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VERTICAL DISTRIBUTION OF *DAPHNIA HYALINA* LEYDIG IN LAKE BLED WITHIN THE FIRST YEAR AFTER THE OCCURRENCE OF *DAPHNIA GALEATA* SARS

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ABSTRACT

Before 1994, only Daphnia hyalina *was present in Lake Bled. Intensive study of* D. hyalina *distribution in the water column of Lake Bled was carried out in 1988. In April 1995,* D. galeata *was recorded in the lake for the first time. In August,* D. galeata *built up approximately 25 % of the* Daphnia *community.*

From June to November of 1995, we studied vertical distribution of both Daphnia *species in the water column of the lake to test two hypotheses: a) are there differences in vertical distribution of* D. hyalina *between 1988 and 1995 during the 24-hour period; b) are there differences in the vertical distribution of* D. hyalina *and* D. galeata *during the day. For 1995 both hypothesis were rejected.*

Key words: *Daphnia hyalina, Daphnia galeata,* vertical distribution, eutrophic lake, competition

INTRODUCTION

Lake Bled is an eutrophic, subalpine lake (470 m a.s.l.; area: 1.47 km², max. depth: 30 m) in the northwestern part of Slovenia (Brancelj, 1991; Brancelj & Blejec, 1994). From 1988 onward, zooplankton samples have been taken once a month to check the structure and abundance of the plankton community, with special attention to the Cladocera. Until the end of 1994, only one *Daphnia* species was found (Brancelj *et al.*, 1996). According to Negrea (1983), Margaritora (1985) and Glagolev (1986), it was recognised as *D. hyalina* (Leydig, 1860) (Fig. 1).

In April 1995, a new form of *Daphnia* occurred in the lake, eventually recognised as *D. galeata* Sars, 1864 (Fig. 1). The newcomer was becaming more and more abundant. In August/September it represented approximately 25% of the *Daphnia* community. The hybrids of the two main forms were also being observed *(i.e. Daphnia hyalina* x *galeata)* confirmed also by electrophoresis (Spaak, *pers. com.).*

The question arises, how these two species will behave in Lake Bled: will they be subjected to a long-term coexistence or will a competitive exclusion occur? In deep Lake Constance both species show fundamental ecological differences: *D. galeata* lives epilimnetically and is absent from the lake during the winter, while *D. hyalina* is present throughout the year and shows pronounced diurnal vertical migrations (DVM) (Geller, 1985; Berberovic, 1990). *D. hyalina* x *galeata* hybrids also undergo large migrations, whereas *D. galeata* remains in the warm epilimnion (Stich & Lampert, 1981). Spaak (1994) found that the spatial distribution of hybrid and parental taxa in the shallow Lake Tjeukemeer do not indicate the existence of a hybrid zone. In the deep Lake Geneva the different species of the *Daphnia* complex *(D. hyalina x galeata),* and also different classes, have a distinct DVM which leads to a temporal and spatial segregation (Angeli *et al.*,1995).

The difference in vertical distribution of the two coexisting species, *D. hyalina* and *D. galeata,* may indicate that the food spectra of these two species are different and that they may differ on the threshold of food concentrations for the maintenance of a viable population (Geller, 1985). The ability to gather food particles is determined by the filter mesh-size and filtration area (Korinek & Machaček, 1980). In coexisting species this means a reduced competition (Brandelberger, 1985; Brandelberger & Geller, 1985).

