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Macrobenthic communities in water bodies and streams of Svalbard, Norway

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Abstract

Diversity of macrobenthic communities was studied from water bodies and streams of Spitsbergen, Svalbard archipelago, Norway. All together 162 quantitative samples from different regions of Spitsbergen were analysed in relation to environmental variables. Macrobenthic communities were found on all kinds of substrates (except for periglacial zone) representing wide range of biological communities: solid-bottom, soft-bottom, macrophytes and small brook associated. However, taxonomical structure is very simplified, with a particular dominants from Chironomidae family. The chironomids larvae dominated highly as for diversity, abundance and biomass. Overall macrobenthic communities were characteristic with remarkable dominance of one species and general omnipresent taxonomical scarcity (avg. 2.8 species per sample). All together we found 30 taxa. We distinguished 16 types of macrobenthis communities, characteristic with the dominance of different taxa: chironomids (11 types), oligochaete Enchytraeidae family (3), caddisfly *Apatania zonella* (1) and gammarid amphipod *Gammarus setosus* (1).

As to environmental variables, temperature and pH had the most significant influence on the abundance of macrobenthic organisms.

It is hypothesized that the structural convergence of different types of communities is their common response to extreme high Arctic living conditions. On the other hand, different chironomids may dominate in the same habitats and water bodies. This gives the effect of lower average similarity of communities and high β-diversity.

Keywords: macrobenthos, Chironomidae, Svalbard, Arctic, environmental factors.

Introduction

Benthos organisms and water habitats in Svalbard have two main features. First, it is a very cold climate in the high Arctic, somewhat mitigated by the influence of warm sea currents. Lowland areas are dominated by tundra often underlined by permafrost (Haldorsen et al., 2011). There is no snow for about two to three months long period. The highest temperature in the lakes and its outflowing rivers is usually no more than 10 ˚C to 12˚C. The width of the tundra strip along the coast is usually a few kilometres, and a large part (~ 60%) of archipelago is covered with glaciers (Umbreit, 2005). It is considered that over the past two hundred years glaciers have gradually retreated from the sea (Brooks & Birks, 2004). Hence, the age of all the thawed areas of the land does not exceed a few hundred years.

The second feature is an insular nature of the region in conjunction with the allegedly low age of its thawing. The distance from the continent (the Scandinavian Peninsula) is about 1000 km. Accordingly, the freshwater fauna in Svalbard is of clearly insular nature and is much poorer than for instance the tundra fauna of the Eurasian Arctic mainland (Umbreit, 2005). Svalbard fauna lacks many typical freshwater groups (Mollusca, Decapoda, Odonata, Plecoptera, Heteroptera, most of the Diptera families, etc.) Several groups (Trichoptera, Ephemeroptera, Coleoptera) are represented by single species, and only two groups (Chironomidae and Enchytraeidae) are relatively diverse. Most of the freshwater macrofauna is accounted for chironomids, numbering, according to the recent data, 86 species (Coulson, 2007, 2013). This number can be further refined considerably, as part of these forms is only noticed in the larval stage, hence it is not always possible to determine the species reliably.

Thus, a variety of freshwater communities in this region is drastically limited by two factors at once. It is difficult to live in this area and even more difficult to get here. This extreme combination has resulted in a forceful prevalence of chironomids, what are able both to settle and to dwell effectively in the ephemeral, ultra-cold water and other extreme biotopes (Brooks & Birks, 2004).

Among the high Arctic regions, Spitsbergen from Svalbard archipelago is the most studied one because of governmental support and available facilities. The most significant works on freshwater benthos of the archipelago are those on chironomids' associations in the lakes (Brooks & Birks, 2004) and streams (Lods-Crozet et al., 2007), as well as on benthos drift in streams (Marziali et al., 2009). There are also works on the comparative analysis of the taxonomic diversity of communities of Spitsbergen and other mountainous and Arctic regions (Heiri et al., 2011, Jacobsen & Dangles, 2012), as well as of the similar areas of Greenland (Friberg et al., 2001) and Iceland (Gislason et al., 2000). Still, available knowledge is fragmentary and mechanism of long-term influence from environmental factors is not completely understood. Therefore, the goal of this study is to describe the features and diversity of macrobenthic communities from different regions of Spitsbergen, Svalbard archipelago, as well as the environmental factors defining it.

Materials and methods

Study site

Sampling was conducted in different parts around Isfjorden (Longyearbyen, Aldegondabreen, Randvika, Barentsburg, Ymerbukta, Pyramiden, Kapp Napier, Diabassoden) in August 18 to 24, 2014 and in the Aldegondabreen, Grønfjordbreen and Ny-Ålesund area in August 17 to 22, 2015 (see Fig. 1). Study site has characters associated with the high Arctic climate. Moreover, large part of the studied habitats has formed recently due to nearby glaciers retreated. Due to the hilly, foothill terrain, and the proximity of the rocky bedrock, almost all the watercourses of the region are of piedmont or mountainous nature (with small depth, rapid flows, deep valleys and represent continuous rocky shoals). The exceptions are some of the streams flowing through the flat sections of wetlands, overgrown with moss. Majority of the small water bodies are located in the hollows of glacial moraines.

The study material consists of 162 quantitative samples (of 0.1 or 0.2 m^2) from 96 sampling sites. Both, remote sites and close to settlements located were sampled.

The study involved habitats of varying depth and nature. Observed streams included origin by glaciers, springs and lakes. Water bodies included also oligohaline and mesohaline lagoons and the coastal zone of two large lakes: Linné Lake (surface area 4.6 km^2) and Bretjørna Lake (surface area 1.3 km^2). Those were also the only sites with fish present. See detailed description of all sampling sites in Supplement 1.

Sampling, data processing and analysis

Samples number per site depends on present habitat variability. Each sample was assigned to a particular benthic substrate, as well as to flow depth and velocity. In small waterbodies only one (dominant) substrate was studied, in larger waterbodies the whole diversity of habitats (usually 2 to 4 types of present substrates) was studied.

All samples were collected from the littoral zone with a manual hemisphere sampler (diameter 16 cm, sampling area of 0.02 m^2, mesh size 0.5 mm) at a depth of maximum 1m. In order to grade spatial heterogeneity of macrobenthos communities, each quantitative sample was consisted of 5 to 10 subsamples, taken at a distance of 1 to 5 meters. All samples were preserved with 96% ethanol.

