Internat. Rev. Hydrobiol.	**86**	2001	2	147–163

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The Effects of Ultraviolet Radiation and Nutrient Additions on Periphyton Biomass and Composition in a Sub-Alpine Lake (Castle Lake, USA)

key words: Periphyton, nutrients, UV radiation, lakes

Abstract

Rising levels of ultraviolet radiation (UVR) striking the Earth's surface have led to numerous studies assessing its inhibitory effects on phytoplankton and periphyton in aquatic systems. Mineral nutrients such as nitrogen (N) and phosphorus (P) have been shown to increase aspects of algal metabolism and compensate for UVR inhibition. An *in situ* substratum enrichment technique and UV shielding was used to assess the effects of nutrient additions on periphyton exposed to different levels of UVR in Castle Lake, California during July-August, 1997. UV shielding had no effect on total periphyton biomass, but caused shifts in species composition. The dominant periphyton species, *Anabaena circinalis* RAB., demonstrated sensitivity to ambient levels of UV radiation possibly due to UV inhibition of N_2-fixation. Total diatom biovolume decreased when shielded from UVR. Phosphorus additions continually elicited an increase in periphyton biovolume at all levels of analysis. These results suggest an interaction between nutrient status/availability and UV sensitivity.

1. Introduction

The anthropogenic depletion of stratospheric ozone has led to an increase in the amount of ultraviolet radiation (UVR) that strikes the Earth's surface, although the consequences of current UV radiation on biota is largely unknown (CALKINS and THORDARDOTTIR, 1980; CRUTZEN, 1992; CULLEN *et al.*, 1992; SMITH et al., 1992). Observed increases in ultraviolet-B (UV-B; 290–320 nm) radiation in high-latitude regions have raised further concern about the responses of northern lakes to climate change (VINEBROOKE and LEAVITT, 1996; 1999). High elevation lakes are characteristically highly transparent, oligotrophic ecosystems in which nutrient supply limits productivity (VINCENT and PIENITZ, 1996), and where UV radiation can affect a large portion of biota (VINEBROOKE and LEAVITT, 1999). UV-B exposure can affect a large number of algal metabolic processes, including primary production (BEARDALL *et al.*, 1997; LESSER *et al.*, 1994; MASKE, 1984), nitrogen uptake (e.g., BEHRENFELD *et al.*, 1995), and cell division (e.g., BOTHWELL *et al.*, 1993), and may indirectly affect community structure by altering species interactions such as competition and predation (BOTHWELL *et al.*, 1994; VINEBROOKE and LEAVITT, 1996).

Periphyton assemblages may be especially sensitive to UV radiation (BOTHWELL *et al.*, 1993; VINEBROOKE and LEAVITT, 1996). Epilithic (attached) periphyton are composed pri-

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marily of immobile species that cannot reposition themselves in response to changes in light unlike phytoplankton, which can undergo vertical migration (VINEBROOKE and LEAVITT, 1996). Interestingly, recent evidence suggests that epipelic (sediment-dwelling) periphyton have the potential to avoid harmful doses of UV radiation by migrating into the sediment and may be less sensitive to exposure (MALTAIS and VINCENT, 1997; VINEBROOKE and LEAVITT, 1999). In shallow, clear lakes, where light can penetrate deeply into the water column, periphyton production can make a substantial contribution to the total production observed in the primary trophic level, which is critical to the ecology and food webs of these lake systems (WETZEL, 1983; LOWE, 1996). Therefore, algal response to UVR stress may have consequences that apply to entire ecosystems.

Previous studies suggest that algal sensitivity to UV radiation may be influenced by their nutritional status. Nitrogen and phosphorus have been shown to stimulate periphyton growth in lakes under natural conditions (e.g. CARRICK and LOWE, 1988), and enrichment with these nutrients may minimize the harmful effects of UV radiation. BEHRENFELD *et al.* (1995) demonstrates that both ammonia and nitrate uptake can be reduced by solar UV-B radiation by more than 50% in oceanic phytoplankton assemblages. Conditions in which usable nitrogen occurs in comparatively low quantities to phosphorus produce algal cells that contain less protein, free amino acids, and chlorophyll (RHEE, 1978; BOTHWELL *et al.,* 1993). The absence of these components, all of which are major absorbers of UVR in cells, increases the risk of nuclear DNA damage, and may aggravate the effects of UV exposure (BOTHWELL *et al.*, 1993). In an enclosure experiment, BERGERON and VINCENT (1997) showed that separate treatments of phosphorus enrichment and UV exposure both altered phytoplankton community structure by changing the relative abundance of different species, implying possible interactions between UV exposure and nutrient enrichment.

Although the ultimate concern for increased ultraviolet radiation lies in how UV affects whole communities and ecosystems, the majority of the research on algal response to UVR has focused on species-level responses. Studies such as HILL *et al.* (1997) that found no community-level response to ambient UV manipulations suggest that this is a legitimate approach as well as demonstrate the variability of algal response to UVR. In ecosystems that are exposed to high levels of UVR, selection pressure for UVR-tolerant algal taxa may make shifts in species composition more common than dramatic changes in community and ecosystem processes (WILLIAMSON, 1995). Thus, to understand algal response to UVR, the cumulative and interactive response of algal assemblages must be examined. In the present study, we performed an *in situ* bioassay using point-source nutrient additions and UVR-attenuating filters to evaluate the effects of nutrient additions on periphyton biomass and composition exposed to different levels of UVR at the community, division, and species level in Castle Lake, California.

2. Materials and Methods

2.1. Study Site

Castle Lake is a relatively small (surface area = 0.2 km^2), meso-oligotrophic body of water that lies in a granitic cirque basin in the Klamath mountains of northern California (Figure 1a; Table 1). The basin (maximum depth 34 m) occupies approximately 2/3 of the surface area of the lake, while the remaining 1/3 is compromised of a shallow littoral shelf <5m in depth. The lake has an elevation of 1706 m, and is very transparent during the ice-free season (May – November; AXLER and REUTER, 1996).

Previous assays have indicated that the phytoplankton community may be limited by the availability of N (GOLDMAN, 1960; AXLER *et al.*, 1980; 1982). The primary nitrogen inputs to the lake occur in the form of snowmelt and precipitation in spring. Mixing and turbulent diffusion of N from the sedi-

Table 1. Environmental conditions in Castle Lake during the July-August, 1997 period. PAR, SRP and CHL refer to photosynthetically active radiation, soluble reactive phosphorus, and chlorophyll, respectively.

