Hydroacoustic fish stock assessment in southern and northern boreal lakes – potential and constraints

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Academic dissertation

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Author’s contribution

I TM planned the study, participated in hydroacoustic analyses and wrote the first version of the manuscript. AT participated in analyses and HP in writing the article.

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Abbreviations of authors: AT=Antti Tuomaala, HP=Heikki Peltonen, KKK=Kimmo Kalevi Kahilainen, TM=Tommi Malinen

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Abstract

Modern echosounders produce very accurate and versatile information on observed fish, but applicability of hydroacoustics in fish stock assessment is still largely determined by the behaviour of aquatic animals. A valid assessment is possible only when the target species avoid the inaccessible zones of echo sounder: surface blind zone, bottom dead zone and shallow areas. In addition, it requires an applicable method for eliminating echoes from other targets, especially phantom midge (*Chaoborus*) larvae, which are abundant in clay-turbid lakes. In Fennoscandia, acoustics has been widely used in vendace (*Coregonus albula* (L.)) stock monitoring due to its high economic value but other species have been less frequently assessed.

In the present study, the applicability of hydroacoustics in fish stock assessment was investigated in two contrasting environments, in eutrophic, clay-turbid lakes dominated by smelt (*Osmerus eperlanus* (L.)) located in southern Finland and in oligotrophic, clear-water lakes dominated by whitefish (*Coregonus lavaretus* (L.)) located in northern Lapland. In both lake groups, the suitable diel periods and seasons for acoustic assessment were sought. In southern lakes, a new method was developed for eliminating the disturbance of *Chaoborus*. In northern lakes, the differences of the applicability of acoustics between whitefish populations were explored.

The developed method enabled valid smelt density estimation also in lakes with abundant *Chaoborus* population. Without the new method, the smelt density would have been seriously overestimated. In southern lakes, the pelagic occurrence of smelt favours acoustic assessment. Both day and night surveys can be used and the suitable seasonal sampling window lasts from late July to October. However, because young-of-the-year smelt may occasionally inhabit shallow areas, acoustics should be supplemented by trawling in these areas. In highly turbid lakes, the surface blind zone may be a considerable source of bias and acoustics should be supplemented by surface trawling. Hydroacoustics appeared to be a very useful method in smelt population monitoring and it enables versatile studies on pelagic food-web dynamics of eutrophic lakes.

In northern whitefish lakes, the diel period and season have dramatic effects on the applicability of acoustics. The only suitable conditions for an acoustic survey was occurred at night-time in autumn. In summer, under the midnight sun, and during the day in autumn, the pelagic fish density was very low as most whitefish remained in the bottom dead zone. The applicability of acoustics differed highly between the whitefish populations. In lakes with polymorphic whitefish, the applicability was good for densely-rakered (DR) whitefish due to its pelagic occurrence, but poor for large sparsely-rakered whitefish (LSR) inhabiting shallow areas and small sparsely-rakered (SSR) whitefish inhabiting a bottom dead zone. In lakes with monomorphic whitefish, the level of utilization of the pelagic habitat, and hence the applicability of acoustics differed highly between lakes. The duration of the autumnal sampling window remained unknown and more frequent surveys would be informative for determining the applicability of hydroacoustics in northern whitefish lakes. In addition, surveys revealed that very small-sized nine-spined stickleback (*Pungitius pungitius* (L.)) is abundant in some northern lakes. The composition of trawl catches indicated very low catchability of this species and their proportion was estimated from target strength (TS) distributions. The abundance of nine-spined stickleback suggests that its role in the pelagic food web of northern Fennoscandian lakes should be explored.

In conclusion, considerable differences exist in a suitable timing for a survey and in the most serious sources of bias between the lake groups. Northern whitefish lakes are more challenging subjects to hydroacoustic assessment and the applicability of acoustics may differ dramatically between whitefish populations. The results highlight that prior knowledge of the pelagic food-web is essential for successful hydroacoustic fish stock assessment.

Contents

1. Introduction

1.1 Hydroacoustic estimation of fish populations

Hydroacoustics is a widely applied estimation method for pelagic fish populations in both marine and freshwater ecosystems (Johanneson & Mitson 1983, Simmonds & MacLennan 2005). The method is based on transmitting ultrasonic signals and measuring the intensity of echoes reflected from fish. Acoustic data is collected along sailed transects, placed usually either equidistantly or in a 'zig-zag' pattern. The data is stored on the computer and analysed with post-processing software to obtain fish density and biomass estimates. They can be computed by two different approaches: (1) echo counting, which is based on counting the echoes from individual fish per ensonified water volume (Kieser & Mulligan 1984), and (2) echo integration, where the energies of received fish echoes are integrated and the fish density is given by dividing the integral with the mean reflected energy by a single fish (Midttun & Nakken 1977). Echo counting is suitable for estimating the density of dispersed fish, whereas the density of schooled fish should be estimated by echo integration.

Hydroacoustics has many advantages compared with other assessment methods: it is independent of catch statistics and the estimate can be produced very quickly, even based on data from a single survey. However, the ease of the method is somewhat misleading. It can be used only in the estimation of pelagic fish, it should be supported to experimental fishing preferably with an active gear such as a trawl, and it has many serious sources of bias (Shotton & Bazigos 1984, Simmonds & MacLennan 2005). During the last three decades, the technical development of hydroacoustic equipment has been rapid and modern echo sounders produce very accurate and versatile information on ensonified fish. This has not, however, diminished the need of biological understanding about the studied ecosystems, communities and fish populations. For instance, seasonal, diurnal and ontogenetic migrations of fish will always be present and may strongly restrict the duration of the suitable time window for a hydroacoustic survey. Hence, the inappropriate timing of the survey may produce seriously biased estimates for fish abundance in spite of highly developed hydroacoustic techniques.

1.2 The biological prerequsities for hydroacoustic assessment

The boundary conditions for hydroacoustic assessment are largely set by the behaviour of fish and other aquatic animals. The behaviour of fish affects the applicability of acoustic assessment in various ways (Freon & Misund 1999). The most essential is the habitat selection of the target species. The occurrence of fish in the three habitats unavailable for echo sounding, the surface blind zone, bottom dead zone and shallow areas would bias the population estimate (Shotton & Bazigos 1984). For this reason, many fish stocks are never assessable with hydroacoustics. The height of the surface blind zone is determined by the location and properties of the transducer, varying from about two meters with a high-frequency transducer in a towed body to more than ten meters with a hull-mounted and low-frequency transducer in a large sea vessel. The height of the bottom dead zone depends e.g. on the water depth, the slope of the bottom and the properties of transducer, varying from a few centimetres with a high-frequency transducer in a shallow lake (Tuser et al. 2013) to several metres with low-frequency applications in deep oceans (Mitson 1983). The importance of shallow areas as a source of bias depends on the bathymetry of the study area as well as the size and properties of the survey vessel.

The other important behavioural factor affecting the hydroacoustic estimation is the schooling behaviour of fish. In generally, the schooling complicates assessment, because the echo integration is based on more assumptions than echo counting (Simmonds & MacLennan 2005). One of the most severe sources of bias in echo integration is acoustic shadowing (Røttingen 1976). The phenomenon takes place in dense fish schools, where the uppermost fish attenuate the transmitted sound so that the reflected echo from the lowermost fish is weakened. Shadowing has been reported cause considerable underestimation of schooling pelagic fish (Misund 1993, Appenzeller & Leggett 1992, Røttingen et al. 1994).

In addition to habitat choice and schooling behaviour, also fish avoidance can bias the acoustic density estimate. When a survey vessel approaches, fish may either move away from the acoustic beam, causing underestimation of density, or dive within the beam, when the tilt angle changes, diminishing the reflected echo (Olsen et al. 1983 a and b). The avoidance may be a serious source of bias in sea surveys carried out with large vessels (Olsen 1990) but less dramatic in lakes where smaller boats are used (Drastik & Kubecka 2005, Wheeland & Rose 2015).

Furthermore, also the behaviour of fish other than the target species, and even that of invertebrates may affect the accuracy of fish stock assessment. The pelagic presence of unwanted species complicates estimation, because the echoes from these species must be discriminated from echoes from the target fish species. Under favourable conditions, discrimination can be based on the strength of reflected echoes, more exactly the target strength (TS) (Lindem 1983, Parker-Stetter et al. 2006), but very often the strength of echoes from the wanted and unwanted targets are so close to each other that such a discrimination is not possible. Typically, the proportions of different fish species are determined by simultaneous fishing but this inevitably increases uncertainty of density estimates. It may be difficult to attain sufficient coverage of fishing (in both vertical and horizontal direction) (Yule et al. 2013b) and the variable catchability of different fish species may induce bias to the estimates (Gunderson 1993). The presence of invertebrates, such as large crustaceans in oceans (Madureira et al. 1993) and phantom midge (*Chaoborus*) larvae or opossum shrimps (*Mysis*) in lakes (Eckmann 1998, Rudstam et al. 2008a), may complicate fish density estimation. Especially *Chaoborus* may induce considerable bias to fish density estimates and such situations may exist, where the discrimination between fish and *Chaoborus* is not possible (Eckmann 1998). The echoes from these unwanted targets are generally called reverberation (Simmonds & MacLennan 2005).

For these reasons, the most accurate population estimates are obtained when the target fish species occur dispersed within the pelagic layer, avoiding surface blind zone, bottom dead zone and shallow areas and the pelagic densities of other fish species and disturbing invertebrates are low. The fish density of surface and bottom layers can be estimated using an active gear, typically a trawl (Aglen et al. 1999, Olin & Malinen 2003, Kotwicki et al. 2013), but attaining reasonable coverage may be challenging and trawling may be impossible for many reasons, e.g. bathymetry of the study area. Furthermore, many of the above-mentioned sources of bias can be alleviated by modern technology and approaches. Horizontal and upward-looking beaming may detect most fish hidden in the surface blind zone (Jurvelius et al. 1996, Kubecka & Wittingerova 1998, Knudsen, & Sægrov 2002, Baran et al. 2017) and various techniques have been developed for estimating the fish density in the bottom dead zone (Ona & Mitson 1996, Tuser et al. 2013). Species identification can be at least partly solved by broadband transducers (Reeder et al. 2004), by computational methods based on the properties of fish schools (Robotham et al. 2010) and by a stereo camera applications (Boldt et al. 2018). Additionally, multi-frequency applications improve possibilities to discriminate between fish and invertebrates (Knudsen et al. 2006, Jurvelius et al. 2008). However, because the suitability of these methods vary between study environments and subjects, and they are not always available, the knowledge of fish and invertebrate behaviour is still essential for a successful hydroacoustic survey.

1.3 Habitat selection and schooling behaviour

The habitat choice (here particularly the use of pelagic habitat) and schooling behaviour of the target species are probably the most important behavioral aspects affecting the applicability of acoustic assessment. These are determined by many abiotic, e.g. temperature and light, and by biotic factors, e.g. food availability and predation risk (Whitney 1969, Helfman 1981, Werner et al. 1983, Kramer 1987, Clark & Levy 1988, Freon & Misund 1999). In addition, all of these factors may have interactions with each other affecting the habitat choice of fish.

In temperate lakes, the changes in water temperature are strong between seasons and often vertical stratification develops during the summer. This has strong impacts on the suitability of pelagic habitat and different depth layers (epi-, meta-, hypolimnion) for different fish species (Ferguson 1958, Rudstam & Magnuson 1985, Mehner et al. 2010). For instance, during the summer stratification, warm-water species (e.g. roach) prefer the warm epilimnion and cold-water species (e.g. vendace) prefer the cooler hypolimnion (Northcote & Rundberg 1970, Eloranta & Eloranta 1978, Beier 2001). The temperature preferences of a given species may also change during the ontogeny: young-of-the-year fish prefer generally warmer water than older individuals (Tin & Jude 1983, Dufour et al. 2007). The temperature also has indirect effects on the habitat choice. For instance, it affects the food resources in the pelagic habitat, where the abundance of zooplankton fluctuates dramatically (e.g. Tallberg et al. 1999).

The vertical light profile and the diel cycle of light have dramatic effects on the suitability of a given habitat for fish, because the light intensity largely determines the food detectability and the predation risk (Clark & Levy 1988, Gjelland et al. 2009). Light has pronounced impacts on the use of pelagic habitat with occasionally abundant food resources but no refuges against predation. As the light intensity increases, both the food detectability and the predation risk increase. Depending on the species, the optimal time window for utilizing pelagic habitat may be during darkness or twilight periods (Clark & Levy 1988, Helfman 1993). In turbid waters, however, low illumination reduces the predation risk, enabling the use of a pelagic habitat also during daytime (e.g. Mous et al. 2004). Light intensity also considerably affects the schooling behaviour of fish. Schooling takes place, if it benefits fish, for instance, through better predator avoidance or more effective feeding (Pitcher & Parrish 1993). However, irrespective of the ultimate reason behind schooling, schools generally disperse as the light intensity decreases (Whitney 1969).

The large seasonal or/and diurnal variation of these determinants implies that the pelagic habitat use and schooling behaviour fluctuates considerably with season and diel period. Fishes show diurnal and seasonal migrations in both vertical and horizontal directions, affecting considerably the applicability of acoustic assessment. Due to the general pattern of diurnal vertical migration (DVM), ascending at dusk and descending at dawn, fish may occur in the bottom dead zone during daytime (Jurvelius et al. 1988) or in the surface blind zone at night (Horppila et al. 2000, Knudsen & Saegrov 2002). Due to the general pattern of horizontal migration, offshore movement at dusk and onshore movement at dawn, fish may be outside the acoustic sampling during the day but detectable at night (Bohl 1980, Gliwicz & Jachner 1992). However, reverse diurnal migrations have also been documented (Engel & Magnuson 1976, Imbrock et al. 1996, Staby et al. 2011, Ahrenstorff & Hrabik 2016). Similarly, due to seasonal movements, e.g. spawning migrations, fish may be occasionally inaccessible for acoustics (Eckmann 1995). The importance of light intensity for schooling induces large variation in the degree of schooling between day and night (Dembinski 1970, Helfman 1981) and may limit the applicability of acoustics to night-time (Appenzeller & Leggett 1992). Although numerous studies have compared day and night surveys and investigated the seasonal sampling window (Jurvelius & Heikkinen 1988, Winfield et al. 2007, Drastik et al. 2009, Yule et al. 2009), more reseach is still needed, because the migration patterns are evidently species- and environment-specific.

1.4 Hydroacoustic studies in Fennoscandian lakes

The development of hydroacoustic fish detecting accelerated after the Second World War, when sea fishers and researchers started to apply the techniques developed by the military, and the first attempts at acoustic fish density estimation were made in the 1950s (Cushing 1952, Tungate 1958, Richardson et al. 1959). In Fennoscandian lakes, hydroacoustics has been used since the late 1960s in studies concerning pelagic fish distribution (Northcote & Rundberg 1970) and since the early 1980s in quantitative fish density estimation (Lindem 1983, Lindem & Sandlund 1984, Jurvelius et al. 1984). Especially in Finland, a great majority of freshwater acoustic studies has been aimed at vendace (*Coregonus albula* (L.)) because of its high economic importance. It is the dominant species of many lakes in Central Finland, supporting considerable commercial and subsistence fisheries. Numerous vendace-oriented studies (e.g. Jurvelius 1991, Marjomäki & Huolila 1995, Nyberg et al. 2001, Axenrot & Degerman 2016) have shown that acoustics is applicable in density estimation of this pelagic species. However, in lakes not supporting harvestable vendace stock, acoustics have been less frequently applied (but see Horppila et al. 1996, Jurvelius et al. 2005, Keskinen et al. 2012). Especially in southernmost and northernmost Finland, the pelagic fish communities of many lakes are dominated by species other than vendace. In southern Finland, these include eutrophic and turbid lakes dominated by smelt (*Osmerus eperlanus* (L.)) (Sammalkorpi & Turunen 1995, Sammalkorpi 2000, Olin et al. 1998). In northern Lapland, outside the natural distribution of vendace, these include oligotrophic and clear-water lakes dominated by whitefish (*Coregonus lavaretus* (L.)) (Sarjamo et al. 1989, Lehtonen & Niemelä 1998).

Although the economic importance of smelt in southern lakes and whitefish in northern lakes is generally low, the estimation of their density and biomass may be of crucial importance because both may play a key role in the pelagic food web. In northern lakes, the pelagic coregonids determine prey resources for the most abundant predator, brown trout (*Salmo trutta* L.) (Jensen et al. 2008, 2015), which is the most valuable target of fisheries. In southern smelt lakes, pelagic predatory fish, e.g. pikeperch (*Sander lucioperca* (L.)), usually have abundant prey resources but the dense pelagic fish assemblage may induce considerable top-down effects in the food-chain possibly contributing the formation of cyanobacterial blooms (Sarvala et al. 1998, Elser et al. 2000, Jeppesen et al. 2003).

1.5 Smelt

Smelt (*Osmerus eperlanus*) is a small-sized salmonid species inhabiting freshwaters and coastal areas in northern Europe. It is widely distributed especially in the catchment of the Baltic Sea. It is sometimes also referred to as European smelt, but in this thesis only the term 'smelt' is used from here forward. Smelt has two close relatives, rainbow smelt (*Osmerus mordax*) distributed in eastern North America, and Pacific rainbow smelt (*Osmerus dentex*) living in North Pacific and Arctic waters (Nellbring 1989, Mc Cusker et al. 2013). The species belonging the genus *Osmerus* are considered very similar and results from the more extensively studied rainbow smelt have been generally utilized in studies focused on smelt. However, because differences between these two species have not been comprehensively studied, primarily smelt studies are referred to in the present thesis.

