Cloud cover does not clearly affect the diurnal vertical distribution of crustacean zooplankton in naturally fishless alpine lakes

ROCCO IACOBUZIO & ROCCO TIBERTI

1 DISTA-Dipartimento di Scienze della Terra e dell’Ambiente, Sezione di Zoologia, University of Pavia, Via Adolfo Ferrata 9, I-27100, Pavia, Italy
2 Alpine Wildlife Research Centre, Gran Paradiso National Park, Degioz 11, I-11010 Valsavarenche, Aosta, Italy

Received 27 May 2011; Accepted 27 September 2011

Abstract: The diurnal vertical distribution of zooplankton have been compared on a sunny and on a cloudy day in two shallow, oligotrophic and fishless alpine lakes, exploring the role of cloud cover in shaping zooplankton movements. UV ray avoidance is considered the ultimate reason for zooplankton vertical migration in the lakes, which are naturally devoid of zooplanktivorous fish. Thus, as a thick cloud cover reduces the visible and UV radiation, a shallower diurnal distribution was expected on cloudy days, since migrant zooplankton should balance the amplitude of migration with the light intensity. However, we found very little field evidence that zooplankton change their vertical distribution according to daytime light conditions.

Key words: Alps, diel vertical migration, Gran Paradiso National Park, light intensity, UV rays

Zooplankton Diel Vertical Migration (DVM) is considered as the biggest animal migration, in terms of biomass, on our planet (Hays 2003, Hansson et al. 2007a) and the usual DVM pattern is to spend the daylight hours deep in the water and to rise toward the surface at night (Dodson 1990). The avoidance of visually feeding fish predators is generally suggested to be the ultimate reason for such migrations (Stich & Lampert 1981, Gliwicz 1986, Lampert 1989, 1993, Hansson et al. 2007b), but DVM has also been reported in lakes without predatory fish, suggesting that there is at least another cue that can trigger migration (Williamson et al. 2001, Hansson et al. 2007b); actually DVM is also considered as a behavioral response to DNA damage induced by ultraviolet (UV) rays (Hansson et al. 2007b, Cooke et al. 2008), since depth highly attenuates UV radiation (Losey et al. 1999, Quickenden & Irvin 1980).

Whatever the ultimate cue controlling DVM is in each particular ecosystem, changes in light intensity is the proximate cause (Cohen & Forward 2009, Brönmark & Hansson 2006). Migrant zooplankton should balance the amplitude of migration (the migratory cost) with the light intensity and they are expected to reach greater depths with higher brightness.

We tested this study hypothesis with a non-manipulative approach in two alpine lakes in the Gran Paradiso National Park (south-western Alps, Italy), by comparing the vertical distribution of zooplankton in bright sunlight on a sunny day, and in poor sunlight on a cloudy day, to simulate a treatment with two light levels. The study sites are particularly suitable for studies concerning zooplankton movements since they are naturally affected by high UV irradiance (increasing with altitude and with lower extinction coefficients in oligotrophic waters) (Caldwell et al. 1980, Scully & Lean 1994), they host abundant populations of migrant zooplankton (Tiberti & Barbieri 2011) and they are naturally devoid of fish.

Gran Paradiso National Park includes both the studied lakes belonging to the catchments of rivers Orco and Dora di Savarenche. Losere (in the following, LOS) and Nivolet Superiore (in the following, NIV) are not affected by hydromorphological alterations, they are both above the local tree line and their watersheds belongs to the Alpine belt. Geographical, morphological and watershed data are based on Tiberti et al. (2010) and are reported in Table 1. The lakes are close to each other and their watersheds are covered by the same geological formation, dominated by acidic gneiss (Compagnoni et al. 1974). The geology affects the development of vegetation in the watershed as well as the hydrochemistry of the lakes. The lakes are well protected from acidification processes, with their pH approaching neutral values, they are oligotrophic and ultra-oligotrophic and phosphorus-limited (Tiberti et al. 2010). Zooplankton distribution was observed on a day with complete cloud cover (18 August 2010 in LOS and 7 September 2010 in NIV) and on a sunny day (22 August 2010 in LOS and 28 August 2010 in NIV). The number of days elapsing between the first and second surveys was reduced as much as
possible to avoid large variations induced by the ecological dynamics of the lakes. The sampling protocol includes five interventions and provides for the procedural method and timing of each survey.

