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Patterns of benthic copepod assemblages in an oligotrophic lake

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The benthic copepod assemblages in an oligotrophic lake were studied from quantitative samples collected from 57 sites at depths of 0.2—65 m. Numerical classification and ordination of sites resulted in six site groups: stony shores, emergent macrophyte (*Equisetum*) stands, and depth zones of 1—2 m (littoral), 2—5 m (littoriprofundal), 5—10 m (upper profundal) and below 10 m (lower profundal). Classification and ordination of species showed that the stony shores and the lower profundal had characteristic species assemblages. The total number of benthic copepod species decreased from the littoral (23 species) to the profundal (14—16 species); in the littoral it was lowest among *Equisetum*. Both the harpacticoid and omnivorous cyclopoid guilds showed parallel trends. Several other diversity measures (Hill's numbers, Kempton & Taylor's mid-range statistic and rarefied species numbers) showed approximately similar patterns. Dominance was inversely related to diversity: it was lowest on littoral soft bottoms, and increased with depth and towards the shoreline; it was higher among emergent macrophytes than on stony shores.

The benthic copepod diversity in the *Equisetum* stands, the most productive area in the lake, was probably restricted by poor oxygen conditions in the sediment, which excluded burrowing forms, mainly harpacticoids. The stony shores, the most diverse littoral area relative to productivity, probably offered the most varied microhabitats. The decreasing species diversity pattern on the soft bottoms from the open littoral towards the depths probably reflected partly the decreasing productivity of the benthic subsystem and partly the abundance of two main faunal components: littoral, warm-water species decreased with depth, and a group of cold-water adapted species favoured the deep profundal. The fluctuating summer temperatures around the thermocline depth perhaps contributed to this faunal turnover, restricting the reproduction of cold-adapted species.

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1. Introduction

Rules governing the organization of ecological communities are at present the subject of a lively debate (e.g. Strong et al. 1984), and especially the role of interspecific interactions is controversial (e.g. Brown 1981, Hebert 1982, Simberloff 1982). The interpretation of community data has turned out to be difficult: usually the patterns observed in the field do not tell anything about the mechanisms regulating species diversity and coexistence (e.g. Hebert 1982, Ranta 1982, Strong et al. 1984). Yet, although an experimental approach based on specific hypotheses is likely to yield more understanding of these mechanisms, studies on real natural communities still form the starting point for hypotheses and sophisticated experiments.

The abundance, the great diversity of different life forms and inhabited environments (Noodt 1971), and the relatively short life cycles of meiobenthic animals in general, and benthic copepods in particular, make them ideal organisms for studies on the basic questions of contemporary population and community ecology (see reviews by Fenchel 1978 and Hicks & Coull 1983). Most studies on meiobenthic communities derive from the marine environment, and the earliest concerned the interstitial meiofauna of sandy beaches (see e.g. Mielke 1976 and Moore 1979a for copepod studies). Later the patterns of muddy littoral, phytal and sublittoral cope-

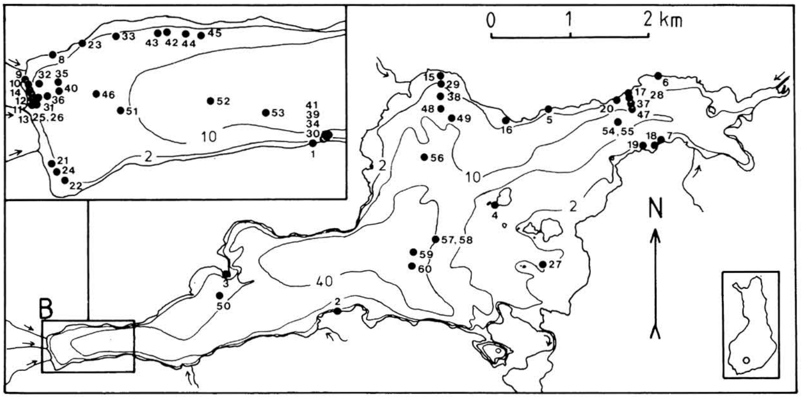

Fig. 1. The location of sampling sites in Lake Pääjärvi. B = Lammi Biological Station.

pod assemblages have also been assessed (e.g. Castel & Lasserre 1979, Coull et al. 1979, Moore 1979b, 1979c, Castel 1980, Fleeger 1980, Hicks 1980, Ivester 1980, Warwick & Gee 1984). In recent years, the traditional descriptive approach has been enriched by accompanying field experiments (e.g. Gee et al. 1985; see a review by Coull & Palmer 1984), and benthic copepod communities have also been used for the explicit testing of different diversity hypotheses (Thistle 1980, 1981, 1983a, 1983b, Reidenauer & Thistle 1981).

Much less is known of the freshwater meiobenthos (see e.g. Holopainen & Paasivirta 1977 and Anderson & DeHenau 1980). Qualitative information on the ecology of freshwater benthic copepods is abundant, but quantitative knowledge on the structural patterns of the copepod assemblages is scarce. The harpacticoid community of subterranean waters has been intensively studied by Rouch (e.g. 1980, 1984, Rouch & Carlier 1985), and a few other studies have elucidated the distributional patterns of microcrustaceans in epigeous waters (Ponyi 1969, Rey & Dupin 1973, Thaler 1977, Frenzel 1979, Adalsteinsson 1979, Amoros 1980). However, there are no thorough analyses of benthic copepod assemblages in any northern lake.

I studied the ecology of benthic copepods in 1972–1974 as part of a comprehensive investigation on the energy flows in the ecosystem of the oligotrophic lake Pääjärvi, southern Finland (Ruuhijärvi 1974, Sarvala et al. 1981). In the present paper I shall analyze the patterns of the benthic copepod assemblages in Pääjärvi, as a basis for future papers on the life histories, production and interspecific relationships of benthic copepods, and discuss the reasons for these regularities in relation to other meiofaunal communities and to general hypotheses on community organization.

2. Study area

Lake Pääjärvi (Fig. 1) is a mesohumic, oligotrophic lake in southern Finland (approx. 61°04′N, 25°08′E; altitude 103 m). Its maximum length is 10 km, area 13.4 km^2, shoreline development 2.5, mean depth 14.4 m, maximum depth 85 m, and volume 205.7 million m^3. The catchment area is 244 km^2 and consists of coniferous forests, bogs and agricultural areas. The lake is dimictic, and the depth of the epilimnion increases from about 5 to 10 m from early June to early September. The ice cover forms in November–December and melts in early May. In summer, the near-bottom temperatures approach 20–24°C along the shores and 5–7°C in the lower profundal zone; in winter the temperatures range from below 1°C in the littoral to about 2–3°C in the lower profundal. Even the deepest parts are fairly well oxygenated all through the year; at the greatest depth the minimum saturation in late winter usually varies from 60 to 70%, but may in extreme years approach 40%. Whole lake means and ranges of some important chemical and physical characteristics are given in the following table (compiled from Ruuhijärvi 1974, Ryding 1980, Salonen 1981 and unpublished data of the Pääjärvi project):

	Mean	Range
Theoretical water residence time (a)	4.1	2.1–7.4
Conductivity ($\mu S_{20°C}$)	69	52–77
pH	6.9	6.4–7.5
Colour (Pt-units)	..	55–65
Transparency (m)	2.6	1.5–3.0
Dissolved inorganic carbon (mg/l)	2.8	2.7–4.6
Dissolved organic carbon (mg/l)	10.0	..
Total phosphorus (mg/m^3)	10	5–19
Total nitrogen (mg/m^3)	948	700–1500
$KMnO_4$ consumption (mg/l)	38	25–49
Calcium (mg/l)	6.1	5.5–6.6
Alkalinity (mMol/l)	..	0.17–0.19

Along the shores the environmental conditions are more extreme than is indicated by the above figures. During winter, the shallowest parts down to a depth of

Table 1. Ranges of some chemical and physical properties of the surface (0—1 or 0—2 cm) sediment at different depths in Lake Pääjärvi. Sources: (1) Sarvala et al. (1982), Kairesalo et al., unpublished: summers 1978—1980; (2) National Board of Waters, Holopainen (1979): April 1975; (3) National Board of Waters: March 1972; (4) data of Simola & Uimonen-Simola (1983): October 1980. DM = dry mass.

	Sediment among *Equisetum* (1)	Sediment at 1.0—2.3 m (2)	Profundal sediment (3), (4)
Dry mass mg/cm^3	290—995	187—518	22—236
Carbon mg/g DM	3.4—10.4	21.9—74.8	15.8—43.1
Total nitrogen mg/g DM	0.14—0.87	1.5—4.5	2.0—2.9
Total phosphorus mg/g DM	0.20—0.43	0.9—1.6	1.1—1.5
N:P ratio (by mass)	0.6—3.7	1.7—3.1	1.7—2.2
C:N ratio (by mass)	ca. 15	13.1—22.1	10—15
Calcium mg/g DM	..	3.5—5.8	5.8—7.8
Iron mg/g DM	..	30.8—72.5	47—81

about 0.5 m are frozen to the bottom, and in summer there are, at least within macrophyte vegetation, pronounced diel variations in temperature and pH and in the concentrations of dissolved substances. In the inner parts of dense helophyte stands, total phosphorus concentration may be tenfold, and chlorophyll *a* concentration and zooplankton biomass five- or sixfold compared to the open water, while oxygen deficiency may occur during the night (Sarvala et al. 1982, Kairesalo 1983).

Macroscopic vegetation extends to a depth of 1.5 m, covering about 11 % of the lake area (Kansanen & Niemi 1974 and unpublished); the emergent macrophytes, *Carex rostrata* Stokes, *Equisetum fluviatile* L., and *Phragmites australis* (Cav.)Trin. ex Steudel as the dominants, make up 2.4 % of the lake area. Microscopic algae are abundant down to a depth of about 3 m, and their lower limit lies at 4—5 m (Kairesalo & Nenonen 1974, Kairesalo 1976, 1977).

At depths of more than 5 m (in the profundal zone) the sediments are fairly uniform, usually having a 2—3 cm thick soft surface layer of brown clayey gyttja with high water content, and often a layer of iron hydroxide at a depth of about 1.5 cm; deeper reduced layers are grey or dark grey ooze with more or less visible annual laminations (Simola & Uimonen-Simola 1983). Along shores, at depths of less than 5 m (the littoriprofundal and littoral zones) sediment quality is more variable, depending on the shore type. In sheltered places sediments of the profundal type extend to a depth of 1—2 m, in exposed areas firm gravel, sand or sandy silt bottoms predominate, while off rich macrophyte vegetation and around the river mouths the bottom is soft with a large proportion of silt and coarse detritus and with a 1.5—3 cm thick brown surface layer. Some chemical and physical characteristics of the bottom sediments are shown in Table 1. Dry weight per volume generally decreases towards depth. Organic content is highest in the littoral, being around 30 mg/cm^3 down to a depth of 5 m; values of about 15 mg/cm^3 are found in the whole profundal. A basic description of Lake Pääjärvi is given by Ruuhijärvi (1974); additional information can be found in Holopainen (1979) and Ilmavirta (1981). The ecological energetics of the lake have been characterized by Sarvala (1974) and Ilmavirta (1979), and in a revised form by Sarvala et al. (1981). Low nutrient contents lead to low productivity: in 1972—1973 the whole annual primary production in Lake Pääjärvi was on an average 1454 kJ/m^2/year, the majority of which was due to phytoplankton production. During the same years, the mean gross input of allochthonous organic matter into the lake was 2466 and outflow 1398 kJ/m^2/year.

3. Sampling methods

In June—August and October—November, 1972, the bathymetric and horizontal distribution of benthic copepods was studied by sampling 37 sites at depths between 0.2 and 65 m in different parts of the lake; five of these sites were also sampled regularly through all seasons in 1972—1974. These surveys were complemented with occasional samples from other seasons. Usually 3—10 replicate cores with single corers of different sizes (7.9—54.6 cm^2; Hakala 1971 and unpublished) were taken at each site; when sampling depths of less than 3 m, the corers were attached to the end of a rod. In addition, 13 quantitative samples taken with a 0.1 mm hand-net from within a 900 cm^2 box (Coffman et al. 1971) from 7 stony shore localities of the lake were kindly placed at my disposal by Miss Anja Leisma, M.Sc. One large littoral sample derived from Ranta & Sarvala (1978). In all, data from 57 sites were used for the present analyses (Fig. 1, Appendix 1). Although represented by only two small samples, the emergent macrophyte stands were included in the analyses, since data from a three-year study of zooplankton among *Equisetum* (Lehtovaara & Sarvala 1984) were available for comparison.

The vertical distribution of copepods within the sediment was examined by cutting some cores into 1-cm slices with a piston-operated device (Hakala 1971). In routine sampling, only the top 2—2.5 cm (in the littoral) or 3 cm (in the profundal) of mud were retained as the sample.

The samples were sifted through a series of sieves with 0.4, 0.2 and 0.1 mm meshes. In 1973, a lower sieve of 0.05 mm mesh was routinely used at the seasonally sampled sites, but for the present purpose only adults and copepodites of cyclopoid and harpacticoid copepods recovered from these samples were considered. Residues remaining on the sieves were usually stored in 4 % formaldehyde, and examined at 12× and 25× magnifications on a grooved disc (Hakala 1971) under a dissecting microscope. Each groove was examined twice, and all copepods found were removed for identification. In some samples, the sieved residues were washed in a Barnett's trough (Barnett 1968); in such cases the heavy residues were also inspected.