The phenotypic plasticity of smelt is exceptionally high: stunted and more rapidly growing forms exist, and they can live both in allopatry or sympatry (Nellbring 1989). While the heredity and the existence of two or more sympatric populations as in rainbow smelt (Saint-Laurent et al. 2003) cannot not be completely excluded, the population parameters (e.g. growth, maturation and mortality) of a certain genotype has found to vary according to physical and biological characteristics of the environment (Kriksunov & Shatunovskiy 1979, Ivanova 1982, Volodin & Ivanova 1987). Smelt is a cold-water species. Adult smelt prefer a temperature of 12°C (Ivanova 1982) while younger smelt tolerate warmer water. During the summer stratification, young-of-the-year (0+) smelt may occur continuously in the warm epilimnion, but older smelt mostly inhabit colder meta- or hypolimnion (Ivanova 1982).

Smelt is an omnivorous species utilizing all food resources available in offshore habitats. Larval smelts feed in their early stages on copepods, rotifers and diatoms (Næsje et al. 1987, Jachner 1991). After that, the diet of young-of-the-year smelts consists almost exclusively on crustacean zooplankton (Næsje et al. 1987, Jachner 1991, Rogala 1992, Karjalainen et al. 1997, Salujõe et al. 2008). Yearlings and older smelt prefer larger food items, typically *Chaoborus* larvae or relict crustaceans, e.g. *Mysis relicta* or *Pallasea quadrispinosa* if available (Nilsson 1979, Sandlund et al. 1985, Vinni et al. 2004, Northcote & Hammar 2006). The proportion of fish in the diet increases with smelt size and also cannibalism is common (Sterligova 1979, Vinni et al. 2004, Hammar et al. 2017).

The strong preference of smelt to pelagic habitat favours hydroacoustic assessment. Although acoustics has been applied frequently in estimation of rainbow smelt populations in North America since the early 1980s (Heist & Swenson 1983), only a few estimates from European lakes have been reported (Peltonen et al. 1999, Nyberg et al. 2001, Jurvelius et al. 2005, Keskinen et al. 2012). From the sources of bias originating from fish inaccessibility, the surface blind zone is obviously the most serious one. Observations from a variety of lakes suggest that smelt ascend up to the surface blind zone at night (Dembinski 1971, Jurvelius 1991, Gliwicz & Jachner 1992, Horppila et al. 2000). In turbid conditions, smelt may occur in the surface layer even during daytime (Mous et al. 2004). Moreover, at least rainbow smelt occasionally form surface schools during daytime (Kendall 1927). The bias induced by surface blind zone obviously differs between seasons. In general, it is a more serious problem in cool-water seasons, whereas during summer the warm epilimnion sets the upper boundary for ascending smelt (Northcote & Rundberg 1970, Dembinski 1971, Jurvelius & Louhimo 1991). However, in some circumstances, smelt may ascend to the surface layer even in mid-summer (Horppila et al. 2000). In addition, fish in the shallow areas outside the hyrdoacoustic sampling may be a relevant bias source. While smelt generally avoid shallow areas during summer (Sandlund et al. 1985, Lammens et al. 1990, Jeppesen et al. 2006), they can utilize them in cold seasons (Sterligova 1979). In addition, young-of-the-year (0+) smelt, being relatively tolerant of warm water, may inhabit shallow areas also during summer. The bottom dead zone of echosounder may be a relevant source of bias in oligotrophic lakes with abundant benthic crustacean populations. In these lakes, smelt may feed frequently on crustaceans and remain at the near-bottom layer (Nilsson 1979, Sandlund et al. 1985). In eutrophic lakes, however, these resources are generally scarce, and the occurrence of smelt in the near-bottom layer may also be restricted by hypolimnetic oxygen depletion (Jurvelius & Louhimo 1991, Keskinen et al. 2012).

As a species forming schools, acoustic shadowing may be a considerable source of bias in smelt density estimation. Shadowing was considered to cause dramatic underestimation of rainbow smelt density in Lake Memphremagog during daytime (Appenzeller & Leggett 1992). However, the occurrence of this phenomenon in smelt, or lakes of different types has not been documented. It is reasonable to expect that many factors, such as the density and size of schools as well as the size of fish strongly affect the magnitude of acoustic shadowing.

While the behaviour of smelt favours hydroacoustic estimation, in some lakes, the estimation is seriously disturbed by *Chaoborus* larvae (Horppila et al. 2000). The two air sacs of a *Chaoborus* larva are relatively strong scatterers and larvae may form dense aggregations, which are difficult to distinguish from fish (Northcote 1964, Unger & Brandt 1989). Furthermore, the applicability of the only existing quantitative discrimination method is questionable for typically small-sized smelt, because it requires relatively large size-difference of *Chaoborus* and fish targets (Eckmann 1998).

The low catchability of smelt by gill-nets may hamper traditional monitoring of fish stocks (Peltonen et al. 1999, Olin & Malinen 2003, Olin et al. 2008). It is likely that the prevailing monitoring practice based on gill-netting has undervalued of the role of smelt in food-webs of Fennoscandian lakes. Other estimation methods have shown that smelt is numerically the dominant pelagic species in a wide variety of Fennoscandian lakes (Northcote & Rundberg 1970, Nyberg et al. 2001, Jurvelius et al. 2005). A dense smelt population may have considerable effects on both upper and lower trophic levels of the food web and may hence be a key species in the pelagic fish assemblage (e.g. Nellbring 1989, Sandlund et al. 2005, Hammar et al. 2017).

1.6 Whitefish

Whitefish is a very diverse species distributed throughout northern and central Europe. It is often called European whitefish, because it has a close relative, lake whitefish (*Coregonus clupeaformis* Mitchill) living in North America. In the present thesis, only terms 'whitefish' and 'lake whitefish' are hereafter used. Whitefish show divergent phenotypic traits and niche occupation especially in high-altitude lakes and in the northernmost part of its distribution area (Svärdson 1979, Østbye et al. 2005, Hudson et al. 2007).

In northern Lapland, whitefish is the dominant species in many lakes (Sarjamo et al. 1989, Lehtonen & Niemelä 1998). In most cases it occurs as a monomorphic population utilizing both pelagic and littoral prey resources (Amundsen et al. 2004, Harrod et al. 2010). In many large, deep and slightly more productive lakes, however, the adaptive radiation has divided whitefish into two or more sympatric morphs, which have specialized in feeding different prey resources. In these lakes, whitefish morphs often dominate all available habitats (Harrod et al. 2010, Siwertsson et al. 2010). Whitefish morhps differ considerably in morphometric and meristic traits. The most pronounced phenotypic difference is the number of gillrakers (Kahilainen & Østbye 2006). The three most comprehensively documented sympatric morphs living in northern lakes are (1) densely rakered morph (DR), (2) large-sized sparsely rakered morph (LSR) and (3) small-sized sparsely rakered (SSR) morph (Kahilainen & Lehtonen 2002, Kahilainen & Østbye 2006). The DR morph is a highly specialized zooplanktivore, LSR morph is specialized to feed on littoral benthic macroinvertebrates and SSR morph is specialized to utilize profundal benthic macroinvertebrates (Palomäki 1981, Lehtonen & Kahilainen 2002). However, the taxonomy of sympatric morphs has not been comprehensively explored and other morphs may still be discovered (Kahilainen et al. 2014). Furthermore, whitefish morphs may hybridize and introgress with other morphs, or even with vendace (Kahilainen et al. 2011a, Bhat el. al. 2014) hampering morphological and meristic identification of morphs in some lakes.

Whitefish is generally a cold-water species but the temperature preference differs considerably between whitefish morphs (Kahilainen et al. 2014). While deep-dwelling dwarf morphs occur continuously at very low temperature (< 8°C, Helland et al. 2007), littoral-dwelling LSR whitefish tolerate 10-20°C summertime temperatures (Kahilainen et al. 2014). In addition, young-of-the-year whitefish prefer warmer water than adults (Dufour et al. 2007).

Hydroacoustics has been applied in whitefish assessment especially in large Alpine lakes. Whitefish has proved relatively optimal for acoustics in these environments because of the pelagic behaviour of whitefish and the small overlap of horizontal and vertical distributions with other species (Dahm et al. 1985, Appenzeller 1995, Yule et al. 2013a). In addition, hydroacoustic has been used in whitefish assessment in northern Germany (Emmrich et al. 2010), in the U.K. (Winfield et al. 2013) and in southern Fennoscandia, where the occurrence of whitefish outside of the pelagic habitat, and the presence of other pelagic species, especially vendace, typically complicates the assessment (Sandlund et al. 1985, Enderlein & Appelberg 1992, Linløkken 1995). In northern Fennoscandia, hydroacoustics has been applied in food-web studies in two subarctic Norwegian lakes, where two native whitefish morphs (densely rakered and sparsely rakered) co-exist with introduced vendace (Gjelland 2008). In these lakes, acoustics has proved to be useful in density estimation of densely rakered whitefish and vendace throughout the open water period, whereas sparsely rakered morph exist mainly in benthic habitats and hence outside the range of acoustic sampling (Amundsen et al. 1999, Gjelland 2003). In early use of hydroacoustics in northern lakes, pioneering attempts were made to estimate vendace and whitefish densities in the large Lake Inari but these encountered problems, connected especially with unexpected diel vertical migration patterns of target species (Jurvelius & Louhimo 1991).

Due to the great diversity of whitefish habitat choice, the applicability of hydroacoustics obviously varies widely between whitefish populations. Planktivorous whitefish populations may strongly prefer pelagic habitats, favouring acoustic assessment but benthivorous populations may occur mostly in the bottom dead zone or in shallow areas. Many whitefish populations, however, use several food resources and utilize the pelagic habitat when it is profitable to do so. Especially monomorphic whitefish and sympatric DR whitefish may utilize all habitats of the lake (Næsje et al. 1991, Amundsen et al. 1999, Hayden et al. 2014a). The profitability of the pelagic habitat is determined mainly by food resources and predation risk, which fluctuate with diel period and season (Clark & Levy 1988, Næsje et al. 1991, L'-Abée-Lund et al. 1993, Kahilainen et al. 2009). In northern lakes, these changes are more pronounced due to northern climate and light regime. Short summer induces large and rapid changes in zooplankton resources (Amundsen 1988, Kahilainen et al. 2005, Hayden et al. 2014b), and polar light regime with midnight sun in summer but dark nights in autumn induce substantial changes in the predation risk of whitefish (Gjelland et al. 2009, Kahilainen et al. 2009). Hence, the applicability of acoustics in whitefish population estimation in northern lakes can vary dramatically with population, season and diel period and all the aforementioned three sources of bias (the shallow areas, surface blind zone and bottom dead zone) may be relevant. So far, exhaustive studies on seasonal and diurnal changes in habitat use of various northern whitefish populations and the applicability of hydroacoustic assessment have not been conducted (but see Gjelland 2003).

2. Objectives of the thesis

The aim of the present thesis was to determine the applicability of hydroacoustics in estimation of pelagic fish populations in two contrasting freshwater environments: eutrophic and turbid, smelt-dominated lakes in southern Finland and oligotrophic and clear-water, whitefish-dominated lakes in northern Finland.

In southern lakes, the more detailed objectives were: (1) to develop an efficient method for eliminating *Chaoborus* reverberation, which seriously disturbs fish density estimation in clay-turbid lakes (**I**), (2) to estimate the bias caused by *Chaoborus* on fish density estimate if the reverberation is not taken into account (**I**), (3) to determine whether night surveys are necessary or if day surveys are adequate for estimating the pelagic smelt density (**II, extra results**), (4) to describe the seasonal distribution pattern of smelt population (**III**) and (5) to determine a suitable seasonal sampling window for hydroacoustic monitoring of the smelt population (**III**).

In northern lakes, the more detailed objectives were: (6) to establish which of the studied whitefish populations can be estimated by vertical echosounding with an acceptable accuracy (**IV,V**) and (7) to examine the suitability of two seasons (mid-summer and autumn) and two diel periods (day and night in autumn) for hydroacoustic surveying of different whitefish morphs (**IV, V**).

3. Material and methods

3.1 Study lakes

The thesis consists of hydroacoustic studies conducted in five lakes located in southernmost Finland (Fig. 1) and in six lakes locating in the northernmost Finland (Fig. 2). Hereafter, these two groups are referred to ‘southern lakes’ and ‘northern lakes’. Southern lakes are ice-covered generally from December to April and the epilimnetic water temperature reaches 20-25°C in late summer. Northern lakes are ice-covered generally from November to May-June and the summertime maximum water temperature stays generally below 20°C (Jensen et al. 2015). In northern lakes, the polar light regime governs the dynamics of pelagic food web (Gjelland et al. 2009, Kahilainen et al. 2009). In mid-summer, the water column is well-illuminated all the time, whereas in autumn both day and night photoperiods occur.

3.1.1 Southern lakes

Most of the studies concerning the southern lakes (**I**,**II**,**III**) were conducted in Lake Hiidenvesi, a eutrophic and clay-turbid lake (Table 1). The lake consists of several basins differing greatly in morphology and water quality (Horppila 2005). The acoustic surveys were done in Kiihkelyksenselkä and Retlahti basins, which form a relatively large continuous area – the strait between basins is > 0.5 km wide and > 15 m deep. Kiihkelyksenselkä is a deep (max. depth 33 m) and comparatively turbid (Secchi depth ca. 1 m) basin, where strong thermal stratification develops bringing on recurrent oxygen depletion in the lower hypolimnion in late summer. Retlahti is a shallower basin (max. depth 13.3 m) with relatively similar water quality and stratification characteristics. Trawling was conducted also in two shallower basins, Kirkkojärvi (mean depth 0.9 m) and Mustionselkä (mean depth 2.0 m) (**III**). These basins are highly turbid (Secchi depth 0.2-0.9 m) and eutrophic (average total phosphorus concentration 70-100 µg/l).

The fish assemblages of deep basins are dominated by smelt, which is a key species in the pelagic food web (Vinni et al. 2004). Pikeperch (*Sander lucioperca*) is the most important predatory fish in pelagic areas. Other abundant species include white bream (*Abramis björkna*), blue bream (*Abramis ballerus*), bream (*Abramis brama*), roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*) and perch *Perca fluviatilis*, but their populations are generally concentrated in shallower areas (Olin & Ruuhijärvi 2005).

The larvae of phantom midge (*Chaoborus flavicans*) play a central role in the pelagic food web of L. Hiidenvesi. They are the most important predators of zooplankton probably contributing to the development of cyanobacterial blooms (Liljendahl-Nurminen et al. 2003 and 2005). In addition, the abundant *Chaoborus* population controls the zooplanktonic food resource for fish; the first biomass peak of zooplankton in spring, typical of temperate, dimictic and eutrophic lakes (Sommer et al. 1986) is regularly missed (Tallberg et al. 1999, Horppila et al. 2005). The *Chaoborus* population itself is a relevant food resource for smelt (Vinni et al. 2004, Salonen 2004) but is easily available only in early summer before the emergence period (Vinni et al. 2004). The high density of *Chaoborus* seriously disturbs acoustic fish density estimation (Horppila et al. 2000).

Lake Rehtijärvi is a small canyon-shaped lake (max. depth 29 m), which is highly eutrophic and clay-turbid (Table 1). The average Secchi depth is only 0.5 m (Niemistö, J., unpublished). The summer stagnation is strong and long-lasting resulting in regular oxygen depletion episodes in the hypolimnion during late summer. The pelagic fish assemblage is relatively diverse with no clear dominant species. According to experimental trawling and gill-net fishing (Malinen et al. 2006), abundant species include roach, perch, pikeperch, smelt, bleak and bream. The lake is inhabited by dense *Chaoborus* population inducing similar effects on zooplanktonic succession (Horppila et al. 2009) and simirarly serious interference to acoustic fish stock assessment as in L. Hiidenvesi.

Lake Tuusulanjärvi is a relatively shallow lake, which is highly eutrophic and clay-turbid (Table 1). It has been originally, at least temporarily, thermally stratified during summer (Pekkarinen 1990). Since the late 1990's its hypolimnion has been aerated by pumping epilimnetic water, which has prevented the formation of thermal stratification and oxygen depletion episodes (Horppila et al. 2017). Soon after the beginning of the pumping, the originally abundant smelt population collapsed due to the lack of cool hypolimnion (Sammalkorpi 2000, Malinen et al. 2004). After that, the pelagic fish assemblage has become more diverse containing mainly smelt, white bream, bream, roach, pikeperch and perch (Malinen 2017, Ruuhijärvi et al. 2017). The *Chaoborus* density is negligible in the water column but occasionally methane bubbles rising from anoxic sediment disturb acoustic analyses. In this lake, the low proportion of area deep enough for vertical echosounding reduces the accuracy of acoustic assessment of total fish density and biomass. Especially the pelagic occurrence of cyprinid fish fluctuates considerably (Malinen 2017). Anyhow, the concentration of the smelt population in deep areas is favorable for hydroacoustic assessment.

