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Hydromorphological Literature Reviews for Lakes

Integrated catchment science programme

Science report: SC060043/SR1

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Steve Killeen

Steve Killeen

Head of Science

Executive summary

This report forms part of a larger project reviewing the linkages between hydro-geomorphology and the biological quality elements required for assessing the ecological status of water bodies under the Water Framework Directive (WFD). This report focuses on lakes; other reports in the series focus on rivers and transitional and coastal (TRaC) waters.

The main aim of this review is to identify how hydro-geomorphology impacts on the ecology of the main biological elements. This knowledge is extremely important for implementing the WFD as it demonstrates the importance of hydro-geomorphology for underpinning good ecological status and allowing better measurement and prediction of the ecological effects caused by hydromorphological mitigation measures (such as programmes of measures). This information will be used to improve the management of water bodies to comply with the WFD.

This review synthesises the linkages between hydrological and geomorphological processes and the five core biological elements of interest for lakes under the WFD (phytoplankton, phytobenthos, macrophytes, macroinvertebrates and fish). Direct and indirect effects of hydromorphology on the hydro-geomorphological processes or physicochemical parameters that impact the biota are reported, together with the effects of direct hydromorphological pressures. Findings related to each biological element are outlined below, grouped into process-biotic interactions and pressure-biotic interactions.

Hydro-geomorphological process-biotic interactions

<u>Phytoplankton:</u> Phytoplankton abundance, community structure and diversity are influenced by the rate of water entering and leaving the lake, changes in nutrient loading and mixing, interactions with the substratum and light availability – all of which are impacted by changes in hydrology.

<u>Phytobenthos:</u> Considerably less information is available on the hydro-geomorphological process impacting phytobenthos (primarily benthic diatoms). However, phytobenthos communities are highly dependent on water flow, substratum and light availability.

<u>Macrophytes:</u> Light, temperature, nutrients and substratum all affect the production and diversity of macroalgae. Lake depth is considered to be the single most important geomorphological parameter impacting macroalgae, as it controls light availability and the extent of littoral habitat available for colonisation, as well as impacting on temperature, nutrient cycling and wave disturbance.

<u>Macroinvertebrates</u>: Many lake macroinvertebrates rely on the macrophyte community for refuge, and so all of the pressures that affect macrophytes apply to macroinvertebrates by association. Sediment-dwelling macroinvertebrates depend on suitable habitats and are therefore impacted by pressures affecting sedimentary processes. Acidity, nutrients and water depth also affect macroinvertebrate communities.

<u>Fish:</u> There is very strong evidence to demonstrate that lake depth, connectivity (to streams and other lakes) and sedimentation all affect fish abundance, diversity and community composition, as well as the smothering of fish eggs. Nutrient loading, dissolved oxygen concentration and acidification are other water chemistry parameters, related to hydro-geomorphology, that impact on fish communities.

Hydromorphological pressure-biotic interactions

Direct pressures

Abstraction – removal of phytoplankton and invertebrate or fish larvae.

Recreational activity – trampling and propeller damage impacts macrophytes.

Dredging – removal of phytobenthos and sediment-dwelling invertebrates (also potentially macroalgae and fish).

Damming – impacts water flow and supply of sediment to/through a lake.

Indirect pressures

Damming – affects phytoplankton, macrophytes, macroinvertebrates and fish by impacting residence times.

Abstraction – abstraction from the lake affects residence times, impacting phytoplankton, macrophytes, macroinvertebrates and fish; abstraction of groundwater can also affect the water level, again impacting phytoplankton, macrophytes, macroinvertebrates and fish.

Dredging – impacts on phytoplankton, phytobenthos and macrophytes by altering turbidity and therefore light availability.

Agriculture/forestry – fertiliser run-off increases nutrient concentrations, land drainage can cause a reduction in the water level, and land run-off can increase sediment loading and turbidity (and therefore light availability). All of which can impact phytoplankton, phytobenthos and macrophytes.

Recreation – increased trampling along shorelines can lead to increased bank erosion and increased concentration of suspended sediment, reducing light availability and impacting phytoplankton, phytobenthos and macrophytes. Increased sedimentation impacts phytobenthos, macroinvertebrates and fish eggs.

Effluent – effluents containing suspended matter can increases turbidity and can impact phytoplankton, phytobenthos and macrophytes. Increased sedimentation impacts phytobenthos, macroinvertebrates and fish eggs.

What does this review mean for the strategic assessment and subsequent work on regulatory measures for lake hydromorphology?

1. The literature on hydromorphological pressure impacts need to be reviewed more thoroughly to determine the evidence base for developing measures and to analyse which sectors are responsible for each pressure. Some pressure-response linkages (direct and indirect) may require further research.

2. The importance of hydro-geomorphology on wider issues (such as eutrophication, diffuse pollution and contamination) needs to be better understood and highlighted. Further work is needed to demonstrate the importance of these processes when managing human pressures that are not considered hydromorphological but are strongly mediated by hydro-geomorphological processes.

3. In the short-term, further analysis of the literature on human pressure-hydro-geomorphology-biotic response is required. In the medium-term, a concerted research programme will be required to allow the implementation of adaptive management measures as part of the second and third WFD cycles.

4. This review can be used to highlight the relative dearth of information on hydro-geomorphological processes and pressures in lakes.

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1 Introduction

1.1 Project background

The Water Framework Directive (WFD) is considered to be the most substantial piece of EU water legislation to date. It also provides a major opportunity to improve the whole water environment and to promote the sustainable use of water for the benefit both of people and wildlife (Council of the European Communities 2000). The main objective of the WFD is that all inland, transitional and coastal waters should reach 'good status' by 2015. It will accomplish this by establishing River Basin District management plans, which will set demanding environmental objectives including ecological targets for surface waters. The WFD requires the creation of a holistic and co-ordinated framework for the sustainable management of water resources based on introducing objectives and environmental standards. Hence, implementing the WFD requires sound science for developing classification tools/criteria to determine the ecological status of the biological elements. For lakes, these biological elements include macrophytes, macroinvertebrates, fish, phytoplankton and phytobenthos.

The classification tools/criteria developed to define ecological quality in these biological elements must accommodate the effects of both the natural and anthropogenic processes influencing any water body. This requires a clear understanding of the relationships between these tools/criteria and the processes/pressures affecting the ecological status being measured. This understanding then needs to link with management options for water bodies.

This report identifies the known relationships between hydro-geomorphological aspects (pressures and processes) and biological elements in lake systems. It specifically examines the relationships between hydro-geomorphological processes and pressures and the WFD biological criteria of macrophytes, macroinvertebrates, fish, phytoplankton and phytobenthos. These relationships are of central importance to fulfilling the WFD, in that the criteria for change must be related to the ecological sensitivity of waters with respect to changes in hydro-geomorphology. However, it should be emphasised that there are many other pressures that link only indirectly to hydro-geomorphology, such as chemical pollution and the presence of alien species, and these pressures are not covered in the present report.

Furthermore, it should also be emphasised that, under the WFD, any heavily modified water body (HMWB), as a result of anthropogenic hydro-geomorphological modifications, will need only to be classified as a good ecological potential rather than good ecological status (Freeman *et al.* 2003). Hence the implications of those modifications on the biota, and thus the HMWB designation, have to be defined.

The aim of this project is thus to:

'*provide the Environment Agency's Water Framework Directive Programme and ultimately Defra [Department for Environment, Food and Rural Affairs] with a review of the current state of understanding on the relationships between the biological classification tools/criteria for good ecological status (potential) for lakes to both hydro-geomorphological processes and pressures.*'

It is understood that Defra will ultimately be using the Environment Agency's input to the Strategic Review to determine whether new regulatory powers are required to meet the hydromorphology requirements of the WFD. It is further understood that the present report will inform the Environment Agency's input to Defra.

1.2 Lakes

Lakes are large bodies of standing water, either formed naturally or man-made for amenity, water resources or energy generation purposes. A common definition of a lake is a waterbody where wind-induced turbulence plays a major role in mixing the water column (Brönmark and Hansson 1998). Friedman and Sanders (1978) described a lake as ‘a landlocked body of water occupying some kind of basin’. In Great Britain (England, Wales and Scotland), there are approximately 14,300 lakes greater than 1 hectare (ha) in surface area (Hughes *et al.* 2004).

The WFD (EC Parliament and Council, 2000) aims to achieve good ecological status for all surface waters by 2015. Each EU member state must identify and classify water bodies and also define reference conditions. Lakes are classified according to their hydromorphological and biological parameters. The reference conditions on which management decisions will be based are defined as background conditions that have no or minimal anthropogenic stress. Reference conditions should reflect totally or nearly undisturbed conditions for general physicochemical water quality elements and biological water quality elements (Räsänen *et al*. 2006). In the UK, it has generally been agreed that 1850 AD is a suitable reference date for assessing anthropogenically-driven aquatic impacts, as it is considered to represent pre-industrial conditions (Leira *et al.* 2006).

The WFD uses macroinvertebrates, fish and macrophytes as biological parameters and requires that the final ecological classification be based on the current status of all these biotic elements. Annex V, 1.2.1 to 1.2.2 of the WFD provides definitions for high, good and moderate ecological status in rivers and lakes for each biological element. Good ecological status prevails when the total effect of anthropogenic pressures is insufficient to cause more than a slight deviation in the composition and abundance of the flora and fauna from their natural condition (Bragg *et al.* 2003, WFD 2006).

There are specific hydromorphological quality elements that are required to determine high ecological status. For other status classes, the hydromorphological elements are required to have ‘conditions consistent with the achievement of the values specified for the biological elements’. Table 1.1 details the quality elements that should be used for assessing ecological status in lakes, based on the list in Annex V, 1.2 of the WFD.

Table 1.1 Quality elements for assessing ecological status in lakes

Biological elements	Hydromorphological elements supporting the biological elements	Chemical and physicochemical elements supporting the biological elements
• Composition, abundance and biomass of phytoplankton • Composition and abundance of other aquatic flora • Composition and abundance of benthic invertebrate fauna • Composition, abundance and age structure of fish fauna	Hydrological elements • Residence time • Connection to the ground water body • Lake depth variation Morphological elements • Structure and substrate of the lake bed • Structure and condition of the lake shore	• Transparency • Thermal conditions • Oxygenation conditions • Salinity • Acidification status • Nutrient conditions • Specific pollutants • Pollution by priority substances identified as being discharged into the body of water • Pollution by other substances identified as being discharged in significant quantities into the body of water

Source: WFD Annex V, 1.1.2

This review will cover the following biological elements (as well as the main hydromorphological elements that support them): macrophytes, phytoplankton, phytobenthos, macroinvertebrates and fish. Chemical and physicochemical elements will not be specifically addressed, but will be discussed where appropriate. An introduction to the hydromorphological elements is followed by a discussion of the effects of these elements on each biological element. Anthropogenic pressures that may impact on lakes and the associated biological and hydromorphological elements are also reviewed.

1.2.1 Lake hydrology and morphology

The biological, hydromorphological and physicochemical elements outlined in Table 1.1 cannot be considered in isolation. The conceptual diagram in Figure 1.1 illustrates the linkages between the three elements in Table 1.1.

Bragg *et al.* (2003) and Acreman *et al*. (2006) provide a review of each of the hydromorphological quality elements for lakes, which are briefly discussed in Table 1.2. Readers requiring further details should consult the original reviews.

