VARIATION IN THE BIOMASS OF FUNCTIONAL GROUPS COMPRISING THE OPEN-WATER PLANKTON OF SHALLOW LAKES IN IRELAND

Elvira de Eyto and Kenneth Irvine

ABSTRACT

The open-water plankton form a complex food web that is crucial to the cycling of nutrients through the ecosystem. This food web consists of two interconnected loops: the classical grazer loop and the microbial loop. Here, we describe in detail the seasonal composition and biomass of the planktonic food web of six Irish shallow lakes. The lakes were sampled three times in 2000, and the biomass of zooplankton, phytoplankton, ciliates, flagellates and bacteria was measured. Total biomass ranged from 0.08μg C ml^{-1} to 1.47μg C ml^{-1}, and a significant portion of the biomass comprised microbial elements. Zooplankton biomass was generally highest in April, corresponding with large amounts of *Daphnia*. With the exception of zooplankton, all other group biomasses were correlated with physicochemical parameters indicative of nutrient status.

Elvira de Eyto (corresponding author; e-mail: elvira.deeyto@marine.ie), Marine Institute, Furnace, Newport, Co. Mayo; Kenneth Irvine, Department of Zoology, Trinity College, University of Dublin.

Received 11 September 2003. Read 31 January 2005. Published 31 March 2005.

INTRODUCTION

Although Ireland has a wealth of lakes, very little study has been focused on the open-water plankton communities and the factors that contribute to their structure. In particular, the planktonic microbial communities of Irish lakes (comprising bacteria, autotrophic picoplankton, heterotrophic flagellates and ciliates) have been generally ignored, even though recognition of the importance of the microbial component of the open-water plankton in the functioning of lake food webs has increased in recent years (Porter 1996; Carrick *et al.* 2000). The relative importance of the microbial component in the productivity of the open-water plankton is still unclear, although it is has been shown in several studies that its significance decreases with increasing trophic state (Porter *et al.* 1988; Weisse and Stockner 1993; Jeppensen *et al.* 1998), even though the actual abundance of microbes may increase. While the cascading effects of fish stock changes on zooplankton and phytoplankton can be dramatic, the effects may be diminished by the time they reach the microbial components (Jeppensen *et al.* 1998). Nevertheless, the importance of microbial interactions should not be underestimated simply because they are harder to observe and enumerate, as classical food web theory may not be sufficient to explain ecological changes resulting from biomanipulation or lake restoration. This is particularly true for lakes where *Daphnia* is not the primary grazer, as it has been shown that, in the absence of *Daphnia*, the microbial community can be much more abundant and diverse (Ventelä 1999; Straškrabová *et al.* 2000).

The microbial component of the open-water food web is perhaps more complex than the classical grazer (metazooplankton and phytoplankton) component, as there are many links between the groups making up the microbes. APP (autotrophic picoplankton) and bacteria can be considered the primary producers within the microbial component. In the case of bacteria, they may be autotrophic themselves, or they may utilise particulate and soluble nutrients released by algae, crustacean zooplankton and fish, as well as other microbes (Azam *et al.* 1983). In lakes, 50–100% of phytoplankton carbon production may pass through bacterioplankton (Simon 1987). It is thought that most bacterial production is transferred primarily to protozoan microzooplankton and does not reach higher trophic levels directly (Simon 1987). Flagellates provide the link between picoplankton (APP and heterotrophic bacteria) and ciliates, as they are the main bacterivores in freshwater (Jürgens and Stolpe 1995). Ciliate assemblages in lakes are mixed assemblages of species that live on a wide range of food types, including bacteria and flagellates (Müller 1989). It is assumed that group-cannibalism occurs among ciliates and flagellates, but estimates of its extent are unknown (Weisse 1990). The main link between the microbial and classical components of the open-water food web is grazing by zooplankton. *Daphnia* are thought to be the most important grazers of microbial animals, and hence have the largest ability to suppress microbial biomass in the open-water plankton (Pace and Funke 1991). This is largely owing to sizes on which they can feed, which range from bacteria to larger ciliates. However, copepods and rotifers can also significantly impact on microbial biomass primarily through grazing on ciliates. This, in turn, has cascading effects on flagellate and bacterial biomass (Jürgens and Jeppensen 2000).

