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Impacts of increased sediment loads on the ecology of lakes

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ABSTRACT

Increased sediment loading comprises one of the most important and pervasive anthropogenic impacts on aquatic ecosystems globally. In spite of this, little is known of the overall effects of increased sediment loads on lakes. By modifying both bottom-up and top-down ecological processes and restructuring energy flow pathways, increased sediment loads not only alter biotic assemblage structure and ecological functioning significantly, but frequently result in reduced biological diversity and productivity. Although lake food-webs can be subsidised to some extent by the adsorption of organic carbon to fine sediments, trophic structure and the composition of biotic assemblages remain likely to be modified considerably. The mineralogy and particle size of sediments and the availability of nutrients, by influencing both the scale and nature of impacts, are key determinants of the overall effects of increased sediment loads on lake ecosystems. Although interactions with other global anthropogenic pressures, such as invasion by exotic species and climate change, are likely to be significant, little remains known about the nature or likely strength of those interactions. Widespread increases in sediment loading to lakes have, therefore, profound implications for the conservation and management of global aquatic biological diversity.

Key words: siltation, turbidity, soil erosion, aquatic, diversity, productivity

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I. INTRODUCTION

Excess loading with sediment comprises one of the most significant, widespread and pervasive forms of aquatic pollution (Clarke, Haverkamp & Chapman, 1985; Ryan,

1991; Waters, 1995; Parkhill & Gulliver, 2002). Although a natural and important component of lake ecosystems, the delivery of sediment increases typically five- to tenfold following major human impact (Dearing & Jones, 2003), with considerable implications for biological diversity,

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ecological functioning and productivity. Increased sediment loading of aquatic systems comprises the most important off-site impact of soil erosion (Pimentel *et al.*, 1995; Waters, 1995), which itself represents one of the most important environmental and social problems facing humanity (Pimentel *et al.*, 1995; Helming, Rubio & Boardman, 2006; Pimentel, 2006). Human-induced soil erosion has resulted in an increase of 2.3 billion metric tonnes of sediment being transported by rivers globally every year (Syvitski *et al.*, 2005). Only 1.4 billion metric tonnes of this actually reaches coastal waters, however, owing to the retention of sediments in reservoirs and lakes or in rivers and their floodplains (Walling *et al.*, 2003; Syvitski *et al.*, 2005). Increased delivery of sediment to aquatic systems can, however, also be a consequence of other human activities, including, for example, mining, urban development, construction and the presence of roads (e.g. Sorensen *et al.*, 1977; Ryan, 1991; Gruszowski *et al.*, 2003; Motha *et al.*, 2004; Rijsdijk, Bruijnzeel & Sutoto, 2007).

Although the delivery of sediment to lakes has reduced in some regions owing to the introduction of sediment control programmes and improved soil conservation practices (see Lal, 2001), excessive sediment loading remains one of the primary forms of anthropogenic disturbance of aquatic ecosystems in both tropical and temperate regions (Ryan, 1991; Waters, 1995; USEPA, 2000; Parkhill & Gulliver, 2002). In addition to affecting natural lake systems, the retention of eroded sediments in reservoirs is a major environmental, social and economic concern globally as high sedimentation rates reduce hydropower efficiency and viability, increase costs of dam maintenance and water treatment and have important consequences for water supply, fisheries and tourism (Clarke *et al.*, 1985; Robertson & Colletti, 1994; Pimentel *et al.*, 1995).

Multiple and varied effects of high sediment loads on aquatic ecosystems have been documented (see reviews by Cordone & Kelley, 1961; Chutter, 1969; Bruton, 1985; Clarke *et al.*, 1985; Lloyd, 1985; Appleby & Scarratt, 1989; Newcombe & MacDonald, 1991; Ryan, 1991; Kerr, 1995; Harvey & Pimentel, 1996; Wood & Armitage, 1997). In spite of this, little work has focussed on lakes and less still is known of the overall impacts of increased sediment loads on lake ecosystems. Lakes comprise highly complex systems with the overall effects of increased sediment loads likely to be determined by multifaceted interactions among numerous physical, chemical and biotic factors. Indirect effects are, therefore, likely to be highly important, with increased sediment loads likely to affect both bottom-up and top-down ecological processes. By linking the research that has been done and placing it into a holistic ecosystem context, the aim of this review is to provide a synthesis which describes both the likely consequences of increases in sediment loading for lake ecosystems and their biological diversity and the key factors that determine those consequences.

II. INTERACTIONS WITH PHYSICAL AND CHEMICAL PROCESSES

Decreased transmission of light through the water column is among the most important of the physical effects of

increased sediment loads on aquatic ecosystems (Ellis, 1936). The absorption and scattering of light by suspended particles reduces the compensation depth, below which light intensity is insufficient to sustain photosynthesis, thus diminishing the volume of water supporting primary production (Kirk, 1985; Lloyd, 1985; Lloyd, Koenings & LaPerriere, 1987; Krause-Jensen & Sand-Jensen, 1998; Whalen *et al.*, 2006). Lloyd (1985) reported sharp reductions in the compensation depths of different Alaskan lakes following minor variations in turbidity [2–10 Nephelometric Turbidity Units (NTU)], with dramatic changes in their productive volumes (–75% following a turbidity increment of 5 NTU). Increased mineral turbidity has also been shown to attenuate blue light more rapidly than red light (Ellis, 1936; Grobbelaar & Stegmann, 1976; Kirk, 1979), and to increase the frequency of light fluctuations (Grobbelaar, 1985), with considerable implications for photosynthetic production (Kirk, 1985). Differential light attenuation may also be responsible for the modification of behavioural responses of lacustrine biota to those processes driven by photoperiod and light intensity. Cuker (1987) observed, for example, a significant diurnal shallowing of vertical migration of the zooplankton in a small piedmont lake as a consequence of increased mineral turbidity.

