A Global Review of the Spatial, Taxonomic and Temporal Scope of Freshwater Fisheries Hydroacoustic Studies and an Investigation into the Measurement of Within- and Between-Season Fish Population Fluctuations in a Boreal Reservoir

by

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Abstract

Hydroacoustics for studying fisheries ecosystems has been developed and improved upon since the practice was first used in the inter-war era, with observational and analytical approaches constantly being adapted for a better understanding of aquatic environments. Recently the application has been gaining popularity for use in freshwater ecosystems, improving the study of lakes, reservoirs and rivers. This thesis aims to advance freshwater hydroacoustics by testing size-based approaches for assessing the status of Lac du Bonnet, a boreal reservoir in Manitoba, Canada. There, 11 systematic acoustic surveys were conducted in order to determine fish abundance and changes in that abundance over two summers in 2011 and 2012. This technique shed light on aquatic ecosystem dynamics, namely within-season fish mortality and recruitment variability between two years. A global ecological review of the scope of freshwater fisheries hydroacoustics was first undertaken in order to determine the spatial, temporal, and taxonomic research gaps that must be addressed if a thorough understanding of global freshwater systems is to be obtained through hydroacoustics. This review provides guidance for the implementation and improvement of the size-based techniques elaborated on later.

Acknowledgements

The completion of this thesis would not have been possible without the efforts and support of a large group of colleagues, friends and family. My family is thanked for their contributions and endless words of encouragement throughout my academic career, and especially during my time at MUN.

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This work most definitely would not have been possible without the assistance of my advisor, Dr. George Rose. My sincerest gratitude goes to him for giving me a chance and for providing me with so many opportunities beyond my thesis, most notably the unforgettable research expeditions to the North Atlantic aboard the *RV Celtic Explorer* in 2011 and 2012. The opportunity to undertake my studies in Newfoundland proved enjoyable far beyond expectation.

Last and certainly not least, my partner Tracy Strauch deserves accolades for her enduring patience and devotion to us during my prolonged study.

Table of Contents

List of Tables

List of Figures

Introduction and Overview

Biologists gain an understanding of freshwater ecosystems through a wide variety of methods, one of the most promising being hydroacoustics (Simmonds and MacLennan 2005). Any attempt at the management of a fishery or aquatic ecosystem requires baseline information on how biotic components of the ecosystem interact with each other and the abiotic environment (Jackson *et al.* 2001). Specifically this includes life-history characteristics (Winemiller 2005), predator-prey interactions (Christensen 1996), food availability (McIvor and Odum 1988), and information on how population dynamics relate to habitat structure (Hayes *et al.* 1996) for each species of interest, all of which interact to determine species distribution and abundance (Jackson *et al.* 2001). Such data are extremely cost-intensive and time-consuming to collect at the regional or watershed scale using traditional net-based methods, which also lead to unintended mortality in study specimens. In addition, the vast majority of limnological studies have focused at the scale of individual lakes. By and large, freshwater ecologists lack the resources to carry out the necessary amount of field research to comprehend broader macroecological processes that move beyond local-scale conclusions and predictions of fish diversity and population dynamics (e.g. Rosenfield 2002; Heino 2011).

Scientific hydroacoustics, the practice of sending calibrated sound pulses through the water column and analyzing the returned echoes, has much to contribute to the understanding of fish population dynamics and aquatic ecosystems, and has advanced at a rapid pace over the last several decades (Simmonds and MacLennan 2005; Kubecka *et al.* 2009). Hydroacoustics technology has potential to provide valuable data useful for limnologists, fisheries managers, and conservationists.

Gaining a more comprehensive knowledge of freshwater ecosystems at the macro scale will depend on research questions that further our understanding of i) mechanistic interactions between lakes and rivers within watersheds, ii) the ecological state of multiple watersheds within regions, and iii) seasonality and long-term variability in abiotic conditions and population dynamics within watersheds. The breadth of taxonomic and size-based coverage possible with hydroacoustic measures further enables the investigation and testing of many aspects of ecological theory and application.

This thesis first elaborates on the state of the field of freshwater fisheries hydroacoustics and future research needs, and follows with a promising first exploration into the use of fish size-based acoustic methods for systematically monitoring the health of freshwater fisheries ecosystems.

The first chapter of this thesis aims to review the current state of science in hydroacoustic studies of freshwater ecosystems. It presents a review of the taxonomic, spatial, and temporal scope covered by 279 research articles that studied freshwater fisheries through hydroacoustics in a total of 294 systems.

Chapter 2 contributes to the temporal component of acoustics research by testing the methods for use in long-term monitoring. Namely, a series of 11 hydroacoustic surveys were undertaken on a boreal reservoir to determine fish abundance over the summer season for two years. Size-based fish data collected on Lac du Bonnet in

Manitoba suggest that hydroacoustics can detect within-season and between-year fluctuations in fish abundance, with implications for monitoring and fisheries management. I first turn to review freshwater acoustic research on a global scale prior to describing these local applications for monitoring. Together these chapters reveal the vast potential for hydroacoustics to further our understanding of freshwater ecosystems.

Co-authorship Statement

This thesis consists of two manuscript chapters, both co-authored by myself and my advisor, Dr. George Rose. Chapter 1 is intended for submission in the near future. A version of Chapter 2 was published in PLOS ONE on April 15th, 2015 (doi: 10.1371/journal.pone.0124799; available at http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0124799).

Chapter 1 - A global review of the taxonomic, spatial and temporal scope of freshwater hydroacoustic studies

1.1 Abstract

Although fisheries hydroacoustics has been used by ecologists and managers of freshwater systems for several decades, there have not yet been any attempts at unifying this burgeoning field to systematically increase our understanding of global watersheds at regional or biogeographical scales. Generalizations about acoustic methodologies, the effects of fish morphology and behavior on target strength, and hydro- and ecological variability across systems are all poorly parameterized by empirical observation. This chapter aims to assess the status and scope of freshwater hydroacoustic research in three areas crucial to a broader biogeographical understanding of global aquatic ecosystems and watersheds: i) the spatial scope of hydroacoustic studies to date ii) the taxonomic extent of freshwater hydroacoustics at the species and family levels (restricted to bony fishes), and iii) the temporal scope of hydroacoustic studies to date. This review presents a summary of 279 research contributions that studied freshwater fisheries through hydroacoustics in 294 systems. The study points to critical gaps in the freshwater fisheries acoustics literature, and provides recommendations for more systematic and fruitful research and monitoring efforts that will contribute to effective management and conservation of fisheries and freshwater ecosystems.

1.2 Introduction

Great strides have been made in the use of hydroacoustics for the study of fish populations since the inception of their use. The literature focusing on freshwater hydroacoustics has showcased substantial methodological progress, however no efforts have yet been made to unify the field in an analysis of global research. In addition, efforts to integrate acoustic research into systematic studies of whole watersheds and across space, time, and taxa have been sorely lacking. This chapter aims to provide a global review of published freshwater hydroacoustic research that is focused on fish. Although this review is not an attempt at a synthesis of the results obtained through acoustic studies, the field is reviewed through these crucial lenses of space (single water bodies to catchments, watersheds and regions), time (one-time or seasonal surveys to long-term monitoring), and taxonomy (single species to ecological communities and higher orders of taxonomic organization such as genera and families).

It is thought that a more systematic approach is needed in order for freshwater hydroacoustics to be implemented in a maximally beneficial manner. A primary conclusion drawn from this literature survey is that methodological approaches are now sufficiently well-advanced that the time is right for hydroacoustics to be applied more broadly using a biogeographical approach. The purpose of this chapter is to identify critical research gaps that form barriers to a holistic understanding of the production, ecology and evolution of freshwater fish communities through hydroacoustic methods. Although other complementary methods are necessary for ground-truthing and to investigate portions of the water column that are inaccessible, hydroacoustics offers much reduced bias and unintended mortality compared to traditional net methods.

Grey literature, conference proceedings, and laboratory or simulation studies are beyond the scope of this study, as are acoustic studies of non-fish organisms such as mammals or phytoplankton. The current study is the first attempt at a comprehensive review of the scope of freshwater acoustics research to date, restricted to the English literature. The ecological rather than the technical aspects of these technologies are reviewed (but see Foote 2009), with the hopes of furthering this area of research for the benefit of global fisheries and freshwater ecosystems.

1.2 Spatial Scope of Freshwater Hydroacoustics Research to Date

In spite of the frequent application of marine hydroacoustic surveys, assessments of freshwater ecosystems have to date largely clustered in only a few regions, thus hampering scientists' abilities to make comparisons and macro-scale interpretations of data. The patterns observed in this regard are at times an artifact of developed countries having access to the resources needed to make the up-front investment to purchase hydroacoustic equipment, however exceptions exist and there are still large spatial gaps, even in developed regions. Spatial coverage is crucial for making comparisons among systems to better understand the ecological diversity underpinning the observable differences they exhibit – essentially providing a natural set of 'experiments' where scientists can test hypotheses (Poole 2002; Johnson *et al.* 2007). Discovering more about the responses of hydroacoustic hardware and software across these systems is equally important (Wanzenböck *et al.* 2003).

By far the most published literature on freshwater hydroacoustics comes from studies done in North America and Northern Europe (Figure 1-1). The Pacific Northwest region of the United States and Canada is a hotspot for such studies, a result of the economic importance of anadromous salmonids in the region. Ransom *et al.* (1998) reviewed side-aspect monitoring of salmonid (*Oncorhynchus* and *Salmo spp.*) escapement in European (Finland and the UK) and Pacific North American rivers. Such studies have been undertaken on more than 14 rivers in order to better understand declines in salmon populations, especially in light of their economic importance and the degree of local adaptation they exhibit (Fraser *et al.* 2011). Beauchamp *et al.* (1997; 1999) studied abundance, diel distribution and predator-prey dynamics of salmonids in Washington and Idaho. Sockeye salmon (*Oncorhynchus nerka*) in Lake Washington have been studied extensively using hydroacoustics since the 1970s (Thorne and Dawson 1974; Eggers 1978; Thorne 1979), and the Columbia River has received similar attention for its salmonid species that have been impacted by widespread hydroelectric development (Johnson *et al.* 1992; Skalski *et al.* 1993; Steig and Johnston 1996; Johnson and Moursund 2000).

