Fisheries and Oceans Canada

Pêches et Océans Canada

Ecosystems and Oceans Science

Sciences des écosystèmes et des océans

Freshwater Cage Aquaculture: Ecosystems Impacts from Dissolved and Particulate Waste Phosphorus

Megan K. Otu[1], Dominique P. Bureau[2], Cheryl L. Podemski[1]

[1] Fisheries Ecology Section
Central and Arctic Region
Fisheries and Oceans Canada
501 University Crescent
Winnipeg, MB R3T 2N6

[2]Fish Nutrition Research Laboratory
Department of Animal and Poultry Science
University of Guelph
Guelph, ON N1G 2W1

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Correct citation for this publication:

Otu, M.K., Bureau, D.P., and Podemski, C.L. 2017. Freshwater Cage Aquaculture: Ecosystems Impacts from Dissolved and Particulate Waste Phosphorus. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/059. v + 55 p.

TABLE OF CONTENTS

ABSTRACT

Open net-pen finfish aquaculture operations in freshwaters release waste directly into aquatic environments. These wastes contain phosphorus (P) in the form of particulate P (e.g., faeces and uneaten feed) or dissolved P (e.g., soluble P released from feed, faeces, and metabolic excretions of the fish). Phosphorus is the nutrient most often limiting primary production (i.e., photosynthetic rates and biomass) in freshwater and, thus, anthropogenic additions of P raise concerns for potential impacts on lake productivity. Assessing and mitigating the adverse effects of P loading is critical to proper management of freshwater resources.

This Canadian Science Advisory Secretariat (CSAS) review does not constitute a formal risk assessment of P inputs from cage aquaculture operations in Canadian freshwaters, but instead, synthesizes the current state of science with regards to two key components necessary to understanding the potential for effects of P waste from aquaculture: the estimated P loads per tonne of Rainbow Trout (*Oncorhynchus mykiss* Walbaum) produced and the lake response to such P loads. Estimation of P release from cage aquaculture has been best accomplished through bioenergetics models and one such model has been designed for and tested in commercial Rainbow Trout cage culture operations within Canada. The complex physical, chemical, and biological interactions that may occur within the P cycle mean that impacts of P loading from aquaculture or other anthropogenic sources are challenging to predict. The complexities of the P cycle are particularly well documented in the Laurentian Great Lakes, and here we have drawn on this literature. Attempts to better predict the effect of anthropogenic P loads have prompted the development of water quality models to predict P concentrations; P fractionation techniques to assess bioavailable P fractions in particulate form; whole lake mass balances to quantify the P loss to sediments; and total P loading estimates from the catchment to contextualize P loads in an area of interest.

Aquaculture en cage en eau douce : impacts écosystémiques des déchets de phosphore dissous et sous forme de particules

RÉSUMÉ

Les activités de pisciculture en cage en filet dans les milieux d'eau douce relâchent des déchets directement dans l'environnement aquatique. Ces déchets contiennent du phosphore (P) sous la forme de particules (p. ex. fèces et aliments non consommés) ou de phosphore dissous (p. ex. phosphore soluble émanant de la nourriture, des fèces et des excrétions métaboliques des poissons). Le phosphore est le nutriment qui limite le plus souvent la production primaire (c.-à-d. le rendement photosynthétique et la biomasse) dans l'eau douce et, par conséquent, les apports anthropiques de phosphore soulèvent des préoccupations concernant les répercussions possibles sur la productivité des lacs. Il est essentiel d'évaluer et d'atténuer les effets nocifs de la charge en polluants phosphorés pour gérer adéquatement les ressources d'eau douce.

Cet examen du Secrétariat canadien de consultation scientifique (SCCS) ne constitue pas une évaluation officielle des risques des apports en phosphore provenant des activités de pisciculture en cage en filet dans les eaux douces canadiennes, mais résume plutôt la situation actuelle de la science concernant deux composantes clés nécessaires pour comprendre les effets possibles des déchets phosphorés de l'aquaculture : les charges estimées de phosphore par tonne de truite arc-en-ciel (*Oncorhynchus mykiss* Walbaum) produites et la réaction du lac à l'égard de ces charges. L'estimation des rejets de phosphore des activités de pisciculture en cage se fait mieux par des modèles bioénergétiques, et l'un de ces modèles a été conçu pour les activités commerciales d'élevage en cage de truite arc-en-ciel au Canada et mis à l'essai dans le cadre de ces activités. Les interactions physiques, chimiques et biologiques complexes pouvant survenir dans le cycle du phosphore signifient que les répercussions de la charge de phosphore provenant de l'aquaculture ou d'autres sources anthropiques sont difficiles à prévoir. La complexité du cycle du phosphore est particulièrement bien documentée dans les Grands Lacs laurentiens, et nous nous sommes fondés sur ces renseignements. Pour tenter de mieux prévoir l'effet des charges anthropiques de phosphore, nous avons élaboré des modèles de qualité de l'eau visant à prévoir les concentrations de phosphore, des techniques de fractionnement du phosphore en vue d'évaluer le phosphore biodisponible sous forme de particules, des bilans massiques de l'ensemble du lac pour quantifier la perte de phosphore par les sédiments, et des estimations de la charge totale de phosphore du bassin versant afin de mettre en contexte les charges de phosphore dans une zone d'intérêt.

INTRODUCTION

Open net-pen finfish aquaculture operations in freshwaters release waste directly into aquatic environments. These wastes contain phosphorus (P) in the form of particulate P (e.g., uneaten feed and faeces) or dissolved P (e.g., soluble P released from feed, faeces and metabolic excretions of the fish). Phosphorus is the nutrient most often limiting primary production (i.e., photosynthetic rates and biomass) in freshwater. Additions of P to freshwater can have diverse effects on the ecosystem, such as increased primary productivity, changes in algal community composition and bottom-up enhancement of fisheries. Excessive P additions to aquatic ecosystems have historically been associated with nuisance algal production, deep-water oxygen declines (hypoxia) and fish kills (Beeton 1965). There are a few North American aquaculture examples that have raised concerns regarding the risk that the aquaculture industry may pose to receiving waters (e.g., Axler et al. 1997, Boyd et al. 2004). Since commercial fish aquaculture production is predicted to increase as the global demands for protein production increase (Delgado et al. 2003) and production is intertwined with water quality, concerns for the sustainability of the industry need to be addressed (Yan 2005).

Freshwater cage aquaculture, like all animal husbandry practices, inherently produces P-containing waste. Currently, there is a good understanding of Rainbow Trout (*Oncorhynchus mykiss* Walbaum) metabolism and digestion of fish feeds (Coloso et al. 2003, Hua and Bureau 2006, Azevedo et al. 2011). Bioenergetics models designed for Rainbow Trout are available to predict P released in both particulate and dissolved forms (Cho and Bureau 1998, Bureau et al. 2003, Bristow et al. 2008, Bouwman et al. 2013). The P digestibility, which affects the forms of P released from fish, has been characterized for commercial stocks of freshwater Rainbow Trout (Hua and Bureau 2006) and in commercial composite feeds (Cho and Bureau 1997, Coloso et al. 2003, DFO unpubl. data).

Although characterization of waste release is well known, literature on the ecological effects of waste release in freshwaters is sparse. The effects of P from freshwater aquaculture in Canada have not been reviewed previously. Freshwater aquaculture is far less studied than marine operations, and processes involved in P cycling in the marine environment differ substantially (e.g., tidal flows, water volume, nutrient limitations, decomposition processes). Different forms of P released into the freshwater environment affect the fate of P and a number of studies have attempted to predict resulting P water concentrations (McDonald et al. 1996, Axler et al. 1997, Yokom et al. 1997, Håkanson et al. 1998). Phosphorus loading from freshwater aquaculture has been quantified in the context of whole lake P budgets, predominantly in small basins (Håkanson and Carlsson 1998, Hamblin and Gale 2002, Bristow et al. 2008, Milne 2012). Few have quantified the effect of P loading from cage aquaculture on water quality (Reid and Moccia 2007, Bristow et al. 2008, Azevedo et al. 2011, Milne 2012). There is still little known today of the bioavailability of P released from aquaculture operations for primary production. However, there are preliminary estimates of the chemical fractionation and thus bioavailability of P in wastes (DFO unpubl. data).

The complexity of P cycling is such that models to predict the ecosystem response to aquaculture P loading need to be adaptable to site specific conditions and require the integration of limnology, nutrition, and hydrodynamic sciences. This deficiency hinders the ability to accurately predict the fate of P waste from freshwater aquaculture or assess the environmental risks. This Canadian Science Advisory Secretariat (CSAS) review does not constitute a formal risk assessment of P inputs from cage aquaculture operations in Canadian freshwaters. By addressing the following objectives, this review strives instead to provide a synopsis of the current state of the science with regards to P loading from freshwater cage aquaculture, an overriding concern for the sustainability of the industry.

OBJECTIVES

1. Review the importance of P to the freshwater environment, and in particular those Canadian ecosystems where cage aquaculture is prevalent.

2. Review what is known of the cycling and fate of the chemical forms of P in the freshwater environment, focusing on the chemical forms of P that are associated with finfish cage aquaculture activities.

3. Review what is known of the type and amounts of P inputs from freshwater cage farms, including a review of estimation methods, and place inputs in context of other natural and anthropogenic sources.

4. Review what is known of methods to predict, manage, and mitigate effects of cage aquaculture P in the freshwater environment.

5. Assess risk of P inputs from the cage aquaculture industry to Canadian freshwater environments.

6. Identify important knowledge gaps that affect our ability to assess the risk that P release from the cage aquaculture industry poses to freshwater environments.

Due to the nature of the CSAS request for advice, the scope of this paper is limited to a consideration of P wastes from cage aquaculture. There are other non-P related environmental considerations with regards to cage aquaculture operations that are outlined in Yan (2005) that are not addressed in this document. We do not discuss P waste from land-based fish culture operations because they are regulated differently. Land-based facilities may represent a point source discharge to water bodies in a manner similar to other industrial point sources, they may use treatment facilities to manage P in effluent, or they may dispose of effluent on land in a manner similar to terrestrial livestock production.

BACKGROUND

THE PHOSPHORUS CYCLE

Phosphorus is a non-metallic chemical element on the periodic table with the symbol (P) and atomic number 15. Phosphorus is the 11th most abundant element in the Earth's crust and it is an essential component of all life forms on Earth.

In nature, P usually exists as part of a phosphate molecule (PO_4) and pure, "elemental" P is extremely rare (Westheimer 1987). Phosphates in biological systems occur as organic phosphate and inorganic phosphate. Organic phosphate consists of a phosphate molecule associated with a carbon-based molecule such as nucleotides, phospholipids, coenzymes, deoxyribonucleic acid (DNA), and ribonucleic acid. Inorganic P is generally found as orthophosphates ($H_2PO_4^-$, HPO_4^{2-}, and PO_4^{3-}), although more complex inorganic phosphate compounds, such as "condensed phosphates" or "polyphosphates," can also be found in high concentrations under certain conditions.

For the sake of simplicity, acknowledging that there are many forms of P, the remainder of this document will use "P" to indicate a phosphate molecule unless otherwise specified.

Sources of P to lakes

There are a number of naturally occurring and anthropogenic driven processes that contribute P to lakes (Figure 1). Dissolved P is released naturally through chemical weathering of rocks and particulate P through physical weathering of rocks. The chemical release of P from rocks

accelerates with acid rain. Decay of terrestrial organic matter results in the release of dissolved P in the form of inorganic P and organic compounds and/or particulate P in the form of P bound to or contained within iron hydroxides, carbonates, cellular components, and inorganic clays (Hendricks and White 2000). Dissolved P commonly adsorbs to particles such as silt washed into lakes from the catchment.
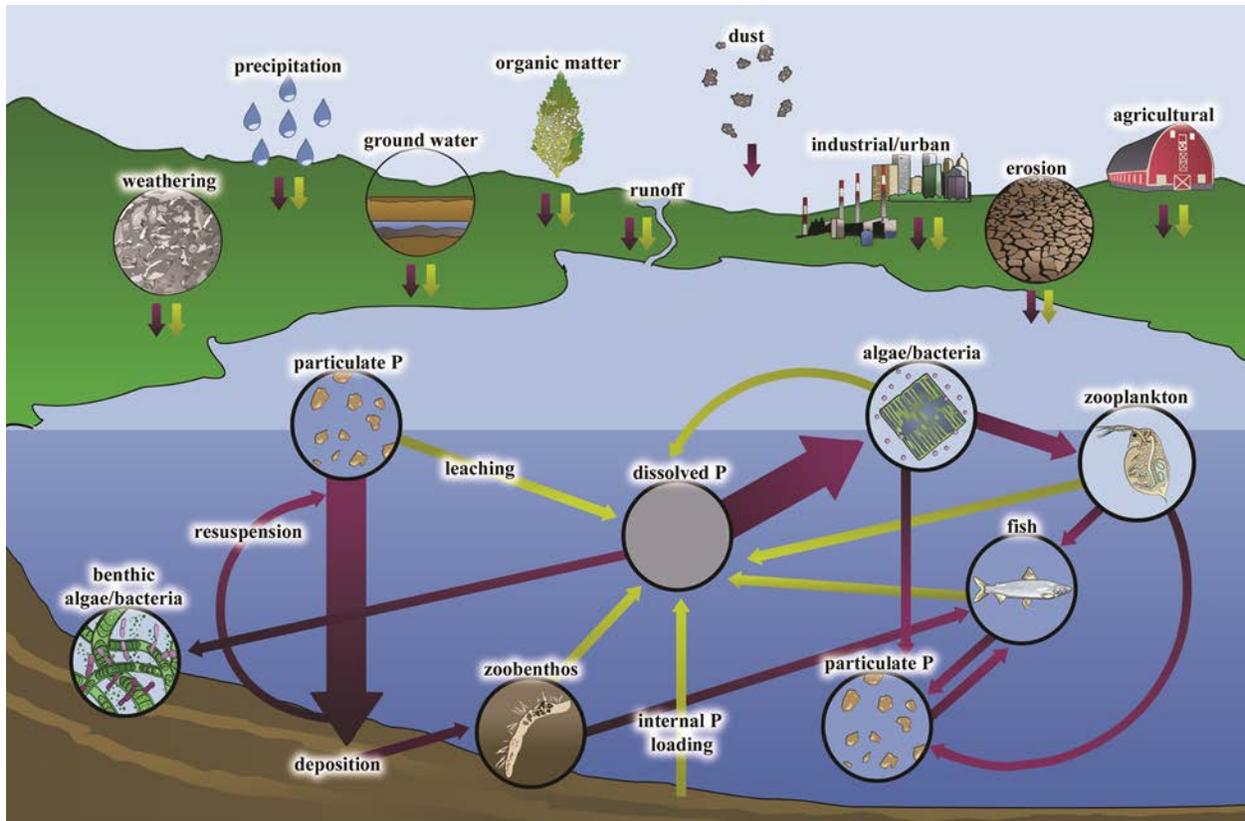

Figure 1. Diagram of phosphorus (P) loads from the catchment and internal P sources to lakes where P can be transformed through biotic and abiotic interactions. Arrows indicate the flux from one P pool to another P pool. Arrows in purple are the particulate P transformations and arrows in green are dissolved P transformations (Graphics by Aldo F. Rios Martinez).

In addition to weathering, processes that lead to P loading of lakes are hydrological (e.g., precipitation, ground water, runoff, and river input) and anthropogenic (e.g., sewage effluent, animal husbandry waste, soil erosion, fertilizer, dust pollution, and industrial waste; Carpenter et al. 1998, Kalff 2002). These external sources of P are transported from the atmosphere or land to rivers and lakes as particulate-bound or dissolved P forms.

Essential nutrients, N and P, are often added to crops by way of either synthetic fertilizers or manure from livestock production to enhance yields. These nutrient applications can exceed crop uptake (Sharpley 1995) and soils have a limited capacity to retain P (e.g., as iron, calcite, clay, and aluminum-bound P; Holtan et al. 1988). Once soil capacity has been exceeded, it can take years to deplete soil P content during which time excess P continues to be released through runoff and seepage (McCollum 1991). The timing of the application of soil amendments and the solubility of P contained within can also affect the amount of P exported because heavy rains accelerate transport of P via surface runoff (Withers et al. 2001).

Certain practices reduce the relative release of particulate P to dissolved P; examples include the use of secondary P treatment of sewage, bank reinforcement, and maintained or restored

riparian zones. Historically, cultivation of highly erodible soils and destruction of riparian buffers led to high particulate P loads downstream. Recently, as a result of practices to improve soil conservation, P loading from the Ohio tributaries of the Great Lakes has changed from predominately particulate P loads originating from topsoil erosion to largely dissolved P loads (Joosse and Baker 2011). In cold, dry climates like the Canadian prairies, snowmelt dominates the transport of dissolved nutrients from croplands (Tiessen et al. 2010). Cultivation techniques like conservation tillage (i.e., leaving the previous year's stubble and stalks on the land during seeding) were once believed to reduce P export from soil erosion, but more recent research shows these practices do not mitigate dissolved P transport during snowmelt runoff in northern temperate zones (Tiessen et al. 2010, Kleinman et al. 2011). Changing P loads from runoff to large lakes (e.g., Lake Winnipeg; McCullough et al. 2012 and Lake Simcoe; Palmer et al. 2013) and flooded agricultural fields (Cade-Menun et al. 2013) may become an even greater concern in P management strategies as climate patterns change.

An additional source of P to the water column is the internal pool of P contained within the lake and its sediment (Nürnberg 1984, Søndergaard et al. 2003). Phosphorus in the water column is found in both dissolved and particulate forms, and biological demand for P often dictates the relative proportions and turnover time (calculated as the P pool in the water column divided by the rate of uptake of radioactive $P^{32}O_4$ by phytoplankton and bacteria; Rigler 1956). Dissolved and particulate P in the pelagic zone are released from biota through decomposition of settling particulate matter, and this P can be recycled in a matter of minutes (Rigler 1964). A greater proportion of P is retained within the sediment than in the water column, with sediment P concentrations measuring at least an order of magnitude greater. Surface sediments have an upper active layer in which biota and biogeochemical reactions can alter the form of P, providing either a source or a sink of P to the overlying waters, while lower layers represent a permanent sink. Over an inter-annual timescale the net flux of P is to the sediments.

Phosphorus transformations in lakes

Phosphorus in freshwaters naturally occurs in concentrations from 1 µg L^{-1} to > 200 mg L^{-1} (Wetzel 2001). The catchment geology strongly influences background P concentrations from P-rich volcanic lakes that have naturally high P concentrations (e.g., 250 µg L^{-1} soluble reactive P; Murphy et al. 1983) to granitic alpine lakes that have naturally low P concentrations (e.g., < 5 µg L^{-1} total P; Leavitt et al. 1994), although both of these examples are rare. Temperate lakes frequently measure around 5–10 µg L^{-1} in late summer (Guy et al. 1994). Once in lakes, P can be transformed through many processes that dictate the water P concentrations.

Phosphorus concentrations in the water column often exhibit temporal trends in deep, temperate, dimictic lakes (i.e., with spring and fall turnover of the water column). Total P concentrations are elevated at ice off in the springtime with inputs from external sources of P (i.e., P in runoff, snowmelt, and atmospheric deposition; Wetzel 2001) and under certain conditions internal loading of P (Søndergaard et al. 2005). With spring turnover and low organic matter deposition, oxygenation of the sediment-water interface facilitates the sorption of P to particulates/substrates (Søndergaard et al. 2005). After spring turnover and into summer, total P (TP) concentrations in the surface waters (0–10 m) may decline due to sedimentation of particulate P and settling of spring phytoplankton (Guy et al. 1994). Midsummer, TP may continue to decline, but the soluble reactive P (SRP) fraction can increase slightly with enhanced rates of photosynthesis (Kalff 2002) and zooplankton grazing pressure that can regenerate SRP (Mazumder et al. 1992). During the late summer months and into the fall, P may become resuspended or released from deep anoxic waters by deep water column mixing in a process known as internal P loading, (Nürnberg 1984, Søndergaard et al. 2003). The oxygen supply to the deep water is largely dependent on the changing seasons which control the

annual thermal mixing regime and organic matter deposition trends. There are also temperate lakes that exhibit little variation in TP seasonally (Johengen et al. 1994). Changing concentrations of P in lakes is the result of a combination of abiotic and biotic factors.

Abiotic factors dictating P concentrations in lakes

Several abiotic processes affect the concentrations of P in lakes, such as water column mixing (i.e., turnover events), rates of water discharge (i.e., flushing time), particulate binding (i.e., adsorption, coagulation, and sedimentation), and physiochemical properties of the sediment-water interface (i.e., oxic versus anoxic pore water space; Wetzel 2001).

Flushing rate is the total volume of lake water relative to the rate of net outflow, and this rate is fundamental when considering the cumulative effects of P loads on lakes (Dillon 1975, Vollenweider 1975). An increase in external P loading to a lake does not necessarily translate to an increase in TP or primary production in the water column because the hydrological regime (i.e., water volume, inflow, and outflow) needs to be factored into the P budget (Dillon 1975). Dillon (1975) examined the P budget of Cameron Lake, located on the Canadian Shield in Ontario, and reported that although the P loading was high for a lake of that depth and should have resulted in eutrophic conditions, the average TP concentrations were only 10.2 µg L^{-1} and maximum chlorophyll a (Chla) concentrations were 2.6 µg L^{-1}, which is more characteristic of oligotrophy. He attributed this to a very high flushing rate. Dillon (1975) pointed out that similar high flushing rates were not uncommon in the larger Great Lakes drainage system and advised that flushing must be considered in future P loading models. Schindler et al. (1971) were the first to explore P additions to a lake-wide nutrient budget in experimentally eutrophied Lake 227 at the Experimental Lakes Area (ELA) in Ontario. Schindler et al. (1987) reported that changes in precipitation patterns that increased lake retention time from an average of 2.3 years during 1969–1974 to 4.1 years during 1975–1982 was responsible for greater P accumulation in the water column of Lake 227 during the later years of the experiment.

In water, P has a high affinity for iron, aluminum, or manganese hydroxides, calcite, aragonite, and clay minerals and, thus, can be quickly bound to particulate form. When oxygen is saturated at the sediment-water interface, redox potentials range from 710 to 800 mV and iron or Fe (III) and manganese or Mn (III and IV) precipitate with phosphate. In Precambrian Shield lakes, there is a high retention of P in sediments because there is an abundance of iron available in sediments (17–31 times more iron relative to suspended organic matter; Nürnberg and Dillon 1993, Dillon and Molot 2005). At the oxygenated sediment-water interface there is typically a settling of Fe and Mn bound P and in anoxic surface sediments an upward diffusion of Fe, Mn and P.

Under anoxic conditions with low redox potential (-100 to -710 mV), P bound to Fe or Mn disassociates into soluble P and soluble Fe (II) or Mn (II) (Hendricks and White 2000). This fraction is called redox-sensitive P and has the potential to be rapidly mobilized should the lake bottom become anoxic. Nürnberg (1984, 1988) reported that internal P loading from anoxic sediments in mesotrophic lakes averaged 12 mg P m^{-2} d^{-1} and in eutrophic lakes averaged 38 mg P m^{-2} d^{-1}. These P dissolution rates are applicable only to the lake bottom area experiencing anoxia. Internal P loading in oligotrophic lakes can occur from anoxia but at much slower rates of 1.5–2.63 mg m^{-2} d^{-1} (Nürnberg et al. 1986). Anoxia, however, is not a necessary condition for P remobilization when bound to iron in sediments because sulfide, too, can play a role (Boström and Pettersson 1982, Søndergaard et al. 2001). Sulfide is the product of microbially-mediated sulfate reduction and therefore sulfide-mediated P release is discussed in the section on biotic factors.