As far as possible, determination of organisms was carried out up to the species level, however, for insufficiently described chironomids' larvae (genera *Diamesa, Cricotopus, Orthocladius* and *Chironomus*), for young larvae and oligochaetes (Enchytraeidae family), animals were identified up to the genus level. Identification was done mainly by applying following identification keys: Makarchenko (2001), Timm (2009), Widerholm (1983). For each species quantity and wet biomass with an accuracy of 1 mg was determined.

The main indicator for taxa abundance was relative taxa metabolism, i.e. taxa share in each sample calculated by the formula of abundance and biomass:

$$R = Q \times N^{0.25} \times B^{0.75},$$

where N is number, B is biomass in g/m^2, Q is the coefficient of proportionality (the exchange level) specific for each taxon (Alimov, 1989). This index reflects the role of the taxon in the community more accurately, since it is directly linked to its feed and breathing.

The environmental and descriptive parameters of water bodies and streams (coordinates, elevation, width, average depth, area, velocity of flow for streams, pH, conductivity, temperature) and types of bottom substrates were evaluated for each station on site. We did approximate estimations for width, average depth and area on site. Since most of the habitats were rather small, those parameters can vary annually and within the season drastically. Therefore sampling sites were categorized in six classes according to their size and approximate average depths/width. This classification was based on already existing concept presented by CAFF (Conservation of Arctic Flora and Fauna) Freshwater Expert Monitoring Group for Pan-Arctic Monitoring program and from other literature sources (Culp et al. 2012; Rautio et al. 2011). For sampling site classification, see Table 1. Large area (> 1 ha) flooded waterbodies were categorized as large ponds.

Temperature, conductivity and pH was measured by applying Hanna Instruments testers HI98129 and HI98130. For more detailed sampling sites description and environmental parameters see Supplement.

We used Shapiro-Wilk test of normality first and since data were not normally distributed we used Spearman's correlation analysis with ρ coefficient afterwards for correlation and its significance determination (IBM SPSS Statistics version 23.0.). We used the cluster analysis for the community type differentiation (Past 3.11 software (Hammer et al. 2001), Euclidean distance measurement for the relative taxa metabolism).

Results

Study area and environmental parameters

Due to poor development of both terrestrial and aquatic vegetation, the bottom substrates of the sampling sites were dominated by the mineral ones, which are stones (frequency within 96 sampling sites – 64.9 %), clayed silt (41.5 %), as well as pebbles and clay (28.7 %). In streams, rocky bottom prevails everywhere, whereas lakes and ponds have alternating stones and pebbles with varying degrees of silting. There are also deep silt sedimentation areas present, often anaerobic. Many small water bodies have coastal area abundantly overgrown with moss. Moss is also occasionally present down to depth of 0.5 m (in 47.9 % of all 96 sampling sites).

The pH values varied between 6.23 (site no. 78, small pond) and 9.48 (site no. 60, small pond). Conductivity in most of the waterbodies is relatively high due to freely soluble basement rocks (typically from 100 to 1500 μS/cm). The exception is watercourses and waterbodies fed by glaciers (typically from 10 to 100 μS/cm) and two mesohaline lagoons with strong tidal saliny gradient (typically from 2000 to 15000 μS/cm). The summer daytime temperature varied between 0.9 ˚C (site no. 27, fast running river close to a glacier) and 12.1 ˚C (site no. 44, large flooded pond). In rivers and streams fed by lakes it is about the same, in those fed by glaciers and ground, temperature never exceeds 3 to 5˚C (Fig. 2). For more detailed study sites description see Supplement.

According to Spearman's correlation analysis, in general, there was no significant correlation detected between specimens' amount, frequency and environmental parameters like temperature, pH, conductivity and elevation. The only significant (P_ρ ==1,05 x10^{-2}), still weak (ρ =0.26) correlation was found between specimens' amount and conductivity. This however can be rather explained by the presence of few brackish water habitats with high conductivity and particular fauna composition.

Current velocity is a key factor separating all macrobenthos communities into groups inhabiting lotic and lentic water bodies. Flowing waters such as rivers and streams are usually constantly dominated by chironomids genus *Diamesa* (other taxons are usually absent at all). Still waters such as lakes, puddles and lagoons are dominated by other chironomid genera.

Substrate was a second most important factor, what is determining the distribution of macrozoobenthos animals. In rivers and streams as a rule there is a little variation – rocky bottom with a single genus *Diamesa* is dominating. In still waters, substrate determines main existing communities. On muddy sediments there are *Chironomus* and *Procladius* communities, on mosses there are mainly *Cricotopus*, *Orthocladius*, *Psectrocladius, Metriocnemus* communities, on rocky bottoms there are *Paratanytarsus* and other communities present.

Origin and outlet type impact is partly interfaced with the water temperature. Is has more significant role for flowing waters. For instance, there are marked differences in the chironomid *Diamesa* species composition in streams with glacier and underground origin: in former, there is usually *D.* gr. *arctica* present, while in latter it is *D. aberrata* Lundbeck, 1898 or *D. bertrami* Edwards, 1935. In glacial streams there are no macrobenthic animals at a distance of approximately 200 m from the glacier. Moreover, there are particular communities of spring species present with prevalence of *Hydrobaenus conformis* (Holmgren, 1869). On the other hand, there are no clear conformities as to macrobenthos density changes in running waters depending on the outlet type as shown particularly for the Svalbard (Blaen et al., 2014) and western Greenland (Friberg et al., 2001), for the larger rivers. According to our data, there were no significant temperature differences depending on the stream origin type unlike Blaen et al. (2014) findings. In majority of all the studied watercourses, the water temperature is below or hardly exceeds 5 ˚C (see Fig. 2. and Supplement).

Size (surface area) and depth does not play a significant role in most of the study sites. The exception is the smallest puddles drying up periodically during the season. In some of those puddles there was no macrobenthos detected. In some other there were typical soil species found – chironomids *Smittia* sp., *Paraphaenocladius brevinervis* (Holmgren, 1869) and oligochaeta *Lumbricillus*. Macrobenthos collected from the coastal zone of large lakes such as Lake Linné and Lake Bretjørna turned out not to be more rich than macrobenthos from smaller waterbodies, on average there were three species per sample. As to animal abundance, there was slightly higher average abundance in large lakes (0.35 g/m^2) in comparison with regional average (0.25 g/m^2).

