A Global Review of the Spatial, Taxonomic, and Temporal Scope of Freshwater Fisheries Hydroacoustics Research

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1 A Global Review of the Spatial,
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4 Research

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Abstract

This review assessed the status and scope of freshwater hydroacoustic fisheries research in global aquatic ecosystems with emphasis on i) geographical and spatial scope, ii) taxonomic range at the species and family levels (restricted to bony fishes of the Actinopterygii and Sarcopterygii), and iii) temporal scope. Hydroacoustic measures have been used by ecologists and managers of freshwater systems for several decades, with major progress in technology and methods in recent years. A literature review indicated research contributions that employed hydroacoustics to study freshwater fisheries in different aquatic ecosystems. Spatially, hydroacoustics research in freshwater systems have thus far been concentrated in developed countries, particularly in North America and Northern and Central Europe (83% of the studies reviewed here). Most studies were small in spatial scale and short-term, with 80% including only a single body of water and 63% conducted over a single year or season (75% spanning less than two years). In addition, effects of fish morphology and behavior on acoustic target strength (TS) and taxonomic identification are not well parameterized, with only 21 species receiving empirical study of TS. Despite progress, the present study reveals gaps in the knowledge needed for wider applications to management. These include larger biogeographical and temporal scales of study and further empirical research on TS and taxonomic identification. Recent advances in size rather than species-based methods and theory offer potential solutions to this issue but require further investigation. We conclude with recommendations for systematic hydroacoustic research to enable more effective monitoring, management, and conservation of fisheries and freshwater ecosystems.

46 **Key Words:** *freshwater hydroacoustics, target strength, TS, body size, species ID, fisheries*
47 *surveys, inland fisheries.*

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Introduction

Fisheries and plankton hydroacoustics utilizes scientific echosounders to interpret density differences in water columns, in particular those caused by living organisms. Scientific echosounders utilize calibrated sound waves travelling at approximately 1500 m.s⁻¹ with known power, transmission and reception characteristics to measure the power and “backscatter” of returned echoes. Most scientific echosounders use a narrow range of frequencies centred on 38, 120, and 200 kHz, although other frequencies are sometimes used and broadband echosounders using a wider range of frequencies are gaining increasing application. Returned echoes from single or integrated multiple targets can be converted to target size or density. Such conversions rely on knowing the conversion factor, or target strength (TS), which is the power of the echo returned from an individual of the target type of a specific size. TS depends on the cross-sectional area impacted by the advancing sound wave and hence the body size and existence and form of a swim bladder, which is the main sound scatterer in fishes. The swimming aspect of the fish is also a key determinant of returned echo power. Returned echoes are typically displayed and analyzed on an echogram, which depicts the water column, detected targets and bottom substrate, and forms the basis for editing, noise or interference removal, and determination of target type (Figure 1). Targets isolated as single organisms in sequential transmissions may be singled out using tracking algorithms and counted. In many cases, however, the majority of targets cannot be isolated, for example from schooling fishes, in which case echo integration uses the average backscatter within a given volume to estimate density. More complete descriptions of scientific hydroacoustics are referred to Simmonds and MacLennan (2005)

and Kalikhman and Yudanov (2006), and relevant online resources from acoustics technology manufacturers (HTI 2015; BioSonics 2016).

Progress in the use of hydroacoustics for the study of fish populations has been substantial over the past few decades, particularly in marine ecosystems. Scientific-grade calibrated echosounders have been utilized for decades in marine environments to quantify the distribution and abundance of many species of fishes and plankton (e.g., Sund 1935; Thorne 1983; Pieper and Holliday 1984; Hampton 1987). The advantages of hydroacoustic methods relative to capture netting are well known, and include coverage of much more of the water column, especially pelagic regions where netting is often problematic, less size selectivity, and non-lethality (MacLennan 1992; Simmonds and MacLennan 2005). In addition, the abilities of digital and multi-frequency echosounders to assess a much broader range of organism sizes and spatial and temporal distributions within the water column than is feasible with net technology is now well established (Latour et al. 2003; Koslow 2009; Trenkel et al. 2011). In freshwater ecosystems, hydroacoustic applications have also made major methodological advances (e.g. Wanzenbock et al. 2003; Everson et al. 2013; Wheeland and Rose 2014), albeit arguably less so than in marine ecosystems. With most reviews and textbooks on the topic of hydroacoustics focusing on marine applications (Johannesson and Mitson 1983; Simmonds and MacLennan 2005, Kalikhman and Yudanov 2006), the extent and scope of freshwater applications of hydroacoustics worldwide has received far less attention, despite the importance of freshwater fisheries globally (Lynch et al. 2016).