The Kajaanselkä basin of L. Vesijärvi and the Karjalohjanselkä basin of L. Lohjanjärvi are mesotrophic and relatively clear-water basins (Table 1). They have stabile and long-lasting summer stratifications but oxygen concentration stays generally at a high level even during late summer. Based on trawling and experimental gill-net fishing, the pelagic fish assemblage is highly dominated by smelt and the other relatively abundant species are roach, perch and vendace (Sammalkorpi et al. 2006, Ruuhijärvi & Ala-Opas 2014, unpublished). The density of *Chaoborus* is negligible (Malinen et al. 2003).

3.1.2 Northern lakes

Lake Kilpisjärvi is located in the north-western corner of Finland, whereas the other northern lakes; L. Vuontisjärvi, L. Rahajärvi, L. Vastusjärvi, L. Muddusjärvi and L. Paadar (hereafter termed without Finnish word 'järvi') are located in north-eastern Finnish Lapland (Fig. 2). The study lakes are relatively deep, except L. Vastus (Table 1). All the study lakes are oligotrophic (tot P 4-8 µg/l and tot N 120-240 µg/l), neutral (pH 7.0-7.2) and the water transparency varies from very clear L. Kilpis (Secchi depth 10 m and colour 8 Pt/l) to slightly brownish L. Vastus (Secchi depth 2 m and colour 25 mg Pt/l).

Whitefish is the dominant fish species in all the six northern lakes where it exists as either monomorphic (L. Kilpis, Vuontis and Raha) or as two or more polymorphic populations (L. Vastus, Muddus and Paadar). Allopatric LSR whitefish in L. Kilpis, Vuontis and Raha has generalist diet and niche utilization (Harrod et al. 2010, Kahilainen et al. 2011a). In L. Raha, the pelagic niche is inhabited also by the introduced vendace (Kahilainen et al. 2011a). Large and deep lakes, L. Muddus and L. Paadar have trimorphic whitefish populations consisting of pelagic zooplanktivorous DR morph, littoral benthivorous LSR morph and profundal benthivorous SSR morph (Kahilainen & Lehtonen 2002, Lehtonen & Kahilainen 2002, Harrod et al. 2010). The small and shallow L. Vastus has only DR and LSR morphs (Kahilainen et al. 2011b).

The most important pelagic piscivore in the northern study lakes is brown trout (Kahilainen & Lehtonen 2002, Jensen et al. 2008). Other piscivores include pike (*Esox lucius* L.), burbot (*Lota lota* (L.)) and Arctic charr (*Salvelinus alpinus* (L.)), which is the most abundant predator in L. Kilpis. These species consume whitefish as their main prey, but prefer benthic habitats (Kahilainen & Lehtonen 2003). The littoral habitat of most lakes is inhabited also by perch, grayling (*Thymallus thymallus* (L.)), minnow (*Phoxinus phoxinus* (L.)), three-spined stickleback (*Gasterosteus aculeatus* L.) and nine-spined stickleback (*Pungitius pungitius* (L.)).

3.2 Study strategy

3.2.1 Southern lakes

In L. Hiidenvesi, hydroacoustic surveys were originally aimed at estimating the size of cyprinid populations and monitoring the effects of a large-scale mass removal project (Olin et al. 2006). However, the scope of the studies changed completely when the first surveys during 1997-1999 had revealed the overwhelming dominance of smelt in the pelagic fish assemblage (Vinni et al. 2004) and extremely abundant *Chaoborus* population inhabiting the pelagic of deep basins (Liljendahl-Nurminen et al. 2002). It therefore became evident that smelt is the key species in the food-web of L. Hiidenvesi, and, at the same time, the only species which might be assessed by hydroacoustics. Moreover, it was soon realized that the most serious challenge to smelt density estimation was how to eliminate the reverberation due to *Chaoborus* larvae.

The present thesis utilizes a large dataset containing results from surveys conducted with hydroacoustics and adjoining experimental trawling during the years 1997-2001, in order to explore the suitability the hydroacoustics in smelt stock assessment. To achieve valid density estimates, the first challenge was to develop a new approach to eliminating the reverberation by *Chaoborus* (**I**). This proved to be a difficult and lengthy process. When an applicable approach was finally developed, the studies were directed towards exploring the suitable seasons and diurnal periods for a survey aimed at smelt stock assessment (**II, III**).

The *Chaoborus* elimination method was developed using acoustic data from 26 surveys conducted during 1999-2001 (**I**). The daytime and night-time density estimates were compared using data from four surveys in 2000 (**II**). The suitable seasons for assessment was explored using data from 5-8 echo-surveys conducted between early June and late October in 1997, 1999 and 2001 (**III**). In addition, in order to study the lake-wide horizontal distribution of smelt, the acoustic data from deeper basins were complemented by trawl data from two shallower basins during 2001-2007 (**III, extra results**). The hydroacoustic density and biomass estimates for comparison with other lakes were computed from data from 2007, when concurrent echo sounding and trawling were made in June, August and October (**extra results**).

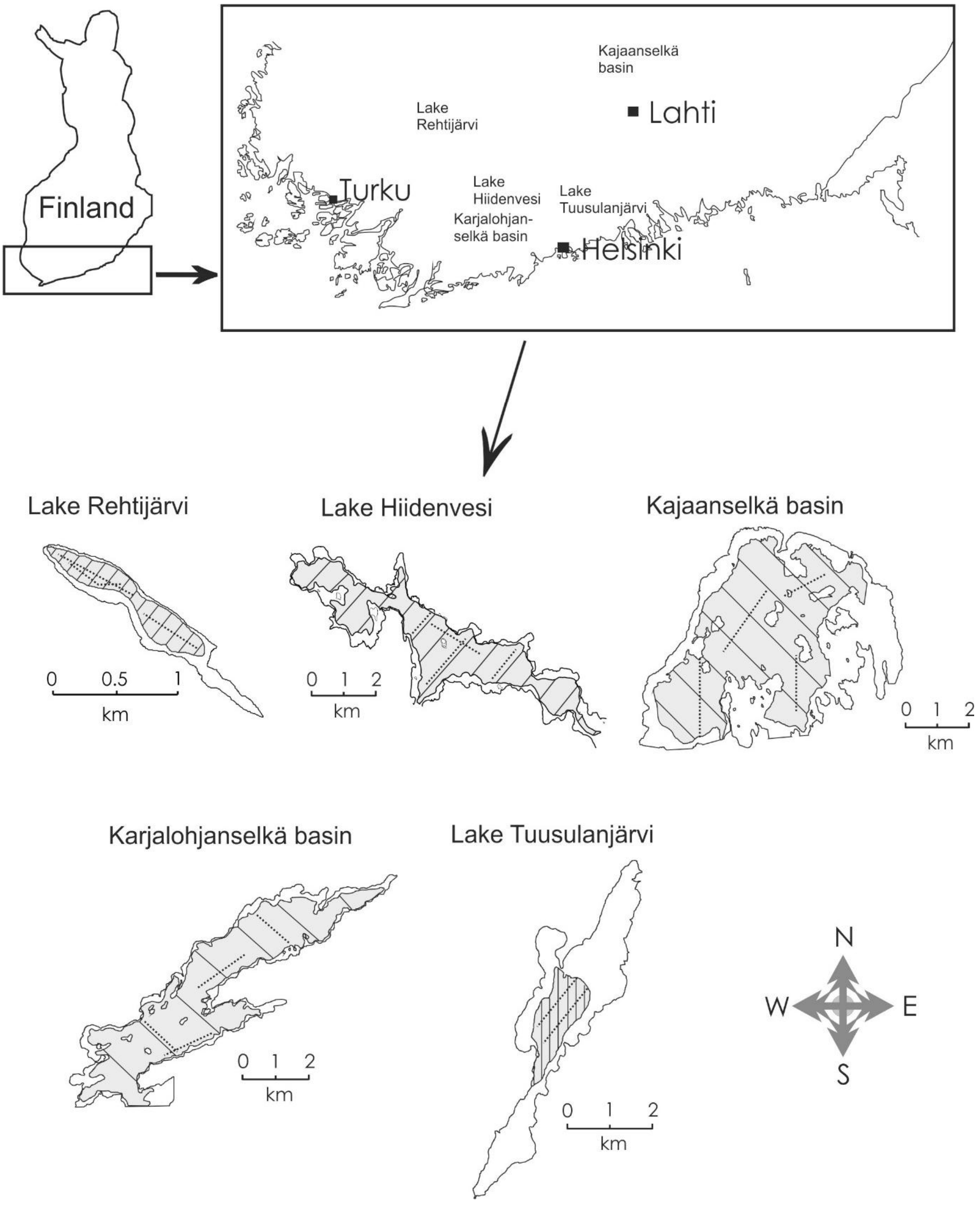

Fig. 1. Map of southern Finland indicating the location of southern study lakes. Shaded areas represent the study area of hydroacoustics, solid lines indicate echo sounding transects and broken lines are examples of trawl sampling during one hydroacoustic survey.

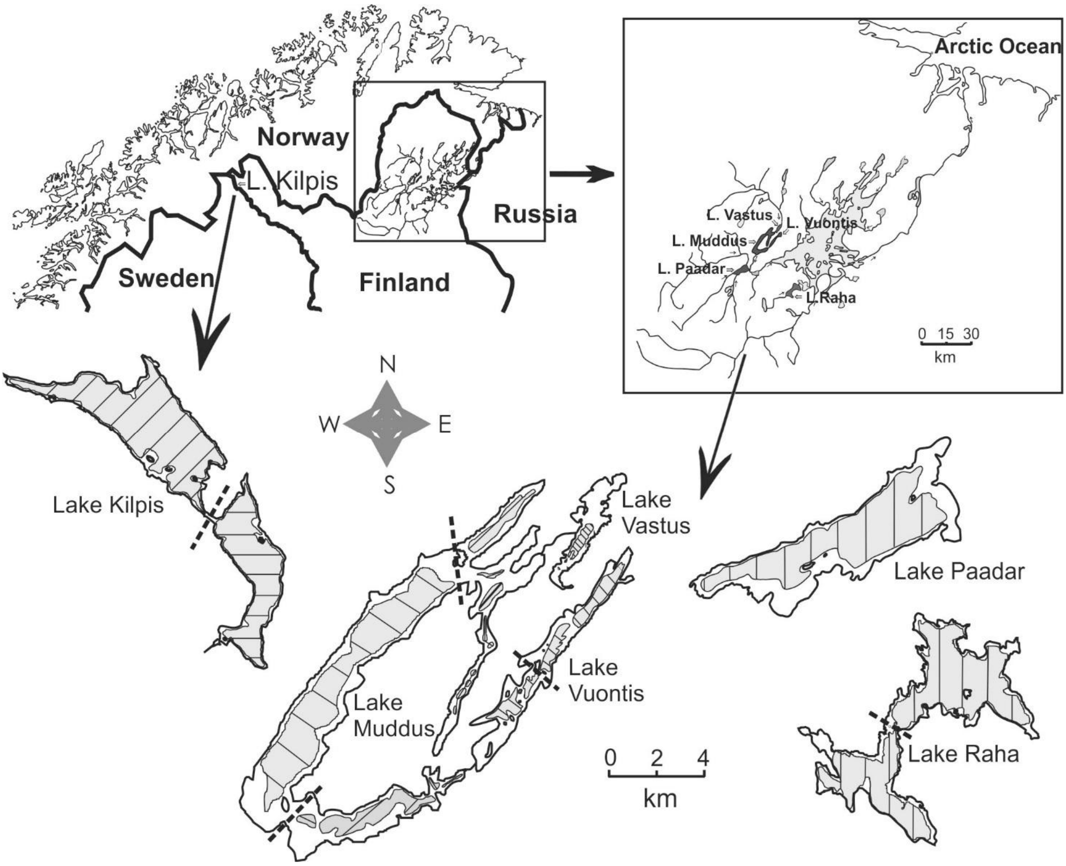

*Fig. 2. Map of northern Fennoscandia indicating the location of northern study lakes. Shaded areas represent the study area of hydroacoustics, solid lines indicate echo sounding transects and broken lines indicate boundaries between strata in lakes, where stratified sampling was applied (modified from **V**).*

The generality of findings from L. Hiidenvesi concerning the suitable timing of the hydroacoustic survey were studied in four other southern lakes (**extra results**); in two highly turbid lakes (L. Rehtijärvi and L. Tuusulanjärvi) as well as in two clear-water lakes (Kajaanselkä basin of L. Vesijärvi and Karjalohjanselkä basin of L. Lohjanjärvi). All the lakes were surveyed four times, during the day and at night in late summer and in late autumn. In addition, L. Tuusulanjärvi was surveyed in late summer and in late autumn during 2004-2010 in order to estimate the pelagic fish density and biomass (**extra results**).

Table 1. Background data on morphometry and water quality of the study lakes. Abbreviations for lake names used in some figures are also given.

	Lake Hiidenvesi[§]	Lake Rehtijärvi	Lake Tuusulanjärvi	Kajaanselkä basin	Karjalohjanselkä basin	Lake Kilpisjärvi	Lake Vuontisjärvi	Lake Rahajärvi	Lake Vastusjärvi	Lake Muddusjärvi	Lake Paadar
Abbreviation	Hii	Reh	Tuu	Kaj	Kar	Kil	Vuo	Rah	Vas	Mud	Paa
Latitude	60°22’	60°50’	60°26’	61°08’	60°16’	69°00’	69°01’	68°45’	69°03’	69°00’	68°52’
Area (km^2)	10.5	0.4	6	44	19	37	11	23	4	48	21
Altitude (m a.s.l.)	32	97	38	81	32	473	151	132	146	146	144
Max depth (m)	33	29	10	42	41	57	31	46	15	73	56
Secchi depth (m)	1.1	0.5	0.6	3.3	2.3	10	8	6.5	3	3	6
Colour (mg Pt/l)*	60	60	90	5	30	8	8	8	25	25	20
Tot P (µg/l)*	43	51	68	20	17	4	7	4	7	5	6
Tot N (µg/l)*	1200	1300	730	430	770	120	170	100	240	160	160
Type of lake											
Clay-turbid	x	x	x								
Clear-water				x	x	x	x	x	x	x	x
Type of fish assemblage											
Smelt-dominated	x			x	x						
Diverse assemblage		x	x								
Monomorphic whitefish						x	x	x			
Polymorphic whitefish									x	x	x

[§] Values of Kiihkelyksenselkä basin

*Data from Hertta-database, Finnish Environment institute

3.2.2 Northern lakes

In L. Muddus, the suitability of hydroacoustics for the assessment of different whitefish morphs was studied with surveys conducted in September 2000, June 2001 and August 2001 (**IV**). To determine a suitable diel periods for assessment, the vertical migration and schooling behaviour of pelagic fish were studied on selected area during each survey. The diurnal study was conducted from afternoon to morning by frequently repeated echo soundings and simultaneous experimental fishing with trawl and gill-nets. On the basis of the diurnal study, more extensive sampling aimed at population estimation was conducted at night. In order to study the effect of timing of survey on assessment more comprehensively (**V**), the data was complemented with a respective daytime survey in September 2006.

To study the applicability of hydroacoustics in the assessment of different whitefish morphs living in a variety of northern lakes (**V**), mid-summer and autumn surveys were conducted in five other lakes; three lakes (Kilpis, Vuontis and Raha) have monomorphic whitefish population, while two lakes (Paadar and Vastus) has polymorphic whitefish populations. In addition, surveys done in L. Muddus, which has polymorphic whitefish population, were included in the dataset.

Each lake was surveyed three times during the years 2000-2010; in mid-summer (no apparent dark period due to the midnight sun), sampling was done only at night, whereas in autumn (distinguishable light and dark periods) sampling was done during the day and at night. In addition to evaluating the applicability of hydroacoustics, approximate species/morph-specific density and biomass estimates were computed from the data sampled at the most suitable moment (**V**).

3.3 Hydroacoustic sampling

In all the lakes, areas deeper than 5 or 6 m (depending on the lake) were surveyed along equidistant transects (Figs. 1 & 2). The distance between transects varied from 0.1 km in the smallest L. Rehtijärvi to 1.5 km in the largest L. Muddus. The location of the first transect was randomized. In four lakes (Kilpis, Muddus, Vuontis and Raha) stratified sampling with lake basins as strata was applied. In smaller lakes, the study area was surveyed during one day and one night but in larger lakes sampling took 2-3 successive days/nights.

Hydroacoustic data was collected with a SIMRAD EY-500 echosounder equipped with a split-beam transducer ES120-7F or ES120-7C (operating frequency 120 kHz with a half-power beam angle of 7°). The transducer was mounted on a towed body, which was lowered to a depth of 0.6 m on the left side of the boat. Pulse duration was set at 0.3 ms, pulse interval to ‘minimum value’ and minimum TS to -65 dB. The transducer was calibrated using a standard copper sphere (TS = -40.4 dB) with SIMRAD LOBE-program. Determined calibration parameters were entered to EY 500-program. The speed of sound was set according to measured temperature and relationship between the temperature and sound speed (Del Grosso & Mader 1972). In addition, EY 500-program contains many parameters which need to be set according to prevailing circumstances, such as depth and bottom quality.

