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Testing the benthic lake type concept based on chironomid associations in some Finnish lakes using multivariate statistical methods

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The profundal chironomid associations in 9 Finnish lakes were analyzed using a hierarchial cluster analysis technique in order to test the usefulness of the lake typology of Brundin in the study area. The classification results were evaluated by analyzing the corresponding physico-chemical water quality data with discriminant analysis. The same procedure was also applied with the shallow water associations.

The results showed that the lake typology of Brundin is a valid basis for monitoring stratified lakes. They supported the thesis holding that the availability of food is the primary controlling mechanism in the profundal chironomid communities.

In the shallow water region the difficulties in creating benthic lake typologies are apparent. The best classification results in relation to the water quality and trophic status were achieved at a depth of 3-5 m. It is necessary to divide the littoral and sublittoral into subzones and to compare lakes separately in them. The results showed that it is possible to find characteristic benthic types in shallow lakes as well, these being typical to Finland. Further supporting taxonomic research on quantitatively important lake chironomids is required before a useful lake typology can be established for the shallow water region.

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1. Introduction

The biological variables have many advantages over the conventional physico-chemical parameters in lake monitoring. The most important advantage is that they integrate the effects of several environmental variables over a long period of time and also permit the detection of occasional disturbancies. The use of zoobenthos, in particular, has great potentiality in monitoring programmes (cf. Wiederholm 1979, 1980b). The palaeolimnological investigation of zoobenthos may also widen the monitoring programmes over a longer period of time (e.g. Hofmann 1971, Warwick 1975).

The benthic lake typologies form a basis for the use of zoobenthos in lake monitoring. The lake typology used by Brundin (1949, 1956, 1958) is the most precise in this field (Brinkhurst 1974). It is based on the profundal chironomid fauna in regularly stratified and harmonic lakes in North Europe. Brundin's typology was later developed by Saether (1975, 1979) and Wiederholm (1980a), which considered the causal relationship between the composition of the profundal chironomid fauna and the trophic status of lakes.

The use of chironomid benthos in lake monitoring does, however, still have some shortcomings. The lake typologies are restrictred to relatively deep lakes, which are not very common, at least in Finland. The benthic lake typologies of Valle (1927) and Järnefelt (1953) clearly demonstrate the difficulties in classifying Finnish lakes. Both of them contain several shallow water associations whose relation to the trophic status is confusing (Brinkhurst 1974). Another shortcoming is that these typologies are based solely on a few type species which may be absent from the benthos or occur there only in small numbers. Thirdly, the lake type may often be recognised intuitively without any statistical method being employed (Wiederholm 1981).

The aim of this study is to test the benthic lake type concept in a lake area typical of Finland and to attempt to find answers to the following questions:

1) Is it possible to classify the total profundal chironomid fauna with multivariate statistical methods so that the produced types are relevant to the real differences in trophic status and water quality?

2) Is it possible to apply the classification to shallow water associations as well, these being typical to Finnish lakes?

2. Study area

The study area comprises the southern part of the drainage basin of the river Kokemäenjoki (Fig. 1). The lakes studied were Pyhäjärvi (stations 2-3), Vanajavesi (stations 4-12), Mallasvesi (stations 13-14), Ilmoilanselkä (station 15), Hauhonselkä (station 16), Iso-Roinevesi (station 17), Pälkänevesi (station 18), Roine (station 20) and Längelmävesi (stations 21-23). A general description of the study area has been presented elsewhere (Ryhänen 1962, Aho 1966, Särkkä & Aho 1980, Kansanen & Aho 1981).

Morphometrically the lakes of the study area can be divided into three categories:

1) Shallow (max. depth 15 m), unstratified basins with a warm profundal zone. The renewal time is usually short (flow-through basins typical of Finnish watercourses). Stations 3, 4, 9, 11, 12 and 16.

2) Relatively shallow basins, where the depressions (max. 25 m) are small in volume. The thermal stratification is unstable and therefore the profundal is occasionally warm. Stations 2, 5, 6, 7, 8, 10, 13 and 14.

3) Deep (30-65 m), regularly stratified basins with a cold profundal zone. Stations 17, 18, 20, 21, 22 and 23.

As there were insufficient direct measurements of the primary production capacity of phytoplankton, the trophic state of the lakes is expressed by the total phosphorus and nitrogen concentration of the surface water, Secchi disc transparency (Forsberg & Ryding 1980) and the mean total phytoplankton biomass values (Heinonen 1980, Table 1). It can be seen that lakes Pyhäjärvi and Vanajavesi are both eutrophic water bodies, some of the stations even being hypereutrophic. In both of them this is due to the edaphic factors and Man's impact. The lakes are more or less polluted by industrial effluents and municipal sewage. The rest of the study area is in an almost natural condition. Lakes Ilmoilanselkä and Hauhonselkä are clearly slightly eutrophic or mesotrophic, the others being oligotrophic. There are only a few restricted areas in these lakes which are slightly polluted by municipal sewage.

Table 2 indicates the most important differences in water quality characteristics between the polluted and unpolluted lakes. The most striking difference in the surface water is seen in the values of specific conductivity, because there is no overlapping at all between these lake groups.

The high content of humus substances is typical of Finnish lakes. Because the total area of peatlands is small in the southern drainage basin of the river Kokemäenjoki, polyhumic lakes are lacking. Stations 2-12 are mesohumic lakes (mean water colour 51-83 mg Pt l^{-1}), while the others are oligohumic lakes (mean water colour 11-36 mg Pt l^{-1}).

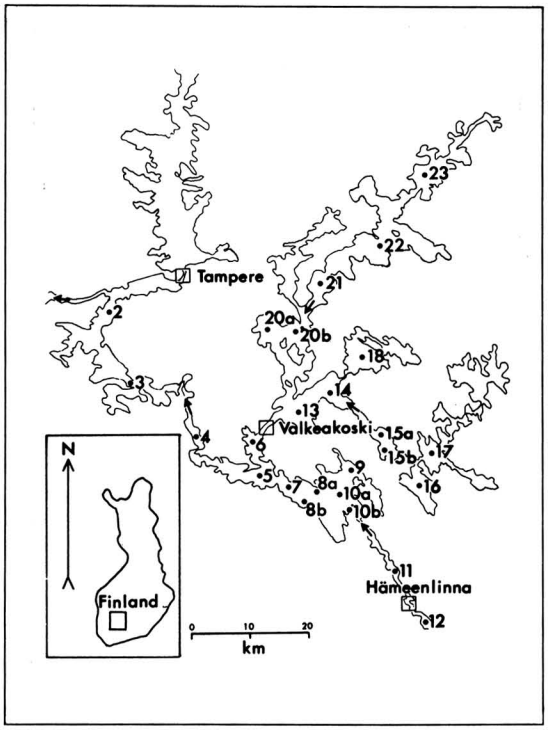

Fig. 1. The study area and sampling stations. The arrows indicate the direction of flow.

Variations in the distribution and abundance of oligochaete worms, especially as a function of the varying degrees of eutrophication and pollution, were studied by Särkkä & Aho (1980) in the same area using the same benthos material. Because the statistical methods used in the analysis of oligochaete material were different in the present study, any direct comparison between these studies was difficult. The comparison between oligochaete and chironomid fauna will be made later, when a synthesis of the benthos in the study area is published.

3. Material and methods

This study is based on two sets of data. The first set is composed of the number of individuals for each chironomid taxa (usually species, but also genus or larval type). The collections were made between 2 July and 20 August in the years 1965-1967 at 22 stations (labelled 2-23 in Fig. 1).

The methods used in sampling have been described previously by Särkkä & Aho (1980). The samples were taken, as a rule, from two sampling transects in each station (Fig. 1). The sampling transects were situated in opposite directions from the deepest place and the samples were taken once at each station, except for stations 5, 7, 15 and 17, which were sampled in two (stations 15 and 17) or three (stations 5 and 7) successive years. Each sample usually consisted of six hauls with an Ekman-Birge dredge (263 cm^2 in area, height 23 cm,

Table 1. Trophic classification of the lakes studied according to the total phosphorus and total nitrogen content of the surface water, Secchi disc transparency (Forsberg & Ryding 1980) and the mean total phytoplankton biomass (Heinonen 1980). H = hypereutrophic, E = eutrophic, M = mesotrophic, O = oligotrophic and U = ultraoligotrophic.

Lake (stations)	*n*	Total-P (mg/m^3)	Total-N (mg/m^3)	Secchi (m)	Biomass (mg/l)
Pyhäjärvi (2-3)	2	75 E	1250 E	1.6 E	1.92 M
Vanajavesi (4-12)	10	103 H	1280 E	1.4 E	11.50 H
Mallasvesi (13-14)	3	20 M	330 O	3.7 M	0.13 U
Ilmoilanselkä (15)	1	40 E	500 M	2.1 E	0.24 O
Hauhonselkä (16)	1	10 O	600 M	1.8 E	2.48 M
Iso-Roinevesi (17)	1	10 O	400 M	3.8 M	0.29 O
Pälkänevesi (18)	1	10 O	300 O	4.5 O	0.06 U
Roine (20)	2	10 O	300 O	3.6 M	0.13 U
Längelmävesi (21-23)	6	15 M	350 O	2.9 M	0.45 O

Table 2. Means and ranges of some water-quality characteristics measured during the summer stagnation in the years 1962-1967 at a depth of 1 m. After Särkkä & Aho (1980).

	Subarea, stations:	Polluted, 2-12		Unpolluted, 13-23	
		Mean	Range	Mean	Range
Oxygen content (mg/l)		7.7	0.1-9.8	9.1	8.0-10.6
Spec. conductivity (18° C, μS/cm)		97	73-188	48	35-61
$KMnO_4$ consumption (mg/l)		69	48-193	24	11-55
pH		6.9	5.7-7.5	7.1	6.6-7.8
Colour of water (mg Pt/l)		62	30-100	26	5-80
Total phosphorus (mg/l)		0.10	0.02-0.48	0.02	0.01-0.09
Total nitrogen (mg/l)		1.3	0.4-3.1	0.4	0.1-0.6
Secchi disc visibility (m)		1.4	0.8-1.9	3.3	1.8-4.5

weight 6.7 kg), the hauls being made at standard depths of 1, 3, 5, 7, 10, 15, 20, 30, 40, 50, 60 m and at the greatest depth in the lake basin. In some cases the number of hauls was reduced to from two to five because large amounts of detritus or lake ochre interfered with sampling, but the reduced number of samples constituted only 9.2 % of the total number of samples (n=315). The total sampled area of the whole study was 49.1 m^2. Despite certain criticism which has been levelled at the use of the Ekman dredge (e.g. Hakala 1971), the sampling technique is in accord with the aims of this study.

The samples were sieved through a 0.6 mm mesh. The material left on the sieve was studied carefully on the same day. The organisms were preserved in 80 % alcohol. The whole material consisted of about 42 300 individuals, of which chironomids formed the most important group.

The second data set consists of the environmental variables obtained by the National Board of Waters of Finland and the local association of water protection, as a vertical series of observations in the main deep of the lake basin. The references for the environmental variables are given in detail by Aho (1978). The water analysis technique is described by Laaksonen (1972).

The environmental variables used in this study were measured in the years 1962-67. Most of these measurements (82.7 %) were made either in the same years as the zoobenthos collections were made, or in the year preceding these (1964). The mean values used in this study are based on from three to six observations.

The variables used can be classified into three categories:

1) Variables describing physico-chemical condition in the environment of benthos near the bottom surface. For each chironomid observation there is a corresponding measurement of temperature, oxygen concentration, specific conductivity, $KMnO_4$ consumption, pH and water colour from the same depth. Both summer and winter measurements were used in the analysis, except for water colour, which was measured only in summer.

2) Variables describing trophic conditions in the trophogenic layer. The impact of these variables on benthos is merely indirect (through phytoplankton production). These variables were total phosphorus and nitrogen concentration of the surface water (1-5 m) and Secchi disc transparency. Only summer averages were used. Nutrient concentration values were corrected by dividing them with the mean depth of the basin (cf. Saether 1979, Wiederholm 1980a).

3) Variables describing the morphometric features of the basin. One variable, the mean depth, was chosen and this was also used to correct the nutrient concentrations.

The numerical treatment of the biological data was made using the hierarchial classification analysis technique. The original data matrix was reduced in size by the substitution of zero values for all species having a lower abundance than 2 % of the total number of chironomids at a single station. This was done to eliminate inconsistencies generated by the different sample sizes employed for different stations (Clifford & Stephenson 1975). Several similarity indices were used: the percentage similarity of the community (Renkonen 1938), the Bray-Curtis measure (Clifford & Stephenson 1975),

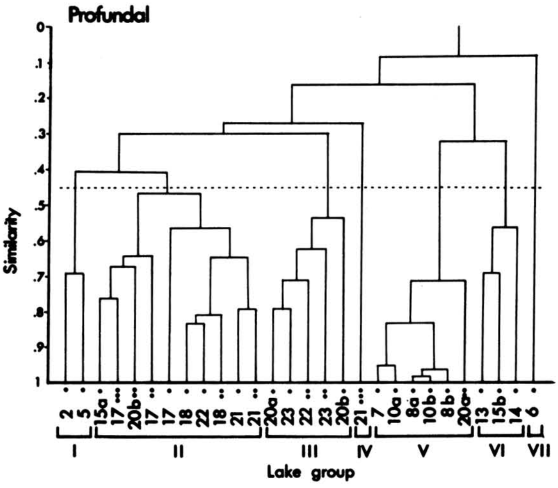

Fig. 2. Hierarchial cluster analysis of profundal stations based on abundancies of 22 chironomid taxa. The vertical axis shows the similarity calculated as the percentage similarity of Renkonen (1938). On the horizontal axis are lake codes and group code numbers. Depth zones are indicated by black dots as follows: one dot 15–20 m, two dots 30–40 m, three dots 50–60 m.