Alterations to sediment budgets can also affect other physical and chemical processes in lakes. Owing to their high oxygen sequestration capacity, whereby sediments are capable of deoxygenating up to sixteen times their own volume of aerated water (Bruton, 1985), increased sediment loads or resuspension of deposited sediments can cause considerable reductions in both oxygen availability (Bruton, 1985; Appleby & Scarratt, 1989) and rates of water column reaeration (Alonso, McHenry & Hong, 1975). Increased mineral turbidity can also influence the heat budgets of lakes through the absorption of heat by suspended particles (Kirk, 1985) or by increased reflection of sunlight back to the atmosphere (Clarke *et al.*, 1985), and can, therefore, depending on the nature of the suspended sediments and lake morphology, cause water temperatures to increase (Ellis, 1936) or decrease (Clarke *et al.*, 1985). This could have highly important physiological and reproductive implications for lacustrine biota (e.g. Sanoamuang, 1993; Gordo, Lubian & Canavate, 1994; Schallau *et al.*, 2008). The ramifications of this often-overlooked effect of suspended sediments are especially important in view of interactions with global climate change (see, for example, Moss *et al.*, 2003; Huber, Adrian & Gerten, 2008; Johnk *et al.*, 2008; Rahel & Olden, 2008; Rosenzweig *et al.*, 2008). Alterations to lake heat budgets may, in turn, affect other sediment-associated processes indirectly. By modifying water viscosity and density, for example, temperature alters the settling velocity of suspended sediment particles, especially those with densities close to that of water (Kerr, 1995).

Increased sedimentation rates can result in the clogging of interstices among lakebed sediments, thus reducing sediment-water exchanges and oxygen penetration and altering biogeochemical and microbial processes considerably (Brunke, 1999; Rehg, Packman & Ren, 2005; Nogaro *et al.*, 2006; Heywood & Walling, 2007). Sediments also concentrate nutrients, trace metals, pesticides and other

pollutants by adsorption to their surfaces (e.g. Oschwald, 1972; Rosales-Hoz, Carranza-Edwards & Lopez-Hernandez, 2000; Jain & Sharma, 2001; Reynolds & Davies, 2001; Walling, Russell & Webb, 2001; Davide *et al.*, 2003; Ricking, Schwarzbauer & Franke, 2003; Walling *et al.*, 2003; Kretzschmar & Schäfer, 2005), facilitating their incorporation into and transfer within lake food-webs. The interactions among the mineralogical properties of sediments and water chemistry determine whether sediments become a source or a sink of nutrients or other contaminants. Periodic anoxia in lake hypolimnia can, for example, result in the desorption of considerable quantities of nutrients or other contaminants from sediments to lake water (e.g. Kilham & Kilham, 1990; Søndergaard, Jensen & Jeppesen, 2001; Jeppesen *et al.*, 2005). Physical and chemical interactions between lake water and influent sediments can, therefore, play a highly important role in determining the outcome of the effects of increased sediment loading on lake ecosystems.

III. EFFECTS ON BIOTA

(1) Clay-organic-bacteria aggregates

The adsorption of dissolved organic carbon (DOC) onto clay particles in suspension can provide a hugely important subsidy to aquatic food-webs (Baylor & Sutcliffe, 1963; Riley, 1963; Arruda, Marzolf & Faulk, 1983; Cuker & Hudson, 1992; Lind, Chrzanowski & Davalos-Lind, 1997) and has been shown to mediate to some extent the impacts of suspended sediments on lakes (Arruda *et al.*, 1983; Gliwicz, 1986; Cuker & Hudson, 1992; Lind *et al.*, 1994). Although clay aggregates may not subsidise significantly food-webs in minerally turbid lakes with low concentrations of organic carbon (Seki, Shortreed & Stockner, 1980; Koenings, Burkett & Edmundson, 1990), and bacterial colonisation may be minimal in these situations (Seki *et al.*, 1980), they may be highly important in systems with sufficient sources of autochthonous or allochthonous organic matter (Cuker & Hudson, 1992; Lind *et al.*, 1997). In a clay-rich North American reservoir with concentrations of suspended sediments close to 100 mg l⁻¹, for example, Arruda *et al.* (1983) estimated that the quantity of organic carbon adsorbed to sediments was over 30 times greater than that available from the phytoplankton. Based on their work in the minerally turbid and nutrient-rich Lake Chapala in Mexico, Lind & Davalos-Lind (1991) and Lind *et al.* (1997) proposed that the concentration of DOC adsorbed onto suspended clay particles as a consequence of their relatively large surface areas can create a concentrated food source for bacterial colonisation and growth. This modification of the traditional heterotrophic microbial loop thereby makes dissolved organic matter available to higher planktivores as particulate food, thus bypassing the intermediate link through heterotrophic nanoflagellates and larger protists (Lind *et al.*, 1997) and improving DOC utilisation efficiency considerably. Under these conditions, aggregate-associated bacteria may represent an important fraction of the total bacterial community. The proportion of

aggregate-associated bacteria in Lake Chapala has been shown to be as large as 77-88% of the total bacterial population and comprises 42% of the total small particle production of the food-web (Lind & Davalos-Lind, 1991; Lind *et al.*, 1997). In these situations, bacterial biomass and production tends to be correlated strongly with inorganic turbidity whilst the coupling between phytoplankton and bacteria, though important, becomes somewhat blurred (Hart, 1986; Lind *et al.*, 1997).

