Vol. 83: 203–209, 2019
https://doi.org/10.3354/ame01917

AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol

Published online September 19

Nutrient pollution degrades microbialites in Lough Carra, an Irish marl lake

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ABSTRACT: Marl lakes often have microbialite crusts in the littoral zone, containing a community of cyanobacteria and algae. Previous work has shown that these crusts are most prevalent in oligotrophic lakes and that crust metrics, such as chlorophyll content and green algal abundance, are correlated with total phosphorus concentration (TP) in lake waters, with no intact crusts being found when mean TP > 0.02 mg l^{-1}. Two experiments were carried out to examine how microbialite crust communities respond to nutrient pollution. A culture experiment exposed crusts to various concentrations of nutrients and measured responses over a 43 wk period. In a parallel controlled field experiment, crusts were moved between areas of different trophic state within Lough Carra, a marl lake in the west of Ireland, to see how the community responded. In both experiments, increased nutrient conditions caused a change in relative abundances of taxa in the crust community, leading to a dominance of green algae and degradation of crusts. There were significant differences in chlorophyll concentrations between crusts grown in different nutrient environments. It was concluded that these metrics offer the prospect of a useful quality assessment method for marl lakes.

KEY WORDS: Marl lake · Microbialite · Eutrophication · Cyanobacteria · Conservation

1. INTRODUCTION

Shallow marl lakes are rare in Europe and are under serious threat from nutrient pollution (Pentecost 2009, Free et al. 2016). Ireland is unusual in having many such lakes and is a European centre for this habitat type. In their natural state, these lakes are alkaline, oligotrophic, and have a characteristic charophyte flora (Pentecost 2009, Roden & Murphy 2013). The upper littoral, to a depth of 1 m or more, is typically covered by a layer of marl crust, which is home to a complex microbial community (Kennedy et al. 2012). Doddy et al. (2019) examined marl crusts in lakes of different nutrient conditions. These crusts had a layered, microbialite structure and contained a diverse community of cyanobacteria, chlorophytes (green algae) and diatoms. Total phosphorus concentrations in lake waters were positively associated with chlorophyte abundance and chlorophyll concentration in the microbial crusts. Phosphorus was the main predictive nutrient factor in relation to chlorophyll *a* concentrations in crusts, and high-P lakes had either no crusts, or crusts that were patchy and partly overgrown by green algae or aquatic bryophytes. It was proposed that nutrient pollution in these lakes was causing a shift from a clear-water state, with abundant phytobenthos, to a turbid state in which much of the phytobenthos, including the microbialite crusts, could no longer survive.

In the present study, we used both experimental mesocosms and a field experiment to test the effects of increased nutrient concentrations on the microbialite crusts of Lough Carra, a marl lake in the west of Ireland. Our mesocosm experiment was facilitated by the ability of the microbialite crust communities to grow in culture for a lengthy period. While planktonic cyanobacteria and algae are commonly grown in culture, and cyanobacterial isolates from stromato-

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lites have been grown as axenic cultures on agar (Sharp 1969) or in liquid media (Goh et al. 2009), it is quite unusual for a complex cyanobacterial and algal community to be grown successfully in culture. Fenchel (1998) showed that marine cyanobacterial mats could be cultured if benthic invertebrates were eliminated, and Liu et al. (2002) cultivated cyanobacterial-algal mats in shallow salt ponds. Havemann & Foster (2008) successfully cultured marine microbialites, proposing that these could be used as experimental models for studying microbialite development. Bebout et al. (2002) grew hypersaline microbial mats for >1 yr while testing the effects of salinity variations. Couradeau et al. (2011) cultured samples of microbialites from an alkaline Mexican lake, noting that microbial diversity was maintained in culture even after 2 yr. Buffan-Dubau et al. (2001) cultured microbial mats from an Antarctic lake, noting that green microalgae proliferated when mats were grown at elevated nutrient concentrations, even though these microalgae had not been detected in field samples.