3.4 Fish sampling

To determine the species/morph distribution of the observed fish, 2-10 mid-water trawl hauls were conducted during most acoustic surveys. The location and depth of these trawl hauls were selected based on the echo sounding, in order to allocate most of the effort to high-density areas and layers. This was an essential procedure, because it was possible to conduct only a limited number of trawl hauls during a survey and the species/morph composition of the densest aggregations has the strongest effect on the accuracy of density estimates. In addition to the mid-water hauls, 2-4 surface hauls were conducted in order to estimate approximately the fish density in the blind zone of the echosounder. The location of these hauls was randomized.

The trawl sampling was made with a small pair-trawl (2-5 m high, 5-8 m wide and cod-end mesh size 3 mm (bar length)). The trawl was towed with two small (length 4-7 m) outboard motor boats (engine power 25-40 hp). It was lowered to the desired depth (0-20 m) using iron weights and the fishing depth as well as the opening of the trawl was confirmed by the echosounder. Each haul took 10-60 minutes and the average towing speed was ca. 3 km/h.

In addition, in the northern lakes, the fish sampling was performed with benthic gill-nets in the shallower areas beyond the hydroacoustic sampling and in the bottom layer of deep areas in order to evaluate species/morph composition and approximate density in these unsampled zones. In L. Kilpis, where no trawling was made, the gill net series were used also in mid-water. Gill-net fishing was done with gill-net series combined of eight 30 m long and 1.8 m high nets with mesh sizes of 12, 15, 20, 25, 30, 35, 45, and 60 mm (knot to knot). The fishing depth of gill-net series was checked with an echosounder and the fishing time was measured to an accuracy of one minute.

The species and whitefish morph distribution of each catch was determined from the whole catch, or in cases of high trawl catch (> 15 kg) from a random sample. The whitefish morphs were identified according to differences in body shape, head shape and gill raker counts (Kahilainen & Østbye 2006). Length and weight of fish were measured to an accuracy of 1 mm and 0.1 g. The gill-net catch-per-unit-effort (CPUE) was calculated as the number of fish captured with one gill-net series per hour.

3.5 Computation of fish density of sampling unit

The first step in hydroacoustic data analysis aiming at fish density estimation is the computation of fish density of each sampling unit. The sampling unit is the section of a cruise track along which the acoustic measurements are averaged to give one sample (Simmonds & MacLennan 2005). In the first northern study (**IV**) ca. 500 m long sections of echo sounding transects were used as sampling units. However, because the serial correlation of successive sampling units complicates the estimation of variance and hence the confidence intervals (Williamson 1982, Jolly & Hampton 1990a), whole transects were used as sampling units in the other studies. The exception was the horizontal distribution analysis of smelt (**III**), where the sections of transect located on each depth zone were used as sampling units.

The fish density of a sampling unit was computed by summing up the densities in all the 1-5 depth layers. The number of layers was chosen based on visual interpretation of the echogram and the composition of trawl catch. The objective was to divide the water column into layers as homogenous as possible in respect to the presence of schools, fish species composition and the magnitude of *Chaoborus* reverberation. Layer-specific analysis enabled using the most appropriate analysis method for each layer. The fish density (ρ) per hectare of each layer was computed by the equation:

$\rho = s_a/\mathrm{mean}(\sigma_{sp})$ (1) , where

s_a = total area scattering coefficient (m^2/ha)
σ_{sp} = spherical cross-section = $4\pi 10^{(TS/10)}$ (m^2) (2) , where
TS= target strength (dB re 1 m^2)

Note: Simrad has introduced a 4π coefficient in the s_a calculation, hence it is not a backscattering coefficient as commonly used but a total area scattering coefficient. Therefore, σ_{sp} should be used instead of a backscattering cross-section (σ_{bs}) (Simrad 1995, MacLennan et al. 2002) when calculating fish density from s_a-value computed by EP 500 -program.

The s_a was computed with the 'Analyze' -option of the EP 500 -program using variable s_v-threshold, which was selected based on water depth and the size of present fish. The s_v-threshold (*i.e.* integrator threshold) is the smallest integral value of the analyzed cell which is taken account when computing the integral from target species – integral values under the s_v-threshold are ignored as 'noise'. Usually, the threshold was set to -60 dB but in cases where small fish inhabited deep water layers, lower thresholds (down to -65 dB) were used. The objective was to choose a threshold low enough to contain all scattering from fish but high enough to exclude scattering from unwanted targets (for example from *Chaoborus* or other invertebrates). When the decision was difficult, the thresholding method of Eckmann (1998) was applied. In cases of high *Chaoborus* reverberation, a special elimination method was used (chapter 3.6).

The mean spherical cross-section (σ_{sp}) was computed either by TS-dirtribution or trawl catch depending on circumstances. TS-distribution was computed as a mean over mean σ_{sp} values of each tracked fish as recommended by CEN (2014). This method is based on the assumption of accurate TS-distribution requiring relatively low fish density (Sawada et al. 1993). In addition, the size distributions of single fish and schooled fish should be identical. Hence, the procedure is the most justifiable when the proportion of echo energy from single fish echoes to total echo energy is high. The great advantage of the method is that the uncertainty connected to trawl sampling does not bias the fish density estimate. TS-distribution was used in northern lakes (**IV** and **V**) and in southern lakes when the TS-distribution was not affected by obvious sources of bias: high fish density, the low proportion of single fish echoes or noticeable *Chaoborus* reverberation (**I, II, III, extra results**). The choice between procedures was made based on visual interpretation only, because the presence of *Chaoborus* complicated the use of Sawada's index (Sawada et al. 1993).

When trawl catch was used, the mean σ_{sp} was computed from the fish length distribution of the trawl catch. The spherical cross-section of each measured fish was computed by equations (2) and:

$TS = 23.4\log_{10}L - 68.7$ (3) (Peltonen et al. 2006) for smelt

$TS = 17.3\log_{10}L - 64.5$ (4) (Tuomaala, unpublished) for other species, where

L= fish total length in cm

Equation (3) has been determined for smelt in L. Hiidenvesi, whereas equation (4) has been determined for species mixtures observed in L. Lohjanjärvi (containing smelt, perch, roach, blue bream, bream, white bream) and for DR whitefish of L. Muddus. It contains 11 observation pairs of modes of length and TS distributions. The range of observations was 4.7 – 35.0 cm in length and -54.0 – -38.5 dB in TS.

The advantage of using trawl catch is the applicability when fish are schooled – it can be used even if no fish can be detected as a single target. However, the procedure relies strongly on the representativeness of trawl sampling. The low coverage of trawl sampling and the possibly biased size-distribution of trawl catch may substantially reduce the precision and accuracy (Cochran 1977, p. 16) of the fish density estimate. In addition, possible errors in TS-length relationship bias the fish density estimate. Hence, it was used only in those cases, when the TS-distribution was considered to be obviously biased (**I**, **II, III, extra results**).

In L. Hiidenvesi (**I**, **II**, **III**) the dominance of smelt was so strong (typically > 95% of numerical trawl catches, Vinni et al. 2004) that the proportion of other species was considered negligible. A corresponding case was found in L. Kilpis (**V**), where the dominance of LSR whitefish in gill-net catches was equally strong. In other study lakes, however, the fish density estimates were divided to species-specific estimates. The fish density by equation (1) was divided into species-specific density estimates according to numerical proportions of each species in the most representative trawl catch to each depth layer of each sampling unit. In cases of low trawl catches, a combination of catches from 2-5 hauls was used.

In four northern lakes, however, the TS-distributions revealed the presence of very small-sized targets. The TS-modes of these targets varied between -55 and -60 dB (see Fig. 14). Since the pelagic of these lakes are not inhabited by large invertebrates (*Chaoborus*, for instance) these targets were most likely small-sized fish. The only small-sized fish which were present in the trawl catch were nine-spined stickleback. However, in the light of TS-distributions and species distributions in trawl catches it was obvious that the catchability of this species was considerably lower than that of coregonids and the use of species proportions in trawl catches would have caused severe overestimation of coregonid density. As it happened, the generally distinct TS-distributions of nine-spined sticklebacks and coregonids enabled the approximation of their proportions. Because the TS-distributions varied between lakes, lake-specific limits for TS of nine-spined stickleback were visually determined from TS-distributions. More sophisticated, computational methods for the allocation of targets to two groups (e.g. Parker-Stetter et al. 2006) were not suitable because nine-spined sticklebacks practically inhabited the whole water column, hampering the modelling of the TS-distribution of coregonids.

3.6 Elimination of *Chaoborus* reverberation

3.6.1 The first methods

In L. Hiidenvesi, already the first hydroacoustic surveys revealed that unbiased estimation of fish density required the elimination of *Chaoborus* reverberation. The applicable method for elimination was explored from a large dataset from the years 1999-2001. At first, the thresholding method developed by Eckmann (1998) was tested using data from 22 transects in 3-4 June, 6 July and 19-20 October 1999. During all surveys, a simultaneous sampling of *Chaoborus* densities was conducted at 53 stations (Liljendahl-Nurminen et al. 2002). In the thresholding method (Eckmann 1998), the acoustic data is analyzed with several volume backscattering (s_V) thresholds and curve of a total area scattering coefficient (s_a) as a function of a s_V-threshold is constructed. If the curve shows some intermediate plateau before reaching the final plateau, the s_a from fish can be calculated for instance with an asymptotic Bertalanffy function (Fig. 3, A and B).

In June, when the vertical distribution of *Chaoborus* larvae was relatively even in L. Hiidenvesi and no dense aggregations existed, the elimination succeeded with the the thresholding method. However, this was the only season when the method was effective enough to eliminate reverberation in all transects. In October, *Chaoborus* aggregations were too dense in near-bottom layers of some transects. In July, circumstances were even more demanding due to dense *Chaoborus* layer in the metalimnion. The thresholding method was not applicable to eliminate reverberation in this layer (Fig. 3, C and D).

Because the volume of the analyzed cell increases with depth due to the beam spreading, the required size of target to be included in s_a with a given s_v-threshold increases with depth. Therefore, it is reasonable to assume that the curve of s_a as a function of s_v-threshold is a subject to variation with depth. In addition, the shape of the curve can be changed by fish size and schooling behaviour, which have been observed to change with depth. In L. Hiidenvesi, the size of smelt increases generally with depth (Vinni et al. 2004, **III**) and smelt form schools only in the uppermost 8 m of the water column (Vinni et al. 2004, **II**). In theory, these effects might mask the presence of an intermediate plateau when the water column is analyzed in a single analysis. Therefore, the applicability of the thresholding method was tested by analyzing the water column as 2-4 layers. The layer-specific-thresholding produced some gain compared with one-layer-analysis but still in too many cases at least one layer remained where no detectable intermediate plateau existed. This problem was present even if thresholding was done in very narrow layers (for example 20 cm thickness). The use of linear scale (σ) instead of logarithmic dB in s_v-threshold gave no solution either. However, the layer-specific thresholding method was successfully applied in a study revealing the effect of Langmuir circulations on transport of *Chaoborus* larvae (Malinen et al. 2001).

Another approach which was tested for eliminating the reverberation was based on the finding of a difference in the frequency distribution of s_a-values in *Chaoborus*-layers and fish-layers. The presence of fish induced also high s_a-values and produced wide, positively skewed frequency distributions, while in layers with only *Chaoborus*, the distributions were composed of small s_a-values only, producing a narrower distribution. The difference between the distributions in these two cases was noticeable when the data were analyzed as small cells (for example a 20 cm vertical layer in one pulse). This approach slightly helped in dividing the water layers into those containing only *Chaoborus*, only fish or both *Chaoborus* and fish. It was applied in determining the vertical distributions of *Chaoborus* and fish (Horppila et al. 2000, Liljendahl-Nurminen et al. 2003, Horppila et al. 2004). However, no solution was found to the quantitative elimination of reverberation, which would make the fish density estimation possible.

3.6.2 The new method

During the course of the studies, theory about the predictable shape of a relationship between s_v-threshold and s_a from fish was developed. Would it be possible to estimate the total s_a from fish, using s_a with such a high s_v-threshold that *Chaoborus* reverberation is eliminated? It was hypothesized that there should be a strong dependence between s_a from fish with a given low threshold (containing all scattering from fish) and s_a from fish with a high threshold (containing only some portion of all scattering from fish). If this relationship could be determined using data containing no *Chaoborus*, it should be possible to analyze the data with a threshold high enough to eliminate reverberation and then to convert the estimate to coincide with the result that would have been achieved with a low threshold containing all scattering from fish.

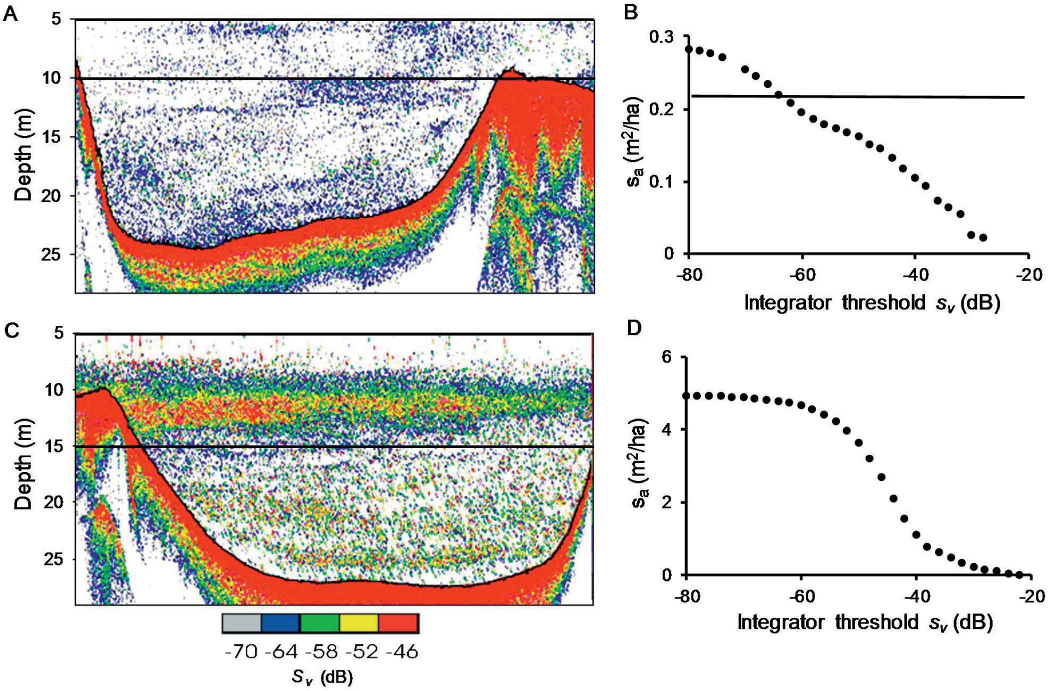

*Fig. 3. An echogram and s_a as a function of s_v-threshold from low Chaoborus density (A and B) where a plateau exists at an intermediate threshold making Eckmann's thresholding method applicable (L. Hiidenvesi in 3 June 1999). An echogram and s_a as a function of s_v-threshold from high Chaoborus density (C and D) requiring a more efficient method (L. Hiidenvesi in 3 August 1999). Horizontal lines in A and C represent the lower boundaries of analyzed water layers and line in B represent the asymptote in the thresholding method. Modified from **I**.*

At first, the relationship between s_v-threshold and s_a from fish was determined using 88 samples (49 day and 39 night observations) containing only fish. The absence of *Chaoborus* was visually interpreted from an echogram. Deep (≥14 m) and shallow (<14 m) water layers were analyzed separately, because it was hypothesized that the relationship changes with depth due to the increasing volume of an analyzed cell in thresholding. Then these relationships were applied in analyzing fish densities by assuming a constant dependence between s_a with a high threshold and s_a with low a threshold for fish.

More exactly, the following formulation was applied for the estimation of a total area scattering coefficient of fish, $s_a(f)$, in either a deep or a shallow layer of a transect:

$$s_a(f) = \frac{s_a[thr(a)] - s_a[thr(h)]}{p[thr(a)]} + s_a[thr(h)] \qquad (5)$$

,where

thr(*a*) = s_v-threshold applied i.e. the lowest threshold eliminating *Chaoborus* reverberation. This was determined visually by thresholding for each sample. Several thresholds were tested in ascending order, and the first one eliminating all reverberation (i.e. also the strongest echoes from *Chaoborus*) was chosen.

thr(*h*) = the upper limit of the analysis (-42 dB in shallow and -44 dB in deep layers). Above this limit, the *p*–value, *p*[*thr*(*a*)], was subject to unacceptably large variation.

$$p[thr(a)] = \frac{s_a[thr(a)] - s_a[thr(h)]}{s_a[thr(l)] - s_a[thr(h)]}, \qquad (6)$$

computed from 88 fish-only samples, where

thr(*l*) = the lower limit of the analysis (-60 dB in shallow and -62 in deep layers). It was chosen to be the highest threshold which still resulted in an asymptotic value of $s_a(f)$ based on the s_a-versus-threshold curve (Eckmann 1998).

The highest and lowest possible *thr*(*a*) in the analysis were *thr*(*h*)-2 dB and *thr*(*l*)+2 dB, respectively.

The new method was validated with a secondary dataset: 48 samples throughout the open water period having a negligible density of *Chaoborus* were analyzed using the traditional analysis (threshold –60 or –62) and with equation (5). The accuracy of the method was tested by comparing the mean $s_a(f)$-value from equation (5), [$s_a(m)$], to the mean $s_a(f)$-value obtained through traditional analysis [$s_a(t)$], and the precision was evaluated based on the percentage mean deviation (MD) of $s_a(m)$ from $s_a(t)$.