Changing weather patterns can affect both external and internal P loading rates, depending on the seasonal or inter-annual variability and catchment size (Soranno et al. 1997). With late

summer thermal stratification in small, eutrophic water bodies, there is often development of anoxia in the hypolimnion (a cell of deeper water that is thermally isolated from the surface water). Hypolimnetic anoxia can also occur in less productive lakes as a result of incomplete turnover (Wagner and Adrian 2009, Taranu et al. 2010) and incomplete turnover can be related to rapidly warming spring weather that leads to quick set-up of thermal stratification and to less wind during periods of isothermal conditions. Phosphorus dissolution from sediments is possible when deep water anoxia occurs, but the amount of dissolution is also dependent on a number of lake characteristics like sedimentation rates (i.e., rapid burial impedes release of P back to the water column), organic matter composition, iron to sulfide ratios, and nitrate concentrations (Gächter and Müller 2003). During stratification, the majority of the dissolved deep-water P remains in the hypolimnion but a small fraction can become entrained in the epilimnion through diffusion across the thermal barrier (Holdren and Armstrong 1980, Soranno et al. 1997). Greater amounts of P can become entrained during stormy, cool years when stratification is weakly established (Soranno et al. 1997).

Biotic factors dictating phosphorus concentrations in lakes

Many biotic interactions influence the concentration of P in water. The most prominent biotic process is the rapid uptake and assimilation of P into living tissue (Hendricks and White 2000). Phosphorus is often the growth limiting nutrient in freshwater and marine environments (Kalff 2002, Schindler et al. 2008) and dictates the production of algal biomass. The high biotic demand for P generally means that soluble P does not build up over time in the water column, but rather tends to be barely detectable. Low nutrient lakes can have P turnover times of minutes (Rigler 1964, Hudson et al. 2000). Dissolved P uptake is dominated by bacteria under many conditions, including in the epilimnion of stratified temperate lakes. Phosphorus is in greatest demand in the euphotic zone, defined as depth to which 1 % of surface light intensity penetrates, where phytoplankton can access light energy to effectively photosynthesize at rates greater than respiration rates. With very high competition for P, some phytoplankton collect reserve P stores or strip P from dissolved organic molecules using alkaline phosphatase, an enzyme that hydrolyzes phosphate for uptake from organic P sources. Particulate P within phytoplankton is recycled when cells are consumed and excreted by grazers, lysed by viruses, or senesce.

Phosphorus availability typically dictates in-lake primary productivity. In the field of limnology, lakes are classified on the basis of their productivity, known as the trophic status. Three basic categories are used:

1) oligotrophic lakes which are low in nutrients,

2) mesotrophic lakes with moderate nutrient concentrations, and

3) eutrophic lakes high in nutrients (Vollenweider 1968, OECD 1982).

Lake trophic status is categorized based on the combination of several limnological metrics (Table 1), the most decisive being total phosphorus (TP) concentrations. This lake classification scheme frames our understanding that changes to P can have whole ecosystem effects.

Table 1. Characteristic features in lakes of different trophic categories based on OECD (1982).

Trophic level	Primary Production (gCm^{-2}y^{-1})	Secchi (m)	Chl-a (µg L^{-1})	Algal Vol.* (gm^{-3})	TP** (µg L^{-1})	TN** (µg L^{-1})	Dominant Fish
Oligotrophic	< 30	> 5	< 2.5	< 0.8	4–10	< 350	trout, whitefish
Mesotrophic	25–60	3–6	2–8	0.5–1.9	10–30	300–500	whitefish, perch
Eutrophic	40–200	1–4	6–35	1.2–2.5	30–100	350–600	perch, roach
Hypereutrophic	130–600	0–2	30–100	2.1–20	> 80	> 600	roach, bream

* mean value for the growing period (May–October)
** mean value for the spring turnover circulation period.

In North America during the 1970s, anthropogenic P additions to lakes were causing widespread eutrophication and the need to manage P loading spurred the development of predictive P models based on empirical evidence. Eutrophication is a nutrient enriched state that is characterized by high levels of organic matter production. Initially, Dillon and Rigler (1974) proposed a predictive model based on a linear regression through the log-log relationship between spring TP and average summer Chl*a* concentrations. Phosphorus concentrations during the spring turnover of temperate lakes provide much of the P used by phytoplankton during the open water season. Dillon and Rigler (1974) found that P values above 30 µg L^{-1} frequently coincided with Chl*a* concentrations above 6 µg L^{-1}, a concentration indicative of a eutrophic lake (Table 1; OECD 1982). However, as our understanding of the P cycle increases, so does the complexity of P modelling.

In some aquatic ecosystems, water column P concentrations may not be a direct function of the total nutrient loading but rather the response by consumers to the nutrients (Mazumder and Lean 1994). Spring TP loads to the water column can persist longer in the euphotic zone when the food web supports a greater proportion of pico-, nano- and microplankton (1–3, 3–20, 20–200 µm, respectively) than larger organisms. These plankton have fast regeneration times, reduced sedimentation rates and greater surface area:volume ratios, which facilitates faster P uptake rates (Taylor 1984, Mazumder et al. 1988). The efficiency of P cycling in the food web is also affected by the top-down predation pressures of zooplankton and fishes, both planktivorous and piscivorous (Schindler et al. 1993, Mazumder and Lean 1994). For example, Mazumder and Lean (1994) found that P additions to mesocosms dominated by large zooplankton-grazers resulted in elevated dissolved P concentrations and declining Chl*a* concentrations due to high clearance rates by zooplankton.

The microbial food web can impact the water P concentration by altering the redox potential, refractory organic matter, and dissolved oxygen concentration in the water column and sediment-water interface (Gächter and Meyer 1993, Baker et al. 2000). For instance, microbially-mediated sulfate reduction to hydrogen sulfide can result in S^{-2} binding to iron to form FeS, and vivianite transformation to pyrite (FeS$_2$). The binding of iron by sulfides results in the dissolution of Fe-bound P and diffusion of P upwards, towards the sediment water interface (Gächter and Müller 2003, Orihel et al. 2013, Molot et al. 2014). Recent assessment of internal P loading in oxic Canadian prairie lakes found that if high amounts of sulfate reduction occur then sulfide can sequester iron and release dissolved P to the water column (Orihel et al. 2013, North et al. 2015). In Lake Diefenbaker, a large prairie reservoir, microbially-mediated sulfate reduction is likely the main mode of P internal loading (North et al. 2015). Microbes can also

metabolize large P molecules (e.g., phytic acids, nucleic acids, humic substances) and thus contribute to the retention or release of dissolved P (Gächter and Meyer 1993).

Sedimentation of biota and biotic wastes contributes to P concentration changes as P is removed from the water column. Up to 60 % of spring turnover P is lost to sedimentation at the onset of thermal stratification (Guy et al. 1994). The decline in total P in the water column is due to sedimentation of phytoplankton at rates of 1.2–1.7 mg P m^{-2} d^{-1}, as measured in 40 oligotrophic to mesotrophic lakes (Guy et al. 1994). The rate of loss to sediments is accelerated by larger particle size (Guy et al. 1994). Phosphorus sedimentation rates are dependent on TP concentrations and algal community composition. Senescing diatoms are negatively buoyant and after the spring peak in diatom biomass in Lake Erie, P deposition rates accelerated to a mean of 2.8 mg P m^{-2} d^{-1} as diatoms rapidly settled at the onset of stratification (Barbiero et al. 2006, Bruce Ronzio 2007). Accelerated P sedimentation during stratification has also been observed in other Laurentian Great Lakes, namely Michigan, Huron, and Superior (Anderson et al. 2005, Evans et al. 2011). A large proportion of the P input to a lake and taken up by biota is ultimately transported to the sediment. For example, 48 % of non-apatite P (apatite is mineral P and is not generally bioavailable) input into the central basin of Lake Erie was retained in the sediments (Burns et al. 1975). Lake 227 is a small temperate Canadian Shield lake in the ELA that was experimentally fertilized and was found to have 77 % or greater of the P input lost to sediments (Schindler et al. 1987).

P concentrations in lakes can change when food webs are restructured by the introduction of invasive species. From 1995 to present, the relationship between Chl*a* and P concentrations of the Great Lakes changed due to the establishment of invasive dreissenid mussels and resulting changes in P cycling (Figure 2). Zebra Mussel *Dreissena polymorpha* (Pallas) and Quagga Mussel *D. rostriformis bugensis* (Andrusov) populations were first reported in 1988 and 1991, respectively (Herbert et al. 1989, Mills et al. 1996, Patterson et al. 2005). In Lake Erie, Chl*a* concentrations declined and water clarity improved, but eutrophic indicators like nuisance algae (e.g., cyanobacteria, *Cladophora*) and nearshore SRP concentrations increased (Nicholls et al. 1999, Conroy et al. 2005, North et al. 2012). Dreissenids re-engineered the nearshore ecosystem by capturing nutrients and organic matter that would have otherwise been transported offshore, a process termed "benthification" (Mills et al. 2003) or "the nearshore shunt" (Hecky et al. 2004). Dreissenid mussels rapidly filter algae, zooplankton, and seston, releasing P waste as dissolved or solid faeces and pseudofaeces (non-ingested particulates consolidated in mucus; Ozersky 2010, Ozersky et al. 2009). The change in P cycling resulting from the invasive dreissenids was first modelled by DePinto et al. (2007), who related late summer P release by dreissenids to nearshore algal blooms. In Lakes Simcoe and Ontario, dissolved P concentrations increased in the littoral zone with rapid P capture and remineralization rates by dreissenids (Ozersky et al. 2010). Increasing littoral SRP release, increased light penetration and substrate restructuring to a shell matrix favoured the growth of *Cladophora glomerata*, and other nuisance algae in the nearshore (Higgins 2005, Higgins et al. 2005, Malkin 2007, Ozersky et al. 2009) despite reducing P concentrations offshore. The presence of Dreissenid populations has shifted P away from the open water zone towards the nearshore zone contributing to a reduced offshore P concentration in lakes (Higgins and Zanden 2010, Evans et al. 2011). Dreissenids also sequester P nearshore in the form of refractory shell material, which has likely contributed to the P-limitation offshore and indirectly to collapse of the open water fisheries (Dermott and Munawar 1993, Lozano et al. 2001, Pothoven et al. 2001, Madenjian et al. 2003, Liskauskas et al. 2007, Riley et al. 2008).
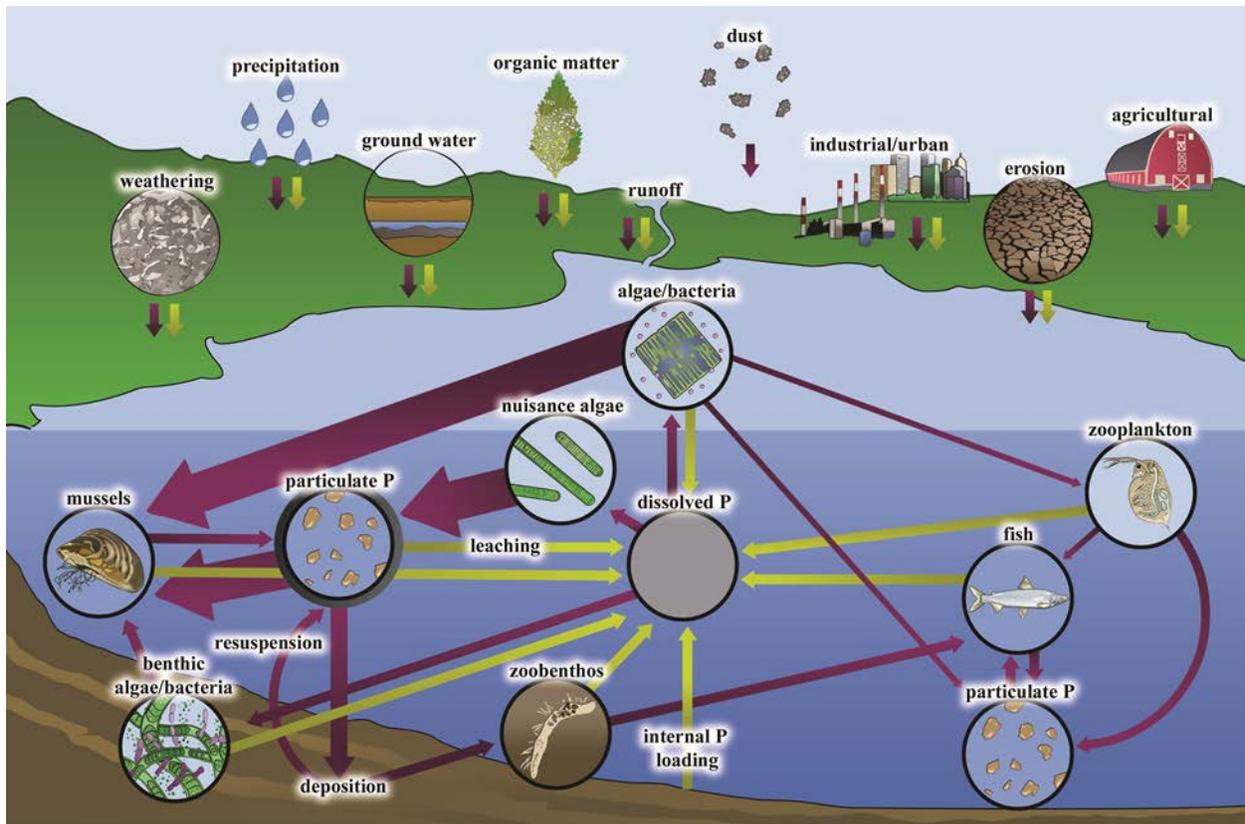
*Figure 2. Diagram of the phosphorus (P) cycle after the proliferation of Zebra Mussels (*Dreissena polymorpha*) in the nearshore of the Lower Laurentian Great Lakes. Phosphorus loads from the catchment and internal P sources in lakes where P can be transformed through biotic and abiotic interactions. Arrows indicate the flux from one P pool to another P pool. Arrows in purple are the particulate P transformations and arrows in green are dissolved P transformations (Graphics by Aldo F. Rios Martinez).*

The changing food web structure and P dynamics require that previous P management strategies be reevaluated for the Laurentian Great Lakes. Declining TP concentrations in the open waters of Lake Michigan have resulted in a decline of over 60 % of the Chl*a* concentrations from 1980–90s to 2007–08 (Evans et al. 2011) and a decline in spring diatom blooms (Barbiero et al. 2006). However, at the same time, in Lakes Erie and Ontario, there are widespread observations of nuisance algae (e.g., *Cladophora*) in the nearshore, similar to the 1970s, prior to the implementation of P control (Depew et al. 2001). In Lake Ontario, and to a lesser extent Huron, Michigan, and Erie, actual P concentrations offshore measured lower than model simulations (Chapra and Dolan 2012). As a result, the International Joint Commission (IJC) will move away from lake-wide P loading targets towards site specific P loadings that depend on the P cycling in the region of the lake (International Joint Commission 2012).

HISTORY OF PHOSPHORUS MANAGEMENT STRATEGIES FOR THE GREAT LAKES

Since freshwater cage aquaculture in Canada predominantly occurs in the Laurentian Great Lake, Lake Huron, we review here the management strategies for P loading in the Great Lakes. The Laurentian Great Lakes have been the site of intensive anthropogenic activity from the time of early settlement with deforestation, rapid population growth, and industrial expansion from

1850 to present (Schelske et al. 1983). Partnered with this massive alteration in land use was the accelerated loading of P and the threat of eutrophication to the lower Great Lakes (Beeton 1965, Burns et al. 1975). In the late 1960s, scientists determined that Lake Erie was markedly degraded because of an oversupply of P that caused excessive algal growth, particularly *Cladophora glomerata* (Linnaeus) in the nearshore and cyanobacteria that produced a bad taste and odour for consumption, and resulted in depletion of deep-water oxygen concentrations.

Efforts to mitigate P loading focused on reducing point sources of P (International Joint Commission 1987). More than $ 8 billion USD were spent on remediation of sewage treatment facilities to add secondary treatment, reducing P in effluent to ≤ 1 mg L^{-1} (Dolan 1993, Conroy et al. 2005). Additional millions were spent on changing farming practices and restricting P content in household items like detergents.

In 1983, TP targets for the Great Lakes were set based on the Dillon and Rigler (1974) TP- Chl*a* model. A maximum acceptable water column P concentration of 10 µg L^{-1} was set for all the lakes as a conservative threshold that would maintain water quality below eutrophic status (Dillon and Rigler 1975). A water column monitoring program was established to assess water quality in the Great Lakes and the P abatement program was deemed successful in the late 1980s when P concentrations declined below 10 µg L^{-1} and suspended solids and Chl*a* concentrations decreased (Chapra and Dolan 2012). Today, we recognize that each lake has a different trophy, and the Lake Huron spring mean open water P target concentration is 5 µg L^{-1} (Table 2).

Table 2. Objectives for phosphorus (P) concentrations in the spring mean open water and TP target loads for the waters of the Laurentian Great Lakes (International Joint Commission 2012, Copyright 2012 reproduced with permission from authors).

Water Body	Interim [TP] in open waters (µg/L)*	Interim TP targets (MTA)
Lake Superior	5	3,400
Lake Michigan	7	5,600
Main Lake Huron	5	2,800
Georgian Bay	5	600
North Channel	5	520
Saginaw Bay	5	440
Western Basin Lake Erie	15	11,000
Central Basin Lake Erie	10	-
Eastern Basin Lake Erie	10	-
Lake Ontario	10	7,000
		31,360

*spring mean

Changes to the P-Chl*a* relationship resulting from food web alterations by invasive species and a shift in particulate:dissolved P loadings from the catchments have led to a reassessment of the P loading targets and management issues of the Laurentian Great Lakes. The International Joint Commission (IJC) is currently reassessing quantity and quality of P target loads and spatial P loading trends in order to redesign the new P targets, which will come into place in 2015 (International Joint Commission 2012).

> *"In establishing Substance Objectives for phosphorus concentrations and phosphorus loading targets, the Parties shall take into account the bioavailability of various forms of phosphorus, related productivity, seasonality, fisheries productivity requirements, climate change, invasive species, and other factors, such as downstream impacts, as necessary." (International Joint Commission 2012)*

HISTORY OF FRESHWATER AQUACULTURE IN CANADA

Canada has had a long tradition of fish cultivation. The earliest fish culture in Ontario is attributed to Samuel Wilmot who reared Atlantic Salmon (*Salmo salar* Linnaeus) and many other native fish species (whitefish, Lake Trout [*Salvelinus namaycush* Walbaum], Walleye [*Sander vitreus* Mitchill], and bass) near Newcastle circa 1865. In 1868, the Canadian government provided funding to construct a permanent hatchery and initiate full-scale production. Research done by Samuel Wilmot led to the development of many culture techniques for trout and salmon that are basically still used today. The federal government invested in fish culture activities starting in 1876 and established many fish hatcheries. Most efforts were devoted to species of importance for commercial fisheries, such as whitefish, Walleye, Lake Herring (*Coregonus artedi* Lesueur), and Lake Trout (Kerr 2006).

The provincial government of Ontario became involved in fish culture around 1910 when it reached an agreement with the federal government to assume responsibility for culturing fish destined to support recreational fisheries. The federal government retained the fish culture activities related to commercial fisheries. Today, the Ontario Ministry of Natural Resources (OMNR) operates 10 fish culture stations that rear 12 species of fish and produce the millions of eggs required to meet stocking targets. The provincial hatcheries currently stock about seven million fish annually in more than 1,000 water bodies.

Since 2000, the commercial aquaculture industry has grown primarily from the expansion of Atlantic Salmon in marine cages (FAO 2011). Production of Rainbow Trout reared in freshwater cages has experienced a more modest growth and production has been relatively constant for the past decade (Figure 3). Rainbow Trout are native to the West Coast of North America, although they are stocked across the country. The province of Ontario is the largest Rainbow Trout producer with both cage and land-based farms (Figure 4) accounting for 57 % of Canadian finfish production (Statistics Canada 2012). In Ontario, the Rainbow Trout industry shifted from initially land-based production to 88 % cage production by 2010 (Figure 5). Lake Huron is the site of most cage based aquaculture in Canada, although there are a few operations in Western Canada (e.g., Lake Diefenbaker, SK, Lois Lake, BC and Lake Georgie, BC). In Ontario, a new freshwater cage aquaculture license has not been issued by the province since 2003. The future growth of the freshwater aquaculture industry in Canada is uncertain due to regulatory and environmental challenges.
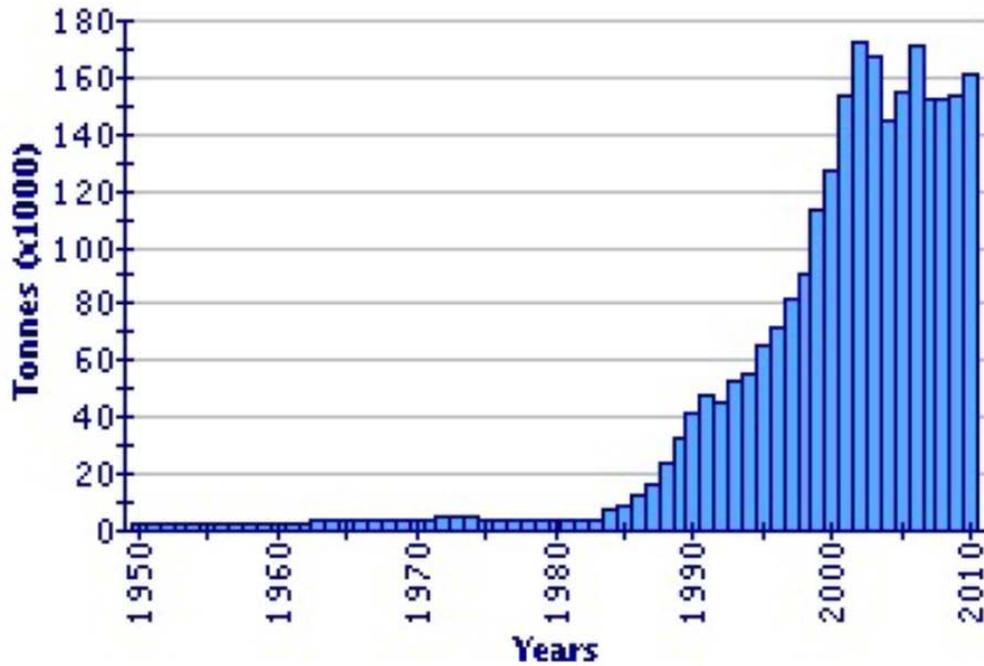
Figure 3. Reported aquaculture production in Canada from 1950 (FAO 2011, Copyright 2011, reproduced with permission from FAO).
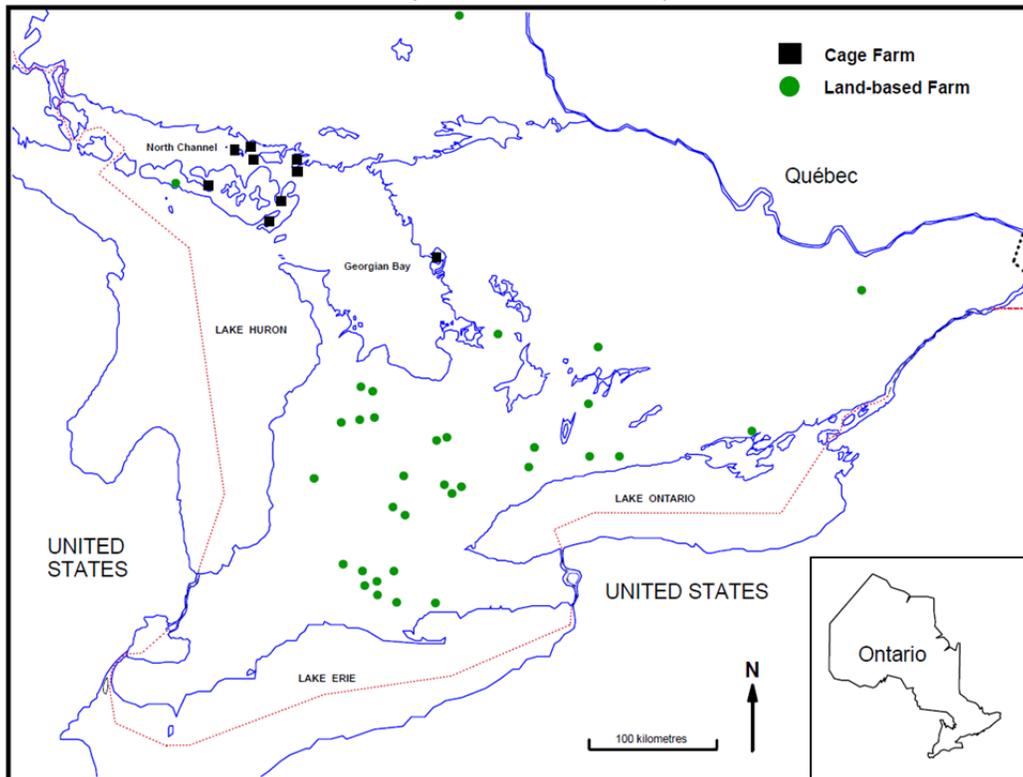

