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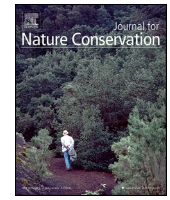

Review

A review of dystrophic lake and pool habitat in Europe: An Irish perspective

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A B S T R A C T

Freshwater lakes and pools contained within peatlands are unique habitats that support rare and specialised species. Despite this, these ecosystems have been overlooked in conservation and management practices. One of these habitats, '3160 Natural dystrophic lakes and ponds', is protected under the European Union (EU) Habitats Directive with a concerning proportion of these habitats having an "unfavourable-bad" or an "unfavourable-inadequate" conservation status across Europe. Our current understanding of the key physico-chemical and ecological features of this habitat is inadequate which is hindering the implementation of effective conservation measures. This review summarises the current knowledge of this protected lake habitat as defined under the EU Habitats Directive. With a focus on Ireland, we demonstrate how the current monitoring and assessment methods used to characterise and assess the structure and function and conservation status of this habitat, which relies largely on the use of macrophyte community composition and surrogate physico-chemical data collected under the EU Water Framework Directive, is ineffective. We propose the incorporation of further or alternative ecological metrics including, but not limited to, algae and macroinvertebrates which are needed to improve our understanding of the structure and function of this priority lake habitat. In addition, application of such data via ecological metrics would allow for the quantification of biodiversity and species rarity metrics which would aid in identifying sites of conservation importance.

1. Introduction

Peatland ecosystems, in particular blanket bogs, are rare and unique habitats containing a suite of specialist species. Peatlands are found predominantly in the northern hemisphere in northern areas of Europe, North America and Asia and in isolated regions of the southern hemisphere (Xu et al., 2018). Peatland ecosystems are a globally important habitat providing several critical ecosystem services including the provision of good quality water, water regulation, flood mitigation, biodiversity, recreation, and carbon storage and sequestration (Evans & Warburton, 2010; Kimmel & Mander, 2010; NPWS, 2015). Europe contains 12.5 % of the world's peatlands (Xu et al., 2018) and a considerable amount of rare blanket bog with Ireland and the UK accounting for 8 % (Foss & O'Connell, 1996) and 13 % (Lindsay et al., 1988) of the worlds resource, respectively. Within European peatland ecosystems, a common freshwater lake and pond habitat type protected under Annex 1 of the European Union (EU) Habitats Directive (formally the Council Directive 92/43/EEC) is '3160 Natural dystrophic lakes and ponds' (referred to '3160 lake habitat' throughout the manuscript) (EEA, 2013).

We are currently facing a freshwater biodiversity crisis with one third of freshwater biodiversity facing extinction due to habitat loss, invasion of non-native aquatic species and pollution (IUCN, 2016), along with an 84 % collapse in freshwater species populations since 1970 (WWF, 2020). Conservation status assessment, monitoring and restoration efforts are therefore imperative if the freshwater biodiversity of protected peatland lake habitats is to receive prominence in future legal and scientific frameworks (Albert et al., 2021; Maasri et al., 2022; van Rees et al., 2020). Furthermore, small lakes and ponds such as those found in peatlands have been overlooked in past conservation efforts (van Rees et al., 2020), but they are gaining increasing recognition for their biodiversity (Biggs et al., 2017; Bolpagni et al., 2019) and role in global biogeochemical processes such as carbon cycling (e.g. Holgerson & Raymond, 2016). Collectively, lakes and pools can cover a significant proportion of the peatland landscape (Connolly et al., 2014) and are therefore important areas for freshwater conservation and habitat

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preservation.

For conservation and restoration objectives to succeed for smaller, less well understood systems such as 3160 lake habitat, they need to be characterised, monitored, and conditions that meet a favourable conservation status established. Therefore, this review aims to i) summarise current knowledge of protected 3160 lake habitat as defined by the EU Habitats Directive and interpreted and implemented within Ireland; ii) assess methods used to derive the current conservation status of 3160 lake habitat under the EU Habitats Directive within Ireland and Europe; and, finally; iii) propose potential ecological monitoring indicators that could aid in characterising, monitoring and determining the conservation status of 3160 lakes and pools under the EU Habitats Directive in Ireland and Europe.

2. Methodology

We aimed to compile all existing peer-reviewed and grey literature that contained data or information on lakes related to '3160 Natural dystrophic lakes and ponds' within peatland areas of Europe. Information was firstly acquired from organisations responsible for implementing the Habitats Directive in Europe (European Environment Agency (EEA)) and within Ireland (National Parks and Wildlife Service (NPWS)). The search was confined to EU member states (MS) with a significant coverage of peatlands which was defined as ≥ 5 % of the land area according to Tanneberger et al., (2017), which were determined as: Denmark (5 %), Estonia (20 %), Finland (27 %), Ireland (21 %), Latvia (12 %), Lithuania (10 %), Netherlands (7 %), Poland (5 %), and Sweden (15 %), the UK (11 %) was also included as it was part of the EU during the most recent reporting period (2013–2018). Searches were then performed within Google Scholar to gather information on how each country characterised 3160 lake habitat using the following key word searches: "Natura 2000″ & "habitat" & "3160″ & "[EU MS]". Google searches were also performed within each country's native language to collate MS habitat interpretation documents which were then translated into English using Google translate. Due to the lack of studies that identify whether their sites contain 3160 lake habitat, additional searches were also performed using other names that can be used to describe these systems including: "peatland lakes", "peatland pools", "bog pools", "dystrophic lakes", "peatland oligotrophic lakes", "acidic lakes" and "*Sphagnum* pools". These alternative names were used in combination with parameters and points of interest including biota ("desmids", "diatoms", "odonata", "coleoptera", "macroinvertebrates"), "water chemistry", "physico-chemical parameters" and "conservation status". Although results of these searches did not identify 3160 lake habitat, they indicated physico-chemical and ecological characteristics that may be indicative of this habitat.

