ABSTRACT: Diel Vertical Migration (DVM) is a widespread behavior in zooplankton. Although considered to be a predator avoidance behavior in most cases, DVM is also influenced by the distribution of food, competitive interactions and UV (Ultraviolet) radiation. In this paper we report the day and nighttime vertical distribution of the common zooplankton species in nine high altitude tropical Andean lakes to obtain an idea of the range in vertical distribution patterns in Andean lakes. The lakes are situated between 4000 and 4545 m a.s.l. The maximum depth of the lakes varied from 5 to 24 m, and the area varied between 0.6 and 20.75 ha. *Daphnia pulex* (Leydig 1860) showed tendencies for a normal vertical migration behavior in all lakes sampled irrespective of whether the lakes contained fish. The population resided deeper in the water column during the daytime than during the night, although migration amplitude differed strongly among lakes. In many lakes, there was an important daytime "deficit" in the number of individuals caught, suggesting that the animals stay close to the bottom of the lake during the day. It suggests that UV radiation is the more likely factor influencing the DVM of *Daphnia*. Copepods and rotifers showed reverse DVM in some lakes. Our data suggest that the DVM behavior of copepods and rotifers in the studied lakes may in part be determined by the avoidance of competition from *Daphnia pulex*.

KEY WORDS: Diel vertical migration, zooplankton, Cordillera de los Andes, Andes lakes, Bolivia, high mountain lakes, *Boeckella titicacae*, *Daphnia pulex*

1. INTRODUCTION

Diel vertical migration (DVM) is a widespread phenomenon in both marine and freshwater zooplankton. DVM patterns differ among species and populations, and may strongly differ with age and sex (De Meester et al. 1999). There is general consensus that the ultimate reason for DVM in many zooplankton populations is the avoidance of visual predators, although other factors may also be involved (Zaret 1976, Lampert 1989, De Meester et al. 1999). Recently, several studies have emphasized that UV radiation may be an important factor determining DVM in high mountain lakes (Ringelberg 1999, Roman and Del Castillo 1999, Leech and Williamson 2001, Sommaruga 2001, Winder et al. 2003). Pigmentation and migration can be considered as two alternative strategies to avoid harmful ultraviolet radiation. Pigmentation offers a good protection against UV light, but it increases visibility and susceptibility to
visual predation. Therefore in lakes with fish, DVM is expected to be the preferred strategy to reduce UV damage (Rhode et al. 2001).

The Cordillera del Tunari is part of the Cordillera Oriental, one of the two important Andean chain mountains in Bolivia (Navarro and Maldonado 2002). There are many lakes of glacial origin scattered over this Cordillera. The high mountain lakes are of moraine origin, and were formed in the Pleistocene during the last retreat of glaciers (Hutchinson 1957). These lakes, which enjoy more or less a constant photoperiod throughout the year, lack ice cover, and have been characterized as cold polymictic (Hutchinson 1957). As the density of the air at an altitude of 4000 m is only 0.6 of that at sea-level, tropical high mountain lakes are subject to a high intensity of direct solar radiation throughout the year. The low humidity in some parts of the Andean range and the generally lower stratospheric ozone concentration in the tropics add to the intensity of solar radiation (Löffler 1961). As a consequence, highly pigmented organisms often dominate in Andean lakes. Unlike Lake Titiaca and neighbouring lakes in the region of Puna that harbour endemic species and subspecies of Orestias (Pices, Microcyprini), the Tunari lakes were originally fishless. Since 1940, however, most of them have been stocked with rainbow trout (Oncorhynchus mykiss (Walbaum 1792)) (Navarro and Maldonado 2002). Introduction of rainbow trout is likely to change profoundly the structure and functioning of mountain lakes (Modenutti et al. 1998). Studies on the effect of fish on zooplankton in Andean lakes in Perú revealed a great variability in zooplankton species composition that have been related to differences in fish assemblage (Hurlbert et al. 1986). Stomach analysis of trout in high mountain lakes in La Paz (Bolivia) showed that early stages of trout feed principally on cladocerans (Hamamitsu and Castañón 1995).

Since at this high altitude the UV radiation seems affect zooplankton species, we expect that if UV is the most important factor, then unpigmented *Daphnia* should migrate in any case even if there are no fish. On the other hand, if fish would be the sole driver factor of DVM, then there should be no migration in fishless lakes.