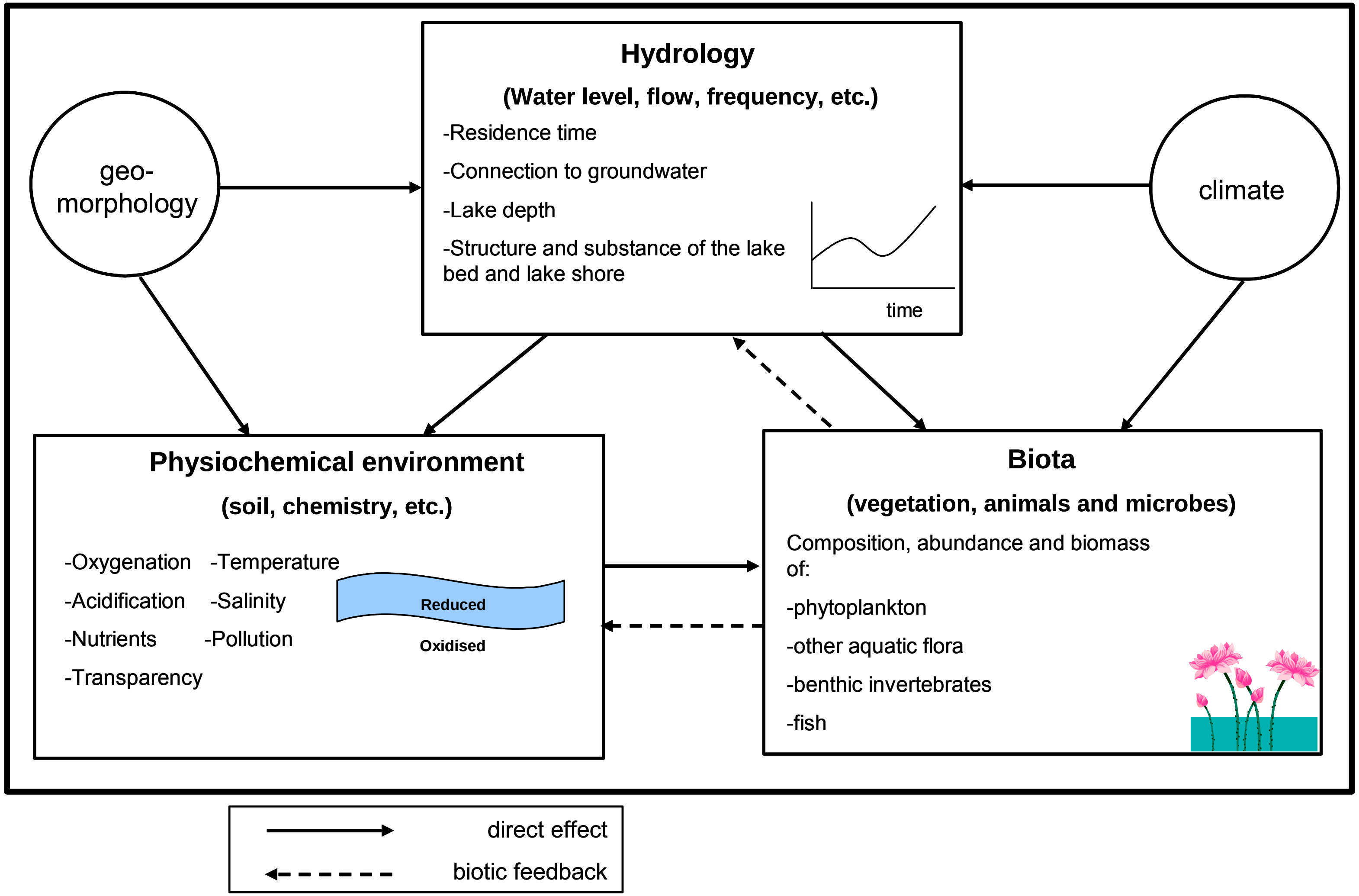

Figure 1.1: Relationships between hydromorphology, biology and physicochemical elements for lakes. Note the considerable role of biotic feedback in the system. (Adapted from Mitsch & Gosselink, 2000, p 27).

Table 1.2 Hydromorphological quality elements in lakes and their ecological signficance

Hydrological regime	
Quantity and dynamics of flow	Flow – the inflow discharge and the outflow discharge – is a fundamental aspect of lake environments, controlling, *inter alia*, lake water level and residence time. Flow can be estimated at an annual time-scale by water balance methods and at finer time resolutions by methods that combine the annual water balance with soils and other information, reflecting the dynamic behaviours of a catchment.
Water level	Water level is of direct ecological significance, since it affects the exposed area of littoral zone and exercises a control on water depths. Water level data is used in many different ways, including annual range, seasonally-defined maxima or minima and the vertical extent of weekly changes in water level (see Smith *et al.* 1987). Changes to inflow to lakes and outflow from lakes will affect water level.
Residence time, T	Residence time is also known as lake water retention time or turnover time. It indicates how long it would take for all the water in a lake to be replaced, and may be calculated as the ratio of lake volume (V) to discharge (Q). It is relevant in lake ecology due to its affect on water quality, as it influences the lake response to catchment nutrient budgets, although seasonal differences in flushing rate must be also taken in to account (Werrity *et al.* 1993, in Bragg *et al.* 2003). Whether or not a lake stratifies will have an effect on residence time. Deep lakes in temperate latitudes, such as those in the UK, display an annual thermal cycle (Figure 1.2; Bragg *et al.* 2003). The spring period is characterised by isothermal conditions, permitting overturn of the entire water column at a temperature close to that of the maximum density of fresh water (3.94°C). Summer insolation (solar radiation) typically leads to stratification of the water column, with relatively warm and circulating surface waters (epilimnion) resting upon cooler non-circulating waters (hypolimnion) and a well-developed thermocline (the region in which the fall of temperature $\geq 1°C\ m^{-1}$) in between. Hypolimnetic waters will be essentially stagnant during such conditions. Autumn is characterised by a return to isothermal and fully-circulating conditions. In winter it is possible for a reverse thermocline to develop as the surface waters become stabilised by further cooling. This thermocline is, however, much less stable than its summer counterpart and can readily be broken down by strong wind action, producing intermittent isothermal and stratified conditions. Once the surface water temperature falls to 0°C, ice begins to form. This process is usually initiated in shallow bays and protected embayments, but it may extend to cover the entire lake surface. With the onset of spring warming, the cycle continues.
Connection to groundwaters	Depending on the permeability of the terrain in which a lake has been created, there will be a degree of connectivity between the basin waters and groundwaters. Thus lakes are not only sensitive to activities in their river catchment areas but also to groundwater

	pollution and abstraction in/from underground areas that may not coincide with the surface catchment.
Morphological regime	
Lake depth variation	Lake depth variation is an important control of habitat availability, particularly in relation to the availability of light (Figure 1.3). In order to determine lake depth variation, information on the basin form must be known. Methods such as those developed by Håkanson (1981) provide mechanisms for broadly predicting basin form for unsurveyed lakes using data readily available from maps. Lakes can be divided into three zones (Figure 1.3): the littoral zone, which is a sloped area close to land that supports an abundance of plant life as light penetrates through the water column and to the sediment; the photic or open water zone, where sunlight is abundant and photosynthesis can occur; and the deep-water profundal or benthic zone, where little sunlight can reach and which is typically below the thermocline. The depth that light can reach in lakes depends on the morphology of the basin and the density and motion of particles in the water. The absorption and attenuation of light in the water column are factors controlling water temperature and potential photosynthesis.
Quantity, structure and substrate of the lake bed	The composition (particle size, distribution, organic content) of the lake bed will act as a control on aquatic communities by contributing to the amounts and types of nutrients available. It is a function of lake sedimentation rates, being controlled both by allocthonous (catchment-derived) and autochthonous (within lake-derived) sediment (Håkanson and Peters 1995). Re-suspension of sediment is considered to be a function of lake size and form. Various processes serve to infill lake basins, with the most obvious process being the transport of sediments by influent rivers draining the catchment areas. However, minor components to the sedimentary deposits come from wind-borne particles (both inorganic, such as silt, and organic, such as leaves) and erosion of shores by both wind-generated waves and ice activity (as in Loch Leven, Kinross). Inorganic sedimentation within a lake is accompanied by the accumulation of organic debris largely derived from the skeletal remains of organisms living in the lake (such as diatoms). Typically, the debris range from coarse deposits in the littoral zone, which are disturbed by wave activity in the shallow waters, to progressively finer deposits in quiescent, deeper waters that are beyond the base of wind-generated waves (Bragg *et al.* 2003; Figure 1.3).
Structure and condition of the lake shore	Shoreline habitat measurement is important for identifying possible causes of ecological impact, as many lakes are impacted on or near the shore zone. Shoreline development through pressures such as housing or industry can have a disproportionate impact on nutrient loadings compared to more distant parts of the catchment. Lake shores are not subject to tidal rises and falls in water level.

	Most lake margins are dominated by forced (wind-generated) waves that are still undergoing active generation right up to the shore (Figure 1.3).

Source: Adapted from Bragg *et al.* (2003)

1.2.2 Linking biology to physical variables

Linkages between hydromorphological and biological elements are illustrated in Figure 1.4 and discussed in the following chapters. Lake depth and water level are considered in detail, as these are the most directly important and the most studied hydrological elements influencing the biological elements covered in this review (macrophytes, phytoplankton, phytobenthos, macroinvertebrates and fish).

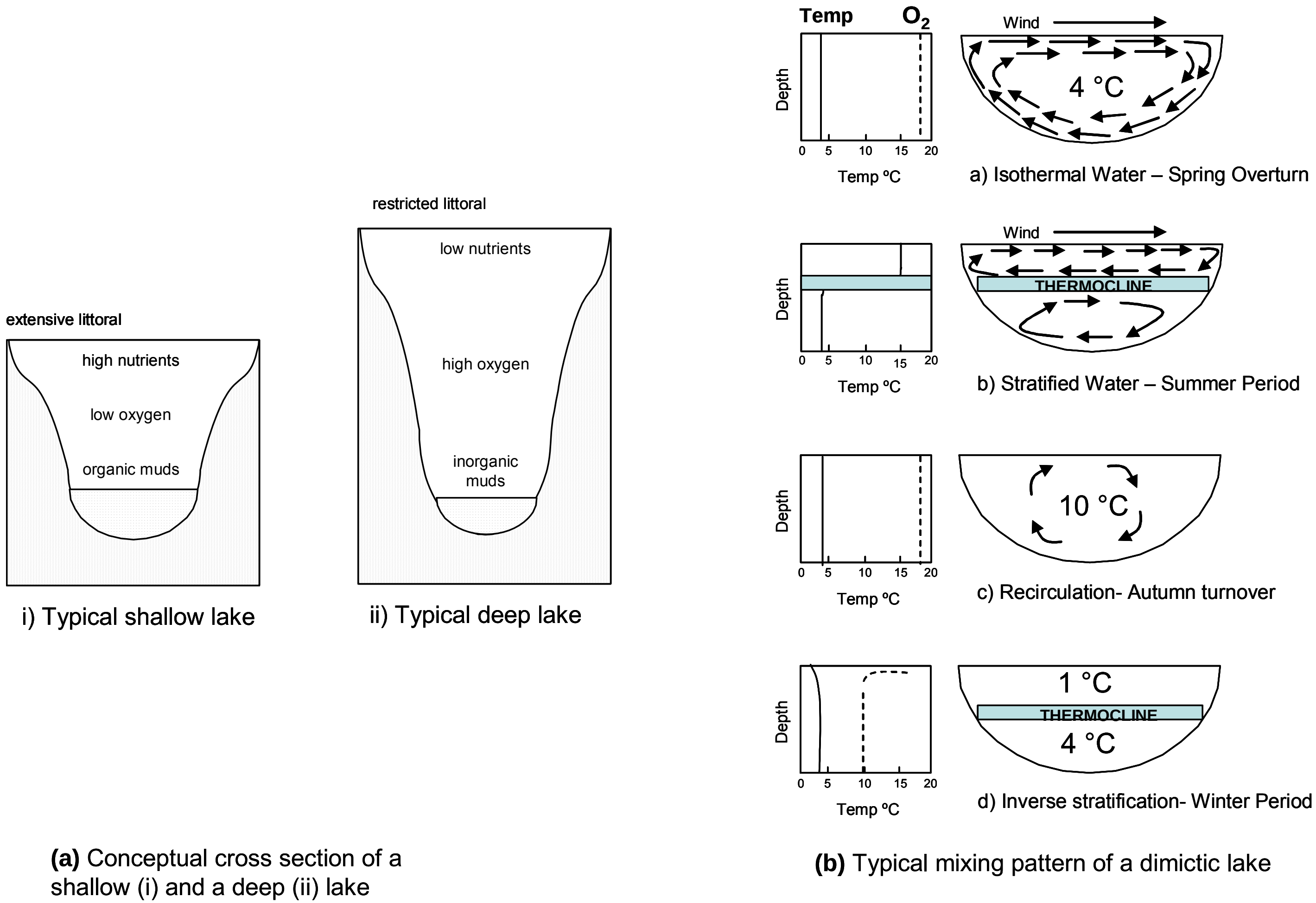

Figure 1.2: Lake depth and thermal cycling. Adapted from Brönmark and Hansson 1998