The objective of the present study is to provide a global review of published freshwater hydroacoustic research on fish and fisheries. The review is not an attempt at a synthesis of results or technical aspects of hydroacoustics studies, but of their ecological scope through the lenses of space (global geography - 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). A summary of acoustic TS research on freshwater species is also compiled. We did not include grey literature reports, conference proceedings, laboratory or simulation studies, or non-English language publications. In total, 296 studies that focused on 294 freshwater ecosystems were reviewed.

Spatial Scope of Freshwater Hydroacoustics Research to Date

Hydroacoustic research in freshwater ecosystems has largely been clustered in more affluent countries. By far the most published literature comes from studies in North America and Northern and Central Europe (Figure 2). Other important work has been undertaken in Australia, China, and the East African Rift Valley, with a minority of studies in South America, Russia, and New Zealand.

North America

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. For example, 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). 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 salmon population dynamics and local adaptation (Fraser et al. 2011). Some of this research has addressed important ecological questions. For example, Beauchamp et al. (1997, 1999) studied abundance, diel distribution, and predator-prey dynamics of salmonids in Washington and Idaho.

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 standard operating procedures are in place for undertaking hydroacoustic fisheries surveys (Rudstam et al. 2009). Smelt body size has been estimated for Lake Erie based on *in situ* TS experiments (Rudstam et al. 2003); other studies on that lake have focused on cluster sampling techniques (Connors and Schwager 2002) and density estimates based on single vs. split-beam hydroacoustic data (Rudstam et al. 1999).

Lake Huron is the site of smelt, alewife, bloater (*Coregonus hoyi*) and cisco (*Coregonus artedii*) fisheries, and several surveys have estimated the abundance of these species (Argyle 1982; Dunlop et al. 2010). Hydroacoustic 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 majority of Great Lakes hydroacoustics 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 TS for pelagic species (Fleischer et al. 1997). Vertical migrations have been investigated in alewives (Janssen and Brandt 1980) and bloaters (Fleischer and Tewinkel 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 (Van Den Avyle et al. 1995; Degan and Wilson 1995; Vondracek and Degan 1995). More recent research on the salmonids Brook Charr (*Salvelinus fontinalis*) and Ouaniche (landlocked Atlantic Salmon *Salmo salar*) in Newfoundland ponds has indicated potential to isolate and measure individual fish (Figure 1).

Europe

In Europe, freshwater hydroacoustic applications are well established in southern Scandinavia, the methods having been adapted from marine fisheries applications in the region, which routinely use hydroacoustic data for fisheries 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, Arctic charr (*Salvelinus alpinus*), whitefish, and vendace (*Coregonus albula*). Several authors (Romakkaniemi et al. 2000; Romare 2001; Knudsen and Sægrov 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 in coregonids (Gjelland and Bohn 2004; Knudsen and Gjelland 2004) and vendace (Hamrin 1986) have been well studied in Scandinavia. Other studies have compared fish echo traces with those of pelagic invertebrates (Knudsen and Larsson 2009; Knudsen et al. 2006), studied factors affecting

recruitment variability (Axenrot and Degerman 2016), and have investigated effects of introduced species (Brabrand and Faafeng 1993) and climate change (Nyberg et al. 2001) on aquatic systems.

(Lilja et al. 2000) studied TS of Atlantic salmon, brown trout (*Salmo trutta*), whitefish and pike (*Esox lucius*) in Finland (see Table 1), where extensive work has been done on fish abundance estimates (e.g. Jurvelius and Sammalkorpi 1995; Jurvelius et al. 1984). 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 hydroacoustic surveys must account for seasonal variability in fish behavior and habitat use to provide comparable measures of fish distribution and abundance. 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 hydroacoustics research. In the UK, one well-studied system is Lake Windermere, with extensive research on Atlantic salmon and Arctic charr having taken place there (Baroudy and Elliott 1993; Elliott et al. 1996; Elliott and Fletcher 2001; Jones et al. 2008; Winfield et al. 2002, 2007, 2015). Winfield et al. (2009) assessed Arctic charr abundance in five 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, Table 1), 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-transducer 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 Vergès 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 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), all of which determined the methods to be complementary and comparable (although gillnetting tended to underestimate 0+ fish that were too small for the mesh). Vertical migrations of pelagic fishes have been characterized on Lake Stechlin as well (Mehner 2006a; Mehner et al. 2010).

