

An assessment of Harpacticoida and resting stages of Cyclopoida as trophic indicators in Finnish lakes

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The early winter assemblages of Harpacticoida and densities of Cyclopoida were compared at the upper profundal and sublittoral zones of two large lakes of contrasting trophic levels in eastern Finland. Supplementary information is given about the not so well known benthic copepod fauna in Finnish lakes. Assuming unimodal relationships between the species' relative abundances and lake productivity, a weighted averaging regression and calibration model to infer lake trophic level from harpacticoid assemblages in upper profundal depth was constructed and evaluated using the available data from Finnish lakes. The epilimnetic total phosphorus was used as the measure of lake trophic level. In different comparisons the harpacticoid-inferred and observed total phosphorus was significantly correlated and the root mean squared error of prediction estimated by bootstrap or cross-validation methods was tolerable (3.3–5.1 $\mu\text{g l}^{-1}$). The results prove harpacticoids as potential trophic indicators and demonstrate the applicability of weighted averaging approach in biological indication using benthic invertebrates. Larger numbers of benthic cyclopoid resting stages were observed in lake areas of higher trophic level, but it was concluded that the phenomenon cannot be explained by decreased fish predation resulting from oxygen deficiency, as recently suggested. Two alternative explanations are hypothesized.

1. Introduction

Freshwater benthic copepods, as meiobenthic animals in general, have attracted little interest considering their diverse and important role in aquatic systems. In the first Finnish quantitative studies of lacustrine meiofauna, published no more than two decades ago (e.g. Särkkä & Paasivirta 1972, Särkkä 1975, Holopainen & Paasivirta 1977), copepods were mainly treated

at a group level. Recently Sarvala (1986) has thoroughly described the benthic copepod assemblages of Lake Pääjärvi, and Särkkä (1992a, b) has investigated the profundal meiofauna of Lake Päijänne with particular reference to Harpacticoida. Not much more has been published on benthic copepod fauna in Finland.

Särkkä (1992a, b) related the abundances of profundal harpacticoid species to water quality variables and suggested harpacticoids as poten-

tial indicators of pollution or a trophic level. Särkkä (1992a) based his conclusions on linear correlations between the species' abundances and the environmental variables within a single lake. However, correlation coefficients are not useful in ranking species in accordance to their environmental preferences, i.e. giving them indicator values. Moreover, linear correlation may not be an approvable approach, since the organism's relationship to an environmental factor can be unimodal instead of monotonic, each species having an optimum value, especially when the observed range is wide enough (e.g. Ter Braak & Prentice 1988). In such instances, the weighted averaging method in the recently introduced form (Ter Braak & Barendregt 1986, Ter Braak & Looman 1986) provides a simple, yet objective measure to derive ecologically meaningful species indicator values and further, a tool to obtain estimates for environmental variables for sites on the basis of species assemblages. The method has been extensively brought forth into biological indication, especially in lacustrine environments and using algae as indicator organisms (e.g. Oksanen et al. 1988, Ter Braak & van Dam 1989, Birks et al. 1990, Hall & Smol 1992, and references therein). The approach has not yet been applied to lake benthic animals (see Johnson et al. 1993), but reliable estimates of stream acidity have been obtained by using macroinvertebrates as indicator organisms (Hämäläinen & Huttunen 1990, and forthcoming).

Särkkä (1979, 1992b) observed increased density of cyclopoid resting stages in profundal sediments of polluted or eutrophicated areas in Lake Päijänne. Consequently, Särkkä (1992b) suggested large numbers of resting cyclopoids as an indication of eutrophic, organically loaded, or poorly oxygenated conditions. The phenomenon was explained by decreased fish predation due to hypolimnetic oxygen deficiency (Särkkä 1979, 1992b). As the planktonic copepodids enter diapause, they are assumed to sink passively to the bottom (e.g. Vijverberg 1977). Accepting this, the benthic copepodid density can be expected to correspond to the number of cyclopoids in the overlying water column preceding the diapausing period. According to the fish predation hypothesis, the benthic populations in unpolluted or oligotrophic areas should, as a result of fish pre-

dation, be smaller than expected. In the polluted or eutrophic areas, in turn, the benthic population should be equal to or differ less from the planktonic population.

In this study we compared the early winter assemblages of Harpacticoida and the densities of the resting stages of Cyclopoida at the upper profundal and sublittoral zones of two large basins of contrasting trophic levels in the Saimaa lake system in eastern Finland. The aim of the study was to provide supplementary information of the poorly known benthic copepods in Finnish lakes and to assess them as trophic indicators. Assuming unimodal relationships, tentative trophic indicator values for harpacticoid species were derived from the available data from Finnish lakes, and a simple weighted averaging model for the assessment of the trophic level in lakes on the basis of harpacticoid assemblages was constructed and evaluated. An attempt was made to test the predation hypotheses in explaining density of benthic cyclopodids by comparing the observed benthic density to that expected on the basis of autumnal planktonic populations.

