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Complete List of Authors:	Pereira, Helder; Trinity College Dublin, Centre for the Environment Allott, Norman; Trinity College Dublin, Department of Zoology Coxon, Catherine; Trinity College Dublin, Department of Geology Naughton, Owen; Trinity College Dublin, Department of Civil, Structural and Environmental Engineering Johnston, Paul; Trinity College Dublin, Department of Civil, Structural and Environmental Engineering Gill, Laurence; Trinity College Dublin, Department of Civil, Structural and Environmental Engineering
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59 60 Title: Phytoplankton of turloughs (seasonal karstic Irish lakes)

Authors:

<u>1. Cunha Pereira, Helder</u> (corresponding author) Centre for the Environment, Trinity College Dublin Dublin 2 Ireland

+353 1 896 1005

cunhapeh@tcd.ie

2. Allott, Norman

Dept. of Zoology, Trinity College Dublin

Dublin 2

Ireland

3. Coxon, Catherine

Dept. of Geology, Trinity College Dublin Dublin 2 Ireland

4. Naughton, Owen; 5. Johnston, Paul; 6. Gill, Laurence

Department of Civil, Structural and Environmental Engineering, Trinity College Dublin

Dublin 2

Ireland

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Abstract

The seasonal succession of phytoplankton communities in turloughs (seasonal karstic Irish lakes) is described for the first time. R-selected species dominated throughout the duration of flooding and a clear succession of communities, with three distinct phases, was found in most turloughs: prevalence of Chlamydomonas, cryptophytes, pennate diatoms and Tribonema in the first few months of flooding followed by dominance in winter by cryptophytes, pennate diatoms and centric diatoms. A final stage in late spring was characterised by filamentous greens and chrysophytes. Algal communities in turloughs resemble those of ponds, lakes or even slow-flowing rivers, depending on the time of the year. Multivariate analysis showed that the variables significantly affecting phytoplankton composition in turloughs were total phosphorus (TP), season and mean depth/colour. Turloughs with higher TP tended to have a higher prevalence of green algae, particularly filamentous forms. Tychoplanktonic algae were also important in turloughs (up to 82% of total biovolume), probably owing to their shallow nature and to the presence of terrestrial vegetation on the bottom of the basins. The results are discussed in relation to Reynolds functional groups and other studies and, in general, it is shown that there is good accordance between the algae found in turloughs and what is presently known of their ecologies.

Introduction

Turloughs are karstic temporary lakes that are virtually unique to Ireland (Sheehy Skeffington et al., 2006). They occur in depressions in karstic areas that flood seasonally usually in September or October and normally persist until late spring or early summer. Turlough basins are usually covered in grassland, which is commonly used as pasture for grazing cattle during the summer (Reynolds, 1982). They occur mostly in the west of Ireland, where the dominant bedrock is pure bedded limestone covered with thin and permeable glacial drift (Coxon, 1987). There are no published studies on the phytoplankton communities of turloughs and, indeed, relatively few on the phytoplankton of temporary lakes in general (Williams, 2006) which contrasts starkly with the extensive literature on the phytoplankton of permanent lakes. Several features of turloughs appear to mitigate against the development of algal communities. Turloughs are hydrologically dynamic systems characterised by a rapid response to rainfall events and short hydraulic residence times (median of 73 days for sites within this study). They fill and empty typically once a year, or in some cases several times a year, and are dry over the late spring and the summer periods, when algal populations in permanent lakes usually reach their peak. Consequently, algal communities in turloughs must develop, at least initially, at low light levels and low temperatures. Additionally, most turloughs are fed by groundwater which is an unlikely source of algal inocula. In spite of the above constraints on growth of algae, turloughs have been shown to develop phytoplankton

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biomass concentrations comparable to those of permanent lakes in summer (Cunha Pereira et al., 2010). Peaks of chlorophyll a (Chl *a*) occur throughout the flooding season, with high values frequently in the middle of winter (up to 69 μ g Chl *a* L⁻¹).

Published studies of temporary lakes usually describe algal communities of one or very few lakes. For example, Alvarez et al. (Alvarez et al., 2006) studied the phytoplankton of three temporary shallow saline lakes and Garcia & Niell (Garcia & Niell, 1993) describe the phytoplankton of one seasonal saline lake in Southern Spain. In this study we focus on a large set of geographically close turloughs, which therefore are subject to a similar climate (particularly relevant is the onset of effective rainfall in autumn, which correlates with the start of flooding) (Moran et al., 2008). By studying the phytoplanktonic communities of a set of turloughs with differing trophic status we have the opportunity to infer much about the ecological adaptations of the taxa present, as well as the factors affecting their occurrence. This study focuses on three specific questions: the ecological characteristics of the predominant algae in turloughs, how algal communities change in response to changing environmental conditions over a flooding season, and which are the most important factors responsible for algal community differences amongst turloughs and over time.

Method

Sampling and water chemical analyses

Twenty-two turloughs in the west of Ireland (Fig. 1) were sampled monthly from the onset of flooding (October 2006) until they were dry or very low (April-June 2007). The turloughs were selected to represent a geo-hydrological range of Irish turloughs and a range of trophic status based on the terrestrial plant communities present (Working Group on Groundwater, 2004; Goodwillie, 1992). Table I presents chemical and hydrological characteristics of the turloughs sampled.

Samples were collected by throwing a 5 L weighted bottle attached to a rope from the shore into an area of open water to avoid disturbance of the sediment. The estimated depth of the sampled points was of about 0.5 m. Chemical analyses were done for total phosphorus (TP), total nitrogen (TN), chlorophyll a (Chl a), colour and alkalinity, following standard methods (Eaton et al., 2005). Further details on the exact methods used for each parameter can be found in Cunha Pereira et al. (Cunha Pereira et al., 2010). Additionally, silicates were measured in filtered samples following an acid colorimetric method (Grasshoff et al., 1999).

Phytoplankton analysis

Phytoplankton was preserved with Lugol's iodine solution. Identification and counting was carried out according to Utermöhl (Utermöhl, 1958). Samples were observed at 200x or 400x

 magnification with an inverted microscope (Leica Leitz DM-IL) after at least 24h in a sedimentation column (Uwitec, http://www.uwitec.at). Between 300 and 400 individuals in a number of transects were counted. Cell biovolume for each taxon was calculated by approximation of cell shape to known geometrical forms (Hillebrand et al., 1999; Sun & Liu, 2003). Chl *a* was positively correlated with algal biovolume (R=0.83, N=170, Spearman's), with a slightly better fit than when correlated with cell abundance (R=0.80, N=170, Spearman's). Biovolume was therefore used as the measure of algal biomass.

Taxa were identified to the species level where possible following John et al. (John et al., 2002), Cox (Cox, 1996) and Bourrely (Bourrelly, 1970, 1981, 1990). Some taxa were not discriminated beyond general groupings, such as small ($d \le 10 \mu m$) centric diatoms (considered to be either Cyclotella spp. or Stephanodiscus spp.), dinoflagellates, unidentified pennate diatoms (i.e. diatoms that were too small for correct identification, or in ambiguous girdle view; they were generally small with average biovolume of 302 μ m³). Synedra sp. was discriminated between small (<70 µm long) and big (>70 µm long); Synedra nana was found in one turlough only (Coolcam). Non-identified dinoflagelates were always small (average length= $21.4 \mu m$, SD= $7.3 \mu m$) and morphologically similar to Peridinium, Peridiniopsis, Gymnodinoum or Katodinium. The term nonidentifiable alone (or n.i.) was reserved for rare cases where specimens were not identifiable. Discrimination between n.i. filament, n.i. flagellate, n.i. colony, n.i. green filament was made when applicable. A common small cryptophyte with a typical pointy apex was named Chroomonas/Rhodomonas (Palsson & Graneli, 2004; Leitao & Leglize, 2000), as it is morphologically similar to Chroomonas acuta but also to Rhodomonas minuta/Plagioselmis nannoplanctonica (Barone & Naselli-Flores, 2003; Novarino, 2002; Novarino et al., 1994); correct discrimination was therefore not possible. Taxa richness was the number of taxa found in each monthly sample; averages per turlough were calculated as the mean across turlough samples.

