Microfaunal primary succession on the volcanic island of Surtsey, Iceland

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The island of Surtsey, Iceland, was formed in 1963 by a volcanic eruption. Since then, it has served as a unique natural laboratory for scientists interested in primary succession. In this study we investigated the state of the soil microfauna succession in 1995. We examined locations on the island with different vegetation types (unvegetated soil, soil with one or two plant species, and bird colony soil with a diverse vegetation). We recorded at least 16 nematode taxa and 13 flagellate taxa. Most of these were not reported in previous surveys from Surtsey. On the location with unvegetated soil, ciliates and nematodes were absent and only amoebae and heterotrophic flagellates were found. Most of the protozoan populations we examined were unable to survive salinity levels corresponding to seawater. We therefore conclude that many of soil protozoa populations on Surtsey arrived to the island as airborne cysts brought there from nearby land. However, in the bird colony soil with a high input of salts from the bird droppings, several flagellate species survived and multiplied at seawater salinity. This indicates that the bird colony soil harbours microhabitats where marine flagellate populations have been established.

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Iceland is located on the Mid-Atlantic Ridge. Since the last ice age, a series of submarine volcanic eruptions has created a row of islands south of the main island: the Vestmann Islands (Vestmannaeyjar) (Fridriksson 1994). In November 1963, an eruption formed Surtsey, the youngest naturally formed island in the world (Fig. 1). Volcanic activity on Surtsey continued until 1967. The island is located at 63.4º N, 20.3º W. It has an area of 2.8 km^2, is located 33 km south of the main island of Iceland and is 20 km south-west of Heimaey, the largest of the Vestmann Islands.

During the last 30 years, Surtsey has served as a unique "laboratory" for scientists interested in primary succession (Fridriksson 1989). Plant cover has been established on part of the island. However, the substrate on Surtsey is poor in available nutrients and organic matter, and has an extremely low water-retention capacity. In 1985 gulls, primarily *Larus fuscus* and *L. argentatus*, started nesting on the lava fields. This resulted in a dramatic increase in the nitrogen level, and several more N-demanding vascular plants established themselves in these areas (Fridriksson 1992). The organic input from birds and plants has resulted in increasing populations of bacteria and fungi, which may serve as food for members of the microfauna, mainly protozoa and nematodes.

The first study of soil protozoa from Surtsey dates back to 1968, when at least six species of heterotrophic flagellates were recognized (Schwabe

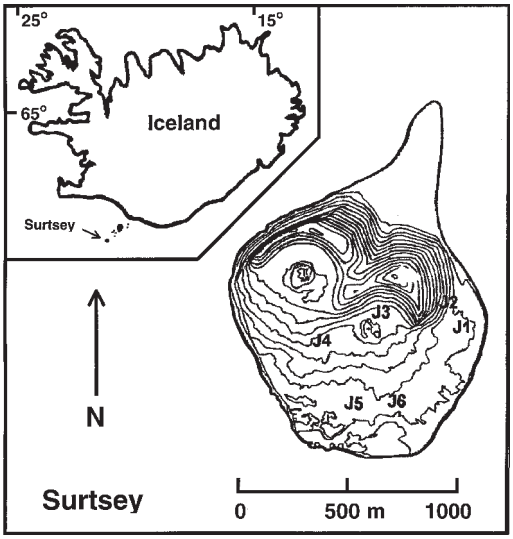

Fig. 1. Map of Surtsey showing the position of the six experimental plots (modified from Jakobsson et al. [1993], with permission from S. Fridriksson). See Table 1 for details.

1970; Smith 1970). Surveys in the 1970s demonstrated that a more complex microfauna was gradually developing (Holmberg & Pejler 1972, 1974). The most recent study of the Surtsey soil microfauna was performed in 1976 (Hedin 1978). This investigation focused primarily on ciliates, but the presence of naked and testate amoebae, flagellates, rotifers and nematodes was reported.

During an expedition in the summer of 1995, six permanent plots for survey of the soil fauna were established, and the microfaunal composition in them was investigated. In this paper we deal with successional aspects of the heterotrophic flagellate and nematode communities in the Surtsey soil.

Materials and methods

Sampling

Sampling sites (Fig. 1) were chosen to provide a plant community gradient of increasing complexity. The plots (3 x 3 m) can be classified in three groups according to their vegetation: unvegetated soil (J4), *Honckenya* communities (J1-J3), and bird colony plots (J5, J6) (Table 1). The position of the plots is given with reference to the plots established for botanical surveys by Magnusson et al. (1996), as well as the coordinate system that divides the island into 100 x 100 m quadrants (Fridriksson 1992). Perpendicular distances to the nearest coastline are also indicated (Table 1).

Samples were taken on 19 July 1995. A 4 cm wide plastic tube was pressed into the soil to a depth of 5 cm. Sub-samples were taken at 10 randomly chosen spots at each plot. The soil samples were transferred to airtight plastic bags and stored at 5 ºC prior to analysis.

C/N content

Five mg air-dried, sieved (2 mm) soil from each sub-sample (N = 10) placed in tin capsules (0.07 ml) was analysed in a C/N-ANALYZER (NA 1500, Carlo Erba instruments) using d-phenylalanine as a standard.