Comparisons were made for all *thr*(*a*)-values applied in the present study, to find out whether the practice of using transect-specific values, i.e. the lowest threshold eliminating *Chaoborus* in each transect as *thr*(*a*), gave some gain in accuracy or precision. Otherwise a rational choice would be a constant threshold, high enough to eliminate reverberation in all transects, because this would make the analysis more straightforward and faster.

In order to evaluate possible overestimation of fish density if *Chaoborus* reverberation is not subtracted, smelt densities were computed using two approaches: (a) a traditional analysis in which thresholds were -60 or -62 dB, and (b) using equation (5). The surveys included in the analysis were selected to represent different phases in the seasonal development of the *Chaoborus* population (Liljendahl-Nurminen et al. 2003). The smelt density was estimated as in section 3.7.

3.7 Estimation of fish density and biomass in the study area

The following step after the fish densities for each sampling unit have been computed, is to generalise this information to concern the whole study area. The fish densities of sampling units were not transformed, because the gain of transformations is questionable (Jolly & Hampton 1990b, Malinen & Peltonen 1996). The species/morph-specific density estimates were computed with post-stratified sampling (Cochran 1977), using lake basins as strata in multi-basin lakes Kilpis, Vuontis, Raha and Muddus, whereas in the other lakes equations of simple random sampling were applied (Figs. 1 and 2). The variance of mean fish density in a stratum *h* [$Var(\bar{y}_h)$] was computed using the equation (Shotton & Bazigos 1984):

$$Var(\bar{y}_h) = \frac{\sum_{i=1}^{n}\left[(y_i - \bar{y})^2 * l_i\right]}{\sum_{i=1}^{n} l_i * (n-1)} \qquad (7)$$

,where

y_i = fish density in ith transect
$\bar{y}$ = mean fish density
l_i = length of ith transect
n = number of transects

The variance of the mean density in the whole study area, $Var(\bar{y})$, was computed using the equation (Cochran 1977):

$$Var(\bar{y}) = \sum_{h=1}^{L}\left[\left(\frac{A_h}{A}\right)^2 * Var(\bar{y}_h)\right] \qquad (8)$$

,where

A_h = area of hth stratum
A = study area
L = number of strata

Species/morph-specific biomass estimates (**V**, **extra results**) were computed by multiplying the density estimate of each sampling unit with the mean weight of species/morph in mid-water trawl catches, excluding L. Kilpis and L. Vuontis, where mean weights obtained from gill-net catches were used. The biomass estimates for the whole study area and their variance estimates were computed with equations (7) and (8). The approximate 95% confidence limits for the fish density and biomass estimates were calculated on the basis of Poisson distribution (Jolly & Hampton 1990a).

3.8 On the concept of density estimate

In most quantitative hydroacoustic studies, results are reported as fish density estimates, which are typically presented as fish per hectare within an acoustically sampled area. In lakes, the study area is typically outlined as an area deep enough to give reliable density estimates by hydroacoustics. This kind of density estimate can be very useful in studies concerning the dynamics of pelagic fish assemblage, such as food web studies, and they can be used also in fish population monitoring. However, valid population monitoring requires that no considerable changes take place in the proportion of population occurring the pelagic habitat. In addition, it is important to realize that this type of acoustic density estimate for a given species may be a very accurate measure of its pelagic abundance but still a strongly biased indicator of its population size. Valid estimation of population size with vertical echo sounding is possible only if the target species prefer the pelagic habitat so strongly that the density is negligibly low in all the three unsampled zones; surface blind zone, bottom dead zone and shallow areas at the time of the survey. Alternatively, plausible population estimates may be obtained if a realistic assumption of fish density in these unsampled zones relative to acoustically sampled can be justified.

In the present thesis, the densities were estimated always by acoustically sampled area and were considered to represent the size of the population based on the assumption that the density of target species/morph in the unsampled volumes of water is zero. One might argue that this is not the most realistic assumption and instead some other assumption should be used, for instance similar volumetric density in these unsampled zones as in the acoustically sampled zone. The simple ‘zero density’ hypothesis is, however, very useful when comparing the accuracy of a population estimate obtained in various seasons or diel periods, or differences in accuracy between various populations: higher gill-net catch-per-unit-effort (CPUE) in bottom layers or shallow areas indicates univocally lower accuracy. Because gill-net catch-per-unit-effort cannot be converted into fish density, problems would arise with all other hypotheses. It is impossible to know which level of CPUE indicates similar density as in the acoustically sampled zone, and hence also impossible to know whether higher CPUE of certain sampling moment or population would indicate lower or higher accuracy.

3.9 Comparison of daytime and night-time surveys

In southern lakes, results given by daytime and night-time surveys were compared using hydroacoustic smelt density estimates from a successive day and night (**II** and **extra results**). In addition, the smelt density in the surface blind zone of the echosounder was estimated by surface trawling (swept-area-estimate) during each survey. It was hypothesized that in general, day surveys result in lower density estimates than night surveys due to acoustic shadowing (Appenzeller & Leggett 1992). However, if smelt ascend to the surface blind zone at night (Horppila et al. 2000), the opposite may be true. Therefore also surface trawling was conducted on all sampling occasions.

In northern lakes, minimal trawl catches during daytime hampered the determination of species/morph distribution from catches. Therefore, daytime and night-time surveys were compared using echo integrals [integrated s_v over area, resulting in a total area scattering coefficient (s_a, m^2/ha), MacLennan et al. 2002]. Echo integral is, in general, linearly related to fish density (e.g. Simmonds & MacLennan 2005). The fish density in the surface blind zone was estimated by surface trawling (swept-area-estimate) during the day and at night. In addition, the magnitude of the bottom dead zone as a source of bias was evaluated based on benthic gill-net CPUEs during the day and at night. In the study concerning all six northern lakes (**V**), it was hypothesized that night surveys would result in higher echo integrals than day surveys based on the first diurnal study in L. Muddus (**IV**).

The possible differences between daytime and night-time density estimates (L. Hiidenvesi) or echo integrals (northern lakes) were tested with a non-parametric sign-test, by considering day and night estimates for each transect as one observation pair (**II** and **V**). In northern lakes, differences in daytime and night-time integrals over study lakes were tested with Mann-Whitney U-test.

3.10 Comparison of survey seasons

To evaluate the suitability of different seasons for smelt stock assessment, the density estimates from surveys conducted during daytime in early June - late October were compared in L. Hiidenvesi. The accuracy of estimates for different seasons was evaluated based on (1) the density in shallow basins outside the hydroacoustic sampling (**III** and **extra results**), (2) density in the shallowest stratum in deep basins (**III**), (3) density in the surface blind zone (**III**) and (4) the seasonal succession of the density estimate (**extra results**).

In northern lakes, the suitability of two seasons was studied by comparing night-time echo integrals in mid-summer (under the midnight sun), and in autumn (dark nights). Based on the experience gained in the first study in L. Muddus (**IV**), no mid-summer-trawling was made in the other northern lakes. Confidence limits for echo integrals were computed by Poisson-distribution (**extra results**) and differences between seasons were tested with Mann-Whitney U-test (**V**).

4. Results

4.1 Southern smelt lakes

4.1.1 Elimination of *Chaoborus* reverberation

The developed method for *Chaoborus* elimination, equations (5) and (6), enabled the estimation of the smelt density in L. Hiidenvesi (**I**). With the method, estimation of fish density was possible even when *Chaoborus* density was relatively high, approximately 200-300 ind./m^3. In almost all samples, at least one threshold was found, which was high enough to eliminate *Chaoborus* reverberation but low enough to enable the estimation of fish scattering, $s_a(f)$, by equations (5) and (6). Only a few metalimnetic aggregations of *Chaoborus* in July were so dense that reverberation extended beyond the highest threshold, hampering the application of the method.

Based on validating samples, the new method gave accurate estimates of $s_a(f)$: on average, the difference between the new method and traditional analysis was less than 1%. The difference between means with a given threshold varied between –2.5% and +3.5% and no noticeable trend existed. Therefore, $s_a(f)$ computed by equations (5) and (6) could be used as a reference value for traditional analysis when evaluating the bias caused by *Chaoborus*. This analysis showed that the bias can be high if the threshold is chosen to contain all $s_a(f)$ while *Chaoborus* reverberation is not taken into account. The degree of overestimation of fish density varied widely between seasons: in June it was as high as 35-55%, whereas in August, after the emergence period of *Chaoborus*, it was only 3%-16% (Fig. 4).

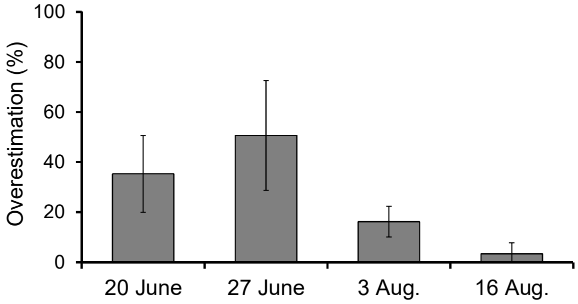

*Fig. 4. The overestimation of smelt density (older than 0+) by normal hydroacoustic analysis resulting from reverberation by Chaoborus in June 2000 and August 1999. The mean density was 8000 ind./ha in June 2000 and 12000-14000 ind./ha in August 1999 (**I**).*

Two important features of the method were found during the study. At first, the fish-only data set confirmed that the relationship between s_v-threshold and scattering from fish was a subject to high variation with depth (Fig. 5). Therefore, the accuracy of the new method can be increased by determining threshold-fish scattering-curves for several depth layers.

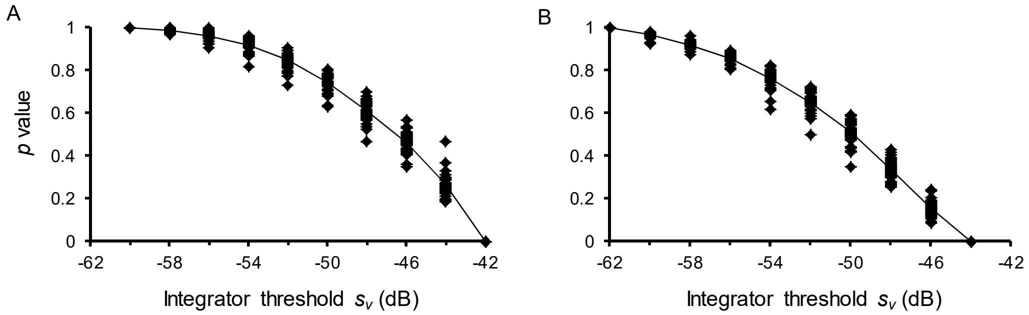

Fig. 5. The relationship between s_v *-threshold and p value (equation 6) i.e. relative* $s_a(f)$ *in the range of the new analysis in shallow (<14m) layers (A) and in deep (≥14 m)layers (B) (**I**).*

Secondly, the variation of estimated $s_a(f)$ increased with the threshold applied as indicated by increasing mean deviation (MD) between actual $s_a(f)$ and estimated $s_a(f)$ (Fig. 6). In the shallow layer, MD was less than 3% with *thr*(*a*) up to -46 dB and increased only slightly thereafter. In the deep layer, however, MD increased rapidly after -52 dB, up to 20% with the highest *thr*(*a*). Hence, the most precise estimates are achieved when the lowest threshold eliminating *Chaoborus* is applied. Because this threshold varies considerably with *Chaoborus* density, precise fish density estimation requires sampling-unit-specific determination of the lowest threshold eliminating *Chaoborus* reverberation.

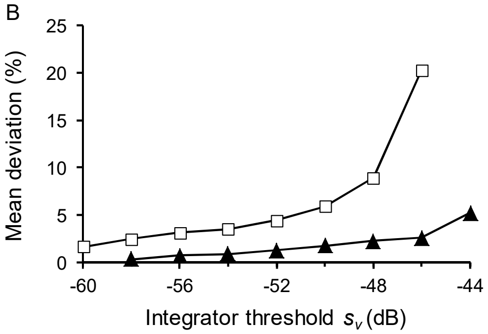

Fig. 6. Mean percent deviation between actual $s_a(f)$ *and estimated* $s_a(f)$ *by equation (5) as a function of thr(a) in shallow (-▲-) and deep (-□-) layers in fish-only validating samples (**I**).*

4.1.2 Comparison of day and night surveys

Lake Hiidenvesi

The data collected from L. Hiidenvesi during August-November 2000 did not support the hypothesis that night-time density estimates are higher than daytime estimates (Fig. 7). Density estimates for successive day and night were close to each other excluding the November survey. Similarly, the concern that the smelt density might be high in the surface blind zone at night, proved to be unnecessary. The occurrence of smelt in the surface blind zone was a considerable source of bias for the hydroacoustic estimate only in November. At this time, the direction of DVM appeared to be mainly opposite than generally documented: 0+ smelt, which formed a majority of the population, occurred in the surface layer during daytime (Fig. 7). However, results suggested that older smelt had normal DVM, because they appeared in the surface layer at night.

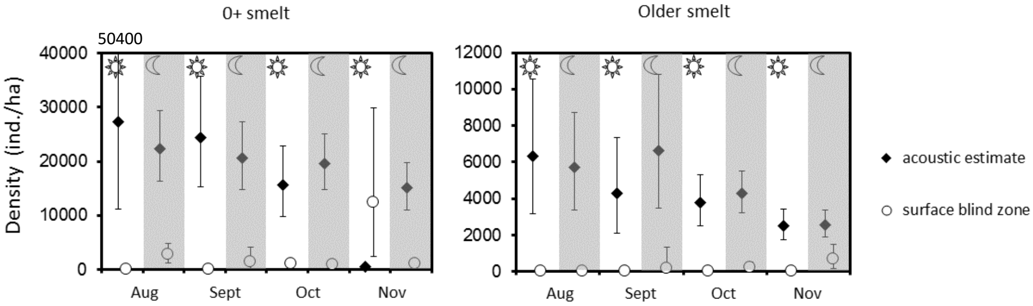

*Fig. 7. Diurnal density estimates with 95% confidence limits by hydroacoustics and surface trawling for two groups of smelt, young-of-the-year (left panel) and older smelt (right panel) in L. Hiidenvesi during August-November 2000. Modified from **II**.*

Results suggested that no gain in accuracy could be achieved using more troublesome and expensive night sampling compared with day sampling. Daytime and night-time estimates can be considered comparable during August-October. In late autumn the DVM of smelt was unexpected and differed between age-groups decreasing the accuracy of both day and night sampling. The analyses highlighted one reason why day sampling can result in even more accurate estimates than night sampling. In L. Hiidenvesi, smelt of different age-groups occurred in typically in different depth layers during daytime, 0+ smelt higher in the water column than older smelt (**III** and Fig. 8). In this case, it is possible to achieve accurate size distribution of smelt population by a relatively low number of trawl hauls. On the contrary, at night smelt of different ages appeared to be dispersed throughout the water column (Fig. 8), probably in a non-random pattern, in which case the estimation of size distribution of the population requires trawl hauls from many depth layers. In L. Hiidenvesi, unbiased trawl samples are important, because mean σ is computed from trawl catches. Furthermore, although in the present study the night-time smelt density in the surface layer was low throughout the study period, observations by Horppila et al. (2000) suggest that at least occasionally smelt ascend until the surface blind zone, which favours day surveying. On the other hand, night surveys had one advantage over day surveys: the precision of the smelt density estimate was higher at night (**II**). However, the introduction of bias in exchange for some increase in precision is not regarded as a reasonable trade-off. The results suggest that both day and night surveys can be used in the monitoring of smelt population in L. Hiidenvesi, but day sampling can be favoured as a cheaper and probably slightly more accurate alternative.

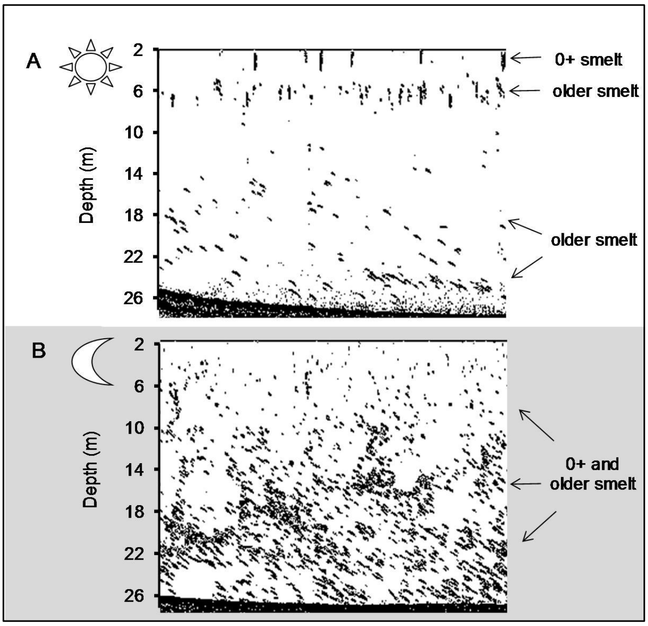

*Fig. 8. Echograms from the same transect in Lake Hiidenvesi in September 2000 during the day (A) and at night (B). During daytime, a great majority of smelt were concentrated in two narrow epilimnetic layers whereas at night they existed in the whole water column. Modified from **II**.*

Five-lake study

In the two clearest lakes, Karjalohjanselkä and Kajaanselkä basins, daytime and night-time estimates resembled those found in L. Hiidenvesi: the difference between estimates was small (Fig. 9). Similarly, the surface blind zone was a notable source of bias only in late autumn, when the night-time density estimate for a surface blind zone was even higher than the acoustic estimate in Kajaanselkä basin. In Karjalohjanselkä basin, however, no smelt occurred in the surface layer even in October. As in L. Hiidenvesi, both daytime and night-time estimates declined between August and November-December pointing to the high natural mortality of the smelt population.