2. Study area

Sediment and zooplankton samples were gathered in two humic lakes, Lake Pyhäselkä (area 229 km², mean depth 10 m, max. depth 70 m) and Lake Paasivesi (area 108 km², mean depth 21 m, max. depth 72 m), in eastern Finland (Fig. 1). Lake Pyhäselkä receives a loading of nutrients from the surrounding agriculture. Additional loading, mainly via the river Pielisjoki by purified sewage waters of the city of Joensuu and by effluents of a pulp mill 30 km upstream, produces a decreasing trophic gradient from north to south (Mononen & Niinijö 1993, Holopainen et al. 1993, Karjalainen et al. 1994, Table 1). The summer thermal stratification is rather weak and the temperature in hypolimnion (below 15–20 m) usually exceeds 10°C during the summer period. Oxygen saturation is low in the greatest depths during the winter stagnation period (Table 1), but not remarkably low during summer. Lake Paasivesi is oligotrophic, loaded only by nonpoint sources and with little spatial variation in trophic variables (Mononen & Niinijö 1993,

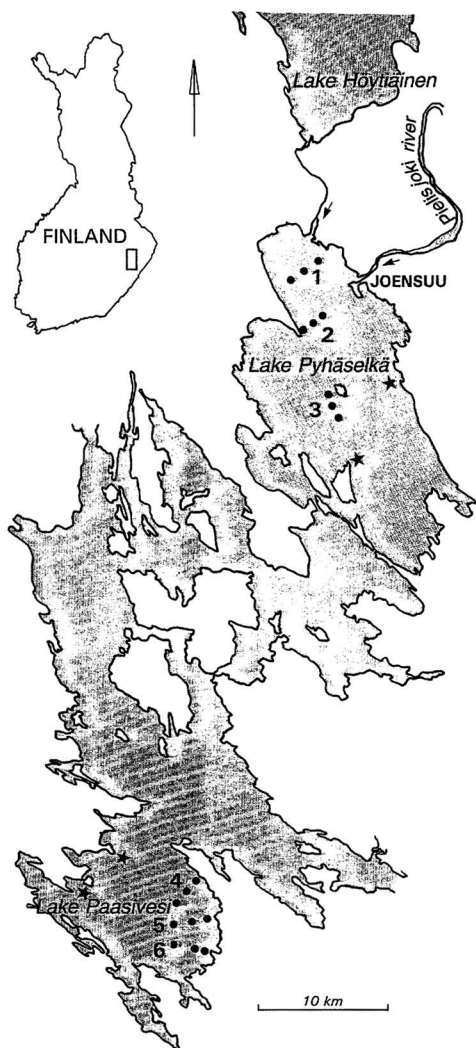


Fig. 1. The study area and location of benthic sampling sections (indicated by numbered dots) and plankton sampling stations (indicated by an asterisk if different from the benthic sampling sites).

Holopainen et al. 1993, Table 1). The lake is thermally well stratified, with cold ($< 6^{\circ}\text{C}$), well oxygenated hypolimnion ($< \text{c. } 20 \text{ m}$) throughout the year.

Three benthic and five zooplankton sampling stations were placed in both lakes (Fig. 1). The water quality information for Lake Pyhäselkä was compiled from the data collected for monitoring purpose in 1990 (Holopainen & Huovinen 1991). The epilimnetic total phosphorus values

for Lake Paasivesi were adopted from Mononen & Niinioja (1993) and the oxygen saturation measurements were from a monitoring station located nearby the benthic sampling stations (data supplied by the Water and Environment District of North Karelia).

3. Material and methods

Benthic samples were taken from three depths representing the sublittoral (5 m) and upper profundal zones (15 m and 25 m, 19 m at st. 1) at each of the six stations on December 14th – 19th 1990. Three replicate samples were taken from each depth through bore holes in ice using a Kajak corer with an inner diameter of 45 mm ($A = 15.9 \text{ cm}^2$). The topmost 5 cm of each replicate haul was separately transferred to a plastic container and preserved in 4 % neutralized formaldehyde. In the laboratory, the samples were washed through a $80 \mu\text{m}$ sieve, stained by the method of Thiel (1966) and sorted from a grooved disk (Hakala 1971) under a dissecting microscope at $12\times$ magnification. Harpacticoid adults and copepodids were identified to species from whole mounts in polyvinyl-lactophenol and counted. Cyclopoids were grouped into benthic and diapausing planktonic forms and counted.

Zooplankton samples were collected in five stations located in the littoral and pelagial zone of the lakes in 1989–1991. Composite samples representing the pelagial zone consisted of 10 subsamples taken with the tube sampler (volume 6.79 l, length 1 m) from the 0–5 m and 5–10 m depth zones in 1989 and 1990. The total water

Table 1. Some limnological characteristics of the benthic sampling stations.

