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Response by macrozoobenthos biomass to water level regulation in some Finnish lake littoral zones

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Abstract

The relationship of the macrozoobenthos biomass in the littoral area to the yearly fluctuation in water level and the characteristics of the area or lake are studied using data collected from sheltered bays in regulated and natural waters. Most of the lakes were clear and oligotrophic. The benthos biomass at all depths in the littoral decreased with increased water level fluctuation, provided that the transparency of the water was uniform.

The macrozoobenthos biomass in the 0–3 m depth zone could be predicted from

$$\text{log macrozoobenthos biomass (mg ODW m}^{-2}) = 4.25 - 1.33\ (\text{log Biomass Index})$$

in which the Biomass Index is calculated as

$$\text{Biomass Index} = \frac{\begin{array}{c}\text{water level fluctuation in the previous year}\\ \text{(m; calculated from monthly mean values)}\end{array}}{\text{Secchi disk value in the same open water season (m)}} \times 100.$$

The whole illuminated littoral shifts due to water level fluctuation, which disturbs the zonation of the benthos. Such an increase or decrease in benthic biomass has been observed after one year of disturbance due to water level fluctuation. It need, however, a study based on the carefully planned and collected data, in which it can be taken account by a multivariate statistical analysis also the interactions between the important factors affected the littoral benthos.

Introduction

The trophic status of a lake affects the macrozoobenthos biomass (Kajak & Rybak, 1966; Alley & Powers, 1970; Jonasson, 1972; Dermott *et al.*, 1977; Brylinsky, 1980; Rasmussen, 1984; Hanson & Peters, 1984; Rasmussen & Kalff, 1987), which often correlates directly with the biomass of net plankton (Deevey, 1941; Rawson, 1942). An experimental addition of nutrients (Smith,

Table 1. Sampling dates and methods in the lakes included in the analysis.

Lake		Date		Sampler	Sieve (mm)	Author
1	Inarijärvi	VI	1977	Ekman-Birge	0.4	Palomäki 1990
2	Inarijärvi	VIII	1977	Ekman-Birge	0.4	Palomäki 1990
3	Pyhäjärvi (O.l.)	VIII	1979	Ekman-Birge	0.4	Palomäki & Koskenniemi 1993
4	Pääjärvi	VIII	1973	Tube	0.4	Haka et al. 1974
5	Pyhäjärvi (T.l.)	VIII-IX	1980	Ekman-Birge	0.5	Mölsä 1981
6	Kultsjön	VI	1960	Ekman-Birge	0.6	Grimås 1965a
7	Oulujärvi	IX	1974	Ekman-Birge	0.5	Granberg & Hakkari 1980
8	Lentua	VIII	1984	Morduchaj-Boltovskoj-tube	0.5	Tikkanen et al. 1989
9	Ontojärvi	VIII	1984	Morduchaj-Boltovskoj-tube	0.5	Tikkanen et al. 1989
10	Pohjois-Konnevesi	V	1976	Ekman-Birge*	0.4	Särkkä 1983
11	Etelä-Konnevesi	V	1976	Ekman-Birge*	0.4	Särkkä 1983
12	Pohjois-Konnevesi	VIII	1975	Ekman-Birge*	0.4	Särkkä 1983
13	Etelä-Konnevesi	VIII	1975	Ekman-Birge*	0.4	Särkkä 1983
14	Alajärvi	IX	1986	Ekman-Birge	0.4	Palomäki 1990

* Dendy at depth 1 m.

1969; Hall *et al.*, 1970) or an increase in total phosphorus in the water due to eutrophication (Dermont *et al.*, 1977) have been shown to have a correlation with the total biomass of macrozoobenthos in the sublittoral zone. In addition to the quantity of phytoplankton, the chlorophyll content, total phosphorus content of the water, Secchi transparency, and the morphometry of the lake (mean depth, Hayes, 1957; Rawson, 1955, 1960; morphoedaphic index, Johnson, 1974; or several morphometric variables combined, Rasmussen & Kalff, 1987) have been presented to have a close relationship with the biomass of the macrofauna in the sublittoral and profundal areas. The total biomass of zoobenthos among the richest vegetation of the littoral area is explained by the chlorophyll content of the water, the exposure and the slope of the shore (a series of Quebec lakes (Canada), Rasmussen, 1988).