The main aim of this paper is to describe for the first time the total open-water planktonic community of several different Irish lakes. We describe the biomass of functional groups in the open-water plankton of six Irish shallow lakes (mean depth <3 metres), sampled in spring, early summer and late summer. The five functional groups are defined as and separated into bacteria, flagellates (heterotrophic nanoflagellates or HNF), ciliates, phytoplankton (including autotrophic picoplankton or APP) and zooplankton (comprising rotifers, copepods and cladocerans). We also analysed whether standard physicochemical variables can account for the observed variation in the biomass of functional groups in the six lakes.

METHODS

STUDY SITES AND FIELD SAMPLING

The six lakes chosen for this study cover a range of the physicochemical and ecological conditions found in Ireland (Table 1). The lakes were sampled in April, June and August 2000. Composite water samples were collected on each sampling occasion from the deepest point of each lake using a three-metre plastic tube. In lakes with a maximum depth of less than three metres, the water samples were taken at 30–50cm depth. Portions of these water samples were preserved with Lugol's iodine for phytoplankton and ciliate counts and with Formalin (final concentration 1.5%) for counts of bacteria, heterotrophic nanoflagellates (HNF) and autotrophic picoplankton (APP). The rest of the water was used for chemical analysis. Zooplankton were sampled by vertical hauls of the water column using a conical zooplankton net (53μm mesh). A flow meter was used to correct results for filtering efficiency. Where the lake was too shallow for effective use of the net, ten litres of water were collected using a perspex tube (diameter 5.5cm, volume 2276cm^2). Four samples were taken from the deepest point of each lake, and preserved in $>70\%$ ethanol.

CHEMICAL ANALYSIS AND BIOMASS DETERMINATION

Total phosphorus (μg l^{-1}), chlorophyll *a* (μg l^{-1}), pH, alkalinity (mg $CaCO_3$ l^{-1}), conductivity (μ siemens cm^{-1}), turbidity (NTU) and colour (PtCo) were measured in the laboratory using standard methods. To count and measure bacteria, HNF and APP, aliquots were filtered onto black 0.22μm Isopore filters, stained with DAPI and counted using epiflouresence, following the methodologies of Porter and Feig (1980) and Kemp *et al.* (1993). Digital photographs of the fields of view at × 1000 magnification were taken, and individuals were counted and measured using the computer programme Scion Image, version 4.0.2. Phytoplankton, ciliates and rotifers were counted and measured using an inverted microscope (× 400 magnification) and an eyepiece graticule. Zooplankton samples were subsampled using a 5ml-wide bore pipette, and counted and measured using a dissecting microscope (× 30).

Individual measurements were converted into biomass (pg carbon) using the conversion factors in Gaedke (1992). The body sizes of bacteria, APP, HNF, phytoplankton and ciliates were calculated from standard geometric formulas. Colonial phytoplankton were treated as individuals only in

Table 1 — Characteristics and morphometric data for the six Irish lakes in this study.

Lake (basin)	*Position*	*Mean depth (m)*	*Catchment composition*	*Annual retention time (yrs)*	*Area (ha)*	*Trophic status*
Carra (north)	53°42′N 09°15′W	2.0	Calcareous	0.20	1500	Oligotrophic
Gara (south)	53°55′N 08°27′W	1.0	Calcareous	0.02	202	Mesotrophic
Gur	52°31′N 08°32′W	1.5	Calcareous	0.21	78	Highly eutrophic
Maumwee	53°28′N 09°32′W	2.0	Organic	0.10	27	Oligotrophic
Mullagh	53°49′N 06°57′W	2.3	Siliceous	1.34	35	Highly eutrophic
Ramor	53°49′N 07°04′W	3.0	Siliceous	0.17	741	Hypertrophic

Trophic status is classified according to the modified version of (OECD 1982) used by the Irish EPA (Lucey *et al.* 1999) according to maximum values of chlorophyll *a*.

cases where it was too difficult to differentiate between cells that shared a common surface area. In general, therefore, the individual cells of the colony were counted and measured. Measurements of rotifers were converted to dry weight using the methods of Latja and Salonen (1978) and Telesh *et al*. (1998). Measurements of the larger crustaceans were converted to dry weights using length–weight regressions calculated for various species from each lake during the course of the study (Table 2), or using values from Bottrell *et al*. (1976). Physicochemical and biological variables were averaged over the three sampling occasions and log$_e$ transformed where necessary, and bivariate relationships were examined using Pearson correlation coefficients.

