus* (L., 1758), *P. pubescens* Krøyer, 1838 and *Anapagurus laevis* (Bell, 1845) were found on the shelf, the two first being by far the most common and often occurring together (Hoydal, 2001). Access to empty gastropod shells is a necessity for the hermit crabs, and almost all shells found are occupied. In the above study it was found that the two species utilize shells from the same genera, which were *Buccinum*, *Colus*, *Gibbula*, *Lacuna*, *Littorina*, *Lunatia*, *Thais*, *Trophonopsis*, *Trichotropis* and *Trophon*. Only for a few shells of *Neptunea* and *Natica* there was no overlap, *P. bernhardus* using the first and *P. pubescens* the last. *Buccinum*, *Gibbula*, *Thais* and *Lacuna* were the most often occupied. Availability of the 'next size' up in shell has been shown to influence the growth rate of *P. bernhardus* (Markham, 1968).

Brachiopods

In all regions of the N Atlantic the phylum Brachiopoda is represented by rather few species, mostly living along the continental margin, on the outer shelf and upper slope (Zezina, 1976; 1997). In places, single species may occur in high densities and form a dominant constituent of the benthic fauna (Rudwick, 1970; Brunton and Curry,

1979; Witman and Cooper, 1983; Zezina, 2001). Among the species showing such patchy mass occurrence *Macandrewia cranium* (Müller, 1776), *Terebratulina retusa* (Linné, 1758) and *T. septentrionalis* (Couthouy, 1838) are regularly found to provide substrate for an incrusting fauna of other sessile organisms; this is especially the case for larger, older individuals (Logan and Noble, 1971; Noble *et al.*, 1976; Brunton and Curry, 1979; Tendal, unpubl. obs.; scattered notes in the literature). The habitat represented by the single brachiopod shell is rather insignificant, but in cases of mass occurrence the combined area is considerable as to the size, although it is broken up into a mosaic.

Brachiopods offer a substrate in localities with good water movement (Thomsen, 2004), and it has been suggested that the brachiopod's own movement in relation to current direction is taken advantage of by some of the commensals growing on the shell (LaBarbera, 1977; Zumwalt and DeLaca, 1980). Although there may be some competition for food particles between the brachiopod and its epiphytes, even heavy overgrowth does not seem to be of significant inconvenience to the brachiopod, neither in its movements, nor in its growth and reproduction (Rudwick 1970; Tendal, unpubl. obs.). An advantage for the brachiopods might be a certain protection against predators, especially fish, allowing the slow-growing brachiopods to live for a long time undisturbed in a rather obvious position.

Six brachiopod species have been found in Faroese waters (Thomsen, 2001). *W. cra-*

nium and *T. retusa*, both common all around the islands, mostly at depths of 200 to 500 m, have been observed to house a fauna comprising foraminiferans, sponges, hydrozoans, serpulids, bivalves, bryozoans and other brachiopods, dominated by thinly encrusting sponges and bryozoans (Thomsen and Tendal, in prep.). The total number of species found on Faroese brachiopods can not be given. For one group, the sponges, 16 species have been recorded on *W. cranium* and *T. retusa* from the Swedish West coast (Skagerrak) (Tendal, unpubl. obs.), and there are reasons to believe that the number will be higher in the populations around the Faroes.

Conclusions

The main goal of the BIOFAR programmes was to provide knowledge on the composition and distribution of the benthic fauna and flora within the Faroese EEZ. Numerous specialists and students took part, and with the rather plentiful resources it was possible also to support and encourage quite a number of personal investigations with different aims and purposes (training, graduate students projects, Master's, Ph.Ds). All these efforts that led to a wealth of diverse, but also very scattered results. Many of these were in the fields of biogenic substrates and habitats, and associated fauna.

Three lines of work can be distinguished, especially carried out by participants from the Zoological Museum, University of Copenhagen. One is the delimitation, description and mapping of mass occurrences of large-sized species of corals, sponges

and bivalves (Frederiksen *et al.*, 1992; Klitgaard *et al.*, 1997; Dinesen and Bruntse, 2001; Bruntse and Tendal, 2001b; Klitgaard and Tendal, 2001; 2004; Dinesen and Ockelmann, 2004;). Another is the investigation of fauna associated with corals, sponges, bivalves, coral weed and large brownalgae (Jensen and Frederiksen, 1992; Klitgaard, 1992; 1995; Dinesen, 1994; 1996; 1999; Kristensen, 1995; 1996; Worsaae, 1996; 1998; Bruntse *et al.*, 1999; Kongsrud, 2000 (University of Bergen)). The third is the effort to create a map of bottom types around the Faroes, including of biogenic habitats composed of live organisms, initially comprising corals and existing information from many sources, followed by the addition of sponge dominated bottoms, hydroid mass occurrences, *Modiolus* banks and octocorals (Frederiksen and Jensen, 1990; Klitgaard, 1992; Thorsen, 1992; Dinesen, 1996; Bruntse and Tendal, 2001a: fig. 1).