Taxa were categorised into "tychoplanktonic" (including metaphytic) or "true planktonic". As most raphid diatoms (Kelly, 2000, Round et al., 1990, Cox, 1996), and most filamentous chlorophytes and *Tribonema* spp. (Irfanullah & Moss, 2005; Berry & Lembi, 2000; John et al., 2002), are usually associated with the benthos (streams, rivers, or shallow lakes and ponds), these were considered tychoplanktonic, while all other algae were considered planktonic. Non-identified algae were ignored and the biovolume of n.i. pennates was considered half planktonic and half tychoplanktonic (as an estimate).

The functional group approach (Reynolds et al., 2002; Reynolds, 2006) was applied to help interpret the data and to put the work in a wider research context. This approach has been found to provide a higher discriminatory power than classical taxonomic groups in ecologically interpreting community data (Kruk et al., 2002) and it has thus been extensively applied in research studies of

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phytoplankton (Padisák et al., 2009). Functional groups are groups of algae (often cross-phyletic) that have similar adaptive features (e.g. surface area to volume ratios, motility, nutrient use efficiency, sensitivity to grazing). Algae belonging to the same functional group are therefore often found in the same habitat type or similar environmental conditions (Reynolds et al., 2002). Dominant taxa in turloughs were assigned to functional groups based on the classification of Reynolds et al. (Reynolds et al., 2002) and the recommendations of Padisák et al. (Padisák et al., 2009).

Hydrological and environmental data

Water levels were recorded at hourly intervals using Schlumberger Divers[®] (http://www.swstechnology.com/groundwater-monitoring/groundwater-dataloggers) placed at or near the lowest point in each turlough. Sites were instrumented between September 2006 and January 2007. Topographic mapping of the basins allowed the determination of volume and surface area measurements based on the measured water levels. Mean depth was calculated by dividing the volume by the surface area at any given time (Wetzel, 2001).

Water temperature was measured using a field mercury thermometer. The sunset-sunrise time period duration of the days sampled ('day length') was calculated according to 'Time and Date AS' (http://www.timeanddate.com) for Dublin, Ireland. 'Number of days flooded' (at a given sampling date) is the number of days a turlough had been flooded until that date; this variable takes into account periods of dryness that could occur in the middle of the flooding season (the case in two turloughs). 'Hydroperiod' was calculated as the total number of days a turlough was flooded during the flooding season. The first sampling date was used for all turloughs as a surrogate for onset of flooding (not known for a number of turloughs) and the last day was when a turlough was found dry at the end of the season or with an estimated volume of less than 10% of its peak volume in the case of turloughs with persisting water throughout the year.

Data analyses

Predominant taxa were determined after ranking the taxa found by frequency of occurrence, mean biovolume, coefficient of variation of biovolume, and percentage biovolume, across samples and across turloughs. The coefficient of variation was calculated by dividing the standard deviation of biovolume across samples or turloughs by the mean biovolume across samples or turloughs; this was considered to be a measure of evenness of occurrence; the lower the value the more evenly distributed a taxon is across samples or turloughs.

Algal community biovolume data was 4th root transformed and the Bray-Curtis similarity coefficient was applied as recommended by Clarke & Warwick (Clarke & Warwick , 2001).

 CLUSTER analysis (Clarke & Gorley, 2006) was used to determine similarity relationships between taxa and between turlough communities (averages of biovolumes within turlough samples were used in order to compare turlough communities). SIMPROF analysis was applied to test statistically significant clustering (at p<0.05 level) of turloughs and taxa (Clarke & Gorley, 2006). MDS ordination was used to plot similarity relationships between turloughs. A stress factor < 0.20was considered a reasonable threshold for accurately interpreting the ordinated MDS plots (Clarke & Warwick, 2001). Statistical t-tests (Field, 2005) were used to compare biovolume contribution (log-transformed to assure normal distribution) of algal taxonomic groups between the significant turlough clusters identified with the SIMPROF routine. A SIMPER analysis (Clarke & Gorley, 2006) was additionally done to determine which taxa contributed the most to the dissimilarity found between the significant turlough clusters. Biovolumes were also "standardised": the biovolume of each taxon in each sample was divided by the total biovolume of that sample and averages per turlough (across months) were taken. This eliminates differences in total biovolume across samples and enables the comparison of the relative contribution of each taxon to the total biovolume of each turlough. All multivariate statistical analyses were run with both non-standardised and standardised biovolume data.

The relationships between phytoplankton communities and the environmental variables were assessed using direct gradient analysis. First a detrended correspondence analysis (DCA) of the phytoplankton taxa data was run to determine whether linear or unimodal ordination methods should be applied (Ter Braak & Šmilauer, 2002). Because the length of the first axis resulting from the DCA was less than three, a linear method (Redundancy Analysis or RDA) was used (Ter Braak & Prentice, 1998). Only relevant environmental variables with low covariance (r<±0.60, p<0.001, Spearman rank correlations) were included in the analysis: TP, TN, silicate, alkalinity, colour, water temperature, number of days flooded and mean depth; significant correlations and r values were: TP and TN (0.39), silicate and number of days flooded (-0.53) and silicate and colour (0.59). Significant explanatory variables were determined by automatic forward selection (Ter Braak & Šmilauer, 2002) after Bonferroni correction of the P-value (Abdi, 2007). Only samples without missing values in any of the environmental variables were included (April samples were omitted (no colour measurements), as were some others owing to lack of hydrological data). In total 100 samples (from a total of 171) were included in the initial RDA. Forward selection results showed that colour did not contribute significantly to explain the variance in the phytoplankton data (p>0.05). Because colour was discarded, April samples could be included and a final RDA was run with 116 samples (reported herein).

PRIMER 6 and CANOCO for Windows 4.5 were used for multivariate statistical analyses.

Results

Phytoplankton taxa in turloughs

Cryptophytes and pennate diatoms were the most prominent taxa in turloughs (Table II). Cryptophytes had overall high biovolume ratings (particularly *Cryptomonas* spp.), the highest evenness, and the highest average percentage of biovolume per turlough. Pennate diatoms, such as small *Synedra* sp. (small), *Achnanthidium minutissimum*, *Nitzschia* spp., *Navicula* spp., and other unidentified pennates, were prominent in all turloughs. Less widespread across turloughs, but with high contributions when occurring, were *Gomphonema* spp., *Synedra* sp. (big) and centric diatoms.

Chlamydomonas spp. occurred in roughly half of the turloughs and 28% of all samples and made a considerable contribution to overall biovolume. Other chlorophytes, such as *Monoraphidium* spp. and *Scenedesmus* spp., were common but contributed little to overall biovolume. Some green filamentous algae were common; *Mougeotia* spp., *Spirogyra* spp. and *Oedogonium* spp. in particular were important contributors to overall biovolume and were present in 12 to 18 turloughs and 17% to 30% of all samples. *Tribonema* spp., a non-chlorophyte filament, also contributed considerably to total biovolume in samples.

Dinoflagellates were present in 15 turloughs and 25% of samples, with considerable evenness across turloughs but in low biovolume. Virtually all were n.i. small dinoflagellates, though *Ceratium hirundinella* was found in low abundance in one sample (in May). Chrysophytes were fairly well represented in turloughs. *Mallomonas akrokomos* was present in 17 turloughs and almost 50% of samples (although in low biovolume), with high evenness. *Dinobryon* spp. was present in slightly fewer samples but in much larger biovolumes. This taxon was the second largest contributor to overall measured biovolume indicating that, when present, it was in great numbers. cyanophytes, desmids and euglenophytes were poorly represented in the turloughs and *Oscillatoria/Planktothrix, Cosmarium* spp. and *Euglena* spp. were the most noticeable taxa within these groups (Table II).