Except for a temperature related to the outlet type, water summer temperature had no significant role. Apparently, temperature variations in still water habitats are associated with the present weather conditions and the entire regional macrobenthos community has adapted to these variations. Contrary to expectations, summer temperature from still water habitats turned to be weakly linked to the distance from the glacier. It does not form a strong, regular gradient, which could lead to the formation of the communities' gradient. Resembling gradient is marked for rheophilic communities of western Greenland (Friberg et al., 2001), but it is linked to significant summer water temperature variations (from 2 to 17 ˚C).

In the majority of the studied habitats conductivity does not have a significant role. Exceptions are brackish lagoons (up to 10–15 ppt at high tide). In those habitats there were no typical freshwater chironomids associations present, dominating species was oligochaetes *Enchytraeus* sp.

In the majority of the studied habitats the distance from the glacier does not have a significant role. Exception is approximately 200 m wide pre-glacial zone where no macrobenthos specimens were found. Otherwise, there were no significant changes as to macrobenthos communities diversity and composition at a distance from approximately 300 m to 5 km from the glacier.

In the majority of the studied habitats antropogenic impact did not have a significant role. The exception was few habitats, obviously transformed by human activity. For instance, stream of Westbyelva with an outlet located at coal mine near to Ny-Ålesund village was almost with no macrobenthos animals. The only found specimens were few, mostly dead chironomids, possibly they have felt into the watercourse from the side streams. Apparently, the water in the watercourse is not appropriate for macrobenthos animals. Another examples,depletion of macrobenthos abundance is associated with water-pipe system (particularly in Barentsburg settlement). We suggest this is probably due to the strong fluctuations of the water level. Outside mines and settlements areas, human impact on freshwater ecosystems can be considered as insignificant.

Faunal composition

The samples revealed 30 macrozoobenthos taxa, see Supplement 2. Including 24 taxa of chironomids larvae, 3 taxa of Enchytraeidae oligochaetes, as well as caddisfly *Apatania zonella* (Zetterstedt, 1840), amphipod *Gammarus setosus* Dementieva, 1931 and Arctic tadpole shrimp *Lepidurus arcticus* (Pallas, 1776). On average, chironomids constitutes 92% as for number and 91% as for biomass. Enchytraeidae oligochaetes, *A. zonella* and *G. setosus* dominated in 10, 4 and 1 sample correspondingly. In addition, in many samples of ponds, there was *L. arcticus* present, a large actively swimming organism inhabiting all the water column of ponds, but often grazing closer to the bottom. As to bottom substrates, an average number of found species was not significantly variable for different substrates. The highest number (4.0) was found on boulders, the lowest (2.67) on pebbles.

Svalbard macrobenthos regional features

Our study showed that despite strong taxonomic depletion of freshwater fauna, almost all the surveyed sites were populated by macrobenthos. The exceptions are a few habitats of glacial origin: a stream located at a distance of 300 m from the glacier and small lake on the border of the glacier: no macrobenthos was found there (sampling sites 17 and 89 accordingly, for more details see Supplement). Overall, approximately 200 m area around the glacier can be considered uninhabited by macrobenthos. The rest of studied area had all the typical substrates equally inhabited by macrobenthos. Exception is the ice surface of permafrost.

The average number of macrobenthos is 770 specimen/m^2 and biomass is 0.25 g/m^2; metabolic rate here is 112.9 ml O_2/m^2 per hour. These values are small but generally typical for the cold-water oligotrophic water bodies and correspond with the trophic status of the surveyed habitats (Chertoprud & Palatov, 2013). On the other hand, many freshwater macrobenthic communities of insect larvae in temperate Eurasia are not using all the trophic resources of ecosystem. There is no direct relation between water trophy and abundance of macrobenthos detected (Chertoprud, 2011).

In our survey, local diversity of macrobenthos (number of species per sample and abundance uniformity) is decreased drastically. Most species associations from the small water bodies were single-species dominant, with substantial dominance of one of the many chironomids species. Except for one (rarely two) dominant species, the species from other habitats of the particular water body occur sporadically in the samples, but this, in general, happens occasionally and can be explained by mosaic like substrate nature in small water bodies. The metabolic rate of the most dominant taxon is 77.8 %, that is approximately twice as high as in the macrobenthos communities of the Palearctic moderate zones (Chertoprud, 2011). Only in few samples it is less than 50%. Average number of species per sample is 2.8, in contrast for most Palaearctic communities there are approximately from 10 to 20 species (Chertoprud, 2011; Palatov & Chertoprud, 2012). Usually, the number of all species from all habitats of a particular single water body does not exceed 4 to 5 species. This result is generally typical for high Arctic and periglacial communities (Jacobsen & Dangles, 2012).

In addition to the typical benthic species, the macrobenthos samples often contain the large eurybiontic species Arctic tadpole shrimp *L. arcticus*. It occurs on all substrates (except for habitats with fast current) and often dominates by the abundance. Apparently, it has no effect on the development of benthic chironomids' associations.

Community types

Cluster analysis for highlighting macrobenthic community types was carried out based on metabolic rate matrix for macrobenthos organisms at the genus level (Fig. 3). Genera instead of species were chosen since in many samples it was not possible to identify the species and habitat preferences for several species of the same genus (in particular *Cricotopus* and *Diamesa*) greatly overlap. Cluster analysis identifies 16 samples groups (Table 2), each corresponds to one dominant taxon. Below there is a brief descriptions of all community groups, according to water body/stream type and habitat.

Hard-bottom macrobenthic communities. Associated with the rocky and, particularly, with pebbly bottoms – substrates, what are solid and stable for macrobenthos:

1. *Diamesa* community. The community is typical for rocky bottoms of streams and small rivers, occupying them almost completely. In all the samples, the dominance of *Diamesa* chironomids is expressed. Other taxa are usually not presented. There are several species of the *Diamesa* genus in the surveyed area. They are not always recognizable by the larvae. We distinguish three subtypes:

1.1. *Diamesa* gr. *arctica*, *Diamesa aberrata*. Found on rocky bottoms of streams and small rivers, usually in those with predominance of ice feed. One of the two species of the *Diamesa* genus usually dominate, but the species of the *arctica* group are not always identifiable. Hence, it is possible, there can be found even more species of this group.

