

Importance of the microbial food web in large lakes (USA)

Hunter J. Carrick, Aneal Padmanabha, Laurie Weaver, Gary L. Fahnenstiel
and Charles R. Goldman

Introduction

The traditional view of food web structure categorizes all organisms within an ecosystem into one of several feeding guilds (i.e. primary producers, decomposers, herbivores, and consumers), where energy is transferred from one guild to the next (LINDEMAN 1942). The biomass of these guilds decreases geometrically with successive trophic levels to form a pyramid, with a large biomass of plants at the base (FITTON 1927). Metabolic inefficiencies, such as excretion and sloppy feeding, produce significant losses at each trophic level, with the greatest loss at the highest trophic level (RICH & WETZEL 1978).

Deviations from this paradigm have been described for planktonic communities in the ocean, where the biomass of heterotrophic organisms can rival phytoplankton, thus indicating a tight coupling between plants and animals (e.g. ODUM 1971). However, our view of food web structure in aquatic ecosystems is being further revised based upon the knowledge that small heterotrophic organisms are more quantitatively important than previously thought (AZAM et al. 1983). Recent technological advances now allow more accurate censusing of natural microbial populations, as well as measurement of their high rates of metabolic activity (KEMP et al. 1993). Furthermore, large concentrations of non-living pools of organic carbon and detritus are common features of aquatic ecosystems, and appear to be responsible for fueling a portion of this high microbial metabolic activity (e.g. DUCKLOW 1994). In this way, organic wastes produced at all levels of the food chain are available to support significant levels of heterotrophic production, that can often rival rates of primary production (e.g. SCAVIA 1988).

Despite this, comprehensive measures of heterotrophic plankton are scarce, thus making it difficult to draw inferences about their relative contribution to planktonic food web structure. Herein we present information about the planktonic food web structure in four large lakes in the United States. Our objectives are: (1) to estimate the biomass of heterotrophic pico-, nano-, and microplankton

among lakes using rigorous microscopic enumeration techniques; (2) to measure the variation in microheterotrophic biomass through time (season) and space (depth); and (3) to put forth a hypothesis concerning the role of microheterotrophs in the plankton of large lake ecosystems. Our findings indicate that the biomass of microheterotrophic plankton was large in all the lakes we studied, with HpicO (bacteria) representing the largest fraction of heterotrophic biomass and exhibiting the least variance in time and space.

Materials and methods

Lake sampling

A total of four large lake ecosystems from two major geographic regions in the United States of America (temperate and subalpine) were sampled during the 1987–1996 period. All samples were taken at a representative offshore station in each lake. In the St. Lawrence chain of Great Lakes, Lakes Huron and Michigan were sampled monthly during December 1986–November 1987. The subalpine lakes, Crater Lake (Oregon) and Lake Tahoe (California–Nevada), were sampled on 25 July and 1 August in 1996, respectively.

On each sampling date, water column temperature and light profiles were measured with either an electronic bathythermograph or Seabird SBE-19 CTD. All water samples were collected using opaque 5-l Niskin bottles from the surface depths (5 m) during isothermal mixing periods and at 6–10 m depths during thermal stratification. Chlorophyll *a* concentrations were determined fluorometrically on extracted samples (STRECKLAND & PARSONS 1972). Duplicate subsamples were transferred into 250-mL amber bottles and preserved with glutaraldehyde and Lugol's solution for subsequent microscopic analyses (both 1% final conc.).

Microscopic analysis of the microplankton community

The biomass and composition of microheterotrophic

plankton collected from each lake was measured using a combination of light and epifluorescence microscopy (BOOTH 1993, CARRICK & SCHELSKE 1997). Picoplankton (cells 0.2–2 μm in size) and nanoplankton (cells 2–20 μm in size) were enumerated using epifluorescence analysis of glutaraldehyde preserved samples (stored cold at 5 °C). Microplankton (cells 20–200 μm in size) were enumerated using inverted light microscopy of the Lugol's preserved samples.

