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Evidences of zooplankton vertical migration in stocked and never-stocked alpine lakes in Gran Paradiso National Park (Italy)

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Abstract

Zooplankton vertical migration was described in four high altitude lakes in Gran Paradiso National Park (Northern Italy) during 2008 summertime. The authors succeeded in describing the vertical distribution of 6 species: diel vertical migrations were observed in the case of adult crustacean species (*Cyclops* gr. *abyssorum*, *Arctodiaptomus alpinus* and *Daphnia* gr. *longispina*), whereas the remaining rotifer species (*Keratella quadrata*, *Polyarthra* gr. *dolichoptera* and *Synchaeta* gr. *stylata-pectinata*) and naupliar stages of copepods did not undergo migrations. Migratory behavior of *Daphnia* gr. *longispina* and *Cyclops* gr. *abyssorum* was influenced by the size of individuals, especially larger individuals use to migrate deeper during the day compared to the smaller conspecific. This study provides new evidences of zooplankton vertical migration in never-stocked lakes and highlights the need to consider the zooplankton migration as result of multiple causal factors.

INTRODUCTION

Handling the DNA damage induced by UV radiation, zooplankton commonly synthesize photoprotective compounds and produce DNA repair systems (Zagarese et al. 1994, Leech and Williamson 2000, Hairston 1976, Hessen 1994, Vinebrooke and Leavitt 1999, Mcfadyen et al. 2004). Moreover, zooplankton can reply to UV damage also with behavioral responses and, since the depth highly attenuates UV radiation (Tonolli 1964, Losey et al. 1999, Quickenden & Irvin 1980), Diel Vertical Migration (DVM) may serve as a dark refuge (Dawidowicz & Loose 1992, Hansson 2007, Cooke et al. 2008). As a whole, it is a system where phenotypic plasticity and behavioral escape mechanisms function as complementary traits (Hansson et al. 2007). At the same time, DVM within water bodies have been considered as a defense mechanism against visually hunting predators according to which the irradiated surface is avoided during the daytime to prevent fish predation (Stich & Lampert 1981, Gliwicz 1986, Lampert 1989, Lampert 1993, Hansson et al. 2007).

Since UV radiation intensity increases with altitude (Caldwell et al. 1980) and its attenuation depth in water is highly correlated with the Dissolved Organic Carbon content (DOC) (Scully & Lean, 1994), DVM behavior in high altitude and oligotrophic alpine lakes (with very low DOC content) would be rather pronounced, and in our opinion this kind of environment is particularly suitable for studies on zooplankton movements. Moreover, in many cases, alpine lakes are naturally devoid of fish, but they often underwent fish stocking, which incidentally provides interesting experimental condition for understanding the connection between predation and DVM.

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During the ice free season of 2008, we completed a study on zooplankton DVM in four high altitude and oligotrophic lakes of Gran Paradiso National Park (GPNP, the Western Italian Alps), two of which were stocked with *Salvelinus fontinalis*, an alien salmonid from North America. Our objective was to describe the vertical distribution of a large number of crustacean and rotifer species inhabiting GPNP lakes, looking for DVM behavior evidences.

MATERIALS AND METHODS

The study area

Gran Paradiso National Park (GPNP) is located between 45°25' and 45°45' N, and between 7° and 7°30' W in the Western Italian Alps (Fig. 1). The protected area shows a large altitudinal extension (between 800 and 4061 m) and a typical alpine climate. GPNP includes all the four studied lakes (Fig. 1) belonging to the catchments of rivers Orco and Dora di Savarenche. In this paper, toponyms of the lakes will be replaced by abbreviations: Nivolet superiore – NIVSUP, Losere – LOSERE, Nero (in the Leynir valley) – LEYNIR, Nero (in the Djouan area) – NERODJ. Main geographical, morphological, watershed and chemical data are based on Tiberti et al. (2010) and presented in Table 1. The lakes are not affected by hydromorphological alterations; they are larger than 10,000 m^2 and are all located above 2500 m a.s.l. and the local tree line, with their watershed belonging to the Alpine and nival belts. They are placed in two geologically separated areas: the first one is entirely dominated by acidic gneiss, while the second one is dominated by thick cover of calcareous schist metamorphosed to a different extent (Leporati et al. 1999). The geology affects the vegetation development in the watershed (Scotta et al. 1999), as well as hydrochemistry of the lakes (Tiberti et al. 2010). Also when they are surrounded by the insoluble rocks, the studied lakes seem to be well preserved from acidification risk. The total phosphorus (TP) concentration (always 2 µg l^{-1}) is an index of ultraoligotrophic conditions and according to Redfield's ratio, phosphorus is the phytoplankton growth limiting element. Also TOC concentration, between 0.2 and 3.7 mg l^{-1}, is consistent with oligotrophy and clear water (Table 1).