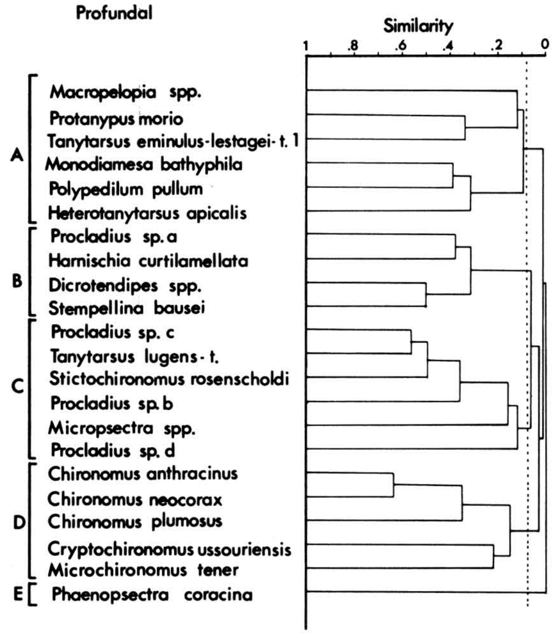

Fig. 3. Inverse cluster analysis of profundal data. The horizontal axis shows the the percentage similarity of taxa. On the vertical axis are the names of taxa and group code letters.

Table 3. The two-way table of coincidence relating the profundal lake groups to species clusters. Zero entries have been made to replace the very low abundancies, see text.

Species clusters / Stations	2 Pyhäjärvi	5 Vanajavesi	15a Ilmoilanselkä	17 Iso-Roinevesi 50 - 60 m	20b Roine 30 m	17 Iso-Roinevesi 30 - 40 m	17 Iso-Roinevesi 15 - 20 m	18 Päläkänevesi 15 - 20 m	22 Längelmävesi 15 - 20 m	18 Pälkänevesi 30 m	21 Längelmävesi 15 - 20 m	21 Längelmävesi 30 - 40 m	20a Roine 15 - 20 m	23 Längelmävesi 15 - 20 m	22 Längelmävesi 30 - 40 m	23 Längelmävesi 30 - 40 m	20b Roine 15 - 20 m	21 Längelmävesi 50 m	7 Vanajavesi	10a Vanajavesi	8a Vanajavesi	10b Vanajavesi	8b Vanajavesi	20a Roine 30 m	13 Mallasvesi	15b Ilmoilanselkä	14 Mallasvesi	6 Vanajavesi
	I		II										III					IV	V						VI			VII
A Macropelopia spp.	-	-	-	-	-	-	2	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-
P.morio	-	-	-	-	-	-	3	0	-	0	8	0	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-
T.eminulus-lestagei t.2	-	-	-	-	-	-	0	-	0	-	6	6	-	-	0	0	-	-	-	-	-	-	-	-	-	0	6	-
M.bathyphila	-	-	-	-	-	6	7	13	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-
P.pullum	-	-	-	-	-	5	2	0	-	-	0	6	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-
H.apicalis	-	-	-	-	-	13	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B Procladius sp. a	-	0	9	-	6	-	-	0	5	-	-	-	-	11	6	-	25	-	0	0	0	0	-	-	0	0	13	-
H.curtimellata	-	-	-	-	-	-	-	0	0	-	-	-	3	-	4	-	3	-	-	-	-	-	-	-	-	0	-	-
Dicrotendipes sp.	-	-	-	-	-	-	-	-	3	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
S.bausei	-	-	-	-	-	-	-	0	6	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-
C Procladius sp. c	19	51	130	6	133	46	13	149	48	152	105	51	19	25	8	22	28	6	0	0	0	0	-	19	-	75	38	-
T.lugens-type	-	-	-	-	19	5	2	113	21	38	81	40	3	11	15	6	0	6	-	-	-	-	-	6	-	0	-	-
S.rosenscholdi	-	-	-	-	-	-	7	138	35	139	29	6	54	72	53	82	35	-	-	-	-	-	-	-	-	-	-	-
Procladius sp. b	3	0	-	2	6	0	5	0	0	-	5	21	10	13	11	13	6	13	0	0	0	-	-	32	0	0	13	-
Micropsectra spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	73	-	-	-	-	-	-	-	-	-	-	-	-
Procladius sp. d	-	-	-	-	-	-	-	-	-	-	-	0	-	3	-	0	-	6	0	0	-	0	-	-	-	-	-	-
D C.anthracinus-type	-	-	-	-	25	-	-	-	0	-	-	-	-	-	8	-	-	-	1217	1191	2422	3276	2422	159	228	0	33	-
C.salinarius-type	16	3	22	-	19	-	-	-	0	-	-	-	-	-	8	-	3	-	436	544	292	484	444	-	558	226	76	-
C.plumosus	16	44	-	-	13	-	-	-	0	-	-	-	-	-	-	-	-	-	38	51	-	0	0	-	19	0	6	-
C.ussouriensis	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	-
M.tener	3	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	0	0	-	-	-	-	0	-	19	-
E P.coracina (Zett)	-	-	-	-	-	-	-	-	-	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-

Table 4. Comparison of profundal lake groups on the basis of the best 'indicator species'. Single-station groups IV and VII were excluded. The *F*-values of group I were calculated from three primary observations. *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$.

Taxon	Mean no. individuals/m²					*F*
	I	II	III	V	VI	(4.22 df)
Chironomus anthracinus-type	0	2.5	1.6	1614.5	88.5	33.5***
Chironomus salinarius-type	4.5	4.1	2.2	366.7	286.7	11.7***
Stictochironomus rosenscholdi	0	35.4	59.2	0	0	9.1***
Procladius c-type	35.0	83.3	20.4	3.1	37.7	8.5***
Harnischia curtilamellata	0	0	2.0	0	0	6.6**
Tanytarsus lugens-type	0	31.9	7.0	1.0	0	5.1**
Chironomus plumosus	30.0	1.3	0	14.8	8.3	4.6**
Microchironomus tener	5.0	0	1.5	0	9.5	3.3*

Kendall's rank correlation test (Ghent 1963) and the Canberra metric coefficient (Clifford & Stephenson 1975) (the first three both with, and without, logarithmic transformation of data). The classification was made as a group average clustering of stations. The classification results were usually slightly different depending on the similarity index used. To save computer time, only one of them was selected for further analysis. This was done on the basis of the knowledge of the trophic status and water quality of the lakes in each group formed (cf. Table 1). Finally, an inverse cluster analysis was made for taxa to form species clusters corresponding to lake groups. They were compared in two-way tables of coindicence. The *F*-statistic, which is the ratio of the among-groups to the within-groups variance of log-abundance, was calculated for each species, and used as an index of degree to which the lake groups are defined by the species. *F*-values were not used here as tests of significance.

The statistical treatment of the environmental data was made using discriminant analysis (SPSS). Fifteen environmental variables were used in the direct analysis as discriminatory variables. Groups of stations were defined by the cluster analysis of the corresponding biological data (Green & Vascotto 1978, Green 1979).

4. Results

4.1. Profundal zone

Because considerable vertical variations are exhibited by lakes, it was appropriate to take into account the morphometric features of lake basins and to compare the corresponding depth zones. When an attempt was made to divide the benthic material into only two zones ('littoral' and 'profundal'), no clear separation of groups was achieved, especially in the shallow water region. Hence, the whole material was divided into four depth classes: littoral, upper sublittoral, lower sublittoral and profundal.

The profundal zone comprises that part of the lake bottom lying between the deepest point of the lake basin and the average upper limit of the hypolimnion (Eggleton 1931). This criterion was also applied to those lakes in which the thermal stratification was more or less labile (hypolimnion occasionally warm). Shallow, unstratified basins have no cold profundal zone and their deeps were classified as the lower sublittoral zone. Stations 3, 4, 9, 11, 12 and 16 were then excluded.

4.1.1. Analysis of the chironomid associations

The original data matrix is composed of 34 taxa, from which 22 were taken into the hierarchial cluster analysis after data reduction. The complete list of species and their abundancies is presented in Appendix 1. The similarity coefficient chosen was the percentage similarity of the community (Renkonen 1938), which would appear to be suitable for the profundal data. A mean value of the chironomid density was calculated at each station by combining depths of 15–20, 30–40 and 50–60 m, respectively. The total number of 'samples' was then 28.

The result of the hierarchial cluster analysis of stations is shown in Fig. 2. Seven lake groups were formed. Five of them comprise several (2–10) stations. Two groups have only one station. Group IV has both qualitatively and quantitatively sparse bottom fauna. Group VII has no fauna at all.

An inverse analysis produced five species clusters (Fig. 3). These two dendrograms are best compared with each other in a two-way table of coincidence (Table 3). All species having an *F*-probability of less than 0.05 are listed in order of the magnitude of their contribution to lake group definition in Table 4 (cf. p. 000).

Species clusters A, B and E contain taxa having a low constancy (Table 3). Clusters A and E are limited almost entirely to lake group II. Species cluster B is characteristic of lake group III. More important are species clusters C and D, which have both common and abundant species.

Lake group I is characterized by a *Chironomus plumosus* association (Table 4). Although dominant, *Procladius c* is not as typical of this lake group as *C. plumosus,* because it has a high dominance and abundance in many other groups as well. Lake group V can easily be relegated according to its dominant species to the *Chironomus anthracinus* lake type. This larval type, which probably belongs entirely to *C. anthracinus* Zett., has a very high indicator value. Lake group VI is almost as easy to name as a *Chironomus salinarius* lake type on the basis of this dominant larval type. Lake groups II and III appear to have similar faunae. The most typical species in both groups are *Stictochironomus rosenscholdi* and *Tanytarsus lugens. Procladius c* is common in both groups. Thus, it is unreasonable to name these lake groups according to a single species. Both are characterized by a *Stictochironomus rosenscholdi - Tanytarsus lugens* Type association. Group separation is mainly due to a slight difference in the abundance of these species and *Procladius c.*

4.1.2. Analysis of the environmental variables

The direct discriminant analysis was used to test whether there is a significant difference in water quality between lake groups defined by the hierarchial classification analysis of the biological variables. The discriminant analysis shows which linear combinations of the fifteen environmental variables give the best separation of the defined lake groups. It also gives an indication of the relative importance of each variable in separation.

The results of the analysis are shown in Table 5. Four discriminant functions were derived. The first two functions collectively contribute up to 85% of the separation. Fig. 4 shows the separation of the lake groups on the first two discriminant functions. Lake groups I and V are separated on the first discriminant function from three other lake groups, which have considerable overlap along the horizontal axis. Table 5 shows that the most important variables in this function are summer pH, summer conductivity, total nitrogen in the surface water, mean depth and summer temperature. It is obvious that this function separates the eutrophic and polluted stations from unpolluted and more oligotrophic lakes. Lake group I (stations 2 and 5) comprises the most polluted stations having, for example, a mean summer specific conductivity of 103.2 µS/cm (range 97-111). The stations in lake group V (7, 8, 10 and 20a) are less polluted but are eutrophic, except for station 20a, which is

Table 5. Discriminant analysis of the profundal data: variables and standardized discriminant function coefficients.

Discriminant function:	1	2
Per cent of separation:	54	31
Summer temperature	0.47	1.26
Winter temperature	-0.35	1.47
Summer oxygen concentration	-0.35	0.10
Winter oxygen concentration	-0.19	0.47
Summer specific conductivity	0.89	-0.30
Winter specific conductivity	-0.17	0.25
Summer $KMnO_4$-consumption	0.26	1.20
Winter $KMnO_4$-consumption	0.20	-0.29
Summer pH	-0.94	0.18
Winter pH	-0.05	-0.50
Summer water colour	-0.32	1.03
Summer total phosphorus[1]	-0.01	1.09
Summer total nitrogen[1]	0.63	0.42
Summer Secchi disc transparency	0.39	3.37
Mean depth	0.52	-0.40

[1] Values in surface water corrected with mean depth

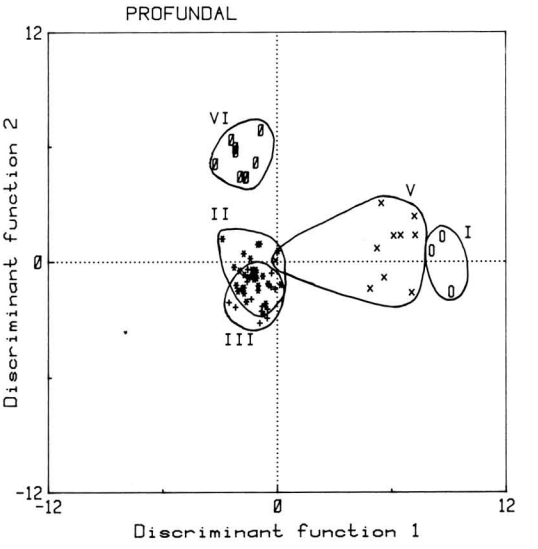

Fig. 4. The separation of the profundal lake groups on the basis of the first two discriminant functions of the fifteen environmental variables.