Because of their high nutrient content, clay-organic-bacteria aggregates represent concentrated sources of nitrogen and phosphorus for potential consumers and may affect nutrient recycling within lake ecosystems significantly (Rothaupt, 1992; Weisse, 2005). Further, bacterial cell size is strongly dependent on the organic matter component of aggregates, which depends both on the available DOC and the capacity of the clay particles to bind the organic matter and form aggregates (Lind & Davalos-Lind, 1991). In general terms, while the relative surface area available for adsorption of organic matter increases as particle size decreases, the chemical composition and physical structure of the clay will determine its capacity for, and the consequent strength of, ion adsorption. This can have important consequences for lacustrine biota. Cuker & Hudson (1992) found, for example, that zooplankton were more sensitive to increased loading with montmorillonite clay than kaolinite. After enrichment with phosphorus, however, montmorillonite was able to sustain zooplankton populations of clay-tolerant taxa at 'normal' abundances by means of clay-organic-bacteria aggregate-formation. The effect of these aggregates on lake food-webs depends not only upon sediment loading rates, mineralogy and organic carbon concentrations but also on the capability of organisms to assimilate them (Arruda *et al.*, 1983). As a result, their contribution to the nutrition, growth and survival of organisms likely varies considerably among species and could trigger shifts in community composition and dynamics of minerally turbid lakes and reservoirs.

(2) Primary producers

Light attenuation by inorganic turbidity decreases the fraction of light absorbed by photosynthesising organisms in lakes (Tilzer, 1983). This has been shown to reduce the density, growth rates and production of lake phytoplankton considerably (Seki *et al.*, 1980; Lloyd *et al.*, 1987; Søballe & Kimmel, 1987; Cuker, Gama & Burkholder, 1990; Dokulil, 1994; Guenther & Bozelli, 2004a). Shifts in phytoplankton assemblage structure owing to increased inorganic turbidity, with enhanced dominance of flagellates at the expense of filamentous blue-greens have also been described (Avnimelech, Troeger & Reed, 1982; Cuker, 1987; Cuker *et al.*, 1990). The relative tolerance of flagellates is thought to be due to their greater motility, which both confers the ability to maintain position in the photic zone and reduces sensitivity to flocculation (Avnimelech *et al.*, 1982; Cuker, 1987), and to the fact that they are facultative heterotrophs, which provides access to a wider range of food resources. The adhesion of clay particles onto algal cells in turbid waters has been shown to increase rates of algal sinking, and thereby reduce

phytoplankton densities, significantly (Avnimelech *et al.*, 1982; Cuker *et al.*, 1990; Guenther & Bozelli, 2004a, b). The effects of clays on sinking rates of different forms of algae are, however, difficult to generalise, owing to complex interactions among algal morphology and physiology, clay mineralogy, and water chemistry (Avnimelech *et al.*, 1982; Cuker *et al.*, 1990; Guenther & Bozelli, 2004a, b).

Turbid lakes tend to be depauperate in submerged angiosperms (Baxter, 1977; Kimmel, Lind & Paulson, 1990). High turbidity and sedimentation rates have been shown to reduce the density (Robel, 1961; Moss, 1977), growth rates (Lewis, 1973), photosynthetic activity (Chandler, 1942), regeneration (Spencer & Ksander, 2002) and maximum depth of colonisation (Canfield *et al.*, 1985) of aquatic plants as well as causing considerable physical damage to their leaves (Lewis, 1973). High mineral turbidity has also been shown to reduce the standing crop of periphyton, although this can be concurrent with increased photosynthetic efficiency (Van Nieuwenhuysse & LaPerriere, 1986). High phosphorus loading can, however, alleviate to some extent the impacts of increased mineral turbidity on periphyton productivity (Burkholder & Cuker, 1991). Coupled with the fact that increased sediment loading can promote flocculation and sinking of phytoplankton (Avnimelech *et al.*, 1982; Cuker *et al.*, 1990; Guenther & Bozelli, 2004a, b), the relative importance of periphyton to total lake primary production may, therefore, increase considerably in shallow lakes under high loading of both sediments and phosphorus (Burkholder & Cuker, 1991). The accumulation of sediment particles and associated reduction of organic content of epilithic periphyton has, however, been shown to reduce considerably its nutritional value for consumers (Cline, Short & Ward, 1982; Graham, 1990; Davies-Colley *et al.*, 1992; Yamada & Nakamura, 2002; Kent & Stelzer, 2008).