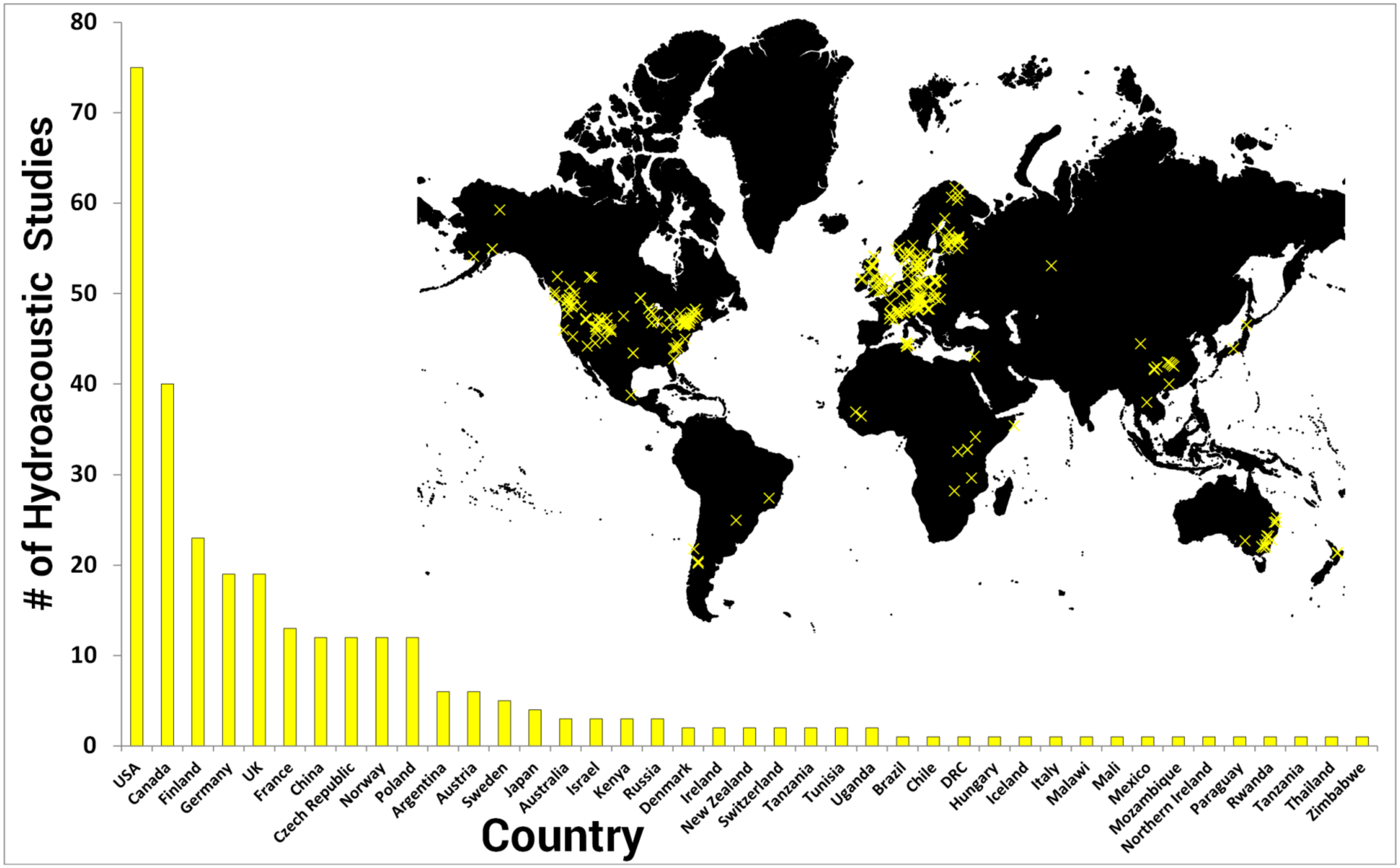

Figure 1-1. Count of published hydroacoustic studies performed in each country. Many studies occurred across national boundaries and so are counted more than once. **Inset:** Map of the locations of hydroacoustic studies included in this review.

The only other well-studied area of North America is the Great Lakes region, with important fisheries for whitefish (*Coregonus spp.*), alewife (*Alosa pseudoharengus*), and smelt (*Osmerus mordax*). Hydroacoustic methods are used across the Great Lakes by several management agencies, and published standard operating procedures are in place for undertaking acoustic surveys (Rudstam *et al.* 2009). Smelt body size has been estimated for Lake Erie based on *in situ* target strength experiments (Rudstam *et al.* 2003); other studies on that lake have focused on cluster sampling techniques (Conners and Schwager 2001) and density estimates based on single vs. split-beam acoustic data (Rudstam *et al.* 1999).

Lake Huron is the site of smelt, alewife, bloater (*Coregonus hoyi*) and cisco (*Coregonus artedi*) fisheries, and several surveys have estimated the abundance of these species (Argyle 1982; Dunlop *et al.* 2010). Acoustic fisheries research on Lake Ontario has been limited to studies on target-strength characterization of alewives (Warner *et al.* 2002) and the effects of power plants on fish communities (Kelso and Minns 1975; Ross *et al.* 1993).

The lion's share of Great Lakes acoustic research has been carried out on Lakes Superior and Michigan. Lake Superior has fisheries for species similar to those in Lake Huron with the addition of the kiyi (*Coregonus kiyi* – a species extirpated from other Great Lakes, COSEWIC 2005), and extensive abundance and biomass estimates for several species have been made there (Heist and Swenson 1983; Mason *et al.* 2005; Stockwell *et al.* 2006; Yule *et al.* 2007, 2008). Diel vertical migrations are exhibited by most of the native pelagic forage fishes in Lake Superior and have been the focus of much attention (Hrabik *et al.* 2006; Jensen *et al.* 2006; Stockwell *et al.* 2007), while other studies have focused on spatial and trophic interactions of forage fish and plankton (Holbrook *et al.* 2006). Surveys have been carried out on Lake Michigan to explicitly compare fish size to target strength for pelagic species (Fleischer *et al.* 1997) – work that is extremely important but lacking when acoustic studies are done in most systems. Vertical migrations have been investigated in alewives (Janssen and Brandt 1980) and bloaters (TeWinkel and Fleischer 1998, 1999). Additional studies have been undertaken to improve survey design (Fabrizio *et al.* 1997; Argyle 1992; Adams *et al.* 2006) and to understand how fish react to heat effluents from Lake Michigan power plants (Spigarelli *et al.* 1973, 1982). General surveys to measure density and abundance were carried out on Lake Michigan as well (Peterson *et al.* 1976; Brandt *et al.* 1991).

Other water bodies in North America with multiple published hydroacoustic studies include Lakes Croche (Gauthier *et al.* 1997; Gaudreau and Boisclair 1998, 2000), Mendota (Hasler and Villemonte 1953; Hergenrader and Hasler 1967; Rudstam *et al.* 1987), Oneida (Arrhenius *et al.* 2000; Rudstam *et al.* 2002) and Texoma (Degan and Wilson 1995; van den Avyle *et al.* 1995; Vondracek and Degan 1995).

In Europe, southern Scandinavia is an area popular for freshwater acoustic studies, the methods having spilled over from the marine fisheries in the region, which rely heavily on acoustic data for management. Abundance estimates in Norway and Sweden have been undertaken in multiple freshwater systems (Brabrand 1991; Linløkken 1995; Balk and Lindem 2000; Romakkaniemi *et al.* 2000) for species including Atlantic salmon (*Salmo salar*), Arctic charr (*Salvelinus alpinus*), whitefish, and vendace (*Coregonus* *albula*). Several authors (Romakkaniemi *et al.* 2000; Romare 2001; Knudsen and Saegrov 2002) investigated the benefits of using horizontal echo sounding complementary to the more common vertical sounding for abundance and behavioral studies. They found that horizontal beaming, combined with vertical acoustics, provided more complete estimates of abundance by allowing researchers to observe fish near the surface and in littoral zones closer to shore. Vertical migrations have been studied thoroughly in Scandinavia for coregonids (Gjelland and Bohn 2004; Knudsen and Gjelland 2004) and vendace (Hamrin 1986). Other useful studies done in the area compare fish echo traces with those of pelagic invertebrates (Knudsen *et al.* 2006; Knudsen and Larsson 2009), and investigate effects of introduced species (Brabrand and Faafeng 1993) and climate change (Nyberg *et al.* 2001) on aquatic ecosystems.

Lilja *et al.* (2000) studied target strength of Atlantic salmon, brown trout (*Salmo trutta*), whitefish and pike (*Esox lucius*) in Finland. The country has also seen extensive work done on fish abundance estimates (e.g. Jurvelius *et al.* 1984; Jurvelius and Sammalkorpi 1995). Several studies have compared the different methods of estimating abundance on Finnish lakes, including electrofishing depletion, gillnetting, seining, trawling, and hydroacoustics (Auvinen and Jurvelius 1994; Horppila *et al.* 1996; Jurvelius *et al.* 2010). These studies concluded that acoustic surveys must account for seasonal variability in fish behavior and habitat use. Vertical migrations of fish have been the focus of many Finnish researchers as well (Sydanoja *et al.* 1995; Jurvelius and Marjomaki 2004, 2008; Kahilainen *et al.* 2004; Malinen and Tuomaala 2005). Valuable long-term studies of vendace density have been performed on Lake Puulavesi (Marjomaki and Huolila 1995, 2001).

The UK and northern mainland European countries such as France, Germany, Poland and the Czech Republic are active areas for freshwater acoustics research. In the UK, one well-studied system is Lake Windermere, where Atlantic salmon and Arctic charr have been focused on heavily (Baroudy and Elliot 1993; Elliot *et al.* 1996; Elliot and Fletcher 2001; Winfield *et al.* 2002, 2007*;* Jones *et al.* 2008). Winfield *et al.* (2009) assessed Arctic charr abundance in five other Scottish Lochs as well. Lake studies in other areas of the UK have examined spatial distribution and patchiness of fish (Duncan and Kubecka 1996; George and Winfield 2000), the distribution of juvenile perch (*Perca fluviatilis*, Goldspink 1990), target-strength body-size relationships for brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon, roach (*Rutilus rutilus*), perch, dace (*Leuciscus leuciscus*), chub (*Leuciscus cephalus*), crucian and common carp (*Carassius carassius* and *Cyprinus carpio*), bleak (*Alburnus alburnus*) and bream (*Abramis brama*) (Kubecka and Duncan 1998), and have estimated brown trout populations in several localities (Kubecka *et al.* 1994).

UK researchers have also been at the forefront of hydroacoustics research in lotic systems. Studies using both mobile and fixed acoustic techniques have been used in rivers such as the Rivers Thames (Hughes 1998; Kubecka and Duncan 1998b), Ouse (Frear 2002), Trent (Lyons 1998), Hull (Peirson and Frear 2003) and Wye (Nealson and Gregory 2000). Ireland has been the site of surveys for pollan (*Coregonus autumnalis* –

Rosell 1997; Harrison *et al.* 2010) and a study of interactions between fish and plankton (Wojtal-Frankiewicz *et al.* 2009).