Parameter	Units	n	Mean ± 1 SD
Physical			
Max. Incident PAR	$\mu E/m^2/s$	12	1936.4 ± 49.0
Max. Incident UV-A	mW/cm^2	12	5.07 ± 0.45
Max. Incident UV-B	$\mu W/cm^2$	12	24.05 ± 1.12
Ext. Coeff. (PAR)	m^{-1}	8	0.27 ± 0.04
Ext. coeff. (UV-A)	m^{-1}	12	0.94 ± 0.09
Ext. coeff. (UV-B)	m^{-1}	12	1.88 ± 0.13
Chemical			
SRP	µg P/liter	12	3.57 ± 1.71
NH_4-N	µg N/liter	12	4.42 ± 4.59
NO_3-N	µg N/liter	12	9.13 ± 6.65
Biological			
CHL	µg/liter	8	0.86 ± 0.23

ments and bottom waters also contribute to the N pool available at the beginning of the growing season (REUTER and AXLER, 1992). This pool of available N is depleted by algal uptake during late spring and ammonia and nitrate levels remain extremely low for the remainder of the growing season. After the spring thaw, summer precipitation is virtually non-existent, and mixing, diffusion and internal cycling may become important sources of N (AXLER *et al.*, 1981).

2.2. Environmental Characteristics

UVR and PAR were monitored daily using a Solar Light radiometer (PMA 2100) and a Li-cor Data Logger (Table 1). UVR was measured hourly (6 am–7 pm) in direct sunlight 15 m from shore and at the water's surface. Average radiation maximums were determined from daily peak radiation measurements (1300 hrs), and average extinction coefficients were determined from radiation depth profiles

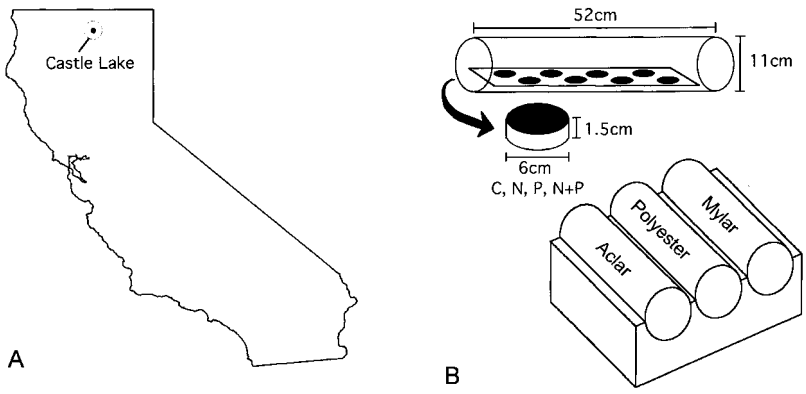

Figure 1. A.) Map of California showing location of Castle Lake. B.) Schematic diagram of bioassay apparatus. Top: single polystyrene tube showing NDS. Bottom: bioassay apparatus showing placement of polystyrene tubes and UV screens.

taken 3 times daily (1100, 1300, and 1500 hrs). All radiation characteristics were calculated from data gathered on cloudless days.

Water column nutrient concentrations (lake center) were averaged from 3 depths (0, 1, and 3 m) on four dates within the study period (July-August, 1997; Table 1). Soluble reactive phosphorus (SRP) concentrations were determined by the phosphomolybdate method (APHA, 1976). Ammonia was quantified by the phenolhypochlorite method of SOLORZANO (1969) and nitrate was analyzed using a diazonitization-coupling reaction (STRICKLAND and PARSONS, 1972). Chlorophyll concentrations were determined fluorometrically from the top 5 m of the epilimnion, using methods described below.

2.3. Nutrient Diffusing Substrata

Nutrient diffusing substrata (NDS) were constructed according to methods used by PRINGLE and BOWERS (1984). Sand was sterilized and packed into disposable plastic petri dishes (60 x 15 mm). Two percent agar solutions made with refined agar (type 1b, Sigma Chemical Co.), alone, or enriched with 0.5 M $NaNO_3$, 0.1 M Na_2HPO_4, or a combination of the two were added to each substrate and thoroughly mixed such that the agar solution filled the interstitial spaces between the sand grains. Each NDS contained approximately 15 ml of agar and 40 g of sediment. Once the agar hardened, each substratum was scraped flush to the top of the petri dish to provide a suitable surface for periphyton colonization.

The diffusion rates of NO_3 and PO_4 from the NDS are characterized by an initial pulse of nutrients followed by an exponential decrease through time (PRINGLE and BOWERS, 1984). Specifically, release rates (0.71 mg N/m^2/day; 2.27 mg P/m^2/day) were determined over a six-day period and are idealized measures of the flux of N and P into distilled water from uncolonized substrates. The presence of a periphyton mat on colonized substrates has been shown to significantly reduce the flux rate of N and P from NDS (PRINGLE, 1987). The release rate of nitrogen from the NDS falls within the range of natural flux of NO_3 from the sediments of Lake Michigan (0.34–1.22 mg/m^2/day), which shares a trophic status similar to Castle Lake (GARDNER *et al.*, 1987). The release rate of phosphorus from the NDS is twofold that of Lake Michigan sediments (0.17–1.12 mg/m^2/day; QUIGLEY and ROBBINS, 1986).

2.4. In Situ UV-Enrichment Manipulation

Nutrient diffusing substrata (NDS) were incubated *in situ* in polystyrene cylinders under three levels of UVR exposure (Fig. 1b). Polystyrene transmits all wavelengths of UVR, thus each NDS received the same quantity of light, while the quality of the light was altered through the use of UVR filters. One cylinder was wrapped in aclar, which allowed the passage of ambient levels of photosynthetically active radiation (PAR) and UV radiation (Fig. 2a). The second and third cylinders were wrapped in polyester and mylar. These screens created a stepwise reduction in UV-A and UV-B radiation in the cylinders, and effectively shielded the NDS contained within from full exposure (Fig. 2a). Ambient UV-B radiation was reduced by 90% under the polyester screen and by 99% under the mylar screen (Fig. 2a). In an experimental design similar to PRINGLE (1990) each UVR attenuating cylinder served as an experimental unit (block) where the patterns of periphyton response to nutrient additions were examined. Simultaneously, each nutrient treatment was considered a blocking factor to examine UVR filter effects. A wooden apparatus secured three flow-through cylinders wrapped in each of the three UVR filters and containing the NDS 10 cm below the surface of the water parallel to wave action (Fig. 1b). This placement ensured continual flushing of the cylinders and prevented a build-up of nutrients inside the tubes. Using the extinction coefficients measured during the experiment and the UVR attenuating qualities of the filters, it was estimated that the aclar cylinder represented a UVR environment similar to that of 0.5 m below the surface of the lake. Polystyrene and mylar were representative of 1.5 m and 3.8 m, respectively. Thus, although incubated at 10 cm, the UVR exposure of the experiment is representative of 90% of the littoral shelf, and 30–35% of the lake itself (AXLER and REUTER, 1996).