The CLUSTER analysis of the taxa contributing more than 1% of total biovolume presented a good overview of the taxa most frequently co-occurring within samples (Fig. 2): *Cryptomonas* spp. and *Chroomonas/Rhodomonas* were the most similarly distributed taxa (about 80% similarity) and the ubiquitous pennate diatoms already mentioned were also largely co-occurring together with these cryptophyes. Other interesting clustering occurred between centric diatoms and *Synedra* sp. (big) (co-occurring particularly in the winter and first months of flooding), *Tribonema* spp. and *Chlamydomonas* spp. (most abundant in the first two months of flooding), and green filamentous algae (*Oedogonium, Spirogyra* and *Mougeotia* species), particularly abundant during spring. This analysis of co-occurrence provides cues for possible functional analogies between linked taxa.

The contribution of tychoplanktonic algae in the 22 turloughs ranged between 5.7% (in Coy) and 81.7% (in Aleenaun) of the total biovolume per turlough, with an average of 31.5% and SD of 19.4%. Figure 3 shows the distribution of the biovolume of tychoplanktonic and planktonic algae in each of the turloughs studied.

Community similarity among turloughs

 CLUSTER analysis showed that the phytoplankton communities in the 22 turloughs were almost half (45.2%) overlapping in composition. At similarity levels between 45.2% and 51.4%, four significant turlough clusters were discriminated through CLUSTER/SIMPROF analysis (Fig. 4a). The clusters were named based on relevant and characteristic chemical and hydrological parameters (Table II): high TP (TP \geq 0.64 µM, N=8), low TP (TP \leq 0.81 µM, N=9), coloured/deep (turloughs with distinctly high colour waters and greater mean depths, N=4), and Turloughmore (turlough with a distinctly short hydroperiod, N=1). The similarity relationships between turloughs remained the same when using standardised biovolumes (Fig. 4b) but the SIMPROF routine did not significantly separate the high TP and the low TP clusters in this case (loss of multivariate statistical sensitivity; the standardised biovolume values are more similar amongst themselves than the absolute values). This suggests that there is a gradient of similarity between these 17 turloughs that broadly corresponds to a TP gradient rather than a clear separation into two distinct trophic groups.

Differences in algal communities between turlough clusters

Fig. 5 shows total biovolume and percentage biovolume of algal groups for each turlough, arranged by the identified significant clusters. Turloughs in the coloured/deep cluster showed very low total abundances and had very few chlorophytes. Their compositions were almost exclusively cryptophytes and diatoms (see also Table III), and at times had taxa virtually absent from other turloughs (e.g. *Asterionella formosa* or *Melosira varians*). The percentage contribution of the different algal groups in Turloughmore was similar to those in the high TP and low TP turloughs, but the actual taxonomic composition differed sufficiently to form a separate cluster (Table III). The t-test of the differences in relative abundance of algal groups between the high TP and low TP turlough clusters revealed that only two groups were significantly different: chlorophytes were more abundant in the high TP cluster and cryptophytes were more abundant in the low TP cluster (log percentage of biovolume of algal groups, p<0.04). The majority of the biovolume of chlorophytes was of filamentous forms (79%) so it was not surprising to find that both sums and percentage biovolume of filamentous algae were also significantly higher in the high TP cluster than in the other clusters (log sum and percentage biovolume t-test, p≤0.01), even though a few turloughs in the high TP group had relatively low filamentous algae abundance and some turloughs in the low

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TP cluster had relatively high filamentous algae biovolume (Fig. 5). SIMPER analysis revealed that the taxa differing the most in abundance between the high TP and low TP groups were *Chlamydomonas* spp., centric diatoms and *Spirogyra* spp. (all more abundant in the high TP group) with a number of other filamentous algae (*Oedogonoium* spp., *Mougeotia* spp. and *Tribonema* spp., also more abundant in the high TP cluster) being important contributors to dissimilarity between these two groups as well (Table IV). This confirms that filamentous algae are more abundant in high TP turloughs, as stated above. High TP turloughs also tended to have the highest taxonomic richness (Table II), with a number of chlorophytes absent from other groups of turloughs, including green filaments (*Binuclearia* spp., *Bulbochaete* spp. and *Chaetonema* spp.) and Chlorococcales (*Actinastrum* sp., *Coelastrum* spp., *Micractinium* sp. and *Tetrastrum* sp.).

Seasonal succession of algae in turloughs

Fig. 6 shows the temporal variation in abundance of the algal groups summarised for all turloughs and Table III shows the most abundant taxa in each month within each turlough cluster. Diatoms and cryptophytes were present in considerable amounts throughout the season and clearly dominated over the winter months (December to February). The most abundant taxa during winter were Cryptomonas spp., Chroomonas/Rhodomonas, Synedra sp. (small and big), and other pennates, including the small pennate diatom Achnanthidium minutissimum at times. Centric diatoms also made large contributions predominantly in winter, appearing in blooms in specific turloughs and months. Xanthophytes (which are almost exclusively represented by the filamentous alga Tribonema spp. (99.95% of this group's biovolume) represented a sizable fraction of the phytoplankton only during the first two months, particularly in the high TP group (Table III). Chlorophytes made higher contributions during the first two months of flooding and during spring (March to June); in the high and low TP turloughs the biovolume of chlorophytes was dominated clearly by filamentous forms (Table III). In October the green flagellate *Chlamydomonas* spp. was a substantial contributor to the high TP and low TP clusters and in Turloughmore (Table III); this taxon was also significant in Turloughmore in November and in March, after the turlough had been dry for a month. Chrysophytes made a particularly noticeable contribution during later months, especially between April and June, and Dinobryon spp. was the taxon mainly responsible for this, although other taxa appeared occasionally in great numbers (Mallomonas sp. in Coy in April or Uroglena sp. in Caranavoodaun in May). Dinobryon spp. and filamentous green algae comprised a large proportion of the biovolume during spring in the high and low TP turloughs (Table III).

All other algal groups constituted a small proportion of the total monthly biovolume and, together with the xantophytes, were not present in all 22 turloughs, unlike the aforementioned four groups. Cyanophytes constituted a sizeable proportion of the phytoplankton only in June (although

they were present in a few turloughs in October and November also) and euglenophytes in October and June only (Fig. 6). Dinoflagellates were found from October to June with varying temporal distribution depending on the turlough, but always as a small percentage of the total biovolume.

As shown elsewhere (Cunha Pereira et al., 2010) algal abundance (as Chl a) over time varied erratically across turloughs, with peaks occurring at varying times in different turloughs. Fig. 7 depicts the taxa dominating the total biovolume in the most important of the peaks. Not surprisingly, some of the peaks are dominated by cryptophytes or pennate diatoms, but of particular interest are the several peaks of filamentous algae and chrysophytes (particularly Dinobryon spp.) when these taxa were often absent or present in low abundance in months preceding or proceeding these peaks. There are also a few examples of sudden blooms of *Chlamydomonas* spp., *Oscillatoria/Planktothrix*, and centric diatoms.

Influence of environmental variables on phytoplankton distribution

Fig. 8 presents the variation over time of relevant environmental factors (mean depth, water temperature, day length and silicates). RDA analysis showed that season (represented by number of days flooded and temperature, the latter significantly correlated with day length), TP and mean depth were the main explanatory variables of phytoplankton composition (Table Va). When standardised biovolumes were used, TP and season were still the main explanatory variables (p<0.007). These results confirm the indications above that TP is an important explanatory variable of phytoplankton composition. The first two axes of the RDA explained 78% and 71% of the species-environment relationship using absolute and standardised biovolumes respectively, and 11% of the species variance in both cases. The samples of the coloured/deep turloughs seem to drive the explanatory value of the mean depth variable, as these samples plot towards the highest end of the mean depth gradient (Fig. 9). When the analysis was rerun without the samples from these turloughs it is seen that mean depth ceases to be a significant explanatory variable for the remainder of the turloughs (Table Vb). It should be borne in mind that the four coloured/deep turloughs are both much deeper but also more coloured than the other 18; thus both mean depth and colour can be responsible for the separation of this group.

