

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 furoid 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 km² 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 km² 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 est-

ablished 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

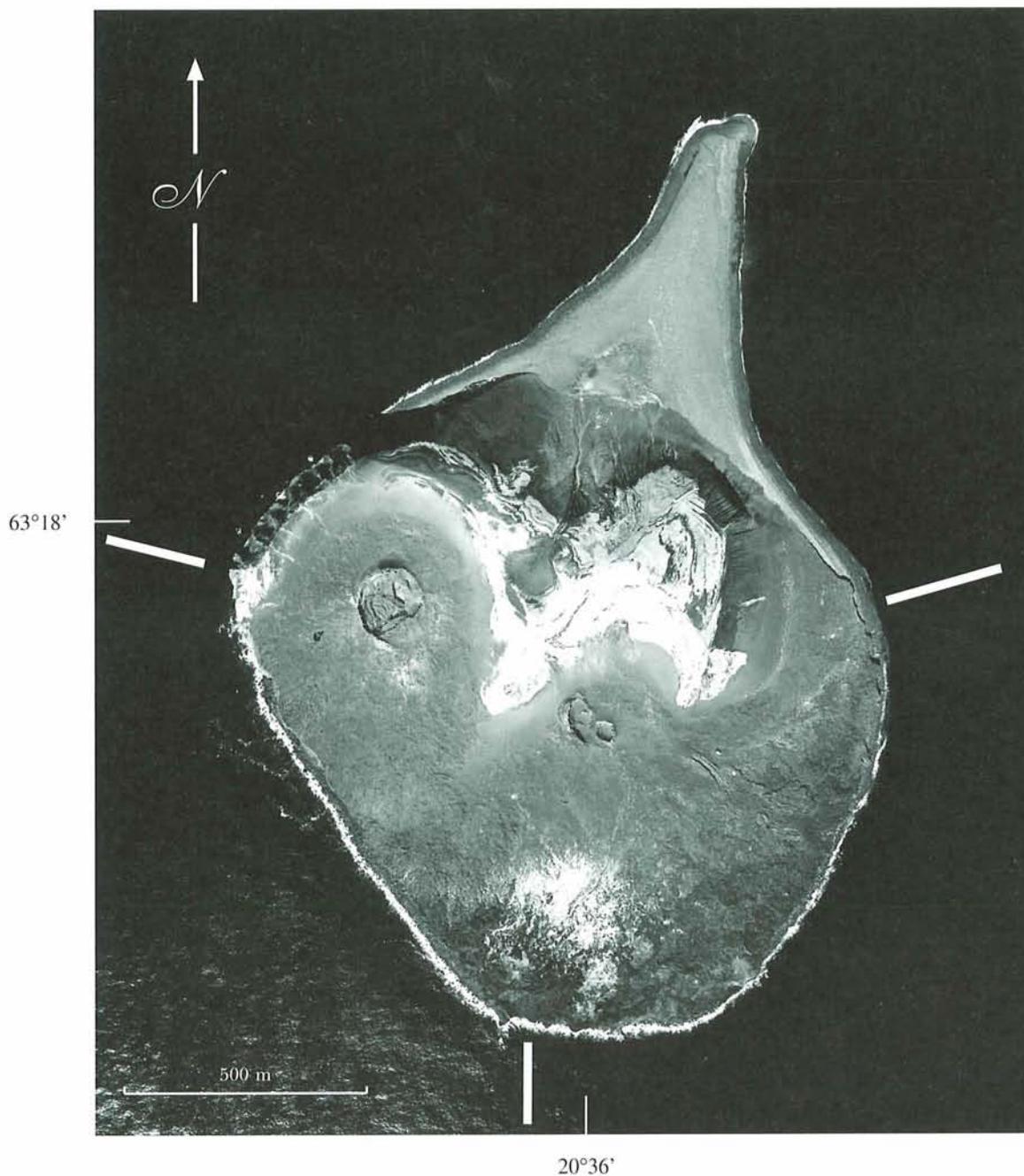


Figure 1. Vertical aerial photograph of Surtsey, July 21, 1996. Transects studied during 1987, 1992 and 1997 are indicated in white. Note the boulders and lava cliffs in the southern part of the island and sand beach in the northern part (courtesy of the National Land Survey of Iceland).