The purpose of the present study was (1) to test experimentally the hypothesis that increases in nutrients are the causative factors in the transition from cyanobacterial to green algal dominance in marl lake crusts, and to determine where the transition point lies, and (2) to characterise the ecological changes that take place in the crust community during this transition. The culture experiment allowed for precisely controlled conditions and regular sampling, whereas the field experiment tested effects of ambient lake conditions on crust structure and persistence.

2. MATERIALS AND METHODS

2.1. Site description

Lough Carra is a shallow, calcareous lake in Co. Mayo, western Ireland, which is well-mixed vertically throughout the year and does not usually freeze over in winter (Hobbs et al. 2005, Huxley & Huxley 2015). A mixture of cattle and sheep farming takes place in much of the catchment. The lake is fed by a combination of small rivers, streams and groundwater and has an area of 18 km^2 (Roden & Murphy 2013), mean depth of 1.75 m, and a maximum depth of 20 m (Irvine et al. 2003). Much of the shore consists of outcropping Carboniferous limestone bedrock, or large boulders or cobbles derived from this rock. Three distinct basins can be defined in the lake: the north basin, mid basin and south basin (Hobbs et al. 2005). Roden & Murphy (2013) documented the vegetation in Lough Carra, finding that cyanobacterial crusts were extremely extensive and sometimes >10 cm thick. In our field experiment, 3 sites were chosen. Site 1 (53.725°N, 9.263°W) and Site 3 (53.724°N, 9.264°W) were both in the north basin, where the cyanobacterial crusts are prevalent, covering most shallow benthic surfaces. Site 2 (53.704°N, 9.217°W), to which experimental stones were moved (see Section 2.3), was in the south basin, near the mouth of the inflowing Annie's River. This area is considered to be nutrient-polluted and has comparatively little crust, with benthic surfaces covered largely by green algae and aquatic bryophytes (Roden & Murphy 2013). Water chemistry in Lough Carra is measured as part of the Irish Environmental Protection Agency (EPA) monitoring programme (EPA 2006). Nutrient data for the north basin (Sites 1 and 3) were taken from an EPA sampling point in the north lake (53.735°N, 9.264°W). Data from a sampling point near the mouth of Annie's River (53.699°N, 9.225°W) was used for Site 2. The results of EPA monitoring of these sites done during our experiment were as follows:

North basin station: Total oxidised N (as N) mean = 0.11 mg l^{-1}, SD = 0.04, n = 7; total P mean = 0.008 mg l^{-1}, SD = 0.003, n = 7.

South basin station (near Annie's River): Total oxidised N (as N) mean = 0.23 mg l^{-1}, SD = 0.18, n = 8; total P mean = 0.009 mg l^{-1}, SD = 0.003, n = 8.

EPA nutrient data for water entering the lake from Annie's River were available for the period May 2016 to May 2017, with the following values: Total oxidised N (as N) mean = 0.77 mg l^{-1}, SD = 0.25, n = 26; total P mean = 0.02 mg l^{-1}, SD = 0.01, n = 26.

2.2. Culture experiment

A preliminary investigation showed that Lough Carra's microbialite crusts can be maintained in culture for at least several months by keeping encrusted stones in containers of lake water or rainwater. In our culture experiment, crusts from Lough Carra were kept in a range of nutrient conditions (see below) over a 10 mo period. Encrusted stones, chosen in order to have an upper (crust-covered) surface of ~400 cm^2, were taken from Site 1 (north basin), transported to Galway-Mayo Institute of Technology, and placed in individual 10 l containers which were kept outdoors, under natural light. These were treated like batch cultures, with the water and nutrients renewed every 6 wk. Chu No. 10 medium (Andersen 2005) was chosen as a growth medium, which was then modified as follows. Series A used a quarter-

strength dilution, Series B used a half-strength dilution, and Series C used full-strength Chu No. 10 medium. Three replicates of each were used, in 3 separate containers. In each case, lake water was substituted for distilled water. All water used in the experiment was collected from Lough Bunny, Co. Clare. This lake is ecologically similar to Lough Carra and was accessible for regular water collection. Results from the Irish EPA showed that mean values for both lakes in the 2010–2016 period were comparable, both having total $p < 0.01$ mg l^{-1}. This lake water (with no additions) was also used for the control series. Sampling was conducted at the start, and at 13, 28, and 43 wk, by taking 19 mm core samples, which were divided and used for chlorophyll analysis and microscopic examination. Relative abundances of selected cyanobacterial and algal groups (Table 1) were assessed during the experiment, which ran from 30 June 2017 until 2 May 2018.