Discussion

Ecological characteristics of the predominant algae in turloughs

Cryptophytes, together with small pennates, were the most widespread groups of algae in turloughs. *Cryptomonas* has been assigned to the **Y** functional group, including taxa known to be

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able to live in virtually all lentic ecosystems where grazing pressure is low (Padisák et al., 2009; Barone & Naselli-Flores, 2003; Reynolds et al., 2002). Although there are no data on zooplankton abundance in turloughs, it is plausible to assume, given this group's temperature sensitivity and ecology (Gyllström & Hansson, 2004), that their abundance during the first months of flooding and during winter (when cryptophytes are particularly prominent) would be low. Studies of European lakes and temporary water bodies, for example, have shown that grazing pressure from zooplankton only becomes important at the onset of spring (Garcia & Niell, 1993; Sommer et al., 1986). *Cryptomonas* is also known to be tolerant of low light and temperature and is assumed to prefer enriched waters (Reynolds et al., 2002). However, some studies suggest that the occurrence of *Cryptomonas* spp. is quite independent of trophic status (Barone & Naselli-Flores, 2003; Ojala, 1993), and we also found that this taxon was abundant in all turloughs, irrespective of trophic status.

The small Cryptophyte *Chroomonas/Rhodomonas* is part of the X_2 functional group, typical of shallow meso-eutrophic waters. Although most turloughs are meso-eutrophic, this taxon was also common (and relatively more abundant) in oligotrophic turloughs. There are numerous examples of the abundance of this taxon in oligotrophic environments in the literature (Dokulil & Teubner, 2003; Pybus et al., 2003; Salmaso, 2002). By contrast, studies of meso-eutrophic systems also found *Rhodomonas/Plagioselmis/Chroomonas* to be present in relative abundance (Kruk et al., 2002, Aktan et al., 2009). Reynolds et al. (Reynolds et al., 2002) indeed note that there is uncertainty on the sensitivity of the X_2 functional group to nutrient status (Table III in that article).

Cryptomonas spp. and *Chroomonas/Rhodomonas* co-occurred in virtually all turlough samples (only in one turlough, Rathnalulleagh, was the latter not present) and this co-occurrence is often found in lakes also (Aktan et al., 2009, Salmaso, 2002). This is evidence, therefore, that these cryptophytes may be largely functionally related. These taxa are often prevalent in turbid waters (Tavernini et al., 2009) or after extreme climatic or hydrological events (Devercelli, 2010), denoting their adaptability to dynamic hydrological environments such as that found in turloughs. They are also found to dominate winter communities in particular. Barone & Naselli-Flores (Barone & Naselli-Flores, 2003), for example, found *Cryptomonas* and *Plagioselmis nannoplanctonica* to be the most common cryptophytes occurring in Sicilian lakes, with particular prevalence during winter, when the lowest values of water temperature, illumination and grazing pressure were recorded. In western Ireland, Allott (Allott, 1990) found that *Cryptomonas* spp. and *Rhodomonas minuta* were the most frequently occurring taxa in six lakes geographically close to the turloughs in this study; these taxa were co-occurring in the majority of samples and were also especially dominant during winter (see also Pybus et al., 2003).

 The diatoms predominant in turloughs were usually small-celled and fast growing, thus able to take swift advantage of the available nutrient resources in turbulent conditions. Most are part of functional group **D** (i.e. *Synedra* spp., *Nitzchia* spp.), known to be tolerant to low light and shallow mixed depths (Reynolds et al., 2002). This functional group has been described as typical of shallow, well-mixed waters, liable to be turbid (including rivers) which again matches well with the environment in turloughs. *Achnanthidium minutissimum*, a characteristically benthic diatom also abundant in the turloughs, is known to colonise periphytic communities and be tolerant of low light (Johnson et al., 1997); it is also known to be able to live in a wide range of habitats, even those characterised by physical disturbance (Peterson, 1996).

Centric diatoms, depending on the species, have different ecological affinities, particularly for nutrient levels and depth of mixed layer. Centrics in turloughs were found abundantly in oligotrophic turloughs (Knockaunroe and Gealain) as well as in more eutrophic ones (as Tullynafrankagh and Carrowreagh). Therefore, they could belong to functional groups D, B or C, depending on the environmental characteristics present where they are found. They were mostly small and occurring in conspicuous blooms, particularly during the winter. This shows a marked colonising r-selected character (see also Kasten, 2003). Similar co-dominance of centrics and cryptophytes during the winter period (when recorded temperatures were at a minimum, turbulence was high, and nutrients were abundant) has been found in a study of a permanent lake (Moustaka-Gouni, 1993).

A notable proportion of the algae found in turloughs can be considered tychoplanktonic, such as the filamentous algae and certain diatoms. These algae are probably associated with the vegetation on the turlough floor and can be suspended in the water column owing to the shallow depth of the sampling points and wind-driven mixing (see also Moustaka-Gouni, 1993). It is interesting to note that these algae can be assigned to the **MP** functional group (including metaphytic, periphytic and epilithic diatoms drifted in the plankton, such as *Achnanthidium minutissimum*) and to **T**_D (including metaphytic filamentous green algae and diatoms). The **MP** group is characteristic of frequently stirred turbid shallow lakes (Padisák et al., 2009) and **T**_D was developed specifically to describe algal assemblages found in the plankton of mesotrophic rivers (Borics et al., 2007). Interestingly, the descriptions of these habitats fit well with the environmental conditions found in turloughs: turloughs can even be likened to "slow-flowing rivers", because of their highly dynamic hydrological nature.

Environmental factors affecting community structure and temporal succession in turloughs

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The coloured/deep turloughs had very low algal biomass throughout the season and lacked a clear succession, with cryptophytes and diatoms dominating throughout. In contrast to most of the turloughs, these turloughs were found not to be P-limited, and high colour (Havens & Nurnberg, 2004; Jackson & Hecky, 1980) and mean depth (Nõges & Nõges, 1999; Garcia et al., 1997) are probable factors limiting the growth of algae in these turloughs (Cunha Pereira et al., 2010). Turloughmore had a distinctly short hydroperiod and probably owing to this fact it showed a truncated succession among the 22 turloughs. In this turlough we find prevalence of r-selected, fast growing and small-celled organisms, such as cryptophytes, pennate diatoms (*Navicula, Nitzschia*), and, at times, centric diatoms, but it does not develop further. Interestingly *Chlamydomonas*, an r-selected, colonising taxa, was particularly notable in this turlough, and was abundant after periods of prolonged dryness (as in March). *Chlamydomonas* was also abundant in many turloughs following the onset of flooding (i.e. October), confirming its rapid colonising character.

Turloughs from the low and the high TP clusters (N=17) showed a clear and similar temporal succession of phytoplankton communities (summarised in Table VI) which can be considered the "norm" among the 22 turloughs in this study. Such typical turloughs were, in general, shallow (mean depth 0.8-3.0 m), continuously flooded during the sampling period, and nutrient limited (Cunha Pereira et al., 2010).

The most noticeable shifts in community structure occurred at the onset of winter (December) and at the onset of spring (March). There are obvious differences in day length and temperature between these periods (Fig. 8), which contributed to the changes in community structure (as indicated in the RDA analysis). Besides these factors, changes in nutrient levels, hydrological regime and grazing pressure over time may have also contributed to changes in community structure. In permanent lakes these are known to be important factors in shaping community structure; see Jeppesen et al. (Jeppesen et al., 2005) and Leitao & Leglize (Leitao & Leglize, 2000) for the influence of nutrient availability, Na & Park (Na & Park, 2006), Nõges & Nõges (Nõges & Nõges, 1999) and Reynolds & Lund (Reynolds & Lund, 1988) for the influence of hydrological factors, and Garcia & Niell (Garcia & Niell, 1993) and Sommer (Sommer, 1986) for the influence of grazing pressure; reviews in Reynolds (Reynolds, 1984, 2006).

Besides the ubiquitous cryptophytes and pennate diatoms, the first two months of flooding were characterised by the abundance of fast growing C-strategists such as *Chlamydomonas*, and of low light tolerant filamentous species such as *Mougeotia* and *Tribonema*. Mean depths are low during this period and fresh nutrients are available for uptake. These conditions suit rapid resource-utilising, fast-growing r-selected species, which can take advantage of the resources under mixed conditions. Temperature and light levels are still sufficient for the growth of green algae (both for the flagellate *Chlamydomonas* and the filamentous forms), which are sensitive to these factors.