Two replicate NDS of each nutrient treatment (Control, N, P, N + P) were incubated under the three UVR filters in randomly determined positions. The partially enclosed design of the flow-through apparatus was an attempt to minimize the effects of incident UV radiation through the ends of the cylinder and that being reflected up from the bottom, thereby maintaining the UV attenuation of each cylinder, without altering the total light each cylinder received.

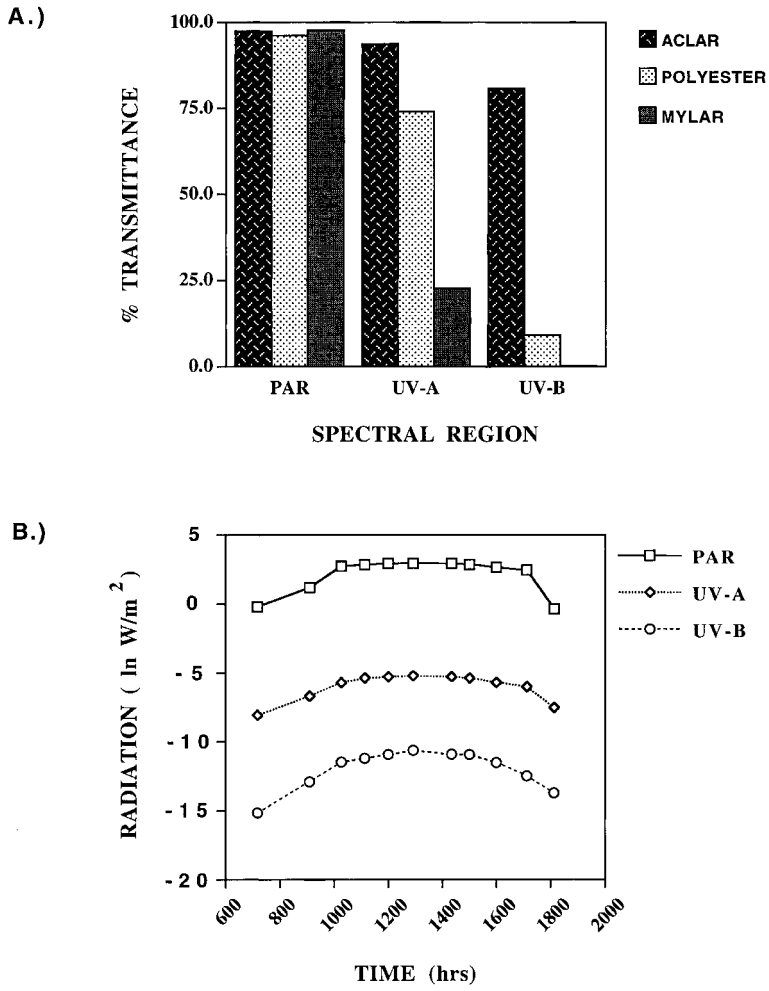

Figure 2. A.) Percentage of ambient radiation transmitted through three UV screens (Dupont Corp.) used in this study. B.) Average incident radiation measured on land over an 11 hour period at Castle Lake during July 26, August 4, and August 6, 1997.

Upon termination of the experiment, each substratum was retrieved by covering the NDS with the top of the petri dish (including as little lake water as possible) and sealing them in zip lock bags, following the methods of PRINGLE and BOWERS (1984). In the laboratory, the top 3 mm of agar and sand were carefully removed with a razor blade, placed in a 250 ml beaker, and diluted to 100 ml with deionized lake water. This suspension was then vortexed for three minutes, stirred with a magnetic stirrer for ten minutes, and decanted into a 250 ml graduated cylinder. The remaining grains were rinsed with 25 ml of fresh distilled water and this second slurry was decanted into the 250 ml graduated cylinder. This procedure of mixing and decanting results in a thorough separation of periphyton and sand grains (PRINGLE and BOWERS, 1984). The separation of periphyton and sand grains was further substantiated in this study through microscopic examination of the grains, and by measuring the relative fluorescence of vortexed and settled samples using a Turner 10-AU fluorometer. The final volume of each slurry was adjusted to 300 ml with deionized lake water and placed in a 500 ml polycarbonate bottle for subsampling and analysis.

2.5. Periphyton Analysis

Periphyton biovolume and general composition were estimated by two independent measures. Chlorophyll-*a* concentrations (corrected for phaeophytin) were determined fluorometrically from each treatment slurry (n = 24) using a 10-AU Turner fluorometer. Sub-samples were filtered onto membranes (Whatman EPM 2000) and pigments were extracted for 1 h in a 50:50 mixture of acetone: DMSO (SHOAF and LIUM, 1976; CARRICK *et al.*, 1993). Periphyton biovolume was also estimated from stratified cell counts (CARRICK and SCHELSKE, 1997). Duplicate sub-samples from each treatment slurry were transferred to separate bottles and preserved with 1% glutaraldehyde (picoperiphyton) or 1% Lugol's solution. Picoperiphyton (< 2 μm in size) biovolume and composition was estimated from prepared slides by using epifluorescence microscopy. Aliquots (0.5 ml) were filtered onto pre-stained (Irgalan Black) 0.2-μm nucleopore filters, and mounted onto microscope slides with immersion oil and coverslips. Slides were stored at –20 °C and counted within 1 month to minimize autofluorescent fading (CARON, 1983). The slides were enumerated using a microscope equipped to distinguish the dominant bright autofluorescent emissions of an individual cell (FAHNENSTIEL and CARRICK, 1992). The biovolume and composition of larger celled periphyton (> 2 μm) were determined from fixed mounts (DOZIER and RICHERSON, 1975). These mounts were prepared by filtering 2.5–5 ml aliquots onto 3 μm millipore filters. The filters were then placed on microscope slides, cleared with glutaraldehyde under low heat (50–70 °C), and permanently mounted with a coverslip (DOZIER and RICHERSON, 1975). Biovolume was estimated by counting an average of 750 cells (< 5% counting error assuming Poisson statistics) for each slide (CARRICK and SCHELSKE, 1997) and approximating cell volume with the most closely related geometric shape based on average dimensional measurements of each species (n = 25). Cell counts were also used to determine the abundance of dominant taxa and general algal composition (phyla) present in the samples. Algal taxonomy conformed to that outlined by PRESCOTT (1973), with modifications made by RIPPKA *et al.* (1979) for the cyanobacteria.