Nematodes

Nematodes were extracted by a modified Baermann wet-funnel system (O'Connor 1962) from a 20 g soil portion from 5 of the 10 sub-samples collected at each site. The tubes connected to the funnels were emptied after 24 h and 48 h. No further nematodes appeared after 48 h. The nematodes were stored in a 4 % formaldehyde solution at 5 °C. Nematodes were examined using a Wild light microscope equipped with Camera Lucida (bright field, 400 or 1000× magnification) to the lowest possible taxonomic level. For each subsample, all nematodes were examined if less than 100 specimens were present. If the sample contained more than 100 individuals, a representative sample of 100 worms was examined, while the rest of the sample was scanned for new species. The literature used for the nematode identification included Anderson (1968), Andrássy (1958, 1976, 1981, 1983), Bongers (1988), Goodey (1963), Maggenti et al. (1987), Sachs (1949) and Sudhaus (1976).

Protozoa

A qualitative examination of the protozoa in the samples was done as follows. Soil from the 10 sub-samples from each plot was thoroughly mixed. Raw cultures were then prepared from

50 mg soil portions (fresh weight) and 10 ml liquid medium in sterilized Nunclon™ 50 ml tissue culture flasks. The liquid media used for the raw culture incubations were mixtures of "freshwater" (Modified Neff´s amoebae saline; Page 1988) and artificial "seawater" (Finley 1930). The final seawater concentrations in the incubations were 0, 10, 30 and 100 %.

Three replicate raw cultures were prepared from each plot for each of the four seawater concentrations. A sterilized wheat grain was added to each culture as a food source (Vørs 1992). Cultures were kept at 15° C, in darkness. After one, two, three and four weeks the culture flasks were inspected using a microscope with inverted lens (Olympus IMT2, 600 × magnification phase contrast). Further details on individual cells were examined using an Olympus BX50 microscope equipped with phase and interference contrast at 1000 × magnification. Flagellates were assigned to the lowest taxonomic level possible on a routine basis; critical identification of difficult taxa was usually not attempted. Some cells remained unidentified, and were not included in the results. The presence of ciliates and amoebae was noted.

Statistics

Results were tested statistically using a Kruskal-Wallis ANOVA on ranks, and all Pairwise Multiple Comparison Procedures using Tukey Test. One-way ANOVA and all Pairwise Multiple Comparison Procedures using Student-Newman-Keuls Method were performed to test for significant differences between the three vegetation types: bare soil (J4), *Honckenya* (J1, J2 and J3) and the bird colony (J5 and J6). The statistical tests were performed using SigmaStat® 2.0 from SPSS Inc.

Results

Soil

Soil carbon and nitrogen content in the six plots are presented in Table 2. The soil samples from site J6 (bird colony B) consisted primarily of roots and plant residues, and it was impossible to separate an appropriate soil fraction. Therefore, the level of soil carbon and nitrogen was not determined in this plot. Nitrogen was below detection

Table 1. Characterization of the six examined localities and their position in relation to the botanical plots defined by Magnusson et al. (1996) and the quadrant system of Fridriksson (1992).

Plot	Characterization	Position in relation to the botanical plots	Location in quadrant system	Perpendicular distance to the nearest shoreline	Plant species at the sampling site
J4 Unveg. soil.	Control site. Unvegetated soil. Bare sand. Some root material found in the soil sample.	Ca. 200 m north-west of plot 11	O10	300 m, southern cliff	
J2 *Honckenya* 1970	Eastern slope, 20º. Sand with *Honckenya* patch est. in 1970.	208º, 18 m south of plot 15	L17	200 m, eastern shore	*Honckenya peploides*
J3 *Honckenya* 1974	Southern slope, 15º. Sand with *Honckenya* patch est. in 1974. Some *Fulmarus glacialis* nesting nearby.	36º, 12 m south of plot 12	L13	550 m, eastern shore	*H. peploides*
J1 *Honckenya–Elymus*	Sand with a *Honckenya–Elymus* association est. in 1970. Some *F. glacialis* nesting nearby.	160º, 27 m south of plot 13	M18	120 m, eastern shore	*H. peploides, Elymus arenarius*
J5 Bird colony A	Plant association on sand, est. in 1983. *Larus fuscus* and *L. argentatus* nesting since 1986.	318º, 22 m south of plot 1	Q12	250 m, southern cliff	*H. peploides, Poa pratensis, Puccinellia retroflexa, Cochlearia officinales, Stellaria media*
J6 Bird colony B	Soil material is a compact layer (3 - 10 cm) of roots and plant residues on top of the lava field. Plants est. in 1985. *L. fuscus* and *L. argentatus* nesting since 1985.	54º, 21 m south of plot 6	Q13	200 m, southern cliff	*P. pratensis, P. retroflexa*