Sampling operations started at 12:00 a.m. and were completed at 02:30 p.m. In-air irradiance was measured close to the lakes using a light meter (LI-COR LI-250) with a submersible sensor; measurements were repeated ten times, at an interval of 10 s. Temperature measurements were taken at 1 m depth intervals throughout the water column, close to the deepest point of the lake, marked by a moored floating buoy. A vertical profile of light intensity was measured at the same point using Photosynthetically Active Radiation (PAR, 400–700 nm) throughout the water column, from a few centimeters below the water surface, with measurements repeated three times at each depth, at an interval of 30 s. Then, quantitative zooplankton samples were collected close to the deepest point of the lake. Water samples were collected from the surface to the bottom with a 4.25-L Van Dorn horizontal bottle, sampling at one meter intervals to 10 m and at 2 m intervals at deeper depth. Zooplankton were filtered from this sampled water on the boat using a large funnel connected to a replaceable cylindrical filter with a 48 μm mesh net; once back on shore, the zooplankton was immediately removed from each filter and fixed in 70% ethanol. Finally, land-based irradiance measurements were repeated at the end of the survey.

Each zooplankton sample was analyzed under a binocular dissecting microscope (Olympus CH-BI45-3), following the methods of Edmondson & Winberg (1971). Zooplankton taxa were identified following Dussart (1969), Hardinger & Smith (1974), Braioni & Gelmini (1983), Stella (1984) and Margaritora (1985). Coarse taxonomic levels, indicating a group of species (gr.) have been clumped in the longispina group, whereas Cyclops belonging to the abyssorum group have been classified as Cyclops gr. abyssorum or when the specific identification was not possible because of morphological deformations due to the fixative medium (e.g. Polyarthra belonging to the doliciopeta group have been classified as Polyarthra gr. doliciopeta). All the zooplankton individuals were counted using a closed counting chamber, their lengths were measured using an eye piece micrometer and the developmental stages of copepods were noted.

Light vertical profiles have been fitted with an exponential curve and the vertical extinction coefficients (k) were estimated. Light intensities were log-transformed in order to test whether, between the first and second surveys, there had been significant changes in k with a test for parallelism, comparing the regression lines between log-transformed light intensity and depth on cloudy and sunny days. Moreover, we tested if there were any significant changes in the size distribution of the total crustacean zooplankton community of of the dominant crustacean species between the sunny and cloudy surveys using a t-test. Finally, we tested if there were significant differences in the depth distributions of zooplankton sampled under sunny or cloudy conditions using a two-sample Kolmogorov-Smirnov non-parametric test statistic modified for patchy distributions (W), testing the null hypothesis of equal depth distributions (Solow et al. 2000). Significance of W was determined using a randomization procedure that pooled the two samples into a single sample. The pooled sample was divided at random into two samples for which W was recalculated. This procedure was repeated 1,000 times and the significance level (p-value) was the proportion of simulated values of W that exceeded the observed value (Manly 1997, Solow et al. 2000). All the statistical analyses were performed thanks to the statistical environment of R, version 2.12.1 (R Development Core Team 2010).

A total of 1475 zooplankton specimens belonging to nine taxonomic groups was counted; the zooplankton communities consisted of rotifers ( Keratella quadrata Müller, Notolca squamula Müller, Polyarthra gr. doliciopeta Ehrenberg and Lecane sp.), copepods (Arctodiaptomus alpinus Imhof and Cyclops gr. abyssorum Sars) and cladocerans ( Daphnia gr. longispina Müller, D. middendorffiana Fischer and Chydorus sphaericus Müller). The full range of zooplankton species was attained only in NIV, while LOS hosted only 4 species (K. quadrata, A. alpinus, C. gr. abyssorum and D. gr. longispina). However, in both lakes the dominant crustaceans were A. alpinus, C. gr. abyssorum and D. gr. longispina; these species were found with a suitable number of animals (at least 20 specimens) at each sampling date, with the exception of D. gr. longispina, which was absent at the second sampling in NIV probably because its life cycle completed after the first sampling. Almost all copepods were adult individuals with the exception of a small number of cyclopoid nauplii, representing respectively 3% and 0% of the C. gr. abyssorum populations in the first and second surveys in LOS and 4% and 6% in the first and second surveys in NIV.

