HYPERTROPHIC PHYTOPLANKTON: AN OVERVIEW

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Introduction

Nowadays, the structure and function of freshwater phytoplankton are reasonably well understood (Reynolds 1984a; Harris 1986). Most phytoplankton studies have been carried out in temperate lakes whose trophic status ranges from oligotrophy to (natural) eutrophy. Unfortunately, in recent years a rapidly increasing trend in nutrient concentrations is clearly seen in many temperate lakes, where no remedial action has been carried out. This situation is especially dramatic in the Third World where water resources are very threatened, but is also common in Western countries as a result of heavy, often industrial pollution in watersheds. This is the reason why many freshwater ecosystems became hypertrophic and many more will be in the near future. Remedial actions, when carried out, often act on discharge, but internal loadings and non-point sources may postpone water quality improvement for a long time.

Despite the increasing number of hypertrophic freshwater ecosystems, reports on hypertrophic limnology are still scarce (Barica & Mur 1980) as compared with those on lakes of lesser trophic status. Furthermore, studies on hypertrophic phytoplankton are uncommon; studies on the ecophysiology and field biology of *Oscillatoria* spp. (e.g., van Liere 1979; Zevenboom 1980; Foy & Gibson 1982; Berger 1987; Meffert 1989) cover only a small part of hypertrophic phytoplankton biology. Although information is highly scattered throughout the literature, we feel it is time to undertake a preliminary approach to hypertophic phytoplankton in order to explore the subject and to suggest uncovered areas of research in this interesting and unfortunately increasingly important theme.

We shall restrict ourselves to stagnant environments. Hypertrophic streams also exist but are even less well known. What do we mean by freshwater, hypertrophic ecosystems? Since mass loadings are sometimes difficult to ascertain, and nutrient concentrations in the water are misleading in view of internal cell quotas (Droop 1983), we have used a community criterion to define hypertrophic environments. They are those whose yearly average of phytoplankton chlorophyll is equal to or higher than 100 mg per cubic metre of water (OECD 1982). Hypertrophic ecosystems could include the shallow polymictic lakes of Ireland (Lough Neagh), Scotland (Loch Leven), England (Norfolk Broads), the Netherlands (Drontmeer, IJsselmeer, Loosdrecht, Wolderwijd), Denmark (Arreskov, Lange, Sobygard, Sollerod), Japan (Kasumigaura, Teganuma), USA (Onondaga, Sebasticook, Sylvan), Spain (Albufera lakes, gravel-pit lakes close to heavily polluted watercourses) and lots more. But they also include the fertilized fish ponds in Central Europe (Poland, Czechoslovakia), India, Israel and China, and aerobic waste-water treatment lagoons (including high rate oxidation ponds) spread throughout the world. Earlier studies on hypertrophic phytoplankton include those of Bursche (1954) in the Locknitz lakes, Steeman-Nielsen (1955) in Sollerod So, Bucka (1960) and Hepher (1962) in Polish and Israeli fish ponds, Wetzel (1966) in Lake Sylvan and Mackenthun et al. (1966) in Lake Sebasticook.

This overview will deal with species composition, diversity, biomass, primary production, losses and seasonal succession of hypertrophic phytoplankton. Other topics, such as population dynamics and ecophysiological issues, either lack information enough to be considered or are well known, e.g. *Microcystis* and *Oscillatoria* ecophysiology (Reynolds 1987).

Species composition and diversity

Hypertrophic phytoplankton is comprised of a small number of taxonomic groups in comparison with other phytoplankton. The main groups are cyanobacteria, Chlorophyceae, Cryptophyceae and Euglenophyceae. Diatoms usually attain biomasses much lower than the preceeding groups. Other groups commonly living in freshwater ecosystems of lesser trophic degree, are either absent or present in very low numbers in hypertrophic sites. These are desmids, dinoflagellates, Chrysophyceae and Xanthophyceae, although some bloom-forming species of these groups sometimes have been reported for hypertrophic areas (see Berger & Sweers 1988; Moss 1973; Sanchez-Castillo 1990).

Hypertrophic cyanobacteria include members *of* the Chroococcales (mainly *Microcystis),* Oscillatoriales *(Oscillatoria, Pseudanabaena)* and Nostocales *(Anabaena, Aphanizomenon).* The dominant hypertrophic species are the following: *Microcystis aeruginosa* (Mackenthun et al. 1966), *Oscillatoria (Planktothrix) agardhii* (Berger 1989; Jones 1977a; Romo 1991), *O. (Limnothrix) redekei, Pseudanabaena* spp. (Jewson 1976; Berger & Sweers 1988), *Anabaena flos-aquae* and *Aphanizomenon* spp. (Fyns Amt 1991a, b).