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.

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

taxa	depth (m):	east section						south section				west section					
		5	10	15	20	25	30	10	15	20	25	5	10	15	20	25	
<i>Acrochaetium secundatum</i>																	o
<i>Acrosiphonia arcta</i>		o															
<i>Alaria esculenta</i>		o		o		o		o	o	o		o	o	o			o
<i>Antithamionella floccosa</i>		o	o	o	o		o	o				o	o	o	o		
<i>Audouinella membranacea</i>																	
<i>Callophyllis cristata</i>				o	o												o
<i>Conchocelis</i> sp.			o		o		o	o									
<i>Delesseria sanguinea</i>			o	o	o	o	o		o					o	o	o	
<i>Desmarestia aculeata</i>		o	o	o	o									o		o	
<i>Desmarestia ligulata</i>				o													
<i>Desmarestia viridis</i>		o	o	o			o			o			o				
<i>Ectocarpus siliculosus</i>		o			o				o					o			
<i>Enteromorpha prolifera</i>							o										
<i>Entodictyon infestans</i>									o								
<i>Epicladia flustrae</i>																	o
<i>Halosiphon tomentosus</i>		o						o				o	o				
<i>Haplospora globosa</i>						o	o			o			o				o
<i>Hincksia granulosa</i>							o										
<i>Hincksia secunda</i>												o					
<i>Hincksia</i> sp.		o															
<i>Laminaria hyperborea</i>			o	o	o	o			o				o	o			o
<i>Lomentaria clavellosa</i>		o	o		o												
<i>Lomentaria orcadensis</i>				o			o	o	o	o			o	o	o		
<i>Membranoptera alata</i>									o								
<i>Monostroma grevillei</i>		o															
<i>Phycodrys rubens</i>			o	o	o	o	o		o	o				o			o
<i>Phyllophora traillii</i>																	o
<i>Polysiphonia stricta</i>		o	o	o	o		o	o	o			o	o	o	o	o	o
<i>Porphyra miniata</i>		o	o	o													
<i>Porphyropsis coccinea</i>		o	o	o													o
<i>Rhodochorton purpureum</i>			o														
<i>Sphacelaria caespitula</i>			o	o	o			o	o				o				o
<i>Ulvaria fusca</i>		o															
<i>Urospora penicilliformis</i>					o												
<i>Urospora wormskioldii</i>		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 m² 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.