	Station					
	1	2	3	4	5	6
Local maximum depth (m)	19	36	57	72	72	72
Minimum O_2 saturation at max. depth (%)	33	18	17	61	61	61
Minimum O_2 saturation at 25 m. (%)	–	59	74	87	87	87
Mean epilimnetic total phosphorus ($\mu\text{g l}^{-1}$)	16	16	14	8	9	9

column in 5 meter intervals was sampled in 1991. In the littoral zone, the samples were gathered in the perpendicular transect from the shoreline to the depth of 4 m. The samples were concentrated with a 48 μm net and preserved in 70% ethanol and in formaldehyde in the laboratory. For counting, three 10–40 ml subsamples were taken from agitated samples with a pipette. The diameter of the mouth of the pipette was 4 mm, and the total volume of the sample 250 ml. All zooplankters were counted in a sedimentation cuvette with an inverted microscope. The different developmental stages of cyclopoids were identified and counted.

Epilimnetic total phosphorus (TP) concentration was selected for the measure of lake trophic level, since phosphorus is usually considered the limiting factor for freshwater production (e.g. Hecky & Kilham 1988, Hessen 1992) and as data for this variable was available for all sites. A simple approach to summarize the species' unimodal response to an environmental variable (TP in this case) is to calculate the average and standard deviation of the environmental variable over all observed sites, weighted by the abundance of the species at each site. On certain conditions the weighted average (WA) is a reliable approximation for the species' optimum along the environmental gradient and the abundance weighted standard deviation an estimate of the species' tolerance or amplitude. The estimation of indicator values is referred to as regression (Ter Braak & Barendregt 1986, Ter Braak & Looman 1986). Supposing the species' response is unimodal we can further assume that the abundance of each species at a given site is proportional to the distance of the species' optimum from the environmental value of the site. Then a simple estimate for the environmental variable at each site is obtained as the abundance weighted average of the species' optima over all species present. Poor indicators with wide amplitude can be downweighted by inverses of their squared tolerances. The estimation of the environmental variable is referred to as calibration. For the theory and further details of weighted averaging regression and calibration see Jongman et al. (1987), Ter Braak & Prentice (1988) and the publications referred therein.

The WA estimates for species' optima and tolerances for the TP (trophic) level were de-

rived from the data of Särkkä (1992a, 20 m) referred to as data set A, and separately from all available data of comparable depths, referred to as data set C. The latter comprises the data set A (see above), and data set B: the present material (15–25 m pooled), unpublished data from Lake Höytiäinen (27 m) (I.J. Holopainen et al., unpublished), and data from Lake Pääjärvi adopted from Sarvala (1986) (mean densities in 10–85 m) (Table 2). The inference model derived from the data set A was cross-validated by using the set B as a test group. To avoid circular logic and overestimation of the prediction power, the prediction error of the full model based on the whole data set (C) was assessed by the bootstrap method (Efron & Gong 1983, Wallach & Goffinet 1989, see Birks et al. 1990). The regression and calibration were performed by the latest version (3.3, J.M. Line, C.J.F. Ter Braak & H.J.B. Birks, unpublished) of WACALIB program (Line & Birks 1990), providing the bootstrapping option (see Birks et al. 1990). In the bootstrapping procedure, the number of resampling cycles was 1000 and the seed value randomized. Percentage abundances, instead of densities, were used in regression and calibration, because they were assumed to be less sensitive to alterations caused by differences in sampling methods and sampling times. Preliminary trials also proved that relative abundances yield least prediction error. Inverse and classical regression were used in 'deshrinking', i.e. correcting the inherent bias of predictions towards the observed mean (Ter Braak & van Dam 1989, see Birks et al. 1990). The prediction power of the models was assessed in terms of the

Table 2. Summary of the three sets of lake sites used in regression and calibration.

Data set	<i>n</i>	TP ($\mu\text{g l}^{-1}$)		
		mean	<i>SD</i>	range
A ¹⁾	9	15.89	4.89	8–24
B ²⁾	8	10.88	3.76	5–16
C ³⁾	17	13.53	5.05	5–24

¹⁾ Särkkä 1992a

²⁾ present study, Holopainen et al. (unpubl.), Sarvala 1986

³⁾ A + B

root mean squared error, RMSE, of the predictions (Wallach & Goffinet 1989) and the correlation coefficient (r) between the predicted and observed values. When the bootstrapping procedure was applied, the correlation was calculated between the mean of the bootstrap estimates (as tabulated by the WACALIB) and the observed values. The apparent RMSE and r refer to estimates without bootstrapping.

Following Särkkä (1979), the expected benthic density of cyclopoids was calculated according to the planktonic densities of C3–C5 copepodids estimated from the vertical samples taken in September 1990. In the littoral zone, the

animals were assumed to sink to the bottom from the overlying 0–5 m water column and in the pelagial zone from the 0–25 m water column. The densities in the 10–25 m column in 1990 were approximated using the estimated densities in the 0–10 m column in the respective year and the relative vertical distribution in 1991.