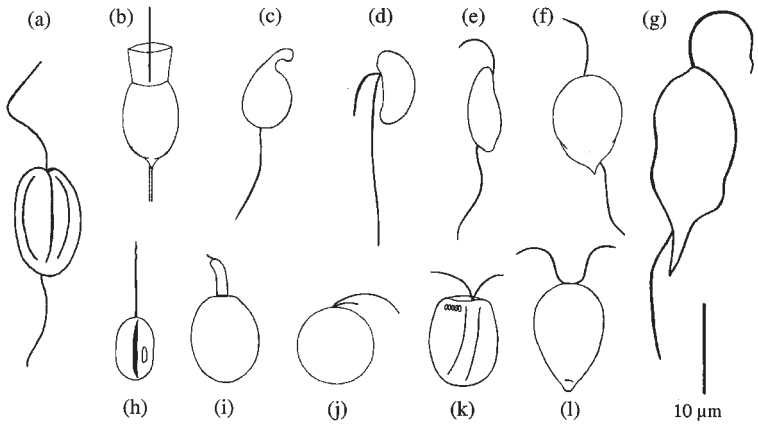

Fig. 2. Flagellate taxa observed in soil incubations from Surtsey: (a) *Entosiphon/Ploeotia* sp.; (b) *Codosiga botrytis* (note that only a minor part of the cell stalk is shown in the drawing); (c) *Rhynchomonas nasuta*; (d) *Bodo saltans*; (e) *Bodo designis*; (f) *Heteromita globosa*; (g) *Cercomonas* sp.; (h) *Petalomonas minuta*; (i) *Apusomonas proboscidea*; (j) *Spumella/Paraphysomonas* sp.; (k) *Goniomonas truncata*; and (l) *Polytoma* sp.

level in the unvegetated soil. The amount of soil nitrogen and carbon was significantly increased in plots with more complex plant communities as compared to sites with less complex communities ($p < 0.05$, one-way ANOVA on arcsine transformed data).

Nematodes

At least 16 different nematode taxa were observed in the soil samples. Basic parameters needed for their identification were measured on selected individuals from each species (Table 3). Mean number and range of the specimens of the recorded nematode taxa at the different sampling sites are listed in Table 4. A few notes are provided below on the nematode taxa where identification was not straightforward.

Protorhabditis cf. *oxyuroides* Sudhaus 1974—The closed peloderan bursa, in combination with absence of a pharyngeal collar, places our specimens in the *oxyuroides*-group (sensu Sudhaus 1976). They are probably best considered as a small strain of *P. oxyuroides* (sensu stricto). All adults came from one sample from plot J6.

Acrobeloides nanus (de Man 1880) Anderson 1968—Two *A. nanus* males were found at site J5. Males of this species have only been reported from very few studies, therefore we include a more detailed description here. The average annule width just behind the stoma region was 1.85 µm. The labial probolae were pointed and the corpus of the pharynx was spindle-shaped. The lateral field was 4 - 5 µm wide and had four lines separated by approximately 1, 2 and 1 µm. In the posterior part (from about anus level) only two lines about 1 µm apart were visible. The lateral fields started 80 µm from the anterior end and ended approximately 9 µm from the tail tip. The 22 µm long spicules were separated and sickle-shaped. The gubernaculum was 11 µm long. The dis-

Table 2. Nitrogen and carbon content in the six examined localities on Surtsey. See Table 1 for locality characterizations. Localities are arranged in order of increasing complexity of the plant communities. Numbers are mean values of 10 replicates. The plots differed significantly with respect to nitrogen and carbon contents ($p < 0.05$, Kruskal-Wallis ANOVA on ranks on arcsine transformed data). Mean values followed by different letters differ significantly ($p < 0.05$, Tukey pairwise comparison). S.e. = standard error, nd = not determined, bd = below detection level.

		J4	J2	J3	J1	J5	J6
%	Mean	bd	0.032a	0.044a	0.114ab	0.293b	nd
Nitrogen	S.e.	bd	0.058	0.001	0.001	0.001	nd
%	Mean	0.117c	0.160cd	0.276de	0.211cd	2.925e	nd
Carbon	S.e.	0.020	0.064	0.001	0.001	1.112	nd

tance from anus to the conspicuous phasmids was 23 µm. Only four lines were present in the lateral field of these males, whereas the females have five lines. According to our knowledge and to Bongers (1988), the number of lines in males of *A. nanus* has not previously been recorded. In other respects the observed males fit the description of this species.

Plectus sp. 1 and 2—Differences in morphometric parameters (Table 3), as well as the position of the amphids in relation to the stoma, suggest that at least two *Plectus* species were present in the samples. Sp. 2 was found only in a single sample from J6.

Panagrolaimus sp.—The corpus:isthmus ratio was 2.0 - 2.1 for the females, and 2.3 - 2.5 for the males. The length of the postvulval sac was 75 - 80 % of the body width, and the length of the gubernaculum was 11 µm. The lateral field of the female had four lines and was 5 µm wide.

Table 3. Morphometric parameters of the observed nematodes: g = gender, n = number of specimens contributing to description, L = total body length, a = body length:body width, b = body length:length of pharynx, c = body length:tail length, c' = tail length:body width at anal opening, st L = greatest length of mouth cavity or length of stylet or spear, st w = greatest width of stoma, a-V = distance from vulva to anus, sp L = length of spicule, V = (distance from anterior end of body to vulva/L) X 100. Unit of measurements is µm. Only juvenile specimens of *Rhabditis* were encountered, so the genus is not listed in the table.