2.6. Statistical Analyses

Final chlorophyll concentrations, and algal biovolumes (from cell counts) were analyzed using one-way analysis of variance (ANOVA; ZAR, 1996) considering UVR quality as a blocking factor to examine nutrient effects, and considering nutrient treatment as a blocking factor to examine UVR effects. Pairwise differences among the fixed factors were tested using Fisher's PLSD test ($\alpha = 0.05$). All statistical analyses were performed using Statview (version 4.01).

3. Results

3.1. Ambient Conditions

UV radiation and PAR showed expected diel patterns (Fig. 2b). Daily peaks occurred at 1300 hrs and the exposure period of the littoral zone of Castle Lake ranged between 0700 and 1800 hrs due to the morphology of the lake basin and surrounding foliage (Fig. 2b). During the period coinciding with the periphyton bioassay, the daily flux of photosynthetically active radiation (PAR) to the lake ranged between 27.7 and 2001 $\mu E/m^2/s$, UV-A ranged between 0.16 and 5.33 mW/cm^2, and the daily flux of UV-B radiation ranged between 0.22 and 25.70 $\mu W/cm^2$ (Table 1; Fig. 2b). These UV-B values correspond to a peak hourly dose of 4.12 meds/hr, and an average cumulative dose of 20.17 meds/d.

Water column nutrient levels in the top 5 m remained low throughout the July-August growing season (Table 1). Mean SRP, NH_4, and NO_3 concentrations were < 10 μg/L, and chlorophyll values were also low, ranging from 0.33 to 1.3 during midsummer (Table 1). During the experiment, there was a lack of algal growth on the tubes themselves, suggesting that there was no build-up of nutrients inside the tubes dues to insufficient flushing. Ambient radiation attenuated rapidly in the water column (Table 1). UV-A and UV-B were attenu-

ated at rates 3.5 and 7 fold higher than that of PAR, respectively, but were still detectable at 3 m. From the depth profile data (n = 9 profiles), we estimate that the NDS at 10 cm were exposed to UVR levels ranging from 5.0–6.4 mW/cm^2 of UV-A and 16.2–23.1 μW/cm^2 of UV-B throughout the study period.

3.2. Periphyton Biovolume Response

Two independent estimates of periphyton biovolume that accumulated on the NDS (Chlorophyll-*a* and total biovolume) were highly correlated ($r = 0.735$, $P < 0.001$; $n = 24$), and exhibited comparable responses to nutrient and UV treatments (Fig. 3). UVR treatments did not significantly affect total periphyton biovolume (Table 2; Fig. 3). Across all screen treatments, periphyton biovolume increased 1.7-fold over controls, 1.8-fold over N additions, and 1.9-fold over N + P additions following enrichment with P ($P < 0.001$; Fig. 3). Enrichment with N + P or N exhibited no significant difference from the control treatments. Under the Aclar filter, P additions increased periphyton biovolume 1.7-fold over all other nutrient treatments. Under mylar, N additions caused a 2.5-fold decrease from controls and N + P additions, and a 3.8-fold decrease from P enrichment (Table 2; Fig. 3). There were no significant differences among the nutrient treatments under the polyester filter (Table 2).

Table 2. Results from one-way analysis of variance (ANOVA) assessing the variation in two estimates of periphytic biovolume (mm^3/m^2) between three UV screens and four nutrient treatments. To examine individual effects of screens and treatments, one-way ANOVA were performed under the indicated blocking factors. Underlined treatments and screens (ranked low to high) were not significantly different when assessed with Fisher's PLSD test (at $P < 0.05$). Where *$P < 0.05$ **$P < 0.01$.

Estimate	Treatment	Block Factor	df	F-value	Fisher's PLSD
Chl-*a*	Screen	None	2	0.587	Mylar Aclar Poly
		C	2	0.256	Aclar Mylar Poly
		N	2	7.278*	Mylar Poly Aclar
		P	2	0.289	Aclar Poly Mylar
		N + P	2	0.891	Poly Aclar Mylar
	Nutrient	None	3	2.916*	N + P N C P
		Aclar	3	1.929	C N + P N P
		Poly	3	1.420	N + P C N P
		Mylar	3	15.533**	N N + P C P
Biovolume	Screen	None	2	0.295	Mylar Poly Aclar
		C	2	0.692	Poly Aclar Mylar
		N	2	4.385	Mylar Aclar Poly
		P	2	3.885	Poly Aclar Mylar
		N + P	2	2.772	Poly Aclar Mylar
	Nutrient	None	3	4.933**	N C N + P P
		Aclar	3	8.035*	C N + P N P
		Poly	3	2.352	C N + P N P
		Mylar	3	6.413*	N N + P C P

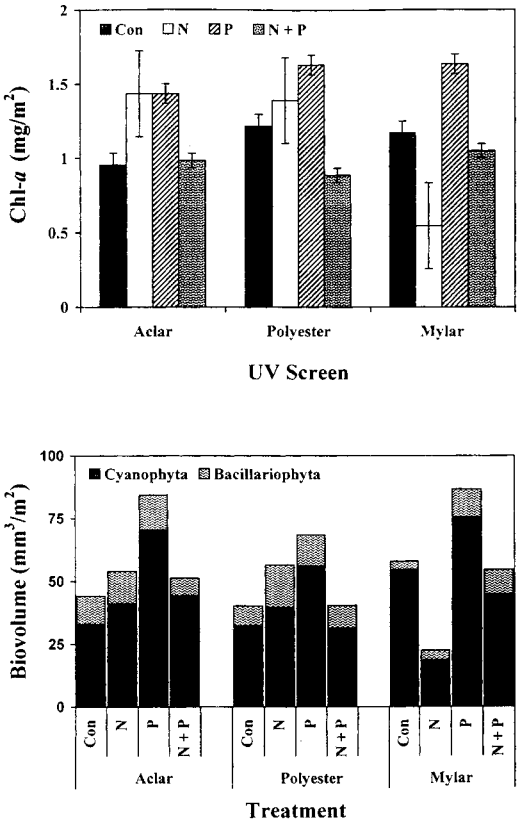

Figure 3. Average chlorophyll-*a* concentrations, total biovolume, and average biovolume for the dominant periphyton phyla among four nutrient treatments and three UV treatments after 17 days of incubation. Vertical bars denote 1 standard error from the mean.