On the dates of sampling the in-air irradiances were markedly higher during the sunny survey (range: 1786–1917 μmol s⁻¹ m⁻² in LOS, 1866–2136 μmol s⁻¹ m⁻² in NIV) than during the cloudy one (range: 688–810 μmol s⁻¹ m⁻² in LOS,
211–459 μmol s⁻¹ m⁻² in NIV (Fig. 1) when the cloud cover was persistent and thick, without bright spells. Light intensity varied with cloud cover also at the lake surface and through the water column (Fig. 1) and decreased with depth with a low vertical extinction coefficient \( k \). Between the first and second surveys, \( k \) ranged between 0.195 and 0.208 in LOS and between 0.176 and 0.167 in NIV. No significant change in \( k \) was observed in LOS (\( t = 1.072, p = 0.290 \)), while water transparency increased in NIV (\( t = 2.105, p < 0.05 \)). Neither of the lakes showed any thermal stratification. Temperature gradients were absent or slightly decreasing in both the lakes and the temperature profiles between the first and second surveys were essentially the same, with the surface layers slightly warmer during the survey with sun (Fig. 1). Also the size structure of the crustacean zooplankton community and of each dominant species did not show significant changes between the sunny and cloudy surveys, with the exception of *Cyclops* gr. *abyssorum* in LOS, which was larger during the sunny survey (Table 2). Therefore between the first and second surveys, the lakes had very similar abiotic vertical gradients and zooplankton size distributions and the only parameter that clearly varied was the irradiance in-air and through the water column. Thus we are reasonably confident that the differences in zooplankton depth distributions between the two surveys was largely the re-

---

**Fig. 1.** (a) Box-plot showing median, quartile and extreme values of the Photosynthetically Active Radiation (PAR) irradiance before (B) and after (A) collecting zooplankton; (b) temperature profiles; (c) Photosynthetically Active Radiation profiles; (d) vertical distribution of crustacean zooplankton on a sunny day (solid line) and on a cloudy day (dotted line). All data were collected in two alpine lakes in the Gran Paradiso National Park (western Italian Alps): lake Losere (LOS) and lake Nivolet superiore (NIV). T: temperature; ARCALP: *Arctodiaptomus alpinus*; CYCABY: *Cyclops* gr. *abyssorum*; DAPLON: *Daphnia* gr. *longispina*; prop: proportions of population in each depth bin.
sult of the light levels.

In Table 2 we report the mean values of depth distribution of the crustacean zooplankton and of each dominant crustacean zooplankton species in lakes LOS and NIV, the statistic \( W' \), its significance levels, the mean size of each taxon and the mean light intensities at which each taxon lived. All the taxa, except *Daphnia gr. longispina* in LOS, showed a decrease in their habitat depth in the presence of clouds, which is consistent with the hypothesis. However only for *Arctodiaptomus alpinus* in NIV was this trend significant. On the other hand, zooplankton always lived at higher light intensities on the sunny days and we found very little evidence supporting the hypothesis that migrant zooplankton should balance the amplitude of migration with the light intensity, going shallower during periods of thick cloud cover.

Despite the fact that the light intensity during the sunny survey was much more intense (twice or four times) than during the cloudy survey, our results show that zooplankton does not change its vertical distribution significantly, remaining at the same depth regardless of light exposure or only weakly reacting to daytime light variations. The absence of predatory fish could reduce or cancel the migratory behavior and therefore the need to balance the amplitude of migration with the light intensity. However DVM has been described at least in LOS (Tiberti & Barbieri 2011) and in this lake the vertical migration of *Daphnia gr. longispina* and *Cyclops gr. abyssorum* showed significant, but small, differences between mean depth distribution at midday and midnight (1.4 m for *C. gr. abyssorum* and 2.3 m for *D. gr. longispina*). The small amplitude of vertical migrations in the studied lakes could explain the difficulty to highlight small depth variations in response to daylight intensity.

### Acknowledgments

We thank Achaz von Hardenberg and Bruno Bassano (Gran Paradiso National Park) and Giuseppe Bogliani (University of Pavia) for their support and contributions to the research program. We thank Roberto Sacchi and Andrew R. Solow for their kind help in data analysis, and Cristiana Callieri and Roberto Bertone for lending us the light meter. Logistic support and funding for this research was provided by the Gran Paradiso National Park within the framework of the FP7 ACQWA Project (Assessment of Climatic change and impacts on the Quantity and quality of Water), Grant Agreement No. 212250.

