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).

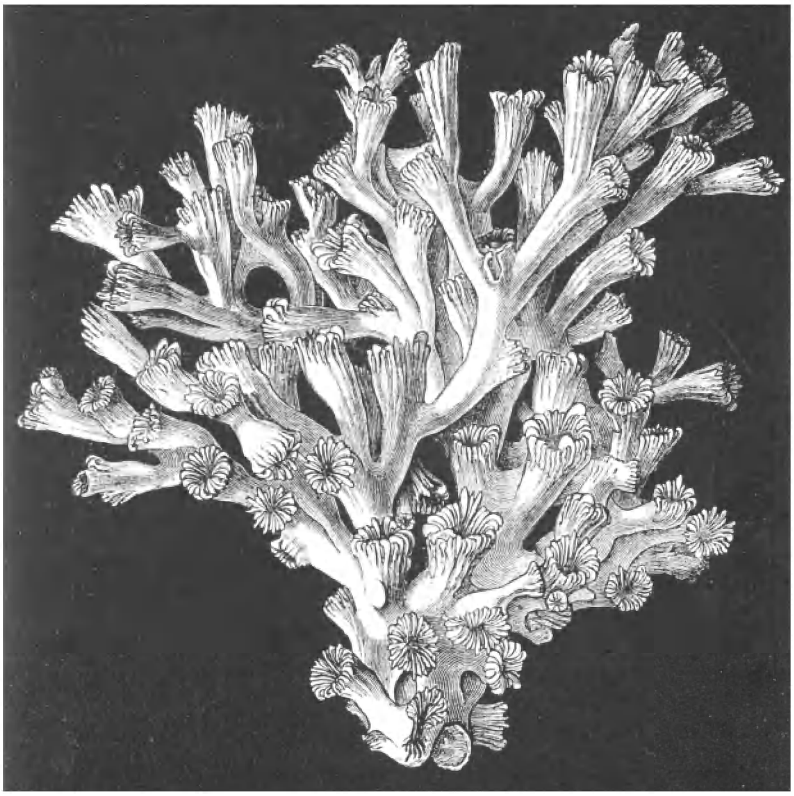

Figure 1.
Lophelia pertusa (from Wyville Thomson 1873).

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 off-shore 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

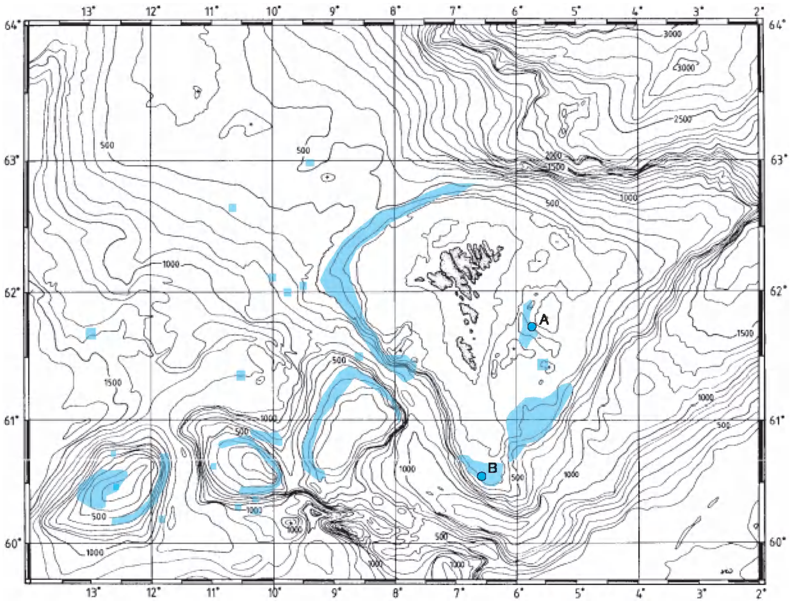

Figure 2.
Distribution of *Lophelia pertusa* in Faroe waters. A and B are localities where coral associated fauna was investigated (see Jensen & Frederiksen 1992).

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).

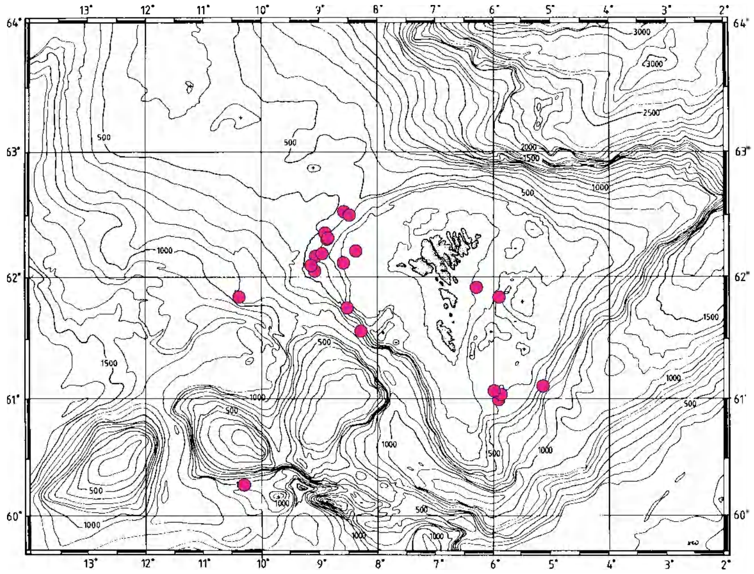

Figure 5.
Distribution of *Primnoa resedaeformis* in the Faroe area.

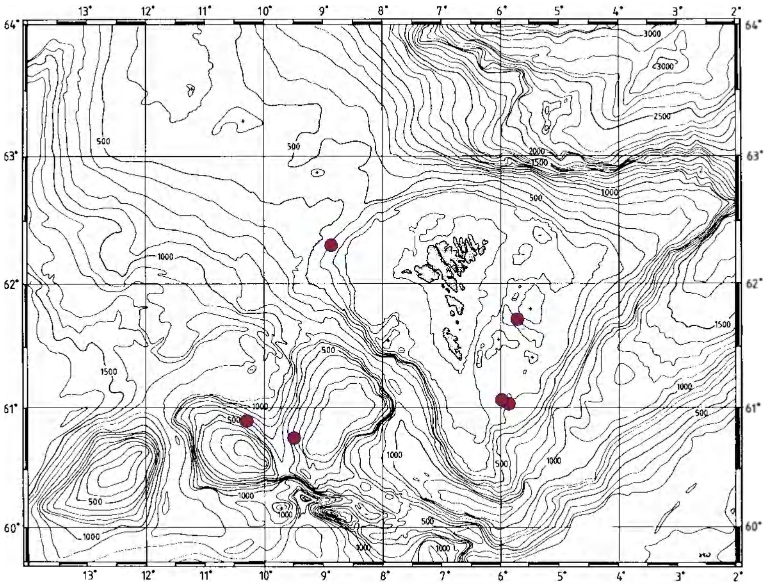

Figure 6.
Distribution of *Paragorgia arborea* in the Faroe area.

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

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 Tåning 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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