In most turbid lakes (L. Tuusulanjärvi and L. Rehtijärvi), however, daytime and night-time density estimates acted in an unexpected way (Fig. 9). In L. Tuusulanjärvi, the acoustic density estimate of 0+ smelt was higher at night than during daytime in August, whereas in late autumn the opposite was true. For older smelt, the daytime estimate was higher than the night-time estimate in both seasons. All these differences were statistically significant ($p<0.01$) because 95% confidence limits were non-overlapping (Austin & Hugs 2002). In L. Rehtijärvi, the acoustic estimates for older smelt acted as in clearer lakes: the differences between daytime and night-time estimates were small within a season but the drop in the density between August and October can be clearly seen in both estimates. However, the estimates for 0+ smelt density acted in a different way: in October, the night-time density was higher than daytime density, and estimates did not decrease between August and October. This suggests that severe sources of bias might exist in both daytime and night-time sampling.

In these turbid lakes, the most likely reason for unexpected differences in acoustic estimates were occasional and unforeseen occurrence of smelt in the surface blind zone (Fig. 9). Most obviously the effect of smelt occurrence in the surface blind zone on the acoustic density estimate can be seen in 0+ smelt estimates for L. Tuusulanjärvi during daytime in August. At that time, the acoustic estimate was exceptionally low and the estimate for a surface layer exceptionally high. A similarly clear case was the 0+ smelt estimates for L. Rehtijärvi in October. However, in August in that lake, the accurate acoustic assessment of 0+ smelt was impossible during both daytime and night-time, because a noticeable part of the age-group occurred in the surface layer.

The effect of the occurrence of 0+ smelt in the surface layer can be seen from the combined data of southern study lakes, when the night-time acoustic estimates are plotted against the daytime estimates (Fig. 10). For 0+ smelt, in all four observation pairs deviating noticeably from the 45° line, the density has been exceptionally high in the surface blind zone. When the point is above the line, the smelt density has been high in the surface layer during daytime decreasing the daytime acoustic estimate (L. Hiidenvesi in November, L. Tuusulanjärvi in August, L. Rehtijärvi in October). When the point is under the line, the high density in the surface layer has reduced the acoustic estimate at night (L. Rehtijärvi in October). The densities of older smelt in the surface layer were generally low and the deviating points could not be explained by smelt occurrence in the surface layer. The reason behind the mostly deviating observation pair (daytime and night-time estimates for L. Hiidenvesi in September), was probably biased trawl sampling (**II**). However, the occurrence of older smelt in the surface layer at night in L. Tuusulanjärvi in both seasons and in Kajaanselkä basin in October are indicated by points located under the line.

The results showed that both daytime and night-time acoustic surveys are suitable for smelt assessment in most cases in relatively clear lakes (Secchi depth ≥ 1 m). The occurrence of smelt in the surface blind zone is a considerable source of bias, whereas the effect of the acoustic shadowing of fish schools appeared to be small. It is recommended to check the occurrence of smelt in the surface layer (and estimate approximately the density) with a trawl. However, because the variance of a swept area estimate seemed to be very high, surveys should be preferably done when low surface layer density can be expected. In the study lakes, these conditions prevailed during daytime in August-October.

In highly turbid lakes (Secchi depth < 1 m) of the present study the occurrence of smelt in the surface layer is so common and unforeseen that an acoustic survey should always be supported by surface trawling or alternatively, by horizontal or upward-looking echo sounding (Jurvelius et al. 1996, Knudsen & Saegrov 2002). The results showed that in turbid study lakes the DVM of 0+ and older smelt differed considerably. While older smelt ascend to the surface layer at night as a general pattern of DVM suggests, 0+ smelt appeared to have in some cases opposite DVM occurring in the surface layer during daytime and descending to deeper layers at night.

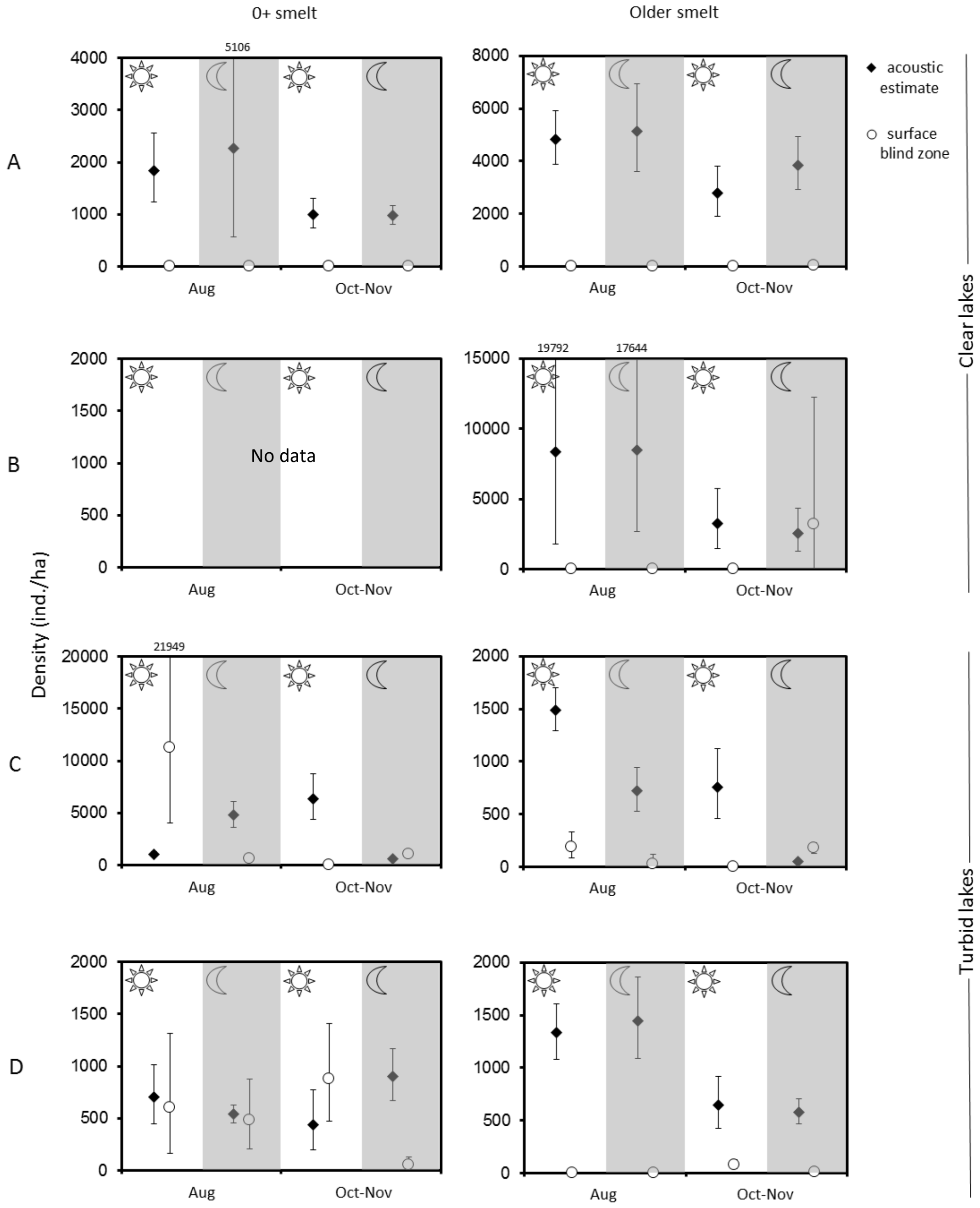

*Fig. 9. Density estimates with 95 % confidence limits by hydroacoustics and surface trawling for two groups of smelt, young-of-the-year (left panel) and older smelt (right panel) in two clear-water lakes (A=Karjalohjanselkä basin, B=Kajaanselkä basin) and in two highly turbid lakes (C=Lake Tuusulanjärvi, D=Lake Rehtijärvi). In all study lakes, two seasons (August and October-November) and two diel periods (day and night) were surveyed. Note different scales of y-axes. In Kajaanselkä basin, the density of 0+ smelt was not estimated due to exceptionally weak year-class (**extra results**).*

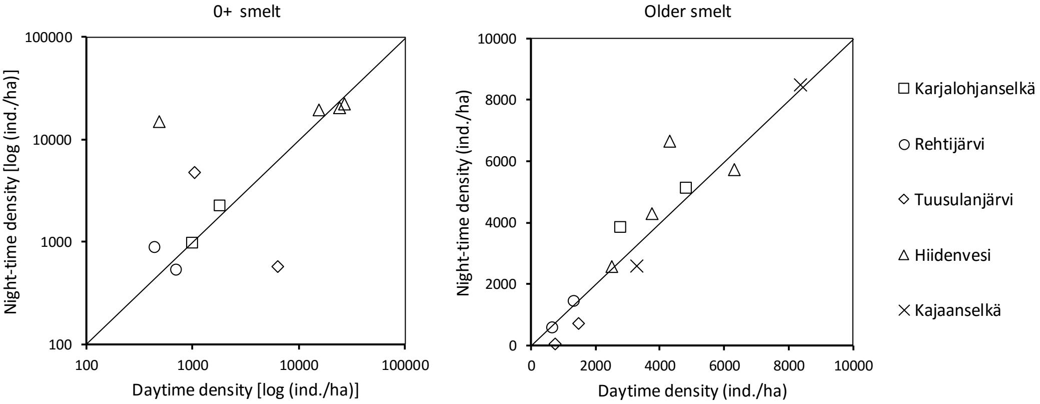

*Fig. 10. Night-time acoustic density estimates plotted against daytime acoustic density estimates for 0+ smelt (left) and older smelt (right) in southern study lakes (**extra results** and recalculated from **II**). The lines of equality are also are shown. Note logarithmic scales in the left-side figure.*

4.1.3 Comparison of survey seasons

Echo-surveys conducted throughout the open water season in L. Hiidenvesi suggested that both the vertical and horizontal distributions of smelt have implications for population estimation (**III**). The daytime vertical distribution of smelt followed a similar pattern from year after year (Fig. 11). The majority of the population (older than 0+) typically inhabited the lowermost epilimnion or uppermost metalimnion, *i.e.* the layer at which the water temperature was slightly lower than in the surface layer. However, in late summer, the density of this aggregation decreased and a considerable part of population shifted to hypolimnion. This hypolimnetic maximum disappeared after the autumn overturn. The density of older smelt in the surface blind zone was negligible during August-October 2000 and 2001 (**II**). This was the case also in June, August and October 2007, when the density estimates were only 14, 0 and 2 ind./ha, respectively (**extra results**). Younger (0+) smelt, which were detectable with acoustics since mid-summer (Fig. 12), showed different depth distributions compared with the older smelt inhabiting mainly epilimnion throughout the late summer and autumn (**III**). The mean of 0+ smelt depth distribution varied slightly within and between years but remained always between 3.5 and 6 meters. The density in the surface blind zone was negligible in August and low in October but very high in November (**II**). Corresponding densities were observed also in August and October 2007: 13 and 614 ind./ha, respectively (**extra results**).

Similarly, the horizontal distribution of smelt (older than 0+) in deep Kiihkelyksenselkä and Retlahti basins followed a similar pattern from year to year. A majority of the older smelt inhabited relatively shallow areas in June. The percentage of population inhabiting deep areas increased gradually until late autumn, when it began to decline (Fig. 13). The experimental trawl data, from shallower Mustionselkä and Kirkkojärvi basins suggested that older smelt did not inhabit these basins during June-October (Table 2). The horizontal distribution of 0+ smelt was different from that of older smelt: in deep basins, 0+ smelt inhabited generally shallower areas than older smelt (**III**). Occasionally even a great majority of the population inhabited the shallowest depth zone analyzed (5-10 m). In addition, the seasonal succession of horizontal distribution of 0+ smelt varied highly between studied years and no general pattern could be found. In the shallow basins, the density of 0+ smelt was low in most cases but the variation was extremely high: on some occasions, very high densities were observed (Table 2).

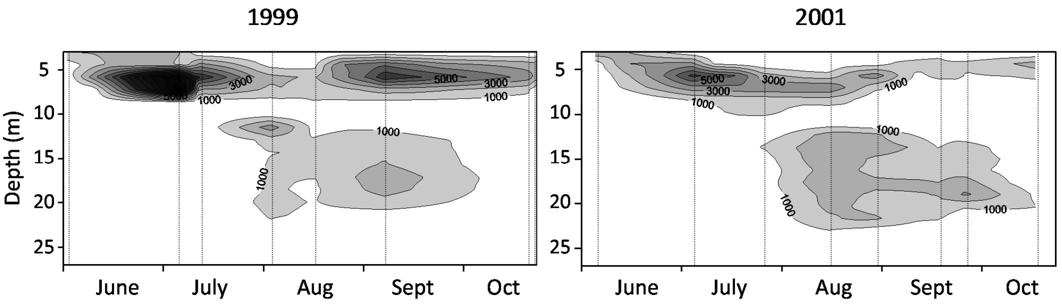

*Fig. 11. The vertical distribution of older than 0+ smelt in areas deeper than 20 m in L. Hiidenvesi obtained by acoustics during 1999 and 2001. The isopleths represent smelt densities per hectare computed for 1-m-high layers. The survey dates are indicated by vertical bars Modified from **III**.*

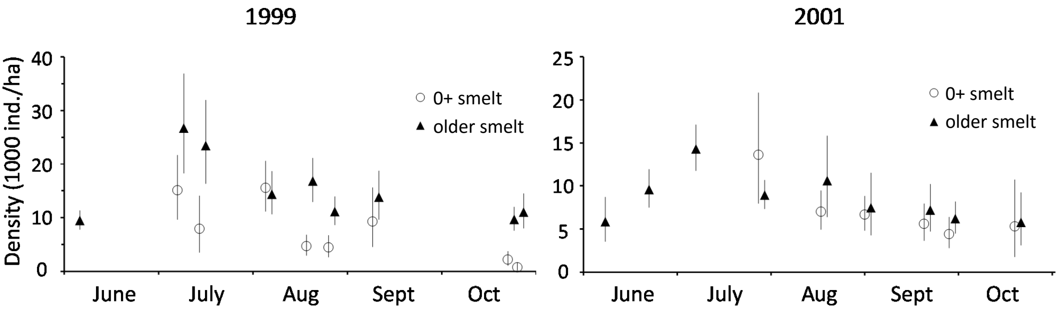

*Fig. 12. Hydroacoustic density estimates for 0+ and older smelt with 95 % confidence limits in >5 m deep areas of L. Hiidenvesi during 1999 and 2001 (**extra results**). Note different scales on y-axes.*

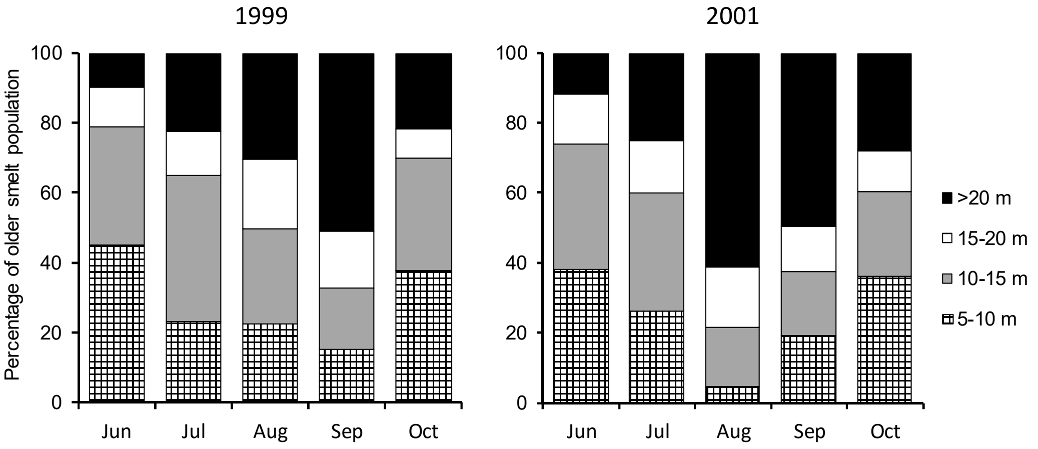

*Fig. 13. Horizontal distribution of older smelt in > 5 m deep areas of L. Hiidenvesi obtained by hydroacoustics during 1999 and 2001. In the figure, for instance 5-10 m depth zone refers to the area where depth is 5-10 m. The 5-10 m depth covered 43%, 10-15 m 32%, 15-20 m 9% and > 20 m 16% of the study area. Modified from **III**.*

*Table 2. Smelt density estimates in two shallow basins of L. Hiidenvesi by experimental trawling (**III** and **extra results**). Confidence limits (95%) are presented for densities ≥ 10 ind.ha.*

Basin	Depth zone	Sampling date	Number of hauls	Density of 0+ smelt (ind./ha) with 95% confidence limits	Density of older smelt (ind./ha)
Mustionselkä	1.5-4.5 m	31 Jul-2 Aug 2001	19	2100 (1740-2590)	<10
		6-8 Aug 2002	22	76400 (31050-141850)	<10
		5 Jun 2007	3	<10	<10
		22 Aug 2007	3	30 (4-66)	<10
		9 Oct 2007	2	<10	<10
Kirkkojärvi	1.5-3 m	5-6 Aug 2003	8	<10	<10
		24-25 Sep 2003	8	70 (48-100)	<10
		4-5 Aug 2004	8	2000 (1030-3330)	<10
		29-30 Sep 2004	8	240 (84-490)	<10
		5 Jun 2007	2	<10	<10
		9 Oct 2007	2	<10	<10
		22 Aug 2007	2	20 (14-28)	<10

The vertical and horizontal distributions of older than 0+ smelt in L. Hiidenvesi favoured hydroacoustic estimation. During June-October, their density was negligible in the surface blind zone as well as in the shallow basins. Therefore the survey conducted in > 5 m deep area is a sufficient measure for monitoring the number of older smelt. However, the relatively high percentage of older smelt population in the shallowest depth zone (Fig. 13) in June as well as the increase in the density estimate from early June to July (Fig. 12) suggested that a considerable part of the population inhabited the < 5 m deep area outside the acoustic sampling in early summer. Hence, a hydroacoustic survey aimed at population monitoring should be preferably timed for late summer or autumn.