Within a particular species, intra-specific competi-

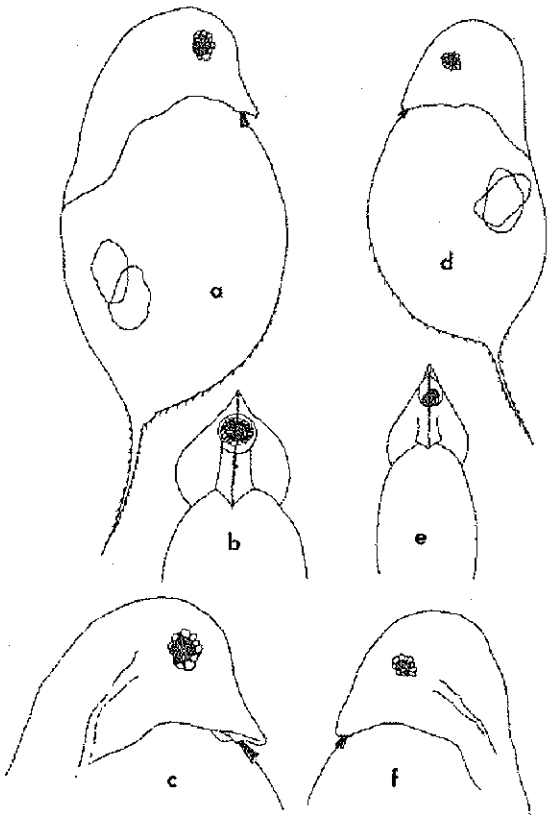


Fig. 1a-f: Differences in body shape in** D. hyalina **(left) and** D. galeata **(right) from Lake Bled (Slovenia). a and d: whole specimen (lateral view); b and e: head (frontal view); c and f: detail of head (lateral view).
Sl. 1a-f: Razlike v obliki telesa med vrstama** D. hyalina **(levo) in** D. galeata **(desno) v Blejskem jezeru (Slovenija). a in d: celo telo (lateralno); b in e: glava (frontalno); c in f: detajl glave (lateralno).

tion can potentially be reduced by a segregation of specimens of different size or status (*i.e.* juveniles, ovigerous females and adult females without eggs) in the water column (Brancelj & Blejec, 1994). This is usually connected with DVM, which is often induced by the presence of predators (Stich & Lampert, 1981; Dodson, 1990; Ringelberg & Flik, 1995).

In this work we tested the hypothesis that spatial segregation between *D. hyalina* and *D. galeata* appeared after the invasion of *D. galeata* in Lake Bled in 1995, through a reduction of the vertical habitat range occupied by *D. hyalina*. For this purpose we compared the differences in vertical distribution of *D. hyalina* before and after the invasion of *D. galeata*.

MATERIAL AND METHODS

Sampling

Zooplankton samples were taken at approximately monthly intervals between June and November 1995 in Lake Bled (Slovenia). We sampled a vertical profile at the deepest point of the lake, at 2.5 m intervals from the surface to a depth of 15 m. Below that depth hypoxia and anoxia regularly appeared during the summer/ autumn. A Friedinger's bottle with a volume of 6.15 l was used. Samples were taken in triplicates at noon and midnight. Samples were preserved in 4% formaldehyde.

Laboratory work

In the laboratory, specimens of *Daphnia* from each sample were separated according to the morphological differences of the species (Fig. 1). At each date, the number of specimens of each taxon from each sample was counted and individuals were separated into juveniles, adult females without eggs and ovigerous females. In both species the body length of all ovigerous females was measured to the nearest 0.01 mm from one sample of each date, depth and time of the day to test for the differences between the species. In addition, the number of eggs per clutch in each specimen was counted.

Statistics

To represent the differences in daytime distribution of *D. hyalina* over the samples taken in 1988 and 1995, the median depth of the population and the 1st and 3rd quartil were plotted. The same method was used to compare the differences in day- and night-time vertical distribution of *D. hyalina* and *D. galeata* population over time in 1995.

The effect of depth in water column and species on the percentage of animals caught was evaluated by two-way ANOVA. As the variables were expressed as a proportion in relation to the whole population, the data were arcsinus transformed. Differences between both species in body length and number of eggs per clutch were tested by one-way ANOVA.