(3) Zooplankton

High suspended sediment concentrations have been associated frequently with altered assemblage composition and reduced abundance and biomass of lake zooplankton (Adalsteinsson, 1979; Hart, 1986, 1987, 1990; Lloyd *et al.*, 1987; Koenings *et al.*, 1990; Cuker & Hudson, 1992; Jack *et al.*, 1993; Dejen *et al.*, 2004). Reduced rates of zooplankton population growth in turbid conditions have been found to be a consequence of both decreased survivorship and fecundity with increased suspended sediment loads (Kirk & Gilbert, 1990; Kirk, 1992), with juveniles generally more susceptible than adults (Kirk & Gilbert, 1990). A decline of 70% in the net reproductive rate of *Daphnia ambigua* with experimentally increased suspended sediment concentrations was recorded by Kirk (1992) while suspended sediments have also been found to increase significantly the age of first reproduction (Kirk & Gilbert, 1990).

Experimentally increased concentrations of suspended sediments have been shown to reduce rates of both zooplankton feeding and the incorporation of carbon into their tissues by up to 99% (Arruda *et al.*, 1983; Hart, 1988; Kirk, 1991b; Bozelli, 1998). Arruda *et al.* (1983) found that exposure to suspended sediment concentrations of 50–100

mg l⁻¹ decreased the incorporation of algal carbon to near starvation levels for daphnids. Rates of ingestion also varied significantly with the size of suspended particles, with significant variability found among species in their responses to particles of differing size. Experimentally increased suspended sediment concentrations have also been shown to lower significantly the body size of *Daphnia ambigua* at maturity (Kirk, 1992), even though the rate of growth was unaffected. This response of cladocerans to increased turbidity mirrors that for decreased food availability, suggesting that the mechanical interference of suspended sediments with their feeding behaviour comprises the primary mechanism resulting in these patterns (Kirk, 1992).

Cladocera in particular appear to be among the more susceptible of the zooplankton to high concentrations of suspended sediments (Kirk & Gilbert, 1990; Koenings *et al.*, 1990; Jack *et al.*, 1993). High filtration rates and greater size ranges of food generally enable cladocerans to outcompete rotifers in clear-water conditions through exploitative competition (MacIsaac & Gilbert, 1991), mechanical interference (Burns & Gilbert, 1986; Gilbert, 1988; MacIsaac & Gilbert, 1991), and predation (Burns & Gilbert, 1986; Pace & Funke, 1991). Large-bodied cladocerans, particularly daphnids, commonly constitute the dominant herbivores in clear-water off-shore lake habitats. Experimental work (Koenings *et al.*, 1990) has, however, found that increased suspended sediment concentrations can reduce cladoceran feeding efficiency significantly, owing to considerable overlap between the sizes of their algal food and inorganic particles in suspension. Increased turbidity has thereby been shown to enhance the dominance of rotifers over cladocerans in lakes as the former are generally more selective feeders and can avoid ingesting large volumes of sediments which reduce the carbon ingestion rate of indiscriminate filter-feeding cladocerans (Kirk, 1991a). Highly variable tolerance to high suspended sediment concentrations has, however, been found within some groups, including the Cladocera. A number of ciliates (Jack & Gilbert, 1993; Jack *et al.*, 1993), rotifers (Kirk & Gilbert, 1990) and daphnids (Schulze *et al.*, 2006) are highly sensitive to increased suspended sediment concentrations while others have been demonstrated to be relatively tolerant, showing strong competitive release in turbid conditions. Further, increased turbidity, by providing a refuge from fish predation in low-light conditions, has also been shown experimentally to modify zooplankton diel migration patterns significantly (Mimer & Stein, 1993), which may further drive the competitive release of sediment-tolerant zooplankton taxa.

In addition to modifying the structure of zooplankton assemblages directly, significant alterations can also be an indirect consequence of increased water column turbidity. Experimental work in the field (Cuker, 1993) has, for example, shown that increased concentrations of suspended sediments can either enhance or reduce the abundance of zooplankton, depending upon the structure of the lake food-web. Where planktivorous fish (*Lepomis macrochirus* and *L. cyanellus*) were present, Cuker (1993) found that the abundance of zooplankton was reduced by a factor of four when suspended sediment concentrations were increased,

Table 1. Direct and indirect effects of increased sediment loads on benthic invertebrates.

Description	References
Reduced feeding rates	Grazers: Broekhuizen <i>et al.</i> (2001); Donohue & Irvine (2004b); Peeters <i>et al.</i> (2006) Filter feeders: Loosanoff & Tommers (1948)
Increased mortality	Ellis (1936); Broekhuizen <i>et al.</i> (2001); Gilmour (2002); Donohue & Irvine (2003, 2004b)
Lower metabolic rates	Aldridge <i>et al.</i> (1987)
Reduced viability of eggs	Harrison & Farina (1965)
Decreased growth rates	Broekhuizen <i>et al.</i> (2001); Peeters <i>et al.</i> (2006)
Enhanced production of pseudofaeces by filter feeders	MacIsaac & Rocha (1995)
Decreased quantity and quality of food	Grobbelaar (1985); Graham (1990); Quinn <i>et al.</i> (1992); McIntyre <i>et al.</i> (2005); Peeters <i>et al.</i> (2006)
Increased incidence of infection and infestation	Lemly (1982); McIntyre <i>et al.</i> (2005)
Clogging of interstices and interference with oxygen availability	Chutter (1969); Ciborowski <i>et al.</i> (1977); Lemly (1982); Radwell & Brown (2006); Bo <i>et al.</i> (2007)
Decreased connectivity among appropriate habitat patches	Cohen (1995)
Alterations to habitat structure and reduced habitat heterogeneity	Chutter (1969); Hynes (1970); Boles (1981)

while in treatments with piscivorous fish (*Micropterus salmoides*) present, zooplankton abundance was greater when exposed to added sediments. Cuker (1993) concluded that the added sediments weakened the link between visual fish predators and the chaoborid invertebrate zooplanktivores *Chaoborus albatus* and *C. punctipennis*, which, in turn, strengthened the effect of predation by chaoborids on the zooplankton. This had the effect of not only altering the abundance of zooplankton, but also changed community composition considerably; only the larger chaoborid instars were affected by sediment addition owing to selective predation by fish on larger individuals, rotifers were largely unaffected by sediment addition as they were mostly preyed upon by smaller chaoborid instars.