Hydroacoustic surveys in France have been undertaken on the Seine (Guillard *et al.* 1994) and Rhône (Guillard and Colon 2000) rivers, as well as on Lakes Pareloup (Brosse *et al.* 1999), Bourget (Guillard and Gerdeaux 1993) and Chalain (Guillard and Verges 2007). Lake Annecy has been studied over a long period of time, with extensive focus on seasonal and ontogenetic changes in fish assemblages (Masson *et al.* 2001; Guillard *et al.* 2004, 2006a, 2006b, 2010). The most important fish species in these areas are European whitefish (*Coregonus lavaretus*), common roach and European perch.

In Germany, several authors have researched fish communities in reservoir systems. For example, avoidance behavior of vendace has been studied on the Bigge reservoir (Schmidt and Gassner 2006; Schmidt 2009), while abundance estimates of vendace and whitefish were conducted in the Henne and Wahnbach Reservoirs, respectively (Brenner *et al.* 1987; Schmidt *et al.* 2005). Lake Constance is a well-studied system where diel vertical migrations of European perch and burbot (*Lota lota*) have been characterized (Imbrock *et al.* 1996; Probst and Eckmann 2009). Seasonal variations in fish schooling and migration in perch and whitefish have drawn attention in other studies (Eckmann and Imbrock 1996; Ptak and Appenzeller 1998).

Lake Stechlin is the most well studied lake in Germany, owing to the presence of the Leibniz Institute of Freshwater Ecology and Inland Fisheries on its shores. Hydroacoustic research there has been extensive, focusing largely on the reliability of acoustic fish population estimates (Wanzenbock *et al.* 2003; Mehner *et al.* 2003, 2005, 2007; Mehner 2006a; Busch and Mehner 2009) and comparison with other stock estimation techniques such as gillnetting and trawling (Mehner and Schulz 2002; Mehner 2006b; Emmrich *et al.* 2010). Vertical migrations of pelagic fishes have been characterized on Lake Stechlin as well (Mehner 2006a; Mehner *et al.* 2010).

Poland is another country where acoustic fisheries research has been active. Lake Pluszne has received considerable attention over the years, including studies on abundance estimates (Doroszczyk *et al.* 2007), vertical distributions (Dembinski 1971; Swierzowski 2001), comparing multiple frequencies (Godlewska *et al.* 2009a), and the effects of seasonal changes on abundance estimates (Swierzowski and Godlewska 2001; Swierzowski and Doroszczyk 2004). Many of the Polish studies are relatively long-term and include multiple bodies of water (Dembinski 1971; Godlewska and Swierzowski 2003; Doroszczyk *et al.* 2007; Godlewska *et al.* 2009b).

The last of the well-studied countries in Europe is the Czech Republic, with widespread research having been carried out on reservoir systems there. Diel migrations (Cech *et al.* 2005), daytime versus nighttime abundance estimates (Drastik *et al.* 2009), and juvenile perch distribution and abundance (Kubecka and Svatora 1993; Frouzova and Kubecka 2004; Cech *et al.* 2005, 2007) are topics that have been focused on in the region. The most intensively studied reservoir in the region is the Rimov Reservoir, a heavily managed system that provides drinking water and recreational fisheries for much of the southern portion of the country. Research at the Rimov has been diverse, with studies ranging from survey differences resulting from horizontal versus vertical beaming

(Kubecka and Wittingerova 1998; Tušer *et al.* 2009), fish swimming behavior (Cech and Kubecka 2002), spatial distributions (Vašek *et al.* 2004; Prchalova *et al.* 2009), to boat avoidance (Drastik and Kubecka 2005) and ontogenetic changes in fish distribution (Cech and Kubecka 2006).

The only study that has attempted to make generalizations and comparisons spatially across different regions of Europe by studying lakes from multiple watersheds was carried out by Emmrich *et al.* (2012). This study found robust compatibility between gillnetting and acoustic surveys in a diversity of systems in Norway, Sweden, Denmark, the UK, Germany, France and Italy.

Beyond Europe and North America, another well-studied area is the African Rift Valley and Great Lakes, including Victoria, Malawi and Kivu. The sustainability of Lake Kivu's fishery for the introduced Tanganyika sardine (*Limnothrissa miodon*) has been assessed (Guillard *et al.* 2012), and the diet and feeding behavior of pelagic fish has been studied using a combination of stomach content analysis and acoustic surveys in Lake Malawi (Allison *et al.* 2008). Lake Victoria has been the focus of considerable hydroacoustics efforts in recent years – likely the result of the introduced Nile perch (*Lates niloticus*) and declining cichlid populations (e.g. Ogari and Dadzie 1988). Target strength measurements and distribution related to stratification have been studied for the Nile perch (Goudswaard *et al.* 2004; Kayanda *et al.* 2012; Taabu-Munyaho *et al.* 2013). The spatial and temporal variation in distribution has also been studied for cichlids (Getabu *et al.* 2003; Tumwebaze *et al.* 2007; Taabu-Munyaho *et al.* 2014). Everson and colleagues (2013a, b) have suggested using acoustics in Lake Victoria for ecosystem-based fisheries management.

In China the onset of large hydroelectric megaprojects has resulted in some of the few published hydroacoustic efforts from Asia. The Yangtze River has been the site of most of this work, and studies on large fishes such as common carp and the endangered Chinese sturgeon (*Acipenser sinensis*) and paddlefish (*Psephurus gladius*) (Qiao *et al.* 2006; Zhang *et al.* 2009, 2011; Wang *et al.* 2013) have been the focus, although some authors have broadened their focus to other species (Tao *et al.* 2010; Lin *et al.* 2013a, 2013b). Other systems studied through acoustics in China include the Pearl River (Tan *et al.* 2011) and Lake Laojianghe (Ye *et al.* 2013).

Acoustic works on inland fisheries in areas other than those outlined above have been few and far between, with scattered research having taken place in Argentina (Oldani and Baigun 2002; Vigliano *et al.* 2008, 2009), Australia (Matveev 2003, 2007), Iceland (Snorrason *et al.* 1992), Israel (Walline *et al.* 1992; Kalikhman *et al.* 1992; Horne *et al.* 2000), Japan (Okamoto *et al.* 1992; Iida and Mukai 1995; Mukai and Iida 1996; Trevorrow 1996; Haga *et al.* 2007), Mali (Coll *et al.* 2007), New Zealand (Rowe 1994; Rowe and Chisnall 1995), Russia (Pavlov *et al.* 1986; Borisenko *et al.* 2006), Thailand (Prchalova *et al.* 2003), Tunisia (Djemali *et al.* 2009, 2010) and Zimbabwe (Begg 1976). Although these studies are widespread, many important watersheds have been untouched by hydroacoustics research globally.

In addition to the dearth of acoustic information available for many of the watersheds around the world, most studies focus entirely on a single body of water (Figure 1-2). Those studies that have investigated multiple systems allow a more holistic understanding of freshwater systems. For example, Emmrich *et al.* (2012) studied 18 lakes in seven different European countries, and were able to make conclusions supporting the correspondence of gillnet catches with hydroacoustics across the entire region. Another author was able to make broad comparisons of Australian freshwater systems with North American ones for a total of eleven reservoirs in the context of food web theory (Matveev 2003).

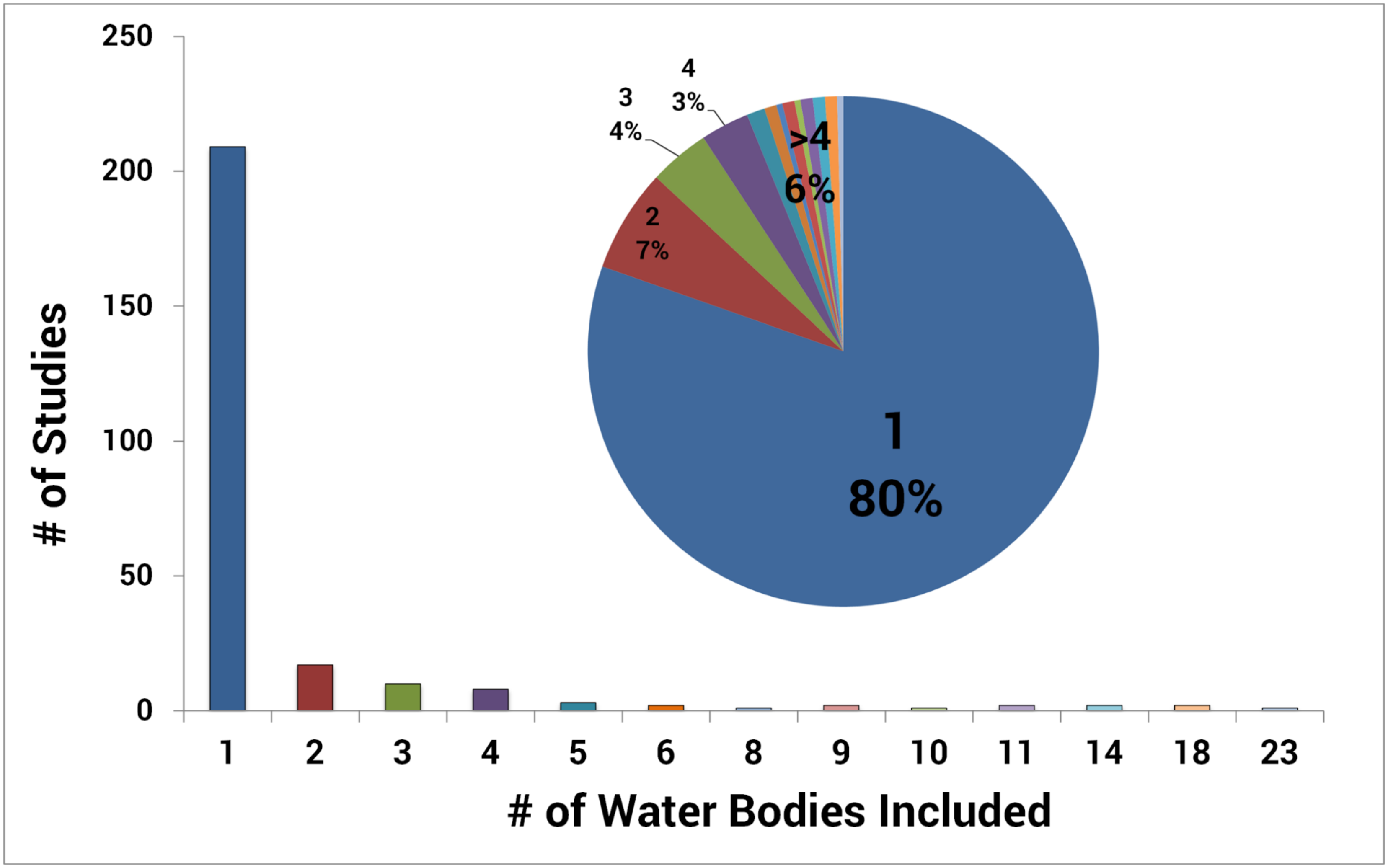

Figure 1-2. Number of water bodies included in the freshwater acoustics publications reviewed in this study. **Inset:** Percentage of studies with different counts of water bodies researched. Very few studies reviewed here involved more than 4 bodies of water (note that proportions do not sum to 100% as a result of rounding).