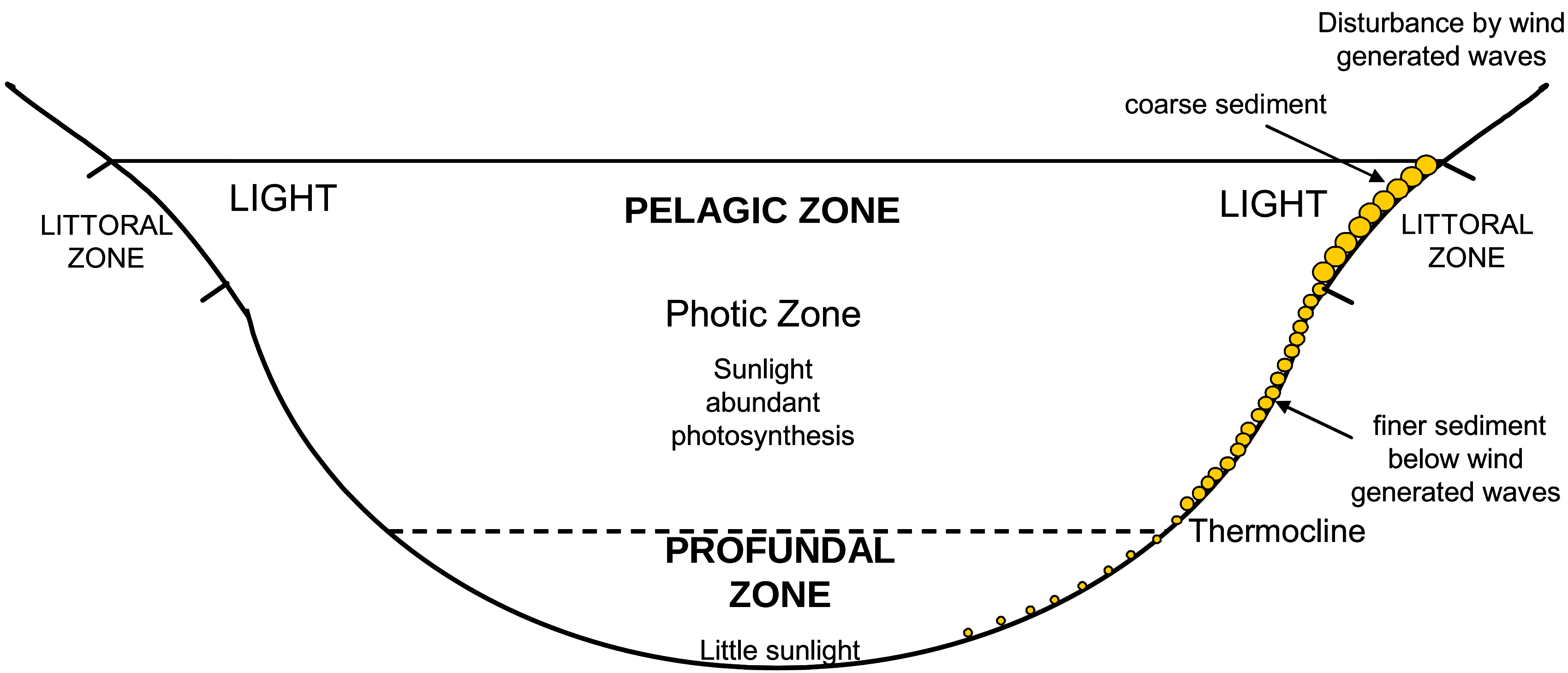

Figure 1.3: Cross section of a medium-depth lake showing interactions within it

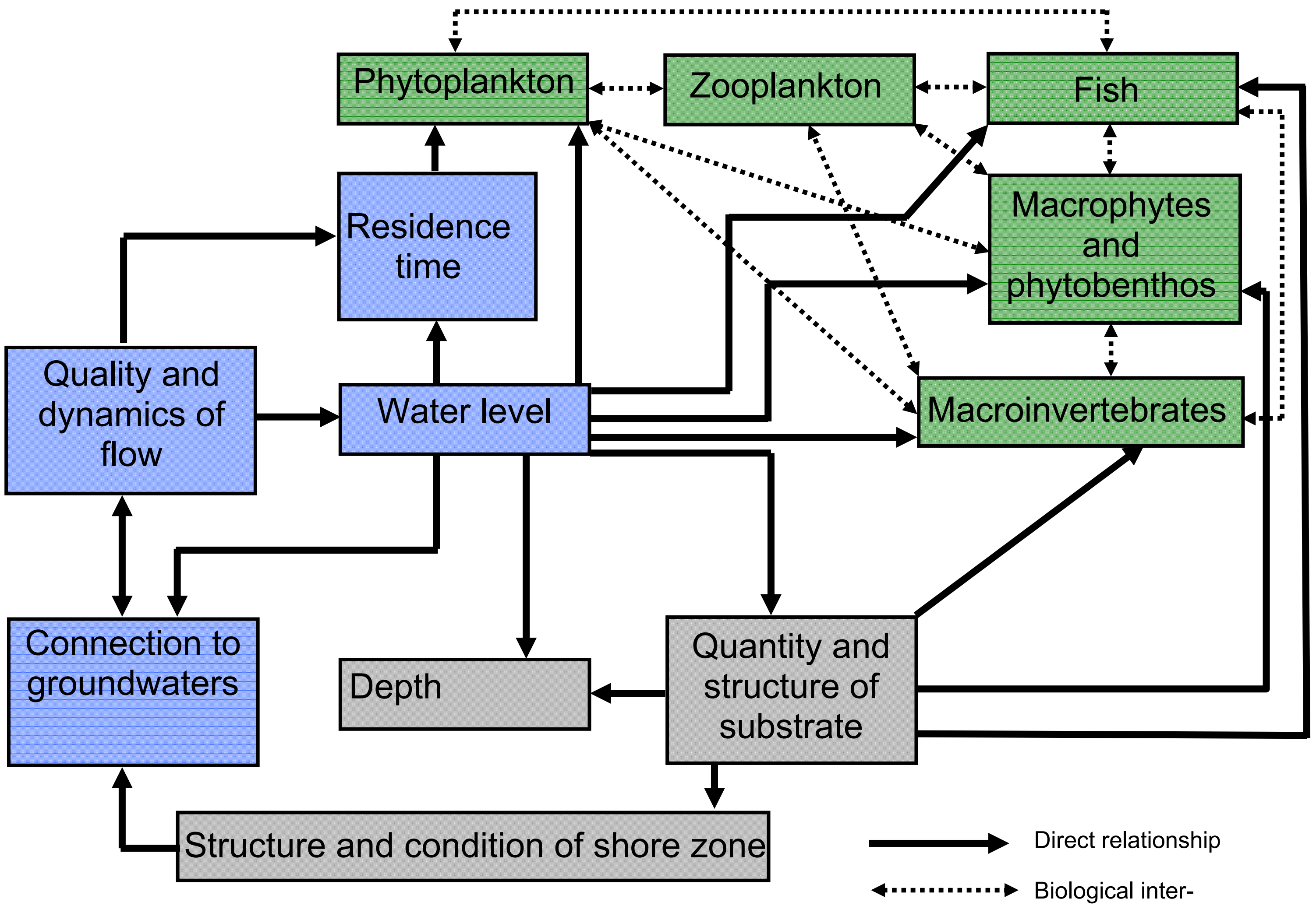

Figure 1.4a: Relationships between hydrological quality elements (blue), morphological quality elements (grey) and biological (green) quality elements in lakes. (Adapted from Acreman *et al.* 2005; WFD 48 Stage 3, p 78).

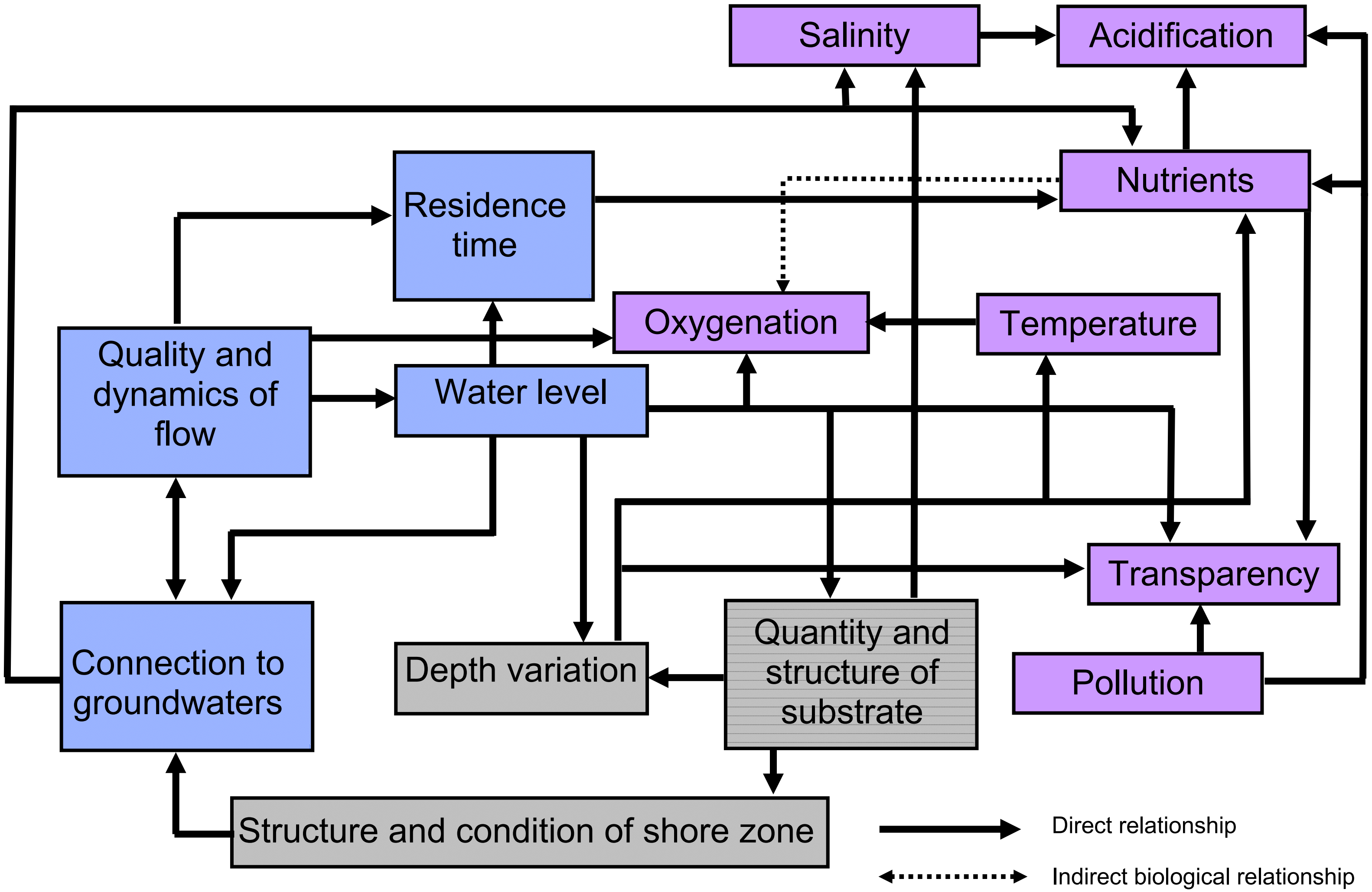

Figure 1.4b: Relationships between hydrological quality elements (blue), morphological quality elements (grey) and physiochemical (purple) elements in lakes. (Adapted from Acreman *et al.* 2005; WFD 48 Stage 3, p 78).

