Surface avoidance by freshwater zooplankton: Field evidence on the role of ultraviolet radiation

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Abstract

The avoidance of surface waters by crustacean zooplankton is a common phenomenon both in marine and freshwaters. The contemporary paradigm interprets such behavior as an antipredator strategy. However, the phenomenon has also been reported in predator-free environments, which suggests that other variables may contribute to this depth-selection behavior. We investigated the possibility that ultraviolet radiation (UVR) could influence the avoidance of surface waters in three interconnected lakes differing in their transparency. Each lake was sampled 17 or 18 times. In the two most transparent lakes, the percentage of the population occurring in the surface layer decreased during spring and summer, but this pattern was not observed in the less transparent lake. Such differences in the patterns of surface-water avoidance were unrelated to the abundance and vertical distribution of the dominant planktivores (early stages of galaxiid fishes) as well as to temperature and food availability. They were inversely related, however, to the average UVR levels within the surface layer. A UV avoidance strategy was predicted for the copepod *Boeckella gracilipes,* on account of its low UV tolerance and lack of photoprotective compounds. Our results support this prediction and strongly suggest that surface avoidance by freshwater Patagonian zooplankton is not just a byproduct benefit of an antipredator behavior but is a direct response to high UVR levels.

Many zooplankton species avoid the upper surface waters of lakes and oceans during daytime. Such a depth-selection behavior may or may not be associated with the more specific pattern of diel vertical migration (DVM). Over the years, a number of different hypotheses have been proposed to explain the deep vertical distribution of zooplankton during the day. Indisputably, the most widely accepted explanation for this phenomenon is the avoidance of visually oriented predators (De Meester et al. 1999). The predator avoidance hypothesis is not only supported by circumstantial field evidence but also, and more importantly, by experimental studies that have shown that fish kairomones enhance (or even trigger) the negative phototaxis of zooplankton (Dodson 1988; De Meester et al. 1999). However, in spite of the importance of predator-induced migration, predation alone does not explain the variety of DVM patterns observed in nature. For example, DVM has been observed in organisms inhabiting fishless systems (Hairston 1980; Williamson et al. 2001).

Ultraviolet radiation (UVR, 280–400 nm) may also pose a risk for zooplankton organisms in the surface waters of transparent aquatic ecosystems (Zagarese and Williamson 2000). Thus, UVR could potentially induce a surface avoidance reaction similar to that documented for visual predators. In fact, the possibility that UVR could be responsible for the deep vertical distribution of zooplankton has long been sug-

Table 1. Optical parameters and PAR and UVR conditions in the surface layer (see the text).

Surface layer lower limit (SLLL) (m)	Morenito		Moreno West		Moreno East	
	2		10		10	
	k_d (m^{-1})	I (%) at SLLL	k_d (m^{-1})	I (%) at SLLL	k_d (m^{-1})	I (%) at SLLL
PAR (400–700 nm)	0.55	33.287	0.21	12.246	0.29	5.500
Blue (at 484 nm)*	0.59	30.605	0.16	20.598	n/a	n/a
Green (at 520 nm)*	0.40	44.933	0.14	24.171	n/a	n/a
Red (>600 nm)	0.53	34.438	0.22	11.080	n/a	n/a
UV at 320 nm	5.50	0.002	0.52	0.552	0.68	0.111

* Data from Pérez et al. (2002).
n/a: data not available.

gested (Huntsman 1924; Klugh 1930), but conclusive experimental evidence (particularly under realistic irradiance conditions) has only recently been produced (Storz and Paul 1998; Leech and Williamson 2001; Rhode et al. 2001). Quite interestingly, Rhode et al. (2001) have recently suggested that UVR could have had an initial role in the evolution of the predator-induced daytime sinking in DVM.

Although there is now experimental evidence available that demonstrates that *Daphnia* can adjust its vertical position in response to UVR (Storz and Paul 1998; Leech and Williamson 2001; Rhode et al. 2001), complementary non-manipulative, whole–lake-scale evidence is still lacking. One of the difficulties of studying the behavioral responses to UVR under field conditions is determining whether a behavior is in response to UVR or visible light (photosynthetically active radiation [PAR], 400–700 nm) (Leech and Johnsen 2003). This is because, within the same environment, UVR and PAR covary in time. Manipulative experiments use artificial filters to break out the correlation between UVR and PAR (Leech and Williamson 2001; Rhode et al. 2001). Similarly, we speculated that a field survey could take advantage of the differences in UVR transparency between lakes to separate the effects of UVR and PAR.

Here, we present the results of a 1-yr survey of a system consisting of three interconnected lakes that differ in UVR and PAR transparency. The three lakes share the same crustacean and fish communities, which simplifies the comparisons between environments. Our objective was to obtain nonmanipulative, whole–lake-scale evidence that could allow us to discriminate between the predator avoidance and the UVR avoidance hypotheses.