The Chlorophyceae are mostly comprised of Volvocales and Chlorococcales. Volvocales are usually unicellular species, mostly belonging to *Chlamydomonas, Carteria* and the like (Rojo 1990; Berger &

Sweers 1988; Elber & Schanz 1989; Wrigley & Toerien 1990), but some colonial forms can also be found, such as *Pandorina* and *Eudorina* (Rojo 1990). Microscopical determinations of Volvocales are difficult since the specimens should be viewed *"in vivo";* this is the reason for the many *"Chlamydomonas* spp." seen in lists of hypertrophic algae. Chloroccocales are by far the most diverse group occurring in hypertrophic phytoplankton. In fact, a great deal of the Chloroccocales cited in the classic monograph by Komarek & Fott (1983) have been reported from highly eutrophic to hypertrophic environments. Many *Scenedesmus, Actinastrum, Chlorella, Coelastrum, Monoraphidium* and *Oocystis* species are found in hypertrophic assemblages (Leah et al. 1980; Sze 1980; Takamura et al. 1989).

Some species of Cryptophyceae attain high biomasses in hypertrophic environments. *Cryptomonas,* mostly *C. erosa* and its varieties, and *Rhodomonas minuta* are the most frequent species (Fott 1975; Elber & Schanz 1989; Rojo 1990).

Euglenophytes are also very common, especially in ecosystems with high organic matter and ammonia concentrations (Pringsheim 1952, 1956). *Euglena, Phacus, Trachelomonas* and some colourless species are the main representatives of this group in hypertrophic environments (Azov et al. 1980; Wrigley & Toerien 1990; Garcia et al., pers. comm.).

Diatoms are mostly comprised of some centric species. *Cyclotella meneghiniana* and *Stephanodlscus hantzschii* (Leah et al. 1980; Rojo 1990) have been recorded very often but some *Melosira (Aulacoseira)* species have also been reported (Bailey-Watts 1978; Gibson et al. 1971). Very interestingly, some typical species of lesser trophic status, such as the pennates *Asterionella formosa* and *Diatoma elongatum,* have also been recorded for hypertrophic environments (Bailey-Watts 1978; Berger & Sweers 1988; Olrik et al. 1984). Another interesting appearance in hypertrophic lakes is that of *Nitzschia* species, mostly belonging to the *lanceolatae* group *(sensu* Hustedt 1930) since they have been rarely recorded in temperate, lacustrine phytoplankton; e.g. Lake El Porcal (Alvarez Cobelas & Rojo 1990) and hypertrophic Danish lakes (Jacobsen, unpublished).

Concerning morphological features, most hypertrophic species experience motility, either by buoyancy mechanisms (cyanobacteria) or flagella (volvocales, cryptophytes, euglenophytes). Filaments, colonies, coenobiae and flagellated unicells are the dominating morphotypes (Bailey-Watts & Kirika 1981; Rojo 1990).

Species diversity has rarely been calculated. Furthermore, the data appear to be very scanty in relation to seasonal cycles, and have been calculated only on an individual, proportional basis ("bits" per individual, Table 1). Values cover almost the whole spectrum of diversity measured in freshwater ecosystems (Margalef 1983) but on the average appear to be lower than that calculated from other non-hypertrophic ecosystems. Studies reporting seasonal phytoplankton diversity in hypertrophic environments found high fluctuations (1.5 bits per individual and week) (Moss 1973; Rojo 1990) throughout the year, and diversity usually changes as a result of either disturbances (Rojo & Alvarez Cobelas 1992) or overlapping algal populations with balanced cell numbers (Moss 1973).

Table 1. Phytoplankton diversity (bits per individual) in hypertrophic lakes. All data refer to phytoplankton *units (filaments, colonies, unicells). Only surface samples are considered.* Oligotrophic (Rosensee), mesotrophic (Priddy Pool) and eutrophic (Kaminsee II) communities are also given for comparison.

