The land-invertebrate fauna on Surtsey during 2002–2006

ERLING ÓLAFSSON & MARÍA INGIMARSDÓTTIR
Icelandic Institute of Natural History, Hlemmur 3, P.O. Box 5320, 125 Reykjavik, Iceland
E-mail: erling@ni.is

ABSTRACT
Formal studies on invertebrate colonizers and establishments on Surtsey started in 1965 and the island was visited regularly for longer and shorter periods till 1984. After a period of sporadic invertebrate studies, yearly visits to Surtsey started again in 2002. Here are presented the results from a five year study period, 2002–2006.

Surtsey is characterized by three kinds of substrates, viz. lava, sand and palagonite rock. The invertebrate collecting is mainly based on pitfall trapping in permanent plots on sand and lava substrates, also informing on the impact of a gull breeding colony that started in the lava field in 1985. Netting and direct picking takes place on all three kinds of substrates of the island. Also, three traps were set up close to the hut and helicopter platform to test for signs of human impact.

Hitherto, 354 species or taxa ranked as species have been found on Surtsey. Thereof 144 are regarded permanent settlers. In 2005 an invasion of flying insects by air mass was witnessed. Transport of invertebrates by birds was probably underestimated in the beginning, but the existence of a number of permanently settled species can hardly be explained differently.

The gull breeding colony was an advantage to the invertebrate diversity on Surtsey. Higher species diversity is found within the colony than outside it and a clear distinction in species composition between plots outside and within the gull colony. Also, a great faunal diversity is within the colony while the fauna is rather homogenous on the sand substrate.

Land-invertebrates have proved to play a very important role in the developing ecosystem on the island, also forming the basis for colonization of invertebrate feeding birds.

INTRODUCTION

Invertebrate colonization and community assembly of islands have been intriguing questions for ecologists. Questions commonly rise on where the invertebrates come from, how they get there and what the community assembly is like. It is a unique opportunity to be able to study young oceanic islands where sterile soil has become invaded by living organisms and formed different kinds of habitats. Colonization of invertebrates on young volcanic islands has been studied on Krakatau Island between Java and Sumatra in Indonesia (e.g. Thornton & New 1988), Long Island near Papua New Guinea (Edwards & Thornton 2001), Nishinoshima Island south of Japan (Abe 2006) and Surtsey Island, south of Iceland.

The first land-invertebrate, the midge *Diameza zernyi*, was found on Surtsey in 1964 (Fridriksson 1964, Oliver 1965). In 1965, while the volcano was still erupting, Surtsey was protected and reserved for scientific research. Organized studies on land-invertebrates started immediately and for gaining knowledge on the nearest invertebrate source, collections were also made on other nearby islands

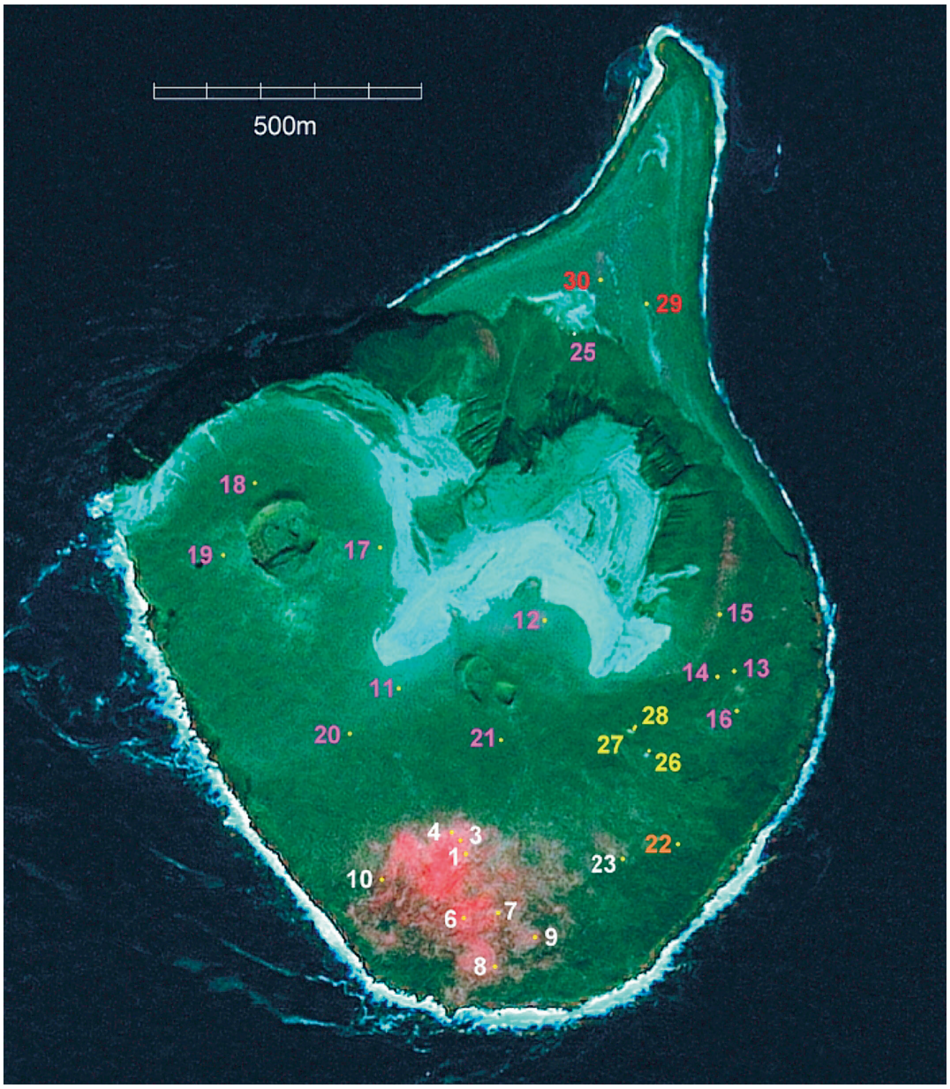

Fig 1. Plots for pitfall trapping invertebrates on Surtsey 2002–2006. Colours indicate different types of surface; white = lava with gull colony; purple = sand-filled lava; orange = bare lava; red = sandy spit; yellow = human effect study. Infra-red SPOT 5 image from July 16, 2003. Dense vegetation appears in red colour, educing the gull breeding colony.

(Vestmannaeyjar) as well as in the closest coastal region of mainland Iceland (Lindroth *et al.* 1973). During 1965–1974 invertebrates were collected every summer on Surtsey, followed by visits during the summers of 1976, 1978, 1981 (Lindroth *et al.* 1973, Ólafsson 1978, 1982, Bödvarsson 1982) and 1984. The research during these first two decades (1964–1984) resulted in a list of 193 species of land-invertebrates found on the island.

Several pairs of lesser black-backed gulls (*Larus fuscus*) and herring gulls (*L. argentatus*) started a breeding colony on Surtsey around 1985. The gull colony increased gradually during the following years. This resulted in a breakthrough in plant succession (Magnússon & Magnússon 2000). Unfortunately the process initiated by the breeding gulls was not followed up by entomological studies until 1995, when soil-invertebrates were explored (Gjelstrup 2000, Sigurdardóttir 2000).

In 2002, invertebrate studies started again on Surtsey. The aim was to follow up the status of invertebrate colonization and the development of invertebrate communities on different substrates in relation to other environmental factors.

METHODS

Study area

In 2004 the constantly eroding Surtsey Island (Fig. 1) covered 1.4 km^2 of land, what was left of a 2.7 km^2 island at the end of the eruption in 1967 (Jakobsson *et al.* 2007). Surtsey is located 32 km off the south coast of mainland Iceland and 4.8 km from the nearest small island, Geirfuglasker, in the Vestmannaeyjar archipelago.

The island is characterized by three kinds of surfaces, e.g. palagonite rock, lava and sand. There are two hills made of palagonite rock mostly devoid of vegetation. The lava makes the slopes and flats south and east of the hills. Part of the lava was colonized by gulls which influenced the plant colonization and succession process so now it has rich vegetation (Magnússon & Magnússon 2002, Magnússon & Ólafsson 2003, Magnússon *et* *al.* 2009). Windblown sand fills the lava adjacent to the hills. On the north side the sea currents have built up a spit from loose material, boulders and sand, originating from the constantly eroding lava and palagonite cliffs (Jakobsson *et al.* 2007). The sandy surfaces are characterized by a beach vegetation community dominated by *Honckenya peploides*, *Mertensia maritima* and *Leymus arenarius* (Magnússon & Magnússon 2002, Magnússon *et al.* 2009).

Data collecting

Each year invertebrates were sampled over a period of four days in July, starting the earliest on 15th and at the latest on 21st of July. The sampling was based on pitfall trapping, netting and direct picking.