The aim of this research was to document DVM behaviour of the zooplankton in nine tropical high mountain lakes, some of them currently stocked with trout and some others having been not stocked for a long period of time. We discuss the occurrence of day- and nighttime "deficits", and compare the day and nighttime distribution of the zooplankton both among lakes and among species within lakes, especially among pigmented and non-pigmented ones.

![Map of Bolivia showing the sampled lakes in the “Peruvian Puna Province” of the Cordillera del Tunari during March 2002 (Navarro and Maldonado 2002)](image-url)
2. STUDY AREA

The study area corresponds to the Cordillera del Tunari located in Cochabamba – Bolivia (Fig. 1). Based on geographical, physiographical, and climatic characteristics, the study area belongs to the “Peruvian Puna Province” characterized by a humid climate and seasonal rainfall (Navarro 1999). It includes altitudes belonging to the orotropical belt (4000–4600 m a.s.l.) (Navarro 1999). These lakes are clear, neutral or weakly acid, and mesoligotrophic, containing relatively high concentrations of chlorine, sodium, bicarbonates and silica (Navarro 1999). Wasson and Barriere (1999) characterized the same area as a region of humid mountains, below the glacial region (3400 to 5000 m a.s.l.).

The study was carried out during March 2002 in nine lakes of the Cordillera del Tunari, clustered along two sides of the mountain chain (Fig. 1). In one area, located near the Lake Taquiña basin in the East part, we sampled three lakes: Lake Taquiña, Lake Santa Rosa, and Lake Wara Wara I. The first two of these lakes are interconnected. In the western part of the study area, we sampled six lakes: Lake Azul, Lake Abuela, Lake Wara Wara II, Lake Toro, Lake Saito, and Lake Cuyuntani. Of these, Lake Abuela and Lake Azul are interconnected.

Landscape characteristics and the area of each lake were obtained from a map (1:50000) provided by de IGM (Instituto Geográfico Militar, Bolivia). The geographical location and the altitude of each lake were recorded by GPS. Other characteristics such as depth, secchi disk depth (SD), and macrophyte coverage were recorded during the sampling sessions. Vertical profiles at 1-m depth interval were taken for dissolved oxygen, pH, conductivity and temperature using electrodes. We also established a vertical profile of chlorophyll a concentration. Chlorophyll a was quantified by filtering water of each depth through a Whatman GF/F filter and extracting the photosynthetic pigments with 90% acetone (Nusch 1980). Information on the presence of fish was obtained through personal communication from inhabitants of local villages for Lake Azul, Lake Santa Rosa, Lake Wara Wara I, Lake Wara Wara II, Lake Saito, Lake Cuyuntani, and Lake Toro. In addition, a standardised fishing effort was carried out in March 2003 in two of the study lakes (Lake Taquiña and Lake Abuela). Four-multiple mesh (8–30 mm) gillnets of 120 meter long and 3 meters high were used in each lake during 20 hours (Table 1).

3. METHODS

In each lake, we sampled the zooplankton community at one meter depth intervals both during the day and night. We sampled at the deepest place of the lakes (except Lake Taquiña of which we only sampled the upper 12 m) as determined by a sonic depth finder. At each depth, we took a 30 l sample using a Shindler-Patalas sampler equipped with a 50 μm mesh net. The daytime profiles were all taken between 11:30 and 15:30 hours, whereas the night samples were taken between 20:30 and 23:00. The samples were fixed with formaldehyde (4% final concentration) saturated with sucrose (Handy and Hall 1973) and stored in 50 ml vials. The organisms were counted and identified to level of species using a stereo-microscope (Olympus SZX 12). For identification, we used the keys of Bayly (1992), as well as Smirnov (1996) respectively for copepods and cladocerans.