Of the eleven categories of biogenic substrate and habitats reviewed here some influence benthic life in large areas of the Faroese shelf and upper slope as secondary substrate (shell-sand and -gravel, *Laminaria*, sponges, corals, scallops and *Modiolus*). Others are well known from investigations outside the Faroe area to provide housing for a rich, characteristic fauna, or otherwise to play a significant ecological role (sponge spicule mats, *Corallina*, octocorals, 'pagurid-shells' and brachiopods). Still others could have been mentioned, both algae (f.i. *Lithothamnion* crusts and *Fucus* species) and animals (e.g. large thecate hydroids and stylasterids, serpulid

crusts, other molluscs, some decapod crustaceans and certain ascidians), but there are for these no or few Faroese observations. Numerous reports treat single categories such as listed and referred to above and point out on a more or less well documented basis their ecological importance. Others are more generalized and have a wider scope in their approach (examples are Sebens, 1991; Lohse, 1993). The overall conclusion is that the presence of stable biogenic structures adds significantly to habitat heterogeneity within a given area or along a gradient, and within this, at a smaller scale, to physical complexity in time and space. Physical structure and age of the biogenic substrate, disturbance of various kinds, succession and isolation are all dynamic features that determine species richness, abundance, and single species' density.

Concerned with substrates and habitats only this paper has not attempted at a further analysis of faunistic differences and similarities between habitats, nor at any kind of division into functional groups, modes of reproduction, growth and recruitment, or fisheries effects. The level of taxonomic identification in the investigations performed during BIOFAR varies according to aim as well as to the time and resources allocated in each case. For sponge spicule-mats, octocorals, scallops and pagurids only scattered observations are present. As a contrast, identification of fauna associated with *Laminaria*, sponges, corals and *Modiolus* are carried through to species level and this may allow for further analyses, including the important interplay with

different life stages and populations of both commercial and non-commercial fish species. Finally, other fauna compositions, such as those associated with shell-gravel and -sand, *Corallina* and brachiopods are known in some detail, mostly to phylum or class, and they are obviously promising for further investigations.