Pitfall trapping was performed under the different conditions on the island. In 1990–1995 permanent plots (10x10 m) were set up for measuring vegetation succession. The sites for the plots were originally chosen to represent two of the main surface types considered, sand and lava (the palagonite surface was omitted), including the gull colony (Magnússon & Magnússon 2000). In 2002–2006, 21 of those plots were still in use and in 2005 two additional ones were set up on the spit. To have the opportunity to process results together with other environmental factors measured, each year a pitfall trap (6.3 cm in diameter, and depth of 6.5 cm) filled up to 1/3 with 4% formaldehyde, was placed in the centre of each plot, collecting for approximately 70 hours. The trap sampling has been limited to a single trap within each plot to have as little impact on the fauna as possible on the by law protected island.

For further invertebrate studies four additional plots were selected. One was located on the north side of the hills, i.e. at the base of the spit, where the sandy surface is unstable and vegetation has little chance to develop (a plot formerly used for measuring plants). Three traps were set up to look for signs of human impact; two of them close to the research hut, one under the terrace, the other behind the hut, and one at the helicopter platform near by. Thus a total of 27 pitfall traps have been utilized in this survey. Five categories of plot sites are defined: 1) lava with gull colony; 2) sand-filled lava, no gulls; 3) bare lava, no gulls; 4) sandy spit; 5) human effect study (Fig. 1).

Manual collecting (i.e. netting and direct picking) has also been performed each year to sample invertebrates that seldom are caught in pitfall traps. Netting takes place primarily in the gull colony as many species tend to fly around there but also on the sand and on the palagonite hills. However, netting is not performed within the plots to prevent effects on the vegetation to be monitored. Direct

Table 1. Land-invertebrates, orders and higher taxa, collected on Surtsey during the 2002–2006 surveys; number of specimens collected annually given.

Species groups	**2002**	**2003**	**2004**	**2005**	**2006**	**Total**
Entognatha						
Collembola	2.545	3,386	645	1,684	1,837	10,097
Insecta						
Coleoptera	222	250	361	344	342	1,519
Diptera	431	590	877	1,240	1,429	4,567
Hemiptera	128	72	132	194	143	669
Hymenoptera	42	211	122	131	81	587
Lepidoptera	8	17	11	15	26	77
Neuroptera					2	2
Thysanoptera	405	473	115	575	320	1,888
Arachnida						
Araneae	221	232	558	405	334	1,750
Neomolgus	19	26	10	119	30	204
Acari	1,617	1,762	4,480	1,997	3,481	13,337
Mollusca						
Gastropoda	6	18	16	6	11	57
Annelida						
Oligochaeta	11	3	4	6	11	35
Total	5,655	7,040	7,331	6,716	8,047	34,789

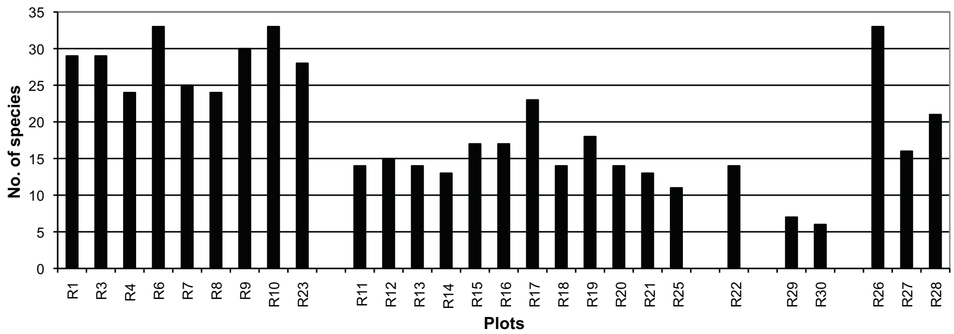

Fig. 2. Land-invertebrates caught by pitfall traps, total number of species (springtails and mites excluded). Plots arranged in five categories, from left: lava with gull colony (9 plots), sand-filled lava (12 plots), bare lava (1 plot), sandy spit (2 plots), human effect study (3 plots).

picking takes place mostly from under stones and under dead birds on the lava and from under driftwood on the spit. Collecting has also taken place around a steaming hot fumarole and in ruins of a lighthouse on top of the island (built in 1973 but no longer in use). The lighthouse has an uncovered door-opening facing north, thus serving as an excellent trap for just arrived flying insects.

Identification

All beetles (Coleoptera), moths (Lepidoptera), thrips (Thysanoptera), lacewings (Neuroptera), spiders (Araneae) and snails (Gastropoda) have been identified to the species level, except for juvenile stages of some. A great majority of flies and midges (Diptera) have been identified to species (Sciaridae and Cecidomyiidae excluded), hemipterans (Hemiptera) to species except for aphids (Aphididae) and hymenopterans (Hymenoptera) either to species or generic level, with several unsolved exceptions. Springtails (Collembola), mites (Acari) and the oligochaete worms of the family Enchytraeidae are still unrecognized.

Some of the older material collected, before 1984, was checked specially and revised in connection with the present work.

Data analysis

DECORANA-ordination (Hill 1979) was used to test the similarities between the pitfall trap samples. From each plot the five year sampling series (2002–2006) was combined to a single data set prior to analyses as samples from a single year are too small to be analysed as such. All species or taxa equivalent to species were considered in the analyses. Also the number of specimens caught, calculated to catch per day (24 hours). Rare species were downweighted.

RESULTS

Annually several thousand specimens have been sampled during the five year period considered. The total material counts 34,789 specimens (including Collembola and Acari), of which 84.5% were achieved by pitfall trapping and 15.5% by manual collecting (i.e. by netting and direct picking).

The species groups considered belong to the large taxa Entognatha, Insecta, Arachnida, Mollusca and Annelida (Table 1, Appendix I). A total of 168 species or species equivalent taxa have been named (Collembola and Acari excluded). The total number is a minimum as some named and not fully treated taxa may include more than a single species (for instance Sciaridae, Aphididae). In such cases the relevant taxon is counted as one species. Of those 168 species, 156 have been collected manually and 83 by pitfall traps, 85 only manually and 12 only by traps.

The invertebrate fauna of different habitats

The lava with gull colony is richest in invertebrate species. Nine plots give an average of 28.3 species and an average daily catch of 17.7 speci-

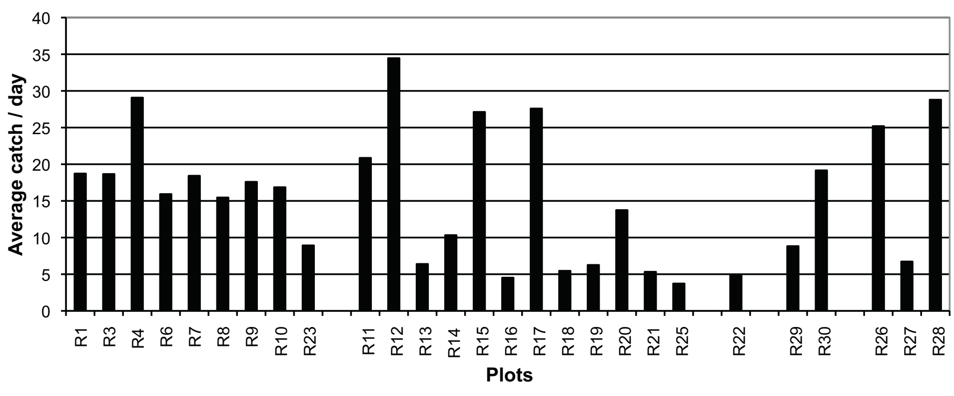

Fig. 3. Land-invertebrates caught by pitfall traps, the average daily catch of specimens (springtails and mites excluded). Plots arranged in five categories, from left: lava with gull colony (9 plots), sand-filled lava (12 plots), bare lava (1 plot), sandy spit (2 plots), human effect study (3 plots).

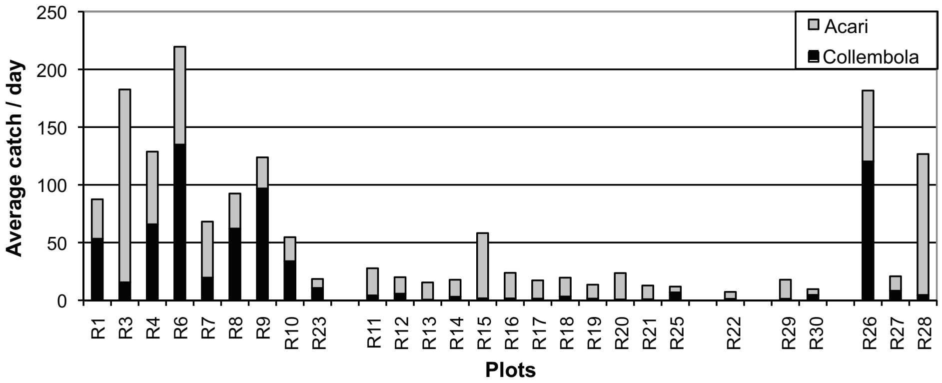

Fig. 4. Land-invertebrates caught by pitfall traps, the average daily catch of springtails (Collembola) and mites (Acari). Plots arranged in five categories, from left: lava with gull colony (9 plots), sand-filled lava (12 plots), bare lava (1 plot), sandy spit (2 plots), human effect study (3 plots).

mens (Figs 2 & 3). These plots show a relative stability in number of species and catch. The catch at plot 4 exceeds the average markedly, with an exceptional number of linyphiid spiders (*Erigone arctica*) caught. Plot 23 is, on the other hand, markedly lower in the same point, the plot being located at the margin of the colony (Fig. 1), thus being under minor influence of breeding gulls.