Aside from a few exceptions, this review indicates that fisheries acousticians have an extremely limited knowledge of how ecosystems can differ across water bodies within and between watersheds. Focusing on one water body necessarily eliminates the possibility of uncovering important differences and dynamics between water bodies, including variations in fish reproductive success and seasonal movement patterns among lakes and rivers. The limited number of water bodies and geographic scope covered to date by hydroacoustic survey methods reviewed here has important consequences beyond spatial representation, to be explored in the coming sections.

1.3 Taxonomic Scope of Freshwater Hydroacoustics Research To Date

One immediate consequence of the lack of spatial coverage of acoustic studies is the limited number of taxa that have been studied in this manner (Figure 1-3). The vastly differing morphological, ecological and life-history traits among disparate fish taxa make the validity in extending generalizations to unstudied groups questionable. This review reveals that an astonishingly limited taxonomic coverage has been achieved to date with freshwater hydroacoustics.

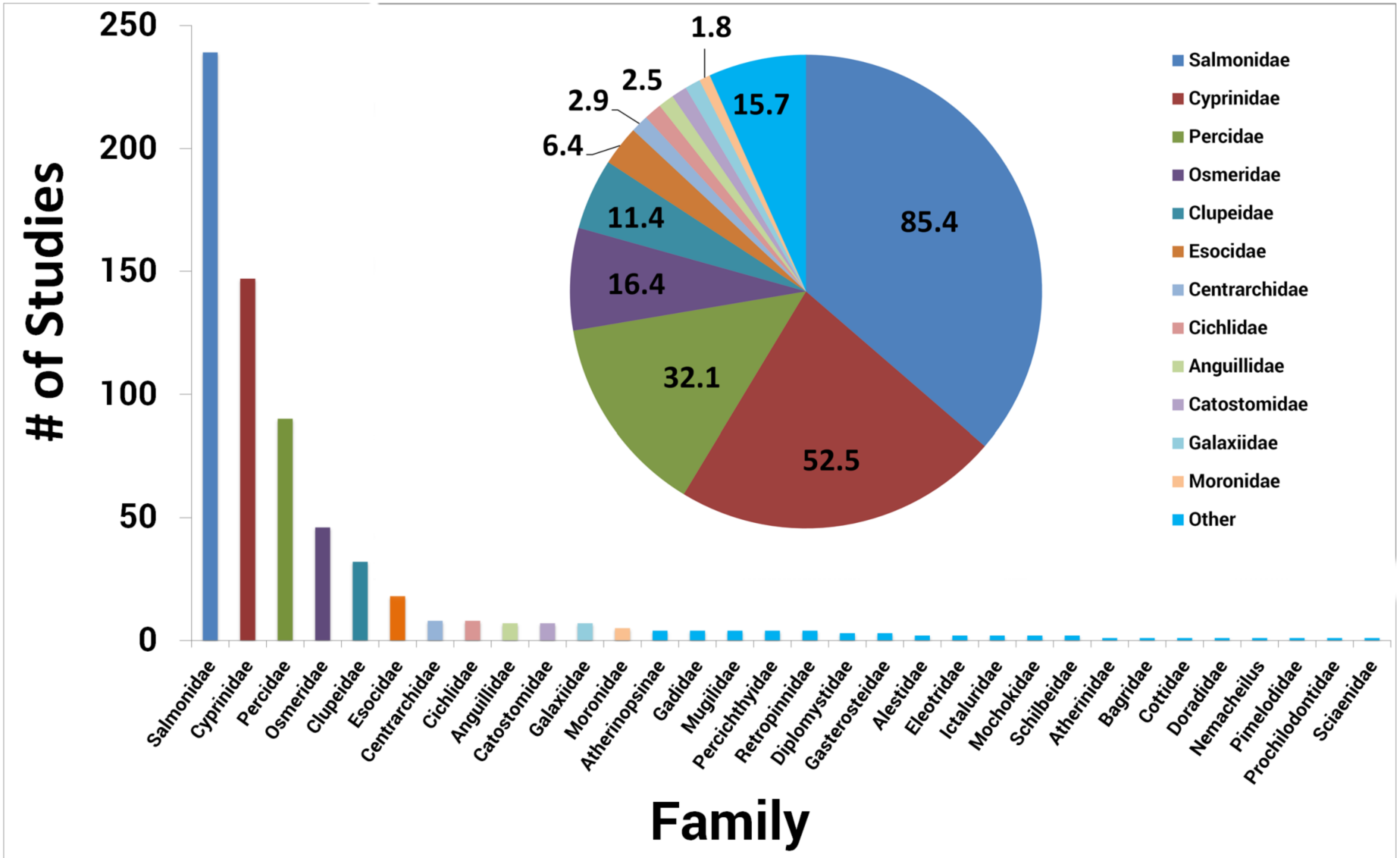

Figure 1-3. Histogram displaying the count of hydroacoustic studies assessed here that focused on or heavily involved each fish family. **Inset:** Proportion of studies reviewed here that involve each fish family (note that proportions do not sum to 100% as a result of rounding).

Globally, estimates of the number of extant freshwater fish species lies somewhere around 15 000 if anadromous species are included, in about 170 families (Leveque *et al.* 2008). The current review documents approximately 109 species in 32 families (Figure 1-3) that have been studied through hydroacoustics, with studies of some commercially valued taxa far outnumbering those focusing on less well-known fish (Figure 1-4).

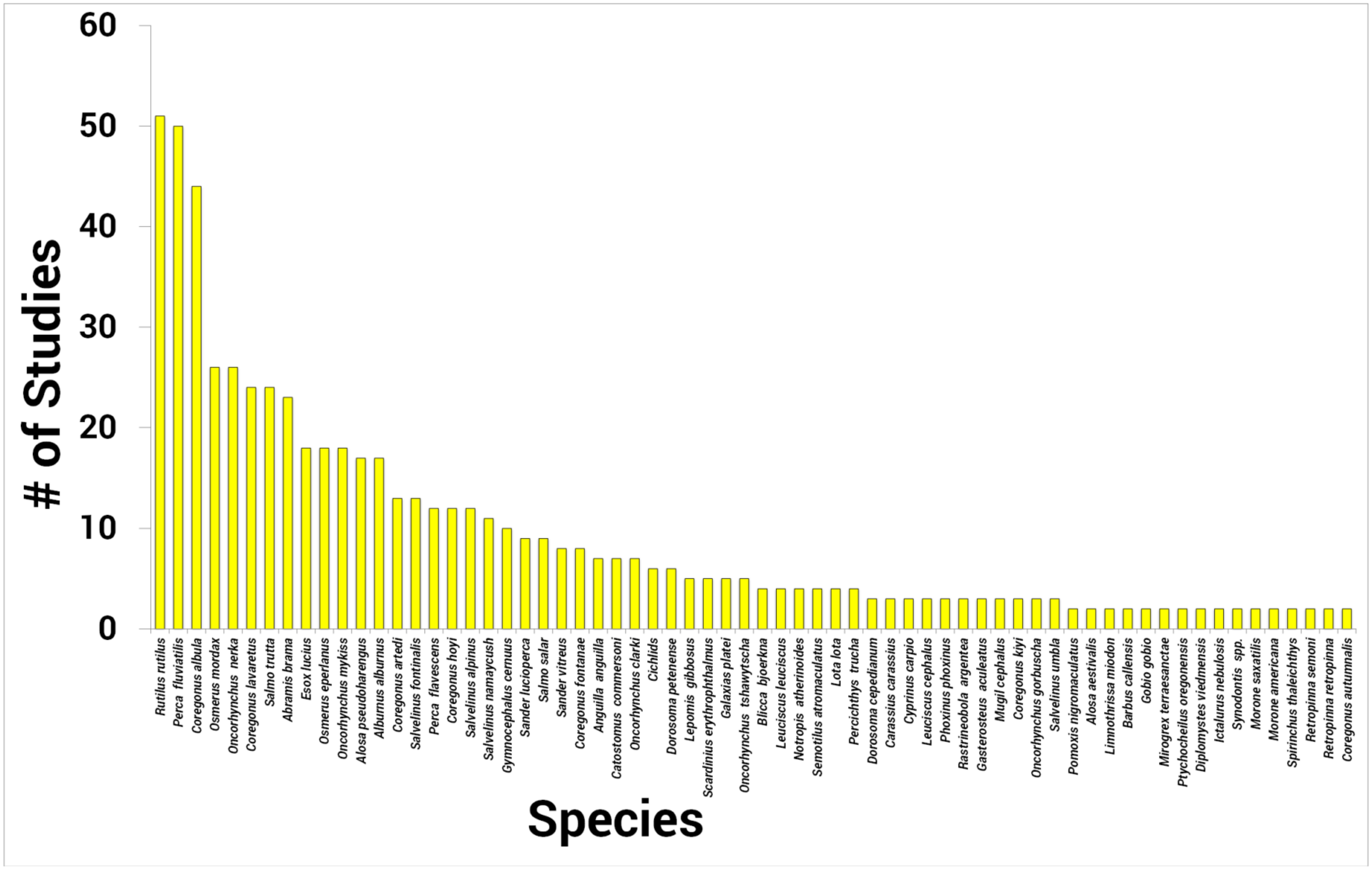

Figure 1-4. Histogram displaying the count of hydroacoustic studies assessed here that focused on or heavily involved each fish species.

In addition to this limited taxonomic coverage, it is evident that very few freshwater species have been singled out and focused on intensively for hydroacoustic study. This is necessary in order to determine individual behavioral traits (e.g. vessel avoidance – Wheeland and Rose 2014), physiological traits and target strength-length relationships (Ona 1990), and variation in target strength as a result of changes in aspect of the fish within an acoustic beam (Kubecka 1994), all of which can affect size and density estimates.

In terms of the taxa that have been studied, by far the most well-studied group is the salmonids – not only anadromous *Oncorhynchus* and *Salmo spp.,* but also landlocked *Salvelinus* and *Coregonus* (whitefish and cisco) spp. Other families that are well-studied include the cyprinids, perch, smelts and herring, although in most cases very few individual species have been studied within a family (Figures 1-3 and 1-4).

An especially disproportionate amount of work in this area has been undertaken on three European species in particular – roach, European perch (*Perca fluviatilis)* and the vendace or European cisco (*Coregonus albula)*. These species are dominant and widespread in northern Europe with active fisheries throughout the region, and more than a quarter of the literature reviewed here involved one or more of these species.

The heavy concentration of hydroacoustic studies on these taxa leave large gaps in our knowledge of other important freshwater taxa. Many groups that include commercially and ecologically important species have so far not been studied, thus limiting our knowledge of how hydroacoustics can help us understand the full gamut of freshwater ecosystems. Some morphologically disparate or diverse groups are yet to be investigated, and it is unclear what these physical differences will imply for echo interpretation and subsequent acoustic abundance estimates.