The vertical distribution of the most abundant species of the zooplankton was visualized by plotting the percentage of the total population sample that was observed at each meter depth. Inspection of the data revealed that in many cases there was a pronounced difference in the total number of animals that were caught during the day and during the night, with the night catches having many more individuals than the daytime samples especially for Daphnia pulex (Table 2). In plotting the data, we therefore added this difference (later called “deficit”) to the number of animals observed in the sample from the deepest layer of the lake (Fig. 3). We performed a paired t-test to test whether the Daphnia daytime “deficit” is significant by using the total number of animals caught during the day and those caught during the night in each lake. We also performed an independent t-test to compare the daytime “deficit”, measured as the ratio of
Table 1. Selected characteristics of the studied lakes. For environmental variables, the mean (SD) values for different depths are given. The period of study was March 2002.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Taquía</th>
<th>Lake Santa Rosa</th>
<th>Lake Wara Wara I</th>
<th>Lake Azul</th>
<th>Lake Abuela</th>
<th>Lake Wara Wara II</th>
<th>Lake Toro</th>
<th>Lake Saito</th>
<th>Lake Cuyuntani</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>17°17'3.1&quot;</td>
<td>17°16'16&quot;</td>
<td>17°17'3&quot;</td>
<td>17°03'0&quot;</td>
<td>17°03'09&quot;</td>
<td>17°06'03&quot;</td>
<td>17°10'5&quot;</td>
<td>17°12'9&quot;</td>
<td>17°13'41&quot;</td>
</tr>
<tr>
<td>Longitude</td>
<td>66°9'5.8&quot;</td>
<td>66°8'43&quot;</td>
<td>66°06'32&quot;</td>
<td>66°32'31&quot;</td>
<td>66°7.734</td>
<td>66°29'38.9&quot;</td>
<td>66°22'42&quot;</td>
<td>66°21'54&quot;</td>
<td>66°23'14&quot;</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>10</td>
<td>4.3</td>
<td>12</td>
<td>10.8</td>
<td>5.08</td>
<td>6.5</td>
<td>4.8</td>
<td>4.1</td>
<td>3.9</td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td>24</td>
<td>5</td>
<td>15</td>
<td>16</td>
<td>6</td>
<td>14</td>
<td>6</td>
<td>6.1</td>
<td>5</td>
</tr>
<tr>
<td>Lake area (ha)</td>
<td>10.25</td>
<td>0.6</td>
<td>20.75</td>
<td>6.12</td>
<td>1.1</td>
<td>18</td>
<td>2.5</td>
<td>5</td>
<td>4.5</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>4090</td>
<td>4363</td>
<td>4000</td>
<td>4513</td>
<td>4545</td>
<td>4310</td>
<td>4412</td>
<td>4327</td>
<td>4423</td>
</tr>
<tr>
<td>Secchi (m)</td>
<td>1.85</td>
<td>3.32</td>
<td>1.55</td>
<td>0.73</td>
<td>0.75</td>
<td>3.48</td>
<td>2.95</td>
<td>1.92</td>
<td>1.52</td>
</tr>
<tr>
<td>Fish stocking history</td>
<td>Once stocked</td>
<td>Once stocked</td>
<td>Regularly stocked</td>
<td>Regularly stocked</td>
<td>Once stocked</td>
<td>No fish in gillnet</td>
<td>Regularly stocked</td>
<td>Regularly stocked</td>
<td>Regularly stocked</td>
</tr>
<tr>
<td>Littoral macrophytes (cover %)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>pH</td>
<td>6.4±0.3</td>
<td>7.9±0.4</td>
<td>7.30±0.3</td>
<td>6.4±0.1</td>
<td>6.4±0.1</td>
<td>6.3±0.2</td>
<td>6.3±0.1</td>
<td>6.8±0.4</td>
<td>6.7±0.1</td>
</tr>
<tr>
<td>T (°C)</td>
<td>11.8±0.5</td>
<td>9.9±0.2</td>
<td>11.7±0.7</td>
<td>10.8±1</td>
<td>8.8±1</td>
<td>11±0.5</td>
<td>11.7±5.3</td>
<td>9.3±0.3</td>
<td>10.5±1.5</td>
</tr>
<tr>
<td>Conductivity (μS cm⁻¹)</td>
<td>19.1±2</td>
<td>22.4±1.4</td>
<td>20.8±0.6</td>
<td>16.3±1.2</td>
<td>30.9±1.3</td>
<td>13.4±07</td>
<td>19.2±5.3</td>
<td>9.7±0.7</td>
<td>14.5±1.3</td>
</tr>
<tr>
<td>Dissolved oxygen (mg l⁻¹)</td>
<td>6.9±0.2</td>
<td>3.6±0.2</td>
<td>6.9±0.3</td>
<td>3.2±0.1</td>
<td>2.6±0.2</td>
<td>4.8±0.1</td>
<td>5.8±0.9</td>
<td>6.5±0.7</td>
<td>4.0±0.2</td>
</tr>
<tr>
<td>Chlorophyll-a (μg l⁻¹)</td>
<td>1.4±1.2</td>
<td>3.6±3.6</td>
<td>3.7±0.6</td>
<td>1.5±1.6</td>
<td>2.2±2</td>
<td>0.7±0.6</td>
<td>0.7±0.2</td>
<td>4.0±0.4</td>
<td>1.5±1.4</td>
</tr>
</tbody>
</table>
The total number of individuals caught during the night on that caught during the day, between lakes with and without fish. All statistical analyses were performed in Statistica version 6.