Figure 4. Map of Ontario trout farms both land-based (green circles) and cage farms (black box) in 2010. (Moccia and Bevan 2011, Copyright 2011, reproduced with permission from authors).
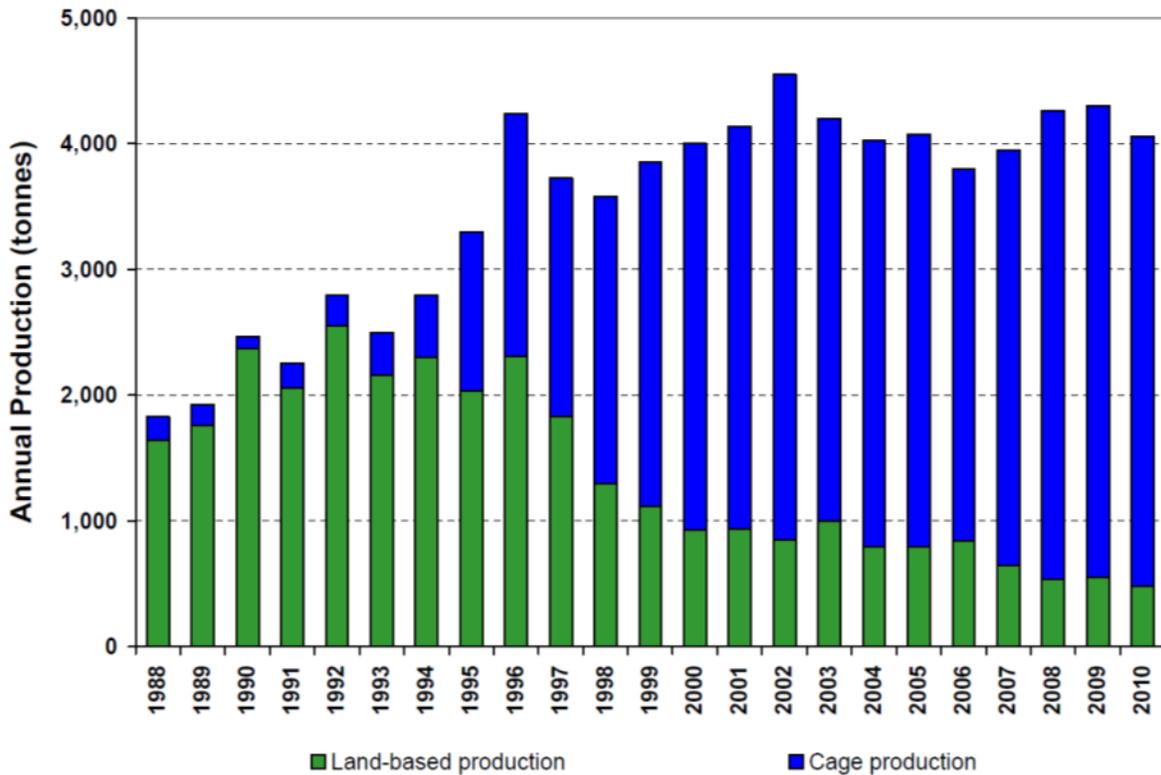
Figure 5. Comparison of Ontario's land-based and cage aquaculture production between 1988 and 2010. (Moccia and Bevan 2011, Copyright 2011, reproduced with permission from authors).

CAGE AQUACULTURE

Sources of P from cage aquaculture

Since 1995, commercial Rainbow Trout production in Canada has been predominantly from freshwater cage operations. Cage aquaculture is one source of P in a lake's P cycle (Figure 6). Cage operations are stocked with small fingerlings, which represent both a P source in the form of fish waste and P storage in the form of fish biomass. An additional source of P to the lake is the fish feed fines and feed waste. Fish are fed one to several times a day, using pelletized feed composed primarily of fish meal, fish oil, and plant meal, often corn meal (Hua and Bureau 2006). Over time, fish grow and retain a portion of the P that is removed from the lake at harvest. Fish are also removed from cages if mortality occurs. Loss of fish due to mortality may amount to a maximum of 15 % of the population during the fingerling stage and 2 % of the population during the adult stage (Steve Naylor, Ontario Ministry of Agriculture, Foods and Rural Affairs, pers. comm.) or a seasonal average of 5 % (Bristow et al. 2008). Release of farmed fish due to non-catastrophic escape is estimated to be on average around 2–4 % of the population (Penczak et al. 1982).
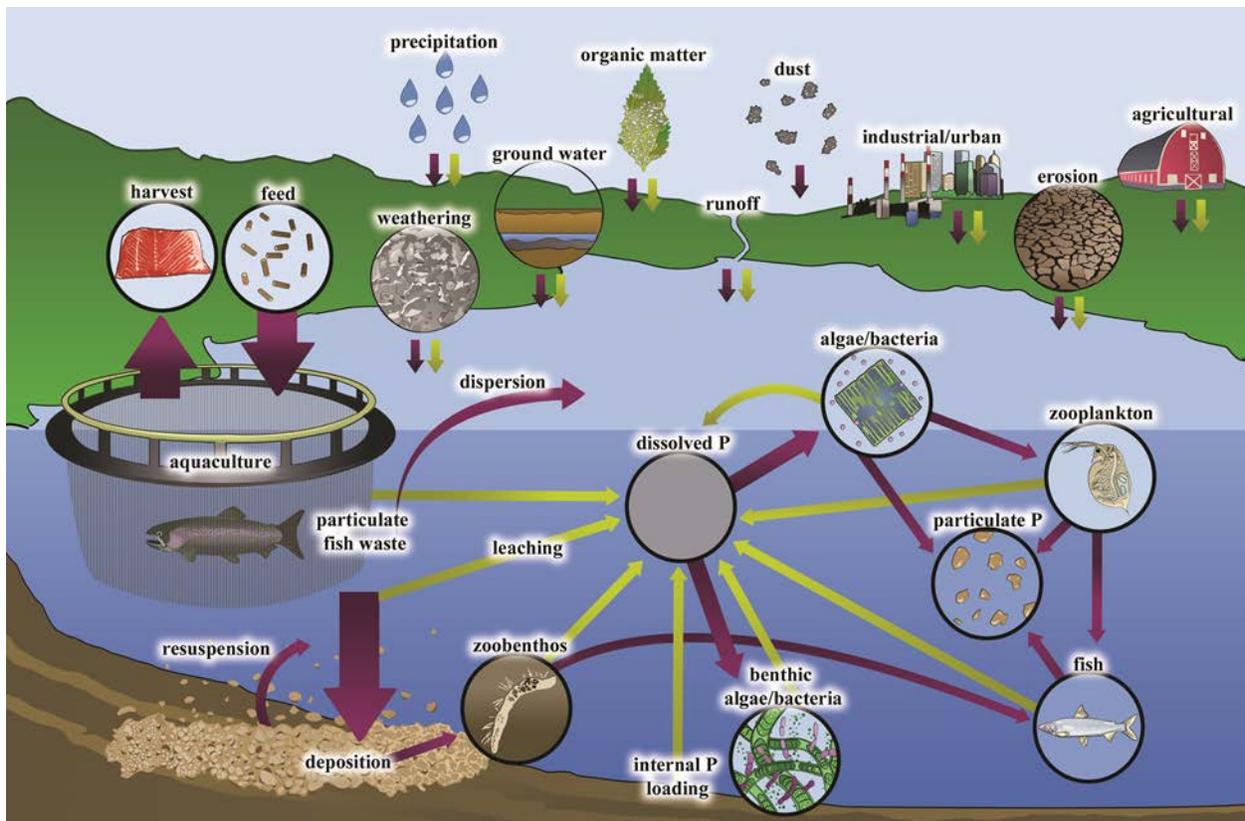
Figure 6. Diagram of phosphorus (P) loads from aquaculture and other external P sources to lakes where P can be transformed through biotic and abiotic interactions. Arrows indicate the flux from one P pool to another P pool. Arrows in purple are the particulate P transformations and arrows in green are dissolved P transformations (Graphics by Aldo F. Rios Martinez).

Phosphorus utilization by fish and the release of P waste by Rainbow Trout culture operations have been the focus of numerous research efforts and are relatively well understood and characterized (Azevedo et al. 2011, Coloso et al. 2003, Bouwman et al. 2013, Bureau et al. 2003, Cho and Bureau 1997, 1998, 2001, Bureau 2006, Bureau and Cho 1999, 2000, Bureau and Hua 2010, Hua and Bureau 2006, 2009a, 2009b, 2010, 2012). Fish ingest P as part of various compounds in their diet. These compounds are digested, absorbed, metabolized, partly retained in the body, and partly excreted by the fish. The particulate P waste (i.e., feed fines, feed waste, and faeces) will settle to the lake bottom, while the dissolved P will enter in the water column (Enell and Löf 1983).

Principles of nutrition can be used to describe or predict the excretion of P wastes by fish and by extension, fish culture operations. Digested and absorbed P is used by the fish to sustain life processes and form various tissues in the body (e.g., hydroxyapatite in bones and scales, phospholipids, nucleic acids). The digestible fraction of P that exceeds fish P requirement is excreted as dissolved P waste (orthophosphates), mostly in the form of urine and to a lesser extent through mucus from the gills (Garcia-Ruiz and Hall 1996). The minimum P requirement of Rainbow Trout is around 0.6 % digestible P in the feed. Trout receiving only the required amount of digestible P requirement for growth will excrete only a minute amount of dissolved P (~ 5 mg P kg^{-1} BW d^{-1}). The quantity of P in the aquaculture waste produced is directly related to the P content and P digestibility of the feed. Reduced P content in feed (from > 3.0 to 1.0 % TP) can result in reduced P waste because fish have the ability to increase P retention efficiencies (Lanari et al. 1995, Coloso et al. 2003). Coloso et al. (2003) measured dietary P (Figure 7) and

found that feeding trials with high P feeds led to greater P waste, particularly dissolved P waste. The relative proportion of solid to dissolved P waste is largely dependent on the P digestibility of the feed. Additional sources of dissolved P to the lake are from P leaching from sedimenting feed and faeces. Composite feeds have a greater proportion of soluble P (50-60 %) that can be leached as compared to faeces (30–40 %); however, there is considerably less feed waste than faeces from farms (Phillips et al. 1993). The global average for aquaculture P waste in 2010 was estimated to be 3.0 kg dissolved P tonne^{-1} fish and 5.0 kg particulate P tonne^{-1} fish (Bouwman et al. 2013). These particulate P wastes accumulate as sediment on the lake bottom where they undergo processes of decomposition and diagenesis.

Phosphorus wastes from cage aquaculture operations are primarily in the form of solid faeces and to a lesser extent as uneaten feed and "fines" which is essentially feed dust that results from the erosion of pellets in feed bags during handling and storage and may measure up to 4 % of feed dry weight (Clark et al. 1985). Feeding is generally well-managed on modern commercial fish culture operations and feed wastage is very limited (less than 1 % of the feed used; DFO unpubl. data). Undigested P-containing compounds are egested as faecal material by the fish and consequently, most of particulate P waste released by fish culture operations is of faecal origin (> 99 %). The quantity of waste produced by a commercial farm is strongly associated with animal husbandry practices and the size of the operation (Hardy and Gatlin 2002). Presently, Ontario and Saskatchewan cage farms average an estimated 240-318 kg manure tonne^{-1} fish (Bureau et al. 2003, DFO unpubl. data). Particulate P waste (i.e., feed fines, feed waste, and faeces) released into lakes is partially consumed by wild fish populations around the cages (Johansson et al. 1998, Gabrielsen 1999, Kullman et al. 2009, Wellman et al. 2017).
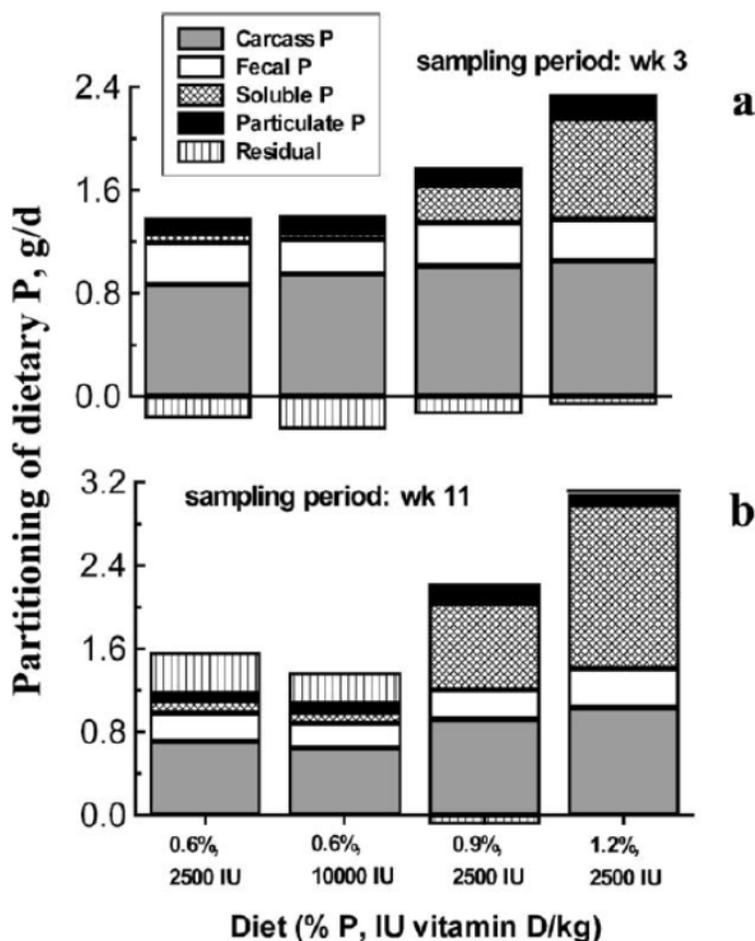
Figure 7. Partitioning of dietary phosphorus (P) consumed by fish during a) week 3 (top) and b) week 11 (bottom) fed diets of varying P content (Coloso et al. 2003). By week 11, fish released considerably greater soluble P when fed high P content diets, as compared to low P diets. (Coloso et al. 2003, Copyright 2003, reproduced with permission from Elsevier)

Particulate farm wastes have limited dispersion in freshwaters and typically accumulate below the cages (Rooney and Podemski 2010). Benthic invertebrates like oligochaetaes and profundal chironomid larvae are known to feed on organic aquaculture deposits around finfish farms (Grey et al. 2004, Wetton 2012). All consumers (primary to tertiary) were found to incorporate organic matter from aquaculture operations in ELA Lake 375 with widespread increases in δ^{15}N signatures by the second year of Rainbow Trout production (Wellman et al. 2017). Pelagic, planktonic, and littoral invertebrate taxa (except *Mysis*) did not show signs of direct consumption of farm waste based on δ^{13}C depleted signatures (Kullman et al. 2009, Wellman 2011, Wellman et al. 2017) but did utilize the waste material indirectly as secondary consumers. Stable isotopic analysis of wild fish species showed signs that they may have consumed waste feed, fines, and faecal material, as well as biota that had assimilated aquaculture waste particularly N in the form of NH_3 released by fish or decomposition of fish waste (Kullman et al. 2009, Wellman 2011, Wellman et al. 2017). Biotic activity, wave action, and resuspension may perturb sediments in the zone of aquaculture waste deposition, focusing the finer, organic-rich silts to the deepest part of the lake basin that over time become permanently buried.

Accurate estimation of the amount and type of P waste released by cage culture operations can be achieved through analysis of production data and the feed used or detailed information about

the feed formulation. Methods to estimate the quantities of P loadings include the mass balance approach, various factorial models (e.g., Fish-PrFEQ model) and direct measures (e.g., sampling under cages with sediment traps). Nutritional models and mass balance methods are the most practical methods to date.

Phosphorus nutritional model for fish

Nutritional modelling has been shown to generate highly accurate estimates of waste outputs from cage aquaculture. Fish-PrFEQ was designed by the Ontario Ministry of Natural resources, developed further by Cho and Bureau (1998) at the University of Guelph and tested at a cage site by Azevedo et al. (2011). Fish-PrFEQ has been shown to generate highly accurate estimates of both P dissolved and particulate waste outputs from Rainbow Trout culture operations. The available information on P nutrition of fish was integrated into a factorial model developed by Hua et al. (2008). This model can be used to estimate P digestibility, retention, and waste outputs of salmonid fish culture operations. This model operates within the framework of the Fish-PrFEQ bioenergetics model (Cho and Bureau 1998, Bureau et al. 2003) and allows theoretical estimation of the different types of P wastes (e.g., dissolved vs. solid, inorganic vs. organic solid P wastes) and should be tested in the field.

Composite feeds are formulated based on the relative proportions of ingredients like fish meal, bone meal, poultry meal, soy protein, wheat middlings, corn meal, and fish oil, with additional supplements (i.e., vitamins and minerals). Phosphorus form and content in each ingredient differs. Thus, engineered composite feeds today contain many forms of P, including bone P (i.e., hydroxyapatite), plant-based phytate P (e.g., myo inositol hexaphosphate), organic P (e.g., protein, lipids, carbohydrates, and nucleic acids), and supplements in the form of monobasic P and dibasic P (Hua and Bureau 2010). Each of these forms of P can have varying rates of P digestibility, which in turn affects the P waste outputs from fish (Table 3).

Table 3. Estimated digestible P concentrations of P compounds in the diet used in Experimental Lakes Area (ELA) Lake 375 experimental trout culture during 2003 and 2004, and solid P waste output according to the model Hua and Bureau (2006). From Azevedo et al. (2011), Copyright 2011 reproduced with permission from Elsevier.

	g kg^{-1} dry matter of feed	%, as feed basis
Dietary total P	12.4	1.15
Dietary apatite P	6.9	0.64
phytate-P	1.4	0.13
organic-P	4.2	0.38
Total solid P waste	5.74	0.53
solid apatite-P waste	3.71	0.34
solid phytate-P waste	1.36	0.13
solid organic-P waste	0.67	0.06

P digestion efficiency is specific to the fish species (Coloso et al. 2003, Hua and Bureau 2010). Rainbow Trout outperformed carp and tilapia in the relative digestion of bone P. The gut of piscivorous Rainbow Trout is acidic and breaks down bone P to orthophosphate, which is readily absorbed by the gut at 68 % (g g^{-1}; Hua and Bureau 2010). Conversely, P digestibility by Rainbow Trout from phytate P is 0 %. Remaining P fractions had high levels of digestibility with organic P, monobasic P, and dibasic P > 62 % (Hua and Bureau 2006). Rainbow Trout do not physiologically have the ability to switch diets from meat-based to plant-based nutrition with regards to P uptake, unless plant-based feed ingredients are further treated to enable digestion (Cheng et al. 2003).

Estimates of P waste by cage aquaculture

Animal husbandry inevitably generates animal waste and aquaculture is no different. Given that direct measurement of fish waste from cage operations is challenging and costly, a good alternative is to use bioenergetics models (Bureau et al. 2003). Using Fish-PrFEQ, the amount and type of P waste outputs from fish culture operations can be estimated from the amount of feed used, the total P concentration of the feed used the digestibility of P in the feed, the whole body P concentration of the fish, the feed conversion ratio, and the feed wastage by fish culture operations.

The amount and types of P waste output of fish culture operations can be quite variable across fish culture operations, seasons, years, and production cycles. FISH-PrFEQ models the fish growth rates, and for poikilotherms, water temperature is a critical component. Based on the production records from the previous growing cycle, fish growth rates are estimated given that the same animal husbandry practices and fish stocks are used from year to year. With measured feed and water temperatures, fish weight gain can be very reliably predicted (Figure 8). The quantity of feed administered and net release of P from aquaculture production varies seasonally (Figure 9) with September typically having the greatest fish biomass and greatest P waste released from cages. In some Canadian freshwater trout operations, the P release curve can appear bimodal with a depression in August due to reduced feed rations at high water temperatures (DFO unpubl. data). In Canadian freshwaters, there are large seasonal variations in temperature (4 to > 20 °C). During the winter, water temperatures are low and feed rations decline to the basic metabolic demands of the fish. During late summer, water temperatures can be high (typically peak in August); feed rations are usually reduced when temperatures exceed 20 °C because fish become more stressed as their metabolic activity increases and oxygen tension decreases. Most farmers will stop feeding when temperatures exceed 22 °C, since continuing to feed in warmer temperatures can result in increased disease incidence and mortality (Steve Naylor, Ontario Ministry of Agriculture, Foods and Rural Affairs, pers. comm.). The upper thermal tolerance for Rainbow Trout is 25 °C.
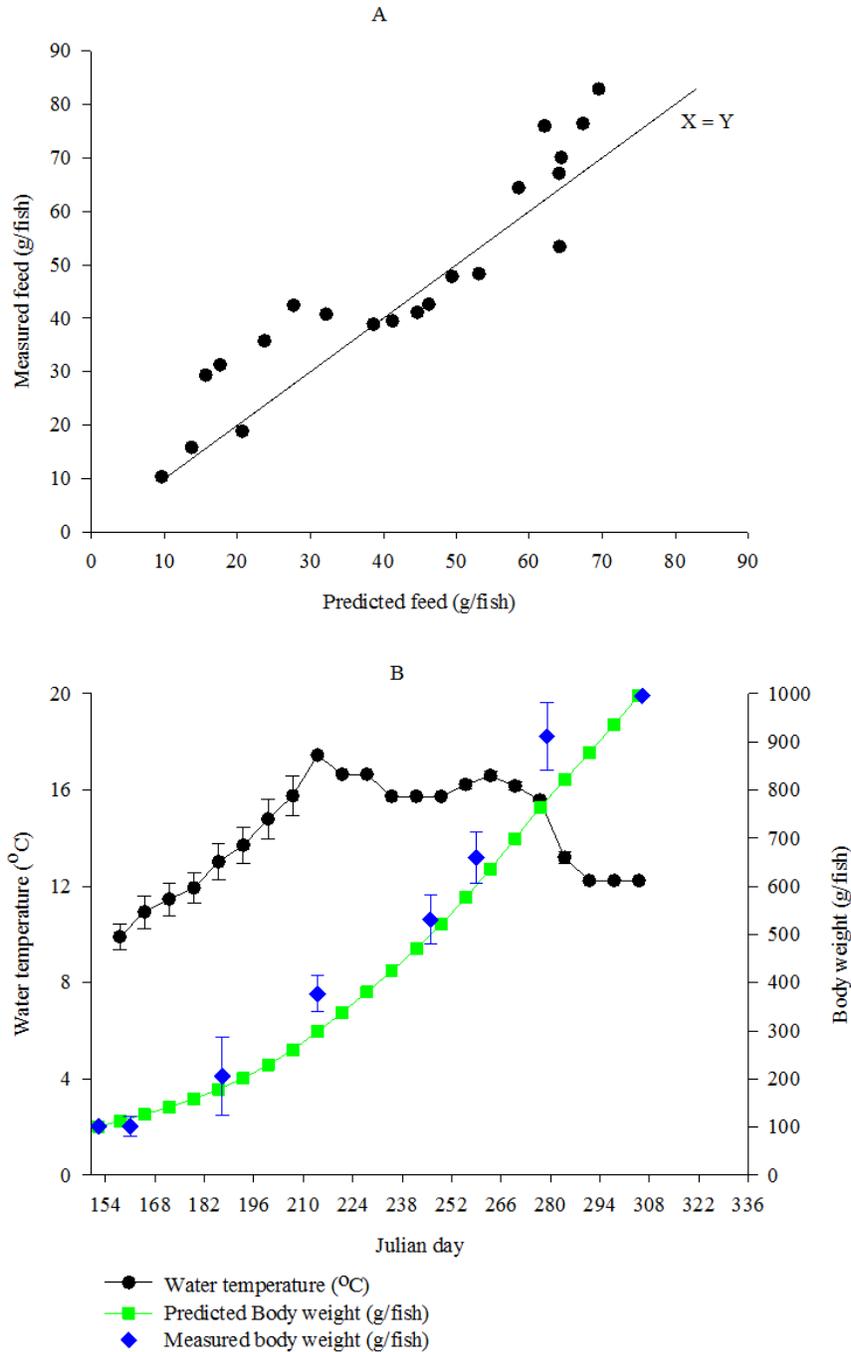
Figure 8. Use of bioenergetics model Fish-PrFEQ to a) predict feed rations, as compared with measured feed for cage cultured Rainbow Trout, and b) measured water temperature (2-6 m depth, mean ± SE, n = 30-127) in relation to predicted fish body weights and measured fish body weights from Rainbow Trout during experimental production trials at Experimental Lakes Area (ELA) Lake 375 (Azevedo et al. 2011, Copyright 2011, reproduced with permission from Elsevier).
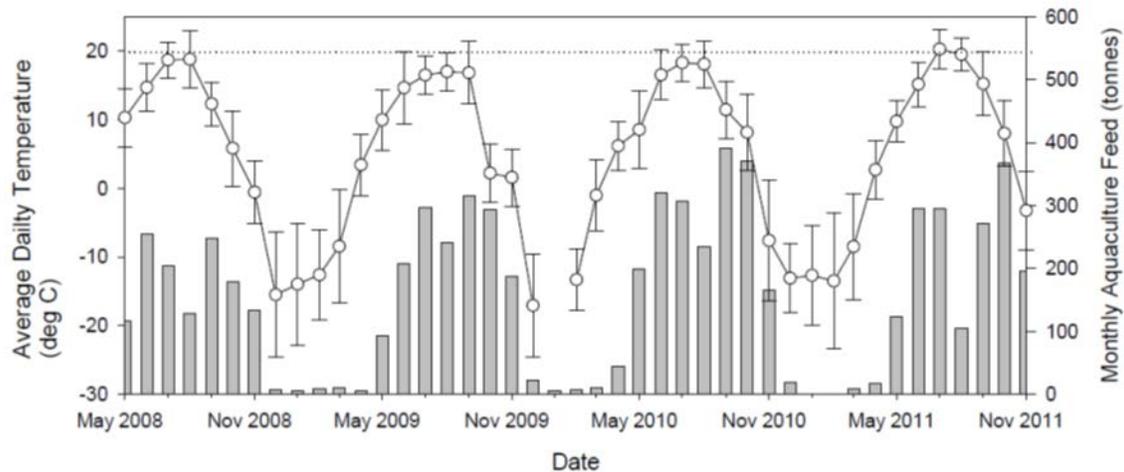
Figure 9. Seasonal variations in average daily air temperature (°C, open circle) and monthly aquaculture feed (tonnes, bar chart) applied for rearing commercial Rainbow Trout in Lake Diefenbaker, SK (DFO unpubl. data).