The sampling efficiency of the 15.2 cm^2 corer used was about 80 % on flocculent gyttja, and that of the 54.6 cm^2 corer better than 95 % (Holopainen & Sarvala 1975). The 7.9 cm^2 corer was as efficient as the 15.2 cm^2 corer on the fairly compact sediments of the 1, 2 and 13 m sites where it only was used (Sarvala, unpublished). The laboratory procedures were also tested in connexion with the seasonal sampling, and their effectiveness was very high, for adults and copepodites better than 99 % (Sarvala, unpublished).

Copepods were identified to species and developmental stage at 125×—625× magnifications from temporary whole mounts in water or from dissected mounts in glycerol. Adult harpacticoids were identified according to Dussart (1967), Gurney (1932), Kiefer (1960), and Lang

(1948); adult cyclopoids according to Dussart (1969), Gurney (1933), and Rylov (1948). The identifications of copepodites were based partly on experience from my own rearing experiments. Abundances were converted to biomass units using mean carbon values for each developmental stage and species (Sarvala, unpublished).

4. Numerical methods

To reveal possible patterns in the benthic copepod assemblages, the abundance and biomass data were subjected to numerical classification and ordination. For each site visited more than once, mean values of abundance and biomass were used; for the seasonally sampled 2, 13 and 40 m sites (25, 26, 54, 55, 57 and 58) mean values for the years 1972 and 1973 were treated separately; they thus formed an internal check for the numerical procedures. For comparison, the actual numbers of individuals counted at each site were also used.

To produce a firm result, several clustering and ordination methods in combination with various measures of ecological distance were applied both on original and $\log_e$-transformed data as well as on data transformed according to Taylor's power law (e.g. Taylor 1961) using a common transformation exponent of 0.3. This latter transformation is slightly stronger than the cube root transformation suggested by Clifford & Stephenson (1975).

The following distance measures were adopted:

A. Indices based on presence-absence data (see Janson & Vegelius 1981): 1. Jaccard index *QJ* as 1−*QJ*. 2. Dice index *QD* as 1−*QD*. 3. Ochiai index *QO* as 1−*QO*.

B. Indices based on quantitative data: 4. Euclidean distance in squared form D^2 (e.g. Sneath & Sokal 1973), or as *D*. 5. Percentage difference *PD* (Odum 1950). 5a. Proportional similarity *PS* (Renkonen 1938; see Kohn & Riggs 1982) as its one-complement 1−PS. 6. Canberra metric *CA* (Clifford & Stephenson 1975); this index was also used so that double zeros were ignored; in zero/nonzero comparisons the zero values were replaced with 0.2 (see Clifford & Stephenson 1975). 7. Cos theta *CT* (see Fasham 1977). 8. Geodesic metric *G* (Orlóci 1978, p. 57). 9. *NESS* index (the normalized expected species shared; Grassle & Smith 1976). 10. Modified Euclidean index *U* (Orlóci 1978, p. 95).

Numerous clustering procedures were also tried (see Sneath & Sokal 1973 for descriptions of the techniques): 1. Nearest neighbour (NN). 2. Furthest neighbour (FN). 3. Centroid (C). 4. Group average (GA). 5. Minimum variance (MV) (= Ward's error). 6. Flexible strategy clustering (FLEX); here values of −0.50 and −0.25 were used for the coefficient β. NN and FN were used with Euclidean distance only, C with squared Euclidean distance, GA with Euclidean distance and proportional similarity, and MV and FLEX with all the mentioned distance measures.

Several ordination methods were also used: 1. Principal components analysis (PCA, starting from a covariance matrix of $\log_e$-transformed values) followed by Varimax rotation of the principal axes. From two to five factor solutions were computed (program of the Computing Centre of the University of Helsinki). 2. Principal coordinates analysis (PCOORD, Gower 1966; program from Mather 1976). 3. Reciprocal averaging (RA, or the analysis of correspondances; Chardy et al 1976; Hill 1973a,1974; the program included in Decorana of the Cornell Ecology Programs). 4. Detrended correspondence analysis (DCA, Hill & Gauch 1980; the program Decorana in the Cornell Ecology Programs). 5. Principal coordinates analysis preceded by a special algorithm for computing distances ("step-across" and "step-along" of Williamson 1978, 1983).

The validity of the site groupings obtained was examined by classification and ordination of the species.

Site groupings mainly based on the numerical analyses were utilized in further structural analyses of the copepod assemblages. Several measures of structure were applied: 1. Total observed number of species per each site group. 2. The expected number of species obtained with rarefaction (Simberloff 1978, 1979). 3. Species density per unit area. 4. The number of species attaining their maximum abundance in each site group. 5. Hill's diversity numbers of the order 1 and 2 (N_1 and N_2; $N_1=\exp(H')$) (Hill 1973b, Peet 1974, Daget 1980); in calculating H′ a correction for sample size was used according to Hutcheson (1970). 6. The mid-range statistic *Q* of Kempton & Taylor (1976). 7. Dominance expressed as N_2 or as the contribution of one (D_1; Berger & Parker 1970) or two (D_2; McNaughton 1967) of the most abundant species to the total abundance, or as *k*-dominance curves (Lambshead et al. 1983). 8. Evenness as $J'=H'/\ln S$ (Pielou 1975), $F_{1.0}=(N_1-1)/(N_0-1)$ (Heip 1974) or $F_{2.1}=(N_2-1)/(N_1-1)$ (Alatalo & Alatalo 1980, Alatalo 1981). 9. Dominance-diversity (ranked abundance) curves (e.g. Pielou 1975).

5. Results

5.1. Identification of patterns

Vertical distribution in the sediment

In the littoral and littoriprofundal, 95 % of the harpacticoids and an even higher proportion of the cyclopoids were found in the uppermost 1 cm, and none were found below 3 cm (Table 2). In the profundal, harpacticoids were more evenly distributed in the top two cm, but only single individuals were found deeper than 2 cm. Cyclopoids were also concentrated in the profundal at the very surface of the sediment, only single individuals being found deeper than 1 cm. Like most other meiofaunal groups in Lake Pääjärvi (Holopainen & Paasivirta 1977), the benthic copepods are thus restricted to the oxidized surface layer, which in the profundal sediment extends to about 1.5 cm.

Copepod fauna

In all, 32 benthic and littoral copepod taxa were identified from the present quantitative material; 13 of them belonged to Harpacticoida and 19 to Cyclopoida (Appendix 2). The four additional cyclopoid taxa found by Lehto-

Table 2. The vertical distribution of benthic copepods in the bottom sediment of Lake Pääjärvi at depths of 2 and 9 m. Numbers found in each mud layer are given as percentages of the total numbers (TN) of each species. N = nauplii, C = copepodites, A = adults.

Depth layers (cm):	0–1	1–2	2–3	>3	TN
2 m, 8 February, 1975					
Canthocamptus staphylinus N	100	–	–	–	2
C. microstaphylinus A	100	–	–	–	9
Attheyella crassa A	93	5	2	–	193
– " – C	100	–	–	–	30
Moraria brevipes A	100	–	–	–	12
– " – C	94	6	–	–	34
M. mrazeki A	90	5	5	–	21
Bryocamptus minutus A	100	–	–	–	1
B. echinatus A	100	–	–	–	17
– " – C	99	1	–	–	67
Paracamptus schmeili A	93	6	1	–	157
– " – C	98	–	2	–	62
Harpacticoida, total	95	4	1	–	604
Paracyclops fimbriatus A	96	4	–	–	27
Other benthic Cyclopoida C	100	–	–	–	7
Benthic Cyclopoida, total	97	3	–	–	34
9 m, 5 March, 1978					
A. crassa A+C	50	50	–	–	2
B. echinatus A+C	92	8	–	–	24
P. schmeili A+C	39	61	–	–	31
Harpacticoida, total	61	39	–	–	57
P. fimbriatus N	–	33	33	33	3
Diacyclops nanus C	93	7	–	–	14
D. abyssicola A+C	100	–	–	–	14
Benthic Cyclopoida, total	87	7	3	3	31

vaara & Sarvala (1984) in the *Equisetum* stands increased the total number of taxa to 36. The harpacticoid taxa were all easily identifiable and taxonomically clear species, with the exception of *Canthocamptus microstaphylinus*, which has often been confused with *C. staphylinus*. In Lake Pääjärvi, these species were clearly distinct, their morphology agreeing with descriptions in Gurney (1932) and Lang (1948); they also had differing life histories and habitats. In Cyclopoida, two forms named in the literature as subspecies of *Diacyclops languidus*, namely *D. l. belgicus* and *D. l. disjunctus*, were kept as separate taxa. *D. l. belgicus* was found only on two stony shores. It was much smaller than *D. l. languidus*, which occurred on one stony shore. *D. l. disjunctus* was found only a few times, mainly in deep water. It was also small, and resembled most *Diacyclops languidoides*; it might in fact be only an aberrant form of this latter species. In the deep profundal, a *Paracyclops* species with short furca was identified as *P. fimbriatus chiltoni* (Lindberg 1957). The treatment of this form as an independent taxon was justified by Frenzel (1977) who demonstrated reproductive isolation between *P. f. fimbriatus* and *P. f. chiltoni*. A large *Eucyclops* form, occurring both in the deep profundal and in the littoral *Equisetum* zone, was treated under the name *E. speratus*. Without crossing experiments, it was impossible to decide whether the littoral and profundal populations were conspecific or not. In the harpacticoid *Moraria brevipes*, separate subpopulations in the littoral and in the deep profundal were wholly interfertile in crossing experiments, confirming their conspecificity.

For more detailed analyses, three guilds were distinguished: 1) harpacticoids, which are mainly detritus-feeders (13 species), 2) omnivorous cyclopoids (16 species), 3) carnivorous cyclopoids (3 species; see Appendix 2). Of the four additional cyclopoid species found among *Equisetum* by Lehtovaara & Sarvala (1984), one was omnivorous and three carnivorous.

The total numbers and biomass of harpacticoids were highest at 1–2 m, around 60 000 exx/m^2 and 35 mgC/m^2, respectively, and from 2 m to the greatest depth they were about one third of these figures (Table 4). Lower numbers were found on stony shores, and among *Equisetum* harpacticoids were almost absent. Omnivorous cyclopoids had their maximum abundance, slightly more than 12 000 exx/m^2, at 5–10 m, although they were almost equally abundant at all depths greater than 2 m; they were much less abundant on stony shores or among emergent macrophytes. Carnivorous cyclopoid abundance was highest on stony shores and at 1–2 m, and decreased steadily towards greater depths. Omnivorous cyclopoid biomass had its maximum, 6–9 mgC/m^2, between 1 and 5 m. In carnivorous cyclopoids, the distribution of biomass was almost identical with that of abundance. In all habitats, harpacticoids were more numerous than cyclopoids. In biomass, however, cyclopoids were clearly dominant among *Equisetum*, and the cyclopoid biomass was almost equal to that of harpacticoids at 2–5 m and on stony shores.

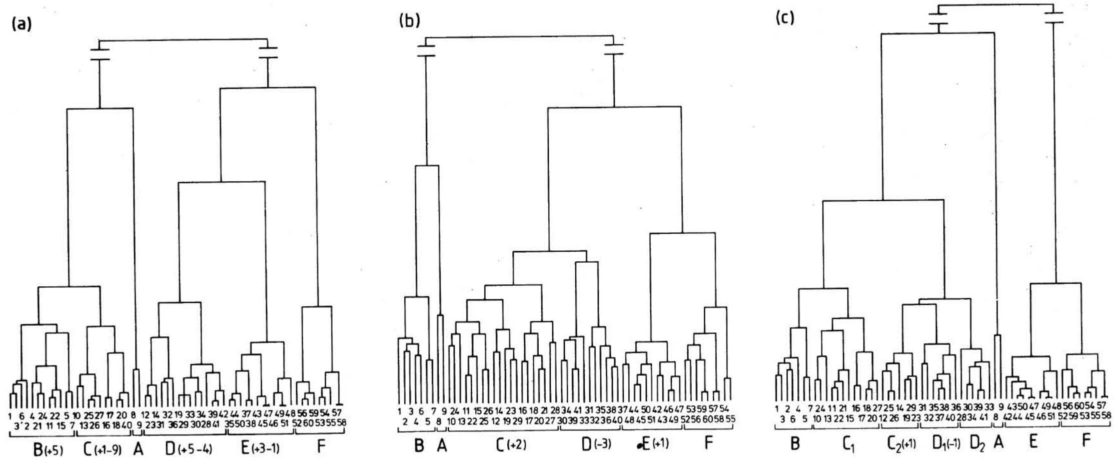

Fig. 2. Flexible strategy clustering of sites with a) the Dice index ($\beta = -0.50$), b) the percentage difference ($\beta = -0.25$; Taylor-transformation), and c) cos theta ($\beta = -0.25$; $\log_e$-transformation). The final site groups established are indicated by the letters A–F (A = *Equisetum*, B = stony shores, C = 1–2 m, D = 2–5 m, E = 5–10 m, F = >10 m); figures in parentheses give the number of extra or lacking sites in each group compared to the final grouping.

Numerical classification of sites

Different clustering methods were compared with quantitative data using Euclidean distance. Stony shores were subjectively judged to have a distinct copepod fauna; therefore, clusters were defined at a level where stony shores formed a separate site group. When untransformed abundances or biomasses were used, sample size strongly affected the clusters and all clustering methods tried gave clearly unacceptable site groupings: the stony shores were not separated as a coherent group.

Even with $\log_e$-transformed data, chaining was a dominant feature of the NN and C clusterings. GA clustering produced partly acceptable clusters, but at the decided level of resolution, many small groups were still produced. MV and FLEX clustering (with $\beta = -0.25$ or -0.50) produced almost identical results: both gave distinct and easily interpretable site groupings.