RESULTS

Differences in vertical distribution of *D. hyalina* between 1988 and 1995

The day-time vertical distribution pattern of the *D. hyalina* population inhabiting Lake Bled slightly changed between 1988 and 1995 (Fig. 2). In the lake the period of the summer thermal stratification lasts, on average, from the middle of May till the end of October. During the thermal stratification in 1988, the median day-depth of the population of *D. hyalina* in May was only 5 m below the surface, whilst it was to 10-11 m from June to September. The median depth rose again to 6-7 m below the surface in October and November (Fig. 2d). In 1995 the median day-depth of the population

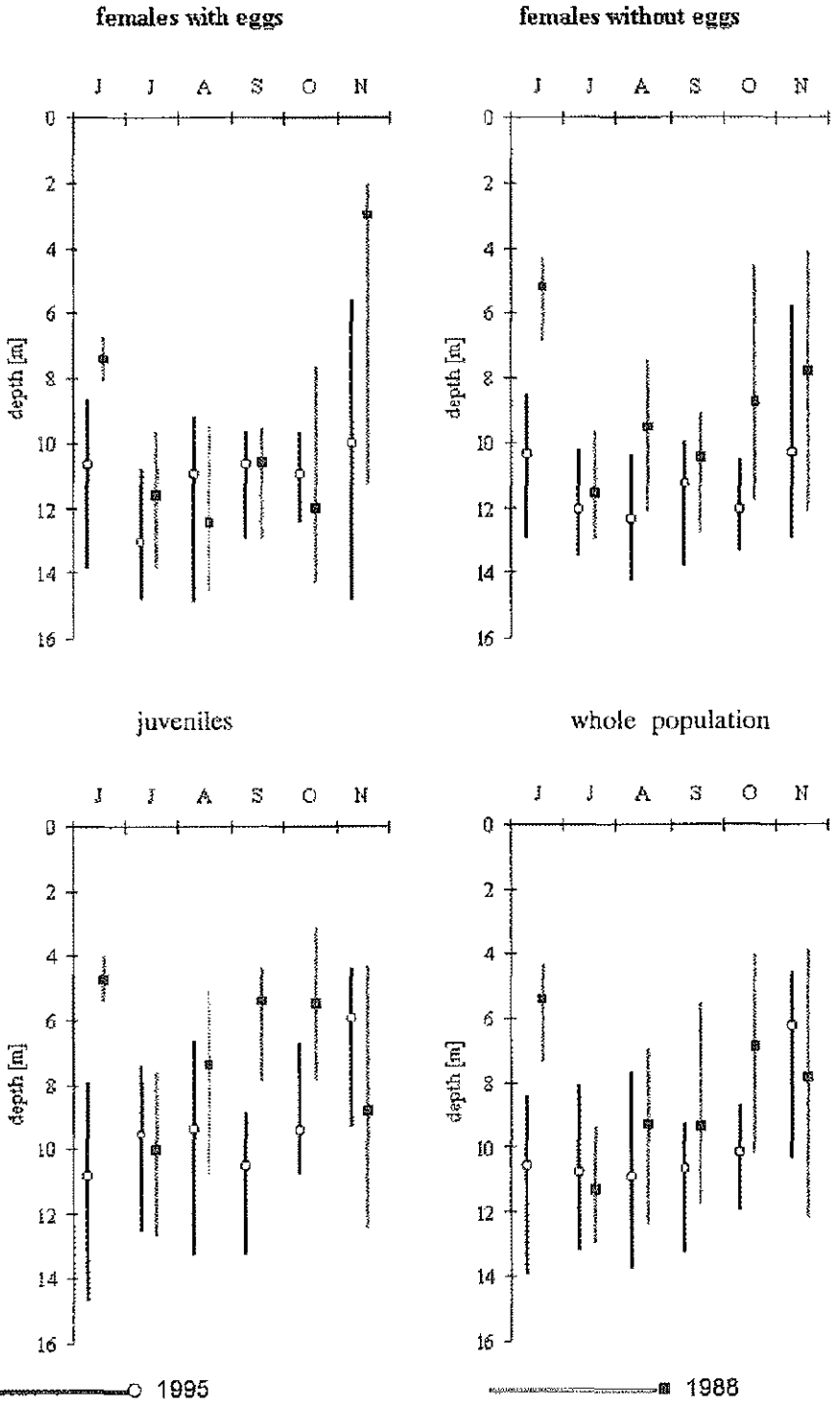


Fig. 2.: Vertical distribution plots of mediana and 1st and 3rd quartil of different categories as well as of the whole population of** D. hyalina **at noon in lake Blejsko Jezero (Slovenia) from June to November in 1988 (squares) and 1995 (circles).