2 Methods

Initial literature searches for the five biological elements (macrophytes, macroinvertebrates, fish, phytoplankton and phytobenthos) were undertaken against three topics (general terms, hydro-geomorphological process and human impacts (pressures)) by the Environment Agency (see Appendices). The reviews were then allocated as follows:

- macrophytes, macroinvertebrates and fish were completed by the Halcrow Group Ltd, UK;
- phytoplankton and phytobenthos were completed by the Environment Agency.

Initial search methods were consistent between teams, with methods varying slightly due to the amount of material on particular topics. The precise methods of each group are detailed below.

The information presented in this report is a summary of the literature reviewed, but it is important to note that time restrictions prevented a full critical review of the articles. It is assumed that each article was critically appraised as part of the normal peer review process of journal publication. However, the lack of a full critical review is a particularly important point to consider when discussing areas where only a few papers have been published. One should bear in mind that conclusions from a single paper or study may not be transferable between lake types and between different parts of the world (indeed, conclusions based on single studies may not even be reliable).

2.1 Phytoplankton and phytobenthos

Due to time constraints, the reviews of phytoplankton and phytobenthos were restricted to material identified by initial searches and articles cited within key papers. Database use was limited to Web of Science. The lack of review papers, and little published material on phytobenthos in lakes as a whole, made extracting the key human-hydromorphic-biota linkages difficult.

2.2 Macrophytes, macroinvertebrates and fish

The literature search for the review on macrophytes, macroinvertebrates and fish for lakes was conducted using a combination of four databases (Web of Science, Cambridge Scientific Abstracts, Biosis and CAB). These were searched with a series of keywords and keyword combinations that reflected the three topic areas of: (i) hydrological and geomorphological processes; (ii) general biogeomorphology; and (iii) hydrological and morphological pressures. The original combined search period covered the years 1990–2006.

Following a study of the references obtained using standard WFD terminology, it was decided to conduct additional literature searches using standard biological and hydrological search terms based on the authors' existing knowledge of the most important hydrological processes and pressures in lakes. In addition, a large number of key studies in lake ecology were conducted well before 1990 and so the additional search period covered all available years in Web of Science and JSTOR (Journal Storage), with the latter covering articles dating back to 1880. Key papers known to the authors were also added to the reference list (for example, studies on acidification pressures in lakes), particularly key review articles from Europe and, where possible, the UK. Relevant North American literature was also referenced. Whilst North

American literature does not directly cover the UK, a significant proportion of the current understanding of lake ecology is based on North American studies. The processes and pressures detailed in those studies have also been found to occur in European lakes, including those in the UK.

Review papers were focused on because: (a) they provide useful syntheses of lake processes and pressures; and (b) because issues such as eutrophication in lakes are the focus of many separate studies that often repeat the same basic information on the processes and pressures affecting macrophytes, invertebrates and fish. Following these literature searches around 15–20 papers were focused on in detail for each biotic group. There was some overlap between the three groups due to the strong focus in the literature on biotic interactions between macrophytes, macroinvertebrates and fish in lakes.

3 Phytoplankton

3.1 Hydrological and geomorphological processes

A significant factor in any lake system, regulating physical, chemical and ecological aspects, is the relative input and output of flow. As part of the natural cycle, variation in flow is to be expected and will have knock-on effects on water level, hydraulic flushing rates and resulting residence times. Huszar and Reynolds (1997) describe an Amazonian lake (Lago Batata) where water level fluctuates on an annual cycle due to seasonal variations in rainfall in the catchment area. With the onset of summer, water level drops from a maximum depth of 12m to a low water mark of a little over 2m. During this period, significant changes to phytoplankton assemblages and overall biomass were observed. From sparse populations of nanoplankton at high water levels, diatoms and then cyanobacteria became dominant as the water level fell. A general trend from small to larger-sized phytoplankton was recorded, as were marked increases in biomass and taxon diversity.

In contrast, flood waters entering lakes of the Parana river floodplain in Argentina were observed to create conditions of disturbance in previously isolated water bodies (de Domitrovic 2003, de Emiliani 1997). This influx appeared to initiate a process whereby phytoplanktic communities reverted back to an earlier successional state associated with higher water levels, similar to those seen at the start of the L. Batata annual cycle. As well as decreases in density, biomass and taxon diversity with increasing depth, changes to the specific composition of assemblages were observed. Chlorophyceae (small, fast-growing algae) and Cryptophyceae (disturbance-tolerant algae) maintained a sustained presence throughout the year, becoming (along with Chrysophyceae) especially prominent during the rising flood phase. Euglenophyceae, Dinophyceae and Cyanophyceae (all slow-growing species) dominated during periods of isolation.

The link between changes in hydrological regime and phytoplankton abundance and diversity are generally explained in relation to nutrient concentrations, mixing of the water column, connection with the sediment and light availability (see Figure 1.1). As Huszar and Reynolds (1997) explain, falling water level initiates a process of greater mixing between previously stratified layers, meaning that resources that have become unavailable get recycled as they are brought up into the euphotic zone. This greater availability of nutrients coupled with good light penetration is said to account for the rapid increase in biomass associated with this phase. Naselli-Flores (2000), on the other hand, points out that a deepening of mixed layers means algal cells spend a longer time in the dark. In his example examining summer-time draw-down in Sicilian reservoirs, he notes that the regular occurrence of this cycle leads to rarer species of phytoplankton, which are able to regulate their buoyancy or tolerate unbalanced dark/light periods, to become more prevalent. Increased competition from species brought up into the euphotic zone and greater levels of predator-prey interaction may further modify community structure (Beisner 2001, Huisman *et al.* 2004).

As water levels reach their lowest points, disturbance of the sediment by thermal and wind-generated currents becomes a governing factor. Sediment suspended in the water column alters light attenuation and may absorb or release phosphates and other nutrients depending on the sediment type and water chemistry (Burkholder 1992). The effect on phytoplankton biomass depends largely on a shift between limiting factors (Northcote *et al.* 2005, Schallenberg and Burns 2004). In established turbid systems, phytoplankton that are resilient to suspended sediment loading may become dominant (Burkholder 1992), while in permanently shallow lakes stands of macrophytes play an important role in preventing this re-suspension process happening in the first place

(Muylaert *et al.* 2003). Sediment-containing clay particles may have an additional effect, which involves the process of adhesion-sinking of algal cells (Guenther and Bozelli 2004).

Shallower lakes and periods of low water are also associated with shorter residence times (RTs). James *et al.* (2002) suggests that shorter RTs could either increase phytoplankton biomass due to nutrient loading or reduce it due to the effect of hydraulic flushing. In fact, Walz and Welker (1998) show that a very strong relationship does exist. Maximum growth rate and high concentrations of chlorophyll were recorded at low RTs (around eight days) in a German lake (Neuendorfer See). Whereas chlorophyll concentrations increased rapidly then levelled-off, their growth rate peaked abruptly at this point. This crucial RT of 8–15 days (James *et al.* 2002, Olding *et al.* 2000, Walz and Welker 1998) – but sometimes as low as three days (Schallenberg and Burns 1997) – beyond which any further reduction causes biomass loss, relates to phytoplankton doubling time and the effect of hydraulic flushing (Rennella and Quirós 2006). A gradual decline in chlorophyll concentrations with increased RT may reflect higher levels of grazing by growing rotifer communities plus sedimentation and light limitation factors.

Dilution is the main force driving down phytoplankton biomass with increasing input and rising water levels (Huszar and Reynolds 1997). Even where floodwaters bring in nutrients from decomposed organic matter, the re-stratification of the lake eliminates them from the euphotic layer (de Domitrovic 2003).

In other studies concerned with scale effects, Karatayev *et al.* (2005) showed high correlations between lake area and phytoplankton diversity and total species richness for samples of over 500 Belarusian lakes. Fee *et al.* (1992) found that midsized lakes in a chain of Canadian shield lakes had higher phytoplankton photosynthesis rates, while Reynolds (1987) suggests that phytoplankton in deeper waters respond more slowly to environmental change compared with their shallow-dwelling counterparts.

3.2 Human pressures

Examples of anthropogenic pressures impacting directly on phytoplanktic development through hydro-geomorphic processes were identified in the literature. These pressures included activities such as urbanisation, power generation, agriculture and mining (see Table 8.1).

At the catchment scale, Karatayev *et al.* (2005) identified a positive correlation between phytoplankton diversity, watershed size and level of development, and speculated that this was in response to an increase in the flow of nutrients into the lake.

Pressures affecting RT included water abstraction for human consumption (Ishikawa *et al.* 2002), diversion of flow for hydroelectric power (James *et al.* 2002) and damming for agricultural purposes (Romo and van Tongeren 1995). Large increases in RT coincided with increased abundances of toxic cyanobacteria and pinnate diatoms in the case of Lake Biwa, Japan (Ishikawa *et al.* 2002), but shorter RTs only had a significant impact when they fell below a critical point (10–15 days; James *et al.* 2002).

Drops in water level and variation in mixing were commonly associated with high anthropogenic demand (Ishikawa *et al.* 2002, Naselli-Flores 2000). At Lake Yogo in Japan, channels and watercourses were built to maintain water levels for irrigation purposes, but the artificial pumping of water from Lake Biwa disrupted layers and brought about the onset of cyanobacterial blooms (Tsukada *et al.* 2006).

The build-up of inorganic suspended sediment in reservoirs located in agricultural watersheds became the controlling factor for phytoplanktic biomass and species composition, over and above that of nutrient loading (Holz *et al.* 1997). Meanwhile, the dumping of bauxite tailings from mining activities caused high levels of turbidity in L. Batata and reduced phytoplankton densities by limiting light levels (Guenther and Bozelli 2004). In the case of two reservoirs that underwent drainage and refilling, it was the undredged reservoir that progressed towards eutrophic conditions in the period afterwards (Maier 2001). In permanently shallow waters, however, dredging might be expected to have the opposite effect due to the importance of established macrophytes in preventing re-suspension and nutrient release (Burkholder 1992).

Where the effects of other human factors specifically relating to hydro-geomorphic processes are noticeably absent from the literature, mechanisms for phytoplankton biomass regulation can still be inferred from the evidence collected on natural systems. Dam construction, for example, would be expected to increase RTs, depth and turbidity (initially) but reduce water-sediment connectivity. The complex interaction of these factors would prove difficult to untangle, but the general direction of phytoplantkic development might still be determined (see Table 8.1).

4 Phytobenthos

4.1 Hydrological and geomorphological processes

Phytobenthos, and more specifically benthic diatoms, although featuring less frequently in the literature with regards to lakes, are shown to have close relationships with various hydro-geomorphic parameters.

From a study on Welsh lakes and streams (Allott and Flower 1997), flow and current velocity were identified as important factors in diatom assemblage diversity. More stable conditions and more diverse microhabitats, formed from mucilage layers and algal growth, were shown to provide greater opportunities for colonisation. In addition, the absence of strong currents allowed a higher proportion of stalked or colonial forms of epilithon to become established.

The close associations between diatoms and particular types of substrate are also important to note. Species with strong preferences for particular habitat types are subject to pressures associated with substrate quality and quantity and macrophyte development. However, as more research is done, species are increasingly identified as having the ability to exploit a broader range of habitats than previously thought (King *et al*. 2006). Epilithic and epiphytic diatoms are more frequently referred to in the literature, as silt-inhabiting species are less sensitive (and therefore of less importance for monitoring purposes) to changes in the water column and to the wider lake environment (King *et al.* 2006).