1.4 Temporal Scope of Freshwater Hydroacoustics Research to Date

One of the most promising avenues for freshwater hydroacoustics is long-term monitoring. Long-term (> one season or year) monitoring of fish stocks is required in order to disaggregate seasonal variation and trends in populations caused by natural or anthropogenic environmental change. This literature review indicated that long-term hydroacoustic studies are also lacking in the literature, with a vast majority of the studies reviewed having taken place within a single year (often only through a few surveys done over months or weeks, and even only days in many cases – Figure 1-5). These studies are thus essentially a snapshot of an aquatic ecosystem and fish population, and may miss important phenological events that are crucial to understanding ecosystems and predicting fisheries performance (e.g. Jeppesen *et al.* 2012).

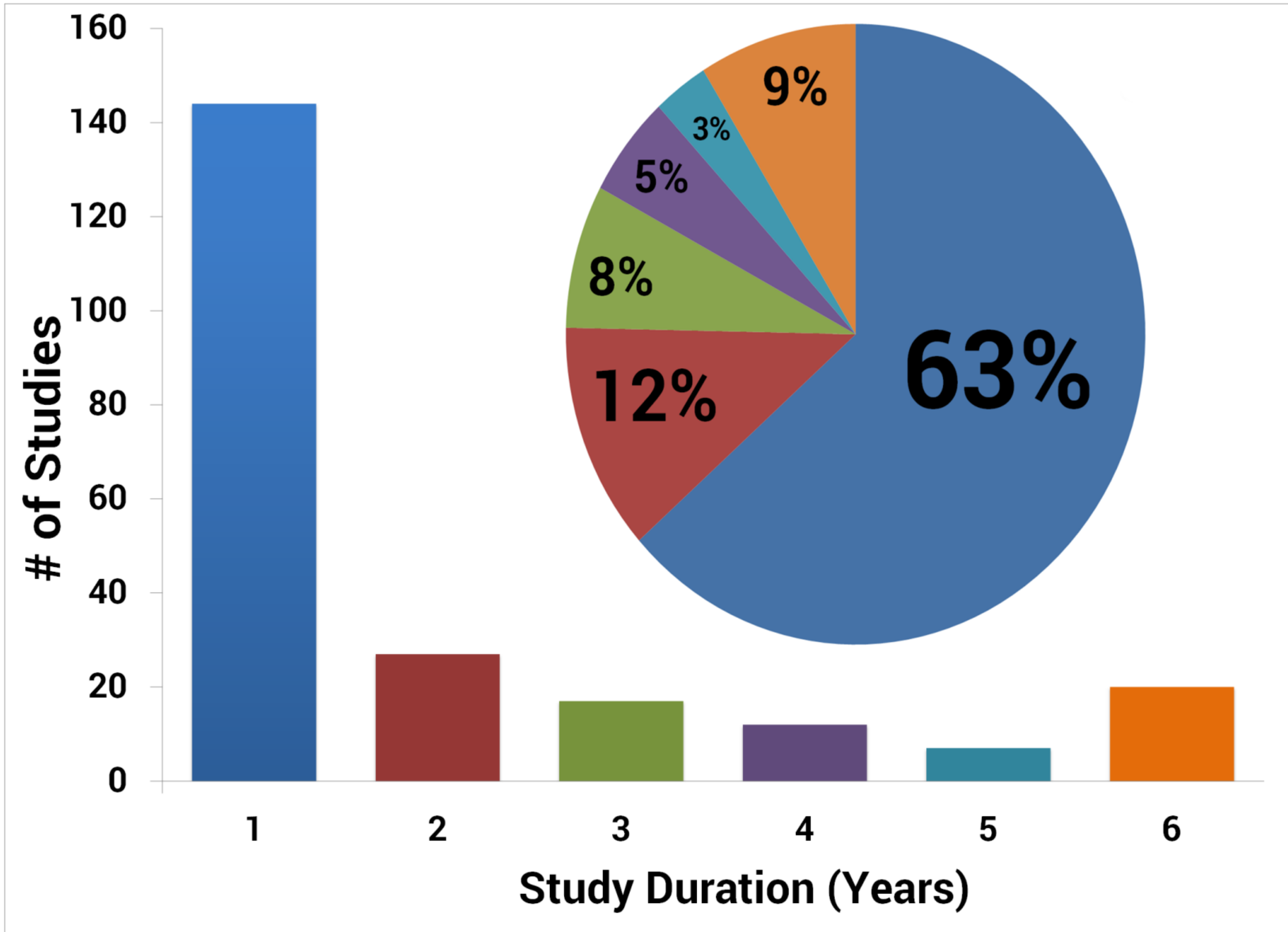

Figure 1-5. Histogram displaying the duration of studies reviewed in years. **Inset:** The proportion of studies in this review for each period of duration (1 year or less, 2-3 years, 3-4 years, 5-6 years, >6years; note that proportions do not sum to 100% as a result of rounding).

Important long-term studies that were encountered in this review reveal ecosystem dynamics much more clearly, and are able to link observations of populations to environmental and anthropogenic variables.

One important aspect of long-term data sets is that they allow for an estimation of error through the seasons. Godlewska *et al.* (2009b) studied Polish lakes for 76 months and were able to make reliable estimates of the relationship between sampling intensity and error, which would not have been possible without such a large dataset. Other advantages of long-term studies include the ability to inquire about seasonal variability (Winfield *et al.* 2007) and observing long-term population dynamics (Brabrand and Faafeng 1993; Johnson and Goettl 1999; Marjomaki and Huolila 2001).

Longer-term data tends to give a more complete picture of how fish communities and ecosystems change over time, and allows for a more adaptive approach to management that can help to avoid the pitfalls of shifting baselines in fishery knowledge and to better manage freshwater ecosystems. Early warning signs of anthropogenic impacts and unwanted ecological changes are easier detected with monitoring in place as well.

1.5 Challenges

Perhaps the biggest challenge in quantitative fisheries acoustics is the identification of targets to some taxonomic level that proves useful for management and research (e.g., Rose and Leggett 1988; Haralabous and Georgakarakous 1996; Lawson *et al.* 2001). Much progress has been made in marine environments since early studies (Horne 2000;

Kang *et al.* 2002; Robotham *et al.* 2010), but not so much in freshwater, where acoustic signal characteristics of various species are still relatively poorly known.

One promising acoustic tool in terms of species identification is the dual-frequency identification sonar (DIDSON), which utilizes high frequencies and a more structured beam array to resolve morphology. The technique is most widely deployed from a fixed transducer in shallow riverine environments that allow all passing fish to be counted (e.g. Mueller *et al.* 2010; Langkau *et al.* 2012; see Martignac *et al.* 2014 for a review).

Another major challenge in acoustic fisheries research is the limitations imposed by turbulent water (i.e. fast-moving sections of river) and shallow littoral regions of a watershed, which usually encompass the majority of higher-order streams and tributaries (Simmonds and MacLennan 2005). These limitations are caused by reverberations, scattering, and absorption of acoustic waves by air bubbles and sediments that are suspended in turbulent water and obscure fish targets (Trevorrow 1998). Other fisheries research methods are required to complement hydroacoustics in such scenarios, and should be incorporated into any comprehensive study of a watershed.

1.6 Ecosystem and size-based methods

Hydroacoustics enables the determination of acoustic size of individual fish which can be isolated in the acoustic beam – a situation thought to be more common in freshwater than marine systems. Early attempts to apply size-based acoustics in marine fisheries ecosystems were thought to be problematic because individual fish were typically distributed in aggregations too dense for reliable isolation of single targets. In freshwater systems, however, there was reason to expect that this problem was not as great (G.A. Rose, early unpublished work in freshwater salmonid lakes in Ontario and Newfoundland). Such size-based methods are directly applicable to monitoring and management of aquatic ecosystems under an ecosystem, rather than single species, approach (and could potentially inform scientists about non-fish species including mammals, plankton and macrophytes). The research presented in Chapter 2 is intended to test that notion, and to investigate if size-based acoustic methods could be applicable to fish in boreal freshwater systems.

1.7 Conclusions

This review revealed substantial progress in freshwater hydroacoustics since their earliest implementation. The research also indicates that in order to move towards a much more comprehensive knowledge of freshwater ecosystems through hydroacoustics, a more systematic approach must be taken. This approach must address shortfalls in the temporal, spatial and taxonomic coverage of freshwater acoustic surveys that have been exposed here.

A major research gap to be addressed is the temporal coverage of hydroacoustic surveys. It is suggested that fisheries managers wishing to use hydroacoustics as a fisheries or ecosystem management tool should invest in sustainable long-term projects with research funding guaranteed for several years. This will ensure that surveys are carried out each year and that long-term trends in fish populations are understood. Knowledge of such trends should lead to better management by informing fisheries regulations as well as mitigation and restoration efforts.

A broader spatial distribution of hydroacoustic studies promises to allow for an extensive comparison of freshwater ecosystems within and across watersheds. Spatially disparate water bodies are subject to and give rise to a countless number of varying ecosystem characteristics. Hydroacoustic comparisons across a diversity of systems will ensure a maximal understanding of how ecosystem components interact with one another to produce unique freshwater communities across space, essentially allowing for macro-scale field 'experiments' that enable freshwater scientists to modulate some variables while keeping others constant.

A spatial extension of these methods necessitates the collection of data on new taxonomic entities, leading to a better understanding of how different species are detected by acoustic systems. A better understanding of species other than the few studied to date would not only reveal novel ecosystem dynamics, but would also elucidate how acoustic biomass and abundance estimates can vary based on nuances between species morphology, behavior and life-history. Research gaps identified here reveal the need for concerted efforts to study multiple systems within watersheds, and to undertake new acoustic surveys in areas that have not yet been studied in this manner whether or not they harbor commercially-valuable species.

The global review of freshwater fisheries hydroacoustics carried out here implies a large number of research gaps in terms of the temporal, spatial, and taxonomic coverage achieved through acoustic surveys to date. This analysis should be seen as a call for action for researchers to strive for a more comprehensive use of hydroacoustics in understanding freshwater ecosystems at multiple scales. Coupled with other traditional sampling methodologies, hydroacoustics offers a wealth of knowledge about freshwater ecosystems that can be tapped with a concerted effort at addressing the future research priorities outlined here. Ultimately the use of hydroacoustics has the potential to become a central tool in a logistic framework to better understand and preserve freshwater fisheries and aquatic biodiversity. Chapter 2 turns toward a boreal system in Manitoba to test how size-based approaches can be used to assess fisheries dynamics within lakes, with the hopes of employing these approaches to make contributions to the broader gaps identified here.