4. Results

Altogether 9 species of Harpacticoida were identified from the samples, and each of the two lakes was represented by 7 species (Table 3).

Table 3. Mean ($n = 3$) density of Harpacticoida and benthic resting stages of Cyclopoida (ind. $m^{-2} \times 10^3$) at different depths in Lake Pyhäselkä (st. 1–3) and Lake Paasivesi (st. 4–6).

Depth/Taxon	Sampling station					
	1	2	3	4	5	6
25 m						
<i>Canthocamptus staphylinus</i>	—	—	—	—	—	—
<i>Attheyella crassa</i>	5.0	5.0	—	—	—	—
<i>Moraria brevipes</i>	—	0.2	—	0.2	0.4	—
<i>Moraria mrazeki</i>	—	—	—	—	—	—
<i>Bryocamptus minutus</i>	—	—	—	0.6	—	0.2
<i>Bryocamptus echinatus</i>	—	—	—	4.8	7.6	8.4
<i>Elaphoidella gracilis</i>	—	—	—	—	—	—
<i>Paracamptus schmeili</i>	6.1	2.9	3.4	0.6	2.5	2.1
<i>Parastenocaris brevipes</i>	—	—	—	—	—	—
Total Harpacticoida	11.1	8.1	3.4	6.3	10.5	10.7
Resting Cyclopoida	123.0	65.4	44.7	20.1	24.3	34.1
15 m						
<i>Canthocamptus staphylinus</i>	0.4	—	—	—	—	—
<i>Attheyella crassa</i>	6.1	10.7	0.6	0.6	0.2	—
<i>Moraria brevipes</i>	0.2	0.4	0.4	0.2	0.4	—
<i>Moraria mrazeki</i>	—	—	—	—	—	—
<i>Bryocamptus minutus</i>	—	—	—	0.2	—	0.4
<i>Bryocamptus echinatus</i>	0.4	—	3.4	8.0	4.2	10.3
<i>Elaphoidella gracilis</i>	1.5	1.9	—	—	—	—
<i>Paracamptus schmeili</i>	2.7	4.8	0.4	2.3	0.4	0.2
<i>Parastenocaris brevipes</i>	—	—	—	—	—	—
Total Harpacticoida	11.3	17.8	4.8	11.3	5.3	10.9
Resting Cyclopoida	82.1	123.1	57.0	12.6	17.0	18.7
5 m						
<i>Canthocamptus staphylinus</i>	0.2	—	—	—	—	—
<i>Attheyella crassa</i>	8.6	2.1	0.8	2.5	1.3	0.4
<i>Moraria brevipes</i>	—	0.4	0.8	0.2	—	—
<i>Moraria mrazeki</i>	—	—	—	—	—	0.2
<i>Bryocamptus minutus</i>	0.2	—	0.4	—	—	0.6
<i>Bryocamptus echinatus</i>	1.7	1.5	1.3	4.2	1.9	3.6
<i>Elaphoidella gracilis</i>	0.6	—	—	—	—	—
<i>Paracamptus schmeili</i>	4.4	2.3	2.5	1.5	3.1	2.5
<i>Parastenocaris brevipes</i>	—	—	—	—	—	0.2
Total Harpacticoida	15.7	6.3	5.9	9.0	6.3	7.6
Resting Cyclopoida	40.5	16.4	2.9	13.4	8.6	10.7