Sl. 2: Grafični prikaz medijane in 1. in 3. kvartila v vertikalni razporeditvi različnih kategorij in celotne populacije** D. hyalina **v Blejskem jezeru (Slovenija) opoldne v času od junija do novembra v letu 1988 (kvadrati) in v letu 1995 (krogi).

remained at 10-11 m below the surface from June until October. It rose to a depth of 6 m in November, during the fall turnover period. The same differences in vertical distribution were observed for females without eggs and juveniles. In 1988 both groups had their median day-depth 5 m below the surface in June and at 10-12 m in July. In July to October/November the mean depth rose gradually toward the surface. In 1995 the animals stayed at a depth of 8-14 m at day-time during the period of thermal stratification (Fig. 2b, c). Ovigerous females, however, behaved similarly in both years, as they always stayed between 8 and 14 m during the day (Fig. 2a).

Vertical distribution of *D. hyalina* and *D. galeata* in 1995

During the thermal stratification of the lake, there were only slight differences between the median day-depths of *D. hyalina* and *D. galeata*. The median depths were in the interval between 8 and 11 m below the surface studied during the whole period, except November. Except for June, the median day-depth of *D. galeata* was somewhat higher (0.5-2.5 m) than that of *D. hyalina* (Fig. 3a).

During the night, the median depth of *D. hyalina* was between 5.5 and 7.7 m below the surface (Fig. 3b). In *D. galeata* the median night-depth of the population gradually decreased from June (4 m depth) to October (9 m depth). In November, the median night-depth of *D. galeata* was at 6 m.

The migration amplitudes of *D. hyalina* ranged from 3 to 6 m in the period from June to October. There was no migration in November. In *D. galeata*, the migration amplitude decreased gradually from 7 m in June to no migration in October. Consequently this was due to a lowering of the night distribution rather than to a change in the daytime distribution.

