

Succession and benthic community development in the sublittoral zone at the recent volcanic island, Surtsey, southern Iceland

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ABSTRACT

The island Surtsey was formed south of Iceland during an eruption that lasted from 1963 to 1967. The settlement of marine benthic organisms has been monitored at the island from the beginning. First with visits every year but after 1971 with some years between each visit. Since 1984 standard photographs have been shot of the hard substrate in the sublittoral to monitor species composition, cover and density. Data collected 1997 are presented here. In the shallower part of the sublittoral, algae are dominant. Below 15 m depth the cover and density of animals increases and at 30 m algae have disappeared. At the eastern coast the substrate seems more stable than elsewhere along the coast. Multivariate analysis shows two separate communities. A community with a mixture of *Mytilus edulis*, hydrozoans, *Alaria esculenta* and *Polysiphonia stricta*, primarily found where the substrate is unstable, and a community with *Laminaria hyperborea*, deep water red algae, sponges and *Alcyonium digitatum* on the more stable substrate.

INTRODUCTION

The island Surtsey (63° 18'N, 20° 36'W) was born from seabed at 120 m depth, in a series of eruptions that started in November 1963 and lasted until 1967. It is situated in the Vestmannaeyjar archipelago, about 30 km south of Iceland and 20 km from Heimaey the largest island in the archipelago. Most of the coastline is covered by basaltic rock, except the northern part which is of sand (Calles et al. 1982). Since its formation the island has diminished considerably due to intensive erosion by heavy waves. The break down of the shore is most severe at the south western part of the island. The part of the shoreline where the erosion has been the least is the eastern part (Jakobsson et al. 2000). The seawater around Surtsey is part

of the North Atlantic current with salinity at 35.1. The surface temperatures reaches 12 to 13 °C during late summer and falls to 6 °C in the winter. Visibility of the waters in the area is reduced by the outflow of several large glacial rivers at the south coast of Iceland.

Monitoring the colonisation of benthos started as soon as rocky shores were formed in Surtsey and the first colonizers of the island were found in the littoral zone on a newly formed lava in August 1964 (Jónsson 1966). Soon after the eruption stopped i.e. in 1967 direct sampling of the hard substrate was initiated in the sublittoral zone by diving (Jónsson 1968, Sigurdsson 1968). In the beginning rapidly colonizing species such as mussels, hydroids, filamentous diatoms and the phaeophyte *Alaria esculenta* dominated the substrate. The number of species found at Surtsey increased rapidly the first 10 years but levelled off after 1975 (Jónsson & Gunnarsson 1982, Hauksson 1992). Relatively stable substrate could then be found off the east coast of the island

Two pioneers in the study of the colonisation of marine life at Surtsey, Adalsteinn Sigurdsson and Sigurdur Jónsson recently passed away. They introduced the authors to the studies at Surtsey. This contribution is a tribute to them.

with perennial species growing on top of the biggest rocks and boulders (Jónsson et al. 1987). Due to difficult working conditions, in this extremely wave exposed area, direct studies of community development were difficult. Since 1980 photographs of defined areas of the bottom have been used to monitor the benthic community development.

Already in the beginning of the 80's Jónsson et al. (1987), distinguished two separate seaweed communities in the sublittoral zone at Surtsey, a shallow water community with nearly 100% cover of seaweeds and dominated by *Alaria esculenta* and *Porphyra miniata* growing at 5 to 15 m and a community at 20 to 30 m with much less seaweed cover and dominated by deep water red algae. But significant elements of the marine benthic biota found in neighbouring islands as e.g. crustose corallines, were still missing in Surtsey (Gunnarsson 2000). In this paper we describe the results of a sublittoral benthic community study in Surtsey in 1997.