Highly turbid zones are likely to have different diatom assemblages from clear water zones, depending on the ability of species to adapt to low light conditions. Interactions between light availability and diatom assemblages are hard to disentangle from the literature (King *et al.* 2006), and whether the decrease in light is due to suspended sediment, eutrophic conditions or both is not always made clear.

Dixit and Smol (1994) identified depth, Secchi depth and lake size as three of the six most important factors explaining the distribution and abundance of taxa in 66 lakes located in the northeastern US. However, the direction that these variables work in and their mechanisms were not made clear. pH is also identified by this and other studies as being particularly significant. In terms of hydro-geomorphic processes, drought-induced acidification, whereby previously deposited acids stored in wetlands seep back into the lake system during times of drought, is highly relevant (Faulkenham *et al.* 2003). This effect was observed from conducting sedimentary core analysis in the lakes of North America, and was shown to affect diatom assemblages over a 20-year period primarily through alterations to water chemistry. Importantly, this acidification process was only detected in lakes with a degree of wetland coverage.

4.2 Human pressures

Few studies give examples of direct human-induced pressures on hydro-geomorphic processes with reference to phytobenthic species. However, one study (Hammer and Stoermer 1997) identified the impact on diatoms of urban construction and observed dramatic changes in the predominant taxa due, in part, to the disruption of the inflow stream bed and the subsequent transport and deposition of clay into the lake. Other sources of inorganic sediment, namely industrial effluent (Davydova *et al.* 1999), logging and recreational-related erosion (Koster *et al.* 2005), are also seen as important, affecting diatom diversity and abundance through processes of pH alteration and nutrient enrichment.

Flower *et al.* (2001) again used sedimentary core analysis to investigate the impact of the hydrological modification of North African wetland lakes. The major alteration to the environment over this period was the construction of the Aswan Dam, but interestingly this was not detected using the diatom records. On the other hand, local land drainage and water diversion programmes, undertaken to alleviate winter flooding and promote summer water availability, were seen as the primary drivers of salinity change in the region during the 20th century. This was reflected in significant alterations to diatom assemblages over this period.

The strength of using diatoms as a monitoring tool lies in the ability to construct past environmental conditions and use them as reference points for comparison with present states. As such, a lot of work has been done on testing the accuracy of sediment core analysis

There was little information on trying to reverse detrimental effects but a great deal of emphasis on the importance of diatom records in being able to assess pre-disturbance conditions.

5 Macrophytes

Macrophytes are strongly influenced by and can have an influence on the morphology of lakes. They also play key roles in determining quality elements such as nutrient levels and the quality of habitat for other biota, including macroinvertebrates, fish and birds. Their importance is reflected in the heavy emphasis on macrophytes in the literature on various aspects of lake ecology ranging from food web interactions to classifying lake types.

The principal hydrological and morphological factor that ultimately determines the quality and nature of macrophyte communities in any lake is its water level regime. The depth of any lake basin is determined by how it was formed, whether through glacial, fluvial or other processes (for example tectonic processes, landslides, volcanic activity, solution basins). The depth of water in a lake basin, and to a great extent its area, dictates in large part two crucial factors for macrophytes: the relative amount of light available and the extent of littoral (shallow) habitat available for them to colonise. Figure 1.2a shows some of the basic differences between deep and shallow lakes.

Lake depth also plays a role in the annual changes of temperature and cycling of nutrients within lakes. Deep lakes will stratify into separate layers according to season (Figure 1.2b), whilst in very shallow lakes the temperature profile is not stratified and nutrients are generally more readily available to macrophytes all the time (Jeppesen *et al.* 1997). There are also reports of changes in groundwater/surface water interactions occurring during droughts, apparently as a response to the climatic change in water level (Glaser *et al.* 1997).

A lake's general bathymetry – its depth and area profile – is also related to the nature of sediments in the lake (whether they are primarily organic or inorganic; see Brönmark and Hansson 1998 for a general review) and the relative influence of effects such as wind. A shallow lake is more likely to have sediments stirred up by wind across its entire surface than a deep lake (Håksanon 2005), and this, combined with wave stresses on macrophytes (see James *et al.* 2002), can prevent effective macrophyte colonisation. In shallow lakes, the ability of macrophytes to colonise the lake, thereby helping to stabilise its sediments (see Horppila and Nurminen 2003), is potentially much more important for achieving good ecological status than in deep lakes. In all lakes, macrophytes also play important roles in nutrient cycling (particularly phosphorus uptake) and in providing habitat for birds, macroinvertebrates and fish.

Other natural factors such as latitude and altitude, whilst important with regard to macrophyte diversity (see Jones *et al.* 2003), are factors outside of regulatory control and have not been investigated fully. Many lake studies have been conducted in temperate latitudes, while few studies in the tropics have done more than focus on single lakes (for example, studies of water hyacinth in Lake Victoria are common but they do not generally consider the wider landscape; Acreman *et al.* 2006). These factors should be given due regard when determining the ecological status of macrophyte quality elements in lakes, but the most crucial and most controllable factor in achieving good ecological status is water level regime.

Macrophytes in natural lakes are adapted to cope with the prevailing water level regime, including situations where the water depth naturally fluctuates quite widely, such as in prairie potholes (Mitsch and Gosselink 2000). However, many of the pressures on macrophytes arise when natural changes are exacerbated through human activities that alter the water level regime, such as drainage, dredging or impoundment (see de Haan *et al.* 1993, van Geest *et al.* 2003). These impacts can include sudden reductions in the amount of available light, reductions in the extent of the littoral zone and changes in nutrient availability (Baxter 1977). All these changes combine to reduce habitat quality for macrophytes, as does direct physical damage from activities such as dredging. Ultimately, many of these impacts will require regulation that minimises changes to natural water level regimes and maximises ecological quality. Drainage and diversion in the agricultural sector is particularly in need of regulation (McParland 2006). The effects of these pressures on macrophytes are explored more fully in Section 2.2.

The importance of depth is clearly shown in the numerous examples of lake eutrophication and its management across the world. Glacially-formed prairie pothole lakes in North America are subject to cultural eutrophication in many of the same ways as floodplain lakes in Europe (see Hanson and Butler 1994, Jeppesen *et al.* 1997), but solutions such as nutrient reduction and dredging do not work as well for shallow lakes as they can for deep lakes (Bachmann *et al.* 1999). Biomanipulation (manipulation of fish and invertebrates) and inserting wave barriers can prove more effective at restoring macrophytes in shallow lakes than in deep lakes (Hanson and Butler 1994, Bachmann *et al.* 1999, Bergman *et al.* 1999, Meijer *et al.* 1999). As a consequence of the interactions between macrophytes, turbidity (suspended sediments), algae-grazing invertebrates and fish, shallow lakes can alternate between a turbid, algal-dominated state and a clear-water, macrophyte-dominated state (Scheffer *et al.* 1993). The vast literature on biomanipulations reflects the importance of these interactions and demonstrates how the state of a shallow lake can be changed by manipulating them (Bachmann *et al.* 1999, Bergman *et al.* 1999 and Meijer *et al.* 1999 provide comprehensive reviews of the field). Deeper lakes (where the littoral zone is restricted, nutrient supplies are affected by stratification and wave impacts on sediments and macrophytes are limited) tend to be better managed through actions like nutrient reduction (Bachmann *et al.* 1999). Intermediate-depth lakes apparently pose major problems for restoration: they are too deep to have their sediments extensively stabilised by macrophytes and are too shallow to benefit from the dilution of nutrients such as phosphorus (Genkai-Kato and Carpenter 2005).

The success of measures such as biomanipulation or nutrient reduction can be assessed by defining the extent and type of the macrophyte communities that develop after management actions have been taken. In Europe, lake macrophytes have been used to indicate the ecological status of German lakes (Schaumburg *et al.* 2004), whilst simpler measures such as the percentage cover of a lake by macrophytes have been used to measure the success of many biomanipulations (see Bergman *et al.* 1999, Hanson and Butler 1994). Macrophyte communities are used to classify lakes and other freshwater habitat types in Britain (see Duigan *et al.* 2005, Rodwell 1995), and these classifications can provide useful reference points for setting macrophyte-based targets of ecological quality.

The above indicates a wide general acknowledgement that deep lakes differ from shallow lakes with regard to the relative importance of the processes and pressures that affect macrophyte diversity and that a lake's depth is geologically determined (see Duigan *et al.* 2005). However, geological processes are rarely linked directly to macrophyte quality. Recent attempts to make such links include Acreman *et al.* (2006), who identified six British lake types based on geological features (coverage of peat or limestone), basin features such as formation, shoreline features and the water environment. The latter includes nutrient status and, by inference, macrophytes. This typology also acknowledges the importance of depth, or water level regime, on macrophyte quality. Given that the current understanding of the links between depth, sediments, nutrients and macrophytes is well developed, it is perhaps not productive at this stage to try to make direct links between the geological processes of lake formation and the status of the macrophytes within that lake.

While links between depth, sediments, nutrients and macrophytes are well understood, there are still major uncertainties regarding the long-term maintenance of good ecological status (whether that involves maintaining a naturally stable state or a naturally variable state, as in Blindow *et al.* 1993). For example, many biomanipulations require maintenance and do not appear to last more than a few years (Carpenter and Lathrop 1999), which may be due to biotic interactions between fish, invertebrates, algae and macrophytes. However, these interactions all occur within an abiotic setting of lake depth, area and sediments, all of which are determined by geomorphological and hydrological processes. The interactions between these elements, as outlined in the introduction, are crucial to a better understanding and management of ecological status for lake macrophytes.

In conclusion, current understanding of the role of the hydrological and geomorphological processes and pressures affecting macrophytes is focused strongly on the depth of lakes and the consequences of lake depth for a range of other factors that affect macrophyte quality, such as light, nutrients, sediments and wave action. The vast array of studies on macrophyte quality in lakes provides a firm basis (only briefly presented above) for regulating activities that alter lake depths unnaturally and/or activities that exacerbate the negative effects of related hydrological/geomorphological processes, including sedimentation and nutrient inputs. This is particularly important in the UK, where utility industries in particular contribute to morphological alterations and to a consequent risk of failing WFD objectives for as much as 46 per cent of lake water bodies in Scotland alone (SEPA 2004). However, more information is needed on how to maintain the long-term good ecological status of lakes, particularly the majority of shallow lakes in Europe, which includes many of the shallow lakes that dominate the southern half of Britain (Acreman *et al.* 2006).

6 Macroinvertebrates

Macroinvertebrates play a key role in lake ecosystems, providing food for wildfowl and fish, and also playing important roles in maintaining the good ecological status of lakes. The wide functional diversity of macroinvertebrates, which can act as predators, prey, primary consumers, detritivores and parasites, makes them excellent indicators of the ecological status of any lake. This is widely acknowledged in the array of macroinvertebrate-based indices of water quality and quantity used in rivers and ponds, such as BMWP (Biological monitoring working party) scoring, PSYM (Predictive SYstem for Multimetrics) assessments (for example, indicators of nutrient status; Ward et al. 1992) or LIFE scoring (Lotic Invertebrate Index for Flow Evaluation; an indicator of flow status).

One of the most important factors influencing the ecological status of macroinvertebrates in any lake is the amount of macrophyte habitat available. Macrophytes provide invertebrates with food, with refuges from predators such as wildfowl, fish and other invertebrates, with habitat for laying eggs and as habitat for their prey, including other invertebrates and larval fish and amphibians. Because of the importance of macrophytes for lake invertebrates, many of the hydromorphological factors that are important for the ecological status of macrophytes in lakes will, by extension, also apply to macroinvertebrates.