Clusterings resulting from the use of different distance measures were then compared using the MV and FLEX clustering methods. With the indices utilizing only presence-absence data, the desired level of resolution could not be attained. Clusters obtained with Jaccard's index were unacceptable. Dice's index gave more distinct groups, but the stony shore sites were erroneously intermingled with deeper soft bottom sites. However, the main site groups had much in common with groupings based on quantitative indices on $\log_e$-transformed data (Fig. 2, cf. later). The cophenetic correlation coefficient (Sneath & Sokal 1973) was 0.44 for *QJ* and 0.49 for *QD* clustering.

Of the distance/similarity indices utilizing quantitative information, *CA* worked about as well both with untransformed and transformed abundances, but with biomasses a transformation was even here necessary to obtain meaningful groupings; moreover, it was necessary to use the modification which ignores double-zero comparisons. *PD, PS, CT, G* and *U* required transformation both for abundance and biomass data; there was little difference between the $\log_e$- and Taylor-transformations. Cophenetic correlation coefficients varied from 0.48 to 0.67, but even clearly unacceptable groupings based on untransformed data attained as high values as the acceptable clusterings. With transformation, results obtained from the actually counted numbers of copepods differed little from those obtained using numbers calculated per m^2, although there was more variation in groupings. Since the use of numbers per unit area makes the seasonally sampled sites more comparable with single visits, final analyses were based on numbers per m^2. Large sizes of random samples in the calculation of the NESS index (see Grassle & Smith 1976) could not be used, since several of my samples were small, and their deletion would have made the analysis meaningless. When the size of the random samples was set at 16 individuals, only site 8 was left out of consideration. Then the lower and upper profundal site groups were distinct, but the 1-m site 10 and the *Equisetum* site 9 were intermingled with stony shore sites.

The present samples were so heterogeneous in respect of size (Appendix 1) as well as seasonal representativeness that no small-scale patterns could have been detected. However, in spite of the limitations of the data, at the level of six clusters the classifications with *CA* (untransformed or transformed data) and PD (transformed data) were almost identical both when based on abundance and when based on biomass. Practically equivalent classifications on transformed data were also obtained using the *PS*, *CT*, *G* or *U* index. Most of the consistent main groupings emerging from the classification could be identified as depth zones (Fig. 2).

A "shore group" was always evident, and in most analyses it broke up into two subgroups representing stony shores (sites 1—7) and *Equisetum* (sites 8—9) stands. The third major group had a nucleus of several sites from 1—1.5 m (sites 10—24) and two or three 2-m sites as usual associates (sites 25—27). Most of these sites were on the western arm of the lake. There was also a subgroup containing sites from the eastern part of the lake (sites 16—18, 20 and 27); this subgroup was characterized by the abundance of *Bryocamptus minutus*. Sites 12,14,19,23, 28 and 29 were somewhat variably included in either this or the next group in different analyses. The fourth group had a nucleus of sites from 3 and 4 m (sites 31—39), often with three 2-m sites (sites 28—30) and usually two 5-m sites (sites 40—41) as associates. Again, some of the sites, especially those from 2 and 5 m, belonged to different groups in different classifications. Site 37 was often grouped with the next cluster. Sites 30, 34, 39 and 41 formed the core of a fairly consistent subgroup; they all came from a transect off the stony shore site 1, and were characterized by abundant occurrence of *Bryocamptus echinatus, Diacyclops nanus* and *Paracyclops fimbriatus.* The fifth group was more distinct, consisting of all sites from 6—9 m (sites 44—51), and, in addition, of two 5-m sites (42—43). The sixth group (sites 52—60) consisted of all sites deeper than 10 m, and it was the most clear-cut cluster, emerging with the same composition in almost all analyses.

The main groups revealed by the numerical classification thus coincided almost perfectly with depth zones; only the shallowest (and most heterogeneous) zone was horizontally divided into two habitat types. Subgroups within these main clusters could partly be correlated with the location in the lake and with the abundant occurrence of certain species. Clear connexions with substrate quality were not found; sites with a fairly hard sandy bottom were combined with soft-bottom sites. The variable boundaries between the 1—2 m, 2—5 m and 5—9 m groups showed that the clusters in this depth area were not discrete. This also means that too much importance should not be attached to the details of the clusters; only the main features may be considered valid.

Ordination of sites

In the ordination with PCOORD, the qualitative indices were again clearly less satisfactory than the quantitative indices. With all indices, the sites were arranged on the two first axes in a horse-shoe shaped figure approximately in depth order (Fig. 3). When the main depth groups established in the classification analyses were plotted on the ordination diagram, the 1—2 m, 2—5 m and 5—9 m site groups were more or less overlapping. Site groups corresponding to stony shores, *Equisetum* and the deep profundal (>10 m) were separate, the upper profundal (5—10 m) sites were almost separate, whereas the sites from 1—5 m lay in a large elongate scatterplot, where no discrete boundaries could be traced. The overlap was larger with the qualitative indices and small with quantitative indices, which differed little from each other, although the clearest configurations with the greatest concentration of variance on the two first axes were always obtained with CT. The contribution of the two first axes of the total variance explained by the first four axes was usually 70—74 %, with CT 76—78 %. The use of actual counts instead of numbers per m^2 as the primary matrix also increased the scatter of sites. Thus, the ordination confirmed that in the depth range of 1—5 m or even 1—9 m there were no discrete site groups but that there was a gradual change in the copepod assemblages.

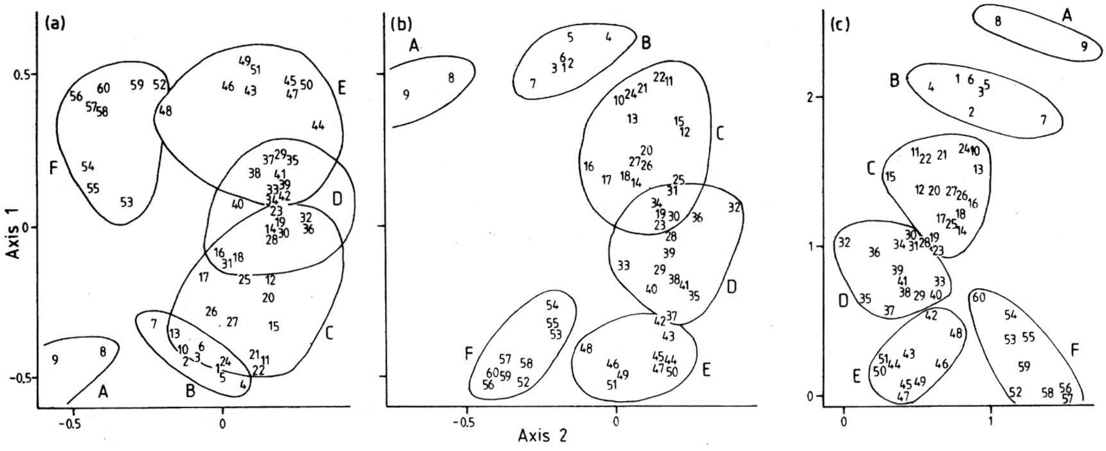

Fig. 3. Ordination of sites with a) principal coordinates analysis and the Dice index, b) principal coordinates analysis and cos theta, and c) detrended correspondence analysis with downweighting of rare species; the two latter with $\log_e$-transformed abundances. A—F = final site groups as in Fig. 2.

However, the width of this transition zone and the weak groups shown in the ordination suggest that it is reasonable to recognize three separate groups within this depth zone, keeping in mind that the division is somewhat arbitrary and the boundaries not exact. The third axis (in some analyses the fourth axis) better separated the *Equisetum* sites from the stony shores. Higher axes added little other new information.

On the first PCOORD axis the composite samples from seasonally studied profundal sites which contained more species than single visit samples, were located closer to shallower sites. The second axis separated the shore sites and the deep profundal group from the intermediate group, and this separation was also visible in a weaker form on axis 4. The third axis separated *Equisetum* sites from the stony shores and also confirmed the separation of the upper and lower profundal.

PCA ordination of sites on $\log_e$-transformed abundances also produced a horse-shoe where sites were arranged approximately according to depth from the *Equisetum* stands over stony shores to the lower profundal. Sites of the upper and lower profundal were almost wholly overlapping on the two first axes, but were separated on the third axis. The first three principal components contributed 53, 17 and 5 %, or taken together 76 % of the total variance. Rotation of axes did not improve the configuration.

RA produced an approximately similar ordination to PCOORD. The sites were arranged on the first two axes in a horse-shoe shaped figure, where the *Equisetum* sites diverged from all others. Stony shores were fairly distinct, but especially the lower and upper profundal site groups considerably overlapped, and the higher axes did not improve the separation.

DCA with $\log_e$-transformation and downweighting of rare species yielded an almost identical ordination plot to PCOORD. A gentle horse-shoe shape persisted, but there was no overlap of depth-based groupings (Fig. 3).

PCOORD with $\log_e$-transformed data, *CT* as distance measure, and with Williamson's modification for calculating distance matrix, produced an ordination plot resembling that of RA analysis, but with better resolution. *Equisetum* sites were here again quite separate, and other sites were arranged according to depth in a gently sigmoid arc. There was more overlap of the depth-based groupings than in the ordinary PCOORD, but this overlap decreased if *Equisetum* sites were removed. The contributions of the first three axes were 57, 20 and 11 %, or altogether 87 % of the total variance, which means that this solution constituted a good description of the original samples-species matrix.

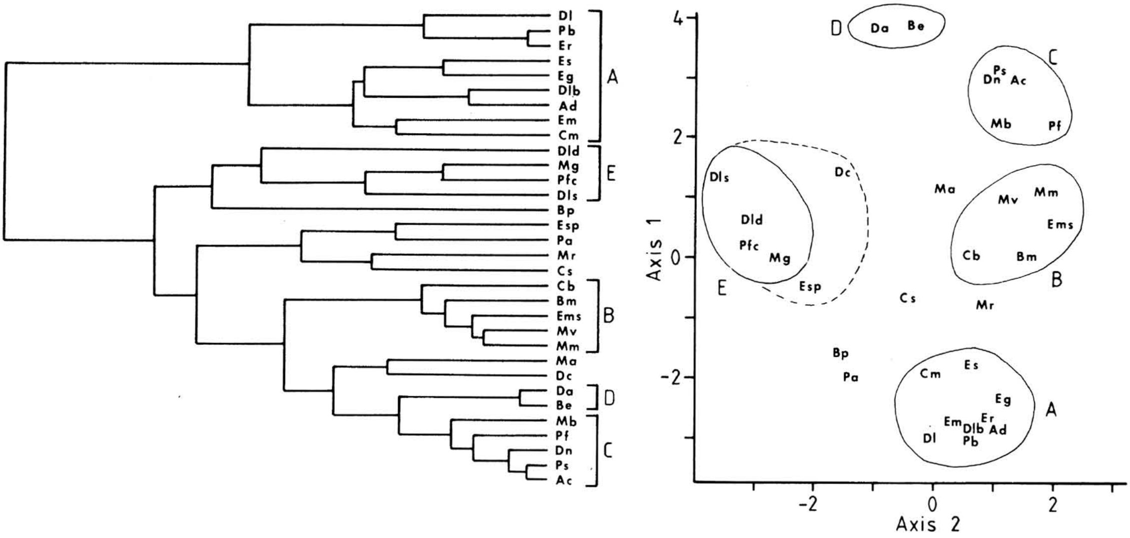

Fig 4. Flexible strategy clustering (left; cos theta, $\log_e$-transformed abundances, $\beta = -0.25$) and principal coordinates analysis (right; presence-absence data, Williamson's modification to calculate distances, $\log_e$-transformed abundances) of the copepod species. Each species is denoted by the first literals of its generic and specific name (Dl = *D. languidus*, Dlb = *D. l. belgicus*, Dld = *D. l. disjunctus*, Dls = *D. languidoides*, Em = *E. macrurus*, Ems = *E. macruroides*, Es = *E. serrulatus*, Esp = *E. speratus*). A = species typical of stony shores, B = species occurring both on stony shores and on shallow soft bottoms, C = common species of shallow soft bottoms, D = widespread species with maximum in deep water, E = species typical of the lower profundal; the broken curve adds two more species to this group.

Classification and ordination of species

Clustering of species with percentage difference and transformed abundances or biomasses was not very useful (Fig. 4). Usually only two of the major clusters could be interpreted: the stony shore species and the deep profundal species.

In Q-mode PCA-analysis, the first three axes contributed 33, 14 and 9 %, or taken together 56 % of the total variance. This species ordination was difficult to interpret; only single species pairs were evident (*B. echinatus* and *D. abyssicola; A. crassa* and *P. fimbriatus; P. schmeili* and *D. nanus; M. viridis* and *E. macruroides*). As such this analysis was less useful than a visual examination of simple correlation matrix. Ordinations of species with PCOORD and quantitative indices on untransformed or transformed abundances or biomasses gave interpretable and essentially similar results. Surprisingly, also Williamson's "step-across" modification using species incidence data gave practically identical configuration to the quantitative indices (Fig. 4). The first two axes separated three more or less coherent groups: the deep-water species, the stony shore species, and the shallow-water soft-bottom species. The deep-water dominants *B. echinatus* and *D. abyssicola* with a wide depth amplitude grouped together between the deep-water and shallow-water groups. The first and third axes served to further separate out a group typical of the depth zone of 5–9 m. Higher axes again contributed little new information. Other species groups were not clearly separate; this is fully understandable, since many of the species occur in several depth zones. Therefore, the lists of dominant species in each defined site grouping contained more species than the lists of characteristic species obtained from the ordination of species.