METHODS

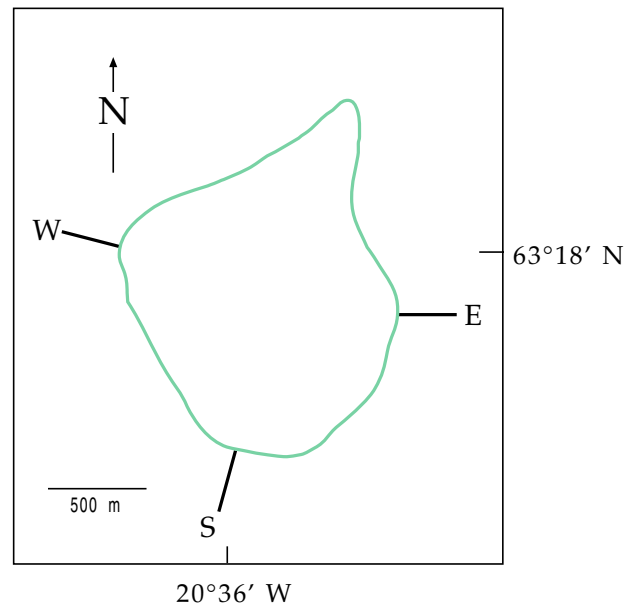
In the 1997 marine expedition to Surtsey three transect were studied to the east, south and west of the island (Fig. 1). Studies were made at 5, 10, 15, 20, 25 and 30 m depths. Pairs of divers visited each station took photographs and collected specimens to assist with the identifications of organisms on the photographs. Samples were hand collected into 1 mm mesh size sampling nets. At each depth station 10 photographs were shot covering an area of 40 x 60 cm of the bottom. Only hard substrate was studied. Due to heavy swell some stations on the south and the west transects could not be visited. The species were determined from fresh samples in the ships laboratory with microscopic examination as necessary. Species that could not be determined onboard were fixed in 5% formalin (algae) or 70% isopropanol (animals) for later identification.

Underwater photographs were projected on a 10 by 10 grid and cover of each species was assessed by counting the number of intercepts hitting the species. Individuals of errant species were counted on the images. As species may overlap the added cover of all sessile species can be much higher than 100%. This is not accounted for by our method which gives maximum cover of 100% for the photographed area. MDS plots of the data were created with MATLAB software, using Jaccard metrics. The metrics were one minus the Jaccard coefficient and percentage of nonzero coordinates that differed between images.

RESULTS

Depth distribution

The substrate in the sublittoral zone at Surtsey consists of rocks and boulders with sand in be-



Figures 1. Surtsey is situated about 20 nautical miles off the south coast of Iceland. Lines shown to the east, south and west of the island represent transects examined in the present study.

tween. Hard substrate could be found at all depths but sand was observed to increase with depth. More sand cover was observed at the southern and western transects than the eastern one. In the shallower part of the sublittoral, algae were dominating on the hard substrate. Below 15 m depth the cover and density of animals increased and at 30 m algae had practically disappeared. On the eastern transect the most abundant algae confined to the shallow water were *Alaria esculenta* and *Porphyra miniata* covering each about 25% of the hard substrate at 5 m and *Polysiphonia stricta* and *Halosiphon tomentosum* covered 13% and 6% of the substrate respectively (Table 1). At 10 m *A. esculenta* and *P. miniata* had reduced their cover by half and similarly *Laminaria hyperborea* and *Desmarestia aculeata* each covered about 12% of the bottom at that depth. At 10 m hydrozoans had the highest cover 17%. At 15 m *A. esculenta* was still prominent with 35% cover and the filamentous brown algae *Ectocarpus siliculosus* had a cover of almost 40%. Below 15 m sessile animals started to dominate the substrate with *Tubularia larynx* and other hydrozoans most common at 20 and 25 m depth. *T. larynx* and *Alcyonium digitatum* dominated at 30 m (Fig. 2). In the deeper part of the sublittoral at 20 to 30 m the only seaweed found were deep water red algal species such as *Phycodrys rubens* and *Lomentaria orchadensis*. The total algal cover at 25 to 30 m was less than 10%.