Planning the research activities we chose two never-stocked lakes, naturally devoid of fish, and two stocked lakes: *Salvelinus fontinalis* has been introduced during the 1960s in NERODJ and LEYNIR, where

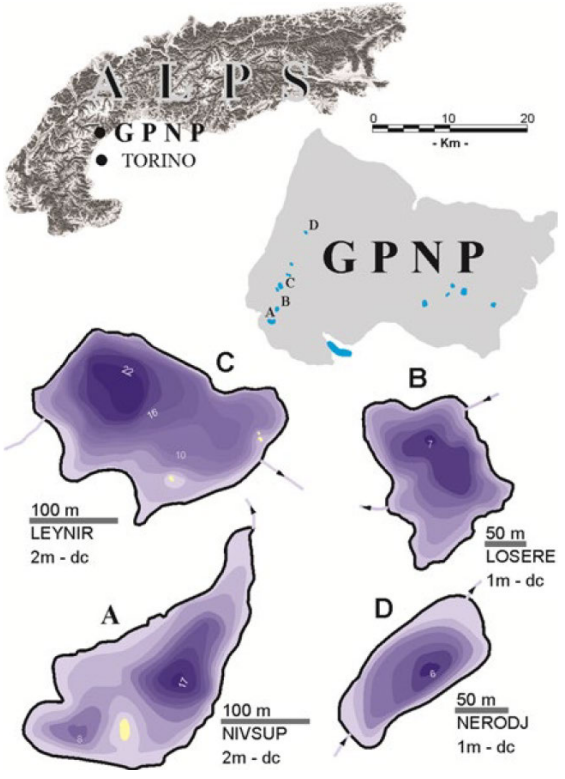


Fig. 1. The study area: the Gran Paradiso National Park hydrographic system, the studied lakes and their bathymetry (modified from Tiberti et al. 2010); dc - depth contours.

Table 1

Geographic and morphometric data on the studied GPNP lakes, their catchment characteristics and chemical properties.

		NIVSUP	LOSERE	LEYNIR	NERODJ
Date of sampling		30/06/2008	29/06/2008	11/07/2008	03/07/2008
Latitude		45°28'41"	45°28'33"	45°30'28"	45°33'07"
Longitude		07°08'55"	07°09'25"	07°09'06"	07°10'07"
Altitude	m	2538	2568	2747	2671
Z_m	m	17.1	7.2	22.1	6.0
A	m^2	34482	21401	44691	17121
L	m	986	684	956	548
V	×10^3 m^3	162.1	70.4	466.4	41.6
B	ha	29.11	43.48	156.47	86.55
Geology		AG	AG	CS	CS
pH		7.14	7.09	7.93	8.05
$C_{20°C}$	µS cm^{-1}	21.7	22.1	107.9	72
T.Alk.	meq l^{-1}	0.168	0.203	1.061	0.63
TP	µg l^{-1}	2	2	2	2
TN	mg l^{-1}	0.14	0.13	0.22	0.2
TOC	mg l^{-1}	0.4	3.7	0.2	0.3

Z_m - maximum depth, A – area, L – perimeter, V – volume, B - catchment area; Geology: AC - catchment entirely composed by acidic gneiss, CS - catchment dominated by a thick cover of calcareous schist; $C_{20°C}$ - conductivity at 20°C, T.Alk. - Total alkalinity, TP - Total Phosphorus, TN - Total Nitrogen, TOC - Total Organic Carbon

this species established reproductive stable populations surviving at the decreased growth rates (Alessio et al. 1987).