Habitat distribution of individual species

Six major habitats were distinguished on the basis of the classification and ordination analysis: 1) *Equisetum* stands (sites 8–9); 2) Stony shores (sites 1–7); 3) 1–2 m depth zone (sites 10–27); 4) 2–5 m zone (sites 28–41); 5) 5–10 m zone (sites 42–51); 6) 10–85 m zone (sites 52–60). The first three of these represent littoral habitats, the fourth approximates the littoriprofundal zone, and the fifth and sixth

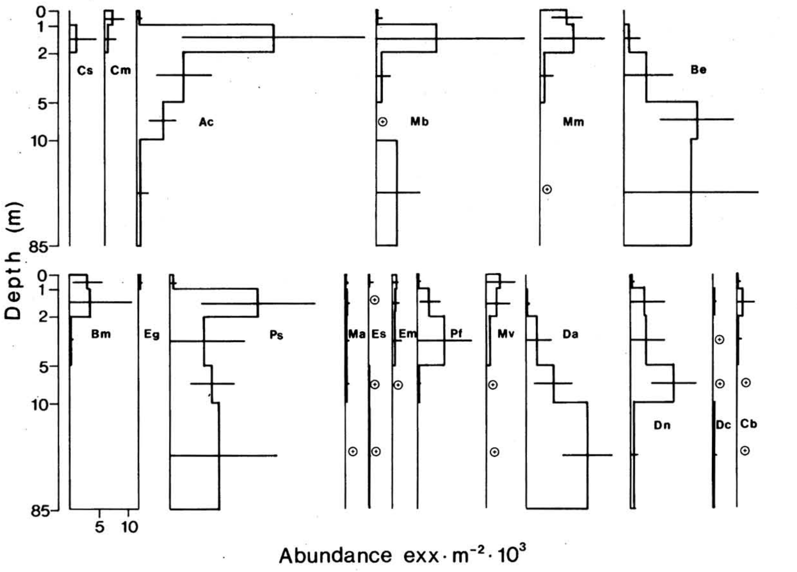

Fig. 5. The bathymetric distribution of the main copepod species (names abbreviated as in Fig. 4 except that Es = *E. speratus*; Em = *E. macruroides*) in Lake Pääjärvi, shown as mean abundance values (with *SD*) per depth zone. The vertical scale is construed from the cumulative depth-area curve of the lake so that the areas delimited by the abundance curves show directly the contribution of each depth zone to the whole lake population of the species. Circled + signs indicate the occurrence of a species in a depth zone in very low numbers.

correspond to the upper and lower profundal zones. Most species had well defined peaks of maximum abundance in different habitats (Fig. 5). All species dominant in abundance or biomass in any of the main habitats are listed in Table 3. Seven harpacticoid and six cyclopoid species could be considered characteristic of stony shores. Two of these harpacticoid species and one of the cyclopoid species were common, too, in the 1 – 2 m zone, and one harpacticoid species was common in the *Equisetum* stands. Most of the species of stony shores were not very abundant. Indeed many were scarce here, though they were entirely absent elsewhere: *Attheyella dentata, Elaphoidella gracilis, Epactophanes richardi, Parastenocaris brevipes, Diacyclops languidus, D. l. belgicus.* The most common species of the stony shores were, however, common also elsewhere: *Moraria mrazeki, Bryocamptus minutus, Canthocamptus microstaphylinus, Eucyclops macruroides, Megacyclops viridis.* In the *Equisetum* zone species were few. Of the total of five harpacticoid species known from this zone in Lake Pääjärvi, only one or perhaps two (*C. microstaphylinus, M. mrazeki*) were abundant. Of the cyclopoids, *Macrocyclops albidus* and *Eucyclops speratus* were dominant although not very abundant, but as they were large, their biomass was high. The data of Lehtovaara & Sarvala (1984) showed that *Megacyclops viridis* may also be abundant among *Equisetum.*

The number of abundant species was highest at 1 – 2 m; there were six abundant harpacticoid species and six abundant cyclopoid species (*A. crassa, Paracamptus schmeili, M. mrazeki, M. brevipes, B. minutus, C. staphylinus, D. nanus, Paracyclops fimbriatus, Cryptocyclops bicolor, E. macruroides, M. viridis,* and *Macrocyclops albidus* in biomass). At 2 – 5 m the most abundant species were those which were already most abundant at 1 – 2 m, but here they were in most cases less abundant (*A. crassa, P. schmeili, M. brevipes, P. fimbriatus, M. viridis*); *B. echinatus* appeared as a new abundant species. At 5 – 10 m the commonest harpacticoid species were the same as at 2 – 5 m, but now *M. mrazeki* and *M. brevipes* were almost lacking. There were practically only two cyclopoid species, *D. nanus* and *D. abyssicola,* which were both already present at 2 – 5 m, *D. nanus* was even abundant at 1 – 2 m. At depths greater than 10 m there were again three abundant harpacticoid species (*P. schmeili* and *B. echinatus* everywhere, *A. crassa* in shallower parts and *M. brevipes* in deeper parts). In the deep profundal there was only one really abundant cyclopoid species, *D. abyssicola.*

Table 3. Dominant harpacticoid and omnivorous cyclopoid species in Lake Pääjärvi. The number of sites at which each species was dominant according to abundance (A) or biomass (B) are given for each main habitat.

	Stony shores	*Equisetum* zone	Depth zone (m) 1–2	2–5	5–10	>10
No. of sites	7	2	18	14	10	9
Harpacticoida						
C. staphylinus	–	–	B1	–	–	–
C. microstaphylinus	A1, B2	A2, B2	–	–	–	–
A. crassa	–	–	A9, B12	A6, B9	–	–
M. brevipes	–	–	A3	–	–	–
M. mrazeki	A5, B4	A1	A1	–	–	–
B. minutus	A1, B1	–	A1, B2	–	–	–
B. echinatus	–	–	–	A3, B2	A7, B6	A7, B5
P. schmeili	–	–	A4, B3	A5, B3	A3, B4	A2, B4
Cyclopoida, omnivores						
E. speratus	B1	A1, B1	–	–	–	–
E. macruroides	A6, B5	–	B1	A1, B1	–	–
P. fimbriatus	–	–	A10, B13	A10, B11	–	–
D. abyssicola	–	–	A1	A2, B1	A2, B4	A9, B9
D. nanus	–	–	A6, B5	A4, B1	A9, B6	–
C. bicolor	A1, B1	–	A2	–	–	–

Table 4. Diversity of the benthic copepod assemblages of the main habitats in Lake Pääjärvi. *Q* = the mid-range statistic of Kempton & Taylor (1976); Smax = the number of species attaining their maximum abundance in the site group; species density = the expected number of species per 100 cm^2, obtained by rarefaction. For the *Equisetum* zone, the total number of species found in a three-year study of Lehtovaara & Sarvala (1984) is given in parentheses.

	Stony shores	*Equisetum* zone	Depth zone (m) 1–2	2–5	5–10	>10
No. of individuals studied	2415	153	25404	1698	2823	21348
Mean abundance exx/m^2						
– total benthic copepods	16904	3725	69976	30360	37552	36219
– Harpacticoida	12452	1955	61522	19722	24840	24564
– Cyclopoida, omnivores	1580	1068	6496	10005	12528	11575
– – " – carnivores	2872	703	1957	633	154	80
No. of species observed						
– total benthic copepods	22	7(18)	23	16	14	16
– Harpacticoida	10	2 (5)	9	7	4	5
– Cyclopoida, omnivores	10	3 (8)	11	7	8	8
– – " – carnivores	2	2 (5)	3	2	2	3
Species density /100 cm^2						
– total benthic copepods	15.9	5.9	17.0	14.0	8.6	10.3
SD	1.6	0.9	1.2	1.0	1.2	1.4
– Harpacticoida	8.5	2.0	8.0	5.5	3.2	4.2
SD	0.8	0.1	0.1	0.6	0.4	0.4
– Cyclopoida	7.0	3.6	8.8	8.5	5.4	6.4
SD	1.3	0.9	1.2	0.8	1.1	1.3
Hill's N_1 (=exp(H'))						
– based on abundance	7.26	4.66	7.19	7.71	5.00	4.59
– based on biomass	7.30	3.76	8.30	7.34	5.79	5.72
Mid-range statistic *Q*	5.39	1.75	3.36	3.14	1.28	2.77
Smax	11	4	8	2	2	5

5.2. Analysis of the pattern of the copepod assemblages

Species richness

The simplest measure of species richness is the observed number of species. The highest numbers of species, 22 and 23, were found on the stony shores and in the 1–2 m depth zone (Table 4, Fig. 6). From 1–2 m the number of species decreased to the 5–10 m zone, but increased again in the lower profundal zone. Considering only harpacticoids and omnivorous cyclopoids, the lowest species

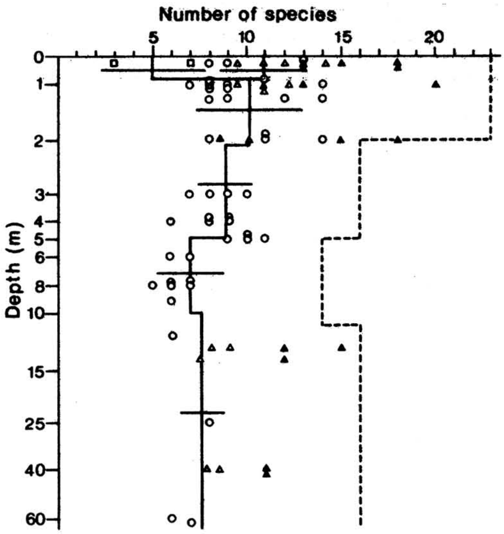

Fig. 6. The total number of species per main habitat (broken line), the corresponding mean number of species per site (thick line, *SD* shown with horizontal bars; at 0—1 m the stony shores and *Equisetum* stands shown separately), and the observed numbers of species per site (circles and triangles). Seasonally sampled sites are indicated by triangles: filled triangles denote values obtained from data combined over seasons, and open symbols denote data reduced to mean values per visit. Open squares = *Equisetum* stands. Overlapping symbols have been slightly shifted vertically for clarity.

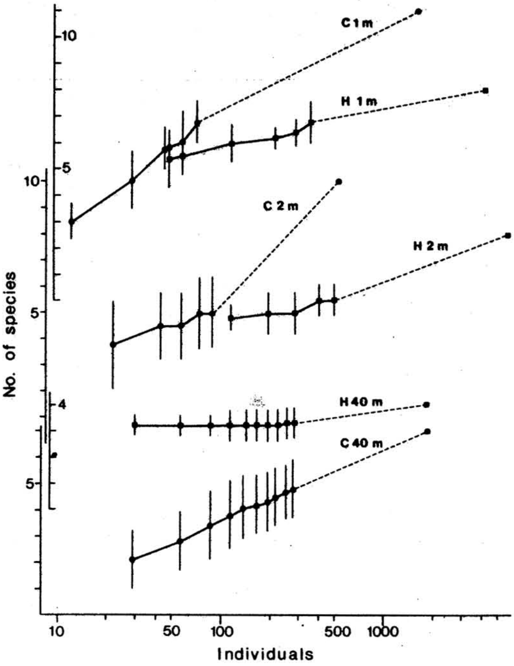

Fig. 7. The cumulative number (± *SD*) of cyclopoid (C) and harpacticoid (H) species plotted against the cumulative number of individuals in successive replicate cores at the 1, 2 and 40 m sites averaged over seasonal sampling series. The total number of species at each site is also shown against the total number of individuals (points joined with broken lines with the appropriate series).

richness was found in the 5—10 m and in the *Equisetum* zone, whereas the latter habitat held the highest number of carnivorous species. The number of species is always a function of the number of individuals examined (Fig. 7). Since the total number of individuals studied was much higher in the lower profundal than in the upper profundal, the slightly higher number of species in the lower profundal may have been a sampling phenomenon. The lower profundal also included three sites which were sampled all through the year, whereas the upper profundal had no such sites. Sampling during an extended period reveals more species than a single visit: this is clearly seen in Fig. 6: the seasonally sampled sites are situated to the right of other sites.

One way of standardizing the sample size for a comparison of species numbers was to calculate the mean number of species encountered on a single visit to each site. This procedure moved the seasonally sampled sites among other sites in the same depth zone (Fig. 6). The mean number of species per site and visit in each depth zone still showed the same pattern as the total number of species; the difference between the upper and lower profundal was not significant. The above procedure does not, however, remove the effect of differing abundances leading to different numbers of individuals obtained per visit. The highest or lowest diversity and evenness values based on biomass were not always in the same site groups as when calculated from abundance data (Table 4). But when the exact values were ignored and the index values classified only as high, intermediate or low, consistent results were usually obtained for both abundance and biomass diversity. When diversity was measured with Hill's number N_1 ($=\exp(H')$), the site groups clearly fell into two groups: three habitats with high diversity (stony shores, 1—2 and 2—5 m), and three habitats with fairly low diversity (*Equisetum* and the upper and lower profundal). According to Hill's

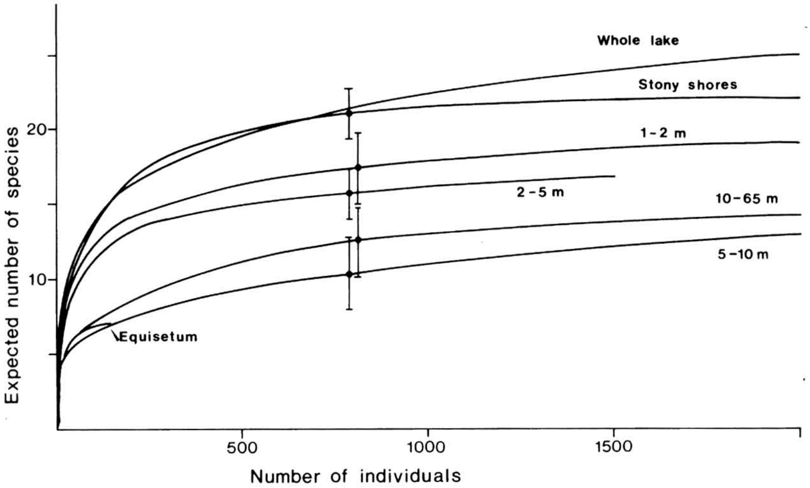

Fig. 8. Rarefaction curves: the expected number of benthic copepod species in the main habitats and the whole of Lake Pääjärvi as a function of the number of individuals studied. The 95 % confidence intervals are indicated by vertical bars for the number of species expected for 800 individuals; for clarity, the bars have been slightly shifted horizontally.

numbers there was no diversity minimum in the 5 – 10 m zone. On the other hand, the midrange statistic *Q* (Kempton & Taylor 1976) showed a clear minimum in the 5 – 10 m zone, a low value in *Equisetum* and a maximum on stony shores.