Mougeotia and other green filaments, for example, are found abundantly in the autumn plankton of deep European lakes (Sommer, 1985, 1986). *Tribonema* is known to tolerate lower temperatures and irradiances than green filamentous algae (De Vries & Hillebrand, 1986), and coincidentally it was found most prominently during the autumn in turloughs, while in spring the green forms dominated.

In winter, when water temperatures and day lengths are at the minimum (Fig. 8a), the turlough communities were almost exclusively dominated by small pennates and cryptophytes. These algae often dominate winter plankton in lakes, even under ice when lakes freeze in winter (Pasztaleniec & Lenard, 2008). In spring there is a rise in temperature and light availability and a decline in silicate concentration (Fig. 8c). These conditions, in addition to a probable increase of zooplankton abundance (as discussed above), seem to account for the decline in the abundance of diatoms and cryptophytes (both sensitive to grazing) and for the increase in the abundances of filamentous green algae (Mougeotia spp., Spirogyra spp., Oedogonium spp. and Bulbochaete spp. in particular, but Ulothrix tenerrima, Binuclearia spp. and Klebsormidium sp. also in lower abundance), and of chrysophytes (particularly *Dinobryon* spp.), which are taxa known to be tolerant to grazing pressure and typical of this time of the year in many water bodies. Green filaments are well adapted to spring temperatures and light intensities (see Graham et al., 1995 and Berry & Lembi, 2000 for Spirogyra; Graham et al., 1996 and Hillebrand, 1983 for Mougeotia) and Dinobryon is also common in the spring plankton in lakes (Olrik, 1998; Sandgren et al., 1995). This taxon, as in turloughs, often appears in "sudden" pulses or blooms, thought to be benefiting from declining diatom populations and the availability of trace metals (Kangro & Olli, 2005; Dokulil & Skolaut, 1991). Blooms of chrysophytes in turloughs also coincide with the decline in diatom abundance, and so these explanations could apply to the case of turloughs as well. Green filamentous algae were more abundant in nutrient rich turloughs, which is in accordance with other studies. McCormick & O'Dell (McCormick & O'Dell, 1996) found that periphyton dominated by cyanobacteria and epiphytic diatoms in oligotrophic waters in the Florida everglades was replaced by green filamentous algae including Spirogyra and Mougeotia in stations with elevated TP concentrations or after experimental enrichment. Also, Hainz et al. (Hainz et al., 2009) studied 133 sites in Central Europe and found that *Spirogyra* grew optimally in meso-eutrophic conditions. Total phosphorus, which was found to influence total algal biomass in turloughs (Cunha Pereira et al., 2010), seems to drive phytoplankton composition towards higher abundances of green algae in general (e.g. *Chlamydomonas*), not only filamentous forms. Overall, green algae have relatively high half P saturation constants (Padisak, 2004), and so it is not surprising that they were found to be more abundant in turloughs with higher phosphorus concentrations.

Main conclusions

The first algae to colonise turloughs in autumn were typically fast-growing flagellates, such as *Chlamydomonas*, and filamentous forms, such as *Tribonema*. Such algae, together with the ubiquitous cryptophytes, pennates and small dinoflagellates, are often typical of small ponds (Reynolds, 2006; Alam et al., 2001; Evans, 1958). The algal communities in winter, dominated by cryptophytes and diatoms, were similar to those of many permanent lakes in winter (Pasztaleniec & Lenard, 2008), and the algae found in spring (dominated by filamentous greens, particularly in nutrient-rich turloughs), were again characteristic of ponds, but also of slow-flowing rivers. In general, and as expected, K selected species (typical of stable water columns, see de Hoyos & Comin, 1999; Jacobsen & Simonsen, 1993; Allott, 1990) did not occur in turloughs.

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Tables and Figure legends

Table I: Geographical coordinates and chemical, hydrological and taxonomical characteristics of each turlough over the study period, arranged by identified clusters (see text) and descending average total phosphorus within clusters.

Table II: Summary statistics for phytoplankton taxa in 22 turloughs: ranking in terms of biovolume (mean or sum of biovolume across samples or turloughs), coefficient of variation of biovolume across samples and turloughs, mean percentage of each taxon's biovolume in total turlough biovolume, occurrence in turloughs and samples (total nr. of samples = 171), and % of each taxon's biovolume from total biovolume (i.e. sum of all samples' biovolumes). Taxa ordered by descending occurrence in samples; showing only taxa with \geq 9.9% occurrence. Also shown are the proposed functional group for each taxa and whether a taxa was considered to be tychoplanktonic or true planktonic.

Table III: Percentage biovolume of algae in each month's samples for each identified cluster (only showing taxa contributing to the upmost 75% of cumulative total month's biovolume). **[2 pages]**

Table IV: SIMPER results of differences between high and low TP turlough clusters (absolute biovolumes and standardised biovolumes). All biovolume values are 4^{th} root transformed $\mu m^3/mL$. Only taxa contributing to the top 25% of dissimilarity are shown.

Table V: Automatic forward selection results of environmental variables including all turloughs (a) (showing only variables that were significant at p<0.0071 after Bonferroni correction, N=116 samples), and (b) excluding coloured/deep turloughs (only the first three variables were significant; p<0.0071, N=97 samples).

Table VI: Overall phytoplankton succession in turloughs with the respective functional associations (Reynolds et al., 2002; Padisák et al., 2009), adaptive strategies (Reynolds, 2006), and habitats where each group is typically found (as described by Reynolds et al., 2002 and Padisák et al., 2009).

Fig. 1: Geographical distribution of the 22 turloughs studied (abbreviations explained in Table I). Shaded areas correspond to areas of pure bedded limestone (geological data from the Geological Survey of Ireland database: http://www.gsi.ie/Mapping.htm). Adapted from Cunha Pereira et al. (2010).

Fig. 2: CLUSTER/SIMPROF analysis of phytoplankton taxa in 22 turloughs. Only taxa that contributed to more than 1% of total algal biovolume are shown. All clustering was significant at p<0.05.

Fig. 3: Biovolume of tychoplanktonic algae (in light grey - filamentous algae; in dark grey - raphid diatoms) and true phytoplankton (in black). Turloughs are arranged by identified clusters and descending average total phosphorus per cluster (clusters are explained in the text).

Fig. 4: MDS plot showing ordination of turloughs in terms of their phytoplanktonic communities' similarity: using absolute values of averages per turlough (a) and after standardisation of values by total per sample (b). Circles represent average total phosphorus per turlough (see Table 1 for explanation of abbreviations of turlough names). Enclosed areas represent statistically significant clusters (with similarity values presented up to the closest maximal decimal place). Legend of clusters for (a): 1 – high TP; 2 – low TP; 3 – coloured/deep; 4 - Turloughmore.

Fig. 5: Percentage biovolume of algal groups (bars), total biovolume (large black symbol) and biovolume of filamentous algae (small white circle) per turlough (arranged by identified clusters and ordered by descending TP within each cluster).

Fig. 6: Sum of biovolume of algal groups per month including all 22 turloughs studied.

Fig. 7: Monthly total algal biovolume of each of the 22 turloughs studied with indication of the taxa dominating the biovolume in peak occasions (>60% of total biovolume); turloughs arranged per identified cluster and descending mean TP per cluster.

Fig. 8: Mean temperature (solid line) and day length (dashed line) (a), mean depth of coloured/deep (dashed line) and rest (solid line) of turloughs (b), and mean silicate concentration over time in the 22 turloughs (c). Error bars are \pm standard deviations.

Fig. 9: First two axis of the RDA analysis including all 22 turloughs showing significant explanatory variables (arrows). Symbols correspond to identified turlough clusters: black circles - high TP, open circles - low TP, grey circles – Turloughmore; x - coloured/deep turloughs.