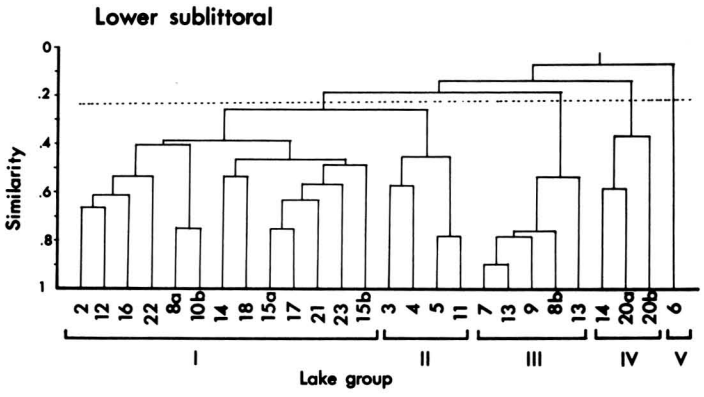

Fig. 5. Hierarchial cluster analysis of lower sublittoral stations based on the chironomid fauna. The vertical axis shows the similarity calculated as the percentage similarity of Renkonen (1938).

oligotrophic. Lake group V has a mean summer specific conductivity of 94.3 μS/cm (range 47–107). Lake groups II, III and VI comprise unpolluted, more or less oligotrophic stations having a mean summer specific conductivity of 51.0 (40–68), 41.3 (36–40) and 55.3 (53–59) μS/cm, respectively. Morphometrically, lake groups I and V differ from other lake groups in having a lower mean depth. The thermal stratification is also usually labile in these lakes. Lake groups II and III are, in particular, deep, regularly stratifying basins.

The second discriminant function separates lake group VI from the other unpolluted lake groups, II and III (Fig. 4). Lake groups II and III still exhibit a considerable overlap. The most important variables in this function are Secchi disc transparency, winter temperature, summer temperature and summer $KMnO_4$ consumption (Table 5). Group VI is a unique combination of lakes which are oligotrophic or slightly eutrophic clearwater lakes, but which have high hypolimnetic water temperatures, especially in winter. As mentioned by Aho (1978), Lake Mallasvesi (stations 13 and 14) is not a typical Finnish oligotrophic water body because its winter temperature is very high (group mean 3.9 C, while even 6.3 C has been measured). This is believed to be caused by ground water upwelling in the deeps. The deeper water layers, especially in winter, are rich in iron and other inorganic compounds.

It can be stated that the classification of the profundal chironomid fauna produces lake types which are ecologically meaningful and have some indicator value. The composition of the chironomid fauna seems to depend on the trophic state and water quality.

4.2. Sublittoral zone

The sublittoral can be defined as the zone between the lower limit of rooted vegetation and the average upper limit of the hypolimnion in stratified lakes (Eggleton 1931). The sublittoral is a far less uniform environment than the profundal zone because there are sharp vertical physical and chemical gradients at these depths (e.g. vertical decrease in wave energy, light penetration, temperature, etc.). There is a clear sublittoral minimum in the bathymetric distribution of the benthos. Hence, it is not possible to calculate any representative means of chironomid abundance for the whole sublittoral zone. In this study sublittoral is divided into two subzones, the lower and upper sublittoral. Although the absolute limit for the sublittoral differs somewhat from lake to lake, all samples taken from depths of 7 m or deeper were defined as lower sublittoral samples (if not profundal samples). The upper sublittoral then comprised depths of 3–5 m. This schematic division into depth zones was seen to be most suitable for the present material and its statistical treatment. Attempts were made to define the limit between littoral zone and sublittoral zone separately at each station on the basis of total macrozoobenthos. In most cases this left room for interpretation at a depth of 3–5 m.

In the hierarchial classification analysis of the biological data in the lower sublittoral zone five lake groups were formed when the percentage similarity of Renkonen (1938) was used as a similarity index (Fig. 5). It is obvious that groups I and III comprise both eutrophic-polluted and oligotrophic stations (cf. Table 1). Instead, groups II (eutrophic-polluted), IV (oligotrophic)

and V (polluted) are uniform in relation to the water quality. This situation did not change when other measures of similarity were applied.

The results of the discriminant analysis of fifteen environmental variables demonstrate this well. Fig. 6 shows that there is considerable overlapping between lake groups (cf. Fig. 4). Discriminant function 1, where the most important variables are summer $KMnO_4$ consumption, winter specific conductivity and pH only sharply separates lake group II from other groups. The overlapping on discriminant function 2 is even more evident than on the first function.

A feature of lake group II is the very high dominance of *Chironomus plumosus,* which is absent or rare in other lake groups. It appears to be difficult to find such ecologically meaningful lake types based on the lower sublittoral fauna as in the profundal zone. Only when eutrophication and pollution have progressed far beyond the natural state may typical *C. plumosus* associations develop at this depth zone. These have some indicator value, just as they have in the profundal zone. A complete list of species together with their abundancies is presented in Appendix 1.

In the upper sublittoral zone (3–5 m) four groups of lakes were formed when the Canberra metric coefficient was used in the classification of biological data (Clifford & Stephenson 1974, Fig. 7). The use of the percentage similarity of Renkonen (1938) gave almost identical results. A mean value of chironomid density was calculated for each station by combining depths of 3 and 5 m. The total number of 'samples' was then 24. Fig. 7 indicates that the faunal differences between lake groups are slight in the upper sublittoral. An inverse analysis of taxa produced 6 species clusters, which are compared with lake groups in a two-way table of coincidence (Table 6). All taxa having a F-probability of lower than 0.05 are listed in Table 7.

The analysis shows that lake groups II and III have a very similar fauna. There are only slight differences in the abundance of species, of which *Procladius* sp. *a* and *b* are the most important. Lake group IV (station 6) differs, in contrast, very distinctly from other groups having only 2 species. *Chironomus plumosus* has a dominance of 98 % in the total fauna at this polluted station. Lake group I also has some distinctive features. *Chironomus plumosus* and *Microchironomus tener* are here distinctly more common than in groups II and III. Complete faunal lists are given in Appendix 1.

Table 7. Comparison of upper sublittoral lake groups on the basis of the best 'indicator species'. Group IV, with only one station, was excluded. Significancies as in Table 4.

	Mean no. individuals/m²			*F*
	I	II	III	(2.21 df)
Chironomus plumosus	193.7	17.0	0	22.2***
Procladius sp. *b*	0	12.9	32.6	21.2***
Microchironomus tener	18.1	1.1	1.1	11.0***
Procladius sp. a	76.7	110.3	37.1	6.9**
Cryptochironomus defectus- type 2	0	0.8	5.6	6.4**
Tanytarsus eminulus-lestagei- type 2	2.1	21.4	3.0	5.5*
Tanytarsus mendax-type	19.7	0.6	0	5.2*
Cladotanytarsus mancus-type	0	5.3	8.1	4.8*
Stictochironomus sticticus	0	10.9	0.7	4.6*
Demicryptochironomus vulneratus	0	0	3.7	4.5*
Stempellina subglabripennis	0	0	11.6	3.8*

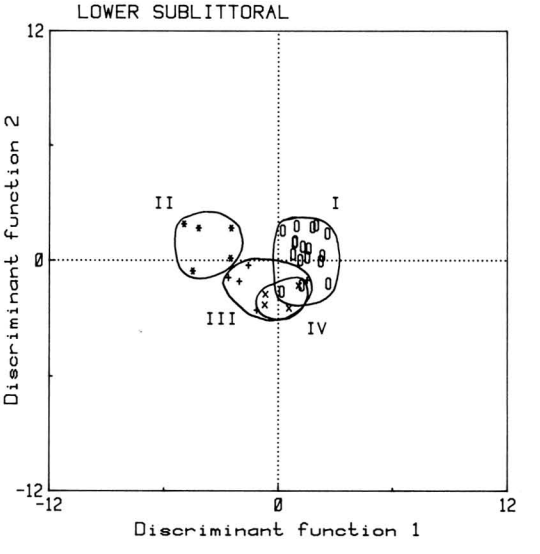

Fig. 6. The separation of the sublittoral lake groups on the basis of the first two discriminant functions of the fifteen environmental variables.

Despite the generally slight faunal differences between upper sublittoral lake groups, these would appear to be meaningful in relation to the trophic status and water quality. The results of the discriminant analysis show this well (Fig. 8). Two discriminant functions were derived (Table 8). Very good separation is achieved on discriminant function 1, which contributes 76 %

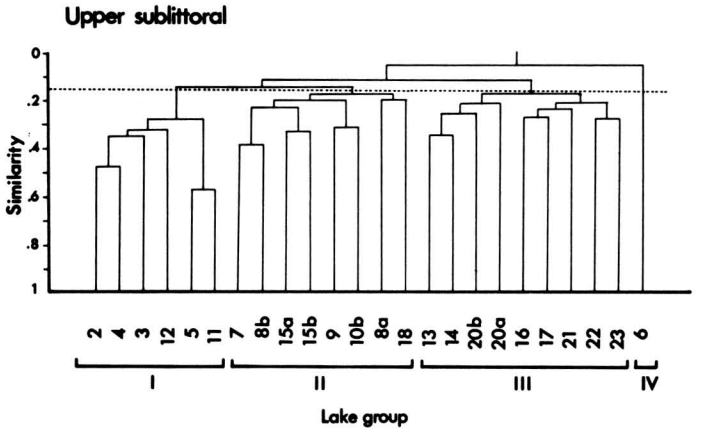

Fig. 7. Hierarchial cluster analysis of upper sublittoral stations based on the abundancies of 39 chironomid taxa. The similarity is calculated as the Canberra metric coefficient (Clifford & Stephenson 1974).

Table 6. The two-way table of coincidence relating the upper sublittoral lake groups to species clusters. Zero entries have been made to replace the very low abundancies, see text.