Materials and methods

Study area and rationale for the sampling design—The study area is composed of three basins of the lake Moreno complex (45°04′S, 71°31′W, 770 m a.s.l.) within Nahuel Huapi National Park (Patagonia, Argentina), which, in spite of being part of an interconnected system, are customarily referred to as three independent lakes: Moreno West, Moreno East, and Morenito. Moreno West (area: 5.22 km²) and Moreno East (area: 5.42 km²) are deep (z_{mean} > 50 m) oligotrophic lakes, with low levels of dissolved organic carbon (DOC; 0.5–0.7 g m^{-3}) and corresponding high PAR and

UVR transparency (k_{dPAR}: 0.21–0.29 m^{-1}, k_{d320}: 0.52–0.68 m^{-1}). On the other hand, Morenito (area: 0.83 km²) is comparatively shallow ($z_{mean} \sim$ 10 m) and has higher levels of DOC (2.4 g m^{-3}) and lower transparency (k_{dPAR}: 0.55 m^{-1}, k_{d320}: 5.5 m^{-1}) (Hargreaves et al. unpubl. data).

The above differences in transparency allowed us to arbitrarily define two layers within the water column of each lake: surface and deep. The surface layer in lakes Moreno East and West was defined between 0 and 10 m, and the deep layer extended from 10 to 50 m (i.e., from 10 m to z_{mean}). The limit at 10 m for the surface layer was set on the basis of a preliminary summer survey, which suggested that very few zooplankton occurred at noon within the upper 10 m in these highly transparent lakes. In addition, available UVR-tolerance data for two common zooplankton species of Patagonian lakes (*Boeckella gracilipes* and *Ceriodaphnia dubia*) indicated that virtually no UVR damage could be expected below 10 meters (Zagarese et al. 1998; Tartarotti et al. 2000). The lower limit of the surface layer in Morenito (set at 2 m) was defined so that the amount of PAR reaching the bottom of this layer were similar (actually, a little higher, to be conservative) than that at the bottom of the surface layer of Moreno East and West. (Notice that such relationship applies not only to the total amount of PAR but also to each of the main regions within this waveband, i.e., blue, green, and red; Table 1.) However, because of the differential absorption within the UVR range, the amount of UVR in the surface layer of Morenito would be much lower than that in the other two lakes. The deep layer in Morenito extended from 2 to 10 m (i.e., $\sim z_{mean}$). For each waveband (305, 320, 340, and 380 nm and PAR), the average irradiance within the surface layers was computed according to the method of Helbling et al. (1994)

$$I_{mean} = I_0 \times \frac{1 - e^{(-k_d \times z)}}{k_d \times z}$$

where I_0 is the irradiance at the surface, k_d is the diffuse attenuation coefficient (for the corresponding wave band), and z is the lower limit depth of the surface layer (i.e., 2 m in Morenito and 10 m in Moreno East and West).

The rationale for this sampling design was that if PAR was used as a cue to avoid the surface layer, then the organisms from Morenito should avoid the upper 2 m as much as those from Moreno East and West should avoid the upper 10 m.

But if the organisms migrate down in response to UVR (but not PAR), then they would avoid the upper 10 m of Moreno East and West but not the upper 2 m of Morenito (Table 1). Clearly, the success of such a sampling design depends heavily on the proper selection of the surface layer lower limit. Despite the obvious risk of failure (i.e., not detecting differences even when they exist), we favored this sampling design over a traditional vertical profile (i.e., samples taken every *n* m from surface to bottom) on the basis of considerations about sample collection and processing time.

Visual planktivores in Patagonian lakes are mostly restricted to larval and juvenile fish (ichthyoplankton) usually galaxiid fishes *Galaxias maculatus*; *Galaxias platei* (Barriga et al. 2002). As mentioned above, a major advantage of the studied environments is that they share the same crustacean zooplankton and ichthyoplankton assemblages. In addition, one of the dominant species (*B. gracilipes*) is known to be present year around (Balseiro and Modenutti 1990), which made it a convenient choice for investigating its tolerance to UVR during the survey period (see below). Moreover, this species has very limited photorepair capacity (Zagarese et al. 1997) and very low levels of photoprotective compounds (Tartarotti et al. unpubl. data). The latter two characteristics suggested that this species could be a good candidate for displaying a UVR avoidance response.

Sampling and data collection—Solar radiation was continuously recorded with a GUV 511 radiometer (Biospherical Instruments) with four channels for UVR (305, 320, 340, and 380 nm) and PAR (400–700 nm) measurements. This instrument is located at the laboratory of photobiology (Universidad Nacional del Comahue), ~10 km southeast of the sampling sites. Underwater profiles were performed with a submersible version of the radiometer (PUV 500) on several occasions. Each lake was sampled on 17–18 occasions between November 1998 and November 1999. Sampling frequency was every 2–3 weeks in summer and roughly monthly in winter. Sample collection took place as close to 1200 h as possible (always between 1100 and 1500 h). For this reason, it was not possible to sample the three lakes on the same day; instead, we sampled two lakes one week and the remaining lake the next week. Variables included (1) temperature profile every 1 m in Morenito and every 5 m in Moreno East and West, (2) zooplankton vertical tows in two strata (surface and deep layers, as defined above), and (3) ichthyoplankton horizontal tows at discrete depths.