Total P content (g fish^{-1}) increases linearly with increased body weight (BW) in Rainbow Trout (P content = 0.174 + 0.0035*Fish weight; Azevedo et al. 2011) and can be influenced by P digestibility of the feed. Digestibility of P in commercial Rainbow Trout feeds used in Canada typically varies between 40 to 60 % of the TP. Improvements in P digestibility of feed have resulted a reduction of P waste outputs from 32 kg t^{-1} to 8 kg t^{-1} from 1980 to 2010, respectively (Bouwman et al. 2013).

One critical metric in modelling P waste output is the feed conversion ratio (FCR), which is the weight of dry feed supplied relative to the wet weight of fish biomass, g g^{-1} (USAID 2011). FCRs of commercial Rainbow Trout culture operations in Canada depend on the quality of feed used (mainly nutritional composition), as well as the environmental factors (i.e., temperatures and seasons) and husbandry practices (i.e., feeding practices and production management). FCRs for commercial Rainbow Trout culture operations in Ontario vary between 1.15 and 1.35 for the entire production cycle (i.e., from a typical stocking weight of 30 g to a typical harvest weight of 1.1 kg; Bureau et al. 2003, Azevedo et al. 2011, Bouwman et al. 2013). Fish feed is 50 % of the gross input costs to the industry and efforts are made to optimize growth and minimize cost (Statistics Canada 2012).

Total P waste output of Rainbow Trout culture operations in Canada is estimated to vary between 8 and 15 kg P tonne^{-1} of fish biomass produced, based on typical commercial production conditions of Rainbow Trout grown from about 30 g to 1100 g harvest weight (Cho and Bureau 1998, Bureau et al. 2003, Bristow et al. 2008, Azevedo et al. 2011, Bouwman et al. 2013). For these same conditions, P wastes are estimated to vary from 3 to 9 kg particulate P and 4 to 6 kg dissolved P tonne^{-1} of fish biomass produced. Table 4 presents recent, as well as historic, records of the average P loading from freshwater salmonid culture (Rainbow Trout and Chinook Salmon [*Oncorhynchus tshawytscha* Walbaum]). As fish husbandry practices and feeds have changed, the P wastes have declined considerably.

Table 4. Published total phosphorus (TP) and total dissolved phosphorus (TDP) load rates per tonne of fish biomass produced and associated FCR feed conversion ratios and P content in fish feed used in freshwater salmonid culture.

Site	Publication	kg TP per tonne fish	kg TDP per tonne fish	FCR (max)	FCR (min)	P in diet (%)
Global average in 2010	Bouwman et al. 2013	8.0	3.0	1.10	-	1.10
Lake 375, ELA Ontario	Azevedo et al. 2011, 5 % waste	8.7	3.1	1.16	1.10	1.10
Canada, several sites	Vandenberg 2009, older CDN feed	8.5-13.3	-	1.60	1.00	-
Canada, several sites	Vandenberg 2009, newer CDN feed	5.1	-	0.99	-	-
Canada, several sites	Vandenberg 2009, Danish feed	4.2-7.3	-	1.19	0.91	-
ON cage cultures	Bureau et al. 2003, widely used feed	7.5	1.7	1.14	-	1.15
ON cage cultures	Bureau et al. 2003, widely used feed	7.9	1.9	1.22	-	0.93
ON cage cultures	Bureau et al. 2003, high P content	15.2	5.5	1.29	-	1.50
Land based operation	Cho and Bureau 1998	5.1	2.0	1.22	1.11	
MN Aquafarm Inc.	Axler et al. 1996	4.8-18.7	-	-	-	0.94-3.6
MN Aquafarm Inc.	McDonald et al. 1996	5-40	-	-	-	-
Laboratory, Scotland	Phillips et al. 1993	13.9-19.8	0.4-1.5	-	-	1.2-2.4
Sweden	Ackefors and Enell 1990	9.5	2.2	1.1	2.3	0.9
NW Germany	Wiesmann et al. 1988	4-18.8	-	1.4	0.7	2.0
Lake Malaren, Sweden	Persson 1988	13-22	-	1.3	2.0	1.3
Sweden	Enell and Löf 1983	8.5-9.0	1.9	1.3	-	1.6
Denmark	Alabaster 1982	36.5	-	-	-	-
Tunison Laboratory, NY	Ketola 1982	9.1-23	-	1.3	1.0	2.2
Glebokie Lake, Poland	Penczak et al. 1982	23.0	-	-	-	-
Global average in 1980	Bouwman et al. 2013	32.0	14.0	6.0	1.5	2.5

Transformation of P from cage aquaculture waste in lakes

Release of dissolved P from aquaculture waste is estimated to be one third of the total P loading (Cho and Bureau 1998, Bureau et al. 2003, Bouwman et al. 2013) and is in part delivered to the surface waters (Figure 6). Most cage aquaculture in Canada uses low P content feeds and takes place in oligotrophic, P-limited Lake Huron. In 2010, Lake Huron had an average open water concentration of 3.4 µg P L^{-1} (Chapra and Dolan 2012). There is little evidence that P additions from aquaculture have resulted in a perceptible rise in TP concentrations in the water column near farms. Water chemistry monitoring at Ontario cage culture sites has not produced any instances of TP regulatory exceedances at fish farms in ON since 1998 (Clerk et al. 2004, Yan 2005). At one fish farm in Lake Huron, water column TP concentrations were higher 30 m downstream (mean 7.1 ± 0.1 µg L^{-1}) than at 30 m upstream of the cages (mean 5.0 ± 0.3 µg L^{-1}; Reid et al. 2006, Reid and Moccia 2007). A similar water column survey at a nearby farm reported no statistical difference between surface TP concentrations at a site 100 m versus 1,000 m distant from cages, but vertical water column sampling did detect slightly elevated TP concentration in bottom water (1 m above lake bottom; Milne and Charlton 2007). Water sampling at a fish farm in Lake Diefenbaker, SK measured detectable increases in TP at the surface water (by a mean 2.6 µg L^{-1}) and 20 m water depth (by a mean of 5.7 µg L^{-1}) at the very edge of farm cages relative to an upstream site 400 m away (DFO unpubl. data). There was, however, no detectable elevation at the sampling site approximately 600 m downstream of the farm.

The fate of most dissolved P is transformation to particulate organic P by uptake or adsorption to particles, cycling through the food web, and then eventual loss of particulate P to the sediments. Dissolved P waste from fish is readily bioavailable (Brabrand et al. 1990) and is rapidly taken up and assimilated by algae, bacteria, and macrophytes because of the prevalence of P-limitation (Garcia-Ruiz and Hall 1996). Reid and Moccia (2007) reported that after dissolved P was released from farmed fish, soluble P concentrations decline to background values with minutes to hours. The turnover time for dissolved P is often less than 10 minutes for phytoplankton in the epilimnion of lakes (Rigler 1964, Wetzel 2001).

The fate of most particulate P is transport to sediments. Particulate P sedimentation is characterized by the settling velocity (Chapra and Tarapchak 1976). Organic bound particulate P in artificially fertilized Lake 227, ELA was largely (77 %) and rapidly (75 kg P y^{-1}) exported to the sediments (Schindler et al. 1987, Bristow et al. 2008). During experimental aquaculture production in Lake 375, a greater proportion of particulate P (88 %) was exported to the sediments at an even faster rate (95 kg P y^{-1}, Azevedo et al. 2011) because faeces from aquaculture waste have much higher sedimentation rates than algae.

The fate of some sedimenting particulate P waste from aquaculture is dissolution via leaching. Phillips et al. (1993) estimated that leaching amounts to 0.43-0.94 kg dissolved P $tonne^{-1}$ fish, but analysis of leaching from modern feed formulation is needed. Newer composite feeds today contain a higher proportion of soy meal, which provides P in the form of phytate. Phytate is not readily absorbed by Rainbow Trout unless the enzyme phytase is provided in the formulated feed (Bureau and Hua 2010).

Although aquaculture wastes elevate sediment P concentrations, they typically do so over a limited surface area. Sediment P concentrations under the fish cage was significantly elevated (39 mg g^{-1}) from pre-cage measures (1.9 mg g^{-1}) at experiment Lake 375, ON after 5 months of fish farming (Rooney and Podemski 2010). However, the area affected was restricted to under the cage and a 1 m radius and a limited spatial distribution is typical of the footprint at farms in Lake Huron (Wetton 2012, DFO unpubl. data). There is limited dispersal of solid P waste from aquaculture because currents are too slow (varying between 2 to 10 cm s^{-1}) for dispersal

beyond 30 m of origin (Boyd et al. 1998, Reid and Moccia 2007, DFO unpubl. data). Fish farm sites are typically located over deeper waters (> 20 m). When high winds, waves and ice loosen or displace cage moorings, the depositional footprint may become larger and aquaculture wastes more diffusely distributed. The restricted footprint provides a limited interface between fish waste and water, and the surface area of the interface is critical in predicting the amount of P released by internal loading (Nürnberg 1988). Internal P loading from deposited aquaculture waste is also determined by the form of P and the background chemistry.

Once deposited on the lake bottom, particulate P can solubilize and diffuse up into the water column. The form of sedimented P from fish farms is largely composed of apatite P; one estimate is 65 % of TP was in the form of apatite P (DFO unpubl. data). Apatite P is a mineral form of phosphate that is highly insoluble and thus not readily bioavailable (Williams et al. 1980, Manning et al. 1991) and unlikely to solubilize unless conditions become highly acidic (otherwise the release of P is on a geological time scale). After 3 years of intensive aquaculture production in Lake 375, background P concentrations doubled in the metalimnion and quadrupled in the hypolimnion (Bristow et al. 2008). The elevated deep-water P concentrations were associated with changes in primary producers, which included metalimnetic cyanobacteria (e.g., *Snowella lacustris* Chodat) and mobile dinoflagellates (Findlay et al. 2009). Phytoplankton composition changes were similar to Lake Glebokie, Poland where aquaculture wastes were prevalent (Wegleńska et al. 1987) and vertical water column P distributions were similar. Mobile plankton like cyanobacteria, dinoflagellates, and cryptomonads migrate through the water column to assimilate dissolved P below the thermocline and photosynthesize in the epilimnion (Ganf and Oliver 1982, Kromkamp et al. 1989). Otherwise, the release of P in the hypolimnion is relatively inaccessible to algae in the surface waters during thermal stratification.

Particulate P waste at the lake bottom can be taken up, assimilated, and recycled by deposit feeding biota like oligochaetes. An estimate of over 4 g m^{-2} of invertebrate biomass or over 30,000 individuals m^{-2} was found within 10-30 m of fish cages at three commercial aquaculture operations studied in Lake Huron (DFO, unpubl. data). Further from the fish cage operations (i.e., 20-50 m), there can be invertebrate biomass that exceeds reference conditions and represents a zone of enhancement (Pearson and Rosenberg 1978, DFO, unpubl. data). Assimilation of organic matter by deposit feeders is reflected in higher relative abundances and increased body size of some taxa (i.e., doubling of individual tubificid biomass; DFO, unpubl. data). A greater biomass of invertebrates will condition greater amounts of sediment with estimates ranging from 0.1-0.3 mg faeces produced hourly per mg of worm biomass (Ivlev 1939, Appleby and Brinkhurst 1970, Cummins and Klug 1979, Thomann et al. 1992). These deposit feeders also play a direct role in recycling P back into the water column (Zhang et al. 2014). Mobilization of dissolved P from sediment by invertebrates is dependent on density and type of invertebrate (Fukuhara and Sakamoto 1987, Zhang et al. 2014).

Latent and labile forms of solid P waste from cage aquaculture

One way to determine the relative labile and latent P in solid aquaculture wastes is to employ P fractionation techniques (Table 5). Phosphorus fractionation was described by Psenner and Pucsko (1988) and outlined by Rydin (2000). This technique is unlike classic ecological analyses, which separate P fractions by size class, but rather classifies P based on its chemical form using a series of extractions. The extraction sequence measures P from loosely sorbed P (SRP), iron P (Fe-P), calcium P (Ca-P), aluminum P (Al-P), organic P (Org-P), and residual P (Res-P) fractions (Psenner and Pucsko 1988, Rydin 2000). Particulate P adsorbed to Fe and Mn under most oxygenated conditions has been readily observed as a potential source of labile P. Aluminum hydroxide bound P is due to electrochemical forcing of charged particles, but less is known about the mobility of Al-P in lake sediments at neutral pH. Apatite P, particularly in

bone meal from fish food, can be extracted with HCl, but is considered refractory in sediments (Boström et al. 1988, Sonzogni et al 1982). Organic P is believed to be the extractant of NaOH digestion but has not been definitively fractionated further into labile and latent forms. For this reason Org-P is calculated as the difference of Al-P from total P from NaOH extraction (Psenner and Pucsko 1988). All P left from the final digestion from the P is deemed the Res-P.

Table 5. List of phosphorus forms and extraction techniques used to separate P fractions.

Fraction	Abbr.	Extraction	Mobility*	Conditions for mobility
Loosely sorbed P to silt and clay	SRP	Ammonium chloride (NH_4Cl-P)	Labile	Soluble
Iron and Manganese bound P	Fe-P, Mn-P	Bicarbonate-dithionite; $NaHCO_3$-$Na_2S_2O_4$ (BD-P)	Highly mobile under low redox potential	Low redox potential (e.g., anoxia)
Aluminum bound P	Al-P	Sodium hydroxide (NaOH-rP)	Permanently bound	Basic pH
Organic P	Org-P	Residual P remaining after sodium hydroxide extraction (NaOH-nrP)	Mobile/immobile	Approximately 60 % mobile with microbial activity
Calcium bound P	Ca-P	Hydrogen chloride (HCl-P)	Permanently bound**	Acid pH
Residual P	Res-P	Calculated, P remaining	Permanently bound**	Not extractable

* *mobility as defined by Rydin (2000)*
** *not mobile under typical environmental conditions*

Phosphorus fractions determined in lake sediments have rarely been tested for their liability (DePinto et al. 1981) and one approach to determine lability is to conduct P release experiments on sediments. Rydin (2000) compared P release rates from sediment cores collected in eutrophic Lake Erken using a flow-through cell with treatments of either oxygenated water or hydrogen sulfide enriched, low redox water (Rydin 2000). Under oxic conditions, 72 % of the Fe-P and 20 % of the Org-P were released during the three week experiment, while the Al-P, Ca-P, and Res-P fractions did not come into dissolution. This is compared to anoxic conditions where 86 % or more of the SRP and Fe-P, 60 % of the Org-P, 60 % of the Al-P, and 28 % of the Ca-P was released. The release rate under oxic conditions was half the speed and half the total amount of P released under anoxic conditions. Based on these results, roughly 45 % of the P pool in Lake Erken sediment was mobile and the other 55 % was bound for permanent burial in the sediments (Rydin 2000). Another study on Esthwaite Waters found that aluminum hydroxide P released phosphate rapidly when pH was increased. In Esthwaite Waters, 75 mg P m^{-2} d^{-1} was released at a pH of 10.5 as compared to 2 mg P m^{-2} d^{-1} at a pH of 7.6 (Drake and Heaney 1987). When pH is high, P desorption was rapid, with 50 % of all extractable Al-P released within 3 hours (Drake and Heaney 1987).

Limited P fractionation analysis has been conducted on surface sediment (0–2 cm) under and around two commercial Rainbow Trout cages and at reference sites (> 1,000 m distant) in oligotrophic Lake Huron (Table 6, DFO, unpubl. data). The relative amounts of P differs statistically between cages and references sites (ANOVA, $P < 0.05$) for all fractions with the exception of the Al-P. By applying Rydin's P mobility trends under conditions typical of Lake Huron farms (oxic surface-water interface, neutral pH, low sulfide) we can estimate that roughly 4 % of the P is readily mobile in sediments under cages and 6 % is readily mobile at reference sites.

Table 6. Preliminary results of the mean proportion of phosphorus (P) fractions (%) extracted using P fractionation techniques from surface sediments under cages, 30 m distance and at reference sites (> 1,000 m distance) for two freshwater commercial trout cage operations in Lake Huron, ON (= 9, 8 and 9 for cage, 30 m and reference sites, respectively; DFO unpubl. data).

SITE	Cage			30 m			Reference		
SRP-P (NH_4Cl-P)	7.8	±	1.4	1.5	±	0.8	0.9	±	0.9
Fe-P (BD-P)	5.1	±	0.1	4.6	±	1.3	3.2	±	2.0
Organic-P (NaOH-nrP)	2.0	±	0.6	5.2	±	3.8	16.8	±	3.1
Al-P (NaOH-rP)	5.5	±	0.7	12.6	±	8.3	9.2	±	5.3
Ca-P (HCl-P)	65.0	±	3.9	50.2	±	23.5	32.4	±	13.9
Res-P (Residual-P)	14.5	±	1.2	25.9	±	12.5	37.6	±	7.8

The most commonly understood mode of internal loading is the release of Fe bound P which occurs if anoxia develops. There are two estimates of Fe bound P from aquaculture waste: Penczak et al. (1982) reported 4.5-7 % of P from aquaculture waste was Fe bound in eutrophic Lake Glebokie, Poland and DFO (unpubl. data) estimates 5.1 ± 0.1 % of waste P was Fe bound at two commercial farms in Lake Huron. Internal P loading is facilitated by anoxia in the hypolimnion of lakes. A factor mitigating the risk of P internal loading from anoxia at aquaculture operations in Canada is the current regulatory and husbandry practices. In Ontario, the Ontario Ministry of the Environment and Climate Change (OMECC) recommends that any aquaculture siting be in a location of adequate flushing rate for the purposes of preventing deep-water anoxia (Boyd et al. 2001).

Release of iron bound P from sediments can also occur under oxic conditions, when within the sediment pore water sulfate reduction occurs and the Fe:P molar ratio falls below 2 (Gächter and Müller 2003). This results in the dissolution of P via the binding of iron to sulfide to form vivianite and pyrite, which is not readily reversible (Gächter and Müller 2003, Orihel et al. 2013, Molot et al. 2014). However, in most oxic freshwater sediments sulfide is not in good supply (e.g., 0-30 μM as compared to marine oxic sediments 50-550 μM; Joye and Hollibaugh 1995, Sutherland et al. 2007). When iron (and secondarily manganese) is in low supply relative to sulfide concentrations, Fe-P release under oxic conditions is more possible; however, release rates are slow (Rydin 2000).

Aluminum hydroxide bound P in deposits under freshwater cage farms is likely to be relatively inert since binding is dependent on alkaline conditions with pH greater than 7.0 (Drake and Heaney 1987). Sediments in Lake Huron, like other Precambrian shield lakes, are glacial sediments with high probability of PO_4 adsorption to hydroxides (Kemp and Thomas 1976). Aluminum-P around two commercial farms in Lake Huron measured from 5.5 % under cages as

compared to 9.2 ± 5.3 % at reference sites (Table 6). However, measures of sediment pH under freshwater fish farms are consistently below 7.0 (DFO unpubl. data) and so Al-P is unlikely to be released.

The P in waste deposits under freshwater cage operations are 65 % calcium bound P and only 2 % Org-P (Table 6). Calcium bound P is considered to be largely unavailable (Boström et al. 1988) and therefore represents the permanent removal of P to sediments. It is possible that some of the Ca-P in fish farm waste may be ingested by organisms with low gut pH and then some of that P would be liberated and assimilated into the foodweb or excreted; however, there is limited knowledge of the gut pH of freshwater invertebrates and from what information is available, it appears that an acidic gut may not be widespread (e.g., Sinsabaugh et al. 1985, Bälocher and Porter 1986, Austin and Baker 1988).

Typically the fate of over 70 % of P from aquaculture waste is lost to sediments (Bristow et al. 2008). This is supported by Håkanson and Carlsson (1998), who reported 74.5 % of P loading to Lake Southern Bullaren, Sweden was transported to the sediments. These results are similar to lakes without aquaculture. For example, Dillon's (1975) study of Four Mile Lake found 84.3 % retention of P in sediments, Bristow et al. (2008) reported P retention of 60, 77, and 87 % in ELA lakes 373, 227, and 302, respectively, and McCullough et al.'s (2012) P mass balance study of Lake Winnipeg reported 70 % of P transported to sediments. Internal P loading from surface sediments is not only dictated by the sediment-water conditions but by the rate of sedimentation, which can be very high under the cages (e.g., 2 g m^{-2} day $^{-1}$ or greater; DFO unpubl. data) and rapidly buries P which in turn limits P release. There is little known of the rate of release of dissolved P from aquaculture affected freshwater sediments.