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References

- Andrews, A.H., Cordes, E.E., Mahoney, M.M., Munk, K., Coale, K.H., Caillet, G.M. and Heifetz, J. 2002. Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia* 471: 101-110.
- Anwar, N.A., Richardson, C.A. and Seed, R. 1990. Age determination, growth rate and population structure of the horse mussel *Modiolus modiolus*. *Journal of the Marine Biological Association of the United Kingdom* 70: 441-457.
- Bacescu, M. 1971. Les spongiaires; un des plus intéressants biotopes benthique marins. *Rapport Commission Internationale pour la Mer Méditerranée* 20: 239-241.
- Barthel, D. 1992a. Do hexactinellids structure Antarctic sponge associations? *Ophelia* 36: 111-118.
- Barthel, D. 1992b. Antarctic hexactinellids: A taxonomically difficult, but ecologically important benthic component. *Verhandlungen der Deutschen zoologischen Gesellschaft* 85: 271-276.
- Barthel, D. and Tendal, O.S. 1993. Sponge spicules in abyssal and bathyal sediments of the NE Atlantic. *Deep-Sea Newsletter* 20: 15-18.
- Barthel, D., Tendal, O.S. and Thiel, H. 1996. A wandering population of the hexactinellid sponge *Pheronema carpenteri* on the continental slope off Morocco, Northwest Africa. *Marine Ecology* 17: 603-616.
- Bett, B.J. and Rice, A.L. 1992. The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic). *Ophelia* 36: 217-226.
- Bett, B., Thurston, M. and Rice, T. 1992. Sponge surprise. *Deep-Sea Newsletter* 19: 19.
- Brattegard, T. and Meland, K. 1997. Mysidacea (Crustacea) in the Faroe area. *Fróðskaparrit* 45: 69-95.
- Brattegard, T. and Rømer, E.I. 1998. Decapoda Natantia (Crustacea) in the Faroe area. *Fróðskaparrit* 46: 91-126.
- Breeze, H., Davis, D.S., Butler, M. and Kostylev, V. 1997. Distribution and status of deep sea corals off Nova Scotia. *Ecology Action Centre, Marine Issues Committee Special Publication* 1. 58 pp.
- Brown, R.A. and Seed, R. 1977. *Modiolus modiolus* (L.), an autecological study. Pp. 93-100 in Keegan, B.F., CÉidigh, P.Ó., and Boaden, P.J.S. (eds). *Biology of Benthic Organisms. Proceedings of the 11th European Symposium on Marine Biology*. Pergamon Press. Oxford. 630 pp.
- Brunton, C.H.C. and Curry, G.B. 1979. British Brachiopods. *Synopsis of the British fauna (New Series)* 17. The Linnean Society of London. 64 pp.
- Bruntse, G., Kongsrud, J.A. and Worsaae, K. 1999. Species associated with stipes and holdfasts of *Laminaria hyperborea*. Pp. 50-65 in Bruntse, G., Lein, T.E. and Nielsen, R. (eds). *Marine benthic algae and invertebrate communities from the shallow waters of the Faroe Islands. A base line study*. Kaldbak Marine Biological Laboratory, The Faroe Islands. 117 pp.
- Bruntse, G. and Tendal, O.S. 2001a. Summary. A new map of benthic faunal associations and bottom types around the Faroes. Pp. 5-7 in Bruntse, G. and Tendal, O.S. (eds). *Marine biological investigations and assemblages of benthic invertebrates from the Faroe Islands*. Kaldbak Marine Biological Laboratory. The Faroe Islands. 80 pp.
- Bruntse, G. and Tendal, O.S. 2001b. *Lophelia pertusa* and other cold water corals in the Faroe area. Pp. 22-32 in Bruntse, G. and Tendal, O.S. (eds). *Marine biological investigations and assemblages of benthic invertebrates from the Faroe Islands*. Kaldbak Marine Biological Laboratory. The Faroe Islands. 80 pp.
- Buhl-Mortensen, L. and Mortensen, P.B. 2004. Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunnerus, 1763). *Journal of Natural History* 38: 1233-1247.
- Choat, J.H. and Kingett, P.D. 1982. The influence of