Zooplankton were sampled with a 25-cm diameter Wisconsin-type closing net (54 μm mesh). Samples were then preserved in 4% formalin and counted in 5-ml Bogorov chambers under a dissecting scope. Ichthyoplankton were collected using two conical nets of different size, to cover a wider range of fish larvae size. The smallest net was 32 cm diameter × 105 cm length, 270 μm mesh, and the largest was 50 cm diameter × 260 cm length, 1,500 μm mesh. Sampling depth could be adjusted by using a 5-kg depressor and varying the length of the towing line. To maintain the sampling depth constant, the towing angle was continually monitored and adjusted as required. Sampling depths were 0, 3, and 5 m in Morenito and 0, 3, 5, 7.5, and 20 m in Moreno East and West. The sampling order was from the

surface to the bottom using the first net and from the bottom to the surface using the second net (the order of nets was arbitrary). For each depth-net combination, horizontal tows were done at a constant speed of ~0.65 m s⁻¹ for 2 min in Morenito and for 5 min in Moreno East and West, which represents distances of ~80 and ~200 m, respectively. Trawls were done along a straight line in a deep limnetic area of each lake. Each depth-net combination was sampled along consecutive segments of that line, to avoid sampling on an already disturbed area.

Tolerance to UV-B radiation—A standardized protocol (Zagarese et al. 1997) was used to assess the tolerance to UVB radiation of zooplankton during the study period. *B. gracilipes* was chosen for this assessment because it was the only species that could be assumed a priori to occur year around. All experiments were run in an incubator at 15°C. Each experimental unit consisted of 30 adult individuals placed in a 55-mm Pyrex Petri dish filled with 15 ml of filtered (0.2 μm) water. The Petri dishes were placed on a built-in, clear acrylic turntable rotating at 1 r.p.m. A Spectroline XX15-B fluorescent lamp (Spectronics) provided the source of UV-B radiation (280–315 nm). The lamp was covered with a new sheet of cellulose diacetate, to remove wavelengths shorter than ~295 nm (*see* Zagarese et al. 1997 for lamp output spectra). The duration of the UV-B exposure was 4 h in all experiments. Differing UV-B intensities (0, 0.1, 0.29, 0.39, and 0.48 J cm⁻²) were obtained by covering the individual Petri dishes with a variable number of layers of plastic window screen.

Dark experiments—The objective of these experiments was to assess the tolerance of the three *B. gracilipes* populations (i.e., from the three lakes) in the absence of recovery radiation (i.e., no photorepair). After exposure to UV-B radiation for 4 h, the animals remained in the dark for 20 additional h and then were moved inside a second incubator with a 14:10 light:dark cycle for an additional 24-h period.

Photorepair experiments—The objective of the photorepair experiments was to assess the potential for photoreactivation of the three populations of *B. gracilipes*. The experimental setup was similar to that of the experiments in the dark, except that the copepods received UV-B and PAR simultaneously for 4 h. After UV-B exposure, the animals continued receiving PAR for at least 10 more h. The following 24-h period was identical to that of the dark experiments. The number of dead individuals was recorded at the end of each experiment. The dose modification factor was calculated for each experiment as the quotient between the LD₅₀ (i.e., the UV-B dose at which 50% of individuals died) obtained in the presence and absence of recovery radiation, respectively. The LD₅₀ values were calculated by linear regression of logit-transformed mortality rates versus UVB dose.

Results

Moreno East and West showed stable temperature stratification during summer, with thermoclines at ~35 and 30 m,
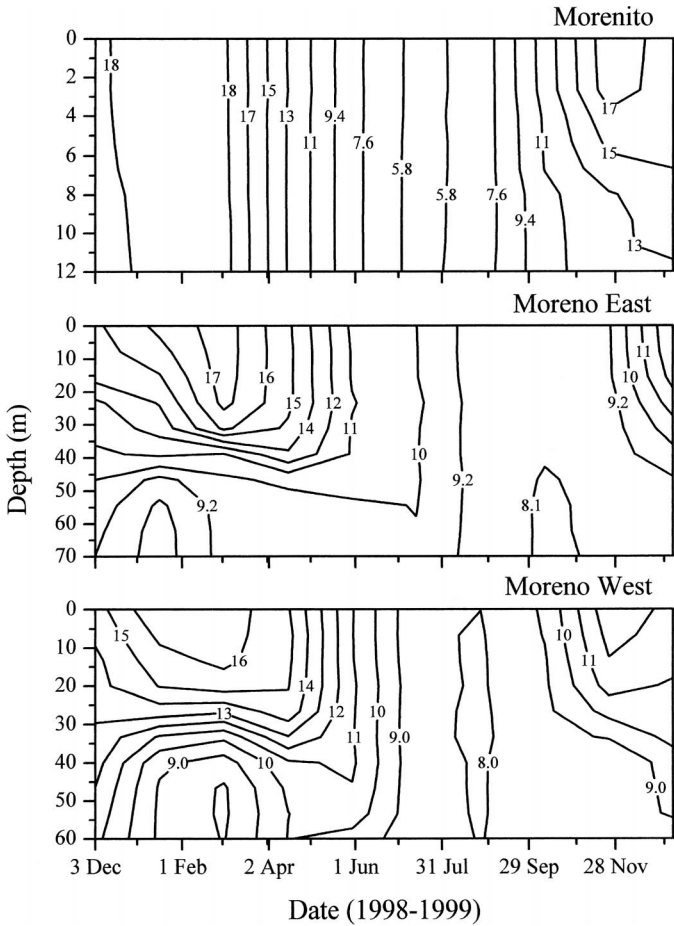
Fig. 1.   Thermal profiles (°C) of the three lakes during the annual study period.