4. RESULTS

The characteristics of the lakes as measured during the sampling period are detailed in Table 1. The lakes are situated between 4000 and 4545 m a.s.l. The transparency (Secchi disk depth) ranged between 0.73 and 3.48 meters. Only two of the lakes (Lake Toro and Lake Cuyuntani) harboured patches of emergent macrophytes. The mean temperature (March) in the lakes varied from 8.8 to 11.8°C.

The vertical profiles indicate that physical and chemical characteristics of the water were homogeneous throughout the whole water column at the time of sampling, both during the day and the night. Chlorophyll a, however, showed a vertical profile in many lakes. In most lakes, there was a higher chlorophyll a concentration in the upper water layers than at greater depth (Fig. 2).

The lakes of the Taquiña basin (Lake Taquiña and Lake Santa Rosa) have been stocked with trout ones nearly 60 years ago. Therefore is likely that those lakes have very few fish or any at present. This was probed when we didn’t catch fish in the gillnets in Lake Taquiña. The local communities, who regularly stock the lakes, but have no clear registration of these stocking efforts, manage the other lakes.

A significant difference in Daphnia pulex was observed between day and night catches (t-test $P = 0.001$, $n = 8$). The ratio of the number of animals caught during the night to the number of animals caught during the day was $> 1.0$ (positive value in Table 2) in all the lakes in which the species was observed ($n = 8$). The difference was also significant for calanoid copepodies ($P = 0.042$, $n = 8$). For this group, however, more individuals were counted in the samples taken during the day than in those taken during the night (ratio $< 1.0$, $n = 8$) (negative value in Table 2). For the other taxa, no overall significant differences in the number of organisms between

<table>
<thead>
<tr>
<th>Species</th>
<th>Lake Taquiña</th>
<th>Lake Santa Rosa</th>
<th>Lake Wara Wara I*</th>
<th>Lake Azul*</th>
<th>Lake Wara Wara II*</th>
<th>Lake Toro</th>
<th>Lake Saito*</th>
<th>Lake Cuyuntani*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia pulex adults</td>
<td>95</td>
<td>88</td>
<td>95</td>
<td>46</td>
<td>84</td>
<td>98</td>
<td>73</td>
<td>93</td>
</tr>
<tr>
<td>Daphnia pulex juveniles</td>
<td>88</td>
<td>17</td>
<td>95</td>
<td>69</td>
<td>39</td>
<td>88</td>
<td>39</td>
<td>64</td>
</tr>
<tr>
<td>Metacyclops leptopus</td>
<td>91</td>
<td>73</td>
<td>41</td>
<td>16</td>
<td>41</td>
<td>34</td>
<td>34</td>
<td>34</td>
</tr>
<tr>
<td>Keratella cochlearis</td>
<td>–95</td>
<td>13</td>
<td>30</td>
<td>30</td>
<td>53</td>
<td>–53</td>
<td>–53</td>
<td>–53</td>
</tr>
</tbody>
</table>

Table 2. Diurnal differences ("deficits") of the density of individuals for the most abundant zooplankton species in the Andean lakes of Cordillera del Tunari. Period of study March 2002. Positive values indicate day "deficit" (day estimates of total population densities expressed as percentage of the total population during the night). Negative values indicate a night "deficit" (night estimates of total populations densities expressed as percentage of the total population during the day). Empty cells: species not found in the sample. Lakes regularly stocked with fish are marked with asterisk*.
the day and night samples were observed. A number of lakes showed strong and specific patterns. For instance, contrary to the general pattern, many more individuals of *Boeckella titicacae* (Harding 1955) were observed in the night than in the day samples in Lake Saito, Lake Taquiña, and Lake Wara Wara I. There was also a day “deficit” for *Metacyclops leptopus* (Kiefer 1827) in Lake Santa Rosa, Lake Taquiña, and Lake Saito (Table 2).