- fish predation on the abundance cycles of an algal turf invertebrate fauna. *Oecologia* 54: 88-95.
- Clausen, C. 2004. Gastrotricha from the Faroe Bank. *Sarsia*
- Conway, K.W., Krautter, M., Barrie J.V. and Neuweiler, M. 2001. Hexactinellid sponge reefs on the Canadian continental shelf: a unique 'living fossil'. *Geoscience Canada* 28: 71-78.
- Christie, H., Rinde, E., Fredriksen, S. and Skadsheim, A. 1994. Økologiske konsekvenser av taretråling: restituering av tareskog, epifytter og hapterfauna etter taretråling ved Rogalandskysten. *Norsk Institutt for Naturforskning. Oppdragsmelding* 295: 1-29.
- Crisp, D.J. and Mwaiseje, B. 1989. Diversity in intertidal communities with special reference to the *Corallina officinalis* community. *Scientia Marina* 53: 365-372.
- Dahl, L. and Dahl, K. 2002. Temporal, spatial and substrate-dependent variations of Danish hard-bottom macrofauna. *Helgoland Marine Research*. 56: 159-168.
- Davis, J., Fosaa, A.M., Gunnarson, K. and Nielsen, R. 1999. Diversity of species. Pp. 37-40 in Bruntse, G., Lein, T.E. and Nielsen, R. 1999. *Marine benthic algae and invertebrate communities from the shallow waters of the Faroe Islands. A base line study*. Kaldbak Marine Biological Laboratory, The Faroe Islands. 117 pp.
- Dayton, P.K. 1985. Ecology of kelp communities. *Annual Review of Ecology and Systematics*. 16: 215-245.
- Dinesen, G.E. 1994. Færøske hestemuslinger og deres logerende. Dyr i natur og museum 1994/2: 6-9.
- Dinesen, G.E. 1996. Hestemuslingen *Modiolus modiolus* (Linn., 1758) og dens associerede fauna ved Færøerne. Specialrapport, Zoologisk Museum. Københavns Universitet. 178 pp.
- Dinesen, G.E. 1999. *Modiolus modiolus* and its associated fauna. Pp. 66-71 in Bruntse, G., Lein, T.E. and Nielsen, R. (eds). *Marine benthic algae and invertebrate communities from the shallow waters of the Faroe Islands. A base line study*. Kaldbak Marine Biological Laboratory, The Faroe Islands. 117 pp.
- Dinesen, G.E. and Bruntse, G. 2001. *Modiolus modiolus* beds. Pp. 33-36 in Bruntse, G. and Tendal, O.S. (eds). *Marine biological investigations and assemblages of benthic invertebrates from the Faroe Islands*. Kaldbak Marine Biological Laboratory. The Faroe Islands. 80 pp.
- Dinesen, G.E. and Ockelmann, K.W. 2004. Spatial distribution and species distinction of *Modiolus modiolus* and synoptic Mytilidae (Bivalvia) in Faroese waters (NE Atlantic). *Proceedings from BIOFAR Symposium, Tórshavn, 24.-26. April 2003. North-East Atlantic marine benthic organisms in the Faroes – taxonomy, distribution and ecology. Supplementum Fróðskaparfelag* 41.
- Dommasnes, A. 1968. Variation in the meiofauna of *Corallina officinalis* with wave exposure. *Sarsia* 34: 117-24.
- Dommasnes, A. 1969. On the fauna of *Corallina officinalis* L. in western Norway. *Sarsia* 38: 71-86.
- Edwards, A. 1980. Ecological studies of the kelp, *Laminaria hyperborea*, and its associated fauna in southwest Ireland. *Ophelia* 19: 47-60.
- Einarsson, H. 1941. Survey of the benthonic animal communities of Faxa Bay (Iceland). *Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelser. Fiskeri*. 11. 46 pp.
- Fosså, J.H., Mortensen, P.B. and Furevik, D.M. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* 471: 1-12.
- Frederiksen, R. and Jensen, A. 1990. Korallen *Lophelia* og dens associerede fauna omkring Færøerne. Specialrapport, Zoologisk Museum. Københavns Universitet. 96 pp.
- Frederiksen, R., Jensen, A. and Westerberg, H. 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. *Sarsia* 77: 157-171.
- Gerken, S. and Watling, L. 1999. Cumacea (Crustacea) of the Faroe Island region. *Fróðskaparrit* 47: 199-227.
- Gotceitas, V., Fraser, S. and Brown, J.A. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. *Marine Biology* 123: 421-430.
- Grahame, J. and Hanna, F.S. 1989. Factors effecting the distribution of the epiphytic fauna of *Corallina officinalis* (L.) on an exposed rocky shore. *Ophelia* 30: 113-129.
- Hagerman, L. 1968. The ostracod fauna of *Corallina officinalis* L. in western Norway. *Sarsia* 36: 49-54.
- Hansen, B. 2000a. *Havið. Føroya Skúlabókagrunnur*. Tórshavn. 232 pp.
- Hansen, J.G. 2000b. Tardigrad-faunaen fra BIOFAR-undersøgelserne. Fagprojekt. Zoologisk Museum. Københavns Universitet. 65 pp.
- Hansen, J.G. 2004. The ongoing investigation of the Faroe Bank tardigrade fauna. *Proceedings from the BIOFAR Symposium, Tórshavn, 24.-26. April 2003*.