3. 3160 lake habitats in Europe and their conservation status

3.1. 3160 Lake habitat description of Europe and Ireland

The EEA describes 3160 natural dystrophic lakes and ponds as being found on peaty soils or heaths and thus have a brown tinted water, due to humic acids, and an acidic pH (pH 3–6) (EEA, 2013; European Commission, 2007). The plant communities are dominated by the order *Utricularietalia* (EEA, 2013). In Ireland, this lake habitat has been interpreted as 'species poor lake and pond systems dominated by *Sphagnum* mosses and restricted to blanket bogs and wet heaths' (O'Connor, 2015).

3160 lake habitat is abundant within peatlands throughout north western Europe where cool temperatures and high precipitation favour the formation of blanket bogs (Lindsay et al., 1988), with Ireland considered a stronghold for this lake habitat within Europe (O'Connor, 2015). However, the description of 3160 lake habitat as defined by the EEA (EEA, 2013) has been criticised as being ambiguous and unclear because classification of lake habitats heavily relies on the description of historical macrophyte community data with little guidance or consideration given to other physico-chemical, morphological, or ecological features (Curtis et al., 2009; O'Connor, 2016). This has led to differences in its interpretation by EU MS, with each MS creating their own definitions and guidance documents in order to determine the conservation status of this habitat (Airaksinen and Karttunen, 2001; Arts et al., 2016; Aunina, 2013; Miljøstyrelsen., 2016; Naturvårdsverket. , 2011; O'Connor, 2015; Paal, 2007; Paulauskas, 2008; SYKE, 2020; Wilk-Woźniak et al., 2012). To make matters more complex, habitat interpretation documents from Ireland (O'Connor, 2015), Poland (Wilk-Woźniak et al., 2012), Latvia (Aunina, 2013), and Denmark (Miljøstyrelsen, 2016) suggest that 3160 lake habitat share overlapping features and similarities with one or more of the following lake habitat types: 'Oligotrophic waters containing very few minerals of sandy plains (Littorelletalia uniflorae) (3110)', 'Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea* (3130)', 'Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp (3140)', and 'Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition* -type vegetation (3150)' making them difficult to distinguish and classify. This can be further complicated by the co-occurrence of different habitats within the same waterbody (Evans, 2006; O'Connor, 2015). This high degree of variation in habitat characteristics, and differences in interpretation makes it difficult to confidently define an individual lake to one habitat type, particularly where data is limited or unknown.

3.2. Conservation status assessment criteria for 3160 lake habitat under the EU habitats Directive

Under the EU Habitats Directive, conservation status of habitats is assessed for each biogeographical region (Alpine, Boreal, Macaronesian, Atlantic, Continental, Pannonian, Black Sea, Mediterranean, Steppic) within each MS according to range, area, structure and functions, and future prospects (EEA, 2017). For lake habitats, range and area are unlikely to change between assessments therefore structure and function parameters are key determinants of conservation status (NPWS, 2019; NPWS, 2013). The status of each parameter (range, area and structure and function) is defined as the rate of loss or distance away from Favourable Reference Values (FRV) defined as "favourable (FV)", "unfavourable-inadequate (U1)", "unfavourable-bad (U2)" or "unknown (XX)" (EEA, 2017). The conservation status of 3160 lake habitat within Europe indicates that 35 % are of favourable status, with the remainder being assessed as unfavourable-inadequate (30%), unfavourable-bad (28 %) or unknown (7 %) (Fig. 1).

There is no requirement under the EU Habitats Directive for lake sites to be continuously monitored, therefore MS assess the conservation status of range, area and structure and function using a combination of 'expert opinion', 'extrapolation of limited data', 'complete surveys' or 'statistically robust estimates' (EEA, 2019). In general, range and area can be estimated and extrapolated using remote techniques such as mapping, whereas the evaluation of structure and function requires field data which is often lacking (EEA, 2019). For example, the condition of habitat structure and functions were estimated based on 'extrapolation from a limited amount of data' (Denmark Atlantic and Continental, Finland Alpine and Boreal, Ireland, Netherlands, Poland Continental, and UK) or 'based mainly on expert opinion with very limited data' (Sweden Alpine, Boreal and Continental, Lithuania, and Latvia) for all MS being evaluated in this review except for Poland (Atlantic) and Estonia (Boreal) which were evaluated based on a 'complete survey or a statistically robust estimate' for the 2013–2018 reporting period (EEA, 2019). Using Ireland as an example, the inadequate stable (2007–2012 and 2013–2018 cycle) conservation status assigned to the 3160 lake habitat was heavily reliant on expert knowledge and judgements of limited macrophyte data along with maps of blanket bog, areas of base-poor geology and current and historical maps of catchment land use, in addition to several extrapolations and assumptions because many of the