At the southern and western transects the species number was much lower and algal cover was less. There, hydrozoans were the dominating element with filamentous brown algae, *A. esculenta*, *P. stricta*

Table 1. Mean cover by depth and transect of benthic species with more than 1% cover in the sublittoral zone at Surtsey.

Transect Depth (m)	East							West						South			
	5	10	15	20	25	30	mean	5	10	15	20	25	mean	15	20	25	mean
Hydrozoa (excl. <i>Tubularia</i>)	2,7	17,5	1,9	23,3	34,5	17,0	16,1	1,9	18,6	38,9	51,6	65,9	35,4	7,8	64,9	58,4	43,7
<i>Alaria esculenta</i>	25,1	12,4	35,7	0,7	0,1	0,0	12,3	0,0	2,4	9,7	0,0	0,0	2,4	22,5	0,0	0,9	7,8
<i>Tubularia larynx</i>	0,0	0,0	0,0	2,0	20,1	36,7	9,8	0,0	0,3	1,4	21,3	12,9	7,2	0,0	0,0	0,0	0,0
Filamentous brown algae	6,4	1,5	38,3	2,1	7,8	1,0	9,5	34,3	39,5	43,4	0,0	0,1	23,4	17,2	0,5	1,0	6,2
<i>Porphyra miniata</i>	26,0	12,0	0,2	3,0	0,0	0,0	6,9	0,2	0,1	0,1	0,0	0,0	0,1	0,0	0,0	0,0	0,0
<i>Alcyonium digitatum</i>	0,0	0,0	0,0	0,1	0,0	28,0	4,7	0,0	0,0	0,1	0,0	0,3	0,1	0,0	0,0	0,6	0,2
<i>Desmarestia aculeata</i>	0,0	11,3	0,0	8,1	8,4	0,0	4,6	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,1
<i>Laminaria hyperborea</i>	0,0	12,0	0,0	9,2	0,0	0,0	3,5	0,0	0,0	0,4	0,0	0,0	0,1	0,0	0,9	0,1	0,3
<i>Polysiphonia stricta</i>	13,0	3,4	1,4	0,9	0,2	0,2	3,2	0,0	24,6	1,1	0,0	0,0	5,1	2,2	0,0	0,0	0,7
<i>Delesseria sanguinea</i>	0,0	0,6	0,0	4,1	6,3	0,0	1,8	0,0	0,0	0,9	0,0	1,5	0,5	0,3	0,0	0,3	0,2
<i>Phycodrys rubens</i>	0,0	2,2	0,1	7,3	0,5	0,7	1,8	0,0	0,0	0,5	0,8	0,2	0,3	0,4	0,4	1,0	0,6
<i>Halosiphon tomentosum</i>	6,1	0,3	0,1	0,0	0,0	0,0	1,1	0,0	0,0	0,0	0,0	0,0	0,0	12,1	0,0	0,0	4,0
<i>Ulvaria fusca</i>	2,8	2,5	0,0	0,0	0,0	0,0	0,9	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
crustose Bryozoa on stones	0,1	1,0	0,0	3,4	0,2	0,2	0,8	0,0	0,1	0,2	0,2	0,3	0,2	0,2	0,6	0,3	0,4
<i>Mytilus edulis</i>	0,0	0,0	4,1	0,1	0,0	0,0	0,7	0,0	0,9	18,1	0,0	0,0	3,8	7,5	0,1	0,0	2,5
Bryozoa on algae	0,0	0,0	0,0	0,4	3,1	0,0	0,6	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,1	0,1
<i>Desmarestia viridis</i>	0,0	0,0	0,0	3,2	0,1	0,0	0,6	0,0	1,2	0,0	0,0	0,0	0,2	0,2	0,0	0,0	0,1
<i>Grantia compressa</i>	0,5	0,2	0,0	0,7	1,8	0,0	0,5	0,0	0,4	0,3	1,0	0,8	0,5	0,0	0,2	0,6	0,3
<i>Lomentaria clavellosa</i>	0,0	2,7	0,0	0,1	0,0	0,0	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,5	0,2	0,0	0,2
<i>Chorda filum</i>	1,9	0,0	0,2	0,1	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,0	3,8	0,0	0,0	1,3
Cirripedia	0,2	0,1	0,3	0,1	0,1	1,0	0,3	0,0	0,0	0,4	0,6	0,7	0,3	0,4	0,5	0,3	0,4
<i>Lomentaria orchadensis</i>	0,0	0,8	0,0	0,5	0,2	0,0	0,2	0,0	0,0	0,6	0,7	1,1	0,5	0,0	0,0	0,0	0,0
<i>Ophiopholis aculeata</i>	0,0	0,1	0,0	0,1	0,0	0,0	0,0	0,0	0,0	2,7	0,0	0,0	0,6	0,0	0,2	0,0	0,1
<i>Alaria esculenta juv.</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,0	0,1	0,0	8,6	0,0	2,9