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- North-East Atlantic marine benthic organisms in the Faroes – taxonomy, distribution and ecology. Supplementum Fróðskapar felag* 41.
- Hansen, O.S., Lundholm, N. and Rømer, A. 1989. Fauna associeret til *Thenia* - specielt med henblik på meiofauna. Student report. Zoologisk Museum. Københavns Universitet.
- Hawkes, A. 2004. A study of attached benthic Foraminifera associated with the deep-sea coral *Prinnoea resedaeformis* on the Scotian margin. M. Sc. thesis. Dalhousie University.
- Haward, N.J.B. and Haynes, J.R. 1976. *Chlamys opercularis* (Linnaeus) as a mobile substrate for foraminifera. *Journal of Foraminiferal Research* 6: 30-38.
- Hayward, P.J. 1988. Animals on seaweed. *Naturalists' Handbooks* 9. Richmond Publishing Richmond (UK), 108 pp.
- Hedley, R.H., Hurdle, C.M. and Burdett, I.D.J. 1967. The marine fauna of New Zealand: Intertidal Foraminifera of the *Corallina officinalis* zone. *New Zealand Department of Scientific and Industrial Research Bulletin* 180 (New Zealand Oceanographic Institute Memoir 38) 180: 1-86.
- Heiner, I. 2003. The Loriciferan fauna of the Faroe Bank, North Atlantic with emphasis on the different types of life cycles. M. Sc. Thesis. Zoological Museum. University of Copenhagen. 110 pp.
- Heiner, I. 2004. Preliminary account of the Loriciferan fauna of the Faroe Bank. *Proceedings from the BIO-FAR Symposium, Tórshavn, 24.-26. April 2003. North-East Atlantic marine benthic organisms in the Faroes – taxonomy, distribution and ecology. Supplementum Fróðskapar felag* 41.
- Henry, L.-A. 2001. Hydroids associated with deep-sea corals in the boreal north-west Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 81: 163-164.
- Hicks, G.R.F. 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of Experimental Marine Biology and Ecology* 44: 157-192.
- Hilldén, N.-O. 1978. On the feeding of the goldsinny, *Ctenolabrus rupestris* L. (Pisces, Labridae). *Ophelia* 17: 195-198.
- Hovland, M., Vasshus, S., Indreeide, A., Austdal, L. and Nilsen, Ø. 2002. Mapping and imaging coral reefs off Norway, 1982-2000. *Hydrobiologia* 471: 13-17.
- Hoydal, K. 2001. Udbredelsen af Paguridea i havområdet omkring Færøerne. Fagprojekt. Zoologisk Museum. Københavns Universitet. 33 pp.
- Hughes, R.G. 1975. The distribution of epizoots on the hydroid *Nemertesia antennina* (L.). *Journal of the Marine Biological Association of the United Kingdom* 55: 275-294.
- Husebø, Å., Nøttestad, L., Fosså, J.H., Furevik, D.M. and Jørgensen, S.B. 2002. Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471: 91-99.
- Jensen, K. 1970. The interaction between *Pagurus bernhardus* and (L.) and *Hydractinia echinata* (Fleming). *Ophelia* 8: 135-144.
- Jensen, K. and Bender, K. 1973. Invertebrates associated with snail shells inhabited by *Pagurus bernhardus* (L.) (Decapoda). *Ophelia* 10: 185-192.
- Jensen, A. and Frederiksen, R. 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinia) on the Faroe shelf. *Sarsia* 77: 53-69.
- Jones, D. J. 1969. The fauna of the kelp holdfast. *Underwater Association Report* 1969: 75-80.
- Jones, D. J. 1971. Ecological studies on macroinvertebrate populations associated with polluted kelp forests in the North Sea. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 22: 417-441.
- Josefson, A.S. 2001. Macrofauna in soft sediments. Pp. 39-43 in Bruntse, G. and Tendal, O.S. (eds). *Marine biological investigations and assemblages of benthic invertebrates from the Faroe Islands*. Kaldbak Marine Biological Laboratory. The Faroe Islands. 80 pp.
- Kay, A.M. and Keough, M.J. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia* 48, 123-130.
- Klitgaard, A.B., 1992. Fauna associeret med svampe (Porifera) i farvandet omkring Færøerne. Speciale-rapport. Zoologisk Museum. Københavns Universitet. 306 pp.
- Klitgaard, A.B. 1995. The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, Northeastern Atlantic. *Sarsia* 80: 1-22.
- Klitgaard, A.B. and Tendal, O.S. 2001. "Ostur" - "cheese bottoms" - sponge dominated areas in the Faroese shelf and slope areas. Pp. 13-21 in Bruntse, G. and Tendal, O.S. (eds). *Marine biological investigations and assemblages of benthic invertebrates from the Faroe Islands*. Kaldbak Marine Biological Laboratory. The Faroe Islands. 80 pp.
- Klitgaard, A.B. and Tendal, O.S. 2004. Distribution and species composition of mass occurrences of large-