Pronounced water level regulation reduces the abundance and diversity of the macrozoobenthos in the littoral of lakes (Grimås, 1961, 1962, 1965a, 1965b), while the effects of the slight water level regulation have not been studied much (Palomäki & Koskenniemi, 1993, see also Palomäki & Paasivirta, 1993).

Because the littoral is very complicated system, the aim here is to study as preliminary mean, which factors, the shifting of the illuminated zone due to water level regulation, water level fluctuation alone or the other morphometric, physical and water quality characteristics of the sampling area or lake, have effect on the macrozoobenthos biomass in the littoral.

Material and methods

Data were collected from the literature, chosing investigations performed by as similar methods

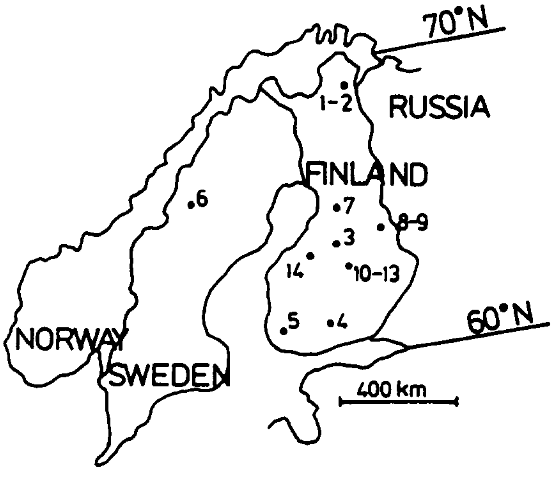

Fig. 1. The lakes studied.

Table 2. Characteristics of the lakes included in the analysis.

Lake	Altitude, m	Drainage area, km^2	Lake area, km^2	Max depth, m	Tot P, mg m^{-3}	pH	Conductivity, mS$_{20°C}$	Colour, mg Pt l^{-1}	Secchi disc value, m
Inarijärvi	119	14575	1153	98	5	7.0	2.6	10	6.5
Pyhäjärvi (O.l.)	139	687	115	31	15	7.2	5.4	20	3.5
Pääjärvi	103	244	13	87	12	7.0	6.9	50	3.0
Pyhäjärvi (T.l.)	45	615	154	25	15	7.4	8.5	20	4.0
Kultsjön	540	–	90	–	2	6.9	–	–	8.0
Oulujärvi	122	19890	928	36	27	6.6	2.9	65	1.5
Lentua	168	2065	90	26	14	6.7	2.2	55	2.0
Ontojärvi	159	5015	102	27	14	6.5	2.2	61	2.0
Konnevesi, N-part	95		69	44	7	7.0	3.7	25	4.4
Konnevesi, S-part	95	5780	119	56	7	6.9	3.7	35	3.8
Alajärvi	103	465	11	6	55	6.0	6.8	150	0.8

as possible (Table 1). Except for one report from Lake Kultsjön in Sweden, all data derived from Finland (Fig. 1). The lakes differ in some of their morphological and limnological characteristics (Table 2), and morphological differences are also noticeable between the transects (Table 3). All the lakes except Lake Lentua and Lake Konnevesi are regulated. Primarily the water level in the regulated lakes are regulated by bower plants. During the period of 12 years studied the water level was low in winter or spring (December–May) in all lakes expect in Lake Pyhäjärvi (T.l.) and Konnevesi, where the low water level was in autumn in some years (August–November). The

Table 3. Slope (to depth 3 m), exposure (exp., Rasmussen, 1988), effective fetch (L_f, Håkanson, 1981) and total macrozoobenthos biomass (mg ODW m^{-2}) of the transects in the lakes (References in Table 1).

	Slope (%)	Exp. (km^2)	L_f (km)	mg ODW m^{-2}, at depth			
				1 m	2 m	3 m	0–3 m, x
Inarijärvi, Spring	21.0	0.97	0.82	133	193	576	301
Inarijärvi, Spring	11.0	0.77	0.46	610	904	656	723
Inarijärvi, Autumn	21.0	0.97	0.82	119	303	276	233
Inarijärvi, Autumn	11.0	0.77	0.46	500	576	424	500
Pyhäjärvi (O.l.)	2.0	6.38	2.44	2690	1090	636	1472
Pyhäjärvi (O.l.)	6.0	2.13	1.05	524	520	566	537
Pääjärvi	2.0	3.97	1.38	2157	958	1090	1402
Pyhäjärvi (T.l.)	1.0	39.68	5.73	2410	1310	1140	1620
Kultsjön	–	–	–	85	–	165	125
Oulujärvi	–	–	–	22	77	13	37
Lentua	1.2	–	2.70	74	171	45	97
Ontojärvi	4.0	–	3.40	2	20	78	33
Konnevesi, N-part, spring	–	6.12	2.44	515	1078	619	736
Konnevesi, S-part, spring	–	1.16	0.78	53	236	291	193
Konnevesi, S-part, spring	–	0.32	0.42	154	351	370	292
Konnevesi, N-part, autumn	–	6.12	2.44	389	693	344	476
Konnevesi, S-part, autumn	–	1.16	0.78	122	282	226	210
Konnevesi, S-part, autumn	–	0.32	0.42	148	560	332	358
Alajärvi	0.5	8.93	2.63	31	38	–	35