In Poland, hydroacoustic research has been conducted for many years. Lake Pluszne has been subject to studies of abundance (Doroszczuk et al. 2007), vertical distributions (Dembinski 1971; Świerzowski 2001), fish coexistence with blue-green algae (Godlewska

et al. 2015), comparisons of multiple frequencies (Godlewska et al. 2009a), and the effects of seasonal changes on abundance estimates (Świerzowski and Godlewska 2001; Świerzowski and Doroszczyk 2004). Many studies in Poland have been relatively long-term and include multiple bodies of water (Dembinski 1971; Godlewska and Swierzowski 2003; Doroszczyk et al. 2007; Godlewska et al. 2009b).

Hydroacoustic research has been carried out on reservoir systems in the Czech Republic. 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 (Čech and Kubecka 2002), spatial distributions (Vašek et al. 2004; Prchalová et al. 2009), to boat avoidance (Draštík and Kubečka 2005) and ontogenetic changes in fish distribution (Čech and Kubečka 2006). Diel migrations (Čech et al. 2005), daytime versus nighttime abundance estimates (Draštík et al. 2009), and juvenile perch distribution and abundance (Kubecka and Svatora 1993; Frouzova and Kubecka 2004; Čech et al. 2005, Čech et al. 2007) have been examined. The only study that has attempted to draw 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 hydroacoustic surveys in a diversity of systems in Norway, Sweden, Denmark, the UK, Germany, France and Italy.

278 *Africa*

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

293 *Asia*

294 Most of the hydroacoustic work in Asia has been conducted in China, where the onset of
295 large hydroelectric megaprojects has resulted in some of the few published hydroacoustic
296 studies from this continent – many more may not be reported in the English language
297 literature. The Yangtze River has been the site of most of this work. Studies on large fishes
298 such as common carp and the endangered Chinese sturgeon (*Acipenser sinensis*) and

paddlefish (*Psephurus gladius*) (Qiao et al. 2006; Zhang et al. 2009, Zhang et al. 2011; Wang et al. 2013) have been the focus, although some authors have broadened their work to other species (Tao et al. 2010; Lin et al. 2013a, b). Other systems studied through hydroacoustics in China include the Pearl River (Tan et al. 2011) and Lake Laojianghe (Ye et al. 2013).

Other Regions

Hydroacoustic research on inland fisheries in areas other than those outlined above has been far less extensive, although some important work has taken place in Argentina (Oldani and Baigun 2002; Vigliano et al. 2008, 2009), Australia (Matveev 2003, Matveev 2007), Brazil (Loures and Pompeu 2015), Iceland (Snorrason et al. 1992), Israel (Walline et al. 1992); Kalikhman et al. 1992; Horne et al. 2000), Japan (Okamoto et al. 1993; 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; Mochek et al. 2015), Spain (Rodríguez-Sánchez et al. 2015), Thailand (Prchalova et al. 2003), Tunisia (Djemali et al. 2009, Djemali et al. 2010) and Zimbabwe (Begg 1976). Although these studies are widespread, many important watersheds have been untouched by hydroacoustics research globally.

Most hydroacoustic surveys and research has focused on a single body of water (Figure 3). A few studies have investigated multiple systems. For example, (Emmrich et al. 2010) studied 18 lakes in seven different European countries, and based on these comparisons were able to provide evidence on the correspondence of gillnet catches with

hydroacoustics across the entire region. Another author was able to make broad comparisons of 11 freshwater systems in Australia and North America in studies of food web theory (Matveev 2003). Overall, however, generalization of patterns observed in hydroacoustic data may be constrained by the clustered distribution of studies which may lead to lakes within a cluster being pseudoreplicates. A broader spatial distribution of data would help resolve this problem and enable larger-scale spatial data comparisons and meta-analyses. Although we emphasize the need to fully understand the acoustic properties of species of interest prior to undertaking larger-scale studies (Kubečka *et al.* 2009), a lack of broader spatial coverage reduces the possibility of uncovering important differences and dynamics between water bodies, including variations in fish reproductive success and timing (Leggett and Carscadden 1978; Jackson *et al.* 2001), and seasonal and daily movement patterns among lakes and rivers (Winemiller and Jepsen 1998; Woolnough *et al.* 2009). The limited number of water bodies and geographic scope covered to date by hydroacoustic survey methods reviewed here has important consequences beyond spatial representation; this will be explored in the coming sections.