respectively. In contrast, Morenito usually did not exhibit such thermal stratification (Fig. 1).

The composition of crustacean zooplankton was similar in the three lakes and included the cladocerans *C. dubia, B. chilensis, B. longirostris, Daphnia* sp. and *Diaphanosoma* sp., the calanoid copepod *B. gracilipes,* and an unidentified cyclopoid copepod. The discussion of the results is limited to the three most abundant species that were present during the whole period of study (*B. gracilipes, C. dubia,* and *Bosmina* spp.), because the remaining species appeared only sporadically and at low densities. Abundance (on a volume basis) was much higher in Morenito than in Moreno East and West (Table 2).

In Moreno East and West, the percentage of occupancy of the surface layer (upper 10 m) was minimal during spring

and summer and increased gradually during fall and winter (Fig. 2), resembling a sinusoidal shape (particularly for *B. gracilipes* and *C. dubia*). More rigorously, the degree of occupancy of the surface layer was significantly lower during the high radiation season (i.e., between 21 September and 20 March) than during the low radiation season (i.e., 21 March to 20 September) for the three species in Moreno East and for *B. gracilipes* and *C. dubia* (but not *Bosmina longirostris + B. chilensis*) in Moreno West (Table 3). In contrast, in Morenito, the occupancy percentage of the surface layer (upper 2 m) did not show any obvious seasonal trend and tended to be higher than in the other two lakes during spring and summer (Table 3 and Fig. 2).

The plots of the percentage of occupancy of the surface layers versus the average radiation (i.e., I_{mean}) within the strata do not show any trend when the radiation band was PAR (Fig. 3). However, when considering the same data but plotted against the average radiation at 305 nm, a definite trend became apparent: most data points plotted below the imaginary diagonal that divides the graph into a lower left and upper right triangle. In other words, at low levels of UVR, the percentage of occupancy appeared to be variable, but, as radiation increased, the percentage of occupancy seemed to be restricted to progressively lower values (Fig. 3). In addition, we used stepwise multiple regression analysis to develop linear models of occupancy percentage versus average radiation in the surface layer. The best models always included one or two radiation bands within the UVR range but left out PAR. The models were *B. gracilipes* (adults and copepodites): predictor variable UV_{305nm}, $r^2 = 0.186$, $P = 0.008$; *Bosmina* spp. predictor variables UV_{305nm} and UV_{380nm}, $r^2 = 0.425$, $P = 0.001$; *C. dubia:* predictor variable UV_{380nm}, $r^2 = 0.456$, $P = 0.001$. Moreover, forcing the inclusion of PAR into the multiple regression model never resulted in a significant increase of the explained variance for any zooplankton species.

B. gracilipes individuals from Morenito consistently showed higher tolerance to UVB exposure than those from either Moreno East or Moreno West (Fig. 4; analysis of variance [ANOVA], Bonferoni test $P < 0.001$). The simultaneous exposure to PAR during UVB exposure resulted in a significant increase in survival (ANOVA, $P < 0.001$) for copepods from the three lakes. But the dose modification factor was low (between 1.35 and 1.49) compared with species that have a strong photorecovery capacity (DMF ∼ 4–14) (Siebeck and Böhm 1991; Rocco et al. 2002).

Ichthyoplankton abundance varied seasonally in the three studied lakes, showing a noticeable maxima during spring and early summer (Fig. 5). During the period of maximal abundance, there were important differences among lakes. In Morenito, the catches were >10 ind. min^{-1} on several oc-

Table 2. Summary statistics on the abundance of zooplankton (individuals m[-3]) in the three lakes during the study period.