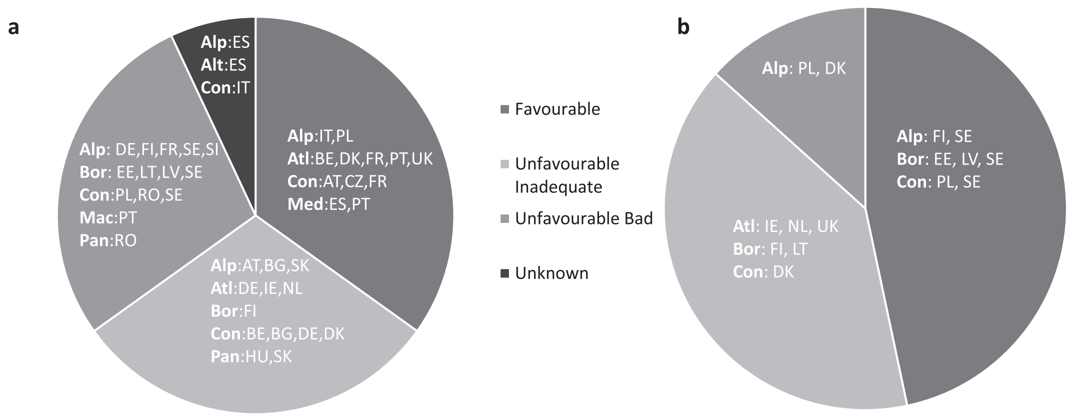

Fig. 1. Proportion of biogeographic (Alp = Alpine, Atl = Atlantic, Bor = Boreal, Con = Continental, Mac = Macaronesian, Med = Mediterranean, Pan = Pannonian and Ste = Steppic) and country (AT = Austria, BE = Belgium, BG = Bulgaria, CZ = Czech Republic, DE = Germany, DK = Denmark, EE = Estonia, ES = Spain, FR = France, HU = Hungary, IE = Ireland, IT = Italy, LT = Lituania, LV = Latvia, NL = Netherlands, PL = Poland, PT = Portugal, RO = Romania, SE = Sweden, SI = Slovenia, SK = Slovakia, UK = United Kingdom) categories which have a favourable (mid-grey), unfavourable-inadequate (dark-grey), unfavourable-bad (black) or an unknown (light grey) overall conservation status for (a) 3160 lake habitat in all EU countries and (b) 3160 lake habitat in countries with an area of peatland exceeding 5% according to Tanneberger et al., (2017). (Based on reported data from each MS for the 2013–2018 reporting period (EEA, 2019)).

lakes were unstudied or had minimal data (NPWS, 2019; NPWS, 2013). In Ireland, where macrophyte community composition data was available it is used to determine the range, area and structure and function of the lake habitat (NPWS, 2019; NPWS, 2013). In contrast, Poland have defined ranges for physical, chemical, and ecological metrics for favourable, inadequate, and unfavourable conservation status and outline standard methodologies for the collection and interpretation of these data (Wilk-Woźniak et al., 2012). This goes beyond the EEA (2013) description of 3160 lake habitat as it includes numerical values for variables such as water colour, dystrophy, and conductivity with the addition of other ecological elements including phytoplankton (Wilk-Woźniak et al., 2012). Although Poland do also highlight there is limited data on this habitat type particularly in the Alpine biogeographical region (EEA, 2019).

These two examples highlight the vast differences in methodological approaches for assessing conservation status between MS, making it difficult to compare the relative condition of 3160 lake habitat collectively across Europe. These difficulties will continue without a standardised approach for assessing the structure and function of 3160 lake habitat across Europe.

3.3. *The Water Framework Directive (WFD)*

Data on surface water bodies, including dystrophic lakes (3160 lake habitat), are also collected under the EU Water Framework Directive (WFD) which aims to protect all EU waters and their habitats, promote sustainable water use, and prevent the deterioration of waters (European Commission, 2019). Therefore, MS such as Ireland, Sweden and Finland use data collected under the WFD to inform conservation status for the Habitats Directive (EEA, 2019).

While the WFD and Habitats Directive have overlapping goals and an ecological focus, their monitoring and assessment approaches, and terminology differ (ETC/ICM., 2015; European Commission, 2011; O'Connor, 2016; Rouillard et al., 2018). For example under the Habitats Directive, site specific monitoring is decided by the individual MS and there are no pre-determined physical, chemical or ecological elements listed as being essential to measure nor are threshold boundaries indicated to determine the appropriate conservation status (Louette et al., 2011; O'Connor, 2016). This absence of a universal monitoring approach across MS hinders cross comparisons at a European scale. In contrast, the WFD follows a prescriptive approach to monitoring that requires a list of physicochemical and ecological metrics to be measured that have been agreed at European level (European Commission, 2019) and with ecological metrics being intercalibrated across MS (Birk et al., 2013; ETC/ICM, 2015; Poikane et al., 2014).

The ecological (macrophytes, phytoplankton, phytobenthos, benthic macroinvertebrates, and fish) and physico-chemical (nutrients, temperature, oxygen, and pollutants) elements monitored under the WFD were predominantly, but not exclusively, designed to identify the impacts of eutrophication (Phillips, 2014). Whilst eutrophication is also a threat to conservation status, other impacts are also important such as hydrological and morphological modifications which may lead to habitat degradation (Poikane et al., 2020). Using data collected under the WFD to inform lake habitat condition and conservation status should therefore be undertaken with caution (Ecke et al., 2010), because critical structure and function information, such as the occurrence of rare or threatened species, is not considered (O'Connor, 2016). As a result, high ecological status according the WFD does not mean that the lake habitat will have a favourable conservation condition under the Habitats Directive, or vice versa (Ecke et al., 2010; European Commission, 2011). Metrics for assessing ecological status under the WFD were also primarily developed for clear-water systems and therefore may not be suitable for assessing the ecological status of dystrophic lakes as they function differently (Alahuhta et al., 2009; Ozoliņš et al., 2021; Rask et al., 2011).