The majority of research on macroinvertebrates in lakes has focused on their responses to changes in nutrients and to impacts such as acidification. For example, the successful management of culturally eutrophied lakes can be monitored by studying invertebrate responses: the typical pattern in shallow lakes is for an increase in zooplankton such as *Daphnia* and a decrease in smaller organisms such as *Bosmina*. As macrophytes in biomanipulated lakes recover, increases in plant-associated snails and isopods occur (Hargeby *et al.* 1994) and invertebrates that are associated with bare sediment, such as Chironomidae and Oligochaeta, become less dominant. This pattern has been identified in Europe and North America (Hanson and Butler 1994, Meijer *et al.* 1999). In acidified, nutrient-poor lakes, invertebrates such as molluscs and crustaceans are generally the first to be extirpated as pH falls (see Bendell and McNicol 1995, Eriksson 1983, Mallory *et al.* 1994), with knock-on effects for organisms that rely on these invertebrates, such as wildfowl. There is generally a predictable shift in acid lakes towards more nektonic (open-water, active) invertebrates such as beetles (see McParland 2005 for a review). This predictability in the changes to macroinvertebrate diversity in response to changes in processes and pressures like eutrophication and acidification adds to the usefulness of macroinvertebrates as indicators of ecological quality in lakes.

However, there are relatively few studies that directly tie macroinvertebrate ecological quality in lakes to hydromorphological factors (but see Smith *et al.* 1987). Instead, many studies focus on the effects of, for example, drawdowns (lowering of water levels) on fish, birds and macrophytes, and mention macroinvertebrates as part of the overall picture. Examples of attempts at direct linkages between hydromorphology and invertebrates include that of Boulton *et al.* (1992), who showed that a large drop in water depth during a drought caused major changes in invertebrate community structure. Other studies note the role of tube-dwelling benthic invertebrates (tubificids and Chironomidae) in suspending sediments and altering oxygen and nutrient availability (see Krezoski *et al.* 1978, Schelske *et al.* 1978., Svensson and Leonardson 1996). All of the latter studies are linked to the quality of water for macrophytes and fish.

Human activities that alter the morphometry of a lake can also alter nutrient availability in lakes and, in conjunction with increased nutrient inputs, can cause major changes to macrophyte quality and hence to invertebrate composition. Quinlan *et al.* (2002) found that agriculture and urbanisation in Canadian prairie lakes caused significant changes to the historical balance between deep-water and littoral invertebrate species. Changes in land use since European settlement has increased the rates of natural change in invertebrate communities by adding nutrients to already naturally nutrient-rich systems. This evidence does not provide a direct link between hydromorphology and invertebrates, but one of the principal changes to Canadian prairie lakes since European settlement has been drainage. This again provides a pressure on lake depth that may, in conjunction with unnatural nutrient inputs, have led to the changes recorded.

Heino and Muotka (2006) found that a combination of limnological factors and landscape factors, such as lake connectivity, appear to determine mollusc diversity in Finnish lakes. Notably, Heino and Muotka (2006) do not appear to have considered depth as an explanatory factor in their analysis, but they point out that local environmental factors in lakes, such as productivity, provide strong environmental filters for invertebrate diversity. It is possible that the strength of the relationships between factors such as productivity and macroinvertebrate ecological status obscures relationships between ecological status and hydromorphological factors. The tentative links to hydromorphological pressures inferred from Quinlan *et al.* (2002) are a useful example of this obscurity.

This means that any biotic-hydrogeomorphic interactions for invertebrates will need to be inferred through studies of the biotic-hydrogeomorphic interactions for macrophytes and fish, which are generally more clearly demonstrable. The strong links between invertebrates, fish and macrophytes are so well documented in lake ecology that there is likely little to be gained by attempting to find direct links between invertebrates and hydromorphological processes and pressures. Macroinvertebrate indices of ecological status offer an excellent means of monitoring the success of conservation efforts in lakes. However, the regulation of drainage, dredging, and other activities that constitute hydromorphological pressures will be more immediately linked to macrophytes, which provide habitat for invertebrates, and to fish, which rely upon and are relied upon by invertebrates.

7 Fish

The relationships between fish survival and hydromorphological factors such as lake depth, lake order (the number of inlet and outlet streams to a lake and the distance to the next nearest lake) and oxygen availability have been well documented in a wide range of lake systems across the globe (for example, Danylchuk and Tonn 2006, Eriksson 1983, 1984, Garcia *et al.* 2006, Håksanon 2005, Hershey *et al.* 2006, Tonn and Magnusson 1982). Large, deep, well-connected lakes are more likely to support salmonids, pike and other large-bodied fish than small, shallow isolated lakes (Tonn and Magnuson 1982, Hershey *et al.* 2006). Small lakes are often fishless or support only small-bodied, anoxia-tolerant species such as the fathead minnow *Pimephales promelas* or the brook stickleback *Culaea inconstans*, which are a feature of prairie potholes (Cox *et al.* 1998, Hanson and Butler 1994, McParland 2004, Robinson and Tonn 1989).

Similar to their effects on macrophytes, the depth and permanence of water in a lake basin (fluctuating or stable water levels) will have direct impacts on fish in terms of available habitat (Tonn and Magnusson 1982). Depth will also have impacts on the availability of oxygen (W. Tonn, personal communication). Oxygen availability, lake productivity and depth are all closely related. Shallow, nutrient rich lakes will be much more prone to anoxia than deep, nutrient-poor lakes, and there are also well-documented cases of lake drawdown resulting in warmer temperatures, greater productivity and reduced oxygen in lakes (see Rowan and Soutar 2005 for a review). Drawdown (the artificial reduction of water level) in lakes has also been shown to impact on the reproductive output of fish, both by inhibiting spawning (see Yamamoto *et al.* 2006) and by causing the mortality of fish eggs in shallow water (Anras *et al.* 1999).

In cold climates, shallow lakes are also much more likely to freeze to the bottom in winter, thereby causing fish extirpations – unless the fish can find some refuge in outlet streams or deep-water refugia (Danylchuk and Tonn 2006, Robinson and Tonn 1989). In temperate regions, where the majority of research has been conducted on fish ecology, winter coverage of ice and snow is also likely to cause oxygen reductions, particularly in shallow, productive lakes where large amounts of organic matter will use up oxygen through decomposition (Danylchuk and Tonn 2006). This depletion can lead to the loss of lake fish in winter, a phenomenon known as 'winterkill'. Thus, depth, in combination with factors such as lake order, latitude and area, will determine the availability of vital resources for fish, such as oxygen. In turn, because oxygen demand for fish is size-dependent, these factors will also determine the diversity of fish in lakes. Pike-dominated lakes, for example, are generally deeper than lakes dominated by small-bodied fish such as minnows within the same geographical region (W. Tonn, personal communication).

Lake depth is also generally reflected in various chemical and biological processes and pressures on fish. Acidification of deep oligotrophic lakes and the resulting effects on fish have been well documented since at least the late 1970s in Europe and North America (see Bendell and McNicol 1995, Eriksson 1979, Eriksson *et al.* 1980, Eriksson 1987). In shallow eutrophic lakes, the roles of depth, oxygen levels and artificial nutrient inputs are equally well documented (see Bergman *et al.* 1999, Danylchuk and Tonn 2006, Fox and Keast 1991, Hanson and Butler 1994, Meijer *et al.* 1999, Robinson and Tonn 1989). Deep lakes at high latitudes are less productive, with generally lower alkalinity, and so are less buffered against impacts such as acid deposition (Brönmark and Hanson 1998). In studies of German lakes, depth and lake volume appear to be more reliable predictors of fish diversity and quality than eutrophication (Mehner *et al.* 2005), and this pattern has also been found in studies of fish communities in North

American lakes (W. Tonn, personal communication). Many of the pressures on lakes, such as dredging, abstraction, impoundment and diversion, can alter a lake's depth, general bathymetry and connectivity to streams and other lakes (Bragg *et al.* 2003).

Whilst depth is clearly an overwhelmingly important hydromorphological determinant of the ecological quality of fish communities in lakes, it is also crucial to consider the effects that fish have on lake hydrological processes, particularly with regard to sedimentation processes. Coarse fish such as bream (*Abramis brama*), roach (*Rutilus rutilus*), tench (*Tinca tinca*) and carp (*Cyprinus carpio*) are often a major cause of sediment re-suspension and mechanical damage to macrophytes, and so these fish have been the focus of many biomanipulation efforts in eutrophic, shallow lakes (Bergman *et al.* 1999, Meijer *et al.* 1999, Scheffer *et al.* 1993). Maintaining good ecological status involves keeping a balance between fish, macrophytes and sediments.

Many fish typical of shallow lakes also eat grazing zooplankton, which would normally control the amount of nuisance algae in a lake. Again, increases in grazing zooplankton, water clarity and macrophytes, and reductions in suspended sediments following the removal of benthivorous (bottom-feeding) and planktivorous (plankton-eating) fish such as those detailed above are well documented in the northern hemisphere (see Bergman *et al.* 2000, Hanson and Butler 1994, Jeppesen *et al.* 1997, Lauridsen *et al.* 1993, Williams and Moss 2003). Fish communities provide an indicator of ecological quality because their diversity is so strongly tied to lake depth and the associated sedimentation, oxygen, temperature and nutrient levels (see Gassner *et al.* 2006). Salmonids will be more likely to occur in deeper, more oxygen-rich waters than cyprinids (Mehner *et al.* 2005).

In summary, fish diversity is influenced by various geomorphological factors including lake order (connectivity), latitude and depth. Of these, depth is by far the most important hydromorphological factor on the ecological status of fish in lakes. This is due to the strong influence of depth on the chemical and biological factors that are important for fish, with oxygen, temperature, nutrient status and sedimentation being the most important. It is therefore just as important to regulate fish stocking operations and lake fisheries directly, as to regulate activities that alter lake depths. Commercial fisheries in British lakes form a relatively low proportion of the industry impacts on the morphology of lakes (see SEPA 2004). However, the role of fish in maintaining problem situations, such as eutrophication and algal blooming, caused by morphological alterations of lakes for utilities, agriculture and urbanisation (including flood defence) should not be ignored.

8 Anthropogenic pressures on lakes and impacts on hydrological, morphological and biological elements

Bragg *et al.* (2003) summarise the anthropogenic pressures on lakes and the resulting impacts on hydromorphology and biota. It is not intended to reproduce that review in this report. However, Tables 3 and 4 of the Bragg *et al.* (2003) review have been adapted in Table 8.1, which incorporates examples from the literature of anthropogenic impacts on lakes.

Human impacts on biota and lake hydromorphological processes may be indirect or direct. Indirect human impacts include climate change, which may increase water temperatures. Direct human impacts and pressures have been identified from the literature as including dredging and the construction of dams for water supply, amenity and power generation. These will impact on residence time, water levels, light transmissivity and nutrient availability (de Haan *et al.* 1993, McParland 2006, Baxter 1977) and consequent changes to community structure (Boulton *et al.* 1992).

In general, the impact of lake water depth on fish, macroinvertebrates and macrophytes has been the most studied hydromorphological parameter.