On the sand-filled lava outside the colony, twelve plots give the average of 15.3 species and the daily catch average of 13.8 specimens (Figs 2 & 3). The number of species is markedly lower than in the gull colony, only one plot approaches the lowest colony plots. Considering the number of species, the sandy plots are comparable mutually. On the other hand the daily specimen catch shows a wide range of results, ranging from 3.7–34.5 specimens. The high scorers are due to a great number of *Thrips vulgatissimus*, dominating in the catches. Plot 25 is the poorest plot on the island, located under extremely unfavourable conditions at the northern side of the hills where surface is so unstable that plants are unable to grow.

The bare lava which is neither affected by gulls nor moving surface sand has been surveyed on a single plot only (plot 22), resulting in 14 species and a poor catch of 4.9 specimens on daily average (Figs 2 & 3).

The sandy spit lies considerably lower over sea level than the sand-filled lava sites and is clearly affected by the vicinity of the beach. The plots are species poor, giving an average of 6.5 species, and 14.0 specimens in average daily catch (Figs 2 & 3). It must be kept in mind that the results are based on catches from two years only. In daily catch plot 30 slightly exceeds the average of plots within the colony on the lava, which is explained by a great catch of *Thrips vulgatissimus* dominating the catch as in some of the plots accounted for above on the sand-filled lava.

The human effect study by two plots at the hut and one at the helicopter platform give an average of 23.3 species and an average daily catch of 20.2 specimens (Figs 2 & 3). The plot at the helicopter platform (plot 26) gives a species number comparable with the lava with gull colony while the other two, by the hut, are more similar to the sand-filled lava plots. When considering the catch in traps, the plot under the terrace of the hut (plot 27) has the fewest specimens of the three.

As stated springtails and mites have not been identified to species or sorted to any higher taxonomic categories for this report. Still, individuals belonging to these two invertebrate groups have been counted. The results indicate low number in all sandy plots, both on sand-filled lava and on the spit (Fig. 4). Two of the plots for human impact studies show similar number as the plots in the lava with gull colony.

DCA-ordination

The results of the DCA-ordination show a clear distinction between plots outside and within the gull colony (Fig. 5). Also, a great faunal diversity is indicated within the colony and the invertebrate fauna is affected by the human activity around the hut.

The results show little variation when plots on sandy soils are considered separately, independent on location on the island. The two plots on the spit (29 and 30), that only were sampled for two years, are the extreme outsiders furthest to the left on ordination Axis 1.

The plots within the gull colony are separated on the right side of the graph from sandy plots. They are also more distributed than the sandy plots. This variation is best explained by the gradually developing vegetation. Plots 1–6 are located in the oldest part of the colony. The locations of plots 7–9 are near this oldest core, but plot 10 and plot 23 are at the margins, gradually being incorporated into the colony, plot 10 well ahead. Plot 22, the only bare lava plot outside colony, is placed close to plot 23 in the eastern part of the lava, still unaffected by the breeding gulls.

The human effect study plots 26, at the helicopter platform, and 27, under the terrace of the hut, take positions on level with the marginal plots in

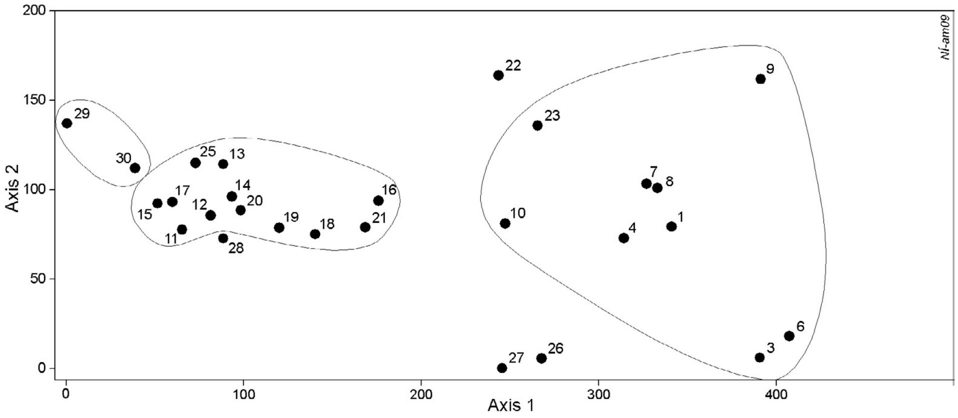

Fig. 5. DCA-ordination results from pitfall trap plots on Surtsey. Encircled from left: sandy spit (2 plots), sand-filled lava (12 plots), lava with gull colony (9 plots); outside circles: bare lava (plot 22), human effect study (plots 26–28). Axis 1 shows 73% of the sample variation and Axis 2 stands for 18%.

the colony, i.e. near the centre of Axis 1, while plot 28, behind the hut, is intermixed with other sandy plots.

DISCUSSION

Dispersal

Several means of transport of invertebrates over open sea to Surtsey have been confirmed and described; 1) by winds or air currents, 2) by sea currents, and 3) by birds (Lindroth *et al.* 1973, Ólafsson 1978).

Aerial dispersal is a favoured explanation for invertebrates (Drake & Farrow 1988, Bell *et al.* 2005, Nkem *et al.* 2006) and flying insects have been shown to be carried along with air masses (Coulson *et al.* 2002a). In 2005 such an invasion was witnessed to Surtsey following northern winds. Numerous individuals were found inside the ruins of the lighthouse and several species not previously

Table 2. Land-invertebrates, orders and higher taxa, collected on Surtsey during the 2002–2006 surveys; total number of species and their evaluated status in 2006.

	Species total no.	Species settled	Status uncertain	Species not settled	Dead in drift only*
Collembola	22	9	5	8	
Protura	1			1	
Diptera	155	45	8	102	
Hymenoptera	41	12	6	23	1
Lepidoptera	21	5	3	13	1
Coleoptera	18	12	4	2	6
Hemiptera	9	6		3	1
Thysanoptera	3	3			
Trichoptera	3			3	1
Neuroptera	2			2	
Mallophaga	1			1	
Siphonaptera	1			1	
Acari	59	41	1	17	
Araneae	14	7	2	5	
Oligochaeta	2	1	1		
Gastropoda	2	2			
Total	354	143	30	181	10*

* Not included in the total number

found on the island were flying around in the gull colony. Some of those species were typical wetland species, e.g. the dipterans *Platycheirus granditarsus*, *Tetanocera robusta*, *Dictya umbrarum* and *Rhamphomyia simplex,* some not capable of surviving on Surtsey due to lack of fresh water on the island.

Invertebrates, such as soil arthropods, can survive long time in sea water (Coulson *et al.* 2002b) and more invertebrate species have been brought to Nishino-shima island by sea than by air (Abe 2006). Invertebrates (springtails, shield bugs, a proturan and mites) have come to Surtsey either floating directly on the surface, hiking with floating objects or in turfs of vegetation and soil (Lindroth *et al.* 1973, Ólafsson 1978). Some species have been found dead in drift only (Table 2).

Invertebrate dispersal by getting a lift with birds has received speculations and some support (Lindroth *et al.* 1973, Smith & Djadjasasmita 1988, Thornton & New 1988, Ashmole & Ashmole 1997, Figuerola *et al.* 2005). When the gulls had established the breeding colony, the importance of birds as transport media became more obvious. The first gull settlers built their nests by plucking mosses around the nesting site, but so it seemed that some of them adopted the act of bringing nesting material from sites outside Surtsey, which led to colonization of new plant species (Magnússon & Magnússon 2000, Magnússon & Ólafsson 2003). Our conclusion is that birds, as transport method, have probably been underestimated by Lindroth *et al.* (1973) and that birds must have carried invertebrates with the nesting material, like aphids and thrips, and most likely also hidden in their feather coats, like springtails, mites, beetles and gastropods; some of which certainly could also have been carried with nesting material. However, dispersal of molluscs by birds to Krakatau has been considered unlikely (Smith & Djadjasasmita 1988) and aerial dispersal suggested for smaller invertebrates like thrips (Thornton & New 1988).

Import of organisms to Surtsey by humans is strictly controlled and it has not been detected that species have been able to colonize due to humans. Two species have been found there, accidentally brought to the island in food supplies, the beetle *Lathridius minutus* and the fly *Drosophila funebris*, neither of which can survive under conditions outside the hut (Jakobsson *et al.* 2007).