high water level was more often in late spring or in summer (May–August, over 2/3 of the years in all lakes) than in autumn or winter (October–January).

The water level fluctuations in the lakes, calculated in different ways, are presented in Table 4, together with the disturbed zone (*i.e.* the zone between the high water level (HW) and the low water level (NW)) as a proportion of the lighted zone (*i.e.* transparency). The Secchi transparency values in the lakes were measured in the same open water season as the benthos was sampled. The information on transparency and water level fluctuation can then be used to formulate a Biomass Index (BmI): water level fluctuation (m) divided by the Secchi transparency of water (m) x 100. This interaction term serves as an indicator of the relative vertical height of the disturbed zone (F) in comparison to that of the undisturbed zone (T) (Fig. 2). Used term empha-

Table 4. Data on water level fluctuations in the lakes included in the analysis. S = in same year as bottom sampling, P = in previous year as sampling, HW, NW = high water level and low water level; Abs = calculated from absolute daily values (cm); M-x = calculated from mean values per month (cm); Biomass Index (BmI) = lighted zone (i.e. transparency) as a proportion of the disturbance zone (i.e. the zone between HW and NW) calculated from the various HW and NW values (above).

Lake	S HW-NW		P HW-NW		S + P, HW-NW		HW (P)-NW (in same spring)	HW-NW, average during 12 years	
	Abs	M-x	Abs	M-x	Abs	M-x		Abs	M-x
Inarijärvi, Spring	197	178	116	88	197	178	125	138	116
Inarijärvi, Autumn	197	178	116	88	197	178	125	138	116
Pyhäjärvi (O.l.)	68	65	61	42	68	58	49	81	72
Pääjärvi	68	46	88	41	88	51	51	80	54
Pyhäjärvi	53	44	24	24	53	44	22	46	36
Kultsjön	–	470	–	440	–	470	430	–	–
Oulujärvi	179	139	152	132	179	168	149	158	141
Lentua	108	89	96	89	108	91	94	97	77
Ontojärvi	423	386	360	308	431	386	415	387	344
Konnevesi, N-part, spring	25	21	69	65	79	75	74	46	40
Konnevesi, S-part, spring	23	19	68	64	77	72	72	44	38
Konnevesi, N-part, autumn	69	65	68	65	72	68	22	46	40
Konnevesi, S-part, autumn	68	64	65	63	68	67	32	44	38
Alajärvi	86	60	98	80	102	83	67	101*	67*

Lake	BmI-1	BmI-2	BmI-3	BmI-4	BmI-5	BmI-6	BmI-7	BmI-8	BmI-9
Inarijärvi, Spring	30	27	18	14	30	27	19	21	18
Inarijärvi, Autumn	30	27	18	14	30	27	19	21	18
Pyhäjärvi (O.l.)	19	19	17	12	19	17	14	23	21
Pääjärvi	23	15	29	14	29	17	17	27	18
Pyhäjärvi (T.l.)	13	11	6	6	13	11	6	12	9
Kultsjön	–	59	–	55	–	59	54	–	–
Oulujärvi (Paltaselkä)	119	93	101	88	119	112	99	105	94
Lentua	54	45	48	45	54	46	47	49	39
Ontojärvi	212	193	180	154	216	193	208	194	172
Konnevesi, N-part, spring	6	5	16	15	18	17	17	10	9
Konnevesi, S-part, spring	6	5	18	17	20	19	19	12	10
Konnevesi, N-part, autumn	16	15	15	15	16	15	5	10	9
Konnevesi, S-part, autumn	18	17	17	17	18	18	8	12	10
Alajärvi	108	75	123	100	128	104	84	126	84

* Period only 4 years.