Species clusters	Stations	2 Pyhäjärvi	4 Vanajavesi	3 Pyhäjärvi	12 Vanajavesi	5 Vanajavesi	11 Vanajavesi	7 Vanajavesi	8b Vanajavesi	15a Ilmoilanselkä	15b Ilmoilanselkä	9 Vanajavesi	10b Vanajavesi	8a Vanajavesi	18 Pälkänevesi	13 Mallasvesi	14 Mallasvesi	20b Roine	20a Roine	16 Hauhonselkä	17 Iso-Roinevesi	21 Längelmävesi	22 Längelmävesi	23 Längelmävesi	6 Vanajavesi
		I						II								III									IV
A	A.monilis-type	–	–	–	–	–	–	–	–	–	–	–	–	–	29	–	10	6	0	–	4	–	–	–	–
	C.viridula	–	0	–	–	0	–	–	–	–	–	–	–	–	19	–	–	13	29	3	3	5	–	0	–
	Macropelopia spp.	–	–	–	–	–	–	0	–	0	5	–	–	–	29	–	–	–	8	–	15	–	–	–	–
	Procladius sp. b	0	–	–	–	0	–	15	6	19	26	–	8	0	29	21	57	16	30	3	26	38	46	56	–
	T.eminulus-lestagei-t.2	0	13	0	–	0	–	13	25	–	39	19	17	0	57	–	–	–	0	2	13	11	0	0	–
	S.sticticus	–	–	–	–	–	–	17	–	–	–	–	13	35	22	–	–	–	0	–	0	6	–	–	–
	T.eminulus-lestagei t.1	–	0	–	0	0	–	0	0	–	0	5	11	32	40	–	–	–	22	2	10	0	10	0	–
	H.marcidus	–	–	–	–	–	–	–	–	–	0	–	0	0	0	–	–	–	19	–	3	–	–	0	–
	P.prasinatus	–	–	–	–	–	–	–	–	0	–	–	–	–	0	–	–	–	16	–	3	–	–	5	–
	N.brayi	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	6	–	13	–	–	0	–	0	–
	C.defectus-t.2	0	–	0	–	–	0	–	–	0	–	6	–	–	0	13	16	0	10	5	3	5	–	0	–
	C.mancus-type	–	–	–	–	–	–	–	–	–	12	30	–	–	0	11	25	13	10	–	–	6	4	3	–
	S.minor	–	–	–	–	–	–	0	0	–	6	6	13	–	0	–	–	0	13	–	–	5	–	–	–
	H.curtilamellata	–	–	0	–	–	–	0	–	0	0	–	0	1	–	–	–	0	10	–	–	0	8	–	–
	S.subglabripennis	–	–	0	–	–	–	–	–	–	–	–	0	–	0	0	–	82	10	–	–	8	4	0	–
	P.morio	–	–	–	–	–	–	–	–	6	0	–	–	–	0	0	–	0	–	–	11	0	6	8	–
	S.psammophilus-type	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–
	C.atridorsum-type	–	–	–	–	–	0	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–	5	–
	G.gripekoveni-type	–	–	–	–	–	–	–	–	–	–	–	–	–	13	–	–	–	–	–	–	–	–	–	–
	T.usmaensis-type	0	–	–	–	–	0	–	–	–	–	–	–	–	15	–	–	–	–	–	–	–	–	–	–
B	C.plumosus-type	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–
	Cryptotendipes sp.	0	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	10	16	0	0	0	–	–	–
	T.verralli-type	–	–	–	–	–	0	0	–	–	–	0	–	–	–	–	–	10	32	5	–	0	–	–	–
	D.vulneratus	–	–	–	–	–	–	–	–	–	–	0	0	–	0	15	–	10	–	3	0	0	6	0	–
	S.bausei	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	0	–	–	0	0	–	–
C	Procladius sp.d	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–	18	70	–	–
	M.bathyphila	–	–	–	–	–	–	0	0	–	–	0	–	6	0	–	–	–	–	–	–	25	–	3	–
D	Procladius sp. a	63	76	126	37	58	100	137	73	146	105	41	49	108	124	124	17	13	117	25	13	6	0	19	–
	Procladius sp. c	32	149	5	15	86	50	15	29	6	4	51	–	10	13	37	10	0	0	6	3	16	13	12	–
	C.plumosus	43	87	14	76	380	564	0	–	–	0	25	93	19	–	0	–	–	–	–	–	0	0	0	283
	M.tener	32	38	14	6	0	18	9	0	–	–	0	–	–	–	6	3	–	–	–	0	0	–	–	–
	T.mendax-type	–	73	36	10	0	0	0	–	–	–	5	0	–	–	–	–	–	–	–	–	–	–	–	–
	T.vilipennis	–	–	–	13	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
E	C.anthracinus-type	–	–	–	0	0	–	48	25	–	–	5	0	–	–	–	–	–	–	–	–	–	–	–	–
	C.salinarius-type	–	–	–	–	0	–	45	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Einfeldia sp.	11	–	8	–	–	0	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	P.bicrenatum	8	10	0	–	–	–	9	13	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–
	T.lucens-type	–	–	–	–	–	–	8	–	–	–	–	–	19	–	–	–	–	–	–	–	–	–	–	–
F	T.kraatzi	–	–	–	–	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6

Table 8. Discriminant analysis of the upper sublittoral data: variables and standardized discriminant function coefficients.

Discriminant function	1	2
Per cent of separation	76	24
Summer temperature	-0.84	0.76
Winter temperature	-0.03	-0.64
Summer oxygen concentration	-1.18	0.27
Winter oxygen concentration	1.47	-0.45
Summer specific conductivity	-0.20	0.68
Winter specific conductivity	-0.90	-0.50
Summer $KMnO_4$-consumption	-0.30	-0.13
Winter $KMnO_4$-consumption	-0.06	1.45
Summer pH	0.93	0.57
Winter pH	0.53	1.91
Summer water colour	-0.09	-1.05
Summer total phosphorus[1]	0.34	0.50
Summer total nitrogen[1]	0.56	-0.02
Summer Secchi disc transparency	-0.74	-1.15
Mean depth	1.03	1.02

[1] Values in surface water corrected with mean depth

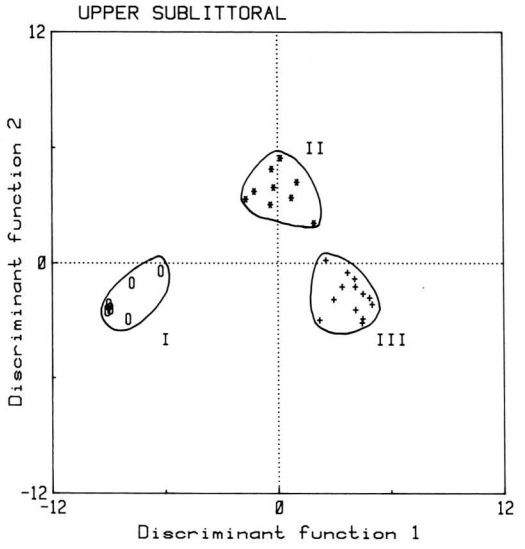

Fig. 8. The separation of the upper sublittoral lake groups on the basis of the first two discriminant functions of the fifteen environmental variables.

of the separation. Lake group I comprises eutrophic and polluted stations which, with the exception of station 2, are shallow unstratified flow-through basins. In contrast, lake group III comprises unpolluted, mostly oligotrophic stations. Group II is something of an intermediate between these two lake groups, having slightly polluted and eutrophic stations, with one oligotrophic station. Group IV (station 6) is very heavily polluted by industrial effluents.

The most important variables in discriminant function 1 are winter and summer oxygen concentration and mean depth (Table 8).

When the classification is based on the sublittoral fauna it seems preferable to divide this zone into subzones and compare the fauna at corresponding depths. In the present work upper sublittoral fauna could to be classified into meaningful groups. The differences in the fauna of oligotrophic and eutrophic lakes were, however, very small. Only lakes of advanced eutrophy and pollution differed markedly from other groups in this respect.

4.3. Littoral zone

The littoral zone can be defined as the zone from the shore line to the lower limit of rooted macrophytes (Eggleton 1931). In this study all samples taken from a 1 m depth were considered littoral samples. The littoral zone is a mosaic of microhabitats (variations caused, e.g. by the quality of vegetation and sediment). It is almost impossible to take quantitative samples with the usual benthic samplers (e.g. Ekman dredge), owing to coarse detritus and hard erosive sediments. For this reason, littoral samples are to be considered qualitative or semi-quantitative.

Of the several similarity coefficients which were attempted in the hierarchial classification analysis, the Kendall's rank correlation coefficient gave well-defined lake groups (Fig. 9). Other indices either did not produce any meaningful groups in relation to the trophic status and water quality, or the differences between groups were negligible.

The extremely polluted station 6 was again isolated in its own group (only 3 species). Lake group II comprises only unpolluted lakes. Large lake groups I and III, however, have both eutrophic-polluted and oligotrophic, unpolluted lakes. It is thus obvious that differences in water quality do not explain the classification results. This can also be seen in Fig. 10. There is overlapping between groups and the actual differences on discriminant functions are far less evident than, for instance, in the profundal zone (cf. Fig. 4) or upper sublittoral zone (Fig. 8). For a complete list of littoral chironomid fauna see Appendix 1.

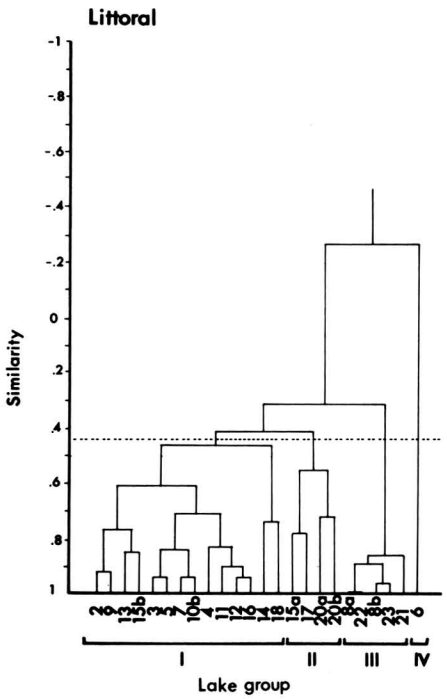

Fig. 9. Hierarchial cluster analysis of littoral stations based on the chironomid fauna. The similarity is calculated as Kendall's rank correlation coefficient (Ghent 1963).

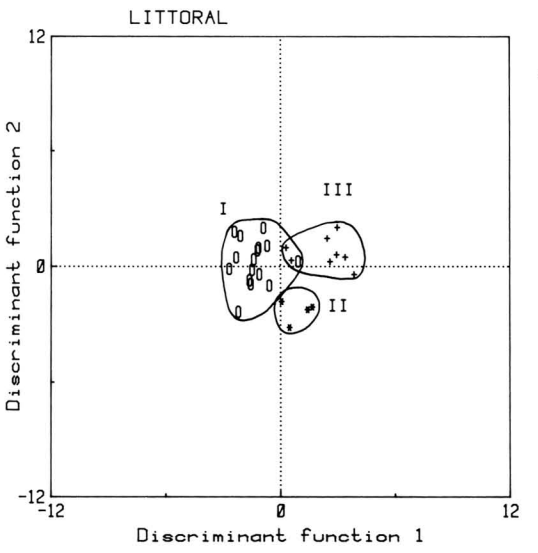

Fig. 10. The separation of the littoral lake groups on the basis of the first two discriminant functions of the fifteen environmental variables.

5. Discussion

5.1. Classification of profundal associations

Brundin (1956, 1958) proposes the following lake type system for regularly stratifying oligohumic lakes:

I *Heterotrissocladius subpilosus* lakes (ultra-oligotrophic)
I/II *Tanytarsus-Heterotrissocladius* lakes (oligotrophic)
II *Tanytarsus lugens* lakes (moderately oligotrophic)
II/III *Stictochironomus-Sergentia* lakes (mesotrophic)
III *Chironomus* lakes (eutrophic)
a) *Chironomus anthracinus* lakes (moderately eutrophic)
b) *Chironomus plumosus* lakes (strongly eutrophic)

This system is not based entirely on the presence or absence of these species, but takes into account several other species having equivalent ecological requirements.

If the results of our classification analysis of the profundal data are compared with this system, it can be seen that the ultraoligotrophic *Heterotrissocladius subpilosus* category is lacking in the study area. The lakes studied most closely resemble the oligotrophic-eutrophic benthic types (II-III).

Our lake groups II and III (Table 3 and 4) have the same dominant species, but their mutual importance is different. This type of fauna seems to be very close to a *Tanytarsus lugens* community. From the ten characteristic species of this community type mentioned by Brundin (1956), *Protanypus morio, Monodiamesa bathyphila, Phaenopsectra (Sergentia) coracina, Micropsectra* spp. (incl. *Lauterbornia*), *Stictochironomus rosenscholdi* and *Tanytarsus lugens* type (probably most larvae belong to the type species) were found almost entirely in these lake groups. The two last mentioned species were most characteristic of these groups. The discriminant analysis showed that there was no significant difference in trophic status or water quality between them. The lakes of both groups are all oligotrophic, oligohumic and regularly stratified water bodies.

Typical mesotrophic *Stictochironomus-Sergentia* lakes in the Brundin sense seem to be absent from the study area. Lake groups I and V belong to eutrophic *Chironomus* lakes. Both groups with good reason can be named according to their

dominant *Chironomus* species: *C. plumosus* and *C. anthracinus,* respectively. Kansanen & Aho (1981) analyzed these associations in detail in a part of the study area. The discriminant analysis revealed differences in their trophic status and water quality. Both lake groups differed significantly from oligotrophic lake groups. The main difference between these associations appears to be in the oxygen conditions, which are poorer in the *C. plumosus* lakes than in the *C. anthracinus* lakes (cf. Kansanen & Aho 1981). It may be said that both lake groups are faunistically well defined and that they are related to differences in environmental variables. All the lakes in both groups are eutrophic and more or less polluted. On the other hand they are mesohumic and their thermal stratification is usually labile.

The third *Chironomus* lake group (VI) is interesting as it has no counterpart in Brundin's system. Discriminant analysis showed that this *C. salinarius* association has its own position in the fifteen dimensional environmental space analyzed. Despite being oligotrophic or slightly eutrophic clearwater lakes, these lakes differ from other unpolluted lakes in having unusual conditions in the hypolimnion. Lake Mallasvesi and the main basin of Ilmoilanselkä belong to this association type. Lake Mallasvesi is irregularly stratified and it has high hypolimnetic temperatures both in summer (labile stratification) and in winter (ground water upwelling?). Although it is stratified, Lake Ilmoilanselkä has a hypolimnion of small volume (the depression is funnel-shaped). As Brundin (1949) points out, this causes abnormally high sedimentation in the deepwater region. Common to both cases are the enrichment of hypolimnetic water layers by organic and inorganic materials (in Mallasvesi due to groundwater upwelling, in Ilmoilanselkä due to the slight eutrophy and morphometry of the lake basin) and high temperatures. This may cause a high oxygen consumption and the development of a *Chironomus* community. A similar phenomenon can be seen in one deep of Lake Roine, which was relegated to lake group V. The abundance of *Chironomus* larvae is, however, in these circumstances lower than in polluted and eutrophic lakes.