Both the vertical and horizontal distribution patterns of 0+ smelt induced considerable limitations on hydroacoustic population monitoring. Late autumn was not suitable for the assessment of 0+ smelt because of their strong preference of a surface layer. While the vertical distribution of 0+ smelt in deep areas favoured acoustics during late summer and early autumn, the unpredictable horizontal distribution complicated estimation. The occasional profusion of 0+ smelt in the shallow basins and in the shallowest strata in the acoustic data suggest that acoustic estimation should be supplemented by experimental trawling in shallow areas.

4.2 Northern whitefish lakes

4.2.1 Pelagic fish assemblage

Whitefish was the dominant fish species in the pelagic of all northern study lakes according to the experimental trawling (gill-netting in L. Kilpis) in September (**V**). In three lakes (Kilpis, Muddus and Paadar) the dominance of whitefish was very strong: the percentage of whitefish was more than 95% of numerical catches. In lakes with polymorphic whitefish (Vastus, Muddus, Paadar) the pelagic catches consisted of mostly the DR morph. In L. Muddus and Paadar the percentage of other fish than DR whitefish was only < 3% but the small pelagic area of L. Vastus was inhabited also by perch (36% of the trawl catch) and LSR whitefish (15%). In a three-season study in L. Muddus, the dominance of DR whitefish was equally strong in June, August and September (**IV**). In L. Raha, the dominant fish was monomorphic LSR whitefish (66%) but the pelagic was inhabited also by vendace (27%, **V**). In all lakes, the catches of other species than coregonids and perch (mainly nine-spined stickleback, brown trout and Arctic charr) were low. However, TS-distributions suggested that in four lakes (Vastus, Raha, Muddus, Paadar) the very small-sized nine-spined stickleback (mean length 33-38 mm) was actually abundant (Fig. 14).

4.2.2 Comparison of day and night surveys

In a first comparison of day and night surveys (conducted in June, August and September in L. Muddus), the pelagic DR whitefish density was significantly higher at night than during the day in all seasons (**IV**). In addition, a clear diurnal vertical migration (DVM) pattern existed in August and September: whitefish occurred higher in the water column at night than during the day. In June, under the midnight sun, most DR whitefish stayed in near-bottom layers also at night. This study, however, was done within a relatively small area of one lake, which reduced the generalization of findings.

In a more extensive diurnal study conducted in six lakes with variable coregonid assemblages (**V**), the observations made in the prior study were supported in four lakes. In three lakes (Raha, Muddus and Paadar), the daytime and night-time echograms were highly different: during the day, only a few fish existed in the water column whereas at night many fish were observed (Fig. 14). This was also seen as a very strong difference between daytime and night-time echo integrals (Fig. 15). The most pronounced difference was detected in L. Raha, where night-time s_a was even 26-fold compared with daytime s_a (**V**). In L. Muddus, the night-time s_a was 10-fold and in L. Paadar 5-fold compared with daytime s_a. In L. Kilpis, the night-time s_a was significantly higher than the daytime s_a, but the difference between estimates was relatively small. In this respect, the other two study lakes (Vuontis and Vastus) were different (Fig 15). In these lakes the echo integrals were higher during the day than at night. In L. Vastus, the high daytime integral most likely originated from the relatively large schools of perch (**V**). In L. Vuontis, the monomorphic whitefish population did not practically utilize the pelagic habitat, neither during daytime nor at night, based on minimal trawl catches and echo integral.

The superiority of night over daytime for hydroacoustic estimation was also indicated by profundal gill-net catches (**V**). The CPUE was significantly higher during daytime than at night, which indicated higher fish density in the bottom dead zone during daytime. However, relatively high CPUEs even at night indicated that the bottom dead zone may be a considerable source of bias also during September nights. The surface blind zone appeared to be a less serious source of bias, because the swept area fish density estimates were negligible during both diel periods in September (**V**).

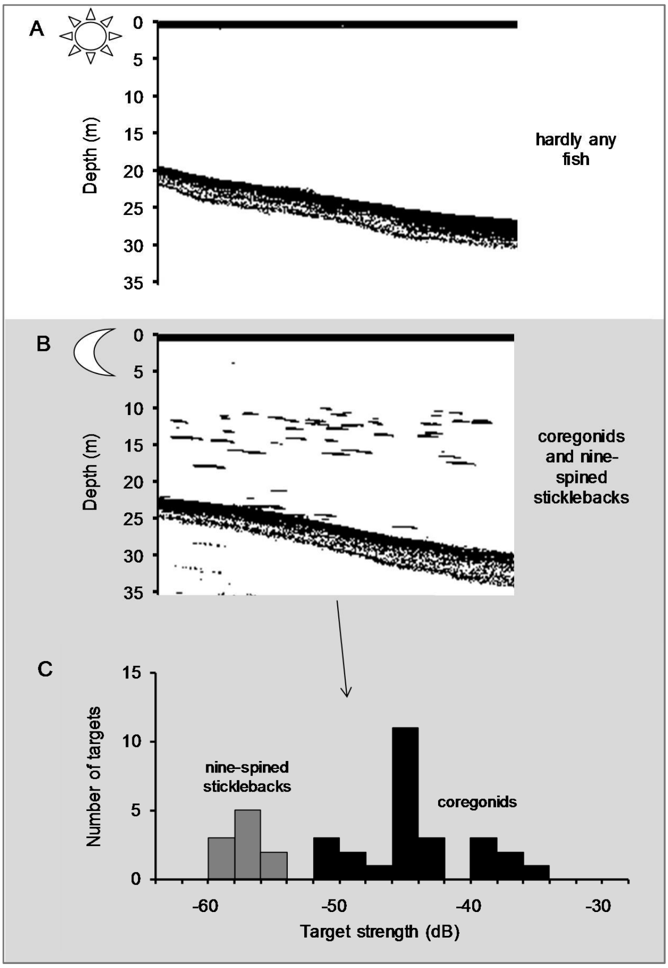

*Fig. 14. Echograms from the same transect in L. Raha in September 2005 during the day (A) and at night (B). During the day, hardly any fish could be seen but at night coregonids (LSR whitefish and vendace) as well as nine-spined sticklebacks have been appeared in mid-water. The target strength distributions of coregonids and nine-spined sticklebacks from the presented echogram were non-overlapping (C) (**extra results**).*

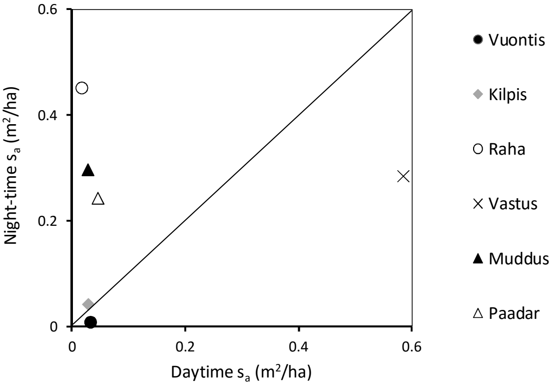

*Fig. 15. Night-time echo integral (mean total area scattering coefficient, s_a) plotted against daytime echo integral in surveys conducted in northern study lakes in September. The line of equality is also shown (recalculated from **V**).*

4.2.3 Comparison of survey seasons

In L. Muddus, the night-time pelagic whitefish density increased clearly from June to August and further from August to September (**IV**). In a more extensive six-lake study, the echo integral was clearly higher in September than in June-July in all lakes excluding L. Vuontis (**V** and Fig. 16). The relative difference was the highest in L. Paadar, where s_a was 22-fold in September compared with s_a in June. In L. Muddus, s_a in September was 18-fold compared with s_a in June while in other lakes s_a in Semtember was 2-6-fold compared with s_a in June (excluding L. Vuontis). The results suggest that the utilization of a pelagic habitat by whitefish became more common towards autumn excluding L. Vuontis, where the monomorphic whitefish population did not practically exist in the pelagic even in September. Hence, autumn is evidently a more suitable season for hydroacoustic assessment than mid-summer in the northern lakes of the present study. This conclusion can be drawn in spite of the lack of fish species distribution data from all sampling occasions, because s_a-values were minimal in mid-summer.

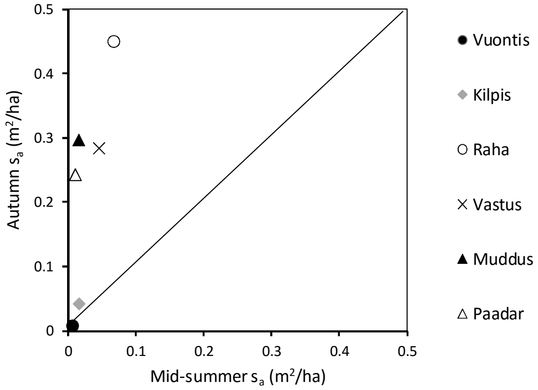

Fig. 16. Night-time ehco integral (mean total area scattering coefficient, s_a) in mid-summer plotted against echo integral in September in northern study lakes. The line of equality is also shown (recalculated from V).

4.2.4 Suitability of acoustics in estimation of different whitefish populations

Even on the most suitable survey occasion (night-time in September), the accuracy of hydroacoustics varied greatly between lakes and between coregonid species/morph (**V**). The accuracy was in most lakes reduced by fish occurring in the bottom dead zone and shallow area outside the acoustic sampling (Fig. 17), while the surface blind zone was only a minor source of bias. In lakes with polymorphic whitefish, acoustics was a suitable estimation method only for DR whitefish, because LSR whitefish strongly preferred shallow areas and SSR whitefish the profundal bottom layer. In L. Vastus, the accuracy of DR whitefish assessment was lowered by the high percentage (79%) of shallow area outside the acoustic sampling and by the difficulties in allocating echo integral between species due to the abundant perch population. In lakes with monomorphic whitefish, the level of utilization of the pelagic habitat, and hence the accuracy of acoustic assessment, appeared to differ greatly between lakes. The most suitable monomorphic whitefish population for acoustic assessment was the LSR population in L. Raha due to its strong preference for the pelagic habitat. The LSR population of L. Kilpis remained partly in the bottom dead zone biasing acoustic estimation. The most unsuitable monomorphic whitefish population for acoustic assessment was found in L. Vuontis, where the LSR whitefish avoided the pelagic habitat. By comparison, the vendace population of L. Raha preferred strongly the pelagic habitat, and this was found to be the most suitable for acoustic assessment among the studied coregonid populations.

When the accuracy of hydroacoustic assessment was evaluated in estimation of total fish density and biomass of each lake, it was considered high in L. Raha, average in L. Muddus and L. Paadar, but low in the other three lakes. The tolerably accurate estimates were 430 fish and 7.4 kg/ha in L. Raha, 640 fish and 9.5 kg/ha in L. Muddus as well 1780 fish and 13.3 kg/ha in L. Paadar.

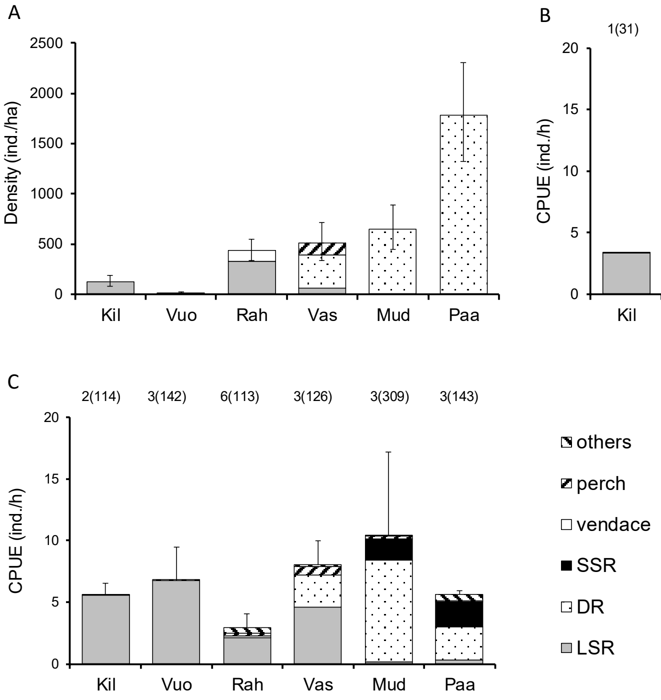

*Fig. 17. Hydroacoustic fish density estimates (with 95% confidence limits) in the pelagic area at night in September (A) and simultaneous catch-per-unit-effort (with standard errors) of benthic gill-net series in shallower areas (B) and in the bottom layer of deep areas (C). For gill-net fishing, also number of catching periods and total catch in numbers (in parenthesis) are indicated above the columns. Modified from **V**. Key: Kil=Lake Kilpis, Vuo=Lake Vuontis, Rah=Lake Raha, Vas=Lake Vastus, Mud=Lake Muddus, Paa=Lake Paadar.*

5. Discussion

5.1 Suitable diel periods

The choice of diel period for a hydroacoustic estimation is much more important in northern clear-water whitefish lakes than in southern turbid smelt lakes. In those northern lakes where the accuracy of acoustics was considered to be at least average (**V**), night-time echo integrals were multifold compared with daytime integrals (Fig. 18) indicating a superiority of night-time surveys. High difference resulted from the habitat choice of whitefish: in all study lakes, whitefish utilize the pelagic layer only at night. This was unexpected especially in the case of planktivorous DR whitefish. The results highlight that habitat shifts of whitefish can be very sudden and extensive. In Lake Skrukkebukta, located on the Norwegian side of the same watercourse, DR whitefish show corresponding but less extensive diurnal habitat shift in autumn (Gjelland 2003, Gjelland et al. 2009). Night-time is generally preferred in hydroacoustic whitefish estimation also in Alpine lakes (Appenzeller 1995 and 1998), where, however, the superiority of night-time is based on schooling behaviour of fish. Whitefish inhabit the pelagic layer also during daytime but form dense schools, which complicates density estimation (Ptak & Appenzeller 1998).

In the southern lakes excluding the very turbid ones, the differences between day- and night-time fish density estimates were small indicating both diel periods to be equally suitable for hydroacoustic surveys (Fig. 18). Results did not support the presence of bias due to acoustic shadowing during daytime nor the presence of bias due to ascending smelt to the surface blind zone at night. The negligible effect of acoustic shadowing in clay-turbid lakes may result from looser and/or smaller schools due to the lower utility of antipredator behaviour in turbid conditions (Abrahams & Kattenfeld 1997). The schooling behaviour of smelt along a turbidity gradient has not been systematically studied, but echograms presented by Gliwitz & Jahner (1992) suggest that the importance of schooling decreases with increased turbidity. The low smelt densities in the surface blind zone at night during August-October were somewhat unexpected. It is possible that high epilimnetic temperature (**III**) prevented smelt from ascending to the surface layer in August (Northcote & Rundberg 1970, Dembinski 1971, Jurvelius & Louhimo 1991), whereas low zooplankton biomass (Tallberg et al. 1999) may reduce the attractiveness of the surface layer during autumn. However, because other studies have shown that smelt ascend up to the surface blind zone at least occasionally (Dembinski 1971, Jurvelius 1991, Gliwicz & Jachner 1992, Horppila et al. 2000), the possibility of night-time occurrence of smelt in the surface blind zone can not be excluded. Therefore, hydroacoustics should be supported by surface trawling when night-time surveys are used.

The original hypothesis that night-time estimates are higher than daytime estimates was not supported by the data and results suggested that estimates may instead be relatively similar. However, since possible similarity was a new finding made in the present study, it cannot be tested with the present data. Testing similarity requires new, independent data set and a hypothesis stated to show similarity, not difference (Schuirmann 1987, Rita & Ekholm 2007). The similarity analysis offers a valid approach for testing the interchangeability of survey timings. However, the analysis requires quantification of the similarity limit *i.e.* a researcher should state how similar estimates are needed for the interchangeable use of survey timings.

