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# SURTSEY RESEARCH

## 11

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# SURTSEY RESEARCH

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# Introduction

The first report on the scientific work on the island of Surtsey was published in February 1965, one year and three months after the beginning of the submarine eruption off the southern coast of Iceland which created the island. The tenth report was published in 1992. In those reports scientists from Iceland and from abroad representing most diciplines of natural sciences of importance in this connection have carefully covered the development of Surtsey from its birth. The reports were published as "Surtsey Research Progress Reports". Due to the somewhat changed characteristics of the publication it was decided to change its name to "Surtsey Research".

During it's early years, the development of Surtsey was rapid. In later years changes have become slower. Yet, the scientific work has continued to create great interest. It continues to produce new information about the geology of a new piece of land and it's settlement by various forms of life.

The creation of Surtsey by a submarine eruption is not unique on Earth. Several new islands have been formed. On the other hand, Surtsey is, we believe, unique in that it was right in the beginning, declared as a nature reserve for the purpose of scientific research. The island has been protected from human influence and is closed to visitors without a special permit. This has made Surtsey unique for a long term study of the formation of an island and it's gradual settlement by life.

The Surtsey Research Society is responsible for control and management of Surtsey. The Society was formed soon after the eruption. Its objectives are to encourage scientific work on Surtsey, assist scientists, manage the island and to publish the results of the scientific work. This would not have been possible without assistance from several sources. The Icelandic Parliament, Althing, has for several years appropriated funds for the Society's operation, the Icelandic Coastguard has from the beginning transported scientists to and from Surtsey without charge and scientific institutions and several individuals have supported the work in various ways. This is much appreciated.

The following three scientists have been in charge of the editing and publication of this volume: Karl Gunnarsson, marine biology, Eythor Einarsson, botany and Sveinn P. Jakobsson, geology. Without their voluntary work this volume would not have been published.

For nearly 40 years dedicated scientists have done research on Surtsey often under difficult conditions. The objective has been to further man's knowledge of nature and thus contribute to life on Earth being handled in a more sustainable way. Hopefully this work will continue as long as it serves that purpose.

For the Surtsey Research Society,

*Steingrímur Hermannsson*
*chairman*

TERRESTRIAL BIOLOGY

# Vegetation succession on Surtsey, Iceland, during 1990-1998 under the influence of breeding gulls

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## ABSTRACT

Vegetation succession and soil development were studied on Surtsey, in 22 permanent plots that were set up in 1990 to 1995. The plots were on sand or lava substrate and outside or inside a gull colony that started forming on the island in 1986. The formation of the colony was followed by enhancement of plant cover in the breeding area and a sharp rise in rate of colonization of plant species not found previously on the island.

Twenty species of vascular plants were recorded within the plots in 1998, when a total of 47 species was found on the whole island. Plots outside the gull colony had on average 2 species and 6% plant cover. *Honkenya peploides* was the most prominent species in the sand plots but *Sagina procumbens* in the lava plots. Inside the gull colony 9 species were found on average in each plot and total cover was 72%. In sand plots inside the colony *Honkenya peoploids, Poa annua* and *Stellaria media* were the dominant species, but *Puccinellia distans* and *Cochlearia officinalis* in the lava plots. The soil outside the colony was high in pH (7.5) and low in total C (<0.1%). Inside the colony the soil pH (6.4) had decreased and total C (1.1%) increased.

Changes in vegetation cover and species richness have been minor in plots outside the gull colony during the study period and the dominant species *Honkenya peploides* appears to have fully colonized the sand areas. Most of the species of these areas are perennials with clonal growth. Within the gull colony plant cover and species richness have, on the other hand, incresed two to threefold. The vegetation of the gull colony is characterized by perennial and annual species adapted to disturbed and nutrient-rich habitats. Most of the species are found in bird colonies on neighbouring islands.

## INTRODUCTION

Colonization of life on Surtsey has been studied since the formation of the island. Investigation carried out in the early days revealed that microbial moulds, bacteria and fungi soon become established in the fresh volcanic substrate (Schwabe 1970, Smith 1970, Fridriksson 1975). In the summer of 1965 the first vascular plant was found growing on Surtsey, mosses became visible in 1968 and lichens were first found on the Surtsey lava in 1970 (Fridriksson 1966, Johannsson 1968, Einarsson 1969, Kristinsson 1972).

Plant colonization on Surtsey has been closely studied, the vascular plants in particular as they have been of far greater significance than mosses and lichens in the vegetation development. The island has been visited every summer and a record kept of colonizing species and their fate. Initially, each individual plant that was found on Surtsey was marked on a map and given a label. Measurements were made of its growth and development, through the summer and from year to year. Such detailed observations were possible while the number of plants on the island was relatively small and it was continued until 1978. After that time the focus has been more on particular sites on the island where the general development has been follwed. Colonization of new species has, however, continued to be monitored for the whole island (Fridriksson 1992, 2000, Magnússon *et al.* 1996).

The first twenty years of vegetation colonization and succession on Surtsey were characterized by invasion and spread of the coastal species *Honkenya peploides, Leymus arenarius* and *Mertensia maritima* which formed a simple community on the unfertile, sandy substrate on the island. Of the other seventeen species discovered on the island during that period only seven managed to become established and spread slightly but they were all insignificant in the vegetation (Fridriksson 1992, Magnússon *et al.* 1996).

In 1986 a few pairs of lesser black-backed gull *(Larus fuscus)* were found breeding on a lava terrain on the southern part of Surtsey. In the following years the number of breeding pairs increased greatly and a distinct colony was formed by the lesser black-backed gull, herring gull *(Larus argentatus)* and great black-backed gull (*Larus marinus*) that also had been breeding in the area. The formation of the gull colony marked a new era in plant colonization and succession on Surtsey as these gulls had considerably stronger impact that other breeding birds earlier established on the island.

The present paper describes a study of vegetation succession on Surtsey between 1990 and 1998. The aim of the study is to investigate plant colonization, vegetation composition and soil development under different substrate conditions and influence of birds (Magnússon *et al.* 1996). The study is based on permanent plots that have been set up in different locations on the island.

## STUDY AREA

### *General*

Surtsey was formed in a volcanic eruption, lasting from November 1963 to June 1967. At the end of the eruption the island had reached 2.7 km² in total area. During the eruption two large tephra cones were built up on the middle of the island by the main craters (Fig. 1). The highest point on Surtsey, 154 m above sea level, is on the eastern hill. The southern part of the island is formed by lava flows descending from the craters. The lava flows have to a large extent been filled in by drifting tephra sand from the hills above them. The lava in the southeasternmost part of Surtsey is though still mostly free of sand, but airborne dust has settled in hollows and fissures. The northernmost part of Surtsey is a low ness, formed by eroded material carried by the surf to the leeward side of the island (Jakobsson 1993, Fridriksson 1975, 1994). During winter sea water may wash over the ness area in extreme storms. The coastal erosion has taken its toll of Surtsey and in 1998 the island had been reduced to 1.5 km² (Jakobsson 1998).

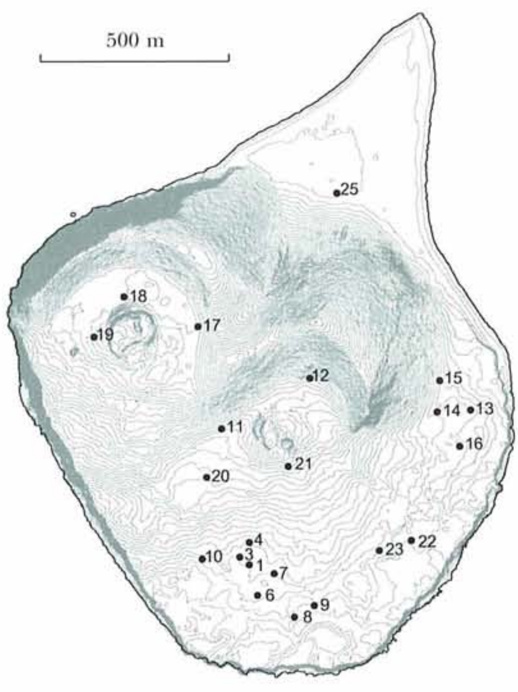


Figure 1. Location of permanent plots on Surtsey, shown on a topographical map of the island from 1998, contour intervals are 2 m. North is up in the figure. (done by: Hans Hansson, Icelandic Institute of Natural History).

Surtsey is the southernmost of the Westman islands, 7 – 35 km off the south coast of Iceland. The climate in the area is mild and oceanic. At the Heimaey weather station, 15 km from Surtsey, the mean annual temperature during 1961-1990 was 4.8°C and the mean annual precipitation was 1590 mm (Fridriksson 1994). The area is generally frost free from the first week of May until the middle of October (Einarsson 1976).

### *Nesting birds and formation of gull colony*

The Westman Islands are known for their abundance of seabirds. In the first weeks of the Surtsey eruption gulls were seen roosting on the shores of the new-born island. Ever since, birds have been important in the development of the ecosystem on Surtsey through enrichment of the soil with their excrements and dispersal of plant seeds to the island (Fridriksson 1975, 1994, 2000, Petersen 1993, Magnússon *et al.* 1996).

Fulmar (*Fulmarus glacialis)* and black guillemot *(Cepphus grylle)* were the first species of birds

Table 1. Breeding bird species on Surtsey, descriptions of nesting sites and relative impact on vegetation development, based on observations. Number of breeding pairs is taken from last bird census in 1990 (Petersen 1993).

| Species | Nesting pairs | Nesting in sea cliffs | Nesting inland | Nest made of vegetation and other materials | Effect on plant cover | Effect on colonization of new plant species |
|---|---|---|---|---|---|---|
| Fulmar | 120 | + | + | | considerable | not evident |
| Black-Guillemot | 15 | + | | | none | none |
| Great Black-backed gull | 7 | | + | + | considerable | not evident |
| Kittiwake | 5 | + | | + | slight | none |
| In gull colony: | | | + | + | profound | profound |
| Lesser black-backed gull | 120 | | | | | |
| Herring gull | 35 | | | | | |
| Great black-backed gull | 28 | | | | | |
| Glaucous gull | | | | | | |

to nest on Surtsey in 1970 when one nest of each species was found in the cliffs on the southern part of the island. In 1974 great black-backed gull started breeding on Surtsey, kittiwake *(Rissa tridactyla)* in 1975, herring gull in 1981, lesser black-backed gull in 1986 and glaucous gull *(Larus hyperboreus)* in 1993 (Petersen 1993). The effect of the bird species on the vegetation development appears to be related to their population size, selection of nesting sites and the type of nest they build (Table 1). The gull species build nests of vegetation, sea-weed, feathers and other available material while the fulmar and black guillemot do not use nest building materials or only slightly arrange pebbles under their eggs. The nests of the black guillemot and the kittiwake are confined to sea-cliffs of the island, which are very unstable and change considerably between years due to wave erosion. Vegetation has not become established at their nest sites. The kittiwake, however, roosts in great numbers on the northern ness of Surtsey and enriches the soil with excrements. In the early years the nests of the fulmar were mostly confined to the sea cliffs but in the last 15 years it has also established nest sites inland, mainly in the cliffs of the old craters where small concentrations of about 5 – 15 pairs are now found in five different locations on the island. Vegetation has not become established at the fulmar nest sites in the unstable sea cliffs but at the inland sites vegetation cover has increased considerably at most of the sites. New plant species for the island have on the other hand never been found at these fulmar nest sites. The great black-backed gull nests inland on Surtsey. During the early years the pairs were solitary with nests far apart. *Honkenya*- and *Leymus*-plants were frequently selected as nest sites but the birds also gather plants and other suitable material when they build the nest (AE. Petersen, personal communication). Plant vigor and cover was enhanced around the nests (Fridriksson 1994) but these soilitary nest sites have never been centres for colonization of new plant species on the island.

In 1986 the first nests of the lesser black-backed gull were found on a lava flat on the southern part of Surtsey. This marked the initiation of the dense gull colony on the island that now consists of the lesser black-backed, herring, great black-backed and glaucous gull (Table 1). These species, with the exception of the great black-backed gull, usually nest in colonies and the nests can be within a short distance (< 10 m) of each other (Sobey & Kenworthy 1979). They build nests that are mostly made of plant material. In the first years of the colony *Racomitrium*-moss was mainly used by the lesser black backed and herring gull for nest building but with increasing cover of vascular plants in the colony grasses and *Honkenya* have also been used (Petersen, unpublished data). The number of breeding pairs in the colony and the extent of the breeding area has increased greatly. In the last thorough bird census on Surtsey in 1990 (Petersen 1993), there were over 150 pairs in the colony (Table 1), and we estimate that the number had risen to at least 300 pairs in 1999. Most of the birds breed within a 7 ha area. The lower part of the colony is on lava terrain but the upper part on lava that has been filled with tephra sand from the slopes above. The forma-

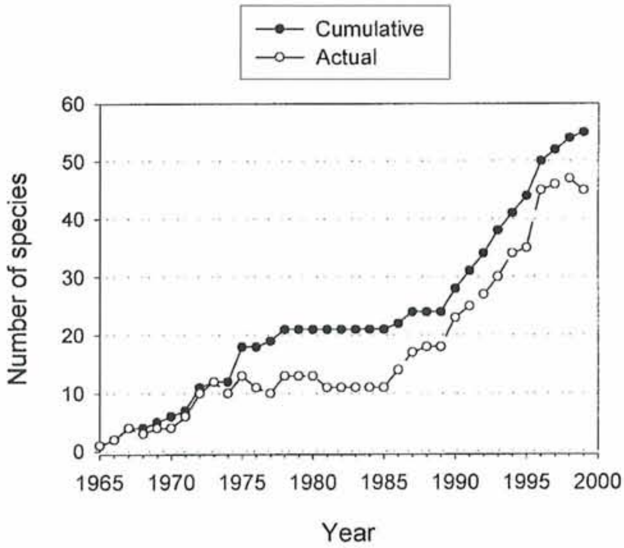


Figure 2. Number of vascular plant species found on Surtsey during 1965-1999, (based on Fridriksson & Magnusson 1992, Fridriksson 1994, 2000).

tion of the colony had immediate effects on vegetation cover within the breeding area. This gull invasion was also followed by a sharp rise in colonization of new plant species on the island (Fig. 2) and most of them were initially found within the colony area (Fridriksson 1994, 2000, Magnússon *et al.* 1996).

## METHODS

### *Permanent plots*

During 1990 to 1995 permanent plots, 10 x 10 m in size, were set up on Surtsey. The location of the plots was chosen subjectively with respect to substrate types (sand or lava) and the influence of the gulls on vegetation development in their colony on the southern part of the island. The first five plots were set up in the gull colony area in 1990, in 1994 fourteen plots were added and six in 1995 (Fig. 1, Table 2). Two of the plots (no. 2 and 5) set up in 1990 were taken out of use in subsequent years and one plot on the northern part of the island (nr. 24) was destroyed by sea-floods during the winter of 1997-1998. Therefore 22 permanent plots are currently on the island.

Eight of the plots (no. 1, 3, 4, 6-10) are within the gull colony on the southern part of the island, four plots (no. 20-23) are a short distance above or to the east of the colony where the effects of the gulls were less pronounced when the plots were established, four plots (no. 13-16) are on the easternmost part of the island, five plots (no. 11-12, 17-19) are up in the crater area and one plot (no. 25) is on the lowland ness to the north of the hills (Fig.1). The plots are 5 – 100 m above sea level, ten of the plots are on lava and twelve on sand or sand filled lava (Table 2). The plots replaced older transects set up in 1987 (Magnússon *et al.* 1996).

Table 2. Location, substrate and sampling frequency for permanent vegetation plots on Surtsey.

| Plot no. | Year of sampling | Substrate type | Location |
|---|---|---|---|
| 1, 3, 4 | 1990, 1992, 1994, 1996, 1998 | sand-filled lava | inside gull colony |
| 6-10 | 1994, 1996, 1998 | lava | inside gull colony |
| 11, 12, 15 | 1994, 1996, 1998 | sand | outside gull colony |
| 13, 14, 16-19 | 1994, 1996, 1998 | sand-filled lava | outside gull colony |
| 20, 21 | 1995, 1996, 1998 | sand-filled lava | outside gull colony |
| 22, 23 | 1995, 1996, 1998 | lava | outside gull colony |
| 25 | 1995, 1996, 1998 | sand | outside gull colony |

### *Vegetation sampling*

Vegetation sampling in the plots has generally been carried out every second year (Table 2). Five 10 m line-transects were laid across each plot, parallel at 1, 3, 5, 7 and 9 m from their western edge. Plant cover was determined by line-intercept method. All vascular plant species intercepting the line were recorded and measured and also the total cover of mosses, lichens and bare ground. Additional vascular species within the plots not intercepted by the line were also recorded.

### *Soil sampling*

In 1998 soil samples were taken from all the permanent plots. Four random samples were taken in each plot with a soil corer (7 cm diameter) down to 10 cm depth. After sampling the four samples were mixed to make a composite sample for each plot. In the laboratory the samples were dried at 40°C and sieved through a 2 mm mesh. Measurements of pH were made in an approximate 1:1 mixture with distilled water, content of organic carbon (C%) was determined using a carbon analyser (Leco Carbon Determinator, C–12) and nitrogen (N%) by the Kjeldahl method.

### *Data analysis*

DECORANA-ordination (Hill 1979) was used to investigate the vegetation similarity between individual plots and successional trends based on the data from the different sampling years. In the input data, species mean cover values were used. The CANOCO-program (ter Braak 1987) was used for the ordination analysis, selecting square-root transformation of the data and downweighing of rare species.

## RESULTS

### VEGETATION AND SOIL IN 1998

*Species richness and cover*

Twenty plant species were recorded in the 22 permanent plots in Surtsey in 1998 (Table 3) when a total of 47 species was found on the whole island. Of the 20 species, 9 were found in plots outside the gull colony and 15 in plots inside it. Only 4 species were found in plots in both areas (Table 3). The most abundant species in the permanent plots in 1998 were *Honkenya peploides, Sagina procumbens* and *Puccinellia distans.* These were the only species occurring in half of the plots or more (Fig. 3).

Vegetation cover in the plots in 1998 was around 30% on the average, with vascular plants dominating and mosses and lichens only contributing around 1% (Table 4). *Honkenya peploides* had the highest mean cover, followed

Table 3. Vascular plants recorded in permanent plots on Surtsey in 1998 and their occurrance with respect to gull colony. Nomenclature follows Kristinsson (1986).

| Species | Plots outside gull colony n=14 | Plots inside gull colony n=8 |
|---|---|---|
| **Monocots**: | | |
| *Agrostis stolonifera* | | x |
| *Agrostis capillaris* | | x |
| *Agrostis vinealis* | | x |
| *Festuca richardsonii* | | x |
| *Juncus alpinus* | x | |
| *Leymus arenarius* | x | x |
| *Poa annua* | | x |
| *Poa pratensis* | | x |
| *Puccinellia distans* | x | x |
| **Dicots**: | | |
| *Armeria maritima* | x | |
| *Cardaminopsis petraea* | x | |
| *Cerastium fontanum* | | x |
| *Cochlearia officinalis* | | x |
| *Empetrum nigrum* | | x |
| *Honkenya peploides* | x | x |
| *Matricaria maritima* | | x |
| *Mertensia maritima* | x | |
| *Sagina procumbens* | x | x |
| *Silene uniflora* | x | |
| *Stellaria media* | | x |
| Total no. of species | 9 | 15 |

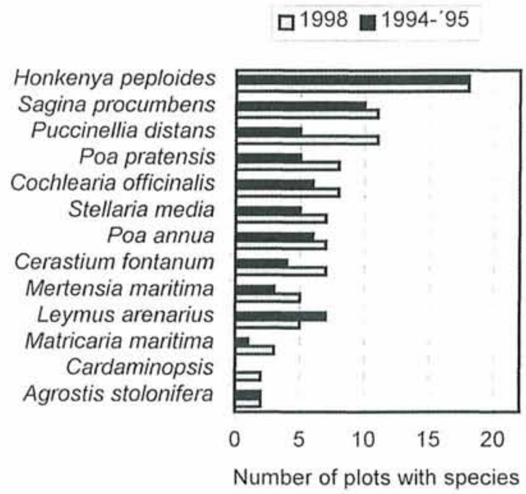


Figure 3. Relative frequency of vascular species in 22 permanent plots in Surtsey at establishment of all plots in 1994 to 1995 and in 1998. Only those species occurring in ≥ 2 plots in 1998 are shown.

by *Puccinellia distans, Poa annua, Stellaria media* and *Cochlearia officinalis,* which all reached over 1% cover.

There was a profound difference in vegetation between plots outside and inside the gull colony (Figs 4-6). Outside the colony the vegetation cover was on average only 5.5% (±2.6 s.e.) and 2.2 (±0.4 s.e.) species were found in each plot. In this area *Honkenya peploides,* was the only species with substantial cover on sand or sand-filled lava (Figs 5 and 10). *Leymus arenarius* and *Mertensia maritima* were most often associated with *Honkenya* but their cover was insignificant. In the two lava plots (no. 22 and 23) located outside the gull colony (Table 2) *Sagina procumbens* was the most prominent species but its cover was very low (<1%).

Within the plots of the gull colony the vegetation cover had reached 71.5% (±11.7 s.e.) in 1998 and 8.6 (±0.8 s.e.) plant species were found in each plot on average (Fig. 11). In the colony *Honkenya* was very abundant in plots with sandy substrate, where its cover was substantially higher than in comparable plots outside the colony. There were however signs of that *Honkenya* had begun to degenerate in the oldest plots in the colony and was giving way to competing species that had invaded the area (Fig. 5). *Poa annua* and *Puccinellia distant* have become very abundant in plots within the gull colony where they were the main dominants with *Honkenya. Puccinellia* was more confined to

Table 4. Average plant cover (%) of vascular species, mosses, lichens and bare ground in the 22 permanent plots in Surtsey in 1994 -'95 and 1998, + indicates that cover was not measureable.

| | 1994 -'95 | 1998 |
|---|---|---|
| Monocots | | |
| *Agrostis stolonifera* | 0.05 | 0.09 |
| *Agrostis capillaris* | 0.01 | 0.01 |
| *Agrostis vinealis* | absent | + |
| *Festuca richardsonii* | + | 0.91 |
| *Juncus alpinus* | + | + |
| *Leymus arenarius* | 0.01 | 0.66 |
| *Poa annua* | 1.84 | 4.67 |
| *Poa pratensis* | 0.17 | 0.48 |
| *Puccinellia distans* | 1.72 | 7.61 |
| Dicots: | | |
| *Armeria maritima* | absent | + |
| *Cardaminopsis petraea* | absent | + |
| *Cerastium fontanum* | 0.14 | 0.97 |
| *Cochlearia officinalis* | 0.53 | 2.03 |
| *Empetrum nigrum* | absent | + |
| *Honkenya peploides* | 9.25 | 9.89 |
| *Matricaria maritima* | + | + |
| *Mertensia maritima* | + | + |
| *Sagina procumbens* | 0.72 | 0.74 |
| *Silene uniflora* | + | + |
| *Stellaria media* | 0.05 | 2.66 |
| Vascular plants total: | 13.71 | 28.71 |
| *Mosses* | 1.32 | 0.79 |
| *Lichens* | + | 0.01 |
| *Bare ground* | 85.49 | 73.28 |

the lava plots while *P. annua* had higher cover in the sandy plots (Fig. 5). Other species that were common in plots of the gull colony and attained considerable cover in one or more plots were *Stellaria media, Cochlearia officinalis, Sagina procumbens, Cerastium fontanum, Festuca richardsonii, Leymus arenarius* and *Poa pratensis* (Table 4).

*Ordination results*

The results of the ordination also show a clear distinction in vegetation between sand and lava areas and the vegetation changes that have occurred within the gull colony (Fig. 7). Tightly clustered to the right on the ordinatation diagram, with the highest scores on axis 1, are plots from sand or sand-filled lava. These plots represent the initial stage in the vegetation succession on sand on Surtsey. It can be described as the *Honkenya*-stage as *H. peploides* is the only species commonly occurring in the plots and with substantial cover (Figs 5 and 10). Other species that were recorded with measureable cover in one or more these plots were *Leymus arenarius, Mertensia maritima* and *Sagina procumbens.* In the lava plots the initial stage of plant succession is characterized by colonization of *Sagina procumbens,* and may therefore be described as the *Sagina*-stage. The two plots (no. 22 and 23) representing this stage have the highest scores on axis 2 on the ordination diagram (Fig. 7). The cover of *Sagina* is, however, very low at this stage as described above.

The changes from these initial stages affected by the breeding gulls are clearly demonstrated on the diagram (Fig. 7). All the plots within the gull colony are far removed from the initial stages. The changes appear greater in the lava plots and their vegetation is also more diverse than in the sand plots within the colony. In the sand plots (1, 3 and 4) *Honkenya peploides, Poa annua* and *Stellaria media* were the dominant species and other species recorded with relatively high cover in one or more of these plots were *Cerastium fontanum, Leymus arenarius* and *Poa pratensis.* Species of less prominence but occurring in all the sand plots in the colony were *Cochlearia officinalis, Sagina procumbens* and *Puccinellia distans.* One of the lava plots (10) is

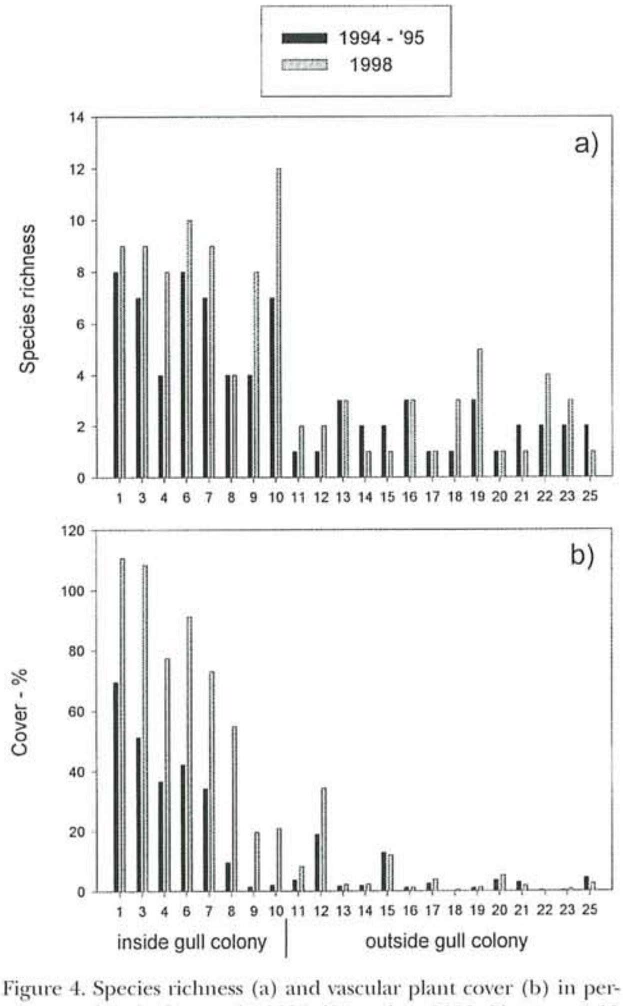


Figure 4. Species richness (a) and vascular plant cover (b) in permanent plots in Surtsey in 1994 -'95 and in 1998. Plots no. 1-10 are inside gull colony, plots no. 11-25 are outside it.

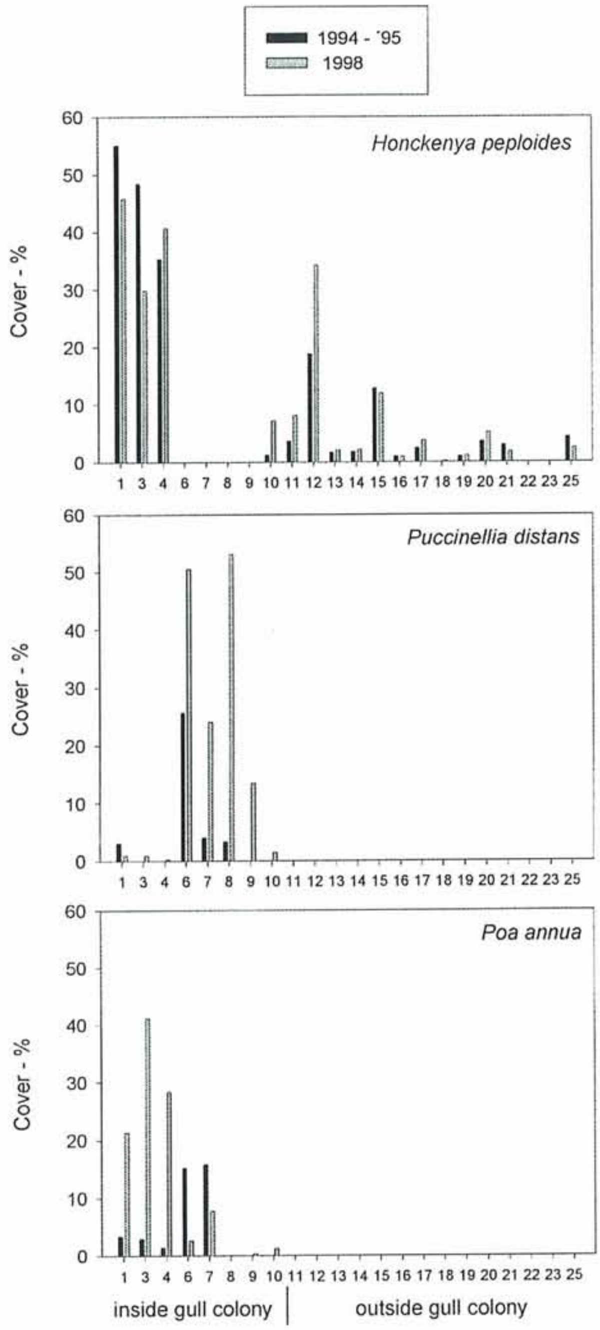


Figure 5. Cover of *Honkenya peploides, Puccinellia distans* and *Poa annua* in permanent plots in Surtsey in 1994 -'95 and 1998. Plots no. 1-10 are inside gull colony, plots no. 11-25 are outside it.

positioned close to the sand plots in the ordination results (Fig. 7). In the plot there is slight sand, which has enabled *Honkenya* to grow in it. In 1998 it was the dominant species in the plot, but otherwise the species were more characteristic of the vegetation of the gull colony. The other lava plots (6, 7, 8 and 9) of the gull colony are separated further to the left on the ordination diagram (Fig. 7). In all of these plots *Puccinellia distans* was the dominant (Fig. 5) and other species that were common to the plots was the initial colonizer *Sagina procumbens* and *Cochlearia officinalis* and *Poa pratensis*. Other species that had considerable cover in one or more of these four plots in 1998 were *Cerastium fontanum, Stellaria media, Festuca richardsonii* and *Poa annua*. It should be noted that *Honkenya* was not found in any of these plots.

*Soil results*

In the soil sampled in 1998 and analysed for pH, total C and N, there was a considerable difference between plots outside the gull colony and inside it. The soil from the gull colony was lower in pH and higher in C and N (Table 5). In plots outside the colony the pH was in the range of 6.83 – 8.04 compared to 6.17 – 6.69 inside. C and N content of the samples taken outside the colony were in most cases below limits of quantification of the methods used (0.105% for C and 0.004% for N). In samples from inside the colony total C ranged from 0.37 – 3.33% and the total N 0.03 – 0.26% (Table 5). The highest C and N levels were from plots (6 and 7) that were in the oldest part of the colony where the first breeding gull pairs were found in 1986.

Table 5. Results of analysis of soil samples taken from permanent plots in Surtsey in 1998. Plots 1-10 are inside gull colony, plots 11-25 outside it. For carbon the limit of quantification was 0,105% and 0,004% for nitrogen.

| Plot | pH | C % | N % |
|---|---|---|---|
| 1 | 6.38 | 0.647 | 0.057 |
| 3 | 6.38 | 0.576 | 0.054 |
| 4 | 6.69 | 0.366 | 0.037 |
| 6 | 6.28 | 2.534 | 0.228 |
| 7 | 6.17 | 3.329 | 0.257 |
| 8 | 6.38 | 0.827 | 0.069 |
| 9 | 6.51 | 0.427 | 0.034 |
| 10 | 6.61 | 0.429 | 0.035 |
| 11 | 8.04 | < 0.105 | < 0.004 |
| 12 | 7.57 | < 0.105 | < 0.004 |
| 13 | 7.52 | < 0.105 | < 0.004 |
| 14 | 7.55 | < 0.105 | < 0.004 |
| 15 | 7.56 | < 0.105 | < 0.004 |
| 16 | 7.39 | < 0.105 | < 0.004 |
| 17 | 8.00 | < 0.105 | < 0.004 |
| 18 | 7.50 | < 0.105 | < 0.004 |
| 19 | 7.44 | < 0.105 | < 0.004 |
| 21 | 7.60 | < 0.105 | < 0.004 |
| 22 | 6.83 | < 0.105 | 0.008 |
| 23 | 6.88 | < 0.105 | 0.006 |
| 25 | 7.67 | < 0.105 | 0.011 |
| Average: | | | |
| 1-10 | 6.42 | 1.141 | 0.096 |
| 11-25 | 7.50 | (<0.105) | (<0.004) |

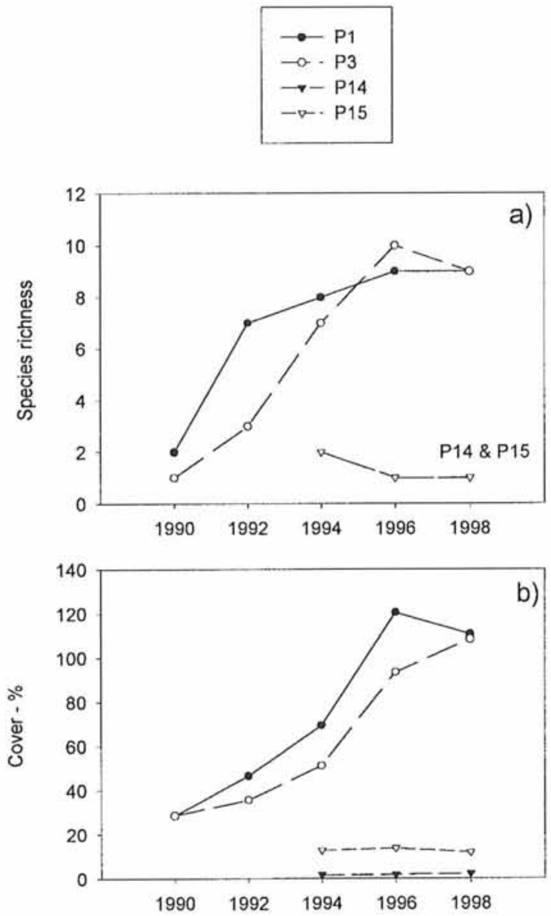


Figure 6. Changes in species richness (a) and cover (b) in plots inside (P1, P3) and outside (P14, P15) gull colony during 1990 – 1998.

The close relationship between vegetation and soil development on Surtsey and how it is affected by the breeding gulls is also demonstrated on Fig. 8, where the results of soil carbon analysis have been superimposed on the ordination results.

## VEGETATION CHANGES FROM 1990

The first permanent plots in Surtsey were set up in a sandy area of the gull colony in 1990. Repeated measurements of vegetation in these plots and other plots set up on the island in subsequent years showed a steady increase in species richness and vegetation cover. This increase is, however, mostly confined to plots within the gull colony. Outside the colony they are not as distinct (Fig. 4-6). There was only a substantial increase in cover in one plot (no. 12) outside the gull colony (Fig. 4). The plot is within 40 m of a small crater where fulmars have been nesting in increasing numbers in the last few years and are probably affecting the site.

When the first plots were established in the gull colony in 1990 the effects of the gulls on the vegetation were noticable. At that time only one to two species were found in each plot and vegetation cover was around 30% (all *Honkenya*) which was high for the island at that time. In 1998 the number of species in the plots had risen to between eight and ten and several species in addition to *Honkenya,* e.g. *Poa annua, Stellaria media, Leymus arenarius* and *Poa pratensis,* had attained a high cover in the plots. Total vegetation cover in the plots at that time had reached 100% (Figs. 6 and 11). In comparable plots, set up in 1994 outside the gull colony, there has not been an increase in species number. *Honkenya* was the only species in these plots in 1998 and its cover has not changed from 1994 (Fig. 6). The two plots (14, 15) shown in the example are from one of the oldest *Honkenya*-areas on Surtsey that was initially colonized by the species in 1968 (Fig. 10).

In the gull colony a similar trend to the sandy plots can also be seen in the lava plots when different years are compared, although the sampling period is shorter. Total vegetation cover in the lava plots in 1998 was generally lower than in the sandy plots but the species richness was comparable (Fig. 4). As described above *Sagina procumbens* was the initial colonizer of the lava plots but in the colony *Puccinellia distans* has become the main dominant. Several other species also occurred in the plots.

The relative vegetation changes in the permanent plots from 1990 to 1998 are also revealed by the ordination, when the placement of the

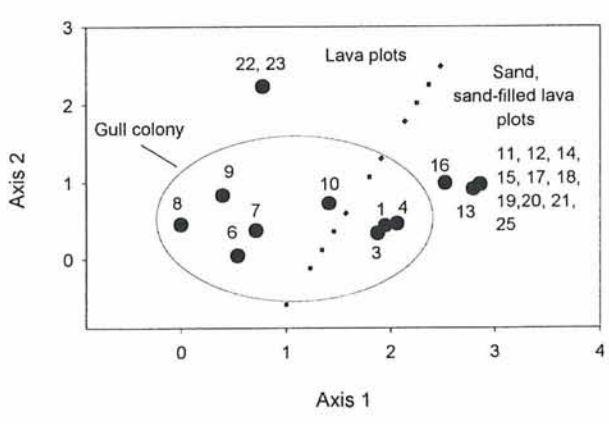


Figure 7. DECORANA-ordination results of the permanent plots on Surtsey for the year 1998.

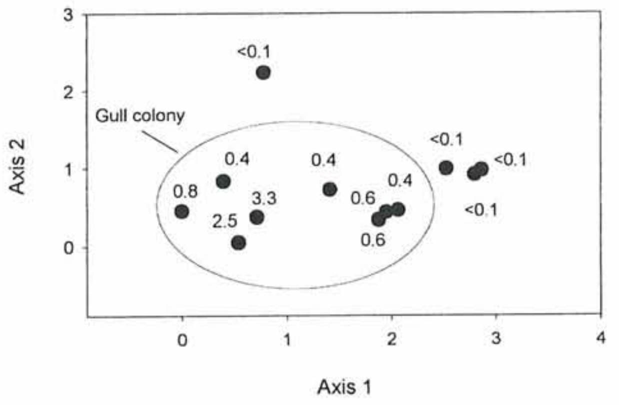


Figure 8. Results of analysis of soil carbon content in permanent plots in 1998 (C%) superimposed on the DECORANA-ordination results. Placement of plots is the same as shown on Fig. 7.

same plot in different years was studied (Fig. 9). The first two DCA axes accounted for 90% (72+18) of the variation extracted by the four axes given in the analysis. As shown on Fig. 7 and described above, the plots with the highest scores on axes 1 and 2 represent the initial stages of vegetation succession on sand (*Honkenya*-stage), (Fig. 10) and lava (*Sagina*-stage) on Surtsey. Changes or movement of plots from these stages represent successional changes influenced by the gulls in the breeding colony. The movement of plots between years on the ordination diagram (Fig. 9) are caused by changes in species composition and relative cover. Changes in species composition are due to new colonization as species have generally not been outcompeted in the plots yet. The ordination results indicate that the vegetation changes have been greatest during the first years, but slow down with increasing species richness and cover in the plots (Fig. 9).

## DISCUSSION

### *Succession outside gull colony*

On most of Surtsey relatively small vegetation changes took place in the permanent plots during the study period. The sand areas had already been colonized by coastal species, mainly *Honkenya peploides, Leymus arenarius* and *Mertentsia maritima* which all are clonal perennials (Davy & Figueroa 1993) adapted to the nutrient-poor habitats. The vegetation cover of this simple community is low (< 20%) and has generally not increased in the last years, which was also found in previous monitoring of the sand areas on eastern Surtsey during 1987 and 1994 (Magnússon *et al.* 1996). *Honkenya peploides* has been the most successful colonizer and is the dominant species on the sand (Fig. 10). The population growth of *Honkenya* on Surtsey was fast in the early years but individuals of the species started producing seeds on the island in 1971, which compares to 1977 for *Mertensia* and 1979 for *Leymus* (Fridriksson 1992, Magnússon *et al.* 1996). *Armeria maritima, Cardaminopsis petraea* and *Silene uniflora* were all recorded in permanent plots outside the gull colony in 1998. These species, which are very common on infertile gravel and sandy flats in Iceland, did not become established on the island until the period 1986-1991 (Fridriksson 1994). They have all been producing seeds on the island for a number of years and will probably become more prominent members of the sand community in the near future.

The permanent plots in the bare lava areas, outside the gull colony, have mostly been devoid of vascular plants. Only *Sagina procumbens* and *Puccinellia distans* have spread onto the lava, but total plant cover remains extremely low (< 1%). The spread of both species onto the lava areas has probably been facilitated by their high abundance within the gull colony where seeds may have been dispersed from.

The soil of Surtsey, apart from the gull colony, is poorly developed and has a relatively high pH and very low content of C and N, comparible to mobile coastal dunes (Lundberg 1987). In spite

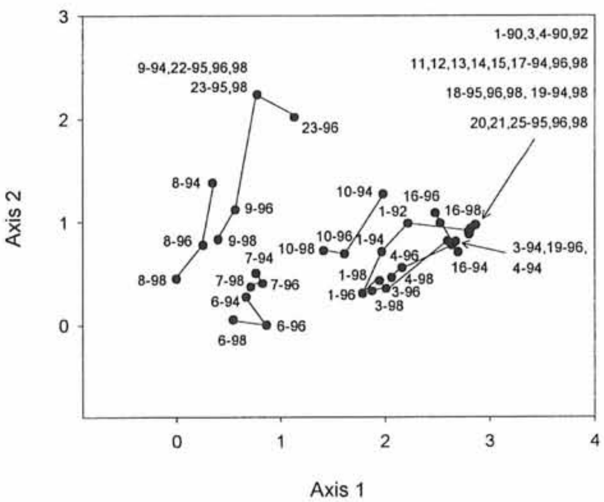


Figure 9. DECORANA-ordination results for permanent plots in the different sampling years. Lines show relative vegetation changes in individual plots between years, 1-90: plot 1 in 1990, etc. (The 1998 plots have the same positions on this diagram as on Fig. 7).

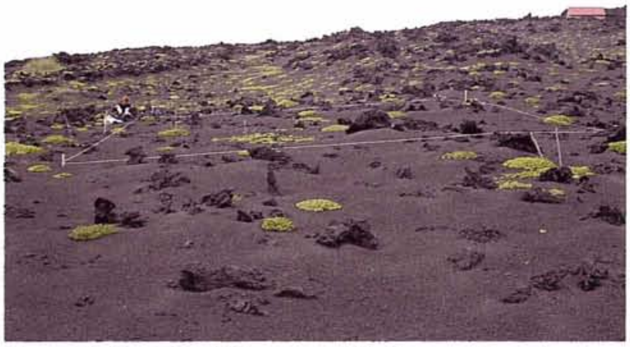

Figure 10. Plot 14 in 1998, on sand-filled lava outside gull colony. *Honkenya peploides*, had 2% cover and was the only species in the plot.

of the poor development the soils of the simple *Honkenya*-community in Surtsey have been shown to have higher root, microbial and microfaunal activity and carbon content than sand areas without vegetation on the island (Magnússon 1992, Frederiksen 1999).

*Succession within gull colony*

There were profound changes in vegetation in permanent plots within the gull colony where vegetation cover and species richness increased greatly over the study period (Fig. 11). The driving force of these changes is the nutrient enrichment of the soil by the gulls and introduction of new plant species, which also appears to be related to the activity of the gulls. At their breeding sites gulls deposit faeces and regurgitate pellets, fish and marine invertebrates are spilled on the ground during feeding of young and corpses of young and adult birds that die within the colony decompose at the sites. Nest material may also be brought into the sites. The most significant of these for the vegetation development are the faeces that have a relatively high content of nitrogen, phosphorus, potassium and minerals (Sobey & Kenworthy 1979).

The rise in the rate of colonization of new plant species on Surtsey, mostly within the gull colony, following the invasion of the lesser black-backed and the herring gull is more difficult to explain and only a speculative attempt can be made. If the colonization is primarily due to improved nutrient status of the soil within the colony, then why have the more dispersed inland nest sites of the great black-backed gull and of the fulmar never been the hotspots of colonization of new plant species? The explanation may be found in the feeding ecology of these bird species.

Both lesser black-backed and herring gull are frequently seen in grassland and hayfields in coastal areas in southern Iceland where they feed on insects and earthworms. Plant seeds may also be selected and eaten directly or indirectly with earthworms. Viable seeds have been found in the digestive tract and casts of earthworms (Grant 1983, Reest & Rogaar 1988, Thompson *et al.* 1994). Some such seeds are from the same species or genus (e.g. *Sagina procumbens, Cerastium fontanum, Stellaria media, Epilobium, Poa annua, Agrostis spp., Capsella bursa-pastoris, Taraxacum ssp.* and *Rumex spp.*) that have been found within the gull colony of Surtsey. In a study of vegetation of gull colonies (lesser black-backed, herring, great black-backed gull) on islands in Britain, Gilham (1956) found that gulls can disperse plant seeds. In regurgitated pellets viable seeds of barley and wheat were found that the gulls had carried from at least 15 – 20 km distance. In the pellets viable seeds of *Cerastium, spp., Festuca, spp., Poa annua, Polygonum aviculare, Rumex, spp., Stellaria media* and other species were also found (Gilham 1956, 1970).

The great black-backed gull depends more on fish, carcasses and spill and feeds more on the shore or out at sea than the two other gull species (Petersen, personal communication). The fulmar gets all its food from the sea and does not visit other inland areas than nesting sites. It may also matter here that the lesser black-backed and the herring gull tend to build as bulky nests as the great black-backed gull, not to mention the fulmar which does not collect material for its nest scrap (Table 1). In a study of the nest-building activities of herring gulls in Scotland it was found that the birds collected most of the plant material used for nest building near the nest sites within the colony area. A few birds, however, brought in material from outside the colony (Sobey & Kenworthy 1979). In the first years of the gull colony in Surtsey grass cover on the island was so scarce that it may have forced some of the gulls to visit the neighbouring islands (≥5 km) to collect plant material for their nests.

The vegetation succession on Surtsey has changed considerably after the formation of the gull colony. A number of new plant species have colonized the island, the nutrient status of the soil has improved which has enabled nutrient demanding plants to become established and also improved the conditions of older species on the island. The main species that have taken advantage of the improved conditions within the colony area are *Sagina procumbens, Poa annua, P. pratensis, Puccinellia distans, Cerastium fontanum, Cochlearia officinalis* and *Stellaria media*. Most of these species prefer disturbed and/or nutrient-rich habitats and have high seed production (Kristinsson 1986, Grime *et al.* 1988). *Poa annua* and *Stellaria media* are annuals, but annual species had not been able to become firmly established on Surtsey before the formation of the gull colony.

In the oldest plots in the center of the gull colony, changes in vegetation composition and cover between years appear to have slowed down in the last few years (Figs 6 and 9). With the formation of a closed sward it will be more difficult for new species to colonize the area and plants of small stature may be outcompeted. In some of the lava plots the cover of *Sagina procumbens* has started to decrease but the species has not disappeared in any of the plots yet. The vegetation of the outer Westman islands is characterized lush grassland and forb communities that are species poor and under strong influences of seabirds (Fridriksson & Johnsen 1967). All the key species of these communities, with the exception of *Angelica archangelica,* have now become established within the gull colony on Surtsey. The vegetation development within the colony will probably be into the direction of the communities found on the other islands. *Festuca richardsonii* is the dominant species in grass swards on the islands (Fridriksson & Johnsen 1967) but in the gull colony on Surtsey the species is rather infrequent in comparison to *Puccinellia distans* and *Poa annua* (Table 4). Where *Festuca* is found within the gull colony it forms very dense patches by vegetative expansion. Only one of the permanent plots (6) contains *Festuca* where its cover increased from less than 1% in 1994 to 20% in 1998, which may be indicative of the growth potential of the species.

The results of the soil analysis showed that there has been a considerable build-up of soil organic matter within the gull colony in the 13 year period from its formation (Table 5). However, the carbon content of the soil within gull colony in Surtsey is still relatively low in comparison to freely drained grassland soils in Iceland where the organic carbon is commonly in the range of 5-15% (Helgason 1968). Recent studies of the soil biota on Surtsey have demonstrated that the activity and diversity of soil organisms is much higher in the gull colony than in other habitats on the island (Frederiksen 1999, Gjelstrup 2000, Sigurdardóttir 2000).

Figure 11. Plot 1 in 1998, on sand-filled lava inside gull colony. The plot had 9 plant species in 1998 and extent of bare ground was only 8%. *Honkenya peploides* was the dominant species with 46% cover, *Poa annua, P. pratensis, Stellaria media, Cerastium fontanum* and *Leymus arenarius* had also a relatively high cover in the plot.

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# Vascular plants on Surtsey, Iceland, 1991-1998

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## ABSTRACT

The vascular plant life on Surtsey has been studied since the first plant was discovered in 1965. The dispersal, colonization and formation of communities have been monitored during the last study period of 1991-1998.

In 1998 there had been 54 vascular plant species recorded growing on Surtsey, about 85% of which are permanent residents, Of these species 75% may have been carried to Surtsey by birds, 11% by sea and 14% by air. About 80% may have derived from the other Westman Islands.

The colonization of the dry sandy lava is slow. The plant cover had increased during the study period from 5.2% to 21.4% in a quadrat, where a sand dune had been formed. In contrast, vegetation in a sea gull colony is rapidly developing, covering 6.3 hectares, about 4% of the dryland of Surtsey. The sea gulls are bringing plant seeds and increasing the soil fertility of that area by their droppings and food wastes.

## INTRODUCTION

Since the first plant was discovered on Surtsey in 1965 an annual study has been made of the vascular plant life on the island. Previously reports have regularly been given of this investigation in the Surtsey Research Progress Reports. The last one covered the period 1981-1990 (Fridriksson 1992). In addition an overview in Icelandic of the Surtsey story including the plant research has been presented in a recent book (Fridriksson 1994) and also in a special publication celebrating Surtsey´s first 30 years (Jakobsson *et al.* 1993). A report on the development of the vegetation on Surtsey as studied on permanent transects and in a number of plots has been written in Icelandic with an English summary (Magnússon *et al.* 1996). Furthermore the ecological studies have been described in an international journal (Fridriksson & Magnússon 1992). Finally it may be pointed out that news about the biological expeditions to Surtsey has annually appeared in the local paper Morgunbladid.

In this article an account will be given of some facts relating to the investigation of vascular plants and their colonization on Surtsey during the years from 1991 to the summer of 1998. A separate paper covers a study of plant succession in permanent plots on the island during the same period (Magnússon & Magnússon 2000).

## RESEARCH METHODS

From the first years of the Surtsey studies attempts have been made to monitor the colonization of vascular plants using similar methods as described by Fridriksson (1992). Individual plant species new to the island were marked on

Table 1. Vascular plant species found on Surtsey during the years 1965–1998

| | Species /Year | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Cakile arctica* | ■ | ■ | ■ |  | ■ |  |  | ■ | ■ | ■ | ■ |  | ■ | ■ | ■ | ■ |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |
| 2 | *Elymus arenarius* |  | ■ | ■ | ■ | ■ | ■ | ■ |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 3 | *Honkenya peploides* |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 4 | *Mertensia maritima* |  |  | ■ | ■ |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 5 | *Cochlearia officinalis* |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 6 | *Stellaria media* |  |  |  |  |  | ■ | ■ | ■ | ■ |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 7 | *Cystopteris fragilis* |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 8 | *Angelica archangelica* |  |  |  |  |  |  |  | ■ | ■ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ |
| 9 | *Carex maritima* |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 10 | *Puccinellia distans* |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 11 | *Matricaria maritima* |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 12 | *Festuca rubra* |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 13 | *Cerastium fontanum* |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 14 | *Equisetum arvense* |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  | ■ | ■ | ■ | ■ | ■ |
| 15 | *Silene acaulis* |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 16 | *Juncus arcticus* |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 17 | *Poa pratensis* |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 18 | *Sagina procumbens* |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 19 | *Atriplex patula* |  |  |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |  |  |
| 20 | *Rumex acetosella* |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 21 | *Cardaminopsis petraea* |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 22 | *Armeria maritima* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 23 | *Poa annua* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 24 | *Agrostis stolonifera* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 25 | *Alchemilla vulgaris* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |  |  |  |  |  |
| 26 | *Epilobium palustre* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |
| 27 | *Capsella bursa-pastoris* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |  |  |  |  |  |  |  |  |
| 28 | *Luzula multiflora* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |  |  |  |  |  |  |
| 29 | *Taraxacum spp.* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |  | ■ | ■ | ■ |
| 30 | *Rumex acetosa* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 31 | *Polygonum aviculare* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |  |  | ■ | ■ | ■ | ■ | ■ |
| 32 | *Agrostis capillaris* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |  | ■ | ■ | ■ |
| 33 | *Alopecurus geniculatus* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 34 | *Ranunculus acris* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| 35 | *Deschampsia beringensis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ |
| 36 | *Empetrum nigrum* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ |
| 37 | *Agrostis vinealis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ |  | ■ |  |  |
| 38 | *Eleocharis quinqueflora* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ | ■ |
| 39 | *Phleum pratense* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |  |
| 40 | *Montia fontana* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ |
| 41 | *Poa glauca* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ | ■ |
| 42 | *Juncus alpinus* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |
| 43 | *Salix herbaceae* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |
| 44 | *Galium normanii* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ | ■ |
| 45 | *Potentilla anserina* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |
| 46 | *Anthoxanthum odoratum* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |
| 47 | *Leontodon autumnalis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |
| 48 | *Rumex longifolius* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |
| 49 | *Polypodium vulgare* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |
| 50 | *Puccinellia maritima* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ | ■ |
| 51 | *Luzula spicata* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ |
| 52 | *Myosotis arvensis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ | ■ |
| 53 | *Salix phylicifolia* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |
| 54 | *Oxyria digyna* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ■ |
| | Total alive | 1 | 2 | 4 | 3 | 4 | 4 | 6 | 10 | 12 | 10 | 16 | 10 | 12 | 13 | 13 | 13 | 11 | 11 | 11 | 11 | 11 | 14 | 17 | 18 | 18 | 23 | 25 | 27 | 30 | 34 | 35 | 45 | 46 | 47 |

a map and staked, but in 1978 the plants had become too numerous so that surveys were carried out to estimate the frequency and cover of the vegetation on transects or in quadrats. To document the appearance of plants and colonies a number of photographs have been taken every summer, and aerial photographs have been used to locate and map individual plants and vegetative areas. The annual expeditions have taken place after mid July and lasted for a few days, except in 1991 when the island was visited in September.

## RESULTS AND DISCUSSION

### *Establishment*

It is one thing to reach a barren island, but quite another to become established and survive the unique conditions met at a sterile site, and then to go on to reproduce and become part of a new community. Considerable diversity may be found in conditions of plant growth on Surtsey. Seeds often arrive on the island, where they fall into an unfavorable habitat and do not manage to germinate or become mature plants. As conditions are relatively harsh, only the hardiest of plants have succeeded in becoming established on the frequently infertile substrate of the island.

Of all the vascular plant species that have been discovered on Surtsey, about 85% of them are permanent residents. The remaining plants have failed due to unsatisfactory conditions on the island, despite their successful arrival and first establishment. For many of them it proved impossible to occupy for any length of time the loose, dry sand, the hard lava surface or the gradually solidifying tuff. Or, as more recently, they have not withstood the rich, fertile soil and been subdued by secondary, more aggressive colonists in the newly established gull breeding area.

### *Succession*

First of the vascular plants found on Surtsey in 1965 was a sea rocket (*Cakile arctica*). A year later, lymegrass (*Elymus arenarius*, also named *Leymus arenarius*) began to grow on the island. By 1967 sea sandwort (*Honkenya peploides*) joined the flora. It has since attained a widespread distribution.

A milestone was reached when the sea sandwort began to produce seed locally. At that point, the population increase of that species was no longer totally reliant upon the accidentally transported seeds. It took six years for the sea sandwort to bear seeds. But when that occurred, thousands of new plants grew annually. Now, sea sandwort has managed to distribute itself widely throughout the island's sand filled lava. It is currently the most common of all vascular plants on Surtsey.

In the thirty-five years since its formation, 54 vascular plant species have started growth on the island (Table 1). To begin with there was on the average an introduction of at least one species of vascular plants per year during the first fourteen years period. These were mostly coastal or fell-field species. During the following seven years period there was a lag in the increase as hardly any new species arrived. It looked like the first 11-14 species would for a while be dominating in the Surtsey flora. However, during the last decade a new invasion of colonists occurred, as on the average there was an annual addition of over three new vascular plant species in the flora of Surtsey. This rapid increase is brought about by the invasion of sea gulls as will be later discussed.

Pioneer species of the vascular plants, which have become established on Surtsey, also grow on the other islands, with a few exceptions. Even though the sample on Surtsey at present is only a fraction of that within the Westman Islands region, it can be said that the new island's biota is comparable to that found elsewhere in the area.

### *Communities*

Indication of the first formation of plant association emerged when lymegrass and sea sandwort began in 1978 to spread over a sandy area in the east part of the island having their territories overlapping. The lymegrass had settled there as early as in 1974. The sandwort joined it later. These two species plus a lungwort (*Mertensia maritima*) have developed into a primitive, coastal community, which has been studied closely ever since it was formed. Here the sandwort serves as a pioneer plant holding the ground stratum, and lymegass grows above it, taking advantage of the moist sand media held in place by the former species. A plot (5x10 m) at this area has been measured, and a chart showing

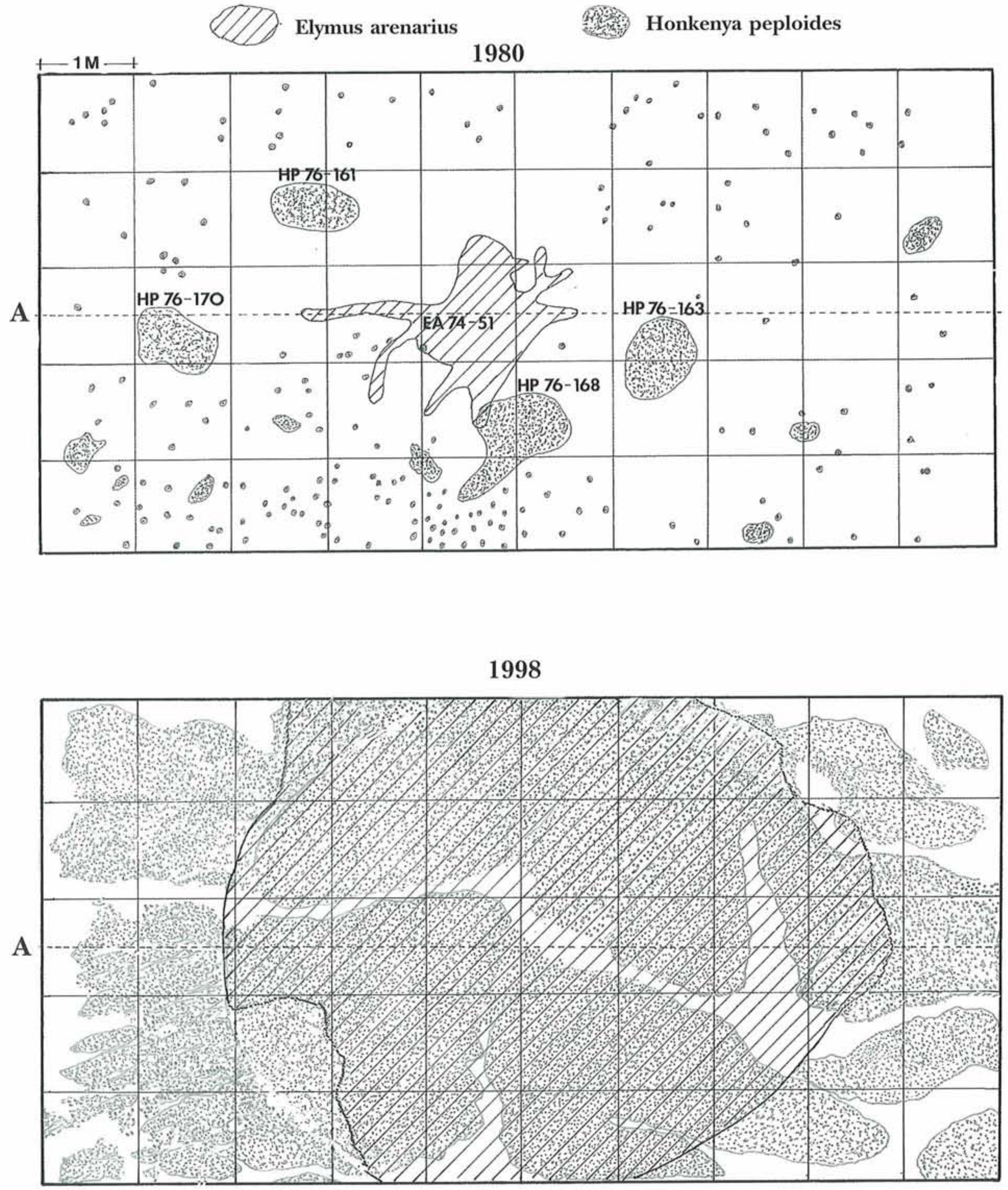


Figure 1. Distribution of two coastal plants forming a dune on Surtsey. The same study area is shown twice, first as it was in 1980 (above) and in 1998 (below). The two species, of *Elymus arenarius* and *Honkenya peploides* are now almost completely covering the plot.