2.3. Field experiment in Lough Carra

A controlled field experiment was carried out over 11 mo in Lough Carra. Because different basins within this lake have different trophic conditions (Roden & Murphy 2013), it was possible to move a set of encrusted stones from an oligotrophic region to a nutrient-polluted region and measure any changes in crust characteristics. The experiment ran from 7 September 2017 until 4 August 2018. Twelve encrusted stones were taken from Site 1 at 30 cm depth. Core samples (19 mm diameter) of microbialite crusts were taken from these for microscopy and pigment analysis. Six of the stones were taken to Site 2 and placed in 30 cm depth of water; the other 6 were taken to Site 3 (the control site) and placed at the same depth. A concrete block was placed as a marker at Sites 2 and 3, and the stones arranged around it at a distance of 30 cm. Small engraved brass plates affixed to the blocks allowed each encrusted stone to be recognised by number. After 11 mo, the sites were revisited, and each encrusted stone was sampled as before.

One sample from each of the 12 stones, at the start of the experiment and again at the end, was used for chlorophyll analysis. A 2-tailed *t*-test was done to test for a significant difference in growth rate, expressed as change over time in chlorophyll *a*, between control and treatment. One sample taken from each stone at the start and end of the experiment was used for microscopy, each divided into subsamples as described below. A Mann-Whitney test was used to test for a significant difference in growth rates of chlorophytes between control and treatment. In addition, 6 stones from Site 2, largely covered by green algae and mosses, were photographed and moved to Site 3; these were again observed and photographed after 11 mo to see if there were any signs of crust recovery.

2.4. Chlorophyll analysis

In all cases, the upper 1 cm of crusts was used for pigment analysis. Samples were ground for 1 min with a mortar and pestle to form a paste. This allowed for more precise measurements of volume. Pigments were extracted in 90% acetone, ground with a glass rod for 3 min and refrigerated at 4°C overnight. Extracts were scanned in a Shimadzu UV-1280 spectrophotometer, and chlorophyll *a* levels were calculated (Parsons et al. 1984). Growth rates, measured as changes in chlorophyll *a*, were calculated as follows:

$$\text{Growth rate} = \frac{\text{natural log (chl } a \text{ conc. at time } x/\text{chl } a \text{ conc. at time 0)}}{\text{time } x \text{ (in wk)}}$$

Table 1. Abundance of cyanobacterial and algal groups were measured during field and culture experiments. Typical representative genera for 2 groups are given in brackets. A detailed list of species present in these lake crusts is given by Doddy et al. (2019)

Group	Description
Group A (*Schizothrix*)	Filamentous cyanobacteria, not tapered, no true branching, heterocysts and akinetes absent, often several trichomes within a common sheath, cells longer than wide, cell width ≤ 3 µm
Group B (*Dichothrix*)	Filamentous cyanobacteria, trichomes tapered, heterocysts present, sheath present and often pigmented, no true branching
Group C (Coccoids)	Cyanobacteria, cells solitary or in colonies, never forming true filaments
Group D (Chlorophytes)	Green algae – members of Phylum Chlorophyta, as defined by John et al. (2011)

2.5. Microscopy

Samples from both experiments were wrapped in aluminium foil and stored at −20°C before analysis. Due to the firm consistency and high inorganic content of these cyanobacterial crusts, standard methods of cell enumeration using an inverted microscope were not possible. Doddy et al. (2019) developed the following method, which was again used in the present study. From each sample, vertical sections (2 × 5 mm) were cut while the crust was still frozen. The upper 1 mm of each was removed. A 1 mm slice was then taken from the top, giving a piece 1 × 2 × 5 mm in size. This was placed on a glass slide, 1 drop of water was added, and the section was homogenised on the slide with a steel, round-tipped rod for 1 min. A 22 × 22 mm cover slip was placed on top and pressed until the homogenised material spread out to its edges. Three slides were prepared from each sample. On each slide, 20 randomised fields of view at 400× magnification were examined (60 per sample), using light microscopy. The presence or absence of organisms from each of the groups listed in Table 1 was recorded. The presence/absence data were then converted to estimated absolute values (Legendre & Watt 1972). Growth rates were then calculated as follows:

$$\text{Growth rate} = \frac{\text{natural log (abundance at time } x\text{/abundance at time 0)}}{\text{time } x \text{ (in wk)}}$$