1.2. *Diamesa bertrami*, *D.* gr. *arctica*. Found at rocky-pebbly bottoms of small streams fed by ground. Those habitats are distinguished by slightly increased temperature and salinity at lower currents, as well as by poor development of vegetation. Lods-Crozet et al. (2007) has already described such associations. According to them *D. aberrata* and *D. bohemani* Goetghebuer, 1932 dominate in glacial streams, *D. bertrami* and *D. arctica* dominate in non-glacial streams.

1.3. *Diamesa* gr. *aberrata*. This species is found on mixed substrates (small stones, pebbles, moss and vegetation) of the brooks at the outlet of lakes and flooded areas, springs and limnocrenes (small ponds fed by springs), in places with lower currents.

Other hard-bottom communities are usually associated with silted rocky and pebbly bottoms in lakes. Here are additional five dominants. The dominant depends on the size and feed of the water body, on the nature and extent of stone silting and, most likely, on some other extra factors.

2. *Paratanytarsus austriacus* (Kieffer, 1924). Found at thin layer silt deposits on various (often rocky) bottoms in stagnant water. It often forms a single-species community. Mixed bottoms show some *Cricotopus*, *Orthocladius* and *Chironomus* genus presence.

3. *Apatania zonella*. The only community in the studied area with the dominance of Trichoptera. Found on stones in shallow waters of relatively deep permanent lakes without significant silting. Benthos density is reduced, with rare lithophile and briophile chironomids.

4. *Hydrobaenus conformis*. Found in limnocrenes on rocky bottoms with a thin layer of silt deposit. This is the only community having species rare for our samples: *Paraphaenocladius brevinervis* and *Oliveridia tricornis* (Oliver, 1976). Also seen in moraine pond located closest to the glacier where macrobenthos can be found at all (sporadic *Hydrobaenus conformis*).

5. ***Micropsectra***. Silted bottoms (including rocky ones) in shallow parts of relatively deep permanent lakes. Two species dominate in different reservoirs: *Micropsectra radialis* Goetghebuer, 1939 and *M. insignilobus* Kieffer, 1924. Benthos density is reduced.

6. *Marionina*. Found in two sampling localities: small stream at the outlet of the lake and limnocrenes in the bed of temporary streams. Stony-pebbly soils. Here, Enchytraeidae oligochaetes dominate, in addition the chironomids of *Diamesa* spp., *Cricotopus* spp., *Metriocnemus* gr. *fuscipes* are sometimes seen.

Moss-associated macrobenthic communities. These communities are the most characteristic for moss undergrowth of low current and standing water bodies, and, to a lesser extent for other solid substrates in same reservoirs (rich in moss). Genera of Chironomids Orthocladiinae dominates in these communities.

7. *Cricotopus.* Usually inhabits moss cushions along the shoreline and shallow waters of small lakes. It is also found on rocky bottoms in small lakes and even on the surface of silty bottoms. Species *Cricotopus* s.str. *tibialis* (Meigen, 1804) and *C. (Isocladius) glacialis* Edwards, 1922 are typical here, though many larvae are not identified at the species level.

8. *Orthocladius*. This community is distributed similarly to the previous one, it is found in mosses, as well as on the surface of stones, pebbles, silt and detritus in small standing water bodies. Despite this, joint communities of genera *Orthocladius* and *Cricotopus* are rare.

9. *Psectrocladius* s.str. *barbimanus* (Edwards, 1929). Likewise, it is mostly found on moss of small standing water bodies and sometimes on the surface of pebble and detrital bottoms. In addition, occasionally, species of *Cricotopus*, *Procladius* and *Paratanytarsus* are observed.

10. *Metriocnemus* gr. *fuscipes*. The community is typical for moss and rocky bottoms in small semi-flowing waters (pools interconnected with streams and springs, and low current streams overgrown with moss).

Silt-associated macrobenthic communities. Those communities are associated with soft bottoms and burrowing species dominance of chironomids (Chironomidae and Tanypodinae subfamilies).

11. *Chironomus*. There are no species identified of this genus. Representatives are found in silty bottoms of usually shallow standing water bodies with high saprobity. Sometimes animals are also found in heavily silted gravel, sand and clay. *C. tibialis* and *P. barbimanus* are found as secondary species.

12. *Procladius.* Community of soft bottoms typical with clays, silt deposits and sometimes with heavily silted gravel. Probably, these bottom types cannot provide the food base needed for detritophages (such as *Chironomus*). Therefore, predatory chironomid species *Procladius (Holotanypus) crassinervis* (Zetterstedt, 1838), feeding on meiobenthos or dead zooplankton organisms, colonize here. This habitat is usually a small area closely bordering with other areas. In low density there are also common other chironomid species.

Temporal macrobenthic communities. Those communities are associated with small drying up reservoirs on the sites of shallow hollows in the plain tundra. Represented by soil species of oligochaetes and chironomids.

13. *Lumbricillus*. Species found in puddles with a predominance of clay and pebbly bottom. The *Lumbricillus* oligochaetes can be found on all sediment types. In one sample taken from a puddle connected to drying out creek, there were also chironomids found.

14. *Smittia.* Animals were found in newly formed puddles with a clay bottom. Dominant species belongs to soil chironomid *Smittia*, in addition soil species *P. brevinervis* and *M.* gr. *fuscipes* were found.

Euryhaline macrobenthic communities. Findings of specimens are associated with penetration of sea water into reservoirs. For instance, in shallow lagoon habitats, usually separated from the sea with a shaft of pebble deposits partially flooded at high tide. The salinity varies from 2 to 15 ppt. Two dominant types of communities were recorded:

15. *Enchytraeus*. This is the main community of brackish lagoons with muddy, sandy and pebbly sediments. The community is considerably dominated by *Enchytraeus* oligochaetes. There were single records of *Orthocladius* chironomid and *M.* gr. *fuscipes*.

16. *Gammarus setosus*. The community is described using a single sample taken at the bottom of brackish lagoon separated from the sea by *Laminaria* thallus. No other species of macrobenthos than *G. setosus* at high density was found. Similar structure associations are described for estuaries of the White Sea, where dominants are *Gammarus duebeni* Lilljeborg, 1852 and *G. zaddachi* Sexton, 1912 (Chertoprud et al., 2004).