Pico- and nanoplankton abundance and composition were determined using epifluorescence microscopic analysis of prepared slides (CARON 1983). Duplicate slides were prepared from each water sample within 1 day of collection (stored at –20 °C). Heterotrophic picoplankton (Hpico, bacteria) slides were prepared by concentrating 1 mL onto darkened filters (0.2- μm Nuclepore) subsequently stained with Acridine Orange (HOBBIE et al. 1977). Phototrophic picoplankton (Ppico, eukaryotic algae and cyanobacteria) slides were prepared by concentrating 10–20 mL onto darkened 0.2- μm filters (FAHNENSTIEL & CARRICK 1992). Both heterotrophic and phototrophic nanoplankton (Hnano and Pnano) were enumerated from slides prepared by filtering 20–50 mL onto darkened filters (0.8- μm Nuclepore) subsequently stained with primulin (CARON 1983). All slides were enumerated within 1 week to minimize the fading of autofluorescence using a research microscope (1000 \times) equipped for autofluorescence (450–490 nm excitation and >515 nm emission), and primulin analysis (320–380 nm excitation and >420 nm emission). All species encountered were identified to their lowest taxonomic category according to the phylogeny outlined by LEE et al. (1985).

Heterotrophic microplankton abundance and composition (Hmicro, ciliates; Dino, dinoflagellates) were determined using the Utermöhl technique (UTERMÖHL 1958). Aliquots (25–100 mL) were settled onto coverslips, and the entire area of the coverslip was systematically scanned with an inverted microscope (200 \times) to avoid counting biases induced

by edge-effects. Organisms were identified to the genus level (LEE et al. 1985); conspecific taxa were delineated by size.

The cell dimensions of all plankton taxa were determined by making microscopic measurements of 10 individuals randomly (400–1,000 \times magnification). Average dimensions were then applied to the geometric configuration which best approximated the shape of each taxon. Cell volumes were calculated and subsequently converted to carbon using the following factors: 0.38 pg C μm^3 for Hpico and Ppico (VERITY et al. 1992), an empirical biovolume–carbon relationship for Hnano and Pnano (VERITY et al. 1992), and a 0.279 wet-to-dry weight conversion for Hmicro and Dinoflagellates (GATES 1984).

Results

Ambient conditions

In terms of our comparison among these four lakes (Table 1), Crater Lake had the smallest surface area (300 km²) and the greatest maximum depth (589 m), while Lake Huron was the largest (>59,000 km²) and most shallow (depth 229 m). Perhaps not surprisingly, the Great Lakes were similar in terms of their morphometric attributes, having larger, shallow basins as a result of glacial scouring, compared with the subalpine Crater Lake and Lake Tahoe, which had smaller, deeper basins formed by volcanic and tectonic processes at relatively high elevations (HORNE & GOLDMAN 1994).

There were apparent differences among the four lakes in terms of their relative productivity and water quality conditions (Table 1). Water column chlorophyll concentrations were highest in Lakes Michigan and Huron (range 0.3–3.7 $\mu\text{g L}^{-1}$), followed by Lake Tahoe

Table 1. Summary of physical characteristics for large lakes in the USA.

Lake type	Physical characteristics			
	Depth (m)	Surface area (km ²)	Elevation (m)	Photic depth (m)
Subalpine				
Lake Tahoe	501	500	1,899	50
Crater Lake	589	300	1,882	100
Temperate				
Lake Michigan	282	57,750	177	31
Lake Huron	229	59,500	177	33

(0.1–1.5 $\mu\text{g L}^{-1}$), while Crater Lake had extremely low chlorophyll levels (0.03–0.5 $\mu\text{g L}^{-1}$). On the contrary, photic zone depth during mid-summer was 100 m in Crater Lake, 50 m in Lake Tahoe, and was most shallow in the two temperate Great Lakes at 31–33 m.

Temporal variation of microheterotrophs in the St. Lawrence Great Lakes

Total microheterotrophs biomass (MH, sum of Hpico, Hnano, and Hmicro) was substantial throughout the year in both Lakes Huron (average 84.0 $\mu\text{g C L}^{-1}$) and Michigan (68.1 $\mu\text{g C L}^{-1}$). In Lake Huron, Hpico carbon was uniform in distribution throughout the year (Fig. 1), ranging from 29 to 37 $\mu\text{g C L}^{-1}$ (coefficient of variation, CV = 14%). Hnano values were variable in occurrence (CV = 41%), being low in the winter (3 $\mu\text{g C L}^{-1}$), and increasing to levels in the range 12–17 $\mu\text{g C L}^{-1}$ for most of the year with a peak in August (23 $\mu\text{g C L}^{-1}$). Hmicro values were the most variable in their occurrence (range 5–67 $\mu\text{g C L}^{-1}$), exhibiting biomass peaks in May and August, and again in October (CV = 59%).