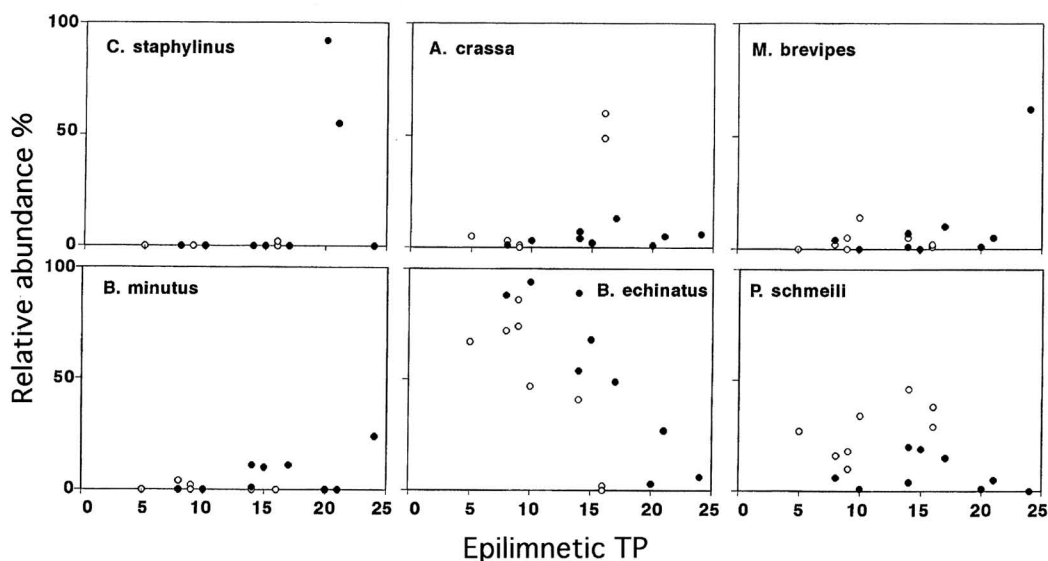


Fig. 2. Relative abundance of harpacticoid species along epilimnetic total phosphorus gradient ($\mu\text{g l}^{-1}$). Filled symbols indicate the data set A (Särkkä 1992a) and open symbols the rest of the data.

Two species, *Parastenocaris brevipes* and *Moraria mrazeki*, were encountered occasionally in the sublittoral zone of Lake Paasivesi. *Canthocamptus staphylinus* and *Elaphoidella gracilis* were confined to the northern part of Lake Pyhäselkä in fairly low numbers (Table 3).

The remaining five species were common to both lakes, but their abundances and bathymetric distributions showed marked distinction between the areas. The most pronounced differences were in the spatial distributions of *Attheyella crassa* and *Bryocamptus echinatus*, particularly in the deeper zone (Table 3). In the profundal, *A. crassa* was almost exclusively restricted to northern Pyhäselkä. *B. echinatus*, conversely, dominated the profundal zone of Lake Paasivesi, but was almost absent from the respective zone of northern Lake Pyhäselkä. In the sublittoral zone, both *A. crassa* and *B. echinatus* occurred in all stations and their abundances showed less spatial variation compared to the profundal zone (Table 3).

Paracamptus schmeili, an abundant species in both lakes, was more or less evenly distributed, and did not show a consistent trend along the trophic gradient. In the deepest zone, however, the abundance tended to increase towards the northern areas of higher trophic level (Table 3). Of the two remaining species, *Moraria*

brevipes was found in almost every station in low numbers. *Bryocamptus minutus* inhabited the profundal zone of Lake Paasivesi, but was restricted to the sublittoral zone in Lake Pyhäselkä, in this respect resembling its congeneric *B. echinatus*.

Some implications of the unimodal relationships of harpacticoid species to the trophic level could be detected, when the species' relative abundances were plotted against the TP (Fig. 2). For example, the abundances of *A. crassa* and *P. schmeili* apparently reach their maxima at the intermediate levels of phosphorus. On the other hand, *B. echinatus* shows a monotonic response, the true optimum lying outside or at the lower edge of the observed range (Fig. 2). The estimated TP optima based on the data set A ranged from $13.1 \mu\text{g l}^{-1}$ for *B. echinatus* to $21.40 \mu\text{g l}^{-1}$ for *M. brevipes* (Table 4). When the whole data set (C) was involved the estimates shifted a little, but the order of the species remained stable, except for *M. brevipes* and *C. staphylinus* which changed places (Table 4).

The indication models constructed from the data set A applied to the test set of remaining lake sites (B), produced considerable prediction errors (Table 5), and the estimates were consistently too high (Fig. 3). The bootstrap error esti-

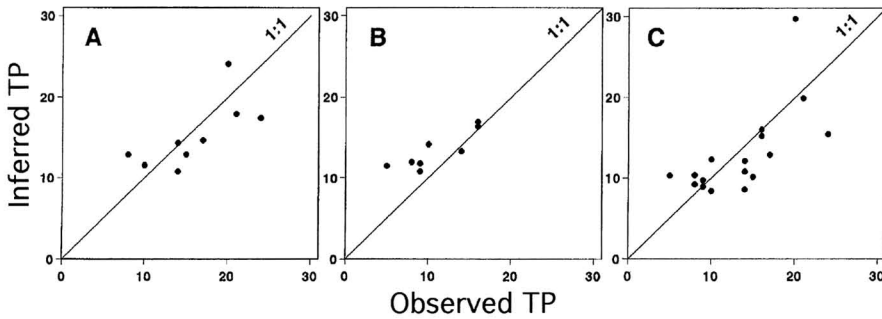


Fig. 3. Relationship between the harpacticoid-inferred (classical deshrinking) and observed epilimnetic total phosphorus ($\mu\text{g l}^{-1}$). A: Inferred (mean bootstrap estimates) vs. observed TP in the group A B: Inferred vs. observed TP in the test group (B) (model derived from the data set A). C: Inferred (mean bootstrap estimates) vs. observed TP in the group C.

mates were still somewhat larger (Table 5). However, the correlation between the observed and the predicted values was quite strong in all cases (Table 5). The error estimates and the correlations for the models based on the whole data set (C) were comparable to those of the models

based on data set A (Table 5). Classical deshrinking generally produced somewhat larger prediction errors, but stronger correlations between the predicted and observed values (Table 5). The tolerance weighting did not improve the models, but instead, yielded slightly larger prediction errors (results not shown).