Discussion

Formally, all the major types of freshwater macrobenthos communities are present in Svalbard: rhithral communities (on the rocky bottom), pelal communities (on the silted bottom) and phytal communities (on the macrophytes). Macrobenthos communities colonize almost all bottom and littoral habitats. However, almost all of these communities are very similar in their taxonomic structure, differing from each other only at the level of chironomids genus and species present. Moreover, there is no considerable difference between communities depending of the habitat size. Thus, the communities of streams and small rivers of all types (i.e. crenal and rhithral) are colonized with *Diamesa* chironomids (species vary only in some cases). Communities of puddles, small and larger ponds, lakes are also very similar in structure, compared, for example, with the communities from moderate climate zone habitats.

Comparison of the data on the structure of macrobenthos communities of Svalbard and other Palearctic regions (Chertoprud, 2011) is shown in Table 3. Evidently, the dominant taxa complex characteristic for each class of the communities in the Arctic is reduced and replaced by different genus of chironomids. Therefore, at the genus and species level, community differences persist, but at the family level those differences disappear.

Hence, we can state a hypothesis for the extreme high Arctic communities' structure – all macrobenthic community classes simplify in structure and get taxonomically common in their high Arctic variants. This effect is partly established in the tundra hypoarctic zone of Eurasia (Palatov & Chertoprud, 2012), but apparently reaches its maximum in areas like Svalbard. One may assume that, in the most cryophile environment (periglacial zone), the communities of all classes are represented by a single *Diamesa* genus, however, this was not true – most close to the glacier present limnophile chironomid *Hydrobaenus conformis*, as well as the rheophile *Diamesa*, both disappear at about 200 to 300 m distance to the glacier.

Perhaps, this consistent pattern is a version of a more general law: in any conditions close to the extreme, there is a simplification of community structure and the structural convergence of various types. This can be observed in cases of high saprobity when all the substrates of all types of water bodies (including different continents' world biomes) are dominated by the *Tubifex* genus oligochaetes (Chertoprud, 2011). Comparably, at extremely rapid currents Simuliidae family species usually dominate on all substrates (Chertoprud & Palatov, 2013). In case of cryophilic communities, the extreme version is the community of glacial streams represented by the genus *Diamesa* chironomids. Similar cases (with the dominance of different *Diamesa* species) were observed from cold streams in alpine zones of Tien Shan, Caucasus and Altai, as well as in the mountain tundra of the Kola Peninsula (Chertoprud & Palatov, 2013). Other studies of the benthos in ultra-cold Holarctic waters also noticed the leading role of *Diamesa*, both in arctic conditions (Gislason et al., 2000) and alpine habitats (Milner & Petts, 1994). As for Svalbard, apart from low water temperature, there is an extreme action of another specific factor, that is areas high isolation combined with geological youth of its reservoirs. Apparently, this effect leads to taxonomic scarcity and monotony of most of its benthic communities (represented, as a rule, by chironomids and enchytraeids larvae). The proximity of the glacier is also seen as a factor reducing biota diversity (Brown et al., 2007), simultaneously this factor is associated with the geological age of the streams and water bodies in Svalbard.

For Svalbard fauna there is well-known model as to stream macrobenthos faunal changes along temperature gradient: Diamesa – Orthocladiinae – Oligochaeta (Blaen et al., 2014, Milner, 2016). Our results however did not support the model mentioned above. Diamesa dominated in almost all rheophilic habitats studied by us.

On the other hand, monodominance of most communities in combination with a rather large number of possible dominance variants (there are 16 possible groups present, excluding the dominance of different species of the genus *Diamesa*, *Cricotopus*, *Micropsectra*) leads to well-differentiated samples, even within the same habitat. For example, four different chironomids genera can dominate in moss, but they do not usually occur together (contrasting the phytophile communities of central Europe biomes where the multispecies complex of dominants persists in most of water bodies). This pattern explains an interesting effect (previously described by Jacobsen & Dangles, 2012) – there is an increase of differences between stations and β-diversity with an increase in the severity of the conditions (at high latitudes and high altitudes).

In conclusion, we would like to emphasize the amazing ability of the Chironomidae family to colonize the habitats extreme both as to abiotic environment and spatial isolation. Unlike other taxa, chironomids colonize the extreme high Arctic not in separate species, but in dozens of species with a variety depending on environmental requirements, which allows them to start their own development here.

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Table 1. Sampling sites classification.

Sampling site class	Number of sites	Area (ha)	Average depth (m)	Width (m)
Puddles	25	< 0.01	≤ 0.25	
Small ponds	23	≥ 0.01 - ≤ 0.1	0.25–1	
Large ponds	22	> 0.1 ha - ≤ 1	1–2	
Lakes	14	> 1	2, usually more	
Streams	6			< 1.5
Rivers	6			> 2

Table 2. Characteristics of selected communities' types.

Community type	Averages: amount (specimen/m^2)	Averages: biomass (g/m^2)	Averages: metabolism (O_2, ml/m^2 h)	Dominant species (relative metabolism, %)
1. Diamesa	637	1.09	0.56	*Diamesa* gr. *arctica 52.3*
				Diamesa gr. *aberrata 32.9*
				Diamesa bertrami 6.1
2. Paratanytarsus	1250	1.40	0.53	*Paratanytarsus austriacus 86.0*
				Psectrocladius barbimanus 4.4
3. Apatania	36	0.15	0.04	*Apatania zonella 55.2*
				Micropsectra radialis 21.6
				Cricotopus tibialis 7.8
				Orthocladius sp. 6.6
4. Hydrobaenus	270	0.30	0.17	*Hydrobaenus conformis 74.2*
				Diamesa gr. *arctica 12.8*
				Diamesa gr. *aberrata 6.1*
5. Micropsectra	1607	1.36	0.83	*Micropsectra radialis 62.3*
				Micropsectra insignilobis 32.0
6. Marionina	776	0.84	0.49	*Marionina* sp. *68.3*
				Diamesa gr. aberrata 16.0
				Metriocnemus gr. *fuscipes 5.6*
7. Cricotopus	1030	1.62	0.62	*Cricotopus tibialis 59.3*
				Cricotopus spp. *10.5*
				Cricotopus glacialis 9.5
				Metriocnemus gr. *fuscipes 4.8*
8. Orthocladius	567	1.29	0.52	*Orthocladius* sp. *69.4*
				Cricotopus tibialis 8.4
				Paratanytarsus austriacus 8.3
				Psectrocladius barbimanus 5.4
9. Psectrocladius	759	3.71	0.96	*Psectrocladius barbimanus 73.1*
				Procladius crassinervis 10.0
				Cricotopus tibialis 6.1
10. Metriocnemus	515	0.51	0.26	*Metriocnemus* gr. *fuscipes 68.0*
				Paraphaenocladius brevinervis 6.3
				Cricotopus tibialis 4.5
11. Chironomus	391	1.90	0.81	*Chironomus* spp. *78.7*
				Psectrocladius barbimanus 6.3
				Cricotopus tibialis 5.4
12. Procladius	380	1.48	0.86	*Procladius crassinervis 69.1*
				Psectrocladius barbimanus 12.8
				Cricotopus tibialis 6.6
				Orthocladius sp. *5.2*
13. Lumbricillus	402	0.51	0.28	*Lumbricillus* spp. *89.5*
				Metriocnemus gr. *fuscipes 8.3*
14. Smittia	317	0.17	0.12	*Smittia* sp. *55.0*
				Metriocnemus gr *fuscipes 32.2*
				Paraphaenocladius brevinervis 13.0
15. Enchytraeus	1424	3.12	1.51	*Enchytraeus* sp. *99.5*
16. Gammarus	60	2.10	0.65	*Gammarus setosus 100.0*