In Lake Michigan, Hpico carbon values varied two-fold over the year (range 15–38 $\mu\text{g C L}^{-1}$) reaching peak levels in the July–August period (Fig. 1); Hpico experienced less seasonal variance compared with other MH (CV = 39%). Hnano were variable in occurrence (CV = 75%), being low in the winter (3 $\mu\text{g C L}^{-1}$), and increasing to levels in the range 8–16 $\mu\text{g C L}^{-1}$ for most of the year with peak abundance also being achieved in the July–August period (30–40 $\mu\text{g C L}^{-1}$). Hmicro biomass was moderately variable through time (range 12–44 $\mu\text{g C L}^{-1}$), and peaked during the April–May period (CV = 41%).

Spatial variation of microheterotrophs with water depth

Total MH biomass varied with depth, such that peak levels were observed in the vicinity of the deep chlorophyll layer (DCL) in each of the three lakes (Fig. 2). Lake Michigan supported the greatest subsurface MH biomass followed by Lake Tahoe and Crater Lake (109, 30, and

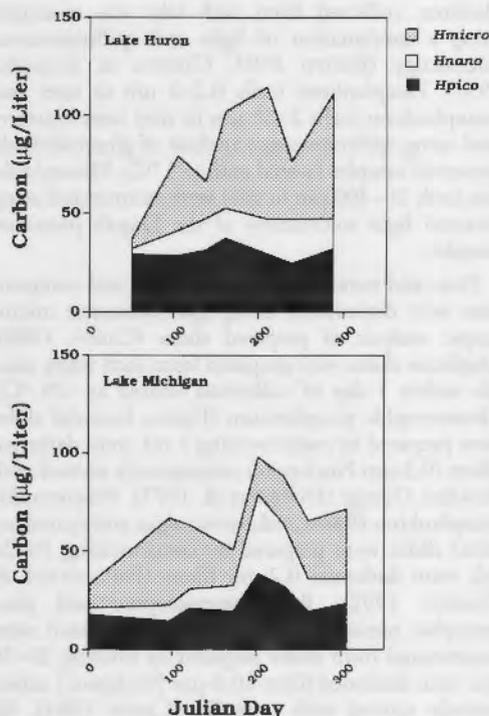


Fig. 1. Seasonal distribution of microheterotrophic (MH) biomass in the surface waters of Lakes Huron and Michigan (1987).

17 $\mu\text{g C L}^{-1}$, respectively). Interestingly, the subsurface concentration of MH biomass in each lake shows a reasonable quantitative correspondence with the relative magnitude of DCL chlorophyll levels in each system (Michigan 3.7, Tahoe 1.5, and Crater 0.5 $\mu\text{g L}^{-1}$).

MH composition also varied with depth in all lakes; however, Hpico became progressively more important with increasing oligotrophy (Fig. 2). Overall, Hpico showed the least variation in biomass with depth (range in CV 28–36%) and their contribution increased from 52% in Lake Michigan, to 68% in Lake Tahoe and 88% in Crater Lake. Lake Michigan supported a significant subsurface assemblage of Hnano and Hmicro that constituted 21 and 27% of total MH biomass, respectively. Hnano were scarce in Lake Tahoe (<6%), while Hmicro represented 25% of MH biomass. In Crater