Taxonomic Scope of Freshwater Hydroacoustics Research

One consequence of the lack of spatial coverage of hydroacoustic studies is the limited number of taxa that have been researched. Globally, estimates of the number of extant freshwater fish species lie 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 4) that have been studied using hydroacoustics (0.0073% of total species diversity and 18.8% of family diversity).

Following marine applications, the majority of research has focused on commercially valued taxa, in particular Salmonids, Cyprinids, Percids, Osmerids and Clupeids (Figure 5). Studies on these taxa accounted for over 85% of all reported research in this area. Three commercially important European species - roach, perch, and vendace – are the focus of the majority of studies undertaken, and in many cases other fishes are only included incidentally (though they may be ecologically important).

The limited overall taxonomic coverage indicates that factors that may affect hydroacoustic properties have been studied in very few freshwater species. Such detailed species-focused studies are necessary in order to determine individual behavioral traits such as vessel avoidance (Wheeland and Rose 2014), physiological traits and TS-length relationships (Ona 1990), and variation in TS as a result of changes in aspect of the fish within an acoustic beam (Kubečka 1994), all of which can affect size and density estimates. Hydroacoustic studies should ideally include fish length-TS research to ensure that the relationship used for length or biomass calculations is locally appropriate for the studied species. To date, such studies are rare, with TS quantified for only 21 species (Table 1).

The TS data for freshwater fishes indicate that the traditional “standard” formula for TS-length models ($TS_{dB} = 20\log_{10}(\text{length}_{cm}) - b$) (Simmonds and MacLennan 2005), which assumes that the scattering area and hence backscatter is proportional to the square of fish length, is not appropriate for many or most species (Table 1). It is also apparent that substantial and unexplained variability exists in the proposed models, which might result from several factors, including site, seasonal or condition factors of the studied fishes (Ona 1990; Rose 1992), in addition to frequency and methodical differences among studies.

Target strength models based on fish length plotted from data in Table 1 show substantial variation (Figure 6). Differences are apparent within species and families and among frequencies, although the differences are inconsistent. Few correspond to the “standard” form that assumes a quadratic relationship to length (Simmonds and MacLennan 2005), which tends to support contentions based on marine fish that the standard form is the exception (McClatchie et al. 1996). When frequency and species are taken into account, the models appear to be more similar, although differences are still apparent. For example, for Coregonids (Figure 6a), all measured at 120 kHz, two independent models are near identical, but for a different but closed related species the model differs substantially. Large differences are apparent in the two models for Clupeids (Figure 6c), although these are confounded by different frequencies and a mix of species in the model of Fleischer et al. (1997). Models for Cyprinids (Figure 6d) are more tightly grouped, but again there are differences among species and frequencies that are not entirely consistent. Some species show higher TS at 200 kHz than at 420 kHz which is consistent with theory, but there are exceptions to that with data mostly from *Carassius carassius*, although even this comparison is confounded by a mix of different species. The most inconsistent TS models have been derived from side aspect studies, shown for Salmonids having similar body forms (Figure 6b). It appears that 200 kHz models predict higher TS than those at 420 kHz, but the single model at 120 kHz is in the middle with slope lower than other models and the standard form (most models are higher). These inconsistencies lead us to caution researchers against transference of TS models across species or frequencies, and to

385 conclude that more work is needed in this area if TS models are to be used to estimate
386 biomass.

387 In terms of the taxa that have been studied, by far the most well-studied group is the
388 salmonids – not only anadromous *Oncorhynchus* and *Salmo* spp., but also landlocked
389 *Salvelinus* (charr) and *Coregonus* (whitefish and cisco) spp. Other families that are well-
390 studied include the cyprinids, perch, smelts, and herring, although in most cases very few
391 individual species have been studied within a family (Figures 4 and 5).