Lake	*Year of study*	*Range*	*Mean ± 1 SD*	*Reference*
Abbot's Pond	1966-1977	0.0–3.0	0.9 ± 1.0	Moss (1973)
Albufera de Valencia	1981-1987	0.8–3.5	2.3 ± 0.7	Romo (1991)
Albufera Honda	1984–1985	0.3–2.2	1.0 ± 0.8	Sánchez-Castillo (1990)
Arreskov	1990	1.2–3.4	2.3 ± 0.7	Fyns Amt (1991*b*)
El Porcal	1984–1985	0.3–3.1	2.2 ± 0.8	Rojo & Alvarez (1992)
Kaminsee I	1984	0.1–2.3	1.4 ± 0.9	Elber & Schanz (1989)
Kaminsee II	1984	1.3–2.8	2.2 ± 0.5	Elber & Schanz (1989)
Lange	1990	0.5–3.3	1.9 ± 0.8	Fyns Amt (1991a)
Priddy Pool	1962–1963	0.8–3.5	2.3 ± 0.8	Moss (1973)
Rosensee	1984	2.6–3.8	3.2 ± 0.5	Elber & Schanz (1989)
Smyslov	1972	0.2–4.5	2.1 ± 1.3	Fott (1975)

Biomass

Hypertrophic phytoplankton experiences high fluctuations during the year (Barica 1981) that can be easily detected using either microscopic counts or measurements of chlorophyll-a. As a result, very broad ranges are depicted (Table 2) for both chlorophyll and total biovolume. Such fluctuations shall be dealt with below. Suffice it here to say that maximal peaks of areal chlorophyll (i.e. milligrams of chlorophyll per square metre of lake surface) are well above those predicted by theoretical approaches (Tailing et al. 1973). The reason for this is not clear yet but an explanation is outlined below.

Primary production

Phytoplankton productivity of hypertrophic environments is the highest in the trophic rankings. These high values are sustained by the high nutrient

Table 2. Ranges of phytoplankton biomass (B, mm^3 fresh weight per litre of lakewater) and Chlorophyll-a (Chla, mg per m^2 or mg per m^3 (*)) in hypertrophic environments. Only surface values have been used for biomass as no other data are currently available. HROP indicates high rate oxidation pond.

Lake	*Year of study*	*B*	*Chla*	*Reference*
Albufera de Valencia	1981–1987	6–377	212–815	Romo (1991)
Albufera Honda	1984–1985	–	50–285	Sánchez-Castillo (1990)
Arreskov	1990	2–63	20–1000*	Fyns Amt (1991b)
El Porcal	1984–1985	5–309	22–420	Rojo (1990)
Field ponds at Turew (Poland)	1983	0.3–183	–	Jurkowska (1987)
Hartbeesport Dam	1981–1982	–	14–738	Robarts (1984)
Hjarbæk Fjord	1980–1981	0.5–26	–	Olrik et al. (1984)
HROP at Barcelona	1989–1990	–	30–1470	García et al. (pers. comm.)
HROP at Jerusalem	–	–	100–520	Abeliovich & Azov (1976)
IJsselmeer	1976	–	50–260*	Berger (1987)
Kasumigaura	1957–1978	5–400	–	Toda et al. (1981)
Kinnego Bay (Lough Neagh)	1973–1974	5–63	30–328	Jones (1977a)
Lange	1990	3–143	5–300*	Fyns Amt (1991a)
Lauwersmeer	1981	–	130–190*	Berger (1987)
Loch Leven	1968–1976	2–93	10–988	Bailey-Watts (1978)
Lough Neagh	1971–1972	3–18	65–165	Jewson (1976)
Sebasticook	1965	15–560	18–161	Mackenthun et al. (1966)
Teganuma	1983–1984	–	250–1000*	Takamura et al. (1989)
Wolderwijd	1971–1982	–	100–300*	Berger (1989)

content of hypertrophic waters, but photosynthetic features are differential too. In Table 3 such features are shown, including some of less eutrophicated lakes for comparison. As a rule, photosynthetic ranges are broader in hypertrophic lakes. The highest net annual productivity ever recorded is that of Hartbeesport Dam, South Africa, mainly resulting from *Microcystis* photosynthesis (Robarts 1984). Maximal quantum yields are in the same range as for other lakes. However, the most outstanding difference is the lower chlorophyll-specific attenuation coefficient of hypertrophic phytoplankton. This low coefficient allows a higher fraction of the incoming irradiance to be used (Table 3), increasing the utilization of photosynthetically active radiation and thus increasing primary productivity, despite the "optically deep" nature of hypertrophic environments, where self-shading by dense populations of algae reduces light at relatively shallow depths (Jewson & Taylor 1978).