Species	Morenito					Moreno West					Moreno East				
	Mean	SD	SE	Min	Max	Mean	SD	SE	Min	Max	Mean	SD	SE	Min	Max
B. gracilipes	3,012	5,848	1,418	27	19,776	136	125	29	6	434	111	95	22	0	352
Bosmina (longirostris + chilensis)	8,755	9,033	2,191	401	35,844	79	222	52	0	946	74	117	28	0	471
Ceriodaphnia dubia	1,002	2,437	591	0	9,466	85	108	26	1	399	25	22	5	0	77

max = maximum, min = minimum.

Table 3. Kruskal-Wallis comparisons on the proportion of the population occurring in the surface layer between samples collected during spring–summer (21 September–20 March) and fall–winter (21 March–20 September).

Species	Morenito		Moreno West		Moreno East	
	n	*P*	*n*	*P*	*n*	*P*
B. gracilipes	17	0.435	17	0.015*	17	0.019*
Bosmina (*longirostris + chilensis*)	17	1	14	0.847	16	0.015*
Ceriodaphnia dubia	17	0.916	16	0.001*	17	0.003*

* Statistically significant.

casions, whereas they never exceeded 5 ind. min⁻¹ in Moreno East or 1 ind. min⁻¹ in Moreno West. Even more important from the perspective of the present study is the fact that the maximum density of juvenile fish occurred well below our definition of the surface layer (i.e., 2 m in Morenito and 10 m in Moreno East and West), particularly during spring and summer (Fig. 5).

Discussion

Seasonal trends in surface layer occupancy (or avoidance)—For the two most transparent lakes, the results show a clear seasonal pattern in the percentage of surface layer occupancy by the crustacean zooplankton. The occupancy was lower during spring-summer (high radiation season) than

during fall-winter (low radiation season). The species displaying this pattern were Moreno East: *B. gracilipes, C. dubia,* and *B. longirostris + B. chilensis* and Moreno West: *B. gracilipes* and *C. dubia.* Such results confirm that our simplified sampling design was able to capture a critical aspect of zooplankton ecology—namely, the avoidance of the surface waters during the day—and agree with our preliminary observations of the scarcity of individuals in the upper layer of deep, transparent Patagonian lakes during summertime. In contrast, in the less transparent Morenito, we did not observe a systematic change in the degree of occupancy of the surface layer. More specifically, the proportion of individuals occu-
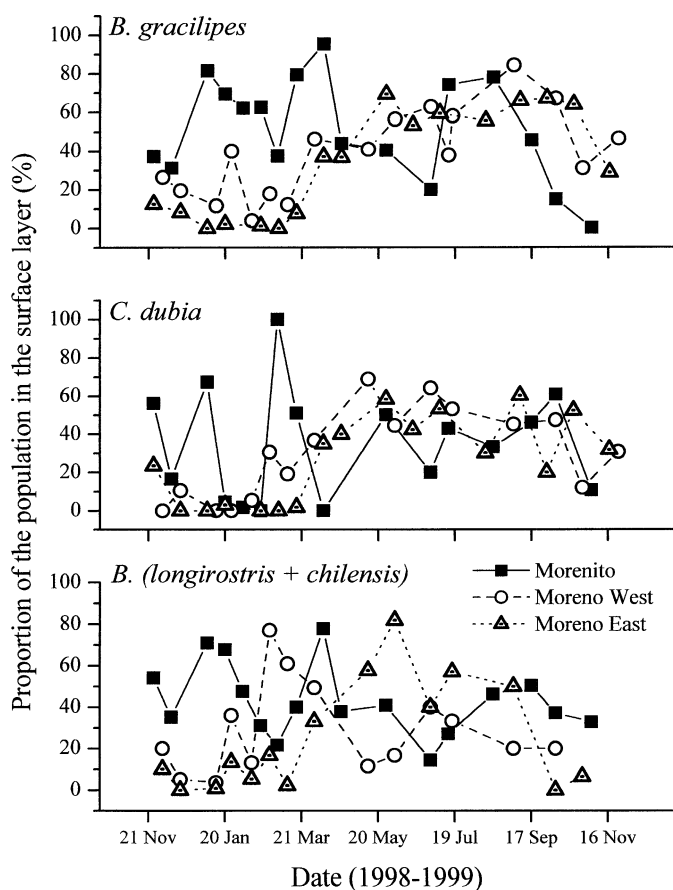