The planktonic densities or the biomass of cyclopoid copepodids and adults did not differ between the lakes (Mann-Whitney U-test, $P < 0.05$). In summer (May–October), the average biomass was in the pelagial zone of Lake Pyhäselkä 47.5, 30.4 and 30.8 and in Lake Paasivesi 64.1, 30.8, 36.2 $\mu\text{gC } 10 \text{ l}^{-1}$ in 1989, 1990 and 1991, respectively. Further, there was no difference in the numbers of cyclopoid copepods in the different parts of Lake Pyhäselkä in 1991 and 1992 (unpublished data, cf. Karjalainen et al. 1994). The samples taken in winter indicated that the vast majority of *Thermocyclops* and *Mesocyclops* populations were in diapause. Only some C1–C3 copepodids were found in the

Table 4. The weighted averaging estimates for the harpacticoid species' optima and tolerances with respect to epilimnetic total phosphorus ($\mu\text{g l}^{-1}$), derived from the data sets A and C.

Species	Optimum		Tolerance	
	A	C	A	C
<i>B. echinatus</i>	13.1	11.2	4.1	4.1
<i>P. schmeili</i>	14.9	12.6	3.4	4.1
<i>A. crassa</i>	16.9	15.6	4.6	3.7
<i>E. gracilis</i>	—	16.0	—	—
<i>B. minutus</i>	19.0	17.8	5.2	6.1
<i>C. staphylinus</i>	20.4	20.3	0.7	1.0
<i>M. brevipetes</i>	21.4	18.8	6.2	7.2

Table 5. Correlation coefficients between the inferred and observed TP and the root mean squared error (RMSE) of the prediction for the different models.

Model	source data	deshrinking type	Correlation coefficient			RMSE ($\mu\text{g l}^{-1}$)		
			apparent	boot	cross	apparent	boot	cross
A		classical	0.89	0.70	0.86	2.5	4.6	3.3
		inverse	0.89	0.65	0.86	2.2	4.4	3.9
C		classical	0.83	0.67	—	3.4	5.1	—
		inverse	0.83	0.64	—	2.8	4.4	—

plankton, and no differences were found in the densities of small cyclopoids in any depth layers between the two lakes.

The density of benthic resting stages of cyclopoid copepodids (*Thermocyclops oithonoides* and *Mesocyclops leuckarti*) differed significantly between Lake Pyhäselkä and Lake Paasivesi (Mann-Whitney U-test, $P < 0.05$) (Table 3). The densities increased with increasing depth, being 4–10 times higher at the profundal zone than at the sublittoral zone in Lake Pyhäselkä and 2–3 times higher in Lake Paasivesi, respectively (Table 3).

The estimated benthic copepodid densities ranged between 44 659–123 076 ind. m^{-2} in the pelagial zone and 2 937–40 464 ind. m^{-2} in the sublittoral zone of Lake Pyhäselkä (Table 3), while the expected values varied from 21 000 to 37 000 ind. m^{-2} in the pelagial zone and from 3500 to 6600 ind. m^{-2} in the sublittoral zone. In the northern parts of the lake, the estimated values were 4–10 times higher than the expected values. On the contrary, the estimated densities (e.g. 20 128–34 174 ind. m^{-2} in the pelagial zone) corresponded well to the expected values (18 400–39 000 ind. m^{-2}) in the oligotrophic Lake Paasivesi.

5. Discussion

The number of harpacticoid species and the species composition in the lakes studied were comparable to those reported in other Finnish lakes. All 9 species detected were also found in Lake Pääjärvi, which was represented by 13 species (Sarvala 1986). The 4 additional species in Lake Pääjärvi were restricted to stony shores or other littoral habitats, which were not sampled in the present study. The profundal harpacticoid fauna of Lake Päijänne consists of 7 species (Särkkä 1992a, b) of which 6 (*M. brevipes*, *A. crassa*, *P. schmeili*, *B. minutus*, *B. echinatus*, and *C. staphylinus*) are common to all of the lakes studied.

In all, the recorded harpacticoid fauna of the three Finnish lakes or lake systems studied amounts to 14 species, of which only 4 seem to be constant inhabitants of profundal depths: *B. echinatus*, *A. crassa*, *M. brevipes* and *P. schmeili*. *B. minutus* could be included as the fifth species

in this group although it seems, according to Sarvala (1986), to be lacking in the profundal zone, if *B. echinatus* is abundant. Accordingly, the species was not detected in the profundal zone (27 m) in the oligotrophic part of Lake Höytiäinen (draining to Lake Pyhäselkä, see Fig. 1), where *B. echinatus* is present in a high density (6200 ind. m^{-2}) (I.J. Holopainen et al., unpublished data). Sarvala (1986) postulated competitive interactions as a possible explanation for such distributions. However, the two species have been met together in considerable numbers in the profundal zone of Lake Päijänne (Särkkä 1992a), and in the present study *B. minutus* was confined (even though in low numbers) to profundal areas with the highest densities of *B. echinatus*. According to their estimated TP optima the two species, nevertheless, seem to segregate along the trophic gradient.