and *Halosiphon tomentosum* abundant at 5 to 15 m and at 15 m *Mytilus edulis* covered nearly 20% of the bottom. Deeper, *T. larynx* and other hydroids, were dominating.

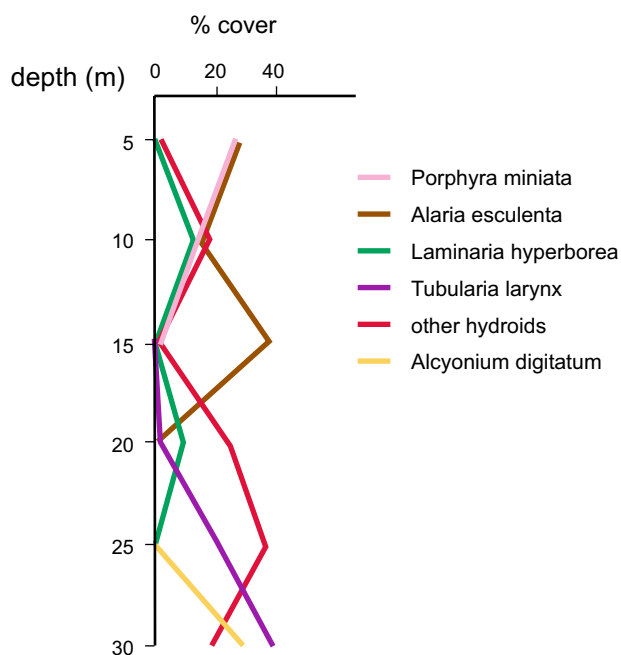


Figure 2. Cover of the most common sessile organisms in the sublittoral zone in relation to depth on the east transect.

Community structure

Multivariate analysis indicate the presence of two separate communities. A community in shallow water with a mixture of brown and green algae and shallow water red algae and a community in deeper water with deep water red algae, barnacles, gastropods, sponges (Fig. 3). Species occurring mainly in the shallow water community include hydrozoans and the algae *Alaria esculenta*, *Porphyra miniata*, *Polysiphonia stricta* and *Halosiphon tomentosum* (Fig. 4). In the deeper community *Laminaria hyperborea*, *Phycodrys rubens*, *Alcyonium digitatum* and *Tubularia larynx* dominate (Fig. 5 and 6).

Multivariate analyses of picture data showed a rather clear separation of pictures from the south and west coast from pictures taken in the east. Also most of the pictures taken at the deeper stations clustered together and the pictures from the shallower stations on the east coast grouped into another less distinct cluster (Fig. 7).