3.3. Phyla-Level Responses

Total periphyton biovolume was comprised of representatives from several algal phyla. Cyanobacteria comprised 77–87%, and diatoms accounted for 12–22% of the total periphyton biovolume. Members of the Chlorophyta were found sporadically, and accounted for < 0.5% of the total periphyton biovolume (Table 3).

Total cyanobacteria biovolume increased significantly when enriched with P (Table 3; Fig. 3), while enrichment with N or N + P did not significantly alter their biovolume (Table 3). When blocked by the aclar treatment, P enrichment caused a 1.6-fold increase over N and N+P additions and a 2.1-fold increase over controls (Fig. 3). Cyanobacteria biovolume under the mylar screen underwent a nearly 3-fold decrease following enrichment with N. No nutrient effect on biovolume was observed under the polyester screen. There were no detectable screen effects on cyanobacteria biovolume when nutrient treatments were considered blocked effects (Table 3).

There was no nutrient effect on total diatom biovolume (unblocked; Table 3). However, enrichment with P and N + P caused an increase in biovolume over controls under the mylar

Table 3. Results from one-way analysis of variance (ANOVA) assessing the variation in the biovolume (mm^3/m^2) of three phyla of periphyton between three UV screens and four nutrient treatments. To examine individual effects of screens and treatments, one-way ANOVA were performed under the indicated blocking factors. Underlined treatments and screens (ranked low to high) were not significantly different when assessed with Fisher's PLSD test (at $P < 0.05$). Where *$P < 0.05$ **$P < 0.01$.

Group	Treatment	Block Factor	df	F-value	Fisher's PLSD
Cyanophyta	Screen	None	2	0.277	Poly Mylar Aclar
		C	2	1.736	Poly Aclar Mylar
		N	2	2.593	Mylar Poly Aclar
		P	2	2.213	Poly Aclar Mylar
		N + P	2	2.641	Poly Aclar Mylar
	Nutrient	None	3	5.493**	N C N + P P
		Aclar	3	12.218**	C N N + P P
		Poly	3	2.052	N + P C N P
		Mylar	3	5.109*	N N + P C P
Bacillariophyta	Screen	None	2	4.064*	Mylar Aclar Poly
		C	2	7.879*	Mylar Poly Aclar
		N	2	32.616**	Mylar Aclar Poly
		P	2	0.77	Mylar Poly Aclar
		N + P	2	0.619	Aclar Poly Mylar
	Nutrient	None	3	1.463	C N + P N P
		Aclar	3	1.541	N + P C N P
		Poly	3	2.240	C N + P P N
		Mylar	3	7.731*	C N N + P P
Chlorophyta	Screen	None	2	0.478	Poly Aclar Mylar
		C	2	2.896	Poly Aclar Mylar
		N	2	0.540	Aclar Mylar Poly
		P	2	0.323	Poly Aclar Mylar
		N + P	2	0.611	Aclar Mylar Poly
	Nutrient	None	3	0.164	C N + P N P
		Aclar	3	0.353	N + P N C P
		Poly	3	0.678	C P N + P N
		Mylar	3	0.678	N N + P C P

filter (Fig. 3). Total diatom biovolume was significantly less under the mylar screen when compared to the aclar and polyester screens. When blocked by N-enrichment, NDS under the mylar screen exhibited a 3.2 and 4.3-fold decrease in biovolume when compared to N-enriched NDS under the aclar and polyester screens, respectively (Table 3; Fig. 3).

3.4. Population-Level Responses

The cyanobacteria *Anabaena circinalis* RAB. and *Chroococcus limneticus* W. SM. accounted for 48–54% of the biovolume among all substrata. Both species demonstrated significant responses to UV treatments (Table 4). *A. circinalis* RAB. biovolume was highest under the mylar screen and decreased 2-fold under the aclar screen (Fig. 4). In contrast, *C. limneticus* W. SM. biovolume was highest under the aclar screen and underwent 4.1 and 13.1-fold decrease under the polyester and mylar screens, respectively (Fig. 4). The biovolume of *A.*

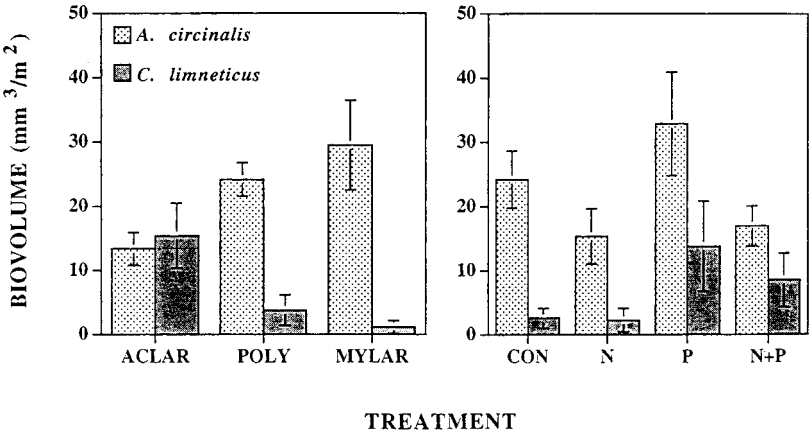

Figure 4. Average biovolumes for the dominant species of cyanobacteria *(Anabaena circinalis, Chroococcus limneticus)* among four nutrient and three UV treatments. Vertical bars denote 1 SE from the mean.

circinalis decreased following N enrichment under the mylar screen, but showed no other response to nutrient treatment. The biovolume of *C. limneticus* increased following enrichment with P, although this response was not significant (Table 4; Fig. 4). Pico-sized periphyton consisted primarily of *Synnechoccus* sp. and exhibited little response to nutrient or UVR treatments (Table 4). When blocked by N+P enrichment, pico-periphyton biovolume under the mylar screen was higher than under the polyester screen, but was not significantly different from the aclar screen (Table 4).