Chapter 2: Size-Based Hydroacoustic Measures of Within-Season and Inter-Annual Fish Declines in a Boreal Freshwater Ecosystem

2.1 Abstract

Eleven sequential size-based hydroacoustic surveys conducted with a 200 kHz split-beam transducer during the summers of 2011 and 2012 were used to quantify seasonal fluctuations in fish abundance in a boreal reservoir in Manitoba, Canada. Fish densities were sufficiently low to enable single target resolution and tracking. Target strengths converted to log_2-based size-classes indicated that smaller fish were consistently more abundant than larger fish by an average factor of approximately 3 for each halving of length. For all size classes, in both years, abundance (natural log) declined linearly over the summer at rates that varied from -0.067.day^{-1} for the smallest fish to -0.016.day^{-1} for the largest (R^2 = 0.24-0.97). Inter-annual comparisons of size-based abundance suggested that for larger fish (>16 cm), mean winter decline rates were an order of magnitude lower (-0.001.day^{-1}), and overall survival higher (71%) than in the main summer fishing season (mean loss rate -0.038.day^{-1}; survival 33%). We conclude that size-based acoustic survey methods have the potential to assess within-season fish abundance dynamics, and may prove useful in long-term monitoring of productivity and hence management and conservation of boreal aquatic ecosystems.

2.2 Introduction

In aquatic ecosystems, the relative abundance and dynamics of size-classes of organisms are keys to understanding energetics and production (Blanchard *et al.* 2009). In these ecosystems, predators and prey often display distinct and predictable body size ratios (Brose *et al.* 2006) that may reflect trophic levels (Lindeman 1942; Cohen *et al* 2003). A positive relationship between body size and trophic level is likely in aquatic systems because fish are morphologically constrained by gape limitation, and hence limited to prey within a specific size range (Persson *et al.* 1996; Romanuk *et al.* 2011).

Aquatic net sampling methods have been used to examine size structure among fishes, but are typically too size-selective to represent all size classes without major bias (Anderson 1998; Beamesderfer and Rieman 1998). Net surveys also cause unintentional mortality of fish and crustaceans and are expensive when sampling large systems (Chopin and Arimoto 2005).

Hydroacoustic methods enable more comprehensive, non-lethal and cost-effective assessments of the pelagic portion of the aquatic environment (Koslow 2009), with potential quantification of the distribution and abundance of organisms ranging in size from zooplankton to large predatory fish at high resolution (Simmonds and MacLennan 2005). Most applications of acoustics to date have been based on echo integration techniques that do not depend on isolation of single organisms in the acoustic beam (Emmrich *et al.* 2012). Size-based acoustic measures have been less successful, as densities often exceed a threshold above which echoes cannot be isolated as single targets (Sawada *et al.* 1993). There may also be bias in the availability of size classes to the acoustic beam in the so-called surface and bottom exclusion dead zones (Patel *et al.* 2009), or at increasing ranges from the acoustic beam axis. These biases may be minor, however, in shallow boreal freshwater ecosystems surveyed at relatively high acoustic frequencies where the exclusion zones are small and the majority of fish targets are encountered individually (Wheeland and Rose 2014).

For fisheries management, indicators of within-season abundance and mortality are important to setting catch restrictions and monitoring the current state of the fisheries ecosystem. Moreover, within-season dynamics may enable better predictions of ecosystem productivity across systems and in coming years (e.g., strong or weak recruitment, low or high mortality). In theory, natural and fishing mortality in aquatic ecosystems should be reflected in seasonal declines in abundance and a more pronounced negative slope of size-frequency data (Gislason and Rice 1998; Graham *et al.* 2005; Shin *et al.* 2005). In addition, inter-annual dynamics of various size classes of fish should be reflected in surveys. There have been few attempts, however, to test whether acoustic survey methods are sufficiently sensitive to measure such dynamics (Emmrich *et al.* 2012).

The main objective of this study was to test if size-based hydroacoustic surveys could describe seasonal and inter-annual variation in fish abundance in a boreal freshwater ecosystem. Expectations of theory were tested, namely that: 1) larger fish would be less abundant than small fish; 2) smaller fish would decline at rates greater than would larger fish over seasons; and 3) inter-annual abundances of size classes would be consistent with mortality expectations from year to year. Based on our findings, I discuss how size-based acoustic methods could contribute to the management and long-term monitoring of freshwater ecosystems.

2.3 Methods

2.3.1 Study Area

Lac du Bonnet is a hydroelectric reservoir on the Winnipeg River in southeastern Manitoba (50° 22'N 95° 55'W), located between the Seven Sisters and MacArthur dams, two large run-of-river hydroelectric operations. The area is moderately developed, with several small communities as well as many summer homes and cabins along its banks, and is heavily used for recreational boating and fishing.

The Lac du Bonnet reservoir comprises three distinct basins (Figure 2-1). The largest basin is the flooded main channel of the Winnipeg River, which runs south to north on the western side of the reservoir during this stretch and covers approximately 38.5km^2. Other than the main channel, which reaches a maximum depth of 26 m, this basin generally has depths of <5 m. The middle basin is deeper (~10-12 m), covers 27 km^2 and is distinguished by several large bays with small creek tributaries and wetlands. The northeast basin is deepest (15-20 m) and covers close to 18.5 km^2. This latter basin is fed by the lower-flow Lee River from the south and has mostly steep rocky banks.

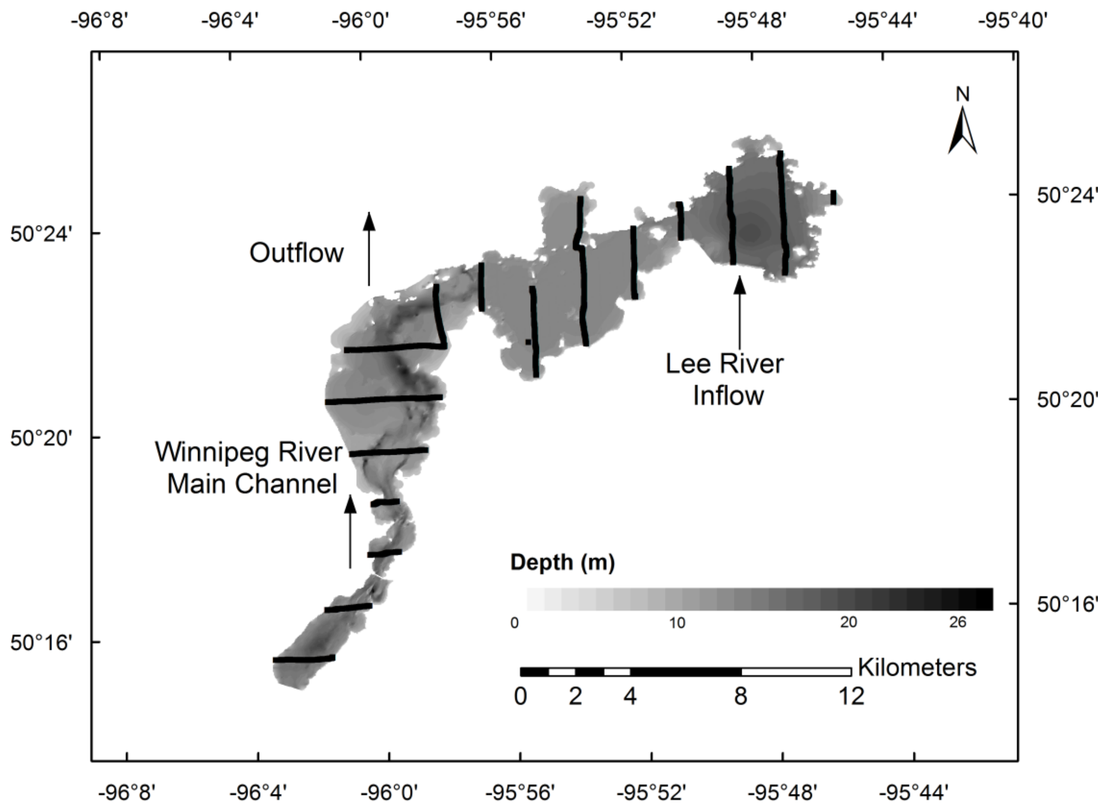

Figure 2-1. Map of Lac du Bonnet with depth contours and GPS-recorded transect lines from Survey 2. Note that surveys were conducted offset from one another and rarely overlapped in order to cover the entire reservoir over the season.

The Lac du Bonnet reservoir has a maximum depth of 30 m, with a summer temperature of approximately 22°C. Flow levels in the reservoir are sufficient to prevent stratification and thus summer temperatures are relatively constant throughout all depths and locales within the reservoir. The waters of Lac du Bonnet can be classified as mesotrophic to eutrophic, with high turbidity (a secchi depth of ~1.2 m) and occasional phytoplankton blooms in late summer. The system's catchment area lies in the transition zone between the aspen parkland with its underlying sedimentary substrate and the boreal forest on the igneous and metamorphic rocks of the Canadian Shield. The reservoir is characterized by a diverse array of large fish that include species such as walleye (*Sander vitreus*), sauger (*Sander canadensis*), northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*), in addition to smaller cisco (*Coregonus* spp.) and shiners (*Notropis* spp.) (authors' personal observations; Stewart and Watkinson 2004). In all, 27 fish species were observed during summer net surveys conducted concurrently in the pelagic and littoral zones of the reservoir in 2011 and 2012 for an adjacent study (D. Boisclair *Université de Montréal*, personal communication).

2.3.2 Acoustic Surveys

Eleven daytime hydroacoustic surveys taking 6-8 hours each were performed in July and August of 2011 and 2012 using a BioSonics split-beam DTX echosounder (BioSonics, Seattle, WA, USA) with 200, 430, and 1000 kHz transducers (only the 200 kHz data are used here; this transducer had a half-power beam angle of 6.5° and transmitted at 6 pings.$^{s-1}$) (Table 2-1). All acoustic data were georeferenced with an integrated GPS (Garmin 17xHVS, Garmin Ltd., Olathe, KS, USA) and collected using

Visual Acquisition Software version 6.0.2 (BioSonics Inc., Seattle, WA, USA). Transducers were deployed on a custom-built aluminum arm mounted off the port side of a 17' Boston Whaler with a foam-cored hull and 90 hp four-stroke engine to reduce noise (Lazarus 2012). During surveys, the transducer faces were between 40 and 50 cm below the water surface. Transducers were calibrated using tungsten carbide spheres to well-established standards (Foote *et al.* 1987). Parallel straight-line transects were run at approximately 9-11 km.h^{-1} (5-6 knots) along the short axis of each basin (Figure 2-1), as close to the shoreline as possible (typically to ~2 m depth on the sounder) (Simmonds and MacLennan 2005; Guillard and Verges 2007). The first transect position was chosen at random; thereafter transects were spaced 1850m apart spanning the entire reservoir. After the first survey, transects were offset by approximately 150 m in each subsequent survey to provide more comprehensive bathymetry and spatial data across the reservoir.