RESULTS

Total open-water planktonic biomass ranged from 0.08μg C ml^{-1} in Lough Gara in April to 1.47μg C ml^{-1} in Lough Mullagh in August. Generally, Lough Ramor and Lough Mullagh had the highest biomass, Lough Gara and Lough Maumwee the lowest, with biomass in Lough Carra and Lough Gur intermediate between the two. When the total open-water biomass was divided into the five functional groups—bacteria, ciliates, flagellates (heterotrophic nanoflagellates), phytoplankton (including autotropic picoplankton) and zooplankton—a more detailed picture of the variation between lakes and months emerged (Fig. 1). Bacterial biomass ranged from 0.009μg C ml^{-1} to 0.189μg C ml^{-1}. In the majority of lakes, bacterial biomass tended to increase from April to June, and drop again in August. Bacteria often made up a large component of the total open-water biomass. On two occasions half of the total biomass in Lough Gara was bacterial. Ciliate biomass ranged from 0.0006μg C ml^{-1} to 0.023μg C ml^{-1}. It was highest in August, except in Lough Mullagh. The biomass of flagellates ranged from 0.001μg C ml^{-1} to 0.176μg C ml^{-1}. There were no obvious trends in the flagellate biomass over the sampling period, except that in most lakes it was lowest in April. The biomass of flagellates and ciliates was generally low in all lakes, comprising on average only about 9% of the total biomass. Phytoplankton biomass ranged from 0.006μg C ml^{-1} to 1.281μg C ml^{-1}. For the three most productive lakes, Gur, Mullagh and Ramor, the highest phytoplankton biomass occurred in August. The high phytoplankton biomass in August in Lough Mullagh and Lough Ramor was made up largely of cyanophytes such as *Anabaena* and *Oscillatoria*. Cyanophytes also made a large contribution to the total biomass in Lough Gur in June, although by August, chlorophytes, in particular *Kirchneriella* sp., had replaced the cyanophytes and dominated the phytoplankton. Phytoplankton was consistently the group with the highest biomass in Lough Maumwee. In June and August, a large proportion of this biomass was a chlorophyte

Table 2—Linear regressions relating length (mm) with dry weight (μg) in freshwater crustaceans from Irish lakes using the equation $\mathrm{LnW} = \mathrm{Ln}a + b\,\mathrm{LnL}$.

Lake	*Date*	*Species*	*Range in length (mm)*	*n*	*Lnza*	*b ± 95% c.i.*	*rms*	*d.f.*	*F*	*P*
Ramor	Sept. 2000	*Cyclops* sp.	0.49–1.09	33	1.583	1.820 ± 0.612	0.1969	1:31	39	< 0.01
		Daphnia hyalina Leydig	0.39–1.30	44	2.086	2.293 ± 0.422	0.1509	1:42	201	< 0.01
		Leptodora kindti (Focke)	2.10–7.35	17	0.077	2.406 ± 0.372	0.0698	1:15	200	< 0.01
Mullagh	Sept. 2000	*Daphnia hyalina* Leydig	0.49–1.19	35	1.916	2.104 ± 0.466	0.1186	1:33	92	< 0.01
		Diaptomus gracilis (Sars)	0.49–1.30	43	1.924	2.067 ± 0.327	0.0767	1:41	229	< 0.01
		Cyclops sp.	0.49–1.02	30	2.235	2.548 ± 0.505	0.1199	1:28	100	< 0.01
		Ceriodaphnia dubia Richard	0.32–0.49	13	1.820	1.497 ± 0.833	0.1347	1:11	7	< 0.01
Maumwee	Oct. 2000	*Cyclops* sp.	0.49–1.09	34	1.713	1.451 ± 0.651	0.2309	1:32	22	< 0.01
		Holopedium gibberum Zaddach	0.60–1.09	30	2.163	2.410 ± 0.472	0.0879	1:28	86	< 0.01
		Bosmina coregoni Baird	0.32–0.60	16	2.326	1.959 ± 0.817	0.2068	1:14	17	< 0.01
Carra	May 2001	*Daphnia hyalina* Leydig	0.81–1.72	43	2.545	1.207 ± 0.343	0.0692	1:41	35	< 0.01
		Diaptomus gracilis (Sars)	0.70–1.30	35	2.597	2.334 ± 0.784	0.3050	1:33	25	< 0.01