Mass balance models for cage aquaculture

Lake 375, Experimental Lakes Area (ELA), ON

A whole-lake aquaculture experiment was conducted in Lake 375 at the ELA from 2002-2009. The Lake 375 experiment was a highly detailed scientific study of ecosystem impacts of aquaculture and it provides the most precise mass balance model of a freshwater aquaculture site available. In whole ecosystem manipulation studies, generally, researchers study both a manipulated system and one or more reference systems for the purposes of comparison. Lake 373 was the reference for Lake 375, where intensive Rainbow Trout aquaculture production began in 2003. Lake 373 flows into Lake 375 and has similar limnological and geological features. Both basins have simple hydrology with no groundwater inputs. In 2002, before experimentation, the P mass balance model parameters were measured for both lakes. Mass balance models quantify P inputs from the atmosphere, inflow, and fish waste relative to P outputs from outflow, lake water retention, and sedimentation. Table 7 summarizes results from 2002-2005. In many other anthropogenically disturbed lakes, tributaries play a larger role in transporting external sources of P to lakes (e.g., P loads from the Red River alone to Lake Winnipeg can measure 61 % of the P inputs; McCullough et al. 2012) and tributary loading can be highly responsive to meteorological change.

Table 7. Annual phosphorus budgets for Experimental Lakes Area (ELA) study, Lakes 373 reference and Lake 375 aquaculture production experiment from 2003-2005 (Bristow et al. 2008, Copyright 2008 reproduced with permission from NRC Research Press).

kg P per year	Lake 373				Lake 375			
	2002	2003	2004	2005	2002	2003	2004	2005
Atmospheric deposition	13.7	3.5	3.6	8.3	11.6	3.0	3.1	7.0
Inflow	2.2	0.5	2.6	1.9	6.3	1.3	9.1	6.1
Aquaculture waste	0.0	0.0	0.0	0.0	0.0	66.8	76.5	99.9
Total Input	15.9	4.0	6.2	10.2	17.9	71.1	88.7	113.0
Outflow	1.1	0.2	3.0	1.6	3.5	0.8	7.9	6.8
Lake water	21.5	21.8	22.4	27.3	15.6	19.5	23.7	35.0
Change in lake water	3.0	0.3	0.6	4.9	0.7	3.9	4.2	11.3
Sedimentation	11.8	3.4	2.6	3.6	13.7	66.3	76.6	94.9
% Sedimentation	74 %	85 %	42 %	35 %	77 %	93 %	86 %	84 %

While the Lake 375 experiment used commercial methods as much as possible, it did not attempt to simulate commercial aquaculture loading rates in this small lake. The P loading delivered by the experimental aquaculture farm (0.27-0.41 g P m^{-2}) to Lake 375 was designed to be comparable to previous fertilization studies conducted at the ELA (0.34-0.48 g P m^{-2} for Lake 227). A comparison of water volume, biomass of fish produced, and residence time of the water body suggest that the P loading in the experiment was approximately two orders of magnitude greater than what would occur in a commercial setting. Therefore, any observed impacts would be an extreme, "worst case" scenario. FISH-PrFEQ was used to predict P loading from aquaculture waste during 2003-2005 production years (Bristow et al. 2008). Feed waste was not a significant contributor to total aquaculture P load estimates (Bristow 2005, Azevedo et al. 2011), and was determined to be < 1 % total feed (Azevedo et al. 2011, DFO unpubl. data). Total P waste was predicted to be 8.7 kg P tonne^{-1} of fish produced (Azevedo et al. 2011). Total P loading to Lake 375 ranged from 67–100 kg P y^{-1} because of changing annual production amounts and FCR values (Table 7; Bristow et al. 2008).

Over three years of intensive cage production, an average of 88 % of the annual P load was exported to sediments, while P export via outflow (5 %) and P retention in the water column (7 %) were minimal. Phosphorus loads to Lake 375 were the greatest in the fall when fish biomass was the greatest (typical of commercial farm stocking-harvest trends). Over the first three years of farm operation, P sedimentation increased from 14 kg P y^{-1} in the pre-farm year to 95 kg P y^{-1} (Bristow et al. 2008). Results of the Lake 375 experiment were compared to two previous whole lake fertilization experiments: Lake 227 epilimnetic fertilization and Lake 302 hypolimnetic fertilization (Bristow et al. 2008). The proportion of P retained by sediments was similar in Lake 302 (87 %) and to a lesser extent in Lake 227 (77 %).

Phosphorus loading from the Lake 375 aquaculture operation enhanced phytoplankton productivity and biomass but to a lesser extent than Vollenweider-based models predicted (Bristow et al. 2008). This observation agrees with earlier studies that have shown that

Vollenweider-based models overestimate productivity response to aquaculture P loading (e.g., Håkanson and Carlsson 1998). Over 3 years, cage culture in Lake 375 resulted in elevated nutrients in the epilimnion with TP increasing 133 % from background levels (i.e., 6 µg TP L^{-1} in 2003 to 14 µg TP L^{-1}). The result was an increase in Chl$a$ concentration by 125 % (Findlay et al. 2009), far below predicted TP-Chl$a$ logarithmic relationships and closer to a linear response (B. Taylor, Department of Biology, University of Waterloo, pers. comm.).

Hypolimnetic oxygen in Lake 375 was observed to decline, correlated with a decrease in *Mysis diluviana* (formerly *M. relicta* Lovén) population densities, by 2007/08 (Paterson et al. 2011) and low dissolved O_2 posed a threat of internal P loading. In dimictic lakes, hypolimnetic lake water is typically oxygenated during spring and fall turn over, but Lake 375 underwent several years of incomplete mixing which, combined with increased sediment oxygen demand (SOD) from fish farm waste and associated with increased primary production, resulted in growing hypoxia in the hypolimnion. The relative contributions of SOD by fish waste and senescing phytoplankton are not known, but fish wastes in Lake 375 were confined to a small depositional zone (< 1 m) from cage (Rooney and Podemski 2010) and the oxygen uptake would have been controlled primarily by the surface area (R. Hesslein, Fisheries and Oceans Canada, pers. comm.) and the rate of transport of P through the associated boundary layer (Lorke et al. 2003). Schindler (1975) reported that at the ELA, despite long term nutrient loading and resulting eutrophication of several experimental lakes, no substantial P return from sediment was ever observed regardless of the presence or absence of anoxia. The supply of iron in Canadian Shield lakes is high and readily binds excess P in sediments. In ELA Lake 227, hypolimnetic Fe concentrations average 200 µmol L^{-1}, while sulfate concentrations had a maximum of 22 µmol L^{-1} (Cook 1984) and therefore oxygenated internal P loading by Fe-S production as described by Gächter and Müller (2003) is unlikely. Fish waste may itself be a source of sulfate, but Rooney and Podemski (2010) reported that porewater sulfide concentrations in cores taken under the Lake 375 farm never exceeded the detection limit of 0.008 µg L^{-1}. For these reasons, P in fish waste had a greater likelihood of being permanently lost to sediment rather than release to the water column by internal loading in Lake 375.

Lake Wolsey, Manitoulin Island (Lake Huron, ON)

Lake Wolsey, Manitoulin Island (Lake Huron) has been the site of a commercial Rainbow Trout cage operation since 1986 and is the subject of two P mass balance models (Hamblin and Gale 2002, Milne 2012, Milne et al. 2017). Lake Wolsey has mean water column TP concentrations of < 10 µg L^{-1} in the spring, but is closely managed because TP concentrations rise above 10 µg L^{-1} during the late summer and the lake has restricted hypolimnetic flushing and is therefore believed more sensitive to P loading. This lake is connected to Lake Huron through a man-made channel through which water both enters and leaves the lake at an exchange rate of 14.3–15.1 m^3 s^{-1} (Hamblin and Gale 2002, Milne 2012). Lake Wolsey has a more complex hydrology than Lake 375; it is on limestone bedrock with substantial groundwater exchange, as well as multiple surface inflows, all making mass balancing considerably more challenging than at the ELA. Residence time for Lake Wolsey is relatively short at 0.54 y^{-1} and exchange with Lake Huron is via the epilimnion (Milne 2012). The catchment is 8,104 ha of both forested and agricultural land use (Milne et al. 2017).

In Lake Wolsey, aquaculture production has averaged 250 tonnes y^{-1} since 1986 (Milne et al. 2017). Based on an estimated 8.7 kg P tonne^{-1} fish (Azevedo et al. 2011), P loading from aquaculture should amount to roughly 2,175 kg P y^{-1}. Values provided by Milne et al. (2017) break down aquaculture P loading into 1,383 kg solid P waste, 63 kg apparent feed P waste and 714 kg dissolved P waste (2,160 kg P total). The solid P waste was believed to be an overestimate by Milne, who then reduced the value by 1/10th (or 138 kg), based on Phillips (1993) study and arrived at a total fish farm contribution of 915 kg P y^{-1}. Phosphorus loadings to

the lake were estimated to be largely from overland flow (1,120 kg) and the fish farm (915 kg y^{-1}), in addition to inlet exchange (539 kg y^{-1}), ground water (305 kg y^{-1}), dwellings (219 kg y^{-1}), internal loading (186 kg y^{-1}), precipitation (79 kg y^{-1}) and leaf litter (8 kg y^{-1}; Milne 2012, Milne et al. 2017).

Internal P loading from sediments was estimated to be 6.5 % of the total P loading to Lake Wolsey based on the duration of deep-water anoxia (Milne 2012). Internal loading in Lake Wolsey was restricted by the small surface area (1.7 % lake bottom) that is periodically anoxic. OMECC water quality monitoring has reported that anoxia was more extensive than the area used by Milne (19-42 % total surface area in Lake Wolsey) and that dissolved oxygen (DO) concentrations have been declining in the hypolimnion from 2007–2010 (N. Diep, Ministry of Ontario Environment and Climate Change, Environmental Monitoring and Reporting Branch, Toronto, ON, pers. comm.). Lake Manitou, Manitoulin Island ON has also experienced the same long-term decline in hypolimnetic DO since the 1990s, which has been attributed to regional warming and changing nutrient dynamics in the basin (Nelligan et al. 2016, 2017). For this reason, internal P loading to Lake Wolsey may be expected to increase in the future, as regional warming trends are predicted to continue.

Effects of the fish farm P loads in Lake Wolsey were estimated to increase water column TP concentrations by 5 µg L^{-1} (Hamblin and Gale 2001) and 2 µg L^{-1} (Milne et al. 2017), based on continued loading of P annually from aquaculture activities. Water column TP concentrations have remained relatively constant, averaging 8 µg L^{-1} in spring and 11 µg L^{-1} in fall (Milne 2012). Milne et al. (2017) suggest that Lake Wolsey may have reached steady state based on anthropogenic P inputs, including 30 years of continued aquaculture inputs, and water column TP concentrations remaining relatively constant. The effects of P loading from aquaculture may also be diminished by the high flushing rate of 199 days of Lake Wolsey.

Milne's work surpasses efforts made by Hamblin and Gale (2002), but this P mass balance still contains uncertainty about the accuracy of estimates of both the gain and loss of P from the system because the sampling regime was sparse and the model relied heavily on literature values derived from other sites. Estimates of P from tributaries were generated from few locations infrequently sampled and the majority of the tributary sampling occurred after the year for which the model predictions were generated (2009 and 2010 versus 2007). Furthermore there was no assessment of interannual variability in precipitation and therefore if watershed P loading differed from year to year. Groundwater inputs were estimated from single day deployments of only 5 seepage meters and three piezometers in May 2009 even though groundwater inputs to the lake were believed to be substantial. Phosphorus loading from dwellings, leaf litter, and sport fishing estimates were based on previously published data sometimes from other locations with minor adjustments to account for the Lake Wolsey watershed. Milne estimated P loss to sediments by deploying one sediment trap twice (on August 14 and 18, 2007) at a single location for four to five days. Sedimentation of P for Lake Wolsey was estimated to be 2.0 g m^{-2} d^{-1} from a trap placed directly under a cage but sedimentation rates will be highly variable both seasonally and spatially. However, Wetton (2012) deployed sediment traps in a transect originating under the fish farm in Lake Wolsey in 2007 and reported P sedimentation rate 100 m away from cages was two to three orders of magnitude less than that observed under the cages, depending on the month sampled. Milne's estimation of P sedimentation in Lake Wolsey is therefore likely a substantial overestimate when the rate measured under a cage was applied to the entire lake bottom area. Overall, this mass balance budget of P inputs from aquaculture leaves a good deal of uncertainty regarding the accuracy of the various budget components. Mass balancing a large and complex system like Lake Wolsey is a significant challenge.

Predicting the effects of P waste from cage aquaculture on lakes

Research has improved the understanding of the relationship between P and primary production. Primary production typically has a strong relationship with Chl*a*, the light-sensitive, green pigment essential in absorbing light during carbon fixation via photosynthesis (Håkanson and Boulion 2002). The understanding of P-Chl*a* relationships originated from Vollenweider-based models with the most widely cited being the Dillon and Rigler (1974) model. From 1974–2002, models expanded P-Chl*a* regression to include a number of abiotic variables including lake morphology, dissolved oxygen, and settling velocities (Chapra and Tarapchak 1976, Larsen and Mercier 1976, Dillon and Molot 1997). These empirical P-Chl*a* relationships for primary productivity are based upon P being the growth limiting nutrient, and this may not be applicable to a small number of lakes (Håkanson and Boulion 2002).

P loading to lakes not only affects lake primary productivity, but secondary production in the form of more consumers. Models predicting consumer biomass or production from P have been more successful when consumers are categorized by functional groups (e.g., planktivore or piscivore) rather than taxa (e.g., family or species), and when models incorporate biotic distribution in the lake (e.g., littoral or benthic) (Vadeboncoeur 2002). The demonstration of empirical relationships between P and zooplankton (Brett et al. 2000), zoobenthos (Rasmussen and Kalff 1987), and fish productivity and biomass (Matuszek 1978, Hanson and Leggett 1982) highlights the intrinsic value of P to lake ecosystems.

As mesocosm and whole lake experiments provided new empirical biotic-P relationships, improvements were made to ecosystem response models. When food webs shifted to include larger taxa dominating the phytoplankton, P loss to sedimentation accelerated in temperate lakes (Mazumder et al. 1992, Bruce Ronzio 2007). Models then characterized this loss through changes to particulate P settling rates. Our ability to predict the effect of aquaculture P waste inputs on temperate lakes may benefit from further developing our understanding of loss of particulate P to the sediments and potential for internal P loading.

Predicting ecosystem response to P from cage aquaculture waste

Models for predicting ecosystem response to P loading have been under development since the 1970s and are available for estimating P accumulation, primary production, and biological oxygen demand (BOD) during eutrophication but they have proven less suitable for predicting effects of P loading from aquaculture. Håkanson et al. (1998) warned that Vollenweider-type models (i.e., used in McDonald et al. 1996, Yokom et al. 1997) typically overestimate water column P concentrations in response to aquaculture P loading where actual measures are less than 20 % of estimated TP concentrations in both salt (Nordvarg 2001) and freshwaters (Håkanson et al. 1998, Johansson et al. 1998, Frier et al. 1995). Johansson and Nordvarg (2002) echo this sentiment in their comparison of traditional mass balance models (i.e., Vollenweider and Dillon-Rigler models); they found TP concentrations predicted in lakes with fish farm operations were twice the TP concentrations measured. For this reason, Håkanson and colleagues set out to redesign P response modelling that better represented P loading from different sources.

Håkanson and Carlsson (1998) tested the Lake Eutrophication, Effect, Dose, Sensitivity model, also known as LEEDS model, on mesotrophic Lake Southern Bullaren, Sweden to determine the contribution of fish farming to the occurrence of nuisance algal blooms. LEEDS includes P in both dissolved and particulate forms and eight main internal processes: sedimentation, mineralization, resuspension/advection, diffusion, mixing between strata, burial, biotic uptake, and release of P from biota (Figure 10; Håkanson and Carlsson 1998). Input variables from LEEDS can be modified to suit a diversity of lakes (e.g., Lake Simcoe with latitudinal, trophic diversity from North et al. 2013). In Lake Southern Bullaren, fish farmers were producing 70

tonnes y^{-1} in 1980, but by 1990 harvests were estimated to be at or near 500 tonnes y^{-1} (Håkanson and Boulion 2002) and severe cyanobacterial blooms were recorded in the late summers of 1986–1992 (Johansson et al. 1998). Phosphorus waste from the fish farm was found to be 25 % of the total P loads to the lake (1,727 kg P y^{-1}) and 9 % of the deposited P (Johansson et al. 1998). Particulate P was delivered to the sediment at a rate of 6,316 kg P y^{-1}, 44 % of which was allocated to permanent burial (Figure 10); however, estimates of sedimentation contained the greatest uncertainty in the model. The model estimated that 50 % of the total P deposited was resuspended with 60 % of P resuspension reaching the epilimnion (Håkanson and Carlsson 1998). Rates for TP flux from sediments to the surface waters ranged from 59-279 kg P month^{-1} (Håkanson and Carlsson 1998). The direct uptake of P by wild fish was estimated to be 38 % of the fish farm waste P load (Johansson et al. 1998); this estimate was increased to 49 % by Håkanson and Boulion (2002). Direct uptake of P by wild fish represents a substantial rerouting of P away from primary production and contributes to the overestimation of impacts to water column P and Chl*a* in Vollenweider-type models. LEEDS predicted a rise in wild fish populations (Håkanson et al. 1998) through direct uptake of aquaculture waste, a phenomenon touched on by other studies (Gabrielsen 1999; Kullman et al. 2009, Wellman 2011).

LakeWeb is a modification of LEEDS that includes more complex biotic interactions and predicts changes in biomass and production for nine functional groups: phytoplankton, bacteria, herbivores, predatory zooplankton, prey fish, predatory fish, zoobenthos, macrophytes, and benthic algae in response to changing TP concentrations (Håkanson and Boulion 2002, Håkanson et al. 2003). The LakeWeb model enables both P mass balance models and empirical relationships between biotic-abiotic reactions to combine and simulate lake-wide responses to perturbations like eutrophication, humifications, acidification and climate change (Håkanson and Boulion 2002). An integrated system of biotic and abiotic factors is favoured to better inform managers of the effect of aquaculture on lake systems.

The FISH-PrFEQ model, while accurately predicting P outputs, would result in overestimation of water column P concentrations from aquaculture waste if one simply considers waste output being diluted into the lake water volume. For example, in Lake 375 epilimnetic TDP was predicted to rise from background measures of 6.3 µg L^{-1} in 2002 to 25 µg L^{-1} in 2003 and again to 35 µg L^{-1} in 2004 when only 14.2 µg L^{-1} was measured (Bristow et al. 2008, Azevedo et al. 2011). The fish waste outputs from FISH-PrFEQ are very accurate, but the model does not include any biotic or abiotic reactions that occur once waste P leaves the fish. It is a nutritional model not an ecosystem response model. There is potential for a valuable management tool to be developed were FISh-prFEQ predictions of waste outputs coupled with an ecosystem model that integrates empirical biotic and abiotic processes.
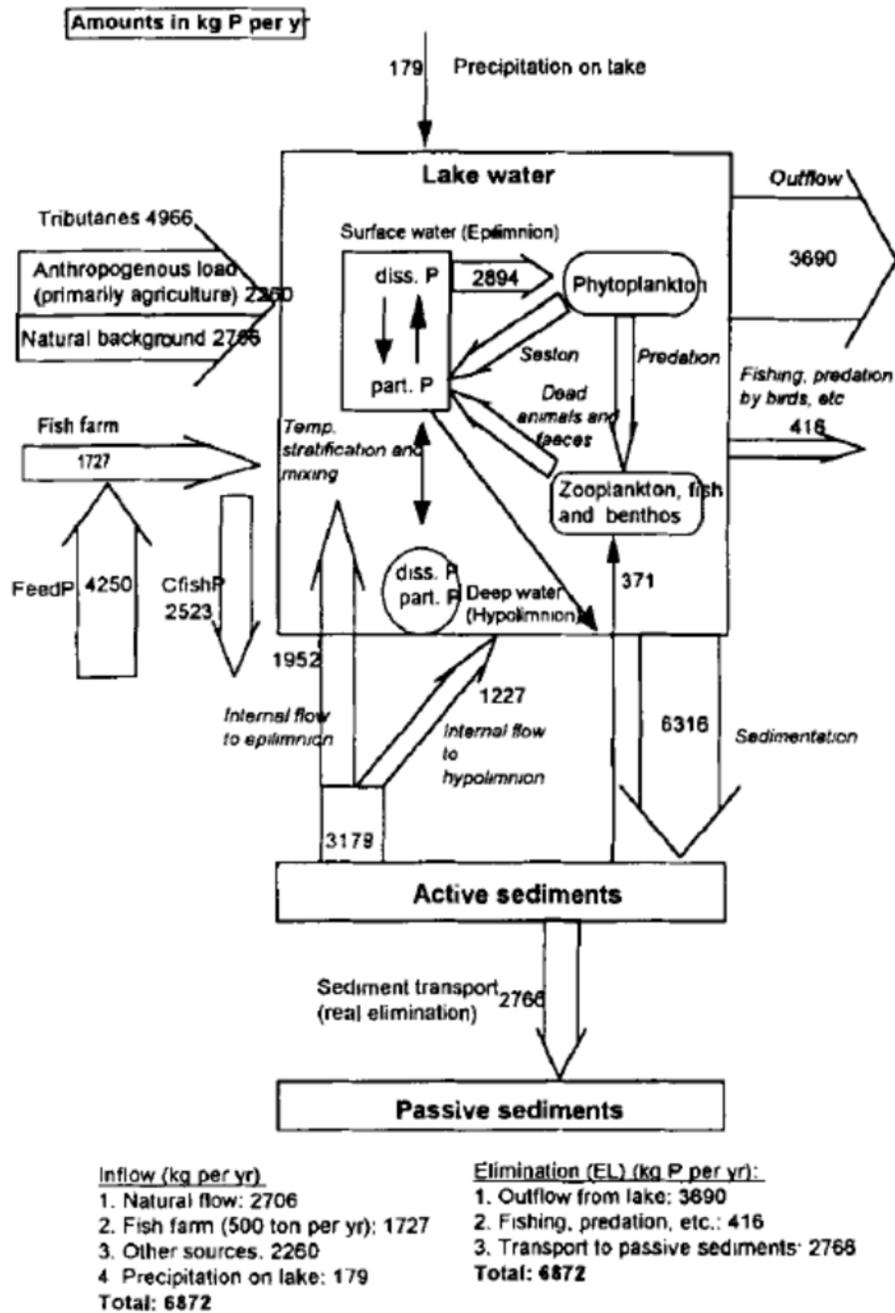
Figure 10. A schematic of the phosphorus (P) budget for Lake S. Bullaren, Sweden with a fish farm of 500 tonnes y⁻¹ generating P loading values in kg P y⁻¹ using the LEEDS model (reproduced from Håkanson and Carlsson 1998, Copyright 1998, with permission from Taylor and Francis).