The distribution of an abundant species, *A. crassa*, within the studied area of Lake Saimaa was apparently controversial to what could be predicted according to Särkkä (1992a). The abundance of *A. crassa*, 'the most obvious indicator of oligotrophy' (Särkkä 1992a), increased towards the higher trophic level (cf. Table 3). The same is true, even though less obviously, for *P. schmeili*, which should prefer oligotrophy at profundal depths (Särkkä 1992a). According to the estimated optima, *A. crassa* and *P. schmeili* favour more or less mesotrophic conditions, instead of true oligotrophy. This accepted, the present findings meet better the expectations. Regarding the epilimnetic total phosphorus as a measure of trophic level, the other species can also be tentatively ordered with respect to their trophic preference according to their weighted averaging estimates for the phosphorus optima (see Table 4). At the upper profundal zone, *B. echinatus* thrives best in oligotrophic conditions. *B. minutus* seems to reach its maximum contribution to the total harpacticoid fauna in mesotrophic lakes, while *C. staphylinus* and *M. brevipes* tend to prefer eutrophy. The large values of tolerance estimates, especially for *B. minutus* and *M. brevipes*, indicates wide trophic amplitude of the harpacticoid species.

What might be the causal link between the distributions of harpacticoid species and the lake trophic level? In the eutrophic or organically

polluted lakes with periodically anoxic hypolimnion, the harpacticoids seem to be totally absent in profundal depths (e.g. Särkkä 1992a, b), indicating that the group as whole does not tolerate low oxygen concentrations. Whether the species differ in their oxygen demands or tolerance is unknown. Moreover, the upper profundal zone, considered in the present study, rarely suffers from oxygen deficiency in lakes of trophic level within the observed range. Therefore the apparent differences in species' trophic preferences are likely to be mediated by some other factor(s) than oxygen. Food resources could serve as an explanation, since the amount of available food in the pelagial zone is strictly dependent on lake productivity. *C. staphylinus*, an indicator of eutrophy (Särkkä 1992a, Table 4), is restricted to the littoral zone in oligotrophic lakes, but it can colonize the profundal depths in eutrophic lakes as well (Sarvala 1979a, and references therein). Sarvala (1979a) stated that the reason for the exclusion of *C. staphylinus* from the profundal zone of oligotrophic lakes might be food shortage, since the species is assumed to have high food demands due to a high intrinsic growth rate (Sarvala 1979a, b). The slowly growing species (e.g. *B. echinatus* and *P. schmeili*) in turn could be expected to thrive in low food conditions (Sarvala 1979b, 1990). If different growth rates in general are adaptive to different levels of food availability, we might expect a relationship between the intrinsic growth rates and the trophic preferences of the species. Accordingly, there is a striking correlation between the experimentally determined species' growth coefficients (Sarvala 1979b, p. 530) and the species' optima for lake phosphorus (trophic) level, derived from the field data in the present study (Fig. 4). *B. minutus*, with intermediate TP optimum (Table 4) has also a moderately high growth rate (Sarvala pers. comm.). On the basis of these considerations, food availability is likely to be an important factor in governing the observed distributions of the harpacticoid species along the lake trophic gradient. This, however, may hold for the upper profundal zone only with no oxygen deficiency or other confounding conditions.

The species and their indicator values might prove useful in biological indication, if the value of the environmental variable(s) of interest at a

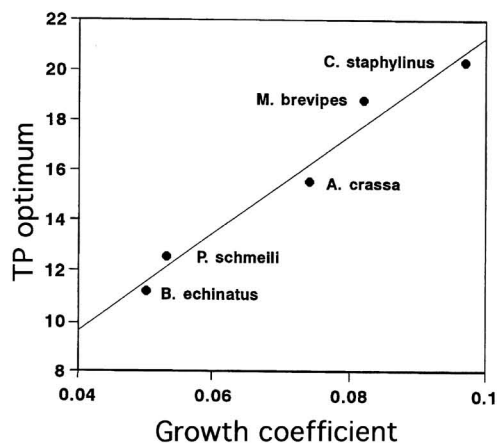


Fig. 4. Relationship between the daily exponential biomass growth (at 15°C) of harpacticoid nauplii (Sarvala 1979b) and the estimated species' optimum for epilimnetic total phosphorus ($\mu\text{g l}^{-1}$). The relationship is almost equally strong for copepodids, but weaker for adults.