n = number of observations; ci = confidence interval; d.f. = degrees of freedom; *F* = variance ratio; *P* = level of significance; rms = residual mean square.

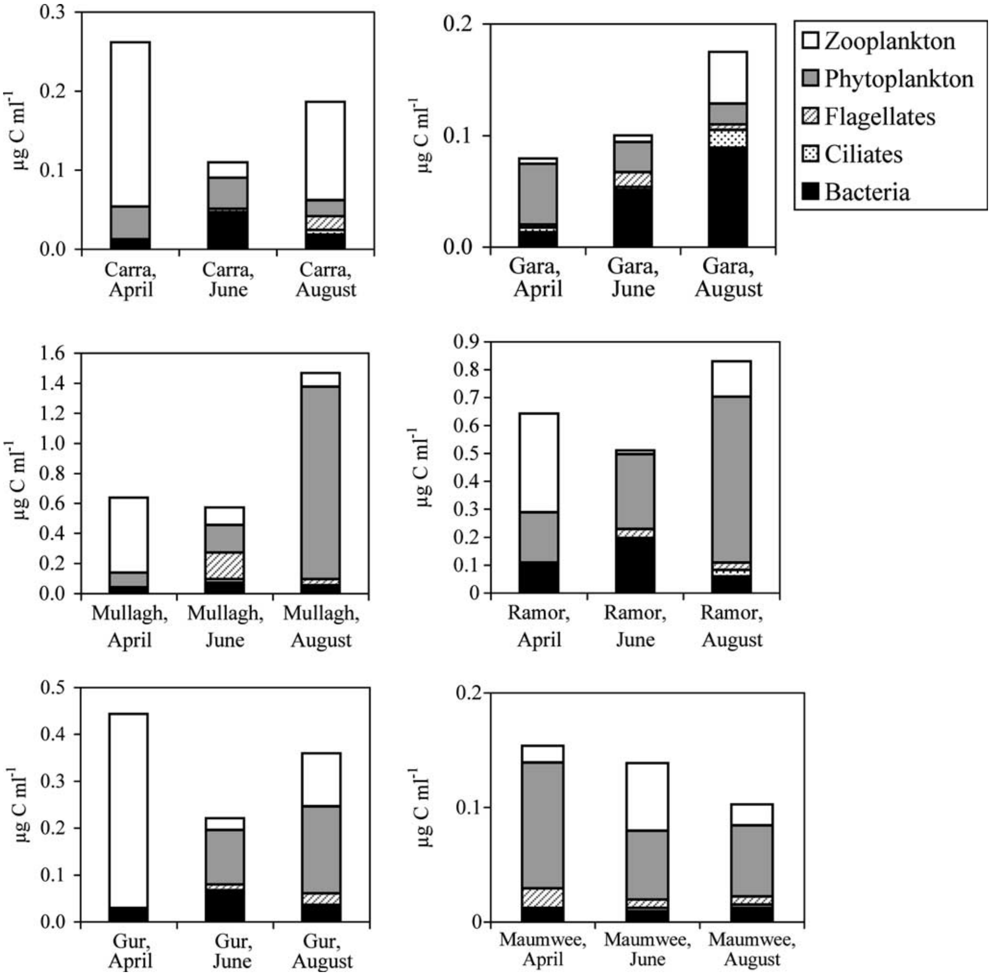

Fig. 1 — Biomass (μg C ml^{-1}) of planktonic functional groups sampled in the open water of six Irish shallow lakes in April, June and August 2000.