The recent introduction of broad lake types by Lyche Solheim et al., (2019) now allow for better cross-comparisons between Habitats Directive habitat types and WFD lake types. For example, broad lake types 5 (lowland, humic and siliceous), 6 (lowland, humic, and calcareous/mixed), 9 (mid-altitude, organic and siliceous), and 10 (mid-altitude, humic, and calcareous/mixed) are comparable with habitat 3160 'Natural dystrophic lakes and ponds' under the Habitats Directive (ETC/ICM, 2015). The utility of this comparison for dystrophic lakes may be limited, however, as the WFD only monitors water bodies of a significant size which is set at a threshold > 0.5 km^2 by many EU MS (EEA, 2003). Many dystrophic lakes and pools are below this size threshold, for example Sweden suggest that 3160 lake habitat is often < 0.1 km^2 and rarely exceed 0.5 km^2 (Naturvårdsverket, 2011). Data from small dystrophic lakes (3160 lake habitat) is therefore likely underrepresented in WFD datasets.

4. Variables used to assess habitat structure and function under the habitats directive

4.1. Macrophytes

3160 lake habitat is considered species poor botanically with a community characterised by bryophytes of the genus *Sphagnum* and sustain the *Utricularietalia* phytosociological order (European Commission, 2007). The European Commission (2013) characterises 3160 lake habitat by the presence of *Utricularia* spp., *Rhynchospora alba*, *R. fusca*, *Sparganium minimum* and *Sphagnum* spp., with *Nuphar lutea*, *N. pumila*, *Carex lasiocarpa*, *C. rostrata*, *Nymphaea candida*, *Warnstorfia trichophylla*, and *W. procera* occurring in boreal regions.

Several macrophyte species occurring in 3160 lake habitat can also occur in other lake habitats for example in Ireland, *Utricularia* spp., *Warnstorfia* spp., and *Nuphar lutea* are also common in 3110 lake habitat (O'Connor, 2015). Therefore, if the macrophyte community of a lake contains these species it can be difficult to assign it to one habitat type. This makes the characterisation and distinction of lakes within peatlands difficult and suggests that information on macrophytes alone is not sufficient for characterising habitat types. This is further complicated by regional differences within these habitat types as certain species are only present within some biogeographical regions due to climatic differences (e.g. boreal species) (European Commission, 2013) and certain species

Table 1
Comparison of chemistry thresholds determined by the EU Water Framework Directive (WFD) for high ecological status broad lake types considered equivalate to 3160 lake habitats (Carvalho et al., 2008; ETC/ICM, 2015; Poikane et al., 2019; Table 4) and 3160 lake habitat interpretations according to the EU (European Commission, 2013), Denmark (Miljøstyrelsen, 2016), Estonia (Loodusveeb, 2021), Finland (Airaksinen & Karttunen, 2001), Ireland (O'Connor, 2015), Latvia (Aunina, 2013), Lithuania (Paulauskas, 2008), the Netherlands (Arts et al., 2016; van Calster et al., 2019), Poland (Wilk-Woźniak et al., 2012), Sweden (Naturvårdsverket, 2011), and the UK (Interagency Freshwater Group, 2015). Poland has separate recommendations for each conservation status FV = favourable, U1 = unfavourable inadequate and U2 = unfavourable bad (Wilk-Woźniak et al., 2012). [abc] literature values for Northern lake types 3a, 8 and 6 respectively as defined under the EU WFD (Carvalho et al., 2008) and which equivocate to new lake types detailed in Lyche Solheim et al., (2019) and ETC/ICM, (2015).

	pH	Alkalinity (meq.l^{-1})	Water colour (Pt mg l^{-1})	Nutrients (mg l^{-1})	Conductivity (μS cm^{-1})	Chlorophyll *a* (μg l^{-1})	Total Dissolved Solids (mg l^{-1})
WFD broad lake types							
5		<0.2 to 1 (Carvalho et al., 2008; Table 4)	>30 (Lyche Solheim et al., 2019; Table 2)	TN 0.7–1.5 TP 0.016–0.3 (Poikane et al., 2019; Table 4)		4.1[a] (median) 7.0[b] (median) (Carvalho et al., 2008; Table 4)	
6			>30 (Lyche Solheim et al., 2019; Table 2)				
9		<0.2 (Carvalho et al., 2008; Table 4)	>30 (Lyche Solheim et al., 2019; Table 2)	TN 0.6 TP 0.013–0.024 (Poikane et al., 2019; Table 4)		3.3[c] (median) (Carvalho et al., 2008; Table 4)	
10			>30 (Lyche Solheim et al., 2019; Table 2)				
Habitats Directive Interpretations							
EU (European Commission, 2013)	3–6		Brown tinted				
Denmark (Miljøstyrelsen, 2016)	3–6		≥60				
Estonia (Loodusveeb, 2021)	4–6						
Finland (Airaksinen & Karttunen, 2001)	4.5–6		Brown	Low nutrient			
Ireland (O'Connor, 2015)	3–6		Brown tinted	TP 0.005 (mean) Total $NH_3 \leq 0.04$ (mean)		<5.8 (growing season mean)	
Latvia (Aunina, 2013)	3–6		≥80				
Lithuania (Paulauskas, 2008)	3–6						
Netherlands (Arts et al., 2016; van Calster et al., 2019)	4.5–5.5	< 0.1		$NH_3 < 0.03$ (annual mean)<0.1 (annual max)	<100		
Poland (Wilk-Woźniak et al., 2012)	FV = 3–7 U1 = 7–8 or 2–3 U2= > 8 or < 2		FV= <50 U1 = 51–100 U2= > 101		FV= <100 U1 = 100–500 U2= >500		FV= <60 U1 = 60–100 U2= > 100
Sweden (Naturvårdsverket, 2011)	<6.2		≥100 (often)	TP < 0.025			
UK (Interagency Freshwater Group, 2015)	<5 (annual mean)		>30	TP ≤ 0.01 (annual mean)			