Table 3. Comparison of macrobenthos community structure from temperate and arctic zones.

Community type	Abundance dominants	
	Temperate zone: Moscow region (by Chertoprud, 2011)	High Arctic: Svalbard (by our data)
Crenal (small brooks and springs)	*Potamophylax, Chaetopteryx, Arctoecia* (Limnephilidae), *Nemoura* (Nemouridae), *Baetis* (Baetidae)	*Diamesa, Hydrobaenus* (Chironomidae)
Rhithral (hard bottom in rivers and streams)	*Ancylus* (Ancylidae), *Baetis* (Baetidae), *Agapetus* (Glossosomatidae), *Hydropsyche* (Hydropsychidae), *Rhyacophila* (Rhyacophilidae)	*Diamesa* (Chironomidae)
Phytal (macrophytes)	*Lymnaea, Radix* (Lymnaeidae), *Bithynia* (Bithyniidae), *Viviparus* (Viviparidae), *Cloeon* (Baetidae) *Galerucella* (Chrysomelidae)	*Cricotopus, Orthocladius, Psectrocladius, Metriocnemus* (Chironomidae)
Pelal (silty and sandy bottom)	*Chironomus, Cryptochironomus, Polypedilum, Orthocladius, Procladius* (Chironomidae), *Eloeophila, Hexatoma* (Limoniidae), *Ephemera* (Ephemeridae), *Unio* (Unionidae), *Sphaerium* (Sphaeriidae), *Pisidium* (Pisidiidae), *Limnodrilus, Tubifex* (Tubificidae)	*Chironomus, Procladius* (Chironomidae)
Ephemeral (temporary pools and puddles)	*Aedes* (Culicidae), *Agabus, Hydroporus* (Dytiscidae), *Helophorus* (Helophoridae), *Chironomus* (Chironomidae), *Limnephilus* (Limnephilidae), *Aplexa* (Physidae)	*Smittia*, *Paraphaenocladius* (Chironomidae)

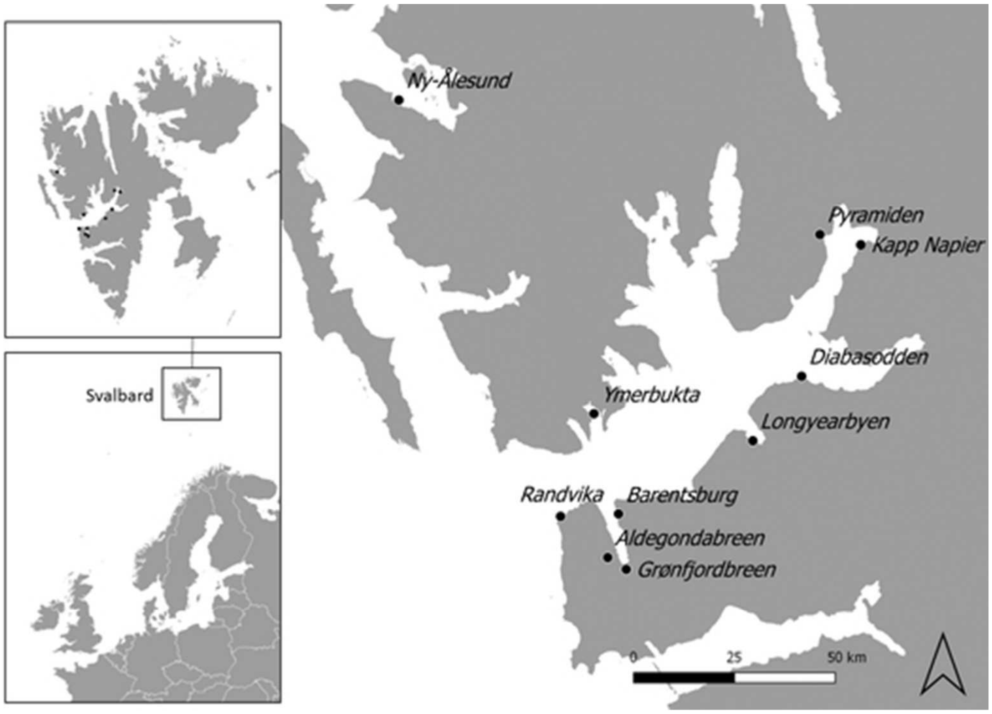

Fig. 1. Map of sampling sites

44x31mm (300 x 300 DPI)