Table I

Turlough	Irish National Grid	Hydro- period (days)	Maximum mean depth (m)	Maximum Volume $(x10^3 m^3)$	Average TP (µM)	Average colour (mg/L PtCo)	Average Chl a (µg/L)	Average algal biovolume (mm ³ /m ³)	Average taxa richness
			Hi	gh TP					
Ardkill (ARD)	M27360 62500	293	2.8	653	2.65	28.3	12.7	75	15.7
Rathnalulleagh (RAT)	M77710 73760	175	3.0	878	1.44	28.3	33.5	193	16.9
Carrowreagh (CARR)	M78420 75080	186	1.9	546	1.38	47.8	12.1	570	16.4
Coolcam (COO)	M57420 71390	346	3.7 ^a	-	1.10	22.9	18.1	698	20.4
Tullynafrankagh (TUL)	M43210 15340	246	1.7 ^a	-	1.07	36.4	18.4	80	20.9
Aleenaun (ALE)	R24740 95440	158	2.6	346	0.99	13.5	9.2	53	16.6
Kilglassaun (KIL)	M27860 64550	223	1.5	709	0.89	27.7	5.0	26	14.9
Brierfield (BRI)	M81600 76560	267	1.7	933	0.64	35.6	5.0	64	16.6
Average		237	2.3 ^b	678	1.27	30.1	14.3	77	17.3
			Lo	ow TP					
Croaghill (CRO)	M59631 70711	348	1.6	636	0.81	43.8	7.6	48	13.2
Skealoghan (SKE)	M24750 62900	213	1.2	382	0.66	26.0	6.9	55	13.3
Termon (TER)	R40920 97350	304	2.3	956	0.48	21.1	3.1	28	13.4
Ballinderreen (BAL)	M41060 14920	211	0.8	529	0.40	17.4	3.0	31	18.6
Caranavoodaun (CARA)	M45450 15450	205	1.3	432	0.36	24.9	2.8	21	14.1
Roo West (ROO)	M38630 02210	213	2.6	1077	0.32	13.6	2.1	13	15.0
Lisduff (LIS)	M84250 55500	234	1.4	765	0.24	20.6	1.4	8	13.5
Knockaunroe (KNO)	R31400 94180	213	2.3	1742	0.14	10.4	1.2	9	13.4
Gealain (GEA)	R31450 94730	212	2.5	870	0.13	7.9	1.1	7	13.9
Average		240	1.8	821	0.39	20.6	3.2	24	14.3
			Colou	ured/deep					
Blackrock (BLA)	M49780 08130	169	6.8	4008	1.69	72.2	1.3	3	13.0
Coy (COY)	M49000 07500	187	5.9	1479	1.40	71.6	5.2	27	16.8
Caherglassaun (CAH)	M41550 06340	200	4.8	2985	1.40	85.1	3.3	21	12.3
Garryland (GAR)	M41750 04050	211	9.1 ^a	-	0.79	79.7	1.1	13	10.0
Average		192	5.8 ^b	2824	1.32	77.2	2.7	16	13.0

			Turlo	ughmore					
Turloughmore (TUR)	R34950 99480	135	1.3	403	0.63	11.0	4.8	18	14.8
no topographic measuremen	nts so maximum abso	olute depth v	alue is given	instead					
only mean depth values we	re used (absolute max	ximum dept	hs were ignoi	red)					
		_	_						

Table II

$\begin{array}{c c c c c c c c c c c c c c c c c c c $	- % biovolume of all samples 5.3 15.9 5.4 0.6 2.6 1.5
n.i. pennatesMP/T _D or DP/T $_{**}^{**}$ 97.1226.673.861.35CryptomonasYP94.72222.412.000.88Chroomonas/RhodomonasX2P91.82110.251.600.79n.i.any-87.7220.7222.191.14Achnanthidium minutissimumMP/T _D T73.7213.3143.471.53NitzchiaDP68.4226.684.901.89ManoraphidiumN 2P62.6200.5213.081.52	5.3 15.9 5.4 0.6 2.6 1.5
CryptomonasYP94.72222.412.000.88Chroomonas/Rhodomonas X_2 P91.82110.251.600.79n.i.any-87.7220.7222.191.14Achnanthidium minutissimumMP/TpT73.7213.3143.471.53NitzchiaDP68.4226.684.901.89ManoraphidiumN.2P62.6200.5213.081.53	15.9 5.4 0.6 2.6 1.5
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	5.4 0.6 2.6 1.5
n.i.any- 87.7 22 0.7 22 2.19 1.14 Achnanthidium minutissimumMP/T _D T 73.7 21 3.3 14 3.47 1.53 NitzchiaDP 71.9 21 1.2 16 5.01 1.80 Synedra (small)DP 68.4 22 6.6 8 4.90 1.89 MonoraphidiumN2P 62.6 20 0.5 21 2.08 1.53	0.6 2.6 1.5
Achnanthidium minutissimumMP/T DT73.7213.3143.471.53NitzchiaDP71.9211.2165.011.80Synedra (small)DP68.4226.684.901.89ManaraphidiumXP62.6200.5213.081.53	2.6 1.5
Nitzchia D P 71.9 21 1.2 16 5.01 1.80 Synedra (small) D P 68.4 22 6.6 8 4.90 1.89 Mon oraphidium N.2 P 62.6 20 0.5 21 3.08 1.53	15
Synedra (small) D P 68.4 22 6.6 8 4.90 1.89 Managraphidium X.2 P 62.6 20 0.5 21 3.08 1.53	1.0
Monoranhidium \mathbf{V}_{2} D (5) (6) (6) (7) (7) (7) (7) (7) (7) (7) (7) (7) (7	5.3
<i>Monoraphian</i> A_{11} r 02.0 20 0.5 21 5.08 1.55	0.7
Navicula MP/T _D T 55.0 21 1.1 20 3.57 1.74	0.7
Mallomonas akrokomos <mark>X₂ P</mark> 45.6 19 0.3 36 2.70 0.97	0.2
n.i. centrics D/B/C P 37.4 17 3.0 4 9.37 3.31	5.7
Dinobryon <u>E</u> P 36.3 17 6.7 2 8.22 3.37	11.3
<i>Gomphonema</i> MP/T _D T 35.1 19 0.3 40 3.04 1.35	0.2
<i>Synedra</i> (big) D P 32.2 18 3.5 9 5.58 1.97	5.3
<i>Mougeotia</i> T _D T 30.4 18 5.6 6 4.15 1.79	5.4
<i>Chlamydomonas</i> X ₂ P 27.5 13 2.3 12 5.00 2.43	2.7
Scenedesmus J P 27.5 19 0.1 41 4.35 1.61	0.1
n.i. dinoflagellate Y P 24.6 15 0.5 27 3.68 1.37	0.4
n.i. filament <u>?</u> T 24.6 19 0.7 19 4.26 1.59	0.7
<i>Eunotia bilunaris</i> MP/T _D T 24.0 16 0.6 25 4.35 1.99	0.5
<i>Cymbella/Encyonema</i> MP/T _D T 22.8 15 0.3 26 8.16 2.85	0.4
<i>Tribonema</i> T _D T 22.2 17 1.9 10 7.86 3.30	4.3
Ochromonas <mark>X₂ P</mark> 21.6 16 0.4 29 4.96 1.67	0.3
<i>Fragilaria capucina</i> D/P P 21.1 13 0.4 24 5.36 1.91	0.5
<i>Eunotia faba</i> MP/T _D T 19.3 14 0.8 18 5.95 2.72	0.7
Nitzchia acicularis <mark>D</mark> P 18.7 13 0.1 35 4.04 1.91	0.2
<i>Closteriopsis acicularis</i> <u>P</u> P 17.5 10 0.4 23 5.45 1.94	0.6
<i>Eunotia minor</i> MP/T _D T 17.5 13 0.7 34 4.30 1.28	0.3
<i>Spirogyra</i> T _D T 17.0 15 7.2 3 6.64 2.30	9.6
Oedogonium T _D T 15.2 12 1.9 11 6.07 1.97	

Oscillatoria/Planktothrix	T _c /S1	<mark>P</mark>	14.0	15	0.0	70	6.28	1.83	0.0
n.i. flagellates	any	P	12.9	14	0.4	45	4.63	1.70	0.1
Cosmarium	N	P	11.7	15	0.4	33	4.74	1.33	0.3
n.i. green cells	any	P	11.7	15	0.0	64	4.47	1.81	0.0
Oocystis solitaria	?	P	10.5	9	0.1	52	4.39	1.93	0.1
Aulacoseira	P/B/C	P	9.9	9	0.1	49	6.58	2.10	0.1
Euglena	W ₁	P	9.9	11	0.1	46	4.84	1.88	0.1
n.i. green colonies	any	P	9.9	12	0.1	42	8.37	3.17	0.1
- functional groups were assign	ned as those that be	etter matched	both the habitat	description ar	d the known se	nsitivities and	tolerances of	each taxon (Padi	sak et al., 2009;

Reynolds et al., 2002)

can have species of both groups and so 50% was considered true-planktonic and 50% metaphytic/tychoplanktonic.