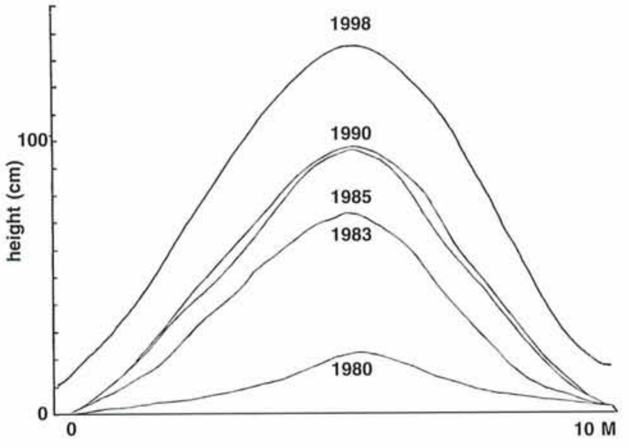


Figure 2. Transect A-B through the coastal community, shown in Fig. 1. The sand has drifted into the vegetated spot and gradually formed a dune 135 cm high.

the location of the individuals of the community has been drawn annually. Examples of the changes in development are presented here (Fig. 1).

Sand from the open beach, at this eastern side of the island, drifts to the vegetative spot, and has gradually built up a dune. This has previously been reported, but a close investigation of the formation of this sand dune has continued in the present study period. In Fig. 2 is shown how the dune has grown both in height and width. In 1998 the dune had reached the height of 135 cm, and had added 17 cm to its height in that last year. The base is over 10 m wide, and the measuring plot (5x10 m) was in 1998 over 90% covered by the two dominant species. However, on the NE side the dune has started to erode.

The lymegrass plant of the dune has flowered since 1979, making that site one of the centers of increase of this species on Surtsey. The production of successful offspring and the part this plant plays in the population increase of the species on the island has previously been discussed (Fridriksson 1992). The number of flowering spikes of the plant (No 74-51) in this dune and on one other lymegrass plant close by (No 74-78) have been counted for a number of years to monitor their fertility from time to time. The increase in flowering spikes of the former plant seems to have continued over a ten year period. After having reached a peak in 1990 the formation of spikes diminished, probably as most of the available nutrients had been used up for the advanced vegetative growth (Fig. 3).

Adjacent to the sand dune, on the eastern side of it, is a quadrat of 10x50 m on sand-filled lava. This plot has been investigated every summer for the last twelve years. The quadrat is occupied by three vascular plant species, that of *Elymus arenarius*, *Honkenya peploides* and *Mertensia maritima*.

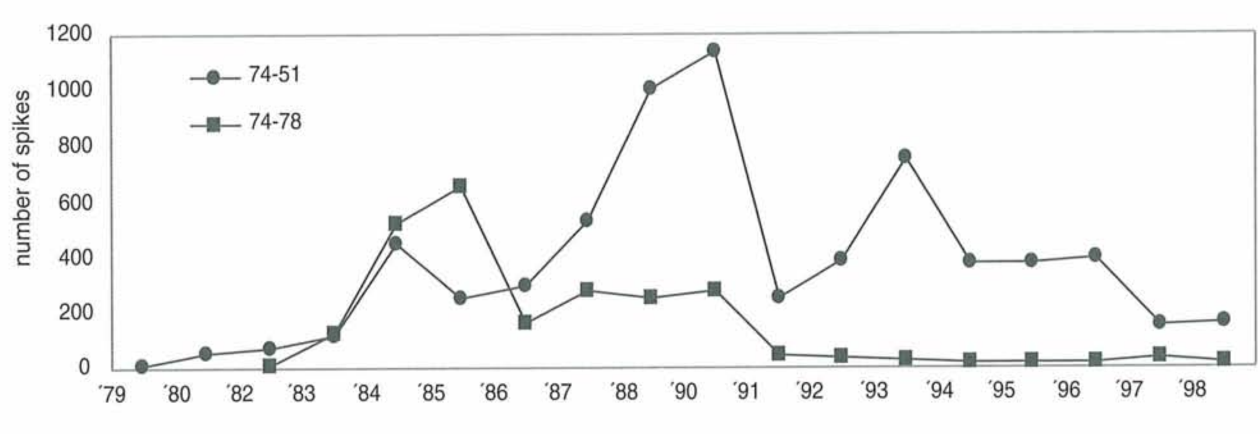


Figure 3. Number of spikes on two *Elymus* plants on Surtsey.

Table 2. Pellets from regurgitating sea gulls in Surtsey

| Contents | 1 | | 2 | | 3 | | |
|---|---|---|---|---|---|---|---|
| | DWg | % | DWg | % | DWg | % | Average% |
| *Fish* | 1.4 | 70.6 | 0.97 | 76.9 | 1.83 | 93.0 | 80 |
| *Feathers* | 0.23 | 11.6 | 0.19 | 14.8 | 0.00 | 0.0 | 9 |
| *Plant material* | 0.21 | 10.8 | 0.09 | 7.4 | 0.12 | 6.0 | 8 |
| *Sand* | 0.14 | 7.0 | 0.01 | 0.9 | 0.02 | 1.0 | 3 |
| Total | 1.98 | | 1.26 | | 1.97 | | |

In 1987 the average plant cover at this site was 5.2%, and in 1998 it had increased to 21.4%. The dominant species was *Honkenya* covering 12% of the area, *Elymus* covered 9%, whereas the *Mertensia* only occupied 0.4% of the quadrat. This site is sheltered from the strong southwestern wind and was colonized early. Black-backed gulls visit the site, but do not influence it much. It was to start with only occupied by these few coastal plant species, and there has been no further introduction of species for the last thirty years. The *Honkenya* plant patches grow to a certain size (up to 1 m$^2$) and gradually the *Elymus* plants are also advancing in size. However, this vegetation is very slowly increasing in cover, due to the limits of the quality of the habitat, and with the same progress the species there will only be forming a simple association in the future. As this vegetation may be considered rather typical of the sand-filled lava elsewhere on the island, a similar development may be expected there in comparable habitats (Fig. 4).

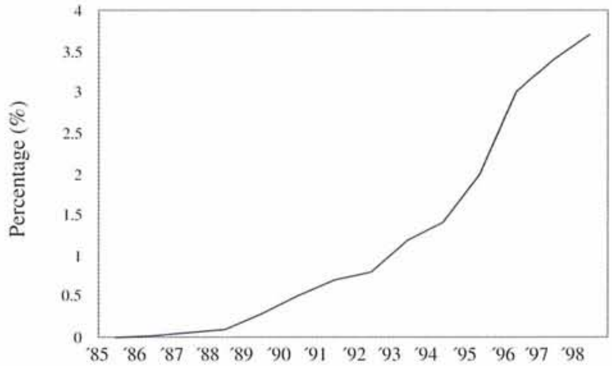

Fig. 5. Development of the vegetative area of the gull colony as percentage of the total dry land area of Surtsey.

In contrast to this slowly advancing coastal community is the rapidly developing vegetation spot on the southern side of the lava apron. Initially a few procumbent pearlworts (*Sagina procumbens*) managed to become established there, on a flat lava surface. Grasses subsequently joined, and now there exists a dense section of nitrophilous species, much like any assortment in a barnyard flora. This rapid development of communities is due to the presence of gulls that carry seeds with them to the nest sites and increase soil fertility with guano and food waste. These gulls are the lesser black-backed gull (*Larus fuscus*) and the herring gull (*Larus*


Figure 4. The sand dune community in 1997.


Figure 6. An aerial photograph of Surtsey, taken 23 August, 1998. The major plant communities appear as a green spot in the central south part of the island. The dune vegetation may be seen as a small, light dot on the central eastern coast of Surtsey. Courtesy of the National Land Survey of Iceland.

*argentatus*) that started nesting at this site in 1985. During the last fourteen years this oasis has rapidly grown in density and total area. From being a small dot on the lava in 1985, that vegetative spot now covers about 6.3 hectares, which amount to about 4 % of the total dry land area of Surtsey (Fig. 5). This may be seen as a green spot in the central southern part on the aerial photograph of

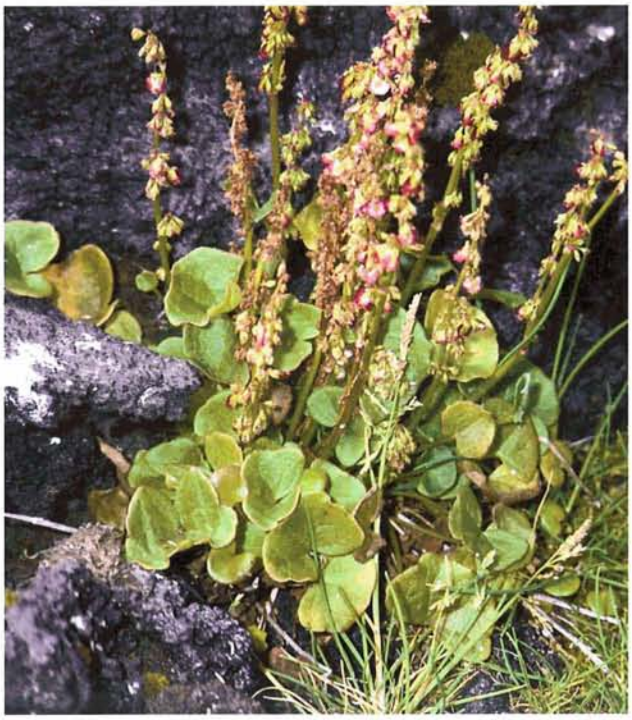

Figure 7. *Oxyria digyna*, the latest newcomer of vascular plant species to Surtsey in 1998.

the island (Fig. 6). Most of the new vascular plant species that have colonized the island since 1990 have been discovered in this area. These are 30 species found during the last nine years, which is a much higher rate of introduction of plant species to the island than in the previous years, being totally due to the various effects of the two kinds of sea gulls that occupy the territory. The latest newcomer of these species was mountain sorrel, *Oxyria digyna,* a common plant in ravines in Iceland and found growing on Heimaey, the largest of the Westman Islands (Fig. 7).

*The source and dispersal*

To demonstrate that sea gulls do carry vegetative material to the area pellets regurgitated by sea gulls at the breeding site were investigated in 1998. The material in those pellets was classed into four categories as shown in Table 2. This observation indicates that about 8 % of the food brought by sea gulls to their youngs may be of vegetative origin. The vegetative material in those pellets was mostly leaves and hulls of *Elymus-* plants. In addition three more pellets were collected. These turned out to be of pure vegetative material, mostly from common scurvygras, *Cochlearia officinalis,* but including also one seed of *Poa sp.* Such a high proportion of vegetative material in the diet might suggest that these birds had been feeding locally on the vegetation on Surtsey.

By investigating the likely dispersal routes of the plant material carried to Surtsey it was proposed (Fridriksson 1992) that 64% of the vascular plant species found on the island might have been carried by birds as to 27% by sea and 9% by air currents. However, with the formation of the sea gull colony, this proportion has changed considerably, as the corresponding figures of the plant material carried to the island in 1998 is 75% of the species by birds, 11% by sea and 14% by air.

At that time, in 1992, it was also estimated from what source the diaspores carried to Surtsey might have derived. It was suggested that some 72% of them had come from the close by source of the Westman Islands, whereas 21% might have derived from the mainland of Iceland and some 7% from a more distant source. This estimate may now also be revised, as a greater proportion of the presently found Surtsey plant species seem to come from the local area or 80%, whereas only 17% come from the mainland and 3% of the diaspores have been brought from a more distant source. These figures once more express the great effects of the lesser black-back and the herring gulls on the development of vegetation on Surtsey.

ACKNOWLEDGEMENTS

I am particularly grateful to my colleagues, who have in many ways contributed to this study. Thanks are also due to the Icelandic Coast Guard for transport to and from the island.

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# Substrate induced respiration and microbial growth in soil during the primary succession on Surtsey, Iceland

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ABSTRACT

The accumulation of organic matter and nutrients within the soil system is essential for the plant succession on Surtsey, and the soil microbial community plays a key role in this process. Microbial biomasses and activity have increased markedly during the succession from bare soil to the complex plant community established in the bird colonies. Parallel to the changes in plant cover, fungi have gained increasing importance in the soil microbial community. Today about 250 pairs of gulls nest on the southern part of the island, and the single main event stimulating succession at present probably is the nutrients deposited by these birds as droppings etc. The microbes in the soil from the bird colony inhabit an unusually nutrient rich environment where a carbon addition without supplementary nutrients will stimulate growth and thereby aid the conservation of nutrients within the system. There are still areas on the island where no plants grow, and here the microbial biomass is very low. The microbial growth in these bare soils takes place at a high rate when nutrients are available, and this could be an adaptive mechanism to retain nutrients in the soil for subsequent plant growth and thereby to mediate the primary succession from bare soil to plant cover.

## INTRODUCTION

The island of Surtsey was created by a series of volcanic eruptions in the period from November 1963 until 1967 (Fridriksson 1994), and during the following decades life became established on the bare volcanic surface. Some of the first colonisers on Surtsey were bacteria and blue-green algae (Schwabe 1970), and already in 1965 the first plants were observed (Fridriksson 1966). The question arises why some areas of the island at present have dense vegetation while others are still mostly without vegetation.

Nitrogen available for the establishment of plant growth on Surtsey may have originated from atmospheric deposition, sea spray and nitrogen fixing microorganisms, but nitrogen from organic matter washed unto the shore and bird droppings is probably more important (Fridriksson 1987). In 1985, seagulls, primarily *Larus fuscus* and *Larus argentatus*, began nesting on the lava-fields of the southern part of the island (Fridriksson 1994). As a consequence, nutrients such as nitrogen and phosphorus from the bird droppings, fish debris and dead gull chicks dramatically increased soil fertility near the nesting sites (Frederiksen *et al.* 2000).

Today the numbers of plant species are much higher and the average plant cover much denser in the bird colony than in the areas under limited influence of birds. Vegetation analyses from 1994 to 1995 (Magnússon *et al.* 1996) showed that plants covered approximately 4% of the area in the surveyed plots outside the colony. Inside the bird colony 30% of the area was covered by plants.

Many of the plants on Surtsey have produced seeds which have spread over most of the island, but in some areas they have been unable to germinate and become established as plants (Fridriksson 1992). The low success of the seeds is probably due to a combination of the sandy tephra being unstable, of the low water retention capacity and low nutrient status of the soil (Fridriksson 1992). Nitrogen and phosphorus were low in these areas due to a small and/or infrequent input, but the soil may also have a low capacity to retain nutrients from the few occasional bird droppings that actually occur in these areas. The microbial community established in these soils must be tolerant to severe food limitations. But when nutrients are introduced into the soil through bird droppings, the microbial biomass must be able to assimilate the nutrients extremely fast in order efficiently to prevent the nitrogen and phosphorus input from leaching. Magnússon (1992) measured the soil respiration, and different microbial activities were found within the different types of plant cover. Soil respiration was low in the bare soil and only slightly higher in soil with *Honkenya peploides* cover, but 50-200% higher in soil with *Elymus arenarius* cover.

The aim of this study was to study which nutrient deficits limited the microorganisms in soil during the primary succession on Surtsey, in three areas that differed in quantity and quality of plant cover, and hence illustrate three stages in the succession. We wanted to study the ability of the microbes in the bare soil to retain and utilise a sudden nutrient input, and thereby to improve the nutrient status of the soil for plant growth. Moreover we wanted to clarify whether the functional differences in the soil microbial communities occurred in parallel to differences in plant cover.

## MATERIALS AND METHODS

### *Study area*

In the summer of 1995, six plots (3x3 m) were established for survey of the soil fauna. The sites were chosen in order to obtain a succession gradient of plant communities of increasing complexity. In July 1996, soil samples were collected in the bare soil plot (J4), in the *Honkenya* plot (J3) and in the bird colony (J5) (Fig. 1).

The positions of the plots are noted in reference to the co-ordinate system which divides the island into quadrants of 100x100 m (Fridriksson 1992), and to plots established for botanical surveys by Magnússon *et al.* (1996) who investigated the plant-cover in the reference plots during 1994-1995.

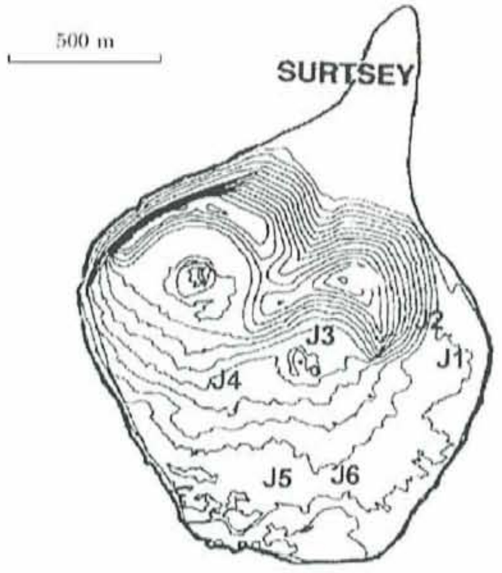


Figure 1. Map of Surtsey, which show the position of the three experimental plots. J3: *Honkenya* plot, J4: bare soil and J5: Bird Colony. No soil samples were colleted at the three other plots. Map from Jakobsson *et al.* (1992), with permission from S. Fridriksson. North is up in the figure.

The *Honkenya* patch (J3) was established in 1974, and positioned in quadrant L13; 36°-12 m south of plot 12 which had a plant cover of 19%. The smallest coastal distance was 550 m to the eastern beach, and the plot was located on a south facing slope (15°). The soil was tephra sand with *Honkenya peploides*, and some *Fulmarus glacialis* were nesting nearby.

The control with bare soil (J4) was positioned in quadrant O10 approximately 200 m northwest of plot 11 which had a plant cover of 4%. The smallest coastal distance was 300 m to the southern cliff. The soil was unvegetated tephra sand, but some root material was found in the soil samples.

The vegetation in the bird colony (J5) was established in 1983, and since 1986 gulls have been nesting. The plot was positioned in quadrant Q12; 318°-22 m south of plot 1 which had a plant cover of 70%. The smallest coastal distance was 250 m to the southern cliff. The soil was tephra sand with a dense vegetation cover primarily consisting of *Honkenya peploides, Poa pratensis, Puccinellia retroflexa, Cochlearia officinalis* and *Stellaria media. Larus fuscus* and *Larus argentatus* were nesting.

### *Sampling*

On July 23rd 1996, bulk samples each consisting of five sub-samples (36 cm², 0-5 cm) were randomly collected from each plot. The samples were placed in airtight plastic bags and stored at 5°C upon arrival in Reykjavik the following day.

*Soil respiration*

In order to investigate which nutrients limit the microbial growth, a respiration experiment was set up. 2 g samples of sieved soil (fresh weight, sieve mesh size: 2x2 mm) were placed in 116 ml serum bottles. Distilled water and nutrient solutions containing factorial combinations of C, N and P were added (i.e. $2^3 = 8$ treatments). Distilled water was added to a final liquid volume of 1.50 ml pr flask, and final concentrations in each flask were 0.278 M C as $C_6H_{12}O_6$; 0.163 M N as $NH_4\ NO_3$ and/or 0.073 M P as $KH_2PO_4$ + 0.088 M P as $Na_2\ HPO_4$. This was equal to 1.5 mg C, 0.34 mg N and/or 0.37 mg P per gram soil (fresh weight). Three replicates were prepared for each of the three soils. The serum bottles were sealed with rubber stoppers, and 10 ml atmospheric air was added in order to avoid partial vacuum during sampling. To prevent any oxygen limitations in the soil slurry, the flasks were shaken at moderate speed during the 48 hour incubation period at room temperature. Headspace gas samples (0.5 ml) were collected every 3-4 hours and analysed on a gas chromatograph equipped with a TCD and a 1.8 m x 3 mm Porapak Q column operated at 35°C.

*Direct counting of bacteria and fungi*

Three replicates from each plot were prepared for direct enumeration of bacteria and fungal hyphae by fixing 2 g fresh soil in 5 ml 0.4% formaldehyde.

Bacteria were stained with Acridine-orange (Hobbie *et al.* 1977). A 100 µl sample of the fixed suspension was added to 5 ml diluted sterile filtered acetic acid (0.15 mM, pH=4). One ml Acridine-orange (0.5 mg/ml) was added to the bacterial suspension, which was left for two min. The suspension was filtered onto a black polycarbonate filter (pore-size: 0.2 µm). Bacteria numbers were determined by direct counting using an epifluorescence microscope equipped with an eyepiece graticule (graticules Ltd, Tonbridge, UK). The number of fields inspected per filter was 30-50, and a minimum of 200 cells were counted. The biovolumes (Jenkinson *et al.* 1976) of 20 cells per filter were estimated using a Porton G12 eyepiece graticule (Graticules Ltd, Tonbridge, UK). Bacterial biomass-carbon was calculated using 310 fgC $\mu m^{-3}$ as biovolume conversion factor (Fry 1990).

The fungal hyphae were stained with Calcoflour-white (West 1988). A 800 µl sample of the fixed suspension was added to 5 ml sterile filtered, distilled water. To the hyphal suspension 1ml Calcofluor-white (6.0 mg/ml) was added, and the suspension was left for one hour at room temperature. The sample was filtered onto a black polycarbonate filter (pore-size: 0.8 µm). The hyphal length was mesured by the grid intersecting method (Olsen 1950) using an epifluorescence microscope equipped with a 10x10 squares eyepiece graticule (graticules Ltd, Tonbridge, UK). The length of a line in the grid, at 500x magnification, was 200 µm and 60 grids were inspected per filter. Fungal biomass-carbon was estimated assuming a diameter of 2 µm, and using 130 fgC $\mu m^{-3}$ as conversion factor (Van Veen & Paul 1979).

*Soil moisture and pH*

Gravimetric water content was determined after drying 10–15 g soil for 24 hours at 105°C. pH was measured in a suspension with 5.0 g (fresh weight) soil and 10ml distilled water. The suspension was shaken for 30 min and left to settle for 30 min before pH was measured. pH was also measured in collected bird droppings.

*Statistics*

Data were analysed using a one-way ANOVA or Kruskal–Wallace ANOVA on ranks and Tukey's multiple range tests were used to analyse for significant differences between the three soils.

It is possible to use the linear increase in ln (respiration rates) during the exponential phase, as an estimate of the first order growth rate of the microbial biomass (Colores *et al.* 1996). The time interval where the regression has the highest r-square is used to find the growth rate as the slope with time. Growth rates, when calculated this way, may only be valid when the microbial growth yield does not change during the period analysed.

Significant difference between two regression lines was tested using the Tukey-Kramer test.

Results from the statistical analyses are presented at the appropriate figures and tables. Sigmastat for Windows, Version 2.03 from SPSS Inc. was used to perform the statistical analyses.

RESULTS

There was a significant difference in the water content in the three soils (Table 1). The bare soil had the least water, and the soil from the colony, with the largest plant biomass, had the

Table 1. Soil pH and content of soil water (dw), standard error in parenthesis. Means with different letters are significantly different (One-way ANOVA, p<0.0001).

| | % Water | pH |
|---|---|---|
| Bare soil | 4.42[a] (0.12) | 7.9 |
| Honkenya | 6.64[b] (0.18) | 7.5 |
| Colony | 12.73[c] (0.02) | 6.5 |

most water. pH in the bare soil and in the *Honkenya* plot was 7.5 and 7.9 (Table 1). pH in the colony soil was 6.5 even though bird droppings alone had a pH of 8.0. The high content of ammonia in the guano (Bedard *et al.* 1980) probably resulted in a high nitrification activity that reduced the pH.

Initial respiration rates were very low in the bare soil and virtually unaffected by C, N and P

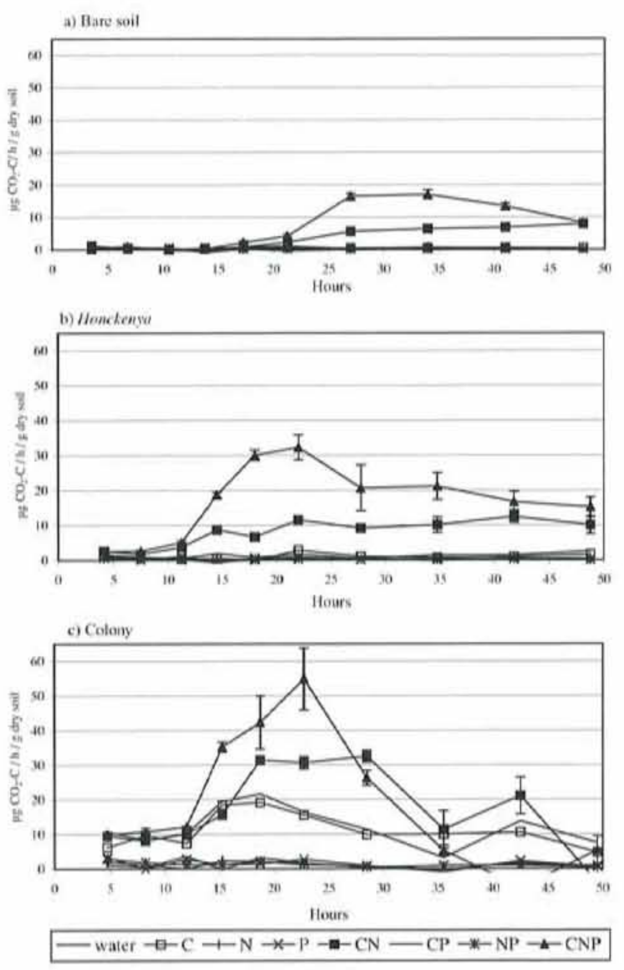


Figure 2. Substrate induced respiration rates in the bare soil plot (a), the *Honkenya* plot (b) and in the bird colony plot (c) for the following amendments: water, C, N, P, CN, CP, NP and CNP. ± standard error bars for the CN and CNP treatment.

amendments (Fig. 2a). In the *Honkenya* soil, similar respiration rates were slightly stimulated by the simultaneous addition of C and N, whereas added P had no effect (Fig. 2 b). The soil from the bird colony showed a marked increase in initial respiration rates upon C addition alone, whereas addition of N and P had no additional effect on the initial rate (Fig. 2c). This indicates that indigenous microbes in the *Honkenya* soil and the soil under the bird colony were capable of increasing their activity if supplied with a suitable substrate, in contrast to the organisms in the bare soil that showed no such response.

The maximal initial substrate induced respiration rate (SIR) has been correlated with the microbial biomass (Anderson & Domsch 1978). Using the CNP amended respiration rates from the first 3-6 hours, the estimated respiration in the three soils were significantly different (Table 2). The initial respiration rate in the bird colony soil and the *Honkenya* soil were 24 and 6 times greater than in the bare soil, indicating a much lower active microbial biomass in the bare soil. The direct counting showed a significantly higher bacterial biomass in the colony soil compared with the *Honkenya* and the bare soil (Table 2). A significant increase was also found in the hyphal biomass, which correlated with the increase in vegetation cover. The difference in fungal biomass resulted in large differences in the ratios between bacteria and fungi. The ratio was 1:1.4 in the bare soil, but 1:34.3 in the *Honkenya* soil and 1:15.2 in the soil under the bird colony. Due to the extreme nature of the bare soil and the very low respiration rate, it was not appropriate to calculate the microbial biomass in accordance with the equation found by Anderson & Domsch (1978).

The addition of C, N and P resulted in the largest respiration rate increase (i.e. growth) for all three plots, but there were differences in the time elapsed before this effect became appar-

Table 2. Initial substrate induced respiration rates after 3-6 hours of incubation with CNP, standard error in parenthesis. Means with different letters within a row are significantly different ([*]One-way ANOVA and [**]Kruskal-Wallis ANOVA on ranks, p<0.005).

| | SIR[*] µg CO2-C/h/g (dw) | Bacteria[*] µg C/g (dw) | Fungal hyphae[**] µg C/g (dw) |
|---|---|---|---|
| Bare soil | 0.41[a] (0.18) | 3.72[a] (0.48) | 5.23[a] (1.27) |
| *Honkenya* | 2.55[b] (0.10) | 2.28[a] (0.47) | 78.21[b] (0.98) |
| Colony | 9.90[c] (0.44) | 9.51[b] (1.54) | 144.36[c] (26.43) |

Table 3. Growth rates and R-square (standard error in parenthesis), estimated from best-fit regressions see text for further explanation. Means with different letters are significantly different (Tukey-Kramer test, $p<0.05$).

| | Growth h-1 | Period h | R square* |
|---|---|---|---|
| CN-addition: | | | |
| Bare soil | $0.196^{b}$ (0.022) | 17.25-27.00 | 0.92 |
| *Honkenya* | $0.176^{ab}$ (0.010) | 7.50-14.50 | 0.54 |
| Colony | $0.078^{a}$ (0.021) | 3.50-17.25 | 0.61 |
| CNP-addition: | | | |
| Bare soil | $0.285^{b}$ (0.040) | 10.50-27.00 | 0.84 |
| *Honkenya* | $0.281^{b}$ (0.029) | 7.50-18.00 | 0.93 |
| Colony | $0.111^{a}$ (0.015) | 6.75-21.25 | 0.84 |

* All regression lines were significant ($p<0.01$).

ent. The bare soil responded slowly, with a maximal respiration rate that occurred after 27-34 hours. In comparison, the *Honkenya* soil and the bird colony soil attained a maximum respiration rate after only 23 hours. Induction of growth required the addition of C as well as N in the bare soil and the *Honkenya* soil (Fig. 2a, 2b), whereas growth was induced by C addition alone, to a lower but comparable level as found with addition of C, N and P in the soil under the bird colony (Fig. 2c).

Estimating first order growth rate of the microbial biomass (Table 3) for CN and CNP addition showed that growth at a detectable level began after 3-7 hours in the soil from the bird colony, and after 8 hours in the *Honkenya* soil. Growth in the bare soil began after 10-11 hours with CNP addition, and after 17 hours when only CN was added. The growth rates were significantly lower for the microbes in the soil from the bird colony, compared with the microbes in the other two plots (Table 3). The addition of P increased growth rates by 40-60% in these soils.

Assuming that a minimum of 40% of the assimilated carbon had been respired into the headspace, it is possible to calculate the maximal percentage of glucose-C that had been mineralised by the microbes (Voroney & Paul 1984). The microbes in the colony soil were able to utilise 90% of the added glucose-C within 24 hours when C, N and P were added (Table 4). In the *Honkenya* soil, 52% were mineralised, whereas the microbes in the bare soil only managed to mineralise 4% of the added glucose-C during 24 hours. This indicates that the microbes in the fully amended incubations from the bird colony were carbon limited after 24 hours.

## DISCUSSION

In the early stages of primary succession the build-up of soil fertility requires that plant nutrients are retained within the system. The nutrients can be stored in the soil system by sorption to the organic matter or within the microorganisms. In the sandy tephra soils of Surtsey, the content of organic matter was extremely low, as 3% carbon and 0.3% nitrogen were found in the bird colony soil, in contrast to 0.2% carbon and no detectable nitrogen in soil without vegetation (Frederiksen *et al.* 2000).

There was a significant increase in the total microbial biomass determined as direct counts or as SIR during the succession. The sum of bacterial and fungal biomass in the bird colony and the *Honkenya* soils were 17 and 9 times, respectively, larger than in the bare soil. Thus there is accordance between the variation in SIR and microscopical biomass estimates between the sites. The direct estimates of fungal and bacterial biomass showed that fungi totally dominated the microbial communities in the plots with vegetation, whereas bacteria comprised 40% of the microbial biomass in the bare soil. The input of plant debris favours fungal decomposition as in the *Honkenya* soil, but the addition of easy decomposable matter such as bird droppings also facilitates bacterial growth. This could explain the relatively lower bacterial:fungal ratio in the bird colony soil

Table 4. Estimated % of glucose-C mineralised in the different treatments after 24 hours, assuming 40% of the assimilated carbon is respired into the headspace, standard error in parenthesis. Means with different letters within a row are significantly different (One-way ANOVA, $p<0.001$).

| | C - addition | CN - addition | CP - addition | CNP - addition |
|---|---|---|---|---|
| Bare soil | $0.13^{a}$ (0.18) | $1.87^{a}$ (0.31) | $1.44^{a}$ (0.28) | $4.10^{a}$ (0.41) |
| *Honkenya* | $2.46^{b}$ (0.18) | $19.27^{b}$ (0.43) | $3.79^{b}$ (0.29) | $52.00^{b}$ (2.97) |
| Colony | $42.49^{c}$ (0.55) | $60.34^{c}$ (1.37) | $48.76^{c}$ (0.66) | $90.91^{c}$ (2.57) |

(1:15.2) compared with the *Honkenya* plot (1:34.3), whereas the fungal:bacterial ratio in the bare soil was much lower (1:1.4).

The exponential growth rates with CNP additions were significantly lower in the colony soil than in the two other plots. This implies that the microbial cells in the colony soil were relatively slow in assimilating the added nutrients, compared with the equivalent microbial biomass in the *Honkenya* plot and in the bare soil. This indicates that the microbial community had a different structure in the different sites, since it is considered unlikely that micronutrients are more limiting to microbial growth in the bird colony soil than in the bare soil and *Honkenya* soil.

Communities, which are dominated by bacteria would be able to perform exponential growth in response to a sudden input of nutrients and thus exhibit a faster response than would a community dominated by fungal hyphae with a more linear growth pattern. The bird colony soil, with the highest fungal biomass, also had the lowest growth rate as compared with the two simpler communities. This could indicate that the microbial communities in the *Honkenya* soil and in the bare soil were dominated by r-strategists, whereas the bird colony soil was dominated by a mixture of r- and K- strategy microbes, which corresponds well with the theories on succession (Odum 1962).

Carbon was the primary limiting factor for microbial activity and growth in both the *Honkenya* soil and the bird colony soil communities at Surtsey, as in most decomposer communities (Swift *et al.* 1979). Carbon was able to stimulate activity but not growth in the bare soil community, and the overall respiration rate was very low in the bare soil as compared with both the colony soil and the *Honkenya* soils. The level of available nutrients was unusually high in the bird colony soil, since addition of carbon alone could induce an initial growth response similar to the response when carbon and nitrogen were added. The effect of N and in part also P was secondary, and addition of N and P resulted in an increased and prolonged growth response, but only when these nutrients were supplied in addition to C.

A depletion of the organic nutrient source could explain the decrease in growth rate at late stages of the inoculation (Stotzky & Norman 1964). In the colony soil and *Honkenya* soil with C, N and P addition, 52-90% of the added C mineralised after 24 hours. Growth also decreased in the bare soil during the late stages of incubation with C, N and P, but in this case less than 5% of the added C was mineralised. Therefore, other explanations than reduced carbon supply, for example production of inhibitory substances and/or depletion of micronutrients, were probably involved in the reduced growth rates in the bare soil.

The capacity of a soil community to utilise and store a sudden supply of nutrients has been important for the development of the Surtsey ecosystem. The ability to do so depends on the specific growth rate of the microorganisms combined with the response time and the standing biomass of the microbial community. The high growth rate of the microbes in the bare soil shows a great capacity of the cells to retain nutrients when available, and this adaptation is probably important for the accumulation of nutrients in the bare soil. But despite the higher growth rate, the microbial community in the bare soil may only be able to utilise a minor fraction of a sudden nutrient input such as a bird dropping. The long time intervals between occasional bird droppings or inputs from other nutrient sources prevent the formation of a sufficient microbial biomass, allowing the bare soil to efficiently immobilise the nutrients in a bird dropping before the nutrients are lost. In spite of the lower growth rate, the microbes in the colony soil have a great potential for utilising a sudden nutrient input as this community has a much higher standing biomass, and therefore a higher net-production rate. However, here the microbial capacity to store nutrients may be less important, due to the high concentration of soluble nutrients available for the plants.

During the more than 30 years that have elapsed since the eruptions began, a new ecosystem has evolved on Surtsey. Bacteria were established early on the island, even before the eruptions ceased (Ponnamperuma *et al.* 1967). In the following years life forms colonised the moist areas near the thermal vents and in craters, in what Schwabe (1971) called the oases of ecogenesis. Our investigations indicate that the birds currently may be the single most important factor for the further development of the ecosystem, as the level of microbial activity is significantly higher compared with the simpler communities.

The potentially fast growth of the microbial community in the bare soil is a mechanism evolved to retain introduced nutrients within the system for eventual use in plant growth. The small biomass of microbes in the bare soil and the low ability to store nutrients result in a very slow accumulation of organic matter in the bare soil, however. These results show that the establishment of plants in the bare areas on Surtsey is still strongly limited by the low nutrient status of the soil.

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# Microbial biomass and community composition in soils from Surtsey, Iceland, studied using phospholipid fatty acid analysis

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## ABSTRACT

Soil samples from Surtsey were analysed for chemical properties, number of fungal colony forming units and phospholipid fatty acid (PLFA) profiles. The temperature in the samples varied from 16 to 74°C. The microbial biomass in the samples was rather low, which may be due to environmental stress. There was a separation of the microbial communities in hot and temperate habitats as evaluated by principal component analysis. The dominating phospholipid fatty acids in hot soils were branched fatty acids, which primarily are found in Gram-positive bacteria. There are also a significant decrease in fatty acids characteristic of Gram-negative bacteria with increasing temperature.

## INTRODUCTION

One method to estimate the total microbial biomass is the extraction and quantification of phospholipid fatty acids (PLFAs), which are located in cell membranes of all living organisms (Ratledge & Wilkinson 1988). Results from the PLFA technique have been shown to correlate well with other methods for estimating microbial biomass (Federle 1986, Frostegård *et al.* 1991, Tunlid & White 1992, Zelles *et al.* 1995), and the turnover rates of PLFA after death of the organisms seem to be rather fast (White *et al.* 1979, Tollefson & McKercher 1983, Klamer & Bååth 1998).

The major advantage of using this technique is, however, the possibility to separate the microbial biomass into major taxonomic groups. This can be achieved because different groups of organisms have PLFAs, which are almost exclusively found within the group. For example 10Me16:0 (for the nomenclature of the PLFA see Materials and Methods) has been suggested as marker for *Desulfobacter* spp. in marine sediments (Dowling *et al.* 1986), and 10Me18:0 has been suggested as a marker for actinomycetes (Tunlid & White 1992). 18:2ω6,9 is almost exclusively found in eucaryotes, mainly in fungi and plants (Federle 1986, Wellburn *et al.* 1994, Zelles 1997), although it has been found in some marine bacteria (Johns & Perry 1977). In the same way one group of PLFAs are mainly found in Gram-negative (Federle 1986, Zelles 1997) and one in Gram-positive bacteria (O'Leary & Wilkinson 1988, Tunlid & White 1992, Zelles 1997). Thus compared to classic methods like, e.g. direct counts of cells and hyphae (Domsch *et al.* 1979, Elmholt & Kj¢ller 1987) and fumigation-extraction techniques (Jenkinson & Powlson 1976, Anderson & Domsch 1978), it is possible to estimate the viable biomass of both fungi and bacteria with the same technique and even within the same sample (Lechevalier & Lechevalier 1988, Frostegård & Bååth 1996).

Therefore the PLFA technique has been widely used to estimate changes in the composition of the microbial community in natural systems, e.g. aquatic systems (King *et al.* 1977, Gillan & Hogg 1984, Kieft *et al.* 1997), soils (Zelles *et al.* 1994, Bååth *et al.*

1995, Frostegård & Bååth 1996, Zogg *et al.* 1997), manure "hot spots" (Frostegård *et al.* 1997) and composts (Hellmann *et al.* 1997, Herrmann & Shann 1997, Klamer & Bååth 1998). But to our knowledge this technique has not previously been used to investigate soils with high temperatures.

In the studies of composts mentioned above the microbial communities were dominated by PLFAs common in Gram-positive bacteria during the heating phase, while marker PLFAs for fungi and Gram-negative bacteria were low or absent (see, e.g. Klamer & Bååth 1998). The marker PLFA for actinomycetes was at a constant low level during the composting experiments. The changes in PLFA profile with changes in temperature can be caused by two mechanisms. Either it is change in the composition of the cell membranes of the microorganisms present or probably more important it is a shift in the composition of the microbial community. There is some evidence that microorganisms can change the composition of the PLFAs in the cell membranes in order to tolerate increased temperature (Sumner & Morgan 1969, Mumma *et al.* 1971, Oshima & Miyagawa 1974, Suutari *et al.* 1990). These changes can be either chain elongation (Oshima & Miyagawa 1974), more saturation of the fatty acids (Mumma *et al.* 1971) or changes in the ratio of *iso*/*anteiso* branched fatty acids. These characteristics can also be found in thermophilic organisms. Thus, by just looking at these ratios it can not be elucidated if changes are due to other organisms thriving in high temperature environments, or if they are due to cell membrane changes in the same organisms that are present also in habitats with lower temperatures. However, Kaneda (1991) divided the membrane lipids in two families on basis of their synthetic pathways. One group consisted of straight-chain fatty acids, and a second group having branched fatty acids. Thus a change in the composition of PLFA to a profile containing, e.g. more branched fatty acids must be caused by a change in the composition of microorganisms in the community.

The aim of this study was to measure the microbial biomass in natural high temperature soils, and to investigate whether the changes in composition of the microbial community due to changes in temperature could be detected by the PLFA technique. In order to obtain this the PLFA profile of soil samples ranging from 16 to 74°C in temperature were compared. The PLFA profiles were evaluated by studying the main chain length of the PLFA by calculating the ratio C16/C18, the degree of unsaturation of the PLFA and the ratio between *iso* and *anteiso* branched PLFA. Finally the profiles from all samples were subject to a principal component analysis, and the changes in different subsets of the microbial community were evaluated by comparing marker PLFAs for the groups.

## MATERIALS AND METHODS

### *Sampling*

During the summer 1996 soil samples were collected at Surtsey in an area between Surtur I and II close to a crevice. Samples were taken from areas dominated with *Honkenya peploides* (L.) Ehrh., bare soil and moss, respectively. In 1997 additional samples were collected from Surtsey and Japan. On Surtsey the sample location was also between Surtur I and II, but south to the sample area of 1996. This area was characterised by scattered vegetation of *H. peploides* and *Puccinellia distans* (L.) Parl., total cover was less than 5%. The distance between hot and temperate samples was about 5 m. The soil samples from Japan were collected at the Zigokudani hot springs, Yamanouchi, Nagano, an area dominated by various coniferous trees.

The samples were air dried and stored at 5°C until analysed.

### *Chemical and fungal analysis*

pH and conductivity were measured by mixing 5 g soil with 25 ml deionised water, and at least 24 hours of extraction. The total amount of nitrogen (totN) was measured on a Leco automatic nitrogen analyser (FP-428). The total amount of carbon (totC) was calculated from loss on ignition after heating at 550°C for 6 hours, assuming the organic matter contained 50% carbon.

From the samples collected in 1996 the number of fungal colony forming units (CFU) was counted by using the soil plate technique (Warcup 1950). 0.1 g soil was plated in petri dishes and 15 ml malt extract agar (20 g/l malt extract, 15 g/l agar and 150 ppm penicillin/-streptomycin) was added. The Petri dishes were incubated at 24 and 40°C in the dark.

### *Phospholipid fatty acid analysis*

The PLFA extraction, fractionation, mild alkaline methanolysis and GC analysis used here were described in detail by Frostegård *et al.* (1991, 1993). Shortly, lipids were extracted from the soil samples in a one-phase mixture of chloroform-methanol-citrate buffer and the polar lipids were separated using silicic acid columns, followed by a mild alkaline methanolysis to form fatty acid methyl esters before GC analysis.

Fatty acids were designated in terms of total number of carbon atoms:number of double bonds, followed by the position of the double bond from the methyl end of the molecule. The prefixes a and i indicate *anteiso-* and *iso*-branching, cy indicates a cyclopropane fatty acid and methyl branching (Me) is indicated as the position of the methyl group from the carboxyl end of the chain.

The sum of the following fatty acids was considered to represent Gram-positive bacteria: i15:0, a15:0, i16:0, i17:0, a17:0 and 10Me17:0. The Gram-negative bacteria were represented by the sum of 16:17t, 16:15, cy17:0, 18:17 and cy 19:0. As marker for actinomycetes and fungi, 10Me18:0 and 18:26.9, respectively, were used.

The C16/C18 ratio was obtained by summarizing all PLFAs with a chain length of 16 and 18 carbon molecules, respectively, and calculate the ratio. The degree of unsaturation was calculated using: (12(mol% monoene) + 22(mol% diene) + 32 (mol% triene))/100.

The principal component analysis was obtained by using the mole percent data and scaling each variable to unit variance.

RESULTS

The soil samples used in this study together with temperature, chemical and microbial properties are listed in Table 1 and 2. The amount of organic matter and nitrogen in the samples from Surtsey is low compared to the samples from Japan. pH and conductivity in the samples from Surtsey showed little variation, while sample no. 16 and 17 from Japan had low pH values and high conductivity, which probably was due to high amounts of sulphur in these samples.

Table 1. Location, temperature and number of colony forming units of soil samples from Surtsey, 1996.

| Sample no. | Location | Temp. (°C) | CFU, 24°C (g soil-1) | CFU, 40°C (g soil-1) |
|---|---|---|---|---|
| 32 | Surtsey, bare soil | 21 | 45 | 20 |
| 34 | Surtsey, bare soil | 21 | 23 | 13 |
| 33 | Surtsey, bare soil | 26 | 130 | 125 |
| 31 | Surtsey, bare soil | 43 | 26 | 20 |
| 35 | Surtsey, moss | 49 | 230 | 240 |
| 37 | Surtsey, *Honkenya* | 16 | 20 | 10 |
| 39 | Surtsey, *Honkenya* | 16 | 6 | 10 |
| 41 | Surtsey, *Honkenya* | 17 | n.d. | 56 |
| 38 | Surtsey, *Honkenya* | 20 | 93 | 50 |
| 40 | Surtsey, *Honkenya* | 25 | 60 | 63 |
| 36 | Surtsey, *Honkenya* | 26 | 60 | 43 |

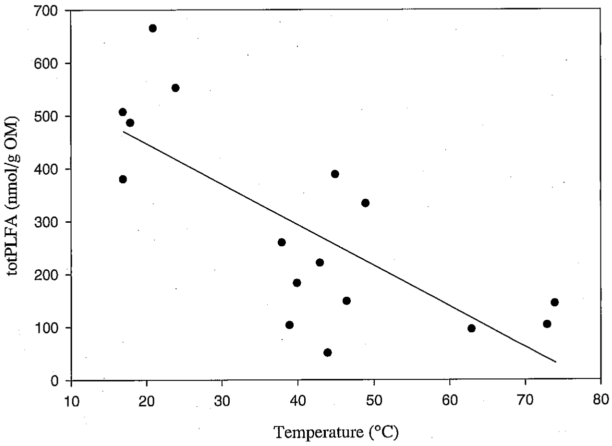


Figure 1. Total amounts of phospholipid fatty acids found in soil samples from 1997 with different temperatures.

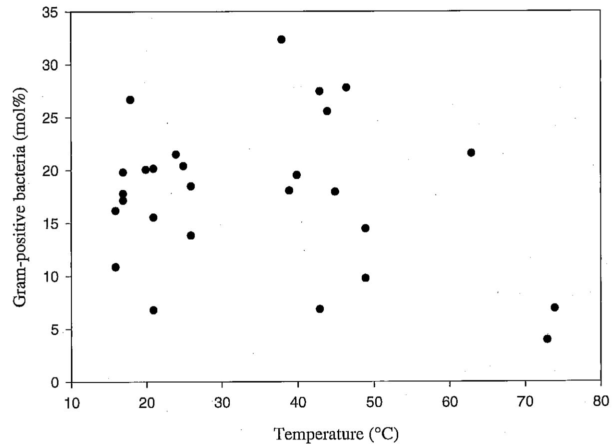


Figure 2. The relative amount of PLFAs characteristic of Gram-positive bacteria found in soil samples with different temperatures.

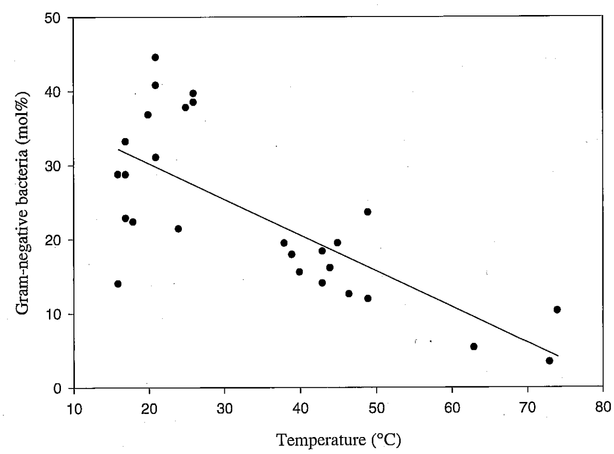


Figure 3. The relative amount of PLFAs characteristic of Gram-negative bacteria found in soil samples with different temperatures.

Table 2. Location, temperature and chemical analysis of soil samples collected in 1997.

| Sample no. | Location | Temp. (°C) | totC (% of dw) | totN (% of dw) | C/N ratio | PH | Conductivity (µS) |
|---|---|---|---|---|---|---|---|
| 1 | Surtsey 1 | 63 | 1.4 | 0.06 | 24.2 | 7.8 | 129 |
| 2 | Surtsey 2 | 73 | 1.2 | 0.12 | 9.7 | 7.6 | 91 |
| 3 | Surtsey 3 | 61 | 0.8 | 0.10 | 7.3 | 7.5 | 70 |
| 4 | Surtsey 4 | 49 | 0.6 | 0.06 | 9.6 | 7.1 | 41 |
| 5 | Surtsey 5 | 45 | 0.5 | 0.12 | 4.3 | 7.2 | 56 |
| 6 | Surtsey 6 | 74 | 1.1 | 0.10 | 11.6 | 7.6 | 90 |
| 7 | Surtsey 7 | 21 | 0.2 | 0.06 | 3.9 | 7.3 | 49 |
| 8 | Surtsey 8 | 17 | 0.3 | 0.05 | 5.9 | 7.2 | 70 |
| 9 | Surtsey 9 | 17 | 0.3 | 0.05 | 7.3 | 7.2 | 57 |
| 10 | Surtsey 10 | 18 | 0.3 | 0.04 | 7.8 | 7.4 | 58 |
| 11 | Surtsey 11 | 24 | 0.3 | 0.01 | 32.1 | 7.4 | 56 |
| 12 | Surtsey 12 | 17 | 0.3 | 0.01 | 20.7 | 7.3 | 59 |
| 16 | Japan 1 | 44 | 7.5 | 0.32 | 23.4 | 2.4 | 9320 |
| 17 | Japan 1 | 38 | 7.4 | 0.63 | 12.0 | 3.4 | 4940 |
| 18 | Japan 2 | 40 | 3.9 | 0.22 | 17.9 | 4.9 | 451 |
| 19 | Japan 3 | 43 | 4.6 | 0.22 | 20.9 | 7.2 | 146 |
| 20 | Japan 3 | 39 | 2.4 | 0.09 | 27.3 | 4.1 | 252 |
| 21 | Japan 4 | 47 | 4.7 | 0.13 | 36.9 | 6.9 | 32 |

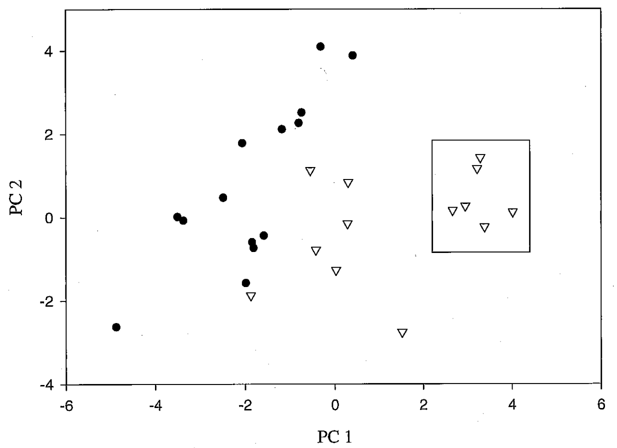


Figure 4. Principal component analysis of the soil samples. (•) samples in the temperature range 16-26°C. (∇) samples in the temperature range 38-74°C. The samples in the frame are from Japan.

In total 40 different PLFAs were detected and 34 were identified on basis of their relative retention time to the standard (19:0). In Fig. 1 the total amount of PLFA per g organic matter (nmol/g OM) found in each sample is plotted against temperature for the samples collected in 1997. There was a significant decrease in microbial biomass with increasing temperature ($r^2$=0.59, $p<0.05$). Sample no. 3 and 12 were omitted, since the amount of the most usual fatty acid, 16:0, was very low.

The marker PLFAs for Gram-positive bacteria had a tendency to increase in relative amount in the temperature interval 40-50°C (Fig. 2), although there was a large variation. The same patterns were observed for the marker PLFA for actinomycetes (data not shown).

A significant decrease in the relative amount of marker PLFAs for Gram-negative bacteria with increasing temperature was observed ($r^2$=0.52, $p<0.05$) (Fig. 3).

A principal component analysis based on the PLFA profiles of all the samples is shown in Fig. 4. A clear separation of the temperate and the high temperature soil samples was demonstrated with the temperate samples to the left and the high temperature samples to the right. The first principal component explained 20.0% of the variation and the second 12.8%. There was a significant correlation between principal component one and temperature ($r^2$=0.44, $p<0.05$), indicating that the separation along PC 1 can be explained at least partly by the changes in temperature. In addition the samples from Japan were rather close, indicating a similar microbial community in these samples. The degree of unsaturation showed a significant negative correlation with temperature ($r^2$=0.46, $p<0.05$) (Fig. 5), while C16/C18 and *iso/anteiso* ratios did not show any clear relationship with temperature (data not shown).

DISCUSSION

The total amounts of PLFA found in these soils (Fig. 1) were lower than normal. For example, Frostegård & Bååth (1996) studied a range of soils and found between 374 and 4694 nmol PLFA/g OM (mean around 2000 nmol/g OM). Using a conversion factor of 340 nmol PLFA/mg

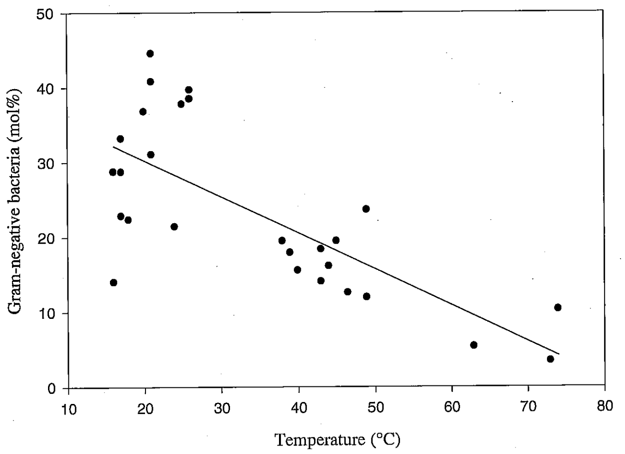


Figure 5. Correlation between the degree of unsaturation of the PLFA profiles found in soils and temperature. Sample no. 7 excluded, hence it has a degree of unsaturation of 1.33.

microbial biomass carbon and 50 % carbon of the biomass dry weight (Frostegård *et al.* 1991), the more temperate soils had around 3 mg microbial biomass decreasing to about 1 mg/g OM in the soils at higher temperature. This is very low compared to normal soil values of 10 to 30 mg/g OM (Wardle 1992). This might indicate that the soil organisms had a stressful situation even in the more temperate soils, and that increased temperatures made these conditions even more pronounced.

There was a clear separation of the temperate and high temperature samples, as seen from the PCA (Fig. 4). It is also interesting that the samples from Japan all clustered together, despite the large variation in chemical parameters (Table 2). This indicates that temperature was the main factor determining the composition of the microbial community, despite large variation also in for example pH and organic matter content between samples.

The results from this study indicate that Gram-positive bacteria are common not only in transient thermophilic habitats like composts, but also in more stable hot environments, while Gram-negative bacteria decrease in relative amount with increasing temperature. These findings are supported by data from traditional isolation techniques (see, e.g. Brock 1978, Strom 1985).

The PLFA marker for fungal presence, 18:2w6,9, constituted from 0 to 10 mol% in all the samples, without a clear relationship to temperature. This is probably caused by the fact that this PLFA also is present in plants and that a very limited number of fungi are present in the soil of Surtsey. This was illustrated by the fact that in the samples from bare soil 18:2w6,9 was absent, and a low number of fungal CFU was found (Table 1).

The degree of unsaturation seemed to be a good indicator for the temperature adaption in the community, while the ratio's C16/C18 and *iso/anteiso* did not correlate. This is partly in agreement with the findings by Klamer & Bååth (1998), who studied the PLFA profile in composts, and found good correlation between degree of unsaturation and temperature, while *iso/anteiso* ratios did not correlate.

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# Soil mites and collembolans on Surtsey, Iceland, 32 years after the eruption

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ABSTRACT

This paper represents a field study of mites and collembolans on the 32 year old eruptive island Surtsey, 30 km south of Iceland. The data were collected in July 1995. Five squares, each 3x3 $m^2$ were investigated, representing different successional communities on the island. Mites were the most numerous soil arthropods followed by collembolans. 80,000-240,000 mites and 68,000-97,000 collembolans per $m^2$ were found in and close to a gull *(Larus argentatus)* colony, dominated by the grasses *Puccinellia retroflexa*, the common meadow grass (*Poa pratensis*) and the plant common scurvy-grass *(Cochlearia officinalis)*. In a pioneer community dominated by the sea purlane *(Honkenya peploides)* and the sea lyme grass *(Leymus arenaria)* about 190,000 mites and 10,000 collembolans per $m^2$ were collected. Oribatid mites (Oribatida) were unexpectedly represented on Surtsey with 22 species, two of the species may have arrived from North America (Nearctic). All other species found on Surtsey most likely have spread from Iceland or Western Europe.

## INTRODUCTION

Lindroth *et al.* (1973) listed the mites found on Surtsey in the period from 1963-1970, (see Table 1). A survey of the occurrence of collembolans found on Surtsey in the period from 1963-1978 was made by Bödvarsson (1982). The first registration of mites on Surtsey was in 1965 and it was found on a Orthocladiin midge (fly). The first Oribatid mite (Oribatida) was found in 1966 on driftwood. The first collembolans were found on the shore in 1967 and apparently they had floated to the island on the sea. New mites and collembolans arrived each year. Most of the firstly appearing mites were found on flies and in connection with the little hut on Surtsey, whereas all collembolans collected in the period from 1965-1972 were found in connection with the shore. However, in 1976 collembolans were for the first time found in mossy vegetation on the southern lava fields far from the shore (Bödvarsson 1982).

Lindroth *et al.* (1973) and Bödvarsson (1982) found 16 species of mites and 16 species of collembolans on Surtsey. Mites most likely have arrived to the island by flies, birds, driftwood, the wind (in stormy weather) or even by man, whereas collembolans may have arrived either by the sea, the birds or the wind. However, a permanent soil fauna was not observed. Therefore it was a big challenge to investigate the soil fauna on Surtsey in July 1995.

## METHODS

The soil fauna was investigated by taking soil samples from 5 squares 3x3 m in different successional plant communities and later extracted in a modified MacFadyan apparatus. The samples in this paper were collected by the author. However, mites from samples collected by the icelandic Hólmfrídur Sigurdardóttir are also included in the results.

*Samples collected by the author were handled as follows:*

Ten samples each 5.6 cm in diameter (24.62 $cm^2$) and to a depth of 8 cm (if possible) were taken from a mini-grid, 30 x 45 cm, thrown back into each of the 3x3m grid by chance. From 10 fixed positions in the mini-grid, soil samples were taken (see Figs 1 and 2).

The samples were extracted in a modified high gradient MacFadyan (Gjelstrup & Patersen, 1987) apparatus a month later in the Mols-laboratory, The Natural History Museum, Aarhus, Denmark.

Samples were collected at different other locations on the island and the results are included in the results (Tables 2-6). 80 samples were taken on Surtsey in 1995.

Figure 1. Collection sub-area in J1. Samples were taken in the mini-grid squares to the right of string marked with white tape. Surtsey, July 1995.

*Samples collected by Hólmfrídur Sigurdardóttir were handled as follows:*

Ten samples, 7 cm in diameter (38.46 $cm^2$), and to a depth of 5 cm were taken from different fixed squares (30x30 cm) in each of the 3x3 $m^2$ areas. The samples were extracted in a modified MacFadyan apparatus a week later in Reykjavik, Iceland.

The mites from these samples were included in this paper (see Table 1-5). In another paper Sigurdardóttir (2000) publishes the results on the collembolans from her samples.

In the old bird colony (J6) it was sometimes difficult to take samples to a depth of 5-8 cm because of the lava just beneath the grass.

The main localities investigated:

J1: A *Honkenya-Leymus* community growing on loose tephra sand in the eastern part of the island, 120 m from the eastern coast line (Figs 1–2). Here *Honkenya* appeared for the first time in 1967. (The mites from this square, collected by Hólmfrídur Sigurdardóttir were lost when sent by post from Iceland to Denmark).

J3: *Honkenya peploides* community growing on loose tephra sand on the rather steep eastern slope of the island. Here *Honkenya* appeared in 1974 (Hólmfrídur Sigurdardóttir coll.).