Monitoring of cage aquaculture P waste

Licensing of fish farming currently falls within the jurisdiction of the Provinces, except in British Columbia where Fisheries and Oceans Canada is the licensing agency. Ontario produces 59 % of the total trout production in Canada (Figure 11; FAO 2011) and an even greater proportion of cage production: all but two of the Canadian freshwater cage operations are located in Ontario. In Ontario, the Ontario Ministry of Natural Resources (OMNR) issues aquaculture licences and the OMECC advises the OMNR on the water quality monitoring program that is attached as a condition to the aquaculture licence in order to ensure that water quality objectives continue to be met. The OMECC monitoring protocol is based on advice in Boyd et al. (2001). Those recommendations were influenced heavily by examining the decommissioned fish farm situated in the La Cloche region of North Channel, Lake Huron. The most significant contributor to the development of deep water anoxia and algal blooms at La Cloche was the lack of circulation, or hypolimnetic flushing, which is driven largely by bathymetry (Gale 1999). A multi-agency workshop held in 1998 classified habitat types based on suitability for aquaculture production. Sites were classified into three groups (Boyd et al. 2001): Type 1 was defined as an enclosed basin with limited flushing, hence greater vulnerability to eutrophication and thus deemed inappropriate for aquaculture; Type 2 was defined as a partially exposed site with good epilimnetic and metalimnetic flushing rates, but where the hypolimnion does not exchange water and aquaculture needs to proceed with caution; and Type 3 was defined as a very exposed site with hypolimnetic waters flushed frequently. La Cloche would have been defined as a Type 1 site because of poor flushing; average water depths of 14–16 m were locally bounded, residence times were 160 days and the area was prone to deep water anoxia (Boyd et al. 1998, 2004, S. Naylor, Ontario Ministry of Agriculture, Foods and Rural Affairs, pers. comm.). Based on water quality monitoring from 1998 to 2008 from up to 6 active aquaculture sites and including La Cloche Channel, OMECC states that "nutrient pollution and oxygen depletion effects can manifest themselves over entire basins at Type 1 sites (e.g., La Cloche Channel in 1998) but Type 3 sites are not susceptible to these problems" (N. Diep, Ministry of Ontario Environment and Climate Change, Environmental Monitoring and Reporting Branch, Toronto, ON, pers. comm.).
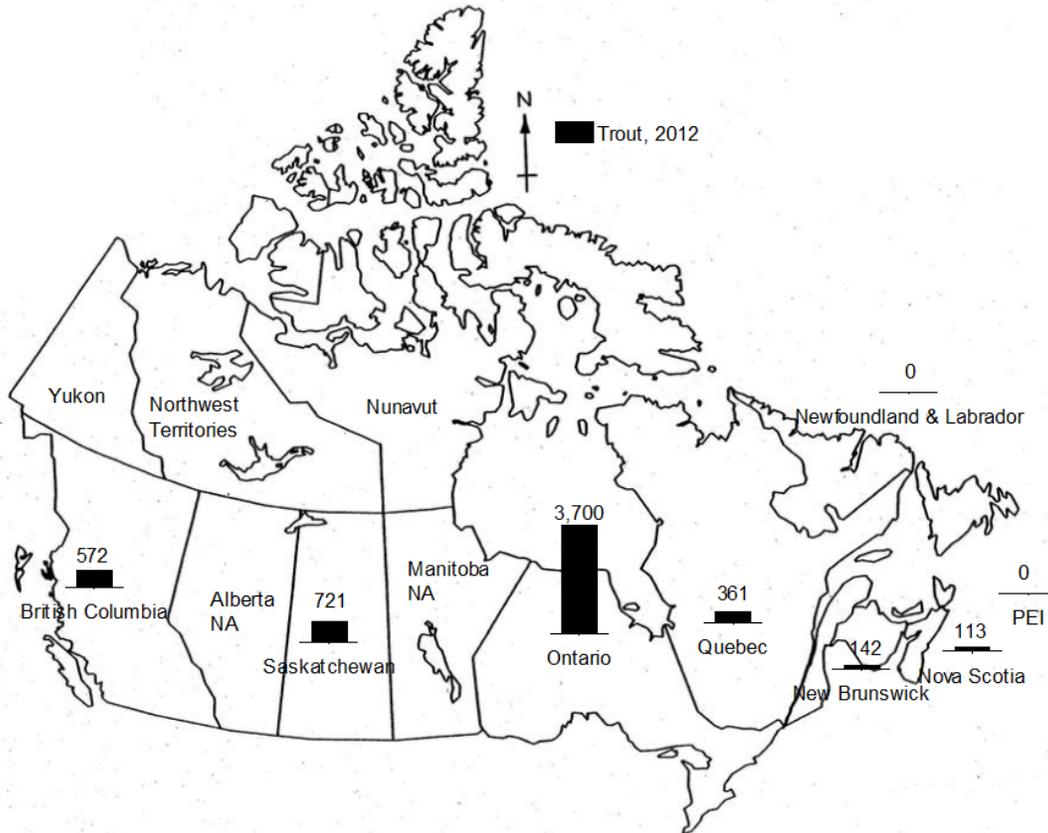
Figure 11. Canada's cultured trout production (tonnes fish year^{-1}) based on data from Statistics Canada 2012 and C. Podemski, Fisheries and Oceans Canada, pers. comm. No data available for Alberta, Manitoba or Northern Canada.

Water quality monitoring protocols developed by the OMECC were based on studies of the water column profiles (dissolved oxygen, temperature, pH), nutrient (P, N) and elemental concentrations, biological oxygen demand, water clarity (turbidity, Secchi disk depth) and sediment cores around commercial cage aquaculture sites in Lake Huron (Boyd et al. 1998, 2004). Today's operational water quality monitoring focuses on dissolved oxygen and TP concentrations, and detecting exceedances relative to up and downstream reference sites (Boyd et al. 2001).

The water sampling regime includes: a) five regional background water quality samples collected and analyzed by OMECC to provide information on spatial and inter-annual variability at reference sites; b) three or four cage water quality samples taken at 30 m from the cages or at the distance of the land use permit (whichever is shorter); and c) two reference sites proximal to the cages that have similar water depth, circulation, and exposure upstream and downstream of the fish cages (Anonymous 1994, Boyd et al. 2001). At these water sampling sites, TP is to be sampled 11 times during the open water season (i.e., three during spring turnover, five during stratification, and three during fall turnover). Samples are not taken at discrete water depths, but rather integrated over the depth of the fish cages. A regulatory threshold (Provincial Water Quality Objective or PWQO) of the median water TP concentration of 10 μg L^{-1} was set at all sites except where background TP measures were > 10 μg L^{-1}, then special consideration and consultation was to be given to identify a more appropriate limit (e.g., Lake Wolsey; Boyd et al. 2001, Milne 2012).

Water quality analyses also include weekly to monthly temperature and dissolved oxygen measures profiled at 1 m intervals. Dissolved oxygen and temperature profiles are used to assess impact to warm- or cold-water fish habitat (based on the site characteristics); these are also parameters that farmers routinely monitor to assess conditions for their livestock. Monitoring results are presented in the form of an annual report generated by a third party (a qualified consultant), that outlines the site locations, results of chemical analyses (to be conducted at a laboratory accredited by the Canadian Association for Laboratory Accreditation), and feed inputs.

The monitoring of water chemistry ensures that a change to local trophic status (as measured by dissolved oxygen and P concentrations) will be detected so that any necessary mitigative actions can be undertaken. Measurements of dissolved oxygen below the PWQO, for example from 10–15 °C the PWQO is 6 mg L^{-1} (54 %), will trigger restricted feeding allowances and greater frequency of monitoring until levels return above the PWQO (Boyd et al. 2001). The onus is on the operator to improve DO conditions (Boyd et al. 2004) and if conditions are not improved then a reduction in production may be required. Median turnover P values must be ≥ 10 μg L^{-1} and statistically greater than at the reference location to trigger action; this P concentration limit may be adjusted to take into consideration elevated background P levels for a Type 2 site (Boyd et al. 2004). Actions in response to a TP exceedance may include an audit, increased P sampling frequency, P abatement planning, reduced feed usage, and confirmation that algal assemblages adjacent to the farm lack nuisance taxa. Today, no reports of elevated Chla or phytoplankton community composition change at fish farms have occurred in Lake Huron (N. Diep, Ministry of Ontario Environment and Climate Change, Environmental Monitoring and Reporting Branch, Toronto, ON, pers. comm.) or Lake Diefenbaker (Otu et al. 2017). Under extreme cases, the OMNR does have the right, if necessary, to revoke a Land Use permit; however, this has only been done once (at La Cloche, Type 1 site) and has not been required during the past 15 years.

Aquaculture licence agreements can include stipulations like annual feed limits (kg y^{-1}), maximum number of cages, and restricted P content (%) in feed. Currently, freshwater Rainbow Trout operations must feed only low P diets (≤ 1.3%). Since the P content of fish feed is directly related to P release, low P diets are essential to decreasing dissolved and particulate P waste.

Phosphorus loads to the North Channel, Lake Huron

Estimation of TP loading to the Great Lakes began in 1967 in an effort to mitigate the effects of eutrophication (IJC 1972). The IJC published annual reports of TP loading to the Lakes Superior, Michigan, Huron, Erie, and Ontario from 1974 to 1979, after which time, annual reporting ceased. In 2012, Dolan and Chapra published TP loading estimates for 1994-2008 following the IJC procedures (Figure 12; Dolan and Chapra 2012). Dolan and colleagues retrieved the federal, state, and provincial monitoring data needed to estimate loads (Dolan et al 2011). The method of estimating loads included the mass balance of P from point sources (monitored industrial and municipal), atmospheric deposition (wet and dry), tributary inputs, and inter-lake exchange (Dolan 1993, Dolan and Chapra 2012), based on DePinto et al. (2007). This method does not account for other P inputs from groundwater, cottage developments or cage aquaculture. Spatially, there were only a handful of meteorological stations to estimate wet deposition (and no dry atmospheric deposition was collected) for all the Great Lakes, which span a great geographic area that has a variety of local weather patterns. Dry deposition was deemed to be equivalent to wet deposition; however, some research shows this would likely be an underestimate (Jassby et al. 1994; Anderson and Downing 2006). Tributaries are the largest contributors of water and P to the lakes (Figure 13; Dolan and Chapra 2012).
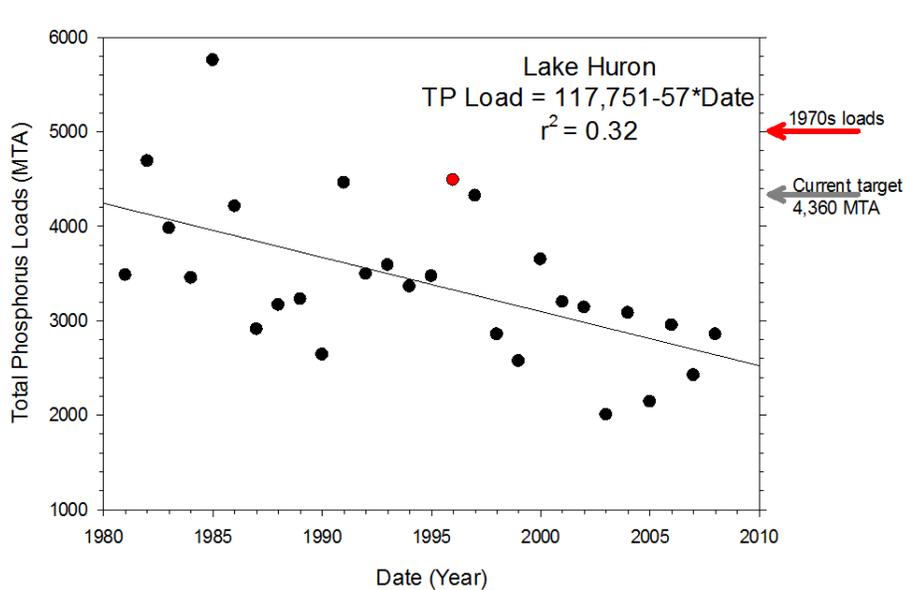
Figure 12. Total phosphorus loads (MTA) to Lake Huron from 1980 to 2008 with linear regression (based on supplementary data from Dolan and Chapra 2012). Data point in red, 1996, was the only year that International Joint Commission (IJC) phosphorus loading targets were exceeded during the study period 1994-2008.
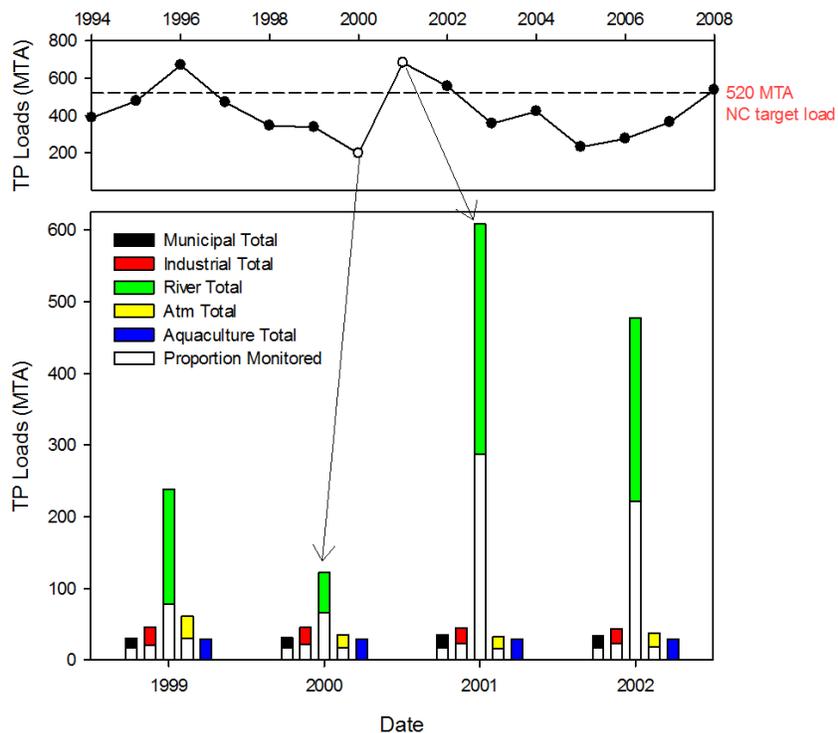

Figure 13. a) Total phosphorus loads (MTA) to the North Channel, Lake Huron from 1994-2008 with the dashed line indicating International Joint Commission (IJC) target loads. b) The breakdown of each contributing phosphorus (P) loads to the North Channel during 1999 to 2002. Vertical bars are blocked off in white to present the proportion of P directly monitored and coloured proportion denotes the unmonitored P loads that were estimated (based on supplementary data from Dolan and Chapra 2012).

P loads to Lake Huron have been well below P targets (Figure 12; Dolan and Chapra 2012, IJC 2012). There were, however, taste and odour issues in Saginaw Bay, Lake Huron in 13 of the 14 years presented (Dolan and Chapra 2012). Net P loads for the whole lake basin do not adequately present the spatial heterogeneity of P sources and regional responses to P loads. For this reason, P loads for Lake Huron were segmented into North and South Main Huron, North Channel, Georgian Bay, and Inner and Outer Saginaw Bay (IJC 1987).

Dolan and Chapra (2012) reported that the target load of 520 MTA for the North Channel, Lake Huron was exceeded during 4 of the 14 years analyzed (in 1996, 2001, 2002, and 2008). The waters around Manitoulin Island are the site of most cage aquaculture. The North Channel catchment has very few municipalities (Saulte St. Marie, Espaniola) or industrial point sources, but extensive areas of crown land, provincial parks (Little White River, Mississagi, Matinenda, La Cloche, and Kilarney), and reserve land (Atikameksheng, Sagamok, Serpent River, Mississauga, Thessalon, Garden River, and Batchewana First Nations). When examining the P loads more closely (Table 8), the years of P exceedances occurred during wet years when rainfall was high and tributaries contributed a greater proportion of the P load (Dolan and Chapra 2012). The years 2000 and 2001 were plotted to show the large inter-annual variability of P loads to the North Channel, which depend strongly on annual precipitation (Figure 13). This is typical of P pollution from diffuse sources. Estimates of P loads have also been found to have greater uncertainty when tributaries have high catchment populations, low base flow or low frequency sampling (Johnes 2007).

Long-term monitoring of P loads has tracked an increased amount of dissolved P entering the Laurentian Great Lakes since 1995 via Ohio tributaries from agricultural fields (Joosse and Baker 2011), whereas total P and dissolved P from Ontario tributaries may be declining (Dolan and McGunagle 2005). The IJC will now begin a program to monitor P loads in both dissolved and particulate forms (IJC 2012). Dissolved P is often bioavailable and does not remain long in dissolution in the water column as biotic uptake is rapid, and SRP turnover rates can be measured in minutes (Berman 1988, Boström et al. 1988, Guy et al. 1994). For this reason, measurement of SRP is difficult to accurately obtain, and is why most monitoring programs have focused on total P until now.

For the purposes of estimating the contribution of aquaculture to P loading in the North Channel, 2006 was the most recent year for which both published cage aquaculture trout yields in ON (Moccia and Bevan 2007) and published P loading data for Lake Huron (Dolan and Chapra 2012) were available. A P load estimate from the cage aquaculture industry in 2014 was approximately 8.7 kg P tonne^{-1} fish. Aquaculture yields in 2006 from Ontario were estimated to have been 3,800 tonnes of fish (note: slightly more than 1,000 tonnes of Ontario production is believed attributable to a farm in Georgian Bay, which is not part of the North Channel) and the industry therefore is estimated to have contributed 33.1 MTA of TP, of which 11.8 MTA would have been in the form of dissolved P. This quantity of P is much less than the wet atmospheric P load to the North Channel (Figure 13; Dolan and Chapra 2012). The proportion of total P loading due to aquaculture was 12 % of the total P and 10 % of the TDP to the North Channel and will likely need to be included in future P management strategies to the region. It should be noted that 2006 was a dry year with low catchment P loading so the estimate of proportional loading may be high. With climate change, it can be expected that hydrological changes will also lead to more frequent years of high catchment P loading, while aquaculture production from licenced farm sites has remained more or less constant since 2000 (Figure 4).

Table 8. Total phosphorus (P) loads to the North Channel in 2006 (data from Dolan and Chapra 2012) including an estimate of total cage Rainbow Trout aquaculture P loading (Moccia and Bevan 2007). Note: North Channel Total P load targets are set at 520 MTA.

North Channel TP Sources	Total Area (km^2)	TP load - Low value	TP load - High value	Low TP/Total (%)	High TP/Total (%)	TDP loads (MTA) 2006
Aquaculture Production (2006 production 1.660 tonnes)	0.15[1]	14.6	14.6	5.4 %	4.6 %	5.3
Industrial point sources (St. Mary's River)		8.7	29	3.2 %	9.1 %	6.3
Municipal point sources (Sault St. Marie waste water treatment plant outflow)		5.1	5.1	1.9 %	1.6 %	3.6
Channel (municipal waste)		1	1	0.4 %	0.3 %	1
Unmonitored Indirect source	8,912	16	16	5.9 %	5.0 %	3
Atmospheric Wet Deposition		48	48	17.8 %	15.0 %	33
Atmospheric Dry Deposition		48	48	17.8 %	15.0 %	0
Spanish River[2]	12,194	98	98	36.3 %	30.7 %	32
Mississagi River	9,300	20	20	7.4 %	6.3 %	2
Les Cheneaux Delta Complex	1,980	0.9	30	0.3 %	9.4 %	0.2
Serpent River	1,313	2	2	0.7 %	0.6 %	0.4
Blind River	1,088	2	2	0.7 %	0.6 %	0.3
Garden River	1,052	2	2	0.7 %	0.6 %	0.3
Thessalon River	938	2	2	0.7 %	0.6 %	0.2
Root River	109	2	2	0.7 %	0.6 %	0.1
Big Carp River	52	0.1	0.1	0.0 %	0.0 %	0.01
East Davignon Creek	18	0.04	0.04	0.0 %	0.0 %	0.005
TOTAL		270.4	319.8	100.0 %	100.0 %	87.7

[1]In the North Channel the fish waste was based on only a few farms. Aquacage and Lake Wolsey sites were removed as sources of P to the North Channel
[2] Spanish River comprises of 40 MTA from point sources
Low P loading estimated that only 3 % of Les Cheneaux flowed to North Channel (Zhao et al. 2012) and that only 30 % St. Mary's River (includes Saulte St. Marie WWTP) entered the NC (David Schwab, NOA, pers. comm.).
High P load estimations assumed 100 % of Les Cheneaux River and St. Mary's River P loads would enter the North Channel.

ASSESSMENT OF THE P INPUTS FROM CAGE AQUACULTURE WASTE

This review does not constitute a formal risk assessment of P inputs from freshwater aquaculture operations, but rather aims to characterize some of the risks that might be associated with P loads from freshwater cage aquaculture.

The threat of P inputs from cage aquaculture causing eutrophication or anoxia in Canadian freshwaters has been declining in Ontario since 2001 recommendations (Environment Canada 2001, Boyd et al. 2001) and today's aquaculture industry presents a small risk. In Ontario, the risks of eutrophication are minimized by conditions for water and sediment quality attached to the licence agreements. Legislation permits the regulation of the industry and monitoring agreements enable provincial bodies to identify non-compliance. There are fish farm operations that fall outside of the provincial and federal authorities jurisdiction to regulate, such as aquaculture production conducted by First Nations, which are regulated under their own governing bodies. That does not prevent First Nations operators from using the same government guidelines to ensure environmental sustainability. In the past some First Nations operators have participated in scientific evaluations of water quality and sediment core benthic invertebrate populations around trout farms (C. Podemski, Fisheries and Oceans Canada, pers. comm.).

Although the freshwater cage aquaculture industry is currently sustainable in Lake Huron, growth of the industry (or expansion of any activity that contributes to the P loading) requires careful consideration of the total amount of P loadings and the location. The IJC is in the process of revising P target loads (520 MTA North Channel) and in the future is anticipated to include nearshore and offshore limits. It is anticipated that redistribution of P loadings will result in areas of concern in the nearshore that will be identified for lower P targets, SRP loadings in particular, and potentially higher P loading targets will be allowable in the offshore. The P loading from aquaculture industry in North Channel today is much less than wet atmospheric P inputs. Because Great Lakes P loadings depend highly on diffuse sources of P pollution, high rainfall years can wash in greater P from tributaries and result in P exceedances, but reduced annual precipitation and lower water levels could reduce the likelihood of P exceedances. Long term monitoring of tributaries is essential in anticipating P loads under future climate change trends. Any expansion of the aquaculture industry will need to continue to follow changes to the management strategies in the Great Lakes by the IJC.

Expansion of freshwater cage aquaculture in Lake Huron also requires appropriate site locations. Currently, operations cannot expand cages, docks or anchorage points without written authorization by the OMNR District Manager. Operators must secure and maintain a Land Use Permit specific to the location. Today, there are restrictions on sites based on proximity to other cage sites, cottage developments, navigation lanes, spawning grounds, national parks, tributary outlets, and species at risk habitat (Table 9; DFO, unpubl. data). Should the industry expand, sites still must meet the licence agreements with high flushing rate (Type 3 sites) and adequate water depths (> 16 m) that will continue to ensure a sustainable industry. Future expansion requires careful placement and consultation to meet these regulations.

Furthermore, confounding variables like the introduction of invasive species or climate change may challenge our current understanding of the threats of P from freshwater cage operations. Sound modelling of biotic and abiotic factors that can be calibrated with current monitoring values will better aid future predictions of lake wide responses to P loads.

Table 9. Rules used for demarcating areas inappropriate for cage culture siting for GIS layers (DFO unpubl. data).

Layer	Red Zone Ruling
Operational Cage Sites	No new cage site within 3000 m of an existing site
Water Protection Act Obstructions	No cage site within a minimum of 100 m of an existing NWPA obstruction
Navigable Waters Protection Act (NWPA) Obstructions	No cage site within a minimum of 100 m of an existing NWPA obstruction
Whitefish Spawning Area	No cage site within 100 m of spawning area
National/Provincial Parks and NGO Reserves	No cage site within 100 m of park/reserve boundary
Tributary Mouth	No cage site within 1000 m of tributary mouth
Species At Risk	No cage site within 5000 m of a location where SAR has been found

SOURCES OF UNCERTAINTY

There is considerably more uncertainty in the measurement of watershed P inputs to lakes than the P inputs from aquaculture operations. Measurement of external P loadings (particularly from non-point sources of P) needs to be improved upon to capture the annual total loads, inter-annual variability, the dissolved and particulate P fractions, and event-based loads. Inadequate monitoring compromises the ability to calculate accurate P loadings, to set target loads or to predict cumulative effects in the nearshore. Current monitoring excludes a number of rivers, dry deposition, adequate spatial assessment of atmospheric deposition, event-based P measures from tributaries, and dissolved P concentrations to name a few.

There is uncertainty whether other lake conditions (i.e., different trophic state, $Fe:SO_4$, size, and flushing rate) respond similarly to P loads from aquaculture waste as compared to other watershed P inputs. Modelling and monitoring of lake environments other than Lake Huron (the site of most freshwater aquaculture presently occurring in Canada) will better enable the accurate prediction of the effects of P loading from aquaculture wastes. There were a number of papers on Lake Diefenbaker, SK in a special issue with Journal of Great Lakes Research that may provide valuable insight into P cycling in a reservoir with a large commercial aquaculture operation (Dubourg et al. 2015, Hewlett et al. 2015, Hudson and Vandergucht 2015, Lucas et al. 2015, North et al. 2015).