	Character										
	g	n	L	a	b	c	c'	st L	st w	V	a-V/sp L
Bunonema reticulatum	f	1	211	16	2.9	10	2.6	12	1	65	53
Protorhabditis cf. *Oxyuroides*	f	4	481 - 519	18 - 19	3.6 - 4.1	5.3 - 5.5	6.7	19 - 25	2	46 - 51	148 - 182
Protorhabditis cf. *Oxyuroides*	m	3	362 - 492	14 - 19	2.9 - 3.4	13 - 18	7.4	18 - 21	2	-	25 - 28
Mesorhabditis monhystera	f	3	438 - 461	18 - 22	3.3 - 4	5.7 - 6.8	5.8 - 6	14 - 15	3 - 4	70 - 73	62 - 67
Mesorhabditis monhystera	m	1	324	14	3.3	7.5	3.3	-	-	-	21.5
Metaterato-cephalus sp.	f	2	486 - 500	18 - 22	4 - 4.3	7 - 8.1	5.5 - 6.9	5 - 7	3.5 - 4	49 - 53	163 - 179
Acrobeloides nanus	f	4	394 - 480	16 - 19	2.9 - 3.6	12 - 15	1.9 - 2.3	-	-	62	121 - 140
Acrobeloides nanus	m	1	414	22	3.5	14	1.8	-	-	-	22
Plectus sp.1	f	5	349 - 383	19 - 31	3.2 - 3.6	6.6 - 9.3	3.8 - 6.7	10 - 12	2	48 - 52	121 - 139
Plectus sp.2	f	2	964 - 968	19 - 21	4.8	10 - 13	2.7 - 3.8	24 - 27	5 - 6	50	384 - 405
Panagrolaimus sp.	f	2	599 - 622	19 - 21	3.7 - 3.8	12 - 13	2.8 - 2.9	15 - 16	2 - 3	59 - 61	101 - 104
Panagrolaimus sp.	m	2	597 - 620	20 - 21	3.8 - 3.9	13 - 14	2.2 - 2.4	15	-	-	23 - 24
Aphelenchoides/ *Bursaphelenchus* sp.	f	3	454 - 695	26 - 36	-	13 - 15	3.6 - 3.8	12 - 15	-	28 - 31	94 - 169
Aporcelaimidae sp.1	f	1	1006	22	4.5	44	0.74	13	-	45	560
Aporcelaimidae sp.1	m	1	728	15	3.8	28	0.79	21	-	-	-
Aporcelaimidae sp.2	f	1	1600	30	4.2	29	1.6	-	-	52	712
Eumonhystera sp.	f	3	322 - 327	29 - 33	4.2 - 4.5	3.4 - 3.8	14 - 15	-	-	51 - 55	58 - 64
Teratocephalus terrestris	f	1	429	33	4.5	3.1	11	-	-	48	85
Prismatolaimus sp.	j	1	586	-	-	-	-	6	3	-	-
Tylenchoidea sp.	j	1	750	39	-	8.2	-	10	-	-	-

Aphelenchoides/*Bursaphelenchus* sp.—Since we only observed females of *Aphelenchoides*/*Bursaphelenchus*, it was impossible to discriminate between the two genera (Bongers 1988).

Aporcelaimidae sp. 1 and 2—The specimens in the samples differed with respect to tail morphology. They had either a conical-pointed tail or a conical-rounded tail. This indicates that at least two species were present.

Tylenchoidea sp.—The low lips, which are not separated from the head by a constriction, the pharynx, which does not overlap the intestine, the ad-anal bursa and the conical tail place the specimen within either the Anguinidae or the Tylenchidae.

With the exception of *Aphelenchoides*, Aporcelaimidae, and Tylenchoidea, the taxa listed in Table 4 are all considered bacterial feeders (Boström & Sohlenius 1986; Yeates et al. 1993). The largest number of nematode genera as well as individuals in our samples are bacterial feeders (Table 4). *Aphelenchoides* comprises nematodes, which feed on hyphae as well as plants

Table 4. Bongers (1990) maturity index (c - p), mean number and range of different nematode taxa in 20 g soil samples (ww), and Shannon diversity index. Nematodes were extracted from five sub-samples from each of the six examined localities on Surtsey (see Table 1). Localities are arranged in order of increasing complexity of the plant communities.

Bongers (1990) c - p	J4	J2	J3	J1	J5	J6
Bunonema reticulatum[a] 1	-	-	-	-	-	+
Protorhabditis cf. *oxyuroides* 1	0	0	0	0	10.5 (0 - 40)	86 (0 - 410)
Mesorhabditis monhystera 1	0	2 (0 - 10)	3 (0 - 15)	874 (0 - 4345)	0	0.8 (0 - 4)
Rhabditis sp. 1	0	0	0	0	2 (0 - 10)	0.4 (0 - 2)
Metateratocephalus sp. 3	0	0	0	0	49 (10 - 105)	0
Acrobeloides nanus. 2	0	42 (10 - 60)	32 (0 - 110)	28 (0 - 90)	511 (158 - 960)	32 (2 - 60)
Plectus ssp. 2	0	14 (0 - 40)	4 (0 - 10)	41 (0 - 140)	32 (0 - 80)	15 (0 - 50)
Panagrolaimus sp. 1	0	58 (0 - 140)	1 (0 - 5)	6 (0 - 30)	60 (0 - 180)	81 (1 - 370)
Aphelenchoides/ *Bursaphelenchus* sp. 2	0	0	2 (0 - 10)	19 (0 - 95)	0	8.6 (0 - 30)
Aporcelaimidae spp. 5	0	0	0	0	90 (15 - 180)	12 (0 - 45)
Eumonhystera sp. 2	0	2 (0 - 10)	0	0	9 (0 - 45)	0
Teratocephalus terrestris[b] 3	-	-	-	-	-	+
Prismatolaimus sp. 3	0	0	3 (0 - 15)	2 (0 - 10)	75 (0 - 160)	4.4 (0 - 20)
Tylenchoidea sp. 2	0	2 (0 - 10)	0	0	0	0
Nematoda total	0	120 (15 - 250)	45 (0 - 150)	970 (0 - 4700)	838 (460 - 1490)	240 (70 - 1170)
Shannon diversity index	-	1.17	1.04	0.45	1.35	1.55
MI (Bongers 1990)		1.5	2.0	1.1	2.4	1.3