Sampling and analytical methods

We collected quantitative samples of zooplankton from different depths with a Van Dorn Bottle (with a capacity of 9.6 liters) at the point of the maximum depth. Each lake has been sampled 4 times during the day, every 6 hours: the first time early in the morning at 6:00 or 7:00, the second one at 12:00 or 13:00, then at 18:00 or 19:00 and finally at 0:00 or 1:00 during the night. The sampling depth in NIVSUP were 14, 12, 9, 7, 5, 3, 0 meters; in LOSERE were 7, 6, 5, 4, 3, 2, 1, 0 meters; in LEYNIR were 20, 16, 12, 8, 4, 0 meters; in NERODJ were 6, 5, 4, 3, 2, 1, 0 meters. Each sample was filtered directly in the field and immediately fixed in 4% formaldehyde. We analyzed the collected samples during the following months in the Laboratory of Zoology - Animal Biology Department at the University of Pavia, according to Edmonson & Winberg (1971). Zooplankton taxa in the samples were identified according to Dussart (1969), Harding and Smith (1974), Braioni and Gelmini (1983), Stella (1984) and Margaritora (1985). Coarse taxonomic levels, indicating a group of species (gr.), have been used instead of the species name for those organisms with uncertain taxonomy (e.g. *Daphnia longispina* and *Daphnia rosea* have been recorded in the *longispina* group) or when the specific identification was not possible because of morphological deformations due to the preservation medium (e.g. *Synchaeta* gr. *stylata-pectinata*), and in the case of larval stages (e.g. nauplii). All the zooplankton individuals were counted and their length was measured with a calibrated eye-piece micrometer.

Data analysis

To enable the analysis of data and to ascribe the observed variation in vertical distribution to DVM behavior, we fixed three conditions:

- Condition 1 (C1): the sample size (the number of individuals of each species per sampling time) has to be greater than 5, as the condition for the application of Kruskal-Wallis test (Siegel & Castellan 1988).
- Condition 2 (C2): precondition of DVM behavior detection is that changes in the vertical distribution of zooplankton during the day have to be significant. We tested C2 with the Kruskal-Wallis non parametric analysis of variance preferred to parametric ANOVA for the reason of the non-normal distribution of data (tested with the Shapiro test for normality).
- Condition 3 (C3): changes in the vertical distribution of C2 have to be consistent with the kind of movements we are looking for, namely, the depth at midday has to be larger than the depth at midnight, and the depths in the morning and in the evening have to range between the maximum diurnal depth and the minimum nocturnal depth. We tested this condition using the multiple comparison median test (Mann-Whitney test).

Only when C1, C2 and C3 were satisfied, we tested if the vertical distribution of the taxon was influenced by the body size of individuals; in particular if larger individuals use to migrate deeper during the day compared to the smaller conspecific. We tested this hypothesis with the Generalized Linear Model (GLM), which enables to highlight any significant effect of the interaction between the sampling hours (H) and the length of individuals (L) on the depth (D) as a dependent variable. All the statistical analyses have been performed owing to statistical environment R version 2.12.1 (R Development Core Team, 2010).

RESULTS

We sampled 27819 individuals belonging to nine zooplankton species. Four crustacean species were identified: *Cyclops* gr. *abyssorum* (collected in all the lakes), *Daphnia* gr. *longispina* (collected in LOSERE and NERODJ), *Arctodiaptomus alpinus* (collected in NIVSUP, LEYNIR and NERODJ) and *Chydorus sphaericus* (collected in NIVSUP, LOSERE and NERODJ); moreover we collected a considerable number of naupliar stages of copepods in all the studied lakes. Five other rotifer species, such as *Keratella quadrata* (in all the lakes), *Keratella cochlearis* (in NERODJ), *Polyarthra* gr. *dolichoptera* (in NIVSUP and NERODJ), *Synchaeta* gr. *stylata-pectinata* (in NIVSUP) and *Notholca squamula* (in NIVSUP, LOSERE and LEYNIR) were identified.

Chydorus sphaericus, *Notholca squamula* and *Keratella cochlearis* never matched the limits set by C1, while the other species satisfied C1 at least in one of the studied lakes. Nauplii satisfied C1 in all the lakes, *Cyclops* gr. *abyssorum* and *Daphnia* gr. *longispina* just in LOSERE, *Arctodiaptomus alpinus* just in LEYNIR,

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Keratella quadrata in all the lakes, *Polyarthra* gr. *dolichoptera* in NIVSUP and NERODJ, *Synchaeta* gr. *stylata-pectinata* in NIVSUP.

Only when C1 was satisfied, we tested C2 and C3 with the Kruskal Wallis analysis of variance and the multiple comparison Mann – Whitney tests. We obtained different results for rotifers and crustaceans: even if the changes in their distribution were usually significant and C2 was satisfied, the data concerning rotifer movements never fulfilled C3. On the other hand, all the crustacean species satisfied C2 and C3, with the exception of naupliar stages of copepods whose behavior did not show any strong evidence of migration. In Table 2 we present the results of the Kruskal-Wallis test for rotifer populations fulfilling C1.

Table 3

Kruskal-Wallis test for rotifer populations following C1.