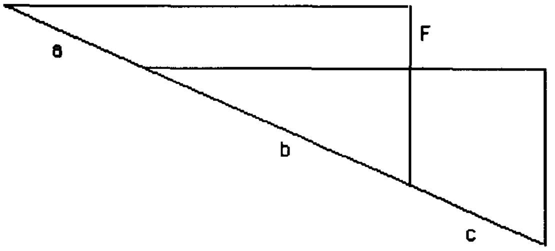

Fig. 2. Schematic profile of a littoral and the variables measured. F = water level fluctuation, T = transparency of water, a = zone affected by the direct water level fluctuation, b and c = zones affected by the shift of the lighted zone.

size the importance of the disturbed zone (zone a in Fig. 2) in the lighted zone.

The limnological and water level data were obtained from the Finnish National Board of Waters and Environment. The water quality characteristics of the lakes are presented as the mean values during the open water season in the year, when the zoobenthos samples were taken (Table 2).

The sampling areas were situated in sheltered bays (bay opens to the offshore at an angle of ≤ 90 °) and the sampling depths were the same (1, 2 and 3 m; measured from the long-term mean water level). Samples have been taken along transects (3–5 samples per station). Emergent macrophytes lacked in the sampling stations of all lakes studied, but submersed plants, especially *Isoetes* spp., occurred in Lake Pyhäjärvi (O.l.), Pääjärvi, Pyhäjärvi (T.l.) and Lentua. An Ekman-Birge sampler was used in most cases (Table 1), the mesh size of the sieve being 0.4–0.6 mm. The samples were taken either in autumn (August–September) or just after the melting of the ice (May–June). The macrozoobenthos biomasses, given in some papers as wet weights, were recalculated to organic dry weight *i.e.* ash free dry weight (1 g ww = 0.11 g ODW, Mölsä, 1981; Paasivirta, 1984). The conversion coefficient falls within the range of published values (0.10–0.15, Waters, 1977, Lindegaard, 1989). The value of the coefficient depends markedly on the quantity of molluscs and gastropods. The coefficient for only *Pisidium* alone is 0.08 (Holopainen, 1979).

The relationships between the biomass of littoral zoobenthos (Table 3) and the chosen variables (Table 2, 3 and 4) were studied by correlation analysis (Pearson's correlation coefficient), and a linear regression model was fitted between the best explanatory variable and the littoral benthos biomass. The mean macrozoobenthos biomass for all the transects in a lake was used in the analyses. The normality of the distribution of all the variables was tested and log-transformation was used if necessary.

Table 5. Correlation of macrozoobenthos biomass at different depths with various characteristics of the lake. Significances: * = $p < 0.5$, ** = $p < 0.01$ and *** = $p < 0.001$ (in parentheses = df).

Log mg m^{-2}, at depth	1 m		2 m		3 m		0–3 m, x	
Slope, log (%)	-0.03	(9)	0.14	(9)	0.08	(8)	0.14	(9)
Exp., log (km^2)	0.45	(13)	0.18	(13)	0.62*	(12)	0.28	(13)
L$_f$, log (km)	-0.01	(15)	-0.16	(15)	-0.10	(14)	-0.08	(15)
Altitude Log (m)	-0.39	(12)	-0.51	(11)	-0.41	(11)	-0.43	(12)
Drainage area (km^2)	-0.27	(9)	-0.14	(9)	-0.48	(8)	-0.27	(9)
Lake area Log (km^2)	-0.06	(12)	0.07	(11)	-0.31	(11)	-0.01	(12)
Max depth (m)	0.37	(11)	0.45	(11)	0.39	(10)	0.45	(11)
Tot P (mg/m^3)	-0.32	(12)	-0.59*	(11)	-0.53	(11)	-0.51	(12)
pH	0.78***	(12)	0.88***	(11)	0.84***	(11)	0.88***	(12)
Conductivity (mS$_{20}$°C)	0.54	(11)	0.33	(11)	0.63*	(10)	0.44	(11)
Colour (Pt-units)	-0.54	(11)	-0.73**	(11)	-0.73**	(10)	-0.70**	(11)
Secchi disc value (m)	0.35	(12)	0.65*	(11)	0.42	(11)	0.42	(12)

Table 6. Correlation of macrozoobenthos biomass at various depths with water level fluctuations and Biomass Index, both calculated in a number of ways (see table 4). Significances: * $= p < 0.5$, ** $= p < 0.01$ and *** $= p < 0.001$ (in parentheses = df).