species, probably *Pseudobulbochaete* sp., whereas *Dinobryon* dominated in April. Zooplankton biomass ranged from 0.004μg C ml^{-1} to 0.502μg C ml^{-1}. In four out of the six lakes, zooplankton biomass was highest in April, which corresponded with large numbers of large cladocerans, particularly *Daphnia hyalina* (Fig. 2). Rotifers also had highest biomass in April. By August, copepods made up the majority of zooplankton biomass in most lakes. Small cladocerans were abundant in April, and again in August in some lakes, but had very low biomass in June. In contrast, predatory cladocerans such as *Leptodora kindtii* and *Polyphemus pediculus* generally had highest biomass in June, although there was a very large biomass of *Leptodora* in Lough Mullagh in August (Fig. 2).

Predictably, many of the physicochemical variables formed autocorrelating groups, specifically alkalinity, pH and conductivity, and chlorophyll *a*, turbidity and total phosphorus. In addition, all of the functional groups except zooplankton biomass were significantly correlated with at least one physicochemical variable (Table 3). Bacterial biomass was positively correlated with turbidity and total phosphorus, ciliate biomass was positively correlated with turbidity and increasing phytoplankton, and flagellate biomass was reflected in increasing chlorophyll *a* values.

DISCUSSION

Our results highlight the two interconnected parts of the open-water food web — one comprising bacteria as the main primary producers, being fed on by ciliates and flagellates, and the other comprising phytoplankton as the primary producers, being fed on by zooplankton. However, the microbial loop is not a separate web, and it is connected to the classical grazer loop by many direct and indirect pathways (Jürgens and Jeppensen 2000). It has been shown that the main link

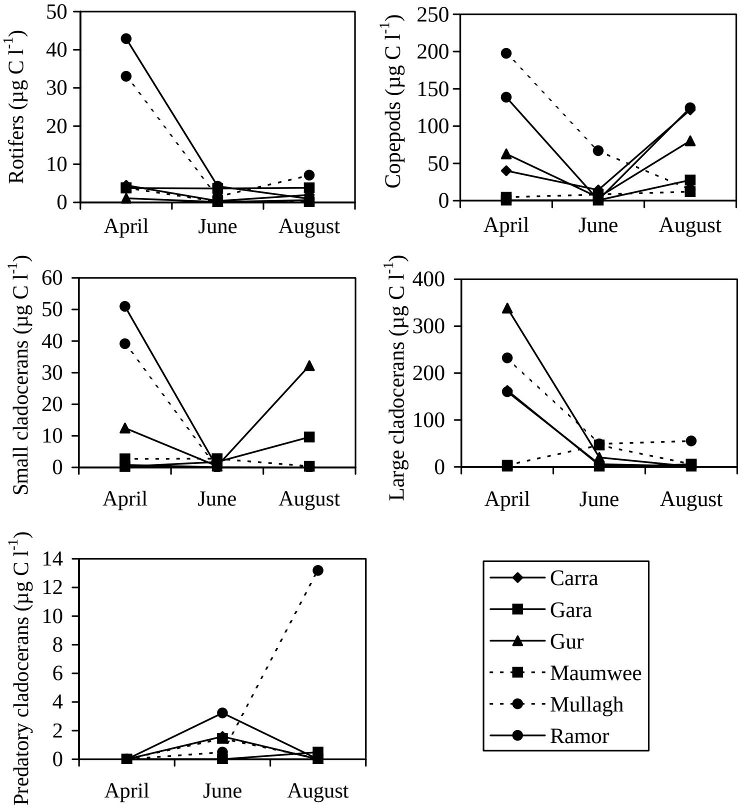

Fig. 2—Biomass (µg C l^{-1}) of zooplankton components sampled in the open water of six Irish shallow lakes in April, June and August 2000. 'Large cladocerans' does not include the predatory species.

between the microbial and classical grazer loop is grazing by rotifers, copepods and cladocera on the microbes. We did not find any direct evidence of this interaction, although lowest levels of microbial biomass (bacteria, flagellates and ciliates) were found in the presence of *Daphnia*, which occurred chiefly in April. While it is very likely that the five functional groups do follow predictable seasonal cycles, it is likely that the temporal resolution of our data is not sufficient to enable their detection, as weekly or fortnightly samples are probably required to accurately describe seasonal succession. Nevertheless, our data do indicate that there are large-scale changes over the year in the relative contribution each group makes to the total biomass.