[a] *Bunonema reticulatum* was not included in total number of nematodes since the extraction method did not allow quantification of this genus.

[b] *Teratocephalus terrestris* was not included in total number of nematodes, as the sole recorded specimen encountered appeared when scanning a sample that was not treated quantitatively.

including algae (Yeates et al. 1993). Nevertheless, the genus is often considered fungivorous in ecological studies (Parmelee & Alston 1986; Sohlenius & Sandor 1987). The nematodes in Tylenchoidea are likewise considered plant/fungal feeding. The Aporcelaimidae are generally considered omnivorous (Yeates et al. 1993); they may feed on smaller nematodes and oligochaetes as well as on algae and moss (Small 1987). The relatively large size of the extracted nematodes from Aporcelaimidae (Table 3) results in a higher nematode biomass in the bird colonies than at the other sites.

Protozoa

The distribution of the recorded protozoan taxa at the different sampling sites is listed in Table 5. Information about the highest seawater concentration tolerated by the individual taxa is also listed in Table 5. The recorded flagellates are sketched in Fig. 2. Brief notes concerning the flagellates where identification was not straightforward are provided below. For flagellates with clear identities only size measurements from the observed populations, and references where more detailed information can be obtained, are provided.

Cercomonas Dujardin 1841—Cell length: 10 - 20 µm. We assigned amoeboid, most often gliding cell, with one active anterior and one posterior passively trailing flagellum to the genus (Karpov 1997). The genus is in need of revision, and identification to species level is very difficult, in many cases impossible. We saw several different forms in the samples, which probably belong to different species.

Heteromita globosa (Stein 1878) Kent 1880—Cell length: 10 - 15 µm. More detailed morphological notes on *H. globosa* are provided by Sandon (1927), Robertson (1928) and MacDonald et al. (1977). *H. globosa* may be confused with some other soil flagellates, e.g. *Protaspis simplex* Vørs 1992 and *Sciviamonas terricola* Ekelund & Patterson 1997. See discussion in Ekelund & Patterson (1997).

Paraphysomonas de Saedeleer 1929/*Spumella* Cienkowsky 1870—Flagellates, which must be referred to either *Spumella* or *Paraphysomonas*, occurred abundantly in our samples. Their cells were 5 - 10 µm long with a roundish to elongate outline. They had one long, arched, forward-directed flagellum, as well as one short, often hardly visible, accessory flagellum. *Paraphysomonas* differs from *Spumella* because it has surface scales, whereas *Spumella* cells are naked (Preisig et al. 1991). In most cases, however, *Paraphysomonas* scales are only visible by electron microscopy. *Paraphysomonas vestita* de Saedeleer 1929 with roundish 10 - 20 µm long cells covered with scales visible by light microscopy occurred in some samples. Morphology of the scales was confirmed by electron microscopy (data not shown).

Polytoma sp. Ehrenberg 1838—Cell length 10 - 15 µm. *Polytoma* is treated by Ettl (1983).

Codosiga botrytis (Ehrenberg 1838) Kent 1880—About 10 µm long. The species is discussed in Ekelund & Patterson (1997).

Goniomonas truncata (Fresenius 1858) Stein 1878—Cells about 10 µm long. The taxonomy is discussed by Ekelund & Patterson (1997).

Apusomonas proboscidea Aléxéieff 1924—Cells about 10 µm long. A second species added by Ekelund & Patterson (1997).

Petalomonas minuta Hollande 1942—Cell length: 5 - 10 µm. See Larsen & Patterson (1990) for detailed description.

Entosiphon Stein 1878 /*Ploeotia* Dujardin 1841—Length of observed cells 10 - 15 µm. *Entosiphon* and *Ploeotia* can only be distinguished properly by electron microscopy (Farmer & Triemer 1988). The observed cells probably belong to *Entosiphon sulcatum* (Dujardin 1841) Stein 1878, but the cells were not studied carefully enough to reveal the characteristic surface striation of this species.

Bodo designis Skuja 1948—Cell length: 6 - 11 µm. See detailed description in Larsen & Patterson (1990).

Bodo saltans Ehrenberg 1838—Cell length: 5 - 10 µm. See Vørs (1992) for discussion of nomenclature.

Rhynchomonas nasuta (Stokes 1888) Klebs 1892 —Cell length: 6 - 8 µm. See Larsen & Patterson (1990) for detailed description and discussion.

Protozoan occurrence

Only naked amoebae and four flagellate taxa, but no ciliates were found in the unvegetated soil, whereas six to seven different flagellate taxa were observed in the *Honckenya* soils. In the bird colony soils, 12 to 13 different flagellate taxa were recorded (Tables 5, 6).