The vertical distributions of the most abundant species in the different lakes was illustrated on Fig. 3. In this figure, the vertical profiles were corrected for a day- or night-“deficit” by adding the “deficit” to the number of animals observed in the deepest layer. Overall, *Daphnia pulex* shows a strong nocturnal migration, with most adult animals during the day residing in the deepest water layers (Fig. 3A). In most lakes, the animals are rather homogeneously distributed throughout the water column during the night. In Lake Abuela and especially in Lake Wara Wara I, however, the animals are moving to the superficial water layer during the night, and a clearcut migration pattern is resulting.

Fig. 2. Vertical profiles of pH, temperature, dissolved oxygen and conductivity for each lake at the sampling time (March 2002). Filled symbols represent nighttime and empty symbols daytime distributions. Temperature = circles; pH = rhombus; conductivity (μS cm⁻¹) = triangles pointing downward; dissolved oxygen (mg l⁻¹) = squares; chlorophyll a (μm l⁻¹) = triangles pointing upward.
A

**Daphnia pulex**

- Taquini
- Wara Wara I
- Cuyuntani
- Abuela

![Diagram](image)

**Boeckella titicaca**

- Taquini
- Santa Rosa
- Wara Wara I
- Cuyuntani

![Diagram](image)

Fig. 3. Vertical distribution (percentage of total population observed at each depth) for the most abundant zooplankton species in the different study lakes. Period of study March 2002. Filled symbols represent nighttime and empty symbols daytime distributions. A) *Daphnia pulex* circles = juveniles and triangles = adults. B) *Boeckella titicaca* circles = females and triangles = males. C) *Metacyclops leptopus* (all individuals) D) *Keratella cochlearis* (all individuals) E) immature copepods circles = nauplii, triangles = calanoid copepodites and squares = cyclopoid copepodites. The day-night difference in the density ("deficit") added to the last meter is marked by a dashed line rectangle.
Fig. 3 continued

**Metacyclops leptopus**

**Keratella cochlearis**
The migration pattern for *Boeckella titicacae* is more variable, but with a tendency for a reverse migration in several lakes (Fig. 3B). The populations inhabiting Lake Abuela and Lake Cuyuntani are an exception to the general pattern. In most lakes, *Meta-cyclops leptopus* shows a nocturnal migration pattern, with Lake Abuela and Lake Toro being the exceptions (Fig. 3C). In Lake Toro, there is little indication for any migration at all. The most abundant rotifer, *Keratella cochlearis* (Gosse 1851), showed a clearcut reverse migration in several lakes (Fig. 3D). The pattern is most expressed in Lake Wara Wara I, while there is no reverse migration in Lake Cuyuntani, Lake Abuela and Lake Santa Rosa. Copepodites calanoids present a pattern of reverse migration in most of the lakes (Fig. 3E).