taxa	depth (m)	east section							south section					west section						
		litt.	5	10	15	20	25	30	10	15	20	25	35	5	10	15	20	25		
<i>Alavia esculenta</i>		o	o	o	o				o	o	o	o				o	o	o	o	
<i>Antithamnionella floccosa</i>		o	o	o		o	o		o			o	o		o	o	o			
<i>Audouinella membranacea</i>				o		o														
<i>Audouinella pectinata</i>				o		o														
<i>Blidingia minima</i>		o																		
<i>Callophyllis cristata</i>				o		o	o													
<i>Chorda filum</i>				o		o														
<i>Codiolum sp.</i>		o																		
<i>Conchocelis sp.</i>							o												o	
<i>Delesseria sanguinea</i>				o	o	o	o	o		o		o	o		o	o	o	o	o	
<i>Desmarestia aculeata</i>			o	o	o	o				o					o					
<i>Desmarestia ligulata</i>						o				o										
<i>Desmarestia viridis</i>			o		o	o				o					o	o				
<i>Ectocarpus siliculosus</i>		o	o	o		o	o	o		o	o	o					o			
<i>Enteromorpha compressa</i>		o																		
<i>Enteromorpha flexuosa</i>		o																		
<i>Enteromorpha intestinalis</i>		o																		
<i>Enteromorpha prolifera</i>		o						o												
<i>Fucus spiralis</i>		o																		
<i>Halosiphon tomentosus</i>			o		o	o		o		o	o				o	o				
<i>Haplospora globosa</i>											o					o				
<i>Hincksia granulosa</i>						o														
<i>Hincksia ovata</i>						o														
<i>Hincksia secunda</i>		o	o	o		o	o			o	o		o		o	o	o	o	o	
<i>Laminaria hyperborea</i>				o	o	o						o	o		o		o			
<i>Lomentaria clavellosa</i>			o	o	o	o									o	o				
<i>Lomentaria orcadensis</i>				o	o	o	o			o	o	o	o	o	o	o	o	o	o	
<i>Meiodiscus spetsbergensis</i>				o																
<i>Membranoptera alata</i>				o	o															
<i>Monostroma grevillei</i>							o								o					
<i>Omphalophyllum ulvaceum</i>				o																
<i>Petalonia fascia</i>		o	o																	
<i>Petalonia zosterifolia</i>		o																		
<i>Phycodrys rubens</i>				o	o	o	o				o	o	o		o	o	o	o	o	
<i>Polysiphonia stricta</i>			o	o		o	o	o		o	o				o	o	o	o		
<i>Porphyra miniata</i>		o	o	o	o	o	o	o		o	o	o			o		o	o		
<i>Porphyropsis coccinea</i>				o		o														
<i>Rhodochorton purpureum</i>				o																
<i>Rhodophysema elegans</i>											o									
<i>Sphacelaria caespitula</i>				o		o	o					o	o			o	o	o	o	
<i>Ulothrix flacca</i>		o																		
<i>Ulvaria fusca</i>		o	o	o	o	o	o			o					o	o				
<i>Urospora bangioides</i>		o																		
<i>Urospora penicilliformis</i>		o																		
<i>Urospora wormskioldii</i>		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 of 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 *Pseudotoxonium 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	
<i>Diatoms</i>		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	
<i>Ulothrix flacca</i>					0.5	2.0	8.0	12.0	0.5		0.5				
<i>Blidingia minima</i>							1.0		0.5	2.0					
<i>Codiolum sp.</i>								1.0	0.5	0.5	0.5	0.5	0.5		
<i>Enteromorpha prolifera</i>						2.0	1.0		5.0	1.0	3.0		3.0		
<i>Urospora penicilliformis</i>						2.0	8.0	5.0	0.5						
<i>Petalonia fascia</i>					0.5						1.0	8.0	2.0	15.0	
<i>Ectocarpus fasciculatus</i>									0.5			3.0	8.0	0.5	
<i>Porphyra miniata</i>									0.5	0.5	0.5	0.5		0.5	
<i>Alaria esculenta</i>													0.5	11.0	
<i>Antithamnionella floccosa</i>						0.5									
<i>Pseudotoxonium marinum</i>		12.0	1.0		14.0	1.0									
<i>Cyanophyceae</i>			0.5		2.0	0.5	2.0		0.5						
<i>Bangia fuscopurpurea</i>										0.5					
<i>Urospora wormskioldii</i>											3.0	2.0	0.5	0.5	
<i>Petalonia zosterifolia</i>													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
<i>Alaria esculenta</i>		32.5	39.8	16.8		0.3	
Brown filaments		3.1	0.4	56.8	1.7	2.2	0.6
<i>Halosiphon tomentosus</i>		11.6	1.6	0.6	0.1		
<i>Conchocelis</i> sp.							0.3
<i>Delesseria sanguinea</i>					2.1	0.3	
<i>Desmarestia aculeata</i>			1.32			5.2	
<i>Desmarestia viridis</i>			1.3			0.2	
<i>Laminaria hyperborea</i>			10.7		10.1		
<i>Lomentaria orcadensis</i>						0.2	
<i>Lomentaria clavellosa</i>			3.0				
<i>Membranoptera alata</i>			0.1				
<i>Phycodrys rubens</i>			0.4		12.5	1.8	0.3
<i>Polysiphonia stricta</i>		12.6	3.3	1.1	1.7	1.0	
<i>Porphyra miniata</i>		22.4	13.8	0.4			
<i>Porphyropsis coccinea</i>			0.1				
<i>Ulvaria fusca</i>		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 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*, *Strongylocentrotus droebachiensis*, *Lacuna vincta*, *Padina pel-*



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).

lucida. Elsewhere along the basaltic cliffs the algal growth, although less abundant, represents similar main features as on the east coast (Fig. 4)

DISCUSSION

Fucoids are common in the littoral zone in the Vestmannaeyjar archipelago, including Geirfugla-sker, 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