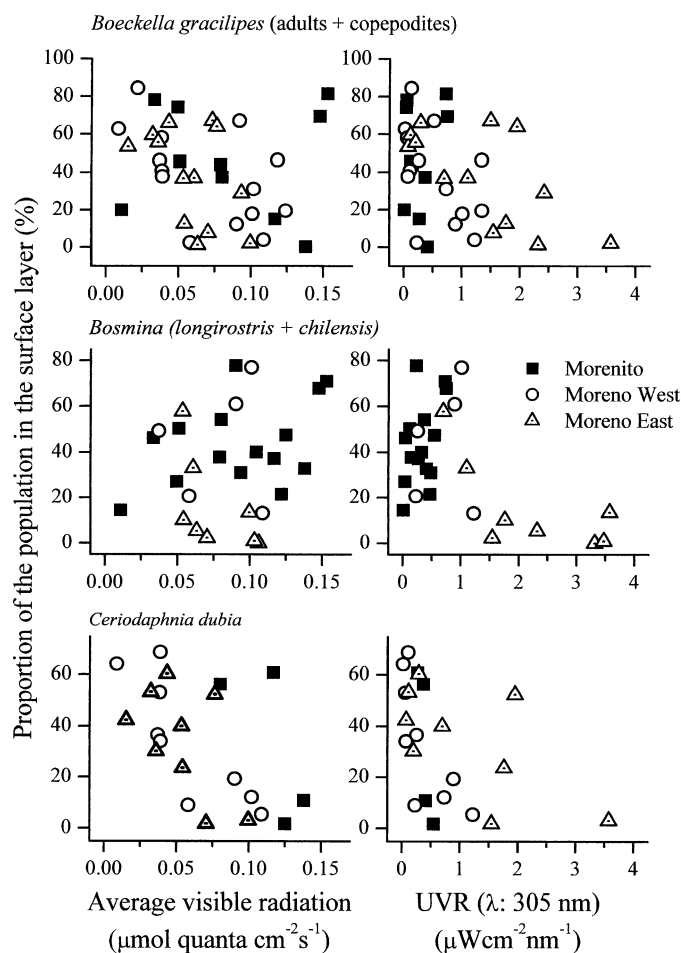Fig. 2. Percentage of occupancy of the surface layer (see text) during the study period.

Fig. 3. Percentage of occupancy of the surface layer (same data as in Fig. 2), plotted against the average level of PAR within the stratum (left) or the average level of UVR (right).
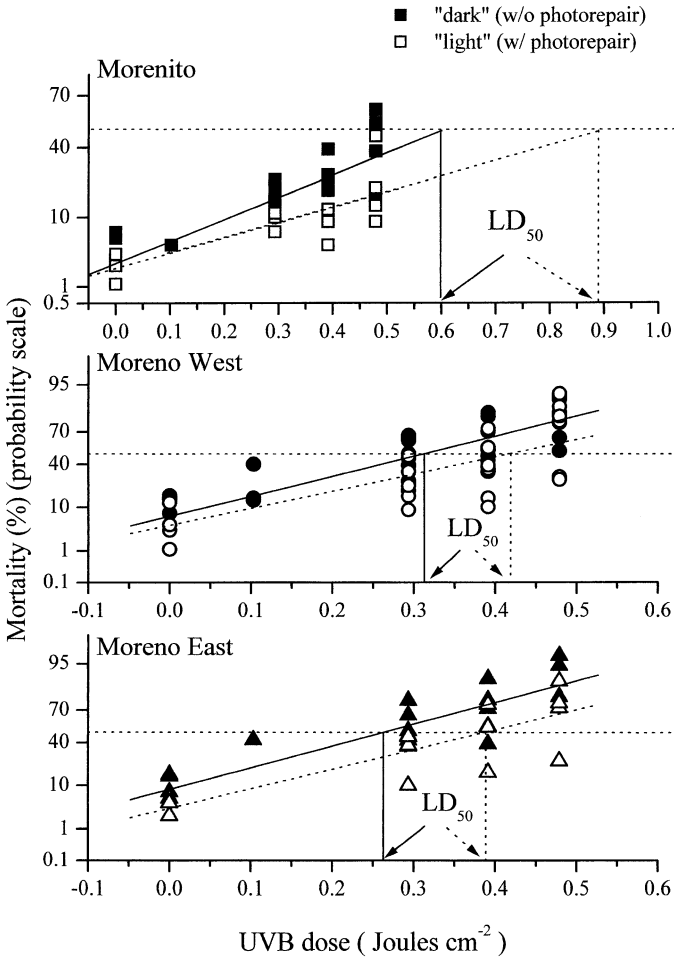
Fig. 4. Tolerance of *B. gracilipes* to artificial UVB radiation. Filled symbols: UVB exposure in the absence of recovery radiation (i.e., PAR), open symbols: UVB exposure in the presence of PAR. For each species, the results of at least four independent test conducted in different seasons were pooled. The lines correspond to a linear fit of logit-transformed mortality rates vs. UVB dose. Arrows indicate the LD_{50} value.

Fig. 5. Fish larvae relative abundance (CPEU) at different depth during the study period.

pying the surface layer did not significantly differ between high (spring-summer) and low (fall-winter) radiation seasons. Collectively, these results suggest that the individuals from Moreno East and West avoid the surface layer during the period of higher solar irradiance by adjusting their vertical position at a deeper depth. On the other hand, the individuals from the less transparent Morenito did not avoid the similar (but always slightly higher) PAR levels present in the upper 2 m of the water column. It seems apparent that PAR alone is insufficient to explain the disparities in the responses between lakes. We will briefly examine alternative environmental factors that could contribute to explain the different responses observed under similar PAR levels.