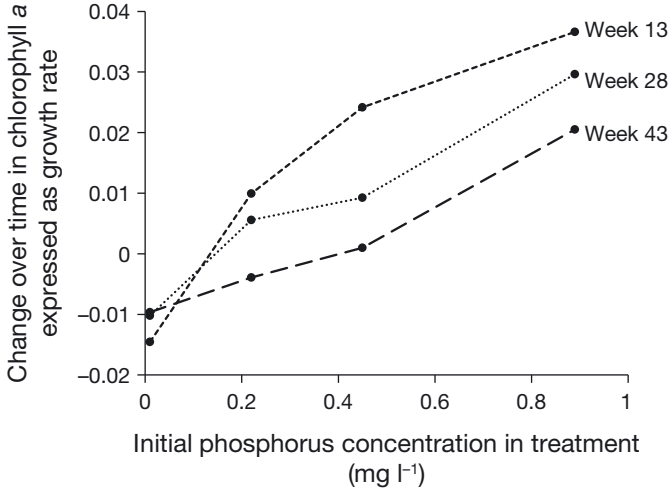

Fig. 1. Changes in chlorophyll *a* in microbialite lake crusts grown in a range of nutrient conditions. Culture media based on modified Chu No. 10 medium (see Section 2), shown here in terms of P content. Water and nutrients renewed every 6 wk. Change over time expressed as growth rate, calculated as: natural log (chl *a* conc. at time *x*/ chl *a* conc. at time 0)/time *x*

3. RESULTS

3.1. Culture experiment

At all elevated nutrient concentrations used in the culture experiment, chlorophyll *a* levels in the microbial crusts initially rose, whereas chlorophyll *a* in the control series declined (Fig. 1). Chlorophyll in the enriched treatments then gradually fell, although by the end of the experiment, the most enriched treatment still maintained elevated chlorophyll concentrations. Chlorophyll in the control series remained low throughout the experiment (Fig. 1).

Groups of organisms within the crust community responded differently to increased nutrient concentrations (Fig. 2). By Week 13, chlorophytes had increased in the most enriched treatment, whereas members of the *Dichothrix* group (Table 1) had increased in the controls. By Week 28, chlorophytes had also increased in the other 2 enriched treatments, in contrast to the cyanobacterial groups. By Week 43, chlorophytes in the most enriched treatment remained elevated, whereas cyanobacterial groups in this treatment had decreased (Fig. 2). Crusts in this treatment had partly fragmented and become greenish in colour. These results indicate that the chlorophyll increase in Fig. 1 is likely mainly due to green algae. In the most enriched conditions, green algae were dominant over all other groups.

3.2. Lake experiment

In the 11 mo field experiment in Lough Carra, crusts moved to a nutrient-polluted part of the lake showed an increase in chlorophyll *a* (Fig. 3), in line with the outcome of the culture experiment. A 2-tailed *t*-test showed a significant difference ($t = 3.166$, $p = 0.010$) between control and treatment. The control crusts experienced a decline in chlorophyll, showing that there appears to be an effect caused by moving crusts, independent of nutrient concentrations. The increase in chlorophytes during the 11 mo (Fig. 4) is in line with the results of the culture experiment. A Mann-Whitney test on growth rates of chlorophytes showed a significant difference ($p = 0.008$) between control and treatment.

Six stones which were moved from Stn 2 (near Annie's River) to Stn 3 (north basin) showed a marked recolonization by microbialite crusts during the 48 wk of the experiment (Fig. 5), indicating that crust degradation can be reversed. However, these regrown crusts were not examined further in the present study.