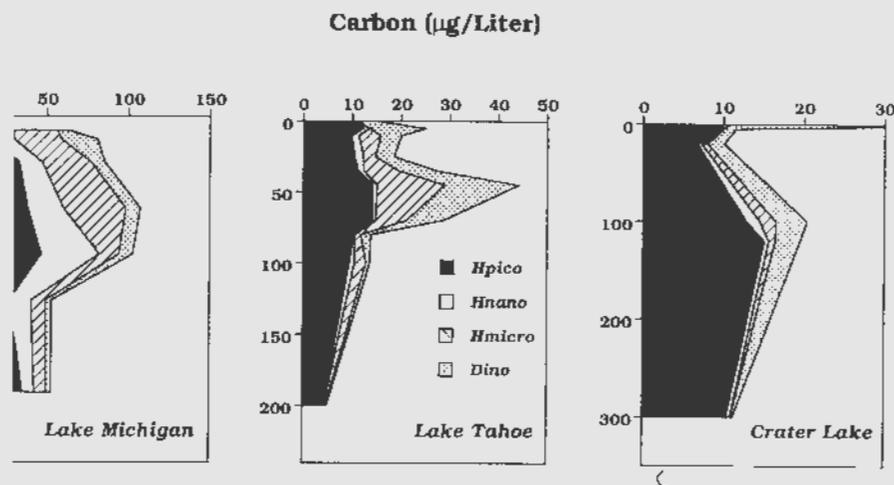


Fig. 2. Spatial distribution of microheterotrophic (MH) biomass with depth in the water column of Lakes Michigan and Tahoe, and Crater Lake.

Lake, Hnano and Hmicro were scarce throughout the water column, making up 12% of MH biomass.

Discussion

The large lake environment

The four lakes investigated here represent some of the largest and deepest lakes in the world (HERDENDORF 1982). Lakes Huron and Michigan are ranked 5th and 6th according to the HERDENDORF (1982) ordination of lakes with the largest surface. Crater Lake and Lake Tahoe are ranked 8th and 11th among the lakes with the deepest maximum depth.

A trophic gradient was evident among these four lakes, although collectively they can be described as low productivity lakes with high water clarity. Crater Lake and Lake Tahoe can be characterized as ultraoligotrophic systems, while Lakes Huron and Michigan are considered oligo- to mesotrophic (WETZEL 1983). In Crater Lake, water column chlorophyll concentrations are some of the lowest measured in any lake in the world, and associated light transparencies are also some of the deepest on record (HORNE & GOLDMAN 1994). These chlorophyll and light transmission values are comparable to those observed in the ultraoligotrophic open oceans (WETZEL 1983). Lake Tahoe is most likely ultraoligotrophic to oligotrophic, with

higher chlorophyll concentrations compared with Crater Lake. In addition, studies by GOLDMAN (1988) show that the photic zone in Lake Tahoe appears to be shrinking, as indicated by a decline in secchi depth of 7 m over the past 20 years; such changes appear to be the result of anthropogenic influences within the lake's basin (e.g. land clearance, human wastes). Lakes Huron and Michigan support higher water column chlorophyll concentrations and more shallow secchi depths (8–20 m); these levels are indicative of mesotrophic lake conditions (FAHNENSTIEL et al. 1998).

Variation in microheterotrophic biomass in time and space

The factors that explain variation in the distribution of microheterotrophs in aquatic ecosystems are difficult to ascertain, perhaps as a result of the complex mix of top-down and bottom-up interactions that influence these organisms. Thus, it is not surprising that the strength of the trophic coupling between bacteria and Hnano is not consistent among ecosystems (GASOL & VAQUE 1993). However in Lake Michigan, Hpico and Ppico abundances are kept in close check by Hnano grazing (SCAVIA & LAIRD 1987, FAHNENSTIEL et al. 1991, respectively), and changes in Hnano biomass are cor-

related with Hpico biomass (CARRICK & FAHNENSTIEL 1989). CARRICK (1990) was able to account for much of the temporal variation in Hnano and Hmicro abundance by balancing growth with grazing losses to mesozooplankton, suggesting that relatively tight coupling must exist between MH and larger metazoa.

The existence of subsurface microheterotroph maxima is not uncommon, and may be linked to higher prey abundances at depth (BOOTH et al. 1993). Subsurface MH maxima have been typically observed in both fresh- and saltwater ecosystems with sufficient light penetration to support a DCL (e.g. WETZEL 1983), and these environments usually support very diverse and plentiful phototrophic assemblages (e.g. FAHNENSTIEL & SCAVIA 1987, CAMPBELL et al. 1994). In the lakes we studied, MH biomass was nearly two times higher in the vicinity of the DCL compared with surface biomass (ratio of 1.7 deep:surface MH biomass). It seems likely that MH in these lakes are responding to changes in prey abundance, other than Hpico which were relatively constant with depth. More recent studies indicate that Hnano and Hmicro probably graze on algae in addition to bacteria, and thus may not rely strictly on bacteria for food (GASOL & VAQUE 1993).