Table 3. **Primary productivity of hypertrophic phytoplankton.** For comparison, values from an oligotrophic lake (Castle), a mesotrophic lake (Constance) and a eutrophic lake (Vombsjön) have been included. When radiocarbon is used as a photosynthetic marker, annual production is considered to be net primary production rather than gross production.

ΣA, areal primary production (mg C m^{-2} h^{-1}); P_{max}, maximal photosynthetic capacity (mg C (mg Chl*a*)$^{-1}$ h^{-1}); I_k, onset of light saturation of photosynthesis (µmol m^{-2} s^{-1}); k_c, chlorophyll-specific PAR attenuation coefficient (m^2 mg^{-1}); F, fractional absorption of PAR irradiance by chlorophyll-*a* (%); PSR_{max}, maximal quantum yield (mol C E^{-1}); $\Sigma\Sigma A$, annual primary production (g C m^{-2} $year^{-1}$).

*Calculated from k_{min} values.

Lake	*Year of study*	ΣA	P_{max}	I_k	k_c	*F*	PSR_{max}	$\Sigma\Sigma A$ *net*	$\Sigma\Sigma A$ *gross*	*Reference*
Castle	1980	–	0.2–3.3	–	0.016	3–40	0.020–0.098	57	–	Priscu (1984)
Constance	1981	13–260	2.7–6.4	72–708	0.015	6–51	0.022–0.092	330	–	Tilzer (1984a)
El Porcal	1984–85	30–500	1.0–16.0	30–1000	0.009	25–75	0.004–0.118	756	900	Alvarez Cobelas et al. (1992)
Hartbeespoort	1981–82	47–3381	1.5–14.3	54–737	–	–	–	1470	–	Robarts (1984)
Kinnego Bay (Lough Neagh)	1973–74	30–520	0.7–6.3	28–161	0.009*/ 0.027	47–60	–	–	854	Jones (1977b)
Loch Leven	1968–71	7–600	0.7–7.5	16–248	0.009*	up to 86	–	–	597–971	Bindloss (1976)
Lough Neagh	1971–72	19–375	1.1–4.9	28–68	0.011*	20–80	–	–	560	Jewson (1976)
Teganuma	1983–84	–	1.0–6.7	–	–	–	–	–	1450	Takamura et al. (1989)
Vombsjön	1973	38–550	1.0–8.0	–	0.020	–	–	655	–	Gelin (1975)
Wolderwijd	1981	–	1.9–4.5	–	0.010	11–59	–	656	–	Berger (1989)

Factors controlling phytoplankton primary production in hypertrophic environments are not yet well known. For some time now it has not been supposed that primary production is simply controlled by chemical features (Jewson 1976; Robarts 1984) as hypertrophic sites are thought to have plenty of nutrients. Consequently, physical factors have been suspected to play a key role. Thus, Jewson (1976) considers water temperature and day length to be the main variables controlling phytoplankton photosynthesis in Lough Neagh. Robarts (1984) states that wind and water-column stability control primary production in Hartbeesport, and Takamura et al. (1989) point to the significance of incoming irradiance and water temperature for the phytoplankton productivity in Teganuma Lake. Anyway, an interplay of factors is recognized (Jewson 1976; Robarts 1984; Takamura et al. 1989). However, recent studies of primary production and environmental factors in Lake El Porcal have demonstrated that dissolved inorganic carbon and soluble reactive phosphorus are also important for controlling seasonal primary productivity, in addition to irradiance and water-column stability. Furthermore, the variance of phytoplankton primary production explained by abiotic features is below 60%, suggesting that food-web interactions could be important too (Alvarez Cobelas et al. 1992).

Phytoplankton losses

Little is known about zooplankton grazing on hypertrophic phytoplankton. Olrik et al. (1984) and Jeppesen et al. (1990) state that zooplankton could trigger off a clear-water phase in the hypertrophic Hjarbaek Fjord and Sobygard So. Crazing in sewage-treatment algal ponds is very common and often results in population crashes within a few days (Lincoln & Earle 1990; Carcfa et al., pers. comm.).

Sedimentary losses have seldom been ascertained. Molongoski & Klug (1980) show two distinct patterns in Wintergreen Lake: in 1976, carbon sedimentation peaked at late stratification and early mixing, whereas in 1977 such peaks occurred during early stratification. In Lake El Porcal, they have been computed as one-fourth of overall phytoplankton losses *on a* yearly basis (Alvarez Cobelas, unpublished data), with losses being higher during mixing.