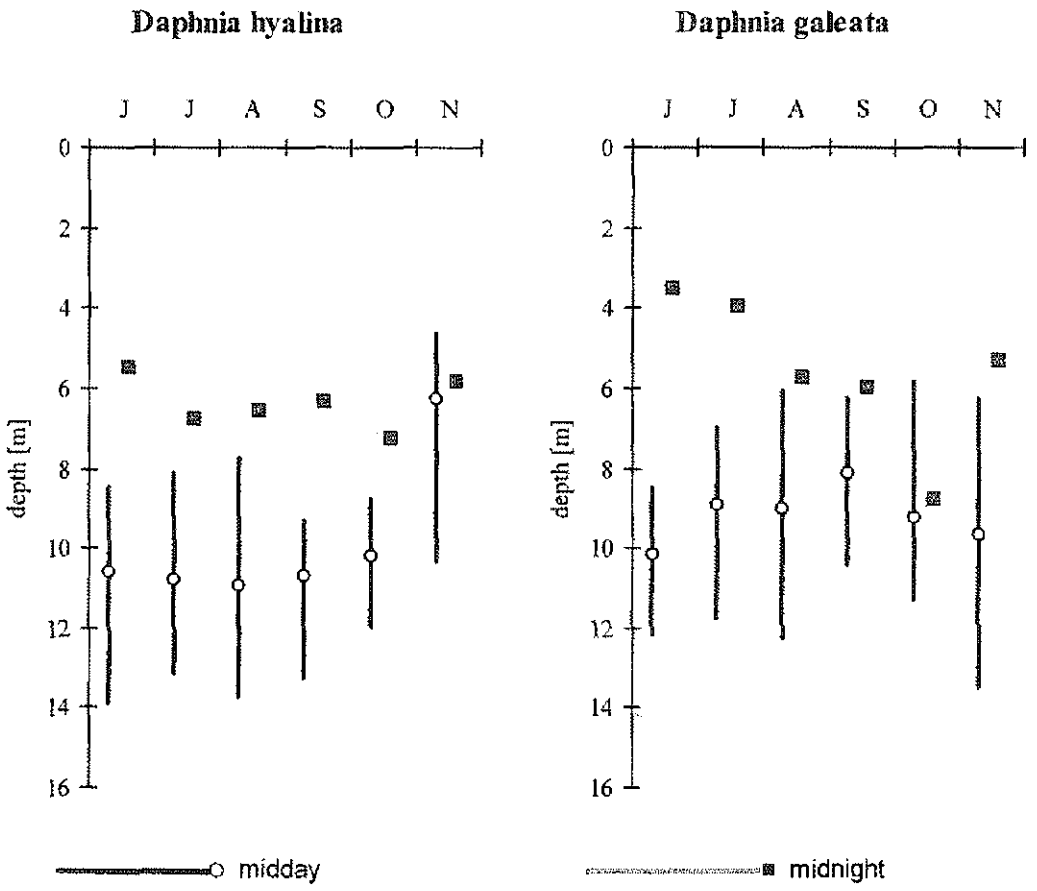


Fig. 3: Vertical distribution plots of mediana and 1st and 3rd quartil of the whole population of** D. hyalina **and** D. galeata **at noon (circles) and midnight (squares) in Lake Bled (Slovenia) from June to November in 1995.
Sl. 3: Grafični prikaz medijane in 1. in 3. kvartila v vertikalni razporeditvi celotne populacije vrst** D. hyalina **in** D. galeata **v Blejskem jezeru (Slovenija) opoldne (krogi) in opolnoči (kvadrati) v času od junija do novembra v letu 1995.

Tab. 1: Results of two-factor ANOVA interaction between species and depth for different category, time of day and date (arcsinus transformed data on proportions in relation to each status were used) *(D. hyalina* ***and*** *D. galeata* ***from June to November 1995). The corrected level of significance with sequential Bonferoni test is 0.00142.***
Tab. 1: Rezultati dvo-faktorske analize variance interakcij med vrstama in globino za različne kategorije živali, dnevni čas in datum (uporabljena je arcsinusna transformacija podatkov, ker so bili le-ti podani v razmerjih) *(D. hyalina* ***in*** *D. galeata* ***od junija do novembra v letu 1995). Popravljena stopnja značilnosti sekvenčnega Bonferonijevega testa je 0,00142.***

date	category					
	juveniles		females without eggs		ovigerous females	
	F	P	F	P	F	P
DAY						
14.06.95	2,290	0,0659	6,607	0,0002	3,544	0,0107
14.07.95	5,788	0,0006	2,206	0,0748	0,579	0,7437
16.08.95	5,738	0,0007	1,110	0,3836	1,303	0,2906
14.09.95	6,066	0,0005	1,185	0,3447	2,494	0,0485
20.10.95	1,892	0,1203	6,607	0,0002	3,544	0,0107
23.11.95	4,042	0,0054	1,238	0,3195	2,151	0,0812
NIGHT						
14.06.95	5,049	0,0015	2,305	0,0644	4,209	0,0043
14.07.95	3,230	0,0166	3,600	0,0099	4,188	0,0045
16.08.95	1,089	0,3947	0,892	0,5150	1,535	0,2062
14.09.95	1,612	0,1836	1,032	0,4271	2,235	0,0716
20.10.95	19,975	0,0000	2,267	0,0682	2,394	0,0564
23.11.95	3,464	0,0119	1,044	0,4206	0,379	0,8857

	species: depth interaction	total	error
d.f.	6	41	26

Tab. 2: One-factor ANOVA testing for the effect of species on the number of eggs in *Daphnia* ***from June to November 1995. Average of the number of eggs (± std) carried by female in*** *D. hyalina* ***and*** *D. galeata* ***are also reported. The corrected level of significance with sequential Bonferoni test is 0.0085.***
Tab. 2: Eno-faktorska analiza variance za testiranje vpliva vrste na število jajc pri samicah rodu *Daphnia* ***od junija do novembra v letu 1995. Prikazano je tudi povprečno število jajc (± SD) pri samicah vrst*** *D. hyalina* ***in*** *D. galeata.* ***Popravljena stopnja značilnosti sekvenčnega Bonferonijevega testa je 0,0085.***

date	d.f.				D. hyalina		D. galeata	
		error	F	P	avg.	st. d.	avg.	st. d.
14.06.95	1	198	1,53	0,2181	1,82	0,86	1,65	0,74
13.07.95	1	181	13,22	0,0004	2,50	1,40	1,59	1,14
16.08.95	1	297	5,52	0,0195	1,59	0,74	1,33	0,52
15.09.95	1	77	1,80	3,9651	1,58	0,70	1,39	0,55
20.10.95	1	142	14,86	0,0002	1,84	0,80	1,37	0,49
24.11.95	1	130	0,64	0,4253	1,93	0,84	1,80	0,61