While total diatom biovolume was affected by both UV screening and nutrient enrichment (Table 3), few differences were observed at the population level. Both *Tabellaria flocculosa* (LYNGB.) KÜTZ. and *Epithemia adnata* (EHR.) KÜTZ. demonstrated a strong negative response to UVR shielding under the mylar screen. The biovolume of other diatom species was negatively affected by mylar, but these differences were not significant.

4. Discussion

UVR can influence periphyton assemblages, however this influence may depend on algal nutritional status (BOTHWELL *et al.*, 1993). The relative consistency in total periphyton biovolume, despite substantial changes in species composition, suggests that the periphyton community in Castle Lake is able to compensate for the changes brought on by UV radiation through changes in the abundance of different species. This idea is consistent with the recent work of HILL *et al.* (1997) who tested the effects of ambient UV radiation on total periphyton biomass and grazers in a small, clear water stream in Tennessee, USA. Their results showed that total periphyton biomass and photosynthesis were not significantly affected by reduced levels of ambient UV radiation, leading them to conclude that the periphyton may be adapted to naturally high levels of UV radiation. However, alterations in UV radiation may have caused shifts in species composition that would have gone unnoticed, given their level of analysis (chl-*a*, and afdw). Enhanced UVR levels may bring about shifts within the community, but biomass and net community processes such as primary production may be buffered against dramatic changes in species composition (WILLIAMSON, 1995).

Table 4. Results from one-way analysis of variance (ANOVA) assessing the variation in the biovolume (mm^3/m^2) of Pico-sized periphyton, *Anabaena circinalis,* and *Chroococcus limneticus* between three UV screens and four nutrient treatments. To examine individual effects of screens and treatments, one-way ANOVA were performed under the indicated blocking factors. Underlined treatments and screens (ranked low to high) were not significantly different when assessed with Fisher's PLSD test (at $P < 0.05$). Where $*P < 0.05$ $**P < 0.01$.

Species	Treatment	Block Factor	df	F-value	Fisher's PLSD
A. circinalis	Screen	None	2	2.908*	Aclar Poly Mylar
		C	2	2.845	Aclar Poly Mylar
		N	2	2.199	Mylar Aclar Poly
		P	2	2.119	Aclar Poly Mylar
		N + P	2	2.892	Aclar Poly Mylar
	Nutrient	None	3	1.217	N N + P C P
		Aclar	3	0.184	N + P P N C
		Poly	3	0.391	N + P N C P
		Mylar	3	7.246*	N N + P C P
C. limneticus	Screen	None	2	7.455**	Mylar Poly Aclar
		C	2	0.213	Poly Mylar Aclar
		N	2	1.554	Mylar Poly Aclar
		P	2	4.188	Mylar Poly Aclar
		N + P	2	24.330**	Mylar Poly Aclar
	Nutrient	None	3	0.890	C N N + P P
		Aclar	3	1.709	C N N + P P
		Poly	3	1.268	C N P N + P
		Mylar	3	0.122	N N + P P C
Pico-algae	Screen	None	2	3.148	Poly Mylar Aclar
		C	2	4.235	Poly Aclar Mylar
		N	2	3.091	Mylar Poly Aclar
		P	2	2.188	Poly Mylar Aclar
		N + P	2	10.334*	Poly Aclar Mylar
	Nutrient	None	3	1.286	C N + P N P
		Aclar	3	3.792	N + P C P N
		Poly	3	3.197	N + P C N P
		Mylar	3	2.812	N C P N + P

In this experiment, total periphyton biovolume changed little with respect to UV treatments; however statistical blocking by UVR filters revealed the effects of nutrient enrichment. This deduced interaction occurred at both the species and division level as demonstrated by the antagonistic occurrence of *A. circinalis* RAB. and *C. limneticus* W. SM. under the UV screens and the decrease in diatom biovolume under the mylar screen. Our results indicate that periphyton growth in Castle Lake is primarily limited by phosphorus. Phosphorus was the only nutrient that consistently promoted an increase in periphyton biovolume over controls, while the biovolume on NDS enriched with N, or N + P did not differ from controls on any level of analysis.

4.1. Nutrient Limitation of Algae in Castle Lake

Although periphyton growth appears to be P-limited, a variety of studies indicate that both N and P can be important factors in regulating phytoplankton growth. Studies on the nitro-

gen limitation of Castle Lake have focused on internal cycling of N (AXLER *et al.*, 1981; 1982), and strategies for N-assimilation related to the ionic form and availability of this resource (PRISCU *et al.*, 1984; REUTER and AXLER, 1992). In 1994, work by BRETT *et al.* (1994) indicated that phytoplankton growth can become P-limited due to disproportionate recycling of NH_4, following a late-summer shift in the zooplankton community to taxa with low internal N : P ratios (such as *Daphnia*). ELSER *et al.* (1995) reported that both N and P were potentially limiting to phytoplankton growth in short-term bioassays (4–5 days) and further supported the idea that phytoplankton are co-limited by N and P.

Because periphyton occupy a different niche from phytoplankton (WETZEL, 1983; LOWE, 1996), there is no *a priori* reason to assume that these two distinct groups should exhibit similar limitations in terms of nutrition. PRINGLE (1987) examined the possibility of an interaction between nutrient sources of overlying waters and substrate and their effects on stream periphyton communities. Periphyton biovolume responded strongest when both the substrate and overlying waters were enriched, and suggests that periphyton are able to utilize both as nutrient sources. Further, her study also indicated that the flux rate of nutrients from her experimental substrata decreased exponentially following periphyton colonization, leading her to conclude that periphyton can act as mediators of nutrient release from underlying sediment. Castle Lake has a rich history of environmental monitoring and research (GOLDMAN, 1960), but surprisingly little information exists on the benthic community of the lake. Thus, the present study adds another dimension to an already well-understood lake ecosystem. Our results indicate that the periphyton, unlike the phytoplankton, have access to an adequate supply of nitrogen through N-fixation, or are more efficient at assimilating available N resources in Castle Lake (AXLER and REUTER, 1996).