As a test of the diversity differences between depth zones the rarefaction technique (Simberloff 1978, 1979) was used. Complete rarefaction curves for the site groups (Fig. 8) showed the highest numbers of species for a given number of individuals on stony shores. When the number of individuals obtained from the stony shores was drawn randomly from the larger sample of the 1 – 2 m zone, the number of species expected fell significantly below that actually observed on stony shores. Similarly, in comparison both to stony shores and to the 1 – 2 m zone, the number of species among *Equisetum* was significantly lower than expected. The number of species in the 2 – 5 m zone might have been drawn from the 1 – 2 m sample, but if drawn from the combined sample of these two zones, the expected number of species for each zone was significantly higher than the number of species actually observed. The difference in the number of species between the 2 – 5 m and the 5 – 10 m zones was significant judged in both ways, whereas the number of species observed in the upper profundal might have been drawn randomly from the sample of the lower profundal. Thus, the lower total number of species in the 5 – 10 m zone was most probably due to the smaller total number of individuals caught from this zone. On the other hand, when the samples from these zones were pooled, the expected number of species for the number of individuals obtained from the lower profundal was markedly higher than that actually observed, indicating that the species assemblages in these zones were different.

There was significant heterogeneity also within the established main habitats (Table 5). When the small samples from *Equisetum* were excluded, the observed number of species at a site fell below the 95 % confidence limits for the expectation based on the pooled species distribution of the zone in 29 out of the possible 58 cases (50 %). In this respect, there was an interesting difference between harpacticoids and cyclopoids. In harpacticoids, the spatial heterogeneity was high in the littoral zone and low in the profundal, whereas in cyclopoids, spatial heterogeneity of the species assemblages was low in the littoral but

Table 5. The number of sites at which the observed number of species was significantly less than expected from the pooled species distribution of the corresponding depth zone (percentages of total number of sites per zone in parentheses). *Equisetum* stands excluded.

	No. of sites	Harpacticoida	Cyclopoida	Total
Stony shores	7	5 (71)	2 (29)	5 (71)
1 – 2 m	18	15 (83)	0 (0)	15 (83)
2 – 5 m	14	4 (29)	2 (14)	5 (36)
5 – 10 m	10	0 (0)	2 (20)	1 (10)
>10 m	9	3 (33)	4 (44)	3 (33)
The whole lake	58	27 (47)	10 (17)	29 (50)

Table 6. Indices of evenness and dominance in the benthic copepodassemblages of the main habitats in Lake Pääjärvi. (1) = Stony shores, (2) = *Equisetum* zone, (3) = 1−2 m, (4) = 2−5 m, (5) = 5−10 m, (6) = >10 m.

	Values based on abundance						Values based on biomass					
	(1)	(2)	(3)	(4)	(5)	(6)	(1)	(2)	(3)	(4)	(5)	(6)
N_2	4.93	4.11	5.04	6.11	4.40	3.91	5.03	3.04	5.53	5.41	5.04	4.51
J'	0.64	0.79	0.63	0.74	0.61	0.55	0.64	0.68	0.68	0.72	0.67	0.63
$F_{1.0}$	0.30	0.61	0.28	0.45	0.31	0.24	0.30	0.46	0.33	0.42	0.37	0.32
$F_{2.1}$	0.63	0.85	0.65	0.76	0.85	0.81	0.64	0.74	0.62	0.70	0.84	0.74
D_1 − total Copepoda	34	34	34	27	35	33	35	46	35	31	30	28
D_2 − total Copepoda	56	58	56	46	54	62	55	75	51	55	50	54
D_1 − Harpacticoida	46	64	38	41	52	48	38	85	49	50	44	41
D_2 − Harpacticoida	76	100	63	71	81	82	61	100	71	78	74	81
D_1 − Cyclopoida omnivores	53	86	38	46	59	92	64	88	54	73	49	86
D_2 − Cyclopoida omnivores	68	98	70	72	97	97	74	98	76	84	92	90
D_1 − Cyclopoida carnivores	99	97	85	74	90	57	99	99	75	70	75	66
D_2 − Cyclopoida carnivores	100	100	100	100	100	80	100	100	99	100	100	96

increased appreciably in the profundal; overall, spatial heterogeneity was much lower in cyclopoids than in harpacticoids.

Species density, or the number of species per unit area, was also derived with the aid of the rarefaction curves and mean abundances for each zone. The number of species expected for a sample of $100\ \mathrm{cm}^2$ (a realistic size for a meiofauna sample) was read from the rarefaction curves. The expected number of species was highest at 1−2 m and on stony shores, and minimal in *Equisetum* and the upper profundal (Table 4). There was a slight difference between the expectations for harpacticoids and cyclopoids. In the harpacticoids, the maximum species density was expected on stony shores, whereas in cyclopoids expectations were highest at 1−2 and 2−5 m.

The number of species attaining their maximum density or biomass produced a pattern greatly resembling that given by the midrange statistic Q (Table 4). The highest values were obtained on stony shores and at 1−2 m, the lowest ones in *Equisetum*, at 2−5 m and in the upper profundal, the value for the lower profundal being intermediate. Essentially the same pattern was found if species attaining more than half of their maximum abundance were enumerated for each zone. This pattern suggests that there is a strong littoral faunal element, which already starts to disappear at a depth of a few metres, and the deep-water fauna does not increase in importance until the lower profundal.

Evenness and dominance

When evenness was measured with $F_{2.1}$ (see Table 6), two of the habitats with high diversity showed low evenness (stony shores and 1−2 m), and all other habitats fairly high evenness. On the other hand, $F_{1.0}$ and J' both gave a similarly deviating pattern with high evenness values for *Equisetum* and 2−5 m, and low values for all other sites. Low values of Hill's N_2 indicating high dominance were obtained for *Equisetum* and the lower profundal. The highest values, indicating low dominance, were obtained for the 2−5 m an 1−2 m zones. When dominance relations were examined from the proportion of the most abundant species (D_1; Berger & Parker 1970) or from the summed proportion of the two most abundant species (D_2; McNaughton 1967), a somewhat different result was obtained; moreover, abundance and biomass suggested different patterns (Table 6). Abundance proportions for the total Copepoda indicated minimum dominance in the 2−5 m zone, and intermediate values with little differences for all other habitats. Biomass proportions showed a higher degree of dominance in *Equisetum*, but again little variation among other habitats. Harpacticoid assemblages showed a high dominance in *Equisetum*, intermediate or low dominance on stony shores and slightly decreasing (D_1 on biomass), or, in contrast, increasing dominance towards depth (D_2). Omnivorous cyclopoids had higher dominance than harpacticoids especially according to biomass and in the lower profundal. In carnivorous cyclopoids dominance was very high in the littoral but decreased markedly with depth.

Another way to approach the relative abundance of species is to examine the ranked importance curves (Fig. 9). The best measure

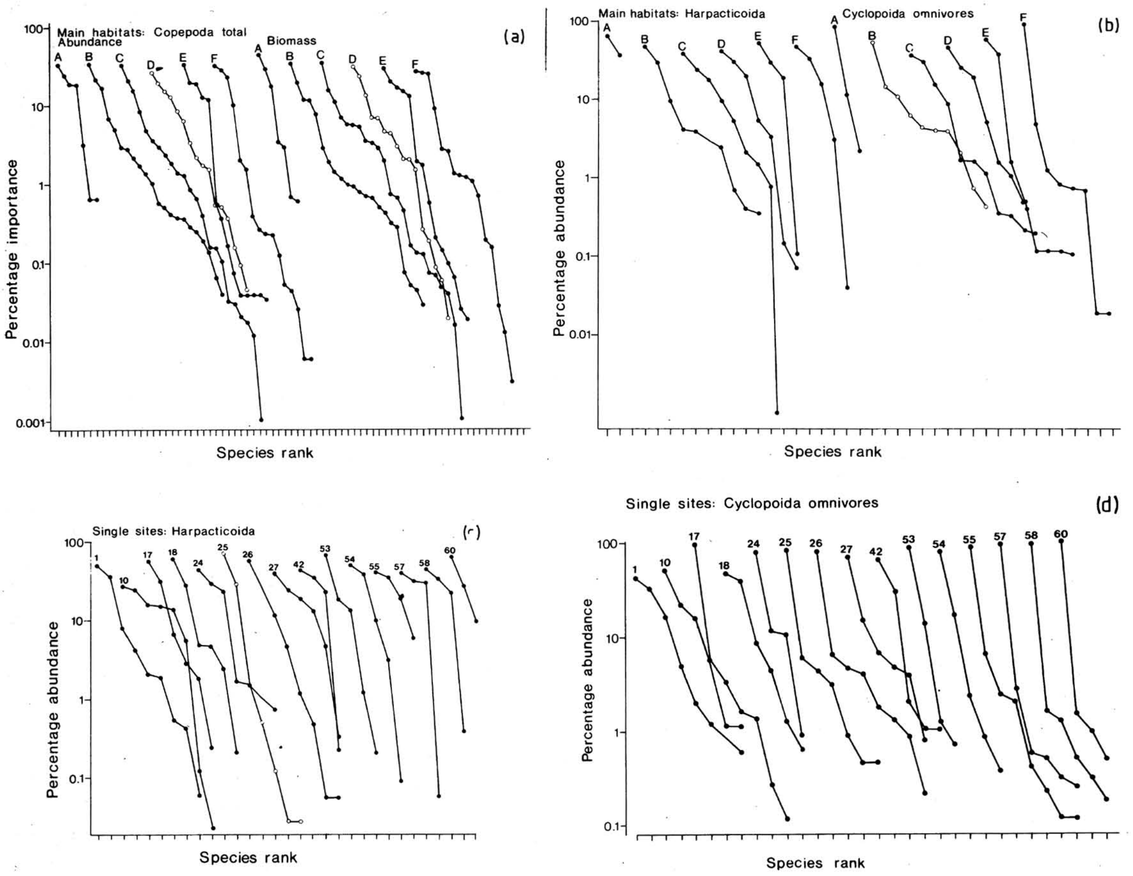

Fig. 9. Ranked abundance curves of benthic copepods in Lake Pääjärvi: a) total copepod abundance and biomass, main habitats, b) harpacticoid and omnivorous cyclopoid abundance, main habitats, c) harpacticoid abundance, single sites, d) omnivorous cyclopoid abundance, single sites. A—F = main habitats as in Fig. 2; single site numbers given above the curves.

of importance would be annual food consumption; population production or respiration might also be used as they are closely correlated with food consumption. However, production measurements exist only for some sites and some species of the present study (own unpublished data), and therefore abundance and biomass must be used as rough measures of importance. Both are unsatisfactory, since the species pool includes small and large species, and there are considerable differences in the production to biomass ratios of different species.

When all benthic copepod species were treated together, the resulting curves were slightly sigmoid on stony shores and at 1—2 m, gently convex at 2—5 m, and with an inverted sigmoid shape among *Equisetum* and in the profundal. Steepness increased from the stony shores to the deep profundal, but the steepest curves indicating highest dominance occurred in *Equisetum* stands and at 5—10 m. The variation caused by imperfect measures of importance could be considerably diminished by analyzing the harpacticoid and omnivorous cyclopoids guilds separately, since the range of variation of both size and productivity are much less within these guilds than between them (own unpublished data). In harpacticoids there was a clear change from a nearly log-linear or gently sigmoid, gradually sloping curve on stony shores towards a steeper convex curve at greater depths. The same trend was visible both in abundance and in biomass. In omnivorous cyclopoids, in contrast, the sigmoid curve type of stony

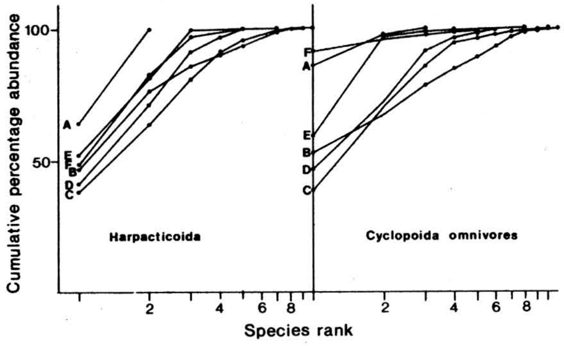

Fig. 10. Abundance-based *k*-dominance curves for the harpacticoid and omnivorous cyclopoid guilds in the main habitats of Lake Pääjärvi. A – F = main habitats as in Fig. 2.