The number of flagellate taxa we recorded in the 50 mg soil samples generally decreased as we increased the seawater concentrations in the raw cultures (Table 6). No amoebae were able to survive 100 % seawater and in the unvegetated soil, no flagellates appeared in 100 % seawater. In the soil from the *Honckenya* communities, no ciliates survived 100 % seawater, whereas several ciliate species from the bird colony soils survived that concentration (Table 6). The fraction of seawater tolerant flagellate taxa (Table 6) was significantly higher in the bird colony than in the simpler plant communities ($p < 0.05$, one-way ANOVA on arcsine transformed data). Table 5 indicates the maximum percentage of seawater in which the observed protozoan taxa could survive and multiply. We note a seeming inconsistency with regard to the flagellate taxa which were able to tolerate 100 % "seawater". *Bodo designis, Spumella/ Parphysomonas, Cercomonas* and *Heterometa globosa* were present at all sites, including the unvegetated soil. Tolerant strains of all of these four types exist in some of the plots. But none of the forms are salt tolerant in all of the plots.

Discussion

Our investigation of microfauna in three vegetation types on Surtsey—unvegetated soil, the *Honckenya* community, and the bird colony soil—revealed a strong relationship between plant community type and the number of nematode and flagellate taxa present in the soil. This is probably caused by the increased content of carbon and nitrogen in the soil of the more complex plant communities.

In the unvegetated soil we found neither ciliates nor nematodes (Tables 4, 5). We recognize, however, that the method we used for studying protozoan diversity possibly only reveals part of the ciliate community. Implementation of other techniques, e.g. the non-flooded Petri dish method of Foissner (1987), might have allowed detection of

Table 5. Presence of ciliates, naked amoebae and different flagellate taxa at the six examined localities (see Table 1). x: Specimens of this type of organism were present; s: specimens of this type of organism capable of survival in 100 % seawater were present. The salt tolerance limit for the different types of organisms is indicated (max. % seawater). Localities are arranged in order of increasing complexity of the plant communities. Nearest waterline: * = southern cliffs; # = eastern beach.

	Max. % seawater	J4	J2	J3	J1	J5	J6
Distance to waterline		300 m*	200 m#	550 m#	120 m#	250 m*	200 m*
Ciliates	100 %		x	x	x	x s	x s
Naked amoebae	30 %	x	x	x	x	x	x
Flagellates							
Bodo designis	100 %	x	x s	x	x	x s	x s
Heteromita globosa	100 %	x	x	x s	x	x	x
Cercomonas spp.	100 %	x	x	x	x	x	x s
Spumella/Paraphysomonas	100 %	x	x	x	x s	x s	x s
Paraphysomonas vestita	100 %					x s	x
Polytoma sp.	100 %		x	x	x	x s	x
Codosiga botrytis	0 %		x		x		x
Goniomonas truncata	30 %			x	x	x	x
Apusomonas proboscidea	10 %					x	x
Petalomonas minuta	30 %					x	x
Rhynchomonas nasuta	100 %					x s	x s
Entosiphon/Ploeotia	30 %					x	x
Bodo saltans	100 %					x s	x s
Mean no. of taxa per culture		2	4	4	5	12	13

ciliates in the unvegetated soil, e.g. the mycophagous, autochthonous ciliates (Petz et al. 1985, 1986). The four flagellate types, *Bodo designis, Spumella/Paraphysomonas, Cercomonas* spp. and *Heterometa globosa*, which were present in the unvegetated soil are all extremely common flagellates, which are found in practically all sites all over the world (Sandon 1927; Foissner 1991; Ekelund & Patterson 1997; Ekelund unpubl. data). The amount of soil organic matter needed to maintain populations of these forms is probably much lower than the amount needed to support ciliate and nematode populations (see Griffith 1990). We attribute this to food limitation, as the small flagellates are able to survive and divide in patches containing relatively few bacteria, whereas the larger ciliates and nematodes require much more bacteria to produce a new generation. Furthermore, the soil flagellates are able to remain in the soil as cysts for long periods. This factor also reduces the need for food. It has been demonstrated that Antarctic flagellates are able to maintain large populations, though they are only active for extremely short periods. Most of the time is spent in the inactive encysted stage (Hughes & Smith 1989). This is probably also the case in the unvegetated soil of Surtsey. Nevertheless, we lack exact information because no reliable methods exist to discriminate between active and encysted flagellates (Foissner 1987; Ekelund & Rønn 1994).