There is uncertainty whether aquaculture cage siting is best characterized by Type 1-3 classifications scheme given the number of limnological tools available to date. There is a desire to identify site characteristics other than flushing that could be considered during the site licensing process.

There is uncertainty in the lake response models applied to today's aquaculture P wastes. Current models fail to adequately predict water column P concentration and result in uncertainty of the lake response to aquaculture P loadings, largely in the form of faeces. There is a need to develop and improve P models for prediction, management and mitigation of aquaculture P waste. Several sophisticated P response models exist (e.g., LEEDS, Håkanson and Carlsson

1995, 1998). There is also well established modelling and data on *Cladophora*, dreissenid populations, P and Chl*a* concentrations in the nearshore of Lake Ontario, Erie, Michigan, and Simcoe (e.g., North et al. 2013). These tools should be applied to refine the effects of P loading to the nearshore.

KNOWLEDGE GAPS

Improved knowledge of the physical (e.g., climate, water depth, water temperature), chemical (e.g., redox, Fe, sulfate), and biological (e.g., invertebrate, microbial interactions) processes acting on the accumulated fish waste is needed to understand the remobilization of P. This information will help to assess the potential effects associated with the addition of aquaculture P loads to the nearshore.

Should fallowing be implemented as a mitigation strategy against the effects of P loading, there is a need to better understand the timeframes for P remediation at sites. Given that aquaculture waste is largely deposited below cages and results in P being exported to the sediments, an effective fallowing strategy requires further knowledge on waste decomposition rates and P mineralization and burial rates.

Offshore freshwater cage operations are anticipated to become a viable means of industry expansion in the coming years with advances in remote feeding and cage design. Due primarily to the deeper water sitings, there is a need to understand how aquaculture P wastes would be dispersed during sedimentation and how the potential for internal P loading may change in offshore areas. A cost-benefit analysis would be useful in comparing offshore and nearshore aquaculture sites, given that enhanced P loading to Lake Huron's offshore may counter current oligotrophication trends (potentially leading to more favourable food web effects) and fewer stakeholders would have opposition to the cage aesthetics.

REFERENCES

Ackefors, H., and Enell, M. 1990. Discharge of Nutrients from Swedish Fish Farming to Adjacent Sea Areas. Ambio 19: 28–35.

Alabaster, J.S. 1982. Report of the EIFAC Workshop on Fish-Farm Effluents, Silkeborg, Denmark, 26–28 May 1981. EIFAC technical paper no. 41. 166 p.

Anderson, K.A., and Downing, J.A. 2006. Dry and wet atmospheric deposition of nitrogen, phosphorus and silicon in an agricultural region. Water Air Soil Pollut. 176: 351–374.

Anderson, N.J., Jeppesen, E., and Soendergaard, M. 2005. Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. Freshw. Biol. 50: 1589–1593.

Anonymous. 1994. Water Management: policies, guidelines, provincial water quality objectives of the Ministry of Environment and Energy. Ministry of Environment and Energy, Ontario.

Appleby, A.G., and Brinkhurst, R.O. 1970. Defecation rate of three tubificid oligochaetes found in the sediment of Toronto Harbour, Ontario. J. Fish. Res. Board Can. 27: 1971–1982.

Austin, D.A., and Baker, J.H. 1988. Fate of bacteria ingested by larvae of the freshwater mayfly, *Ephemera danica*. Microb. Ecol. 15(3): 323–332.

Axler, R., Larsen, C., Tikkanen, C., McDonald, M., Yokom, S., and Aas, P. 1996. Water quality issues associated with aquaculture: A case study in mine pit lakes. Water Environ. Res. 68: 995–1011.

Axler, R., Tikkanen, C., Henneck, J., Schuldt, J., and McDonald, M. 1997. Characteristics of effluent and sludge from two commercial Rainbow Trout farms in Minnesota. Prog. Fish-Cult. 59: 161–172.

Azevedo, P.A., Podemski, C.L., Hesslein, R.H., Kasian, S.E.M., Findlay, D.L., and Bureau, D.P. 2011. Estimation of waste outputs by a Rainbow Trout cage farm using a nutritional approach and monitoring of lake water quality. Aquaculture 311: 175–186.

Baker, M.A., Dahm, C.N., and Valett, H.M. 2000. Anoxia, anaerobic metabolism, and biogeochemistry of the stream-water-groundwater interface. *In* Streams and ground waters. Edited by J. B. Jones and P. J. Mulholland. Academic Press, San Diego, USA. p. 260–286.

Bälocher, F., and Porter, C.W. 1986. Digestive enzymes and feeding strategies of three stream invertebrates. J. North Am. Benthol. Soc. 5(1): 58–66.

Barbiero, R. P., Rockwell, D.C., Warren, G.J., and Tuchman, M.L. 2006. Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of Dreissena spp. Can. J. Fish. Aquat. Sci. 63: 1549–1563.

Beeton, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

Berman, T. 1988. Differential uptake of orthophosphate and organic phosphorus substrates by bacteria and algae in Lake Kinneret. J. Plankton Res. 10: 1239–1249.

Boström, B., and Pettersson, K. 1982. Different patterns of phosphorus release from lake sediments in laboratory experiments. Hydrobiologia 91: 415–429.

Boström, B., Andersen, J., Fleischer, S., and Jansson, M. 1988. Exchange of Phosphorus Across the Sediment-Water Interface. Hydrobiologia 170: 299–244.

Bouwman, A., Beusen, A., Overbeek, C., Bureau, D., Pawlowski, M., and Glibert, P. 2013. Hindcasts and future projections of global inland and coastal nitrogen and phosphorus loads due to finfish aquaculture. Rev. Fish. Sci. 21: 112–156.

Boyd, D., Hobson, G., and McBride, J. 1998. Conditions near the coldwater fisheries Eagle Rock sites during June and July 1998 Environmental Monitoring and Reporting Branch. Ontario Ministry of the Environment and Climate Change. Queens Printer for Ontario. 15 p.

Boyd, D., Thorburn, M., Benoit, N., and Howell, T. 2004. 1999/2000 Water and sediment quality conditions in the vicinity of freshwater net pen aquaculture sites. Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment and Climate Change. Rexdale, ON, Canada. 123 p.

Boyd, D., Wilson, M., and Howell, T. 2001. Recommendations for operational water quality monitoring at cage culture aquaculture operations. Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment and Climate Change. Rexdale, ON, Canada. 16 p.

Brabrand, A., Faafeng, B.A., and Nilssen, J.P.M. 1990. Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. Can. J. Fish. Aquat. Sci. 47: 364–372.

Brett, M.T., Muller-Navarra, D.C., and Park, S.-K. 2000. Empirical analysis of the effect of phosphorus limitation on algal food quality for freshwater zooplankton. Limnol. Oceanogr. 45(7): 1564–1575.

Bristow, C. 2005. Short-term Effects of Aquaculture on the carbon dioxide budget and metabolism of a boreal lake. Thesis (M.Sc.). Ottawa-Carleton Institute of Biology, University of Ottawa. Ottawa, Ontario. 200 p.

Bristow, C.E., Morin, A., Hesslein, R.H., and Podemski, C.L. 2008. Phosphorus budget and productivity of an experimental lake during the initial three years of cage aquaculture. Can. J. Fish. Aquat. Sci. 65: 2485–2495.

Bruce Ronzio, S. 2007. Phytoplankton community composition effects on phosphorus sedimentation dynamics in Lake Erie. Thesis (M.Sc.) Department of Biology, University of Waterloo, Waterloo, ON. 125 p.

Bureau, D.P., Gunther, S.J., and Cho, C.Y. 2003. Chemical Composition and Preliminary Theoretical Estimates of Waste Outputs of Rainbow Trout Reared in Commercial Cage Culture Operations in Ontario. N. Am. J. Aquacult. 65: 33–38.

Bureau, D.P., 2006. Rendered products in fish aquaculture feeds. *In* Essential rendering: all about the animal by-products industry. Edited by D.L. Meeker. p. 179–194.

Bureau, D.P., and Cho, C.Y. 1999. Phosphorus utilization by Rainbow Trout (*Oncorhynchus mykiss*): estimation of dissolved phosphorus waste output. Aquaculture 179: 127–140.

Bureau, D.P., and Cho, C.Y. 2000. An introduction to nutrition and feeding of fish. Fish Nutrition Research Laboratory, Dept. of Animal and Poultry Science, University of Guelph. 36 p.

Bureau, D.P., and Hua, K. 2010. Towards effective nutritional management of waste outputs in aquaculture, with particular reference to salmonid aquaculture operations. Aquacult. Res. 4: 777–792.

Burns, N.M., Williams, J.D.H., and Jaquet, J.-M. 1975. A phosphorus budget for Lake Erie. J. Fish. Res. Board Can. 33: 564–573.

Cade-Menun, B.J., Bell, G., Baker-Ismail, S., Fouli, Y., Hodder, K., McMartin, D.W., Perez-Valdivia, C., and Wu, K. 2013. Nutrient loss from Saskatchewan cropland and pasture in spring snowmelt runoff. Can. J. Soil Sci. 93(4): 445–458.

Carpenter, S.R., Caraco, N.F., Correl, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. 8: 559–568.

Chapra, S.C., and Dolan, D.M. 2012. Great Lakes total phosphorus revisited: 2. Mass balance modeling. J. Great Lakes Res. 38: 741–754.

Chapra, S.C., and Tarapchak, S.J. 1976. A chlorophyll *a* model and its relationship to phosphorus loading plots for lakes. Water Resour. Res. 12: 1260–1264.

Cheng, Z.J., Hardy, R.W., and Usry, J.L. 2003. Plant protein ingredients with lysine supplementation reduce dietary protein level in Rainbow Trout (*Oncorchynchus mykiss*) diets, and reduce ammonia nitrogen and soluble phosphorus excretion. Aquaculture 218: 553–565.

Cho, C.Y., and Bureau, D.P. 1997. Reduction of waste output from salmonid aquaculture through feeds and feeding. Prog. Fish-Cult. 59: 155–160.

Cho, C.Y., and Bureau, D.P. 1998. Development of bioenergetic models and the fish-PrFEQ software to estimate production, feeding ration and waste output in aquaculture. Aquat. Living Resour. 11: 199–210.

Cho, C.Y., and Bureau, D.P. 2001. A review of diet formulation strategies and feeding systems to reduce excretory and feed wastes in aquaculture. Aquacult. Res. 32: 349–360.

Clark, E.R., Harman, J.P., and Forster, J.R.M. 1985. Production of metabolic waste products by intensively farmed Rainbow Trout *Salmo gairdneri* Richardson. J. Fish Biol. 27: 381–393.

Clerk, S., Selbie, D.T., and Smol, J.P. 2004. Cage aquaculture and water-quality changes in the LaCloche Channel, Lake Huron, Canada: a paleolimnological assessment. Can. J. Fish. Aquat. Sci. 61(9): 1691–1701.

Coloso, R.M., King, K., Fletcher, J.W., Hendrix, M.A., Subramanyam, M., Weis, P., and Ferraris, R.P. 2003. Phosphorus utilization in Rainbow Trout (*Oncorhynchus mykiss*) fed practical diets and its consequences on effluent phosphorus levels. Aquaculture 220: 801–820.

Conroy, J.D., Kane, D.D., Dolan, D.M., Edwards, W.J., Charlton, M.N., and Culver, D.A. 2005. Temporal trends in Lake Erie phytoplankton biomass: roles of external phosphorus loading and dreissenid mussels. J. Great Lakes Res. 31: 89–110.

Cook, R.B. 1984. Distributions of ferrous iron and sulfide in an anoxic hypolimnion. Can. J. Fish. Aquat. Sci. 41(2): 286–293.

Cummins, K.W., and Klug, M.T. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147–172.

Delgado, C.L., Wada, N., Rosegrant, M. W., Meijer, S., and Ahmed, M. 2003. Outlook for fish to 2020: Meeting Global Demand. International Food Policy Research Institute Issue Brief 15. Washington, D.C. 36 p.

DePinto, J.V., Young, T.C., and Martin, S.C. 1981. Algal-available phosphorus in suspended sediments from the lower Great Lakes tributaries. J. Great Lakes Res. 7(3): 311–325.

DePinto, J.F., Lam, D., Auer, M.T., Burns, N., Chapra, S.C., Charlton, M., Dolan, D.M., Kreis, R., Howell, T., and Scavia, D. 2007. Examination of the status of the goals of Annex 3 of the Great Lakes Water Quality Agreement.

Depew, D.C., Houben, A. J., Guildford, S. J., and Hecky, R. E. 2011. Distribution of nuisance *Cladophora* in the lower Great Lakes: patterns with land use, near shore water quality and dreissenid abundance. J. Great Lakes Res. 37: 656–671.

Dermott, R., and Munawar, M. 1993. Invasion of Lake Erie offshort sediments by *Dreissena*, and its ecological implications. Can. J. Fish. Aquat. Sci. 50: 2298–2304.

Dillon, P.J., 1975. The phosphorus budget of Cameron Lake, Ontario:the importance of flushing rate to the degree of eutrophy of lakes. Limnol. Oceanogr. 20: 28–39.

Dillon, P.J., and Molot, L.A. 1997. Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments. Water Resour. Res. 33: 2591–2600.

Dillon, P.J., and Molot, L.A. 2005. Long-term trends in catchment export and lake retention of dissolved organic carbon, dissolved organic nitrogen, and total iron, and total phosphorus: The Dorset, Ontario, study, 1978-1998. J. Geophys. Res. 110: G01002.

Dillon, P.J., and Rigler, F.H. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

Dillon, P.J., and Rigler, F.H. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

Dolan, D.M. 1993. Point source loadings of phosphorus to Lake Erie: 1986–1990. J. Great Lakes Res. 19: 212–223.

Dolan, D.M., and Chapra, S.C. 2012. Great Lakes total phosphorus revisited: 1. Loading analysis and update (1994–2008). J. Great Lakes Res. 38: 730–740.

Dolan, D.M., Chapra, S. C., Maccoux, M. J., Schmitt Marquez, H., 2011. Great Lakes total phosphorus models and loads: A fifteen year update. Final Report. EPA Grant No. GL 00E58501. EPA-GLNPO, Chicago, IL. National Service Center for Environmental Publications: 905R11012. 16 p.

Dolan, D.M., and McGunagle, K.P. 2005. Lake Erie total phosphorus loading analysis and update: 1996–2002. J. Great Lakes Res. 31: 11–22.

Drake, J.C., and Heaney, S. 1987. Occurrence of phosphorus and its potential remobilization in the littoral sediments of a productive English lake. Freshw. Biol. 17: 513–523.

Dubourg, P., North, R.L., Hunter, K., Vandergucht, D.M., Abirhire, O., Silsbe, G.M., Guildford, S.J., and Hudson, J.J. 2015. Light and nutrient co-limitation of phytoplankton communities in a large reservoir: Lake Diefenbaker, Saskatchewan, Canada. J. Great Lakes Res. 41: 129–143.

Enell, M. and Löf, J. 1983. Environmental impact of aquaculture - sedimentation and nutrient loadings from fish cage culture farming. Vatten 39: 364–375.

Environment Canada. 2001. Environmental assessment of land-based freshwater aquaculture projects: guidelines for consideration of Environment Canada expertise information. Atlantic Region. 35 p.

Evans, E.D., Fahnenstiel, G., and Scavia,D. 2011. Incidental oligotrophication of North American Great Lakes. Environ. Sci. Technol. 45: 3297–3303.

FAO (Fisheries and Aquaculture Department). 2011. National Aquaculture Sector Overview - Canada. 10 p.

Findlay, D. L., Podemski, C.L., and Kasian, S.E.M. 2009. Aquaculture impacts on the algal and bacterial communities in a small boreal forest lake. Can. J. Fish. Aquat. Sci. 66: 1936–1948.

Frier, J. -O., From, J., Larsen, T., and Rasmussen, G. 1995. Modelling waste output from trout farms. Water Sci. Technol. 31: 103–121.

Fukuhara, H., and Sakamoto, M. 1987. Enhancement of inorganic nitrogen and phosphate release from lake sediment by tubificid worms and chironomid larvae. Oikos Mar. 1: 312–320.

Gabrielsen, S.E. 1999. Effects of fish-farm activity on the limnetic community structure of brown trout, *Salmo trutta*, and Arctic charr, *Salvelinus alpinus*. Env. Biol. Fishes 55(3): 321–332.

Gächter, R., and Meyer, J.S. 1993. The role of microorganisms in mobilization and fixation of phosphorus in sediments. Hydrobiologia 253: 103–121.

Gächter, R., and Müller, B. 2003. Why the phosphorus retention of lakes does not necessarily depend on the oxygen supply to their sediment surface. Limnol. Oceanogr. 48: 929–933.

Gale, P. 1999. Water quality impacts from aquaculture cage operations in the La Cloche/North Channel of Lake Huron. *In* Addressing concerns for water quality impacts from large-scale Great Lakes aquaculture. Edited by Lisa Tulen. p. 51-57.

Ganf, G., and Oliver, R. 1982. Vertical separation of light and available nutrients as a factor causing replacement of green algae by blue-green algae in the plankton of a stratified lake. J. Ecol. 70(3): 829–844.

Garcia-Ruiz, R., and Hall, G.H. 1996. Phosphorus fractionation and mobility in the food and faeces of hatchery reared Rainbow Trout (*Onchorhynchus mykiss*). Aquaculture 145: 183–193.

Grey, J., Waldron, S., and Hutchinson, R. 2004. The utility of carbon and nitrogen isotope analyses to trace contributions from fish farms to the receiving communities of freshwater lakes: A pilot study in Esthwaite Water, UK. Hydrobiologia 524: 253–262.

Guy, M., Taylor, W.D., and Carter, J.C.H. 1994. Decline in total phosphorus in the surface waters of lakes during summer stratification, and its relationship to size distribution of particles and sedimentation. Can. J. Fish. Aquat. Sci. 51: 1330–1337.

Håkanson, L., and Boulion, V.V. 2002. The lake foodweb - modeling predation and abiotic/biotic interactions. Bakchuys Publishers, Leiden, Netherlands. 344 p.

Håkanson, L., and Carlsson, L. 1995. Flows and effects of phosphorus - calibrations and simulations using the LEEDS-model (Lake Eutrophication, Effect-Dose-Sensitivity model) in Lake S. Bullaren, Sweden. Vatten 51: 183–218.

Håkanson, L., and Carlsson, L. 1998. Fish farming in lakes and acceptable total phosphorus loads: Calibrations, simulations and predictions using the LEEDS model in Lake Southern Bullaren, Sweden. Aquat. Ecosyst. Health and Manag. 1: 1–24.

Håkanson, L., Carlsson, L., and Johansson, T. 1998. A new approach to calculate the phosphorous load to lakes from fish farm emissions. Aquacult. Eng. 17: 149–166.

Håkanson, L., Ostapenia, A.P., and Boulion, V.V. 2003. A mass-balance model for phosphorus in lakes accounting for biouptake and retention in biota. Freshw. Biol. 48: 928–950.

Hamblin, P.F., and Gale, P. 2002. Water Quality Modeling of Caged Aquaculture Impacts in Lake Wolsey, North Chawnnel of Lake Huron. J. Great Lakes Res. 28: 32–43.

Hanson, J.M., and Leggett, W.C. 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci. 39 (2): 257–263.

Hardy, R.W., and Gatlin, D. 2002. Nutritional strategies to reduce nutrient losses in intensive aquaculture. Avances en Nutrición Acuícola VI. Memorias del VI Simposium Internacional de Nutrición Acuícola 3. 12 p.

Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., and Howell, T. 2004. The nearshore phosphorus shunt: A consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 61: 1285–1293.

Hendricks, S.P., and White, D.S. 2000. Stream and groundwater influences on phosphorus biogeochemistry. *In* Streams and ground waters. Edited by J. B. Jones and P. J. Mulholland. Academic Press, San Diego. p. 221–236.

Herbert, P.D.N., Muncaster, B.W., and Mackie, G.L. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. 46: 1587–1591.

Hewlett, C., North, R.L., Johansson, J., Vandergucht, D.M., and Hudson, J.J. 2015. Contribution of shoreline erosion to nutrient loading of the Lake Diefenbaker reservoir, Saskatchewan, Canada. J. Great Lakes Res. 41: 110–117.

Higgins, S.N. 2005. Modeling the growth dynamics of *Cladophora* in eastern Lake Erie. Department of Biology, PhD thesis. University of Waterloo, Waterloo, ON. 169 p.

Higgins, S.N., and Zanden, M.V. 2010. What a difference a species makes: A meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80: 179–196.

Higgins, S.N., Hecky, R.E., and Guildford, S.J. 2005. Modeling the growth, biomass, and tissue phosphorus concentration of *Cladophora glomerata* in Eastern Lake Erie: model description and field testing. J. Great Lakes Res. 31: 439–455.

Holdren, G. C., and Armstrong, D.E. 1980. Factors affecting phosphorus release from intact lake sediment cores. Environ. Sci. Technol. 14: 79–87.

Holtan, H., Kamp-Nielsen, L., and Stuanes, A.O. 1988. Phosphorus in soil, water and sediment : An overview. Hydrobiologia 170: 19–34.

Hua, K., and Bureau, D.P. 2006. Modelling digestible phosphorus content of salmonid fish feeds. Aquaculture 254: 455–465.

Hua, K., de Lange, C.F., Niimi, A.J., Cole, G., Moccia, R.D., Fan, M.Z., and Bureau, D.P. 2008. A factorial model to predict phosphorus waste output of Rainbow Trout (*Oncorhynchus mykiss*). Aquacult. Res. 39(10): 1059–1068.

Hua, K., and Bureau, D.P. 2009a. Development of a model to estimate digestible lipid content of salmonid fish feeds. Aquaculture 286: 271–276.

Hua, K., and Bureau, D.P. 2009b. A mathematical model to explain variations in estimates of starch digestibility and predict digestible starch content of salmonid fish feeds. Aquaculture 294: 282–287.

Hua, K., and Bureau, D.P. 2010. Quantification of differences in digestibility of phosphorus among cyprinids, cichlids, and salmonids through a mathematical modelling approach. Aquaculture 308: 152–158.

Hua, K., and Bureau, D.P. 2012. Exploring the possibility of quantifying the effects of plant protein ingredients in fish feeds using meta-analysis and nutritional model simulation-based approaches. Aquaculture 356: 284–301.

Hudson, J.J., Taylor, W.D., and Schindler, D.W. 2000. Phosphate concentrations in lakes. Nature 406: 54–56.

Hudson, J. J., Vandergucht, D. M. 2015. Spatial and temporal patterns in physical properties and dissolved oxygen in Lake Diefenbaker, a large reservoir on the Canadian Prairies. J. Great Lakes Res. 41: 22–33.

IJC (International Joint Commission). 1972. Great Lakes Water Quality Agreement. International Joint Commission United States and Canada, Ottawa, ON.

IJC (International Joint Commission). 1987. Revised Great Lake Water Quality Agreement of 1978. International Joint Commission United States and Canada, Ottawa, ON,Canada. 69 p.

IJC (International Joint Commission). 2012. Great Lakes Water Quality Agreement. International Joint Commission United States and Canada, Ottawa, ON, Canada. 56 p.

Ivlev, V. S. 1939. Transformation of energy by aquatic animals. Coefficient of energy consumption by *Tubifex tubifex* (Oligochaeta). Internationale Revue der Gesamtem Hydrobiologie und Hydrographie 38: 449–458.

Jassby, A. D., Reuter, J. E., Axler, R. P., Goldman, C. R., Hackley, S. H. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada). Water Resources Research 30: 2207–2216.

Johansson,T., L. Håkanson, K. Borum, and J. Persson. 1998. Direct flows of phosphorous and suspended matter from a fish farm to wild fish in Lake Southern Bullaren, Sweden. Aquacultural Engineering 17: 111–137.

Johansson, T. and L. Nordvarg. 2002. Empirical mass balance models calibrated for freshwater fishfarm emissions. Aquaculture 212: 191–211.