Table 8.1 Anthropogenic pressures on hydromorphological and biological quality elements in lakes (modified from Bragg *et al.* 2003)

Pressures	Activity	Impacts on lake hydromorphology	Impacts on biota	Number of papers demonstrating the effect	Geographic regions demonstrating the effect (from published literature)	Duration of impact and adaptability of the ecology to the impact	Cumulative cross pressure impact analysis (other factors contributing to ecological responses)	Published remedies to impact	Number of lakes (for key papers)	References for most salient three papers and for all UK lakes
Agriculture	Clearing natural forest; increase in sheep stocks; increase in nutrient inputs	Increase in sedimentation rate; change in composition of sediment load	Decrease in photosynthetic rates; degradation of lake bottom habitats	16	UK, Europe, North America	90 per cent of volume of upland UK reservoir lost in 100 years due to erosion derived sediment Eutrophication widespread	Change in lake bathymetry, surface area, volume Changes in primary production	>1000 examples of remedies to eutrophication; global examples from N America and Europe in particular	16 (UK), 3 (Sweden), 2 (New Zealand), 18 (Netherlands)	67, Rowan *et al.* 2004 in Rowan and Soutar 2005; 70, Scheffer *et al.* 1993; 59, Meijer *et al.* 1999; 8, Bergman *et al.* 1999.
Forestry; timber harvesting	Ploughing, drainage, harvesting	Increase in suspended sediment production and lake sedimentation rate	Decrease in photosynthetic rates due to increased turbidity	3	UK, North America	Depends on residence time of lake			1 (UK)	14,15
Military activities	Army training using live ammunition	Disintegration of shoreline peat rafts	Loss of shoreline communities	1	UK				1 (UK)	61, Morey 1976 in Bragg *et al.* 2003
Recreation	Hill walking, power boating,	Erosion of shoreline and paths; trampling	Loss of shoreline communities	2	UK, North America		Water-based activities such as power		1 (UK)	22

Pressures	Activity	Impacts on lake hydromorphology	Impacts on biota	Number of papers demonstrating the effect	Geographic regions demonstrating the effect (from published literature)	Duration of impact and adaptability of the ecology to the impact	Cumulative cross pressure impact analysis (other factors contributing to ecological responses)	Published remedies to impact	Number of lakes (for key papers)	References for most salient three papers and for all UK lakes
	angling	of wetland					boating			
Road building	Construction; culverting of lake outflow	Accelerated catchment erosion and lake sedimentation rates	Retreat of reed fringe; decrease in photosynthetic rates	2	UK		Alteration of shoreline profile and substrate		2 (UK)	20
Urbanization	Urban development Sewage discharge	Increase in sedimentation rate and suspended sediments Increase in sedimentation rate due to increased deposition of persistent algal remains	Increase in algal growth rate. Emergent macrophytes (*Typha, Phragmites*) favoured	7	Sweden, US, Europe, Scotland	Retention time important for variance in concentration of particulates bound to sediment	Decrease in fish productivity Decrease in emergent and floating leaf plants, agricultural nutrient inputs and inappropriate fish stocking	Suction dredging to remove phosphorous rich sediment	60 (50 in Scotland)	10, Blindow *et al.* 1993; 63, Quinlan *et al.* 2002; 72, SEPA 2004.
Mineral exploitation	Mining; gravel extraction from lake bed	Changes in sediment deposition and distribution patterns	Degradation of fish spawning grounds; decrease in invertebrates and associated wildfowl	>10 examples in UK of gravel pit lake effects	UK	Initial management of fish stocks in gravel pit lakes important for maintaining quality		Drawdown and removal of bottom-feeding fish improves macroinvertebrate and macrophyte quality, and thus provides better habitat	1 (UK)	55, also Giles *et al.* 1990

Pressures	Activity	Impacts on lake hydromorphology	Impacts on biota	Number of papers demonstrating the effect	Geographic regions demonstrating the effect (from published literature)	Duration of impact and adaptability of the ecology to the impact	Cumulative cross pressure impact analysis (other factors contributing to ecological responses)	Published remedies to impact	Number of lakes (for key papers)	References for most salient three papers and for all UK lakes
								for wildfowl		
Navigation	Dredging	Increase in water depth and turbidity	Siltation of fish spawning grounds	1	UK		Destruction of lake bed habitat		1 (UK)	57
Upstream water use	Change in inflow rate	Change in flow dynamics Change in water level, residence time, connection to groundwater	Phyto-plankton favoured	1	Canada					
Water supply	Direct water abstraction from lake Groundwater abstraction	Increase in residence time Change in rates of exchange between lake and groundwater; change in water quality (for example, salinity)	Changes in plankton, macrophyte populations; increases in frequency of algal blooms	11	Europe, Italy, Armenia, Israel, Australia, Germany, UK, Japan, Norway, Sweden, Netherlands, Denmark	Some apparent permanent impacts	Increase in nutrient and pollutant impacts from agriculture and urban sewage Sediment re-suspension by wind generated turbulence; deposition of fine sediment in spawning ground gravels Dredging to allow boat clearance on	Re-flooding (to counter sediment re-suspension)	1 (UK)	57

Pressures	Activity	Impacts on lake hydromorphology	Impacts on biota	Number of papers demonstrating the effect	Geographic regions demonstrating the effect (from published literature)	Duration of impact and adaptability of the ecology to the impact	Cumulative cross pressure impact analysis (other factors contributing to ecological responses)	Published remedies to impact	Number of lakes (for key papers)	References for most salient three papers and for all UK lakes
							drawndown lakes and reservoirs.			
Construction of barrages and dams, including hydropower generation	Water diversions Damming	Reduction in residence time Increase in area Changes in water level Changes in patterns of water level fluctuations Changes in Retention time Effect on erosion, deposition and sediment transport dynamics; freezing of sediments if lake bed exposed. Landslides in lake bed sediments.	Decline in frequency of algal blooms; changes in plankton populations Changes to vegetation communities Changes to growth rates of fish communities (increase in fish productivity rates) Changes to phytoplankton communites Changes to littoral communities and littoral	41	Ireland, UK, Africa, Argentina, Norway, Spain, US, Canada, Finland, Sweden, Japan, Australia, Malaysia, Czech Republic, Brazil, Israel, New Zealand.	Depends on frequency of water level changes and duration of flooding.	Low water levels lead to reduction of hypolimnion volume and increases in the end products of organic decomposition. Changes to size of pelagic zone Alteration of shoreline profile Changes to lake temperature and light transmissivity Changes in primary productivity rates in phytoplankton Changes in re-suspension of sediments	Promoting re-vegetation of shoreline by light application of fertiliser Reduce designated fluctuation range Set water levels to favour biota Not allowing rapid water level changes; this does not allow flora and fauna to migrate or adapt	2 (UK)	45, 73, Frost 1956 in Bragg *et al.* 2003

Pressures	Activity	Impacts on lake hydromorphology	Impacts on biota	Number of papers demonstrating the effect	Geographic regions demonstrating the effect (from published literature)	Duration of impact and adaptability of the ecology to the impact	Cumulative cross pressure impact analysis (other factors contributing to ecological responses)	Published remedies to impact	Number of lakes (for key papers)	References for most salient three papers and for all UK lakes
		Bank erosion Discolouration of water supplies due to trapping of sediments	fauna				arising from lake-level lowering			
Drainage	Construction of drainage canal; agricultural drainage	Decrease in water level Decrease in surface area Reduced volume Restricted littoral zone Reduced residence time	Loss of spawning habitat Reduced oxygen availability Increased chances of winterkill	2	UK Canada	70 per cent of Canadian wetlands drained	Changes in primary production and resuspension	Plugging of drainage ditches can reverse losses to biodiversity in prairie wetland complexes	1 (UK)	68, Munro 1994 in Rowan and Soutar 2005

9 Discussion and conclusions

Lakes are complex systems and this review of the available literature has demonstrated that few studies have attempted to tackle the three-way interplay between chemical, biological and hydro-geomorphological processes at large spatial or temporal scales. There is, therefore, limited quantitative material on which to base programmes of measures.

The main problem in attempting to quantify such processes is that it is difficult to separate the role of hydro-geomorphological processes from that of other processes driving lake ecosystems. For example, climate and the physicochemical parameters that hydrological and geomorphological parameters influence also impact lake ecology, and their effects are closely linked with hydro-geomorphology. Similarly, it is often difficult to separate the impacts of human activities from those caused by natural processes. However, it is clear that human activities, including hydromorphological pressures, do impact on the ecological function of the WFD-relevant biota.

Given the strong links between all of these processes, it may be that managing pressures in isolation exacerbates rather than reduces human pressures on lake ecosystems. Achieving good ecological status for one biological element in isolation may impact negatively on other biological communities. For example, some biological parameters (such as phytoplankton) are more sensitive to hydrological processes, while others (such as fish) are more sensitive to geomorphological processes. Nevertheless, most are responsive to hydro-geomorphological processes coupled with other environmental and biological forcing factors.

There is less quantitative evidence to underpin the more indirect process or pressure relationships between hydro-geomorphology and the WFD biota. However, indirect relationships are equally important and should therefore be given equal priority for WFD considerations. The following example demonstrates why this is the case. Phytoplankton, phytobenthos and macrophyte communities are strongly affected by light availability, which is a topic that has received considerable attention. One of the dominant controls on light availability is turbidity. This is caused by a suite of processes such as erosion-accretion cycles and sediment fluxes, which are in turn controlled by hydrological and geomorphological conditions. Thus, if we want to enhance light availability in order to improve ecological quality under WFD, we need to understand which human pressures disturb or increase the supply or quality of sediments to systems. In order to do this, hydrological and/or geomorphological studies are required to help identify regulatory measures that mitigate dominant causes of poor light availability.

This literature review has highlighted that all five biological elements (phytobenthos, phytoplankton, macrophytes, macroinvertebrates and fish) are interlinked and that they all affect, and are affected by, the hydromorphology of their surroundings. The interdependence of lake biota should be considered when setting targets and implementing strategies for achieving and maintaining good ecological status in lakes. Recognising the importance of this biotic interdependence is critical to improving the understanding of the interactions between hydromorphological, biological and physicochemical quality elements in lakes.

Of all the hydromorphological factors that affect lake biota, the influence of depth is most well understood. Depth is arguably the most important factor in determining: nutrient status, light availability and oxygen availability; the quantity and diversity of phytoplankton and phytobenthos, the establishment of macrophytes and the types of fish and invertebrates present; and the relative importance of processes such as eutrophication and sedimentation. Although factors such as latitude and altitude may also be important for lake biota, these factors cannot be subject to regulatory measures to reduce impacts to the ecological status of lake biota.

The relationships between lake order and lake biota are still poorly understood, and may often be clouded by the strong relationships between lake depth and lake biota. Hydromorphologically-based measures to reduce or reverse human impacts to lakes should therefore focus in the first instance on regulating activities that change the depth of a lake, as well as changing its general bathymetry. This approach, in conjunction with physicochemically- and biologically-based measures (such as nutrient reduction or fish removals), has been shown in numerous case studies (reviewed by Bergman *et al.* 1999, Meijer *et al.* 1999, Perrow *et al.* 1999) to have positive effects on the ecological status of lake biota.

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List of abbreviations

BMWP	Biological monitoring working party
Defra	Department for Environment, Food and Rural Affairs
HMWB	Heavily modified water body
JNCC	Joint Nature Conservation Committee
JSTOR	Journal Storage
LIFE	Lotic Invertebrate Index for Flow Evaluation
RT	Residence time
SEPA	Scottish Environmental Protection Agency
SNIFFER	Scotland and Northern Ireland Forum for Environmental Research
WFD	Water Framework Directive

Glossary

Abiotic – non-living elements of an ecosystem.

Anoxia – low or no oxygen availability in water, leading to 'suffocation' of fish and invertebrates. Also known as hypoxia (see below).

Anthropogenic – effects and processes generated by human activity.

Bathymetry – depth/area profile of a lake, the 'shape' of its basin and the volume of water in it.

Benthivorous – bottom-feeding: often refers to feeding on invertebrates that live in sediments at the bottom of lakes, known as benthos.

Biomanipulation – the manipulation of aquatic food webs to improve water quality; generally involving removal of fish that stir up sediments and/or prey on the grazing invertebrates that normally keep nuisance algae in check. Can be used in combination with nutrient reduction efforts in culturally-eutrophied lakes.

Biotic – living elements of an ecosystem.

Epilimnion – relatively warm and circulating lake surface waters.

Eutrophic – rich in nutrients, particularly those of importance for primary production (nitrates and phosphates). Can be natural, but human activities can also unnaturally increase nutrient availability.

Eutrophication – excess input of organic nutrients, primarily nitrates and phosphates, which results in declines in water quality.

Hydromorphology – the physical characteristics of the boundaries of a water body.

Hypolimnion – cooler non-circulating deeper waters in a lake.

Hypoxia – low oxygen availability in lakes, which can be natural or human-induced. Arises in productive lakes where large amounts of algal or plant material are produced and then decompose after death. This decomposition process uses up oxygen.

Lake order – the connectivity of a lake to outlet and inlet streams and, in some cases, the distance to the next nearest lake.