- sized sponges in the northeast Atlantic. *Progress in Oceanography* 61: 57-98.
- Klitgaard, A.B., Tendal O.S. and Westerberg, H. 1997. Mass occurrences of large-sized sponges (Porifera) in Faroe Island (NE-Atlantic) shelf and slope areas: characteristics, distribution and possible causes. Pp.129-142 in Hawkins, L.E. & Hutchinson, S. with Jensen, A.C. Williams, J.A. and Shearer, M. (eds). *The responses of marine organisms to their environment*. University of Southampton. 362 pp.
- Kongsrud, J.A. 2000. Flora og fauna tilknyttet stortarestipes (*Laminaria hyperborea* (Gunnerus) Foslie) ved Færøylene. Hovedfagsoppgave i marinbiologi. Institutt for fiskeri- og marinbiologi, Universitetet i Bergen.
- Krieger, K.J. and Wing, B.L. 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* 471: 83-90.
- Kristensen, R.M. 2004. Fifteen years investigation of the meiofauna of the Faroe Bank (NE Atlantic). *Proceedings from the BIOFAR Symposium, Tórshavn, 24.-26. April 2003. North-East Atlantic marine benthic organisms in the Faroes – taxonomy, distribution and ecology. Supplementum Fróðskapar felag* 41.
- Kristensen, T.W. 1995. Den associerede fauna til *Coralina officinalis* på Færøerne. Fagprojekt. Zoologisk Museum. Københavns Universitet. 26 pp.
- Kristensen, T.W. 1996. Korallagens mange beboere. *Dyr i natur og museum* 1996/2: 24-27.
- Kunzmann, K. 1996. Die mit ausgewählten Schwämmen (Hexactinellida und Demospongien) aus dem Weddellmeer, Antarktis, vergesellschaftete Fauna. *Berichte zur Polarforschung* 210: 1-93.
- Larsen, K.R. 1998. Caprellida (Crustacea; Amphipoda) from Faroe Island waters, with a key to the North-Atlantic species. *Fróðskaparrit* 46: 81-90.
- Logan, A. and Noble J.P.A. 1971. A recent shallow-water brachiopod community from the Bay of Fundy. *Maritime Sediments* 7: 85-91.
- Lohse, D.P. 1993. The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology and Ecology*. 166: 1-17.
- LaBarbera, M. 1977. Brachiopod orientation to water movement. I. Theory, laboratory behaviour, and field orientations. *Paleobiology* 3: 270-287.
- Magnussen, E. 2002. Demersal fish assemblages of the Faroe Bank: species composition, distribution, biomass spectrum and diversity. *Marine Ecology Progress Series* 238: 211-225.
- Markham, J.C. 1968. Notes on growth-patterns and shell-utilization of the hermit crab *Pagurus bernhardus* (L.). *Ophelia* 5: 189-205.
- Mills, C.E. 1976. The association of Hydractiniid hydroids and hermit crabs, with new observations from north Florida. Pp. 467-476 in Mackie, G.O. (ed.). *Coelenterate Ecology and Behaviour*. Plenum Press. New York. 744 pp.
- Moore, D.R. and Bullis, H.R. 1960. A deep-water coral reef in the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean* 10: 125-128.
- Mortensen, P.B. 2000. *Lophelia pertusa* (Scleractinia) in Norwegian waters. Dr. scient. Thesis. University of Bergen. 42 pp (synthesis).
- Mortensen, P.B., Hovland, M., Brattegard, T. and Farestveit, R. 1995. Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64°N on the Norwegian shelf: structure and associated megafauna. *Sarsia* 80:145-158.
- Mortensen, P.B. and Rapp, H.T. 1998. Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L.) (Anthozoa, Scleractinia): Implications for determination of linear extension rates. *Sarsia* 83: 433-446.
- Navarro, J.M. and Thompson, R.J. 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dyllwyn) during the spring diatom bloom. *Journal of Experimental Marine Biology* 209: 1-13.
- Nelson, W.A. and Gordon, D.P. 1997. Assessing New Zealand's marine biological diversity - a challenge for policy makers and systematists. *NZ Science Review* 54: 58-66.
- Nicolajsen, Á. 1997. The history of the queen scallop fishery of the Faroe Islands. *NOAA Tech. Rep. NMFS* 129: 49-56.
- Nielsen, R. and Gunnarsson, K. 2001. Seaweeds of the Faroe Islands. *Fróðskaparrit* 49: 45-108.
- Noble, J.P., Logan, A. and Webb, G.R. 1976. The recent *Terebratulina* community in the rocky subtidal zone of the Bay of Fundy, Canada. *Lethaia* 9: 1-18.
- Nørrevang, A. 1993. Bunddyrfaunaen på Færøbanke. *Seminar om Færøbanken, Tórshavn, 12.-13. november 1992*: 116-122.
- Nørrevang, A. 1997. Livet på havets bund ved Færøerne. *Carlsbergfondet Årsskrift* 1997: 46-53.
- Nørrevang, A., Brattegard, T., Josefson, A.B., Snæli, J.-A. and Tendal, O.S. 1994. List of BIOFAR stations. *Sarsia* 79: 165-180.
- Ojeda, F.P. and Dearborn, J.H. 1989. Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine, seasonal and bathy-