5. DISCUSSION

We studied the vertical distribution of zooplankton in nine Andean lakes in the Cordillera del Tunari in Bolivia to obtain an idea of the range in vertical distribution patterns. The lakes are situated at an altitude that is characterized by quite constant climatic factors. The physico-chemical characteristics of the lakes were in general quite similar, not only among lakes, but also throughout the whole column during night and day, corresponding with the characteristics of cold polymictic lakes and consistent to previous observations (Hutchinson 1957, Navarro 1999, Wasson and Barrere 1999). As the physico-chemical variables did not show much variation along the water column of
the different lakes, these variables cannot be used to explain the vertical distribution of the zooplankton. From this perspective, most of zooplankton species could be expected to occur throughout the whole water column. Yet, the different zooplankton species often showed a pronounced vertical distribution and DVM, which often strongly differed among species and, to a somewhat lesser extent, also among lakes. This is also reflected in the strong daytime or nighttime “deficit” in number of individuals observed in some species, especially *Daphnia pulex* and calanoid copepods. DeStasio (1993) has discussed several mechanisms that may explain the occurrence of such a strong daytime “deficit” of individuals. We see three possible mechanisms: better avoidance of the sampler during the day than during the night, diel horizontal migration (with animals hiding in the littoral during the day) and diel vertical migration (with animals hiding just above the bottom during the day). The explanation that the animals avoid the sampling equipment during the day is unlikely because one would expect this behaviour to be stronger in copepods than in cladocerans, as they are faster swimmers than cladocerans (DeStasio 1993). Diel horizontal migration is also unlikely, as the lakes studied do not have a littoral zone with macrophytes, and the ratio of *Daphnia* and *Boeckella* in the community was similar in both pelagic and littoral zones (paired t-test *P* = 0.37 n = 7). We therefore came to the conclusion that the only reasonable mechanism that can explain the daytime “deficit” is the performance of strong diel vertical migration. We assumed that animals stayed so close to the lake bottom sediment that they could not be sampled with the Schindler-Patalas sampler and it causes the daytime “deficit”. The fact that *Daphnia* in lakes without fish still migrates indicates that UV may drive vertical migration, independently of whether fish is present or not. For the lakes with fish, it may be both UV and fish that drive DVM. Strongly pigmented species such as *Boeckella*, did not show a strong DVM behaviour, indicating that UV is the main driving force for DVM for *Daphnia*.

The vertical distribution of *Daphnia pulex* and *Metacyclops leptopus* in another Andean lake called Lake Mynas Kkota (4640 m a.s.l.) shows a density peak at intermediate depth during the daytime, whereas the animals tended to move to more superficial water layers during the night (Román and Del Castillo 1999). Contrary to our observations, females of *Boeckella occidentalis* (Marsh 1921) showed a normal vertical distribution in this lake. Modenutti et al. (1998) had pointed out the vertical distribution of large ciliates in a number of southern Andean lakes in Argentina. They attributed the preference for deeper water layers during the daytime to high levels of irradiation, which is characteristic at large oligotrophic lakes of the higher altitude and with low amounts of dissolved organic carbon.

The presence of predators is known to be a very important factor influencing the vertical distribution of zooplankton. In the Andean lakes studied, the introduced rainbow trout is the only fish species. Whereas some lakes have been stocked regularly, others have been stocked only once, and the success of stocking is not properly documented. We can therefore not make strong statements on the relationship between the presence of fish and DVM of the zooplankton in the studied lakes. The behavioural response of zooplankton to fish depends on many factors such as species composition, population structure and abundance of the predators (Ringelberg 1999, Winder et al. 2003). We observed that *Daphnia pulex* tends to migrate strongly in all lakes, whereas the calanoid copepodes show a reverse migration in most of the lakes. This difference in behaviour can be related to a difference in pigmentation: whereas the copepods are strongly pigmented, the *Daphnia* observed in the study lakes are transparent and not melanic. It has been hypothesized, especially for high altitude lakes, that UVB radiation influences the vertical distribution of zooplankton (Leech and Williamson 2001, Rhode et al. 2001). We expected the zooplankton to be pigmented in lakes without fish and to migrate in lakes with fish. *Boeckella titicacae* has pigments that effectively protect the individuals against UV damage (Helbling et al. 2002), but it is quite visible
to fish and has been observed to disappear from lakes that are heavily stocked with fish (Hurlbert et al. 1986). This may explain why this species is absent in two of the nine lakes studied by us. If so, then its presence in the remaining lakes would indicate that fish densities are moderate to low in these lakes. *Daphnia* is in general more susceptible to fish predation than calanoid copepods, and this would explain why the *Daphnia* are not melanic, and perform diel vertical migration. Whether the *Daphnia* perform DVM to avoid fish or UV-radiation is difficult to say. Most likely, they perform DVM to avoid UV-radiation because they are not melanic, and the latter is caused by the presence of fish. Even if predation risk by fish would be so low that being non-melanic is sufficient as a defence, vulnerability to UV-radiation would still force the *Daphnia* to perform DVM. The reverse migration of *B. titicacae* in some of the lakes can be explained as an avoidance of (interference) competition with *Daphnia* (Winder et al. 2003). The reverse migration of rotifers like *Keratella cochlearis* similarly can be explained as a strategy to avoid competition with larger zooplankton.

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