DISCUSSION

The sublittoral zone at Surtsey is extremely exposed to wave action especially at the south and the western part as prevailing winds are south-westerly. The heavy waves, that can reach significant wave heights of about 17 m, have caused rapid breakdown of the island which has been reduced to about half of its original surface area (Viggósson et al. 1994, Jakobsson et al. 2000). Jakobsson et al

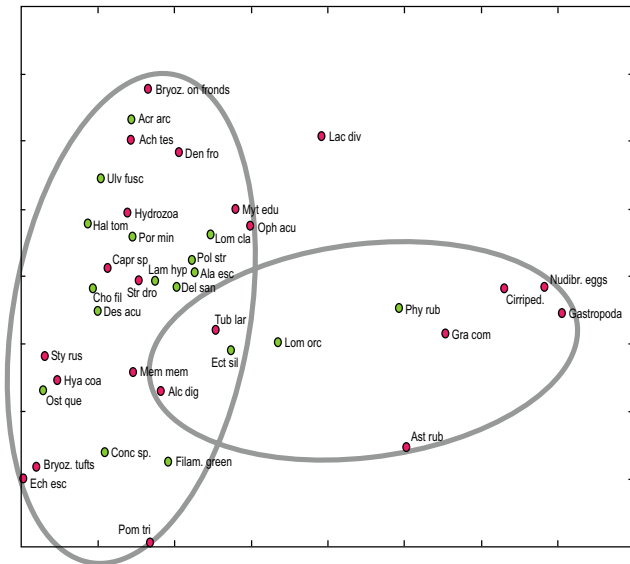


Figure 3. Multidimensional scaling (MDS) plot of the most abundant species in the shallow water (on the left) and deep water community (on the right) encircled by two ellipses. Red dots: animals; green dots: seaweeds.

Key to symbols on the plot: Ach tes, *Achmaea tessulata*; Acr arc, *Acrosiphonia arcta*; Ala esc, *Alaria esculenta*; Alc dig, *Acyonium digitatum*; Ast rub, *Asterias rubens*; Bryoz on fronds, bryozoans forming crusts on algae other than *Membranacea membranacea*; Byoz. tufts, tuftlike bryozoans; Capr sp, *Caprella* sp; Cho fil, *Chorda filum*; Cirriped., includes primarily *Balanus balanus* but also *Balanus hammeri* and *Verruca stroemia*; Conc sp., *Conchocelis* sp; Del sang, *Dellesseria sanguinea*; Den fro, *Dendronotus frondosus*; Des acu, *Desmarestia aculeata*; Ech esc, *Echinus esculentus*; Ect sil, *Ectocarpus siliculosus*; Filam. green, *Urospora* sp.; Gastro-poda includes *Gibbula tumida*, *Margarites groenlandicus*, *Margarites helicinus*, *Nassa incrassata*; Gra com, *Grantia compressa*; Hal tom, *Halosiphon tomentosum*; Hya coa, *Hya coarctatus*; Hydrozoa; several species of hydrozoans; Lac vin, *Lacuna vincta*; Lam hyp, *Laminaria hyperborea*; Lom cla, *Lomentaria clavellosa*; Lom orc, *Lomentaria orcadensis*; Mem mem, *Membranipora membranacea*; Myt edu, *Mytilus edulis*; Nudibr. Eggs, nudibranch eggs; Oph acu, *Ophiopholis aculeata*; Ost que, *Ostreobium quekettii*; Phyrub, *Phycodryis rubens*; Pol str, *Polysiphonia stricta*; Pom tri, *Pomatoceros triquetter*; Por min, *Porphyra miniata*; Str dro, *Stroglyocentrodus droebachiensis*; Sty rus, *Styela rustica*; Tub lar, *Tubularia larynx*; Ulv fusc, *Ulovaria fusca*.

(2000) predict that the islands recession will continue at a relatively fast albeit diminishing rate for more than a century to come. Gradually the lava covering the southern half of Surtsey will disappear and the island will take on the same form as many of the other, older islands, of the Vestmannaeyjar archipelago that are mainly made of palagonite tuff with steep cliffs all-around. In light of the likely geological development, the biota of the littoral and sublittoral zone in Surtsey is probably still far from any final or climax stage in its development.