J4: Control area with bare and loose tephra sand about 300 m from the southern coast line (Hólmfrídur Sigurdardóttir coll).

J5: Young bird colony established in the southern lava field in 1986, 250 m from the southern coast line. The plant community was dominated by *Honkenya peploides*, *Poa pratensis*, *Puccinellia retroflexa*, *Cochlearia officinalis* and the Common Chickweed (*Stellaria media*). (Hólmfrídur Sigurdardóttir coll. included).

J6: Old bird colony (with breeding birds since 1985) is situated in the middle of the southern lava field about 200 m from the southern coast line. The plant community here was dominated by *Poa pratensis* and *Puccinellia retroflexa* (Hólmfrídur Sigurdardóttir coll. included).

Besides a special area east of the old gull colony was investigated:

J6 E: A community with vegetation of *Cochlearia officinalis* and different grasses.

The above mentioned 3x3 m squares except J6 E are permanently marked. Therefore it will be possible to follow the succession of soil arthropods in those areas in the following years.

## RESULTS

*Mites- earlier arrivals*

The 16 mite species found on Surtsey in the period from 1963-1970 (Lindroth *et al.* 1973) are listed in Table 1. In the period from 1971-1976 918 specimens of mites have been collected, but not determined to species level (Ólafsson 1978).

*Oribatida (Oribatid mites)*

From 1963-1970 only 1 species of Oribatid mite *Oribotritia faeroensis* was found on Surtsey (Table 1). In 1995, however, Oribatid mites were found in most places with vegetation including in the main squares as seen from Table 2.

Table 1. Mites found on Surtsey 1963-1970.

| | 1965 | 1966 | 1967 | 1968 | 1969 | 1970 | way of transport |
|---|---|---|---|---|---|---|---|
| *Thinoseius spinosus* | 5 | | >1,000 | | | | I |
| *Oribotritia faeroensis* * | | 11 | | | | | D |
| *Myianoetus digiferus* *** | | many | | 8 | | 52 | I |
| *Ixodes ricinus* # | | | 1 | | | | B |
| *Myianoetes vesparum* *** | | | 281 | | | | I |
| *Pygmephorus mesembrianae* ** | | | | 20 | 27 | | I |
| *Tyrophagus dimidiatus* *** | | | | 27 | | 1 | H |
| *Dendrolaelaps oudemansi* | | | | 14 | | | H |
| *Haemogamasus nidi* | | | | | 1 | 1 | H D? |
| *Ixodes uriae* # | | | | | | 2 | B |
| *Caloglyphus reglei* *** | | | | | | 1 | I |
| *Machrocheles matrius* | | | | | | 1 | I |
| *Arctoseius cetratus* | | | | | | many | H |
| *Halolaelaps suecicus* | | | | | | 12 | H |
| *Cocceupodes clavifrons* ** | | | | | | 5 | H |
| *Rhagidia* sp.** | | | | | | 1 | H |
| *Protereunetes agilis* ** | | | | | | 53 | H |
| | 5 | 21 | 1,306 | 70 | 4 | 148 | 1,554 |

Gamasida (6) — I: spread by insects (6)
* Oribatida (1) — B: spread by birds (2)
** Actinedida (4) — D: spread by driftwood (1)
*** Acaridida (4) — H: possibly spread by man - found under boards near the hut or in or under the hut (8)
\# Ixodida (2)

Table 2. Oribatid mites from different communities on Surtsey, July 1995.

| | J1 | J5 | J6 | J6 E | J3F | J5F | J6F | J4F | Ex |
|---|---|---|---|---|---|---|---|---|---|
| *Hypochthonius rufulus* * | 4 | | | | | | | | |
| *Liochthonius lapponicus* * | 33 | 41 | | | 4 | 28 | 6 | | 12 |
| *Lichthonius muscorum* * | | | 8 | 1 | | | | | 28 |
| *Liochthonius propinquus* ** | 1 | | | 227 | | | | | 257 |
| *Eniochthonius minutissimus* ** | | 1 | | | | | | | |
| *Hermannia* sp. nov. *** (~*pseudonodosa*, Alaska) | | | 3 | 300 | 18 | | 23 | 6 | 2,309 |
| *Tectocepheus velatus* | 10 | 7 | | | | | | | |
| *Suctobelba subcornigera* | 2 | | 1 | | | | | | |
| *Suctobelba sarekensis* * | | | 1 | | | | | | |
| *Suctobelba acutidens* | 1 | | | | | | | | 3 |
| *Quadroppia quadricarinata* | 1 | | | | 27 | | | | 1 |
| *Quadroppia* sp. nov. *** (~*illinoiensis*, USA) | | | | 2 | | | | | |
| *Oppiella nova* * | | 1 | | | | | | | |
| *Oppiella splendens* * | | | | | 85 | | | | 106 |
| *Oppiella subpectinata* * | 1 | | | | | | | | |
| *Autogneta longilamellata*** | | | 1 | | | | | | |
| *Ameronothrus linetaus* | | | 2 | | 1 | 69 | | 71 | |
| *Ameronothrus nigrofemoratus** | | | | | | | | | 1 |
| *Zygoribatula exilis* * | | 2 | | | | | | | |
| *Chamobates cuspidatus* ** | | | 2 | | | | | | |
| *Ophidiotrichus connexus* ** | | 1 | | | | | | | |
| *Achipteria coleoptratus* | 1 | | | | | | | | |
| Total number | 54 | 53 | 18 | 530 | 135 | 28 | 98 | 6 | |
| Species | 9 | 6 | 7 | 4 | 5 | 1 | 3 | 1 | |

*: Found for the first time on the Westman Islands (16).
**: Species new to Iceland (7)
***: Species new to science (2)
~: Closely related to
J1: *Honkenya-Leymus* 1970 — J1F: (Hólmfrídur Sigurdardóttir coll.)
J5: bird colony, young — J5F: (Hólmfrídur Sigurdardóttir coll.)
J6: bird colony, old — J6F: (Hólmfrídur Sigurdardóttir coll.)
J6 E: East of the old bird colony — J4F: Control area, tephra without vegetation (Hólmfrídur Sigurdardóttir coll.)
Ex: Found elsewhere on Surtsey, 1995

Table 3. Actinedida mites found in different communities, Surtsey, July 1995.

| | J1 | J5 | J6 | J6 E | J3F | J5F | J6F | J4F | Ex |
|---|---|---|---|---|---|---|---|---|---|
| *Tarsonemus fusarii*** | 4,410 | 945 | 1,675 | 1,515 | | | | | 3,174 |
| *Nanorchestes arboriger* | | | | | | | | 3 | 4 |
| *Rhagidia mordax* | | 1 | | | 4 | 4 | 2 | | 1 |
| *Penthalodes ovalis* | | 1 | | | | 9 | | | |
| *Petrobia apicalis*** | 3 | | | | | | | | |
| *Bdella* sp | 2 | | | | | | | | 4 |
| *Neomolgus littoralis* | | | | | | | | | >50 |
| *Anystis* sp.** | 4 | | | | | | | | |
| *Bakerdania* sp. nov. *** | | | | | | | 2 | | |
| Total | 4,419 | 947 | 1,675 | 1515 | 4 | 13 | 4 | 3 | 3,233 |
| Number of species | 4 | 3 | 1 | 1 | 1 | 2 | 2 | 1 | |

Abbreviations as in Table 2

More than 3700 Oribatid mites were found representing 22 different species, which all are new to Surtsey. 5 species belong to Oribatei Inferiores (species 1-5), 11 species to Oribatei Superiores (sp. 6-18) and 4 species to Oribatei Pterogasterina (sp. 19-22). Two of the species seem to be new to science, 7 of the species new to Iceland, and 16 species new to the Westman islands.

By far the most numerous and widespread Oribatid mite species on Surtsey in 1995 were *Hermannia* sp nov. followed by *Liochthonius lapponicus* and *Liochthonis propinquus.* Most of the other species were found in very few specimens. Outside the 5 main squares investigated only 8 of the 22 oribatid mite species were found, and only one species *Ameronothrus nigrofemoratus* was found in green algae growing at two nests of the Fulmar (*Fulmarus glacialis*) on the volcano cone Surtur 1. Unexpectedly Oribatid mites were also found in soil samples from the control area without vegetation (J4) collected by Hólmfríður Sigurðardóttir. 9 species were found in the pioneer square J1 dominated by *Honkenya* and *Elymus.* In or close to the bird colony 4-7 species were found in each square, and in all 15 species were found. Oribatid mites were not found under driftwood or close to the sea. *Hermannia* sp. nov. to science were numerous in patches with single specimens of *Puccinellia pratensis* growing in the lava field close to the southern coast line of Surtsey and in many other places investigated including the zero plot J1 without vegetation at all. Most Oribatid mites are mycophagous mites or bacteria feeders.

Figure 2. Collection site J1 3x3 m with *Honkenya peploides* and *Leymus arenaria*, Surtsey, July 1995.

*Actinedida (Prostigmatic mites).*

From 1963-1970, 4 species were found on Surtsey (Table 1). None of them, however, were found in 1995 although 3 of the species, *Cocceupodes clavifrons, Rhagidia* sp. and *Protereunetes agilis* are soil living mites. In 1995 *Tarsonemus fusarii* was by far the most numerous species on Surtsey (more than 11,000 specimens collected, see Table 3). This mite species may feed on tissue of plants and/or may be a fungus feeder (Cooreman 1941). *T. fusarii* was especially numerous in the pioner community J1 with *Honkenya* and *Elymus.* Many of the other Actinedid mites found are predaceous mites eating other soil organism. One species, *Nanorchestes arboriger* is phycophagous and may consume microalgae, and *Petrobia apicalis* and *Bakerdania* sp. nov. are phytophagous.

*Neomolgus littoralis* were numerous on the shore, whereas the rest of the species are soil living species.

Table 4. Acaridida mites found on Surtsey, July 1995.

| | J1 | J5 | J6 | J6 E | J3F | J5F | J6F | J4F | Ex |
|---|---|---|---|---|---|---|---|---|---|
| *Tyrophagus similis* | | 127 | 120 | 1742 | 5 | 454 | 73 | | 379 |
| *Schwiebia cavernicola*** | 163 | | 16 | 56 | | | | | |
| *Histiostoma feroniarum* | 33 | 584 | 50 | 1518 | 1 | 1,087 | 291 | | 213 |
| *H. (hypopus)* | | | | | | 852 | | 2 | |
| Total | 196 | 711 | 186 | 3,316 | 6 | 2,393 | 364 | 2 | |
| Number of species | 2 | 2 | 3 | 3 | 2 | 2 | 2 | 1 | |

Abbreviations as in Table 2

*Acaridida (Astigmatic mites, mites of stored products)*

From 1963 - 1970, 4 species were found on Surtsey, see Table 1. Only 1 species, *Tyrophagus dimidiatus* may live in the soil. This species (= *Tyrophagus similis*, Table 4) was numerous in many of the soil samples investigated in 1995, but a new species *Histiostoma feroniarum* often dominated. The latter was mainly numerous in the bird colonies. *H. feroniarum* was found on Heimaey in 1967 by Lindroth *et al.* (1968).

A species new to Iceland, *Schwiebea cavernicola* was found in some of the samples from the gull colonies but dominated in the pioneer area J1. This species may be the same species as *Schwiebea talpa*, mentioned from northern Iceland (Hudges 1961).

The Acaridid mites found on Surtsey are supposed to be mycophagous or detritus feeders. Species of the family Anoetidae, to which the genus *Histiostoma* (Table 4) and *Myanoetus* (Table 1) belong, however, are bacteria feeders. Many acaridid mite species have a highly mobile second instar (hypopus) with suckers adapted to attach on other animals including insects, which then act as vectors (Table 1, Table 4).

On Surtsey Acaridid mites were especially numerous in and close to the gull colonies, localities J5, J6 and J6 E.

*Gamasida (Mesostigmatic mites)*

Gamasid mites were the first mites to be found on Surtsey in 1965. The species found in 1995 are soil living species. In 1995 about 2000 specimens were found, many being subadults and difficult to determine to species level. The most dominating and widespread species seems to be *Eviphis ostrinus* and *Zercon triangularis*, species new to Surtsey. In 1966-1968, however, both species were found on Heimaey and other islands south of Iceland (Lindroth *et al.* 1973).

The other species were found in few specimens. Gamasid mites were especially found in or close to the gull colonies J5, J6 and J6E.

Gamasid mites are predaceous and some species attach themselves to insects and in this way may be spread (especially *Thinoseius*, Table 1, and *Eviphis* Table 5).

Table 5. Gamasida mites found on Surtsey, July 1995.

| | J1 | J5 | J6 | J6 E | J3F | J5F | J6F | J4F | Ex |
|---|---|---|---|---|---|---|---|---|---|
| *Eviphis ostrinus* | 5 | 250 | 854 | 631 | 8 | 406 | 94 | 5 | 602 |
| *Zercon triangularis* | | 1 | 55 | | | 42 | 39 | | 38 |
| *Arctoseius* sp. nov. *** | | | | | | | | | |
| ~ *cetratus* | | | | | 5 | | | | 8 |
| *Eugamasus kraepelina* | | | 2 | | | | | | 2 |
| *Halolaelaps* sp. nov.*** | | | | | | | | | |
| ~ *porulus* | | | | 1 | | | | | |
| *Parasitus halophilus* | 1 | | | | | | | | |
| Total | 6 | 251 | 917 | 638 | 13 | 453 | 133 | 5 | |
| Species | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | |

Abbreviations as in Table 2

Table 6. Collembolans per m² found on Surtsey, July 1995.

| | J1 | J5 | J6 | J6 E | Ex |
|---|---|---|---|---|---|
| *Ceratophysella succinea** | 2,397 | | | | n |
| *Hypogastrura purpurescens** | | 55,448 | 58,332 | 90,951 | n |
| *Mesaphorura macrochaeta** | 6,134 | 2,397 | 5,037 | 4,875 | n |
| *Isotoma notabilis* | 1,503 | 14,014 | 2,437 | 609 | n |
| *Isotoma anglicana** | 130 | 325 | 1,137 | 934 | n |
| *Isotomiella minor** | | 81 | | | n |
| *Pseudisotoma sensibilis** | | 41 | | | n |
| *Onychiurus duplopunctatus#* | | | | | 78 |
| | 10,033 | 72,956 | 67,797 | 97,369 | |

EX: Other localities. *: new to Surtsey. n: not counted.
# Found under driftwood.

*Collembola (Collembolans)*

16 species of collembolans were found on Surtsey in the period from 1963-1978 (Bödvarsson 1982). In 1995, 7 species were found in the soil samples investigated, and 1 species on driftwood on the northern sea shore. The occurrence of collembolans per m² in the different areas are calculated in Table 6. Six of the eight species are new to Surtsey.

The dominating species in the gull colonies were *Hypogastrura purpurescens, Mesaphorura macrochaeta* and *Isotoma notabilis.* In the pioneer plant community J1 with *Honkenya peploides* and *Leymus arenarius, Mesaphorura macrochatea* and *Ceratophysella succinea*, new species to the fauna of Surtsey, dominated.

*The distribution of soil mites and collembolans*

When investigating soil animals on a young island as Surtsey, it is interesting to see how aggregated the animals are distributed. In Fig. 3 a Box Plot has been made for the number of mites and collembolans found in samples from the investigated areas. The boxes in Fig. 3 indicate where the central 50% of the values falls and the vertical line the median. Extreme values are indicated by a "o" and less extreme values with an asterix.

Fig. 3 illustrates that in and close to the birds colonies the central 50% values are high and rather close to each other. In samples from the pioneer areas J4 and J3 many zero-values were included in the results. Fig. 3 also illustrates that extremely high numbers of animals were found in some of the samples from the bird colony. Thus the soil fauna may be much aggregated or patchy in distribution even in the bird colony with dense vegetation of grasses.

*Total number of mites and collembolans per m² in the different sampling areas*

The total number of mites and collembolans per m² found in the plant communities have been calculated in Table 7. From the table it is seen, that mites are the most numerous group. Actinedid mites are dominating followed by acaridid and/or gamasid mites.

DISCUSSION

*Tyrophagus dimidiatus* (=*T. similis*) and *Halolaelaps cetratus* were found on Surtsey already in

Table 7. Mites and collembolans per m² in different plant communities, Surtsey, July 1995.

| | J1 | J5 | J6 | J6 E | J3F | J5F | J6F | J4F |
|---|---|---|---|---|---|---|---|---|
| Oribatida | 2,194 | 2,153 | 731 | 21,529 | 3,510 | 728 | 2,548 | 156 |
| Actinedida | 179,506 | 38,468 | 68,041 | 61,541 | 104 | 338 | 52 | 78 |
| Acaridida | 7,962 | 28,882 | 7,556 | 134,700 | 156 | 62,212 | 9,463 | 52 |
| Gamasida | 203 | 10,155 | 37,006 | 25,673 | 208 | 11,647 | 3,406 | 130 |
| Total mites/m² | 189,846 | 79,658 | 113,334 | 243,443 | 3,978 | 74,925 | 15,469 | 416 |
| Collembola/m² | 10,033 | 72,956 | 67,797 | 97,369 | 806* | 74,702* | 17,680* | 0* |
| Total/m² | 199,879 | 152,614 | 181,131 | 340,813 | 4,784 | 149,627 | 33,149 | 416 |

*: values from Hólmfridur Sigurdardóttir (2000)

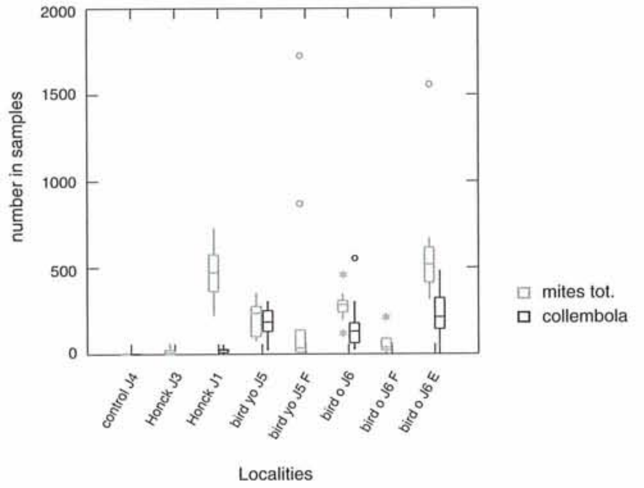


Figure 3. Box plot showing numbers of specimens of Mites and Collembolans in samples from main localities, Yo=young bird colony, o=old bird colony, Honk = *Honkenya*, Control J4=control area.

1968 and 1970 (Lindroth *et al.* 1973). The latter species may be the same as *Halolaelaps* sp. nov. in this paper. Only *T. similis* was common and widespread in 1995. Of the 16 species of collembolans found in the period from 1963-1978 (Bödvarsson 1982) only *Isotoma notabilis* was common and widespread in 1995. This confirm Bödvarsson (1982) saying that "a permanent colonization is as yet extremely doubtful".

In 1995, however, a new soil fauna was found, dominated by the Actinedid mites *Tarsonemus fusarii*, the Acaridid mite *Tyrophagus similis* and *Histiostoma feroniarum*, the Gamasid mite *Eviphis ostrinus*, the Oribatid mite *Hermannia* sp.nov. and the collembolans *Hypogastrura purpurescens*, *Mesaphorura machrochaeta* and *Ceratophysella succinea*. Especially *Eviphis ostrinus* and *Histiostoma feroniarum* may easily be spead by insects. In all 40 species of mites and 8 species of collembolans were found. 38 of the mite species and 6 species of the collembolans are new to Surtsey. Most species were found in small numbers and probably will not survive on the island.

The number of individuals per m$^2$ is very high considering Surtsey as a young island, and the number of mites were exceptionally high for pioneer communities. In comparison with these results samples from Dyrhólaey, southern Iceland, 1995 a pioneer plant community with *Honkenya peploides* and *Leymus arenara* as found on Surtsey only revealed few specimens of mites and collembolans (Gjelstrup, unpublished).

As illustrated in this paper a numerous and well established fauna of some mite and collembolan species existed on Surtsey in 1995, 32 years after the eruption. However, the combination of species may change in the future until more stable and diverse plant communities evolve. It is concluded, that many species of soil living animals easily spread to Surtsey.

The respiration of the soil arthropods may be of interest in future studies. The soil respiration was measured on Surtsey by Magnússon (1992). Also the nutrient cycling and nutrient mobilization is influenced by the soil fauna. (see also Henriksson & Henriksson 1974, 1982, Frederiksen *et al.* 2000).

Future investigations should focus on the development of the food-chains of soil animals. It would also be of interest to follow the vertical distribution of animals and if this distribution of the fauna follows the roots of the plants into the tephra material. The fauna may survive deeply in the tephra soil when the climatic conditions close to the soil surface are too extreme.

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# Status of collembolans (Collembola) on Surtsey, Iceland, in 1995 and first encounter of earthworms (Lumbricidae) in 1993

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## ABSTRACT

The distribution of collembolans was studied in plots of five different plant successional stages outside and inside the gull colony on Surtsey in 1995. Six species of collembolans were found, three of them new to the island. The dominant species were *Mesaphorura macrochaeta* outside the colony and *Hypogastrura purpurescens* inside it. In sparsely vegetated areas outside the gull colony 0 - 935 individuals $m^{-2}$ of collembolans were found on the average but in the more developed grass swards inside the colony the density was much higher or 17,680 – 74,724 individuals $m^{-2}$. The total C and N levels of the soil in the gull colony were higher than in plots outside the colony. The gull colony on Surtsey with its nutrient enrichment has had an impact on the development of the soil fauna.

In 1993 the first earthworms were found on Surtsey when two juveniles of the species *Lumbricus castaneus* (Sav.) were extracted from soil samples taken in the gull colony. In spite of a thorough search and sampling on the island in 1995 earthworms were not reencountered.

## INTRODUCTION

Colonization of soil fauna has not been closely studied on Surtsey but detailed surveys of the occurrence of mites and collembolans were made by Lindroth *et al.* (1973), Bödvarsson (1982) and Ólafsson (1978). In the first ten years after the formation of the island collembolans were found at and near the coastline but when vegetation development began upon the island the collembolans were also found there (Bödvarsson 1982). In 1986 and the following years a distinct gull colony was formed on a lava terrain on the southern part of the island. The formation of the gull colony was a turning point in plant colonization and influenced the development of the ecosystem due to enrichment of the soil by the gulls (Fridriksson 1994, Magnússon *et al.* 1996).

Collembolans together with the mites, enchytraeids and nematodes constitute the soil mesofauna. Collembolans live in the air-filled pore system of the soil and cannot make their own burrows like larger soil animals (macrofauna) as earthworms. Collembolans and earthworms also inhabit the litter layer at the soil surface.

The aim of the study, which was carried out in 1995, was to describe the collembolans at five different plant successional stages on Surtsey and to see if gulls were having an impact on the soil fauna. A second aim was to investigate if earthworms found on the island in 1993 had managed to survive.

## STUDY AREA

The soil fauna was investigated by taking soil samples from 5 plots, 3 x 3 m in size, in the vicinity of permanent vegetation study plots (Magnússon *et al.* 1996) on the southern part of the island (Fig. 1). The sampling was carried out on July 19, 1995.

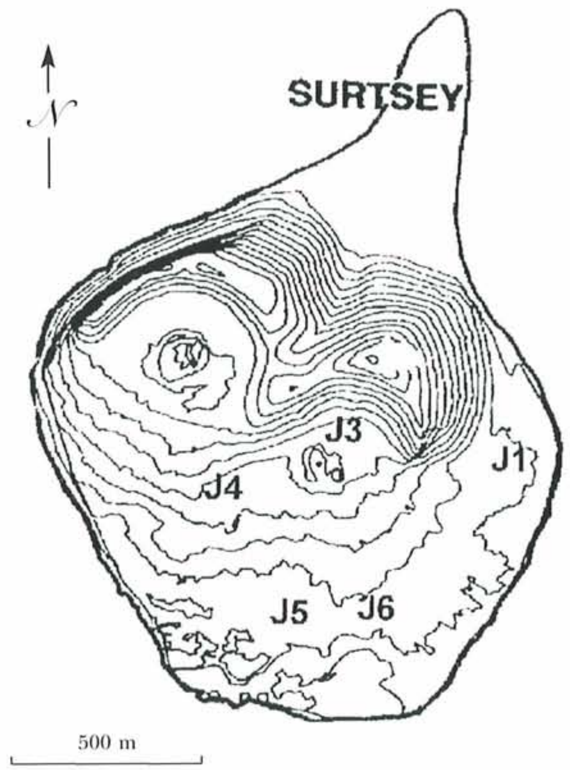


Figure 1. Location of the soil fauna plots on Surtsey.

*Unvegetated reference plot (J4).*

The plot was considered as a base-line reference. The plot was on mostly unvegetated sand. Only 4-5 seedlings of *Honkenya peploides* were found within the plot. The plot was approximately 200 m northwest of the permanent plot no. 11 in the crater area.

Honkenya *plot (J3).*

The plot was grown with developed *Honkenya peploides* colony on sand. The plot was 36° and 12 m northeast of permanent plot no. 12 in the crater area.

Honkenya-Leymus *plot (J1).*

The plot was grown with developed *Honkenya peploides* colony and *Leymus arenarius* on sand. The plot was 160° and 27 m south of permanent plot no. 13 on the easternmost part of the island.

*Young gull colony plot (J5).*

The vegetation was dominated by *Honkenya peploides, Poa pratensis, Pucinellia retroflexa, Cochlearia officinalis* and *Stellaria media*. The plot was 318° and 22 m south of permanent plot no.1 within the gull colony on the southern part of the island.

*Old gull colony plot (J6).*

Vegetation association of *Pucinellia retroflexa* and *Poa annua*. Compact layer of roots and plant residues on top of a flat lava terrain. The plot was 54° and 21 m south of permanent plot no. 6 in the old gull colony on the southern part of the island.

## METHODS

*Soil fauna sampling*

Ten random soil samples were taken in each plot with a soil corer (7 cm diameter) down to 5 cm depth. Within 3 days the collembolans and mites were extracted from the soil separately in a modified Macfadyen high gradient extractor kept running for 8 days, during which time temperature was increased from 10 to 60°C (Sigurdardóttir 1990). Total number of collembolans was determined. A small subsample of specimens from different samplings and plots was sent to Dr Arne Fjellberg, Norway who identified them to species. The aim was strictly to ascertain which species were dominant in the plots and no attempt was made to find difference in species composition between plots. Extracted mites were sent to Dr Peter Gjelstrup, the Natural History Museum, Aarhus, Denmark. Enchytraides were also extraxted from the soil samples but not identified to species.

In the annual expedition of plant ecologists to Surtsey, soil samples were taken in the gull colony with a soil corer (7 cm diameter) down to 5 cm depth, on August 15, 1993. Earthworms were extracted from the soil separately in a modified Macfadyen high gradient extractor as described above.

*Soil sampling*

Three random samples were taken in plot J1, J5 and J6 with a soil corer (7 cm diameter) down to 5 cm depth and mixed for each plot. The samples were sieved through 2 mm mesh and dried at 40°C. Organic carbon content (% C) and nitrogen (%N) content was determined.

## RESULTS

*Collembolans*

Five species of collembolans were found in the plots on Surtsey in 1995 and one species in *Racomitrium*-moss in the crater Gamli Surtur on Surtsey. Four of these six species have not been

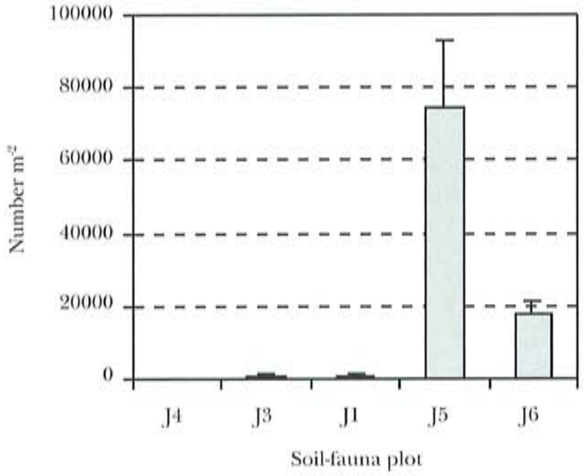


Figure 2. Number of collembolans per square meter found in plots of different plant successional stages outside and inside the gull colony on Surtsey in 1995 (mean SD). J1= *Honkenya-Leymus* plot, J3= *Honkenya* plot, J5= Young gull colony plot with *Honkenya* and grasses and J6= Old gull colony plot with a dense grass sward. No collembolans were found in the unvegetated reference plot, J4.

found previously on the island. The dominant species in the plots outside the gull colony were *Mesaphorura macrochaeta* and *Hypogastrura purpurescens* in the plots inside the colony (Fjellberg 1980). Four of the species listed in Table 1 were also found in samples taken by Gjelstrup (2000) on the same expedition, who found two additional species in the plots.

Abundance of collembola is summarized in Fig. 2. There was a great difference in the average number of collembolans inside and outside the gull colony.

No collembolans were found in the unvegetated reference plot J4, but in plot J3 and J1 a density of 806 - 936 individuals m$^{-2}$ was found. Within the gull colony, on the other hand, the density was 74,724 and 17,680 individuals m$^{-2}$ in plots J5 and J6 respectively. Enchytraeidae were found in all plots except the unvegetated reference plot, J4.

*Earthworms*

In soil samples taken in the gull colony in 1993, earthworms were found for the first time on Surtsey. Two approximately 3 cm long juvenile individuals of the species *Lumbricus castaneus* (Sav.). This species is usually found in the litter layer and soils with high organic content (Sims & Gerard 1985). No earthworms were found on Surtsey in July 1995 in spite of a thorough search and sampling of the same area.

*Soil fertility*

Soil samples taken in the fauna plots in 1995 and in the permanent vegetation study plots in 1998 revealed that the total C and N levels in the gull colony were much higher than in plots outside the colony (Table 2).

## DISCUSSION

The numbers of collembolans in the gull colony were considerably higher compared to the plots outside the colony where the soil was not as developed, has lesser microbial activity and vegetation cover (Magnússon 1992, Frederiksen *et al.* 2000, Magnússon & Magnússon 2000). The gulls no doubt enrich the soil and vegetation by depositing droppings that have high content of nutrients (Sobey & Kenworthy 1979). The abundance of collembolans in the colony is surprisingly high considering the

Table 1. Collembola species found on Surtsey in 1995. J1= *Honkenya-Leymus* plot, J3= *Honkenya* plot, J5= Young gull colony plot with *Honkenya* and grasses and J6= Old gull colony plot with a dense grass sward. No collembola were found in the unvegetated reference plot, J4.

| Species | Plots outside the gull colony | | Plots inside the gull colony | | *Racomitrium* in Gamli Surtur crater |
|---|---|---|---|---|---|
| | J3 | J1 | J5 | J6 | |
| *Ceratophysella succinea** | X | X | | | |
| *Hypogastrura purpurescens** | | X | X[1] | X[1] | |
| *Mesaphorura macrochaeta** | X[1] | X[1] | | | |
| *Isotoma anglicana** | | X | X | X | |
| *Isotoma notabilis* | | X | X | X | |
| *Folsomia brevicauda* | | | | | X |

* Species of Collembola not found previously on Surtsey.
[1] Dominant species.

Table 2. Chemical properties of soil outside and inside gull colony (sampling depth 5 cm and 10 cm*).

| Plot | C% | N% |
|---|---|---|
| Outside gull colony: | | |
| Plant plot 11* (near J4) | < 0.105 | < 0.004 |
| Plant plot 12* (near J3) | < 0.105 | < 0.004 |
| *Honkenya Leymus*, J1 | < 0.105 | 0.07 |
| Inside gull colony: | | |
| Young gull colony, J5 | 0.5 | 0.34 |
| Old gull colony, J6 | 3 | 1.62 |

* Results from Magnússon & Magnússon 2000.

Figure 3. *Lumbricus castaneus* found in Skaftafell in Southern Iceland.

young age of the island and can be compared to numbers of collembolans extracted from grasslands in southern Iceland (Sigurdardóttir 1998). The low numbers of collembolans in plots outside the bird colony is comparable to numbers found in eroded areas in Iceland with sparse vegetation cover (Sigurdardóttir 1990, Sigurdardóttir unpublished).

There is no simple answer to the question how the earthworm, *Lumbricus castaneus,* in the gull colony was dispersed to Surtsey. Most likely they were dispersed by birds from the other islands or from the mainland of Iceland. Earthworms will not survive going through the digestive tract of gulls and it is doubtful that they have dispersed directly to the island as juvenile or adult individuals. On the other hand it is potential that gulls have carried earthworm cocoons, clinging to dirt on their feet or feathers, with them to the island. The gull species (*Larus fuscus* and *L. argenteus)* most abundant in the gull colony on Surtsey are frequently seen in grasslands, hayfield and heathland in Iceland foraging on insects and earthworms (Magnússon & Magnússon 2000). *Lumbricus castaneus* has also been found on Heimaey on the Westman Islands (Lindroth *et al.* 1973) and in Skaftafell in southern Iceland (Fig. 3). Alltogether eleven earthworm species have been found in Iceland (Sigurdardóttir 1994). Enchytraeides were found in all plots but the unvegetated reference plot, J4 and were first discovered on Surtsey in 1972 (Ólafsson 1978). The Macfadyen high gradient extractor method does not ensure a detailed assessment of numbers of enchytraides so no attempt was made to find difference in number between plots.

Collembolans and earthworms are part of the decomposition food web and their consumption of dead plant material leads to fragmentation, thereby increasing the availability of this material to microorganisms. Their activity leads to release of nutrients into the soil where they become available to plants and microorganisms. It is obvious that the gull colony on Surtsey, with its nutrient rich habitat, has had an impact on the soil fauna that has managed to disperse and to develop on the island. In this fragile environment the soil fauna will no doubt change considerably through time. It is of interest here that slugs were found for the first time on Surtsey in 1998 and they were also present in 1999. The slugs were found in a dense grass sward in the gull colony. Identification to species has not been carried out, but the specimens found on Surtsey are similar to slugs commonly found in moist grassland and gardens in southern Iceland (Magnússon & Magnússon, personal communication).

Many questions concerning development and succession of the soil formation and soil fauna on Surtsey and its possible interaction with the vegetation and gull colony development still remains a challenging subjects for future research.

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# MARINE BIOLOGY

# Seaweed colonisation at Surtsey, the volcanic island south of Iceland

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## ABSTRACT

A study of the colonisation by benthic marine algae in Surtsey was conducted as a continuation of the monitoring of the island that started in 1964, a year after the eruption. Three expeditions were undertaken to the island in the summers of 1987, 1992 and 1997. Species samples were collected directly in the littoral zone and by divers in the sublittoral zone. Cover was measured directly in the littoral zone and by measuring cover of species on photographs taken in the sublittoral. A fucoid was found for the first time in Surtsey when *Fucus spiralis* was detected growing in a crevice on the east coast. A total of 65 species were found in the present study of which 11 had not previously been recorded in Surtsey. Since the beginning of the studies, 76 taxa have been recorded around the island. The algal cover in the littoral zone fluctuates unpredictably due to harsh environmental conditions. In the sublittoral zone the algal cover is more stable and seems to increase slowly.

## INTRODUCTION

A unique opportunity to study the colonisation of benthic marine algae on a new volcanic lava isolated from other vegetated bottom areas was offered by the occasion of the volcanic eruption in Surtsey in 1963. The submarine eruption lasted until 1967, creating an island on a bottom of 120 m depth. The island rapidly attained 2.7 km$^2$ in area and a height of 174 m. Most of the coastline was covered by basaltic rock, except the northern part which was of sand (Thórarinsson *et al.* 1964, Jakobsson & Moore 1980). Due to intensive erosion the island has diminished considerably and is presently only about 1.5 km$^2$ in area and the coastline measures approximately 4.5 km.

No studies on colonisation by marine algae have been done elsewhere on an entire virgin island, initially totally devoid of vegetation. Only few studies have been done on algal colonisation on new lava flows in direct contact with established marine vegetation (Dawson 1954, Doty 1967, Gulliksen 1974). A lava flow originating in an eruption in 1973 in Heimaey about 10 nautical miles from Surtsey has recently been studied (Gunnarsson 2000) allowing an interesting comparison with the algal colonisation in Surtsey.

The colonisation by benthic marine algae on Surtsey has been monitored on a regular basis since 1964, a year after the eruption started (Jónsson *et al.* 1987). The first algae to colonise the shores and actually the first plants discovered on the island were diatoms found in August 1964 on new lava solidified a few months before (Jónsson 1966a, 1970). The number of species found on the shores of Surtsey increased rapidly from 1964 to 1971 when about 40 taxa were recorded (Jónsson & Gunnarsson 1982). After 1971 the number of species increased slowly and in 1984, 34 species were found, while the total number of algal species that had been found in the island since the beginning was 69 (Jónsson

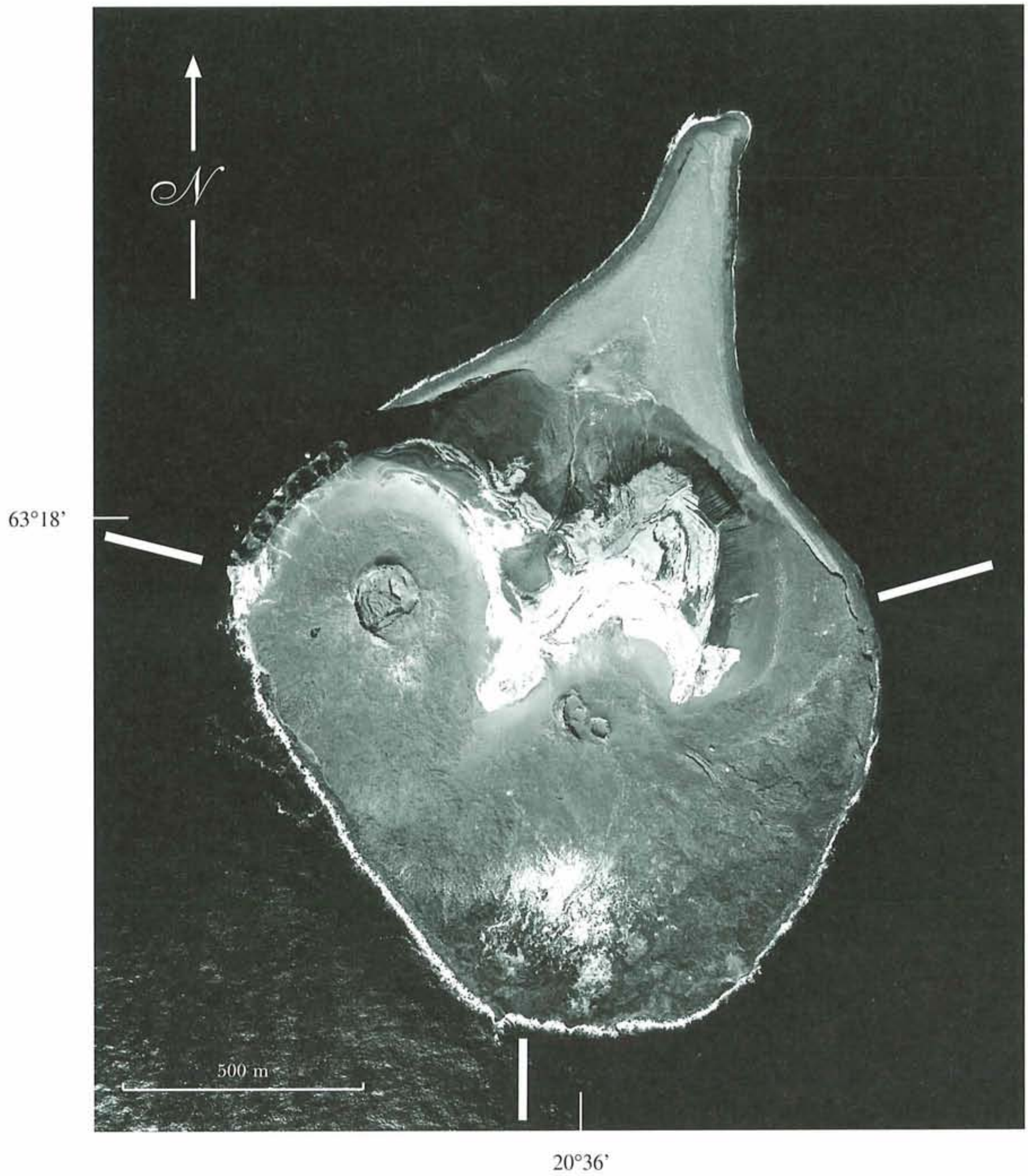


Figure 1. Vertical aerial photograph of Surtsey, July 21, 1996. Transects studied during 1987, 1992 and 1997 are indicated in white. Note the boulders and lava cliffs in the southern part of the island and sand beach in the northern part (courtesy of the National Land Survey of Iceland).

*et al.* 1987). The vegetation in the littoral zone was divided into two associations, an upper one dominated by *Ulothrix* and a lower one dominated by diatoms. In the sublittoral zone the vegetation was equally divided into two associations, an upper one dominated by *Alaria esculenta* and a deeper one at 20 to 30 m depth dominated by the red algae *Phycodrys rubens*, *Lomentaria orcadensis* and *Delesseria sanguinea*.

In this study the species composition and cover of the algal flora and vegetation in the bottom in Surtsey are presented for the years 1987, 1992 and 1997.

## MATERIAL AND METHODS

The present study was carried out during the periods July 2 to 6 1987, June 19 to 26 1992, and July 4 to 9 1997, in the waters around Surtsey. The sampling was done from research vessels of the Marine Research Institute in Reykjavík, rs Bjarni Sæmundsson in 1987 and rs Árni Friðriksson in 1992 and 1997. Samples were collect-

Table 1. Vertical and horizontal distribution of marine algal species found in Surtsey in July 1987.

| | east section | | | | | | | south section | | | | | | west section | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| taxa depth (m): | litt. | 5 | 10 | 15 | 20 | 25 | 30 | 5 | 10 | 15 | 20 | 25 | 30 | 5 | 10 | 15 | 20 | 25 | 30 |
| *Acrochaete viridis* | | | | | o | | | o | | | | o | | | | | | o | |
| *Acrochaete wittrockii* | | | | | | o | | | | | | | | | | | | | |
| *Alaria esculenta* | o | o | o | o | | | | o | o | o | o | o | o | o | o | o | o | o | o |
| *Antithamnionella floccosa* | o | o | o | o | o | | o | o | o | o | o | o | o | o | o | o | o | o | o |
| *Audouinella membranacea* | | | | o | o | o | | | | | o | | | | | | o | o | |
| *Audouinella pectinata* | | | | o | o | o | | | | | o | o | | o | | o | | o | |
| *Bangia artropurpurea* | o | | | | | | | | | | | | | | | | | | |
| *Blidingia minima* | o | | | | | | | | | | | | | | | | | | |
| *Callophyllis cristata* | | | | o | o | o | | | | | | | | | | | | o | |
| *Chorda filum* | | o | | | | | | | | | | | | | | | | o | |
| *Codiolum sp.* | o | | | | | | | | | | | | | | | | | | |
| *Conchocelis sp.* | | | o | | o | o | o | | | | o | o | o | | | | o | o | |
| *Delesseria sanguinea* | | | | o | o | o | o | | | | o | o | o | | | | o | o | o |
| *Derbesia marina* | | | | | o | | | | | o | o | o | | o | | o | | | |
| *Desmarestia aculeata* | | | | | o | | | | | | | | | o | | | o | | |
| *Desmarestia ligulata* | | | o | o | | | | | | | | | | | | | | | |
| *Desmarestia viridis* | | | o | o | o | | | o | o | | o | o | | | | | o | o | |
| *Ectocarpus fasciculatus* | o | | | | | | | | | | | | | | | o | | | o |
| *Ectocarpus siliculosus* | o | | | o | | | | o | | o | o | o | | o | o | | o | | |
| *Enteromorpha prolifera* | o | | | | | | | | | | | | | | | | | | |
| *Epicladia flustrae* | | | | | o | | | | | | o | o | | | | | o | o | |
| *Halosiphon tomentosus* | | o | | | | | | o | | | | | | o | o | | | | o |
| *Hincksia granulosa* | | o | | | o | | | o | o | o | o | | | o | o | | | | o |
| *Hincksia recurvata* | | | | | | | | | o | | | | | | o | | | | |
| *Laminaria hyperborea* | | | | o | o | o | | | | | o | o | o | | | | o | o | |
| *Leptonematella fasciculata* | | | | o | | | | | | | | | | | | | | | |
| *Lomentaria clavellosa* | | | o | o | | | | | | | o | | | o | o | | | | |
| *Lomentaria orcadensis* | | | | o | o | o | o | | o | o | o | o | o | o | o | o | o | o | o |
| *Membranoptera alata* | | | | o | | | | | | | o | | | | | | | | |
| *Monostroma grevillei* | | | o | o | | o | | | | | | | | | | | | | o |
| *Omphalophyllum ulvaceum* | o | | | | | | | | | | | | | | | | | | |
| *Petalonia fascia* | o | | | o | | | | | | | | | | | | | | | |
| *Petalonia zosterifolia* | o | | | | | | | | | | | | | | | | | | |
| *Phycodrys rubens* | | | o | o | o | o | o | | | | o | o | o | o | | | o | o | o |
| *Phyllophora traillii* | | | | | | o | | | | | | | | | | | | | |
| *Pilayella littoralis* | | | | | | | | | | | | | | | | | | o | |
| *Polysiphonia stricta* | | o | o | o | o | | | o | o | o | o | | | o | o | o | o | o | |
| *Porphyra miniata* | o | o | o | o | | | | o | o | o | | | | o | o | o | o | | |
| *Porphyra purpurea* | | | | | | | | | o | | | | | | | | | | |
| *Porphyra umbilicalis* | o | | | | | | | | | | | | | | | | | | |
| *Porphyropsis coccinea* | o | | o | o | o | | | | | | o | o | | | | | o | | |
| *Protectocarpus speciosus* | | | | | | | | | o | | | | | o | | | | | |
| *Pseudentoclonium submarinum* | o | | | | | | | | | | | | | | | | | | |
| *Rhodochorton purpureum* | | | o | o | | | | | | | | | | | | | | | |
| *Rhodophysema elegans* | | | o | o | | | | | | | | | | | | | | | |
| *Scagelia pusilla* | | | | o | | o | | | | | | | | | | | o | o | |
| *Sphacelaria caespitula* | | | | o | o | o | | | | | o | o | o | | o | | o | o | |
| *Ulothrix flacca* | o | | | | | | | | | | | | | | | | | | |
| *Ulothrix speciosa* | o | | | | | | | o | | | | | | | o | o | | | |
| *Ulvaria fusca* | o | | o | o | | | | | | | | | | | | | | | |
| *Urospora bangioides* | o | | | | | | | | | | | | | | | | | | |
| *Urospora penicilliformis* | o | | | | | | | | | | | | | | | | | | |
| *Urospora wormskioldii* | o | o | | | | | | o | o | | | o | | | | | o | o | |
| number of taxa: | 21 | 8 | 14 | 25 | 18 | 13 | 5 | 11 | 11 | 8 | 19 | 16 | 8 | 14 | 12 | 9 | 18 | 19 | 9 |

Table 2. Vertical and horizontal distribution of marine algal species found in Surtsey in June 1992.

| | east section | | | | | | south section | | | | west section | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| taxa depth (m): | 5 | 10 | 15 | 20 | 25 | 30 | 10 | 15 | 20 | 25 | 5 | 10 | 15 | 20 | 25 |
| *Acrochaetium secundatum* | | | | | | | | | | | | | | | o |
| *Acrosiphonia arcta* | o | | | | | | | | | | | | | | |
| *Alaria esculenta* | o | | o | | o | | o | o | | o | o | o | o | | o |
| *Antithamnionella floccosa* | o | o | o | o | | o | o | | | | o | o | o | o | |
| *Audouinella membranacea* | | | | | | | | | | | | | o | | |
| *Callophyllis cristata* | | | o | o | | | | | | | | | | | o |
| *Conchocelis sp* | | o | | o | | o | o | | | | | | | | |
| *Delesseria sanguinea* | | o | o | o | o | o | | | | o | | | o | o | o |
| *Desmarestia aculeata* | o | o | o | o | | | | | | | | | o | | o |
| *Desmarestia ligulata* | | | o | | | | | | | | | | | | |
| *Desmarestia viridis* | o | o | o | | | o | | | | o | o | | | | |
| *Ectocarpus siliculosus* | o | | | o | | | | o | | | | | o | | |
| *Enteromorpha prolifera* | | | | | | o | | | | | | | | | |
| *Entodictyon infestans* | | | | | | | | | | o | | | | | |
| *Epicladia flustrae* | | | | | | | | | | | | | | | o |
| *Halosiphon tomentosus* | o | | | | | | o | | | | o | o | | | |
| *Haplospora globosa* | | | | | o | o | | o | | o | | o | | | o |
| *Hincksia granulosa* | | | | | | o | | | | | | | | | |
| *Hincksia secunda* | | | | | | | | | | | o | | | | |
| *Hincksia sp.* | o | | | | | | | | | | | | | | |
| *Laminaria hyperborea* | | o | o | o | o | | | | | o | | o | o | | o |
| *Lomentaria clavellosa* | o | o | | o | | | | | | | | | | | |
| *Lomentaria orcadensis* | | | o | o | | o | o | o | | o | | o | o | o | |
| *Membranoptera alata* | | | | | | | | | | o | | | | | |
| *Monostroma grevillei* | o | | | | | | | | | | | | | | |
| *Phycodrys rubens* | | o | o | o | o | o | | o | | o | | | o | | o |
| *Phyllophora traillii* | | | | | | o | | | | | | | | | |
| *Polysiphonia stricta* | o | o | o | o | | o | o | o | | o | o | o | o | o | o |
| *Porphyra miniata* | o | o | o | | | | | | | | | | | | |
| *Porphyropsis coccinea* | o | o | o | | | | | | | | | | | | o |
| *Rhodochorton purpureum* | | o | | | | | | | | | | | | | |
| *Sphacelaria caespitula* | | o | o | o | | | | o | o | | | o | | | o |
| *Ulvaria fusca* | o | | | | | | | | | | | | | | |
| *Urospora penicilliformis* | | | | o | | | | | | | | | | | |
| *Urospora wormskioldii* | o | | | o | | o | | | | | | | | | |
| number of taxa: | 15 | 13 | 14 | 14 | 5 | 12 | 6 | 7 | 1 | 10 | 6 | 8 | 10 | 4 | 12 |

ed at three sublittoral transects at the east, south and west shores of Surtsey (Fig. 1). For the study of the littoral zone an expedition to Surtsey was done on a helicopter from the Icelandic coast guard in July 16, 1987. In 1992, bad weather prevented studies in the littoral zone and in 1997 we landed on the island by an inflatable.

In the sublittoral zone SCUBA-divers sampled algae at 5 m depth intervals from 5 m down to a depth of 30 m. At each depth specimens of all algal species were sampled by hand. Collecting bags with a 0.5 mm mesh size were used. In the littoral zone species were sampled during low water at spring tide. In the figures the height in the littoral zone refers to the height above 0 cart datum, that is approximately 10 cm below mean low water spring tide in Reykjavik.

The samples were brought fresh to the laboratory on board the ship where they were examined and identified to species. Herbarium specimens were made of the macroscopic species. The specimens are kept at the Marine Research Institute in Reykjavík. A list of species found at the three different sampling sites is given in Tables 1 to 3. Nomenclature is according to Gunnarsson & Jónsson (2000).

The algal cover of the littoral zone was measured directly within a 0.25 $m^2$ quadrant on the east coast in 1987. The quadrant was placed at 40 cm height intervals along a transect line from the uppermost trace of marine vegetation down to the low water at spring tide. In the sublittoral zone data were obtained by photographing 40 x 60 cm quadrants. Percentage cover was derived from the photographs (cf. Jónsson *et al.* 1987).

Table 3. Vertical and horizontal distribution of marine algal species found in Surtsey in July 1997.

| | east section | | | | | | | south section | | | | | west section | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| taxa depth (m) | litt. | 5 | 10 | 15 | 20 | 25 | 30 | 10 | 15 | 20 | 25 | 35 | 5 | 10 | 15 | 20 | 25 |
| *Alaria esculenta* | o | o | o | o | | | | o | o | o | o | | | o | o | o | o |
| *Antithamnionella floccosa* | o | o | o | | o | o | | o | | | o | o | o | o | o | | |
| *Audouinella membranacea* | | | o | | o | | | | | | | | | | | | |
| *Audouinella pectinata* | | | o | | o | | | | | | | | | | | | |
| *Blidingia minima* | o | | | | | | | | | | | | | | | | |
| *Callophyllis cristata* | | | o | | o | o | | | | | | | | | | | |
| *Chorda filum* | | | o | | o | | | | | | | | | | | | |
| *Codiolum sp.* | o | | | | | | | | | | | | | | | | |
| *Conchocelis sp.* | | | | | | o | | | | | | | | | | | o |
| *Delesseria sanguinea* | | | o | o | o | o | o | | o | | o | o | | o | o | o | o |
| *Desmarestia aculeata* | | o | o | o | o | | | | o | | | | | o | | | |
| *Desmarestia ligulata* | | | | | o | | | | o | | | | | | | | |
| *Desmarestia viridis* | | o | | o | o | | | | o | | | | | o | o | | |
| *Ectocarpus siliculosus* | o | o | o | | o | o | o | o | o | o | | | | | | o | |
| *Enteromorpha compressa* | o | | | | | | | | | | | | | | | | |
| *Enteromorpha flexuosa* | o | | | | | | | | | | | | | | | | |
| *Enteromorpha intestinalis* | o | | | | | | | | | | | | | | | | |
| *Enteromorpha prolifera* | o | | | | | | o | | | | | | | | | | |
| *Fucus spiralis* | o | | | | | | | | | | | | | | | | |
| *Halosiphon tomentosus* | | o | | o | o | | o | o | o | | | | | o | o | | |
| *Haplospora globosa* | | | | | | | | | o | | | | | | o | | |
| *Hincksia granulosa* | | | | | o | | | | | | | | | | | | |
| *Hincksia ovata* | | | | | o | | | | | | | | | | | | |
| *Hincksia secunda* | o | o | o | | o | o | | o | o | | o | | o | o | o | o | |
| *Laminaria hyperborea* | | | o | o | o | | | | | o | o | | | o | | o | |
| *Lomentaria clavellosa* | | o | o | o | o | | | | | | | | | o | o | | |
| *Lomentaria orcadensis* | | | o | o | o | o | | o | o | o | o | o | | o | o | o | o |
| *Meiodiscus spetsbergensis* | | | o | | | | | | | | | | | | | | |
| *Membranoptera alata* | | | o | o | | | | | | | | | | | | | |
| *Monostroma grevillei* | | | | | | o | | | | | | | | o | | | |
| *Omphalophyllum ulvaceum* | | | o | | | | | | | | | | | | | | |
| *Petalonia fascia* | o | o | | | | | | | | | | | | | | | |
| *Petalonia zosterifolia* | o | | | | | | | | | | | | | | | | |
| *Phycodrys rubens* | | | o | o | o | o | | | o | o | o | | | o | o | o | o |
| *Polysiphonia stricta* | | o | o | | o | o | o | o | o | | | | | o | o | o | |
| *Porphyra miniata* | o | o | o | o | o | o | o | o | o | o | | | o | | o | o | |
| *Porphyropsis coccinea* | | | o | | o | | | | | | | | | | | | |
| *Rhodochorton purpureum* | | | o | | | | | | | | | | | | | | |
| *Rhodophysema elegans* | | | | | | | | | o | | | | | | | | |
| *Sphacelaria caespitula* | | | o | | o | o | | | | o | o | | | | o | o | o |
| *Ulothrix flacca* | o | | | | | | | | | | | | | | | | |
| *Ulvaria fusca* | o | o | o | o | o | o | | o | | | | | o | o | | | |
| *Urospora bangioides* | o | | | | | | | | | | | | | | | | |
| *Urospora penicilliformis* | o | | | | | | | | | | | | | | | | |
| *Urospora wormskioldii* | o | | | | o | o | o | | | | | | o | | | | |
| number of taxa | 19 | 12 | 23 | 12 | 24 | 14 | 7 | 9 | 14 | 7 | 8 | 3 | 5 | 14 | 13 | 10 | 6 |

RESULTS

In the study years 1987 to 1997, a total of 65 species were found (Table 1-3) (the diatoms are omitted). The highest number, 53 species, was found in 1987, 35 species in 1992 and 45 in 1997. In 1992 the littoral zone was not sampled.

In the littoral zone 21 species was found in 1987 of which 11 were strictly confined to the littoral area (Table 1). Similarly, the number of species found in the littoral zone in 1997 were 19 of which 9 occurred only in the littoral (Table 3).

Among the species found during the three years of study here 11 had not previously been recorded on Surtsey. The most noteworthy of the new records is *Fucus spiralis* that was found in the uppermost part of the littoral zone (Fig. 2). Two juvenile specimens were found growing in a small crevice in the rock on the eastern shore. Most of the new records were small and inconspicuous species and have not been found every year after their discovery. Two species *Ulvaria fusca* and *Membranoptera alata* are exception. They have become relatively abundant in the sublittoral zone.

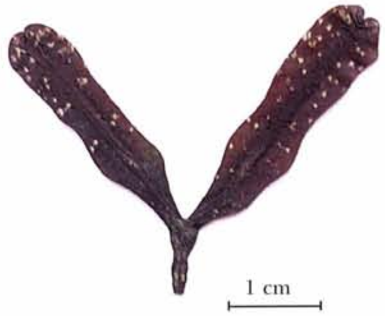

Figure 2. *Fucus spiralis*, a young specimen; the first attached fucoid recorded in Surtsey. Found in the upper littoral on the east shore in July 1997, 34 years after the creation of Surtsey (photo: Karl Gunnarsson).

In the sublittoral zone the total number of species collected in 1987, 1992 and 1997 was 32, 35 and 26 respectively. The greatest number og species was detected east of Surtsey where the coast is less exposed than elsewhere.

The maximum number of species were found at 10 to 15 m depth, more rarely at 20 m and the number was lower both at shallower and deeper waters (Table 1-3). At the lower limit of the vegetation, at about 30 m depth, the number of species fluctuated from 3 to 11 species. In the deepest station a mixture of red, brown and green algae was observed.

The littoral zone was studied quantitatively in 1987. The mean algal cover for the entire littoral zone was about 24 % (Table 4). In the upper part of the littoral zone diatoms and *Pseudentoclonium marinum* were dominant. In the lower part diatoms were still a dominant element associated with *Alaria esculenta* and *Petalonia fascia* in the lowermost part. *Ulothrix flacca, Urospora penicilliformis* and *Enteromorpha prolifera* occupy the middle part of the littoral zone. The total algal cover is lowest in the upper part about 12 %, and increases generally going down the littoral zone reaching 32 % in the lowest part (Table 4). No herbivores were observed in the littoral zone.

In the sublittoral zone the total cover of algae observed off the east coast was highest at 5 m, 86.2 % (Table 5). It diminished gradually with increasing depth and was about 1.6 % on average at 30 m. Inversely the animal cover was lowest at 5 m, 9.7 %, and increased generally with depth and was 89.5 % at 30 m.