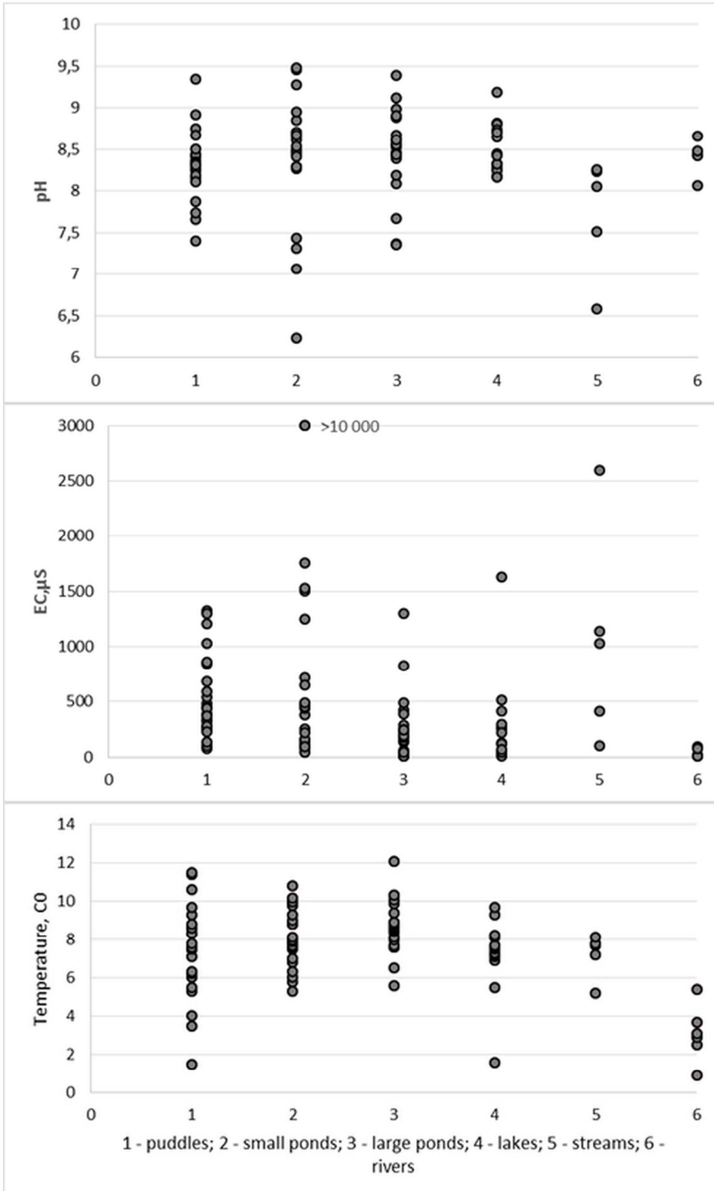

Fig. 2. pH, conductivity and temperature in the different sampling sites. Spitsbergen, Svalbard, 2014–2015.

149x249mm (300 x 300 DPI)

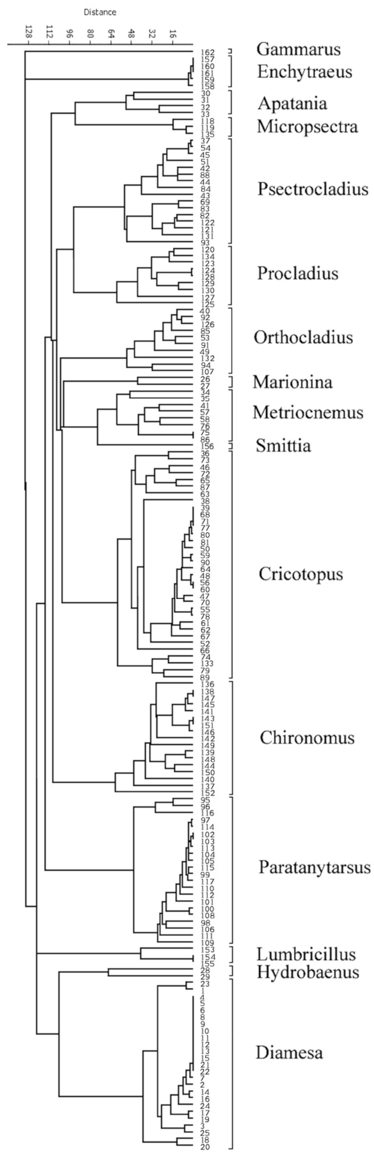

Fig. 3. The dendrogram of samples similarity by the relative metabolism of the macrobenthic genera. Column to the right describes the dominant taxa.

131x302mm (300 x 300 DPI)

Supplement 1

Sampling sites description. Environmental parameters. Sampling sites classes: 1 – puddles. 2 – small ponds. 3 – large ponds. 4 – lakes. 5 – streams. 6 – rivers. 7 – estuarine lagoons. X – no data available.

No.	Sampling site class	Coordinates, E	Coordinates, N	pH	EC,µS	Temperature, C^0	Elevation, m
1	1	15.7625	78.20383	8.30	1320	9.3	13
2	5	15.75853	78.20378	8.23	1140	7.8	15
3	5	15.74727	78.20458	7.51	2600	5.2	20
4	2	15.70602	78.21787	8.85	380	10.0	8
5	1	14.18568	77.99083	7.40	1300	7.5	12
6	1	14.18388	77.99028	7.66	840	3.5	18
7	1	14.17982	77.99102	8.36	390	10.6	25
8	4	14.1685	77.9898	8.45	20	9.7	50
9	3	14.19377	77.99222	8.45	140	8.6	6
10	1	14.1945	77.9922	8.41	80	7.6	8
11	6	14.19438	77.98762	8.43	20	2.9	8
12	1	14.17698	77.98743	8.32	260	6.3	46
13	1	14.15318	77.98637	8.42	480	8.6	41
14	1	14.15015	77.9864	8.75	100	8.3	41
15	1	14.14662	77.98557	8.92	140	7.5	93
16	6	14.13088	77.98373	8.06	10	0.9	54
17	6	14.13088	77.98373	X	X	2.5	X
18	1	14.14562	77.98155	8.15	320	4.0	44
19	6	14.1464	77.98152	8.42	90	3.1	44
20	4	14.17645	77.98463	8.32	260	9.3	28
21	3	14.18697	77.9855	8.43	420	10.3	4
22	5	14.22972	77.97243	8.05	410	7.2	3
23	3	14.23255	77.97052	8.88	830	10.3	5
24	2	14.24205	77.96435	8.66	150	9.8	6
25	3	14.24915	77.95985	9.39	290	9.4	12
26	6	14.266	77.96002	8.66	10	3.7	0
27	2	13.79153	78.0827	8.70	120	8.8	42
28	2	13.79397	78.08118	8.29	720	7.7	16
29	3	13.80405	78.08088	8.46	150	7.7	15
30	3	13.79915	78.0826	8.61	10	8.0	23
31	3	13.81285	78.07383	8.43	10	8.4	73
32	3	13.80758	78.0686	8.39	30	8.4	41
33	5	13.80758	78.0686	X	X	X	X
34	4	13.78307	78.06585	8.18	130	7.1	11
35	4	13.79508	78.07047	8.28	260	8.1	27
36	4	13.79822	78.07178	8.24	410	8.2	28
37	3	13.79817	78.07458	8.56	40	7.6	30
38	2	13.79917	78.07578	8.48	80	6.3	34
39	3	13.7845	78.07335	8.67	60	8.1	34
40	2	14.21617	78.07075	8.45	100	7.9	92
41	2	14.1928	78.09522	8.27	440	8.0	51
42	5	14.07202	78.27885	6.58	100	7.7	20
43	3	14.07755	78.28025	7.67	20	10.1	15