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- metric distribution. *Marine Ecology Progress Series* 57: 147-161.
- Petersen, C.G.J. 1913. Valuation of the sea II. The animal communities of the sea-bottom and their importance for marine zoogeography. *Report of The Danish Biological Station to the Board of Agriculture* 21: 1-68.
- Risk, M.J., McAllister, D.E. and Behnken, L. 1998. Conservation of cold- and warm-water seafans: threatened ancient gorgonian groves. *Sea Wind* 12: 2-21.
- Risk, M.J., Heikoop, J.M., Snow, M.G. and Beukens, R. 2002. Lifespans and growth patterns of two deep-sea corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. *Hydrobiologia* 471: 125-131.
- Rogers, A. 2004. The biology, ecology and vulnerability of deep-water coral reefs. *International Union for Conservation of Nature and Natural Resources*. 10 pp.
- Rudwick, M.J.S. 1970. *Living and fossil brachiopods*. Hutchinson University Library. London. 199 pp.
- Samuelson, T.J. 1970. The biology of six species of Anomura (Crustacea, Decapoda) from Raunefjorden, Western Norway. *Sarsia* 45: 25-52.
- Schander, C. 1995. Pyramidellidae (Mollusca, Gastropoda, Heterobranchia) of the Faroe Islands. *Sarsia* 81: 55-65.
- Schmidt, S.F., Tendal, O.S. and Magnussen, E. 2002. The Faroe Bank - A potential MPA. *WWF Briefing Paper*. 2 pp.
- Schulze, K., Janke, K. and Krüss, A. 1990. The macrofauna and macroflora associated with *Laminaria digitata* and *L. hyperborea* at the island of Helgoland (German bight, North Sea). *Helgoländer Meeresuntersuchungen* 44: 39-51.
- Sebens, K.P. 1985. The ecology of the rocky subtidal zone. *American Scientist* 73: 548-557.
- Sebens, K.P. 1991. Habitat structure and community dynamics in marine benthic systems. Pp. 211-234 in Bell, S.S. (Ed.) *Habitat structure*. Chapman and Hall.
- Seibold, E. and Berger, W.H. 1993. The sea floor. An Introduction to Marine Geology. Springer Verlag. Berlin. 356 pp.
- Sharman, M. 1956. Note on *Capulus ungaricus* (L.). *Journal of the Marine Biological Association of the United Kingdom* 35: 445-450.
- Sneli, J.-A. 1968. The *Lithothamnion* community in Nord-Møre, Norway, with notes on the epifauna of *Desmarestia viridis* (Müller). *Sarsia* 31: 69-74.
- Sneli, J.-A., Schjøtte, T., Jensen, K.R., Wikander, P.B. and Stokland, Ø. 2004. The marine Mollusca of the Faroes. *Fróðskaparrit* (in press).
- Spärck, R. 1929. Preliminary survey of the results of quantitative bottom investigations in Iceland and Faroe waters, 1926-1927. *Rapport et Procès-Verbaux des Réunions. Conseil internationale permanente de l'Exploration de la Mer* 57: 1-28.
- Stachowitsch, M. 1977. The hermit crab microbio-coenosis - the role of mobile secondary hard bottom elements in a North Adriatic benthic community. Pp. 549-558 in Keegan, B.F., Cédigh, P.Ó., and Boaden, P.J.S. (eds). *Biology of Benthic Organisms. Proceedings of the 11th European Symposium on Marine Biology*. Pergamon Press. Oxford. 630 pp.
- Strømgren, T. 1970. Emergence of *Paramuricea placomus* (L.) and *Primnoa resedaeformis* (Gunn.) in the inner part of Trondheimsfjord (West coast of Norway). *Kongelige Norske videnskabernes Selskabs skrifter* 4: 1-6.
- Suchanek, T.H. 1985. Mussels and their role in structuring rocky shore communities. Pp. 70-96 in Moore, P.G. and Seed, R. (eds). *The ecology of rocky coasts*. Hodder and Stoughton. London 453 pp.
- Sørensen, J., Bruntse, G., Gunnarsson, K. and Nielsen, R. 2000. List of BIOFAR 2 stations. *Fróðskaparrit* 48: 61-85.
- Tendal, O.S. 1992. The North Atlantic distribution of the octocoral *Paragorgia arborea* (L., 1758) (Cnidaria, Anthozoa). *Sarsia* 77: 213-217.
- Tendal, O.S., Brattegard, T., Nørrevang, A. and Sneli, J.-A. 2004. The BIOFAR 1 programme: background, accomplishment, and some outcome from inter-Nordic benthos investigations around the Faroe Islands (NE Atlantic). *Proceedings from the BIOFAR Symposium, Tórshavn, 24.-26. April 2003. North-East Atlantic marine benthic organisms in the Faroes - taxonomy, distribution and ecology. Supplementum Fróðskaparfelag* 41.
- Thomsen, E. 2001. Brachiopoda in the Faroe Islands area. *Fróðskaparrit* 49: 109-126.
- Thomsen, E. 2004. Brachiopod-substrate relationships on the continental shelf of the Faroe Islands (NE Atlantic). *Proceedings from the BIOFAR Symposium, Tórshavn, 24.-26. April 2003. North-East Atlantic marine benthic organisms in the Faroes - taxonomy, distribution and ecology. Supplementum Fróðskaparfelag* 41.
- Thorsen, M.S. 1992. Færøernes hydroider (Cnidaria, Hydrozoa). Udbredelse i relation til substrat, dybde og hydrografiske forhold. Specialrapport, Zoologisk Museum Københavns Universitet. 133 pp.