Microbial food web structure in large lakes: a summary

The biomass of MH in all four lakes was large and appears to represent a significant fraction of phytoplankton biomass in each of these ecosystems, suggesting that microheterotrophs are significant components of the pelagic food web. For instance, the range in MH biomass in the surface waters of Lakes Huron and Michigan (68–84 $\mu\text{g L}^{-1}$) is comparable to the range in phytoplankton carbon commonly observed throughout the year in Lake Michigan (50–100 $\mu\text{g C L}^{-1}$, FAHNENSTIEL & SCAVIA 1987). This pattern has been observed in the World's oceans (e.g. BOOTH et al. 1993), and suggests that in large retentive systems, a close match between phototrophic and heterotrophic biomass is probably common (GASOL et al. 1997).

Of the MH size classes we examined, Hpico (bacteria) constituted the greatest portion of

MH biomass and the lowest amplitude of variation along both temporal and spatial scales examined here. Similar distribution patterns have been observed in both freshwater and marine systems. For instance, CAMPBELL et al. (1994) measured nearly constant Hpico biomass with depth in the North Pacific Ocean that was comparable to phototrophic biomass. PICK & CARON (1987) found that Hpico were the most abundant MH throughout the year and with depth in Lake Ontario. A complete analysis of the summer planktonic food web in all five of the St. Lawrence Great Lakes revealed that Hpico constitute approximately 40–50% of the total microheterotrophic biomass (FAHNENSTIEL et al. 1998). Hence, constancy in this relatively large pool of Hpico biomass may act as a stabilizing agent to ecosystems through the regeneration of nutrients and as a food source for a variety of heterotrophic organisms (RICCI & WETZEL 1978, DUCKLOW 1994).

Acknowledgments

This research was supported by National Science Foundation grant nos. DEB-952884 and DUE-9696148 to H. CARRICK. We thank MARK BUKLINSKA and SCOTT GIRDNER of the National Park Service for making it possible to sample Crater Lake. ROBERT RICHARDSON of UC Davis assisted in making field collections on Lake Tahoe. BILL BURNS of NOAA assisted us in field sampling on Lakes Huron and Michigan.

References

- AZAM, E., BENJEDI, J., FIELD, J. G., GRAY, J. S., MEYER-REIL, L. A. & THINGSTAD, E. 1983: The ecological role of water-column microbes in the sea. – *Mar. Ecol. Prog. Ser.* **10**: 257–263.
- BOOTH, B. C. 1993: Estimating cell concentration and biomass of autotrophic plankton using microscopy. – In: KIRBY, P. E., SHERR, B. E., SHERR, E. B. & COLE, J. J. (eds): *Handbook of Methods in Aquatic Microbial Ecology*: 199–205. Lewis Publishers, Boca Raton.
- BOOTH, B. C., LEWIN, J. & POSTELL, J. R. 1993: Temporal variation in the structure of autotrophic and heterotrophic communities in the subarctic Pacific. – *Prog. Oceanogr.* **32**: 57–99.
- CAMPBELL, L., NOLAN, H. A. & VAUGHAN, D. 1994: The importance of *Prochlorococcus* to community structure in the central North Pacific Ocean. – *Limnol. Oceanogr.* **39**: 954–961.
- CARRICK, D. A. 1983: Technique for enumeration of het-

- erotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. *Appl. Environ. Microbiol.* **46**: 491–498.
- CARRICK, H. J., 1990: *Planktonic protozoa in Lake Michigan: distribution, production and fate*. – Ph.D. Dissertation, University of Michigan. 140 pp.
- CARRICK, H. J. & FAHNENSTIEL, G. L., 1989: Biomass, size structure, and composition of phototrophic and heterotrophic nanoflagellate communities in Lakes Huron and Michigan. *Can. J. Fish. Aquat. Sci.* **46**: 1922–1928.
- CARRICK, H. J. & SCHLESKI, C. L., 1997: Have we overlooked the importance of small phytoplankton in productive waters? – *Limnol. Oceanogr.* **42**: 1613–1621.
- DUCKLOW, H. W., 1994: Modeling the microbial food web. *Microbiol. Ecol.* **28**: 303–319.
- ETON, C., 1927: *Animal Ecology*. – Macmillan Press, New York.
- FAHNENSTIEL, G. L. & CARRICK, H. J., 1992: Phototrophic picoplankton in Lakes Huron and Michigan: abundance, distribution, composition, and contribution to biomass and production. – *Can. J. Fish. Aquat. Sci.* **49**: 379–388.
- FAHNENSTIEL, G. L. & SCAVIA, D., 1987: Dynamics of Lake Michigan phytoplankton: recent changes in surface and deep communities. – *Can. J. Fish. Aquat. Sci.* **44**: 509–514.
- FAHNENSTIEL, G. L., CARRICK, H. J. & TURRIAGA, R., 1991: Physiological characteristics and food web dynamics of *Synechococcus* in Lakes Huron and Michigan. – *Limnol. Oceanogr.* **36**: 219–234.
- FAHNENSTIEL, G. L., KRUMH, A. E., MCCORMICK, M. J., CARRICK, H. J. & SCHLESKI, C. L., 1998: The structure of the planktonic food-web in the St. Lawrence Great Lakes. *J. Great Lakes Res.* in press.
- GAME, J. M. & VAUGHN, D., 1993: Lack of coupling between heterotrophic nanoflagellates and bacteria: a general phenomenon across aquatic systems. *Limnol. Oceanogr.* **38**: 657–665.
- GASOL, J. M., DEL GIORGIO, P. A. & DUARTE, C. M., 1997: Biomass distribution in marine planktonic communities. – *Limnol. Oceanogr.* **42**: 1353–1363.
- GATIS, M. A., 1984: Quantitative importance of ciliates in the planktonic biomass of lake ecosystems. *Hydrobiologia* **108**: 233–238.
- GOLDMAN, C. R., 1988: Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California Nevada. *Limnol. Oceanogr.* **33**: 1321–1333.
- HERDENDORF, C. E., 1982: Large lakes of the World. – *J. Great Lakes Res.* **8**: 379–412.
- HOBBS, J. L., DALEY, R. J. & JASPER, S., 1977: Use of Nuclepore filters for counting bacteria by fluorescence microscopy. *Appl. Environ. Microbiol.* **33**: 1225.
- HORNE, A. J. & GOLDMAN, C. R., 1994: *Limnology*. – McGraw-Hill, New York. 576 pp.
- KEMP, P. L., SHERR, B. F., SHERR, E. B. & COLL, J. J., 1993: *Handbook of Methods in Aquatic Microbial Ecology*. – Lewis Publishers.
- LINDEMAN, R. L., 1942: The trophic-dynamic aspect of ecology. – *Ecology* **23**: 399–418.
- LEE, J. J., HUNTER, S. H. & BOWLE, E. C., 1985: *An Illustrated Guide to the Protozoa*. Society of Protozoologists, Lawrence, KS.
- ODUM, E. P., 1971: *Fundamentals of Ecology*. Saunders, New York.
- PICK, F. R. & CARON, D. A., 1987: Picoplankton and nanoplankton biomass in Lake Ontario: relative contribution of phototrophic and heterotrophic communities. *Can. J. Fish. Aquat. Sci.* **44**: 2164–2172.
- RAUB, P. H. & WITZEL, R. G., 1978: Detritus in the lake ecosystem. – *Am. Nat.* **112**: 57–71.
- SCAVIA, D., 1988: On the role of bacteria in secondary production. – *Limnol. Oceanogr.* **33**: 1220–1224.
- SCAVIA, D. & LAIRD, G. A., 1987: Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. – *Limnol. Oceanogr.* **32**: 1017–1033.
- SIBICKAND, J. H. D. & PARSONS, T. R., 1972: A practical handbook of seawater analysis, 2nd Edition. – *Bull. Fish. Res. Board Can.*, Vol. 167. 310 pp.
- ULERMÖHE, H., 1958: Zur Vervollkommung der quantitativen phytoplankton. *Method. Mitt. Int. Ver. Theor. Angew. Limnol.* **9**: 38 p.
- VERTY, P. G., ROBERTSON, C. Y., IRONZO, C. R., ANDREWS, M. G., NELSON, J. R. & SERAUCKI, M. E., 1992: Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. – *Limnol. Oceanogr.* **37**: 1434–1445.
- WITZEL, R. G., 1983: *Limnology*. – Saunders Press, New York.

Authors' addresses:

H. J. CARRICK, A. PADMANABHA, L. WEAVER, Great Lakes Center, SUNY College at Buffalo, Buffalo, New York, USA.

G. L. FAHNENSTIEL, Lake Michigan Field Station, National Oceanic and Atmospheric Administration, Muskegon, Michigan, USA.

C. R. GOLDMAN, Division of Environmental Studies, University of California, Davis, California, USA.