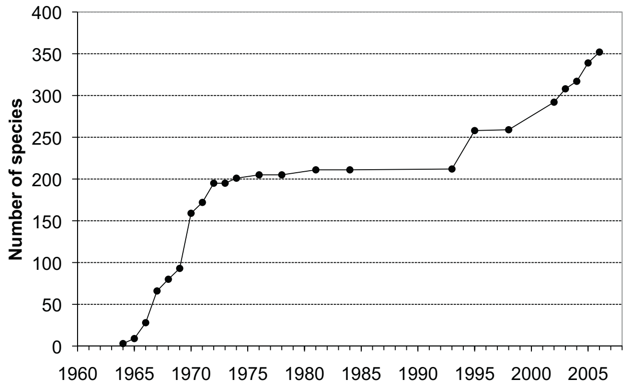

Fig. 6. Land-invertebrate species found on Surtsey, cumulative numbers from 1964–2006 (excluded are eleven species found dead on drift only).

Colonization

Since the first invertebrate was found on Surtsey in 1964 (Fridriksson, 1964, Oliver 1965), 354 species or taxa ranked as species have been listed as found on Surtsey (Appendix I) and as in the case of other young islands the major part of the species in question have a wide distribution (Edwards & Thornton 2001, Abe 2006).

The collecting activity during the first years led to a gradual increase in invertebrate species found (Fig. 6). The more sporadic visits of collectors that followed this active start added only a few species to the list. It should also be kept in mind that during these years the plant succession process was very slow. Species poor beach plant communities were developing in the sandy areas but few new plant species were successful in their colonization attempts (Magnússon & Magnússon 2000, Magnússon & Ólafsson 2003). The soil-invertebrate expedition in 1995 (Gjelstrup 2000, Sigurdardóttir 2000) added 46 species to the list and since the annual visits started again in 2002 gradual additions have been made to the species list (Fig. 6).

In connection with the present work the status of the 171 species obtained during the first 20

Table 3. Land-invertebrates found on Surtsey; number of species during three study periods, 1964–1984, 1995 (soil invertebrates only), and 2002–2006, and their evaluated status for the respective periods.

	1964–1984	1995	2002–2006	Total
Settled species	17	46	99	144
Status uncertain	16		22	29
Not settled	149		52	181
Dead in drift on beach	(11)			(11)

years of studies (1964–1984) has been evaluated, i.e. their status at the relevant survey period. The majority of the species was for the relevant period regarded "not settled" (Table 3). In 2006, 144 invertebrate species are regarded permanent settlers (Table 3, Appendix I). Permanent settlers are here defined as species that have been found under conditions required of the species in question, found annually from 2002 or a later year in increasing number either in traps or netted. Soil animals discovered during the survey in 1995 (Gjelstrup 2000, Sigurdardóttir 2000) are regarded settlers even if not confirmed by a similar survey in later years as most of them were obtained in a great or considerable number in soil. Some of the earlier recorded soil-animal species were not rediscovered during that survey, indicating failed colonization attempts (Gjelstrup 2000).

It can certainly take several years for a population of a settler to grow to a size that is discoverable. Additional 29 species are suspected to be permanent settlers as the conditions required for the species are present on the island, but awaiting further data to approve the actual status is recommended. The remaining 181 species on the list, mainly winged insects, are regarded accidental stragglers to the island, some showing up quite regularly while others are more sporadic. Some of those will have to wait till the ecosystems have developed further, while others, like species with aquatic live forms at some developmental stages or denoted wetland species, will hardly ever find the opportunity to become local citizens on Surtsey.

Invertebrate communities of different habitats

Habitat diversity gives rise to more diverse communities and more species richness than do uniform landscapes. With the gull colony the variety of habitats on Surtsey increased and both the invertebrate fauna and the flora are different within and outside the gull colony and vary more in species composition within and close to the gull colony than outside (Fig. 5; Magnússon *et al.* 2009).

Sand-filled lava and the sandy spit. Both the sand-filled lava and the spit are characterised by a differently scattered *Honckenya peploides*, sometimes accompanied by stands of *Leymus arenarius* (Fig. 7), and nutrient poor soil (Magnússon *et al.* 2009). They are all rather similar concerning invertebrate species composition (Fig. 5). Plots 29 and 30 on the spit are marginal, probably on account of the species poor fauna (Fig. 2), which partly might be affected by only two years of sampling.

Species characterizing the sandy surface are, as on other young and vegetation poor areas, mainly predators and scavengers (Edwards & Thornton 2001, Kaufmann 2001, Hodkinson *et al.* 2004), in this case consisting of beetles, spiders and dipterans. This is the proper habitat for the liniphiid spiders *Meioneta nigripes* and *Islandiana princeps*, also the carabid beetle *Amara quenseli*. The well developed batches of *Honckenya peploides* produce a great number of the thrips *Thrips vulgatissimus*, dominating in the catches. The number of thrips explains the great variety in catches between plots in this habitat, i.e. traps placed within or close to *Honckenya peploides* batches catch numerous thrips (Fig. 3). This similarly explains the high catch at plot 30 on the spit, which is located on a relatively stabilized flat on the inside of the spit with developed *Honckenya* batches (Fig. 8). Plot 29 is closer to the beach and still affected by over-flooding during winter time (Fig. 1).

Human effect study. Plots 26 and 27 are more similar to the plots from the gull colony than other

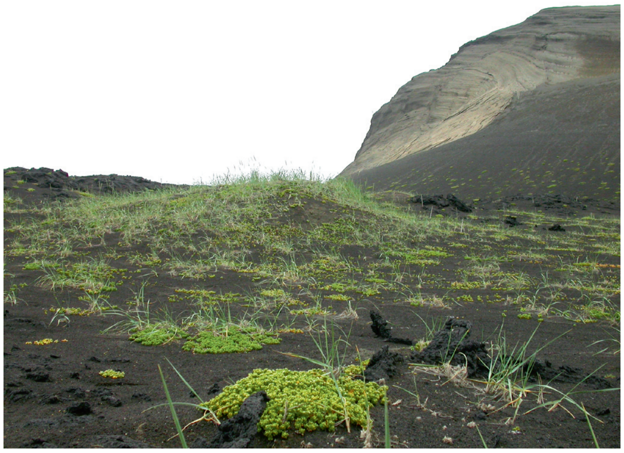

Fig. 7. Sand-filled lava on the eastern side of Surtsey; a beach plant community with *Honckenya peploides* and *Leymus arenarius*. Photo E. Ólafsson, July 11, 2007.

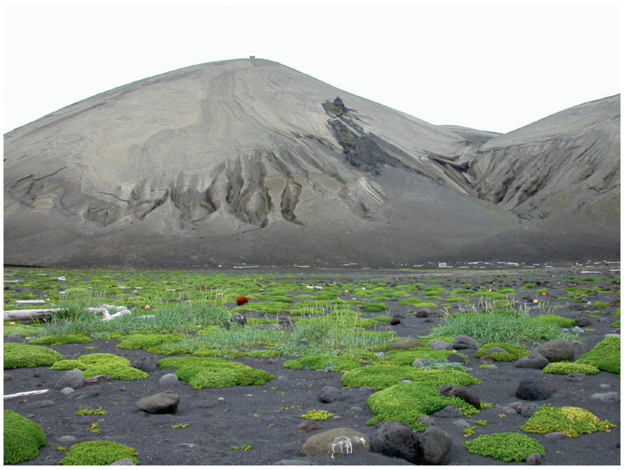

Fig. 8. The sandy flat of the northern spit of Surtsey; a beach plant community with *Honckenya peploides*, *Leymus arenarius* and *Mertensia maritima*. Austurbunki, a palagonite hill, in background. Photo E. Ólafsson, July 11, 2007.

Fig. 9. From the gull colony on Surtsey; *Tripleurospermum maritimum*, *Festuca richardssonii*, *Poa pratensis* and *Leymus arenarius* dominating in luxuriant vegetation. Photo M. Ingimarsdóttir, July 19, 2005.

Fig. 11. The slug *Deroceras agreste*, was discovered in the gull colony on Surtsey in 1998 and has been found regularly since. Photo E. Ólafsson, July 22, 2003.

plots regarding species composition (Fig. 5). The nutrients in soil have not been measured in these plots but we assume those plots are rather nutrient rich. Gulls use the helicopter platform as a roosting site, thus nourishing the soils around it and flourishing the vegetation. Considering plot 26 the species composition and number of species is comparable with plots within the gull colony (Figs 2 & 5). Plot 27 shows a similar tendency but much fewer specimens are caught there, showing more of a typical sandy plot character, also regarding vegetation (Figs 2–4). Still, there must be a reasonable explanation for the plot to be placed beside plot 26 on the ordination graph (Fig. 5). The soil might be richer than generally in this kind of substrate as it is watered by rainwater running from the huts roof and walls, washing off the dust, also from the terrace where gear and supplies are regularly left to stand for undefined hours. Also persons have been caught taking a leak on the spot! Plot 28, behind the hut, is not distinguished from other sandy plots regarding species composition (Fig. 5) but has a high catch of both soil and above ground invertebrates (Figs 3–4). This is probably due to the location of the trap in a well developed batch of *Honckenya peploides* rather than to effects of humans.

Bare lava. The weak information, based on a single plot only, does not allow much discussion. The results indicate that the species composition differs from the sandy substrate fauna even if it similarly has a low number of species and meager general

Fig. 10. The tortricid moth *Eana osseana*, the most common lepidopteran in the gull colony on Surtsey. Photo E. Ólafsson, July 20, 2004.