At depth Biomass		1 m log (mg m^{-2})	2 m log (mg m^{-2})	3 m log (mg m^{-2})	x 0–3 m log (mg m^{-2})
Same year					
HW-NW,	log abs (1)	-0.69** (11)	-0.66* (11)	-0.46 (10)	-0.51 (11)
	log M-x (2)	-0.54* (12)	-0.62* (11)	-0.37 (11)	-0.48 (12)
Previous year					
HW-NW,	abs (3)	-0.80** (11)	-0.76** (11)	-0.51 (10)	-0.64* (11)
	M-x (4)	-0.59* (12)	-0.78** (11)	-0.42 (11)	-0.53 (12)
Same + previous year, HW-NW,					
	abs (5)	-0.72** (11)	-0.67* (11)	-0.44 (10)	-0.56* (11)
	M-x (6)	-0.59* (12)	-0.67* (11)	-0.40 (11)	-0.50 (12)
HW (previous year)- NW (in spring of same year) (7)		-0.64* (12)	-0.71** (11)	-0.43 (11)	-0.54* (12)
HW-NW, average during 12 years					
	abs (8)	-0.74** (11)	-0.73** (11)	-0.47 (10)	-0.59* (11)
	M-x (9)	-0.73** (11)	-0.70** (11)	-0.48 (10)	-0.58* (11)
log Bm INDEX-4		-0.91*** (12)	-0.97*** (11)	-0.86*** (11)	-0.95*** (12)

Results

The relationships between the macrozoobenthos biomass and the slope, exposure or effective fetch of a transect were usually not significant (Table 5). Only one relationship, between pH and macrozoobenthos biomass, was statistically significant in all cases (Table 5). The pH of the water had a close inverse correlation with the water colour ($r = -0.91$, df = 11, $p = <0.001$), and a weak positive correlation with transparency (0.56, df = 12, $p = 0.039$). Transparency of the water had a close inverse correlation with the water color (-0.81, df = 12, $p = <0.001$).

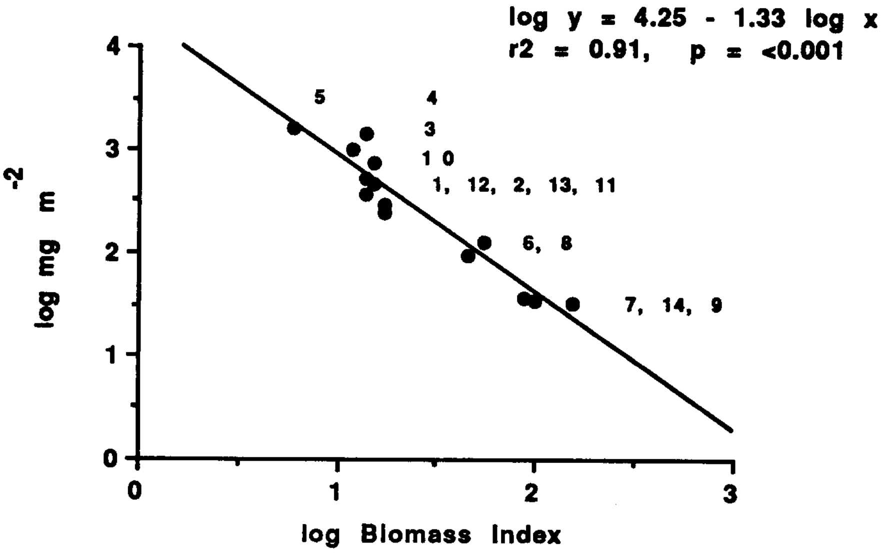

Fig. 3. Regression between total biomass of the littoral macrofauna (mean mg ODW m^{-2} at depth 0–3 metres) and Biomass Index, calculated from the water level data (M-x) for the previous year. The numbers of the lakes are presented in Table 1.

All the correlations between benthos biomass and water level fluctuation or water level fluctuation in relation to the lighted zone were negative (Table 6). The correlations between the littoral benthos biomass and the fluctuation relative to the lighted zone were statistically more significant in all cases than the correlations between benthos biomass and water level fluctuation or secchi transparency alone (Table 5 and 6). The closest correlation was between the littoral benthos biomass and the fluctuation relative to the lighted zone calculated from the water level data of the previous year and especially calculated from the data based on mean values per month (BmI 4, Table 6). The variation in littoral benthos biomass was best explained by Biomass Index 4 in all the littoral depth zones and on an averrage at depth 0–3 metres (Fig. 3).