The data presented here highlight the relative importance of the microbial component of the open-water plankton. When all the sampling dates are combined, the microbial biomass constituted about one quarter of the total biomass, and in several cases, more than half. Irish shallow lakes have quite similar microbial abundances to those found elsewhere. The microbial biomass found in this study is in the same range as that found in Northern European mountain lakes (Straškrabová *et al.* 2000), and the bacterial abundances in this study are also in the same range as those found in Lake Constance (0.01–0.15µg C ml^{-1}) (Simon 1987). The microbial element represents a whole section of the food web capable of transferring significant energy through several successive trophic levels. This is hinted at by the

Table 3—Significant ($P < 0.05$) Pearson product correlation coefficients (r) between physicochemical variables and the biomass of functional groups of openwater plankton, sampled from six lakes in April, June and August 2000 ($n = 18$).

	pH	*Ln conductivity (µ siemens cm^{-1})*	*Ln total alkalinity (mg $CaCO_3$ l^{-1})*	*Ln turbidity (NTU)*	*Ln chlorophyll a (µg l^{-1})*	*Ln total phophorus (µg P l^{-1})*	*Ln colour (PtCo)*
PH	—	—	—	—	—	—	—
Ln conductivity (µ siemens cm^{-1})	0.83	—	—	—	—	—	—
Ln total alkalinity (mg $CaCO_3$ l^{-1})	0.84	0.99	—	—	—	—	—
Ln turbidity (NTU)	—	—	—	—	0.90	—	—
Ln chlorophyll *a* (µg l^{-1})	—	—	—	—	—	—	—
Ln total phosphorus (µg p l^{-1})	—	—	—	0.94	0.96	—	—
Ln colour (PtCo)	—	—	—	—	—	—	—
	—	—	—	—	—	—	—
Ln bacteria (pg C ml^{-1})	—	—	—	0.88	—	0.89	—
Ln ciliate (pg C ml^{-1})	—	—	—	0.87	—	—	—
Ln flagellate (pg C ml^{-1})	—	—	—	—	0.85	—	—
Ln phytoplankton (pg C ml^{-1})	—	—	—	—	0.88	—	—
Ln zooplankton (pg C ml^{-1})	—	—	—	—	—	—	—
Ln total biomass (pg C ml^{-1})	—	—	—	0.89	0.96	0.90	—

results of the correlations, as bacterial, ciliate and flagellate biomass are all positively correlated with physicochemical variables indicative of nutrient status. This suggests that bottom-up control by nutrients is the main determinate of the microbial part of the open-water plankton biomass in shallow lakes. The fact that bacterial biomass was strongly correlated with total phosphorus indicates that phosphorus may be the main limiting factor controlling bacterial production. This is in agreement with the model put forward by Currie (1990) that concluded that bacteria compete with algae for phosphorus in the open water. This has implications for the quantification of phosphorus cycling within Irish shallow lakes, as it seems that the microbial elements may be equally as significant in terms of utilising nutrients as the traditional phytoplankton–zooplankton web.

ACKNOWLEDGEMENTS

The authors would like to thank Peter Stafford, Alison Boyce, Ruth Little and Rossana Caroni for technical support and fieldwork assistance. This work was funded under the European 5th Framework Programme, as part of the ECOFRAME project, *Ecological quality and functioning of shallow lake systems with respect to the needs of the European Water Framework Directive*, project no. EVK1–1999–00261.

REFERENCES

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A. and Thingstad, F. 1983 The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* **10**, 257–63.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. 1976 A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* **24**, 419–56.

Carrick, H.J., Padmanabha, A., Weaver, L., Fahnenstiel, G.L. and Goldman, C.R. 2000 Importance of the microbial food web in large lakes (USA). *Verhandlungen der Internationale Verein für Limnologie* **27**, 3170–5.