Table III [continues in next page]

October		November		December		January		February	
				High TP					
Tribonema	27.1	Spirogyra	41.6	n.i. pennates	23.7	n.i. centrics	49.0	Cryptomonas	42.0
Synedra	18.4	Tribonema	14.4	Synedra	18.5	Cryptomonas	17.4	Synedra	14.0
Cryptomonas	11.8	n.i. pennates	5.5	Fragilaria/Synedra	14.1	Synedra	7.2	Synedra nana	7.8
Chlamydomonas	9.0	n.i. centrics	5.2	Spirogyra	6.4	Synedra nana	5.1	n.i. pennates	6.7
A. minutissimum	6.5	Cryptomonas	5.1	Cryptomonas	5.7			Chroomonas/Rhodomonas	6.1
Chroomonas acuta	3.2	Synedra	4.4	A. minutissimum	5.0				
				Monoraphidium	4.5				
				Low TP					
Chlamydomonas	34.3	Chroomonas/Rhodomonas	23.9	Fragilaria/Synedra	71.9	Cryptomonas	40.0	n.i. pennates	36.0
Cryptomonas	19.0	Cryptomonas	22.9	Chroomonas/Rhodomonas	10.1	Chroomonas/Rhodomonas	19.6	Mougeotia	14.0
Mougeotia	17.8	n.i. filament	12.0			Fragilaria/Synedra	13.3	Fragilaria/Synedra	11.6
Dinobryon	7.6	A. minutissimum	7.4			Synedra	6.7	Achnanthidium minutissimum	10.7
		n.i. pennates	5.9					Cryptomonas	7.1
		Fragilaria/Synedra	5.7						
				Coloured/deep					
Cryptomonas	46.5	Cryptomonas	53.5	n.i. pennates	38.9	Synedra	39.3	Melosira varians	26.3
Chroomonas/Rhodomonas	17.1	Chroomonas/Rhodomonas	20.7	Eunotia bilunaris	20.9	n.i. centrics	25.1	Synedra	19.8
Synedra	11.0	n.i. flagellates	5.2	Cryptomonas	14.1	Cryptomonas	13.9	Fragilaria/Synedra	16.3
Closterium	3.5			Synedra	13.0			Eunotia faba	15.4
				Turloughmore					
Cryptomonas	46.4	Cryptomonas	49.1	Navicula	50.4	Navicula	23.3		
Chlamydomonas	9.7	Chlamydomonas	11.7	n.i. pennates	26.0	n.i. filament	17.4		
Chroomonas/Rhodomonas	7.4	n.i. pennates	10.0			Nitzchia	17.3		
Nitzchia	7.2	Chroomonas/Rhodomonas	7.8			Fragilaria/Synedra	15.0		
n.i. pennates	5.8					n.i. pennates (colonial)	10.4		

Table III [continuation from last page]

March		April		May		June	
			Higl	n TP			
Synedra nana	24.8	Dinobryon	44.1	Dinobryon	21.1	Bulbochaete	18.4
Cryptomonas	21.4	Spirogyra	23.5	Mougeotia	15.1	Dinobryon	14.0
Dinobryon	9.9	Mougeotia	11.2	Spirogyra	14.9	Cryptomonas	12.9
Fragilaria/Synedra	9.7			Oedogonium	9.6	Oedogonium	12.0
Spirogyra	6.0			Chroomonas/Rhodomonas	7.7	Fragilaria/Synedra	9.0
Closteriopsis acicularis	5.2			Cryptomonas	6.3	Spirogyra	7.0
						Mougeotia	4.6
			Low	7 TP			
Spirogyra	23.1	Mougeotia	36.6	Dinobryon	28.4	Dinobryon	32.4
Mougeotia	17.0	Chroomonas/Rhodomonas	18.9	Cryptomonas	14.3	Cryptomonas	26.7
Chroomonas/Rhodomonas	15.4	Oedogonium	13.2	Chroomonas/Rhodomonas	11.7	Chroomonas/Rhodomonas	20.5
Cryptomonas	10.0	Cryptomonas	13.0	A. minutissimum	11.0		
A. minutissimum	8.5			Mougeotia	5.2		
n.i. pennates	6.0			n.i. pennates	4.7		
			Colo	oured			
Cryptomonas	40.1	Cryptomonas	41.7	n.i. pennates	29.3	Chroomonas/Rhodomonas	21.3
Chroomonas/Rhodomonas	39.3	Mallomonas	31.6	Navicula	23.8	Cryptomonas	15.3
		Chroomonas/Rhodomonas	8.3	Cryptomonas	15.8	n.i. flagellates	14.0
				Melosira varians	10.3	n.i. filament	10.4
						Chlamydomonas	9.9
						Navicula	6.2
			Turlou	ghmore			
n.i. centrics	26.8						
Navicula	22.5						
n.i. pennates	12.4						
Chlamydomonas	8.9						
Cryptomonas	6.8						