may be occurring in these habitats due to deviations from their natural water chemistry as a result of anthropogenic stressors (Wilk-Woźniak et al., 2012). For example *Nuphar lutea* is common in eutrophic lake habitats (3150) (Interagency Freshwater Group, n.d.; O'Connor, 2015) and may therefore be an indicator of nutrient enrichment in 3160 lake habitat. Habitat interpretation manuals for 3160 lake habitat from different MS therefore list additional macrophyte species that can also occur in this habitat, such as *Calla palustris* (Poland and Estonia), *Calliergon stramineum* (Poland), *Carex limosa* (Latvia), *Cladium mariscus* (Ireland), *Comarum palustre* (Poland), *Drepanocladus* spp. (Denmark and Estonia), *Eleogiton fluitans* (Ireland), *Equisetum fluviatile* (Finland), *Juncus effusus* (Netherlands), *Molinia caerulea* (Netherlands), *Menyanthes trifoliata* (Poland, Ireland and Finland), *Myriophyllum alterniflorum* (Ireland and Finland), *Phragmites australis* (Poland), *Potamogeton natans* (Poland, Lithuania, Estonia and Finland), *Potamogeton polygonifolius* (Ireland and Finland), *Potamogeton praelongus* (Estonia), *Typha angustifolia* (Poland), *Typha latifolia* (Poland), and *Schoenoplectus lacustris* (Poland) (Airaksinen & Karttunen, 2001; Arts et al., 2016; Aunina, 2013; Herbich, 2004; Miljøstyrelsen, 2016; O'Connor, 2015; Paal, 2007; Paulauskas, 2008; Wilk-Woźniak et al., 2012).

In Ireland, the characterisation of this habitat using macrophytes is hindered by a lack of data. Where available, water chemistry data is substituted to reflect range, area, and structure and function of 3160 lake habitat since physico-chemical characteristics of lake habitats determine which macrophyte species occupy them (O'Connor, 2015). In some instances, the occurrence of macrophytes in dystrophic lakes (3160 lake habitat) can be lacking or non-existent (Rørslett, 1991), but this does not mean that these lakes are barren of life and would not meet favourable conservation status based on alternative ecological assessment. Other ecological elements may therefore be suitable individually or in combination with limited macrophyte data for assessing habitat structure and function thus their conservation status.

4.2. Physico-chemical characteristics

The European Commission (2013) provides limited information on the expected chemical characteristics of 3160 lake habitat, with the only guidance being that their pH is low (pH 3–6) (Table 1). Thus, very few studies have determined chemical thresholds for favourable and unfavourable conservation status for 3160 lake habitat. Efforts to establish physico-chemical thresholds values for 3160 lake habitat in Ireland are, to date, based on limited water chemistry data collected for WFD assessment and expert opinion but do provide a starting point from which 3160 lake habitat may be characterised.

Dystrophic lakes are expected to be dark in colour and have a low transparency (low secchi depth) due to high concentrations of dissolved organic matter (DOM), mainly consisting of humic matter (Carlson & Simpson, 1996; Carpenter & Pace, 1997). This means that the structure and function of these lake ecosystems differ in comparison with clear-water lakes (Solomon et al., 2015). There are numerous ways to evaluate dystrophy within lakes, such as setting threshold values for relevant variables, for example threshold water colour values have been defined for humic (>30 mg l^{-1} PtCo) lake types under the EU WFD (Carvalho et al., 2008; Poikane et al., 2010). MS have also set different thresholds for expected water colour values ranging from < 50 mg l^{-1} PtCo to $>$ 100 mg l^{-1} (Table 1). Alternatively, the Hydrochemical Dystrophy Index (HDI) developed by Górniak, (2017) uses pH, electrical conductivity, dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC) within an equation to evaluate dystrophy. Calculated HDI values, in combination with other lake characteristics, can then be used to determine the level of dystrophy within a lake (e.g. semi-dystrophic or dystrophic) (see Table 6 in Górniak, 2017). Poland have set a HDI threshold for favourable (HDI > 50), unfavourable (HDI 40–50) and bad conservation status (HDI < 40) (Wilk-Woźniak et al., 2012) using previous versions of the HDI (Górniak, 2004, 2006).