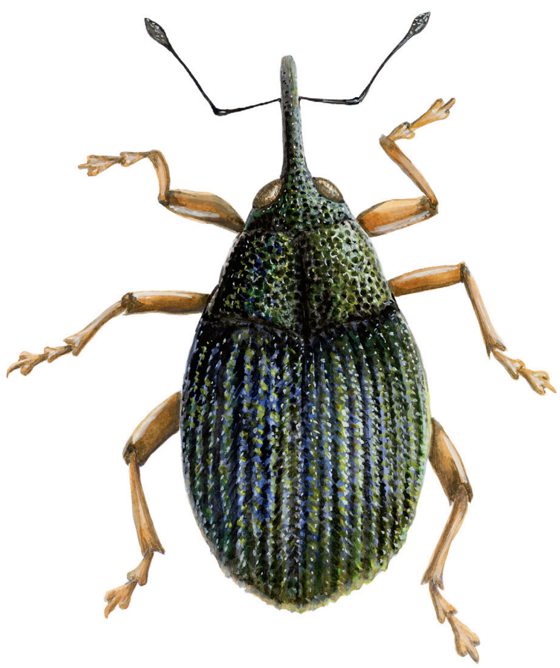

Fig. 12. The weevil *Ceutorhynchus insularis*, a world rarity described in 1971, common on *Cochlearia officinalis* in Surtsey. (The weevil is 2 mm in length). Drawing J.B. Hlídberg.

catch. The fauna seems to be composed of species that have accidentally and randomly drifted in from the nearby margin of the gull colony. Here are found the open surface beetle *Amara quenseli* and the generalist spider *Erigone arctica*, also several dipterans common in the gull colony, like *Dolichopus plumipes*, *Hydrellia griseola*, *Botanophila fugax*, *Delia platura* and *Cynomya mortuorum*. Thus, the bare lava shows a similarity with the nearby margin of the colony (Fig. 5).

Lava with gull colony. Most invertebrate species were found in the gull colony (Fig. 2.) and when compared with the sandy surfaces, the species composition is more diverse (Fig. 5). Soil invertebrates are abundant (Fig. 4) contributing to decomposition of plant remains and formation of organic soil. There are parasitic wasps, both primary and secondary, attacking insect larvae, aphids and spider eggs, and a good number of predators, like the aphid feeding syrphid *Platycheirus manicatus*, the spider *Erigone arctica* and several staphylinid beetles, for instance *Atheta graminicola* and *A. fungi*. Saprophagous dipterans like *Calliphora uralensis*, *Cynomya mortuorum*, *Hydrotaea dentipes*, *Heleomyza borealis* and *Meoneura lamellata* allure decaying bird carcasses.

Invertebrates dependent on this most luxuriously vegetated area of the island (Fig. 9) include the moths *Eana osseana* (Fig 10) and *Xanthorhoe decoloraria*, also anthomyiids and muscids of various species, like *Botanophila fugax*, *B. rubrigena*, *Delia echinata*, *D. radicum* and *Coenosia pumila*. Also commonly swarming around is the fanniid *Fannia glaucescens*, which previously in Iceland was known from a single locality near Reykjavik (unpubl.). The slug *Deroceras laeve* (Fig. 11) is seen in the vegetation after rainfalls, but the snail *Vitrina pellucida* hides under stones.

Active pollinators are present in the gull colony as well as plant eating representatives, both on leaves and roots. The latter include aphids and thrips and a tiny weevil *Ceutorrhynchus insularis* (Fig. 12) which feeds on *Cochlearia officinalis*. It was first found in 1968 on Sudurey, another small island in the Vestmannaeyjar archipelago and described as a new species for science (Dieckmann 1971, Lindroth *et al.* 1973). It was discovered on Surtsey in 2002 when it turned out to be quite numerous on a small spot in the gull colony. Since then it has widened its range and become one of the most common beetles on Surtsey. The validity of *C. insularis* as a species has not been confirmed.

The soils of the gull colony are nutrient rich compared with the sandy surfaces and changes are noted in the vegetation succession as well as in invertebrate communities (Fig. 5; Magnússon *et al.* 2009). A part of the oldest gull colony is approaching the most developed succession stage, comparable with the nearest islands, with dense and luxuriant grassland vegetation dominated by *Festuca richardsonii*. The plots at the margin of the gull colony, plots 10 and 23, were originally on sand-filled and bare lava, respectively, before they were affected by the gull colony and the invertebrate fauna of both plots shows similarities with their origin. Other plots in the gull colony have invertebrate species composition with similarities to both the margins and the most developed stage of the gull colony. The exception is plot 9 that is similar to other plots of the gull colony regarding nutrient and vegetation but has almost twice as many gull nests in its nearest surroundings than other plots of the gull colony (Magnússon *et al.* 2009).

Invertebrates promote bird diversity

Colonization of some of the bird species has certainly been dependent on the developing invertebrate fauna. The first passerine to start breeding on Surtsey was the snow bunting (*Plectrophenax nivalis*), which appeared in 1996. Even if the adults are foremost seed feeding the species is dependent on invertebrates for raising young. In 2002 there were indications of solely insect feeding passerines to be breeding on the island, i.e. the meadow pipit (*Anthus pratensis*) and the white wagtail (*Motacilla alba*); the former has since being a regular breeder on Surtsey (Magnússon & Ólafsson 2003, Jakobsson *et al.* 2007, Petersen 2009). This shows clearly the important role of invertebrates to keep the island's ecosystem functioning and how they accomplish further progresses.

ACKNOWLEDGEMENTS

The Surtsey Research Society has been a firm backstop for this project and previous expeditions from the very beginning, insured on site accommodation and supported the transports. The Icelandic Coast Guard has seen to the transport. The Environment Agency of Iceland has given permits to enter the island to perform the field-work. The Icelandic Institute of Natural History has financed the field-work and processing of material. Colleges and co-operators in the biological research team, guided by Borgthór Magnússon, are thanked, Borgthór also for assisting with the DCA-analysis. Sigurdur K. Gudjohnsen is thanked for preparing the map, Mr. Jón B. Hlídberg for the permit to use his drawing of *Ceutorhynchus insularis*, and Ms. Gudbjörg I. Aradóttir for her contribution during the field-work in 2002. Helene Bracht Jørgensen gets our gratitude for valuable comments on the manuscript.

References

Abe, T. 2006. Colonization of Nishino-shima island by plants and arthropods 31 years after eruption. Pacific Science 60: 355–365.

Ashmole, N.P. and M.J. Ashmole 1997. The land fauna of Ascencion Island: New data from caves and lava flows, and a reconstruction of prehistoric ecosystem. Journal of Biogeography 24: 549–589.

Bell, J.R., D.A. Bohan, E.M. Shaw & G.S. Weyman 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bulletin of Entomological Research 95: 69–114.

Bödvarsson, H. 1982. The Collembola of Surtsey, Iceland. Surtsey Res. Progr. Rep. 9: 63–67.

Coulson, S.J., I.D. Hodkinson, N.R. Webb, K. Mikkola, J.A. Harrison, & D.E. Pedgley 2002a. Aerial colonization of high Arctic islands by invertebrates: the diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species. Diversity and Distributions 8: 327–334.

Coulson, S.J., I.D. Hodkinson, N.R. Webb & J. A. Harrison 2002b. Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. Functional Ecology 16: 353–356.

Dieckmann, L. 1971. Ceutorhynchus-Studien (Coleoptera: Curculionidae). Beitr. Ent. 21: 585–595.

Drake, V.A. & R.A. Farrow. 1988. The influence of atmospheric structure and motions on insect migration. Annual Review of Entomology 33: 183–210.

Edwards, J.S. & I.W.B. Thornton 2001. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VI. The pioneer arthropod community of Motmot. Journal of Biogeography 28: 1379–1388.

Figuerola, J.A. J. Green & T.C. Michot 2005. Invertebrate eggs can fly: Evidence of waterfowl-mediated gene flow in aquatic invertebrates. American Naturalist 165: 274–280.

Fridriksson, S. 1964. Um adflutning lífvera til Surtseyjar. (The colonization of the dryland biota of the island of Surtsey off the coast of Iceland). Náttúrufraedingurinn 34: 83–89, (in Icelandic with an English summary).

Gjelstrup, P. 2000. Soil mites and collembolans on Surtsey, Iceland, 32 years after the eruption. Surtsey Research 11: 43–50.

Hill, M.O. 1979. DECORANA – A FORTRAN program for detrended correspondence analysis and reciprocal averageing. Ecology and Systematics, Cornell University, Ithaca, New York, 52 pp.

Hodkinson, I.D., S J. Coulson & N.R. Webb 2004. Invertebrate community assembly along proglacial chronosequences in the high Arctic. Journal of Animal Ecology 73: 556–568.

Jakobsson, S.P., B. Magnússon, E. Ólafsson, G. Thorvardardóttir, K. Gunnarsson, S. Baldursson & A. Petersen 2007. Nomination of Surtsey for the UNESCO World Heritage List. Editors: S. Baldursson & Á. Ingadóttir. Icelandic Institute of Natural History, 123 pp.