Smith (1970) found four species of heterotrophic soil flagellates on Surtsey in 1968 (*Oikomonas termo*, *Phalansterium solitarium*, *Sainouron mikroteron* and *Helkesimastrix faeicola*). The same year, Schwabe (1970) found two *Petalomonas* species and a "*Bodo*" sp. In samples taken in 1970, Schwabe & Behre (1972) found *Rhynchomonas nasuta* and several species of *Cercomonas* (termed *Cercobodo* by the authors). The identity of some of the above-mentioned forms is uncertain. *Oikomonas termo* may be synonymous with our "*Spumella*/*Paraphysomonas*" and one of the *Petalomonas* species may be our *P. minuta*. The name "*Bodo*" was previously applied to virtually any non-amoeboid heterotrophic nanoflagellate with heterodynamic flagella. Nevertheless, when the list of heterotrophic flagellates presented in this paper (Table 5) is compared to previous records from Surtsey (Schwabe 1970; Smith 1970; Schwabe & Behre 1972), it seems very likely that the soil flagellate diversity has

Table 6. Total and mean number of flagellate taxa per culture flask in 0, 10, 30 and 100 % seawater solutions from the six examined localities (see Table 1). The fraction of salt tolerant taxa is also indicated. Plots are arranged in order of increasing plant community complexity. The plots differed significantly with respect to nitrogen and carbon contents ($p < 0.05$, Kruskal-Wallis ANOVA on ranks on arcsine transformed data). Mean values followed by different letters differ significantly with respect to seawater concentration ($p < 0.05$, Kurskal-Wallis ANOVA on ranks [Tukey pairwise comparison] on arcsine transformed data). Nearest waterline: * = southern cliffs; # = eastern beach. The fraction of salt tolerant taxa is calculated as the number of taxa, whichs were recorded in 100 % seawater divided by total number of taxa for that particular treatment. The fraction of seawater tolerant flagellate species was significantly higher in the bird colony soils as compared to the simpler plant communities ($p < 0.05$, One-way ANOVA [SNK test] on arcsine transformed data).

		J4	J2	J3	J1	J5	J6
Distance to waterline		300 m*	200 m#	550 m#	120 m#	250 m*	200 m*
0% seawater	Total	4	4	5	7	10	12
	Mean	2.33	3.33	4.33ab	4.67	6.33	9.67b
	S.e.	0.58	0.58	0.58	0.58	1.15	1.53
10 % seawater	Total	3	4	6	6	9	11
	Mean	2.33	1.67	4.67b	4.33	7.67	6.67ab
	S.e.	0.58	2.08	0.58	2.08	1.53	2.08
30 % seawater	Total	3	2	6	5	8	5
	Mean	1.33	0.67	3.00a	3.67	4.33	5.00ab
	S.e.	1.53	1.15	1.00	1.15	1.53	0.00
100 % seawater	Total	0	1	1	1	6	5
	Mean	0.00	1.00	0.33a	0.33	2.67	3.33a
	S.e.	0.00	0.00	0.58	0.00	2.08	0.58
Fraction of salt tolerant taxa		0.00	0.25	0.20	0.14	0.60	0.42

increased during the years. Smith (1970) observed neither naked amoebae, testate amoebae nor ciliates. Holmberg & Pejler (1972) found one ciliate species (*Cyclidium citrillus*). In 1976 Hedin (1978) observed several hymostomes, cyrtophores, scuticociliates and hypotrics. In the enrichment cultures from 1995, we saw ciliates that belong to several major taxonomic groups: colpodids, cyrtophores, haptorids, scuticociliates, hypotrichs and heterotrichs.

Sohlenius (1972, 1974) examined nematode communities on Surtsey. He identified *Acrobeloides nanus*, *Plectus rhizophilus*, *Monhystera filiformis* (=*Eumonhystera filiformis* Andrássy [1981]) and *Ditylenchus* sp. In 1981, Boström (1988) extracted two morphological different populations of the nematode genus *Panagrolaimus* from a herring gull nest collected on Surtsey.

We likewise found *A. nanus* in our study. The single specimen of Tylenchiodea we found may be identical to *Ditylenchus* sp. found by Sohlenius (1974). *M. filiformis* sensu Andrassy 1981, *P. rhizophilus* sensu Maggenti (1961) and the *Panagrolaimus* populations described by Boström (1988) do not, however, conform with the characters of specimens from these genera found in our study. Therefore, we extracted at least 14 nematode species which have never previously been reported from Surtsey. They may have immigrated to Surtsey since the studies of Sohlenius (1972, 1974) and Boström (1988).

Nematodes feeding on roots of vascular plants and fungivorous nematodes are extremely poorly represented in our samples. The rootgall-forming nematode *Subsanguina radicicola* is known from *Elymus arenarius* plants on Iceland (Siggeirsson & van Riel 1975). No rootgalls were observed during microscopical inspections of *E. arenarius* roots from the *Honckenya–Elymus* plot. Neither were free-living juvenile specimens present in the samples.

Some groups of nematodes seem to be completely absent on Surtsey. This is true for the predatory nematodes in Mononchoidea, Diplogasteroidea and Nygolaimimoidea and (with the exception of *A. nanus*) the bacteriovorous nematodes in Cephalobidae. Neither have the many specialized diplogasterid bacteriovorous species, which are found in strongly saprobic environments, been reported from Surtsey. With the possible exception of the bacteriovorous diplogasterids, members of these groups are present in beach ecosystems (Yeates 1968; Bussau 1990). Such systems are comparable to the unvegetated and the *Honckenya* sites on Surtsey. In addition to beach habitats, the present study also included bird colonies. Our samples, therefore, were expected to contain an even wider range of forms than the samples of Bussau (1990) and Yeates (1968). The absence of several common nematode groups on Surtsey is probably attributable to the fact that they have yet to arrive and settle successfully in the suitable habitats that are now present.