A number of studies (e.g. Arruda *et al.*, 1983; McCabe & O'Brien, 1983; Gliwicz, 1986; Geddes, 1988; Pollard *et al.*, 1998) have found zooplankton populations in inorganically turbid waters to be similar to those in clear-water lakes. In nutrient-rich turbid waters, suspended clay-organic-bacteria aggregates may provide a hugely important food subsidy to zooplankton and can shift the competitive advantage back to indiscriminate filter-feeders such as the Cladocera (Gliwicz, 1986; Jarvis, Hart & Combrink, 1987; Cuker & Hudson, 1992). Further, laboratory experiments (Arruda *et al.*, 1983) have shown that suspended clay-organic-bacteria aggregates can provide as nutritious a source of food for daphnids as yeast or algae. Moreover, ingestion of these aggregates by zooplankton has been shown to reduce the turbidity of the water column significantly by increasing the sedimentation rate of particles in suspension through their aggregation into larger particles as faeces (Gliwicz, 1986).

(4) Benthic invertebrates

Benthic invertebrates play a highly important role in the food web of lakes and in the sequestration and recycling of

materials (Kolodziejczyk, 1984a, b; Underwood, 1991; Schindler & Scheuerell, 2002). Increased sediment loads, by increasing both inorganic turbidity of the water column and rates of sedimentation of inorganic particles onto the lakebed, have been shown to have a number of significant direct and indirect impacts on benthic invertebrates (Table 1). Further, in streams, benthic assemblages have been shown to be impacted more negatively by increased sediment loads than either planktonic or nektonic assemblages (Iwata, Nakano & Inoue, 2003).

Field studies in lakes (Lloyd *et al.*, 1987; Alin *et al.*, 1999; Donohue, Verheyen & Irvine, 2003; Donohue & Irvine, 2004a) have found that increases in sediment loading tend to reduce the abundance of benthic invertebrate assemblages considerably. Moreover, significant alterations to their taxonomic composition have also been found (Sallenave & Barton, 1990; Hornbach *et al.*, 1993; Alin *et al.*, 2002; Eggermont & Verschuren, 2003; Carew *et al.*, 2007). These alterations frequently include considerable reductions in species richness (Cohen *et al.*, 1993; Alin *et al.*, 1999; Donohue *et al.*, 2003; Donohue & Irvine, 2004a). In addition, Donohue *et al.* (2003) found that benthic invertebrate communities in Lake Tanganyika (Africa) showed extremely low resistance to and resilience after (*sensu* Harrison, 1979; Pimm, 1991; Power, 1999) experimentally increased sediment loading. Further, recent work by Balata, Piazzini & Benedetti-Cecchi (2007) has found that increased sedimentation of inorganic particles can decrease the variability of benthic communities among sites significantly, probably owing to increased homogeneity of habitat structure.

Both experimental work and field surveys (Donohue & Irvine, 2004b; McIntyre *et al.*, 2005) have found that anthropogenically increased sediment loading can alter the size structure of populations of benthic invertebrates significantly. The observed generally downward shifts in population size distributions were hypothesised to be

a consequence of reductions in the quality and quantity of food, but may also be a consequence of size-specific mortality (Gilmour, 2002; Donohue & Irvine, 2004b). Alterations to the size structure of populations can have significant knock-on effects on both intra- and interspecific interactions, population dynamics (De Roos, Persson & McCauley, 2003) and food-web stability (McCann, 2000).

The particle size of sediments can have a hugely important influence on the nature and scale of the impacts of increased sediment loads on benthic invertebrate assemblages. Impacts of fine sediments have been found to be considerably more detrimental to benthic invertebrates than those of coarser sediments, with finer sediments having a greater negative impact on both survivorship (Donohue & Irvine, 2003) and growth rates (Höss *et al.*, 1999). Fine sediments are also more likely to clog interstices among lakebed sediments which can reduce oxygen penetration (Chutter, 1969; Radwell & Brown, 2006; Heywood & Walling, 2007), alter biogeochemical and microbial processes and affect bioturbators negatively, with consequent indirect effects on other benthic organisms (De Haas *et al.*, 2005; Nogaro *et al.*, 2006).