4. DISCUSSION

This study used a combination of culture and field experiments to examine the effects of nutrient increases on lake crusts. In both experiments, increased nutrient concentrations were associated with increases in chlorophyte abundance and chlorophyll *a* concentration. This is in line with our previous investigation of crusts in a range of Irish limestone lakes (Doddy et al. 2019), in which total phosphorus in lake waters was found to be positively associated with both chlorophyll *a* concentration and chlorophyte abundance.

Other studies in various lakes show similar trends. DeNicola et al. (2006) used nutrient-diffusing substrates to examine benthic algal growth in 3 Irish lakes; both mean algal bio-volume and abundance of filamentous green algae increased in high-P treatments in all lakes. Jensen et al. (1994) examined the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes, finding that chlorophytes often became dominant in high-P lakes. It should be noted, however, that other factors can also be significant.

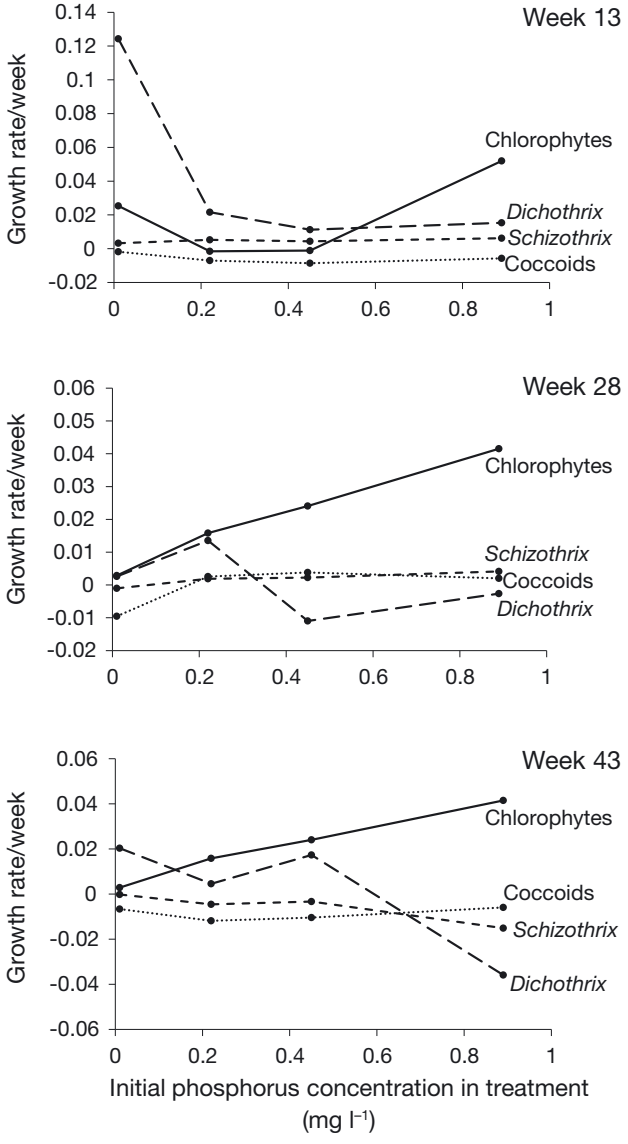

Fig. 2. Growth rates of 4 groups of organisms in microbialite lake crusts grown in a range of nutrient conditions. Culture media based on modified Chu No. 10 medium (see Section 2), shown here in terms of P content. Water and nutrients renewed every 6 wk. All growth rates calculated from the start of the experiment. Taxonomic groups defined fully in Table 1

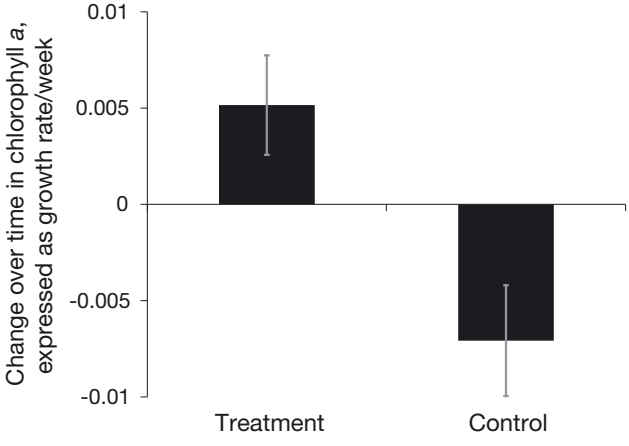

Fig. 3. Changes in chlorophyll *a* concentration in microbial crusts in a 48 wk field experiment in Lough Carra. Mean growth rates and standard error are shown, calculated for the full duration of the experiment, to compare changes from start to end. N = 6 in both cases