- Trygvadóttir, B.V. 2001. Meiofauna associeret til korallalgen, *Corallina officinalis*, i Kaldbaksfjorden, Færøerne. Fagprojekt. Københavns Universitet. 26 pp.
- Tupper, M. and Boutilier, R.G. 1995. Effects of habitat on settlement, growth and postsettlement of Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1834-1841.
- Van Soest, R.W.M. 1993. Distribution of sponges on the Mauretanian shelf. *Hydrobiologia* 258: 95-106.
- Veron, J.E.N. 1995. Corals in space and time. The biogeography and evolution of the Scleractinia. Comstock/Cornell. London. 321 pp.
- Ward, M.A. and Thorpe, J.P. 1991. Distribution of encrusting bryozoans and other epifauna on the subtidal bivalve *Chlamys opercularis*. *Marine Biology* 110: 253-259.
- Warén, A. and Klitgaard, A.B. 1991. *Hanlaya nagelfar*, a sponge-eating ecotype of *H. hanleya* or a distinct species of chiton? *Ophelia* 34: 51-70.
- Wegeberg, S., Nielsen, R. and Gunnarsson, K. 2001. Coralline Red Algae (Corallinales, Rhodophyta) of the Faroe Islands. *Froðskaparrit* 49: 37-43.
- Wiborg, K.F. 1946. Undersøkelser over oskjellet (*Modiola modiolus* (L.)). *Report on Norwegian Fishery and Marine Investigations* 8: 1-85.
- Wilson, J.B., 1979. Biogenic carbonate sediments on the Scottish continental shelf and on Rockall Bank. *Marine Geology* 33 (Letter Section): M85-M93.
- Witman, J.D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecological Monographs* 55: 421-445.
- Witman, J. D. and Cooper, R.A. 1983. Disturbance and contrasting patterns of population structure in the brachiopod *Terebratulina septentrionalis* (Couthouy) from two subtidal habitats. *J. Exp. Mar. Biol. Ecol.* 73: 57-79.
- Worsaae, K. 1996. En undersøgelse af faunaen associeret til haptererne af brunalgen *Laminaria hyperborea* på Færøerne. Biologisk projektarbejde, Zoologisk Museum. Københavns Universitet. (Student report)
- Worsaae, K. 1998. Algehæfterødders etagebyggeri. *Dyr i natur og museum* 1998/2: 13-16.
- Young, H.R. and Nelson, C.S. 1985. Biodegradation of temperate-water skeletal carbonates by boring sponges on the Scott shelf, British Columbia, Canada. *Marine Geology* 65: 33-35.
- Zezina, O.N. 1976. Ecology and distribution of recent brachiopods. *Akademia NAUK USSR*. 138 pp. (In Russian)
- Zezina, O.N. 1997. Biogeography of the bathyal zone. Pp. 389-426 in Blaxter, J.H.S. and Southward, A.J. (eds). *The biogeography of the oceans. Advances in Marine Biology* 32. Academic Press. 596 pp.
- Zezina, O.N. 2001. Articulate brachiopods near Vietnam shores in the belt of suspensionfeeders at the continental slope of Asia. Pp.63-68 in Kuznetsov, A.P. and Zezina, O.N. (Eds.): *Composition and structure of the marine bottom biota. VNIRO Publishing house. Moscow*. 171 pp. (In Russian)
- Zumwalt, G.S. and DeLaca, T.E. 1980. Utilization of brachiopod feeding currents by epizoic Foraminifera. *Journal of Paleontology* 54: 477-484.