Kaufmann, R. 2001. Invertebrate succession on an alpine glacier foreland. Ecology 82: 2261–2278.

Lindroth, C.H., H. Andersson, H. Bödvarsson & S.H. Richter 1973. Surtsey, Iceland. The development of a new fauna 1963–1970. Terrestrial invertebrates. Ent. Scand. Suppl. 5: 1–280.

Magnússon, B. & S.H. Magnússon 2000. Vegetation succession on Surtsey, Iceland, during, 1990–1998 under the influence of breeding gulls. Surtsey Research 11: 9–20.

Magnússon, B., S.H. Magnússon & S. Fridriksson 2009. Developments in plant colonization and succession on Surtsey during 1999–2008. Surtsey Research 12: 57–76.

Magnússon, B. & E. Ólafsson 2003. Fuglar og framvinda í Surtsey. (Birds and succession on Surtsey). Fuglar. Ársrit Fuglaverndar 2003: 22–29, (in Icelandic with an English summary).

Nkem, J.N., D.H. Wall, R.A. Virginia, J.E. Barrett, E.J. Broos, D.L. Porazinska & B.J. Adams 2006. Wind dispersal of soil invertebrates in the McMurdo Dry valleys, Antarctica. Polar Biology 29: 346–352.

Ólafsson, E. 1978. The development of the land-arthropod fauna on Surtsey, Iceland, during 1971–1976 with notes on terrestrial Oligochaeta. Surtsey Res. Progr. Rep. 8: 41–46.

Ólafsson, E. 1982. The status of the land-arthropod fauna on Surtsey, Iceland, in summer 1981. Surtsey Res. Progr. Rep. 9: 68–72.

Oliver, D.R. 1965. Fyrsta skordýrid, er fannst á Surtsey. (The first insect collected on Surtsey, a new Icelandic island). Náttúrufraedingurinn 35: 145–148, (in Icelandic with an English summary).

Petersen, A. 2009. Formation of a bird community on a new island Surtsey, Iceland. Surtsey Research 12: 133–148.

Sigurdardóttir, H. 2000. Status of collembolans (Collembola) on Surtsey, Iceland, in 1995 and the first encounter of earthworms (Lumbricidae) in 1993. Surtsey Research 11: 51–55.

Smith, B.J. & M. Djadjasasmita 1988. The land molluscs of the Krakatau island, Indonesia. Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences 322: 379–400.

Thornton, I.W.B & T. New, T. 1988. Krakatau invertebrates: The 1980s fauna in the context of a century of recolonization. Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences 322: 493–522.

Appendix 1. Land-invertebrate species and species equivalent taxa of Enthognatna, Insecta, Arachnida, Gastropoda and Annelida found on Surtsey during surveys 1964–2006. Their evaluated status is given, i.e. permanently settled species, uncertain settlement, not settled, and found dead in drift only.

1	Settled	Uncertain	Not settled	Dead in drift	2	Settled	Uncertain	Not settled	Dead in drift
ARTHROPODA					**Drepanociphidae**				
ENTOGNATHA					*Euceraphis punctipennis* (Zetterstedt, 1828)			x	
COLLEMBOLA					**Aphididae**				
Hypogastruridae					*Acyrtociphon auctum* (Walker, 1849)	x			
Ceratophysella denticulata (Bagnall, 1941)			x		*Brachycaudus helichrysi* (Kaltenbach, 1843)			x	
Ceratophysella succinea Gisin, 1949	x				Aphididae indet. spp.	x			
Hypogastrura assimilis Krausbauer, 1898		x			**Orthezidae**				
Hypogastrura purpurescens (Lubbock, 1867)	x				*Arctorthezia cataphracta* (Shaw, 1794)			x	
Neanuridae					**THYSANOPTERA**				
Anurida granaria (Nicolet, 1847)			x		**Thripidae**				
Friesea mirabilis (Tullberg, 1871)			x		*Apterothrips secticornis* (Trybom, 1896)	x			
Onychiuridae					*Aptinothrips rufus* Haliday, 1836	x			
Mesaphorura krausbaueri Börner, 1901		x			*Thrips vulgatissimus* Haliday, 1836	x			
Mesaphorura macrochaeta Rusek, 1976	x				**NEUROPTERA**				
Protaphorura armata (Tullberg, 1869)		x			**Hemerobiidae**				
Thalassaphorura duplopunctata (Strenzke, 1954)	x				*Wesmaelius nervosus* (Fabricius, 1793)			x	
Isotomidae					**Chrysopidae**				
Archisotoma besselsi (Packard, 1877)	x				*Chrysoperla carnea* (Stephens, 1836)			x	
Desoria violacea (Tullberg, 1876)			x		**TRICHOPTERA**				
Folsomia fimetaria (Linnaeus, 1758)			x		**Limnephilidae**				
Folsomia quadrioculata (Tullberg, 1871)			x		*Limnephilus affinis* Curtis, 1834				x
Halisotoma maritima (Tullberg, 1871)		x			*Limnephilus elegans* Curtis, 1834			x	
Isotoma anglicana Lubbock, 1873	x				*Limnephilus fenestratus* (Zetterstedt, 1840)			x	
Isotomiella minor (Schaeffer, 1896)	x				*Limnephilus griseus* (Linnaeus, 1758)			x	
Parisotoma notabilis (Schaeffer, 1896)	x				**LEPIDOPTERA**				
Proisotoma minuta (Tullberg, 1871)			x		**Tineidae**				
Pseudisotoma sensibilis (Tullberg, 1876)	x				*Monopis laevigella* (Denis & Schiffermüller, 1775)			x	
Vertagopus arboreus (Linnaeus, 1758)			x		**Plutellidae**				
Neelidae					*Plutella xylostella* (Linnaeus, 1758)			x	
Megalothorax minimus (Willem, 1900)		x			*Rhigognostis senilella* (Zetterstedt, 1839)	x			
PROTURA					**Gelechiidae**				
Protentomidae					*Bryotropha similis* (Stainton, 1854)				x
Protentomon thienemanni Strenzke, 1942			x		**Tortricidae**				
INSECTA					*Eana osseana* (Scopoli, 1763)	x			
MALLOPHAGA					**Pyralidae**				
Menoponidae					*Matilella fusca* (Haworth, 1811)		x		
Eidmanniella pustulosa (Nitzsch, 1866)			x		**Crambidae**				
HEMIPTERA					*Crambus pascuella* (Linnaeus, 1758)			x	
Saldidae					*Nomophila noctuella* (Denis & Schiffermüller, 1775)			x	
Salda littoralis (Linnaeus, 1758)	x				**Nymphalidae**				
Corixidae					*Aglais cardui* (Linnaeus, 1758)			x	
Arctocorisa carinata (Sahlberg, 1819)				x	*Vanessa atalanta* (Linnaeus, 1758)			x	
Miridae					**Geometridae**				
Teratocoris saundersi Douglas & Scott, 1869	x				*Epirrhoe alternata* (Müller, 1764)			x	
Cicadellidae					*Xanthorhoe decoloraria* (Esper, 1806)	x			
Macroseles laevis (Ribaut, 1927)	x				*Xanthorhoe designata* (Hufnagel, 1767)			x	
Delphacidae					**Noctuidae**				
Javesella pellucida (Fabricius, 1794)	x				*Agrotis ipsilon* (Hufnagel, 1766)			x	

Appendix 1, continued.