(5) Fish

Although occasional massive fish mortality has been reported owing to anoxic conditions caused by the resuspension of deposited sediments in shallow lakes (Bruton, 1985), relatively high concentrations of suspended sediments coupled with chronic exposures appear to be required to cause direct mortality in fish (Wallen, 1951; Herbert & Merckens, 1961; Herbert & Richards, 1963; Bruton, 1985; McLeay *et al.*, 1987). Nevertheless, exposure to increased sediment loads may have considerable detrimental effects on fish communities (Table 2), culminating in reduced population sizes (Cordone & Kelley, 1961; Herbert *et al.*, 1961; Peters, 1967; Wilber, 1983; Lloyd, 1985; Rodríguez & Lewis, 1997; Richardson & Jowett, 2002; Mol & Ouboter, 2004), decreased species diversity (Richardson & Jowett, 2002; Mol & Ouboter, 2004) and altered community dynamics and functional characteristics (Berkman & Rabeni, 1987; Rabeni & Smale, 1995; Rodríguez & Lewis, 1997; De Robertis *et al.*, 2003; Donohue *et al.*, 2003; Mol & Ouboter, 2004). Turbidity gradients, which occur regularly during floods as riverine sediment plumes become dispersed and mix with lake water, may, however, also aid fish migration by acting in conjunction with olfactory stimuli to orientate migratory fish through river-fed lakes and reservoirs (Blaber, 1981; Cyrus & Blaber, 1987a, b).

As fish are primarily visual predators, much attention has been given to the effects of inorganic turbidity on their visual perception and foraging activity. In addition to reducing ambient light intensity, turbidity can impair visibility by degrading apparent contrast. Lythgoe (1979) hypothesised that increased turbidity and associated non-image-forming light scatter reduce the visual range of fish considerably by degrading target brightness and contrast. High turbidity levels thus diminish feeding efficiency and, consequently, growth rates of visually predatory fish by

reducing the reactive distance between predators and their prey at the time of detection (Gardner, 1981; Berg & Northcote, 1985; Barrett, Grossman & Rosenfeld, 1992; Gregory & Northcote, 1993; Miner & Stein, 1993; Rowe & Dean, 1998). Decreased reactive distance in turbid waters thus results in smaller volumes of water searched per unit time and reduced encounter rates of both small and large prey (Gardner, 1981; Utne-Palm, 2002). Under moderate turbidity and high ambient light conditions, however, feeding performance and growth rates are frequently higher than those in clear water (Boehlert & Morgan, 1985; Barrett *et al.*, 1992; Miner & Stein, 1993; Bristow & Summerfelt, 1994; Bristow, Summerfelt & Clayton, 1996; Utne, 1997; Utne-Palm, 1999, 2002). This is likely owing primarily to the fact that moderately turbid water can increase the contrast of prey against their background, thus improving their detection under sufficient light conditions (Boehlert & Morgan, 1985; Hinshaw, 1985). The degree of visual prey detection enhancement depends upon the optical and scattering properties of suspended particles, the size and behaviour of the prey and the visual sensitivity of the predator (Utne-Palm, 2002). Because adult piscivores tend to have a larger field of vision, increased turbidity may particularly decrease their prey-detection ability and feeding success (Chesney, 1989; Giske, Aksnes & Fiksen, 1994; Utne-Palm, 2002; De Robertis *et al.*, 2003). By contrast, larval stages and planktivorous fish tend to have a short visual field, and are, therefore less susceptible to contrast degradation, as the effect of turbidity on the detection of close objects appears to be negligible (Utne-Palm, 2002).

Turbid water may provide a refuge from potential predators (Gregory & Northcote, 1993; De Robertis *et al.*, 2003). Visual fish predators tend to avoid turbid areas because of their lowered foraging ability and greater physiological stress while fish with good sensory adaptations to low light are predominant (Rodríguez & Lewis, 1997; Maes *et al.*, 1998). This, in turn, reduces predator avoidance behaviour in turbid areas (Gregory, 1993; Lehtiniemi, Engstrom-Ost & Viitasalo, 2005), while the consequent reduction in energy expenditure can then be invested in foraging for food (Abrahams & Kattenfeld, 1997; Lehtiniemi *et al.*, 2005), resulting in increased rates of feeding and growth (Gregory & Northcote, 1993; Miner & Stein, 1993) and migratory activity (Ginetz & Larkin, 1976).

Impairment of the visual range of fish by increased inorganic turbidity can have important consequences not only for the structure and functioning of fish assemblages but also for the composition of their prey populations, depending on prey size, contrast and behaviour (Utne-Palm, 2002). Both experimental (Vinyard & O'Brien, 1976; Miner & Stein, 1993) and theoretical (Giske *et al.*, 1994) work suggests strongly that increased turbidity increases predation pressure on smaller zooplankton significantly while the risk of predation for larger zooplankton changes little. Gardner (1981) found, however, that the strength of size selectivity of *Daphnia pulex* by bluegill sunfish (*Lepomis macrochirus*) did not vary with turbidity, which suggests that size selectivity was maintained in highly turbid water by active selection upon each encountered individual

Table 2. Direct and indirect effects of increased sediment loads on fish.