The effect of reproductive stage in 1995

The arcsinus transformed data of the proportions of a population caught in a sample were analysed by two-factor ANOVA ($P<0.05$) (Table 1). A significant effect of reproductive category, species, time of the day and depth was observed, as well as a significant effect of interaction between these factors for each date (15 cases out of 36). As 36 sets were carried out, there was a need of applying a sequential Bonferoni test to correct the

Tab. 3: One-factor ANOVA testing for the effect of species on body length of ovigerous females in* Daphnia *from June to November 1995. Average body length (mm) (± std) of ovigerous female in* D. hyalina *and* D. galeata *at different sampling dates are also shown. The corrected level of significance with sequential Bonferoni test is 0.0085.
Tab. 3: Eno-faktorska analiza variance za testiranje vpliva vrste na telesno dolžino samic z jajci rodu* Daphnia *od junija do novembra v letu 1995. Prikazane so tudi povprečne telesne dolžine (± SD) različnih vzorcev samic z jajci vrst* D. hyalina *in* D. galeata. *Popravljena stopnja značilnosti sekvenčnega Bonferonijevega testa je 0,0085.

date	d. f.				D. hyalina		D. galeata	
		error	F	P	avg.	st. d.	avg.	st. d.
14.06.95	1	189	86,59	0,0000	1,47	0,12	1,29	0,11
13.07.95	1	28	22,47	0,0001	1,63	0,13	1,34	0,06
16.08.95	1	56	4,27	0,0435	1,52	0,13	1,43	0,13
15.09.95	1	75	28,68	0,0000	1,47	0,16	1,29	0,13
20.10.95	1	78	35,23	0,0000	1,52	0,11	1,39	0,07
24.11.95	1	44	4,91	0,0319	1,53	0,14	1,42	0,07

level of significance at <0.00142. Taking the different reproductive categories into consideration, significant differences in depth distribution between the species were only observed in 6 out of 36 cases (Tab. 1), indicating that in general the distribution of the species did not differ remarkably.

An average female's body length and number of eggs per clutch

The average clutch size of ovigerous females of both species rarely exceeded two eggs per female during the period studied. Clutch size was significantly larger in *D. hyalina* than in *D. galeata* in July and October (single-factor ANOVA, P<0.0085 corrected with sequential Bonferoni test; Tab. 2). During the day there were no ovigerous females in the upper 5 m of the lake, except in November. During the night ovigerous females were found throughout the vertical profile studied, including close to the surface.

On average, ovigerous female of *D. hyalina* were significantly larger than ovigerous females of *D. galeata* during four of six sampling months (single-factor ANOVA, P<0.0085 corrected with sequential Bonferoni test; Tab. 3). The average body size of ovigerous females ranged from 1.47 to 1.67 mm in *D. hyalina* and 1.29 to 1.43 mm in *D. galeata*.

The size of ovigerous females in both species was randomly distributed in the vertical profile. There was no tendency of aggregation of females of the same size at a particular depth neither during the day nor night.

DISCUSSION

There are two possible scenarios for the sudden occurrence of *D. galeata* in Lake Bled. First, it is possible that the species had been present in the lake before 1995, but its abundance was so low that it was overlooked during the monitoring of the zooplankton. In 1995 yet unknown environmental conditions must have favoured the population growth of *D. galeata*. Alternatively, *D. galeata* may have been introduced recently, either by boats or by migratory birds, and expanded immediately after invading the lake.