3	Settled	Uncertain	Not settled	Dead in drift	4	Settled	Uncertain	Not settled	Dead in drift
Autographa gamma (Linnaeus, 1758)			x		*Homotherus magus* (Wesmael, 1855)			x	
Cerapteryx graminis (Linnaeus, 1758)		x			*Nepiera collector* (Thunberg, 1822)		x		
Chortodes stigmatica (Eversmann, 1855)	x				*Ophion nigricans* (Ruthe, 1859)				x
Diarsia mendica (Fabricius, 1775)	x				Phygadeuontinae indet.			x	
Euxoa ochrogaster (Guenée, 1852)		x			*Pimpla arctica* Zetterstedt, 1838			x	
Noctua pronuba (Linnaeus, 1758)			x		*Pimpla flavicoxis* Thompson, 1877			x	
Peridroma saucia (Hübner, 1808)			x		*Pimpla sodalis* Ruthe, 1859			x	
Phlogophora meticulosa (Linnaeus, 1758)			x		*Plectiscidea collaris* (Gravenhorst, 1829)			x	
COLEOPTERA					*Plectiscidea peregrinus* (Ruthe, 1859)			x	
Carabidae					*Polytribax picticornis* (Ruthe, 1859)			x	
Amara quenseli (Schönherr, 1806)	x				*Saotis* sp.?			x	
Bembidion bipunctatum (Linnaeus, 1761)				x	*Stilpnus tenebricosus* (Gravenhorst, 1829)	x			
Nebria rufescens (Ström, 1768)				x	*Sussaba pulchella* (Holmgren, 1858)			x	
Notiophilus biguttatus (Fabricius, 1779)	x				**Braconidae**				
Patrobus septentrionis (Dejean, 1828)				x	*Alysia manducator* (Panzer, 1799)		x		
Trichocellus cognatus (Gyllenhal, 1827)	x				Alysiinae indet.			x	
Dytiscidae					Aphidiinae indet. spp.	x			
Agabus bipustulatus (Linnaeus, 1767)				x	*Chorebus cf. cytherea* (Nixon, 1837)			x	
Staphylinidae					*Chorebus* sp(p).	x			
Amischa analis (Gravenhorst, 1802)	x				*Dacnusa* sp(p).		x		
Atheta amicula (Stephens, 1832)	x				*Meteorus rubens* (Nees, 1811)			x	
Atheta atramentaria (Gyllenhal, 1810)			x		*Monoctonus caricis* (Haliday, 1833)	x			
Atheta excellens (Kraatz, 1856)	x				**Fitigidae**				
Atheta fungi (Gravenhorst, 1806)	x				*Alloxysta* sp(p).	x			
Atheta graminicola (Gravenhorst 1806)	x				*Trybliographa* sp(p).	x			
Atheta vestita (Gravenhorst 1806)		x			**Pteromalidae**				
Omalium excavatum Stephens 1834	x				*Cyrtogaster vulgaris* Walker, 1833		x		
Omalium rivulare (Paykull, 1789)		x			*Trichomalopsis fucicola* (Walker, 1835)			x	
Oxypoda haemorrhoa Mannerheim, 1830	x				Pteromalidae indet. spp.	x			
Oxypoda islandica Kraatz, 1857		x			**Eulopiidae**				
Parocyusa rubicunda (Erichson, 1837)		x			*Chrysocharis pallipes* (Nees, 1834)	x			
Lathridiidae					**Diapriidae**				
Lathridius minutus (Linnaeus, 1767)			x		*Pantoclis trisulcata* Kieffer, 1907			x	
Coccinellidae					*Polypeza ciliata* (Thomson, 1859)		x		
Coccinella undecimpunctata Linnaeus, 1758				x	*Psilius frontalis* (Thompson, 1859)			x	
Curculionidae					**Scelionidae**				
Barynotus squamosus *Germar, 1824*				x	*Trimorus* sp.	x			
Ceutorhynchus insularis Dieckmann, 1971	x				**Platygastridae**				
Otiorhynchus arcticus (O. Fabricius, 1780)	x				*Platygaster splendidula* Ruthe, 1859			x	
HYMENOPTERA					**Megaspilidae**				
Ichneumonidae					*Dendrocerus bifoveatus* (Kieffer, 1907)	x			
Aclastus gracilis (Thomson, 1884)	x				**DIPTERA**				
Atractodes ambiguus Ruthe, 1859	x				**Tipulidae**				
Atractodes bicolor Gravenhorst, 1829			x		*Prionocera turcica* (Fabricius, 1787)			x	
Campoletis sp.			x		*Tipula confusa* van der Wulp, 1883			x	
Cratichneumon rufifrons (Gravenhorts, 1829)			x		*Tipula rufina* Meigen, 1818			x	
Ctenopelmatinae indet.			x		**Limoniidae**				
Diadegma boreale Horstmann, 1980		x			*Dicranomyia autumnalis* (Staeger, 1840)			x	
Enizemum ornatum (Gravenhorst, 1829)			x		*Symplecta hybrida* (Meigen, 1804)			x	
Homotherus locutor (Thunberg, 1822)			x		**Anisopodidae**				

Appendix 1, continued.

5	Settled	Uncertain	Not settled	Dead in drift
Sylvicola fenestralis (Scopoli, 1763)			x	
Trichoceridae				
Trichocera maculipennis Meigen, 1818			x	
Bibionidae				
Bibio nigriventris Haliday, 1833			x	
Dilophus femoratus Meigen, 1804			x	
Cecidomyiidae				
Cecidomyiidae indet. spp.	x			
Scatopsidae				
Scatopse notata (Linnaeus, 1758)			x	
Sciaridae				
Bradysia cf. *nitidicollis* (Meigen, 1818)			x	
Lycoriella conspicua (Winnertz, 1867)			x	
Lycoriella sp.			x	
Sciaridae indet. spp.	x			
Mycetophilidae				
Allodiopsis domestica (Meigen, 1830)		x		
Brevicornu griseicolle (Staeger, 1840)		x		
Brevicornu sp. (female)				
Exechia borealis Lundström, 1912			x	
Exechia frigida (Boheman, 1865)			x	
Exechia micans Lastovka & Matile, 1974			x	
Exechia nigra (Edwards, 1925)			x	
Exechia pectinivalva Stackelberg, 1948			x	
Leia fascipennis Meigen, 1818			x	
Keroplatidae				
Macrocera parva			x	
Chironomidae				
Chironomus spp.			x	
Cricotopus sp.			x	
Diamesa aberrata Lundbeck, 1898			x	
Diamesa bertrami Edwards, 1935			x	
Diamesa bohemani Goetghebuer, 1932			x	
Diamesa incallida (Walker, 1856)			x	
Diamesa zernii Edwards, 1933			x	
Eukiefferiella minor (Edwards, 1929)			x	
Halocladius variabilis (Staeger, 1839)	x			
Metriocnemus eurynotus (Holmgren, 1883)			x	
Micropsectra atrofasciata Kieffer, 1911			x	
Micropsectra lindrothi Goetghebuer in Lindroth, 1931			x	
Oliverida tricornis (Oliver, 1976)			x	
Paracladopelma laminata (Kieffer, 1921)			x	
Procladius islandicus (Goetghebuer in Lindroth, 1931)			x	
Psectrocladius limbatellus (Holmgren, 1869)			x	
Smitthia sp.	x			
Tanytarsus gracilentus (Holmgren, 1883)			x	
Telmatogeton japonicus Tokunaga, 1933	x			
Ceratopogonidae				
Ceratopogonidae indet. sp.			x	
Simuliidae				

6	Settled	Uncertain	Not settled	Dead in drift
Simulium aureum (Fries, 1824)			x	
Simulium vittatum Zetterstedt, 1838			x	
Empididae				
Clinocera stagnalis (Haliday, 1833)			x	
Rhamphomyia simplex Zetterstedt, 1849			x	
Dolichopodidae				
Dolichopus plumipes (Scopoli, 1763)	x			
Hydrophorus viridis (Meigen, 1824)			x	
Syntormon pallipes (Fabricius, 1794)			x	
Lonchopteridae				
Lonchoptera bifurcata (Fallén, 1810)	x			
Syrphidae				
Eupeodes corollae (Fabricius, 1794)			x	
Eupeodes lundbecki (Soot-Ryen, 1946)			x	
Eupeodes punctifer (Frey, 1934)			x	
Helophilus pendulus (Linnaeus, 1758)			x	
Melangyna lasiophthalma (Zetterstedt, 1843)			x	
Melanostoma mellinum (Linnaeus, 1758)	x			
Parasyrphus tarsatus (Zetterstedt, 1838)			x	
Platycheirus albimanus (Fabricius, 1781)		x		
Platycheirus clypeatus (Meigen, 1822)			x	
Platycheirus granditarsus (Förster, 1771)			x	
Platycheirus manicatus (Meigen, 1822)	x			
Platycheirus peltatus (Meigen, 1822)			x	
Sphaerophoria scripta (Linnaeus, 1758)			x	
Syrphus ribesii (Linnaeus, 1758)			x	
Syrphus torvus Osten-Sacken, 1875			x	
Phoridae				
Megaselia giraudii (Egger, 1862)			x	
Megaselia pumila (Meigen, 1830)			x	
Megaselia sordida (Zetterstedt, 1838)	x			
Piophilidae				
Parapiophila vulgaris Fallén, 1820	x			
Agromyzidae				
Phytomyza farfarella (Hendel, 1935)	x			
Sciomyzidae				
Dictya umbrarum (Linnaeus, 1758)			x	
Pherbellia ventralis (Fallén, 1820)			x	
Tetanocera robusta Loew, 1847			x	
Helcomyzidae				
Heterocheila buccata (Fallén, 1820)			x	
Sepsidae				
Themira arctica (Becker, 1915)	x			
Themira pusilla (Zetterstedt, 1847)		x		
Coelopidae				
Coelopa frigida (Fabricius, 1805)			x	
Anthomyzidae				
Anthomyza socculata (Zetterstedt, 1847)	x			
Chamaemyiidae				
Chamaemyia geniculata (Zetterstedt, 1838)			x	

Appendix 1, continued.