*Alaria esculenta* was the species with the highest cover. It dominated at 5 and 10 m depths in the sublittoral zone, but its cover decreased rap-

Table 4. Percentage cover of littoral algae on the east coast of Surtsey in June, 1987. The height on the shore indicates level above chart datum.

| Taxa | height (m): | 5.5 | 5.1 | 4.7 | 4.3 | 3.7 | 3.3 | 2.9 | 2.5 | 2.1 | 1.7 | 1.3 | 0.9 | 0.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Diatoms* | | 0.5 | 14.0 | 23.0 | 4.0 | 14.0 | 2.0 | 12.0 | 19.0 | 22.0 | 21.0 | 18.0 | 8.0 | 4.0 |
| *Ulothrix flacca* | | | | | 0.5 | 2.0 | 8.0 | 12.0 | 0.5 | | 0.5 | | | |
| *Blidingia minima* | | | | | | | 1.0 | | 0.5 | 2.0 | | | | |
| *Codiolum sp.* | | | | | | | | 1.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | |
| *Enteromorpha prolifera* | | | | | | 2.0 | 1.0 | | 5.0 | 1.0 | 3.0 | | 3.0 | |
| *Urospora penicilliformis* | | | | | | 2.0 | 8.0 | 5.0 | 0.5 | | | | | |
| *Petalonia fascia* | | | | | | 0.5 | | | | | 1.0 | 8.0 | 2.0 | 15.0 |
| *Ectocarpus fasciculatus* | | | | | | | | | 0.5 | | | 3.0 | 8.0 | 0.5 |
| *Porphyra miniata* | | | | | | | | | 0.5 | 0.5 | 0.5 | 0.5 | | 0.5 |
| *Alaria esculenta* | | | | | | | | | | | | | 0.5 | 11.0 |
| *Antithamnionella floccosa* | | | | | | 0.5 | | | | | | | | |
| *Pseudentoclonium marinum* | | 12.0 | 1.0 | | 14.0 | 1.0 | | | | | | | | |
| *Cyanophycea* | | | 0.5 | | 2.0 | 0.5 | 2.0 | | 0.5 | | | | | |
| *Bangia fuscopurpurea* | | | | | | | | | | 0.5 | | | | |
| *Urospora wormskioldii* | | | | | | | | | | | 3.0 | 2.0 | 0.5 | 0.5 |
| *Petalonia zosterifolia* | | | | | | | | | | | | | 0.5 | |
| | total cover: | 12.5 | 15.5 | 23.0 | 20.5 | 22.5 | 22.0 | 30.0 | 27.5 | 26.5 | 29.5 | 32.0 | 23.0 | 31.5 |
| Mean algal cover for the entire littoral zone: | | | | | 24.3 | | | | | | | | | |

Table 5. Percentage cover of sublittoral biota at the east section of Surtsey in July 1997. The numbers in the table are averages of five estimates.

| Taxa depth (m): | 5 | 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|---|
| *Alaria esculenta* | 32.5 | 39.8 | 16.8 | | 0.3 | |
| *Brown filaments* | 3.1 | 0.4 | 56.8 | 1.7 | 2.2 | 0.6 |
| *Halosiphon tomentosus* | 11.6 | 1.6 | 0.6 | 0.1 | | |
| *Conchocelis sp.* | | | | | | 0.3 |
| *Delesseria sanguinaea* | | | | 2.1 | 0.3 | |
| *Desmarestia aculeata* | | 1.32 | | | 5.2 | |
| *Desmarestia viridis* | | 1.3 | | | 0.2 | |
| *Laminaria hyperborea* | | 10.7 | | 10.1 | | |
| *Lomentaria orcadensis* | | | | | 0.2 | |
| *Lomentaria clavellosa* | | 3.0 | | | | |
| *Membranoptera alata* | | 0.1 | | | | |
| *Phycodrys rubens* | | 0.4 | | 12.5 | 1.8 | 0.3 |
| *Polysiphonia stricta* | 12.6 | 3.3 | 1.1 | 1.7 | 1.0 | |
| *Porphyra miniata* | 22.4 | 13.8 | 0.4 | | | |
| *Porphyropsis coccinea* | | 0.1 | | | | |
| *Ulvaria fusca* | 4.1 | 2.1 | | 0.3 | | 0.4 |
| Total plant cover | 86.2 | 78.0 | 75.7 | 28.5 | 11.2 | 1.6 |
| Mean algal cover of the entire sublittoral zone: | 46.9 | | | | | |
| Total animal cover | 9.7 | 16.6 | 5.1 | 36.8 | 74.9 | 89.5 |
| Mean cover of animals over the entire sublittoral zone: | 38.8 | | | | | |

Figure 4. An underwater photograph showing an area of 60 x 40 cm of the bottom at 15 m at the west coast of Surtsey in July 1997. Species appearing in the photo are the seaweed species *Delesseria sanguinea, Phycodrys rubens, Lomentaria orcadensis* and juvenile *Alaria esculenta.* Prominent animal species are sea star, *Asterias rubens,* sponge, *Grantia compressa,* mussel, *Mytilus edulis* and hydroid, *Tubularia larynx* (photo: Karl Gunnarsson).

Figure 3. *Laminaria hyperborea,* a typical view of a *Laminaria*-stand on top of a boulder at the depth of 10 m at the east coast of Surtsey, in July 1997. The highest plants measure about 1.5 m in stipe length (photo: Karl Gunnarsson).

idly with depth. *Laminaria hyperborea* had its highest cover at 10 and 20 m where it formed dense stands on the top of the highest stones (Fig. 3). Brown filaments that consisted of a mixture of filamentous diatoms, *Hincksia* spp. and/or *Ectocarpus* spp. were found at all depths in all years and generally had high cover. In the sublittoral zone the most conspicuous herbivores observed were *Echinus esculentus, Strongylocentrodus droebachiensis, Lacuna vincta, Padina pellucida.* Elsewhere along the basaltic cliffs the algal growth, although less abundant, represents similar main featues as on the east coast (Fig. 4)

## DISCUSSION

Fucoids are common in the littoral zone in the Vestmannaeyjar archipelago, including Geirfuglasker, at about 2.7 nautical miles NE of Surtsey. *Fucus spiralis* is normally found forming the uppermost belt of fucoids on the shore. Fucoids have been found drifted ashore from the early years of Surtsey (Jónsson 1966b). It was therefore not surprising to find *Fucus spiralis* growing on the littoral rocks on Surtsey as anticipated by Jónsson (1967). Perennial vegetation has not established itself in the littoral zone on Surtsey probably due to erosion and scouring action by sand. On Surtsey *F. spiralis* was found in a crevice and thus partially sheltered from the sand scouring.

Another new record, not expected in Surtsey, was *Omphalophyllum ulvaceum.* It was found in the sublittoral zone at the depth of 10 m. This species has not been recorded in southern Iceland before but is a common species in northern Iceland. It has also been found in Greenland and elsewhere in the Arctic (South & Tittley 1986). This species was recently found on the French side of the English Channel (Simon 1985).

In Fig. 5 and Table 6 is shown the increase in the number of species recorded since 1964 a

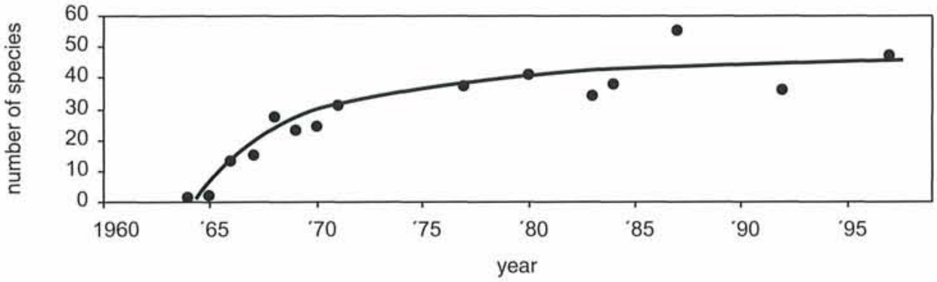

Figure 5. The number of species of seaweed recorded on Surtsey since the beginning of settlement, showing a rapid initial increase in species number and a levelling off after 1970.

year after the eruption started when only bacteria and diatoms were detected on the littoral rocks. The number of species increased rapidly until about 1970 and then levelled off and has increased slowly since with the number of species fluctuating around 40 to 50 species recorded on each sampling occasion the last ten years (Fig. 5).

Most of the species that have been recorded on Surtsey are not permanent residents of the island, but are opportunists that have been found sporadically over the years (Table 6). Some of these species have only been found once after their discovery like e.g. *Laminaria digitata* an extremely common species in the other islands of the Vestmannaeyjar archipelago. One of the species, *Hincksia recurvata,* has not been found elsewhere in Iceland. Some faithful colonisers that were first found shortly after the eruption have been recorded on every occasion since, such as e.g. *Alaria esculenta* that has been common in the sublittoral zone ever since it was first found in 1966. Among the faithful colonisers are both annual species that possibly invade the island every year from a nearby stand, as probably most of the littoral species do, or survive through the winter in a reduced form. Other colonisers are perennial such as *Laminaria hyperborea* that has been found on every occasion since 1968 and plants of up to 9 years have been collected on Surtsey.

Also of interest are species that are common in the Vestmannaeyjar archipelago but have not been found on Surtsey. In Vestmannaeyjar fucoids dominate the littoral zone whereas in Surtsey only small specimens of *Fucus spiralis* have been found. In the case of the littoral species the erosion of the substrate is probably the main factor preventing the development of perennial fucoid vegetation. On the new lava in Heimaey fucoid vegetation was only found in extremely sheltered location while at the more exposed location only annual species were found as has been the case for the extremely exposed littoral zone of Surtsey where the erosion of the substrate and scouring by sand are likely to exert its action (Gunnarsson 2000). Similarly Doty (1967) proposed that the instability of the substrate was the main factor delaying the succession of the littoral vegetation on new lava flows in Hawaii.

In the sublittoral of Surtsey the absence of crustose corallines is striking. These have been found in abundance on the new lava in Heimaey that dates from 1973 and is thus ten years younger than Surtsey (Gunnarsson 2000). Their absence on Surtsey might be due to negative buoyancy of the spores of the crustose corallines that prevents long range dispersal (Okuda & Neushul 1981).

In the littoral zone only thin vegetation covers the rocks. Dominant species in the upper part of the littoral are microscopic and cover only about 1/4 of the rocky surface. In a previous survey in 1983, the algae was estimated to cover 2/3 of the substrate due to an important development of *Ulothrix flacca* in the upper littoral. *U. flacca* is a seasonal species with a relatively short growing period and changes in its cover can be important in a short time span. In comparing the two observations of algal cover in the littoral zone in 1983 and 1987, one can conclude that there are enormous variations between years both in cover and species composition.

The highest cover of sublittoral species was in the depth interval from 5 to 15 m after which the cover decreases rapidly with depth and is down to 1.6 % at 30 m. The main factor influencing the depth distribution of the algae is most likely light, which is very reduced at 30 m depth. Increasing cover of animals coincides with the decrease in algal cover. Below 25 m the algae have almost disappeared and the animals are predominating.

Table 6. Order of arrival of seaweed species in Surtsey from the beginning of colonisation until 1997. Diatoms and Cyanophycea are omitted.

| | species | years | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 77 | 80 | 83 | 84 | 87 | 92 | 97 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Urospora penicilliformis* | | o | o | o | o | o | o | o | o | o | o | o | o | o | o |
| 2 | *Ulothrix flacca* | | | o | o | o | o | o | | o | | | | o | | o |
| 3 | *Enteromorpha flexuosa* | | | o | | | | | | | | | | | | o |
| 4 | *Enteromorpha intestinalis* | | | o | | | | | | | | | | | | o |
| 5 | *Pylaiella littoralis* | | | o | | | | | | | | | | | | |
| 6 | *Ectocarpus siliculosus* | | | o | o | o | o | o | o | o | | | o | o | o | o |
| 7 | *Scytosiphon lomentarius* | | | o | o | o | o | | o | o | | | | | | |
| 8 | *Petalonia fascia* | | | o | o | o | o | o | o | o | o | o | o | o | | o |
| 9 | *Petalonia zosterifolia* | | | o | o | o | o | o | o | o | o | o | o | o | | o |
| 10 | *Alaria esculenta* | | | o | o | o | o | o | o | o | o | o | o | o | o | o |
| 11 | *Porphyra umbilicalis* | | | o | o | o | o | o | o | o | o | o | o | o | | |
| 12 | *Enteromorpha linza* | | | | o | o | | | | | | | | | | o |
| 13 | *Enteromorpha compressa* | | | | o | o | o | o | o | | | | | | | o |
| 14 | *Acrosiphonia arcta* | | | | o | o | o | | | o | | | o | | o | |
| 15 | *Hincksia hincksiae* | | | | o | o | o | o | | | | | | | | |
| 16 | *Desmarestia viridis* | | | | o | o | o | o | o | o | o | o | o | o | o | o |
| 17 | *Urospora wormskioldii* | | | | | o | o | | | | | | o | o | o | o |
| 18 | *Enteromorpha prolifera* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 19 | *Monostroma grevillei* | | | | | o | | | o | o | o | o | o | o | o | o |
| 20 | *Laminaria hyperborea* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 21 | *Desmarestia ligulata* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 22 | *Desmarestia aculeata* | | | | | o | | | o | o | o | | | o | o | o |
| 23 | *Porphyra purpurea* | | | | | o | | | | | | | | o | | |
| 24 | *Porphyra miniata* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 25 | *Lomentaria orcadensis* | | | | | o | | o | o | o | o | o | o | o | o | o |
| 26 | *Antithamnionella floccosa* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 27 | *Phycodrys rubens* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 28 | *Polysiphonia stricta* | | | | | o | o | o | o | o | o | o | o | o | o | o |
| 29 | *Hincksia granulosa* | | | | | | o | | o | o | o | | | o | o | o |
| 30 | *Ulva lactuca* | | | | | | | o | o | | | | | | | |
| 31 | *Laminaria digitata* | | | | | | | o | o | | | | | | | |
| 32 | *Callophyllis cristata* | | | | | | | o | | | | | | | | |
| 33 | *Derbesia marina* | | | | | | | | o | o | o | | o | o | | |
| 34 | *Pseudendoclonium submarinum* | | | | | | | | o | | o | | | o | | |
| 35 | *Ulothrix subflaccida* | | | | | | | | o | | | | | | | |
| 36 | *Hincksia secunda* | | | | | | | | o | o | | | o | | o | o |
| 37 | *Rhodochorton purpureum* | | | | | | | | o | | o | o | | o | o | o |
| 38 | *Delesseria sanguinea* | | | | | | | | o | o | o | o | o | o | o | o |
| 39 | *Hincksia ovata* | | | | | | | | | o | | | o | | | o |
| 40 | *Hincksia recurvata* | | | | | | | | | o | o | | | o | | |
| 41 | *Chorda filum* | | | | | | | | | o | o | o | | o | | o |
| 42 | *Halosiphon tomentosum* | | | | | | | | | o | o | | o | o | o | o |
| 43 | *Plocamium cartilagineum* | | | | | | | | | o | | | | | | |
| 44 | *Rhodophysema elegans* | | | | | | | | | o | o | | o | o | | o |
| 45 | *Lomentaria clavellosa* | | | | | | | | | o | o | o | o | o | o | o |
| 46 | *Scagelia pusilla* | | | | | | | | | o | o | o | o | o | | |
| 47 | *Conchocelis sp.* | | | | | | | | | o | o | o | o | o | o | o |
| 48 | *Audouinella membranacea* | | | | | | | | | | o | o | o | o | o | o |
| 49 | *Ulothrix speciosa* | | | | | | | | | | o | o | o | o | | |
| 50 | *Sphacelaria caespitula* | | | | | | | | | | o | o | o | o | o | o |
| 51 | *Acrochaete viridis* | | | | | | | | | | o | | | o | | |
| 52 | *Acrochaete wittrockii* | | | | | | | | | | o | | | o | | |
| 53 | *Achrochaetium secundatum* | | | | | | | | | | o | | | | o | |
| 54 | *Bryopsis plumosa* | | | | | | | | | | o | | | | | |
| 55 | *Ectocarpus fasciculatus ?* | | | | | | | | | | o | o | o | o | | |
| 56 | *Meiodiscus spetsbergensis* | | | | | | | | | | o | o | | | | o |
| 57 | *Porphyropsis coccinea* | | | | | | | | | | o | | o | o | o | o |
| 58 | *Spongomorpha aeruginosa* | | | | | | | | | | | o | | | | |
| 59 | *Petroderma maculiforme* | | | | | | | | | | | o | | | | |
| 60 | *Blidingia minima* | | | | | | | | | | | o | | o | | o |
| 61 | *Erythropeltis subintegra* | | | | | | | | | | | o | | | | |
| 62 | *Phaeostroma pustulosum* | | | | | | | | | | | o | o | | | |
| 63 | *Leptonematella fasciculata* | | | | | | | | | | | | o | o | | |
| 64 | *Haplospora globosa* | | | | | | | | | | | | o | | o | o |

Table 6 (continued).

| species | years | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 77 | 80 | 83 | 84 | 87 | 92 | 97 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 65 *Audouinella pectinata* | | | | | | | | | | | | | o | | o |
| 66 *Bangia artropurpurea* | | | | | | | | | | | | | o | | |
| 67 *Epicladia flustrae* | | | | | | | | | | | | | o | o | |
| 68 *Membranoptera alata* | | | | | | | | | | | | | o | o | o |
| 69 *Phyllophora traillii* | | | | | | | | | | | | | o | o | |
| 70 *Pilayella littoralis* | | | | | | | | | | | | | o | | |
| 71 *Protectocarpus speciosus* | | | | | | | | | | | | | o | | |
| 72 *Urospora bangioides* | | | | | | | | | | | | | o | | o |
| 73 *Ulvaria fusca* | | | | | | | | | | | | | o | o | o |
| 74 *Omphalophyllum ulvaceum* | | | | | | | | | | | | | o | | o |
| 75 *Endodictyon infestans* | | | | | | | | | | | | | | o | |
| 76 *Fucus spiralis* | | | | | | | | | | | | | | | o |
| Total number of species: | | *1* | *11* | *13* | *25* | *21* | *21* | *28* | *33* | *38* | *31* | *35* | *51* | *33* | *44* |


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# Benthic marine algal colonisation on the new lava at Heimaey, Vestmannaeyjar archipelago, southern Iceland

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## ABSTRACT

A new lava shore was formed during an eruption on the Island of Heimaey, Vestmannaeyjar archipelago, southern Iceland, in 1973. The benthic marine algae that had colonised the littoral and sublittoral zones of the new lava were studied during the summer 1998. A total of 62 species were found of which 21 were confined to the littoral zone. In the sublittoral zone the highest number of species was found at 5 m depth and the number decreased with increasing depth. The lower limit of the vegetation was at about 30 m. On a sheltered site at the entrance of the harbour, prolific fucoid vegetation was found in the littoral zone, on lava outcrops embedded in sand.

A comparison with the marine algal vegetation on Surtsey a volcanic island born 10 years earlier, showed that in terms of species number the colonisation has progressed faster on Heimaey. This is probably due to partly more sheltered habitats and the closeness of mature algal communities to the new lava in Heimaey.

## INTRODUCTION

Marine algal colonisation on introduced substrata or on small artificially or accidentally denuded surfaces in the littoral or the sublittoral zone has been studied extensively (e.g. Dayton 1971, Kain 1975, Sousa 1980, Niell & Varela 1984, van Zyl & Robertson 1991, Williamson & Creese 1996). Studies on the colonisation on new volcanic lava are however scarce. Dawson (1954) studied the algal flora on littoral lava flows of different age in the San Benedicto Island in the Pacific, west of Mexico and noted a marked difference between the flora on the new lava and that of the older lava. Doty (1967) followed the algal colonisation on several lava flows of different age in Hawaii for 7 years. Doty followed successive stages in the colonisation until the algal vegetation reached a semi-climatic stage. The main factor reducing the succession rate was the instability of the substrate. In Jan Mayen Gulliksen (1974) studied the sublittoral vegetation of a lavaflow two years after the eruption stopped. He found five algal species growing on the lava, three of which he did not find on the surrounding old lava.

On Surtsey, a new volcanic island in the Vestmannaeyjar archipelago, southern Iceland, the colonisation by marine algae has been monitored on a regular basis since 1964, a year after the eruption started (see Jónsson *et al.* 1987). The first algae to colonise the shores of Surtsey and actually the first plants found on the island were diatoms found in August 1964 on new lava solidified shortly before (Jónsson 1966, 1970). The number of species found on the shores of Surtsey increased rapidly from 1964 to 1971 when about 40 species were found (Jónsson & Gunnarsson 1982). After 1971 the number of species increased slowly and in 1997, 34 years after the island was born, 47 species were found (Jónsson & Gunnarsson 2000).

A volcanic eruption started on Heimaey, another island of the Vestmannaeyjar archipelago in 1973 and ended in 1975. The lava flowed into the sea on the eastern shore of Heimaey and a new rocky shore of about 10 km in length was formed over part of the east shore (Thorarinsson *et al.* 1973). No studies have been reported on the benthic marine organisms on the new lava in Heimaey. The new lava in Heimaey is in direct contact with established algal communities and it was of interest to see if the colonisation differed from that observed in the isolated shoreline of Surtsey where the nearest algal community is at about 5 km distance. This paper reports results from a study of the benthic marine algae on the new lava in Heimaey conducted in June 1998.

## MATERIAL AND METHODS

The present study was carried out during the period from 8 to 12 June 1998 on the new lava on the north-eastern coast of Heimaey (Fig. 1). Sampling was done on two sublittoral transects separated by about 200 m near the eastern tip of the new lava. In the littoral zone, two sites were studied, a sheltered site near the entrance of the harbour and a more exposed site at the extreme east of the new lava shore.

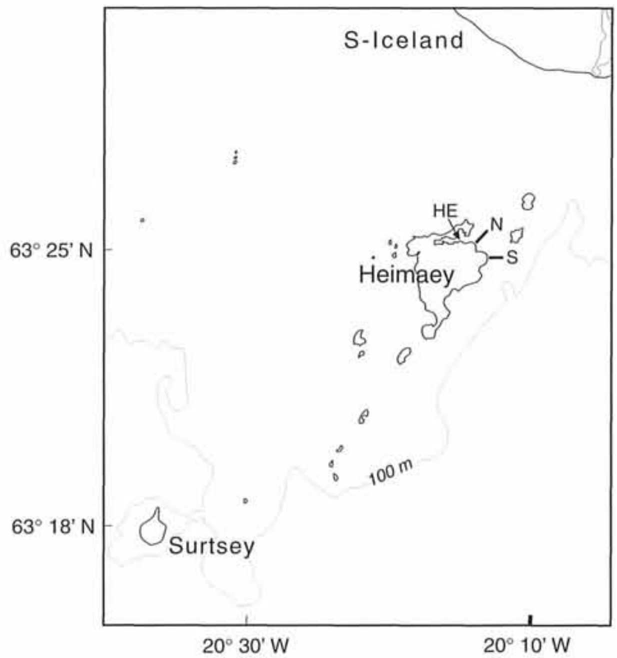


Figure 1. Vestmannaeyjar archipelago. The three transects studied on the new lava at Heimaey, south (S), north (N) and harbour entrance (HE) are marked on the map.

In the sublittoral zone SCUBA-divers sampled algae at 5 m depth intervals from 5 m to 35 m. At each depth the substrate and the general appearance of the vegetation and fauna was registered on a plastic writing pad and specimens of all algal species seen were sampled by hand. An effort was made to sample from as many different kinds of habitats as possible. Collecting bags with a 0.5 mm mesh size were used. In the littoral zone species were sampled during low water at spring tide.

The samples were brought fresh to the laboratory where they were examined and identified to species. Herbarium specimens were made of the macroscopic species and permanent slides were made of the microscopic species by mounting them on microscopic slides in Karo® corn syrup. The specimens are kept at the Marine Research Institute in Reykjavík. A list of species found at the three different sampling sites with author names is given in Table 1. Nomenclature is according to Gunnarsson & Jónsson (2000).

## RESULTS

The substrate on the new lava flow on the north-eastern coast of Heimaey is a mixture of boulders, stones, gravel and sand. In the littoral zone at the more exposed site, the boulders were round and even, while at the sheltered site near the entrance of the harbour the substrate was rough lava bedrock surrounded by fine sand. In the sublittoral zone the stones and boulders get more rough and uneven and cover successively smaller part of the bottom as one goes deeper. The cover of sand and gravel increases with increasing depth.

Dominant sessile animals on the hard substrate in the sublittoral zone are hydrozoans and bryozoans with apparently increasing cover from shallow to deep water. In the deepest collecting sites at 20 to 30 m the octocoral *Alcyonium digitatum* was prominent in the fauna. Of the errant macrofauna sea urchins *Strongylocentrotus droebachiensis* and *Echinus esculentus* were most frequent.

A total of 62 benthic algal taxa were found in the littoral and sublittoral zones on the new lava. Amongst those taxa, 18 belong to the Ulvophyceae, 16 to Fucophyceae and 25 to Bangiophyceae (Table 1). In the littoral zone 33 taxa were found. In the sublittoral zone the highest number of species was found at 5 m depth, 33 species, and the number decreased with increasing depth and at 30 m depth only 3

Table 1. Vertical and horizontal distribution of marine algal species found on the new lava at Heimaey, in June 1998.

| | south section | | | | | | north section | | | | | Harbour entrance, littoral |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| taxa depth (m): | 5 | 10 | 15 | 20 | 25 | 30 | litt | 5 | 10 | 20 | 30 | |
| *Acrochaetiaceae sp.* | | | | | | | | x | x | | | |
| *Acrosiphonia arcta* (Dillwyn) J.Agardh | x | x | | x | | | x | | | | | x |
| *Alaria esculenta* (Linnaeus) Greville | x | x | x | | | | x | x | x | | | |
| *Antithamnionella floccosa* (O.F. Müller) Whittick | | | | x | x | x | | x | | | | |
| *Audouinella membranacea* (Magnus) Papenfuss | | | x | x | | | | | | | | |
| *Blidingia minima* (Nägeli ex Kützing) Kylin | | | | | | | x | | | | | x |
| *Callophyllis cristata* (C.Agardh) Kützing | | | x | | | | | x | x | | | |
| *Chorda filum* (Linnaeus) Stackhouse | | | | | | | | | | | | |
| *Conchocelis sp.* | | | x | | x | | | | x | | | |
| *Corallina officinalis* Linnaeus | x | | | | | | | | | | | |
| *Cruoria pellita* (Lyngbye) Fries | | | | | | | | x | | | | |
| *Crustose corallines* | | x | x | | x | | | x | x | x | | |
| *Delesseria sanguinea* (Hudson) Lamouroux | x | x | x | x | | | | x | | | | |
| *Derbesia marina* (Lyngbye) Solier | | | x | x | x | | | | | | | |
| *Desmarestia aculeata* (Linnaeus) Lamouroux | x | x | x | | | | | x | x | | | |
| *Desmarestia viridis* (O.F.Müller) Lamouroux | x | x | x | | | | | x | x | | | |
| *Ectocarpus fasciculatus* Harvey | | | | | | | x | | | | | |
| *Ectocarpus siliculosus* (Dillwyn) Lyngbye | | x | x | | | | x | x | | | | |
| *Elachista fuciola* (Velley) Areschoug | | | | | | | | | | | | x |
| *Enteromorpha flexuosa* (Wulfen) J.Agardh | | | | | | | | | | | | x |
| *Enteromorpha intestinalis* (Linnaeus) Nees | | | | | | | x | | | | | x |
| *Enteromorpha linza* (Linnaeus) J.Agardh | | | | | | | x | | | | | x |
| *Enteromorpha prolifera* (O.F.Müller) J.Agardh | | | | | | | x | | | | | x |
| *Fimbrifolium dichotomum* (Lepeschin) G.Hansen | | | | x | | | | | | | | |
| *Fucus disticus* Linnaeus | | | | | | | | | | | | x |
| *Fucus spiralis* Linnaeus | | | | | | | | | | | | x |
| *Fucus vesiculosus* Linnaeus | | | | | | | | | | | | x |
| *Haplospora globosa* Kjellman | | | x | | | | | | | | | |
| *Laminaria hyperborea* (Gunnerus) Foslie | x | x | x | x | | | | x | x | | | |
| *Lomentaria clavellosa* (Turner) Gaillon | x | | | | | | | x | | | | |
| *Lomentaria orcadensis* (Harvey) Collins ex W.R.Taylor | x | x | x | x | | | | x | x | | | |
| *Mastocarpus stellatus* (Stackhouse) M.Guiry | | | | | | | x | | | | | x |
| *Meiodiscus spetzbergensis* (Kjellm.) Saund. & McLachlan | | | | x | | | | x | | | | |
| *Membranoptera alata* (Hudson) Stackhouse | x | x | | | | | | x | | | | |
| *Monostroma grevillei* (Thuret) Wittrock | x | | | | | | x | x | | | | x |
| *Palmaria palmata* (Linnaeus) Kuntze | x | | | | | | x | x | | | | x |
| *Petalonia fascia* (O.F. Müller) Kuntze | | | | | | | x | | | | | |
| *Petalonia zosterifolia* (Reinke) Kuntze | | | | | | | x | | | | | |
| *Phycodrys rubens* (Linnaeus) Batters | x | x | x | x | | | | x | | | | |
| *Plocamium cartilagineum* (Linnaeus) Dixon | x | x | x | | | | | x | | | | |
| *Polysiphonia stricta* (Dillwyn) Greville | x | x | x | x | | x | x | x | x | | | |
| *Porphyra miniata* (C.Agardh) C.Agardh | x | x | | | | | | x | x | | | |
| *Porphyra umbilicalis* (Linnaeus) Kützing | | | | | | | x | | | | | x |
| *Porphyropsis coccinea* (J.Agardh) Rosenvinge | | | | | | | | x | x | | | |
| *Prasiola stipitata* Suhr in Jessen | | | | | | | | | | | | x |
| *Pterosiphonia parasitica* (Hudson) Falkenberg | | x | | | | | | x | | | | |
| *Ptilota gunneri* P.Silva, Maggs & L.Irvine | x | x | | x | | x | | x | | | | |
| *Pylaiella littoralis* (Linnaeus) Kjellman | | | | | | | x | | | | | x |
| *Rhizoclonium riparium* (Roth) Harvey | | | | | | | | | | | | x |
| *Rhodochorton purpureum* (Lightfoot) Rosenvinge | | | | | | | x | | | | | x |
| *Rosenvigiella polyrhiza* (Rosenvinge) P.Silva | | | | | | | | | | | | x |
| *Scytosiphon lomentarius* (Lyngbye) Link | | | | | | | x | | | | | x |
| *Sphacelaria caespitula* Lyngbye | | | | | | | | x | | | | |
| *Sphacelaria sp.* | | x | x | x | | | x | | | | | |
| *Spongomorpha aeruginosa* (Linnaeus) van den Hoek | | | | | | | | x | | | | |
| *Ulothrix flacca* (Dillwyn) Thuret in Le Jolis | | | | | | | x | | | | | x |
| *Ulothrix sp.* | | | | | | | | | | | | x |
| *Ulva lactuca* Linnaeus | | | | | | | x | | | | | |
| *Ulvaria fusca* (Postels & Ruprecht.) Ruprecht | x | x | | | | | | | | | | |
| *Urospora bangioides* (Harvey) Holmes & Batters | | | | | | | x | | | | | |
| *Urospora penicilliformis* (Roth) Areschoug | | | | | | | | x | | | | x |
| *Urospora sp.* | | | | x | | | | | | | | |
| Total | 18 | 18 | 17 | 14 | 4 | 3 | 22 | 27 | 12 | 1 | 0 | 23 |

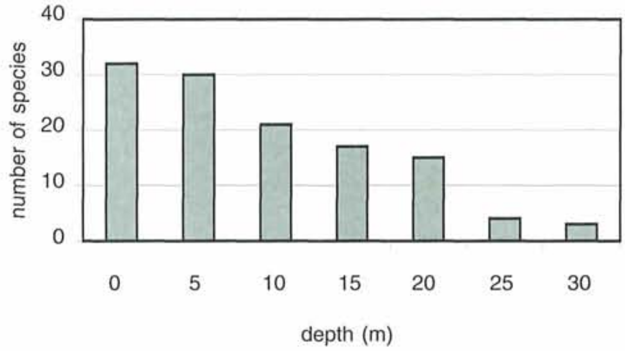


Figure 2. Bar diagram showing the decrease in number of species with increasing depth on the new lava in Heimaey in 1998.

species were recorded (Fig. 2). The flora of the sublittoral zone was similar at the two transects, although 14 of the sublittoral species were confined either to one transect or the other. These were mostly small inconspicuous species that might easily have been overlooked in one of the transects.

The vegetation of the littoral zone was studied at a sheltered site near the entrance to the harbour and at an exposed site at the extreme east of the new lava. About the same number of species was found at the two sites, but the species composition was quite different. Of the 33 species found in the littoral zone, 10 were common to both sites. The littoral vegetation at the exposed site was dominated by *Urospora bangioides* and *Enteromorpha linza* in the lower part, but in the upper part *E. prolifera* and *Sphacelaria* sp. were most abundant. No fucoids were found at the exposed site.

Near the harbour the littoral vegetation was dominated by fucoids with high cover of *Fucus spiralis*, *F. vesiculosus* and *F. distichus*. In addition *Porphyra umbilicalis*, *Enteromorpha prolifera*, *Pilayella littoralis*, *Monostroma grevillei* and *Palmaria palmata* were common (Table 1).

In the sublittoral zone, the vegetation at shallow depths consisted predominantly of *Alaria esculenta* and red algae *Polysiphonia stricta*, *Delesseria sanguinea*, *Phycodrys rubens*, *Plocamium cartilagineum* and *Lomentaria clavellosa*. At about 8 to 13 m depth, dense stands of *Laminaria hyperborea* were found on the top of the highest boulders, but the smaller stones were covered by *A. esculenta* and *Desmarestia aculeata* and the red algae *D. sanguinea*, *P. rubens* and *Porphyra miniata*. At 15 m depth crustose corallines and *Lomentaria orcadensis* were found in abundance amongst *A. esculenta*, *D. sanguinea* and *P. rubens* that were dominant. At 20 m depth the vegetation cover was very low, spread plants of *P. rubens*, *L. orcadensis* and *Derbesia marina* were found on a bottom mostly covered with hydroids and octocorals. At 30 m the plants were primarily small species growing on hydroids.

## DISCUSSION

There was a marked difference in the vegetation between the two littoral study sites on the new lava of Heimaey. At the sampling site near the entrance to the harbour the new lava is sheltered from wave exposure and stable enough to support perennial fucoid vegetation on rock outcrops embedded in sand (Fig. 3). Three species, *Fucus spiralis*, *F. vesiculosus* and *F. distichus* were found growing there. At the more exposed site the vegetation on the rocks was dominated by ephemeral green algae of the genera *Urospora* and *Enteromorpha*. The vegetation at the more exposed site resembled the vegetation found on the extremely exposed littoral zone of Surtsey (Jónsson *et al.* 1987). Similar vegetation of ephemeral green algae has been found to represent the first stages of colonisation in a number of studies (Sousa 1979, 1984, van Zyl & Robertson 1991, Dye 1993). The difference in vegetation between the two littoral sites of equal age on Heimaey is most likely due to the constant erosion of the exposed shore line. The same factor is likely to affect the littoral vegetation in Surtsey where hardly any part of the coastline is un-

Figure 3. Rock outcrops surrounded by sand at the harbour entrance in Heimaey. Fucoids dominate the vegetation on the rocks.

changed from year to year (Norrman & Erlingsson 1992). It was only in 1997, 34 years after the eruption, that the first fucoid was detected in the littoral zone on Surtsey. A juvenile plant of *Fucus spiralis* was found in a small rock crevice in the lava (Jónsson & Gunnarsson 2000). There has probably been no lack of fucoid germlings, as fertile fucoid plants have frequently been observed drifted ashore at Surtsey.

In the sublittoral zone on the new lava in Heimaey stones were embedded in sand that is moved about by current and waves. On the smaller stones, less than 0.5 m in height, only small ephemeral algae were observed. It seems likely that the scouring and burial action of the sand prevents the establishment of perennial vegetation on the smaller stones. On top of the larger stones a dense vegetation of *Laminaria hyperborea* had developed. The *Laminaria* plants were up to 8 years of age (counting growth zones in the stipes). *Laminaria hyperborea* forest is considered to be a climax vegetation in the cold temperate region of the Northwest Atlantic (Svendsen 1972, Kain 1975). Both the number of species and the vegetation cover diminished rapidly below 15 m depth. At greater depths light is the most probable factor limiting the establishment and growth of the vegetation.

In terms of number of species the vegetation of new lava in Heimaey has developed further than the vegetation of Surtsey. A total of 62 species were found on Heimaey in 1998 compared with 44 on Surtsey in 1997. Many of the species that were found on the new lava on Heimaey have never been recorded on Surtsey (Jónsson *et al.* 1987, Jónsson & Gunnarsson 2000). In the littoral zone these are *Elachista fucicola, Fucus distichus, Fucus vesculosus, Mastocarpus stellatus, Palmaria palmata, Prasiola stipitata, Rhizoclonium riparium* and *Rosenvingiella polyrhiza.* All of them were found at the sheltered site at the entrance to the harbour, although *M. stellata* and *P. palmata* were also found growing on the more exposed littoral site.

In the sublittoral zone *Corallina officinalis, Cruoria pellita,* crustose corallines, *Fimbrifolium dichotomum, Pterosiphonia parasitica* and *Ptilota gunneri* were found on the new lava of Heimaey, species but have not been found on Surtsey (Jónsson *et al.* 1987, Jónsson & Gunnarsson 2000). On the new lava at Heimaey the crustose corallines are a prominent element in the sublittoral vegetation found at all depths from 5 to 20 m (Fig. 4). At Surtsey this group is absent.

Figure 4. Crustose coralline algae at depth of 30 m at the north transect on the new lava in Heimaey in 1998.

The most likely explanation for this is that the spores of the crustose corallines are negatively buoyant and therefore have a limited dispersal capacity (Okuda & Neushul 1981). Crustose corallines have succeeded in colonising the new lava in Heimaey from nearby algal communities, while the distance from the nearest mature vegetation (5 km) has presumably prevented the establishment of crustose corallines on Surtsey.

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# A survey of the benthic coastal fauna of Surtsey in 1992 and a comparison with earlier data

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ABSTRACT

This paper consists of a discussion of the results so far obtained from the samples of benthic animals collected from the subtidal zone at Surtsey in June, 1992, and an attempt to compare these results with earlier data from the same area.

## INTRODUCTION

Already during the initial phases of the underwater eruption of 1963, which in the years that followed was to build up the new island of Surtsey, and which first became visible to observers on November 14 of that year, marine biologists had begun speculating on the extent of the influence that such an event might exert on marine life in the area. As a result, during this early period scientists from the Marine Research Institute in Reykjavík embarked upon research surveys of subsequent biological development in the region (Sigurðsson 1965, Skúladóttir 1966).

The first attempt to follow the colonization of benthic fauna at Surtsey was made during the years 1966-1968 by Willy Nicolaisen, who used grabs and dredges (Nicolaisen 1967a, 1967b, 1968, 1970). However, as the underwater slopes off the east, south and west coasts of Surtsey were largely found to be covered by rocks, it was not considered satisfactory to continue the use of such equipment to sample benthos in these areas. Therefore sampling by the method of SCUBA-diving was commenced in 1967 (Jónsson 1968, Sigurðsson 1968), excepting however the sandy subtidal bottom off the north coast, as no scientists were then available for work on the fauna of this type of bottom. As sampling by means of SCUBA-diving of fauna found on the subtidal slopes proved to be the best method available, it has been used exclusively after 1968 (Sigurðsson 1968, 1970, 1972, 1974, Hauksson 1982, 1992).

In the beginning, the sampling was carried out annually; soon, however, the development of the fauna and flora proved to be so slow that it was considered satisfactory to collect samples every third year. It was also necessary to take account of problems imposed by limited economic resources. The interval between the last two samplings was five years. The identification of the animals has as yet not been completed. Thus in Tables 1-3, * after the larger groups means that there are still some species that have not been identified. The bryozoans were identified by Dr. Karen Bille Hansen, while the author is responsible for the identification of the other groups found in the samples from 1992.

## THE SAMPLING

The benthic animals from the subtidal zone off Surtsey down to 30 m were collected by the technique of SCUBA-diving during June 21-25, 1992. Samples were taken on the three main transects off the east, south and west coasts (Sigurðsson 1968, 1970, 1972, 1974, Hauksson 1982, 1992).

Weather conditions being bad, only one transect, that off the east coast, could be worked as planned. The collections of samples taken off the south and west coasts therefore gave limited results, a fact that has to be borne in mind when the present attempt to compare them with earlier faunal records is considered. Particularly at the 5m stations the surf was too heavy for adequate sampling, but the whole of the research work was difficult and some of the stations had to be omitted (see Tables 2 and 3). Adverse weather conditions did not allow access to the littoral zone.

## RESULTS

Tables 1-3 show the distribution by depth of the benthic animals on the three transects at Surtsey which were sampled in 1992. It has, however, to be borne in mind that weather conditions at the time were bad and the sampling, therefore, was ineffective, especially off the south and west coasts. Although the number of species may be different at the various coasts, it is not likely that the difference is as big as might seem to appear from Tables 1-3, where the fauna

Table 1. Benthic animals from the subtidal zone off the east coast of Surtsey in June 1992

| Depth (m) | 5 | 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|---|
| PORIFERA*) | x | x | x | x | x | x |
| HYDROZOA*) | x | x | x | x | x | x |
| ANTOZOA | | | | | | |
| *Alcyonium digitatum* L. | .. | x | x | x | x | x |
| NEMATODA*) | .. | x | x | x | .. | .. |
| POLYCHAETA*) | .. | x | x | x | x | x |
| BRYOZOA | | | | | | |
| *Tubulipora liliacea* (Pallas) | .. | x | .. | x | x | x |
| *Tubulipora sp.* | .. | x | .. | .. | x | x |
| *Diplosolen obelia* (Johnston) | .. | .. | .. | .. | .. | x |
| *Lichenopora verrucaria* (Fabr.) | .. | .. | x | .. | .. | .. |
| *Disporella hispida* (Fleming) | .. | .. | .. | .. | .. | x |
| *Scruparia ambigua* (d´Orbigny) | .. | .. | .. | .. | .. | x |
| *Scruparia chelata* (L.) | .. | x | .. | x | .. | x |
| *Membranipora membranacea* (L.) | .. | x | x | x | x | .. |
| *Electra pilosa* (L.) | .. | x | x | x | .. | .. |
| *Callopora lineata* (L.) | .. | x | .. | .. | .. | .. |
| *Callopora craticula* (Alder) | .. | .. | .. | .. | .. | x |
| *Tegella unicornis* (Fleming) | .. | x | .. | x | x | x |
| *Tegella arctica* (d´Orbigny) | .. | .. | .. | x | x | x |
| *Amphiblestrum flemingii* (Busk) | .. | .. | .. | x | .. | x |
| *Membraniporella nitida* (Johnston) | .. | .. | .. | .. | x | .. |
| *Scrupocellaria scruposa* (L.) | .. | .. | .. | x | .. | .. |
| *Scrupocellaria elongata* (Smitt) | .. | .. | .. | .. | x | x |
| *Tricellaria ternata* (Ellis & Solander) | .. | x | .. | x | .. | x |
| *Cribrilina punctata* (Hassall) | .. | x | .. | .. | .. | .. |
| *Cribrilina cryptooecium* Norman | .. | x | .. | x | x | x |
| *Cribrilina annulata* (Fabr.) | .. | x | .. | x | x | x |
| *Umbonula littoralis* Hastings | .. | x | .. | x | .. | x |
| *Porella alba* Nordgaard | .. | x | .. | x | x | x |
| *Escharella immersa* (Fleming) | .. | x | .. | x | .. | .. |
| *Parasmittina trispinosa* (Johnston) | .. | .. | .. | x | x | .. |
| *Microporella ciliata* (Pallas) | .. | .. | .. | .. | .. | x |
| *Cylindroporella tubulosa* (Norman) | .. | x | .. | .. | .. | .. |
| *Celleporella hyalina* (L.) | .. | x | x | x | x | x |
| *Celleporina hassallii* (Johnston) | .. | x | .. | .. | .. | x |
| *Alcyonidium mamillatum* Alder | .. | .. | .. | .. | x | .. |
| *Alcyonidium mytili* Dalyell | .. | x | .. | .. | .. | x |
| *Alcyonidium parasiticum* (Fleming) | .. | .. | .. | x | .. | .. |
| *Arachnidium fibrosum* Hincks | .. | .. | .. | .. | .. | x |
| CIRRIPEDIA | | | | | | |
| *Verruca stroemia* (Müller) | .. | x | x | x | x | x |
| *Balanus balanus* (L.) | x | x | x | x | x | x |
| ISOPODA | | | | | | |
| *Idotea granulosa* Rathke | x | .. | x | .. | .. | .. |
| *Idotea neglecta* G. O. Sars | .. | .. | x | .. | .. | .. |
| *Janiropsis breviremis* G. O. Sars | .. | .. | .. | x | .. | .. |
| *Janira maculosa* Leach | .. | x | x | .. | .. | .. |
| *Munna kröyeri* Goodsir | x | x | .. | x | .. | .. |
| AMPHIPODA*) | x | x | x | x | x | x |
| DECAPODA | | | | | | |
| *Hyas coarctatus* Leach | .. | x | .. | x | x | .. |
| *Galathea nexa* Embl. | .. | .. | .. | .. | .. | x |
| *Eupagurus bernhardus* L. | .. | .. | .. | .. | .. | x |
| POLYPLACOPHORA*) | .. | x | .. | .. | .. | .. |
| PROSOBRANCHIA | | | | | | |
| *Helcion pellucidum* (L.) | x | x | .. | .. | .. | .. |
| *Acmea testudinalis* (Müller) | .. | x | .. | .. | .. | .. |
| *Margarites groenlandicus* (Chemn.) | .. | .. | .. | .. | x | .. |
| *Margarites helicinus* (Fabr.) | x | x | .. | .. | .. | .. |
| *Lacuna divaricata* (Fabr.) | x | x | x | x | .. | .. |
| *Skenopsis planorbis* (Fabr.) | .. | x | .. | .. | .. | .. |
| *Omalogyra atomus* (Phil.) | .. | .. | .. | x | .. | .. |
| *Neptunea despecta* (L.) | .. | .. | .. | .. | .. | x |
| *Buccinum undatum* (L.) | .. | x | .. | .. | .. | .. |
| *Buccinum undatum var. coeruleum* (G.O.Sars) | .. | .. | .. | x | .. | .. |
| *Nassa incrassata* (Ström.) | .. | x | x | x | x | x |
| NUDIBRANCHIA*) | x | x | .. | x | x | x |
| LAMELLIBRANCHIA | | | | | | |
| *Mytilus edulis* (L.) | x | x | x | x | x | x |
| *Modiolaria discors* (L.) | .. | .. | .. | x | .. | .. |
| *Modiola phaseolina* (Phil.) | .. | .. | .. | x | .. | x |
| *Chlamys islandicus* (Müller) | .. | .. | .. | .. | .. | x |
| *Heteranomia squamula* L. | .. | x | x | x | x | x |
| *Kellia suborbicularis* (Mont.) | .. | .. | x | .. | .. | x |
| *Cardium fasciatum* (Mont.) | .. | .. | .. | x | .. | x |
| *Syndosmya prismatica* (Mont.) | .. | x | .. | .. | .. | .. |
| *Hiatella arctica* (L.) | x | x | x | x | x | x |
| ASTEROIDEA | | | | | | |
| *Asterias rubens* L. | .. | x | .. | x | x | x |
| OPHIUROIDEA | | | | | | |
| *Ophiopholis aculeata* (O.Fr.Müller) | .. | x | x | .. | x | x |
| ECHINOIDEA | | | | | | |
| *Echinus esculentus* (L.) | .. | .. | x | .. | x | x |
| ASCIDIACEA*) | x | .. | x | x | .. | .. |
| *Styela rustica* (L.) | .. | .. | x | x | .. | .. |
| *Halocynthia pyriformis* (Rathke) | .. | x | x | .. | .. | .. |
| *Boltenia echinata* (L.) | .. | .. | .. | x | .. | .. |

*) Species among these were not identified

Table 2. Benthic animals from the subtidal zone off the south coast of Surtsey in June 1992.

| Depth (m) | 5 | 10 | 15 | 25 | 30 |
|---|---|---|---|---|---|
| PORIFERA*) | .. | x | x | x | x |
| HYDROZOA*) | .. | x | x | x | x |
| ANTOZOA*) | .. | x | .. | .. | .. |
| *Alcyonium digitatum* L. | .. | .. | .. | x | x |
| NEMATODA*) | .. | x | .. | x | x |
| POLYCHAETA*) | .. | x | x | x | x |
| BRYOZOA | | | | | |
| *Tubulipora liliacea* (Pallas) | .. | .. | .. | .. | x |
| *Tubulipora* sp. | .. | .. | .. | .. | x |
| *Diplosolen obelia* (Johnston) | .. | .. | .. | .. | x |
| *Scruparia chelata* (L.) | .. | .. | .. | .. | x |
| *Electra pilosa* (L.) | .. | .. | .. | .. | x |
| *Callopora lineata* (L.) | .. | .. | .. | .. | x |
| *Callopora craticula* (Alder) | .. | .. | .. | .. | x |
| *Tegella unicornis* (Fleming) | .. | .. | .. | .. | x |
| *Amphiblestrum flemingii* (Busk) | .. | .. | .. | .. | x |
| *Membraniporella nitida* (Johnston) | .. | .. | .. | .. | x |
| *Scrupocellaria elongata* (Smitt) | .. | .. | .. | .. | x |
| *Tricellaria ternata* (Ellis & Solander) | .. | .. | x | .. | x |
| *Cribrilina punctata* (Hassall) | .. | .. | .. | .. | x |
| *Cribrilina cryptooecium* Norman | .. | .. | .. | .. | x |
| *Cribrilina annulata* (Fabr.) | .. | .. | .. | .. | x |
| *Umbonula littoralis* Hastings | .. | .. | .. | .. | x |
| *Celleporina hassallii* (Johnston) | .. | .. | x | .. | .. |
| *Alcyonidium parasiticum* (Fleming) | .. | .. | .. | .. | x |
| CIRRIPEDIA | | | | | |
| *Verruca stroemia* (Müller) | .. | .. | .. | x | x |
| *Balanus balanus* (L.) | .. | .. | .. | x | x |
| *Balanus hammeri* (Ascanius) | .. | .. | .. | x | .. |
| ISOPODA | | | | | |
| *Munna kröyeri* Goodsir | .. | x | .. | x | x |
| *Janiropsis breviremis* G. O. Sars | .. | x | x | x | .. |
| *Janira maculosa* Leach | .. | x | .. | x | .. |
| AMPHIPODA*) | .. | x | x | x | x |
| DECAPODA | | | | | |
| *Hyas coarctatus* Leach | .. | .. | .. | x | x |
| PROSOBRANCHIA | | | | | |
| *Lacuna divaricata* (Fabr.) | .. | x | x | x | x |
| *Nassa incrassata* (Ström.) | .. | .. | x | x | x |
| NUDIBRANCHIA*) | x | x | .. | x | x |
| LAMELLIBRANCHIA | | | | | |
| *Mytilus edulis* (L.) | .. | x | x | x | x |
| *Modiola phaseolina* (Phil.) | .. | .. | x | x | x |
| *Heteranomia squamula* L. | .. | .. | .. | x | x |
| *Hiatella arctica* (L.) | .. | x | x | x | x |
| *Kellia suborbicularis* (Mont.) | .. | .. | .. | .. | x |
| ASTEROIDEA | | | | | |
| *Asterias rubens* L. | .. | .. | x | x | x |
| OPHIUROIDEA | | | | | |
| *Ophiopholis aculeata* (O. Fr. Müller) | .. | .. | .. | x | x |
| ASCIDIACEA*) | .. | .. | .. | x | .. |
| *Styela rustica* (L.) | .. | x | .. | .. | .. |

*) Species among these were not identified.

at the east coast is represented by twice as many species as at each of the other two transects.

The efficiency of the sampling may have been further affected by other factors than adverse weather conditions. Thus, for instance, some of the animals present may easily have been so small as to have escaped the attention of the divers. An example is the prosobranch *Omalogyra atomus* (Phil.) which is only about 1mm in diameter, being the smallest invertebrate dealt with in the present paper. Such small animals may even have been overlooked during the identification of the samples.

It is noteworthy how few species were found for the first time at Surtsey in 1992 (see Tables 4-9). It is only the bryozoans that include a number of new species, though it should be mentioned that samples from this group for the years between 1971 and 1992 have not been identified, so nothing is said here about new species in the latter year. It is therefore obvious that the development of the benthic fauna at Surtsey has been very slow, and is likely to remain so for a long time to come, especially if compared with the relatively much richer and more advanced benthic fauna at the other islands of the Vestmannaeyjar archipelago.

There would seem to be two main reasons for this slow development. In the first place, the underwater slopes of Surtsey are very unstable and therefore hostile to some of the colonizing species. Every year heavy waves forced by winter storms break off a large quantity of the southern lava field and transport lava blocks, gravel and sand northwards along the west and east coasts, thereby disturbing the settlement of fauna and flora on the subtidal slopes and in the tidal zone. Secondly, difficulties in the way of transport of animals to Surtsey from the adjacent islands can limit the development of the faunal communities, especially in the case of animals with no or short larval stages.

It will clearly take a long time for the benthic communities at Surtsey to develop and stabilize to an extent comparable with what is to be found at the other islands. This holds good both for the underwater slopes and the littoral zone, though development in the latter is a long way behind that found in the former, as a 1997 survey would seem to indicate (Sigurðsson 1999).

## COMPARISON WITH OLDER DATA

Tables 4-9 demonstrate the arrival of benthic animals in the upper part of the underwater slopes and the tidal zone of Surtsey, as far as the present stage of the work of identification allows this to be determined. This topic was treated by Hauksson (1992), but as the data from 1970,

Table 3. Benthic animals from the subtidal zone off the west coast of Surtsey in June 1992

| Depth (m) | 5 | 10 | 15 | 25 |
|---|---|---|---|---|
| PORIFERA*) | x | x | x | x |
| HYDROZOA*) | x | x | x | x |
| ANTHOZOA | | | | |
| *Alcyonium digitatum* L. | .. | .. | x | x |
| NEMATODA*) | x | x | x | .. |
| NEMERTINI*) | .. | .. | x | .. |
| POLYCHAETA*) | x | x | x | .. |
| BRYOZOA | | | | |
| Tubulipora liliacea (Pallas) | .. | .. | x | .. |
| *Tubulipora* sp. | .. | .. | x | .. |
| *Plagioecia patina* (Lamarck) | .. | .. | x | .. |
| *Lichenopora verrucaria* (Fabr.) | .. | .. | x | .. |
| *Scruparia ambigua* (d´Orbigny) | .. | .. | x | .. |
| *Scruparia chelata* (L.) | .. | .. | x | .. |
| *Membranipora membranacea* (L.) | .. | x | x | .. |
| *Electra pilosa* (L.) | .. | .. | x | .. |
| *Scrupocellaria elongata* (Smitt) | .. | .. | x | .. |
| *Tricellaria ternata* (Ellis & Solander) | .. | .. | x | .. |
| *Umbonula littoralis* Hastings | .. | .. | x | .. |
| *Celleporella hyalina* (L.) | .. | x | x | .. |
| *Celleporina hassallii* (Johnston) | .. | .. | x | .. |
| CIRRIPEDIA | | | | |
| *Verruca stroemia* (Müller) | .. | .. | x | .. |
| *Balanus balanus* (L.) | .. | .. | x | .. |
| ISOPODA | | | | |
| *Idotea granulosa* Rathke | .. | .. | x | .. |
| *Janiropsis breviremis* G. O. Sars | x | x | x | x |
| *Janira maculosa* Leach | .. | .. | .. | x |
| *Munna kröyeri* Goodsir | .. | .. | x | .. |
| AMPHIPODA*) | x | x | x | x |
| DECAPODA | | | | |
| *Hyas coarctatus* Leach | .. | .. | x | .. |
| PROSOBRANCHIA | | | | |
| *Margarites groenlandicus* (Chemn.) | .. | .. | x | .. |
| *Margarites helicinus* (Fabr.) | .. | x | .. | .. |
| *Lacuna divaricata* (Fabr.) | .. | x | x | .. |
| *Buccinum undatum* (L.) | .. | .. | x | .. |
| NUDIBRANCHIA*) | x | .. | x | x |
| LAMELLIBRANCHIA | | | | |
| *Mytilus edulis* (L.) | x | x | x | x |
| *Modiola phaseolina* (Phil.) | .. | x | x | .. |
| *Heteranomia squamula* L. | .. | .. | x | .. |
| *Cardium fasciatum* (Mont.) | .. | .. | x | .. |
| *Hiatella arctica* (L.) | x | x | x | x |
| ASTEROIDEA | | | | |
| *Asterias rubens* L. | x | x | x | x |
| OPHIUROIDEA | | | | |
| *Ophiopholis aculeata* (O. Fr. Müller) | .. | .. | x | x |
| ASCIDIACEA*) | x | .. | x | .. |

*) Species among these were not identified.

1971 and 1977 were not available to him, the subject will be resumed here.

No other identifications of nudibranchs than those referred to by Hauksson (1992) are available, so this group will not be treated further here. Hydrozoans, polychaets and amphipods have partly been identified but the results were not available to the present author. These three groups have all been represented in every sampling year since 1967.

Although the samples are not quantitative, I have tried to give a rough idea of the density of the faunal elements at Surtsey by using frequency of individual species in the samples in combination with the divers' reports and underwater photographs.

*Scyphozoa (Table 4)*

*Halyclystus octoradiatus* (Lamarck) is the only species of this group found at Surtsey. It seems to be very thinly scattered as only a few individuals have been found in the samples, and these not every year.

*Anthozoa (Table 4)*

*Alcyonium digitatum* L. This species, which was first found in 1969, and again every sampling year from then on, is very common (Fig. 1).

*Tealia felina* (L.) has only been determined in the samples from 1987.

*Bryozoa (Table 5)*

The bryozoans from Surtsey have only been identified from 4 sampling years, so their immigration to Surtsey cannot be followed in the same measure as for some of the other groups of benthic animals that are treated here. However, as can be seen from the table, the number of species has increased fairly rapidly, 38 of these having been identified, the bryozoans thus being among the most diverse benthic groups at the island. One of

Table 4. Arrival and occurrence of Scyphozoa and Anthozoa at Surtsey.

| Year | 69 | 70 | 71 | 74 | 77 | 80 | 83 | 84 | 87 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|
| SCYPHOZOA | | | | | | | | | | |
| *Haliclystus octoradiatus* (Lamarck) | x | x | .. | .. | .. | .. | x | x | .. | .. |
| ANTHOZOA | | | | | | | | | | |
| *Alcyonium digitatum L.* | x | x | x | x | x | x | x | x | x | x |
| *Tealia felina* (L.) | .. | .. | .. | .. | .. | .. | .. | .. | x | .. |

Table 5. Bryozoa found at Surtsey in 1967, 1968, 1971 and 1992.

| Year | 67 | 68 | 71 | 92 |
|---|---|---|---|---|
| *Membranipora membranacea* (L.) | x | x | x | x |
| *Celleporella hyalina* (L.) | x | .. | x | x |
| *Scruparia ambigua* (d´Orbigny) | .. | x | x | x |
| *Scruparia chelata* (L.) | .. | x | x | x |
| *Electra pilosa* (L.) | .. | x | x | x |
| *Amphiblestrum flemingii* (Busk) | .. | x | x | x |
| *Tricellaria ternata* (Ellis & Solander) | .. | x | x | x |
| *Cribrilina punctata* (Hassall) | .. | x | x | x |
| *Alcyonidium parasiticum* (Flem.) | .. | x | x | x |
| *Alcyonidium polyoum* (Hassall) | .. | x | x | .. |
| *Umbonula littoralis* Hastings | .. | x | .. | x |
| *Flustra foliacea* (L.) | .. | x | .. | .. |
| *Callopora craticula* (Alder) | .. | .. | x | x |
| *Tegella unicornis* (Flem.) | .. | .. | x | x |
| *Membraniporella nitida* (Johnston) | .. | .. | x | x |
| *Scrupocellaria elongata* (Smitt) | .. | .. | x | x |
| *Escharella immersa* (Flem.) | .. | .. | x | x |
| *Parasmittina trispinosa* (Johnston) | .. | .. | x | x |
| *Alcyonidium mamillatum* Alder | .. | .. | x | x |
| *Disporella hispida* (Flem.) | .. | .. | x | x |
| *Porella alba* Nordgaard | .. | .. | x | x |
| *Callopora dumerilii* (Audouin) | .. | .. | x | .. |
| *Porella minuta* (Norman) | .. | .. | x | .. |
| *Porella smitti* Kluge | .. | .. | x | .. |
| *Tubulipora liliacea* (Pallas) | .. | .. | .. | x |
| *Plagioecia patina* (Lamarck) | .. | .. | .. | x |
| *Diplosolen obelia* (Johnston) | .. | .. | .. | x |
| *Lichenopora verrucaria* (Fabr.) | .. | .. | .. | x |
| *Callopora lineata* (L.) | .. | .. | .. | x |
| *Tegella arctica* (d´Orbigny) | .. | .. | .. | x |
| *Scrupocellaria scruposa* (L.) | .. | .. | .. | x |
| *Cribrilina cryptooecium* Norman | .. | .. | .. | x |
| *Cribrilina annulata* (Fabr.) | .. | .. | .. | x |
| *Microporella ciliata* (Pallas) | .. | .. | .. | x |
| *Cylindroporella tubulosa* (Norman) | .. | .. | .. | x |
| *Celleporina hassallii* (Johnston) | .. | .. | .. | x |
| *Alcyonidium mytili* Dalyell | .. | .. | .. | x |
| *Arachnidium fibrosum* Hincks | .. | .. | .. | x |

the species, *Membranipora membranacea* (L.), is very conspicuous, being at once very common and covering extensive parts of algae. It has been found in every sampling year since 1967.

*Cirripedia (Table 6)*

*Verruca stroemia* (O. Fr. Müller) is commonly found living on stones and on shells of other animals at Surtsey and has occurred in every sampling year since 1967, except in 1984.

*Balanus balanoides* (L.) was already found in the tidal zone in 1967, and in every summer and autumn sampling in the same area since, though only in its first year of life. This barnacle is very common in the neighbourhood of Surtsey, where its larvae arrive every spring and settle down in the tidal zone. However, this habitat is so unstable that normal littoral animal communities have still not developed there. During the winter the young barnacles have been destroyed by surf caused by frequent winter storms. This species has occasionally been found down to a depth of 15 m at Surtsey.

Figure 1. *Alcyonium digitatum* at Surtsey in 1974. (Photo. Halldór Dagsson).

*Balanus balanus* (L.) was first found in 1968 and every sampling year since and seems to be fairly common.

*Balanus hammeri* (Ascanius) has only occasionally been found at Surtsey and is presumably rare at the island.

*Isopoda (Table 6)*

*Janiropsis breviremis* G. O. Sars was first found at Surtsey in 1971 and has occurred in subsequent sampling years except in 1983. In that year the sampling was ineffective on account of bad weather conditions. This species is by no means rare at Surtsey.

*Munna kröyeri* Goodsir was first found in 1971 and again in subsequent collections, except in 1984 and 1987. Because of its small size it may well be more common than its occurrence in the samples might seem to indicate.

*Janira maculosa* Leach has only been found in samples from 1977 and 1992, which indicates that it might be rare.

*Idotea granulosa* Rathke has only occurred in samples from 1987 and 1992, and then only some few individuals found at depths from 5 to 20 metres.

*Idotea neglecta* G. O. Sars. Only one specimen was found at a depth of 15 m off the east coast in 1992.