given site can be assessed on the basis of the species assemblage. To detect spatial and temporal variation, accurate estimates may not be needed, but a reliable relationship between real and inferred values will be enough. The prediction error obtained by the WA estimation was tolerable, and the studied lake sites were fairly well ranked according to their TP (trophic) level, even though the resolution was rather poor at the oligotrophic range of the gradient (cf. Fig. 3). Considering the low number of the indicator species, the predictions were surprisingly good. Harpacticoids seem to be reliable indicators of lake productivity, but in eutrophic lakes with oxygen deficiency in hypolimnion, the harpacticoid model does not apply, due to the total lack of the group. The small number of the species in profundal depths in general is a weakness in using harpacticoids as the sole indicators. Much improvement might be achieved by taking into account other meiofaunal groups as well. Thus, rather than a comprehensive model, our attempt should be regarded preliminary and as a further demonstration of the versatility of the weighted averaging regression and calibration approach in biological indication.

In accordance to what could be expected (Särkkä 1979, 1992b) the density of benthic

cyclopoida was higher in the areas of a higher trophic level in the lakes we studied. The diapause of cyclopoids may be induced by temperature, photoperiod, or rapid changes in some other factors affecting the population e.g. heavy predation or desiccation (Frenzel 1977, Vijverberg 1977, Vijverberg & Richter 1982, Elgmork et al. 1990, Næss & Nilssen 1991, Maier 1992). Most of the small cyclopoids (*Mesocyclops* and *Thermocyclops*) are in the resting stage C4–C5 (Sarvala 1979c, Vijverberg 1977). When the copepodids enter diapause, they sink to the bottom (Vijverberg 1977). However, there are some observations that *Mesocyclops* can actively penetrate into the mud (Elgmork et al. 1990). Some copepodids are then found even at the 10 cm depth inside the sediment, although the main part of the small cyclopoid copepodids remain near the surface (80–90% in upper 5 cm; Sarvala 1979c, Elgmork et al. 1990, Maier 1990). The copepodids are very tolerant for oxygen depletion (Frenzel 1977, Gliwicz & Rowan 1984, Maier 1990). In Lake Pääjärvi, the beginning of the diapause occurred in September–November and the termination started in early May (Sarvala 1979c). Generally, the emergence seems to take place during the time of ice break (Elgmork et al. 1990).

A simple explanation of the observed spatial differences in the abundance of resting cyclopoids might have been the difference in the size of planktonic populations. However, no such difference could be detected between the lakes or between separate parts of Lake Pyhäselkä. The lakes did not differ in the timing of ice break or water temperature, and the samples were taken in consecutive days in December. Thus, the population dynamics is not likely to explain the observed differences. The predation hypothesis proposed by Särkkä (1979, 1992b) seems also invalid, because (1) the benthic densities of cyclopoids differed between our study lakes in the sublittoral zone, where no oxygen deficiency occur, and in upper profundal zone, where oxygen depletion is negligible (at least in autumn and early winter), and (2) the observed densities of diapausing animals corresponded well to the expected values in the oligotrophic Lake Paasivesi, where depletion in numbers due to fish predation was expected. Accordingly, Särkkä (1979) himself observed an equivalence between the autumnal planktonic

cyclopoid population and the observed early winter benthic population in the unpolluted part of Lake Päijänne. Moreover, there was great excess of benthic copepodids in Lake Pyhäselkä as compared to the expected numbers.

For the reasons mentioned above we conclude that the explanation for the observed higher densities of the resting cyclopoids in the areas of a higher trophic level cannot be decreased fish predation due to oxygen deficiency. Instead, we offer two alternative explanations. Firstly the diapausing cyclopoids might be concentrated to the studied areas of northern Lake Pyhäselkä because of currents and possibly by drifting from the river Pielisjoki. Diapausing animals are immobile and currents affect their distribution (Vijverberg 1977, Maier 1990). The downstream drift of microcrustaceans is also a well documented phenomenon (Shiozawa 1986). The input of drifting cyclopoids from the river Pielisjoki might be possible, since the watercourse is composed of several lakelike dilatations, which most likely harbour viable zooplankton populations. Similarly, the polluted areas of Lake Päijänne with high densities of resting cyclopoids (Särkkä 1992b) are recipients for large rivers, which could cause currents affecting the distribution of cyclopoids and possibly bring augmentation to the lake populations. The observed high densities of resting cyclopoids might therefore not result from eutrophy at all. The second explanation is based on the observation that a considerable part of the *Mesocyclops* populations can live in the near-bottom water layer and bottom sediments throughout the growing season (Papinska 1984) possibly utilizing detritus as food source (Papinska 1984, 1985). In lakes of a high trophic level, the increased organic sedimentation could allow a large number of *Mesocyclops* cyclopoids to shift from a planktonic to a benthic mode of life. This part of the population would pass unnoticed in plankton sampling, which in turn could explain the unequivalence between the expected and observed benthic densities of the resting stages. Both explanations are tentative and deserve further scrutiny.

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