392 A disproportionate amount of TS research has been undertaken on three European
393 species in particular – roach, European perch (*Perca fluviatilis*) and the vendace or
394 European cisco (*Coregonus albula*). These species are dominant and widespread in
395 Northern and Central Europe with active fisheries throughout the region, and more than a
396 quarter of the literature reviewed here involved one or more of these species.

397 The heavy concentration of hydroacoustic studies on these taxa leaves large gaps in
398 our knowledge of other important freshwater taxa. Many groups that include commercially
399 and ecologically important species have so far not been studied. Some morphologically
400 disparate or diverse groups are yet to be investigated, and it is unclear how various physical
401 differences will impact echo interpretation and subsequent hydroacoustic abundance
402 estimates. Further progress on species identification through hydroacoustics will depend
403 on an improvement in our knowledge of how acoustic signatures vary among species with
404 differing morphologies and ecological niches (Horne 2000).

An alternative to the single species approach is to measure acoustic size rather than species and construct abundance size spectra from hydroacoustic data, which can allow for fish counts or estimates of biomass at various trophic levels and thus insights into system structure and dynamics (Pollom and Rose 2015; Wheeland and Rose 2016; de Kerckhove *et al.* 2016). Taking this approach alleviates the necessity of identifying and classifying species within the hydroacoustic record, in cases in which the majority of individuals can be isolated within the acoustic beam and detectable as single targets. Especially where densities disallow reliable counting of individuals, echo integration may enable more size spectra indicators (de Kerckhove *et al.* 2016).

Temporal Scope of Freshwater Hydroacoustics Research to Date

One of the most promising avenues for freshwater hydroacoustics is long-term monitoring. Long-term (multiple seasons or years) 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 indicates that long-term hydroacoustic studies are rare in the literature, with most studies 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 6). 63% of the studies reviewed here were conducted in one full year or less, and 75% of studies within two years or less. Only 12% of studies endured for five or more years, and very few had a duration of > 10 years, which would arguably be the smallest window needed to uncover important year-to-year and seasonal variability. The majority of published studies were thus essentially snapshots of an aquatic ecosystem and fish population, and may have missed important phenological events that are crucial to

427 understanding such systems and predicting fisheries performance (e.g. Jeppesen et al.
428 2012).

429 Longer-term studies have potential to reveal ecosystem and target species dynamics
430 that are impossible with single year or season studies. Moreover, longer-term research
431 enables evaluations of survey characteristics and error, and allows comparisons to
432 environmental and anthropogenic variables. For example, Godlewska et al. (2009b) studied
433 Polish lakes for 76 months and were able to estimate the relationship between sampling
434 intensity and survey precision. That study showed a sampling error of less than 10% when
435 coverage of the water body was sufficient (~2). Other advantages of long-term studies
436 include the ability to assess seasonal variability (Winfield et al. 2007) and to observe long-
437 term population dynamics (Brabrand and Faafeng 1993; Johnson and Goettl 1999;
438 Marjomaki and Huolila 2001).

439 In all ecological studies, longer-term data tend to give a more complete picture of
440 how communities and ecosystems change over time, allowing for a more adaptive approach
441 to management that can help to avoid the pitfalls of shifting baselines in fishery knowledge
442 and to better manage freshwater resources (Pauly 1995). Early warning signs of
443 anthropogenic impacts and unwanted ecological changes are easier detected with
444 monitoring in place as well, and such datasets allow for the disentangling of how biotic,
445 abiotic, and spatial factors affect fish abundance estimates (Jackson et al. 2001).

1.5 Challenges

Perhaps the biggest challenge in quantitative fisheries hydroacoustics has been the identification of studied targets to some taxonomic level useful for management and research (e.g., Rose and Leggett 1988; Lu and Lee 1995; Scalabrin et al. 1996; Haralabous and Georgakarakos 1996). Much progress in identification has been made in marine environments since those early studies (Horne 2000; Lawson et al. 2001; Kang et al. 2002; Robotham et al. 2010), and the advent of acoustic broadband methods that allow for high-resolution imagery of fish and their swimbladders holds promise (Stanton *et al.* 2010). There has been less focus on this type of research in freshwater, where acoustic signal characteristics of various species are still relatively poorly known. It is noteworthy, however, that the complexities of identification, especially in species-rich ecosystems, may be overcome using size and not species as the basis for characterizations of freshwater fish communities (Pollom and Rose 2015; Wheeland and Rose 2015; de Kerckhove et al. 2016).