It seems obvious that larvae of *Chironomus salinarius*-gr. have a broader niche than other *Chironomus* species. They probably have lower nutritional requirements and a higher tolerance to oxygen depletion than, e.g. *C. anthracinus. C. salinarius*-gr. is common in both *C. anthracinus* and *C. plumosus* associations. It is well adapted to the unfavourable nutritional conditions (compared with eutrophic lakes) and low oxygen concentrations (compared with normal oligotrophic lakes) typical of such oligotrophic lakes as Lake Mallasvesi. The actual identity of the *C. salinarius*-gr. was investigated by rearing larvae to adults (Kansanen, unpublished). They were found to belong to a new species, described by Wülker & Butler (1983) as *Chironomus neocorax* n.sp.

As a conclusion, the hierarchial classification analysis of the profundal chironomid associations produced well-defined groups, which occupy a different position in the multidimensional environmental space analyzed with the multiple discriminant analysis. In the oligotrophic category only two subgroups were formed which were associated with no significant difference in water quality. A contributary factor here was *Procladius* sp. *c.*, which is very common in both groups but differs in abundance in them. It is probable that *Procladius* sp. *c.* still encompasses several species.

The benthic lake type system of Brundin (1958) would appear to be applicable to the study area. It was not possible to test the hypothesis in the ultraoligotrophic and truly mesotrophic categories.

The main advantages of the quantitative classification methods are quite apparent. They objectively take the whole association into account and reduce vast amounts of biological data to clearly-defined groups. Wiederholm (1980) gives a benthic quality index based on a few indicator species having different indicator values. This kind of index is easy to use but it must be modified separately for each biogeographical region. In the study area the benthic quality index failed in many lakes owing to the absence of certain indicator species. A more useful method of defining lake type is the key to chironomid associations of the profundal zones of palearctic and nearctic lakes (Saether 1979). With some modification, it was possible to use the key successfully in the study area (see p. 000).

5.2. Classification of shallow water associations

The difficulties in creating a benthic lake typology based on a littoral or sublittoral fauna are well known. Saether (1975, 1979) gives only

general lists of characteristic sublittoral and littoral chironomids and their relation to trophic status. There are several reasons for this. These depth zones do not constitute as uniform an environment as the profundal zone. The fauna is also more diverse than in the profundal. There are many species with low abundancies and few, if any, really common type species. Due to the taxonomic difficulties, it has not been possible to identify certain taxa to the species level. This causes the loss of a great deal of information. Good examples are the genera *Procladius* and *Tanytarsus*.

When shallow water associations are classified, it is very important that lake comparisons be made in corresponding depth zones. As Brundin (1949) points out, it is not possible to compare the shallow water region with the profundal zone when the trophic status is determined on the basis of the bottom fauna.

The results of the hierarchial classification and discriminant analyses indicated that a similar distinct grouping of lakes, which is related to the trophic status and water quality, is not as easy to achieve in the shallow-water zone as it is in the profundal zone. In the littoral zone (in this study 1 m) there are great variations in bottom quality due to erosion and vegetation. Bottom quality may have a greater impact on benthos than do trophic status and water quality. Besides, it is often impossible to obtain quantitatively representative samples from hard littoral beds with an Ekman-Birge-dredge. In the lower sublittoral zone the general conditions seem to be unfavourable to the whole benthos and there are often clear sublittoral abundance minima at the depth of the thermocline (in these lakes usually 10 m). Even in the upper sublittoral zone (here 3–5 m), where the established lake groups were related to differences in the abiotic factors, the faunal differences were slight, especially those between oligotrophic and moderately eutrophic lakes.

The results indicate, however, that it may be possible to create benthic lake types based on shallow-water chironomid associations. The classification should be based on common species present in lakes. The value of rare species is very limited in this respect. In the present study *Chironomus plumosus* and *Microchironomus tener* were good indicators of strongly eutrophic and polluted habitats in the sublittoral zone. The role of common *Procladius* spp. is interesting in the separation of lakes. This genus might contain several useful indicator species having different ecological requirements in relation to water quality. A good example is *Procladius* sp. *b* (probably *Procladius signatus*) which seems to favour oligotrophic lakes. The same seems to be true with *Procladius* sp. *d* (probably *P. pectinatus*). Types *a* (*?choreus* and *?cinereus*) and *c* (*?nigriventris*) appear to be more or less eurytopic. They may still contain several species. A revision of the systematics of the genus *Procladius* and the production of useful keys to larval types or species would seem to be urgently required. The separation of larval types of the genus *Tanytarsus* in the present work indicates too that more detailed identification, if possible to species level, would produce valuable information about the environment.

5.3. Factors controlling chironomid associations

According to Brundin (1949, 1951), the primary mechanism controlling the profundal chironomid succession from oligotrophy to eutrophy is the annual minimum oxygen concentration. The availability of food is of secondary importance and becomes limiting only in ultraoligotrophic lakes. The third most important factor is temperature. This differs from the statements of Warwick (1975), Saether (1979) and Wiederholm (1980a). According to them, the availability of food is the governing factor, oxygen concentration being of secondary importance.

Although the primary aim of this study was not to elucidate what are the most important factors controlling chironomid associations, some conclusions on the results of the discriminant analysis can be drawn. The discriminant analysis produces a visual display which in itself is convincing evidence of the environmental control of biotic spatial patterns.

If the standardized discriminant function coefficients of temperature, oxygen concentration and variables describing conditions of the trophogenic layer (total-P, total-N and Secchi values) are more closely compared with the profundal data, it can be seen that oxygen concentration is surprisingly unimportant in separating the groups (Table 5). In summer only group I differed remarkably from other groups. Its group mean for oxygen was 0.8 mg/l (cf. other groups: II 6.1, III 6.4, V 4.6 and VI 5.3 mg/l). The within-group variation in both summer and winter values in all groups was great. On the other hand, variables describing trophic conditions in surface waters, especially Secchi disc visibility and total-N corrected with mean

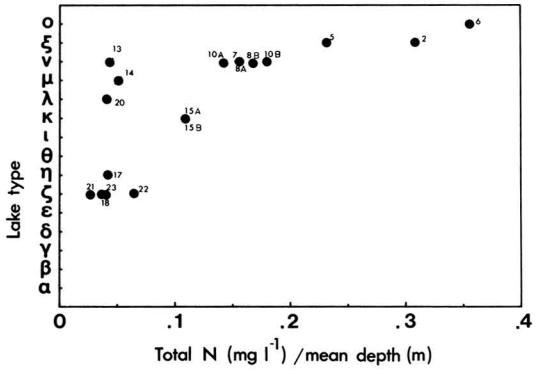

Fig. 11. The relationship between the lake types established by Saether (1979) and the total nitrogen content of the surface water corrected with mean depth.

depth, were among the most important separating variables. The same holds true for temperature.

These results lend support to the theory that it is the availability of food which is important. Saether (1979) and Wiederholm (1980a) found a significant correlation between the composition of the profundal fauna and the total phosphorus or chlorophyll-a concentration of the surface water (both corrected with mean depth). The depth correction allows for the effect of lake morphometry on the eutrophication process. This was also attempted here. The lake types were determined according to the key given by Saether (1979). A slight modification to this key was made. The extremely polluted lake group VII was classed as an *o*-eutrophic type, lake group I as a ξ-eutrophic type despite the presence of *Microchironomus tener,* lake group V as a ν-eutrophic type, lake group VI (station 15) as a κ-eutrophic type and oligotrophic lake groups II and III as ζ-oligotrophic or η-mesotrophic types. The relationship between the benthic lake types of Saether and the total nitrogen content of the trophogenic layer corrected with the mean depth is presented in the form of a scatter diagram in Fig. 11. The fauna of stations 13, 14 and 20a does not seem to fit in with the general trend very well. They are oligotrophic stations with a *Chironomus* fauna inhabiting their profundal. The exceptional nature of these stations was discussed earlier. At these stations other factors would appear to control the faunal composition (morphometry, temperature). The relationship between lake types and total phosphorus concentration (depth corrected) was not as evident. It is possible that in these lakes phosphorus is not the main limiting nutrient.

The conclusion is that Saether (1979) was correct in stating that oxygen concentration comes into effect only in lakes of advanced eutrophy, or lakes where the oxygen level for other reasons is particularly low (humic lakes, morphometrically dependent O_2-deficiency). Kansanen & Aho (1981) analyzed differences in water quality between *Chironomus plumosus* and *C. anthracinus* associations in the study area and found the annual minimum oxygen concentration to be the most important difference between them. The annual hypolimnetic oxygen minimum in the *C. plumosus* area was 4% and in the *C. anthracinus* areas 18% (at 15 m).

In the shallow water region the relationship between benthic associations and trophic status is not as evident. The discriminant analysis of the upper sublittoral data showed that both winter and summer oxygen concentrations were more important discriminating variables than nutrient concentrations of the surface water or Secchi disc transparency. This does not necessarily mean that bottom faunae in this depth zone were primarily controlled by oxygen concentration. It should not be forgotten that eutrophication causes numerous changes in both abiotic and biotic variables and in their interactions within the lake ecosystem. The indirect effects through altered predator-prey interactions are easily forgotten in eutrophication studies (cf. Nilssen 1978). These effects are probably more important in the shallow water region than in the profundal zone. This should be taken into account when the composition of the shallower benthos is used as indicator of certain environmental conditions.

6. Conclusions

1) The hierarchial classification and discriminant analyses of the benthic fauna and water quality data showed that the lake type system of Brundin (1956, 1958) is a valid basis for the monitoring of stratified lake basins in the study area. The composition of the profundal chironomid fauna is dependent on the trophic status. As some earlier authors have pointed out, the primary mechanism governing the chironomid associations in the profundal is the availability of food. The oxygen depletion and other harmful consequences of the intensified saprobic processes come into effect only in lakes of advanced eutrophy or in some special instances.

2) Multivariate statistical methods have many advantages in analyzing benthic associations. With them it is possible to take into account the whole association, not just some indicator species.

3) The use of Brundin's benthic lake type system is most valid in thermally stratified lakes. However, in the Finnish Lake District the lakes are in general shallow and often unstratified. The difficulties in creating a benthic lake typology based on shallow water associations are greater than is the case with the profundal zone. The shallow water region constitutes a far less uniform environment. It is important to divide the littoral and sublittoral into subzones and to compare benthic associations separately at each zone. The best classification of the shallow water fauna was achieved at the upper sublittoral zone. The established lake groups were relevant to the trophic status and water quality. It is not, however, possible to present a lake type system similar to the profundal zone for the shallow-water benthos. The faunal differences between lake groups were too small. This may be due to the fact that several larval types (e.g. *Tanytarsus* and *Procladius*) still comprise many species having different ecological requirements.

4) A need to produce a benthic lake typology based on a sublittoral or littoral fauna is apparent from the practical point of view. This kind of typology would provide a more universal basis for the monitoring of Finnish lakes than Brundin's typology is capable of. A study of this type would call for more comprehensive material (including adults) from all kinds of lakes (ultraoligotrophic and mesotrophic categories, natural polyhumic lakes, larger biogeographic area). It is clear that this kind of study requires supporting taxonomic research on quantitatively important lake chironomid larvae. The results of the present work show that this is not an unreasonable undertaking in conjunction with future investigations.

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APPENDIX 1

Records for the chironomid taxa at each depth zone. The station number is given first, followed by the depth in metres and the average number of specimens, in parentheses, taken in a sample of six hauls with an Ekman dredge (total area 1 578 cm^2). The years and transects of each station are combined.