The monitoring of water colour, DOC and DIC is not mandatory under the EU WFD, with around half of EU MS monitoring one or more organic matter parameters in freshwaters (Sepp et al., 2018). Metrics that assess organic matter are also inconsistent across EU MS making it difficult to evaluate dystrophy on an EU level using existing datasets (Sepp et al., 2018). Secchi depth, a measure of water transparency, is routinely monitored however, and is primarily influenced by DOC, DIC and chlorophyll *a* concentrations. Secchi depth is expected to be shallow for favourable conditions in dystrophic habitats due to natural brown tinting (European Commission, 2007) but this is not defined. Potential values for DOC and DIC could be derived from broader peatland studies, but often habitat type is seldom specified and can be difficult to infer from the presented data.

The EU WFD does require the collection of nutrient and chlorophyll *a* data which may be useful for characterising lake habitat types. According to Poikane et al., (2019) MS have defined a total phosphorus (TP) range of 0.013–0.3 mg l^{-1} and a total nitrogen (TN) range of 0.6–1.5 mg l^{-1} for humic lakes in a good-moderate ecological status (Table 1). Moreover, dystrophic lake habitats are more likely to be impacted by increases in ammonia, yet threshold concentrations have not been specifically defined in Ireland (O'Connor, 2015) although an annual mean of $\leq$ 0.03 mg l^{-1} is used for these lake habitats in the Netherlands (van Calster et al., 2019) (Table 1). Despite the lack of nutrient thresholds for 3160 lake habitat in Ireland it is agreed that naturally unproductive lakes would have stringent, but as yet, undefined targets (Interagency Freshwater Group, 2015). Phytoplankton biomass, approximated as chlorophyll *a* concentration, should also be relatively low, within such humic lake types (3160) (3.3–7.0 μg l^{-1}) (Table 1) (Carvalho et al., 2008) although this can be variable depending on the relative abundance of nutrients and water transparency (Carpenter & Pace, 1997; Carvalho et al., 2008; Poikane et al., 2010) and conductivity is also expected to be low (<100 μS cm^{-1}) (Table 1) (van Calster et al., 2019; Wilk-Woźniak et al., 2012).

Research by Drinan (2012) also points to a clear distinction in physico-chemical characteristics in Irish blanket bog lakes and pools based on altitude, proximity to sea and underlying geology. Lakes and pools below 180 m above sea level (a.s.l) had lower concentrations of TP, chlorophyll *a* and total dissolved organic carbon (TDOC), a lower pH, higher conductivity and higher concentration of major ions (sodium, chloride, magnesium, potassium, and sulphate), compared to those above 180 m a.s.l which were significantly cooler and had higher concentrations of TP (Drinan, 2012). Furthermore, Turner et al., (2016) found significant regional differences in sulphate and chloride ions and fractions of carbon among sites sampled in two areas of Scotland and one area of Northern Ireland suggesting large variability in water chemistry.

In Ireland, information on the physico-chemical parameters of this lake habitat has been gathered from secondary sources such as the EU WFD (NPWS, 2019; NPWS, 2013), the Organisation for Economic Cooperation and Development (OECD) for lake trophic status (Interagency Freshwater Group, 2015; O'Connor, 2015), and broader research on peatland lakes and pools (Drinan, 2012). Data collected from these sources have very different purposes and in most instances lake habitat type is often not distinguished.

It is also difficult to define favourable conservation targets for these physico-chemical parameters without further knowledge of their undisturbed state (Louette et al., 2011; O'Connor, 2015). Some countries, such as Sweden and Finland, have a large number of lakes in relatively pristine condition, where human interference has been limited to atmospheric deposition of substances (EEA, 2019; Poikane et al., 2010). Whereas in other countries, such as Ireland many peatland lakes have been subjected to multiple stressors such as acidification, eutrophication, overgrazing, habitat loss, turf cutting, siltation, drainage, and erosion (Drinan, 2012; Grzybowski, 2019; Moss, 2011; NPWS, 2015; O'Connor, 2015, 2016) that have altered their natural chemistry. It is therefore very difficult to determine natural levels of water colour, nutrients, and chlorophyll *a*. The baseline for many of these variables are also likely shifting with climate change, adding a further complication for setting conservation targets (Lawler et al., 2015).

5. Recommended indicators for assessing structure and functions and conservation status of dystrophic lake habitats

Determining the conservation status of 3160 lake habitat in Ireland is difficult due to limited knowledge on their structure and function and characterisation. At EU level, there is a lack of site specific monitoring coupled with no pre-determined physical, chemical or ecological elements listed as being essential to measure, nor threshold boundaries determining their appropriate conservation status (Louette et al., 2011; O'Connor, 2016). Furthermore, even though lake habitats are comprised of multiple ecological elements, an over reliance on macrophyte data surrogated with physico-chemical data, where available, is concerning because ecological indicators have different response times to environmental change (Kelly et al., 2016) and can react differently to various stressors (Crossetti et al., 2013; Kolada et al., 2016). Therefore, monitoring one ecological element is likely to be insufficient to determine the structure and function and conservation status of such complex lake habitats. This is particularly important for dystrophic lakes (3160 lake habitat) with naturally dark water colour and low transparency meaning macrophytes may be lacking, but this does not mean that they are an unimportant habitat for rare and threatened species (Ozoliņš et al., 2021).