Temperature—The thermal patterns displayed by the lakes were different. Moreno East and West exhibited a typical warm monomictic regime, with thermal stratification during spring and summer. In contrast, Morenito did not show stable stratification. Thus, on most sampling dates, the
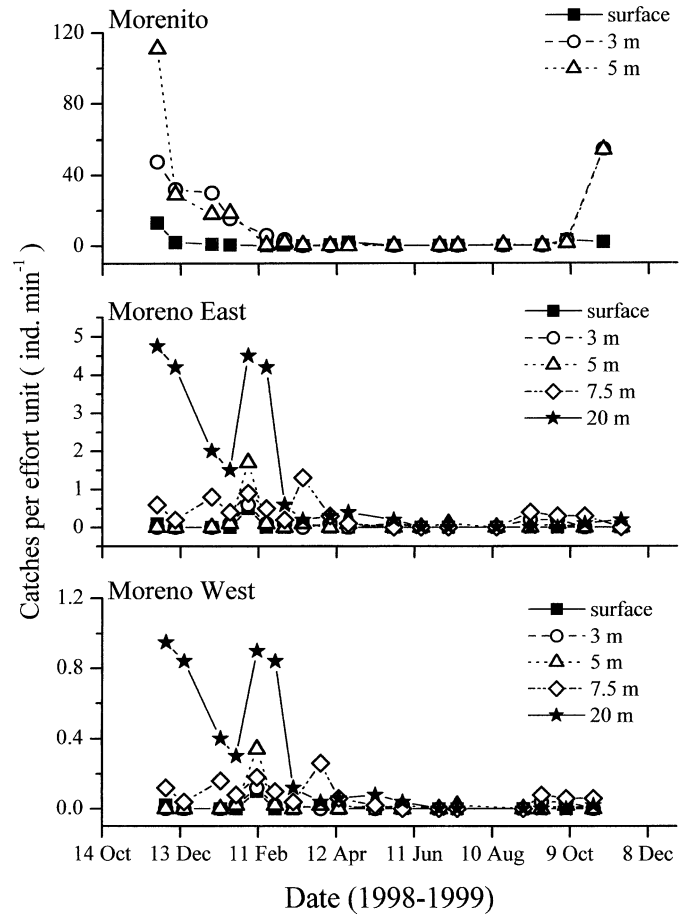
temperature in Morenito was homogenously distributed through the water column. Such thermal patterns have been previously documented for this set of lakes (Quirós and Drago 1985; Pérez et al. 2002) and result from geographic location (latitude) and lake morphology. However, such differences in thermal regime cannot contribute to an explanation of the differences in vertical distributions. Temperature should not have prevented migration into deep water in Morenito because it was homogeneously distributed through the water column during most of the time. The same would be true for Moreno East and West, as long as migrations were restricted to the epilimnion. However, from bioenergetic considerations, it would presumably have tended to reduce the vertical displacement beyond the thermocline (Dawidowicz and Loose 1992). Thus, the temperature gradients observed, particularly during summertime, should not have had an effect on vertical displacements or should have acted in opposition to the observed patterns.

Fish predation—The main visual planktivores in the group of studied lakes are larval stages of galaxiid fishes (*G. maculatus* and *G. platei*). Ichthyoplankton abundance showed a distinct seasonal pattern with maximum in spring and early summer. This kind of seasonal pattern in planktivorous fish abundance is often assumed to induce the vertical migration of crustacean zooplankton into deep waters (De

Meester et al. 1999). However, in the present study, two important pieces of evidence do not provide support to the predator avoidance hypothesis. First, ichthyoplankton density (and, in fact, the overall fish density; Battini pers. obs.) was much higher in Morenito. However, the degree of occupancy of the surface layer did not vary seasonally and, in fact, tended to be higher than in the other two lakes. It is interesting to note that, according to our surface layer definition (see ''Materials and methods''), the overall levels of PAR, as well as the amount of red, green, and blue light, were actually higher in Morenito than in Moreno East and West. Second, the vertical distribution of ichthyoplankton in the three lakes is clearly in conflict with the visual predation avoidance hypothesis, because the highest catches always occurred below what we defined to be the surface layers. In other words, surface avoidance by zooplankton would tend to increase (instead of decrease) the overlap between prey and predators.

Food availability—Although we have not explicitly included a phytoplankton component in our survey, the study by Balseiro et al. (2001) on the vertical distribution of phytoplankton in Moreno West overlapped our study period during summertime (November 1998 to April 1999). In Moreno West, they found a deep chlorophyll maximum at ~30 m. This maximum was mainly due to the distribution of the symbiotic alga bearing ciliate, *Ophrydium naumanni,* which accounted for most of the chlorophyll present at the deep maximum. Such association between the symbiotic *Chlorella* and the ciliate has been previously reported in Moreno West (Queimaliños et al. 1999), which suggests a repeatable event during daytime in summer. However, this ciliate (equivalent spherical diameter: 53 μm) is too large to be eaten by *B. gracilipes,* whose diet include particles up to ~33 μm (Balseiro et al. 2001). On the other hand, the vertical distribution of potential food particles (particularly the nanoplanktonic fraction) was more or less homogeneously distributed from surface to 50 m (Balseiro et al. 2001). Thus, the available evidence, although partial, does not support the idea that avoidance of the surface layer by *B. gracilipes* in Moreno West is related to the vertical distribution of food items.