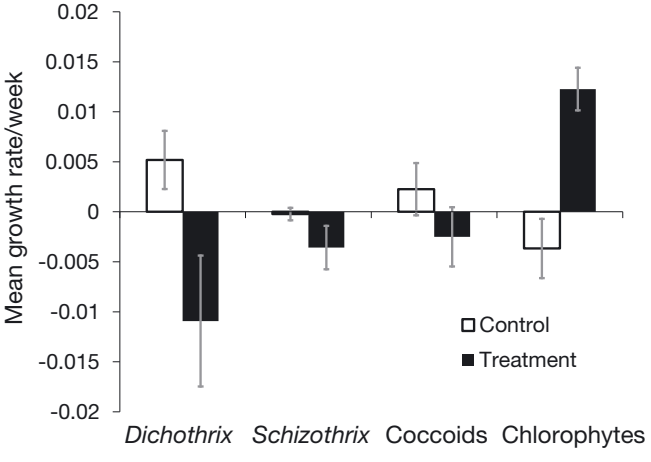

Fig. 4. Changes over time, expressed as growth rates, of microbial groups in lake crusts, in a 48 wk field experiment in Lough Carra. Mean growth rates and standard errors are given for the duration of the experiment, to compare changes from start to end. Taxonomic groups defined in Table 1

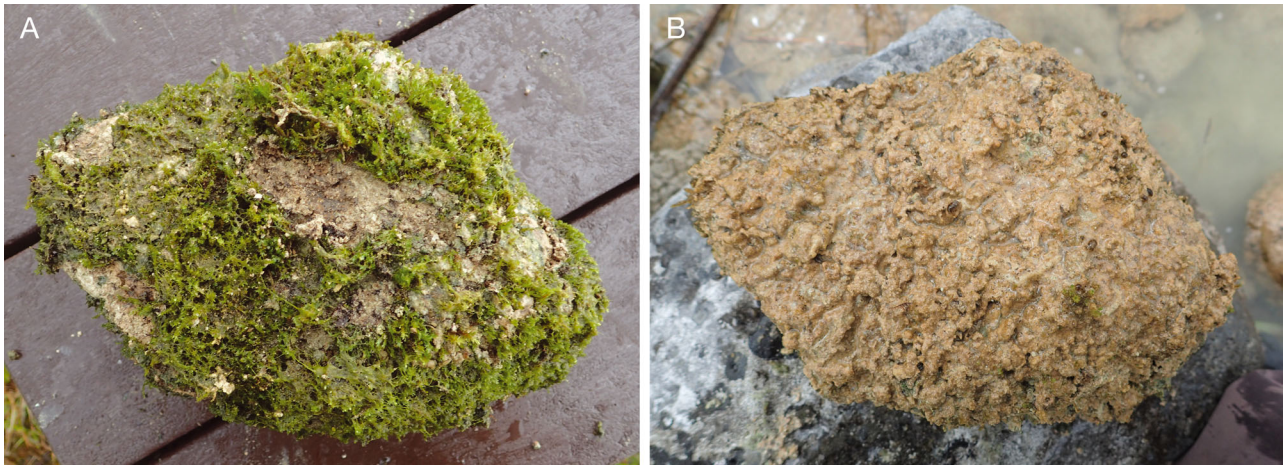

Fig. 5. Stones moved from a nutrient-polluted area (Site 2) to a relatively oligotrophic area (Site 3) in a 48 wk field experiment in Lough Carra showed regrowth of lake crusts. The same stone is shown at the (A) start and (B) end of this period; all 6 replicate stones showed a similar regeneration of crust. Stone is 29 cm across