The variables which explained the littoral benthic biomass best, pH and Log Biomass Index 4, were highly collinear ($r = +0.87$, $df = 12$, $p = <0.001$).

Discussion

Neither the morphometric characteristics of the sampling area nor those of the lake explained the variation in benthic biomass in sheltered lake littoral zones, but a Biomass Index based on water level fluctuation in the previous year and the Secchi depth, and the pH and colour of the water was closely related to the littoral benthic biomass. The pH values varied little, only between 6.0–7.2, and the effects of acidification on the benthos biomass are in any case equivocal (Okland & Okland, 1986). The recent Finnish acidification project showed no correlation between pH and benthic biomass in 140 small lakes (Meriläinen & Hynynen, 1989). The positive correlation between the pH of the water and the littoral benthic biomass obtained here may thus probably be considered an artefact, as pH had a strong positive correlation with the biomass index (Log Biomass Index 4), which explained the benthic biomass even better.

There would appear to be a way of interpreting these results. A reduction in benthos biomass in the shallow depths may results from erosion and a reduction on the deeper bottoms due to light disturbance. But the results also show that the increases or decreases in benthos biomass at all depths of the littoral were dependent on the water level fluctuation if the transparency of the water was uniform. All this points to the conclusion that the whole lighted littoral, in which the benthos has a pronounced vertical zonation, shifts due to the water level fluctuation, and therefore the zonation of the benthos will be disturbed.

Though the colour of the water had a close relationship with the transparency of the water, the phytoplankton has a strong influence the transparency especially in eutrophic waters (f.e. Seip *et al.*, 1992). Therefore transparency may be a better factor than the colour of water, when it described light disturbance in littoral. However, the transparency can't be replaced by the colour of water in the biomass index, because the colour has a different dimension than the water level fluctuation has.

If the transparency of the water remains constant, the illuminated zone of a littoral site will move up or down corresponding to the water level fluctuation. The activity in the littoral area is based on primary production (Lodge *et al.*, 1988) and especially on the benthic algae in clear-water oligotrophic lakes, where benthic primary production may amount to as much as 80% of total primary production in the lake (Welch & Kalff, 1974; Persson *et al.*, 1977). Thus the shifts of the light zone due to water level fluctuation may considerably affect primary production in each depth zone, so that the effect is seen even in the biomass of the macrozoobenthos. This hypothesis is supported by the results of Pike and Welch (1990), who observed that light (ice and thickness of the snow) may be a very important factor determining the quantity of the macrofauna in the Barrow Strait area of Canada. Moreover, Denslow (1980) observed that although a primary effect of disturbance was the opening up of space, space was usually associated with a change in the availability of other resources such as light and soil nutrients in terrestrial systems. Sousa (1985), who studied communities of filter feeders on intertidal rocks, added suspended food to the limiting factors in some aquatic systems. It would indeed seem that light in itself can affect the structure of communities in particular, but that its effect on the biomass of the macrofauna is mediated through food resources. The understanding of this mechanism and the earlier interpretation about light disturbance need to support more studies concerning the ecology of benthic algae and the use of algae as food resources for benthos.

Such mechanism that the light influence on the biomass of invertebrates via its effect on food resources, has been described earlier based on the laboratory experiments (Lamberti *et al.*, 1989). Bottom up control of the lentic ecosystem has been a topic during many years (see Plante & Downing, 1989; Downing & Plante, 1993).

Since water level anomalies seem to be a very important factor in the mechanism of light disturbance, more thorough research is required. F.e. it need study-series, in which it has been taken account both the spatial and temporal heterogeneity of littoral. The benthic biomass in the littoral area is usually highest in wintertime, whereas Paasivirta (1976) observed that the macrozoobenthos biomass in the littoral (at a depth of 0–3 m) of the mesohumic Lake Suomunjärvi in Eastern Finland was usually highest in autumn (October–November) and that it was always over 50% of the highest autumn value in May. The benthic biomass in Lake Inarijärvi was usually highest in spring, whereas in Lake Konnevesi it could be highest in either autumn or spring (Table 3). We do not know exactly how well the dates used to define autumn, winter and spring are comparable, but looking at data for the same months (Fig. 3) we can observe the same trend, which suggests that probably the sampling season did not severely bias the results. However, very many variables in carefully collected data must be taken with into the further studies and treat the data f.e. with a multiple regression analysis. Thus it can be taken account also the interaction of the most important factors affected the benthos of lake littoral.

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