Table 6. Arrival and occurrence of Cirripedia, Isopoda and Decapoda at Surtsey.

| Year | 67 | 68 | 69 | 70 | 71 | 74 | 77 | 80 | 83 | 84 | 87 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CIRRIPEDIA | | | | | | | | | | | | |
| *Verruca stroemia* (O. Fr. Müller) | x | x | x | x | x | x | x | x | x | .. | x | x |
| *Balanus balanoides* (L.) | x | x | x | x | .. | x | x | .. | x | x | x | .. |
| *Balanus balanus* (L.) | .. | x | x | x | x | x | x | x | x | x | x | x |
| *Balanus hammeri* (Ascanius) | .. | x | x | x | .. | .. | x | x | .. | .. | .. | x |
| ISOPODA | | | | | | | | | | | | |
| *Janiropsis breviremis* G. O. Sars | .. | .. | .. | .. | x | x | x | x | .. | x | x | x |
| *Munna kröyeri Goodsir* | .. | .. | .. | .. | x | x | x | x | x | .. | .. | x |
| *Janira maculosa Leach* | .. | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | x |
| *Idotea granulosa Rathke* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | x | x |
| *Idotea neglecta G. O. Sars* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | x |
| DECAPODA | | | | | | | | | | | | |
| *Hyas coarctatus* Leach | x | x | x | x | x | x | x | x | x | x | x | x |
| *Portunus holsatus* Fabr. | x | x | x | .. | x | .. | .. | .. | .. | .. | .. | .. |
| *Eualus pusiola* (Kröyer) | x | .. | x | x | x | x | x | x | .. | .. | .. | .. |
| *Galathea nexa* Embl. | .. | .. | x | x | x | x | x | x | .. | x | x | x |
| *Pandalus montagui* Leach | .. | .. | .. | .. | .. | x | x | .. | .. | .. | .. | .. |
| *Eupagurus bernhardus* L. | .. | .. | .. | .. | .. | .. | .. | x | .. | x | .. | x |

Table 7. Arrival and occurrence of Prosobranchia at Surtsey.

| Year | 68 | 69 | 70 | 71 | 74 | 77 | 80 | 83 | 84 | 87 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| PROSOBRANCHIA | | | | | | | | | | | |
| *Lacuna divaricata* (Fabr.) | x | x | x | x | x | x | x | x | x | x | x |
| *Aporrhais pes-pelicani* (L.) | x | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Odostomia unidentata* (Mont.) | .. | x | x | x | x | x | x | .. | .. | .. | .. |
| *Skenopsis planorbis* (Fabr.) | .. | .. | .. | x | .. | .. | x | .. | .. | .. | x |
| *Velutina velutina* (Müller) | .. | .. | .. | .. | x | x | x | .. | .. | .. | .. |
| *Buccinum undatum* (L.) | .. | .. | .. | .. | x | x | .. | .. | .. | .. | x |
| *Margarites groenlandicus* (Chemn.) | .. | .. | .. | .. | .. | x | x | x | x | x | x |
| *Nassa incrassata* (Ström.) | .. | .. | .. | .. | .. | x | x | x | .. | x | x |
| *Acmaea testudinalis* (Müller) | .. | .. | .. | .. | .. | x | .. | .. | x | .. | x |
| *Onoba striata* (Mont.) | .. | .. | .. | .. | .. | x | x | .. | .. | .. | .. |
| *Lacuna pallidula* (da Costa) | .. | .. | .. | .. | .. | x | .. | .. | .. | x | .. |
| *Helcion pellucidum* (L.) | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | x |
| *Acmaea virginea* (Müller) | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | .. |
| *Natica clausa* (Brod. & Sow.) | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | .. |
| *Gibbula tumida* (Mont.) | .. | .. | .. | .. | .. | .. | x | .. | .. | .. | .. |
| *Margarites olivaceus* (Brown) | .. | .. | .. | .. | .. | .. | .. | .. | x | x | .. |
| *Omalogyra atomus* (Phil.) | .. | .. | .. | .. | .. | .. | .. | .. | .. | x | x |
| *Margarites helicinus* (Fabr.) | .. | .. | .. | .. | .. | .. | .. | .. | .. | x | x |
| *Neptunea despecta* (L.) | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | x |

*Decapoda (Table 6)*

*Hyas coarctatus* Leach, having occurred in the samples since 1967, appears to be quite common at Surtsey

*Portunus holsatus* Fabr. was sparsely represented in the samples from Surtsey in 1967-69 and again in 1971, but has not been found later.

*Eualus pusiolus* (Kröyer) occurred in samples from 1967-80, except for 1968. This is a swimming decapod which is probably still in the area.

*Galathea nexa* Embl. has been found at Surtsey since 1969 and is probably not rare there.

*Pandalus montagui* Leach has only occurred twice in the samples from Surtsey; nevertheless, it is not uncommon in the surrounding region.

*Eupagurus bernhardus* (L.) was found at Surtsey in 1980, 1984 and 1992 only, which might point to its rarity at the island.

*Prosobranchia (Table 7)*

*Lacuna divaricata* (Fabr.) was first found at Surtsey in 1968. Its frequent occurrence in later sampling years shows it to be common at the island.

*Aporrhais pes pelicani* (L.). Only one juvenile individual was found at Surtsey in 1968, but none later. This must be considered natural as a convenient habitat for this species is absent from the sampling area. However, the species has been found in the surroundings of Surtsey, and its shells were brought to the surface during the eruption and were found in the tephra part of the island.

*Odostomia unidentata* (Mont.) occurred first at Surtsey in 1969 and was found in the next 5 collections, but not later, being represented by a small number of individuals only. However, as it is a very small prosobranch, it may have been more frequent than the records indicate, and might still be living at the island.

*Skenopsis planorbis* (Fabr.). This prosobranch was first found at Surtsey in 1971, and again in 1980 and 1992. It seems to be rare, but might have escaped the divers' attention on account of its small size.

*Velutina velutina* (Müller) occurred in the samples in 1974, 1977 and 1980. It is rare at Surtsey, and likewise not frequent at the south coast of Iceland.

*Buccinum undatum* (L.) has been found in the samples from 1974, 1977 and 1992. It is still infrequent at Surtsey.

*Margarites groenlandicus* (Chemn.) occurred first in 1977 and has been found in every sampling year since then. However, up to now it does not seem to be common at Surtsey.

*Nassa incrassata* (Ström.) has been found at Surtsey since 1977, except in 1984, and appears to be fairly common.

*Acmaea testudinalis* (Müller) was only found to occur in the samples from 1977, 1984 and 1992.

*Onoba striata* (Mont.) is one of the small prosobranchs which were only brought up in samples with other animals or algae and are only found in the samples from 1977 and 1980.

*Lacuna pallidula* (da Costa) only occurred in the samples from 1977 and 1987.

*Helcion pellucidum* (L.) was only found in the samples from 1977 and 1992.

*Acmaea virginea* (Müller) was only found once, i.e. in 1977.

*Natica clausa* (Brod. & Sow.) like the last-mentioned species, only occurred in the samples from 1977, so nothing further can be said about its presence at Surtsey.

*Gibbula tumida* (Mont.) has only been found in samples from 1980, and must thus be considered to be very rare at Surtsey.

*Margarites olivaceus* (Brown), found in 1984 and 1987, did not occur in the 1992 samples, and can thus be presumed to be still uncommon.

*Omalogyra atomus* (Phil.) was rare in the 1987 and 1992 samples. As this prosobranch is extremely small, it can easily have been missed by the divers, and even by sorters of the samples.

*Margarites helicinus* (Fabr.) was first found in 1987; again in 1992 several individuals were discovered at 3 stations at the east and west coasts, so it can now be assumed to be a resident in the fauna at Surtsey.

*Neptunea despecta* (L.). Only one individual has

Table 8. Arrival and occurrence of Lamellibranchia at Surtsey.

| Year | 67 | 68 | 69 | 70 | 71 | 74 | 77 | 80 | 83 | 84 | 87 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LAMELLIBRANCHIA | | | | | | | | | | | | |
| *Mytilus edulis* (L.) | x | x | x | x | x | x | x | x | x | x | x | x |
| *Heteranomia squamula* L. | x | x | x | x | x | x | x | x | x | x | x | x |
| *Hiatella arctica* (L.) | x | x | x | x | x | x | x | x | x | x | x | x |
| *Chlamys pusio* (L.) | .. | x | x | .. | .. | x | x | x | x | .. | .. | .. |
| *Cardium fasciatum* (Mont.) | .. | x | x | .. | x | .. | x | .. | .. | .. | x | x |
| *Syndosmya nitida* (Müller) | .. | x | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Modiola phaseolina* Phil. | .. | .. | .. | x | .. | .. | .. | x | .. | .. | x | x |
| *Spisula solida* (L.) | .. | .. | .. | x | .. | .. | x | .. | .. | .. | .. | .. |
| *Mya truncata* (L.) | .. | .. | .. | .. | x | .. | x | .. | .. | .. | .. | .. |
| *Chlamys tigrina* (Müller) | .. | .. | .. | .. | x | .. | .. | .. | .. | .. | .. | .. |
| *Lyonsia norvegica* (Chemn.) | .. | .. | .. | .. | x | .. | .. | .. | .. | .. | .. | .. |
| *Kellia suborbicularis* (Mont.) | .. | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | x |
| *Modiolaria discors* (L.) | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | x | x |
| *Chlamys islandicus* (Müller) | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | x | x |
| *Syndosmya prismatica* (Mont.) | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | x |

Figure 2. Colony of *Mytilus edulis* with *Asterias rubens* feeding on it at 20 m depth at Surtsey in 1970. (Photo. Halldór Dagsson).

been found, in 1992. This large prosobranch is not likely to settle down on the hard bottom sampled at Surtsey although it is common in the surrounding area.

*Lamellibranchia (Table 8)*

*Mytilus edulis* (L.). The common mussel had already settled down at Surtsey in 1967, having in the years that followed formed quite extensive colonies on the underwater slopes (Fig. 2), and being now the most common bivalve at the island.

*Heteranomia squamula* L. has been found at Surtsey in every sampling year since 1967, being common at the island.

*Hiatella arctica* (L.) is very common at Surtsey, being first recorded there in 1967.

*Chlamys pusio* (L.) occurred first in the samples of 1968, and then on five subsequent occasions, though not after 1983, which points to its being relatively rare.

*Cardium fasciatum* (Mont.) was first found at Surtsey in 1968, but is not common there.

*Syndosmya nitida* (Müller) has only been collected once at Surtsey, i.e. in 1968, so it is hardly an inhabitant of the underwater slopes of the island.

*Modiola phaseolina* Phil. was first recorded at Surtsey in 1970, and three times subsequently. This small bivalve might easily have been missed in some of the samplings, but as it was fairly frequent in the samples of 1992, it seems to be getting common in the area.

*Spisula solid*a (L.) was only found at Surtsey in 1970 and 1977, thus being very rare.

*Mya truncata* (L.) only occurred in the samples of 1971 and 1977. It is an unlikely inhabitant on the hard bottom from which samplings are made at Surtsey.

*Chlamys tigrina* (Müller) was only found in 1971 and is thus hardly an inhabitant at Surtsey.

*Lyonsia norvegica* (Chemn.). As was the case with the previous species, this was only collected in 1971, and the same observation applies to its inhabitation at Surtsey.

*Kellia suborbicularis* (Mont.) was found in the samples from 1977 and again in those of 1992. The latter year so many individuals were found that it is obviously one of the inhabitants at Surtsey.

*Modiolaria discors* (L.) occurred at Surtsey in 1987 and again in 1992. In the latter year some few animals were collected from a depth of 20 m

Table 9. Arrival and occurrence of Asteroidea, Ophiuroidea, Echinoidea and Ascidiacea at Surtsey.

| Year | 68 | 69 | 70 | 71 | 74 | 77 | 80 | 83 | 84 | 87 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ASTEROIDEA | | | | | | | | | | | |
| *Asterias rubens* L. | x | x | x | x | x | x | x | x | x | x | x |
| *Hippasteria phrygiana* (Parelius) | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | .. |
| OPHIUROIDEA | | | | | | | | | | | |
| *Ophiopholis aculeata* (O. Fr. Müller) | .. | .. | .. | .. | x | .. | x | x | x | x | x |
| ECHINOIDEA | | | | | | | | | | | |
| *Echinus esculentus* (L.) | .. | .. | .. | .. | .. | x | x | .. | .. | x | x |
| *Strongylocentrotus droebachiensis* (O. Fr. Müller) | .. | .. | .. | .. | .. | x | x | .. | .. | x | .. |
| ASCIDIACEA | | | | | | | | | | | |
| *Ascidia callosa* Stimpson | x | .. | .. | .. | x | x | .. | .. | .. | .. | .. |
| *Styela rustica* (L.) | .. | x | .. | x | x | x | x | x | .. | x | x |
| *Boltenia echinata* (L.) | .. | .. | .. | x | .. | x | .. | .. | .. | .. | x |
| *Halocynthia pyriformis* (Rathke) | .. | .. | .. | .. | .. | x | x | x | x | x | x |
| *Ascidia obliqua* Alder | .. | .. | .. | .. | .. | x | .. | .. | .. | .. | .. |

at the east coast, so this appears to be a beginning to permanent settlement.

*Chlamys islandicus* (Müller) was only found in 1987 and 1992. In the latter year only a solitary young individual was collected, so little can be said about its settlement except that it is rare at Surtsey.

*Syndosmya prismatica* (Mont.). Only one young animal was brought up in the samples of 1992.

*Asteroidea (Table 9)*

*Asterias rubens* L. is very common at Surtsey, having been found there since 1968, grazing on the colonies of the common mussel.

*Hippasteria phrygiana* (Parelius) has only been recorded at Surtsey on one occasion, i.e. in 1977, thus hardly being a permanent member of the fauna at the island.

*Ophiuroidea (Table 9)*

*Ophiopholis aculeata* (O. Fr. Müller) was first found at Surtsey in 1974, being now common locally.

*Echinoidea (Table 9)*

*Echinus esculentus* (L.) occurred first in samples from 1977. Although by no means rare by now, it was not found in 1983 and 1984.

*Strongylocentrotus droebachiensis* (O. Fr. Müller) was first found at Surtsey in 1977, and again in 1980 and 1987. It seems to be rather uncommon.

*Ascidiacea (Table 9)*

*Ascidia callosa* Stimpson only occurred in the 1968 and 1974 samples.

*Styela rustica* (L.) was first found at Surtsey in 1969. Although it has not occurred in every subsequent collection, it is probably not uncommon.

*Boltenia echinata* (L.) was only found in the 1971 and 1992 samples.

*Halocynthia pyriformis* (Rathke) has been found in all sampling years since 1980, and is thus now one of the inhabitants on the underwater slopes at Surtsey.

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# A survey of the benthic coastal fauna of Surtsey, Iceland, in 1997

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## ABSTRACT

During the period of 4th to 10th of July 1997, samples of benthic animals were collected by diving at Surtsey, South-Iceland, on three transects, east, south and west off the island, in the shore and on 5, 10, 15, 20, 25 and 30 meters depths.

Number of species was similar in the collection depths of the east and south transects, but at 15 and 25 meters depths number of species were somewhat lower off the west coast, than the east and south coasts. The species composition of the three transects was quite similar. The isopod, *Janiropsis breviremis* was only found off the south coast, whereas the gastropod *Patina pellucida* was only found off the east coast. Many of the species most frequently collected had wide depth distribution. The exception from this was the octocoral *Alcyonium digitatum* that was only found below 15 m depth.

No new species was found in 1997 and not all of the species recorded in 1992 were found again in 1997. The total number of species was similar in 1997 as in 1992.

## INTRODUCTION

The colonisation of marine organisms on the new land formed in the Surtsey eruption in 1963, has been followed ever since (Sigurdsson 2000). From the year of 1997 the author has been responsible for the marine invertebrate part of the investigation.

The geological development of the island of Surtsey has been spectacular. The erosion of the island due to wave-exposure is immense and the island has decreased considerably since its formation. The heaviest erosion occurs on the southern coast of the island, due to prevailing southerly winds and intense wave exposure. The most stable shores are on the eastern side of the island, where some parts of the cliffs have endured since 1984.

## MATERIAL AND METHODS

During the period of 4$^{th}$ to 10$^{th}$ of July 1997, samples of benthic algae and animals were collected by diving, at the same time photographs were taken of the bottom in order to estimate the cover of the benthic biota. Orginally the plan was to collect samples of flora and fauna, as well as taking photographs, on three transects, east, south and west,

Table 1. Number of species of marine animals found at each depth on each of the three transects investigated.

| Depths (m) | Littoral | 5 | 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|---|---|
| East | 3 | 16 | 22 | 21 | 20 | 23 | 22 |
| South | - | - | 20 | 27 | - | - | 20 |
| West | - | 2 | 22 | 15 | 19 | 18 | 4 |

Table 2. Benthic animals from the intertidal and subtidal zone off the east coast of Surtsey in July 1997.

| Depth (m) | Intert. | 5 | 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|---|---|
| PORIFERA | | | | | | | |
| *Sycon ciliatum* (Fabr.) | | | | | | X | |
| *Grantia compressa* (Fabr.) | | X | X | X | X | X | X |
| SCYPHOZOA | | | | | | | |
| *Haliclystus octoradiatus* (Lamarck) | | | | X | | | |
| HYDROZOA | | X | X | X | X | X | X |
| ANTHOZOA | | | | | | | |
| *Alcyonium digitatum* L. | | | | | X | X | X |
| NEMERTEA | | | | | X | | X |
| POLYCHAETA | X | X | X | X | X | X | X |
| BRYOZOA | | X | X | X | X | X | X |
| CIRRIPEDIA | | | | | | | |
| *Balanus balanus* (L.) | | X | X | X | X | X | X |
| *Balanus balonoides* (L.) | X | | | | | | |
| *Balanus hammeri* (Ascanius) | | | | | | X | |
| *Verruca stroemia* (Muller) | | | | | | X | |
| ISOPODA | | | | | | | |
| *Idotea granulosa* Rathke | | X | X | X | X | | |
| *Idotea pelagica* Leach | | X | | | | | |
| *Idotea neglecta* G. O. Sars | | X | X | X | | | |
| *Janira maculosa* Leach | | | X | X | | | |
| *Munna kroyeri* Goodsir | | | X | | | | |
| AMPHIPODA | | X | X | X | X | | X |
| DECAPODA | | | | | | | |
| *Eupagurus bernhardus* L. | | | | | | | X |
| *Hyas coarctatus* Leach | | | | | X | X | X |
| PROSOBRANCHIA | | | | | | | |
| *Acmaea virginea* (Muller) | | | X | | | | |
| *Acmea testudinalis* (Muller) | | | | X | X | | |
| *Buccinum undatum* (L.) | | | | X | | X | X |
| *Lacuna divaricata* (Fabr.) | | X | X | X | | X | |
| *Margarites groenlandicus* (Chemn.) | | | | X | | X | |
| *Margarites helicinus* (Fabr.) | | X | X | | | | |
| *Nassa incrassata* (Ström) | | X | X | X | X | X | X |
| *Patina pellucida* (L.) | | X | X | | | | |
| NUDIBRANCHIA | | | | X | | | |
| *Doto coronata* (Gmelin) | | | | X | X | | |
| *Archidoris pseudoargus* Rapp | | | | | | | X |
| LAMELLIBRANCHIA | | | | | | | |
| *Heteranomya squamula* L. | | | X | | X | X | X |
| *Hiatella arctica* (L.) | | X | X | X | X | X | X |
| *Kellia suborbicularis* (Mont.) | | | | | | | X |
| *Modiola phaesolina* (Phil.) | | | | | | | X |
| *Modiolaria discors* (L.) | | | | | | X | |
| *Mytilus edulis* (L.) | X | X | X | X | X | X | X |
| ASTEROIDEA | | | | | | | |
| *Asterias rubens* L. | | X | X | X | X | X | X |
| OPHIUROIDEA | | | | | | | |
| *Ophiopholis aculeata* (O. Fr. Muller) | | | X | X | X | X | X |
| ECHINOIDEA | | | | | | | |
| *Strongylocentrotus droebachiensis* (O. Fr. Muller) | | | | X | X | | |
| *Echinus esculentus* (L.) | | | | | | X | X |
| ASCIDIACEA | | | | | | | |
| *Styela rustica* (L.) | | | | | | | X |
| *Halocynthia pyriformis* (Rathke) | | | | X | | X | X |
| PISCES | | | | | | | |
| *Liparis montagui* (Donovan) | | | | | | X | |

both in the shore and on 5, 10, 15, 20, 25 and 30 meters depths. It turned out to be impossible to take samples at all depth on each transect (Table 1). Sampling in the intertidal zone on the south and west shores had also to be abandoned, due to heavy surf. The 5, 20 and 25 meters stations of the south transect had to be left out due to heavy winds, and on the 30 meter station off the west coast little or no hard substrate could be found.

Samples were processed on-board of the

Table 3. Benthic animals from the subtidal zone off the south coast of Surtsey in July 1997.

| Depth (m) | 10 | 15 | 30 |
|---|---|---|---|
| PORIFERA | | | |
| *Sycon ciliatum* (Fabr.) | X | X | X |
| *Grantia compressa* (Fabr.) | X | X | X |
| *Halichondria panicea* (Pallas) | | | X |
| HYDROZOA | X | X | X |
| ANTHOZOA | | | |
| *Alcyonium digitatum* L. | | X | X |
| POLYCHAETA | X | X | X |
| BRYOZOA | X | X | X |
| CIRRIPEDIA | | | |
| *Verruca stroemia* (Muller) | X | | |
| ISOPODA | | | |
| *Idotea granulosa* Rathke | X | | |
| *Idotea pelagica* Leach | X | | |
| *Idotea neglecta* G. O. Sars | X | X | |
| *Janira maculosa* Leach | X | X | |
| *Janiropsis breviremis* G. O. Sars | | X | |
| AMPHIPODA | X | X | X |
| DECAPODA | | | |
| *Hyas coarctatus* Leach | X | X | X |
| *Pandalus montagui* Leach | | | X |
| PYCNOGONIDA | | | |
| *Nymphon* sp. | | X | |
| PROSOBRANCHIA | | | |
| *Lacuna divaricata* (Fabr.) | X | X | |
| *Margarites groenlandicus* (Chemn.) | | | X |
| *Margarites helicinus* (Fabr.) | X | X | |
| *Nassa incrassata* (Ström) | X | | X |
| *Onoba striata* (Mont.) | | | X |
| NUDIBRANCHIA | | X | |
| *Eubranhus pallidus* (Alder & Hancock) | | X | |
| *Dendronotus frondosus* (Ascanius) | | X | X |
| *Tergipes tergipes* (Forskal) | | X | |
| *Coryphella verrucosa* (M. Sars) | | X | |
| *Onchidoris bilamellata* (L.) | | | X |
| *Doto coronata* (Gmelin) | X | X | X |
| LAMELLIBRANCHIA | | | |
| *Hiatella arctica* (L.) | X | X | X |
| *Modiola phaesolina* (Phil.) | X | X | |
| *Mytilus edulis* (L.) | X | X | X |
| ASTEROIDEA | | | |
| *Asterias rubens* L. | | X | X |
| OPHIUROIDEA | | | |
| *Ophiopholis aculeata* (O. Fr. Muller) | X | X | X |
| ASCIDIACEA | | | |
| *Halocynthia pyriformis* (Rathke) | | X | |
| PISCES | | | |
| *Cyclopterus lumpus* L. | | X | |

Table 4. Benthic animals from the subtidal zone off the west coast of Surtsey in July 1997.

| Depth (m) | 5 | 10 | 15 | 20 | 25 | 30 |
|---|---|---|---|---|---|---|
| PORIFERA | | | | | | |
| *Grantia compressa* (Fabr.) | | X | X | X | X | |
| *Sycon ciliatum* (Fabr.) | | X | X | X | X | |
| SCYPHOZOA | | | | | | |
| *Haliclystus octoradiatus* (Lamarck) | X | | | | | |
| HYDROZOA | | X | X | X | X | X |
| ANTHOZOA | | | | | | |
| *Alcyonium digitatum* L. | | | | X | X | |
| POLYCHAETA | | X | X | X | X | X |
| BRYOZOA | | X | X | X | X | X |
| CIRRIPEDIA | | | | | | |
| *Balanus balanus* (L.) | | X | | | X | |
| *Verruca stroemia* (Muller) | | | X | | X | |
| ISOPODA | | | | | | |
| *Idotea granulosa* Rathke | | X | X | | X | |
| *Idotea pelagica* Leach | | X | | | | |
| *Idotea neglecta* G. O. Sars | X | X | | | | |
| *Janira maculosa* Leach | X | X | X | | X | |
| AMPHIPODA | | X | X | X | X | X |
| DECAPODA | | | | | | |
| *Hyas coarctatus* Leach | | | | X | | |
| PROSOBRANCHIA | | | | | | |
| *Acmaea virginea* (Muller) | | X | | X | | |
| *Buccinum undatum* (L.) | | | | X | | |
| *Gibbula tumida* (Mont.) | | | | | X | |
| *Lacuna divaricata* (Fabr.) | | X | X | | | |
| *Margarites groenlandicus* (Chemn.) | | | X | | | |
| *Margarites helicinus* (Fabr.) | | X | | | X | |
| *Nassa incrassata* (Ström) | | X | | X | X | |
| NUDIBRANCHIA | | | | | | |
| *Coryphella verrucosa* (M. Sars) | | | | X | | |
| *Onchidoris bilamellata* (L.) | | X | | | | |
| *Onchidoris muricata* (Muller) | X | | | | | |
| *Ancula cristata* (Alder) | | | X | | | |
| *Doto pinnatifida* (Montagu) | | X | X | X | X | |
| *Eubranhus pallidus* (Alder & Hancock) | | | | | X | |
| LAMELLIBRANCHIA | | | | | | |
| *Chlamys pusio* (L.) | | | | | X | |
| *Hiatella arctica* (L.) | | X | X | X | | |
| *Mytilus edulis* (L.) | | X | X | X | | |
| ASTEROIDEA | | | | | | |
| *Asterias rubens* L. | | | | X | | |
| OPHIUROIDEA | | | | | | |
| *Ophiopholis aculeata* (O. Fr. Muller) | | X | X | X | X | |
| ECHINOIDEA | | | | | | |
| *Strongylocentrotus droebachiensis* (O. Fr. Muller) | | | | X | | |

research vessel, identified to species or species groups and preserved in iso-propanol. Invertebrates belonging to the following groups were identified to species; porifera, isopoda, cirripedia, gastropoda, lamellibranchiata, echinodermata and ascidiacea. Animal groups like amphipods, nudibranchs, hydroids, bryozoans, pygnogonids and polychaetes are undergoing more thorough identification work. Identification of several species is under revision and hence these are not represented at the species level.

## RESULTS

*Intertidal zone*

Only three species were found on the rocks in the intertidal zone on the east coast of Surtsey: the barnacle *Balanus balanoides*, the polychaete *Pomatoceros* sp. and the edible mussel *Mytilus edulis*. The individuals found were all young-of-the-year.

*Subtidal zone*

The most frequently recorded invertebrates on 5-30 m depth range were the poriferan *Grantia compressa*, the edible mussel, the bivalve *Hiatella arctica*, the ophiurid *Ophiopholis aculeata* and the sea-star *Asterias rubens*, which occurred on almost all depths on the three transects. Other frequently recorded animals were; the isopods *Idotea granulosa* and *I. neglecta*, the poriferan *Sycon ciliatum*, gastropods *Margarites groenlandicus* and *M. helicinus*, and *Nassa incrassata*. The octocoral *Alcyonium digitatum* was common too, especially in the deeper parts of the area.

Number of species was similar in the collection depths of the east and south transects, but at 15 and 25 meters depths number of species were somewhat lower off the west coast, than the east and south coast (Table 1).

The species composition of the three transects was quite similar, the same species being the most frequently recorded (Table 2, 3 and 4). The isopod, *Janiropsis breviremis* was only found off the south coast, whereas the gastropod *Patina pellucida* off the eastern coast only.

Many of the species most frequently collected had wide depth-distribution and were found on depths from 10 to 30 meters (Table 2, 3 and 4). The exception from this was the octocoral *Alcyonium digitatum* that was most frequently recorded in the deeper part of the subtidal area and only found below 15 m depth.

## DISCUSSION

No new species was found in 1997 and not all of the species recorded by Sigurdsson (2000) were found again in 1997. The number of species seems to be similar as five years ago, as far as is comparable.

The further enrichment of the marine subtidal algae and invertebrates community off

Surtsey is hard to foresee occurring the next decades. The constant erosion of the shores must have pronounces influences on the settlement and development of the marine biota. Unstable substrate must retards the succession of the community and make it rather stochastic.

ACKNOWLEDGEMENTS

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Dr Anton Galan identified some of the isopods collected (see Galan 2000).

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# Benthic Amphipoda and Isopoda (Crustacea) from the sublittoral zone off Surtsey and Heimaey south of Iceland

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ABSTRACT

The volcanic island Surtsey, in the Vestmannaeyjar archipelago, was formed in a series of submarine eruptions, during the years 1963 to 1967. When the rocky shores began to build up, research of the marine colonization started. The most common crustacean groups in the epifaunal assemblage of subtidal hard bottoms are Amphipoda and Isopoda. This paper deals with studies on these groups in the nineties. Species abundance, faunistic changes and differences in distribution pattern of 30 species of peracaridans are discussed. The group of peracaridan crustaceans was found to have a diversity index of 2.3 on a transect at the east coast of Surtsey, both in 1992 and in 1997. The same value was found on a comparative transect surveyed in 1996 at the old lava grounds west of Heimaey, the main island of the Vestmannaeyjar archipelago. Therefore it is concluded that during the 25 years since the formation of the island, the colonization of crustaceans in the subtidal marine communities east of Surtsey has reached the same successional level as the older islands. The more eroded south and west coasts of Surtsey have not yet reached the same successional level due to the instability of the hard bottom.

Four species of amphipods are recorded herein new for the Icelandic fauna: *Gammarellus angulosus, Metopa borealis* and *M. solsbergi* from off Surtsey and *Jassa pusilla* from off Heimaey.

## INTRODUCTION

The colonization of marine organisms of the new lava grounds formed during the Surtsey eruption, started in the year 1963 and has been studied periodically ever since (Sigurdsson 1999). The author has taken part in the collection of samples from Surtsey during the summer expeditions of 1987, 1992 and 1997, noticing differences and similarities with nearby islands. Lack of information about peracaridan crustaceans (Hauksson 1992) initiated studies on these abundant groups: amphipods and isopods. For comparative studies, similar samples were collected in the summer 1996, off two nearby islands in the Vestmannaeyjar archipelago.

Amphipods and isopods are mainly sedentary-epibenthic crustaceans with eggs-carrying brood-pouch (not planktonic larval stages) and are very conspicuous and numerous on hard bottom substrates. They are important secondary producers, ranging in size from about 2 to 20 mm, and are an important component of the macrofaunal benthic-communities. In the present paper, a diversity index is used to compare the number of amphipod and isopod species and their relative abundance in samples of the hard bottom communities, between new and old lava grounds in the sublittoral zone off Surtsey and Heimaey.

## STUDY AREA, MATERIAL AND METHODS

Surtsey (63° 18´N, 20° 36´W) lies about 30 km southwest off the Icelandic mainland in the Vestmannaeyjar archipelago. It was formed in a

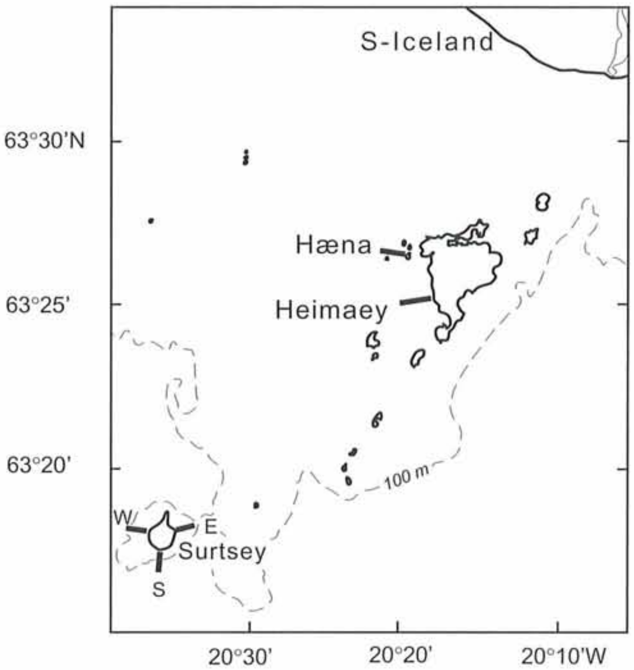


Figure 1. The Vestmannaeyjar archipelago. The study transects are shown with thick lines.

series of submarine eruptions, during the years 1963 to 1967. The biggest island of the archipelago is Heimaey and close to it, to the west is a small island, Hæna (Fig. 1). The waters around the Vestmannaeyjar archipelago are very productive and diving-visibility is frequently less than 5 meters during summer. The waters around Surtsey originate from the North Atlantic current with temperatures about 10 to 11°C during summer and 5 to 6 °C during winter and salinity of 35.2 (Stefánsson 1969). The prevailing southwesterly winds and surf activity constantly erode the exposed southwestern part of Surtsey, shaping the island severely since its formation.

The rocky bottom around Surtsey and Heimaey, generally extends to a water depth of about 30 meters, which marked the lower depth limit of the sampling. The tides are semidiurnal with amplitude of about 2.5 meters at spring tide in the area of study. In Surtsey sampling and photography of the subtidal area were carried out by scuba-diving along three different transects, east, south and west of the island (Fig. 1). The slope of the bottom along the transects is about 30°. Six sampling stations were at each transect, at five meters depth intervals, from 5 to 30 meters depth. The collections were made on one dive at each station. Three divers worked at each station: one collecting algae, one animals and one taking photographs. The main emphasis of the diving work was a biological surveying, therefore the collections were qualitative. However, the same stations were resampled in each of the years: 1987, 1992 and 1997, by the same diving team. Therefore, the samples offer some semi-quantitative information, as well as data for studying the distributional pattern of organisms.

During the period from the June 20 to June 26, 1992 the east transect off Surtsey was sampled at six different depths 5, 10, 15, 20, 25 and 30 meters. On the south transect it was impossible to dive at the 5 m station due to heavy surf, and the 20 m station had to be left out due to strong wind. At the 30 m station on the west transect no hard substrate was found, only sandy bottom, and hence no collection of hard substrate organisms was possible. During the period from the $4^{th}$ to the $10^{th}$ of July in 1997 the same thing happened, with the further limitation that the weather did not allow diving at the 25 m station on the south transect.

The collection of animals in the last three Surtsey expeditions, as well as the collection at the island of Heimaey and the adjacent Hæna island (Fig. 1), were mainly done by the same diver. From the $11^{th}$ to the $22^{nd}$ of August in 1996, two transects, one almost horizontal west of Heimaey and the other near vertical at Hæna, were sampled with 5 meter depth intervals, in a similar way as in the Surtsey survey. Two or three dives were conducted at each station. The emphasis was on the collection of all organisms, in a quarter of square meter, randomly selected by throwing a frame some meters above the bottom, at every sampling depth of each transect. All organisms were collected in 0.5 mm mesh plankton nets, until the diver had scraped the hard bottom bare.

In the Surtsey expeditions the material was sorted on board a research vessel under a dissecting microscope and transferred to 70 % isopropanol with seawater. The Hæna and Heimaey samples were fixed in 5% filtered seawater formalin on board and later sorted under a dissecting microscope in the laboratory and then transferred to alcohol for preservation. The crustaceans were sorted and identified to species. The individuals of each species were counted. The proportion of males, females, gravid females and juveniles were also evaluated, when appropriate for assessment of the species life cycle. The diversity index (Margalef 1974) is defined as the total number of species (S) minus one divided with the natural logarithm of the total number (N) of individuals ((S-1)/ln N).

Table 1. Species and number of individuals collected in Surtsey in 1992.

| Surtsey 1992 | East transect | | | | | | | South transect | | | | | West transect | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth meters: | 5 | 10 | 15 | 20 | 25 | 30 | A* | 10 | 15 | 25 | 30 | A* | 5 | 10 | 15 | 20 | 25 | A* | B° |
| *Idotea granulosa* | 9 | | | | | | | | | | | | | | | | | | |
| *Janira maculosa* | | 2 | 1 | | | | | 1 | | 2 | | | | | | 1 | | | |
| *Janiropsis breviremis* | | | | | | | | | | | | | | | | 1 | | | |
| *Muna kroyeri* | 1 | | | | | | | | | | | | | | | | | | |
| *Hyperia galba* | 1 | | | | | | | | | | | | | | | | | | |
| *Gammarellus angulosus* | | 1 | | | | | | 58 | 22 | 1 | | | 3 | | 3 | 1 | | | |
| *Parapleustes bicuspis* | | | 1 | | | | | | | | | | | | | | | | |
| *Pleusymtes glaber* | | 1 | 2 | | | | | | | 4 | 1 | | | | 2 | 1 | | | |
| *Stenothoe monoculoides* | | 5 | 6 | | | | | | | 7 | 5 | | | | 15 | 10 | | | |
| *Metopa solsbergi* | | | | | | 3 | | | | | | | | | | | | | |
| *Gamaropsis nitida* | | | | | | 17 | | | | | | | | | | | | | |
| *Ischyrocerus anguipes* | 36 | 47 | 65 | 7 | 1 | | | 5 | 8 | 51 | 45 | | 6 | 3 | 70 | 26 | 1 | | |
| *Jassa falcata* | 2 | | 7 | | | | | | | 2 | | | | | 29 | | | | |
| *Caprella linearis* | | 1 | | 2 | | | | | | 1 | | | | | | | | | |
| *Caprella septentrionalis* | | 3 | 21 | 13 | | | | | | 40 | 24 | | | | 22 | 20 | | | |
| **N** | 49 | 60 | 103 | 22 | 1 | 20 | 255 | 64 | 30 | 108 | 74 | 276 | 9 | 3 | 141 | 60 | 1 | 214 | 746 |
| **S** | 5 | 7 | 7 | 3 | 1 | 2 | 14 | 3 | 2 | 8 | 4 | 8 | 2 | 1 | 6 | 7 | 1 | 8 | 15 |
| **(S-1)/ln N** | | | | | | | 2.3 | | | | | 1.2 | | | | | | 1.3 | 2.1 |

* For total transect °For total survey

The diversity index was calculated for each of the transects and for each year.

## RESULTS

*Faunal composition and distribution*

A total of 6,164 peracaridan animals were counted and identified to 30 species: 22 species of Amphipoda and 8 species of Isopoda (Tables 1, 2 and 3).

The number of animals found in Surtsey indicates how common the species are. Below is a list of species arranged in phylogenetic order, with general comments on their distribution and biology. New records for the Icelandic fauna are marked with an asterisk.

Order Isopoda

Family Idoteidae

*Idotea granulosa* Rathke, is a common species resident between tidemarks and below. It has predominantly been found in our study at 10

Table 2. Species and numbers of individuals collected in Surtsey in 1997.

| Surtsey 1997 | East transect | | | | | | | South transect | | | | West transect | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth meters: | 5 | 10 | 15 | 20 | 25 | 30 | A* | 10 | 15 | 30 | A* | 5 | 10 | 15 | 20 | 25 | A* | B° |
| *Idotea granulosa* | | 1 | 1 | 1 | | | | 1 | | | | | 1 | 1 | | 1 | | |
| *Idotea pelagica* | 1 | | | | | | | 2 | | | | | 4 | | | | | |
| *Idotea neglecta* | | 1 | 1 | | | | | 1 | 1 | | | 1 | 1 | | | | | |
| *Janira maculosa* | | 1 | 1 | | | | | 1 | 1 | | | 1 | 2 | 1 | | 1 | | |
| *Janiropsis breviremis* | | | | | | | | | 1 | | | | | | | | | |
| *Muna kroyeri* | | 1 | | | | | | | | | | | | | | | | |
| *Hyperoche medusarum* | 1 | | | | | | | | | | | | | | | | | |
| *Gammarellus angulosus* | | 1 | | 1 | | | | 38 | 30 | 1 | | 30 | 24 | 1 | 2 | 2 | | |
| *Apherusa jurinei* | | | | | | | | | 4 | | | | | | | | | |
| *Stenothoe monoculoides* | | | 1 | | | | | | 1 | | | | | 1 | | | | |
| *Metopa borealis* | | | | 2 | | 2 | | | | 1 | | | | | | | | |
| *Pleusymtes glaber* | | | | 1 | | 1 | | | | 1 | | | 1 | | 1 | | | |
| *Ischyrocerus anguipes* | 47 | 17 | 38 | 10 | | | | 14 | 18 | 1 | | 3 | 20 | 18 | 12 | 11 | | |
| *Jassa falcata* | 4 | 12 | 37 | 12 | | | | | 2 | | | 1 | 1 | 2 | | | | |
| *Caprella linearis* | | | 1 | 7 | | | | 3 | 5 | 5 | | 2 | | | 8 | | | |
| *Caprella septentrionalis* | 1 | 3 | 21 | 38 | 2 | 1 | | | | | | | | | | 2 | | |
| **N** | 54 | 37 | 101 | 72 | 2 | 4 | 270 | 60 | 63 | 9 | 132 | 38 | 54 | 24 | 23 | 17 | 156 | 558 |
| **S** | 5 | 8 | 8 | 8 | 1 | 3 | 14 | 7 | 9 | 5 | 13 | 6 | 8 | 6 | 4 | 5 | 11 | 16 |
| **(S-1)/ln N** | | | | | | | 2.3 | | | | 2.4 | | | | | | 1.9 | 2.3 |

* For total transect °For total survey

Table 3. Species and number of individuals collected at the Hæna and Heimaey transects in 1996

| 1996 | Hæna transect | | | | | | | Heimaey transect | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth meters: | 5 | 10 | 15 | 20 | 25 | 30 | A* | 5 | 10 | 15 | 20 | 25 | 30 | A* |
| *Idotea granulosa* | 1 | | | 1 | | | | 83 | | 2 | | | | |
| *Idotea pelagica* | 4 | 81 | | | | 1 | | 8 | 3 | | | 2 | | |
| *Idotea neglecta* | 1 | | | | | | | | | | | | | |
| *Idotea baltica* | | | | | | | | 6 | | | | | | |
| *Jaera albifrons* | 1 | | | | | | | | | | | | | |
| *Janira maculosa* | 10 | 18 | 1 | | 3 | | | 2 | 4 | | | 2 | | |
| *Janiropsis breviremis* | 15 | 83 | 1 | 2 | | | | 34 | | | | | | |
| *Muna kroyeri* | 18 | 105 | 15 | 17 | 11 | 6 | | 14 | 22 | 44 | 21 | | | |
| *Gammarellus homari* | | | 2 | | | | | | | | | | | |
| *Gammarellus angulosus* | 1 | 2 | | 3 | 2 | 6 | | | | | | | | |
| *Apherusa jurinei* | | 53 | | | | | | 404 | 69 | 5 | | | | |
| *Pleusymtes glaber* | 27 | 155 | 37 | 81 | 33 | 22 | | | 2 | | 20 | 4 | | |
| *Parapleustes bicuspis* | | 26 | 35 | | | | | | | | 8 | 4 | | |
| *Stenothoe monoculoides* | 12 | 110 | 18 | 11 | 26 | | | 62 | 16 | | 32 | | | |
| *Metopa borealis* | | 2 | 12 | 3 | 15 | | | | | | 2 | | | |
| *Metopa alderi* | | | | | | 3 | | | | | | | | |
| *Acanthonotozoma serratum* | | | | | | | | | | | | 1 | | |
| *Dexamine thea* | | | 2 | | | | | | 5 | 57 | 11 | 2 | | |
| *Ampithoe rubricata* | | | 2 | | | | | 263 | 5 | | 2 | | | |
| *Ischyrocerus anguipes* | | 130 | 1 | | 15 | 26 | | | | | 54 | | | |
| *Jassa falcata* | 45 | 159 | 23 | 115 | 17 | 1 | | 855 | 278 | 195 | 130 | 14 | | |
| *Jassa pusilla* | | | | | | | | | | | 2 | | 7 | |
| *Parajassa pelagica* | 31 | 77 | | | | | | 40 | | | | | | |
| *Corophium bonelli* | | | | | | | | | | | 1 | | | |
| *Caprella linearis* | | 53 | | 43 | 12 | | | | | | | | | |
| *Caprella septentrionalis* | 38 | | 7 | 10 | 7 | 55 | | | 30 | 58 | 12 | 2 | | |
| **N** | 204 | 1054 | 156 | 286 | 141 | 120 | 1961 | 1771 | 434 | 361 | 295 | 31 | 7 | 2899 |
| **S** | 13 | 14 | 13 | 10 | 10 | 8 | 22 | 11 | 10 | 6 | 12 | 8 | 1 | 20 |
| **(S-1)/ln N** | | | | | | | 2.7 | | | | | | | 2.3 |

* For total transect

meters depth. Some females had brood pouch with eggs, and juveniles were observed, suggesting at least a two year life span.

*Idotea pelagica* Leach, was the next common species in our study that was predominantly found at a depth of 10 meters, replacing the preceding species on the more exposed transects. Off Surtsey it first appeared in the samples in 1997.

*Idotea neglecta* Sars, is a sublittoral species found in small numbers, along all transects off Surtsey.

*Idotea baltica* (Pallas), has only been found occasionally in our study off Heimaey, but not off Surtsey.

Family Janiridae

*Jaera albifrons* Leach, is mainly a littoral species found only off the island of Hæna at a 5 meter depth.

*Janira maculosa* Leach, is a sublittoral species found only in small numbers in the samples off Heimaey and Hæna in 1996 and off Surtsey in 1992 and 1997.

*Janiropsis breviremis* Sars, is another common sublittoral species found in moderate numbers.

Family Munnidae

*Muna kröyeri* Goodsir, is a sublittoral species. It is often overlooked because it is very small although it is very numerous, and is found along the east transect off Surtsey, Heimaey and Hæna.

Order Amphipoda

Family Hyperiidae

*Hyperia galba* (Montagu), is a pelagic species, normally associated with jellyfish. Its appearance in benthoic samples was considered accidental. One individual was found off Surtsey in 1992.

*Hyperoche medusarum* (Muller), is also a pelagic species probably accidentally occurring in benthos samples. Only one animal was found off Surtsey in 1997.

Family Calliopidae

*Gammarellus angulosus* (Rathke)*, is a shallow sublittoral species common and locally abundant in southwestern Icelandic waters. It appeared in samples off Surtsey in 1992 and 1997, well represented by males, females, some with eggs and juveniles of different size. The same applied to the island of

Hæna. This suggests that *G. angulosus* produces successive broods in a one year life cycle. It was found clinging to algae and other growths in highly exposed areas. The author has observed it preying upon newly dead seabirds (Alcidae) in large quantities.

*G. angulosus* is recognized herein as a different species from *G. homari*, therefore it is a new record for the fauna of Iceland. Previously, *G. homari* has been reported for Iceland by Stephensen (1940) who wrote: "*G. homari* and *G. angulosus* are no doubt synonymous; most of the Icelandic specimens are big and belong to the form *G. homari*." This synonymy has been maintained in the literature (Enckell 1980). Steele (1972) has however shown them to be separate species as is also considered in the present paper.

*Gammarellus homari* (Fabricius), is a large sublittoral species for an amphipod, solitary but widespread around Iceland. It is up to 40 mm in length, double that of *G. angulosus*, with which it has often been confused. *G. homari* occurred only in the sample from 15 meters depth at Hæna.

*Apherusa jurinei* (Milne-Edwards), is a shallow sublittoral species that was locally common amongst algae off the islands Heimaey and Hæna. It was also found at 15 meters depth off Surtsey in 1997.

Family Pleustidae

*Parapleustes bicuspis* (Kroyer), is a sublittoral species found in moderate numbers in the Heimaey and Hæna samples. It appeared on the east transect of Surtsey in 1992 but it was not found there in 1997.

*Pleusymtes glaber* (Boeck), is a moderately common species on rocky subtidal areas. It was collected along all transects, with some females carrying eggs.

Family Stenothoidae

*Stenothoe monoculoides* (Montagu), is a sublittoral species common amongst algae and hydroids, it was found along all transects with the females frequently carrying eggs.

*Metopa alderi* (Bate), is a rocky sublittoral species, that was only found at 30 meters depth off Hæna.

*Metopa borealis* Sars*, is a rocky sublittoral species found off Hæna and Heimaey in 1996 and Surtsey in 1997. It is a Northeast-Atlantic species distributed from Norway to the English Channel, but it is not widely recorded and it is reported herein for the first time in Iceland.

*Metopa solsbergi* Schneider*, is a sublittoral species rarely recorded from Greenland and Norway. It was found for the first time in Iceland off Surtsey in 1992 at a depth of 30 meters at the east transect.

Family Acanthonotozomatidae

*Acanthonotozoma serratum* (Fabricius), is a sublittoral species found on just one occasion off Heimaey.

Family Dexaminidae

*Dexamine thea* Boeck, is a shallow sublittoral species, which appeared locally abundant off the islands of Hæna and Heimaey.

Family Amphithoidae

*Amphithoe rubricata* (Montagu), is a sublittoral species which lives in tubes attached to hard substratum. It was found locally abundant at the islands Hæna and Heimaey. It was not collected at Surtsey in 1992 and 1997 but it appeared in some samples from 1987.

Family Isaeidae

*Gamaropsis nitida* (Stimpson), is a sublittoral species that was found only at a depth of 30 meters, east off Surtsey in 1992. Of the animals 50% were females and one half of them carried eggs.

Family Ischyroceridae

*Ischyrocerus anguipes* Kroyer, is a sublittoral species locally very common all around Iceland. It was the most abundant species off Surtsey in 1992 and 1997. It was also common off the islands Hæna and Heimaey, most abundant between 10 and 20 meters depth, usually in the company of *Jassa falcata*. It is a filter feeder, which constructs tubes amongst algae or hydroids. The proportions of animals found in summer were about 30% males, 30% females with brood pouch, 20% females without brood pouch, and 20% juveniles of different sizes, suggesting successive broods in a one year life cycle.

*Jassa falcata* (Montagu), is a sublittoral species, very abundant locally. It was found to be the most abundant species off the islands Hæna and Heimaey and was also quite common off Surtsey, along with *Ischyrocerus anguipes*. It is also a filter feeder constructing tubes on solid surfaces and the sex and age proportions of animals are similar to those of *I. anguipes*.

*Jassa pusilla* (Sars)*, is a sublittoral species recorded in Icelandic waters for the first time, off Heimaey in 1996, at 20 and 30 meters depth, associated with sponges, hydroids, and carapace of spider crabs. This is a species not widely recorded, distributed from northern Norway to the Bay of Biscay.

*Parajassa pelagica* (Leach), is a shallow sublittoral species locally common at 5 and 10 meters depth off the islands Hæna and Heimaey. This is a filter feeding amphipod, which builds nests amongst algae, hydroids, and bryozoans.

Family Corophiidae

*Corophium bonelli* (Milne-Edwards), is a shallow sublittoral tube-building amphipod that was only present in one sample off Heimaey.

Family Caprellidae

*Caprella linearis* Kroyer, is a benthic species found in moderate numbers off Surtsey in 1992 and 1997, as well as off Hæna in 1996.

*Caprella septentrionalis* (Linnaeus), is a benthic species extremely common, found in almost all the samples off Surtsey, Hæna, and Heimaey. The proportions of males, females, ovigerous females and juveniles were about 25 % each.

*Faunal differences in space and time*

There is a difference in the species composition and numbers of individuals of the peracaridan crustaceans, between the Vestmannaeyjar islands, as well as within Surtsey in the years 1992 and 1997. A list of the 30 species found during the surveys with their relative abundance is shown in the table 4.

A total of 21 species were collected off Surtsey, 15 species were collected on the transects of Surtsey in 1992 and 16 at Surtsey in 1997. There were 22 species collected at Hæna and 20 at Heimaey. The species lists of the different surveys at Surtsey were similar, even though 4 species collected at Surtsey in 1992 were lacking in 1997, and 5 species found in 1997 were missing in 1992. Likewise, 4 species collected along the Heimaey transect did not appear in the Hæna samples which contained 5 species not found at Heimaey. Further comparisons revealed that 4 species collected on the Surtsey transects were not found in the samples from Hæna and Heimaey in which 9 species were lacking from the Surtsey samples.

Considering the vertical distribution of species and the number of individuals sampled, the stations at 15 meters depth off Surtsey, particularly on the east transect, both in 1992 and 1997, yielded the highest number of species and animals. However, off the Hæna island the maximum number of species and animals was found at 10 meters depth. Off Heimaey island the highest number of species and animals was found at 5 meters depth.

Finally, from a total of 30 species, 17 were common to Surtsey, Hæna, and Heimaey. These species are very typical of hard bottom benthos all around Iceland.

Table 4. List of species and relative abundance (x= 1-10 animals; xx= 10-100 animals; xxx> 100 animals).

| Transects: | Surtsey 1992 | Surtsey 1997 | Hæna | Heimaey |
|---|---|---|---|---|
| *Idotea granulosa* | x | x | x | xx |
| *Idotea pelagica* | | x | xx | xx |
| *Idotea neglecta* | | x | x | |
| *Idotea baltica* | | | | xx |
| *Jaera albifrons* | | | x | |
| *Janira maculosa* | x | x | xx | x |
| *Janiropsis breviremis* | x | x | xxx | xx |
| *Muna kroyeri* | x | x | xxx | xxx |
| *Hyperia galba* | x | | | |
| *Huperoche medusarum* | | x | | |
| *Gammarellus homari* | | | x | |
| *Gammarellus angulosus* | xx | xxx | xx | |
| *Apherusa jurinei* | | x | xx | xxx |
| *Parapleustes bicuspis* | x | | xx | xx |
| *Pleusymtes glaber* | xx | x | xxx | xx |
| *Stenothoe monoculoides* | xx | x | xxx | xxx |
| *Metopa alderi* | | | x | |
| *Metopa borealis* | | x | xx | x |
| *Metopa solsbergi* | x | | | |
| *Acanthonotozoma serratum* | | | | x |
| *Dexamine thea* | | | x | xx |
| *Ampithoe rubricata* | | | x | xxx |
| *Gamaropsis nitida* | x | | | |
| *Ischyrocerus anguipes* | xxx | xxx | xxx | xx |
| *Jassa falcata* | xx | xx | xxx | xxx |
| *Jassa pusilla* | | | | x |
| *Parajassa pelagica* | | | xxx | xx |
| *Corophium bonelli* | | | | x |
| *Caprella linearis* | x | xx | xxx | |
| *Caprella septentrionalis* | xxx | xx | xxx | xxx |

*Species diversity*

The diversity indices (Tables 1-3) of the transects off Surtsey in 1992 show the highest value of 2.3, for the east transect. The number of animals was very similar for each transect but the number of species was different, 14 on the east transect and 8 on the south and west transects. Combining the three Surtsey transects gives an index value of 2.1, with a total of 15 species. The survey off Surtsey in 1997 gives similar results, the east transect had a diversity index of 2.3 and 14 species and the combined index for the survey was 2.3, with a total of 16 species.

On the almost vertical slope transect off Hæna the diversity index reached the highest value, 2.7, with 22 species. On the near horizontal slope transect off Heimaey the index was 2.3, with 20 species.

The diversity index shows this natural variability from one transect to another and at different times of collection; but the index from the east transect of Surtsey both in 1992 and 1997 was 2.3, the same as for Heimaey in 1996. In addition the total number of species found on the east transects of Surtsey in both year surveys together was 19, very similar to the 20 species found in the survey at the island Heimaey.

## DISCUSSION AND CONCLUSION

The new lava grounds at Surtsey have a steep slope and large parts of the shoreline of the island was eroded away by the action of the sea. The rocky shore in the southwestern area has been most severely affected and several hundred meters of seashore have been washed away. The east area is the most stable and there the community at the upper 5 and 10 meters depth, comprises seaweeds as the most conspicuous organisms, mainly: *Alaria esculenta*, which is replaced by *Laminaria hyperborea* at 15 meters depth (Jónsson *et al.* 1987). A deep water community situated between 20 and 30 meters depth is dominated by a faunal assemblage of filter feeders, where the soft coral *Alcyonium digitatum* and hydroids are dominant (Fig. 2).

Figure 2. The faunal assemblage of *Alcyonium digitatum* at a depth of 30 meters off the island Hæna.

On the old gently sloping lava grounds off Heimaey the kelp forest of *L. hyperborea* is dominating at 5 m water depth. At the nearby vertical transect off Hæna, *A. esculenta* is the most prominent species at 5 m water depth and *L. hyperborea* at 10 m. On both transects the deep water communities are dominated by the faunal assemblage of *A. digitatum* and hydroids (Galan 2000).

Amongst the crustaceans 4 species of Cirripedia and 6 of Decapoda are known off Surtsey (Hauksson 1992), which were also found at Hæna and Heimaey in 1996. Cirripeds with pelagic larval stages are early invaders on hard substrates. Decapods have a pelagic larval stage, are relatively large and are very mobile. In contrast amphipods and isopods are mostly sedentary, developing youngs from eggs carried in a brood-pouch or marsupium, therefore with limited dispersal capabilities. In spite of their small size, they are important secondary producers because of their abundance in the benthos (Calman 1911). Therefore, the 30 species of amphipods and isopods dealt with here are an important component of the benthos off Surtsey and Heimaey.

In general, the highest value of the diversity index for the peracaridan crustaceans and the highest number of species and animals, in the present study were at the sampling sites where the kelp forest of *L. hyperborea* was dominant. This was at 15 m water depth off Surtsey in 1992 and 1997, 10 m off Hæna and 5 m off Heimaey in 1996. *Ischyrocerus anguipes, Jassa falcata, Caprella septentrionalis* and few other species are most numerous in the kelp forest of *Laminaria hyperborea*. The reason for their abundance is most likely the extensive space, which the holdfast of this kelp species provides. The first two species mentioned are actually tube builders and the caprellids hang amongst hydroids and other sessile organisms. The difference in biomass and depth distribution of *L. hyperborea* at different transects are mainly the combined outcome of physical and biological factors (Galan 2000).

The new record of *Gammarellus angulosus* was found in the exposed southwestern transects off Surtsey and vertical one off Hæna. It was however absent from the horizontal transect off Heimaey and it was rare in the more stable one of east Surtsey. This is likely an opportunistic species because it has a short life cycle, numerous broods, it is resistant to exposure and it has diverse feeding habits. *Metopa borealis, M. solsbergi* and *Jassa pusilla* are new records for the Icelandic fauna, being rarely recorded in the Northeast Atlantic. At least 23 species of the genus *Metopa* are reported from the area, all small species and thus easily overlooked. *Jassa pusilla* is very difficult to distinguish from *J. falcata* and *Ischyrocerus anguipes.* The females and young males of these three species are apparently identical and sometimes present in large quantities in one sample. These facts may explain their recent discovery.

The new records for the Icelandic fauna are not only from Surtsey but also from Heimaey, which probably is the result of a lack of studies on hard substrates. Faunal studies of hard bottom subtidal fauna around Iceland is needed.

There are fewer species present off Surtsey than off the nearby islands (Table 4) and there are also fewer animals collected off Surtsey than off the nearby islands (Tables 1-3). This can partly be explained by the difference in working methods between the two areas. The sampling methods were relatively qualitative at Surtsey and quantitative at the nearby islands. Although, taking into account that we are dealing with motile animals in different space and time, the differences in the total number of species and animals collected in the surveys can also be explained by natural variability. If we assume that the relative abundance of each species is reflected in the number of individuals of the species in the sample. Thus the differences in numbers of species and individuals between transects, can be considered reasonably comparable. In the present paper the natural logarithm of the total number of animals related to the number of crustacean species in the benthos is used as diversity index (Margalef 1974) in order to evaluate the colonization off Surtsey with reference to nearby islands with caution and some reserve.

The diversity indices of the south and west transects of Surtsey are very variable and lower than indices of the east transect in Surtsey and those of the nearby islands. This may be explained by the fact that the southwestern area of Surtsey is in constant renovation because of the retreat of the shoreline and sometimes the addition of huge rocks from above, due to the erosive forces of weather and sea. Therefore, the number of species is lower off the south and west transects. In addition high numbers of the opportunistic species *Gammarellus angulosus* further reduces the index. The almost vertical transect off Hæna presents a different picture. Algal cover is less and sessile macrofauna is more abundant in the shallow water depths. Overhanging cliffs adjacent to the transect reduces daylight reaching the sublittoral zone. The number of species and the diversity index was highest off Hæna. However, the highest number of animals, was in the kelp forest off Heimaey. The number of species and the indices are very similar in the east transect of Surtsey in 1992 and 1997, and off Heimaey in 1996.

For comparison the new lava grounds, formed off Jan Mayen in 1970, had established shallow water subtidal communities, which had after 10 years reached a successional stage similar to that of the old grounds; because the severe physical conditions, like sea-ice, limited the complexity of the community, resulting in a low faunal diversity on both grounds (Gulliksen *et al.* 1980). Biogeographical reasons like latitude and the lack of kelp forest in Jan Mayen, might help to explain longer time of colonization compared with Surtsey.

By comparing the diversity indices for amphipods and isopods it can be stated that colonization and successional evolution of the east subtidal area of Surtsey has reached a similar level of maturity to that of the old lava grounds at Heimaey, after 25 years. How long it will take the subtidal biocenosis of the south and west coast of Surtsey to reach the same successional stage is a question, that can probably be answered by future studies.