UVR—We believe that the data presented in Fig. 3 (as well as the multiple regression analyses) provides crucial support to the UVR avoidance hypothesis. By combining lakes that differed in the concentration of DOC, we were able to distinguish the effects of PAR and UVR on the degree of occupancy of the surface layer. When considering the data from the three lakes together, there is no relationship between the percentage of occupancy in the surface layer and the average level of PAR within that same stratum. However, when the same data are plotted against UVR, the pattern that emerges is one in which there is very low occupancy of the surface layer at high UV levels. In other words, at times of high UV irradiance, the zooplankton appear to avoid the surface stratum. This strongly suggests some sort of boundary condition imposed by the levels of UVR.

Although the radiation waveband that produced the best statistically fit corresponded to 305 nm, we do not claim that the organisms respond to this specific wavelength. Moreover, the actual perceptual mechanism that elicits the observed avoidance patterns in the species included in our study remains unknown. Many aquatic organisms have extended vision into the UV range (Leech and Johnsen 2003), but very few, if any, have visual receptors below ~350 nm. However, UV vision is not necessarily the only possible mechanism by which an organism can perceive that is being exposed to UVR. As has already been mentioned, UVR and PAR covary within the same environment. Thus, populations adapted to their environment could use longer wavelengths of UVA or even wavelengths within the PAR region as proxy signals for the more damaging, shorter wavelengths within the UVA and UVB. In addition, it is also conceivable that the propioception of early tissue damage may elicit an unspecific avoidance reaction from the damaging source, as has recently been suggested for rainbow trout (Alemanni et al. 2003).

Physiological and behavioral responses to PAR and UVR—The results from the UVR tolerance test consistently showed significantly higher UV tolerance in *B. gracilipes* individuals from the less transparent but shallower Morenito. UV tolerance has been shown to increase as an adaptation to elevated UV exposure (Stutzman 1999). Of interest, the assumption that this higher tolerance is an adaptation to higher exposure to UVR would lead us to the counterintuitive conclusion that the copepods from the less transparent Morenito are the most exposed to UVR. Moreover, the differential patterns of surface occupancy between the three lakes appear to provide additional support for this previous statement. Considering these arguments, we suggest that UVR avoidance by vertical displacement may be more efficiently achieved in deep, stratified lakes than in shallow, continuously mixed ones. Of course, such a conclusion remains to be tested, and we acknowledge the fact that other factors, such as a better nutritional status, may contribute to UVR tolerance (Zellmer 1996).

Planktonic organisms have evolved three basic mechanisms to counteract the risk of UVR exposure: avoidance (e.g., deep distribution), photoprotection (e.g., the presence of sunscreen compounds and antioxidant mechanisms), and photorepair (e.g., enzymatic DNA repair systems) (Zagarese and Williamson 1994). *B. gracilipes* has been reported to have a very limited capacity for photorepair (Zagarese et al. 1997), and our results confirm this. On the other hand, the individuals of *B. gracilipes* from these lakes have very low levels of photoprotective compounds (i.e., mycosporine-like amino acids) (Tartarotti and Zagarese unpubl. data). For these reasons, it has been already suggested that this species must relay almost exclusively on the avoidance strategy (i.e., deep vertical distribution) as the sole mechanism to counteract summer UVR levels (Zagarese et al. 1997). However, it was not clear whether the deep vertical distribution that protects *B. gracilipes* from UV damage in highly transparent lakes was a direct response to UV levels or was elicited by the presence of visual hunting predators, such as ichthyoplankton, and only indirectly resulted in UV protection. In other words, was the deep vertical distribution a direct response to UVR or just a byproduct of a predator avoidance behavior, such as has been speculated for *Daphnia* from

North American lakes (Zagarese et al. 1994)? On the grounds of the present results, we are inclined to believe that the zooplankton form deep and transparent lakes in Patagonia avoid the upper portion of the water column in response to high UVR levels.

A few experimental studies have recently demonstrated that *Daphnia* can adjust its vertical position in a water column in response to UVR (Hessen 1994; Storz and Paul 1998; Leech and Williamson 2001; Rhode et al. 2001). However, to our knowledge, this is the first field evidence of such behavior observed at the whole-lake scale. If one considers that early stages of fish, including the embryos of one of the dominant ichthyoplankton species, *G. maculatus,* are highly sensitive to UVR (Battini et al. 2000; Zagarese and Williamson 2001), then the picture that emerges is that not only the crustacean zooplankton but also their potential predators are excluded from surface layer of the most transparent lakes because of the risk of UV damage.

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