In the MDS-plots it can be seen that in the shallow sublittoral zone there was little difference between transects. The substrate was dominated by small *Mytilus edulis*, hydroids, *Alaria esculenta*, *Ectocarpus siliculosus*, and *Polysiphonia stricta*. These

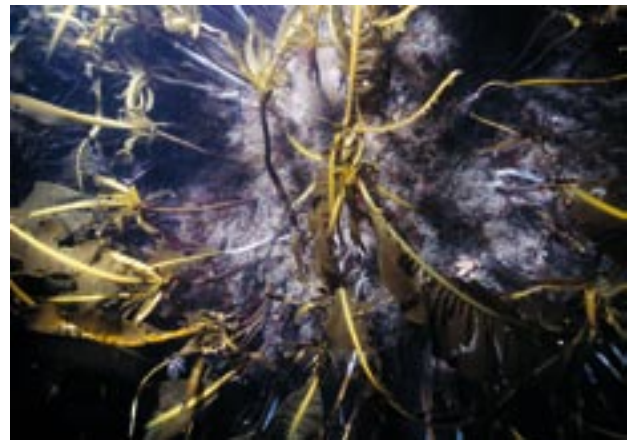


Figure 4. Shallow water benthic community at Surtsey is dominated by rapid colonising species as e.g. in this case hydroids and *Alaria esculenta*. *Lacuna vincta* snails can be seen on the fronds of *A. esculenta* that has grazing marks from the snail.

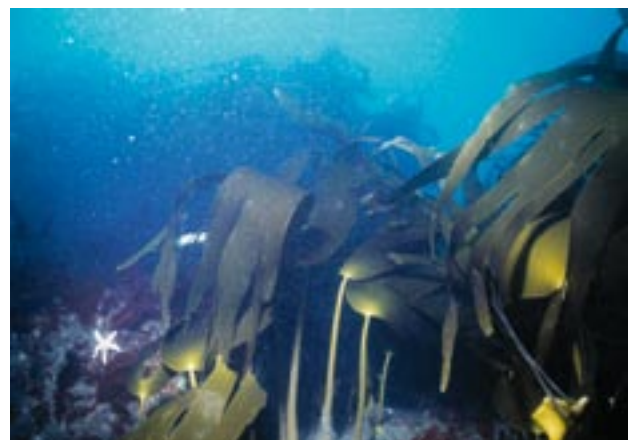


Figure 5. Patches of perennial *Laminaria hyperborea* forest have developed on upper surfaces of large rocks sheltered from moving sand and gravel at the east coast of Surtsey.

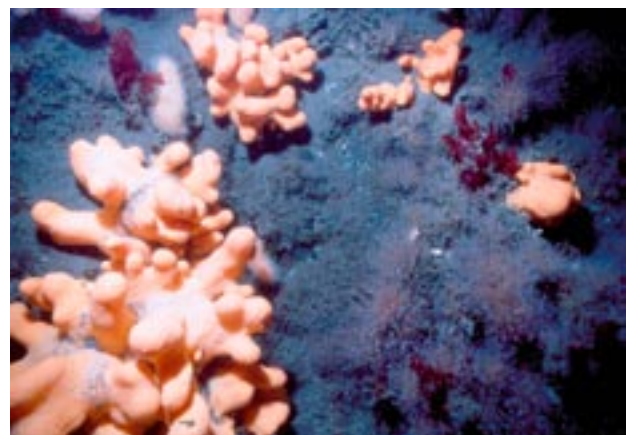


Figure 6. At depths below 20 meters the community is dominated by hydroids, especially *Tubularia larynx* and the octocoral *Alcyonium digitatum*.