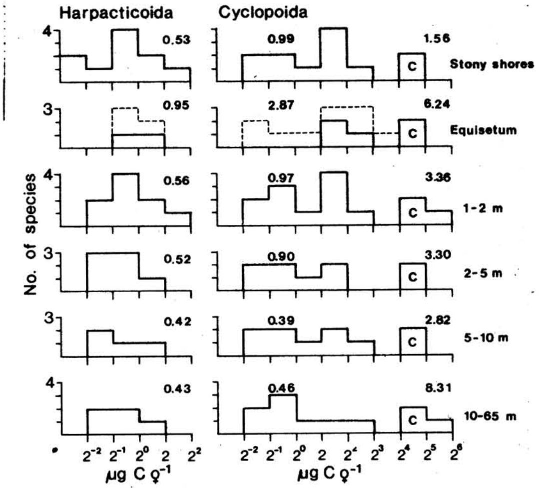

Fig. 11. Size distribution of adult females (μg C/ind) of the harpacticoid and cyclopoid species in each main zone. The actual mean sizes in the harpacticoid, omnivorous cyclopoid and carnivorous cyclopoid guilds are inserted.

shores changed to an inverted sigmoid type at 1 – 2 m and then gradually to a concave curve in the lower profundal. Both harpacticoid and omnivorous cyclopoid curves gave the impression of a consistent increase in dominance from 1 – 2 m to the lower profundal and towards the shore, where dominance was higher among *Equisetum* than on stony shores.

The possible effect of the between-site heterogeneity of the species assemblages was studied by comparing ranked-abundance curves based on single sites to the composite curves in Fig. 9. In harpacticoids, although there was much heterogeneity in the D_1 dominance, there was a general trend towards steeper curves deeper in the lake. The curve form could differ widely between different sites in the same depth zone, especially in the littoral, but many of the curves were convex, as in the main habitats. Most of these single site curves were still based on seasonally lumped data, although at most sites this should not bias the analysis (cf. Fig. 7). Only four single-visit samples (24, 27, 42, 60) were large enough for comparison. The inverted sigmoid or convex curves of three of these (sites 24, 27 and 42) suggested that the harpacticoid curves may be basically similar at all depths: at each site there may be two or three simultaneously abundant species, with no, or only a few rare, species. The rare species are more numerous in the littoral and decrease with depth. In the profundal, owing to the less heterogeneous assemblages, this pattern was revealed even in the pooled data, whereas in the littoral the combination of numerous, different assemblages produced a composite sample tending towards a log-normal distribution of species. The single site curves of the omnivorous cyclopoids were strikingly different from the composite main habitat curves: where the main habitat curves showed convexity, the single site curves were mostly concave. This suggests that the local omnivorous cyclopoid assemblages typically consisted of only one abundant species, and of more numerous, more or less equiabundant rare species, and that the dominant species could vary from site to site within the same depth zone. This difference between the harpacticoids and omnivorous cyclopoids is surprising in view of the greater between-site heterogeneity of the harpacticoid species assemblages (Table 5), but is consistent with the fact that the proportion of species dominant at some site is higher in the harpacticoid species pool than in the cyclopoid species pool.

The *k*-dominance curves (Fig. 10) further clarified the analysis. The crossing curves explained the conflicting suggestions of the different dominance measures. But the *k*-dominance curves revealed some consistent dominance arrangements. According to the abundance of harpacticoids and omnivorous cyclopoids, dominance increased from the 1 – 2 m zone towards greater depths and to the *Equisetum* zone, which had the highest dominance. The stony shores had a lower dominance than the *Equisetum* zone or the

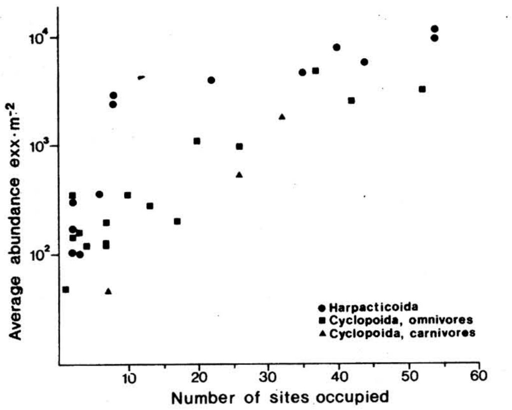

Fig. 12. Relationship between average abundance per site and number of sites occupied in the harpacticoid (dots), omnivorous cyclopoid (squares) and carnivorous cyclopoid (triangles) guilds in Lake Pääjärvi.

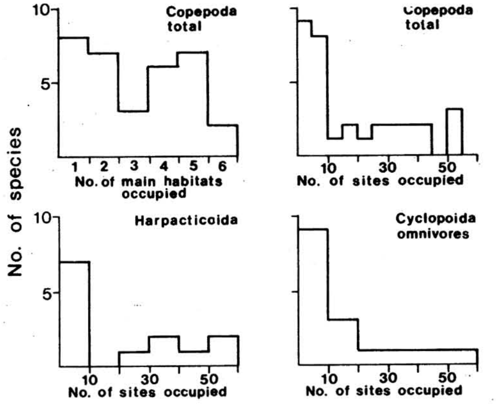

Fig. 13. Frequency distribution of species' distributions in the benthic Copepoda in Lake Pääjärvi: total Copepoda in main habitats, total Copepoda at single sites, Harpacticoida at single sites, and omnivorous Cyclopoida at single sites.

profundal zones, but crossing curves prevented a comparison of the 1—2 and 2—5 m zones.

Size distribution of the copepod species

Size distribution among the benthic copepod species in the different main habitats of Lake Pääjärvi is shown in Fig. 11. In harpacticoids the size range of species was widest on the stony shores, with both large and small species (the smallest were the interstitial forms). From the littoral to the profundal the size distribution shifted towards smaller species. This trend was evident also in the average individual size in the present samples, which thus also included variations in species abundance and population structure. Among *Equisetum*, harpacticoids were larger, and in the profundal smaller, than elsewhere. Exactly similar trends existed in the omnivorous cyclopoid guild, although the minimum size was larger and the whole size range wider than in harpacticoids. Except on stony shores, the size distribution of harpacticoids was unimodal, while the omnivorous cyclopoid distribution was bimodal. The smaller cyclopoid mode coincided with the larger harpacticoid mode. Carnivorous cyclopoids formed a third peak at the larger end of the cyclopoid distribution; their mean size showed no significant variation between habitats, except for a possible increase in the deep profundal due to the increasing contribution of the largest species, *M. gigas*. The small average for stony shores was biased, since the adults of carnivorous cyclopoids were under-represented in the meiofauna subsamples utilized.

Species commonness vs. abundance

The patterns of relative abundance prompted a comparison to the core and satellite species hypothesis of Hanski (1982). Indeed, in accordance with the hypothesis, the average local abundance was in statistically significant positive correlation with the number of sites occupied both in harpacticoids and in omnivorous cyclopoids, and the trend was similar in carnivorous cyclopoids (Fig. 12). The distribution of species frequencies according to the number of sites occupied (Fig. 13) was clearly bimodal in harpacticoids but not in omnivorous cyclopoids.

6. Discussion

6.1. Methodological considerations

Numerical classification and ordination

Numerical classification and ordination of the benthic copepod fauna in Lake Pääjärvi was successful and resulted in the separation of six major site groups, which largely coincided with the limnological depth zones of the lake. Indeed, one of the features of a good classification is that it should be able to predict things that were not included in the analysis. A meaningful analysis might produce site groups homogeneous as to depth, bottom quality, exposure to waves, sampling season, etc. Since many details of the methods are known to affect the results, a variety of exploratory techniques were applied to ensure that the patterns identified were real and not methodological artefacts. It was thought that only such features which would be repeated in varied analyses would represent real patterns present in nature. Indeed, at the level of six groups the numerical analyses were fairly robust, several methods resulting in largely similar groupings. The number of groups was determined by two *a priori* criteria. (1) Since samples originated mainly from two years, between-year variation was not allowed to affect final groupings. To ascertain this, it was required that samples from the same site in successive years should belong to the same group. In most analyses this requirement was fulfilled. (2) The stony shores should be distinguished from other habitats. Some methods failed to fulfill this condition.

An extensive literature exists on the application of multivariate classification and ordination methods to ecological data (see Orlóci 1978, Gauch 1982); therefore, brief comments will suffice here. A rigorous statistical evaluation of different methods would be desirable, but this has turned out to be very difficult (e.g. Gauch 1982). In the present study, cophenetic correlation coefficients of different classifications had little to do with the ecological relevance. A statistical comparison of different ordinations is possible through repeated analyses of randomized subsets of data (Wilson 1981), but requires a larger data set (around 250 samples) than was now available. Moreover, statistical comparisons are made more difficult by the variable degree of the horseshoe curvature, which need not hamper an effective visual interpretation of the ordination diagram (cf. PCOORD and DCA scatterplots; Fig. 3). Therefore, and since the various classification and ordination methods were here mainly used to obtain a sound result, I have given up attempts at statistical analysis and been content with a subjective evaluation of the methods.

A transformation was necessary for meaningful groupings to appear, but then even great variation in sample size could be overcome. The results of classification were especially dependent on the transformation, as well as on the choice of an appropriate distance measure and clustering algorithm. Ordinations with PCA (with or without subsequent rotation of axes), PCOORD (with or without Williamson's modification), RA and DCA produced much more consistent results, especially in the 1 − 9 m depth zone where no clearly distinguishable groups existed. On the other hand, MV or FLEX clusterings were useful aids in making practical decisions on the group boundaries. A combination of classification and ordination was thus obviously advantageous. In studying species relationships, clusterings were less useful, but ordinations were easier to interpret.

Quantitative distance measures were essential for a good analysis. *PD, PS, CT, G* and *U* produced practically equivalent results with transformed data. Although *PD* has been widely used (e.g. Field et al. 1982), Orlóci (1978) and Kohn & Riggs (1982) have, with sound arguments, recommended against its use. *CT* was the best index in Fasham's (1977) comparison; *PS* is independent of sample size and has other desirable properties (Bloom 1981, Kohn & Riggs 1982); *G* and *U* are mathematically correct metrics (Orlóci 1978). Any of these can be successfully used.

Diversity, evenness and dominance measures

The different diversity and evenness indices were of little use in the present study. All diversity measures essentially confirmed the information already contained in the observed number of species. In contrast, different evenness indices suggested contradictory patterns. I must agree with Alatalo (1981) who warned of the difficulties in measuring the evenness. Dominance was not much easier to evaluate, although the simplicity of the dominance indices D_1 and D_2 is attractive. However, in complete agreement with James & Rathbun (1981), the most efficient description of the structure of the copepod assemblages was obtained simply by examining the observed number of species, complemented with rarefaction techniques, and assessing the relative abundance distributions from ranked abundance curves. The advantage of ranked abundance curves over all dominance or evenness indices is that, with sampling restrictions, the whole distribution is available for examination. Visual comparison of trends is unexpectedly effective, and might in principle be complemented by statistical tests. However, the calculation of log-linear slopes for the ranked abundance curves as done by Rouch (e.g. 1980) was not feasible in the present study, since at species-poor sites the presence or absence of some rare species could radically change the value of the slope. It is true that the visual inspection of the curves is prone to the same source of error, and therefore it may be better to use the cumulative *k*-dominance curves advocated by Lambshead et al. (1983).

The concave form of the ranked abundance curve is common at least in marine benthic communities (Hughes 1984) and in avian communities (James & Rathbun 1981); and is predicted by Hughes' (1984) model from general principles of recruitment behaviour, competition and mortality. Convex (or inverted sigmoid) ranked abundance curves like those of the present study seem to be rare: the curves for nematodes and copepods at the middle estuarine site with sparse macrofauna in Warwick & Gee (1984) are the only ones I have seen depicted in the literature. To my knowledge, the only model that is consistent with such ranked abundance curves is the core and satellite species hypothesis of Hanski (1982).

6.2. Diversity of benthic copepods in Pääjärvi in worldwide perspective

The freshwater copepod fauna, possibly containing about 1000 species, is greatly impoverished compared to the marine species pool of about 6000 species. The free-living marine copepod fauna consists of at least 12 more or less specialized benthic or phytal ecological types (Noodt 1971). The reduction in the number of species from a fully marine milieu to a freshwater environment is parallelled by a decrease in the number of ecological types. The benthic copepods of Lake Pääjärvi can be classified into four or five ecological types: (1) actively-swimming herbivorous, carnivorous or omnivorous cyclopoids of different sizes, (2) small, infaunal omnivorous cyclopoids, (3) swimming and burrowing, but mostly infaunal harpacticoids, and (4) small, more or less vermiform burrowing harpacticoids that are poor swimmers and live in interstitial systems. *P. schmeili* might be included in the fourth group or separated as its own group, characterized by a larger size and stronger body form than in typical mesopsammic species. A comparison of these ecological types with the marine fauna reveals a distinct difference: in Lake Pääjärvi, as in lakes in general, actively-swimming phytal harpacticoids are wholly or almost lacking, and cyclopoids of the first group fill their role. Of the few abundant harpacticoid species of the *Equisetum* zone in Lake Pääjärvi, only *C. microstaphylinus* is a fairly good swimmer.