The lack of positive response to N and N + P by Castle Lake periphyton may be explained by a decrease in the abundance of *Anabaena circinalis* RAB. on these treatments. *Anabaena* spp. are known heterocystous fixers of nitrogen (WETZEL, 1983; PAERL, 1998). The ability to fix N may provide this species with a competitive advantage in N-limited Castle Lake (AXLER *et al.*, 1980; 1981; AXLER *et al.*, 1982; REUTER and AXLER, 1992), which may be lost following enrichment with nitrogen. REUTER and AXLER (1992) previously described the littoral periphyton community as dominated by *Calothrix* spp., *Tolypothrix* spp., and *Nostoc* spp., all of which are heterocystous blue greens. In contrast, >95% of the midsummer phytoplankton community of Castle Lake is made up of *Chroococcus limneticus, Gloecapsa granosa,* and *Microcystis aeruginosa*, all of which lack the ability to fix nitrogen (AXLER *et al.*, 1981). The periphyton may then rely on nitrogen fixation as the primary strategy to meet their N requirement while the phytoplankton rely on dissolved inorganic sources of N, commonly found to limit their growth.

4.2. Effects of UV Radiation on Cyanobacteria

The absence of *Anabaena circinalis* RAB. under the aclar screen (ambient UV), and its proliferation under the mylar screen (no UV), suggests that UV may inhibit the growth of this species. The prevalence of *A. circinalis* RAB. under low levels of UV that do not inhibit N-fixation, a process that gives this organism a nutritional advantage in Castle Lake, is compelling evidence for the suppression of N-fixation by natural levels of UV radiation.

UV radiation has been previously shown to inhibit N-fixing enzymes in species of *Anabaena* (NEWTON *et al.*, 1979) and *Nostoc* (AGRAWAL, 1996) under controlled laboratory conditions, and it has been speculated that this enzyme inhibition may be the result of interference of ATP synthesis by UV-B (HADER *et al.*, 1998). However, a suite of other possible mechanisms exist that may explain the inhibition of N-fixation by UV radiation. During the differentiation of proheterocysts into N-fixing heterocysts, cells undergo changes in pigmentation which signal accompanying changes in photosystems I and II (PAERL, 1988). UV

radiation has been previously shown to significantly reduce algal pigment concentrations (MASKE and LATASSA, 1997); such a reduction in pigment may interfere with the pigment alterations involved in the differentiation of heterocysts, thereby disabling N-fixation. Also, UV radiation has been shown to interfere with the electron transport system (BEARDALL *et al.*, 1997). During N-fixation, high energy electrons are transferred to a nitrogenase complex situated in the heterocyst (PAERL, 1988), indicating the possibility for UV interference with this transport and subsequent N metabolism within the heterocyst. Lastly, heterocysts require high rates of respiration to produce the energy required for N-fixation. BEARDALL *et al.* (1997) demonstrated that the respiratory rates of some species may be impaired by UV interference with the electron transport system. This could limit the energy available for N-fixation and reduce its effectiveness as a source of N.

Chroococcus limneticus W. SM. dominated the periphyton communities grown on substrata under the aclar screen, and is a major constituent of the phytoplankton community in the epilimnion of Castle Lake (AXLER *et al.*, 1981). Because UV radiation can penetrate to 3 m in the lake, it is likely that this species of cyanobacteria is resistant to ambient levels of UV radiation. This resistance may result from one or a combination of physiological and morphological factors that have been proposed to compensate for the damage caused by UV radiation. BOTHWELL *et al.* (1993) suggested that inter-specific variation in terms of UV-absorbing proteins, pigments, and DNA characteristics may make some species more susceptible to UV damage than others. The resistance of *Chroococcus limneticus* W. SM. to current UV levels at Castle Lake may be better explained in terms of the morphology of the species. *C. limneticus* W. SM. is surrounded by a mucilaginous sheath which may offer some protection against UV radiation (PAERL, 1988). KARSTEN and GARCIA-PICHEL (1996) demonstrated the presence of UV screening compounds in the sheathes of *Microcoleus*, which offered protection from UV radiation to these organisms. Also, *C. limneticus* W. SM. is a relatively large (65 μm^3 in this study), spherical and colonial species, which may afford more protection to its DNA than single, smaller sized cells (KARENTZ *et al.*, 1991).

4.3. Effects of UV Radiation on Diatoms

UV shielding caused a decrease in diatom biovolume, and this trend was common among most diatom taxa. These results are consistent with the idea that sediment dwelling diatoms are able to burrow into the substrate, and that this may be an adaptation for the avoidance of harmful agents, such as UV radiation. Most photosynthetic organisms orient themselves with respect to external factors to optimize their position in the water column (RAI and MALLICK, 1998). Active avoidance may be the most immediate option available to sediment-dwelling organisms to compensate for elevated UV levels, thereby allowing them to position themselves within the substrate so as to avoid potentially damaging doses of UV radiation, yet take advantage of periodically enhanced PAR availability (VINEBROOKE and LEAVITT, 1999).

Epipelic diatoms have been known to undergo vertical migration in sediment in previous studies. Using sand-based substrates in an enrichment study of a northern Michigan stream, PRINGLE and BOWERS (1984) found that diatoms were present in the substrate to a depth of 4 mm. Although not concerned with vertical migration in the context of UV avoidance, this study clearly demonstrated the ability of periphyton to invade the NDS to exploit nutrient resources. VINEBROOKE and LEAVITT (1999) later reported direct effects of UV radiation were habitat as well as taxon-specific in a study of an alpine lake in Alberta, Canada. They found that UV suppressed the development of epilithon (unglazed ceramic tiles) by inhibiting the dominant diatom component, whereas epipelic diatom abundance was actually enhanced.

Previous experiments have demonstrated the UV sensitivity of diatoms colonizing epilithic (hard) surfaces (BOTHWELL *et al.*, 1993; VINEBROOKE and LEAVITT, 1996). The UV sus-

ceptibility of epilithic diatoms may result from their inability to actively avoid the harmful effects of UV radiation. Epipelic diatoms may tolerate higher levels of UV radiation because of the potential to exploit their habitat as a physical refuge (VINEBROOKE and LEAVITT, 1999). The locomotive mechanism of diatoms is raphe-dependent, and involves the passing of secreted muccopolysaccharides through pores, across the raphe, and back into the cell (PATERSON, 1989). The diatom community of Castle Lake is dominated by bi-raphic and keeled species, thus it is conceivable that these diatoms are able to migrate into the sediments under high levels of UV. When UV avoidance no longer offers competitive advantage under the mylar screen, the biovolume of these diatoms would diminish.