#### References

Braithwaite R (2007) *The puddle-feeding caddis fly (Trichoptera: Rhithrogenidae) of the Salish Sea*. Ecology of Freshwater Systems. Cambridge University Press, Cambridge, 398 pp.

Caldwell MM, Robberecht R, Billings WD (1980) A steep latitudinal gradient of solar ultraviolet-B radiation in the Arctic-Alpine life zone. Ecology 61: 600–611.

Cohen HH, Forward RJB (2009) Zooplankton diel vertical migration: a review of proximate control. Oceanogr Mar Biol Annu Rev 47: 77–110.

Compagnoni R, Elter G, Lombardo B (1974) Eterogenità stratigrafica del complesso degli “Gneiss Minuti” nel massiccio cristallino del Gran Paradiso. Mem Soc Geol It 13: 227–239. (In Italian)

Dussart B (1969) Les copépodes des eaux continentales d’Europe occidentale. Editions N Boubée et Cie, Paris, 292 pp. (in French)

Edmondson WT, Winberg GG (1971) A Manual on methods for the Assessment of Secondary Productivity in Fresh Waters. IBP Handbook No 17. Blackwell Scientific Publications, Oxford, 500 pp.

Gliwicz M (1986) Predation and the evolution of vertical migration in zooplankton. Oxford University Press, New York, 285 pp.

Acknowledgments

We thank Achaz von Hardenberg and Bruno Bassano (Gran Paradiso National Park) and Giuseppe Bogliani (University of Pavia) for their support and contributions to the research program. We thank Roberto Sacchi and Andrew R. Solow for their kind help in data analysis, and Cristiana Callieri and Roberto Bertone for lending us the light meter. Logistic support and funding for this research was provided by the Gran Paradiso National Park within the framework of the FP7 ACQWA Project (Assessment of Climatic change and impacts on the Quantity and quality of Water), Grant Agreement No. 212250.

#### References

Braithwaite R (2007) *The puddle-feeding caddis fly (Trichoptera: Rhithrogenidae) of the Salish Sea*. Ecology of Freshwater Systems. Cambridge University Press, Cambridge, 398 pp.

Caldwell MM, Robberecht R, Billings WD (1980) A steep latitudinal gradient of solar ultraviolet-B radiation in the Arctic-Alpine life zone. Ecology 61: 600–611.

Cohen HH, Forward RJB (2009) Zooplankton diel vertical migration: a review of proximate control. Oceanogr Mar Biol Annu Rev 47: 77–110.

Compagnoni R, Elter G, Lombardo B (1974) Eterogenità stratigrafica del complesso degli “Gneiss Minuti” nel massiccio cristallino del Gran Paradiso. Mem Soc Geol It 13: 227–239. (In Italian)

Cooke SL, Williamson CE, Leech DM, Boeing WJ, Torres L (2008) Effects of temperature and ultraviolet radiation on diel vertical migration of freshwater crustacean zooplankton. Can J Fish Aquat Sci 65: 1144–1152.

Dodson S (1990) Predicting diel vertical migration of zooplankton. Limnol Oceanogr 35: 1195–1200.

Edmondson WT, Winberg GG (1971) A Manual on methods for the Assessment of Secondary Productivity in Fresh Waters. IBP Handbook No 17. Blackwell Scientific Publications, Oxford, 500 pp.

Gliwicz M (1986) Predation and the evolution of vertical migration in zooplankton. Oxford University Press, New York, 285 pp.

**Table 2.** Kolmogorov-Smirnov test for differences in vertical distribution of crustacean zooplankton (Solow et al. 2000) under sunny or cloudy conditions in two alpine lakes from Gran Paradiso National Park (western Italian Alps), \( t \)-test for differences of average body size in zooplankton and average light intensity where the zooplankton live. Cru: crustacean zooplankton; Arc: *Arctodiaptomus alpinus*; Cyc: *Cyclops gr. abyssorum*; Dap: *Daphnia gr. longispina*; LOS: lake Losere; NIV: lake Nivolet superiore; \( W' \): two-sample Kolmogorov-Smirnov test statistic modified for patchy distribution; N: number of counted specimens on each sampling date.