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 passing fish to be counted (e.g. Mueller et al. 2010; Langkau et al. 2012; see Martignac et al. 2014 for a review and Tušer et al. 2014 for potential biases). DIDSON methods can also be deployed simultaneously with side-scan sonar in order to emit sound horizontally for the purposes of studying shallow or littoral zones (Hughes and Hightower 2015).

Another major challenge in freshwater hydroacoustic 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 most 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). Nonetheless, many successful hydroacoustic monitoring programs in such environments have been conducted, particularly on migrating salmonids, with progress made in species identification and size estimations (Ransom et al. 1998; Banneheka et al. 2011). Noise reduction techniques such as cross-filtering between echograms have shown promise in such environments (Balk and Lindem 2000).

A logistic challenge in the advancement of freshwater monitoring programs in much of the developing world, where fisheries are of particular importance (Lynch et al. 2016), and where hydroacoustics could play an important role, is the lack of available equipment and trained personnel. In countries where hydroacoustic applications are well developed, progress in limiting these shortcomings can be made (and has been in some cases, e.g. Lake Victoria) by encouraging advanced training, collaboration, and re-use of older hydroacoustic equipment.

Summary and Conclusions

This review revealed substantial expansion and progress in freshwater hydroacoustics since the earliest implementations, with applications in 42 countries. 124

fish species have been investigated, although only 21 intensively so, and in a limited number of water bodies with concentrations in North America and Europe. There have been relatively few long-term (more than a decade) studies. It is thought that more comprehensive temporal, geographical and taxonomic coverage would elevate knowledge of freshwater ecosystems and fisheries dynamics. In addition, the acoustic properties of most freshwater species remain poorly known, even for some species that have been studied intensively. Further research on the backscatter characteristics and acoustic TS of these and other species are required to enhance the quantitative aspects of hydroacoustic surveys. At the same time, recent size-based monitoring that may be particularly relevant to freshwater ecosystems and fisheries and does not require species identification should be further explored as an alternative to traditional species-based approaches. Overall a more systematic approach to the use of hydroacoustics in freshwater ecosystems shows promise in helping to fulfill the goal of sustainable ecosystem-based fisheries management for inland fisheries globally.

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Tables

Table 1. A summary of fish length-target strength relationships that have been quantified in freshwater. The equation is**TS = $a \log(TL) + b$, where TS=target strength in decibels, TL = fish total length (cm), and a and b are constants.**

<i>Species</i>	<i>Family</i>	Acoustic Frequency (kHz)	Aspect	<i>a</i>	<i>b</i>	Region	Reference
<i>Alosa pseudoharengus</i>	Clupeidae	70	dorsal	20.53	-64.25	Laurentian Great Lakes, NE United States	Warner et al. 2002
<i>Alosa pseudoharengus</i> , <i>Osmerus mordax</i> , <i>Gasterosteus aculeatus</i> , <i>Pungitius pungitius</i>	Clupeidae, Osmeridae, Gasterosteidae	120	dorsal	52.60	-100.00	Laurentian Great Lakes	Fleischer et al. 1997*
<i>Coregonus albula</i>	Salmonidae	120	dorsal	25.50	-70.90	Germany	Mehner 2006b
<i>Coregonus albula</i>	Salmonidae	120	dorsal	20.00	-65.40	Poland	Swierzowski and Doroszczyk 2004
<i>Coregonus hoyi</i>	Salmonidae	120	dorsal	52.60	-107.00	Laurentian Great Lakes	Fleischer et al. 1997*