Our hypothesis was that the increase of *D. galeata* population in Lake Bled would result in a change in vertical distribution of *D. hyalina*. It was expected that the species with the smaller body size, *D. galeata*, should occupy the upper strata of the lake, and that the larger body size species, *D. hyalina*, would occupy deeper strata during the period of thermal stratification of the lake. This pattern has been observed in Lake Constance (Berberovic, 1990). When thermal stratification is broken down in fall, a strong decrease of the *D. galeata* population occurs in Lake Constance, while *D. hyalina* becomes more evenly distributed in the water column.

When the vertical distribution of *D. hyalina* in the water column of Lake Bled was compared between 1988 and 1995, two differences were observed: the median day-depth of the population was lower in 1995 than in 1988, and the change in median day-depth position during thermal stratification was slightly different. The result was a change in the amplitude of DVM. In the population of 1988, the amplitude of DVM gradually decreased from July/August toward October/November. In 1995, the population resided at the same day-depth and engaged in a comparable DVM during the whole period of thermal stratification. In November, when the thermal stratification collapsed, the amplitude of DVM almost disappeared.

There were no significant differences in the overall day-time distribution of *D. galeata* and *D. hyalina* in 1995, though there was a tendency for *D. galeata* to remain closer to the surface and for *D. hyalina* to remain closer to the metalimnion. Significant differences were

only observed in average body length of adult females. *D. galeata* females had, on average, smaller body length but similar clutch size compared to *D. hyalina*. Though ovigerous females of *D. galeata* were significantly smaller than those of *D. hyalina*, both taxa were absent from the upper strata of the lake during the day. This excluded a hypothesis that females with smaller clutch sizes are less vulnerable to fish which have a vision search-mode of prey (Geller, 1989). This means that fish, as a driving force for the potential spatial separation of both *Daphnia* species are excluded in the case of Lake Bled.

As there were no significant differences in the vertical distribution between the juveniles of both species, predation by larvae of *Chaoborus* probably did not play an important role in the vertical distribution of *Daphnia*. This opposes to observations made by Brancelj & Blejec (1994), who found in 1988 that larvae were important in the vertical distribution of different categories of *D. hyalina*.

Differences in filter mesh-size between taxa can explain spatial coexistence of competing *Daphnia* during the day (Liebold, 1991). According to data from Brendelberger (1985) and Brendelberger & Geller (1985), filter mesh-size in *D. galeata* range from 0.25 to 0.62 μm and filtering area between 0.107 and 1.036 mm². Values for *D. hyalina* range between 0.28 and 0.43 μm for mesh-size and between 0.128 to 1.550 mm² for filtering area.