| Taxon | Lake | N      | sunny | cloudy | mean depth (m) | difference (m) | \( W' \) | \( P \)  | mean size (µm) | \( t \) | \( P \)  | mean light intensity (µmol s\(^{-1}\) m\(^{-2}\)) |
|-------|------|--------|-------|--------|----------------|----------------|-------|--------|----------------|-------|--------|---------------------------------------------|
| Cru   | LOS  | 106    | 205   | 6.0    | 5.5            | 0.5            | 0.942 | 0.142 | 1056          | 1042  | 0.462 | 0.644                                      |
| Cru   | NIV  | 197    | 104   | 12.1   | 10.5           | 1.6            | 0.905 | 0.174 | 1295          | 1256  | 0.799 | 0.425                                      |
| Arc   | LOS  | 20     | 48    | 4.8    | 4.4            | 0.4            | 0.503 | 0.868 | 1199          | 1160  | 1.334 | 0.265                                      |
| Arc   | NIV  | 68     | 29    | 12.3   | 10.9           | 1.4            | 1.203 | 0.002 | 1206          | 1226  | 0.500 | 0.619                                      |
| Cyc   | LOS  | 74     | 63    | 5.9    | 5.0            | 0.9            | 0.935 | 0.146 | 1040          | 941   | 2.344 | 0.021                                      |
| Cyc   | NIV  | 91     | 66    | 13.1   | 10.5           | 2.6            | 0.931 | 0.139 | 1413          | 1320  | 1.480 | 1.040                                      |
| Dap   | LOS  | 22     | 94    | 6.0    | 6.5            | −0.5           | 0.805 | 0.350 | 1048          | 1048  | −0.005 | 0.996                                      |

**Clouds and zooplankton vertical distribution**

213
plankton. Nature 320: 746–748.
Hansson LA, Becares E, Fernández-Aláez M, Fernández-Aláez C, Kaire-salo T, Miracle MR, Romo S, Stephen D, Vakkilainen K, van de Bund W, van Donk E, Balayla D, Moss B (2007a) Relaxed circadian rhythm in zooplankton along a latitudinal gradient. Oikos 116: 585–591.
Hansson LA, Hylander S, Sommaruga R (2007b) Escape from UV threats in zooplankton: a cocktail of behavior and protective pigmentation. Ecology 88: 1932–1939.
Harding JP, Smith WA (1974) A Key to the British Freshwater Cyclopid and Calanoid Copepods. Scientific Publications of the Freshwater Biological Association, Ambleside, 53 pp.
Hays G (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiol 503: 163–170.
Lampert W (1989) The adaptive significance of diel vertical migration of zooplankton. Funct Ecol 3: 21–27.
Lampert W (1993) Ultimate cause of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. Ergeb Limnol 39: 79–88.
Losey GS, Cronin TW, Goldsmith TH, Hyde D, Mcfarland WN (1999) The UV visual world of fishes: a review. J Fish Biol 54: 921–943.
Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Second edition. Chapman & Hall, London, 399 pp.
Margaritora F (1985) Fauna d’Italia. Cladocera. Edizioni Calderoni Bologna, Bologna, 399 pp. (in Italian)
Quickenden TI, Irvin JA (1980) The ultraviolet absorption spectrum of liquid water. J Chem Phys 72: 4416–4428.
R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/. (accessed on 22 May 2011)
Scully NM, Lean DRS (1994) The attenuation of ultraviolet radiation in temperate lakes. Erg Limnol 43: 135–144.
Solow AR, Bollens SM, Beet A (2000) Comparing two vertical plankton distributions. Limnol Oceanogr 45: 506–509.
Stella E (1984) Fauna d’Italia. Copepoda: Calanoida (d’acqua dolce). Edizioni Calderoni Bologna, Bologna, 101 pp. (in Italian)
Stich HB, Lampert W (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 293: 396–398.
Tiberti R, Barbieri M (2011) Evidences of zooplankton vertical migration in stocked and never stocked alpine lakes in Gran Paradiso National Park (Italy). Oceanol Hydrobiol Stud 40: 36–42.
Tiberti R, Tartari GA, Marchetto A (2010) Geomorphology and hydrochemistry of 12 Alpine lakes in the Gran Paradiso National Park, Italy. J Limnol 69: 242–256.
Williamson CE, Olson OG, Lott SE, Walker ND, Engstrom DR, Hargreaves BR (2001) Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. Ecology 82: 1748–176.