Description	References
Reduced survival of eggs and larvae	Turnpenny & Williams (1980); Cambray (1983); Wilber (1983); Reynolds <i>et al.</i> (1989)
Gill damage and increased gill-flaring	Herbert & Merkens (1961); Berg & Northcote (1985); Reynolds <i>et al.</i> (1989); Martens & Servizi (1993); Sutherland & Meyer (2007)
Reduced individual growth rates, decreased maximum size and reduced length at sexual maturity	Herbert & Richards (1963); Sykora <i>et al.</i> (1972); Crouse <i>et al.</i> (1981); Gardner (1981); Wilber (1983); Sigler <i>et al.</i> (1984); Bruton (1985); McLeay <i>et al.</i> (1987); Miner & Stein (1993); Suttle <i>et al.</i> (2004); Sutherland & Meyer (2007)
Increased mortality	Wallen (1951); Herbert & Merkens (1961); Herbert & Richards (1963); Bruton (1985); McLeay <i>et al.</i> (1987); Suttle <i>et al.</i> (2004)
Emigration from affected areas	Sigler <i>et al.</i> (1984)
Impaired feeding activity	Vinyard & O'Brien (1976); Confer <i>et al.</i> (1978); Berg & Northcote (1985); McLeay <i>et al.</i> (1987); Crowl (1989); Gregory & Northcote (1993); Utne (1997)
Induced colour changes	Herbert & Merkens (1961); McLeay <i>et al.</i> (1987)
Instigation of stress responses such as increased blood sugar levels	McLeay <i>et al.</i> (1987); Servizi & Martens (1992)
Increased susceptibility to toxicants	McLeay <i>et al.</i> (1987)
Disrupted migration patterns through avoidance	Bruton (1985); Boubée <i>et al.</i> (1997); Richardson <i>et al.</i> (2001)
Altered territorial behaviour	Berg & Northcote (1985)
Altered dynamics and functional characteristics of communities	Berkman & Rabeni (1987); Rabeni & Smale (1995); Donohue <i>et al.</i> (2003); Mol & Ouboter (2004)
Altered breeding behaviour	Wilber (1983)
Increased incidence of infection	Herbert & Merkens (1961); Alabaster (1972); Servizi & Martens (1991)
Increased risk of injury through increases in aggressive interactions among fish	Suttle <i>et al.</i> (2004)

according to perception of zooplankton size and availability in relation to past encounter rates. Others (Rowe & Dean, 1998; Rowe *et al.*, 2003) have suggested that size selectivity can be maintained in highly turbid waters by means of non-visual predation mechanisms such as the olfactory sense or the lateral line system. Like size, prey mobility can also affect the area stimulated on the predator retina, thus increasing significantly the predator reaction distance for more mobile prey organisms (Eggers, 1977; Utne-Palm, 1999). Prey motion, for example, more than doubled the maximum distance at which phantom midge larvae (*Chaoborus* sp.) could be detected by white crappie (*Pomoxis annularis* Rafinesque) (Wright & O'Brien, 1982).

IV. AN ECOSYSTEM PERSPECTIVE

The increased loading of lakes with inorganic sediments has substantial overall negative implications for the diversity, abundance and productivity of their biotic assemblages. Even though some factors, including, for example, the availability of phosphorus (e.g. Cuker, 1987; Cuker *et al.*, 1990; Burkholder & Cuker, 1991; Cuker & Hudson, 1992) or DOC (e.g. Arruda *et al.*, 1983; Cuker & Hudson, 1992; Lind *et al.*, 1994), may mitigate impacts at some trophic levels, ecological functioning and assemblage composition are likely to be altered considerably. Further, the homogenisation of biotic assemblages with increased sediment loading (Balata *et al.*, 2007), owing to reductions in habitat

heterogeneity (*cf.* Passy & Blanchet, 2007) or increased environmental 'harshness' (Chase, 2007), could have considerable ecological and evolutionary consequences (Olden *et al.*, 2004). The direct and indirect effects of increased sediment loads could, therefore, have dramatic consequences for the biological diversity, productivity and ecological functioning of lakes globally.

The physical and chemical characteristics of sediments, in particular their particle size distribution, are key determinants of the impacts of increased sediment loading on lakes (Fig. 1). Sediment particle size distribution governs not only the nature of impacts, by determining the extent of water column turbidity, sediment deposition and the bacteria-clay-organic aggregate heterotrophic pathway, but also their spatial coverage. Fine sediment particles stay in suspension both for longer periods of time and for greater distances from their source, thus impacting considerably larger areas than coarse sediments. Further, fine sediments are more likely to become resuspended in windy or otherwise turbulent conditions, particularly in shallow lakes, and can adsorb substantially greater quantities of nutrients and other substances to their surfaces. Although the transport of sediments by snowmelt or wind is important in some lakes, the majority of sediment entering most lakes is transported by influent rivers. Impacts of increased sediment loads are, therefore, likely to be manifested most strongly in the littoral zones of lakes close to the mouths of rivers, where both sedimentation rates and turbidity are maximal. Both biological and habitat diversity, however, also tend to be greatest in the lake littoral (e.g. Wetzel, 2001; McCabe & Cyr,