A more holistic approach is now needed where the representation of 3160 lake habitat ecology is urgently addressed. This can be achieved through monitoring alternative or a combination of key ecological components to identify the occurrence of rare and threatened species to help assign a biodiversity and conservation value. Here we suggest that monitoring of algae (particularly diatoms and desmids) and macroinvertebrates should be prioritised for this lake habitat. These elements are already monitored as part of the EU WFD, and monitoring methodologies could be adapted and applied to assess the conservation status of 3160 lake habitat, with a number of MS already including information on these ecological elements in their Habitat's Directive guidance documents for 3160 lake habitat (Arts et al., 2016; Aunina, 2013; Paulauskas, 2008; Wilk-Woźniak et al., 2012). Lowering the lake size threshold to include smaller lakes in permanent WFD monitoring would be expensive and time intensive, but short-term 'snapshot' sampling of smaller dystrophic lakes and pools could be beneficial for addressing the current data gap and therefore help make a more informed decision on their current conservation status.

5.1. Suggested alternative ecological monitoring indicators for dystrophic lake habitats

5.1.1. Algae

Algal species are known ecological indicators of physico-chemical differences and stressors in freshwater systems (Stevenson, 2014). Macrophytes are often lacking or non-existent in dystrophic lakes (3160 lake habitat) (Rørslett, 1991) therefore monitoring phytoplankton may be a suitable alternative for determining habitat structure, function and conservation status as they are ubiquitous across lakes. Poland have described the phytoplankton community composition of 3160 lake habitat as being comprised of cryptophytes, chrysophytes, diatoms, dinoflagellates, green algae, desmids, and some small colonies of cyanobacteria (Herbich, 2004). Phytoplankton community composition has also been defined for different levels of conservation status (Wilk-Woźniak et al., 2012). Lakes with a favourable conservation status consist of mixotrophic taxa, diatom species that indicate low nutrients, and acidophilic species; unfavourable-inadequate status habitats have large abundance of *Gonyostomum semen*; and unfavourable-bad status habitats are dominated by species present in eutrophic waters and cyanobacteria blooms (Wilk-Woźniak et al., 2012).

Additional understanding of algal community composition in dystrophic lakes is derived from broader peatland research, where lake habitat types are not defined. In 3160 lake habitat, benthic algal monitoring (i.e. diatoms and desmids) may provide important ecological structure and function clues as they typically have slower turnover times than phytoplankton and are sensitive to changes in the physico-chemical environment, especially changes in pH and alkalinity (Coesel, 1983, 2001, 2003; Coesel & Meesters, 2007; DeNicola et al., 2004; Free et al., 2006). Desmids are particularly abundant in acidic dystrophic systems for example, Free et al., (2006) found that desmid abundance increased rapidly in Irish lakes of low alkalinity (<10 mgl^{-1} $CaCO_3$) with *Cosmarium depressum*, *Staurodesmus indentatus,* and *Xanthidium octocorne* showing a preference for peaty humic waters (Lally et al., 2012), while strongly acidic sites ($pH < 4$) were more likely to be dominated by *Cylindrocystis brebissonii*, *Staurastrum margaritaceum,* and *Staurastrum hirsutum* var. *muricatum* (Štěpánková et al., 2008, 2012). Furthermore, Coesel and Meesters, (2007)' extensive research has already categorised 241 desmid species as being oligotrophic and acidophilic while extensive desmid surveys conducted in peatland lakes in western Ireland by West, (1892) and John and Williamson (2009) have recorded a total of 476 desmid species and 706 subspecies.

These studies on planktonic and benthic diatoms and desmids demonstrate their reliable occurrence in acidic lakes and, due to their sensitivity to changing physico-chemical conditions, could make them suitable ecological indicators for the assessment of structure and function of 3160 lake habitat. Research by Wilk-Woźniak et al., (2012) is a welcome starting point in providing expected evidence of phytoplankton community composition for various conservation statuses within 3160 lake habitat. A similar approach could be adopted by other EU MS to define the phytoplankton and phytobenthic community composition of 3160 lake habitat, and for each MS separate, reliable taxon lists could be compiled including lists of rare and endangered taxa.

5.1.2. Macroinvertebrates of peatlands

A recent study by Ozoliņš et al., (2021) demonstrated that macroinvertebrate communities are a useful indicator for assessing the ecological status of humic lakes for the EU WFD where macrophytes are often lacking (Rørslett, 1991). The metrics developed in this study used data from peatland lakes in raised bog areas of Latvia which could be tested in other MS which have a high proportion of humic lakes. Similar metrics could also be adapted to address the aims of the EU Habitats Directive.

To date, there is a lack of knowledge on macroinvertebrate community composition typical of 3160 lake habitat within Ireland. This is despite the fact that macroinvertebrates are commonly found in peatland lakes and ponds (Ozoliņš et al., 2021) and their distribution and rare species occurrence is well documented with red lists for Coleoptera and Odonata in Ireland, the UK, and Poland as well as for Europe (Daguet et al., 2008; Foster, 2010; Foster et al., 2009; Kalkman et al., 2010; Nelson et al., 2011; Pawłowski et al., 2002). A number of MS list Coleoptera and Odonata in 3160 lake habitat guidance documents, for example Coleoptera species include *Dytiscus lapponicus* (Latvia) and Odonata species include *Somatochlora arctica* (Latvia), *Leucorrhinia albifrons* (Latvia), *Leucorrhinia dubia* (Netherlands), and *Leucorrhinia pectoralis* (Lithuania) (Arts et al., 2016; Aunina, 2013; Paulauskas, 2008).