Table 2-1. Hydroacoustic Surveys conducted over the study period on Lac du Bonnet. Survey coverage is defined as the total transect length divided by the square root of the reservoir area (Simmonds and MacLennan 2004).

Survey Number	Date	Total Transect Length (km)	Coverage
1	July 26th, 2011	37.39	4.08
2	August 2nd, 2011	40.68	4.44
3	August 3rd, 2011	38.41	4.19
4	August 15th, 2011	35.23	3.84
5	August 18th, 2011	40.91	4.46
6	August 27th, 2011	35.15	3.83
7	July 28th, 2012	36.39	3.97
8	August 2nd, 2012	40.23	4.39
9	August 8th, 2012	35.74	3.90
10	August 11th, 2012	39.66	4.33
11	August 24th, 2012	41.39	4.52

2.3.3 Data Analysis

Echograms from all transects were scrutinized then edited using Echoview version 5.0 (Myriax Inc., Hobart, TAS, Australia). The lakebed was delineated using a smoothing filter on the best bottom candidate line picks, with manual edits where necessary to include data as close to the lake bottom as possible while excluding the strong signal associated with the substrate. A surface line was imposed at a depth below the majority of surface noise (a minimum of 2 m was excluded – actual values varied among surveys depending on wind conditions – there was no trend in the exclusion over time). Manual edits removed minor extraneous noise.

A single target detection algorithm identified individual fish and provided target strength (TS_{dB}, hereafter TS) data along each transect. Detection parameters included a TS threshold of -52.6 dB (equivalent to a freshwater fish of 4 cm length with a swim bladder according to the model of Love 1971), a pulse length determination level of -6 dB, and minimum and maximum normalized pulse lengths of 0.7 and 1.50, respectively (Table 2-2). Attempts to decrease the threshold below -52.6 dB were abandoned as a consequence of uncertainties about separation of fish without clouds of large zooplankters that were abundant in the reservoir (unpublished data). A maximum beam compensation larger than typically used was allowed in studies of TS, which increased the effective beam volume and number of fish that could be measured. Tests comparing narrower and wider allowable beam compensations indicated the expected increase in measured targets with larger compensation, but no significant differences in TS characteristics, although a small bias towards larger targets further from the beam axis with increased allowed compensation was evident in some samples. Initial tests of single target and integrated densities indicated that Sawada's N_v never exceeded 0.01, hence single target data were considered to be unbiased (Sawada *et al.* 1993).

Table 2-2. Single target settings. Single target detection settings and fish track detection properties used in Echoview 5.0 (Myriax Inc., Hobart, TAS, Australia).

Single Target Settings	
TS threshold	-52.6 dB
Pulse length determination level (PLDL)	6 dB
Minimum normalized pulse length	0.7
Maximum normalized pulse length	1.5
Beam compensation model	BioSonics
Maximum beam compensation	15 dB
Maximum standard deviation of minor-axis angles	1.2
Maximum standard deviation of major-axis angles	1.2
Fish Track Detection Properties	
Minimum number of single targets	1
Minimum number of pings in track	1
Maximum gap between single targets	2

Tracking of individual fish was based on sequential TS echoes and track acceptance parameters were designed to include all single targets but to group sequential TS values presumed to come from single fish (Table 2-2). Small ranges and relatively rapid survey speeds led to most tracks being single TS echoes. For tracks with n>1 the maximum TS was used. Tracks were manually edited where necessary to limit perceived grouping errors in rare cases where two or more fish were close together. The so-called acoustic near bottom dead zone ranged from approximately 0.5-0.6 m and no doubt resulted in missing some benthically-oriented fish. Any bias was thought to be constant, however, as all surveys were conducted during daylight hours (night-time surveys were also attempted but plankton was sufficiently thick to make isolation of small fish targets problematic).

Fish tracks were separated into five $\log_2$ scale size classes based on the target-strength length relationship outlined in Love (1971). In its modified form taking into account the 200kHz frequency at which the data were collected, Love's equation indicates:

$$\textit{Fish Length (cm)} = 10^{((TS_{dB}+64.09)/19.1)}$$

These size classes span a range from large predatory fish important to recreational fisheries to 4 cm forage fish and juveniles that would be prey for both medium and large fish (size classes of 4-7.9 cm, 8-15.9 cm, 16-31.9 cm, 32-63.9 cm, and >64 cm). Love's equation may not be entirely applicable to all fishes measured in this study, but it provided a consistent relative basis to scale the acoustic TS to biological size of the surveyed fish community. Counts of fish of each size class were then tabulated for each survey, and their natural logarithms plotted against size class. Linear regressions were performed using XLSTAT Version 2014.2.03 (Addinsoft, Belmont, MA, USA).

2.4 Results

The acoustically-derived fish counts surveyed at Lac du Bonnet during the summers of 2011 and 2012 indicated that TS distributions ranged from approximately -53 dB (threshold limited) to a very few tracks that measured in the low -20 dB range (Figure 2-2). All survey counts were strongly skewed right. There was little indication of a shift of counts from one size class to the next largest during the study periods (33 days in 2011 and 28 in 2012), but a decline in all classes over the summer was evident. There was little indication of recruitment to the smallest size class within either year. Fish were on average at similar depths in all surveys (Figure 2-3).

Figure 2-2. Acoustic target strength (dB) counts of fish tracks for the 11 surveys of Lac du Bonnet in 2011 (a-h) and 2012 (g-k). The white dividing lines represent the breaks among assigned size classes.

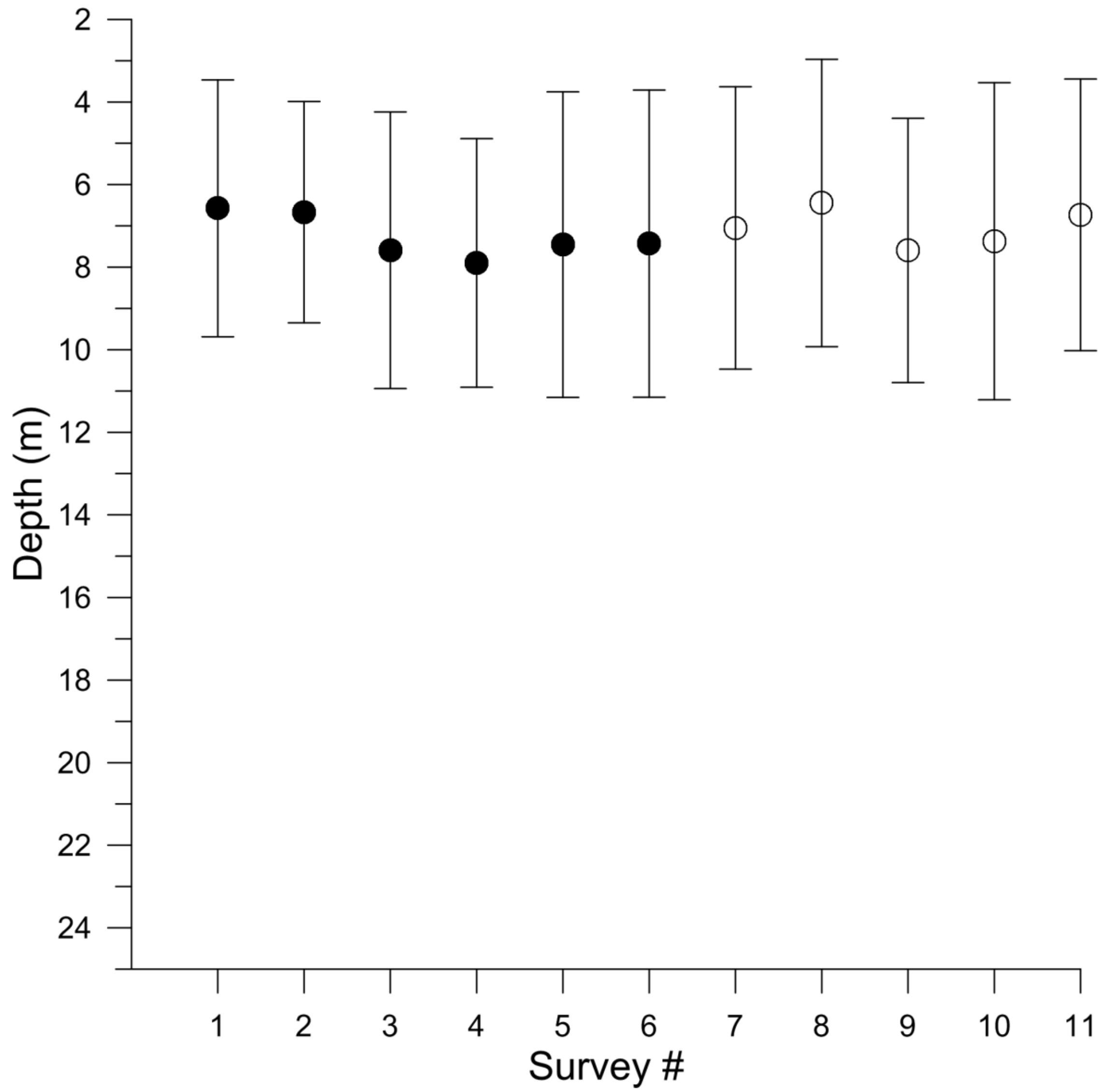

Figure 2-3. The average depth distribution and 95% confidence interval of all targets for each acoustic survey of Lac du Bonnet in 2011 (closed circles) and 2012 (open circles). There was no trend in target depth.

Natural log-transformed counts of all size classes of fishes declined linearly throughout the summer season (Figure 2-4). All surveys showed abundance declining between adjacent size classes by approximately 1 natural logarithm unit or a factor of approximately 3 (e.g., size 4 cm fish were on average approximately 3 times as abundant as size 8 cm fish). Day of year explained between 74.7 and 97.4% of variation in seasonal abundance declines for the five size classes with the exception of the largest size class in 2012 which declined over the season but with greater variability among surveys (Table 2-3).