	Littoral	Upper sublittoral	Lower sublittoral	Profundal
Ablabesmyia longistyla Pittkau	18, 1m (2.5)	8a, 3m (1); 18, 3m (1)		
A. monilis -type	7, 1m (0.5); 9, 1m (0.5); 14, 1m (1); 16, 1m (0.5); 17, 1m (0.5); 18, 1m (2); 20a, 1m (9); 21, 1m (2.5); 22, 1m (0.5)	13, 5m (1); 14, 5m (3); 17, 3m (0.5); 17, 5m (0.7); 18, 3m (6); 18, 5m (3); 20a, 5m (1.5); 20b, 3m (2)	4, 10m (1.2); 14, 10m (1); 17, 10m (0.2); 18, 7m (0.5); 20a, 10m (1)	15b, 23m (0.3); 23, 15m (0.3)
Anatopynia plumipes (Fries)	11, 1m (1)		4, 10m (3.6)	
Macropelopia spp.	16, 1m (0.5)	7, 5m (1.5); 15a, 5m (1); 15b, 3m (0.3); 15b, 5m (1); 17, 3m (8); 17, 5m (2.5); 18, 3m (1); 18, 5m (8); 20a, 3m (1); 20a, 5m (1.5); 22, 3m (1)	7, 7m (10.3); 15a, 7m (1); 15a, 10m (1); 15b, 7m (3); 15b, 10m (0.7); 17, 10m (0.8); 18, 7m (2.5); 18, 10m (2.5)	15b, 15m (0.4); 17, 20m (0.5); 18, 20m (1)
Procladius sp. a	2, 1m (9.6); 3, 1m (10); 4, 1m (26); 5, 1m (15); 7, 1m (14.5); 8a, 1m (4); 9, 1m (9.5); 10b, 1m (2.5); 11, 1m (6.5); 12, 1m (2); 13, 1m (5); 15a, 1m (24); 15b, 1m (16); 16, 1m (2); 18, 1m (9.5); 20a, 1m (3); 20b, 1m (2); 21, 1m (1); 22, 1m (1)	2, 3m (11.5); 2, 5m (8.5); 3, 3m (21.7); 3, 5m (17); 4, 3m (23); 4, 5m (1); 5, 3m (36); 5, 5m (2.9); 7, 3m (34.7); 7, 5m (11.8); 8a, 3m (26); 8a, 5m (8); 8b, 3m (29); 8b, 5m (20); 9, 3m (5.5); 9, 5m (7.5); 10b, 3m (10); 10b, 5m (6.5); 11, 3m (22.5); 11, 5m (9); 12, 3m (9.5); 12, 5m (2); 13, 3m (6.5); 13, 5m (32.6); 14, 3m (24); 14, 5m (30); 15a, 3m (41); 15a, 5m (4); 15b, 3m (23.1); 15b, 5m (7.4); 16, 3m (6.3); 16, 5m (1.5); 17, 3m (0.5); 17, 5m (2.5); 18, 3m (49.5); 18, 5m (21); 20a, 3m (39); 20b, 3m (2); 20b, 5m (2); 21, 3m (1); 21, 5m (1); 22, 3m (2); 22, 5m (2); 23, 3m (2); 23, 5m (4)	2, 7m (12.5); 2, 10m (3.5); 3, 7m (21); 3, 12m (17); 4, 7m (6); 4, 10m (6); 5, 7m (2.3); 5, 10m (1); 7, 7m (8.7); 7, 10m (2.3); 8a, 7m (14); 8a, 10m (12); 8b, 7m (15); 8b, 10m (5); 9, 7m (5); 9, 9m (5); 10b, 7m (2); 10b, 10m (8); 11, 7m (3); 11, 11m (1); 12, 8m (0.5); 13, 7m (7.5); 13, 10m (5); 13, 15m (1); 14, 7m (2); 14, 10m (3); 14, 15m (2); 15a, 7m (1); 15a, 10m (7); 15b, 7m (12); 15b, 10m (7); 16, 7m (1); 16, 10m (6.7); 17, 7m (3); 17, 10m (1.5); 18, 7m (23); 18, 10m (8); 20a, 10m (1); 20b, 7m (5); 20b, 10m (11); 21, 7m (5.5); 21, 10m (7); 22, 7m (4.5); 22, 10m (1.5); 23, 7m (4.5); 23, 10m (8.5)	5, 15m (0.3); 7, 15m (0.8); 8a, 15m (6); 10a, 18m (3.5); 10b, 16m (0.5); 13, 20m (1); 14, 20m (2); 15a, 20m (3); 15b, 15m (0.2); 15b, 20m (0.3); 15b, 23m (0.3); 17, 15m (0.2); 18, 15m (1.5); 18, 20m (0.5); 20b, 15m (4); 20b, 20m (4); 20b, 30m (1); 22, 15m (1.5); 22, 30m (1); 22, 40m (1); 23, 15m (2.5); 23, 20m (1)
Procladius sp. b	9, 1m (5.5); 10b, 1m (0.5); 13, 1m (7); 15b, 1m (35); 17, 1m (9.8)	2, 3m (0.3); 2, 5m (0.5); 5, 3m (0.7); 7, 3m (1.3); 7, 5m (3.3); 8a, 3m (1); 8b, 3m (2); 10b, 5m (2); 13, 3m (5); 13, 5m (1.6); 14, 3m (12); 14, 5m (6); 15a, 3m (3); 15a, 5m (3); 15b, 3m (4.6); 15b, 5m (4.3); 16, 5m (1); 17, 3m (4.5); 17, 5m (4.0); 18, 3m (7.5); 18, 5m (1.5); 20a, 3m (8); 20a, 5m (1.5); 20b, 3m (5); 21, 3m (6.5); 21, 5m (5.5); 22, 3m (18); 22, 5m (7.5); 23, 3m (18); 23, 5m (7)	3, 7m (0.6); 7, 10m (1.8); 8a, 7m (1); 8b, 7m (1); 8b, 10m (6); 9, 7m (1); 9, 9m (0.5); 10b, 7m (1); 10b, 10m (6); 13, 7m (1.5); 13, 10m (0.5); 14, 15m (1); 15a, 7m (2); 15b, 7m (3); 15b, 10m (0.3); 16, 7m (0.5); 16, 10m (0.7); 17, 7m (1); 17, 10m (1); 18, 10m (1); 21, 10m (1); 22, 7m (1); 22, 10m (3.5); 23, 7m (1.5); 23, 10m (1.5)	2, 18m (1); 7, 15m (0.3); 7, 20m (0.7); 8a, 15m (4); 10a, 15m (7); 10a, 17,5m (2); 13, 20m (2); 14, 20m (2); 15b, 15m (0.4); 15b, 20m (0.3); 15b, 23m (0.8); 17, 15m (0.5); 17, 20m (1); 17, 50m (1); 18, 15m (0.5); 18, 20m (1.5); 20a, 20m (3); 20a, 30m (5); 20b, 20m (2); 20b, 30m (1); 21, 20m (1.5); 21, 30m (4.5); 21, 40m (1); 21, 50m (2), 22, 20m (0.5); 22, 30m (1.5); 22, 40m (2); 23, 15m (0.5); 23, 20m (3.5); 23, 30m (1.5); 23, 40m (1)
Procladius sp. c	2, 1m (2.4); 4, 1m (6); 8b, 1m (1); 9, 1m (4.5); 11, 1m (5); 20b, 1m (1); 22, 1m (0.5)	2, 3m (3); 2, 5m (6.1); 3, 3m (0.7); 3, 5m (1); 4, 3m (14); 4, 5m (33); 5, 3m (16.7); 5, 5m (12.2); 7, 3m (0.7); 7, 3m (3.8); 8a, 3m (1); 8a, 5m (2); 8b, 3m (4); 8b, 5m (5); 9, 3m (5); 9, 5m (11); 10b, 3m (1); 10b, 5m (0.5); 11, 3m (6); 11, 5m (9.5); 12, 3m (2); 12, 5m (4.5); 13, 3m (11.5); 14, 5m (3); 15a, 5m (2); 15b, 3m (0.3); 15b, 5m (1); 16, 3m (1.5);	2, 7m (14.5); 2, 10m (14.5); 3, 7m (3.3); 3, 12m (4); 4, 7m (26); 4, 10m (37.2); 5, 7m (25.3); 5, 10m (13.8); 7, 7m (3.7); 7, 10m (5.8); 8a, 7m (3); 8a, 10m (7.5); 8b, 7m (2); 8b, 10m (2); 9, 7m (4); 9, 9m (0.5); 10b, 7m (5); 10b, 10m (2); 11, 7m (3); 12, 8m (1.5); 13, 7m (1.5); 13, 15m (1); 14, 10m (2); 14, 15m (1); 15a, 7m (3); 15a, 10m (2); 15b, 10m (11); 16, 10m (7);	2, 15m (5); 2, 18m (1); 5, 15m (8.0); 7, 15m (5.5); 7, 20m (2); 8a, 15m (1); 10a, 15m (1); 10a, 19m (1); 10b, 17m (2.5); 10b, 22m (2); 14, 20m (6); 15a, 15m (9); 15a, 20m (32); 15b, 15m (11.4); 15b, 20m (15.4); 15b, 23m (6.5); 17, 15m (3.2); 17, 20m (1); 17, 30m (8.5); 17, 40m (5); 17, 50m (2); 17, 60m (0.5); 18, 15m (9.5); 18, 20m (37.5); 18, 30m (24); 20a, 15m (1); 20a, 20m (5); 20a, 30m (3);

	Littoral	Upper sublittoral	Lower sublittoral	Profundal
		16, 5m (0.5); 17, 5m (0.5); 18, 5m (4); 20a, 3m (2); 20b, 3m(1); 21, 3m (2); 21, 5m (4); 22, 3m (3); 22, 5m (9.5); 23, 3m (3); 23, 5m (0.5)	17, 10m (2.3); 18,10m (4.5); 20b, 7m (2); 20b, 10m (1); 21, 7m (7.5); 21, 10m (3); 22, 7m (13); 22, 10m (13); 23, 7m (3.5); 23, 10m (2.5)	20b, 15m (4); 20b, 20m (5); 20b, 30m (21); 21, 15m (11); 21, 20m (22); 21, 30m (9); 21, 40m (6); 21, 50m (1); 22, 15m (9.5); 22, 20m (5.5); 22, 30m (4.5); 22, 40m (1); 23, 15m (5); 23, 20m (3); 23, 30m (3); 23, 40m (4)
Procladius sp. d		7, 3m (7); 21, 3m (5.5)		7, 15m (0.5); 7, 20m (0.3); 10a, 18m (3.5); 10b, 16m (4); 10b, 22m (2); 17, 22m (2.3); 21, 40m (1); 21, 50m (1); 23, 20m (1); 23, 30m (1)
Psectrotanypus varius (Fabricius)			11, 7m (2);	
Tanypus kraatzi (Kieffer)		5, 3m (1); 5, 5m (0.5); 6, 3m (2); 11, 3m (1); 11, 5m (2.5)	11, 7m (2); 12, 8m (0.5)	
T. punctipennis (Meigen)	2, 1m (3)	5, 5m (0.2); 5, 10m (0.1); 18, 5m (0.5)		
T. vilipennis (Kieffer)	6, 1m (0.8)	5, 3m (0.7); 5, 5m (1.4); 11, 5m (1); 12, 3m (2); 12, 5m (2)	5, 7m (0.3); 5, 10m (0.1); 11, 7m (9.5); 11, 11m (4); 12, 8m (0.5)	
Thienemannimyia-gr.	11, 1m (6.5); 21, 1m (0.5)		20b, 10m (1)	18, 20m (0.5)
Monodiamesa bathyphila Kieffer		7, 5m (0.3); 8a, 5m (2); 8b, 5m (1); 9, 5m (0.5); 18, 3m (35); 21, 3m (8); 23, 5m (1)	2, 7m (1.5); 2, 10m (1.5); 7, 7m (0.7); 8a, 7m (2); 8a, 10m (6); 8b, 7m (3); 9, 7m (6.5); 10b, 7m (2); 10b, 10m (1); 18, 10m (3); 22, 7m (2.5)	10a, 15m (2); 17, 15m (1.7); 17, 23m (0.5); 17, 30m (1.5); 18, 15m (4)
Potthastia gaedii (Meigen)	8a, 1m (1); 10b, 1m (3)			
P. longimanus Kieffer	8a, 1m (1); 9, 1m (2); 10b, 1m (8), 22, 1m (1)	10b, 3m (1)		
Protanypus morio (Zetterstedt)		13, 3m (1); 15a, 5m (2); 15b, 5m (1); 18, 5m (1); 20b, 5m (1); 21, 3m (1); 22, 5m (1.5); 23, 3m (1); 23, 5m (1.5)	14, 7m (1); 15a, 7m (2); 15a, 10m (2); 15b, 10m (1); 17, 10m (1.3); 18, 10m (1); 20a, 10m (1); 20b, 10m (2); 21, 7m (1.5); 21, 10m (3.5); 23, 10m (2.5)	15b, 15m (1); 17, 15m (0.5); 17, 23m (0.3); 18, 15m (2); 18, 20m (0.5); 18, 30m (1); 21, 15m (2.5); 21, 30m (0.5)
Cricotopus sylvestris-t	3, 1m (1); 6, 1m (0.8); 10b, 1m (3); 13, 1m (0.5); 21, 1m (0.5)	13, 3m (0.5)	2, 7m (1.5); 4, 7m (2)	
Cricotopus spp.	10b, 1m (0.5); 13, 1m (1); 18, 1m (1)	18, 3m (0.5)		
Epoicocladius flavens (Malloch)	9, 1m (1)	18, 3m (0.5)		
Heterotanytarsus apicalis (Kieffer)				17, 23m (0.3); 17, 30m (3)
Heterotrissocladius marcidus (Walker)	8a, 1m (1); 10b, 1m (0.5); 20a, 1m (1.5); 20b, 1m (1)	8a, 3m (1); 10b, 5m (0.5); 15b, 3m (0.1); 17, 5m (0.5); 18, 3m (0.5); 20a, 5m (3); 23, 5m (0.5)	22, 7m (0.5)	18, 15m (0.5)
Orthocladius saxicola-t.			2, 10m (1)	
Paracladius conversus (Walker)	5, 1m (1); 7, 1m (4.5); 8b, 1m (2); 10b, 1m (1)			
Pogonocladius consobrinus (Holmgren)		18, 3m (0.5)	2, 7m (0.5)	