Respiration might be the highest fraction of energetic losses in hypertrophic environments. Jewson (1976), Jones (1977b) and Takamura et al. (1989) show high rates of plankton respiration. Unfortunately, it is still very difficult to measure phytoplankton respiration using routine methods. This is the reason why no values on respiratory losses of hypertrophic phytoplankton have been published. A correlation analysis suggests that they could roughly account for 50% of overall plankton community respiration in a Spanish hypertrophic lake (Alvarez Cobelas, unpublished data).

Anyway, phytoplankton losses in hypertrophic lakes might follow the same pattern as those occurring in other environments. If one compares unpublished data on Lake El Porcal with those of Tilzer (1984b) and Forsberg (1985), the pattern is very much the same: phytoplankton biomass is lost as fast as it is built. Phytoplankton production and loss rates are equal, slightly lagged and counterbalanced (Table 4).

Table 4. Phytoplankton potential production, losses and growth (means per day ± standard deviation), in lakes of contrasting trophic status (TS). Calculations follow Forsberg's (1985) method. O, oligotrophic; M, mesotrophic; E, eutrophic; H, hypertrophic.

Lake	*Year of study*	*TS*	*Production*	*Losses*	*Growth*	*Reference*
Castle	1968	O	0.33 ± 0.11	0.34 ± 0.13	0.048 ± 0.047	Forsberg (1985)
Constance	1981	M	0.65 ± 0.35	0.67 ± 0.31	0.110 ± 0.090	Tilzer (1984b)
Erken	1957	E	0.36 ± 0.26	0.35 ± 0.25	0.048 ± 0.041	Forsberg (1985)
El Porcal	1984–85	H	0.44 ± 0.28	0.44 ± 0.30	0.001 ± 0.001	unpubl. data

A feature that might explain the high areal chlorophyll concentrations found in hypertrophic sites is the high turnover rates in the phytoplankton community. These high rates have been recorded for the very eutrophic Lake Norrviken prior to sewage diversion (Ahlgren 1970) and in Lake El Porcal (Alvarez Cobelas et al. 1992).

A characteristic event of phytoplankton losses in hypertrophic environments is that of plankton collapses. They have been reported very often (Barica 1975; Fott 1975; Bailey-Watts 1978; Olrik et al. 1984; Jeppesen et al. 1990) and are sudden decreases of phytoplankton biomass which can be reduced 100-fold within a few days. The consequences for ecosystem management are dramatic because fish-kills very often follow the collapse (Barica 1975). The reasons for phytoplankton crashes in hypertrophic lakes have not been entirely elucidated but it appears as if nutrient depletion could be responsible for the collapse of bloom-forming species (Barica 1981; Jeppesen et al. 1990).

Seasonal succession

Seasonal succession patterns are difficult to establish neatly in hypertrophic environments. The same patterns are seldom recurrent throughout a series of years in the few lakes that have been studied for long periods (Bailey-Watts 1978; Jeppesen et al. 1990). Nevertheless, four different types can be suggested from the cases to hand (Table 5). They can be located on a Cyanobacteria-Flagellates continuum. We tentatively

Table 5. Hypertrophic seasonal succession types (I-IV) based upon the dominating phytoplankton biomass. DOM, dissolved organic matter.

	Type	*Autumn–Winter*	*Early Spring*	*Spring*	*Summer*	*Reference*
Low	I	--------	Cyanobacteria	--------	--------	Berger (1989)
						Romo (1991)
	II	Cyanobacteria	Diatoms	------ Cyanobactera	-----	Jewson (1976)
		Diatoms	-------	Chlorococcales	--------	Jones (1977a)
						Bailey-Watts (1978)
						Berger & Sweers (1988)
Ammonia						Mackenthun et al. (1966)
						Sze (1980)
DOM						Takamura et al. (1989)
	III	Flagellates	Diatoms	------ Cyanobactera	-----	Leah et al. (1980)
			-------	Chlorococcales	--------	
				---- Flagellates	------	Olrik et al. (1984)
						Rojo (1990)
						Fott (1975)
						Marvan et al. (1978)
						Urbaniec-Brózda (1985)
	IV	--------	Flagellates	--------	--------	Elber & Schanz (1989)
			------	Chlorococcales	--------	Azov et al. (1980)
High						Wrigley & Toerien (1990)

Table 6. Means (± standard deviations) and ranges of ammonia concentrations (mg l⁻¹) in some hypertrophic environments. Phytoplankton successional types are those of Table 5. HROP = high rate oxidation pond.