<i>Species</i>	Family	Acoustic Frequency (kHz)	Aspect	<i>a</i>	<i>b</i>	Region	Reference
<i>Coregonus lavaretus</i>	Salmonidae	200	side (full side vs head/tail)	39.70	-90.00	Finland	Lilja et al. 2000**
<i>Cyprinus carpio</i>	Cyprinidae	120	side (full side vs head/tail)	23.97	-103.90	Czech republic	Frouzova et al. 2005
<i>Esox lucius</i>	Esocidae	200	side (full side vs head/tail)	28.60	-74.00	Finland	Lilja et al. 2000**
<i>Lates niloticus</i>	Latidae	70	side (-90° to +90°	32.11	-86.79	East Africa	Kayanda et al. 2012
<i>Lates niloticus</i>	Latidae	120	side (-90° to +90°	30.15	-84.14	East Africa	Kayanda et al. 2012
<i>Morone americana</i>	Moronidae	120	dorsal	26.48	-69.45	NE United States	Hartman and Nagy 2005
<i>Morone saxatilis</i>	Moronidae	120	dorsal	15.37	-56.26	NE United States	Hartman and Nagy 2005
<i>Osmerus mordax</i>	Osmeridae	70, 120	dorsal	19.90	-67.80	Laurentian Great Lakes	Rudstam et al. 2003
<i>Perca fluviatilis</i>	Percidae	120	side (full side vs head/tail)	20.96	-97.05	Czech republic	Frouzova et al. 2005
<i>Rutilus rutilus</i>	Cyprinidae	70	dorsal	18.40	-69.30	France	Guillard and Gerdeaux 1993

<i>Species</i>	Family	Acoustic Frequency (kHz)	Aspect	<i>a</i>	<i>b</i>	Region	Reference
<i>Rutilus rutilus</i>	Cyprinidae	120	side (full side vs head/tail)	17.02	-87.37	Czech republic	Frouzova et al. 2005
<i>Salmo salar</i>	Salmonidae	200	side (full side vs head/tail)	25.60	-73.00	Finland	Lilja et al. 2000**
<i>Salmo trutta</i>	Salmonidae	120	side (full side vs head/tail)	10.96	-76.79	Czech republic	Frouzova et al. 2005
<i>Salmo trutta</i>	Salmonidae	200	side (full side vs head/tail)	28.90	-78.00	Finland	Lilja et al. 2000**
<i>Salmo trutta</i>	Salmonidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	34.20	-114.00	UK	Kubecka and Duncan 1998a
<i>Rutilus rutilus</i>	Cyprinidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	29.30	-96.70	UK	Kubecka and Duncan 1998a
<i>Rutilus rutilus</i>	Cyprinidae	200	side (full side vs head/tail aspect vs mean all-aspect – 360°)	15.80	-78.00	UK	Kubecka and Duncan 1998a

<i>Species</i>	Family	Acoustic Frequency (kHz)	Aspect	<i>a</i>	<i>b</i>	Region	Reference
<i>Carassius carassius, Cyprinus carpio</i>	Cyprinidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	19.60	-76.20	UK	Kubecka and Duncan 1998a
<i>Carassius carassius, Cyprinus carpio</i>	Cyprinidae	200	side (full side vs head/tail aspect vs mean all-aspect – 360°)	22.60	-89.80	UK	Kubecka and Duncan 1998a
<i>Leuciscus leuciscus, Leuciscus cephalus</i>	Cyprinidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	27.30	-93.50	UK	Kubecka and Duncan 1998a
<i>Leuciscus leuciscus, Leuciscus cephalus</i>	Cyprinidae	200	side (full side vs head/tail aspect vs mean all-aspect – 360°)	17.90	-82.10	UK	Kubecka and Duncan 1998a
<i>Perca fluviatilis</i>	Percidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	30.30	-98.90	UK	Kubecka and Duncan 1998a
<i>Perca fluviatilis</i>	Percidae	200	side (full side vs head/tail aspect vs mean all-aspect – 360°)	18.20	-83.00	UK	Kubecka and Duncan 1998a

<i>Species</i>	Family	Acoustic Frequency (kHz)	Aspect	<i>a</i>	<i>b</i>	Region	Reference
<i>Abramis brama</i>	Cyprinidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	31.40	-102.10	UK	Kubecka and Duncan 1998a
<i>Abramis brama</i>	Cyprinidae	200	side (full side vs head/tail aspect vs mean all-aspect – 360°)	18.20	-81.60	UK	Kubecka and Duncan 1998a
<i>Onchorhynchus mykiss</i>	Salmonidae	420	side (full side vs head/tail aspect vs mean all-aspect – 360°)	26.90	-96.00	UK	Kubecka and Duncan 1998a
<i>Onchorhynchus mykiss</i>	Salmonidae	200	side (full side vs head/tail aspect vs mean all-aspect – 360°)	18.60	-87.20	UK	Kubecka and Duncan 1998a

* Parameters converted from those published to correspond with $TS_{dB} = a \log_{10}(\text{length}_{cm}) - b$ for comparison.