Johengen, T., Johannsson, O. E., Pernie, G. L., Millard, E. 1994. Temporal and seasonal trends in nutrient dynamics and biomass measures in Lakes Michigan and Ontario in response to phosphorus control. Can. J. Fish. Aquat. Sci. 51: 2570–2578.

Johnes, P. 2007. Uncertainties in annual riverine phosphorus load estimation: impact of load estimation methodology, sampling frequency, baseflow index and catchment population density. Journal of Hydrology 332: 241–258.

Joosse, P.J., and Baker, D.B. 2011. Context for re-evaluating agricultural source phosphorus loadings to the Great Lakes. Can. J. Soil Sci. 91: 317–327.

Joye, S.B., Hollibaugh, J.T. 1995. Influence of sulfide inhibition of nitrification on nitrogen regeneration in sediments. Science. 270: 623.

Kalff, J. 2002. Limnology: inland water ecosystems. Prentice Hall, New Jersey. 592 p.

Kemp, A., and Thomas, R. 1976. Sediment Geochemistry: Cultural Impact on the Geochemistry of the Sediments of Lakes Ontario, Erie and Huron. Geoscience Can. 3: 191–207.

Kerr, S.J. 2006. A historical review of fish culture stocking and fish transfers in Ontario, 1865–2004. Fish and Wildlife Branch, Ontario Ministry of Natural Resources. Peterborough, Ontario. 154 p. + appendices.

Ketola, H.G. 1982. Effect of phosphorus in trout diets on water pollution. Salmonid 6: 12–15.

Kleinman, P.J., Sharpley, A.N., McDowell, R.W., Flaten, D.N., Buda, A.R., Tao, L., Bergstrom, L., and Zhu, Q. 2011. Managing agricultural phosphorus for water quality protection: principles for progress. Plant and soil 349: 169–182.

Kromkamp, J., van den Heuvel, A., and Mur, L.R. 1989. Phosphorus uptake and photosynthesis by phosphate-limited cultures of the cyanobacterium *Microcystis aeruginosa*. Brit. Phycol. J. 24: 347–355.

Kullman, M.A., Kidd, K.A., Podemski, C.L., Paterson, M.J., and Blanchfield, P.J. 2009. Assimilation of freshwater salmonid aquaculture waste by native aquatic biota. Can. J. Fish. Aquat. Sci. 66: 1965–1975.

Lanari, D., D'Agaro, E., and Ballestrazzi, R. 1995. Effect of dietarty DP/DE ratio on apparent digestibility, growth and nitrogen and phosphorus retention in Rainbow Trout, *Oncorhynchus mykiss* (Walbaum). Agriculture Nutrition 1: 105-110.

Larsen, D., and Mercier, H. 1976. Phosphorus retention capacity of lakes. J. Fish. Res. Board Can. 33: 1742–1750.

Leavitt, P.R., Hann, B.J., Smol, J.P., Zeeb, B.A., Christie, C.E., Wolfe, B., and Kling, H.J.1994. Paleolimnological analysis of whole-lake experiments: an overview of results from Experimental Lakes Area Lake 227. Can. J. Fish. Aquat. Sci. 51(10): 2322–2332.

Liskauskas, A., Johnson, J., McKay, M., Gorenflo, T., Woldt, A., and Brendin, J. 2007. A report of the environmental objectives working group of the Lake Huron Technical Committee. Great Lakes Fishery Commission. 80 p.

Lorke, A., Muller, B., Maerki, M., and Wuest, A. 2003. Breathing sediments: The control of diffusive transport across the sediment-water interface by periodic boundary-layer turbulence. Limnol. Oceanogr. 48(6): 2077–2085.

Lozano, S.J., Scharold, J.V., and Nalepa, T.F. 2001. Recent declines in benthic macroinvertebrate densities in Lake Ontario. Can. J. Fish. Aquat. Sci. 58: 518–529.

Lucas, B.T., Liber, K., and Doig, L.E. 2015. Spatial and temporal trends in reservoir physicochemistry and phosphorus speciation within Lake Diefenbaker, a Great Plains reservoir, as inferred from depositional sediments. J. Great Lakes Res. 41: 67–80.

Madenjian, C.P., Holuszko, J.D., and Desorcie, T.J. 2003. Growth and condition of alewives in Lake Michigan, 1984-2001. Trans. Am. Fish. Soc. 132: 1104–1116.

Malkin, S.Y. 2007. The ecology of the nuisance macroalga, *Cladophora glomerata,* and its resurgence in Lake Ontario. Thesis (Ph.D.), Department of Biology, University of Waterloo, Waterloo, ON. 149 p.

Manning, P.G., Murphy, T.P., and Prepas, E.E. 1991. Intensive formation of viviantite in the bottom sediments of mesotrophic Narrow Lake, Alberta. Can. Minerolog. 29: 77–85.

Matuszek, J.E. 1978. Empirical predictions of fish yields of large North American lakes. Trans. Am. Fish. Soc. 107(3): 385–394.

Mazumder, A., and Lean, D.R.S. 1994. Consumer-dependent responses of lake ecosystems to nutrient loading. J. Plankton Res. 16: 1567–1580.

Mazumder, A., McQueen, D.J., Taylor, W.D., and Lean, D.R.S. 1988. Effects of fertilization and planktivorous fish (Yellow Perch) predation on size distribution of particulate phosphorous and assimilated phosphate: large enclosures experiments. Limnol. Oceanogr. 33: 421–430.

Mazumder, A., Taylor, W.D., Lean, D.R.S., and McQueen, D.J. 1992. Partioning and fluxes of phosphorus:mechanisms regulating the size-distribution and biomass of plankton. Ergebnisse der Limnologie 35: 121–143.

McCollum, R. 1991. Buildup and decline in soil phosphorus: 30-year trends on a Typic Umprabuult. Agron. J.83: 77–85.

McCullough, G.K., Page, S.J., Hesslein, R.H., Stainton, M.P., Kling, H.J., Salki, A.G., and Barber, D.G. 2012. Hydrological forcing of a recent trophic surge in Lake Winnipeg. J.Great Lakes Res. 38: 95–105.

McDonald, M., Tikkanen, C., Axler, R., Larsen, C., and Host, G. 1996. Fish simulation culture model (FIS-C): A bioenergetics based model for aquacultural wasteload application. Aquacult. Eng. 15: 243–259.

Mills, E L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., Makarewicz, J.C., Millard, E.S., Munawar, I.F., Munawar, M., O'Gorman, R.,. Owens, R.W., Rudstam, L.G., Schaner, T., and Stewart, T.J. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Can. J. Fish. Aquat. Sci. 60: 471–490.

Mills, E.L., Rosenberg, G., Spidle, A.P., Ludyanskiy, M., Pligin, Y., and May, B. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. Am. Zool. 36: 271–286.

Milne, J. E. 2012. Monitoring and modeling total phosphorus contributions to a freshwater lake with cage-aquaculture. Animal and Poultry Science. Thesis (M.Sc.), University of Guelph, Guelph, ON, p. 145.

Milne, J.E., and Charlton, M.N. 2007. Water quality observations near a working cagedaquaculture farm in the North Channel, Manitoulin Island, Ontario. Burlington, Ontario, Canada: Environment Canada. Water Science and Technology Division. Report No. 07-320. 19 p.

Milne, J.E., Marvin, C.H., Yerubandi, R., McCann, K., and Moccia, R.D. 2017. Monitoring and modeling total phosphorus contributions to a freshwater lake with cage-aquaculture. Aquacult. Res. 48: 283–297.

Moccia, R.D., and Bevan, D.J. 2007. Maintenance of Ontario's Aquaculture Statistics Program: AQUASTATS 2006. Aquaculture Center, University of Guelph, Guelph, ON. 2 p.

Moccia, R.D., and Bevan, D. 2011. Maintenance of Ontario's Aquaculture Statistics Program: AQUASTATS 2010. Aquaculture Center, University of Guelph, Guelph, ON. 15 p.

Molot, L., Watson, S., Creed, I., Trick, C., McCabe, S., Verschoor, M., Sorichetti, R., Powe, C., Venkiteswaran, J., and Schiff, S. 2014. A novel model for cyanobacteria bloom formation: the critical role of anoxia and ferrous iron. Freshwater Biology 59: 1323–1340.

Murphy, T.P., Hall, K.J., and Yesaki, I. 1983. Coprecipitation of phosphate with calcite in a naturally eutrophic lake. Limnology and Oceanography 28(1): 58–69.

Nelligan, C., Jeziorski, A., Rühland, K., Paterson, A., and Smol, J. 2016. Managing lake trout lakes in a warming world: a paleolimnological assessment of nutrients and lake production at three Ontario sites. Lake and Reservoir Management 32: 315–328.

Nelligan, C., Jeziorski, A., Rühland, K., Paterson, A., and Smol, J. 2017. Tracking temporal trends in total phosphorus and hypolimnetic dissolved oxygen in an Ontario lake trout lake. The Society of Canadian Limnologist Conference January 5–8, Montreal, PQ.

Nicholls, K.H., Hopkins, G.J., and Standke, S.J. 1999. Reduced chlorophyll to phosphorus ratios in nearshore Great Lakes waters coincide with the establishment of dreissenid mussels. Can. J. Fish. Aquat. Sci. 56: 153–161.

Nordvarg, L. 2001. Predictive models and eutrophication effects of fish farms. Thesis (PhD), Uppsala University, Villav 16, Uppsala, Sweden. 44 p.

North, R.L., Barton, D.R., Crowe, A.S., Dillon, P.J., Dolson, R.M.L., Evans, D.O., Ginn, B.K., Håkanson, L., Hawryshyn, J., Jarjanazi, H., King, J.W., La Rose, J.K.L., Leon, L., Lewis, C.F.M., Liddle, G.E., Lin, Z.H., Longstaffe, F.J., Macdonald, R.A., Molot, L.A., Ozersky, T., Palmer, M.E., Quinlan, R., Rennie, M.D., Robillard, D., Rühland, K., Schwalb, A., Smol, J., Stainsby, E., Trumpickas, J., Winter, J., and Young, J. 2013. The state of Lake Simcoe (Ontario, Canada): the effects of multiple stressors on phosphorus and oxygen dynamics. Inland Waters 3: 51–74.

North, R.L., Johansson, J., Vandergucht, D.M., Doig, L.E., Liber, K., Lindenschmidt, K.-E., Baulch, H., and Hudson, J.J. 2015. Evidence for internal phosphorus loading in a large prairie reservoir (Lake Diefenbaker, Saskatchewan). J. Great Lakes Res. 41: 91–99.

North, R.L., Smith, R.E.H., Hecky, R.E., Depew, D.C., Leon, L.F., Charlton, M.N., and Guildford, S.J. 2012. Distribution of seston and nutrient concentrations in the eastern basin of Lake Erie pre- and post-dreissenid mussel invasion. J. Great Lakes Res. 38(3): 463–476.

Nürnberg, G.K. 1984. The prediction of internal phosphorus load in lakes with anoxic hypolimnia. Limnol. Oceanogr. 29: 111–124.

Nürnberg, G.K. 1988. Prediction of Phosphorus Release Rates from Total and Reductant-Soluble Phosphorus in Anoxic Lake Sediments. Can. J. Fish. Aquat. Sci. 45: 453–462.

Nürnberg, G.K., and Dillon, P.J. 1993. Iron budgets in temperate lakes. Can. J. Fish. Aquat. Sci. 50: 1728–1737.

Nürnberg, G.K., Shaw, M., Dillon, P.J., and McQueen, D.J. 1986. Internal phosphorus load in an oligotrophic Precambrian Shield lake with an anoxic hypolimnion. Can. J. Fish. Aquat. Sci. 43: 574–580.

OECD (Organization of Economic Cooperation Development). 1982. Eutrophication of waters: monitoring, assessment and control, Final Report. OECD Cooperative Programme on Monitoring of Inland Waters (Eutrophication Control). Paris: Environment Directorate, OECD. 154 p.

Orihel, D.M., Hadas, O., Pinkas, R., Viner-Mozzini, Y., and Sukenik, A. 2013. Internal nutrient loading may increase microcystin concentrations in freshwater lakes by promoting growth of Microcystis populations. Ann. Limnol.-Int. J. Lim. 49(3): 225–235.

Otu, M., Zhang, J., Raper, J., Findlay, D., Wlasichuk, C., and Podemski, C. 2017. Seasonal and inter-annual variability of phytoplankton in central Lake Diefenbaker (Saskatchewan, Canada) proximal to a large commercial aquaculture farm. J. Great Lakes Res. 43: 265–279.

Ozersky, T. 2010. Dreissenid mussels and large lakes: effects on littoral ecology. Thesis (M.Sc.) Department of Biology, University of Waterloo, Waterloo, ON. 126 p.

Ozersky, T., Malkin, S.Y., Barton, D.R., and Hecky, R.E. 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of the Lake Ontario shoreline. J. Great Lakes Res. 35: 321–328.

Palmer, M.E., Hiriart-Baer, V.P., North, R.L., and Rennie, M.D. 2013. Summary of Lake Simcoe's past, present, and future Preface. Inland Waters 3(2): 119–124.

Paterson, M.J., Podemski, C.L., Wesson, L.J., and Dupuis, A.P. 2011. The effects of an experimental freshwater cage aquaculture operation on *Mysis diluviana*. J. Plankton Res. 33: 25–36.

Patterson, M.W.R., Ciborowski, J.J.H., and Barton, D.R. 2005. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. J. Great Lakes Res. 31: 223–237.

Pearson, T.H., and Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16: 229–311.

Penczak, T., Galicka, W., Molinski, M., Kusto, E., and Zalewski, M. 1982. The enrichment of a mesotrophic lake by carbon, phosphorus and nitrogen from the cage aquaculture of Rainbow Trout, *Salmo gairdneri*. J. Appl. Ecol. 19: 371–393.

Persson, G., 1988. Environmental impact by nutrient emissions from salmonid fish culture. Eutrophication and lake restoration. Water Quality and Biological Impacts. p. 215–226. Available at: University of Toronto Library.

Phillips, M.J., Clark, R., and Mowat, A. 1993. Phosphorus leaching from Atlantic salmon diets. Aquacult. Eng. 12: 47–54.

Pothoven, S., Nalepa, T., Schneeberger, P., and Brandt, S. 2001. Changes in Diet and Body Condition of Lake Whitefish in Southern Lake Michigan Associated with Changes in Benthos. N. Am. J. Fish. Manag. 21: 876–883.

Psenner, R., and Pucsko, R. 1988. Phosphorus fractionation: advantages and limits of the method for the study of sediment P origins and interactions. Archiv für Hydrobiologie–BeiheftErgebnisse der Limnologie 30: 43–59.

Rasmussen, J.B. and Kalff, J. 1987. Empirical models for zoobenthic biomass in lakes. Can. J. Fish. Aquat. Sci. 44: 990–1001.

Reid, G.K., McMillan, I., and Moccia, R.D. 2006. Near-field loading dynamics of total phosphorus and short-term water quality variations at a Rainbow Trout cage farm in Lake Huron. J. Environ. Monitoring 8(9): 947–954.

Reid, G.K., and Moccia, R.D. 2007. Estimating aquatic phosphorus concentrations 30 metres down-current from a Rainbow Trout cage array. J. Environ. Monitor. 9: 814–821.

Rigler, F.H. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37: 550–562.

Rigler, F.H. 1964. The phosphorus fractions and the turnover time of inorganic phosphorus in different types of lakes. Limnol Oceanogr. 9(4): 511–518.

Riley, S.C., Roseman, E.F., Nichols, S.J., O'Brien, T.P., Kiley, C.S., and Schaeffer, J.S. 2008. Deepwater demersal fish community collapse in Lake Huron. Trans. Am. Fish. Soc. 137: 1879–1890.

Rooney, R.C., and Podemski. C.L. 2010. Freshwater Rainbow Trout (*Oncorhynchus mykiss*) farming affects sediment and pore-water chemistry. Mar. Freshw. Res. 61: 513–526.

Rydin, E. 2000. Potentially mobile phosphorus in Lake Erken sediment. Water Res. 34: 2037–2042.

Schelske, C.L., Stoermer, E.F., Conley, D.J., Robbins, J.A., and Glover, R.M. 1983. Early eutrophication in the Lower Great Lakes:new evidence from biogenic silica in sediments. Science 22: 320–322.

Schindler, D.W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen and carbon. Verhandlungen des Internationalen Verein Limnologie 19: 3221–3231.

Schindler, D.E., Kitchell, J.F., He, X., Carpenter, S.R., Hodgson, J.R., and Cottingham, K.L. 1993. Food web structure and phosphorus cycling in lakes. Trans. Am. Fish. Soc. 122: 756–772.

Schindler, D.W., Armstrong, F.A.J., Holmgren, S.K., and Brunskill, G.J.1971. Eutrophication of Lake 227, Experimental Lakes Area, Northwestern Ontario, by addition of phosphate and nitrate. J. Fisher. Res. Board Can. 28: 1763–1782.

Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R., Paterson, M.J., Beaty, K.G., Lyng, M., and Kasian, S.E.M. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. Proc. Natl. Acad. Sci. 105(32): 11254–11258.

Schindler, D.W., Hesslein, R.H., and Turner, M.A. 1987. Exchange of nutrients between sediments and water after 15 years of experimental eutrophication. Can. J. Fish. Aquat. Sci. 44: 26–33.

Sharpley, A.N. 1995. Soil phosphorus dynamics:agronomic and environmental impacts. Ecol. Eng. 5: 261–279.

Sinsabaugh, R.L., Linkins, A.E., and Benfield, E.F. 1985. Celulose digestion and assimilation by three leaf-shredding aquatic insects. Ecology 66(5): 1464–1471.

Søndergaard, M., Jensen, P.J., and Jeppesen, E. 2001. Retention and internal loading of phosphorus in shallow, eutrophic lakes. Scientific World J.1: 427–442.

Søndergaard, M., Jensen, J.P., and Jeppesen, E. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506–509: 135–145.

Søndergaard, M., Jensen, J.P., and Jeppesen, E. 2005. Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. Freshw. Biol. 50: 1605–1615.

Sonzogni, W. C., S. C. Chapra, D. E. Armstrong, and T. J. Logan. 1982. Bioavailability of phosphorus inputs to lakes. J. Environ. Qual. 11: 555–563.

Soranno, P., Carpenter, S., and Lathrop, R. 1997. Internal phosphorus loading in Lake Mendota: response to external loads and weather. Can. J. Fish. Aquat. Sci. 54: 1883–1893.

Statistics Canada. 2012. Aquaculture Statistics 2012. Statistics Canada, Catalogue number 23-222-x. 28 p.

Sullivan, A.B., Snyder, D.M., and Rounds, S.A. 2010. Controls on biochemical oxygen demand in the upper Klamath River, Oregon. Chem. Geol. 269: 12–21.

Sutherland, T.F., Petersen, S.A., Levings, C.D., and Martin, A.J. 2007. Distinguishing between natural and aquaculture-derived sediment concentrations of heavy metals in the Broughton Archipelago, British Columbia. Mar. Pollut. Bull. 54: 1451–1460.

Taranu, Z.E., Koster, D., Hall, R.I., Charette, T., Forrest, F., Cwynar, L.C., and Gregory-Eaves, I. 2010. Contrasting responses of dimictic and polymictic lakes to environmental change: a spatial and temporal study. Aquat. Sci. 72: 97–115.

Taylor, W.D. 1984. Phosphorus flux through epilimnetic zooplankton from Lake Ontario: relationship with body size and significant to phytoplankton. Can. J. Fish. Aquat. Sci. 41: 1702–1712.

Thomann, R.V., Connolly, J.P., and Parkerton, T.F. 1992. An equilibrium model of organic chemical accumulation in aquatic food webs with sediment interaction. Environ. Toxicol. Chem. 11: 615–629.

Tiessen, K., Elliott, J., Yarotski, J., Lobb, D., Flaten, D., and Glozier, N. 2010. Conventional and conservation tillage: influence on seasonal runoff, sediment, and nutrient losses in the Canadian prairies. J. Environ. Qual. 39: 964–980.

USAID (United States Agency for international Development). 2011. Feed Conversion Ratio. Page 2 US AID Technical Bulletin #07. US AID.

Vadeboncoeur, Y., Vander Zanden, M.J., and Lodge, D.M. 2002. Putting the Lake Back Together: Reintegrating Benthic Pathways into Lake Food Web Models: Lake ecologists tend to focus their research on pelagic energy pathways, but, from algae to fish, benthic organisms form an integral part of lake food webs. Bioscience 52(1): 44–54.

Vandenberg, G. 2009. Use of high-quality trout feeds to improve growth performance and decrease phosphorus waste. Aquaculture Collaborative Research and Development Program (ACRDP) Fact Sheet. Issue 1. Ottawa: Aquaculture Science Branch, Fisheries and Oceans Canada, DFO/2008-1493. 4 p.

Vollenweider, R.A. 1968. The scientific basis of lake eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Technical Report DAS/DIS 27: 68–77.

Vollenweider, R.A. 1975. Input-output models. Schweizerische Zeitschrift fur Hydrobiologie 37: 53–84.

Wagner, C., and Adrian, R. 2009. Cyanobacteria dominance: quantifying the effects of climate change. Limnol. Oceanogr. 54: 2460–2468.

Wegleńska, T., Bownik-Dylinska, L., Ejsmont-Karabin, J., and Spodniewska, I. 1987. Plankton structure and dynamics, phosphorus and nitrogen regeneration by zooplankton in Lake Glebokie polluted by aquaculture. Ekologia Polska 35: 173–208.

Wellman, S.J. 2011. Nutrient Flow in a Freshwater Food Web During and After an Experimental Aquaculture Operation. Thesis (M.Sc.) Department of Biology, University of New Brunswick. 130 p.

Wellman, S., Kidd, K.A., Podemski, C.L., Blanchfield, P.J., and Paterson, M.J. 2017. Incorporation of wastes by native species during and after an experimental aquaculture operation. Freshw. Sci. 36(2): 387–401.

Westheimer, F.H. 1987. Why nature chose phosphates. Science. 235: 1173–1178.

Wetton, M.S. 2012. Effect of waste loading from freshwater cage aquaculture on benthic invertebrates and sediment chemistry. Thesis (M.Sc.) Entomology Department, University of Manitoba, Winnipeg, MB. 239 p.

Wetzel, R.G. 2001. The phosphorus cycle. *In* Limnology: Lake and River Ecosystems. Academic Press, San Diego, CA. p. 275–283.

Wiesmann, D., Scheid, H. and Pfeffer, E. 1988. Water pollution with phosphorus of dietary origin by intensively fed Rainbow Trout (*Salmo gairdneri* Rich.). Aquaculture 69: 263–270.

Williams, J.D.H., Shear, H., and Thomas, R.L. 1980. Availability to *Scenedesmus quadricauda* of different forms of phosphorus in sedimentary materials from the Great Lakes. Limnol. Oceanogr. 25(1): 1–11.

Withers, P.J.A., Clay, S.D., and Breeze, V.G. 2001. Phosphorus transfer in runoff following application of fertilizer, manure, and sewage sludge. J. Environ. Qual. 30(1): 180–188.

Yan, N.D. 2005. Research needs for the management of water quality issues, particularly phosphorus and oxygen concentrations, related to salmonids cage aquaculture in Canadian freshwaters. Environ. Revis. 13: 1–19.

Yokom, S., Axler, R., McDonald, M., and Wilcox, D. 1997. Recovery of a mine pit lake from aquacultural phosphorus enrichment:Model predictions and mechanisms. Ecol. Eng. 8: 195–218.

Zhang, X., Liu, Z., Jeppesen, E., and Taylor, W.D. 2014. Effects of deposit-feeding tubificid worms and filter-feeding bivalves on benthic-pelagic coupling: Implications for the restoration of eutrophic shallow lakes. Water Res. 50: 135–146.

Zhao, J., Rao, Y.R., and Sheng, J. 2012. Numerical study of dispersion and hydrodynamic connectivity of near-surface waters in Lake Huron. Water Qual. Res. J. Can. 47: 238–251.