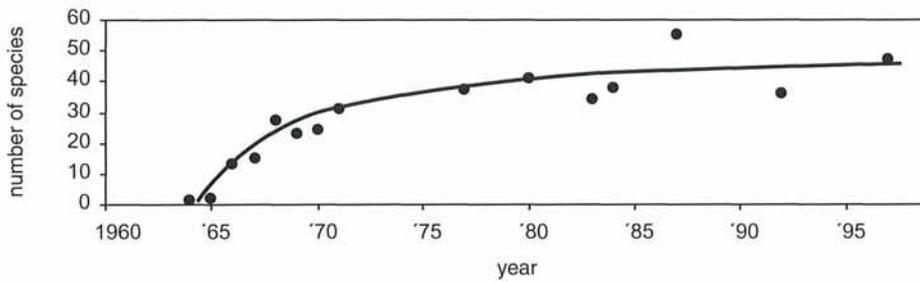


Figure 5. The number of species of seaweed recorded on Surtsey since the beginning of settlement, showing a rapid initial increase in species number and a levelling off after 1970.

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 furoids 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 furoid vegetation. On the new lava in Heimaey furoid 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 Cyanophyceae are omitted.

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

Table 6 (continued).

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

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References

- Dawson, E.Y. 1954. The marine flora of Isla San Benedicto following the volcanic eruption of 1952-1953. *Allan Hancock Foundation Publications*, 16: 1-25.
- Doty, M.S. 1967. Pioneer intertidal population and the related general vertical distribution of marine algae in Hawaii. *Blumea* 15: 95-105.
- Gulliksen, B. 1974. Marine investigations at Jan Mayen in 1972. *K. norske Vidensk. Selsk. Museet, Miscellanea* 19: 1-46.
- Gunnarsson, K. 2000. Benthic marine algal colonisation on the new lava at Heimaey, Vestmannaeyjar archipelago, Southern Iceland. *Surtsey Res.* 11: 69-74.
- Gunnarsson, K. & S. Jónsson 2000. Benthic marine algae of Iceland: revised checklist. *Cryptogamic-Algologie* (in press).
- Jakobsson, S.P. & J.G. Moore 1980. Through Surtsey. Unique hole shows how volcano grew. *Geotimes*, 25: 14-16.
- Jónsson, S. 1966a. Le commencement du peuplement benthique des côtes rocheuses de Surtsey, la nouvelle île volcanique dans l'Atlantique nord. *C. R. Acad. Sci. Paris* 262: 915-918.
- Jónsson, S. 1966b. Initial settlement of marine benthic algae on the rocky shore of Surtsey the new volcanic island in the North Atlantic. *Surtsey Res. Progr. Rep.* 2: 35-48.
- Jónsson, S. 1967. Further settlement of marine benthic algae on the rocky shore of Surtsey. *Surtsey Res. Progr. Rep.* 3: 46-55.
- Jónsson, S. 1970. Meeresalgen als Erstbesiedler der Vulkaninsel Surtsey. *Schr. Naturv. Ver. Schlesv.-Holst. Sonderband*: 21-28.
- Jónsson, S. & K. Gunnarsson 1982. Marine algal colonization at Surtsey. *Surtsey Res. Progr. Rep.* 9: 33-45.
- Jónsson, S., K. Gunnarsson & J.-P. Briane 1987. Évolution de la nouvelle flore marine de l'île volcanique de Surtsey, Islande. *Rit Fiskideildar, J.Mar.Res.Inst. Reykjavík*, 10(1): 1-30.
- Okuda, T. & M. Neushul 1981. Sedimentation studies of red algal spores. *J. Phycol.* 17: 113-118.
- Simon, M.-F. 1985. Présence d'une Phéophycée arctique *Omphalophyllum ulvaceum* Rosenvinge, dans la région de Roscoff (Finistère, France). *Cah. Biol. Mar.* 25 (3): 355-359.
- South, R.G. & I. Tittley 1986. A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. *Huntsman marine Laboratory and British Museum, Natural History, St. Andrews and London*, 76 pp.
- Thórarinnsson, S., Th. Einarsson, G.E. Sigvaldason & G. Elíasson 1964. The submarine eruption off the Vestman Islands 1963-1964. *Bull. Volc.* 27: 435-446.