**Side aspect TS, with mean estimated in the logarithmic domain; approximately 1 dB lower than in the more appropriate arithmetic domain (MacLennan and Simmonds 1992).

Figure Captions

Figure 1. Echogram from Cold Spring Pond, Newfoundland, showing salmonid targets at 200 kHz in July 2010. The echogram spans approximately 1 km with lakebed depths ranging around 30 m and surface temperatures 18.8° C.

Figure 2. 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. Map created using Esri Data and Maps (Esri 2016: Redlands, California. Available at <http://www.arcgis.com/home/item.html?id=170b5e6529064b8d9275168687880359>).

Figure 3. Number of water bodies included in the freshwater hydroacoustics publications reviewed in the present study. **Inset:** Percentage of studies with different counts of water bodies researched. Very few studies reviewed here involved more than 4 bodies of water.

Figure 4. Histogram displaying the count of hydroacoustic studies assessed here that focused on or heavily involved each fish family. **Inset:** Comparison of counts of studies reviewed here that involve each fish family.

Figure 5. Histogram displaying the count of hydroacoustic studies assessed here that focused on or heavily involved each fish species.

Figure 6. Some TS-length models for a) Coregonids (dorsal aspect), b) *Salmo trutta* (side aspect), c) Clupeids (dorsal aspect), and d) Cyprinids (dorsal aspect). Colours indicate authors: black (Kubecka and Duncan 1998); red (Fleischer et al. 1997); blue (Mehner 2006b); brown (Swierzowski and Doroszczyk 2004); green (Frouzova et al. 2005); orange (Lilja et al. 2000); purple (Warner et al. 2002). Line styles indicate acoustic frequency: 70 kHz (dash dot); 120 kHz (solid); 200 kHz (small dash); 420 kHz (large dash). For panel b) open arrowhead indicates *S. salar*, closed arrowhead *O. mykiss*; panel d) open arrowhead indicates *Carassius carassius*, filled arrowhead *Leuciscus* spp., double arrowhead *Abramis brama*, no arrowhead *Rutilus rutilus*.

Figure 7. 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, >1-2 years, >2-3 years, >3-4 years, >5-6 years, >6 years; note that proportions do not sum to 100% as a result of rounding).

Echogram from Cold Spring Pond, Newfoundland, showing salmonid targets at 200 kHz in July 2010. The echogram spans approximately 1 km with lakebed depths ranging around 30 m and surface temperatures 18.8° C.

112x34mm (72 x 72 DPI)

Draft

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.
205x118mm (300 x 300 DPI)

Number of water bodies included in the freshwater hydroacoustics publications reviewed in the present study. Inset: Percentage of studies with different counts of water bodies researched. Very few studies reviewed here involved more than 4 bodies of water.

161x101mm (300 x 300 DPI)

Histogram displaying the count of hydroacoustic studies assessed here that focused on or heavily involved each fish family. Inset: Comparison of counts of studies reviewed here that involve each fish family.
251x155mm (300 x 300 DPI)

Histogram displaying the count of hydroacoustic studies assessed here that focused on or heavily involved each fish species.
266x163mm (300 x 300 DPI)

Some TS-length models for a) Coregonids (dorsal aspect), b) Salmo trutta (side aspect), c) Clupeids (dorsal aspect), and d) Cyprinids (dorsal aspect). Colours indicate authors: black (Kubecka and Duncan 1998); red (Fleischer et al. 1997); blue (Mehner 2006b); brown (Swierzowski and Doroszczyk 2004); green (Frouzova et al. 2005); orange (Lilja et al. 2000); purple (Warner et al. 2002). Line styles indicate acoustic frequency: 70 kHz (dash dot); 120 kHz (solid); 200 kHz (small dash); 420 kHz (large dash). For panel b) open arrowhead indicates *S. salar*, closed arrowhead *O. mykiss*; panel d) open arrowhead indicates *Carassius carassius*, filled arrowhead *Leuciscus* spp., double arrowhead *Abramis brama*, no arrowhead *Rutilus rutilus*. 202x196mm (300 x 300 DPI)

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, >1-2 years, >2-3 years, >3-4 years, >5-6 years, >6 years; note that proportions do not sum to 100% as a result of rounding).

262x167mm (300 x 300 DPI)