7	Settled	Uncertain	Not settled	Dead in drift
Carniidae				
Meoneura lamellata Collin, 1930	x			
Heleomyzidae				
Heleomyza borealis (Boheman, 1866)	x			
Heleomyza serrata (Linnaeus, 1758)			x	
Neoleria prominens (Becker, 1897)	x			
Tephrochlaena oraria Collin, 1943			x	
Drosophilidae				
Drosophila funebris (Fabricius, 1787)			x	
Scaptomyza graminum (Fallén, 1823)	x			
Scaptomyza pallida (Zetterstedt, 1847)	x			
Sphaeroceridae				
Copromyza equina Fallén, 1820			x	
Copromyza nigrina (Gimmerthal, 1847)		x		
Crumomyia nigra (Meigen, 1830)			x	
Ischiolepta pusilla (Fallén, 1820)			x	
Minilimosina fungicola (Haliday, 1836)	x			
Minilimosina vitripennis (Zetterstedt, 1847)			x	
Phthitia empirica (Hutton, 1901)			x	
Rachispoda lutosa (Stenhammar, 1855)			x	
Spelobia clunipes (Meigen, 1830)			x	
Spelobia luteilabris (Rondani, 1880)			x	
Spelobia pseudosetaria (Duda, 1918)			x	
Spelobia rufilabris (Stenhammar, 1855)		x		
Thoracochaeta zosterae (Haliday, 1833)			x	
Ephydridae				
Gymnoclasiopa bohemanni (Becker, 1896)			x	
Hydrellia griseola (Fallén, 1813)	x			
Parydra pusilla (Meigen, 1830)			x	
Philygria vittipennis (Zetterstedt, 1838)	x			
Scatella stagnalis (Fallén, 1813)			x	
Scatella tenuicosta Collin, 1930			x	
Scathophagidae				
Chaetosa punctipes (Meigen, 1826)			x	
Scathophaga calida Haliday in Curtis, 1832			x	
Scathophaga furcata (Say, 1823)	x			
Scathophaga litorea Fallén, 1819	x			
Scathophaga stercoraria (Linnaeus, 1758)	x			
Anthomyiidae				
Botanophila betarum (Lintner, 1883)		x		
Botanophila fugax (Meigen, 1826)	x			
Botanophila profuga (Stein, 1816)			x	
Botanophila rubrigena (Schnabl, 1915)	x			
Delia angustifrons (Meigen, 1826)	x			
Delia echinata (Séguy, 1923)	x			
Delia fabricii (Holmgren, 1872)	x			
Delia platura (Meigen, 1826)	x			
Delia radicum (Linnaeus, 1758)	x			
Delia setigera (Stein, 1920)	x			
Fucellia fucorum (Fallén, 1819)			x	

8	Settled	Uncertain	Not settled	Dead in drift
Fucellia maritima (Haliday, 1838)			x	
Lasiomma picipes (Meigen, 1826)	x			
Pegomya bicolor (Wiedemann, 1817)			x	
Pegoplata infirma (Meigen, 1826)	x			
Zaphne brunneifrons (Zetterstedt, 1838)			x	
Zaphne divisa (Meigen, 1826)			x	
Zaphne frontata (Zetterstedt, 1838)			x	
Muscidae				
Coenosia pumila (Fallén, 1825)	x			
Graphomya maculata (Scopoli, 1763)			x	
Helina annosa (Zetterstedt, 1838)			x	
Hydrotaea armipes (Fallén, 1825)		x		
Hydrotaea dentipes (Fabricius, 1805)	x			
Limnophora pandellei Séguy, 1923			x	
Limnophora sinuata Collin, 1930			x	
Musca domestica Linnaeus, 1758			x	
Mydaea palpalis Stein, 1916			x	
Myospila meditabunda (Fabricius, 1781)	x			
Spilogona baltica (Ringdahl, 1918)	x			
Spilogona contractifrons (Zetterstedt, 1838)			x	
Spilogona micans (Ringdahl, 1918)			x	
Spilogona pacifica (Meigen, 1826)	x			
Thricops rostratus (Meade, 1882)	x			
Trichops cunctans (Meigen, 1826)			x	
Fanniidae				
Fannia canicularis (Linnaeus, 1761)	x			
Fannia lucidula (Zetterstedt, 1860)	x			
Calliphoridae				
Calliphora uralensis Villeneuve, 1922	x			
Calliphora vicina Robineau-Desvoidy, 1830			x	
Cynomya mortuorum (Linnaeus, 1761)	x			
Protophormia terraenovae (Robineau-Desvoidy, 1830)			x	
Hippoboscidae				
Ornithomya avicularia (Linnaeus, 1758)			x	
Ornithomya chloropus Bergroth, 1901			x	
SIPHONATERA				
Ceratophyllidae				
Dasypsyllus gallinulae (Dale, 1878)			x	
ARACHNIDA				
ARANEAE				
Lycosidae				
Pardosa palustris (Linnaeus, 1758)			x	
Linyphiidae				
Allomengea scopigera (Grube, 1859)	x			
Erigone arctica (White, 1852)	x			
Erigone atra Blackwall, 1833			x	
Erigone tirolensis L.Koch, 1872			x	
Improphantes complicatus (Emerton, 1882)		x		
Islandiana princeps Brændegaard, 1932	x			
Leptothrix hardyi (Blackwall, 1850)			x	

Appendix 1, continued.

9	Settled	Uncertain	Not settled	Dead in drift
Meioneta nigripes (Simon, 1884)	x			
Savignya frontata (Blackwall, 1833)	x			
Tenuiphantes mengei Kulczynski, 1887			x	
Tenuiphantes zimmermanni Bertkau, 1890		x		
Walckenaeria clavicornis (Emerton, 1882)	x			
Walckenaeria nudipalpis (Westring, 1851)	x			
ACARI				
Gammasina				
Arctoseius cetratus (Sellnick, 1940)	x			
Dendrolaelaps oudemansi Halbert, 1915			x	
Eugamasus kraepelina (nomen dubium)	x			
Eviphis ostrinus (C.L. Koch, 1836)	x			
Haemogamasus nidi Michael, 1892			x	
Halolaelaps sp.	x			
Halolaelaps suecicus Sellnick, 1957			x	
Macrocheles matrius Hull, 1925			x	
Parasitus halophilus (Selnick, 1957)	x			
Rhodacarus roseus Oudemans, 1902			x	
Thinoseius spinosus Willmann, 1930		x		
Zercon triangularis C.L. Koch, 1836	x			
Ixodida				
Ceratixodes uriae (White, 1852)			x	
Ixodes ricinus (Linnaeus, 1758)			x	
Actinedida				
Anystis sp.	x			
Bakerdalia sp.	x			
Bdella sp.	x			
Cocceupodes clavifrons (Canestrini, 1886)			x	
Ereynetes agilis (Berlese, 1923)			x	
Nanorchestes arboriger (Berlese, 1904)	x			
Neomolgus littoralis (Linnaeus)	x			
Pedeculaster mesembrinae (Canestrini, 1881)			x	
Penthalodes ovalis (Dugès, 1834)	x			
Petrobia apicalis (Banks, 1917)	x			
Rhagidia mordax Oudemans, 1906	x			
Rhagidia sp.			x	
Tarsonemus fusarii Cooreman, 1941	x			
Acaridida				
Caloglyphus regleri (E. Türk & F. Türk, 1957)			x	
Histiostoma feroniarum (Dufour, 1839)	x			
Histiostoma (*hypopus*) - same as above?	x			
Myianoetus digiferus			x	

10	Settled	Uncertain	Not settled	Dead in drift
Myianoetus vesparum			x	
Schwiebia cavernicola Vitzthum, 1932	x			
Tyrophagus dimidiatus (Hermann, 1804)			x	
Tyrophagus similis Volgin, 1948	x			
Oribatida				
Achipteria coleoptrata (Linnaeus, 1758)	x			
Ameronothrus lineatus (Thorell, 1871)	x			
Ameronothrus nigrofemoratus (C.L. Koch, 1879)	x			
Autogneta longilamellata (Michael, 1885)	x			
Chamobates cuspidatus (Michael, 1884)	x			
Eniochthonius minutissimus (Berlese, 1903)	x			
Hermannia sp.	x			
Hypochthonius rufulus C.L. Koch, 1836	x			
Lauroppia falcata (Paoli, 1908)			x	
Liochthonius lapponicus (Trägardh, 1910)	x			
Liochthonius muscorum Forsslund, 1964	x			
Liochthonius propinquus Niedbala, 1972	x			
Medioppia subpectinata (Oudemans, 1900)	x			
Ophidiotrichus connexus (Berlese, 1904)	x			
Oppiella nova (Oudemans, 1902)	x			
Oppiella splendens (C.L. Koch, 1841)	x			
Oribotritia faeroensis (Sellnick, 1923)			x	
Quadroppia quadricarinata (Michael, 1885)	x			
Quadroppia sp.	x			
Suctobelbella acutidens (Forsslund, 1941)	x			
Suctobelbella sarekensis (Forsslund, 1941)	x			
Suctobelbella subcornigera (Forsslund, 1941)	x			
Tectocepheus velatus (Michael, 1880)	x			
Zygoribatula exilis (Nicolet, 1855)	x			
ANNELIDA				
OLIGOCHAETA				
Lumbricidae				
Lumbricus castaneus (Savigny, 1826)		x		
Enchytraeidae				
Enchytraeidae indet. spp.	x			
MOLLUSCA				
GASTROPODA				
Agriolimacidae				
Deroceras agreste (Linnaeus, 1758)	x			
Vitrinidae				
Vitrina pellucida (O.F. Müller, 1774)	x			