Species	Lake	χ^2	df	P
Keratella quadrata	NIVSUP	711.97	3	< 0.0001
Keratella quadrata	LOSERE	54.47	3	< 0.0001
Keratella quadrata	LEYNIR	612.39	3	< 0.0001
Keratella quadrata	NERODJ	20.20	3	< 0.001
Polyarthra gr. *dolichoptera*	NIVSUP	132.69	3	< 0.001
Polyarthra gr. *dolichoptera*	NERODJ	4.82	3	0.19
Synchaeta gr. *stylata-pectinata*	NIVSUP	7.80	3	0.05

As summarized above, regarding the crustaceans, nauplii always fulfilled C2 but never C3. In NIVSUP, the mean depth for nauplii was 3.90 m at 6:00, 4.70 at 12:00, 4.00 at 18:00 and 6.30 at 0:00 and the variation in their distribution was significant (χ^2 = 15.30, df = 3, $p < 0.01$), but when we tested C3 with a multiple comparison at different hours, the results were incoherent. The same is true for the other lakes: in LOSERE, where the mean depth for nauplii was 3.40 m at 6:00, 4.70 at 12:00, 4.50 at 18:00 and 4.10 at 0:00 and C2 was satisfied (χ^2 = 15.30, df = 3, $p < 0.01$) but not C3; in LEYNIR, where the mean depth nauplii was 8.70 m at 6:00, 3.80 at 12:00, 3.00 at 18:00 and 3.00 at 0:00, C2 was satisfied (χ^2 = 15.30, df = 3, $p < 0.01$) but not C3; in NERODJ, where the mean depth for nauplii was 2.60 m at 6:00, 3.60 at 12:00, 3.40 at 18:00 and 3.40 at 0:00, C2 was fulfilled (χ^2 = 15.30, df = 3, $p < 0.01$) but not C3.

Otherwise, adult crustaceans *Cyclops* gr. *abyssorum*, *Arctodiaptomus alpinus* and *Daphnia* gr. *longispina* show migratory behavior following both C2 and C3. In LOSERE, *Cyclops* gr. *abyssorum* shows a significant change in its vertical distribution during the day (χ^2 = 416.82, df = 3, $p < 0.0001$) (Fig. 2); its mean depths were 4.80, 5.50, 4.70 and 4.10 meters and its median depths were 5, 6, 5 and 4 meters respectively at 7:00, 13:00, 19:00 and 1:00. The results of the multiple comparison median test are consistent with C3 and are presented in Table 3. Since C3 was fulfilled we tested the importance of individual size on vertical distribution with the Generalized Linear Model. Fig. 3 presents the vertical distribution of individuals depending on their size. The model enables to highlight a significant effect of the sampling hour (H) ($F_{3,351}$ = 11.57, $p < 0.0001$), but especially of the interaction between H and the length of *Cyclops* gr.

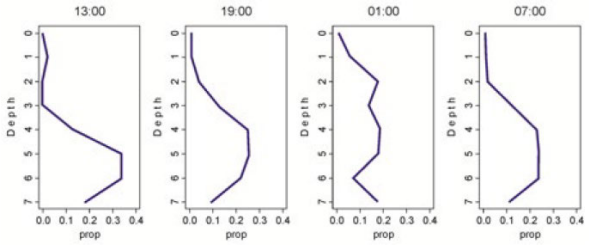


Fig. 2. *Cyclops* gr. *abyssorum* vertical distribution in LOSERE: relative abundances at different depths and times.

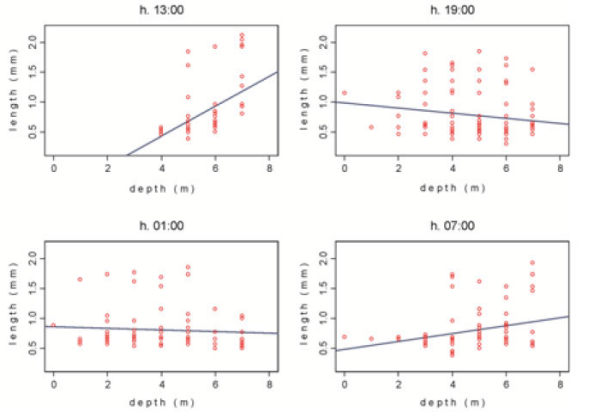


Fig. 3. Scatter plot displaying *Cyclops* gr. *abyssorum* size (length) and sampling depth at different times in LOSERE.