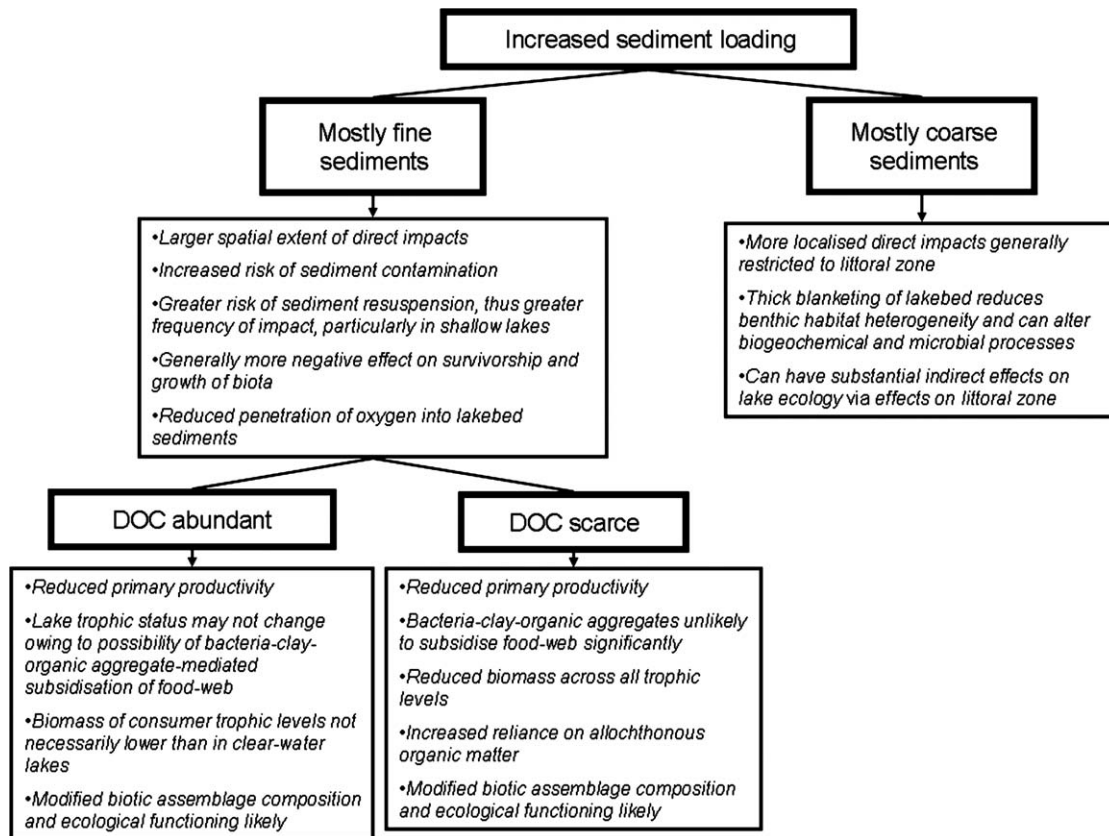


Fig. 1. The importance of sediment particle size in determining the impacts of increased sediment loads on lakes. DOC, dissolved organic carbon

2006; Muirhead, Ejsmont-Karabin & MacIsaac, 2006; Stendera & Johnson, 2008). Moreover, although the direct effects of coarse sediments are more likely to be relatively localised, impacting mostly benthic processes and biota in the littoral zone, off-shore process may be affected indirectly by the impacts of increased loading with fine or coarse sediments on the littoral, *via*, for example, the alteration of biogeochemical and microbial processes at the sediment-water interface (*cf.* Brunke, 1999; Rehg *et al.*, 2005) or because many organisms utilise the littoral zone for recruitment (Hansson, 1996; Graynoth, 1999; Brunberg & Blomqvist, 2003), refuge from predation (Gliwicz, Slon & Szykarczyk, 2006; Sass *et al.*, 2006; Stoll *et al.*, 2008) or as feeding grounds for juveniles (Okun, Lewin & Mehner, 2005; Okun & Mehner, 2005; Dembski *et al.*, 2008).

Establishment of the bacteria-clay-organic aggregate heterotrophic pathway, by effectively bypassing the 'microbial loop' and increasing significantly the efficiency of DOC recycling and uptake by consumers, can provide a highly important subsidy to lake food-webs and may mitigate some of the impacts of increased sediment loading. Lind *et al.* (1994) attributed, for example, the considerably greater productivity of fish in Lake Chapala than that predicted by models based on phytoplankton productivity or biomass to the subsidisation of the food-web by this alternative heterotrophic pathway. Fisheries productivity in the lake remained, however, substantially lower than that predicted

by morphoedaphic models. Further, even if biotic productivity could be subsidised to some extent by this pathway, the composition and functioning of biotic communities would be expected to be modified considerably in lakes with high loading of sediment. Moreover, the pathway would likely subsidise primarily the open-water food-web, while providing little moderation of the impacts of increased sediment loading for the benthos. Further research is needed to quantify the nature and scale of these changes and their effects on biotic diversity throughout the lake ecosystem.

V. CONCLUSIONS

(1) Although some factors, including sediment mineralogy, particle size and the availability of nutrients may moderate to some extent the impacts of increased sediment loads on lake ecosystems, biotic assemblage composition remains likely to be modified. The widespread increases in sediment loading to lakes in recent decades have, therefore, profound implications for the conservation and management of global aquatic biological diversity. This is particularly pertinent when considering that extinction rates for freshwater fauna have been measured as five times greater than those for terrestrial fauna (Ricciardi & Rasmussen, 1999). Further, reductions in fisheries productivity of both lakes and reservoirs owing to high

sediment loading can have substantial negative effects not only on tourism and local economies (e.g. Clarke *et al.*, 1985; Robertson & Colletti, 1994), but, more importantly, on people that rely on them for food.

(2) Little remains known about how increased sediment loads interact with other globally important anthropogenic pressures on lakes. High sediment loading would probably, for example, have considerable influence on the outcome of invasion by exotic species. Further, by affecting heat budgets and the transmission of light through the water column, increased sediment loads could interact significantly with, and may exacerbate considerably, the impacts of climate change on lakes.

(3) In order to maximise our ability to manage lake ecosystems and conserve their biological diversity and ecological functioning effectively, future research is necessary to investigate the nature and strength of the interactions between increased sediment loading and other globally important anthropogenic pressures.

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