4.4. Implications for Alpine Lakes

Rising levels of environmental UV-B can have negative effects on the algal components of aquatic ecosystems and these effects may be mediated by nutrient enrichment (WILLIAMSON, 1995). BOTHWELL *et al*. (1993) indicates that organismal sensitivity to UV may be influenced by internal concentrations of DNA, proteins, and pigments that utilize nitrogen. Thus, it follows that the addition of nitrogen may increase the concentrations of these compounds and resistance to UV. Because of the close coupling of N and P in algal metabolism, it is possible that P additions may also mediate algal response to UV radiation. BOTHWELL *et al.* (1993) tested the effects of UV radiation and P additions in concentrations of up to 2 μg P/L on periphytic diatoms of a river in British Columbia, and found that the degree of P-limitation had no effect on diatom growth rate. However the experimental troughs used in this study were extremely shallow, thereby exposing the periphyton to a high dose of UV that may have outweighed any compensation offered by P-additions. Further, BOTHWELL *et al.* (1993) focused on diatom communities; these results may not apply to communities with a substantial cyanobacterial component.

Our results are likely to be conservative estimates of UV impacts and nutrient additions on periphyton. In conjunction with each other, UV and nutrient additions may have yielded moderate biomass responses, and masked the effects of the opposing variable. Large concentrations of nutrients employed in bioassays can cause the secondary limitation of other nutrients and may reach toxic levels, thereby inhibiting the growth they are used to elicit (SCHELSKE, 1994). To avoid excessive dosage, the nutrient concentrations used in this study were gauged to be relative to the lake. Further, the maximum UV-B flux was much less than that reported in previous studies (24.05 ± 1.12 μW/cm^2 ambient, 16.2–23.1 μW/cm^2 incident on periphyton). VINEBROOKE and LEAVITT (1996; 1999) reported incident UV-B values of 60 μW/cm^2 striking the periphyton in their study of an alpine lake, while BOTHWELL *et al.* (1993) reported 50.8 μW/cm^2 of ambient UV-B in their study of an experimental stream near Alberta, Canada. These studies may then represent worst-case scenarios of the effects of UV on periphyton. The fact that we were able to detect changes in the periphyton community of Castle Lake despite these conservative manipulations suggests that the results of this study apply to a broad range of nutrient and UV conditions.

In 1991, a European program of instrument intercomparisons measured spectral irradiance striking the planet's surface in Panorama, Greece on July 9, and found peak UV-B dosage reached approximately 7 meds/hr (WANG and LENOBLE, 1994). Panorama, located in the mountains of Greece, may represent an accurate comparison to alpine and sub-alpine ecosystems. Maximum ambient UV-B doses encountered in this study (4.12 ± 0.19 meds/hr) fall within the range of doses reported from Panorama. WILLIAMSON *et al.* (1996) reported UV-B attenuation depths (1% of surface radiation) for Lakes in various regions of the United States and Canada ranging from 0.12–4.74 m. In Castle Lake, the 1% UV-B attenuation depth (2–2.5 m) is similar to the reported range for these regions and may be indicative of a variety of clear, freshwater lakes. SCULLY and LEAN (1994) reported integrated UV-B

coefficients for several temperate lakes ranging from 0.62–21.73 m^{-1}, including Snowflake Lake (3.23 m^{-1}) and Pipit Lake (1.43 m^{-1}) studied by VINEBROOKE and LEAVITT (1996; 1999). The extinction coefficient reported in this study (1.88 m^{-1}; Table 1) suggests that UV-B penetration in Castle Lake is high relative to other lakes, and reflects the importance of UV as an environmental influence in this system.

The information provided by our study has predictive importance to future studies in Castle Lake, and other aquatic ecosystems. Increased levels of UV radiation may not always have an impact on net ecosystem processes; rather they may induce subtle shifts in composition and influence physiological processes such as N-fixation. Castle Lake's high elevation, shallow depth, and clear water (owing to its low productivity) create a setting whereby biota are exposed to high levels of UV that can penetrate to significant depths. Therefore, Castle Lake may be useful as an early warning system of global climate change and offer insights into the long-term effects UV radiation has on aquatic biota.

5. Acknowledgements

We appreciate the administrative and financial support provided by the Great Lakes Center and Biology Department at SUNY-College at Buffalo. We acknowledge support from the Castle Lake Research Group, particularly A. MUELLER-SOLGER. G. WHEELER and K. MANLEE who carried out the chemical analysis of our water samples. J. STOCKNER and two anonymous reviewers provided helpful criticisms on the manuscript. This work was supported by NSF grants DUE-9696148 to H. CARRICK, and DEB-9520884 to H. CARRICK, C. R. GOLDMAN, M. T. BRETT, and C. LUECKE.

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Manuscript received January 25th, 2000, revised October 30th, 2000; accepted November 11th, 2000

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Book Review

ZILINSKAS, R. A., BALINT, P. J. (Eds): **Genetically Engineered Marine Organism. Environmental and Exonomic Risks and Benefits.** Kluwer Academic Publishers Boston 1998, 256 pp. ISBN 0-412-15251-7. NLG 250.00.

The book consits of 7 chapters written by different authors and it deals with different aspects of the possible future introduction of genetically engineered organisms (GEO) of different procaryotic and eucaryotic groups, namely *Archea, Bacteria, Cyanobacteria, Fungi, Algae, Protozoa, Molluscs, Crustacea*, viruses, meiofauna, plankton and fish into marine ecosystems. The book combines biological data with laws regulating both GEO and marine ecosystems, directives and risk assesment methods.

There were not yet any field scale releases of transgenic organisms into the marine environment. The degree of uncertainity associated with field trials of transgenic organsims in the marine environment is higher than that associated with terrestial environment, but the perspectives are great.

There are already a lot of cases of genetically modified aquatic organisms, which are released into contained fresh waters and their populations are subjected to experimental studies aimed to detailed risk assesment. There are no limits to the potential dispersal of GEOs with selctive advantage in marine ecosystems and there is great probability of successful establishment of new populations of GEO.

Transgenic microorganisms have the potential of future use as bacterial and cyanobacterial biopesticides and for bioremediation. Concerning transgenic fish species, the main problem is that they proved to be even too successful. The high degree of the effects of transgens in fish can be hardly compared with that in mammals. The excessive growth and/or more rapid development gives the fish selctive advantages and it creates situation with great probability that transgenic fish could replace the original populations. Some of the examples of economicaly interesting transgenic fish are, for instance, transgene coding for the antifreeye protein transferred into atlantic salmon, another transgenic Atlantic salmon reaches sexual maturity in two instead in three years or transgenic in growth hormone gene Pacific salmon which has average mass 11 times larger than the parental genome.

The perspective of utilization of marine biology for human nutrition are very broad. The authors envisage the future “blue revolution” which will be able to bring enough food for the ever increasing human population.

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