Table 2

Multiple comparison of *Cyclops* gr. *abyssorum* vertical distribution at different times (Mann – Whitney median test) in LOSERE.

Hours	Median difference	W	P
13:00 01:00	2	3774	<0.0001
13:00 07:00	1	3266.5	<0.01
13:00 19:00	1	5258	<0.0001
19:00 01:00	1	6526	<0.05
19:00 07:00	0	5080	0.69
01:00 07:00	-1	2722.5	<0.05

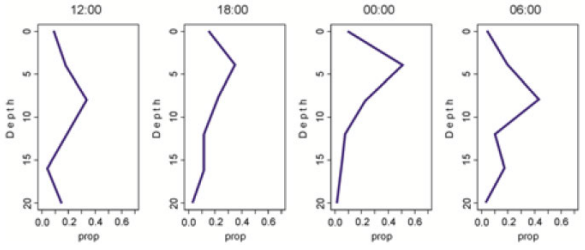


Fig. 4. *Arctodipatomus alpinus* vertical distribution in LEYNIR: relative abundances at different depths and times.

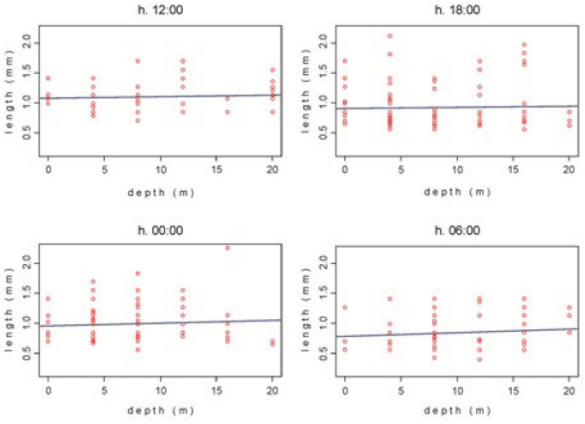


Fig. 5. Scatter plot displaying *Arctodipatomus alpinus* size (length) and sampling depth at different times in LEYNIR.

Table 4

Multiple comparison of *Arctiodiptomus alpinus* vertical distribution at different times (Mann – Whitney median test) in LEYNIR.

Hours	Median difference	W	P
12:00 00:00	4	6187	< 0.0001
12:00 06:00	0	2941.5	0.72
12:00 18:00	4	4798.5	< 0.01
18:00 00:00	0	8596	0.16
18:00 06:00	-4	3788	<0.01
00:00 06:00	-4	3541	<0.0001

abyssorum (L) ($F_{3,348}$ = 5.18, p < 0.01), on the depth as a dependent variable. As shown in Fig. 3, larger *Cyclops* tend to stay deeper at 13:00 (t = 2.48, p < 0.05) and at 7:00 (t = 2.38, p < 0.05).

Also *Arctiodiptomus alpinus* satisfied both C2 and C3 in LEYNIR; its mean depths are 9.10, 9.50, 7.20 and 6.10 meters and its median depths are 8,8,4 and 4 meters respectively at 6:00, 12:00, 18:00 and 0:00. The Kruskal Wallis test is significant (χ^2 = 31.96, df = 3, p < 0.0001) and the Multiple comparison median tests are consistent with DVM movements (Table 4, Fig. 4). We applied the same GLM to *Arctodiaptomus alpinus* distribution data to test the importance of individual size on vertical distribution: we found a significant effect of H ($F_{3,378}$ = 7.43, p < 0.0001) but we did not find any effect of the interaction between H and L as clearly presented in Fig. 5.

The migratory behavior of the last large crustacean species, *Daphnia* gr. *longispina*, was studied in LOSERE and both C2 and C3 were satisfied (χ^2 = 30.73, df = 3, p < 0.0001; Table 5; Fig. 6). The mean and median depth for Daphnia at 7:00, 13:00, 19:00 and 1:00 were respectively 3.70, 5.40, 4.20 and 3.10 meters and 3, 6, 4 and 3 meters. Testing the importance of individual size on the vertical distribution of *Daphnia,* we found a significant effect of H ($F_{3,74}$ = 23.59, p < 0.0001) and of the interaction between H and L ($F_{3,71}$ = 8.16, p < 0.0001); as shown in Fig. 7 larger *Daphnia* specimens tend to stay deeper at 7:00 (t = 3.04, p < 0.01) and at 19:00 (t = 3.62, p < 0.001), even if we did not find a significant relation at 13:00 (t = 0.63, p = 0.53).