Additional evidence from Irish blanket bog lakes and pools indicate *Enochrus fuscipennis*, *Stictotarsus duodecimpustulatus*, and *Haliplus fulvus* are abundant in lowland granite lakes with higher temperatures, conductivity, pH and calcium levels (Drinan, 2012), *Gyrinus minutis*, *Hydroporus obscurus*, and *Haliplus confinis* are acidophilic (Baars et al., 2014), *Coelostoma orbiculare* is strongly associated with *Sphagnum* pools (Hannigan & Kelly-Quinn, 2012) while *Acilius sulcatus*, *Dytiscus lapponicus*, and *Agabus arcticus* are associated with high altitude lakes underlain by sandstone (Drinan, 2012), with *Sympetrum danae* (Drinan, 2012), *Strictonectes griseostriatus*, and *Rhantus suturellus* (Baars et al., 2014) restricted to upland lakes.

These studies suggest that macroinvertebrates may act as good indicators of structure and function within 3160 lake habitat in addition to reflecting physico-chemical environmental shifts. Further work could now be conducted by EU MS including Ireland to determine if the macroinvertebrate community compositions are indicative of 3160 lake habitat and whether they can be used to assess their conservation status under the EU Habitats Directive.

5.1.3. Ecological metrics

Ecological metrics incorporating data on macrophytes, algae and macroinvertebrates may provide a holistic approach for understanding the structure and function of 3160 lake habitat within EU MS along with assisting in comprehensive assessments of their conservation status under the EU Habitats Directive.

Dystrophic lake habitats are often associated with lower species diversity, for example lakes with a highly acidic pH (~4) tend to have low desmid species richness (Štěpánková et al., 2008; Štěpánková et al., 2012). However, such unique environmental conditions are associated with rare taxa and identifying such taxa helps prioritise sites of conservation importance (Coesel, 2001). Lists of endangered or rare taxa developed by MS could be used to inform this. Furthermore, application of such data could assist in the advancement of ecological metrics to determine conservation status of 3160 lake habitat through the modification of existing metrics. One example of this is the Nature Conservation Value (NCV) developed by Coesel, (2001) using desmid assemblages, however substitution of desmids with other ecological elements could further assist in prioritising sites for conservation and restoration.

For many organisms the size of the body differs according to their physico-chemical environment and trophic state. For example, a diatom valve width of < 2 µm for the species *Achnanthidium minutissimum* is attributed to oligotrophic waters (Kahlert et al., 2009; Vilmi et al., 2015) and for desmids smaller sized taxa are associated with ombrotrophic systems (González Garraza et al., 2019; Neustupa et al., 2013). Furthermore, algal morphology and lifeform and ecological guild data (e.g. mobile, colonial, solitary stalked) are intrinsically linked to their function and physico-chemical conditions (Padisák et al., 2009; Reynolds et al., 2002), all having the potential to highlight lake habitat functional differences (Berthon et al., 2011; Passey, 2007). For macroinvertebrates, biological traits such as dispersal ability, time of development, and reproduction also describe variations in communities where species with a high tolerance for harsh conditions, such as acidity, have poor dispersal ability and slower developmental times (Verberk et al., 2008). Findings from Ozoliņš et al., (2021) suggested that the macroinvertebrate abundance, preference for littoral or profundal lake zone, Biological Monitoring Working Party (BMWP) score, and Coleoptera taxa richness were the most useful metrics for assessing ecological status for the WFD in humic lakes in Latvia.

Further research would be required to develop and test these monitoring indicators to determine whether they can be applied across all biotas and climatic regions and to whether they differentiate structure and function of 3160 lake habitat and assist in determining their conservation status under the EU Habitats Directive.

6. Conclusion

3160 lake habitat is a unique system which host several rare species and are therefore important sites for biodiversity. Despite this there is a lack of knowledge on their typical lake habitat characteristics. The current characterisation of this habitat by the EEA is inadequate and relies primarily on macrophyte communities which can be scarce in these lakes and can have several overlapping species with other lake habitat types when they are present. The lack of dedicated monitoring programmes specific to this habitat within MS such as Ireland means that information is lacking on the physical, chemical and, ecological characteristics of this habitat. This means that data is often surrogated from other sources, such as EU WFD monitoring programmes, to assess the structure and function and conservation status of this habitat. The EU WFD is not designed to assess the conservation status of water bodies and lacks information which is key to assessing and prioritising the conservation of individual sites such as the occurrence of rare and threatened species. Therefore, a lake with a 'high ecological status' under the EU WFD does not equate to a 'favourable conservation status' under the EU Habitats Directive. The physico-chemical characteristics of this habitat requires further study and appropriate values need to be set for key variables such as nutrients and water colour. Threshold levels of these variables could also be set to inform conservation status.

A more holistic understanding of 3160 lake habitat ecology is now needed and can be achieved through investigating a broader suite of ecological components including, but not limited to, algae and macroinvertebrates, which would improve our understanding of the ecology of 3160 lake habitat. Ecological metrics that measure biodiversity, traits, and morphology could also be implemented to determine the structure and function and assess the conservation status of this lake habitat. In addition, lists of rare and endangered taxa should be compiled for the habitat to guide the prioritisation of conservation measures within individual sites in EU MS.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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