Table IV

Absolute Biovolumes
Average dissimilarity=48.62%

Species	High TP Average Biovolume	Low TP Average Biovolume	Average dissimilarity	Dissimilarity contribution (%)	Cumulative contribution to dissimilarity (%)
Spirogyra	16.78	6.46	2.00	4.12	4.12
Chlamydomonas	11.55	3.35	1.62	3.32	7.45
Centric diatoms	11.98	3.43	1.50	3.09	10.54
Oedogonium	12.84	4.55	1.48	3.03	13.57
Dinobryon	14.25	9.53	1.36	2.80	16.37
Synedra (big)	12.86	5.99	1.35	2.77	19.15
Mougeotia	13.40	9.25	1.33	2.73	21.87
Tribonema	11.70	5.26	1.30	2.67	24.54
<u>Standardised Biovolumes</u> Average dissimilarity=41.78%			CO		
Species	High TP Average	Low TP Average	Average	Dissimilarity	Cumulative contribution to
	Biovolume	Biovolume	dissimilarity	(%)	dissimilarity (%)
Chlamydomonas	Biovolume 1.14	Biovolume 0.37	dissimilarity 1.38	(%) 3.29	dissimilarity (%) 3.29
Chlamydomonas Centric diatoms	Biovolume 1.14 1.10	Biovolume 0.37 0.59	dissimilarity 1.38 1.09	(%) 3.29 2.62	dissimilarity (%) 3.29 5.91
Chlamydomonas Centric diatoms Spirogyra	Biovolume 1.14 1.10 1.39	Biovolume 0.37 0.59 0.89	dissimilarity 1.38 1.09 1.06	(%) 3.29 2.62 2.53	dissimilarity (%) 3.29 5.91 8.44
Chlamydomonas Centric diatoms Spirogyra Chroomonas/Rhodomonas	Biovolume 1.14 1.10 1.39 1.41	Biovolume 0.37 0.59 0.89 2.13	dissimilarity 1.38 1.09 1.06 1.03	(%) 3.29 2.62 2.53 2.46	dissimilarity (%) 3.29 5.91 8.44 10.91
Chlamydomonas Centric diatoms Spirogyra Chroomonas/Rhodomonas Synedra (big)	Biovolume 1.14 1.10 1.39 1.41 1.32	Biovolume 0.37 0.59 0.89 2.13 0.78	dissimilarity 1.38 1.09 1.06 1.03 1.03	(%) 3.29 2.62 2.53 2.46 2.45	dissimilarity (%) 3.29 5.91 8.44 10.91 13.36
Chlamydomonas Centric diatoms Spirogyra Chroomonas/Rhodomonas Synedra (big) Oedogonium	Biovolume 1.14 1.10 1.39 1.41 1.32 0.98	Biovolume 0.37 0.59 0.89 2.13 0.78 0.62	dissimilarity 1.38 1.09 1.06 1.03 1.03 1.03 1.01	(%) 3.29 2.62 2.53 2.46 2.45 2.43	dissimilarity (%) 3.29 5.91 8.44 10.91 13.36 15.79
Chlamydomonas Centric diatoms Spirogyra Chroomonas/Rhodomonas Synedra (big) Oedogonium Eunotia minor	Biovolume 1.14 1.10 1.39 1.41 1.32 0.98 0.39	Biovolume 0.37 0.59 0.89 2.13 0.78 0.62 0.96	dissimilarity 1.38 1.09 1.06 1.03 1.03 1.01 0.98	(%) 3.29 2.62 2.53 2.46 2.45 2.43 2.35	dissimilarity (%) 3.29 5.91 8.44 10.91 13.36 15.79 18.14
Chlamydomonas Centric diatoms Spirogyra Chroomonas/Rhodomonas Synedra (big) Oedogonium Eunotia minor Dinobryon	Biovolume 1.14 1.10 1.39 1.41 1.32 0.98 0.39 1.15	Biovolume 0.37 0.59 0.89 2.13 0.78 0.62 0.96 1.21	dissimilarity 1.38 1.09 1.06 1.03 1.03 1.01 0.98 0.94	(%) 3.29 2.62 2.53 2.46 2.45 2.43 2.35 2.25	dissimilarity (%) 3.29 5.91 8.44 10.91 13.36 15.79 18.14 20.38
Chlamydomonas Centric diatoms Spirogyra Chroomonas/Rhodomonas Synedra (big) Oedogonium Eunotia minor Dinobryon Mougeotia	Biovolume 1.14 1.10 1.39 1.41 1.32 0.98 0.39 1.15 1.25	Biovolume 0.37 0.59 0.89 2.13 0.78 0.62 0.96 1.21 1.16	dissimilarity 1.38 1.09 1.06 1.03 1.03 1.01 0.98 0.94 0.89	(%) 3.29 2.62 2.53 2.46 2.45 2.43 2.35 2.25 2.14	dissimilarity (%) 3.29 5.91 8.44 10.91 13.36 15.79 18.14 20.38 22.52

Table V

(a)

Marginal	Effects	С	Conditional Effects			
Variable	Lambda1	Variable	Lambda A	Р	F	
nr days flooded	0.05	nr days flooded	0.05	0.001	6.0	
temperature	0.05	TP	0.03	0.001	4.1	
TP	0.03	mean depth	0.04	0.001	4.6	
mean depth	0.03	temperature	0.02	0.001	2.7	
b)						

(b)	

Table VI

Таха	Functional groups	Strategies	Typical habitat
Autumn (October and November)			
Tribonema/Spirogyra/Mougeotia	T_D (possibly)	R	Mesotrophic standing waters, or slow-flowing rivers with emergent macrophytes
Cryptomonas	Y	С	All habitats where grazing pressure is low
Chlamydomonas/Chroomonas/Rhodomonas	X_2	С	Shallow, meso-eutrophic environments
Planktonic diatoms (<i>Synedra</i> (big and small), <i>Nitzchia</i> spp., Nitzchia spp., Nitzchia acicularis, n.i. pennates, and centrics)	D (centrics: D, B or C)	CR	Shallow turbid waters including rivers (D) and species sensitive to stratification (B/C)
Tychoplanktonic pennates (A. minutissimum, Navicula, n.i. pennates)	MP/T _D	CR	Frequently stirred up, inorganically turbid shallow lakes or slow-flowing rivers with emergent macrophytes
Winter (December to February)			
Planktonic and tychoplanktonic pennates (<i>Synedra</i> (big and small), <i>A. minutissimum</i> , n.i. pennates, <i>Nitzchia</i>) and centrics	D and MP/T _D (centrics: D, B or C)	CR	(same as above)
Cryptomonas / Chroomonas/Rhodomonas	Y/X ₂	С	(same as above)
Spring (March to June)			•
Metaphytic green filaments (Spirogyra, Mougeotia and others)	T _D	R	(same as above)
Dinobryon	Е	s	Usually small, shallow, base poor lakes or heterotrophic ponds
Cryptomonas/Chroomonas/Rhodomonas	Y/X_2	С	(same as above)
Small pennates (Synedra (small), A. minutissimum)	D and MP/T _D	С	(same as above)



Fig. 1: Geographical distribution of the 22 turloughs studied (abbreviations explained in Table I). Shaded areas correspond to areas of pure bedded limestone (geological data from the Geological Survey of Ireland database: http://www.gsi.ie/Mapping.htm). 254x190mm (96 x 96 DPI)

http://mc.manuscriptcentral.com/jplankt



CLUSTER/SIMPROF analysis of phytoplankton taxa in 22 turloughs. Only taxa that contributed to more than 1% of total algal biovolume are shown. All clustering was significant at p<0.05. 254x190mm (96 x 96 DPI)





Biovolume of tychoplanktonic algae (in light grey - filamentous algae; in dark grey - raphid diatoms) and true phytoplankton (in black). Turloughs are arranged by identified clusters and descending average total phosphorus per cluster (clusters are explained in the text). 254x190mm (96 x 96 DPI)

http://mc.manuscriptcentral.com/jplankt

2D Stress: 0.13

Similarity %

2D Stress: 0.15

Similarity %

_____51.3 _____53.0

(UB)

----- 46.8 ----- 54.1



MDS plot showing ordination of turloughs in terms of their phytoplanktonic communities' similarity: using absolute values of averages per turlough (a) and after standardisation of values by total per sample (b). Circles represent average total phosphorus per turlough (see Table 1 for explanation of abbreviations of turlough names). Enclosed areas represent statistically significant clusters (with similarity values presented up to the closest maximal decimal place). Legend of clusters for (a): 1 – high TP; 2 – low TP; 3 – coloured/deep; 4 – Turloughmore.

254x190mm (96 x 96 DPI)

Low TP

♦ Biovolume

ARD RAT CARR COO TUL ALE KIL BRI CRO SKE TER BAL CARA ROO LIS KNO GEA BLA COY CAH GAR

descending TP within each cluster).

254x190mm (96 x 96 DPI)

■Chlorophytes «Chrysophytes =Cryptophytes Ucyanophytes ZDiatoms

undetermined

Coloured/deep

 total

TUR

o Filaments

Dinoflagellates

mm

biovolume

High TP

«Euglenophytes 🛛 Xanthophytes



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25

20

15

10

Biovolume (mm³/L)







Xanthophytes

undetermined

Sector Euglenophytes

Cyanophytes

■ Cryptophytes

Chrysophytes

% Diatoms

Sum of biovolume of algal groups per month including all 22 turloughs studied. 254x190mm (96 x 96 DPI)







Monthly total algal biovolume of each of the 22 turloughs studied with indication of the taxa dominating the biovolume in peak occasions (>60% of total biovolume); turloughs arranged per identified cluster and descending mean TP per cluster. 254x190mm (96 x 96 DPI)



Mean temperature (solid line) and day length (dashed line) (a), mean depth of coloured/deep (dashed line) and rest (solid line) of turloughs (b), and mean silicate concentration over time in the 22 turloughs (c). Error bars are ± standard deviations. 254x190mm (96 x 96 DPI)

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First two axis of the RDA analysis including all 22 turloughs showing significant explanatory variables (arrows). Symbols correspond to identified turlough clusters: black circles - high TP, open circles - low TP, grey circles - Turloughmore; x - coloured/deep turloughs. 254x190mm (96 x 96 DPI) R