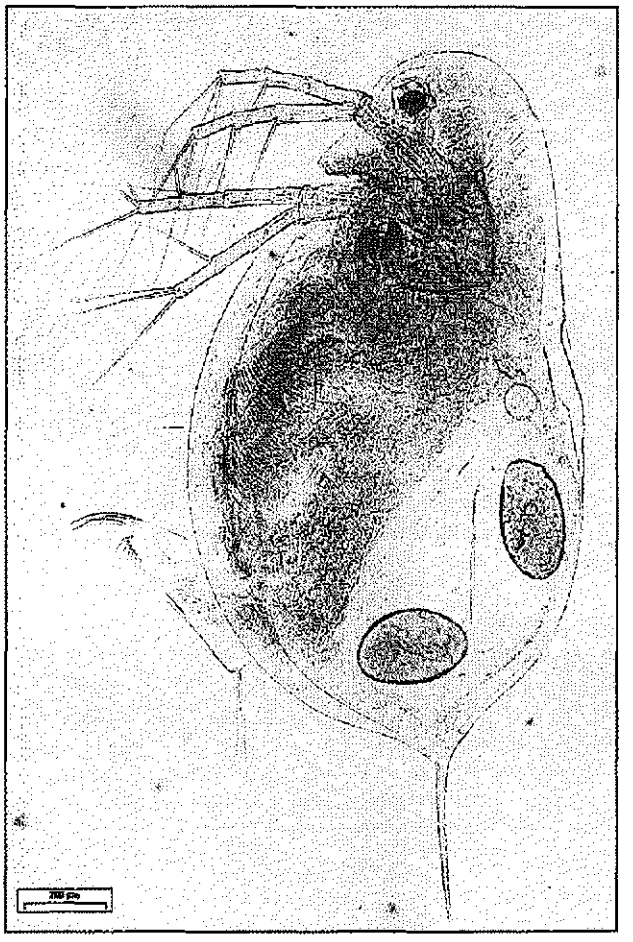
CONCLUSIONS

Comparing the situations in 1988 and 1995, some differences appeared in the vertical distribution of *D. hyalina* in Lake Bled. The median day-depth of *D. hyalina* population was deeper in 1995 compared to 1988, and the amplitude of DVM during the period of thermal stratification differs between both years, but the pattern of distribution did not change significantly.

After the appearance of *D. galeata*, both species occupied similar depth strata during the day, but the median depth of *D. galeata* was always slightly higher in the water column than that of *D. hyalina*. Comparing the distribution of the same categories between species, no significant differences were observed.

Significant differences between both species existed in average body size of ovigerous female, but not in the average clutch size.

Invasion of *D. galeata* in Lake Bled did not significantly effect the vertical distribution of *D. hyalina* in the first year. This is partly a result of interbreeding of both species, producing hybrids, which could make the differences between both species less obvious.



Daphnia galeata, Sars 1863.

VERTIKALNA RAZPOREDITEV VRSTE *DAPHNIA HYALINA* LEYDIG V VODNEM STOLPCU BLEJSKEGA JEZERA LETO DNI PO NASELITVI NOVE VRSTE *DAPHNIA GALETA* SARS

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POVZETEK

Daphnia hyalina *je bila v obdobju 1988-1994 edina znana vrsta iz rodu* Daphnia *v planktonu Blejskega jezera.*

V aprilu l. 1995 smo v vzorcih opazili novo vrsto tega rodu, ki smo jo določili kot D. galeata. *Ta vrsta se je zelo hitro namnožila in je konec poletja že sestavljala okoli 25% celotne populacije rodu* Daphnia. *Pojav* D. galeata *v Blejskem jezeru lahko razložimo na dva načina: a) maloštevilna populacija je v njem živela že dolgo časa, nenadna sprememba življenjskih razmer v jezeru pa je povzročila njeno izrazito povečanje ali b) vrsta se je naselila pred kratkim, potem pa se je njena populacija hitro povečala.*

V letu 1988 smo v času poletne plastovitosti v vodnem stolpcu Blejskega jezera podrobno analizirali razporeditev osebkov vrste D. hyalina. *Enako metodo smo uporabili tudi v letu 1995, ko smo testirali dve hipotezi. Prva naj bi potrdila razlike v razporeditvi osebkov v vodnem stolpcu med letoma 1988 in 1995 tako pri celotni populaciji* D. hyalina *kot tudi pri posameznih skupinah (mladiči, odrasle samice brez jajc in odrasle samice z jajci). Pri drugi hipotezi pa smo ugotavljali razlike v razporeditvi osebkov v vodnem stolpcu med vrstama* D. hyalina *in* D. galeata, *vključno z razlikami med posameznimi skupinami osebkov.*

Vzorec razporeditve osebkov celotne populacije vrste D. hyalina *in tudi posameznih kategorij se v letu 1995 ni bistveno razlikoval od tistega v l. 1988. Manjše razlike so nastale predvsem pri razporeditvi osebkov obeh vrst* (D. hyalina *in* D. galeata) *v nočnem času v l. 1995. Analiza variance (ANOVA) po dveh faktorjih (vrsta in globina) znotraj različnih skupin osebkov ni pokazala bistvenih razlik v vertikalni razporeditvi obeh vrst podnevi. Zato je bila zavrnjena hipoteza, da so osebki enakih skupin pri obeh vrstah rodu* Daphnia *v času poletne plastovitosti jezera različno razporejeni v vodnem stolpcu. To pa je v nasprotju z ugotovitvami iz nekaterih drugih globokih evropskih jezer.*

Ključne besede: *Daphnia hyalina, Daphnia galeata,* vertikalna razporeditev, evtrofno jezero, tekmovanje

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