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GEOLOGY AND GEOPHYSICS

# Geological monitoring of Surtsey, Iceland, 1967-1998

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ABSTRACT

Aspects of the geological monitoring of the volcanic island of Surtsey 1967-1998, are described. A hydrothermal system was developed within the tephra craters in late 1966 to early 1967. Temperatures in a drill hole, situated at the eastern border of the hydrothermal area, indicate that the hydrothermal system at that site has been cooling at an average rate of ≤ 1°C per year since 1980.

The tephra was altered rapidly within the hydrothermal area, producing the first visible palagonite tuff in 1969. A substantial part of the tephra pile above sea level was probably converted to tuff by 1972. The visible area of tuff has gradually increased since then, primarily due to erosion of tephra at the surface. By 1998 52 % of the exposed tephra area had been converted to palagonite tuff. By volume, however, some 80-85% of the tephra pile above sea level had been converted to tuff in 1998.

The area of Surtsey has shrunk from its original 2.65 km$^2$ (1967) to 1.47 km$^2$ (1998) due to marine abrasion. The geological formations on Surtsey have, however, responded quite variably to erosion. The tephra pile was easily eroded, but marine abrasion has also caused rapid cliff recession of the lava field, and longshore currents have deposited a sand-gravel spit on the north shore. The palagonite tuff, however, is very resistant to marine abrasion. The central core of palagonite tuff is estimated to be ≤ 0.39 km$^2$.

Statistical estimation of models of the decrease of Surtsey indicate that it will last for a long time. The numerical experiments indicate that it will take over 100 years until only the palagonite tuff core is left. It is postulated that the final remnant of Surtsey before complete destruction will be a palagonite tuff crag, comparable to those of the other islands in the Vestmannaeyjar archipelago.

## INTRODUCTION

The island of Surtsey was constructed from the sea floor by volcanic activity during 1963-1967, on the Vestmannaeyjar shelf off the south coast of Iceland. The sea water depth prior to the eruption was 130±2 m. The eruption history of Surtsey has been described in detail (Thórarinsson *et al.* 1964, Thórarinsson 1966, 1968), and summarised in numerous papers (e.g. Jakobsson & Moore 1982).

Several research groups have monitored the development of Surtsey within various fields of geology after the eruption ceased in 1967. Some of these projects were initiated during the eruption. Coastal erosion and geomorphological changes until 1993 have been followed by Thórarinsson (1968), Norrman (1980, 1985) and Jakobsson (1995), and the submarine morphology of the Surtsey volcanic group 1967-1989 by Norrman & Erlingsson (1992). The consolidation and palagonitization of the Surtsey tephra and the development of the hydrothermal area 1968-1979 has been reported by Jakobsson (1978), and Jakobsson & Moore (1986).

Geomagnetic field measurements were carried out repeatedly between 1968 and 1973

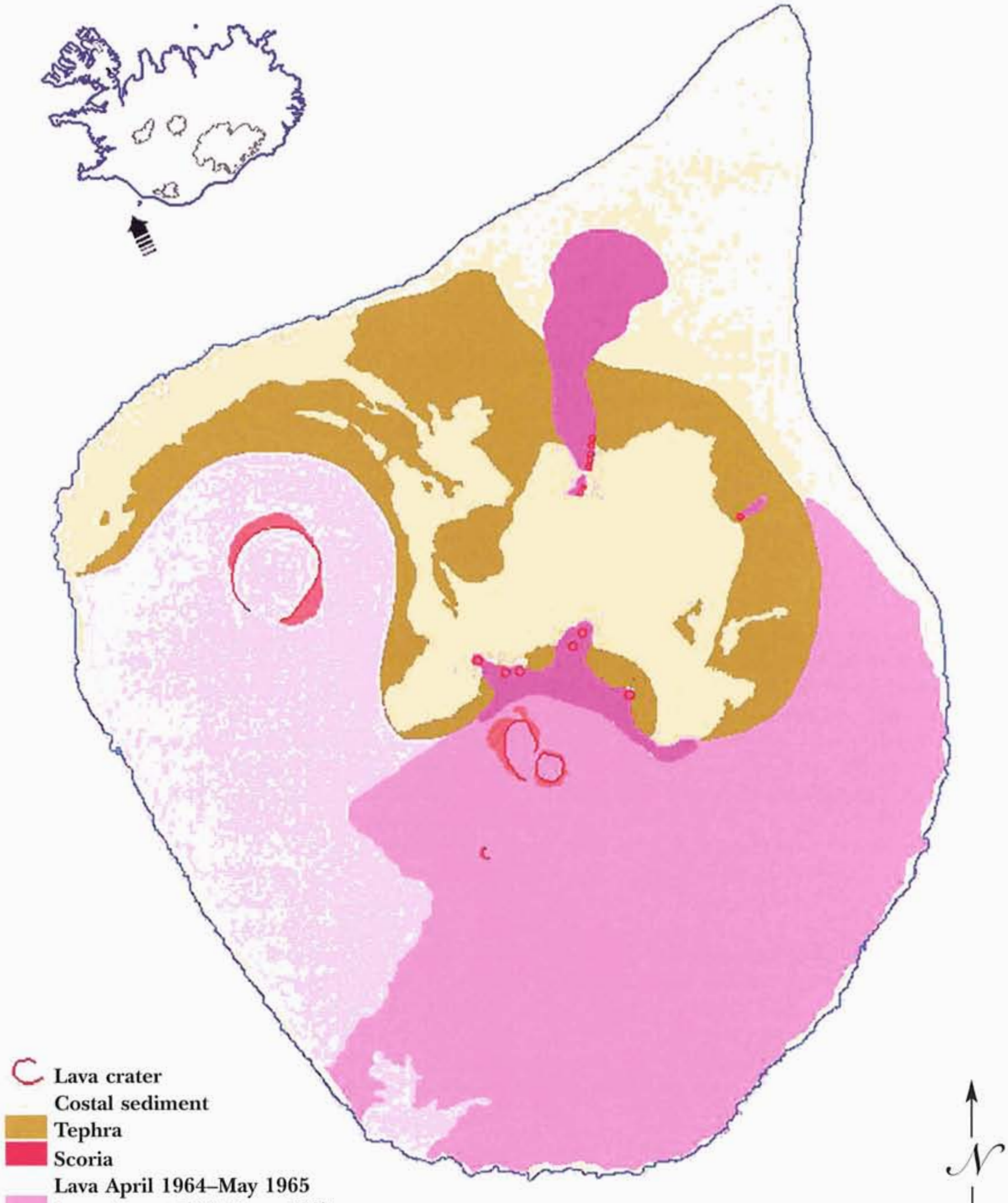


Figure 1. Geological map of Surtsey as in August 1998, modified after Jakobsson (2000).

(Sigurgeirsson 1974). The subsidence of Surtsey until 1991 has been measured by Tryggvason (1972) and Moore *et al.* (1992). Precise GPS measurements, first carried out in 1992 (Einarsson *et al.* 1994) and to be repeated in the summer of 2000, will make it possible to record accurately both vertical and horizontal movements in Surtsey. The area is also closely monitored seismologically, as the Vestmannaeyjar archipelago falls within the area covered by the seismographic net in Iceland (Einarsson & Björnsson 1987, Stefánsson *et al.* 1993).

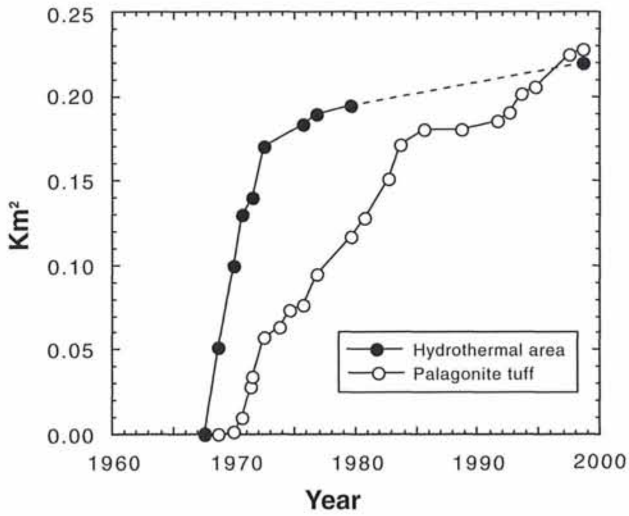


Figure 2. Mapped extent (km²) of the hydrothermal area in the tephra craters and the area of palagonite tuff, 1968-1998. Field observations indicate that after about 1972, the expansion of the hydrothermal area and palagonite tuff is primarily due to aeolian erosion.

During the period 1967-1998, 29 geologic expeditions were made to the island to follow the above mentioned changes and 24 air photo stereo sets were taken by Landmaelingar Islands, at the request of the Surtsey Research Society. The extent of the hydrothermal area and the palagonite tuff has been mapped with the aid of air photos on the scale of 1:5,000. Temperature measurements at the surface were carried out with conventional mercury thermometers until 1979 and after that with electronic thermometers. Temperature measurements in the drill hole were carried out with a thermocouple. Samples of tephra and tuff have been collected regularly to follow the process of palagonitization.

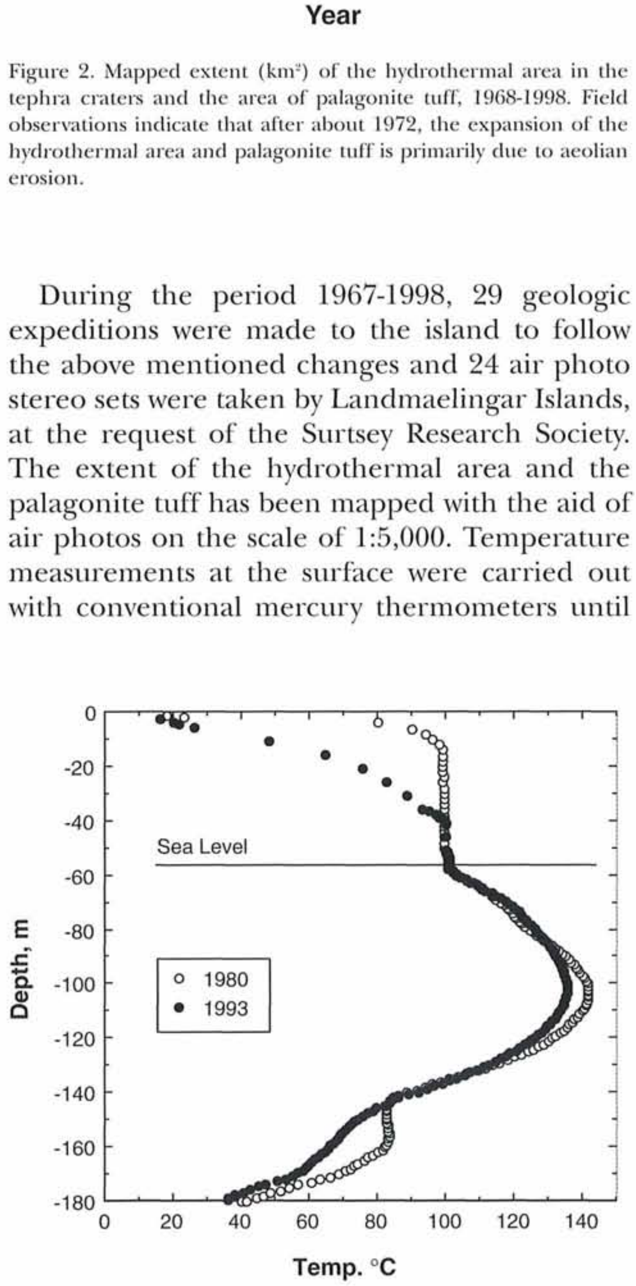


Figure 3. Temperature measurements within the drill hole, as of September 1980 and August 1993. Sea water level is at 58 m depth and the hole is cased down to 165 m depth.

The subject of this report is the monitoring of Surtsey from 1967 to 1998 as regards the development of the hydrothermal system of the volcano, the consolidation of the tephra to palagonite tuff and the marine abrasion of the island (Jakobsson *et al.* 1998). An attempt is also made to predict the future development of Surtsey by simple models, estimated from the observed area.

## ERUPTION HISTORY

During the initial phreatic phase of the eruption, from November 1963 to April 1964, tephra (hyaloclastite) was deposited as air fall tephra and base surge flows, creating two horseshoe-formed craters (Fig. 1). The tephra is generally finely bedded and fine grained, with 60-70 % in the coarse ash (0.06 - 2 mm) fraction. Less than 0.5 % falls into the fraction blocks and bombs (> 64 mm). About 85-90 % of the tephra is basaltic glass, the remainder being olivine and plagioclase phenocrysts, and rock fragments. Initial total porosity of the tephra at surface is as high as 45-50 % (Oddsson 1982).

Lava started to flow from the western crater in April 1964 and continued to do so until May 1965. A lava shield, dipping towards the south and southeast, was gradually built up with foreset-bedded breccia forming at the same time below sea level. This lava shield has a thickness of 100 m at the western lava crater. Lava again erupted from August 1966 to June 1967, this time from a new fissure inside the eastern tephra crater, Surtur, forming an irregular lava shield towards the southeast (Fig. 1). In December 1966 and January 1967 small lava flows erupted from five different fissures in the eastern tephra crater (Thórarinsson 1968). The Surtsey lavas are generally thin and fractured. At the east coast individual lava units average a few meters in thickness, while at the southwest coast the lava flows are often less than 1 m thick. One lava flow at the south coast exceeds 20 m in thickness.

When the eruption ceased the volume of Surtsey itself was about 0.8 km³, of which 0.12 km³ was above sea-level. The island had then reached a maximum height of 174 m above sea level and an area of about 2.65 km². The material erupted is alkali olivine basalt. Morphologically, Surtsey is

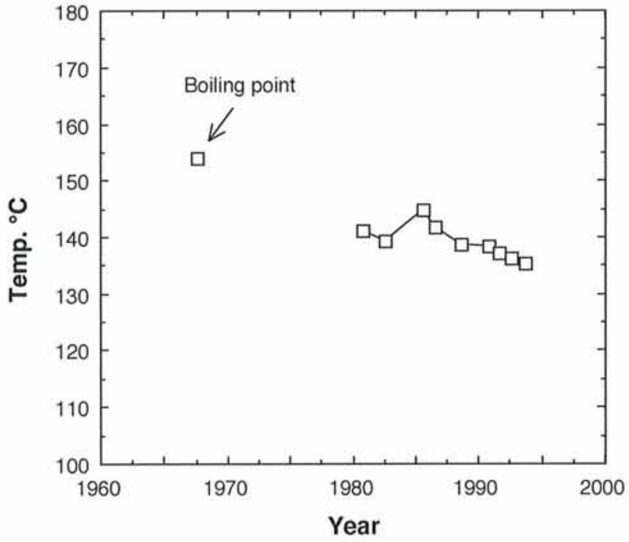


Figure 4. Maximum temperatures (at 101-104 m depth) in the drill hole 1980-1993. The boiling point for sea water at this depth is also indicated for mid 1967, when the hydrothermal system probably was established.

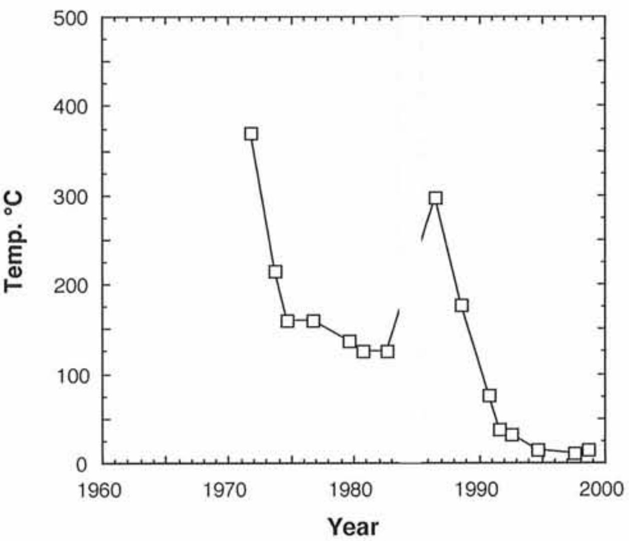


Figure 5. Temperature measurements at surface at a locality on the southern rim of the Surtungur (western) lava crater, 1971-1998. Only maximum temperatures measured each time are registered (cf. Jakobsson 1978, his Fig. 2, curve 1). The vertical shaded area indicates the time period when the fissures at the western lava crater opened up.

a marine tuya (table mountain, stapi), built up in the same manner as the Pleistocene sub- and intraglacial tuyas (Kjartansson 1966).

## THE HYDROTHERMAL SYSTEM

Anomalous temperatures were first detected at the surface in the tephra pile in April 1968 (Jakobsson 1978). A thermal anomaly is clearly visible on the surface of the eastern tephra crater on an infrared image taken on August 22, 1968 (Friedman & Williams 1970). It has been suggested that the hydrothermal system was developed as a consequence of intrusive activity in the eastern tephra crater during December 1966 - January 1967 (Jakobsson & Moore 1986). The hydrothermal system is vapour-dominated above sea level and temperatures around 100° C will therefore prevail in the porous tephra pile, except close to the surface where temperatures were lower because of precipitation and circulation of air.

Since the hydrothermal area was detected in 1968, it has, as measured at the surface, continued to expand within the tephra craters (see Fig. 2). It is tentatively suggested that the birth and development of the hydrothermal system is recorded in the increase in the surface exposure of the hydrothermal area from 1967 to 1970. In 1970 the conversion of tephra to tuff may have started to affect the heat flux, resulting in a slowing down of the expansion of the hydrothermal area. It takes about 1-3 years for the Surtsey tephra to convert to compact tuff at 80-100° C (Jakobsson 1978). The decline in surface temperatures after 1971 is probably also due to the sealing effect of the newly formed palagonite tuff. The surface extent of the hydrothermal area continued to expand in 1972-1979, partly because the vapour was forced to the sides of the almost impermeable core of palagonite tuff, but probably more importantly due to removal of loose tephra from surface by wind and water. After 1979 it was difficult to get accurate estimates on the extent of the hydrothermal area, and in 1998 its extent was estimated to be less than the area of palagonite tuff (Fig. 2).

Temperature measurements in a 181 m deep hole, which was drilled in 1979 at the eastern border of the hydrothermal area (Jakobsson & Moore 1982), show that the hydrothermal system in that area has cooled down in a regular fashion with the greatest cooling occurring near the surface, at the bottom, and at middle depth where the hole is hottest (Fig. 3). The cooling varies with depth in the well. The region of maximum temperatures at 101-104 m depth apparently caused by heat from nearby dykes (Jakobsson & Moore 1986) declined from 154° C in 1967 to 133° C in 1993, or at a general rate of ≤1° C per year (Fig. 4).

Fairly continuous surface temperature measurements are available from a 40x30 m area at the southern rim of the western lava crater (Fig.

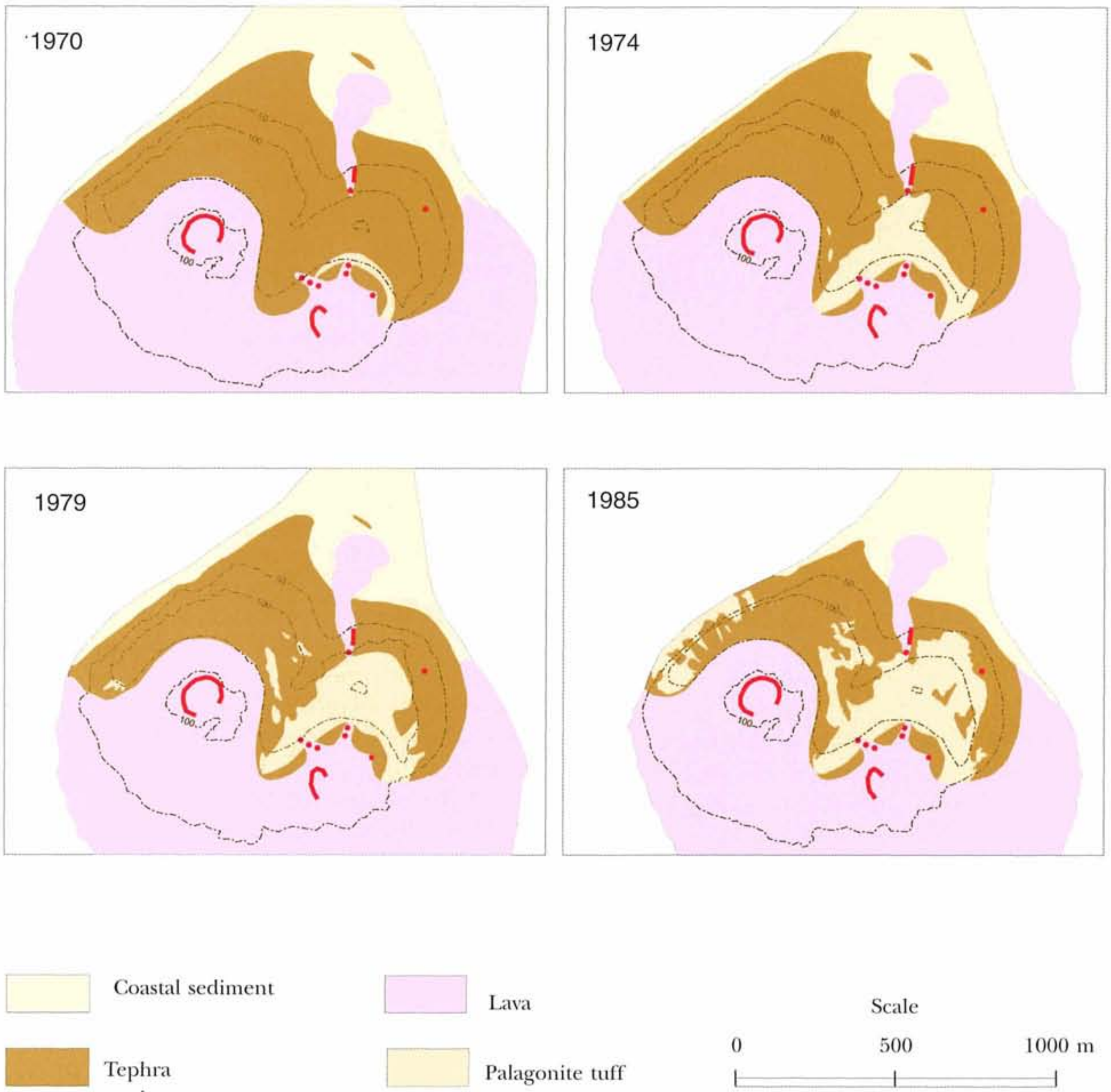


Figure 6. Four simplified geological maps of the central part of Surtsey showing the expansion of the mapped area of palagonite tuff, from 1970 to 1985. Aeolian sand and talus is omitted. Different outlines of the island are traced after air photographs (Landmaelingar Íslands) from respective years. Different height contours are from maps after Norrman (1970), Landmaelingar Íslands (pers. comm. 1977), Norrman (1978) and Norrman & Erlingsson (1992).

5). A series of E-W fissures in the surface lava widened about 10-20 cm between September 1983 and August 1985. An unexpected rise in temperature was observed at this site in 1985 and was apparently caused by subsidence of the southern part of the 100 m thick lava pile, opening of these fissures, and conduction of hot gases from below. A small rise in 1985 of the maximum temperature at 101-104 m depth in the drill hole (Fig. 4) was evidently produced by this event.

## CONSOLIDATION OF THE TEPHRA

The hydrothermal activity caused rapid alteration of tephra, producing the first visible palagonite tuff in 1969, in the southeastern corner of the eastern tephra crater (Jakobsson 1978). Fig. 6 shows how the surface exposure of the palag-

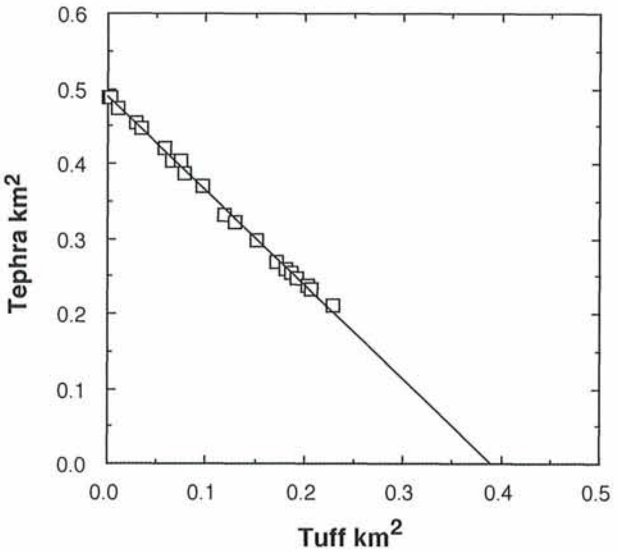


Figure 7. Variations ($km^2$) in the exposed area of palagonite tuff related to the area of unaltered tephra, 1967-1998. It is inferred that the area of palagonite tuff is ≤ 0.39 $km^2$ when all tephra has been altered to tuff or eroded away.

onite tuff has gradually increased from 1969 to 1998, when 52 % of the exposed area of tephra in Surtsey had converted to palagonite tuff. However, the unaltered tephra is a relatively thin blanket encircling the tuff area, and it is estimated that by volume some 80-85 % of the remaining tephra pile above sea level had been altered to palagonite tuff in 1998.

The expansion of the area of palagonite tuff is further elucidated and compared to that of the hydrothermal area in Fig. 2. The expansion of the surface exposure of palagonite tuff is probably directly linked to the expansion of the hydrothermal area in 1969-1972. After that field observations indicate that the mapped expansion of the tuff area is primarily due to removal of loose tephra from the surface by wind and water. The rather irregular curve of the area of palagonite tuff after 1972 (Fig. 2) is probably primarily reflecting the frequency of heavy winter storms. By comparing the variations in the mapped areas of tephra and palagonite tuff from 1967 to 1998 (Fig. 7), it is inferred that the area of palagonite tuff is ≤ 0.39 $km^2$ when all tephra has been altered to tuff or eroded away.

Palagonitization of fine grained air fall and base surge tephra such as found in Surtsey and subsequent deposition of secondary minerals, produces a compact mass of rock, which has turned out to be extremely resistant to marine abrasion. Layering is hardly conspiceous in the tuff and fractures are relatively few.

## EROSION

Heavy storms, mainly during winters, produce high wave activity at the southwest coast of Iceland (Viggósson *et al.* 1994). Marine abrasion has therefore caused rapid sea cliff recession in Surtsey (Thórarinsson 1968, Norrman 1978, Jakobsson 1995). The loose unconsolidated tephra was easily eroded, even during the phreatic phase of the eruption. Since the lava units are generally rather thin and fractured they have also been heavily abraded, particularly the thin pahoehoe sheets. The palagonite tuff, however, is much more resistant to marine erosion. This agrees with observations on the other islands in the Vestmannaeyjar archipelago, where marine erosion of cliffs made of palagonite tuff appear extremely slow, although no reliable records exist on the rate of marine erosion in Vestmannaeyjar.

Longshore currents have deposited a sand-gravel spit on the north side, see Figs 1 and 6. The material is primarily derived from the west and east lava cliffs, carried by heavy surfs towards the north. When marine abrasion reached compact palagonitized tuff at the west coast in 1981 and water depth increased at that site, less and less material was transported to the northern spit. The result was that after 1981 the northern spit has slowly been moved towards the east (Figs 6 and 9).

The unconsolidated tephra is also easily eroded by wind and running water. Exact figures on aeolian erosion in Surtsey do not exist, however, it is estimated that several meters have been eroded from the crest of the tephra craters. In the center of the western bowl of the eastern tephra crater (Surtur), it is estimated that some 10-15 m (vertical thickness) of tephra have been eroded by aeolian action. Much of the eroded tephra has been carried into the sea, the rest being deposited along the sides of the tephra craters and on the lava (Jakobsson 2000). The palagonite tuff is also somewhat sensitive to wind erosion and at places in the eastern tephra crater a few meters of the surface have evidently been eroded after the tephra was consolidated to tuff.

## AREAL CHANGES

The three principal geological formations of Surtsey react quite differently to marine abrasion. Fig. 8 shows the cumulate areal change of Surtsey and separately the changes of its three

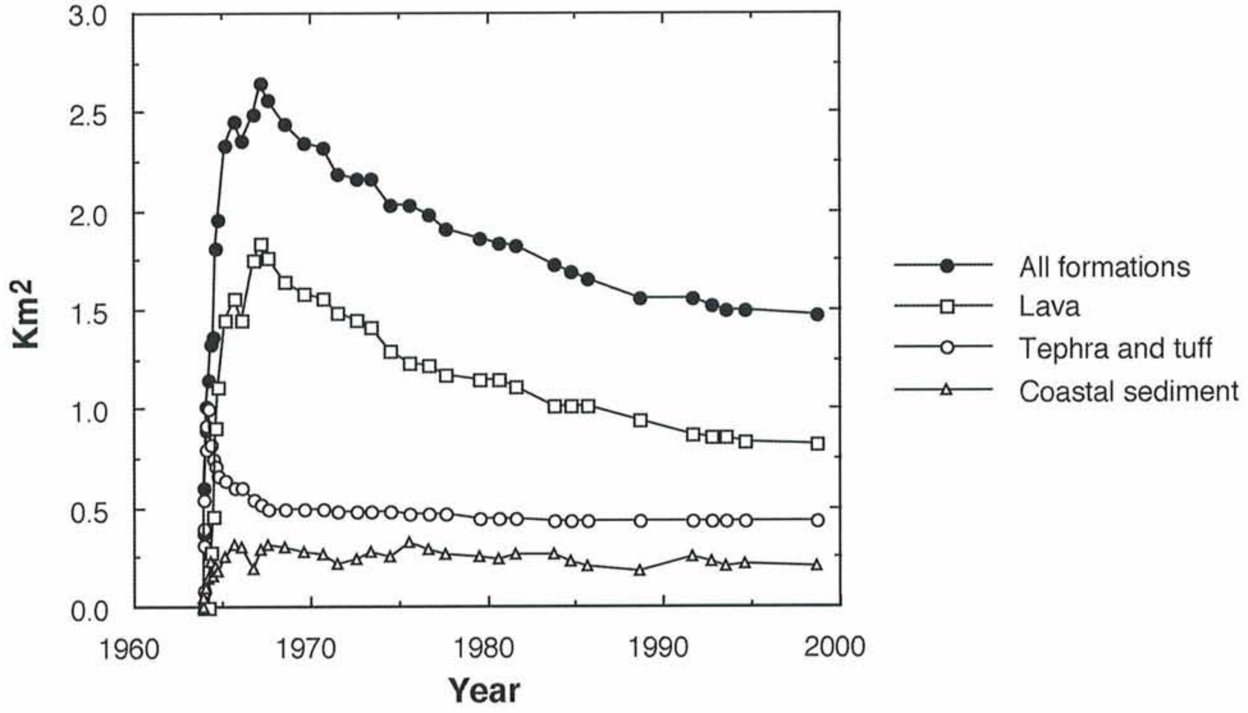


Fig. 8. Aerial changes (km$^2$) of Surtsey and its three principal geologic formations, 1963-1998. The measurements are done on air photographs taken by Landmaelingar Íslands, at the scale 1:5,000. Aerial measurements during the eruption 1963-1967 are mainly from Thórarinsson (1966, 1968).

geological formations during the period of construction in 1963 to 1967 and subsequent destruction after the eruptions ceased in 1967. The diagram demonstrates that the erosion of lava dominates the reduction in size of the island. The total area of tephra plus palagonite tuff has only changed to a minor degree from 1967 to 1998, but the area of lava has been halved in this period. The area of the coastal sediment of the northern spit shows perceptible variations, probably primarily due to variations in intensity of winter storms, and was generally seen to diminish slightly during the period.

Fig. 9 shows changes in the outline of Surtsey from 1967 to 1998. During this period the area of Surtsey shrunk from a maximum of about 2.65 km$^2$ in 1967 to 1.47 km$^2$ in 1998. It appears that the marine abrasion will proceed at a considerable speed until the core of palagonite tuff, volcanic necks and lava resting on palagonite tuff, have been reached. When the core is reached the erosion will slow considerably.

## FUTURE DEVELOPMENT OF SURTSEY

In order to predict the future development of the size of Surtsey with some certainty we would need a credible theoretical model with satisfactory fit to the observed values according to statistical criteria. The shape of the island cannot be closely approximated by any simple geometrical model and the main geological formations, i.e. lava, tephra, tuff and sediment, have different properties with regard to erosion. But the data are not sufficiently accurate or numerous to estimate complicated models with many parameters. Our models are therefore gross simplifications of the actual circumstances and we can only hope to obtain some idea of the order of magnitude of the rate of erosion in the future.

Our observations are measurements of the area of Surtsey at given points in time. The total area at a particular time is

$$Y = Z + B$$

where B is the area of the palagonite tuff, which constitutes the permanent part of the island, and Z is the area of formations subject to erosion.

The rate of erosion at any time depends upon the weather, tides and currents and is highly variable. But our investigation is only concerned with long term changes so we ignore

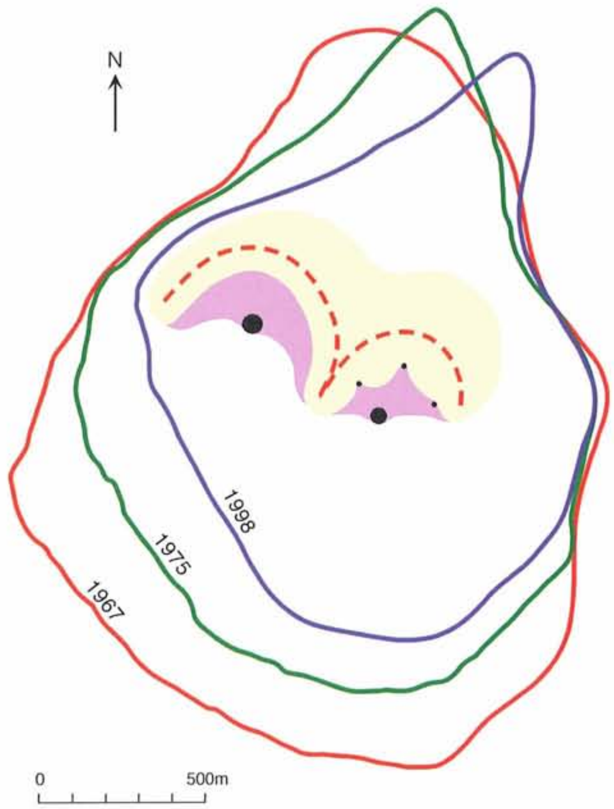


Figure. 9. Changes in the outline of Surtsey from 1967 to 1998, traced after air photographs taken by Landmaelingar Íslands. The estimated extent of the central core of palagonite tuff (brown), volcanic necks (black) and lava resting on tuff (violet), is indicated.

these variations. Let us first consider a rather naïve model and assume that the rate of reduction of the area at any time is proportional to the area of geological formations subject to erosion, i.e.

$$dZ = -\alpha Z dt. \qquad (1)$$

Solution of this equation gives the model

$$Y_i = A^{-\alpha t_i} + B + \varepsilon_i$$

for the observed area at time $t_i$ with $t_1=0$ and Z=A at the first observation. The rate of erosion is determined by $\alpha$. Measurement errors and irregularities in the process of erosion are represented by the residuals $e_i$. Estimation of parameters by least squares gives

$$Y_i = 1.223\ e^{-0.0676 t_i} + 1.309.$$
$$(0.030)\ (0.0045)\ (0.035)$$

Standard deviation of estimated parameters are presented in parentheses below respective value.

$R^2 = 0.994$ (adjusted for degrees of freedom),
$s = 0.026\ km^2$ (estimated standard error of the residuals)
$\log L = 54.72$ (L = likelihood function).

Estimation by least squares is maximum likelihood estimation when the residuals are serially uncorrelated, normally distributed with zero mean, constant variance and independent of $t_i$. The model passes statistical tests based on these premises and also tests whether the parameters are constant in time. (The assumption of constant residual variance is not realistic for this equation but an estimation, taking into account decreasing variance as the area approaches B, produces similar parameter values).

This statistically satisfactory model predicts that the erosion ceases long before the area has reached the estimated size of the palagonite tuff, which contradicts the geological evidence about the future development of the size of Surtsey. The mathematical model of equation (1) is widely applied to describe the decline of mass or populations where each element of Z is equally liable to elimination at any moment of time. But the assumption that the rate of eroded area is proportional to the total area is implausible. The sea is the main erosive force and it is only active along the coastline.

Let us now try and derive a formulation based only on consideration of erosion by the sea. We ignore the actual shape of the island and different properties of the eroded geological formations and consider the erosion of a regular cone of initial height H and radius R. We assume uniform erosion along the coastline so that the circumference remains a circle. When the erosion proceeds the height at the coastline becomes h and the radius r. Let us now assume that the rate of erosion by the sea is proportional with the perimeter so that the change of volume in time interval dt is

$$dV = -2\pi rk dt, \qquad (2)$$

where the constant k is a property of the eroded material and erosive forces. The change in volume when r changes by dr is

$$dV = 2\pi rh dr$$

where h is the height at the perimeter. From the geometry we have $H/R = h/(R-r)$ so that

$$dV = 2\pi rH(1 - r/R) dr. \qquad (3)$$

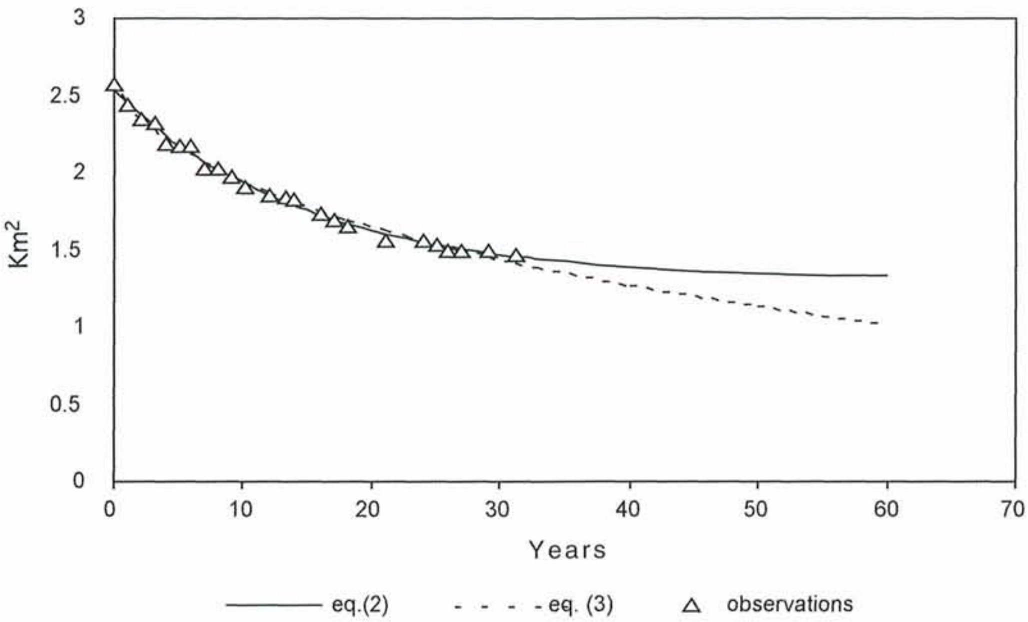


Figure 10. Observed area, fitted models and extrapolation, 3 decades ahead.

Equations (2) and (3) provide a differential equation for the change of r and with the initial value r=R at t=0 the solution is

$$(R-r)^2 = 2kRt/H.$$

In this equation t=0 must be when r=R and this may not coincide exactly with the first observation so we add a constant to t. By inserting the area for r we obtain the model

$$Y_i = (Y_0^{0.5} - (\beta(t_i - t_0))^{0.5})^2 + \varepsilon_i$$

for the observed area. $Y_0$ is the initial area, $t_0$ the time between r=R and the first value and

$$\beta = 2\pi kR/H.$$

Estimation by least squares gives

$$Y_i = (1.673 - (0.00738(t_i+0.62))^{0.5})^2$$
$$(0.016) \quad (0.00052) \quad (0.37)$$

$R^2 = 0.992$,
$s = 0.030$ km$^2$,
logL = 51.39.

The fit of this model is slightly worse than the exponential decay and it fails the test of constant parameters. According to this model the time when the area reaches 0.39 km$^2$ is 148 years after the first observation, i.e. about year 2115. But as the model fails the test of constant parameters this is not a reliable forecast. In view of the impeccable fit of the model with exponential decay a much longer time until only the palagonite formation is left is hardly inconsistent with the data.

Both models are based on the assumption of a homogeneous material with respect to erosion. Obviously the actual geological formations have different physical properties, geometry and exposure to the erosive forces. Fig. 8 shows that the rate of erosion has in fact differed considerably between the formations. However, the fits obtained when the models above (or simple polynomials) are estimated with the area of each formation were worse than we obtained for the total area. One reason for this is probably that the geometry of each formation is less regular than the whole island. We have not attempted any interpretation of these results.

Fig. 10 shows the observed values of the total area, fitted models and extrapolation, 3 decades ahead. The two curves are hardly distinguishable until the end of the interval of observations, but the predicted courses diverge rapidly. Future observations will therefore soon provide valuable additional information for this kind of model building.


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# Physical volcanology of lava flows on Surtsey, Iceland: A preliminary report

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## ABSTRACT

The Surtsey volcano is situated off the central-south coast of Iceland and was formed by a prolonged submarine volcanic eruption between November 1963 and June 1967. The prominent features on Surtsey are two abutting ~140 m high tuff cones and small pahoehoe lava flow field that caps the southern half of the island. Although best known for its surtseyan explosive activity, the eruption featured two distinct subaerial effusive phases that produced two small pahoehoe lava shields. The first effusive phase lasted for 13.5 months and produced a 100 m high lava shield with a total volume of 0.25–0.30 km³. The second effusive phase formed a 70 m high lava shield (volume ~0.1 km³) and lasted for 9.5 months. The observations presented here show that the Surtsey lava shields consist of two principal structural units, the lava cone and the outer lava apron. The lava cones formed during the early stages of each effusive phase by surface flows that emanated from lava ponds in the summit lava craters and produced shelly pahoehoe and sheet flows. The lava apron is a later stage construction, formed when the level of the lava ponds had dropped well below the rims of the summit lava craters. At this stage the flow of lava to the active flow fronts was essentially confined to internal pathways such as lava tubes. As the lava emerged from the tubes it spread to form either a series of small budding lava lobes or broad but thin sheet lobes.

## INTRODUCTION

Surtsey island is a small (~2.5 km²) volcanic island situated about 33 km off the central-south coast of Iceland that belongs to the mildly alkalic Vestmannaeyjar volcanic system which is located on the seaward extension of the Eastern Volcanic Zone (Jakobsson 1979). The prominent features on Surtsey are two abutting ~140 m high tuff cones and a small pahoehoe lava flow field that caps the southern half of the island (Fig. 1). The island is the subaerial part of the larger Surtsey volcano, a 6 km long east-northeast (E65°N) trending submarine ridge that rises from a depth of 125 m and covers ~14 km² (Fig. 2). The volcano was produced by a prolonged eruption that began in early November 1963 and lasted until June 1967. Although best known for its explosive ('surtseyan'; Walker 1973) activity, the eruption featured several distinct eruptive phases including two prolonged subaerial effusive phases that produced two small partly overlapping pahoehoe lava shields and five much smaller a'a lava flows (Table 1). Effusive phase I lasted for 13.5 months (4 April 1964 - 17 May 1965) and produced a 100 m high lava shield with a subaerial coverage of 1.53 km². The total volume of lava produced by this phase was about 0.25 -0.30 km³ when the volume of the submarine foundation is included. Effusive phase II lasted for 9.5 months (19 August 1966 - 5 June 1967) and produced an ~70 m high lava shield that above sea level covered ~1 km², of which 0.5 km² was a new addition to the island. The total volume of lava produced by

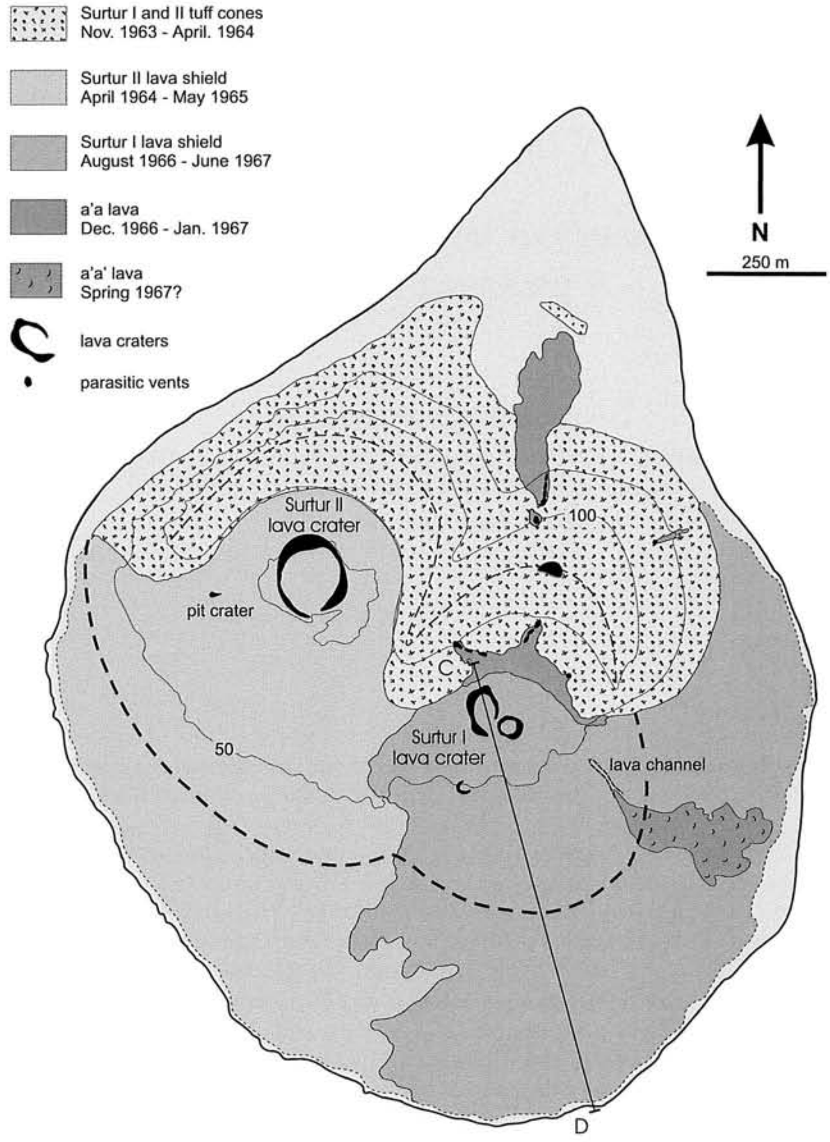


Figure 1. Simplified geological map of Surtsey showing the outlines of the island as they were in 1975. Heavy broken line indicates the boundary between the lava cones and the lava aprons, which are the main structural units of the lava shields. Solid line C-D indicates location of the cross section shown in Figure 3. See key for other explanations. Modified from Jakobsson and Moore (1982).

the Surtur I lava craters was ~0.1 km³. The total volume of tephra and lava produced by the Surtsey eruption amounts to 1.0 - 1.2 km³, of which ~30% (0.3 - 0.4 km³) were erupted as lava. The original volume of lava above sea level did not exceed 0.1 km³ and most likely was of the order of 0.07 km³.

Here I report on miscellaneous volcanological observations made on the Surtsey lavas during a weeklong visit to the island in the summer of 1991. The implications of these observations for the characteristic lava emplacement mechanisms at Surtsey are briefly discussed and will be reported in more detail elsewhere. The terminology used here to describe lava flows and structures is adapted from Macdonald (1967), Swanson (1973), Walker (1991), Self *et al.* (1997), and Thordarson & Self (1998). However, it should be noted that here the terms *sheet flow* and *sheet lobe* are used to describe two distinct lava types. Sheet flow is used here to describe broad and sheet-like surface flows, which originated in the lava craters as fountain-fed or overbank flows similar to those described by Swanson (1973). On the other hand, the term sheet lobe is used to describe tube-fed inflated pahoehoe flows of sheet-like geometry (e.g., Self *et al.*, 1998).

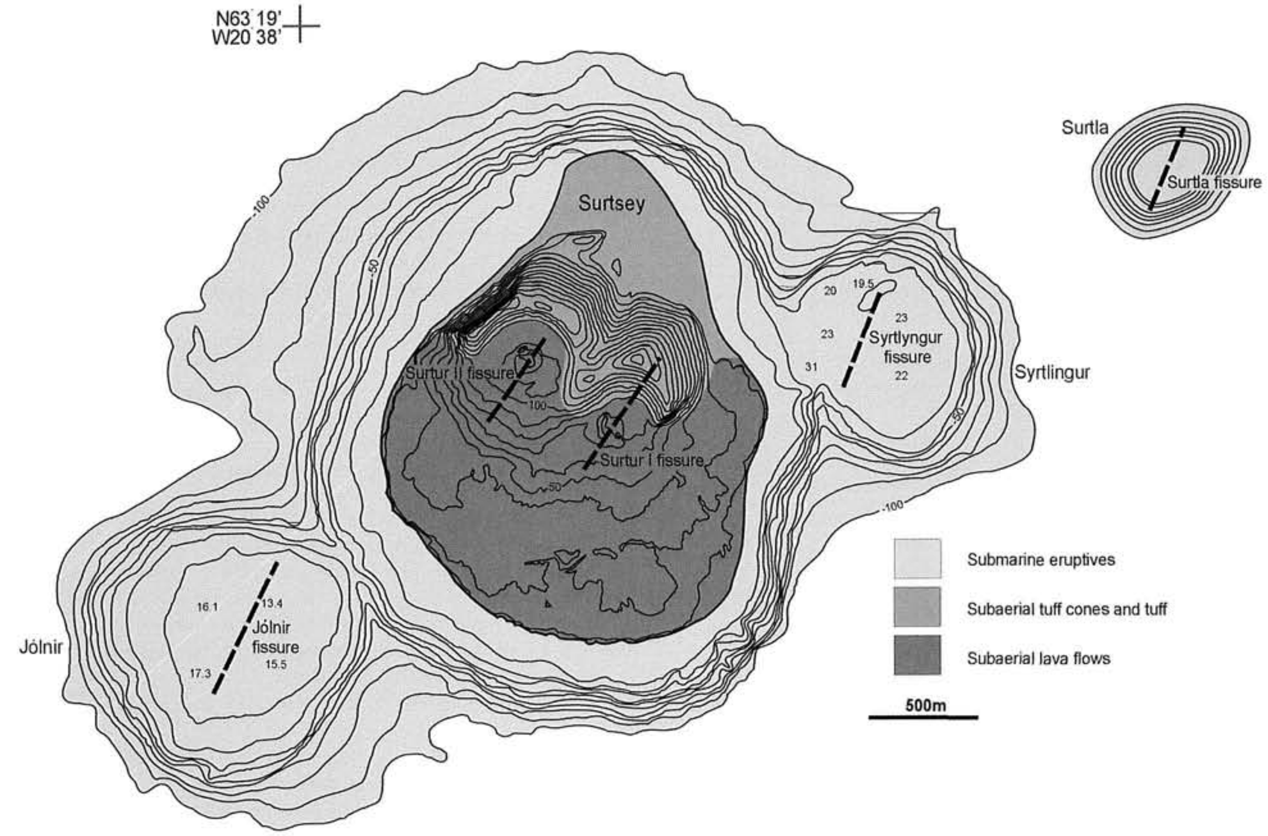


Figure 2. Map of the Surtsey volcano showing the submarine (July, 1967) and subaerial (July 1968) topography. Also shown are the volcanic fissures, submarine and subaerial cones and the lava flow field on Surtsey.

## THE SURTSEY LAVA FLOW FIELD

*Geometry and general structure*

As pointed out in previous studies (e.g. Einarsson 1965, Thórarinsson 1966, 1968, Kjartansson 1966a 1966b, 1967, Jakobsson & Moore 1982), the geometry and profile of the subaerial parts of the Surtur I and II lavas are identical to that of other lava shields in Iceland (Fig. 3). Consequently, the Surtsey lava flow field can be viewed as consisting of two small overlapping half-shields. The shields are capped by 70 m to 130 m wide lava craters encircled by 48 m high spatter rings. The lava craters are nested in the earlier formed Surtur I and II tuff cone craters (Fig. 1). The spatter ramparts, standing 10 to 20 m above the current crater floors, consist of red to black spatter bombs intercalated with centimetre-thick layers of lava. Individual spatter bombs are 150-300 cm long and 20-30 cm thick. The lava craters are flanked by a relatively steeply sloping lava field, which forms the most elevated part of the shields and referred to as the "lava cone". The Surtur I lava cone has an average slope of about 6.5° (range 6-7°), whereas the slopes of Surtur II lava cone are somewhat steeper, or 9.5° on average (range 8-11°). The outer limits of the lava cones are marked by sharp change in surface slope, which occurs at a distance between 350 m and 450 m from the lava craters (Fig. 1). Beyond the lava cones the Surtsey shields consist of broad and gently sloping (average 2.5°; range 0.5-4.5°) lava field, which formed a 400-500 m wide "lava apron" that originally bordered the southern half of the island. Large parts of the lava apron have been removed by erosion, especially on the western side of the island (Fig. 4).

A small pit crater is on the Surtur II lava cone (Figs 1 and 4). Rim to rim distance of the pit crater ranges from 14 m to 27 m, and its depth extends to 21 m. It occurs above a large lava tube (≤15 m wide) that lies from the Surtur II lava crater towards the western coast of Surtsey (Hróarsson 1990). Aerial photographs show that it was formed during the eruption sometime

Table 1. Main eruption episodes identified during the Surtsey eruption. Data from Thórarinsson (1965, 1966, 1967a, 1967b, 1968) and Jakobsson and Moore (1982).

| | Eruption phase and type of activity | Eruption site | Date | Events |
|---|---|---|---|---|
| 1 | Submarine activity early 11.63-14.11.63 | Surtur I fissure | early.11.63 | Start of eruption on sea floor |
| 2 | Subaerial explosive activity 14.11.63-31.01.64 | Surtur I and Surtla | 14.11.63 | Visible explosive hydromagmatic eruption on Surtur I fissure |
| | | | 15.11.63 | Appearance of Surtsey island |
| | | | 28.11.63 | Submarine activity on Surtla fissure first noticed |
| | | | 6.01.64 | Submarine activity ceased on Surtla fissure |
| | | | 31.01.64 | Explosive hydromagmatic eruption ceased at Surtur I vent |
| 3 | Subaerial explosive activity 2.02.64-4.04.64 | Surtur II | 1.02.64 | Explosive hydromagmatic eruption began at Surtur II fissure |
| | | | 1-8.02.64 | Concurrent hydromagmatic eruption and hawaiian fountaining at two vents on Surtur II fissure |
| | | | 9.02.64 | Change to purely hydromagmatic eruption at Surtur II vents |
| | | | 1.03.64 | Northern lagoon on Surtsey formed |
| 4 | Subaerial effusive activity 4.04.64-17.05.65 | Surtur II | 4.04.64 | Transformation from explosive hydromagmatic eruption to effusive lava eruption. ~120m wide lava pond forms in Surtur II crater |
| | | | 4-29.04.64 | Effusive activity dominated by surface flows produced by overspills from the lava pond or directly fed by lava fountains |
| | | | 29.04.64 | Emission of surface flows stops at Surtur II crater; lava pond remains active but its level subsided well below the crater rims |
| | | | 0506.64 | Tube-fed lava from Surtur II crater extruded on seafloor southwest of Surtsey |
| | | | 9.07.64 | Emission of surface flows resumes at Surtur II lava crater |
| | | | 07-08.64 | Gradual transition from surface flows to channel- and tube-fed flows: Surface flows become more and more intermittent and transport of lava from vent increasingly confined to lava channels and tubes |
| | | | mid 08.64 | Lava transport almost exclusively confined to lava tubes, although featuring short periods of surface flow activity. |
| | | | 17.05.65 | Eruption and lava effusion ceased at Surtur II lava crater |
| 5 | Submarine activity 11.05.65-17.10.65 | Syrtlingur | 11.05.65 | Beginning (?) of submarine activity at Syrtlingur eruption site |
| | | | 22.05.65 | Visible explosive hydromagmatic eruption in Syrtlingur fissure |
| | | | 28.05.65 | First appearance of Syrtlingur island |
| | | | 17.10.65 | Eruption ceased at Syrtlingur fissure |
| | | | 24.10.65 | Syrtlingur island completely washed away |
| 6 | Submarine activity late 10.65-24.08.66 | Jólnir | end 10.65 | Beginning (?) of submarine activity at Jólnir fissure |
| | | | 26.12.65 | Visible explosive hydromagmatic activity on Jólnir fissure |
| | | | 28.12.65 | First appearance of Jólnir island |
| | | | 10.08.66 | Eruption ceased at Jólnir fissure |
| | | | 31.10.66 | Jólnir island completely washed away |
| 7 | Subaerial effusive activity 19.08.66-5.06.67 | Surtur I and parasitic vents | 19.08.66 | Resumed effusive activity on Surtsey by eruption on a short fissure in the Surtur I tuff cone crater: Lava emission principally via surface flows |
| | | | end 08.66 | Activity centred on northernmost vent on the fissure, which became the Surtur I lava crater that contained a small lava pond |
| | | | 08-11.66 | Initially effusive activity dominated by surface flows produced by overspills from the lava pond or directly fed by lava fountains, followed by gradual transition from surface flows to channel- and tube-fed flows |
| | | | 1.12.66 | Lava transport almost exclusively confined to lava tubes, although with short periods of surface flow activity. |
| | | | 12-17.12.66 | Effusive eruption on a vent on inner northwest wall of Surtur I tuff cone and produced a small a'a lava flow |
| | | | 14.01.67 | Effusive eruption on vents on outer north slopes of Surtur I tuff cone that produced a small a'a lava flow, which flowed into the lagoon |
| | | | 18.01.67 | Effusive eruption on a vent on inner north wall of Surtur I tuff cone, produced a small a'a lava flow that flowed south past the drill hole |
| | | | 2.01.67 | Effusive eruption on a vent on outer northeast slopes of Surtur I tuff cone that produced a tiny a'a lava flow |
| | | | 27.01.67 | Two ring faults formed on inner east wall of Surtur I tuff cone; a vent on the lower erupted a tiny a'a lava flow |
| | | | 5.06.67 | Eruption and effusion of lava ceased at the Surtur I lava crater |

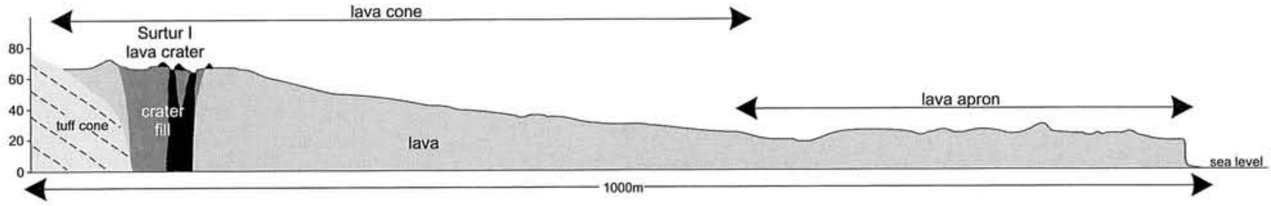


Figure 3. Profile illustrating the geometry of the Surtur I lava shield in cross section. The profile is constructed from topographic map by Norrman (1978). The extent of the lava cone and the lava apron is indicated. Location of the profile is shown on Fig. 1.

between June 1964 and October 1966, presumably by piecemeal collapse of the tube roof and overlying lavas into a partly filled and/or hollow tube.

At the end of the eruption the Surtsey lava flow field terminated at the shoreline in 3-20 m high cliffs, which due to continued marine erosion now reach heights of ~50 m on the western side of the island. These cliffs provide excellent outcrops, revealing the internal structure of the lava shields. In general they show that the shields are built of multiple lava flows of variable thickness and lateral extension. The most conspicuous units are a meter to a few meters thick and several tens to hundreds meters wide (or long) sheet-like lava bodies that most commonly are of the sheet lobe variety and to lesser extent of the sheet flow type.

The lava shields rest on ~130 m thick submarine foundation, assumed to be a foreset-bedded lava delta constructed by submarine lava effusion and disintegration of the subaerial lava flows by wave erosion and/or quenched fragmentation of lava as it entered the sea (Einarsson 1965, Thórarinsson 1966, 1968, Kjartansson 1966a, 1966b, 1967, Jakobsson & Moore 1982).

*Lava surface morphology*

The following descriptions of surface morphologies are based on reconnaissance on-site examination that only cover the lava cones and the Surtur I lava apron because the rest of the flow field was removed by erosion (Fig. 4). Information on diagnostic surface structures within the parts of the flow field that have been removed by erosion was obtained from analysis of aerial photographs taken by the National Land Survey of Iceland in July 1967.