44	3	14.09213	78.27953	7.37	10	12.1	16
45	3	14.11742	78.28312	7.36	40	9.9	15
46	2	14.11542	78.28145	7.31	40	10.8	21
47	4	16.18358	78.65613	8.32	10	7.6	110
48	4	16.19015	78.65492	8.65	40	8.1	61
49	2	16.20888	78.6544	8.70	1750	5.3	50
50	2	16.20372	78.65273	9.46	120	5.8	52
51	4	16.11822	78.63975	8.82	40	7.5	166
52	3	16.73427	78.6381	9.12	1300	8.7	6
53	2	16.74245	78.63752	8.49	1500	10.0	8
54	3	16.73313	78.63592	8.99	390	8.8	8
55	1	16.7371	78.63448	8.67	680	11.4	15
56	2	16.73733	78.63217	8.61	1530	10.2	15
57	1	16.74383	78.63567	8.43	1210	9.7	10
58	1	16.34157	78.6518	8.24	1030	7.1	8
59	6	16.33622	78.64502	8.48	75	5.4	1
60	2	16.10828	78.3609	9.48	160	7.9	28
61	5	16.15575	78.3573	8.26	1030	8.1	20
62	2	16.16838	78.35838	8.46	1250	9.0	4
63	4	11.87755	78.9235	8.81	292	7.7	49
64	4	12.05912	78.9144	8.42	1630	7.3	18
65	2	12.07118	78.9049	9.28	254	9.3	42
66	3	12.06355	78.90418	8.91	182	8.9	29
67	3	12.06702	78.9003	8.52	219	8.5	73
68	3	12.0623	78.89883	8.56	246	5.6	69
69	2	12.07915	1257.039	8.54	470	7.9	38
70	4	11.86367	78.91645	8.74	224	7.2	56
71	2	11.9252	78.91787	7.43	650	8.1	62
72	4	11.93852	78.92518	8.16	514	6.9	23
73	2	11.92332	78.92578	8.41	456	7.0	27
74	1	11.95372	78.92077	8.27	334	5.5	77
75	1	11.96213	78.91868	8.33	450	6.2	18
76	1	11.97552	78.91572	8.34	438	6.0	19
77	2	11.97723	78.91595	7.07	10001	6.0	13
78	2	11.95372	78.9235	6.23	10001	6.8	11
79	7	11.79922	78.93565	8.95	97	7.6	60
80	7	11.81643	78.93433	8.44	195	6.5	54
81	3	14.25063	77.95955	8.09	486	7.6	0
82	1	14.25958	77.95617	8.19	272	7.5	37
83	1	14.25958	77.95617	8.34	265	7.8	37
84	3	14.26343	77.95443	8.19	248	8.9	34
85	1	14.26698	77.95407	8.33	265	8.6	47
86	4	14.28123	77.9551	8.70	116	5.5	12
87	1	14.28115	77.95365	8.11	368	1.5	27
88	1	14.26068	77.95048	8.31	540	8.8	52
89	4	14.26048	77.9404	9.19	65	1.6	35
90	2	14.25022	77.94255	8.29	222	7.5	61
91	1	14.26067	77.96378	9.34	861	11.5	26
92	1	14.15318	77.98637	7.74	283	7.5	41
93	1	14.15055	77.9863	8.5	226	5.3	41

94	1	14.17982	77.99102	7.87	591	8.3	25
95	3	14.1945	77.9922	8.61	242	8.6	6
96	2	14.171	78.00127	8.67	487	8.8	34

Supplement 2

Taxa list and distribution. Sampling sites classes: 1 – puddles. 2 – small ponds. 3 – large ponds. 4 – lakes. 5 – streams. 6 – rivers. 7 – estuarine lagoons.

Taxa	1	2	3	4	5	6	7
Crustacea, Notostraca							
Lepidurus arcticus (Pallas, 1793)	+	+	+				
Crustacea, Amphipoda							
Gammarus setosus Dementieva, 1931							+
Trichoptera, Apataniidae							
Apatania zonella Zetterstedt, 1840			+	+	+		
Diptera, Chironomidae							
DIAMESINAE							
Diamesa aberrata Lundbeck, 1898					+	+	
Diamesa bertrami Edwards, 1935					+		
Diamesa gr. *arctica*					+	+	
Diamesa sp.1					+		
Diamesa sp.2					+		
ORTHOCLADIINAE							
Paraphaenocladius brevinervis (Holmgren, 1869)	+						
Smittia sp.	+						
Cricotopus (s. str.) *tibialis* (Meigen, 1804)		+	+	+	+		
Cricotopus s.str. sp.		+	+	+	+		
Cricotopus (Isocladius) *glacialis* Edwards, 1922		+	+	+	+		
Psectrocladius barbimanus (Edwards, 1929)		+	+	+			
Metriocnemus gr. *fuscipes*	+	+	+	+	+		+
Oliveridia tricornis (Oliver, 1976)					+		
Hydrobaenus conformis (Holmgren, 1869)				+	+		
Paraphaenocladius brevinervis					+		

(Holmgren, 1869)							
Orthocladius s.str.	+	+	+	+			
Chaetocladius s.str.					+		
Limnophyes gr. *edwardsi*				+			
TANYPODINAE							
Procladius crassinervis (Zetterstedt 1838)		+	+	+			
CHIRONOMINAE							
Paratanytarsus austriacus (Kieffer 1924)		+	+				
Micropsectra insignilobus Kieffer 1924				+			
Micropsectra radialis Goetghebuer 1939			+	+			
Micropsectra sp.				+			
Chironomus sp.		+	+	+			
Oligochaeta, Enchytraeidae							
Enchytraeus sp.							+
Lumbricillus sp.	+	+			+		
Marionina sp.	+	+					