Lürling et al. (2012) measured growth rates in cyanobacteria and chlorophytes at various temperatures, finding that, at 20°C, chlorophytes significantly outgrew cyanobacteria. No significant differences were found at other temperatures. Tang et al. (1997) noted that in cold climates, cyanobacteria could out-compete chlorophytes by taking up nutrients more efficiently. In milder conditions, the situation was reversed, with chlorophytes proliferating due to their faster growth rates. Clearly, environmental variables, as well as the particular species present in different situations, are important. We conclude from the results presented herein, and from previous work (Doddy et al. 2019), that increasing chlorophyte numbers in lake crusts, with an associated increase in chlorophyll *a*, signals eutrophication and ecological decline in marl lakes. This increase of chlorophytes, and the eventual decline of *Schizothrix* in the high-nutrient treatment (Fig. 2), may also explain the fragmentation of crusts in this treatment, as well as the previously noted reduction in crust cover in high-P lakes (Doddy et al. 2019). Filamentous cyanobacteria, especially *Schizothrix* spp., are known to be important in binding microbial crusts together (Schneider 1977, Schneider & Le Campion-Alsumard 1999).

It is difficult to directly compare the nutrient concentrations used in our culture experiment with those measured in the lake, due to a number of factors. The nutrient measurements from Lough Carra are spot-checks from the water column, and it is difficult to account for the rate of uptake of nutrients by the crust, the phytoplankton, and submerged plants. In addition, it is likely that some degree of nutrient precipitation and/or internal loading take place at times in the lake. In our culture experiment, the nutrients were renewed every 6 wk, and the rate at which they were used up after each renewal is unknown. In any case, direct comparisons are not appropriate due to the high surface area available for precipitation in the experimental containers compared to the lake. Given these uncertainties, it is best to regard the results of the culture experiment as evidence for the principle that eutrophication has clear and measurable effects on crust metrics, whereas the field experiment shows that the same sorts of responses also occur in nutrient-polluted conditions in nature.

Considering the conservation requirements of marl lakes, Moss (2015) and Free et al. (2016) emphasised the need for better ecological assessment methods, rather than relying on chemical data or using biological metrics purely as proxies for chemical data. Such ecological methods are required by the European Water Framework Directive. While water chemistry data (from the Irish EPA) noted above for 2 stations in Lough Carra appear to detect little difference between the north basin and the Annie's River area during our experiment, our results show clear differences in crust metrics between these 2 areas. Indeed, to an aquatic ecologist on the ground, it is abundantly obvious that the Annie's River mouth area suffers from eutrophication to a greater degree than the north basin; yet, expressing such differences clearly in figures is not always easy. The crust metrics we have presented here offer a solution to this challenge, and the results of our culture experiment bolster the case that these metrics genuinely reflect nutrient factors. Free et al. (2016) emphasised the

sensitivity of marl lakes to nutrient pollution and the need to develop better ecological assessment methods tailored to such lakes. The results presented here show that the microbial crusts of these lakes can be used for this purpose.

Acknowledgements. This research was partly funded by the Irish National Parks & Wildlife Service. We thank Chris and Lynda Huxley, Áine O'Connor, John T. Kennedy, S. O. Baldrick, and Bryan Kennedy.

LITERATURE CITED

Andersen RA (ed) (2005) Algal culturing techniques. Elsevier Academic Press, Burlington, MA

Bebout BM, Carpenter SP, Des Marais DJ, Discipulo M and others (2002) Long-term manipulations of intact microbial mat communities in a greenhouse collaboratory: simulating Earth's present and past field environments. Astrobiology 2:383–402

Buffan-Dubau E, Pringault O, De Wit R (2001) Artificial cold-adapted microbial mats cultured from Antarctic lake samples. I. Formation and structure. Aquat Microb Ecol 26:115–125

Couradeau E, Benzerara K, Moreira D, Gérard E, Kaźmierczak K, Tavera R, López-García P (2011) Prokaryotic and eukaryotic community structure in field and cultured microbialites from the Alkaline Lake Alchichica (Mexico). PLOS ONE 6:e28767