In the proximity (<100 m distance) of the lava craters the surface of the steeper (6°-11°) lava cones are largely covered by ≤2 m thick lava consisting of numerous small, often budding pahoehoe lobes. Typically the lobes have very thin crusts (1-5 cm thick) and hollow interiors, which are either large gas-blisters formed by exsolving gases or small lava tubes formed as the lava was draining of the molten interior. The appearance of this lava strongly resembles the cavernous lava type called shelly pahoehoe described by Swanson (1973) from the summit region of the 1969-1973 Mauna Ulu lava shield at Kilauea in Hawaii. Patches of slabby pahoehoe also occur in this area and in places larger, smooth- or ropy-surfaced pahoehoe lobes outcrop between the smaller lobes. These lavas resemble those exposed in the walls of the pit crater, which consist of a few 1-2 m thick and poorly vesicular sheet flows that are either capped by smooth pahoehoe or cavernous slabby pahoehoe flow surfaces (Fig. 5a). On-site observations during the Surtsey eruption show that slabby pahoehoe or clinkery a'a-type surfaces were commonly formed on the rapidly advancing sheet-like surface flows, although such flows also featured smooth and ropy pahoehoe surface morphologies (Einarsson 1965, Thórarinsson 1967b).

On the outer slopes of the lava cones at 100-300 m distance from the lava craters the surface lava type is typically slabby pahoehoe, which is distinguished by its mishmash of crustal fragments that often are piled up in untidy heaps as high as 1 m (Fig. 5b). Small lava channels flanked by levees and copious subsidiary overflows are common in this sector of the lava field. Some channels are partly crusted over and downslope they transform into tumuli ridges.

The more gently sloping lava apron has a hummocky surface morphology (Fig. 3) and chiefly consists of tube-fed pahoehoe flows, ranging in size from small pahoehoe toes to broad sheet lobes. Two of the distinguishing

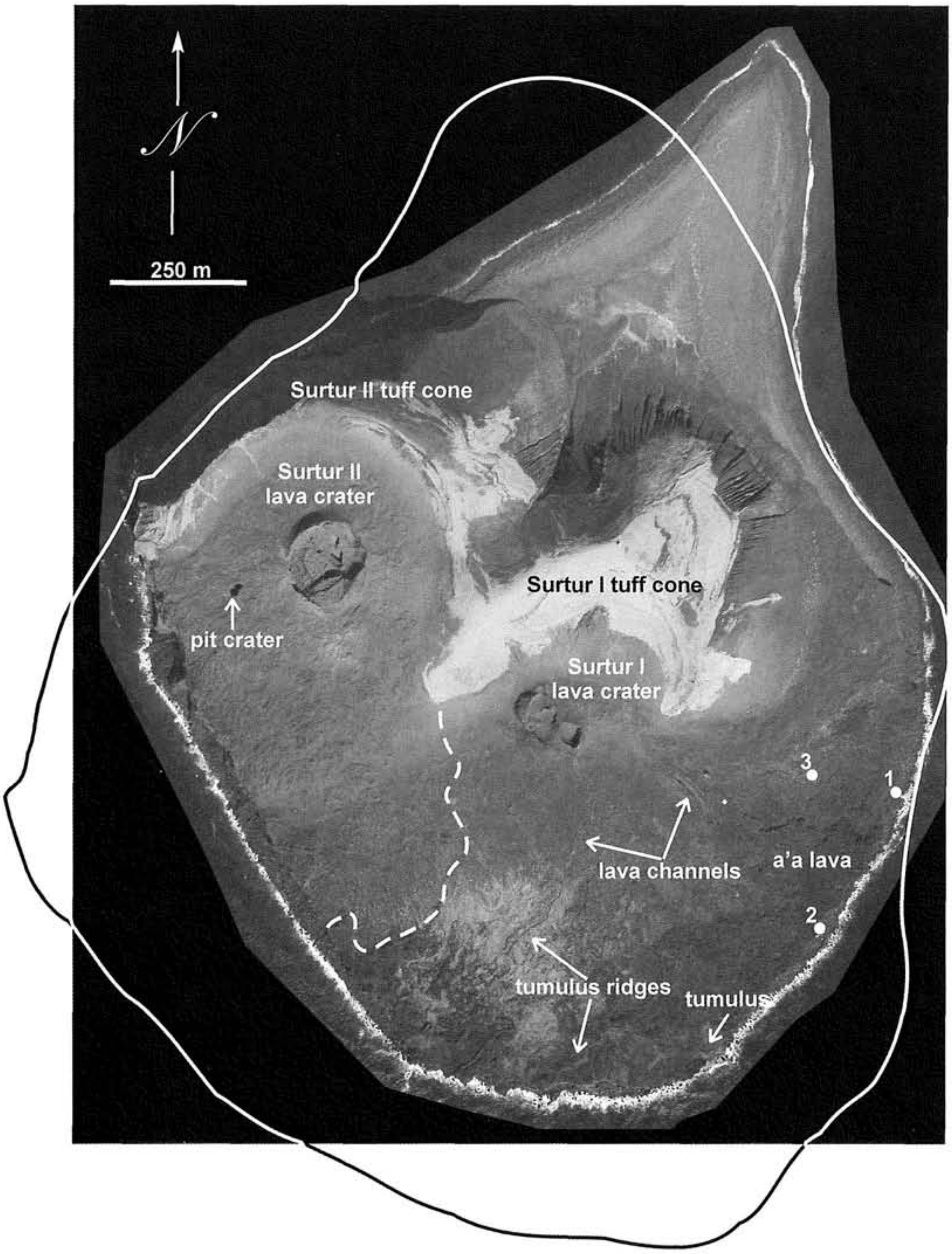


Figure 4. Recent (August 1998) aerial photograph of Surtsey with annotations referring to lava structures and localities referred to in the text. Broken line shows the western margins of the Surtur I lava shield. Also shown is the outline (black and white line) of Surtsey in July 1967. Courtesy of the National Land Survey of Iceland.

structures in this sector of the lava field are tumuli and tumuli ridges (Fig. 5c). Tumuli are isolated cupola-shaped mounds that protrude from the lava surface and typically are 1.5-3 m high (maximum 8 m) and 5-15 m in diameter (maximum 70 m). They consist of tilted crustal slabs that are split by inflation clefts and are genetically linked to lava tubes (see below). Tumuli ridges are similar structures except they have an elongate form and are as long as 350 m (Fig. 5d). Although many tumuli structures are well-exposed, others are completely coated with small surface breakouts, such that they sometimes look like heaps of entrail pahoehoe (Fig.

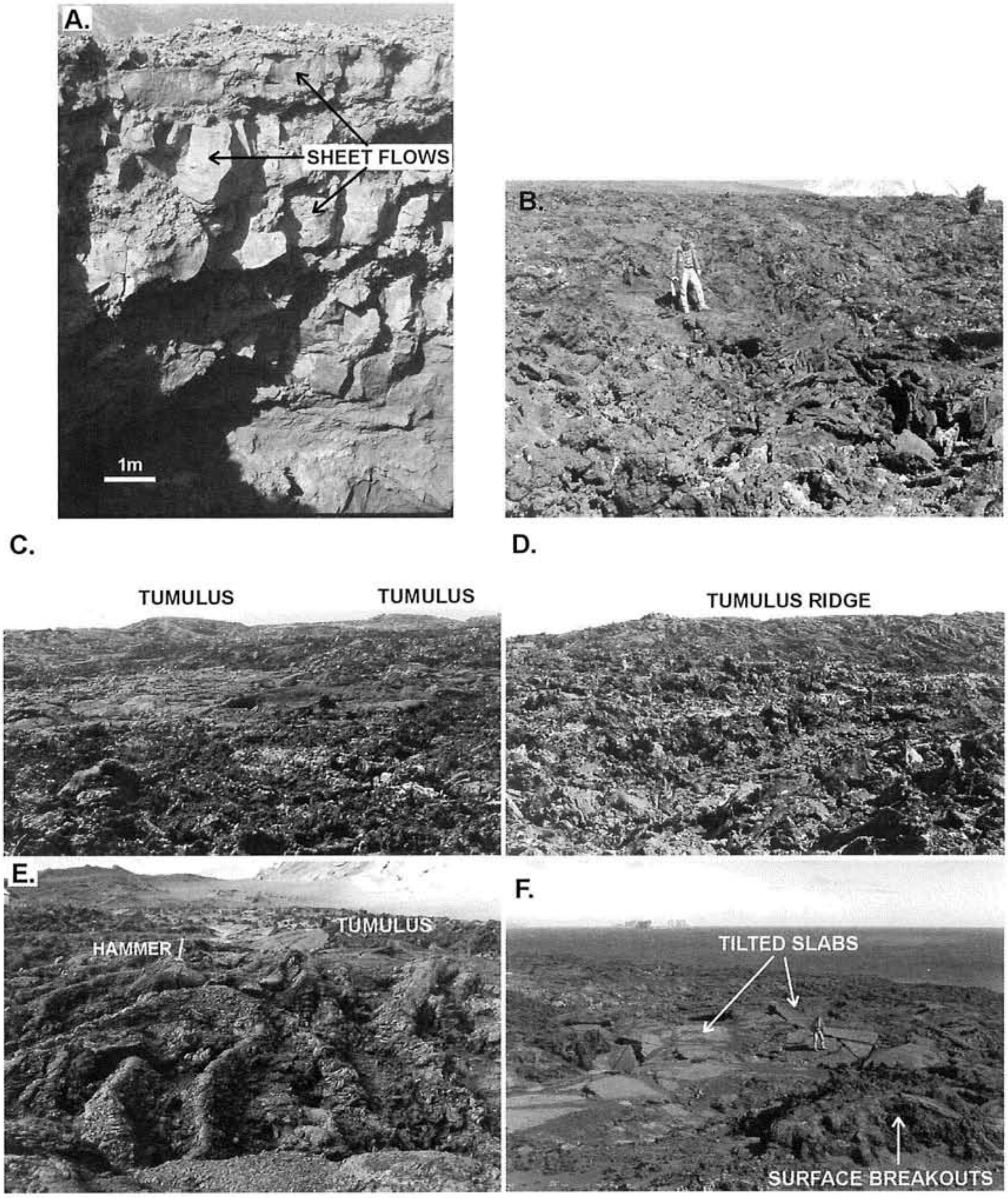


Figure 5. Photographs of lava flows and their surface structures at Surtsey. (A) Lavas in wall of pit crater. Scale bar is ~1 m. (B) Surface of slabby pahoehoe lava on the lowers slopes of the lava cone of the Surtur I lava shield. Person for scale. (C) Tumuli in Surtur I lava apron. Largest tumulus is ~5 m high. (D) A ~3 m high tumulus ridge within the Surtur I lavas almost completely disguised by small surface breakouts. (E) A pile of small flow lobes resembling heaps of entrail pahoehoe, but where formed as surface breakouts from the tumulus in the upper right corner of the photograph. Hammer is 35 cm long. (F) Large slightly tilted crustal slabs on the surface of a sheet lobe. Person for scale.

5e, Macdonald 1967). These surface breakouts are one of the characteristic features of the Surtsey lava flow field and typically occur as a stack of small lava lobes (≤1 m wide and 0.2 - 0.5 m high) that are superimposed on the original sheet lobe or tumulus surface. In places they completely disguise the original surface morphology of the flow. Field evidence show that these surface breakouts emerged through cracks in the lava surface or through skylights above lava tubes. Surfaces of broad sheet lobes are partly exposed in places as large but variably tilted crustal slabs (Fig. 5f).

Many of the tumuli that were inspected are

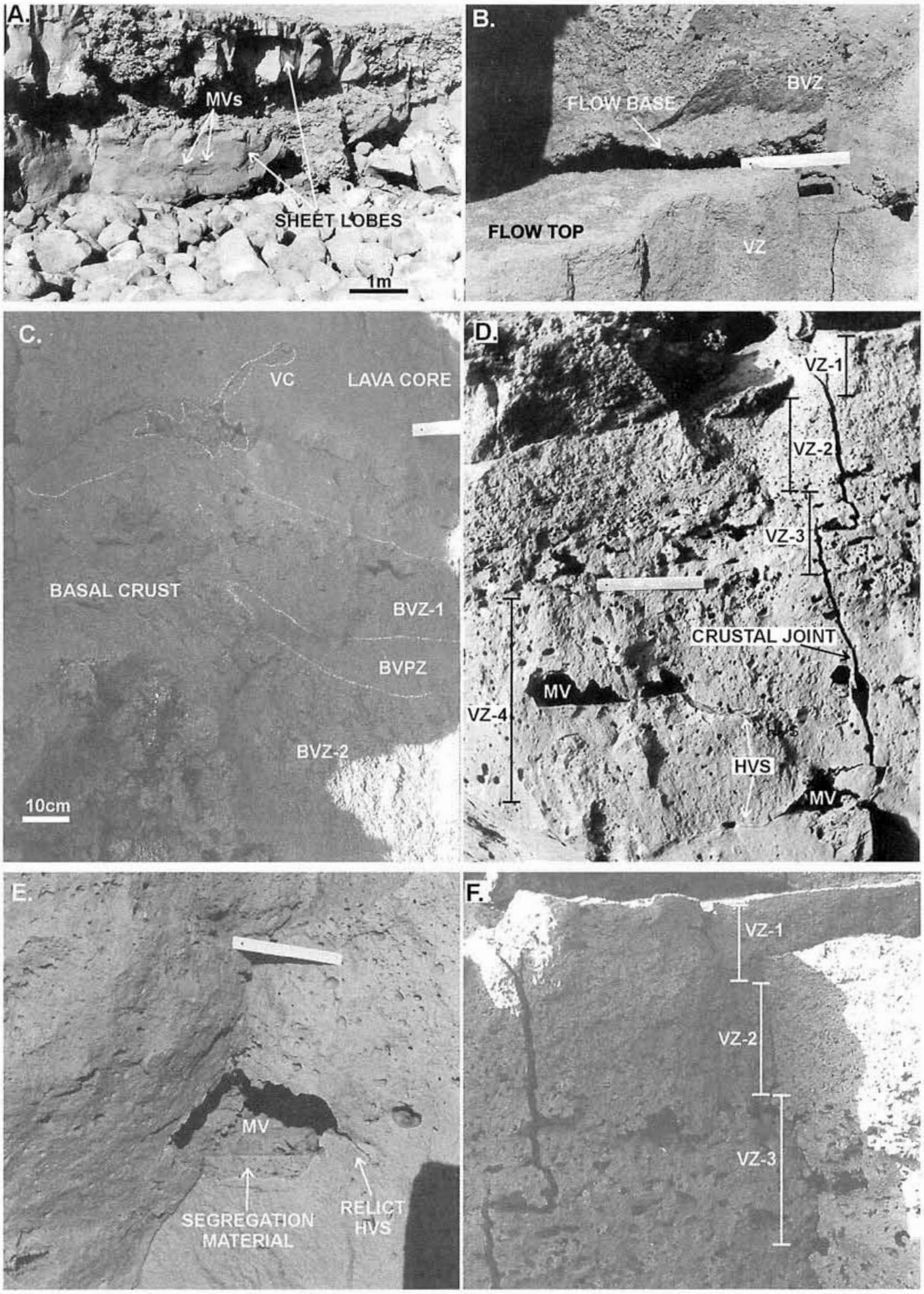


Figure 6. Photographs showing relevant examples of internal structures in a sheet lobe. (A) Terminus of two sheet lobes in the Surtur I lava shield in the cliffs at the eastern shores of Surtsey. The lower lobe features megavesicles (MVs). (B) Typical basal and upper lava surfaces on sheet lobes. Ruler is 20 cm long. (C) Close-up view of the basal crust and a vesicle cylinder extending from the basal crust up into the lava core. (D) Vesicular lava crust of a sheet lobe underlain by megavesicles and associated horizontal vesicle sheets. From sheet lobe at locality 1 (see also Figs 5 and 7 and Table 2). Ruler is 20 cm long. (E) A megavesicle, close-up view showing its characteristic dome-shaped geometry and vesicular segregated material at its base. Ruler is 20 cm long. (F) Close-up of the vesicular lava crust, showing the top three vesicular zones of the sheet lobe at locality 1 (see also Figures 5 and 7 and Table 2). Scale bar is 10 cm. Abbreviations are BVZ, basal vesicular zone, VZ, vesicular zone, BVPZ, vesicle poor zone in the basal crust, VC, vesicle cylinder, MV, megavesicle, HVS, horizontal vesicle sheet.

Table 2. Detailed log from a vertical section measured through the second sheet lobe from the top of the cliff face at the eastern shores of Surtsey (Locality 1 on Fig. 4). The sheet lobe belongs to the Surtur I lava succession. Graphic log is illustrated on Fig. 7. Abbreviations are as follows: VZ, vesicular zone; VPZ, vesicle-poor zone, VC, vesicle cylinder; MV-HVS, horizon of megavesicles (MV) and horizontal vesicle sheets (HVS).

| Structural component | Thickness | Internal structures | Description |
|---|---|---|---|
| Flow top | 40-70 cm | | Purple to red oxidised flow-top rubble of pahoehoe slabs and clinker, intercalated with small (≤0.5 m) flow lobes produced by surface breakouts. Smooth and coherent pahoehoe surface is exposed nearby. |
| Lava crust | 100 cm | | Vesicular upper crust consisting of hypohyaline to hypocrystalline lava with downward increase in crystallinity. Joints are irregular with typical spacing of 0.4-0.7 m. When the original pahoehoe surface is preserved it features distinct flow top jointing where 20-30 cm long regular joints are spaced at 10-20 cm. The lava crust features distinct vesicle zonation, which is as follows: |
| | | VZ-1 15-20 cm | Bluish purple to rusty red oxidised vesicular zone with average vesicularity of 30-35 vol.% and featuring 0.2 cm vesicles at the top increasing to ≤3.0 cm at the base. In top 5-7 cm, the vesicle size is 0.2-0.4 cm. Vesicle outlines are spherical. In the next 7-10 cm, the average vesicle size is 0.5-1.0 cm. Vesicle outlines are irregular and slightly elongated. In the lowest 3 cm the vesicle size ranges from 0.5 cm to 3.0 cm. Vesicles are normally elongated with irregular and convoluted outlines and show evidence of having grown by coalescence of smaller bubbles. |
| | | VZ-2 20 cm | Vesicularity 30-35 vol.% with 0.2 cm spherical vesicles at the top increasing to 0.5-1.0 cm spherical or slightly elongate vesicles at the base. These vesicles have convoluted outlines reflecting growth by coalescence of smaller bubbles. Indistinct centimetre-thick banding is seen in places in the vesicle fabric. |
| | | VZ-3 15-20 cm | A distinct horizon featuring 5-12 cm long and 1-5 cm high elongate segregation vesicles and scattered 1-2 cm spherical vesicles. The base of larger vesicles is flat due to accumulation of segregated material. Vesicularity is ~25 vol.%. |
| | | VZ-4 40-50 cm | Vesicularity 5-20 vol.% with decreasing vesicle abundance from top to bottom. It features 1-6 cm spherical vesicles and a gradual downward increase in vesicle size. This vesicle zone partly overlaps the megavesicle horizon below. |
| Lava core | 205 cm | | Poorly vesicular holocrystalline lava exhibiting the following features: |
| | | MV-HVS 40-50 cm | A distinctive horizon of megavesicles and horizontal vesicle sheets. The MVs are 10-50 cm long and 7-28 cm high. Although the MVs have somewhat irregular and convoluted outlines, they generally feature arched roofs coated by 0.5 cm thick smooth-surfaced glassy skin. The MVs have flat floors and a 3-8 cm thick bottom fill of vesicular segregated material that often connects laterally to 1-2 cm thick discontinuous horizontal vesicle sheets. Overall vesicularity is ~15-20 vol.% |
| | | Lava with VC 170 cm | Poorly vesicular holocrystalline lava with irregular and crooked 1-4 cm wide vesicle cylinders. Each cylinder can be followed vertically for 10-15 cm, and the outcrop pattern shows that some extend up into the megavesicle horizon. One 20 cm long and 2-4 cm wide vesicle cylinder was found to terminate within the lava core. It had risen from amoeboid-shaped blob of vesicular material that extended from the basal vesicular zone. Boulders of poorly vesicular holocrystalline lava on the shore in front of the cliff feature well-developed vesicle cylinders up to 10 cm in diameter, and some were found to connect to 2-4 cm thick horizontal sheets. |
| Basal crust | 55 cm | | Hypohyaline to holocrystalline lava with the following vesicle zonation: |
| | | BVZ-1 10 cm | Vesicularity 5-10 vol.% with 0.2 cm spherical vesicles at the base and ≤11 cm elongate segregation vesicles at the top. |
| | | BVPZ 10-15 cm | Non-vesicular lava. |
| | | BVZ-2 20-40 cm | Vesicularity ~25-30 vol.% with 0.5-2 cm spherical and elongate (stretched) vesicles at the top, decreasing to 0.1-0.2 cm spherical vesicle at the base |
| Basal surface | | | Convoluted base with spinous basal surface and discontinuous horizons of centimetre-large clinker. |

hollow inside, featuring a large chamber roofed by relatively thin crust. The surface of these tumuli are usually covered by numerous surface breakouts illustrating that at some stage their chamber was full to the brim with lava. Inspection of their interiors shows that individual

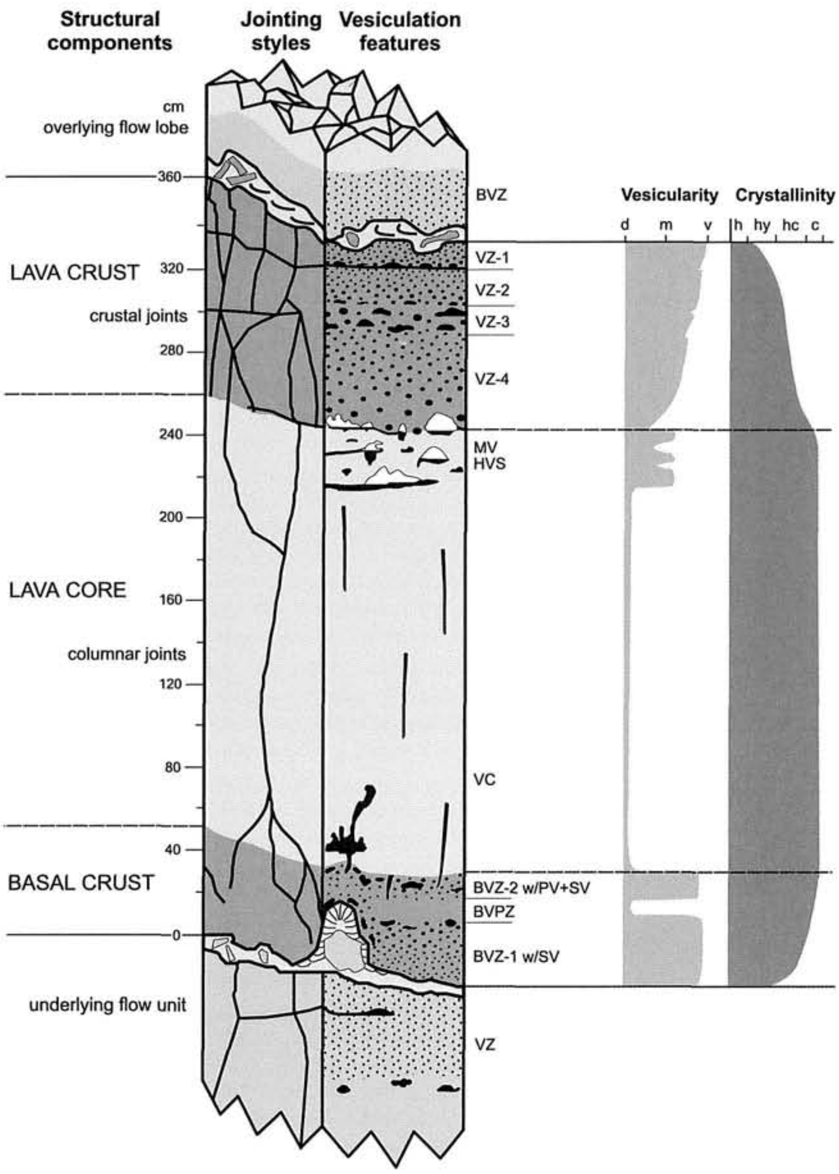


Figure 7. Representative graphic log showing vertical distribution of internal structures in a sheet lobe within the Surtur I lava flow (Locality 2 in Fig. 4). The main structural components; the lava crust, lava core, and basal crust are shown on the left. The left column illustrates the jointing of the lava, thin lines indicate crustal joints and thick line denote columnar joints (Thordarson and Self, 1998). The right column shows vesiculation features. Abbreviations are as follows: VZ, vesicular zone; MV, megavesicle; HVS, horizontal vesicle sheet; VC, vesicle cylinder BVZ, basal vesicular zone; SV+PV, segregation and pipe vesicles. Also shown are profiles depicting vertical changes in vesicularity and crystallinity as determined by visual estimates in the field aided by microscopic examination of a representative suite of hand samples and thin sections. Vesicularity scale is modal percent and intervals of crystallinity are h, hyaline (0-10% crystals); hy, hypohyaline (10-40% crystals); hc, hypocrystalline (50-90% crystals); and c, holocrystalline (90-100% crystals).

tumulus chamber connects to lava tubes on the upflow and the downflow side. At locality 3 in Fig. 4 the tumulus roof is partly collapsed and allowed for easy access to the chamber. This tumulus chamber is 5-8 m wide and ~10 m long. Originally it must have been 3-4 m deep with its roof standing at least 2 m above surrounding lava surface although the original tumulus geometry is now somewhat obscured by numerous surface breakouts that cover the outer slopes (Fig. 5e). The chamber has one 2 m high and 4 m wide tube entry on the upflow side, but three 1-3 m wide tube exits on the downflow side. These observations show that the tumulus formed by inflation of the crust over a rather broad pool of molten lava that was fed by a relatively large lava tube. Tumuli with partly collapsed roofs and empty tumulus pools are scat-

Table 3. Detailed log from a vertical section measured through a tumulus in the third sheet lobe from the top of the cliff face at the southeastern shores of Surtsey (Locality 2 in Fig. 4). The lobe most likely belongs to the Surtur I lava succession. Graphic log is illustrated on Fig. 8 and a sketch of the tumulus is shown in Fig. 9. Abbreviations are as in Table 2.

| Structural component | Thickness | Internal structures | Description |
|---|---|---|---|
| Lava crust (tube roof) | 55 cm | VZ-A 30-40 cm | Vesicularity is ~20 vol.%. Vesicle size increases downwards, from ≤0.4 cm spherical vesicles at the top to ≤2 cm elongate stretched vesicles at the base. A gas-parting surface and a gas-blister separate zones A and B. |
| | | VZ-B 20 cm | Vesicularity is ~15 vol.%. Vesicle size increases downwards from ≤0.4 cm spherical vesicles at the top to ≤5 cm elongate stretched vesicles at 15cm depth. Lowest 5 cm, however, contain ≤1 vol.% of small (≤1.0 cm) spherical vesicles. |
| | | | These zones connect directly with the uppermost vesicular zones in the lava on either side of the tumulus. |
| Hollow tube | 70 cm | | Void bounded by an arched roof and a flat floor. |
| Tube-fill | 180 cm | VZ-1a 10 cm | Vesicularity ~25-30 vol.% with ~0.1 cm spherical vesicles at the top, increasing in size downwards to ~0.5 cm. |
| | | VZ-1b 10-15 cm | Sharp transition to a horizon that is dominated by 3-7 cm long and 1-3 cm high segregation vesicles with arched roofs and a flat base |
| | | VZ-1c 35-40 cm | Vesicularity ~25-30 vol.% with 1-2 cm spherical vesicles at the top decreasing to ≤1.0 cm vesicles at the base. Lower contact is sharp and undulating. |
| | | VPZ-1 40 cm | Vesicularity ≤5 vol.% with a few 0.5-3 cm vesicles evenly dispersed throughout the zone. Vesicles are usually spherical, but a few are elongated (stretched) in horizontal direction. |
| | | VZ-2 20-25 cm | Vesicularity 15-25 vol.% with ≤1 cm spherical vesicles at the top, decreasing to ≤0.5 cm vesicles near base. Upper contact is diffusive because some of the larger vesicles were buoyant enough to rise across it and into VPZ-1. Lower contact is knife sharp and the lava contains scattered ≥1cm long stretched vesicles in the 5 cm immediately above the contact. Midway through the tube-fill VZ-2 thins sharply and continues as a parting surface. Near this transition a vertical ~7 cm wide vesicular band cuts through VPZ-1, linking VZ-2 to VZ-1c, and appears to have formed by a diapiric rise of vesicular mush derived from VZ-2. |
| | | VPZ-2 40-50 cm | Very vesicle-poor (<1 vol.%) lava, with only a few 1 cm spherical vesicles. This zone has elongate and concave upward geometry and apparently a part of the tube itself, in similar fashion as VPZ-1. |
| | | VZ-3 10-15 cm | Vesicularity ~10-15 vol.% with ≤0.4 cm spherical vesicles at the top increasing to ≤1.0 cm vesicles of spherical or elongate (stretched) shape. In places this zone is in contact with the basal vesicular zone of the tumulus and the lava on either side. |
| Basal crust | 30 cm | BVPZ 0-10 cm | Discontinuous, wedge shaped zone of vesicle poor lava within the basal crust of the tumulus |
| | | BVZ 20-25 cm | Vesicularity ~25 vol.% with 2 cm spherical to irregular vesicles in the top 10 cm showing evidence of upwards migration. Next 5 cm features ≤3.0 cm long elongated (stretched) segregation vesicles, whereas lowest 5cm contain small (≤0.3 cm) spherical vesicles. |

tered about in the lavas at Surtsey. On one occasion, I saw that a surface flow had reentered a tube system through such an opening, which is probably a common occurrence in this type of lava.

*General characteristics of the Surtur I lava flows in a vertical succession*

The eastern shores of the island feature 3-10 m high sea cliffs that provide readily accessible exposures through the lava succession of the Surtur I shield. Here, as well as elsewhere along the shores of the lava field, the cliff consists of numerous flow lobes of variable thickness and lateral extension. The thickest lobes are 2-6 m and the thinnest 0.5 m. Most of these flow lobes are pahoehoe or slabby pahoehoe. A few small a'a flow lobes are present in the succession, which is also capped by small, 1.5 to 2.0 m thick, a'a lava flow further to the south (Fig. 1). The beach in front of the cliffs is covered

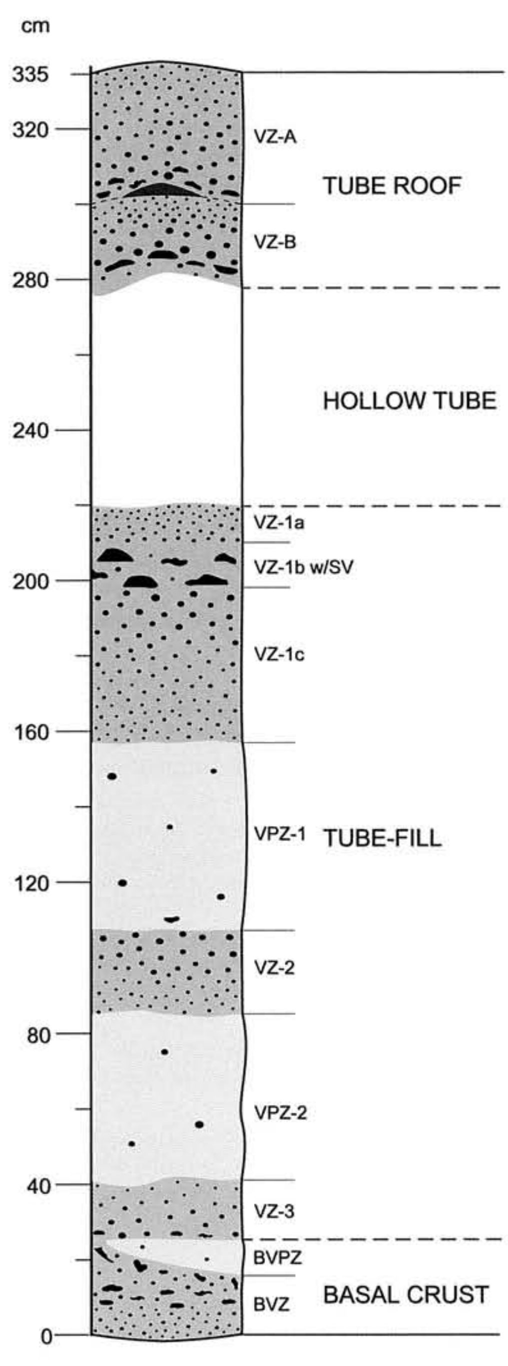


Figure 8. A graphic log illustrating the vertical arrangement of internal structures in the tumulus at locality 2 (see Fig. 4). Abbreviations as in Fig. 7.

by large (0.5 m) angular to subrounded lava boulders formed during the breakdown of the 1966-1967 lava flows by wave erosion. However, this sector of the Surtsey lavas has suffered much less erosion than other parts of the flow field, today the shoreline is just inside its original position at the end of the eruption in June 1967 (Fig. 4). The descriptions that follow are based on observations made along these cliffs, which represent the distal sector of the Surtur I lava apron.

The most prominent lava units in these cliffs are pahoehoe sheet lobes that typically are 50 m to 200 m wide (or long) and 2-4 m thick (maximum measured thickness is ~6 m). For the most part the thickness of each sheet lobe is rather uniform or between 1.5 and 2.5 m (Fig. 6a). However, the sheet lobes commonly swell above 0.5-1.0 m deep lows in the underlying lava surface to more than double the thickness of the lava on either side. In profile these local swells have shapes of a tumulus and hollow lava tubes are routinely found in their centres (see below). A 0.5-1.0 m thick stack of much smaller pahoehoe lobes, with typical dimensions between 0.2-1.0 m, often separate the sheet lobes. Lobes with slabby pahoehoe and a'a surface morphologies are also present. Discontinuous layer of flow-top rubble, up to 0.5 m thick and 20 m long, consisting of a mixture of spinous clinker and slabs of pahoehoe crust sometimes separates the sheet lobes.

*Internal structures of sheet lobes*

The sheet lobes exposed in the cliffs along the eastern shores have similar internal structures. They exhibit the threefold division of vesicular basal crust, crystalline lava core, and an upper vesicular lava crust that is common to this type of pahoehoe lava (e.g., Self *et al.*, 1998). The general arrangement of internal structures and textures in Surtsey sheet lobes are described below. The details of a section measured through a sheet lobe at locality 1 (Fig. 4) is given in Table 2 and illustrated in Fig. 7.

The basal surface of the sheet lobes is either convoluted and spinous or smooth and billowy pahoehoe surface with a 1-4 cm thick glassy selvage that marks the very bottom of the basal crust (Fig. 6b). The basal crust is normally <10% of the total flow thickness. It consists of hypohyaline to hypocrystalline lava featuring a distinct basal vesicular zone with vesicularity between 25-35 vol.%. Sometimes the basal crust is locally split into two by a thin horizon of vesicle-poor lava, which terminates abruptly when followed for several meters. Crystallinity and vesicle size generally increases upwards in the basal crust, and the upper part of the basal vesicular zone sometimes features irregular and elongate segregation vesicles and, more rarely, pipe vesicles. Small cylinders and amoeboid-shaped patches are often present above local irregularities in the basal lava surface, extending tens of centimetres into the overlying

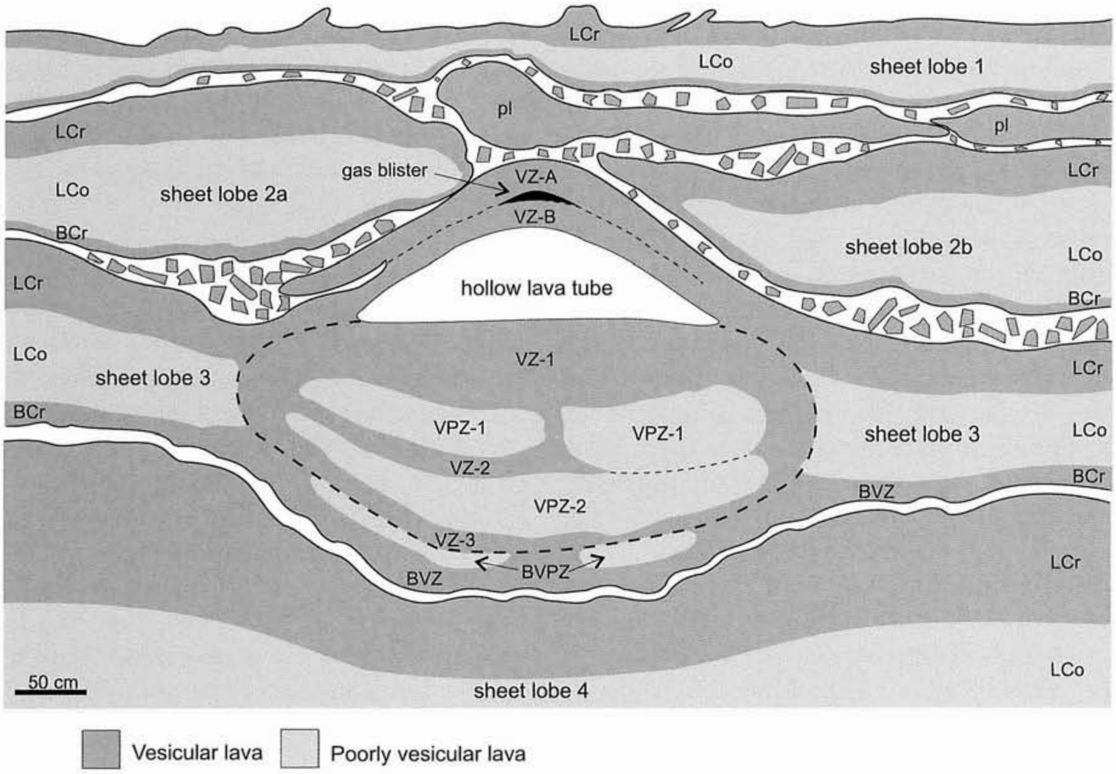


Figure 9. A field sketch of the tumulus at locality 2 (see Fig. 4) outlining its morphology and its relationship with the surrounding lava. Bold broken line outlines the tube-fill lava, whereas thin broken lines indicate parting surfaces. The threefold division lava crust (LCr), lava core (LCo), and basal crust (BCr) are indicated for the sheet lobes; pl stands for small pahoehoe lobe (surface breakout). Other abbreviations are as in Fig. 7.

lava core (Fig. 6c). These structures clearly originate within the basal vesicular zone and contain vesicular (~40 vol.%) segregated material.

The lava core is uniformly holocrystalline and is normally the thickest component of each flow unit or between 50% and 55% of the total thickness (Fig. 7). Joints are irregular and typically spaced at 0.5-1.0 m. The lava core contains 2 vol.% of centimeter-sized spherical vesicles and features scattered 0.5-4.0 cm wide vesicle cylinders that can be followed vertically for 10-15 cm. Outcrop patterns indicate that originally most of these cylinders extended all the way through the lava core, although some clearly terminate within the lava core (e.g. Fig. 6c). Vesicle cylinders were never found within the upper lava crust. In many sheet lobes a distinct horizon of megavesicles (i.e., large segregation vesicles) occurs at the top of the lava core, immediately below the vesicular lava crust. At locality 1 these megavesicles are 8-50 cm long and 9-20 cm high with irregular outlines, flat floors, and arched roofs (Fig. 6d). At the bottom of each megavesicle is a 2-9 cm thick accumulation of segregated material with 3-15 vol.% vesicularity (Fig. 6e). Horizontal vesicle sheets, 1-3 cm thick, are frequently found in direct continuation of the segregated material in the megavesicles. Field relations imply that the megavesicles are formed by localised gas accumulation within the horizontal vesicle sheets that develops into a giant gas bubble rising from the upper surfaces of the sheets into the viscous lava above.

Closely spaced (0.3-0.7 m), highly irregular joints and a progressive upward decrease in crystallinity characterise the vesicular lava crust, which makes up between 35% and 40% of the total flow thickness (Fig. 7). Approximately two out of every three crustal joints terminate abruptly at the lava core/lava crust boundary, whereas the reminder merges with the joints of the lava core. The lava crust usually features several vesicular zones, each with 20-35 vol.% vesicularity and a downward increasing vesicle size (Figs 6f and 7). The sheet lobes are either capped by smooth pahoehoe flow surfaces (Fig. 6b), thin rubble of pahoehoe slabs and clinker, and/or small lava lobes (surface breakouts).

*Internal structures of a tumulus*

The descriptions presented below are based on a detailed vertical section measured through a tumulus within a sheet lobe in the lava cliffs along the southeastern shores of Surtsey (Locality 2 in Fig. 4). Section measurements and descriptions are presented in Table 3 and illustrated by the graphic log in Fig. 8. The tumulus geometry and arrangement of internal structures are shown in Fig. 9. The tumulus is ~3.5 m high and 5 m wide and laterally it connects with an ~2.0 m thick pahoehoe sheet lobe that can be followed in the cliffs for several hundreds of meters. The tumulus is located where there is an ~1 m deep and ~5 m wide low in the underlying lava flow, suggesting that the tumulus formation may have been initiated by irregularities in the subsurface. The lowest 2.1 m of the tumuli are composed of solid lava overlaid by a 0.7 m high and 3 m wide cupola-shaped lava tube (Figs. 8 and 9). The tube is capped by 0.6 m thick arched roof that is partly covered by small surface breakouts and flow top rubble. The tube roof contains two vesicular zones, which when followed sideways merge with the vesicular lava crust in the sheet lobe on the either side of the tumulus. The upper vesicular zone (VZ-A) connects the topmost vesicular zone of the sheet lobe, whereas the lower zone (VZ-B) merges with the underlying one. Below the hollow tube is flat-topped lava representing the tube-fill, which is ~1.8 m thick, implying that at time of solidification the tube was about two-thirds full of lava. The tube-fill features a complex zonation of strongly vesicular and poorly vesicular lava and contains higher number zones than the lava on both sides (Figs 8 and 9). Vesicular zones VZ-1 and VZ-2 and vesicle poor zones VPZ-1 and VPZ-2 are exclusively confined to the tumulus. The lowest vesicular zone (VZ-3), however, merges with the basal vesicular zone that underlies the tube-fill and continues laterally along the base of the sheet lobe on either side of the tumulus (Fig. 9). The continuity of the basal vesicular zone and the vesicle zones in the tube roof show that the tumulus is an integral part of the sheet lobe. The internal structures of the tube-fill, however, demonstrate that it represents a separate lava batch emplaced later than the main body of the sheet lobe. The surface breakouts that cover the tumulus confirm that at some stage the tube was completely full of lava, in fact so full that it inflated to form the arched tumulus roof. About 5 m to the west is another smaller tumulus in the same sheet lobe, and it displays similar internal arrangement of structures as the one described above. However, it does not feature a hollow tube and most likely represents a confined internal lava pathway or lava tube that was not drained of its lava before solidification.

## DISCUSSION

Contemporary descriptions (*e.g.,* Thórarinsson 1965, 1966, 1967a, 1967b, 1968, Einarsson 1965) of the effusive activity clearly show that the construction of the Surtsey shields involved two distinct lava transport and emplacement mechanisms, exemplified by surface flows on one hand and tube-fed flows on the other. As is commonly the case in natural systems these mechanisms represent two end members in a continuous spectrum of processes that in detail are more complex. However, these flow types are useful descriptors of these mechanisms because they encompass the principal processes involved in construction of the Surtsey lava shields. As will be shown these mechanisms produce distinct lava types that can be related to specific eruption processes, which are responsible for the construction of the two principal structural units of the Surtsey lava shields, the lava cone and the flanking lava apron (Figs 1 and 3).

The Surtur I and II lava cones are capped by lava craters, which at the time of the eruption were occupied by small lava ponds. In the vicinity of the lava craters the surface lavas are typically cavernous shelly pahoehoe and, to a lesser extent, sheet flows. The outer slopes of the lava cones are typically covered by slabby pahoehoe flows, although it also features levee-bounded lava channels and subsidiary channel overflows. However, the dominance of sheet flows in the pit crater exposure suggests that this lava type is more common in this sector of the shields than indicated by the surface exposures. The overall morphology and structure of the lava cone flows at Surtsey show a striking resemblance to the fountain-fed and overbank surface flows produced by the summit lava pond at Mauna Ulu (e.g., Swanson 1973) and descriptions of lava effusion at Surtsey show that they were formed in a similar manner (see below).

Contemporary descriptions show that surface flows were the dominant type of lava extrusion in the early stages of each effusive phase (Table 1), when the activity was characterised by periodic rise and drop of lava in the craters and episodic lava fountaining. The short periodicity of these episodes suggests that they were driven by pulsating degassing of the magma during its rise to the surface rather than variations in magma discharge. Some surface flows were fed directly from lava fountains (i.e., fountain-fed flows), whereas others were formed as the gas-inflated lava pond rose to its brim and spilled lava over the crater rims (i.e., overbank flows). Flowing away from the crater as broad sheets or wide and braided lava tongues they often advanced at relatively high velocities (10-20 m/s) and commonly featured spectacular red-glowing surfaces. Such flows are characterised by high cooling rates and rapid changes in lava rheology during emplacement, imposing stringent conditions on how far they can flow (e.g., Keszthelyi & Self 1998). Although a number of surface flows reached the sea, they typically advanced a short distance from the lava craters and were the essential agents that built up the lava cones. This is confirmed by data on the summit elevation of the cones, which show that they grew most rapidly in the early stages of each effusive phase when surface flow activity was most vigorous. Later, when lava transport was essentially confined to tubes and surface flows were rare, the growth of the lava cones was virtually reduced to a standstill (Thórarinsson 1966, 1967a, 1967c, 1968).

The gently sloping lava aprons at Surtsey feature distinct hummocky topography where tumuli, tumulus ridges and small lobes formed by surface breakouts are the distinguishing surface structures. Vertical sections, however, show that the apron chiefly consists of compound pahoehoe. Furthermore it shows that tube-fed sheet lobes and, to a lesser degree, stacks of small pahoehoe lobes are the characteristic lava types. The overall morphology and structure of the Surtsey lava aprons show strong resemblance to that of inflated pahoehoe flows, which make up the distal sectors of tube-fed lava fields in Hawaii (e.g., Mattox *et al.* 1993) and on Icelandic shield volcanoes (Rossi 1996, 1997, and unpublished observations by the author). Contemporary observations show that tube-fed lavas were the main contributors to the construction of the lava apron (Table 1) and were largely responsible for the lateral growth of the Surtsey lava shields. It is therefore appropriate to examine in more detail the chief components of the lava apron and their importance for assessing the lava emplacement mechanism.

The sheet lobes at Surtsey have strikingly similar internal structures to that of inflated sheet lobes from the currently active Pu'u O'o-Kupaianaha pahoehoe lava flow field in Hawaii, as well as to structures of sheet lobes from other inflated pahoehoe lava flows around the world (e.g., Fig. 20 in Thordarson & Self 1998). The three-part structural division of the sheet lobes into basal crust, lava core, and lava crust are equivalent to the bottom crust, molten lava core, and upper crust of actively inflating lobes (Hon *et al.* 1994, Thordarson 1995). These divisions provide the keys for understanding the emplacement mechanism of the Surtsey sheet lobes.

Studies of segregation structures in basaltic lavas (e.g., Goff 1977, 1996, Thordarson 1995, Thordarson & Self 1998) have shown that the segregation principally occurs at the lower solidification front (i.e., basal crust to lava core boundary) and that it is an integral part of the lava emplacement process. As the flow of lava is coming to halt and immediately thereafter, the buoyant segregation melt rises as vertical vesicle cylinders through the molten lava core. When the cylinders meet the upper solidification boundary (i.e., lava core to lava crust boundary) they spread out as horizontal vesicle sheets. Megavesicles form at the upper surfaces of the sheets as a consequence of gas accumulation initiated by local instabilities or irregularities within the sheets. They acquire their dome and flat-based shapes because they rose into the lowest, and then viscous, part of the lava crust (Thordarson & Self 1998). The outcrop pattern of segregation structures in sheet lobes at Surtsey is consistent with this representation (e.g., Fig., 7). The estimated rise velocity for the segregation melt in a typical cylinder of basalt lava is of the order of $3.5 \times 10^{-3}$ cm/s (~3 m per day). Accordingly, at that speed it would have taken just over a day (<29 hr) for the vesicle cylinders to rise to the top of the lobe. However, the transformation from vesicle cylinders to horizontal vesicle sheets and megavesicles in the Surtsey sheet lobe occurs well within the lobe or at normalised height $h/l = 0.47–0.58$ ($h$ = height to sheets and megavesicles in lava; $l$ = total thickness of lobe). This illustrates that the solidification front was positioned at ~1 m depth when the vesicle cylinders were transformed into horizontal vesicle sheets. Thus, it would have taken about half to three-quarters of a day (12-18 hrs) for the cylinders to rise this far. If the Surtsey sheet lobe at locality 1 was entirely molten when they came to rest, then the law of conductive cooling predicts that the depth to the solidification front after 1 day would be at 0.4 m (e.g., Hon *et al.* 1994). Also it would take ~7 days (range 5.6-8.3 days) for it to reach the depth of ~1 m. There is a clear contradiction here and the logical conclusion is that a surface crust of considerable thickness was formed during the emplacement of the sheet lobe. This is an important conclusion because formation of such crust is one of the trademarks of lava inflation and endogenous growth (e.g. Hon *et al.* 1994, Thordarson 1995, Kauahikaua *et al.* 1998 Self *et al.* 1998,).

The general increase in vesicle size with depth in the lava crust is consistent with the conclusion that the crust grew in thickness during lava emplacement. If the lobe was wholly molten when it came to rest, the largest vesicles should be concentrated towards the top of the crust and the smaller ones at the base because larger vesicles rise faster than smaller ones (Vergniolle & Jaupart 1986). The fact that a reverse trend is observed is concordant with incremental growth of the lava crust during emplacement, because as the crust thickens the cooling rate decreases and, consequently, the bubbles that are trapped lower in the crust have progressively more time to grow (Cashman & Kauahikaua 1997). The same results are obtained from evaluations of the two-tiered jointing pattern, crustal joints of the lava crust versus columnar joints of the lava core (Fig. 7). The highly irregular crustal joints are formed by jostling of the lava crust during lava inflation, whereas columnar joints form under a more relaxed stress field in a stagnant lava body (Thordarson & Self 1998).

The distribution of internal structures of Surtsey sheet lobes are best explained in terms of endogenous emplacement, characterised by steady injection of lava into a molten core surrounded by insulating crust and wholesale inflation of the upper lobe surfaces (e.g. Hon *et al.* 1994, Thordarson & Self 1998).

Tumuli and tumulus ridges are one of the most distinguishing lava inflation structures at Surtsey. They are surface manifestation of lava tubes or preferred internal lava pathways. However, their relationship to inflating sheet lobes may not be instinctively obvious and thus are examined here in more detail. The basal and top vesicular zones in the tumulus at locality 2 clearly show it is an integral part of the sheet lobe, whereas the internal structures of the tube-fill indicate that it evolved separately from the main lava body at a later stage in the emplacement. Not only did lava continue to flow through the tube after flow had ceased within the main body of the sheet lobe, but the roof above the tube continued to inflate as is evident by its arched geometry.

Observations in Hawaii show that lava tubes and tumuli structures can form during later stages of sheet lobe emplacement because of the localisation of flow along preferred internal pathways and continued inflation above active tubes (e.g., Mattox *et al.* 1993, Peterson *et al.* 1994, Kauahikaua *et al.* 1998). Consequently, the formation of tumuli (or tumulus ridges) and associated lava tubes, such as the one described previously, can be viewed as follows. Initially the sheet lobe is emplaced as an inflating sheet driven by steady transport of lava through a molten core surrounded by insulating crust. At that stage the upper surface of the sheet lobe is essentially horizontal, whereas its basal surface generally follows the irregularities in the underlying surface. Thus, from the start, the lava flux through the molten core is somewhat greater above lows than above highs. With continued inflation of the sheet lobe, the flow of lava gradually becomes more and more redirected towards regions of higher flux. Eventually, thinner regions of the sheet lobe stagnate, and flow of lava is entirely restricted to a few preferred pathways or lava tubes that feed lava to the steadily advancing flow front where new lobes are formed. Inflation of the tube roof continues as long as the tube is full with lava and the flow maintains excess hydrostatic pressure. Hollow tubes are formed when the supply of lava is reduced or terminated and the slope is enough to promote drainage of the internal lava pathway. At Surtsey slopes as small as 1-2° appear to be sufficient to promote such draining from the tubes.

The formation of cupola-shaped tumuli and tumulus ridges are easily explained by the mechanism described above. The tumuli are formed by localised inflation of the lava crust above small pools in the internal lava rivers, whereas the tumulus ridges are formed by inflation above relatively straight sections of preferred internal lava pathways or tubes. The fact that the tumulus chamber at locality 3 has more than one tube exit suggests that the lava pools may sometime initiate bifurcation within the lava tube system.

In summary, the observations presented here show that the Surtsey lava flow field consists of two small lava shields produced by two prolonged effusive eruption phases. Each shield features two principal structural units, the lava cone and the outer lava apron. The lava cones were constructed in the early stages of each effusive phase by surface flows that emanated from small lava ponds contained within the summit lava craters. This activity produced shelly pahoehoe and sheet flows. The lava apron was constructed in the later stages of each phase when the level of the lava ponds had dropped well below the rims of the summit lava craters and the flow of lava to the active flow fronts was essentially confined to internal pathways or lava tubes. As the lava emerged from the tubes it spread to form either a series of small budding lava lobes or broad but thin (tens of centimetres thick) sheet lobes. As the sheet lobes spread and inflated, they attained lateral dimensions of tens to hundreds of meters and thicknesses of several meters. The existing tube system was extended by flux-induced localisation of flow within the sheet lobes, which carried the lava further to produce more lobes in front of new tube exits and thus gradually enlarging the lava apron. Lava emerging from tubes near or at the shorelines was the chief agent in extending the lateral dimensions of the lava aprons, whereas lava breaking out from tubes farther up in the lava field piled on top of existing lobes and added to their vertical dimensions.

## CONCLUSIONS

The Surtsey lava shields consist of two principal structural units, the lava cone and the flanking lava apron. These structural units were formed by discrete lava emplacement mechanisms and consist of distinct lava types and facies associations. Despite their mild alkalic affinity, the Surtsey lava shields have morphologies that are strikingly similar to that of tholeiitic monogenetic pahoehoe lava shields in Iceland. This similarity in geometry and morphology implies that the effusive activity at Surtsey and the lava types it produced can be used as an analogue to establish a conceptual model shield volcanoes, their eruption mechanism and their mode of construction. This could be accomplished by:

(a) more comprehensive study of lava morphologies, types, and facies associations at Surtsey than presented in this report,

(b) systematic analysis of the effusive activity as revealed by contemporary descriptions and other documents (i.e., photographs and films), and

(c) all-encompassing study comparing the Surtsey lava shields to other Holocene lava shields in Iceland.

Such a study is highly desirable because it will enlighten us about the processes involved in construction of shield volcanoes and provide us with a valuable tool to recognise and map various components of shield volcanoes in older volcanic succession.


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# Volumetric evolution of Surtsey, Iceland, from topographic maps and scanning airborne laser altimetry: 1968 – 1998

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## ABSTRACT

The volumetric evolution of Surtsey has been estimated on the basis of digital elevation models derived from NASA scanning airborne laser altimeter surveys (20 July 1998), as well as digitized 1:5,000-scale topographic maps produced by the National Land Survey of Iceland and by Norrman. Subaerial volumes have been computed from co-registered digital elevation models (DEM's) from 6 July 1968, 11 July 1975, 16 July 1993, and 20 July 1998 (scanning airborne laser altimetry), as well as true surface area (above mean sea level). Our analysis suggests that the subaerial volume of Surtsey has been reduced from nearly 0.100 km$^3$ on 6 July 1968 to 0.075 km$^3$ on 20 July 1998. Linear regression analysis of the temporal evolution of Surtsey's subaerial volume indicates that most of its subaerial surface will be at or below mean sea-level by approximately 2100. This assumes a conservative estimate of continuation of the current pace of marine erosion and mass-wasting on the island, including the indurated core of the conduits of the Surtur I and Surtur II eruptive vents. If the conduits are relatively resistant to marine erosion they will become sea stacks after the rest of the island has become a submarine shoal, and some portions of the island could survive for centuries. The 20 July 1998 scanning laser altimeter surveys further indicate rapid enlargement of erosional canyons in the northeastern portion of the partial tephra ring associated with Surtur I. Continued airborne and eventually spaceborne topographic surveys of Surtsey are planned to refine the inter-annual change of its subaerial volume.

## INTRODUCTION AND BACKGROUND

The topographic evolution of isolated volcanic islands has been uniquely observed at Surtsey, classified geomorphologically as a table mountain (e.g., Williams *et al.* 1983). Aerial photography acquired during the volcanic constructional phase of island development (15 November 1963 through 5 June 1967) (Thórarinsson 1965, 1967, 1968) has continued on a near-annual basis until present, thanks to the efforts of the Surtsey Research Society and the National Land Survey of Iceland. While qualitative assessment of the subaerial landscape evolution of Surtsey has been described by Norrman and associates (e.g. Norrman 1980, Calles *et.al.*, 1982 and Norrman & Erlingsson 1992), it has previously been difficult to estimate quantitatively the change in subaerial island volume. A number of studies have estimated the rate of erosion by area (Thórarinsson 1965, 1968, Calles *et al.* 1982, Jakobsson *et al.* 1998). Because Surtsey represents an unprecedented opportunity to evaluate the volumetric evolution of a recently formed volcano in an isolated, marine setting, we have focused on measuring its volumetric change using newly available remote-sensing methods. Here we present the first high-resolution digital elevation model (DEM) of Surtsey acquired exclusively by means of NASA-based scanning airborne laser altimetry (SALA). The laser-altimeter-based DEM provides ~ 20 cm vertical accuracy across all of the sub-

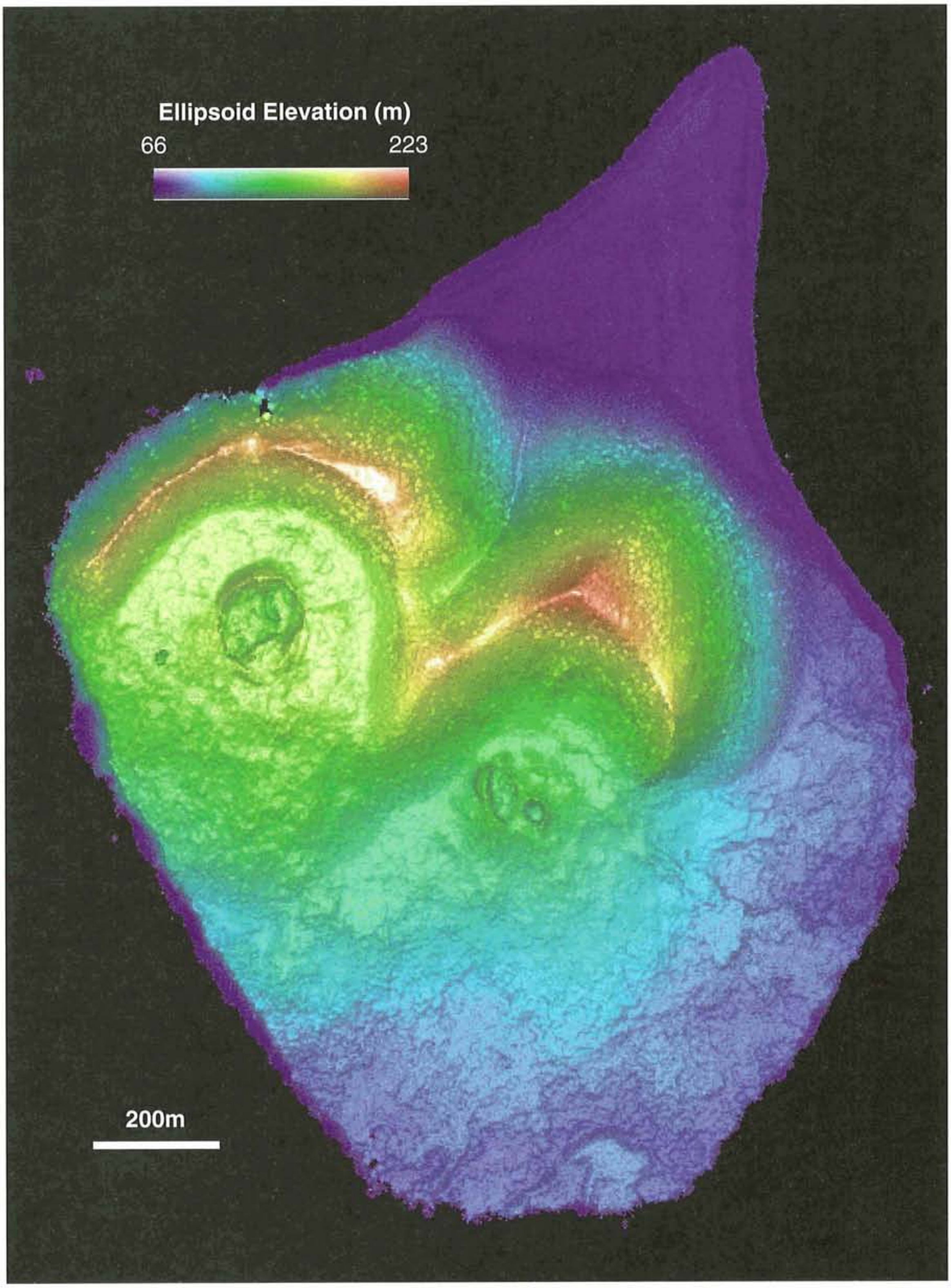


Figure 1. Digital Elevation Model (DEM) of Surtsey acquired 20 July 1998 via scanning airborne laser altimetry using the NASA ATM sensor. Colors represent elevation relative to mean sea level. Shading is based upon local topographic gradient computed from the DEM. The spatial resolution of this image is 3 m, while the vertical accuracy is ~ 20 cm RMS. Colors range from near sea-level (blue) to ~ 150 m (red). Corner coordinates are as in Jakobsson (1998). North is up in this image. Mean sea level corresponds to an ellipsoidal elevation of 66 m.

aerial landscapes of the island and permits computation of whole-island subaerial volumes at unprecedented accuracy. We have taken the SALA-based DEM (Fig. 1), acquired on 20 July 1998, and compared it to independently-derived DEM's from 6 July 1968, 11 July 1975, and 16 July 1993. All of the DEM's prior to 20 July 1998 were generated by digitizing contours on high-resolution topographic maps (Norrman & Erlingsson 1992) and by subsequently converting the data to a rasterized DEM format on a uniform spatial grid. Inter-DEM comparisons were facilitated only after careful co-registration at pixel-scales as fine as 2-3 m (spatial) and less than 1 m (vertical). The temporal evolution of the subaerial volume (V) and of the true surface area (SA) of Surtsey from 6 July 1968 to 20 July 1998 can then be assessed. Here we distinguish projected basal area (i.e., the coastal outline of the island) from true surface area, in which the local relief is utilized in the computation of area.