DISCUSSION

We succeeded in describing the vertical distribution of six species (satisfying C1) and we identified three migrant crustacean species, potentially dominant in GPNP lacustrine zooplankton communities (Tiberti, paper in preparation). A clear model of vertical migration was not observed in diurnal distribution of rotifers. *Synchaeta* gr. *stylata-pectinata* remained within the same water layer (between 0 and 5 m) for the 24-hour cycle, while no noticeable patterns in the distribution of *Keratella quadrata* and *Polyarthra* gr. *dolichoptera* were observed. Moreover, the distributions of the latter two species were very different, depending on the studied lake, indicating that the observed changes in the spatial distribution occurring within the day in all the lakes do not respond to coordinated and predictable movements of the entire population. We suggest that the observed data could be related to the aggregated distribution strongly affecting the number of rotifers in the samples. Unlike our results, the migration behavior of rotifers has been often reported (Paggi 1995, Karabin & Ejsmont-Karabin 2005, Obertegger et al. 2008), and various environmental factors or ecological requirements, as well as predation risk are considered to be involved in the determination of the rotifer vertical

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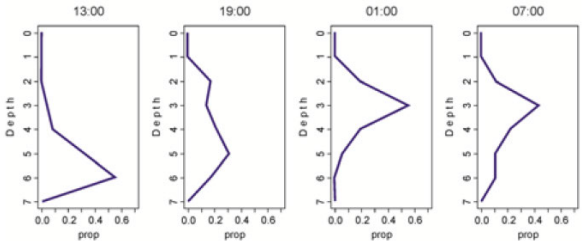


Fig. 6. *Daphnia* gr. *longispina* vertical distribution in LOSERE: relative abundances at different depths and times.

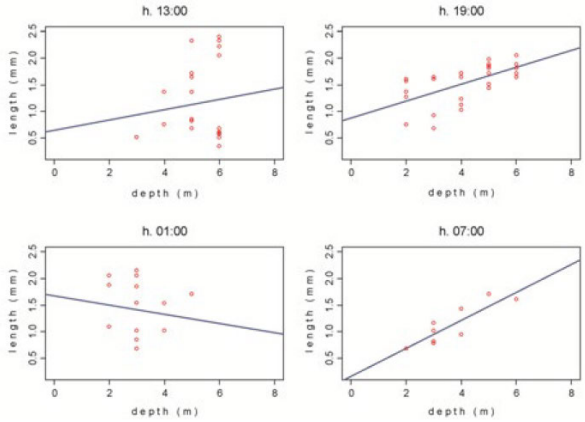


Fig. 7. Scatter plot displaying *Daphnia* gr. *longispina* size (length) and sampling depth at different times in LOSERE.

Table 5

Multiple comparison of *Daphnia* gr. *longispina* vertical distribution at different times (Mann – Whitney median test) in LOSERE.

Hours	Median difference	W	P
13:00 01:00	3	382.5	<0.0001
13:00 07:00	3	194	<0.001
13:00 19:00	2	558	<0.001
19:00 01:00	1	338	<0.01
19:00 07:00	1	160.5	0.29
01:00 07:00	0	54	0.26

distribution (Grzegorz et al. 2006, Obertegger et al. 2008). Rotifers exhibit different species-specific strategies dealing with factors, such as UV exposure, temperature and food availability, often without resorting to the migratory behavior. This great behavioral variability could include the observed distributions, however, the data collected in GPNP lakes are not suitable for conclusive assessment which factors determine the vertical distribution of rotifers, and we postpone any conclusion for the future and more detailed studies.

On the other hand, DVM involves all the non-larval crustaceans. DVM within water bodies have been clearly related to predation risk (Stich & Lampert 1981, Gliwicz 1986, Lampert 1989, Lampert 1993), but the evidence that it occurs in never-stocked lakes too, as in the case of *Daphnia* gr. *longispina* and *Cyclops* gr. *abyssorum* in LOSERE, is a convincing argument supporting the involvement of other causes, such as UV threat (Hansson et al. 2007). In our opinion, this is the most challenging result arising from our study area, because it implies the interaction of at least two main causes in the determination of DVM, and it offers the opportunity to study their relative importance in GPNP by increasing the number of lakes and comparing the zooplankton distribution in fish lakes and fishless lakes. However, understanding some results is problematic: for example larger *Cyclops* and *Daphnia* migrate deeper during the day: this will be a predation-induced mechanism or just the consequence of a better mobility; the same puzzle arises when we consider that adult and larger copepods migrate, while the smaller nauplii do not.

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