DeNicola DM, De Eyto E, Wemaere A, Irvine K (2006) Periphyton response to nutrient addition in 3 lakes of different benthic productivity. J N Am Benthol Soc 25: 616–631

Doddy P, Roden CM, Gammell MP (2019) Microbialite crusts in Irish limestone lakes reflect lake nutrient status. Biol Environ 119:1–11

EPA (2006) Water framework directive monitoring programme. Environmental Protection Agency, An Ghníomhaireacht um Chaomhnú Comhsaoil, Johnstown Castle

Fenchel T (1998) Formation of laminated cyanobacterial mats in the absence of benthic fauna. Aquat Microb Ecol 14:235–240

Free G, Tierney D, Little R, Kelly FL and others (2016) Lake ecological assessment metrics in Ireland: relationships with phosphorus and typology parameters and the implications for setting nutrient standards. Biol Environ 116: 191–204

Goh F, Allen MA, Leuko S, Kawaguchi T, Decho AW, Burns BP, Neilan BA (2009) Determining the specific microbial populations and their spatial distribution within the stromatolite ecosystem of Shark Bay. ISME J 3:383–396

Havemann SA, Foster JS (2008) Comparative characterization of the microbial diversities of an artificial microbialite model and a natural stromatolite. Appl Environ Microbiol 74:7410–7421

Hobbs W, Irvine K, Donohue I (2005) Using sediments to assess the resistance of a calcareous lake to diffuse nutrient loading. Arch Hydrobiol 164:109–125

Huxley C, Huxley L (2015) Lough Carra. Carra Books, Belcarra

Irvine K, Donohue I, Wemaere A, Styles D, Hobbs W (2003) Connecting land-use with water quality: sources, sinks and time-bombs. Diffuse Pollution Conference, 17–21 August 2003, Dublin

Jensen JP, Jeppesen E, Olrik K, Kristensen P (1994) Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish Lakes. Can J Fish Aquat Sci 51:1692–1699

John DM, Whitton BA, Brook AJ (eds) (2011) The freshwater algal flora of the British Isles. Cambridge University Press, Cambridge

Kennedy B, O'Grady M, Whitton BA (2012) Cyanobacteria of Western Ireland. In: Whitton BA (ed) Online supplement to Ecology of Cyanobacteria II, Chap 31. Springer, Dordrecht

Legendre L, Watt WD (1972) On a rapid technique for plankton enumeration. Ann Inst Océanogr Paris 48:173–177

Liu Z, Li P, Liu X (2002) Culturing artificial algal mats to improve the salt yield and quality in saltworks. Ecol Eng 18:379–383

Lürling M, Eshetu F, Faassen EJ, Kosten S, Huszar VLM (2012) Comparison of cyanobacterial and green algal growth rates at different temperatures. Freshw Biol 58: 552–559

Moss B (2015) Lakes, loughs and lochs. William Collins, London

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford

Pentecost A (2009) The marl lakes of the British Isles. Freshw Rev 2:167–197

Roden C, Murphy P (2013) A survey of the benthic macrophytes of three hard-water lakes: Lough Bunny, Lough Carra and Lough Owel. Irish Wildlife Manuals, No. 70. National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Ireland

Schneider J (1977) Carbonate construction and decomposition by epilithic and endolithic micro-organisms in salt- and freshwater. In: Flügel E (ed) Fossil algae. Springer-Verlag, Berlin, p 248–260

Schneider J, Le Campion-Alsumard T (1999) Construction and destruction of carbonates by marine and freshwater cyanobacteria. Eur J Phycol 34:417–426

Sharp JH (1969) Blue-green algae and carbonates- *Schizothrix calcicola* and algal stromatolites from Bermuda. Limnol Oceanogr 14:568–578

Tang EPY, Vincent WF, Proulx D, Lessard P, De la Noüe J (1997) Polar cyanobacteria versus green algae for tertiary waste-water treatment in cool climates. J Appl Phycol 9: 371–381

Editorial responsibility: Tom Fenchel, Helsingør, Denmark

Submitted: February 11, 2019; Accepted: July 11, 2019
Proofs received from author(s): September 9, 2019