In spite of the restricted variety of ecological types, the total number of benthic copepod species found in Lake Pääjärvi is quite high compared to the total species pool of southern Finland. From 17 to 20 harpacticoid species are known to live in southern Finland (Enckell 1980, Sarvala, unpublished), of which 13 occur in Lake Pääjärvi. Including the cyclopoid species found in later studies in *Equisetum* stands (Lehtovaara & Sarvala 1984), 23 of the 29 nonpelagic cyclopoid species occurring in southern Finland inhabit Lake Pääjärvi. In zooplankton, the number of species in each lake is usually only a small fraction of the regional species assemblage (see e.g. Hebert 1982). Even the absolute number of species in Lake Pääjärvi is high compared to numbers reported from elsewhere (e.g. Pelosse 1934, Rey & Dupin 1973, Eie 1974, Daggett & Davis 1975, Adalsteinsson 1979, Anderson & DeHenau 1979, Fryer & Forshaw 1979), although Dussart (1966) listed 13 harpacticoid, but only 12 benthic cyclopoid, species from Lake Geneva, Rouch (1980) found 13 epigeous and eight hypogeous harpacticoid species in the Baget karstic system in the Pyrenees, and Monakov (1968) found 16 cyclopoid species (excluding planktonic species) in the littoral of the Rybinsk reservoir. The diversity of benthic cyclopoids in Lake Pääjärvi is higher than in the ancient and very large Lake Baikal, where Mazepova (1978) identified 21 benthic cyclopoid taxa; Fryer (1985) recently noticed that Baikal and several other very large and deep lakes have a very poor chydorid fauna, and related this with their monotonous and exposed littoral. The copepod species richness in Lake Pääjärvi in fact exceeds the highest hitherto recorded species richness of a freshwater copepod community, found in a tropical wet campo in Brazil (Reid 1984: 29 harpacticoid and four cyclopoid species). Thus, contrary to Reid's (1984) suggestion, the copepod communities of previously glaciated temperate areas do not always have few species.

The reasons for the high copepod diversity of Lake Pääjärvi are not yet clear. It might be argued that the depth and large profundal of Lake Pääjärvi would explain the diversity of at least the deep-water fauna. However, 31 of the 32 benthic copepod taxa were found in the 0—2 m depth zone. Depth alone thus does not seem to be very important, although the existence of large profundal populations may make possible the occurrence of deep-water species in the shallow areas. A partial explanation may be that the Finnish lake area with its very numerous, closely positioned chains of lakes offers extraordinary possibilities both for the dispersal and for the survival and coexistence of numerous species of aquatic invertebrates. The size of an individual lake of course affects the number of species (e.g. Fryer 1985), although the number of benthic copepod species seems to be clearly dependent on lake size only in rather small basins, of less than 0.5—1 km^2 (Sarvala, unpublished). This suggests that the variety of microhabitats available may be decisive for the microcrustacean fauna. Lake Pääjärvi belongs to the category of medium-sized lakes which have a fairly complete set of microcrustacean habitats and have the potential for a diverse fauna.

In comparison to other northern lakes, the contribution of meiofauna in general to the total zoobenthos biomass and production is also exceptionally high in Lake Pääjärvi (Morgan et al. 1980), although methodological differences may provide a partial explanation for this difference. In more eutrophic lakes the reason for the paucity of the benthic meiofauna is obviously the bad oxygen conditions in the hypolimnion and in sediments. The abundance, biomass and number of species of meiobenthic nematodes in the profundal are higher in oligotrophic than in mesotrophic or eutrophic lakes (Prejs 1977), and a similar correlation between lake trophic status and benthic copepod diversity seems plausible. Lake Pääjärvi as a whole is oligotrophic, but it is worth noting that many of the emergent macrophyte stands of Lake Pääjärvi are obvious eutrophic habitats, and offer suitable local environments for species favouring eutrophy.

The large difference in the total species pool between marine and freshwater environments makes a comparison of within-habitat diversities interesting. Local diversity is determined by short-term ecological mechanisms and may be quite loosely related to regional diversity determined by evolutionary mechanisms (or ecological mechanisms on an evolutionary time-scale). From four to 17 copepod species were counted from three estuarine intertidal mudflat sites in England (Warwick & Gee 1984). During 11 years, Coull & Dudley (1985) found a total of 47 copepod species on a North-American subtidal mud site, and 56 species on a sand site, but the average number of species on each date was 6.9 at the mud site and 5.7 at the sand site, or slightly less than at corresponding depths in Lake Pääjärvi. These comparisons indicate that a certain type of benthic environment can only support a limited number of copepod species at a time, and that benthic habitats might thus be saturated.

6.3. Factors behind the diversity patterns

Dispersal abilities of benthic copepods both in water (e.g with currents: Bell & Sherman 1980) and between isolated water bodies (Fryer 1985) are unexpectedly good, irrespective of the presence of resting stages. In Lake Pääjärvi, some faunal exchange between the main habitats is known to occur. In winter, the deep-water species *B. echinatus* and *D. abyssicola* may be found in the littoral area, and at the time of the autumn turnover littoral species may appear in deep profundal samples (e.g. *A. crassa* at 40 m). Floating algal mats and resuspended sediment may transport copepods over long distances. Therefore, the existing patterns of species distributions must be the result of a dynamic equilibrium between immigration and local extinction. The causes of the latter may be related to the specific autecological requirements of the species or to species interactions.

Huston's hypothesis

Huston (1979) suggested that the diversity of a community is determined by a dynamic equilibrium between the frequency of disturbance and the rate of competitive displacement of species. Usually the latter can be correlated with the productivity of the environment. This general diversity hypothesis predicts highest diversities at intermediate frequencies of population reduction, and at intermediate growth rates of the competing species. Huston's hypothesis is thus an extension of the intermediate disturbance hypothesis of Connell (1978).

Of the main habitats distinguished in Lake Pääjärvi, the littoral macrophyte zone is by far the most productive, if total primary production is considered (Sarvala et al. 1982, Kairesalo 1983). The production of the macrophytes, however, is not directly available as food for benthic copepods, and it might be more realistic to compare the contributions of epipelic, epilithic and epiphytic algae as well as benthic bacteria in different habitats. In summer 1973, the average daily production of epilithiphyton at a depth of 1 m at the stony shore site 1 in Lake Pääjärvi was only 3 mgC_{ass}/m^2 (Kairesalo 1976), whereas close to site 23 the daily production of epipelic algae at 1 m was 30 mgC_{ass}/m^2 (Kairesalo 1977), and similar values were later found for the epiphytic algae between sites 9 and 10 (Kairesalo 1980). With increasing depth, algal productivity decreased exponentially down to the lower limit of epipelic algae at about 5 m. No direct information on bacterial biomass or production is available, but measurements of benthic community metabolism allow rough comparisons between habitats. Within an *Equisetum* stand the total benthic daily respiration varied during summer from 300 to 900 mgC/m^2 (estimated from Bergström 1984), while values decreased from 250—230 mgC/m^2/day at 1—2 m, to 120—90 at 5—10 m, and to 45—30 at 20—40 m. Since winter respiration values were at all depths 5—10 mgC/m^2/day, the seasonal variability decreased correspondingly. At an annual level, the differences between depths somewhat decreased, but the trends remained. Dividing these figures by three gives a rough guess for benthic bacterial production. The emergent macrophyte stands were thus the most productive areas even in terms of algal and bacterial production. Annual productivity was halved from 1 to 5 m and once again from 5 to 20 m. The decrease in benthic productivity beyond 10 m was slight, but evidently significant: the life cycle of *P. schmeili* took two years at 13 m and three years at 40 m (Sarvala, unpublished). Other species of the deep profundal zone also grew very slowly. Thus, although copepod numbers remained at a similar level through littoriprofundal and profundal, the changed species composition in the deep profundal resulted in a lowered biomass turnover in accord with the decreased productivity. The decrease of mean size of both harpacticoids and omnivorous cyclopoids in the profundal may also reflect a more acute food shortage; a similar decrease in the mean size of benthic animals with decreasing productivity of the environment is noticeable from the coastal areas to the deep-sea (Thiel 1975).

Physical disturbances are most frequent and severe in the littoral zone. In Lake Pääjärvi, winter ice extends to a depth of about 50 cm, and due to the late winter decrease in the regulated water level, the ice often lies on the bottom down to a depth of 80—90 cm. On stony shores, however, the stones prevent the ice from immediate contact with sediment, thus improving the survival of zoobenthos (E. Alasaarela & S. Hellsten, unpublished). Moreover, several littoral species may survive winter freezing (Enckell 1969), and other species escape to deeper water for the winter. Probably more important for the copepod assemblages are differences in summer conditions. On stony shores, wave action moderates diel variations in temperature, pH and chemical parameters; most importantly, oxygen levels always remain high. In contrast, the sediments in the inner parts of dense macrophyte stands experience wide diel variations in many parameters: temperature and pH vary from high during day to low at night, and oxygen concentration may vary from oversaturation in the afternoon hours to severe deficiency during the night (Sarvala et al. 1982, Kairesalo 1983).

Littoral bottoms with submerged, especially isoetid, macrophytes are still productive but almost free of severe physical disturbances. At depths of less than 1 m, part of the surface sediment may be resuspended during windy days, and on bright calm days the algal mat on the surface of the sediment may become covered by oxygen bubbles; eventually small patches of this mat loosen and are lifted up to the water surface, floating far before sinking.

The annual and diel temperature range are widest in shallow water and decrease towards deep water. On the other hand, during the thermal stratification in summer, temperature is fairly stable both above and below the thermocline, but around the thermocline depth, at about 5—10 m, there are frequent, fairly large and unpredictable fluctuations of temperature due to wind-induced tilting of the thermocline. Considerable near-bottom currents may also occur in this area. It is uncertain whether the temperature fluctuations *per se* have any unfavourable influence on the benthic copepods, but it is quite conceivable that the intervening warm-water periods can restrict the development of some cold-adapted species.

Selective predation has been shown to be an important ecological force acting on the deep-sea (Thistle 1982) and estuarine (Hicks 1984) harpacticoids. Non-selective predation can also be considered as a kind of disturbance of the system. In Lake Pääjärvi, differences in the level of predation pressure between the main habitats are difficult to evaluate. Several invertebrate predators fed on benthic copepods, but there were no species specialized on this group (Haka et al. 1974). The production of benthic predators relative to their potential prey was highest on the stony shores, and about similar at all depths below 1 m. Exact data from the *Equisetum* zone are still lacking, but large and mobile invertebrate predators (e.g. corixids) are known to be abundant. Predation by young fish is probably concentrated in areas immediately outside and in the outer part of belts of emergent vegetation at a depth of about 1 m; on stony shores, predation by the stone loach, bullhead and young perch and burbot may also be important. The invertebrate predation probably occurs at least partly within the sediment, whereas fish predation falls most heavily on the epibenthic species (Hicks & Coull 1983), hence in Lake Pääjärvi mainly on the larger herbivorous-omnivorous and carnivorous cyclopoids. Further speculations are, however, fruitless, since the different types of predation cannot be quantified in Lake Pääjärvi.

The predictions of Huston's (1979) hypothesis, derived from the environmental quality of each main habitat, cannot be rejected by the data. As highly productive and relatively disturbed environments, the *Equisetum* stands should have the lowest diversity and highest dominance. As a less productive but moderately disturbed environment, the stony shores should have a higher diversity than the more productive but less disturbed littoral bottoms at 1—2 m. And the diversity should decrease towards the deepest parts of the lake due to the restrictively low productivity. The generally higher dominance among the more rapidly growing cyclopoids relative to the slow-growing harpacticoids is also consistent with Huston's hypothesis. However, the basic assumption of Huston's hypothesis is that competitive displacement, although interrupted by various disturbances, is going on in the community. In the benthic copepod assemblages of Lake Pääjärvi, there is little evidence of actual competition between species: Microdistribution of benthic copepod species in the littoral of Lake Pääjärvi was indistinguishable from random combinations of species (Ranta & Sarvala, unpublished). The growth rates of the dominant harpacticoids at 1 and 2 m usually seemed to agree fairly well with rates obtained in the laboratory with abundant food and no interspecific competition; in contrast, intraspecific competition seemed at times to decrease fecundity in *A. crassa* (Sarvala, unpublished). The probability of interspecific interactions in the littoral is also decreased by a partial seasonal succession of the production peaks of individual species (Sarvala, unpublished). Competition might be more probable in the deep profundal zone with its very low productivity and broadly overlapping peaks of production. The number of abundant species is here very low, but there seems to be at least partial vertical separation of two of the harpacticoid species (Table 2): *B. echinatus* is restricted to the mud surface, whereas *P. schmeili* lives in deeper layers, at least as an adult. In contrast, the cyclopoid species, although capable of moving in the sediment, usually reside at or very close to the sediment surface. This difference in the vertical use of sediment may be the reason why 2—3 harpacticoid but only one cyclopoid species can be abundant in the low-food environment of the deep profundal. Moreover, different food preferences for each species are quite probable (cf. Gray 1968, Vanden Berghe & Bergmans 1981, Montagna 1984, Carman & Thistle 1985).

When considering potential interspecific interactions, the scale of observations is important, and this scale may be different for harpacticoids and cyclopoids. Owing to the usually larger size and greater mobility of cyclopoids, each cyclopoid individual probably utilizes the resources of a larger area than a harpacticoid. In adult harpacticoids, the spatial scale for interactions may be of the order of 10 cm^2, or about the size of a single meiofauna core, whereas in cyclopoids it may be of the order of several square metres, or about the area from which a series of replicate meiofauna cores may be collected. In laboratory cultures, if food is abundant, harpacticoid nauplii may even remain throughout their whole development in or on the same piece of a decomposing leave not larger than a few mm^2. The species which are found in ten replicate sediment cores are not necessarily all living in exactly the same environment.

Thus, although my results do not contradict the predictions of general diversity hypotheses, other, more concrete reasons for the observed patterns are worth examining. The same environmental factors hypothesized as affecting the competitive interactions may well regulate the community organization through direct effects on the individual species.