	Ammonia		*Successional*	
Locality	*Mean*	*Range*	*Type*	*Reference*
Wolderwijd	0.10 ± 0.15	0–0.81	I	Zevenboom et al. (1982)
El Porcal	0.85 ± 0.62	0.10–3.00	III	Alvarez Cobelas et al. (1990)
Kaminsee I	0.91 ± 0.97	0.10–3.21	IV	Elber & Schanz (1989)
HROP at Jerusalem	27.2 ± 14.2	14.4–48.6	IV	Abeliovich & Shilo (1976)

suggest that such an ordination could co-occur along with an increasing trend in ammonia and dissolved organic matter (DOM) concentrations. The small number of data-sets available on ammonia concentrations in hypertrophic environments suggests such a trend (Table 6). Data on DOM are lacking but its increase, along with the trophic degree, has been recently suggested (Burney 1990).

Therefore, in communities dominated by cyanobacteria, both factors would be comparatively low, whereas in environments dominated by flagellates, ammonia and DOM concentrations would be high. Flagellates could probably tolerate higher ammonia concentrations without suffering the acute toxic effects that occur in Chloroccocales and cyanobacteria (see Abeliovich & Azov 1976). Furthermore, their ability to use DOM substrates for growth (Pringsheim 1952, 1963) is another advantage for flagellates.

The first type of seasonal succession occurs in those environments with a cyanobacteria-dominant phytoplankton community throughout the whole year, e.g. Wolderwijd (Berger 1989) and Albufera de Valencia (Romo1991).

The next pattern is that of short episodes of dominating diatoms (autumn-winter to early spring) with blue-green dominance for the rest of the year, as in Lough Neagh (Gibson et al. 1971; Jones 1977a); some very short, intruding green algal peaks also can be observed, e.g. Loch Leven (Bailey-Watts 1978), IJsselmeer (Berger & Sweers 1988), Lake Onondaga (Sze 1980) and Lake Sebasticook (Mackenthun et al. 1966).

As the chlorophyte fraction increases, we arrive at the third type, where cyanobacteria dominate in late spring and summer, and green algae dominate in the remainder of the year, with some diatoms intermingled. Th is is the case in the pond I of the Norfolk Broads (Leah et al. 1980) and Hjarbaek Fjord (Olrik et al. 1984). A deviation of this pattern includes cryptophytes in-between green algal dominance; this occurs in Lake El Porcal (Rojo 1990) and temperate fishponds (Fott 1975; Fott et al. 1974; Marvan et al. 1978; Urbaniec-Brozda 1985).

Finally, the fourth pattern is entireley comprised of flagellates and some chloroccocal populations. If only small amounts of DOM are present but high ammonia concentrations exist, then a mixed assemblage of Volvocales and cryptophytes develops, e.g. Kaminsee I (Elber & Schanz 1989). If there are high DOM concentrations as well, an algal community highly tolerant of ammonia and DOM occurs, such as euglenophytes, Volvocales and Chlorococcales *(Micractinium);* e.g. in high rate oxidation ponds (Azov et al. 1980; Wrigley & Toerien 1990; Garcfa et al., pers. comm.).

Factors influencing the seasonal succession of hypertrophic phytoplankton have been scarcely explored. Anyway, changes in autogenic (within the phytoplankton community) as well as allogenic factors (outside the community) usually occur (Reynolds 1984b). Autogenic changes could occur in the shifts of summer assemblages in Lake El Porcal, whereas allogenic changes occur during mixing, driven by changes in the mixed depth and light climate (Rojo 1990). However, the variability in resource ratios is equally important in shaping hypertrophic communities, and nutrient limitation (hence autogenic changes) could not be discarded for phytoplankton dynamics during mixing (Rojo 1990). In oxidation ponds, temperature is thought to control community structure on a seasonal basis (Abeliovich 1986), but organic matter content might also play a role 'in assembling such communities (Azov et al. 1980; Garcfa et al., pers. comm.).

Concluding remarks

Hypertrophic phytoplankton biology and ecology are not well understood despite recent efforts. Obscure topics include the unexpected significance of nutrients to phytoplankton production rates, relationships between phytoplankton and zooplankton, toxic effects of nitrogen compounds, and respiratory as well as sedimentary losses. Also some recent findings on the significance of flushing rates on phytoplankton ecology (Bailey-Watts et al. 1990) could help to explain some processes, such as the reversal from hypertrophic conditions to less eutrophic ones, as occurred in the formerly hypertrophic Loch Leven (see Bailey-Watts et al. 1990, fig. 4).

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