	Littoral	Upper sublittoral	Lower sublittoral	Profundal
Psectrocladius psiloptenus-t.	7, 1m (0.5); 10b, 1m (5); 13, 1m (0.5); 14, 1m (2); 16, 1m (1); 18, 1m (5); 20a, 1m (2); 20b, 1m (2); 21, 1m (2); 22, 1m (0.5)	18, 3m (1.5); 21, 3m (0.5)		
P. septentrionalis-t.	18, 1m (0.5)			
Chironomus anthracinus-t.	10b, 1m (1); 15b, 1m (25);	5, 5m (0.1); 7, 3m (1.3); 7, 5m (12.3); 8b, 3m (4); 8b, 5m (4); 9, 5m (1.5); 10b, 5m (0.5); 12, 5m (0.5)	2, 7m (0.5); 4, 7m (2); 7, 7m (29.7); 7, 10m (47.3); 8a, 7m (17); 8a, 10m (20); 8b, 7m (12); 8b, 10m (138); 9, 7m (9.5); 9, 9m (71.5); 10b, 7m (1.5); 10b, 10m (4.5); 13, 10m (1); 13, 15m (38); 16, 10m (2.7)	7, 15m (180); 7, 20m (208); 8a, 15m (233); 8a, 20m (531); 8b, 16m (382); 10a, 15m (128); 10a, 18m (208); 10b, 17m (462); 10b, 22m (626); 13, 20m (36); 14, 20m (6); 15b, 15m (0.2); 15b, 20m (0.7); 15b, 23m (0.3); 20a, 30m (25); 20b, 30m (4); 22, 20m (0.5); 22, 40m (4)
C. plumosus L.	2, 1m (17.4); 3, 1m (2); 4, 1m (17); 5, 1m (15); 7, 1m (22.5); 8a, 1m (11); 8b, 1m (1); 9, 1m (7.5); 10b, 1m (59.5); 11, 1m (114.5); 12, 1m (6); 13, 1m (0.5); 16, 1m (4)	2, 3m (6); 2, 5m (4.8); 3, 3m (1.7); 3, 5m (3); 4, 3m (2); 4, 5m (25); 5, 3m (38.7); 5, 5m (69); 6, 3m (87.3); 6, 5m (2); 7, 3m (0.3); 7, 5m (1); 8a, 5m (6); 9, 5m (7.5); 10b, 3m (16); 10b, 5m (14); 11, 3m (93.5); 11, 5m (84.5); 12, 3m (11); 12, 5m (12.5); 13, 3m (1); 15b, 5m (0.2); 21, 5m (1); 22, 5m (0.5); 23, 5m (0.5)	2, 7m (4.5); 2, 10m (0.5); 3, 7m (10.1); 3, 12m (17); 4, 7m (50); 4, 10m (6); 5, 7m (103); 5, 10m (21.2); 7, 7m (0.7); 7, 10m (4.3); 8a, 7m (6); 8a, 10m (2); 8b, 7m (2); 8b, 10m (1); 9, 7m (27); 9, 9m (31.5); 10b, 7m (4); 11, 7m (49.5); 13, 10m (2.5); 13, 15m (7); 18, 10m (0.5)	2, 15m (3); 2, 18m (2); 5, 15m (7); 7, 15m (10.3); 7, 20m (0.3); 8b, 16m (4); 10a, 15m (7); 10a, 18m (8.3); 10b, 17m (3); 11, 11m (5); 13, 20m (3); 14, 20m (1); 15b, 15m (0.4); 15b, 20m (0.1); 20b, 30m (2); 22, 20m (0.5)
C. plumosus -t.	22, 1m (0.5)	16, 5m (0.5)	4, 10m (1.2)	
C. salinarius -t.		5, 3m (0.3); 5, 5m (0.5); 7, 5m (12.5)	5, 7m (2.7); 5, 10m (0.3); 7, 7m (34.3); 7, 10m (108); 8b, 7m (11); 8b, 10m (127); 9, 7m (8.5); 9, 9m (121); 10b, 10m (1); 10b, 17m (80.5); 13, 10m (26.5); 13, 15m (78); 16, 10m (2.3)	2, 15m (4); 2, 18m (1); 5, 15m (0.4); 7, 15m (78); 7, 20m (56.3); 8a, 15m (23); 8a, 20m (69); 8b, 16m (70); 10a, 15m (26); 10a, 18m (105.7); 13, 20m (88); 14, 20m (12); 15a, 15m (4); 15a, 20m (3); 15b, 20m (99.9); 15b, 23m (21); 20b, 20m (1); 20b, 30m (3); 22, 20m (0.5); 22, 30m (2)
Cladopelma viridula (Fabricius)	2, 1m (0.6); 3, 1m (1); 4, 1m (1); 5, 1m (4); 7, 1m (1.5); 8b, 1m (1); 9, 1m (1); 11, 1m (1); 15b, 1m (2); 18, 1m (1)	4, 5m (2); 5, 3m (1); 7, 3m (0.3); 15b, 3m (1); 16, 3m (0.8); 18, 3m (5.5); 18, 5m (0.5); 20a, 3m (6); 20a, 5m (3); 20b, 3m (2); 20b, 5m (2); 21, 3m (1); 21, 5m (0.5); 23, 3m (0.5)	4, 7m (4); 17, 5m (0.7)	18, 20m (0.5)
Cryptochironomus defectus-t.1	7, 1m (4); 8a, 1m (5); 8b, 1m (6); 10b, 1m (2.5); 15a, 1m (1); 15b, 1m (1)	7, 3m (0.3); 10b, 3m (2); 15b, 3m (0.1); 15b, 5m (0.4); 17, 5m (0.2)	8a, 7m (1)	7, 15m (0.5); 8a, 15m (2); 8b, 16m (1)
C. defectus -t.2	2, 1m (3.6); 3, 1m (1); 7, 1m (4); 9, 1m (4); 11, 1m (6); 12, 1m (1); 13, 1m (2); 14, 1m (5); 15b, 1m (2); 16, 1m (7.5); 17, 1m (1); 18, 1m (4.5); 21, 1m (2.5); 22, 1m (1); 23, 1m (0.5)	2, 3m (1.3); 3, 3m (0.3); 5, 3m (1); 5, 5m (0.4); 7, 3m (0.3); 9, 3m (2); 11, 3m (2.5); 11, 5m (1.5); 13, 3m (3); 13, 5m (1); 14, 3m (3); 14, 5m (2); 15a, 5m (1); 15b, 3m (0.3); 15b, 5m (0.7); 16, 3m (0.5); 16, 5m (0.5); 17, 3m (0.5); 17, 5m (0.3); 18, 3m (2); 18, 5m (0.5); 20a, 3m (3); 20b, 3m (1); 21, 3m (1.5)	2, 10m (1.5); 3, 12m (1); 7, 10m (0.3); 13, 7m (0.8); 13, 10m (0.5); 15b, 10m (0.7); 17, 7m (0.5); 17, 10m (0.2); 20b, 7m (2); 21, 10m (1)	5, 15m (0.1); 7, 15m (0.3); 15b, 23m (0.3)
C. ussouriensis Goetghebuer			3, 7m (0.5); 5, 7m (1.3); 5, 10m (1.6)	5, 15m (0.4); 7, 15m (0.3); 10a, 15m (1); 10a, 18m (0.3)
Cryptotendipes spp.	2, 1m (0.5); 9, 1m (1); 10b, 1m (0.5); 13, 1m (0.5)	2, 3m (0.5); 13, 3m (2.5); 17, 5m (0.4); 20a, 3m (2.5); 20b, 3m (3); 21, 5m (0.5)	14, 7m (1); 18, 7m (1)	

	Littoral	Upper sublittoral	Lower sublittoral	Profundal
Demicrypto-chironomus vulneratus (Zetterstedt)	10b, 1m (2); 13, 1m (0.5); 15a, 1m (1); 15b, 1m (1); 16, 1m (1.5); 17, 1m (0.8); 18, 1m (1.5); 20b, 1m (1); 22, 1m (1)	9, 3m (1); 10b, 3m (2); 13, 3m (2); 13, 5m (3); 15b, 3m (0.1);15b, 5m (0.4); 16, 5m (1); 17, 5m (0.2); 18, 3m (1); 20b, 5m (3); 21, 3m (1); 22, 3m (1); 22, 5m (1); 23, 5m (0.5)	10b, 7m (1); 15a, 7m (2); 15b, 10m (1.9); 17, 7m (1); 17, 10m (0.5); 18, 7m (0.5); 21, 10m (1); 22, 7m (0.5); 23, 10m (1)	17, 23m (0.3)
Dicrotendi-pes spp.	6, 1m (0.6); 7, 1m (4.5); 8a, 1m (3); 9, 1m (17); 10b, 1m (2.5); 13, 1m (1.5); 15b, 1m (6); 16, 1m (1); 18, 1m (4.5); 21, 1m (6)	15b, 3m (1.7);15b, 5m (0.2); 18, 3m (1.5); 20a, 5m (1.5); 20b, 3m (1)	13, 7m (0.8);15b, 10m (0.2); 18, 7m (0.5); 21, 10m (1.5)	22, 15m (1); 22, 30m (0.5)
Einfeldia spp.	2, 1m (27.4); 3, 1m (4); 11, 1m (0.5)	2, 3m (61.3); 3, 3m (1.7); 3, 5m (0.5); 7, 3m (3.3); 11, 3m (0.5)		
Endochirono-mus albipen-nis-t.	15b, 1m (20)			
E. intextus (Walker)	15b, 1m (160)	18, 3m (4)		
Glyptotendi-pes gripeko-veni-t.	2, 1m (3); 3, 1m (2); 5, 1m (19); 7, 1m (78.5); 8b, 1m (1); 9, 1m (8); 10b, 1m (50); 11, 1m (3); 12, 1m (1); 15b, 1m (1)	20a, 3m (5)		
Harnischia curtilamel-lata (Malloch)	15a, 1m (1); 18, 1m (0.5)	3, 3m (1); 7, 3m (1.3); 8a, 5m (3); 10b, 3m (2); 15a, 3m (1); 15b, 3m (0.3); 15b, 5m (0.2); 20a, 5m (3); 20b, 5m (1); 21, 3m (0.5); 22, 5m (2)	2, 7m (1); 14, 7m (1); 14, 10m (5); 15a, 7m (1); 15a, 10m (1); 15b, 7m (2); 15b, 10m (0.7); 18, 7m (0.5); 20a, 10m (1); 20b, 7m (1); 20b, 10m (136); 20b, 7m (2); 23, 7m (2.5)	15a, 15m (1); 15b, 20m (0.8); 18, 15m (0.5); 20a, 15m (1); 20b, 15m (1); 20b, 15m (0.5); 22, 30m (1)
Microchiro-nomus tener (Kieffer)	2, 1m (38.2); 4, 1m (5); 5, 1m (1); 7, 1m (1); 9, 1m (1.5); 11, 1m (1)	2, 3m (8.7); 2, 5m (4.2); 3, 3m (3); 3, 5m (1); 4, 3m (10); 4, 5m (2); 5, 3m (2.3); 5, 5m (1); 7, 3m (1); 7, 5m (1.3); 8b, 3m (1); 9, 5m (0.5); 11, 3m (5.5); 12, 3m (0.5); 12, 5m (1.5); 14, 3m (1); 15b, 5m (0.2); 17, 5m (0.2); 21, 3m (0.5)	2, 7m (5.5); 2, 10m (6.5); 3, 7m (4.7); 3, 12m (12); 4, 7m (8); 4, 10m, (12); 5, 7m (3.3); 5, 10m (0.4); 7, 7m (2.7); 7, 10m (2.8); 8a, 10m (2); 8b, 10m (1); 9, 7m (3); 9, 9m (0.5); 11, 7m (0.9); 13, 10m (5.5); 13, 15m (2); 16, 7m (0.5); 16, 10m (0.3); 20b, 10m (1); 21, 7m (2); 21, 10m (2.5); 23, 7m (0.5)	2, 18m (1); 5, 15m (1.1); 7, 15m (1.8); 10a, 15m (1); 13, 20m (1); 14, 20m (3); 20b, 15m (1)
Microtendi-pes spp.	2, 1m (1); 3, 1m (1); 7, 1m (2); 8a, 1m (1); 9, 1m (3.5); 10b, 1m (39); 13, 1m (2.5); 14, 1m (1); 15a, 1m (1); 21, 1m (1.5); 22, 1m (1)	13, 3m (0.5); 18, 3m (0.5)	17, 10m (0.2)	
Nilothauma brayi (Goetghebuer)	7, 1m (0.5); 14, 1m (1); 17, 1m (0.5)	7, 3m (0.7); 13, 5m (2); 14, 3m (1); 14, 5m (1); 18, 3m (1); 18, 5m (0.5); 20a, 3m (1); 20a, 5m (3); 21, 3m (0.5); 23, 3m (0.5)	14, 7m (1)	
Pagastiella orophila (Edwards)	13, 1m (1.5)	18, 5m (0.5)		
Parachiro-nomus spp.	18, 1m (1.5)			
Paracladopelma camptolabis-t.	7, 1m (0.5); 10b, 1m (0.5)	17, 5m (0.2); 22, 5m (0.5)	17, 10m (0.2); 21, 10m (3.5)	18, 20m (0.5)
Paralauterborniella nigrohalteralis (Malloch)	9, 1m (1); 13, 1m (1)	2, 3m (1); 3, 3m (1); 4, 3m (1); 7, 3m (0.3); 10b, 3m (1); 20a, 3m (1)		