Diversity of microhabitats

The importance of habitat structural complexity, or the number of microhabitats, to the diversity of marine phytal harpacticoids was demonstrated by Hicks (1980). The kind and number of microhabitats in the main habitats of Lake Pääjärvi differ. Emergent macrophyte stands offer only two microhabitats: soft organic sediment with abundant plant detritus and bad oxygen conditions, and the epiphytic community on the macrophytes. Although the macrophyte stands have the highest food production, the unfavourable oxygen conditions of the sediment exclude the burrowing benthic copepods, and only the epibenthic, epiphytic and swimming species can thrive. The only harpacticoids abundant in the *Equisetum* zone, *C. microstaphylinus* and *M. mrazeki*, seem to be living on the periphyton on *Equisetum* stems; judging from the colour of their gut contents in this environment and on the stony shores, they probably feed on littoral algae (cf. Carman & Thistle 1985). The cyclopoid species in the *Equisetum* zone are very motile herbivorous-omnivorous or carnivorous species; true meiobenthic burrowing species like *P. fimbriatus* or *D. nanus* are practically lacking. Three of the four additional cyclopoid species found in the *Equisetum* zone in the very large material of Lehtovaara & Sarvala (1984), *Acanthocyclops vernalis, Diacyclops bicuspidatus* and *D. b. odessanus*, are most probably bound to the near-shore, shallow parts of the stand, where the environmental conditions greatly resemble those of shallow pools; these species are elsewhere common in pools. Environmental factors thus probably mainly explain the dominance of cyclopoids over harpacticoids in the *Equisetum* stands. The shift from a diverse harpacticoid-dominated copepod assemblage on the soft bottoms of open littoral at a 1 – 2 m depth to a less diverse assemblage dominated by highly mobile herbivorous and carnivorous cyclopoids within the stands of emergent macrophytes, probably reflects both the increase in algal food and cladoceran, oligochaete and chironomid prey available and the major change in sediment quality. The productive but unpredictable environment among macrophyte vegetation is also suitable for cyclopoids that have shorter generation times and higher investments in reproduction than harpacticoids (Sarvala 1979 and unpublished). Favourable food conditions make possible the large individual size of copepods among Equisetum, and the large size allows of larger clutches.

The greater abundance of cyclopoids in the littoral zone, and their dominance especially within stands of macroscopic vegetation, agree also with the findings of Gee et al. (1985), who showed that experimental organic enrichment resulted in a significant increase of epibenthic and surface-dwelling copepod species and a simultaneous increase in dominance and decrease in diversity; at a low level of enrichment diversity slightly increased. Similar changes of copepod dominance and diversity were found in field experiments by Hockin (1983).

The stony shores probably offer the largest variety of microhabitats: on the stones the algal mat, between stones sediment with abundant terrestrial plant detritus, and between and below the stones a well oxygenated interstitial milieu; and in general the range of particle sizes is large, allowing for different sizes of sheltered crevices. The interstitial copepods of Lake Pääjärvi, *P. brevipes* and *E. richardi* and most probably also *D. languidus belgicus*, were found solely on stony shores.

The psammic environment is also present at and above shoreline on sandy shores (but was not sampled in this study; previous data in Fennoscandia given by Enckell 1969), but in Lake Pääjärvi does not extend to deeper bottoms: the limited movement of sediment allows packing of the interstitial spaces with fine particles; then space and oxygen become limiting. The narrow range of sediment quality in Lake Pääjärvi, especially the lack of coarse, well-oxygenated gravel and sand bottoms, explains the fact that substrate quality had a minor effect on the copepod assemblages in Lake Pääjärvi. In the sea, in contrast, sediment quality, taken broadly to include the abundance of microbial food organisms (e.g. Ravenel & Thistle 1981), has usually turned out to be the decisive factor determining meiofaunal assemblages, depth having only a minor role (e.g. Moore 1979b, Ivester 1980, Hockin 1982, Decho et al. 1985).

Littoral vs. deep-water species

The faunal turnover around a depth of 10 m may be really influenced by the fluctuating temperature conditions at 5—10 m. There is a strong littoral faunal element in the copepod assemblage of Lake Pääjärvi. These littoral species decline towards depth, partly with decreasing productivity, partly with decreasing temperature which prevents their reproduction (e.g. the eggs of *A. crassa* do not develop at all at 2.5°C; Sarvala 1979). The number of species attaining their maximum abundance in each site group reflected this decrease quite clearly. Then at a depth exceeding 10 m, another faunal element appears, the cold-adapted deep-water species which find suitable conditions in the stable, cool conditions of the deep profundal. Their occurrence in the upper layers may be restricted by the warm summer temperatures (cf. Fryer & Joyce 1981), which may in some cases wholly hinder reproduction (*M. brevipes, B. echinatus*, probably *D. abyssicola*). Such species as occur both in the littoral and in the deep profundal, restrict their reproduction in the littoral only to winter (*M. brevipes*) or to spring and autumn (*P. schmeili*). In shallower lakes in Finland, where such a deep-water faunal element is lacking, the decrease in species diversity with increasing depth is steep and quite like in Lake Pääjärvi down to 10 m (Sarvala, unpublished).

But this explanation does not tell the whole truth. Some of the species becoming more abundant in the deep profundal are elsewhere known as inhabitants of small, even temporary pools (e.g. *D. crassicaudis*). On the other hand, *B. minutus* which was restricted to stony shores and other littoral areas in Lake Pääjärvi, was one of the dominant profundal species in Lake Toisvesi in Central Finland, where *B. echinatus* was scarce, but was lacking in the profundal of Lake Keitele, where *B. echinatus* was dominant (meiofauna material collected by Paasivirta & Särkkä 1978). *B. minutus* was also the only freshwater harpacticoid species at 10 and 28 m in the brackish-water Bothnian Bay ($0.4^0/_{00}$ salinity; Räisänen & Sarvala, unpublished). Competitive interactions may be important in such cases: *B. minutus* seems to be absent from the profundal if *B. echinatus* is abundant. Competition experiments and more information of the actual food and microhabitat requirements of each species are needed before more extended conclusions can be reached.

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Appendix 1. List of sampling sites with sample size, total abundance of copepods per m^2, and a subjective characterization of each site. C = clay or silt, G = gravel, O = soft organic gyttja, S = sand, St = stony shore site, exp. = exposed.

Site no.	Depth m	Sample exx.	size cm^2	Total abundance	Habitat characteristics
1	0.3	904	414.8	21 788	St, N-exp., shady
2	0.3	390	207.4	18 783	St, N-exp.
3	0.3	274	207.4	13 200	St, S-exp.
4	0.3	355	207.4	17 136	St, SW-exp., open
5	0.3	170	103.7	16 416	St, S-exp., much detritus
6	0.3	207	103.7	19 968	St, S-exp., much detritus
7	0.3	115	103.7	11 040	St, N-exp., sheltered
8	0.2	3	7.9	3 774	*Equisetum* stand, CS
9	0.3	150	408.0	3 676	dense *Equisetum* stand, O
10	1.0	5780	811.5	71 226	O off *Equisetum*
11	1.0	314	45.6	68 820	O with plant detritus
12	1.0	180	45.6	39 413	O
13	1.0	140	45.6	30 723	hard S
14	1.0	36	7.9	45 288	O with plant detritus
15	1.0	208	45.6	45 532	hard CO, S-exp., off emergent vegetation
16	1.0	86	7.9	108 188	S-exp., hard SG
17	1.0	491	79.0	62 115	hard S
18	1.0	1607	159.9	100 499	7−8 cm thick brown O on grey C
19	1.0	38	7.9	47 804	O
20	1.0	318	45.6	69 681	hard S
21	1.5	326	38.0	85 892	compact CO
22	1.5	382	38.0	100 473	compact CO
23	1.5	315	109.2	28 849	hard S
24	1.5	3492	400.0	87 309	compact CO
25	2.0	4672	532.0	87 815	compact CO
26	2.0	6140	513.5	119 570	compact CO
27	2.0	879	152.0	57 840	hard S + CG and Fe-concretions
28	2.0	180	45.6	39 413	S
29	2.0	151	45.6	33 164	S-exp. fairly hard O
30	2.0	78	15.2	51 324	G with coarse detritus
31	3.0	183	91.2	20 078	O with coarse detritus
32	3.0	135	91.2	14 806	O with coarse detritus
33	3.0	39	15.2	25 662	brown O
34	3.0	39	15.2	25 662	C with S and coarse detritus
35	4.0	198	45.6	43 495	medium hard grey C with S
36	4.0	94	45.6	20 662	C with S
37	4.0	132	45.6	28 885	compact O
38	4.0	68	45.6	14 803	compact O
39	4.0	43	15.2	28 293	C with S and coarse detritus
40	5.0	118	45.6	25 926	compact grey C with S and brown surface layer
41	5.0	240	45.6	52 618	brown O with S and coarse detritus
42	5.0	630	136.5	46 177	brown soft O
43	5.0	270	68.3	39 565	brown soft O
44	6.0	265	76.0	34 864	brown soft O
45	6.0	388	152.0	25 534	brown soft O
46	8.0	243	45.6	53 231	brown soft O
47	8.0	307	45.6	67 313	brown O
48	8.0	322	152.0	21 188	brown O
49	8.0	214	45.6	46 315	brown O
50	8.0	96	45.6	21 056	brown O with Fe-concretions
51	9.0	88	45.6	19 303	brown soft O
52	12.0	130	76.0	17 109	brown soft O
53	14.0	1874	1064.0	17 611	brown soft O
54	13.0	7417	912.0	81 330	grey C with brown surface layer
55	13.0	3961	474.0	83 560	grey C with brown surface layer
56	25.0	152	152.0	10 003	brown soft O
57	40.0	3654	1064.0	34 339	brown soft O
58	40.0	3680	1064.0	34 581	brown soft O
59	60.0	102	45.6	22 305	brown soft O
60	65.0	378	152.0	24 872	brown soft O

Appendix 2. List of benthic and littoral copepod species found in Lake Pääjärvi, and their food according to Monakov (1976) and own observations. D = detritus and associated bacteria, A = benthic and epiphytic algae, P = Protozoa, Rotifera and other small invertebrates, C = Oligochaeta, benthic and planktonic Cladocera and Copepoda. The occurrence of each species in the main habitats of Lake Pääjärvi is indicated by plus signs; those in parentheses refer to finds by Lehtovaara & Sarvala (1984). Main habitats: 1 = stony shores, 2 = *Equisetum* stands, 3 = 1–2 m, 4 = 2–5 m, 5 = 5–10 m, 6 = >10 m.

	Food	Main habitats					
	type	1	2	3	4	5	6
Harpacticoida							
Canthocamptus staphylinus (Jurine 1820)	D	–	–	+	–	–	–
C. microstaphylinus Wolf 1905	D, A?	+	+	+	–	–	–
Attheyella crassa (Sars 1863)	D, A?	+	(+)	+	+	+	+
A. dentata (Poggenpol 1874)	D, A?	+	–	–	–	–	–
Epactophanes richardi Mrázek 1893	D?	+	–	–	–	–	–
Moraria brevipes (Sars 1863)	D	+	–	+	+	+	+
M. mrazeki T. Scott 1903	D, A?	+	+	+	+	–	+
Bryocamptus minutus (Claus 1863)	D, P, A?	+	–	+	+	–	–
B. pygmaeus (Sars 1863)	D, A?	–	(+)	+	+	–	–
B. echinatus (Mrázek 1893)	D	–	–	+	+	+	+
Elaphoidella gracilis (Sars 1863)	D, A?	+	(+)	–	–	–	–
Paracamptus schmeili (Mrázek 1893)	D, A	+	–	+	+	+	+
Parastenocaris brevipes Kessler 1913	D?	+	–	–	–	–	–
Cyclopoida							
Macrocyclops albidus (Jurine 1820)	C, P	+	+	+	+	+	+
Eucyclops serrulatus (Fischer 1851)	A, P	+	–	+	–	–	–
E. speratus (Lilljeborg 1901)	A, D, P?	+	+	+	–	+	+
E. macrurus (G.O. Sars 1863)	A, P?	+	+	–	–	–	–
E. macruroides (Lilljeborg 1901)	A, P	+	–	+	+	+	–
Paracyclops fimbriatus (Fischer 1853)	A, P?	+	–	+	+	+	–
P. f. chiltoni (Thomson 1882)	D, P?	–	–	–	–	–	+
P. poppei (Rehberg 1880)	A?, P?	–	(+)	–	–	–	–
P. affinis (G. O. Sars 1863)	A, D?, P?	–	+	+	–	–	–
Acanthocyclops vernalis (Fischer 1853)	C, P	–	(+)	–	–	–	–
Megacyclops viridis (Jurine 1820)	C, P	+	+	+	+	+	+
M. gigas (Claus 1857)	C	–	–	+	–	–	+
Diacyclops bicuspidatus (Claus 1857)	C?	–	(+)	–	–	–	–
D. b. odessanus (Schmankevitch 1875)	C?	–	(+)	–	–	–	–
D. crassicaudis (G. O. Sars 1863)	D, P?	–	–	+	+	+	+
D. abyssicola (Liljeborg 1901)	D, P?	–	–	+	+	+	+
D. languidus (G. O. Sars 1863)	A, P?	+	(+)	–	–	–	–
D. l. disjunctus (Thallwitz 1927)	D?	–	–	+	–	–	+
D. l. belgicus Kiefer 1936	D?	+	–	–	–	–	–
D. nanus (G. O. Sars 1863)	D, A, P	+	(+)	+	+	+	+
D. languidoides (Lilljeborg 1901)	D, P?	–	(+)	–	–	+	+
Cryptocyclops bicolor (G. O. Sars 1863)	D, P	+	(+)	+	+	+	+
Microcyclops rubellus (Lilljeborg 1901)	D, P?	+	–	+	+	–	–

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