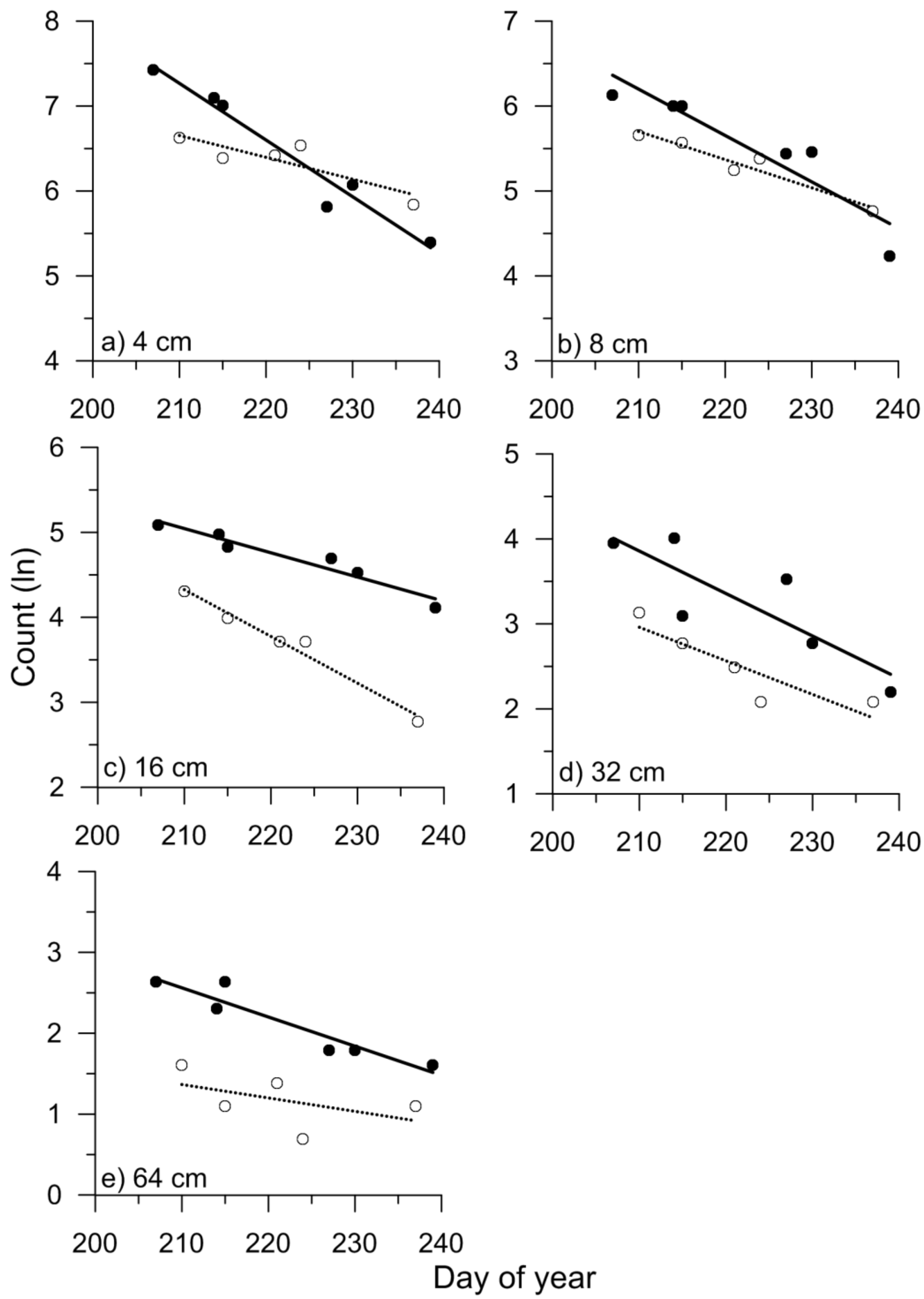

Figure 2-4. Counts of fish (natural logarithms) of 5 target strength size classes (a-e representing size groups 4-7.99, 8-15.99, 16-31.99, 32-63.99 and >64 cm, respectively) from the 11 acoustic surveys carried out on Lac du Bonnet in 2011 (closed circles) and 2012 (open circles). Results of regression analysis are given in Table 2-3.

Table 2-3. Linear regression of survey counts of fish for each size class by year. Slope is an estimate of decline (~mortality) rate.day^{-1}.

Maximum Target Strength (dB)	Year	Ln Initial Count	Slope	p Value	R^2
-46.85	2011	7.423	-0.067	0.001	0.96
-46.85	2012	6.624	-0.026	0.059	0.75
-41.05	2011	6.131	-0.055	0.008	0.86
-41.05	2012	5.659	-0.033	0.007	0.93
-35.35	2011	5.088	-0.029	0.002	0.94
-35.35	2012	4.304	-0.055	0.002	0.97
-29.6	2011	3.951	-0.050	0.034	0.72
-29.6	2012	3.135	-0.039	0.044	0.79
-23.85	2011	2.639	-0.036	0.005	0.89
-23.85	2012	1.609	-0.017	0.398	0.24

Instantaneous loss rates in the counts over both study periods were variable but generally lower with increasing fish size (Figure 2-5). Decline rates over the approximately 30-day study periods in both years ranged from -0.067 to -0.016.day^{-1}. From the end of surveys in 2011 to the first survey in 2012, for the largest 3 size classes, loss rates ranged from approximately -0.0026 to near 0.day^{-1}, an order or magnitude lower than during the summer study period. The smallest size classes were not considered because recruitment, not growth, was almost certainly the main factor in their abundance dynamics from year to year. Based on these data, the mean instantaneous loss in size classes (> 16cm) was approximately 0.001.day^{-1} over the approximately 11 months that were not surveyed, or a fall to summer retention of 71% of fish. In contrast, summer retention of fish during the present study period averaged 33% for the same large size classes. Loss rates of the largest 2 size classes of fish were considerably higher during the summer fishery than during the rest of the year (Figure 2-5).

Figure 2-5. Daily loss rates (declines in counts) within the summer study periods for the five size classes in 2011 (crosses) and 2012 (circles), scale on left axis. Inter-annual loss rates from the last survey in 2011 to first survey of 2012 (squares) for size classes (>16cm) (64 cm class to same class - crossed square), scale on right axis.

2.5 Discussion and Conclusions

The results obtained in this study indicate that size-based hydroacoustic assessments of boreal freshwater ecosystems have potential to enable monitoring of the density and abundance of various size classes of fish both within and between years. During the summer study periods the highest rates of loss occurred with the smallest fish and the lowest in the largest in both years, consistent with size-based and population dynamics theory (e.g. Elton 1927). Comparisons of incremented size classes from 2011 to 2012 gave a similar result, but with much lower losses and higher apparent survival. The instantaneous loss rates are equivalent to estimates of mortality, which during summer is likely a result of the intensive recreational fishery, assuming little emigration from the survey area (Shin and Cury 2004).

The data for the largest three size classes of fish are likely to be of most interest to the sport fishery (>-35.35dB target strength or 16 cm). Their decline, especially in 2011, was in line with the relatively high fishing pressure in Lac du Bonnet (Doug Leroux, Manitoba Conservation, Lac du Bonnet, Manitoba, personal communication). Summer mortality appeared to be of the order of that observed annually in walleye in heavily fished lakes in New York (Irwin *et al*. 2008).

Although inter-annual comparisons can only be made over a single year with the present data, the apparently low losses of larger fish compared to those that occurred during the summer study periods suggest that the fishery is the main source of mortality of larger fishes in this ecosystem. In addition, the initial number of small fish (both 4 and 8 cm size groups) in 2011 was higher than in 2012, which suggests variable production (recruitment), and suffered a higher loss rate over the season, which is consistent with density-dependent mortality. The larger size classes do not show this effect. These findings must be considered preliminary given the limited comparisons, but nonetheless are at least suggestive that further information on population dynamics could be garnered from longer time series of such surveys.

Size-based measures have potential to provide a method to characterize ecological relationships among fish of multiple size classes, and perhaps trophic levels. Counts of individual fish of the various size classes were negatively related to body size, as metabolic theory and trophic transfer efficiency predict (Dickie *et al.* 1987; Kerr and Dickie 2001; Jennings *et al.* 2002; Trebilco *et al.* 2013). Previous studies have linked fish body size to trophic level on regional and global scales in marine systems (Jennings *et al.* 2001; Romanuk *et al.* 2011) as well as in temperate lakes in Ontario near Lac du Bonnet having similar fish communities (Persaud *et al.* 2012). This latter study however found body size predictions of δ^{15}N-derived trophic level to be relatively weak, suggesting factors other than body size may also be involved. Additional research is recommended to further explore these potential relationships as they relate to fish productivity.

It was not clear when this study was planned that hydroacoustic methods could be successful in describing size-based fish communities in the study system. We found, however, that potential limitations, particularly densities too high to reliably extract single targets, were not encountered during this study (nor were they in exploratory companion studies of freshwater salmonid ecosystems in Newfoundland. Variations in TS and hence allocated size as a consequence of behavioural dynamics and variations in the crosssection aspect of fish might also make size-classes problematic, but the consistency of the present results suggest that any such variations did not systematically bias the results of this study. Validation in future studies could affirm this.

It is pertinent to acknowledge several limitations of the present study. The work was conducted over two summers, which limited inter-annual comparisons. In addition, only acoustic targets with TS > -52.6 db (4 cm by Love's 1971 equation) were extracted, thereby excluding the smallest and likely most abundant organisms. It is very likely that counts of the smallest fish were underestimated relative to those of larger fish as a consequence of decreased signal to noise ratios. That there were more 8 cm fish counted at the start of the 2012 study than 4 cm fish at the end of the 2011 study is consistent with that interpretation. In addition, for the largest and perhaps more benthically-oriented fish, a negative bias could potentially exist with the near-bottom dead zone exclusion. It is equally likely, however, that any bias was constant over the summer, making the time series of relative abundance comparable.

It can be concluded that size-based hydroacoustic methods have the potential to monitor seasonal and inter-annual fish mortality and provide information fundamental to the state of fisheries and freshwater ecosystems. These methods are essentially less intrusive, more cost-efficient and perhaps less biased than traditional net-based surveys, and could prove to be an effective tool for ecosystem-based, rather than single species-based fisheries management (Trenkel *et al*. 2011). Further studies and longer time series will be necessary to corroborate these findings and provide further insights into the novel patterns observed here. These early explorations suggest that size-based acoustic methods would bear fruitful insight into aquatic ecosystem management and conservation.

Thesis Summary

The fields of freshwater fisheries ecology and limnology have much to gain through the thoughtful and systematic deployment of hydroacoustic surveys. This thesis took aim at providing a comprehensive review of the work done to date, with an informative foray into the application of acoustic technology to observe changes in fish populations over time. The review in Chapter 1 served to synthesize the spatial, temporal and taxonomic breadth of freshwater acoustics thus far, and revealed areas of strength as well as large knowledge gaps in all three areas. The second section of the thesis aimed to explore acoustic monitoring protocols in order to determine whether within- and between-season fish population fluctuations could be detected in a boreal reservoir through the use of mobile acoustic surveys. This study revealed that acoustics can indeed detect declines in populations of fish in various size classes, and are therefore an invaluable tool to monitor the state of freshwater fishery ecosystems. If such protocols are used repeatedly over the long term they can contribute to addressing some of the temporal research gaps outlined in the review. The systematic deployment of acoustic surveys across space, time and fish taxa has the potential to revolutionize our understanding of freshwater ecosystems and the fisheries that are part of them. It is hoped that these research findings lead others to utilize and elaborate on these methods in order to acoustically illuminate the depths of lakes and reservoirs across Canada and further afield.

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