The patchy spatial distribution of the nematodes (note the ranges in Table 4) presumably reflects a distribution of the nematode habitats (food sources) in "hot spots". These are most likely related to bird droppings, food spills or bird cadavers, which offer a sudden burst of available nutrients of a low C:N ratio. However, the "hot spots" will change radically during decomposition and must be considered a very unstable resource, and hence be a typical habitat of *r*-strategists. *Protorhabditis* cf. *oxyuroides*, *Mesorhabditis monhystera*, some *Panagrolaimus* species and *A. nanus* are *r*-strategists, i.e. habitat generalists with good reproduction potentials (Sohlenius 1973; Sudhaus 1976) typically found in such habitats.

Teratocephalus terrestris (Andrássy 1958), *Bunonema reticulatum* (Sachs 1949), many of the Plectidae (Maggenti 1961), some Aporcelaimidae (see Small 1987), species of *Eumonhystera*, *Tylenchus*, *Acrobeloides* (Gadea 1988), *Metateratocephalus* (Bongers 1988) and *Aphelenchoides* (Georgievska 1990) have been associated with moss. Moss is a persistent environment, relatively stable with respect to the amount and quality of food offered to the nematode society. Therefore, moss-associated habitats will generally favour *K*-strategists, while bird-associated habitats will favour *r*-strategists.

We have calculated the maturity index (MI) of Bongers (1990) for the nematodes at the five sites (Table 4). The MI values range from 1.1 to 2.4. The highest MI value (2.4) was found at one of the bird colony sites (J5). The value at this site is mainly the result of the high abundance of *Acrobeloides nanus* and Aporcelaimidae. *A. nanus* is a generalist and is probably associated with the bird debris at this site, whereas the nematodes of Aporcelaimidae most likely are associated with the moss layer, which was very dense at this site (J5). The lowest MI value (1.1), which was found at the *Honckenya–Elymus* site (J1), was a result of a high abundance of *Mesorhab-*

ditis monhystera at this site. The occurrence of *M. monhystera* is probably caused by droppings from the *Fulmarus glacialis* nesting nearby. Consequently, we suggest that the MI values of the sites simply reflect the balance between moss and bird debris related nematode species. The Shannon diversity index gives an integrated measurement of the number and frequency of species, and seems to reflect the succesional stage at the site better than the MI (Table 4). However, both the MI and the Shannon diversity indexes are very sensitive to occurrence of patches with an exceptional high abundance of certain species. Therefore, the successive state of the sites is better illustrated directly by the type, number and frequency of species as well as the lack of potential inhabitants of the sites.

The origin of the protozoa and nematodes on Surtsey

Protozoa are dispersed as cysts via the air (Kingston & Warhurst 1969; Lawande 1983). The soil protozoa on Surtsey may have reached the island in this manner. An alternative explanation is that they have their origin in the sea (Ponnamperuma et al. 1967). To test these two alternative hypotheses we extracted protozoa from soil samples incubated at different "seawater" concentrations. We had expected a positive relationship between nearest distance to the sea and the fraction of salt tolerant species, but we found no such relationship (Table 6). In the bird colony soils about 50 % of the heterotrophic flagellate taxa tolerated seawater, but in the other vegetation types, only a minority of the heterotrophic flagellates tolerated 100 % seawater. This suggests that most of the soil flagellates on the island originate from other soils—possibly brought to Surtsey as cysts dispersed via the air.

Nonetheless, there was a considerable fraction of salt tolerant flagellate species in the *Honckenya* and particularly the bird colony soils. Samples of Danish field or forest soils incubated in "seawater" in the same manner as described above contained only 0 - 1 salt tolerant species (Ekelund unpubl. data). Our results therefore suggest that part of the protozoa have a marine origin. The bird colony populations could also have their origin in other bird colonies; and may have been brought to Surtsey attached to the feet of the birds. Viable protozoa have even been observed in bird droppings (Bamforth 1980). Birds deposit large amounts of guano and fish debris. The content of salt and other ions in ornithogenic soil may locally be extremely high (Hogg & Morton 1983), and ornithogenic soil may be an acceptable microhabitat for halophile flagellates.

Many nematodes, including *A. nanus* and *Protorhabditis* cf. *oxyuroides* are able to enter a stage of anhydrobiosis, and it has been suggested that they can be dispersed via the air in this condition (Sudhaus 1976; Nicholas & Stewart 1989). This is supported by the finding of *A. nanus* among the first nematodes reported from Surtsey (Sohlenius 1972). Some nematodes use beetles, flies or mites as phoretic hosts (Sudhaus et al. 1988) and may have arrived to Surtsey in this manner. Birds with debris attached to their feet may likewise act as vectors for the nematodes. The genus *Eumonhystera* includes species found in both marine, brackish, freshwater and soil habitats. Some of the marine species may be able to invade terrestrial habitats directly from the sea.

During the first years after formation of Surtsey, the microfauna community developed in the humid areas near the thermal vents (Schwabe & Behre 1972), but communities have now been established all over the island. Most of the new species of nematodes and flagellates found in this study were associated with the bird colonies, which rendered the establishment of diverse plant communities possible. The bird droppings fertilize the soil, and provide nutrients for the vegetation, but also for large populations of bacteria and fungi. The combination of high amounts of organic matter, high humidity and a continuous supply of nutrients provide perfect conditions for the microfauna. We hypothesize that it is the soil from the bird colonies which provides the best environment for the microfauna to further increase in diversity.

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