Littoral – the shallower edges of a lake, generally where light penetrates to the bottom and where most of the macrophytes are established.

Macroinvertebrates – invertebrates large enough to be seen by the naked eye; generally excludes organisms like zooplankton.

Macrophytes – aquatic plants (can be submerged, floating or emergent).

Morphometry – the shape of a lake basin.

Oligotrophic – low in nutrients.

Phytobenthos – plants living on or near the lake bed.

Phytoplankton – planktonic plants and algae.

Planktonic – free-floating, generally microscopic organisms.

Planktivorous – feeding on planktonic organisms.

Reference conditions – for any surface water body, reference conditions or high ecological status is a state in the present or in the past where there are no, or only very minor, changes to those values of the hydromorphological, physicochemical and biological quality elements that would be found in the absence of anthropogenic disturbance. Reference conditions should be represented by relevant values of the biological quality elements in calculations of ecological quality ratios and the subsequent ecological classification.

Thermocline – the region of a lake in which the fall in temperature is greater than 1°C per metre.

Winterkill – extirpation of fish in lakes over the winter period due to factors such as freezing, isolation from inlet and outlet streams, and hypoxia.

Zooplankton – planktonic animals.

Appendices

Appendix 1 Web of Science literature searches for macrophyte terms

Macrophyte		Number of articles found
General	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	6
Hydro-morphology	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and (TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape")) OR (TS= (depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*))) OR (TS=((lake* same (catchment* or sediment*)) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	76
Human pressures	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) same TS=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not TS=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	72

Appendix 2 CSA literature searches for macrophyte terms

Macrophyte		Number of articles found
General	KW=(macrophyt* and lake*) not KW=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and KW=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT KW=((“salt lake*” or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or KW=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	66
Hydro-morphology	KW=(macrophyt* and lake*) not KW=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and (TI=((shore zone) NEAR (condition* or structur*)) OR TI=((substrat*) NEAR (structur* or quantit* or qualit*)) OR AB=((shore zone) NEAR (condition* or structur*)) OR AB=((substrat*) NEAR (structur* or quantit* or qualit*)) OR KW=(turbid* or basin form or catchment shape) OR KW=(depth-change* or depth change* or hydraulic retention time or surface area or water level fluctuations or residence time)) or ((TI=((flow) NEAR (dynamics)) or TI=((quantit*) NEAR (flow*)) OR TI=((lake*) NEAR (catchment* or sediment*)) OR AB=((flow) NEAR (dynamics)) or AB=((lake*) NEAR (catchment* or sediment*) NEAR (input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*)) OR TI=((lake*) NEAR (catchment* or sediment*) NEAR (input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT KW=(tropical or swamp* or estuar* or alpine or lagoon or salt lake or boreal or arid or late quaternary or holocene or pluvial lake or glacial lake or post*glacial lake))	
Human pressures	KW=(macrophyt* and lake*) not KW=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) same KW=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not KW=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	

Appendix 3 Biosis literature searches for macrophyte terms

Macrophyte		Number of articles found
General	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	6
Hydro-morphology	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and (TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape")) OR (TS= (depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*))) OR (TS=((lake* same (catchment* or sediment*)) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	55
Human pressures	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) same TS=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not TS=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	45

Appendix 4 CAB literature searches for macrophyte terms

Macrophyte		Number of articles found
General	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	2
Hydro-morphology	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and (TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape")) OR (TS= (depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*))) OR (TS=((lake* same (catchment* or sediment*)) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	17
Human pressures	(TI=macrophyt* and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) same TS=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not TS=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	36

Appendix 5 Web of Science literature searches for macroinvertebrate terms

Macroinvertebrate		Number of articles found
General	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	13
Hydro-morphology	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) and (TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape")) OR (TS=(depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*))) OR (TS=((lake* same (catchment* or sediment*)) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	37
Human pressures	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) same TS=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not TS=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	64

Appendix 6 CSA literature searches for macroinvertebrate terms

Macroinvertebrate		Number of articles found
General	KW=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and (lake*)) not KW=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and KW=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT KW=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or KW=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	16
Hydro-morphology	KW=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and (lake*)) not KW=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) and (TI=((shore zone) NEAR (condition* or structur*)) OR TI=((substrat*) NEAR (structur* or quantit* or qualit*)) OR AB=((shore zone) NEAR (condition* or structur*)) OR AB=((substrat*) NEAR (structur* or quantit* or qualit*)) OR KW=(turbid* or basin form or catchment shape) OR KW=(depth-change* or depth change* or hydraulic retention time or surface area or water level fluctuations or residence time)) or ((TI=((flow) NEAR (dynamics)) or TI=((quantit*) NEAR (flow*)) OR TI=((lake*)NEAR (catchment* or sediment*)) OR AB=((flow) NEAR (dynamics)) or AB=((lake*)NEAR(catchment* or sediment*) NEAR(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*)) OR TI=((lake*)NEAR(catchment* or sediment*) NEAR(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT KW=(tropical or swamp* or estuar* or alpine or lagoon or salt lake or boreal or arid or late quaternary or holocene or pluvial lake or glacial lake or post*glacial lake))	41
Human pressures	KW=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and (lake*)) not KW=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal or arid) same KW=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not KW=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	52

Appendix 7 Biosis literature searches for macroinvertebrate terms

Macroinvertebrate		Number of articles found
General	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	5
Hydro-morphology	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) and (TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape")) OR (TS= (depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*))) OR (TS=((lake* same (catchment* or sediment*)) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	27
Human pressures	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) same TS=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not TS=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	39

Appendix 8 CAB literature searches for macroinvertebrate terms

Macroinvertebrate		Number of articles found
General	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	7
Hydro-morphology	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) and (TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape")) OR (TS= (depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*))) OR (TS=((lake* same (catchment* or sediment*)) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	14
Human pressures	TI=((macroinvert* or mayfl*or stonefl* or mollusc* or chironomid* or oligochaete* or caddisfl* or dragonfl*) and TS=(lake*)) not TS=("salt lake*" or tropical or alpine or lagoon or swamp or estuar* or boreal* or arid) same TS=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not TS=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	44

Appendix 9 Web of Science literature searches for fish terms

Fish		Number of articles found
General	TI=((fish* or salmonid* or trout* or salmon* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") and TS=(lake*)) not TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach*) and TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological) NOT TS=(("salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	62
Hydro-morphology	((TS=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") same TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape") OR TS=(depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*)) OR TS=((lake* same (catchment* or sediment*))) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*)) SAME TS=lake*) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach* or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	109
Human pressures	((TI=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") SAME ((TI=(human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina* or dock* or agricult* or mining or mine or recreat* or navigat* or jetski* or boat* or "water ski*"or waterski* or "water sport*" or watersport*)) SAME (TI=(disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*)))) AND TS=lake*) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach*terrestrial or marine or infection or "molecular genetics" or dune* or cliff* or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	79

Appendix 10 CSA literature searches for fish terms

Fish		Number of articles found
General	((TS=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") SAME TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological)) AND TS=lake*) NOT (TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach* or "salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	55
Hydro-morphology	KW=((fish* or salmonid* or trout* or salmon* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") and KW=(lake*)) not KW=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach*) and (TI=((shore zone) NEAR (condition* or structur*)) OR TI=((substrat*) NEAR (structur* or quantit* or qualit*)) OR AB=((shore zone) NEAR (condition* or structur*)) OR AB=((substrat*) NEAR (structur* or quantit* or qualit*)) OR KW=(turbid* or basin form or catchment shape) OR KW=(depth-change* or depth change* or hydraulic retention time or surface area or water level fluctuations or residence time)) or ((TI=((flow) NEAR (dynamics)) or TI=((quantit*) NEAR (flow*)) OR TI=((lake*)NEAR (catchment* or sediment*)) OR AB=((flow) NEAR (dynamics)) or AB=((lake*)NEAR(catchment* or sediment*) NEAR(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*)) OR TI=((lake*)NEAR(catchment* or sediment*) NEAR(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*))) NOT KW=(tropical or swamp* or estuar* or alpine or lagoon or salt lake or boreal or arid or late quaternary or holocene or pluvial lake or glacial lake or post*glacial lake))	72
Human pressures	KW=((fish* or salmonid* or trout* or salmon* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") and KW=(lake*)) not KW=(tropical or swamp* or estuar* or	25

	alpine or lagoon or "salt lake" or boreal or arid or cockroach*) same KW=((human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina or dock* or agricult* or min* or recreat* or navigation* or (water same (ski* or sport*) or jetski* or boat*) same (disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*))) not KW=(terrestrial or marine or estuar* or tropical or infection or "molecular genetics" or dune* or lagoon* or cliff* or swamp or alpine or lagoon or "salt lake" or boreal or arid or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	

Appendix 11 Biosis literature searches for fish terms

Fish		Number of articles found
General	((TS=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") SAME TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological)) AND TS=lake*) NOT (TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach* or "salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	37
Hydro-morphology	((TS=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") same TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape") OR TS=(depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*)) OR TS=((lake* same (catchment* or sediment*))) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*)) SAME TS=lake*) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach* or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	83
Human pressures	((TI=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") SAME ((TI=(human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina* or dock* or agricult* or mining or mine or recreat* or navigat* or jetski* or boat* or "water ski*"or waterski* or "water sport*" or watersport*)) SAME (TI=(disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*)))) AND TS=lake*) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach*terrestrial or marine or infection or "molecular genetics" or dune* or cliff* or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	74

Appendix 12 CAB literature searches for fish terms

Fish		Number of articles found
General	((TS=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") SAME TS=(biogeomorph* or ecogeomorph* or hydromorph* or hydro-morph* or ecohydrol* or hydroecol* or geomorph* or morphological)) AND TS=lake*) NOT (TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach* or "salt lake*" or tropical* or alpine* or lagoon* or swamp* or estuar* or boreal* or arid* or histolog* or genetic* or deformit* or molecular* or phylogen*) or TS=((morphol*) same (stasis or deform* or abnormal* or larva* or feed* or body*)))	24
Hydro-morphology	((TS=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") same TS=("shore zone" same (condition* or structur*)) or TS=(substrat* same (structur* or quantit* or qualit*)) OR TS=(turbid* or "basin form" or "catchment shape") OR TS=(depth-change* or "depth change*" or "hydraulic retention time" or "surface area" or "water level fluctuations" or "residence time") OR TS=((flow same dynamics) or (quantit* same flow*)) OR TS=((lake* same (catchment* or sediment*))) SAME TS=(input or load or eros* or erod* or geomorph* or hydro*morph* or hydro*geomorph* or connect* or sensitiv* or disturb*)) SAME TS=lake*) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach* or "late quaternary" or "holocene" or "pluvial lake" or "glacial lake" or "post*glacial lake")	25
Human pressures	((TI=(fish* or salmon* or trout* or charr or lamprey* or shad* or eel* or minow* or pike or perch or ruffe or cyprinid* or bream or carp or gudgeon or roach or rudd or "silver bream" or tench or whitefish or vendace or coregonid* or pike* or "three-spined stickleback*") SAME ((TI=(human* or anthropogenic or man* or fishing* or fisher* or trawler* or marina* or dock* or agricult* or mining or mine or recreat* or navigat* or jetski* or boat* or "water ski*"or waterski* or "water sport*" or watersport*)) SAME (TI=(disturb* or impact* or effect* or harm* or variab* or variab* or respons* or resil* or recover*)))) AND TS=lake*) NOT TS=(tropical or swamp* or estuar* or alpine or lagoon or "salt lake" or boreal or arid or cockroach*terrestrial or marine or infection or "molecular genetics" or dune* or cliff* or quaternary or holocene or "pluvial lake" or "glacial lake" or "post*glacial lake")	29

Appendix 13 JSTOR literature searches for all three biota

Fish		Number of articles found
General	lake+depth+fish	23
	lake+depth+invertebrate	6
	lake+depth+macrophyte	7
	flood+nutrient+lake	10
	macrophyte+light	9

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