were represented by young individuals and the substratum seems to have been recolonized every year by the same group of species since the eruption stopped (Sigurdsson 1968, Jónsson 1968, Jónsson et al. 1987, Hauksson 1992, 2000). The shallow

community is considered to represent an early successional stage. The abrasion caused by sand and gravel put into motion by the waves, especially during winter, is preventing the organisms to become permanently established in the shallow sublittoral zone all around the island. Due to continuous breakdown of the shoreline at the southwestern part of the island, gravel and stones roll down the submarine slopes killing the biota in their path and provide new substrate for colonisation. Here the succession is also at an early stage. The eastern transect differed from the other transects. At middle depths it was characterised by the large perennial *Laminaria hyperborea* growing on the largest rocks and with *Alcyonium digitatum* dominating at the greater depths. This is in accordance with the fact that the substrate at the east coast of Surtsey is more stable than at other parts of the coast. At this transect the species diversity was also highest. These communities are considered to represent later successional stages.

No previous studies on the benthic colonisation of a whole island, isolated from other communities are available. A few studies have been undertaken on colonisation of lava flows that have partly covered areas with established benthic communities. Gulliksen et al. (1980) studied benthic colonisation of a lava flow in the sublittoral zone at Jan Mayen, eight years after its formation. In the shallow part of the sublittoral the fauna found on the new lava was similar to the fauna of the area not affected by the lava but at deeper stations the animal diversity was still significantly lower than on the old ground. Studies of a new lava flow at Heimaey, that was formed 10 years after Surtsey, indicated that the proximity of the established biota greatly affects the colonisation rate (Gunnarsson 2000).

Connell & Slatyer (1977) proposed three models to explain how early successional species could affect their replacement by late successional species. The early successional species could (1) facilitate, (2) tolerate or (3) inhibit the establishment of the late successional species. It is likely that, at Surtsey, space limitation caused by rapid colonisation of mussels and hydrozoans and the shading provided by *Alaria esculenta* might have retarded the settlement and growth of perennial species such as *Laminaria hyperborea* and *Alcyonium digitatum*. Similarly experimental studies on rocky shores indicate that early successional species most often delay the establishment of late successional species (Dean & Hurd 1980, Sousa 1984).

Further influence on the successional process is likely to come from several species of consumers that have increased their abundance in the sublittoral zone in Surtsey. Those are particularly *Asterias rubens* feeding on mussels, nudibranch species feeding on hydrozoans and *Lacuna vincta* feeding on al-

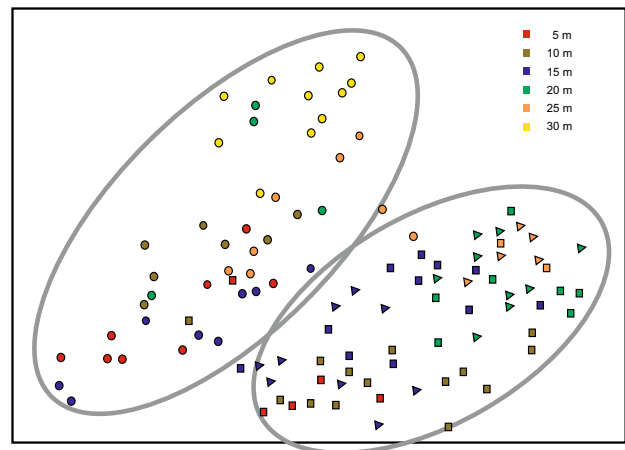


Figure 7. Multidimensional scaling (MDS) plot of pictures from the sublittoral zone at Surtsey in 1997. Circles: east transect; triangles: south transect; squares: west transect.

gae, in particular *Laminaria hyperborea* and *Alaria esculenta* (Hauksson 1992). By selectively feeding on early successional species we expect that these consumers will have accelerated the establishment of late successional species. Similar results have been obtained elsewhere for the littoral and the sublittoral zone (Lubchenco 1983, Kennelly 1983, Kim 1997). The results from Surtsey therefore seem to indicate that the inhibition model of Connell & Slatyer (1977) best describes the successional processes in operation in the sublittoral zone, but that complex interactions between different trophic levels may affect the rate of succession.

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