Currie, D.J. 1990 Large-scale variability and interactions among phytoplankton, bacterioplankton, and phosphorus. *Limnology and Oceanography* **35**, 1437–55.

Gaedke, U. 1992 The size distribution of plankton biomass in a large lake and its seasonal variability. *Limnology and Oceanography* **37**, 1202–20.

Jeppensen, E., Søndergaard, M., Jensen, J.P., Mortensen, E., Hansen, A. and Jørgensen, T. 1998 Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: an 18-year study of a shallow hypertrophic lake. *Ecosystems* **1**, 250–67.

Jürgens, K. and Jeppensen, E. 2000 The impact of metazooplankton on the structure of the microbial food web in a shallow hypertrophic lake. *Journal of Plankton Research* **22**, 1047–70.

Jürgens, K. and Stolpe, G. 1995 Seasonal dynamics of crustacean zooplankton, heterotrophic nanoflagellates and bacteria in a shallow, eutrophic lake. *Freshwater Biology* **33**, 27–38.

Kemp, P.F., Sherr, B.F., Sherr, E.B. and Cole, J.J. 1993 *Handbook of methods in aquatic microbial ecology*. Chelsea, MI. Lewis.

Latja, R. and Salonen, K. 1978 Carbon analysis for the determination of individual biomasses of planktonic animals. *Verhandlungen der Internationale Verein für Limnologie* **20**, 2556–60.

Lucey J., Bowman, J.J., Clabby, K.J., Cunningham, P., Lehane, M., MacCarthaigh, M., McGarrigle, M.L. and Toner, P.F. 1999 *Water quality in Ireland, 1995–1997*. Wexford. Environmental Protection Agency.

Müller, H. 1989 The relative importance of different ciliate taxa in the pelagic food web of Lake Constance. *Microbial Ecology* **18**, 261–73.

OECD 1982 Eutrophication of waters, monitoring, assessment and control. Paris. OECD.

Pace, M.L. and Funke, E. 1991 Regulation of planktonic microbial communities by nutrients and herbivores. *Ecology* **72**, 904–14.

Porter, K.G. 1996 Integrating the microbial loop and the classic food web into a realistic planktonic food web. In K.O. Winemiller (ed.), *Food webs. Integration of patterns and dynamics*. New York. Chapman and Hall.

Porter, K.G. and Feig, Y.S. 1980 The use of DAPI for identifying and counting aquatic microflora. *Limnology and Oceanography* **25**, 943–8.

Porter, K.G., Paerl, R., Hodson, R., Pace, M.L., Priscau, B., Riemann, D., Scavia, D. and Stockner, J. 1988 Microbial interactions in lake food webs. In S.R. Carpenter (ed.), *Complex interactions in lake communities*. New York. Springer-Verlag.

Simon, M. 1987 Biomass and production of small and large free-living and attached bacteria in Lake Constance. *Limnology and Oceanography* **32**, 591–607.

Straškrabová, V., Šimek, K., Macek, M., Hartman, P., Fott, J. and Blazo, M. 2000 Pelagic food webs and microbial loop in low-alkalinity mountain lakes. *Verhandlungen der Internationale Verein für Limnologie* **27**, 513–16.

Telesh, I.V., Rahkola, M. and Viljanen, M. 1998 Carbon content of some freshwater rotifers. *Hydrobiologia* **378/388**, 355–60.

Ventelä, A. 1999 Lake restoration and trophic interactions: is the classical food chain theory sufficient. Turku. University of Turku.

Weisse, T. 1990 Trophic interaction among heterotrophic microplankton, nanoplankton, and bacteria in Lake Constance. *Hydrobiologia* **191**, 111–22.

Weisse, T. and Stockner, J. 1993 Eutrophication: the role of microbial food webs. *Memorie dell'Istituto Italiano di Idrobiologia* **52**, 133–50.

The subvention granted by Trinity College Dublin, towards the cost of publication of papers by members of its staff is gratefully acknowledged by the Royal Irish Academy.