It is our intent to discuss the evolution of the subaerial volume of Surtsey in the context of those erosional processes presently known to be at work (Norrman 1980, Calles *et al.* 1982, Jakobsson *et al.* 1993). This report develops the remote-sensing methods that were utilized and treats the preliminary interpretation of the volumetric history of the island. Finally, simple predictions about the future erosional evolution of the subaerial expression of Surtsey are presented. We acknowledge that additional data are needed, including repeat SALA surveys, to adequately refine and interpret the geomorphic history of the island. However, we assert that the trends presented herein are valid and useful in the context of landscape-erosion rates in high latitude environments. There are additional surtseyan landforms within Iceland, Jan Mayen, and elsewhere whose present state of erosion can be better understood on the basis of the results for Surtsey that are presented in this paper.

The National Aeronautics and Space Administration (NASA) is interested in advanced orbital and airborne remote-sensing approaches that permit direct measurement of landscape rates of change in response to natural forcings such as climate, severe meteorological phenomena, volcanic eruptions, and others. NASA is presently operating an orbital laser altimeter to map the topography of landscapes on Mars (Smith *et al.* 1999), and has flown similar instruments in Earth orbit aboard the Space Shuttle (Garvin *et al.* 1998). Near-term plans call for Earth-orbiting laser altimeters to be launched in the 2001-2002 for the purpose of documenting the dynamics of terrestrial ice sheets, as well as for measuring the relief of vegetation on a global basis. Scanning airborne laser altimeters (SALA) such as the Airborne Topographic Mapper (ATM) are presently used to provide "airborne ground-truth" for local areas in anticipation of future orbital monitoring efforts (Krabill *et al.* 1995). At present, SALA systems such as the NASA Wallops Flight Facility ATM can acquire spatially-dense (i.e., measurements every meter) topographic sampling over local areas on the basis of laser pulse repetition frequencies exceeding 3000 pulses per second. We operated the ATM sensor at 5000 pulses per second (i.e., 5000 Hz) at an altitude of approximately 500 m (above mean sea level) in order to acquire adequately dense spatial sampling to facilitate construction of a 3-m (per DEM grid cell) digital elevation model for Surtsey. This was accomplished by flying the ATM sensor in a NASA Wallops Flight Facility P-3B aircraft, together with differential GPS equipment, at an altitude that maximizes instrument swath width (i.e., 0.5 *{P-3 altitude}), while minimizing laser ranging errors. Thus, we required 13 passes to exhaustively map the topography of Surtsey on a 3 m grid (Fig. 1). In places, the ATM scans overlapped to allow for dynamic cross-over error analyses. We have assessed some of these and the data from independent swaths agree to within 20 cm (RMS) under most circumstances. For more details concerning NASA's aircraft laser altimetry efforts, the reader is referred to Krabill *et al.* (1995), Garvin (1996), and to Garvin & Williams (1992). Additional details concerning the ATM sensor system can be found at the following web site: http://aol.wff. nasa. gov/ aoltm.html.

Detailed characterization of the topographic evolution of isolated, small islands is largely unknown in the extant literature. Surtsey affords an ideal target for undertaking such an experiment on the basis of its isolation, as well as the wealth of existing data about the island since the time of its formation. Prior to the 1998 SALA surveys, we conducted profiling laser altimeter experiments at Surtsey to understand the meter-scale topographic characteristics of its key landscape features, including for example the volcanic collapse crater Surtur I, the northern ness, and the primary tephra rings (Garvin & Williams 1992). Improvements in laser transmitter technology and in differential GPS tracking

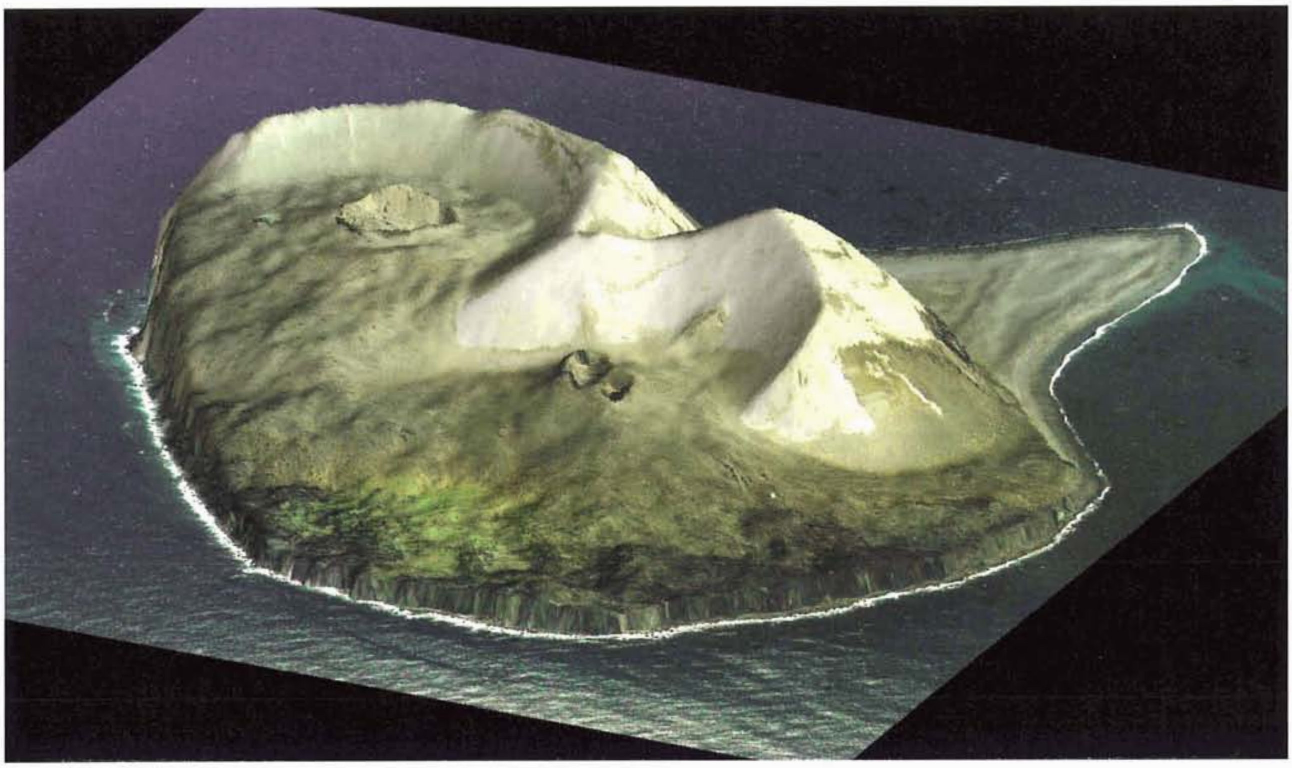

Figure 2. Aerial photograph of Surtsey draped atop the DEM that is illustrated in Fig. 1. The 23 August 1998 aerial photograph was acquired by the Iceland Geodetic Survey (photo ID: O-9542) and digitized by NASA, before being "ray traced" atop the DEM, and then converted to a perspective view from the southeast. The resolution of this image is equivalent to that of the DEM in Fig. 1 or 3 m per pixel. Special thanks to the National Land Survey of Iceland (courtesy S. M. Thorvaldsson, Permit no. 216). Vertical exaggeration is ~20:1.

methods have now allowed us to adopt the SALA approach to completely characterize the landscapes of the entire island in three dimensions. On 20 July 1998, we conducted the ATM surveys of Surtsey under excellent conditions. What follows is a brief description of the data and our preliminary interpretations of it in comparison with previous topographic mapping data from independent sources.

## THE LASER-ALTIMETER DIGITAL ELEVATION MODEL

By combining more than a dozen SALA swaths of topographic data, and correcting for aircraft motion, radial position, and other factors, a seamless DEM can be constructed, as depicted in Fig. 1. This false-colored topographic map combines more than one million independent laser measurements into one image in which color represents elevation above mean sea level. In Fig. 1, the "colder" colors such as blue represent the lowest elevations, while the "hotter" colors such as red indicate the greatest relief. We have modulated the topography with a shaded rendition of the topography of Surtsey derived from the DEM to provide texture on the image. This texture reflects the 3 m scale "roughness" of the surface as measured from the local distribution of slopes at 3 to 6 m horizontal scales. Other than a berm of wave-emplaced boulders, the northern ness appears lower and smoother than all other regions on Surtsey. Individual flow fronts and other crenulations related to the emplacement of the lavas that form the carapace covering the southern half of the island are readily visible. Several topographic/roughness "units" can be observed from the DEM displayed in Fig. 1. First, the depositional northern ness appears as a smooth, low unit, with few features except the berm of boulders that outlines its margins. Second, the middle of the island is dominated by arcuate tephra-rings that extend for 180 degrees in an "m-shaped" pattern. These high-standing features appear to be flanked by aprons of mass-wasted material that transitions into the northern ness lowlands to the north. The third major surface unit is that of the lavas and collapse craters that dominate the southern 40% of the island. Surtur II, to the west, is most clearly expressed as a nearly cylindrical volcanic "pit crater" reminiscent of many similar landforms in the Kilauea region of Hawaii. The lava flow fields that encircle Surtur II appear to form a discrete,

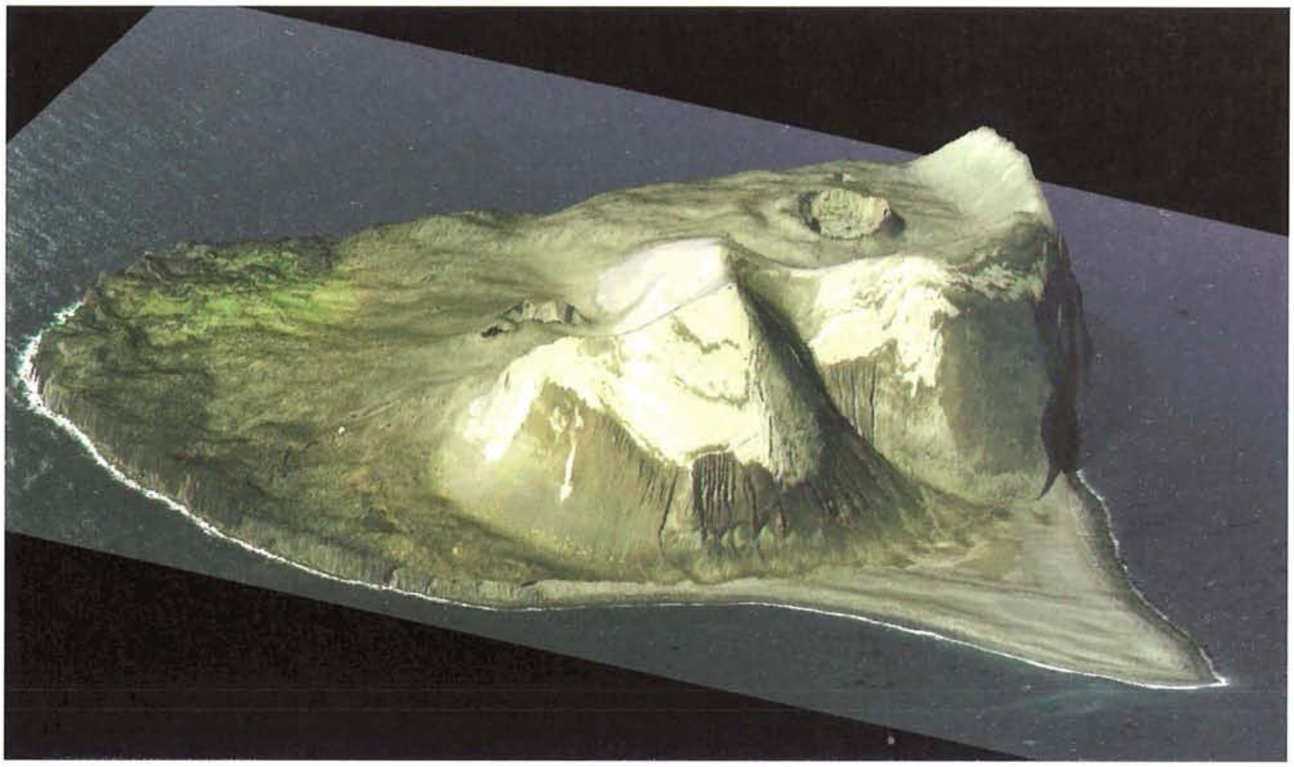

Figure 3. As in Fig. 2, but the perspective view is from the northeast to better feature the erosional canyons being formed in the tephra ring materials (palagonitized tephra). Observe how the albedo of surface materials correlates with the topography. There appears to be local topographic control of the erosional distribution of materials on Surtsey.

but now eroded, lava shield. The lavas associated with Surtur I to the east are multi-tiered, indicating multiple episodes of emplacement, and less association with a single circular vent. From the DEM displayed in Fig. 1, it is clear that intensive marine erosion has most strongly influenced the southwestern coast of Surtsey, leaving a linear coastline, with dramatic cliffs tens of meters in relief.

On the basis of the DEM illustrated in Fig. 1, one can analyze the recent geomorphic history of the island. This is best accomplished by employing multiple perspectives and by combining datasets. We have digitized vertical aerial photographs acquired on 23 August 1998 by the National Land Survey of Iceland and co-registered them to the SALA-derived DEM acquired on 20 July 1998. We can then "ray trace" the two-dimensional data from the vertical aerial photograph on top of a perspective view of the DEM to provide static views from different vantage points. Fig. 2 is an example of a ray-trace of the aerial photograph draped atop the DEM, as viewed from the southeast. In this view, one can visually correlate changes in surface albedo with topography at the same scale. For example, the palagonitized tephra (Garvin & Williams 1992) that outcrops in the tephra rings appears as a higher albedo "tan" unit in Fig. 2, in contast with tephra-covered lavas to their south. Small debris flows can be seen along the eastern and northeastern margin of the tephra ring complex, indicating water-related transport and subsequent outflow. Grassy surfaces have been established in the wind-protected areas of the southern part of Surtsey on the basis of rapid ecological colonization facilitated by sea birds. Fig. 2 also suggests that periodic overflow of the northern ness has produced a series of subtle topographic ridges that outline patterns of deposition as the water receded (Calles *et al.* 1982). Overwash of this region appears to have influenced the position of albedo features associated with very subtle relief variations.

Fig. 3 presents an alternate perspective of Surtsey, as viewed from the northeast. In this case, the research hut is visible with its red roof. In addition, a series of rapidly developing erosional canyons, some of which are more than 5 m in width, can be observed all along the northern face of the tephra rings. Albedo markings associated with the lowest points of the northern

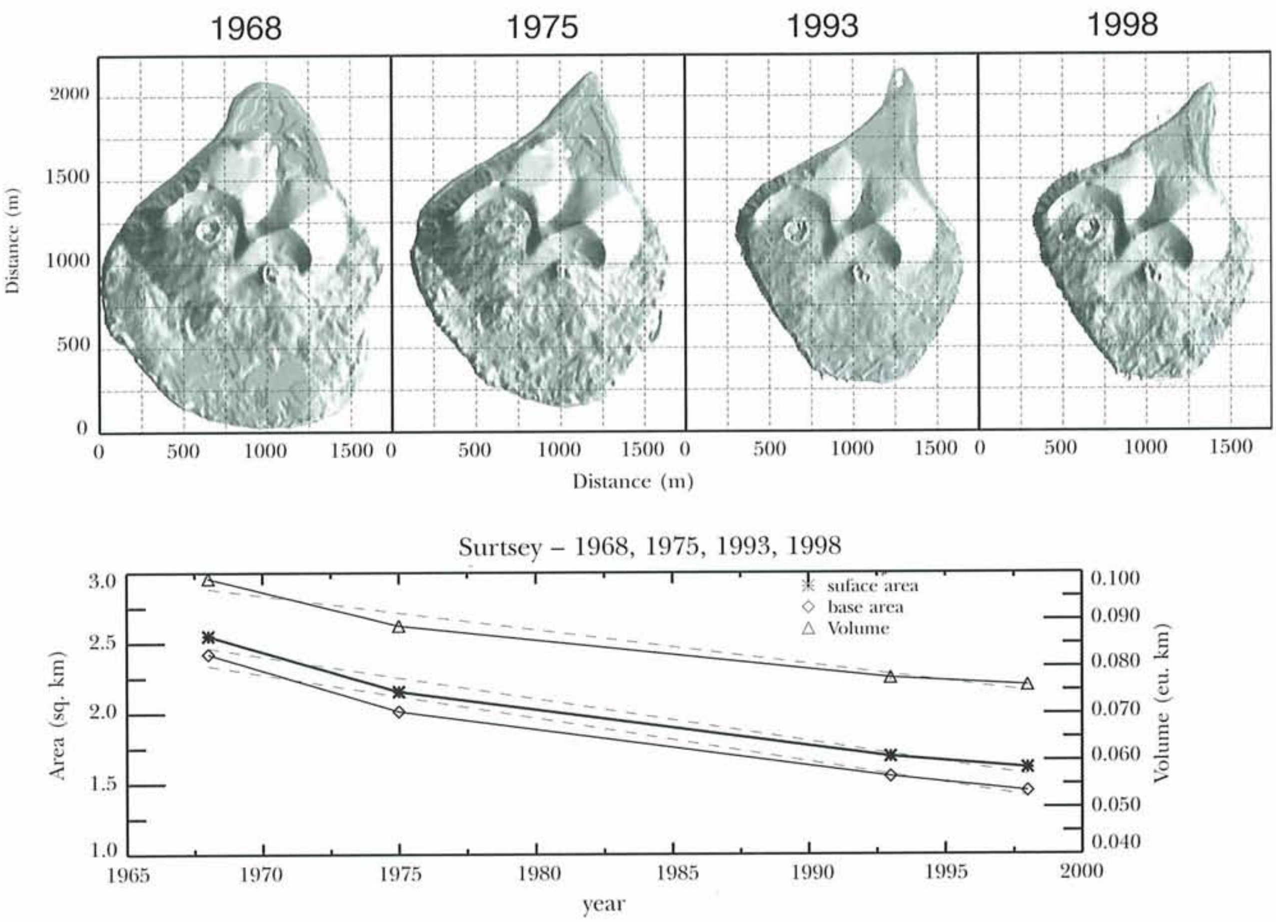


Figure 4. Graphical and pictorial representation of progressive erosion of the subaerial expression of Surtsey from 1968 through 1998. Shaded relief views of the topography of Surtsey in 1968, 1975, 1993, and 1998 are shown at the top, as derived from digitized topographic maps (1968, 1975, 1993) and from scanning airborne laser altimetry (1998). The time-history of the subaerial volume, true surface area (i.e., not projected onto a planar base), and basal area of the island is plotted against year (A.D.) at the bottom, illustrating the pattern of erosional loss over 30 years. More than 25% of the post-eruption subaerial volume of Surtsey has been lost to marine erosion and mass-wasting since 1968. See text for further details and for specific dates associated with each DEM.

ness can also be observed, near the cleft that separates that two sections of the central tephra ring complex. The evolution of the erosional canyons in the tephra rings has increased appreciably since 1991, when field measurements associated with NASA laser altimeter surveys were conducted by the senior author (Garvin & Williams 1992).

## VOLUMETRIC ANALYSIS

The 20 July 1998 SALA surveys produced a geodetic quality DEM of Surtsey, with better than 20 cm vertical accuracy. We have used this dataset as the basis for quantifying the volumetric evolution of the island in a subaerial sense. The subaerial volume of the island was computed by numerical integration of the DEM, yielding a value of 0.075 $km^3$, with an error budget of less than 5%. By co-registering digital elevation models derived by digitizing three different topographic maps of Surtsey, we have been able to compute subaerial island volume for three other time steps. We digitized the 1993 topographic map (1:5000-scale) produced by the Iceland Geodetic Survey (Jakobsson *et al.* 1993) to provide a 3 m DEM for the island from 1993. In addition, we digitized the 1:2000-scale maps produced from aerial photographs acquired on 6 July 1968 and 11 July 1975 (Norrman 1980, Norrman & Erlingsson 1992) to provide additional time steps for reference. In order to accurately co-register four different DEM's to the same reference frame, we used our geodetic-quality 1998 data (i.e., acquired using sub-meter quality GPS positioning) as a reference base and dynamically adjusted each of the other maps so that fixed features were co-aligned to within 1-2 m in a horizontal sense. Once we achieved adequate co-registration, we computed the subaerial volumes of Surtsey for each time step: 6 July 1968, 11 July 1975, 16 July 1993, and 20 July 1998. Fig. 4 illustrates how the topography of the island has evolved from 6 July 1968 to 20 July 1998, as well as how the volume has decreased since 6 July 1968. The true surface area, basal area, and subaerial volume (Fig. 4) all follow the same trend from 6 July 1968 to 20 July 1998. The reduction in subaerial volume from nearly 0.100 $km^3$ to 0.075 $km^3$ in only 30 years of sustained marine erosion from sub-arctic cyclones is remarkable. If one fits a linear relationship to the volume (V) data from 6 July 1968 through 20 July 1998, an equation of the form:

$$V = -0.0007279\ t + 1.53$$

can be derived using least squares regression methods. In this equation, V represents subaerial volume in $km^3$ and t is time in absolute years, such as 1968 and so forth. While it is clear that a linear relationship between volume and time is not expected, this equation fits the existing data with a high confidence factor of nearly 0.98 (i.e., $R^2$ correlation coefficient is 0.98). Using this volume versus time relationship, it can be shown that Surtsey's volume converges to ~0 $km^3$ in only another 100 years. This is a highly simplistic view of the volumetric erosion of Surtsey, because it does not take into consideration that Surtsey itself sits on a submarine socle (Norrman & Erlingsson 1992) and the erosivity of the indurated cores of the conduits of the Surtur I and Surtur II eruptive vents is unknown. However, it shows that the pace of erosion could easily reduce the island to a series of areally insignificant sea-stacks (e.g., indurated cores) in about a century (Jakobsson et al. 1998). Higher-order non-linear least squares regression analyses of the volume versus time data have also been conducted, with largely similar results. In the best-fitting polynomial solution, the subaerial volume of Surtsey approaches zero in approximately 106 years. Power law analysis of the relationship between volume and time involves fitting an equation of the form:

$$V = k\ t^{-n},$$

where k is the pre-exponential coefficient, and n is the power-law exponent. In this case we measure time t in years since 1960 and volume in $km^3$ as before. When we adopt this approach, an equation of the form:

$$V = 0.137\ t^{-0.160}$$

results, which suggests a much longer lifespan for the bulk of the subaerial island. However, this approach implicitly assumes that the relatively rapid pace of erosion Surtsey has experienced over the past 30 years will drastically diminish, allowing for a different style of volumetric erosion in the future. As yet, there is no evidence of a change in the style or magnitude of erosion on the island from recent field observations (Jakobsson 1998). While we believe the linear relationship discussed above is overly pessimistic with respect to the survival of the island, the power-law projection may be considered optimistic. A reasonable projection is likely to lie in between, suggesting a lifespan of several hundred years for the bulk subaerial volume of the island.

The best-fitting linear relationship between true surface area (SA) and time (t) suggests that the majority of the land surface of the island could be reduced to nearly zero in only 50 years. A more optimistic power-law solution ($SA = 4.68\ t^{-0.29}$) would allow for hundreds of years of survival. While more data is needed and increasingly precise geodetic methods could be used to assess inter-annual change, our results suggest that the predicted lifetime of Surtsey as a unique locality for studying the evolution of an island may be limited. Unless the pace of subaerial erosion dramatically shifts, the life span of the island is probably limited to ~ 100 years, although the more resistant sea stacks could survive for centuries.

## SUMMARY

We have used state-of-the-art airborne remote sensing methods to capture the topography of the land surface of Surtsey as of 20 July 1998. The resulting DEM provides more than one million point measurements of the elevation of the island in a geodetic coordinate frame, and facilitates direct computation of the subaerial volume. The subaerial volume computed from the SALA-derived DEM is 0.075 $km^3$, which is ~ 25% less than the volume of the island just after the end of its volcanic construction phase (1968). The best-fitting linear relationship between island subaerial volume and time suggests that most of the island should be reduced to a volumetrically-insignificant group of sea stacks in approximately 100 years. While this prediction is based on very limited snapshots of island volume over a 30 year period, it suggests that monitoring the volumetric erosion of Surtsey over the next few decades could be an important

activity if volcanic island erosion patterns are ever to be quantified. Surtsey is unique in that a high-quality set of DEM's exist for the island since the terminal stages of its constructional phase. Over the past 30 years, there are four snapshots of island volume computed from independent DEM's (6 July 1968, 11 July 1975, 16 July 1993, and 20 July 1998) and prospects for generating new DEM's in future years both from aircraft and spaceborne methods are encouraging. Validating the current volumetric-erosion trend for the island by means of future laser altimetry surveys appears to be amply justified, if only to understand whether there are any shifts in the style or pattern of erosion in this sub-arctic environment.

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# EMISAR mapping of Surtsey, Iceland

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## ABSTRACT

During two measurement campaigns in 1997 and 1998, the Danish airborne Synthetic Aperture Radar (SAR) system, EMISAR, mapped a total of about 16,000 km² along the Northern and Eastern rift zones in Iceland. Although not specifically targeted, Surtsey was included in the mapping of the Eastern rift zone on August 13, 1998. The acquired SAR data have been used to generate a Digital Elevation Model (DEM) of Surtsey with a spatial resolution of 5 m and a polarimetric L-Band SAR image with a resolution of 5 m. The polarimetric SAR image shows differences in surface morphology between the geologic units on Surtsey.

## INTRODUCTION

In the early 1990s, the utilization of satellite radar interferometry to measure the Earth's topography and changes of the Earth's surface became a widespread technique in geophysical research. In topographic mapping, the advantages of radar interferometry over conventional photogrammetric techniques are the rapid data collection, high vertical resolution, and the ability to collect globally consistent elevation data. Surface displacements can be measured with competitive precision, but with a much larger spatial sampling density compared to in-situ techniques. A comprehensive summary of geophysical applications of radar interferometry can be found in Massonnet & Feigl (1998).

The utilization of radar images in classification of lava units and quantitative characterization of lava surface morphology has been discussed in various papers (e.g., Dierking 1999, Campbell & Shepard 1996, Farr 1992, Gaddis 1992, van Zyl *et al.* 1990). The roughness scales typically observed on the surface of lava flows are of magnitudes to which radar sensors operating at frequency bands between C-band (wavelength about 0.05 m) and P-band (about 0.7 m) are very sensitive. Hence, the intensity of the radar signal, which is scattered back from the flow surface to the radar sensor, is in many cases comparatively large.

A major advantage of airborne or satellite radar systems is that large areas (such as the Northern and Eastern rift zones on Iceland) can be imaged in a rather short time independent of light and cloud conditions. The ERS satellites acquire several sets of images per month and airborne systems can perform regional mapping at a much higher rate than aerial photography (2.5 km²/s for the EMISAR).

The Northern and Eastern rift zones in Iceland were mapped with the Danish airborne EMISAR system in the summers of 1997 and 1998 with a two-fold purpose. Firstly, the data were combined with radar data from the European Remote Sensing Satellites ERS-1 and ERS-2 acquired between 1991 and 1997 to study tectonic movements and inflation/deflation events of the magma chambers in the area. Secondly, polarimetric SAR images were used to study aspects of the geology in the area utilizing the fact that the radar signature is related to the morphology of the surface (Dierking & Haack 1998).

SAR studies of terrestrial basaltic lava flows, like those in the active volcanic zones of Iceland are also useful in terms of interpreting the radar signatures of basaltic lava flows on Venus for which the only source of data are the Magellan SAR images (Johnson 1991).

*Principles of SAR mapping*

The EMISAR is an airborne radar system, which transmits and receives radar pulses perpendicular to the flight track. During operation the radar pulses illuminate a strip parallel to the flight track. The width of the strip measured by the EMISAR is usually about 12 km and the altitude of the airplane during mapping is between 7 and 13 km. In a conventional radar the spatial resolution parallel to the flight direction is proportional to the antenna beam width that is smaller for long antennas and larger for short antennas. Due to the limited size of an antenna which can be mounted on an aircraft or a satellite the antenna beam is typically several degrees wide. The resolution is significantly better in the SAR system. Due to the relatively large beam width of the antenna the radar receives many pulses from a particular position on the ground as

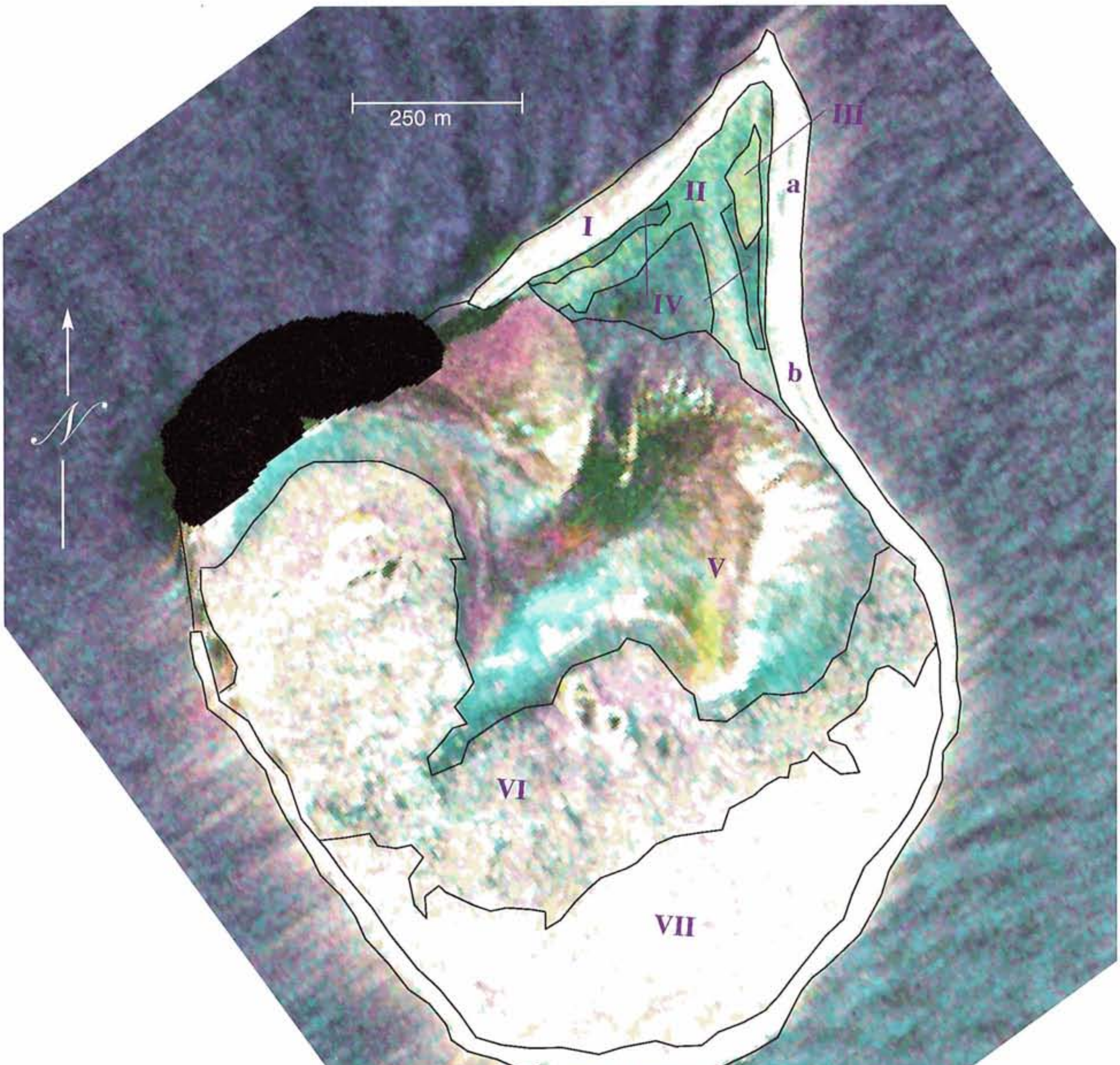


Figure 1. Polarimetric EMISAR image of Surtsey. HV-red, HH-green, and VV-blue. The units shown are described in Table 1.

the radar passes by the target. Since the radar is moving relative to the ground the time interval between consecutive pulses from a particular target is varying (Doppler shift). By combining all pulses received from a particular target and utilizing the Doppler shift information it is possible to generate images similar to those that could have been obtained with a much longer antenna or aperture (length typically in the range of kilometers) - thus the name Synthetic Aperture Radar. Moving targets will, however, not be correctly focussed by this process. For example, reflections from ocean waves are somewhat defocused (Fig. 1).

For each resolution cell on the ground the magnitude and phase of the backscattered signal is calculated for each of the frequencies and polarization used. The magnitude of the backscattered signal depends on the surface roughness and the dielectric properties of the target as well as on the target's orientation relative to the radar beam. In general, a rough surface scatters more of the signal back toward the radar than a smooth surface (unless the surface is facing the radar). In this context rough means that the surface is rough on a scale similar to the wavelength of the radar pulse. The dielectric constant determines the magnitude of the reflected and scattered signals as well as the attenuation of the signal fraction that penetrates into the medium.

The EMISAR currently includes C-band (wavelength 5 cm) and L-band (20 cm), which can be operated simultaneously. Both antennas can transmit horizontally and vertically polarized pulses and can thus be used to generate images utilizing different combinations of polarizations (polarimetric images).

*Polarimetry*

The color-coded polarimetric image shown here (Fig. 1) is based on three L-band EMISAR images, HH (green), VV (blue), and HV (red) where the first letter designates the polarization of the transmitted pulse and the second letter designates the polarization of the received pulse. Note that even though the transmitted pulse is either H or V, the backscattered signal from the Earth surface will in general include both polarizations. A polarization change of a fraction of the signal occurs when the scattering surface is very complex. Many vegetation types and a'a lava flows are examples of scatterers that generate a strong HV (= VH) return. For more details on polarimetric SAR see Ulaby & Elachi (1990).

*Interferometry*

The radar signal carries amplitude and phase information. The phase difference between two different SAR images at a given position on the

Table 1. Interpretation of radar signature and field observation. Units are outlined in Fig. 1.

| | |
|---|---|
| I. | Coastal areas in Surtsey show up as very bright areas in Fig. 1 indicating that the surface is rough on a 20 cm scale. This is in coherence with the morphology of the coastal areas. Field observations during the summer 1998 confirm that the bright areas are covered by boulders in the size range of 0.5 to a few meters in diameter. Two narrow strips covered with sand (a and b) show up as dark units within the bright unit I (Fig. 5). |
| II. | This unit represents the highest benchmarks on the northern peninsula in Surtsey. Densely distributed boulders and tree logs are observed in this area. In between the boulders and the logs we observed that eolian sand medium to coarse grained had accumulated. The darker appearance of this unit relative to unit I can be related to the smoothing effect of the sand (Fig. 5). |
| III. | A small area within the boulder field where the HH reflection is significantly stronger than the VV reflection (Fig. 2). The area in question is characterized by eolian sand, showing ripples in the range of cm to tens of cm (Fig. 5). |
| IV. | Unit 4 is the darkest of the units on the Northern peninsula. The area is covered by a thin layer of eolian sand, where occasional boulders stick out and some beach debris is scattered. The largest area is a remnant of the oldest part of the peninsula. The two smaller areas are similarly built, covered with thin layer of eolian sand and are formed in-between older boulder coasts. Common for the three areas is that they are flooded during winter time. This makes them denser and flatter than other areas covered with eolian sand like area III. |
| V. | The steep and variable slopes in the interior of the island dominate the variation in radar characteristics. The three blue areas on the crater slopes are characterized by large HH and VV backscatter. The HV channel is, however, comparatively weak which is consistent with the smooth surface of these slopes. The surface is composed of smoothly polished hyaloclastite. The reason why these areas are so bright in HH and VV is that they are facing the radar beam, which was transmitted from the SE, and thus reflect the radar pulses like a mirror back toward the plane (Fig. 6) |
| VI. | The unit is relatively dark compared to the southern part of the island. The area inside the Surtur vent and along the crater wall is almost black. This darkening of the unit is correlated with the eolian sand cover. The NW-most area is lightly brighter consistent with the less significant sand cover in Surtungur (Figs 6, 7 and 8). |
| VII. | Southward to the coast, the lava morphology plays a significantly greater role in radar signal scattering, and the image becomes brighter. In this area occasional a'a lava streams are observed. Most significant in the area are heavily fractured pahoehoe flows and shelly type pahoehoe flows. The highly fractured surfaces of these pahoehoe flows make them very rough and therefore give them radar backscattering characteristics similar to the a'a flows. Thin lava plates more or less twisted and tilted characterize shelly pahoehoe flows. The more massive pahoehoe flows show fractures due to deflation (Figs 7 and 9). |

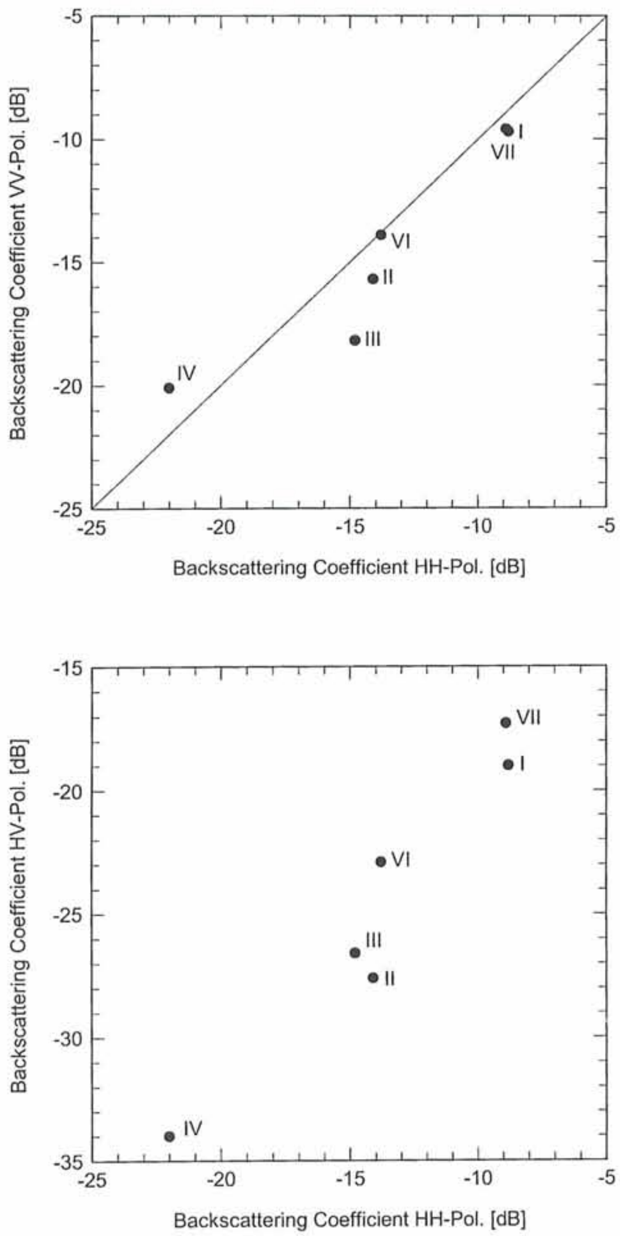


Figure 2. Characteristic backscattering coefficients of the units shown in Fig. 1. The backscattering coefficients are measures of the intensity of the received signals relative to the intensity of the transmitted signals. Units I, and VII are the brightest of all units, both in the HH and VV channel. Unit VI is darker which illustrates the smoothing effect of an increase in the areal extent and/or the thickness of the sand cover on top of the lava flows. Units II and III represent coastal morphologies. Unit III is of particular interest since it has the highest HH/VV ratio, possibly due to sand ripples perpendicular to the incoming radar pulses.

ground is a measure of the difference in distance between the particular ground element and the antenna positions at the two data takes. Images showing the phase difference of two SAR images recorded over the same area are known as interferograms. Interferograms are used for two different purposes.

If the two images are recorded from identical or nearly identical tracks but at different times the phase difference represent displacements of the Earth's surface. Displacements down to 1-2 cm may be detected using C-band SAR images. SAR interferometry is used to study inflation/-deflation of the surface, tectonic movements, glacier motion etc. Until now, this has mainly been done using satellite data since the satellite tracks are smoother than airplane tracks and can be determined with greater accuracy than the tracks followed by an airplane during two consecutive flights.

Alternatively, if the images are recorded at the same time, but with a slight vertical offset, the difference in the distance between ground element and the antennas is due to the difference in viewing angle. Knowing the distance to the target and the difference between the two antennas, it is possible to calculate the elevation of the target. This technique is used to generate Digital Elevation Models. For more details on SAR interferometry see Madsen & Zebker (1998).

## RESULTS

Figs 1-3 show the results from the polarimetric and interferometric analysis of the data. During the measurement the radar illuminated Surtsey from SE (126°) while the airplane was flying toward the NE. The area below the high cliffs along the NW-shore in Figs 1 and 3 was in the radar shadow and was therefore not mapped.

### *Polarimetry*

We have visually classified the surface features on Surtsey into seven major radar units (Table 1). Each unit has a characteristic radar signature due to its particular surface characteristics and morphology. The vegetation on Surtsey is densest in the southern part of the island where large spots of grass have developed. Radar polarimetry can in many cases be used to detect and distinguish different vegetation covers (Ulaby & Elachi 1990, Skriver *et al.* 1999). The low vegetation on Surtsey is too sparse to show up clearly in the L-band polarimetric image. It could possibly be detected using C-band polarimetry because of the shorter wavelength. Although C-band data were also recorded over Surtsey it is not possible to generate a C-band polarimetric image since only vertically polarized pulses were used in the interferometric measurement mode. In Table 1, the field characteristics of the radar units are briefly described and related to the observed radar signatures.

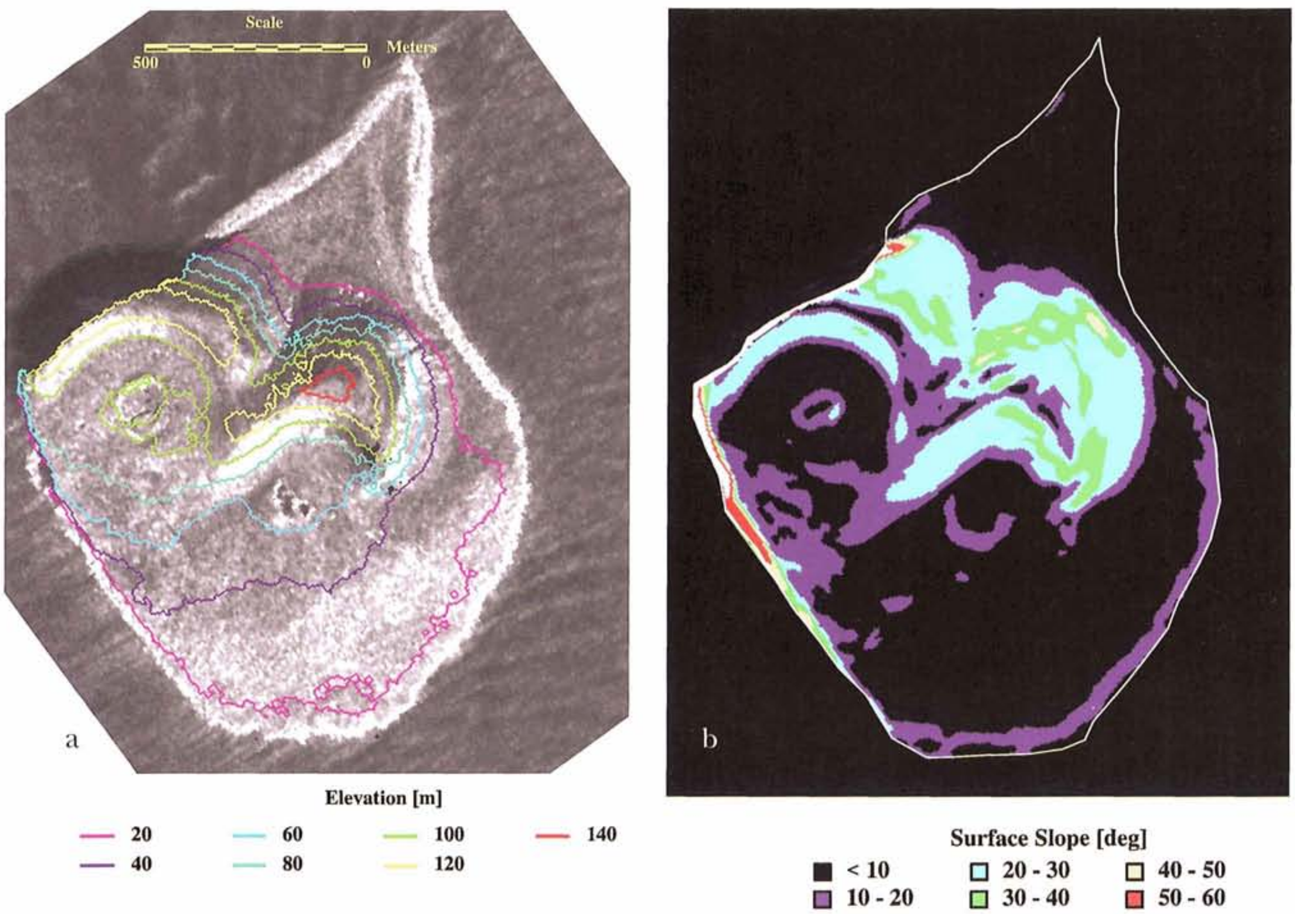


Figure 3. a) Digital Elevation Model of Surtsey superimposed on a C-band intensity image. Contour lines are shown for each 20 m starting with 20 m in red. The height accuracy is about 1 m. b) Slopes calculated on the basis of the DEM shown in 3a. The grey area is an artifact caused by the radar shadow. North is up.

*Comparison of the polarimetric image with the geologic map*

The polarimetric images reflect variations of certain surface characteristics of Surtsey. The radar signature is sensitive to variations in small-scale roughness of the lava flows, thickness and humidity of sand covers, boulder size along the shore line and surface slope relative to the incoming radar signal. These surface characteristics are not necessarily correlated with differences in rock type, mineralogy, or age as shown in the geologic map. Two lava flows of different age may for example have similar surface morphologies and may therefore not be discriminated in the polarimetric image. The polarimetric image may, however, show differences in surface morphology within single units shown in the geologic map. A problem in the interpretation of the radar signatures is the occurrence of variable, partly steep slopes on parts of the island. Variations in signature caused by changes in radar incidence angle are not easily separated from variations due to changes in surface morphology.

The geologic map (Jakobsson 2000) is divided into 9 different units, three types of coastal sediments, three lava flow units and three other types of volcanic units. The two types of beach sediments are readily distinguished in the polarimetric image. The large boulders (Unit 1) have sizes closer to the radar wavelength and are therefore characterized by a very strong backscattered signal. Narrow bands (~20 m wide) of smaller scale coastal sediments (a and b in unit I) NE of Austurbunki clearly show up in the polarimetric image as darker bands. One of these bands is indicated on the geologic map, the other is not (but can be identified in aerial photography).

The spatter cones are not easily distinguished as coherent units in the polarimetric image because of their irregular topography. The rough surface of the spatter is likely to give it radar characteristics similar to that of the lava

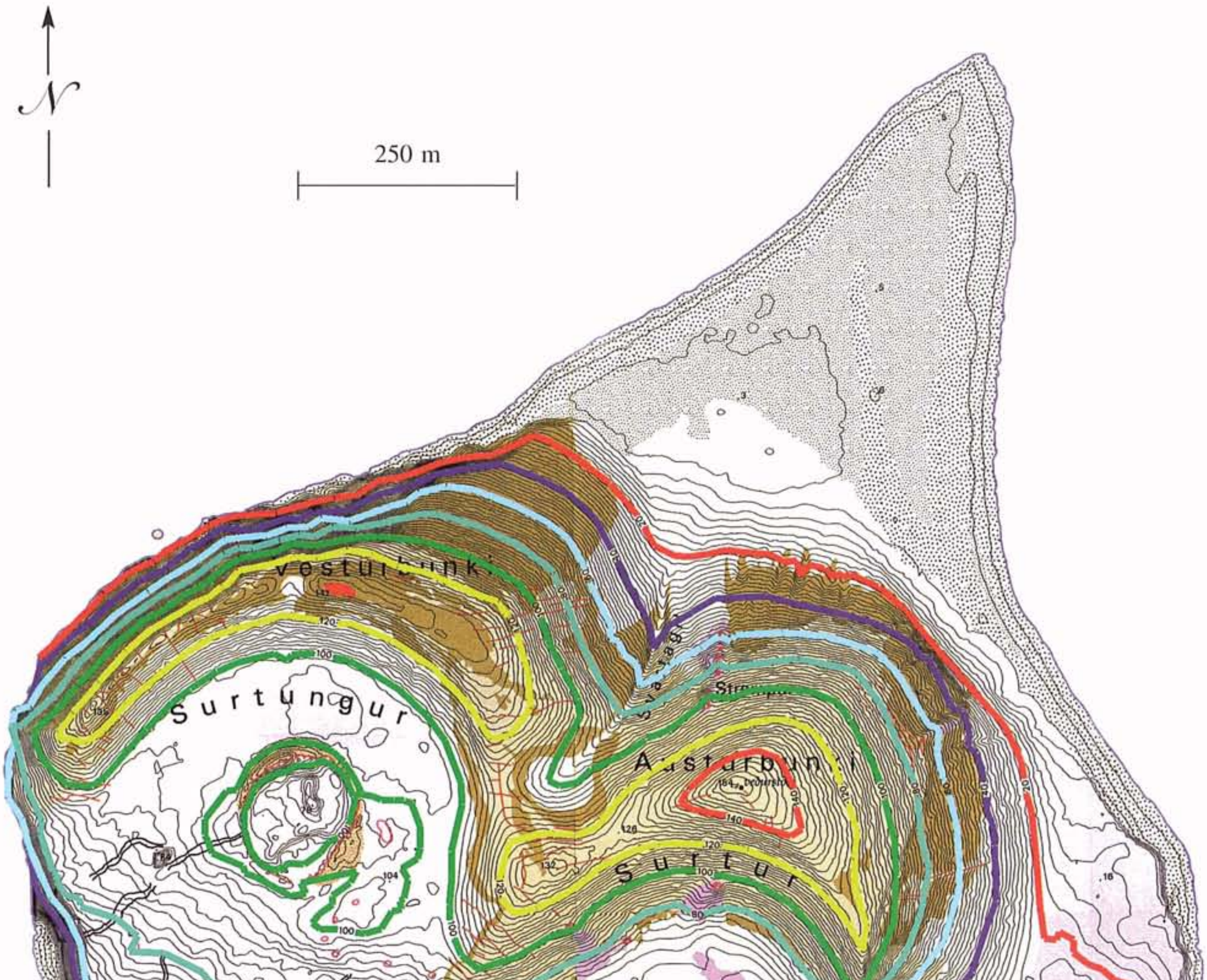


Figure 4. Geologic map of Surtsey (Jakobsson 2000) with the contour lines corresponding to Fig. 3a highlighted and color-coded using the color scheme of Fig. 3a.

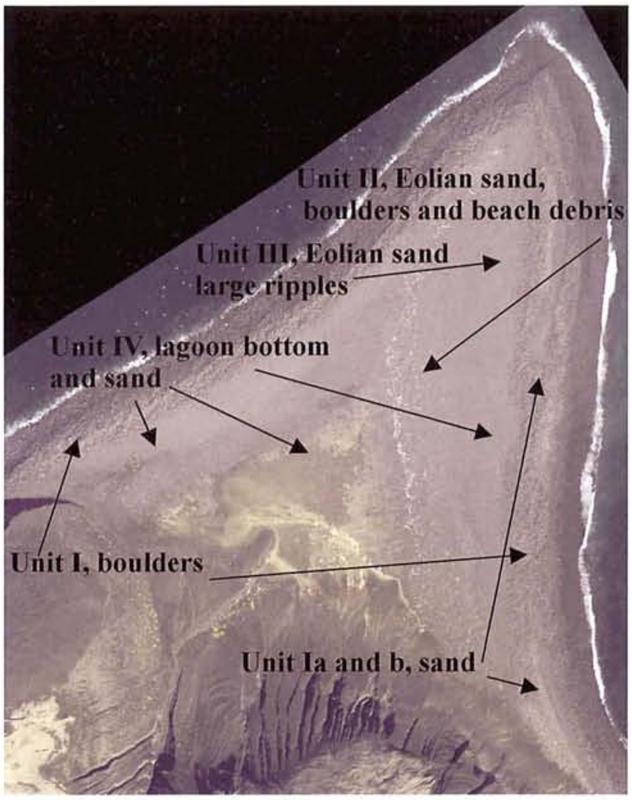


Figure 5. Aerial photograph of the northern tail of Surtsey. The figure shows the four different units that can be distinguished on the tail.

flows. The palagonite tuff and tephra units in the terrain of variable, partly steep surface slopes cannot be distinguished in the polarimetric image, either. It is, however, likely that the similar grain size and surface morphology of these two geologic units also would make it difficult to discriminate them even in areas with modest slope.

The lava type in the three different lava units is mainly shelly pahoehoe with occasional a'a streams. Since both of these types have very rough surfaces and thus high backscattering coefficients they are very difficult to distinguish in the polarimetric image. In general, however, pahoehoe and a'a are easily distinguished in radar images since pahoehoe flows normally have very smooth surfaces.

*The EMISAR DEM*

The digital elevation model and the slope map shown in Fig. 3 are based on two images recorded with the EMISAR's two C-band antennas. The C-band antennas are mounted on the side of the airplane with a vertical spacing of 1.05 m. The elevation contours are superimposed on a greyscale image showing the intensity of the received C-band pulses. The EMISAR DEM was found to closely resemble the elevation data in the geological map (Jakobsson 2000). The elevations in the EMISAR DEM are relative to the mean of the sea surface but seem to reveal a slight offset relative to the elevations of Jakobsson (2000). Since it was difficult to identify a set of reference points in the C-band magnitude image for estimating the offset between the two DEMs, we lack a quantitative number but the offset is approximately 2 m (with the EMISAR elevation numbers being higher than those of Jakobsson 2000). Part of the offset could be due to low tides during the EMISAR mapping. In an interferometric measurement campaign specifically targeted on Surtsey, one can put out radar reflector targets close to the existing GPS stations on Surtsey and thus make it possible to tie the two DEMs together.

In some areas with poor signal to noise ratios such as on the slopes that are facing away from the radar the height accuracy of the EMISAR DEM is deteriorated. This effect may be seen on the N-side of Austurbunki, in particular on the yellow 120 m contour, which reveals high frequency variations. We were able to derive smoother contour lines resembling Jakobsson (2000) in this area by applying a 3x3 median filter to the data (thus reducing the spatial resolution). In other areas with good signal to noise ratio such as the southern lava fields the height accuracy is about 1 m.

An estimate of the volume of Surtsey (above sea level) can be calculated from the EMISAR

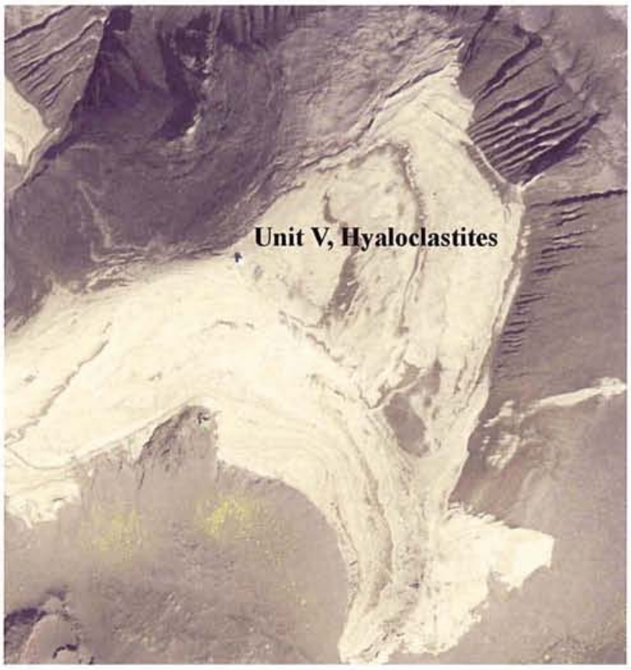


Figure 6. Aerial photograph of the Austurbunki hyaloclastites. The two units marked V and VI can be easily distinguished.

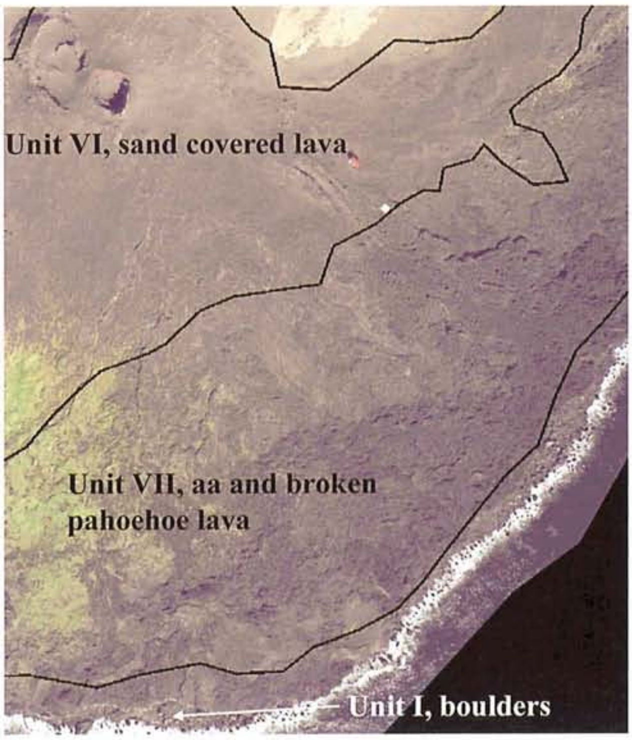


Figure 7. Aerial photograph of the southern most part of Surtsey. The units marked VI and VII are shown on this photograph. The main difference between the two units is the infilling of eolian sand in unit VI. The pahoehoe lavas within unit VII gain their roughness due to inflation and deflation of the surface during formation. Also, note that the width of unit I is larger than the true width seen in the aerial photograph. This is probably due to a combination of the lower resolution of the radar image and a slight broadening of the very strong backscattered signal from the coastal cliffs, boulders and waves along the coast. Multiple reflections from the boulders and vertical cliffs also contribute as these have a longer ray path and thus plot inland of the coast.

DEM. Since a small but very high fraction of the island is in the radar shadow the calculated volume is slightly lower than the actual volume. We estimate that the current volume of Surtsey above sea level as seen by the radar was 0.075 $km^3$. The volume in the radar shadow was of the order of 0.002 $km^3$ and the true 1998 volume therefore ~0.077 $km^3$. The mapped area of the island was 1.40 $km^2$, which excludes about 0.03 $km^2$ in the radar shadow. The total area based on the EMISAR data was therefore 1.43 $km^2$ or 0.05 $km^2$ less than the estimate of Jakobsson (2000).

The DEM determined for Surtsey could be used to correct ERS 1/2 interferometric images for topography. Interferometric images could be of interest because of the large variation in subsidence rate which has been observed across Surtsey (Moore *et al.* 1992). Corrected ERS interferograms may provide information on deformation of Surtsey after 1991 when the ERS satellites came into operation.

## CONCLUSIONS

A polarimetric SAR image, a digital elevation model, and a slope map of Surtsey have been produced based on SAR data recorded on August 13, 1998. The digital elevation model closely resembles the elevation data from the Geological map of Surtsey (Jakobsson 2000). The DEM has been used to calculate an area and volume above sea level of Surtsey of 1.43 $km^2$ and 0.077 $km^3$.

The polarimetric images can be used to dis-

Figure 8. An overview over unit VI. The lavas are mostly filled with eolian sand derived from the volcanic ash formed in the Surtsey eruption. Stick for scale about 0.5 m high.

Figure 9. Overview of the pahoehoe lavas forming unit VII. The lavas are heavily fractured and tilted, although their original surface is smooth. Man for scale.

criminate between lava flows with varying degrees of roughness and/or sediment cover, and areas with different boulder size along the coast. These differences are correlated with field observations from the summer of 1998 and with the most recent geological map of Surtsey (Jakobsson 2000).

Radar mapping specifically targeted at Surtsey could be performed at much higher spatial resolution (down to 75 cm by 1.5 m for C- and L-band using the EMISAR system) than the resolution obtained in the regional mapping setup used here. The regional setup used in the 1998 mapping only allows us to study the large-scale features of Surtsey.

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