	Littoral	Upper sublittoral	Lower sublittoral	Profundal
Phaenopsectra (P.) flavipes (Meigen)	10b, 1m (0.5); 13, 1m (1); 15a, 1m (1); 15b, 1m (1); 18, 1m (0.5); 20a, 1m (2); 21, 1m (1)	18, 3m (1.5)		
Phaenopsectra (Sergentia) coracina (Zetterstedt)				18, 30m (4)
Polypedilum bicrenatum Kieffer	2, 1m (9.5); 3, 1m (1.5); 5, 1m (1); 7, 1m (1); 10b, 1m (0.5); 13, 1m (0.5); 15b, 1m (1)	2, 3m (2.3); 2, 5m (0.6); 3, 3m (0.3); 3, 5m (0.5); 4, 3m (2); 4, 5m (0.5); 7, 3m (2.7); 7, 5m (0.3); 8a, 3m (2); 8b, 3m (4)	2, 7m (0.5); 4, 7m (1); 4, 10m (1.2); 7, 7m (0.3); 8a, 7m (1); 8a, 10m (2); 8b, 7m (1); 21, 10m (2)	
P. brevian-tennatum-t.	2, 1m (3); 8a, 1m (4); 21, 1m (1); 22, 1m (2.5); 23, 1m (3.5)	2, 3m (0.3)		
P. convictum-t.		3, 3m (0.3)	3, 7m (0.5); 5, 10m (0.1)	
P. nubeculo-sum (Meigen)	2, 1m (1.2); 3, 1m (1); 4, 1m (2); 5, 1m (7); 7, 1m (15); 8a, 1m (1); 10b, 1m (5.5); 11, 1m (0.5); 13, 1m (3.5); 15a, 1m (1); 15b, 1m (7)	4, 5m (1); 5, 3m (1); 18, 3m (3.5)	4, 7m (2)	
P. pullum Zetterstedt	14, 1m (8)	2, 3m (0.7); 13, 5m (1.2)	13, 10m (1); 13, 15m (1); 14, 15m (1); 15a, 7m (1); 15b, 7m (1); 15b, 10m (0.2); 16, 10m (0.3); 18, 7m (0.5); 18, 10m (1.5); 21, 7m (0.5); 21, 10m (1.5)	15b, 15m (0.2); 17, 20m (0.3); 17, 23m (0.3); 17, 30m (1); 18, 20m (1); 21, 20m (1); 21, 40m (3)
Pseudochiro-nomus prasi-natus (Staeger)	2, 1m (1.2); 7, 1m (6); 9, 1m (1.5); 10b, 1m (9.5); 12, 1m (8); 13, 1m (1.5); 16, 1m (2); 18, 1m (1); 20a, 1m (1); 20b, 1m (2); 21, 1m (11); 22, 1m (2.5)	15a, 3m (0.5); 16, 3m (0.5); 17, 3m (2); 18, 3m (1); 20a, 3m (2); 20a, 5m (3); 21, 3m (1.5); 23, 3m (1); 23, 5m (0.5)		
Stictochiro-nomus psammo-philus-t.	8a, 1m (52); 8b, 1m (58); 17, 1m (1.5); 21, 1m (70.5); 22, 1m (150); 23, 1m (87)	23, 3m (3)		
S. rosen-schoeldi (Zetterstedt)			15b, 10m (0.1); 18, 10m (1.5); 20b, 10m (2); 22, 10m (5); 23, 7m (4.5); 23, 10m (11)	17, 15m (1.3); 17, 20m (0.7); 18, 15m (18.5); 18, 20m (25); 18, 30m (22); 20a, 15m (12); 20a, 20m (5); 20b, 15m (1); 21, 15m (5); 21, 20m (4); 21, 30m (1); 21, 40m (1); 22, 15m (4.5); 22, 20m (6.5); 22, 30m (12.5); 23, 15m (11.5); 23, 20m (11); 23, 30m (12); 23, 40m (14)
S. sticticus (Fabricius)	3, 1m (13); 5, 1m (2); 7, 1m (28.5); 9, 1m (42.5); 10b, 1m (40); 14, 1m (6); 15a, 1m (1); 16, 1m (0.5); 17, 1m (16.3); 18, 1m (0.5); 20a, 1m (0.5); 21, 1m (11)	7, 3m (6.3); 8a, 3m (11); 10b, 5m (3); 17, 5m (0.3); 18, 3m (7); 21, 3m (1); 21, 5m (1)		
Cladotany-tarsus atridorsum-t.	10b, 1m (1); 11, 1m (8.5); 12, 1m (12); 14, 1m (12); 16, 1m (18.5); 18, 1m (6); 23, 1m (2.5)	11, 3m (0.5); 14, 3m (1); 14, 5m (7); 16, 3m (0.8); 18, 3m (4); 18, 5m (5.5); 23, 3m (1.5)	18, 7m (0.5); 18, 10m (2)	
C. mancus-t.	2, 1m (19.1); 7, 1m (19); 8a, 1m (14); 8b, 1m (11); 9, 1m (68); 10b, 1m (17); 13, 1m (5.5); 14, 1m (12); 15a, 1m (1); 15b, 1m (7); 18, 1m (1); 21, 1m (8); 22, 1m (3); 23, 1m (34.5)	2, 3m (8.3); 9, 3m (7); 9, 5m (2.5); 13, 3m (2.5); 13, 5m (1); 14, 3m (1); 14, 5m (7); 15b, 3m (3.1); 15b, 5m (0.2); 18, 5m (0.5); 20a, 3m (3); 20b, 3m (4); 21, 3m (2); 22, 3m (1); 22, 5m (0.5); 23, 3m (1)	22, 7m (0.5)	
Cladotany-tarsus spp.	5, 1m (3); 17, 1m (51.8)	17, 5m (0.2)		
Micropsectra spp.				23, 15m (1.5); 23, 20m (2.5); 23, 30m (10); 23, 40m (13)

	Littoral	Upper sublittoral	Lower sublittoral	Profundal
Paratanytarsus spp.	17, 1m (0.5); 18, 1m (0.5)	9, 3m (0.5)	9, 7m (0.5)	
Stempellina bausei (Kieffer)	8a, 1m (10); 22, 1m (0.5)	2, 5m (0.6); 20a, 3m (1); 20b, 3m (4); 21, 3m (0.5); 22, 5m (0.5)	2, 10m (1); 15a, 10m (2); 23, 7m (1)	18, 20m (0.5); 20b, 20m (2); 22, 15m (2)
S. subglabripennis Brundin	2, 1m (2); 3, 1m (1); 7, 1m (0.5); 8a, 1m (1); 8b, 1m (1); 9, 1m (6.5); 10b, 1m (1); 11, 1m (10); 13, 1m (0.5); 15b, 1m (1); 16, 1m (2); 20a, 1m (1); 21, 1m (0.5); 22, 1m (1)	3, 3m (0.7); 3, 5m (0.5); 10b, 3m (1); 13, 3m (0.5); 18, 3m (1); 20a, 3m (3); 20b, 3m (26); 21, 3m (2); 21, 5m (0.5); 22, 5m (1); 23, 3m (0.5)	3, 7m (1.2); 13, 7m (0.8)	
Stempellinella minor Edwards	2, 1m (1.1); 7, 1m (2); 8a, 1m (11); 8b, 1m (2); 9, 1m (2); 10b, 1m (2.5); 16, 1m (0.5); 21, 1m (1); 23, 1m (0.5)	2, 3m (2.3); 7, 3m (0.7); 8b, 5m (1); 9, 3m (1.5); 9, 5m (0.5); 10b, 5m (3); 15b, 3m (1.7); 18, 3m (0.5); 18, 5m (2); 20a, 3m (4); 21, 3m (0.5); 21, 5m (1)	8a, 10m (1.5); 15b, 10m (1.2); 21, 7m (0.5)	18, 20m (1.5); 21, 15m (1); 22, 20m (0.5); 22, 30m (0.5); 23, 30m (1)
Tanytarsus chinyensis Goetghebuer	7, 1m (3.5); 8b, 1m (1); 9, 1m (3); 21, 1m (1)	2, 3m (0.3); 7, 3m (0.3); 15b, 5m (0.2); 18, 3m (2)		
T. curticornis Kieffer	10b, 1m (2); 18, 1m (3)		23, 7m (0.5)	
T. eminuluslestagei-t.1	2, 1m (8.3); 7, 1m (3); 9, 1m (9); 10b, 1m (3); 15b, 1m (3); 20b, 1m (1); 21, 1m (3.5)	2, 3m (1.7); 4, 3m (3); 4, 5m (1); 5, 3m (1.3); 5, 5m (0.2); 7, 3m (4.3); 7, 5m (0.3); 8b, 3m (7); 8b, 5m (1); 9, 3m (3); 9, 5m (3); 10b, 5m (4); 12, 3m (0.5); 15b, 3m (10.5); 16, 3m (0.5); 17, 3m (6.5); 17, 5m (0.7); 18, 3m (17); 18, 5m (1); 21, 3m (2); 21, 5m (1.5); 23, 3m (0.5)	2, 10m (3.5); 8b, 7m (1); 9, 7m (3); 10b, 7m (2); 15b, 10m (4.9)	
T. eminuluslestagei-t.2	2, 1m (22.8); 3, 1m (1); 7, 1m (6.5); 8b, 1m (1); 9, 1m (25); 10b, 1m (13); 12, 1m (12); 13, 1m (0.5); 14, 1m (1); 15a, 1m (4); 15b, 1m (8); 16, 3m (0.5); 18, 1m (4.5); 21, 1m (0.5)	2, 3m (0.3); 3, 5m (0.5); 4, 5m (2); 5, 3m (1.3); 5, 5m (0.2); 7, 3m (2.3); 9, 3m (1.5); 10b, 3m (2); 10b, 5m (1.5); 15b, 5m (0.6); 17, 3m (3); 17, 5m (1); 18, 3m (12); 18, 5m (1.5); 20a, 3m (4); 20a, 5m (3); 21, 5m (1); 22, 3m (2); 22, 5m (0.5); 23, 5m (0.5)	3, 7m (1.2); 4, 7m (2); 4, 10m (1.2); 14, 7m (2); 14, 10m (2); 15a, 10m (1); 18, 10m (0.5); 21, 7m (0.5); 21, 10m (1); 22, 7m (1); 23, 10m (1)	14, 20m (1); 15b, 23m (0.5); 17, 15m (0.2); 21, 15m (0.5); 21, 20m (0.5); 21, 30m (0.5); 21, 40m (2); 22, 15m (0.5); 22, 30m (0.5); 23, 40m (1)
T. lugens-t.	7, 1m (1)	7, 3m (3.5); 7, 5m (0.4); 8a, 3m (3); 8a, 5m (3)	7, 7m (1); 8a, 7m (7); 10b, 10m (2); 15b, 10m (0.2); 23, 10m (0.5)	15b, 23m (0.3); 17, 23m (0.3); 17, 30m (0.5); 18, 15m (6.5); 18, 20m (29.5); 18, 30m (6); 20a, 15m (1); 20a, 30m (1); 20b, 30m (3); 21, 15m (13.5); 21, 20m (12); 21, 30m (7); 21, 40m (5); 21, 50m (1); 22, 15m (1.5); 22, 20m (5); 22, 30m (3.5); 23, 15m (2); 23, 20m (1.5); 23, 40m (2)
T. mendax-t.	2, 1m (2.2); 4, 1m (13); 9, 1m (1.5); 10b, 1m (2.5); 11, 1m (1.5); 12, 1m (2)	3, 3m (9); 4, 3m (19); 4, 5m (4); 5, 3m (1.3); 7, 3m (1.7); 7, 5m (0.4); 9, 5m (1.5); 10b, 5m (0.5); 11, 3m (1); 12, 3m (1.5); 12, 5m (1.5)	4, 10m (2.4); 22, 7m (0.5)	
T. recurvatus-t.	18, 1m (3.5); 20b, 1m (1); 21, 1m (0.5)			
T. usmaensis -t.	8a, 1m (2); 9, 1m (2); 21, 1m (1)	2, 5m (1.2); 11, 3m (0.5); 18, 3m (3.5); 18, 5m (1)	8a, 7m (3); 10b, 10m (2); 14, 10m (1); 15a, 10m (1); 18, 10m (1); 21, 10m (0.5)	22, 15m (0.5); 23, 15m (0.5)
T. verralli -t.	7, 1m (12); 8a, 1m (4); 8b, 1m (2); 9, 1m (1); 10b, 1m (2.5); 11, 1m (17); 14, 1m (4); 17, 1m (0.5)	7, 3m (0.3); 9, 3m (0.5); 11, 3m (2.5); 16, 3m (1.5); 20a, 3m (5); 20b, 3m (3); 21, 5m (0.5)	8b, 7m (3); 8b, 10m (2); 10b, 10m (2)	21, 15m (1)