In the most turbid lakes of the present study, the unpredictable occurrence of smelt in the surface blind zone induced a serious source of bias irrespective of diel period. Such high densities in the surface layer (even a majority of smelt population) reduce the applicability of vertical hydroacoustics considerably. The profusion of smelt in the surface layer have been documented also in Lake Ijssel, the Netherlands, during turbid conditions (Mous et al. 2004). Although the results suggest that the importance of the surface blind zone as a source of bias increases with turbidity, general conclusions about the effect of turbidity can not be drawn from the present data. Only two turbid lakes were surveyed, which hampers statistical testing. Furthermore, the turbid lakes differ also in various ways from other study lakes. They were smaller, more eutrophic and had more diverse fish community. It is possible that also these factors affect the depth preference and DVM of smelt. A detailed study on factors controlling the vertical distribution of different age-groups of smelt would help considerably in timing the hydroacoustic surveys.

The results from vendace-dominated lakes prevalent in Central Finland suggest that night-time surveys produce more accurate vendace density estimates than daytime surveys due to the DVM pattern and schooling behaviour of vendace. During the day, vendace form generally dense schools which may appear also in the bottom dead zone. At night, vendace occur scattered in the cool-water hypolimnion, which strongly favours hydroacoustic estimation (Dembinski 1971, Bagenal et al. 1982, Hamrin 1986, Jurvelius et al. 1988). Some vendace may ascend up to the surface blind zone even in warm-water seasons, but this problem is mainly restricted to crepuscular periods (Jurvelius & Louhimo 1991, Lilja et al. 2013). In deep lakes with low vendace density, however, the difference between daytime and night-time density estimates may be small (Jurvelius & Heikkinen 1988).

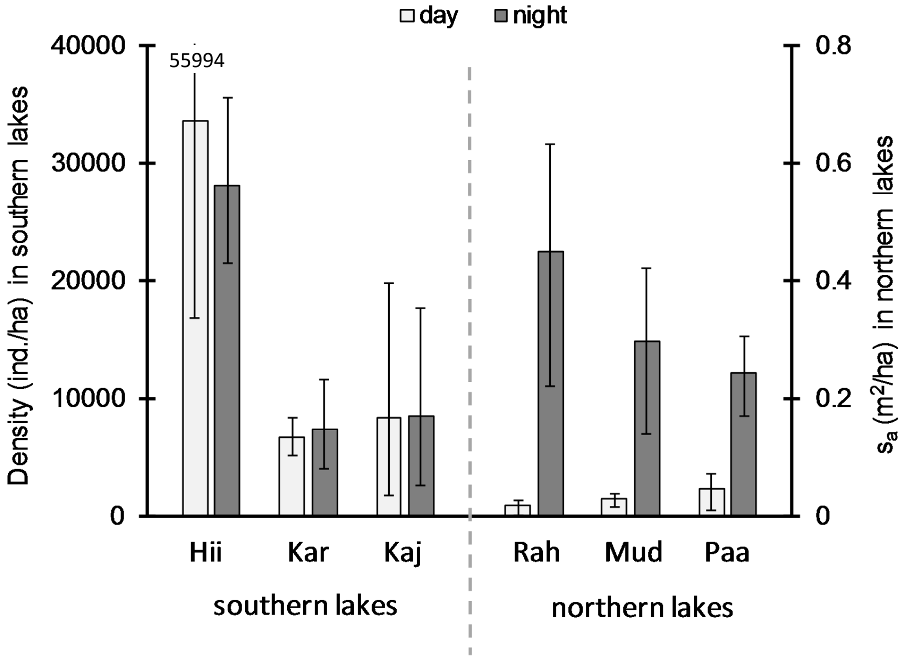

*Fig. 18. Smelt density estimates with 95% confidence limits in southern study lakes (excluding very turbid lakes) during the day and at night in August as well as echo integral (total area scattering coefficient, s_a) with 95% confidence limits in northern study lakes (excluding lakes where the accuracy of hydroacoustics was considered low) during the day and at night in September (**extra results** and recalculated from **II** and **V**). Key: Hii = Hiidenvesi, Kar = Karjalohjanselkä basin, Kaj = Kajaanselkä basin, Rah = Lake Rahajärvi, Mud = Lake Muddus, Paa = Lake Paadar.*

5.2 Suitable seasons

The choice of survey season is also more crucial in northern whitefish lakes than in southern smelt lakes. In northern lakes, the pelagic fish density was minimal in June but remarkably higher, even multifold in September (measured as total area scattering coefficient, **V**). The data from the only lake, L. Muddus, where three surveys were made, suggest that night-time pelagic DR whitefish density increases gradually towards autumn (Fig. 19). Results thus strongly suggest that autumn is the only possible season for hydroacoustic assessment in northern whitefish lakes.

The pelagic occurrence of whitefish in northern lakes is controlled at least by zooplankton succession, the duration of night-time darkness and water temperature. The zooplankton biomass peaks in late summer but may be a valuable resource also after the highest peak for gonad development, especially as the lipid content of copepods increases towards autumn (Eloranta et al. 2013, Hayden et al. 2014b). The duration of darkness and hence the time window of low predation pressure by brown trout (Gjelland et al. 2009) increases towards autumn, which should increase the attractiveness of the pelagic habitat. The temperature may be of crucial importance for the duration of the sampling window, because it likely controls the timing of the spawning migration of whitefish in late autumn. This movement to shallow areas and near-bottom layers determines the deadline for an acoustic survey. Some observations from L. Paadar and Muddus suggest that pelagic whitefish density may drop already in late September with decreasing water temperature (Tuomaala 2008, Kahilainen et al. 2014). Threrefore, the duration of suitable season might be relatively short, possibly only some weeks, depending on the advancement of autumn. During summer, the epilimnetic water temperature is typically <15°C allowing the utilization of the pelagic habitat for DR and LSR whitefish. However, such high temperature may restrict the pelagic occurrence of cold-adapted SSR whitefish (Kahilainen et al. 2014).

In the most intensively studied southern smelt lake, L. Hiidenvesi, the density estimate increases from early June to late July (Figs. 12 and 19). After that, it declines gradually towards autumn. The increase in early summer results from the migration of older smelt from shallower areas to deep area sampled by hydroacoustics while further increase in mid-summer originated from the appearance of 0+ smelt in the estimates. Hence, surveys conducted in June produce underestimates of the size of the population. Because no indications of an increase in the magnitude of bias sources (fish in the surface blind zone or in shallow areas) were noticed, the decrease of the density estimate during autumn was most likely due to natural mortality. Hence, the accuracy of surveys between late July-late October can be considered high but the estimate is still strongly season-dependent. Due to high natural mortality of smelt, the density estimate can be multifold in late July compared with late October. Therefore, it is especially important to fix the survey season in long-lasting monitoring programmes.

The experiences from the vendace-dominated lakes prevalent in Central Finland suggest that the most suitable survey season is late summer when all age-groups of vendace prefer deep areas (Jurvelius & Heikkinen 1988). In some lakes, another suitable survey period may exist just after the thaw, when vendace are concentrated in deep areas (Jurvelius & Heikkinen 1988). During early summer, hydroacoustic estimation of young-of-the year vendace is not possible due to their small size as well as their preference of littoral zone and surface layer (Næsje et al. 1987, Viljanen & Karjalainen 1992, Urpanen et al. 2009). In addition, during that time more rapidly warming shallow waters offering more zooplankton may draw also older vendace (Jurvelius & Heikkinen 1988). Currently, monitoring is carried out in late summer-early autumn (Marjomäki & Huolila 2001, Axenrot & Degerman 2016). However, data on the duration of the suitable seasonal window as well as the succession of density and biomass within this window have not been reported. It would be interesting to know, for instance, whether the suitable window closes with autumn overturn or not until the spawning migrations/activity.

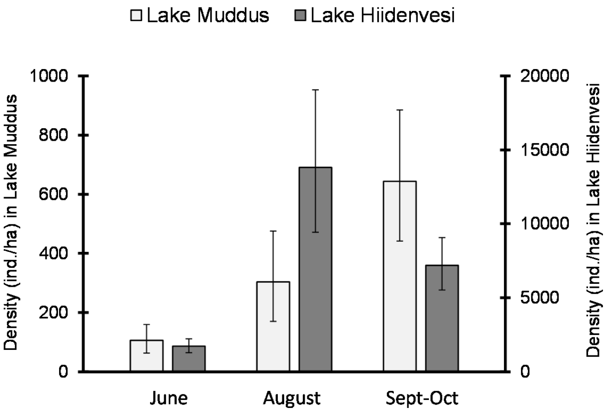

*Fig. 19. An approximate seasonal succession of pelagic DR Whitefish density in Lake Muddus (night-time estimates in June-August 2001 and September 2000) and pelagic smelt density in Lake Hiidenvesi (daytime estimates in 2007) with 95% confidence limits. Note different scales in y-axes (**IV and extra results**).*

5.3 Reverberation

In clay-turbid smelt lakes, the density of *Chaoborus* larvae in the water column may be so high that the reverberation cause serious overestimation of fish density. The presented method broadens the applicability of hydroacoustic fish density estimation in lakes with abundant *Chaoborus* population. While the thresholding method (Eckmann 1998) is an efficient elimination method only during some seasons (Eckmann 1998, Malinen et al. 2001, the present study), the new method seemed to be applicable during the open water period with a few exceptions.

Another way to eliminate reverberation is using low frequency (38 kHz, Knudsen et al. 2006, Jurvelius et al. 2008, Knudsen & Larsson 2009) but it has some disadvantages compared with higher frequency (70-200 kHz) traditionally used in lakes (impractically large-sized transducer, lower vertical resolution and a larger near-field close to a transducer, where density estimation is not possible). In addition, higher frequency enables the estimation of *Chaoborus* density and distribution, which may be also of interest (Eckmann 1998, Knudsen & Larsson 2009). Later data from *ca.* 20 lakes in southern Finland have revealed that *Chaoborus* disturbs fish stock assessment in almost all clay-turbid lakes, which are deep enough for vertical echo sounding, and in some humic lakes, too (Malinen et al. 2009 and unpublished).

The developed *Chaoborus* elimination method, however, does not totally remedy the *Chaoborus* problem. In some lakes, *Chaoborus* larvae may form occasionally such dense swarms that the method is not applicable. This was the case in the Maikkalanselkä basin, a eutrophic, clay-turbid and shallow lake located near Hiidenvesi (Malinen et al. 2003). During the daytime in August, *Chaoborus* larvae occurred mainly in sediment and the reverberation was negligible. At night, however, most larvae had been shifted to the water column causing severe reverberation, which was not eliminated by the method. The observation suggests that in relatively shallow lakes, where sediment is suitable for burrowing *Chaoborus* larvae, their shift to the narrow water column at dusk may result in extremely high density totally hampering night-time fish density estimation.

In addition, even if reverberation could be totally eliminated, the timing of an echo-survey aimed at fish stock assessmnet should be carefully considered. If possible, a survey should be conducted during a season and diel period when the limnetic density of *Chaoborus* is relatively low. There are three reasons for this. At first, even computed by the new elimination method, the precision of fish density estimate increases as *Chaoborus* density decreases (**I**). Secondly, though the developed method was proven to give accurate results with a secondary data set (**I**), it is obvious that changes in fish size, depth distributions and schooling behaviour may induce considerable bias to fish density estimates. Thirdly, the application of the method is time-consuming and analysis is quickened if low *Chaoborus* density enables traditional fish density analysis at least in some transects or water layers. From these viewpoints, the most suitable timing for acoustic fish stock assessment in L. Hiidenvesi is late July-early August, just after the core emergence period of *Chaoborus* (Liljendahl-Nurminen et al. 2003). However, because the life cycle of *Chaobous* varies from lake to lake with a temperature regime (Parma 1971), the optimization of the timing of an acoustic survey may require a prior study on the seasonal succession of *Chaoborus*. In many lakes, the distributions of fish and *Chaoborus* overlap only at night (e.g. Unger & Brandt 1989, Knudsen & Larsson 2009) supporting daytime sampling but in clay-turbid lakes overlapping may take place also during daytime (**I**). Although the timing of the survey can not be selected based on *Chaoborus* existence only, but primarily in accordance with the pelagic occurrence of target fish species, it is one important variable worth considering when planning the sampling strategy.

In general, reverberation by invertebrates is of minor importance in northern whitefish lakes, because of the negligible density of *Chaoborus* (Kahilainen, K., pers. comm.). Based on echograms from L. Kilpis, however, some reverberation may take place even in northern oligotrophic lakes, likely due to the dense aggregations of Chironomidae pupae during the highest emergence period in June and during the peak density of *Eudiaptomus* copepods in September (Kahilainen, K., pers. comm.). Nevertheless, this sporadic and faint reverberation appeared to be negligible bias source in fish density estimation.

Chaoborus have not been reported to disturb fish density estimation in Fennoscandian vendace lakes (but see Jurvelius et al. 2008). The importance of reverberation is diminished by the fact that vendace assessment is typically based on echo counting, where small-sized targets can be excluded. However, in the traditional computation (Lindem 1983, Balk & Lindem 2004), echo integration is applied for schooled fish, exposing vendace assessment to this bias source, too. Because the limnetic occurrence of *Chaoborus* in humic vendace lakes is common (Rahkola-Sorsa et al. 2016), more extensive evaluating of this bias source might be useful. In deep oligotrophic vendace lakes, also the dense aggregations of relict amphipod *Mysis relicta* may disturb hydroacoustic estimation of vendace (Jurvelius et al. 2008). The reverberation by *Mysis*, however, should be considerably weaker than by *Chaoborus* due to its clearly lower target strength (Knudsen et al. 2006, Rudstam et al. 2008b).

5.4 Uncertainty about the composition of fish assemblage

In addition to survey timing and reverberation, which were studied in the present project, hydroacoustics has numerous bias sources (Shotton & Bazigos 1984, Simmonds & MacLennan 2005). These are not extensively discussed here, but the findings made in the course of the study obligated one source to be mentioned: fish sampling.

In the present study, considerable effort was made to assign unbiased fish species composition and length distribution by trawling, which is considered one the most valid sampling gears (Simmonds & MacLennan 2005). It became evident, however, that as a very time-consuming method, the achieved coverage by the trawl during a typical survey was relatively low. This has undoubtedly induced uncertainty for the species/morph-specific estimates, and to a lesser extent, also for the total density and biomass estimates. The low coverage of trawling is also problematic in osmerid and coregonid assessment in the North American Great Lakes and various methods have been developed to alleviate this problem (Yule et al. 2013b and c).

In addition, the used trawling strategy inevitably caused some bias for estimated species proportions: the trawling depths and areas were concentrated on high-density areas based on echo sounding, because they were considered the most critical for total fish density and biomass estimates. This may have led to the underrepresentation of species having dispersal occurrence and/or species favouring different water layers or areas than the dominant/aggregating species. As a consequence, the contribution of some low-density species and morphs have possibly been underestimated. Moreover, the variable catchability by fish size has probably induced some bias to estimates. Trawl avoidance and escape may increase with fish size but very small-sized fish may also escape through trawl mesh (Pearcy 1980, Bethke et al. 1999, McClathie et al. 2000, Jurvelius et al. 2016). In the present study, especially the catchability of very small-sized nine-spined stickleback appeared to be low and serious bias would have introduced if species proportions by trawl catches were blindly applied. It was necessary to discriminate this species from other fish species based on observed TS-distributions. Considering these shortcomings of trawling, possibly underestimated species include e.g. large-sized blue bream and deep-dwelling vendace in southern lakes as well as large-sized piscivores (brown trout, Arctic charr) and deep-dwelling SSR whitefish in northern lakes.

The trawling played an especially important role in assessing the multispecies fish communities of southern L. Rehtijärvi and L. Tuusulanjärvi (**extra results**) and northern L. Vastus (**V**). However, the small pelagic area in these lakes enabled higher coverage of trawling which at least partly compensated the higher uncertainty in species composition. Nevertheless, the estimates for these lakes are more uncertain than in the other study lakes.

As a whole, the hydroacoustics and trawling were considered to give relatively unbiased density and biomass estimates for the total pelagic fish assemblage and these of dominant species/morphs. Nevertheless, the study showed that fish sampling may be the most demanding task in acoustic assessment in southern and northern Finnish lakes and suggested that the time allowable for fishing may strongly contribute to the accuracy of the density and biomass estimates. The study gave a general impression that there may be an exchange between the accurate assessment of a total fish assemblage and that of a given species.

Other fish species also complicates vendace density estimation. Especially the distribution of smelt and vendace may overlap strongly (Northcote & Rundberg 1970, Jurvelius et al. 2005, Northcote & Hammar 2006). In these cases the valid determination of species distribution requires sampling with trawl or seine (Olin & Malinen 2003, Jurvelius et al. 2011). Even then the unbiased estimation of vendace/smelt-ratio may be challenging (Marjomäki & Huolila 1995). Other typically abundant species in the pelagic of Fennoscandian vendace lakes, cyprinids and perch, occur mainly in the warmer epilimnion and typically only during daytime (Northcote & Rundberg 1970, Eloranta & Eloranta 1978, Beier 2001) while vendace are usually surveyed at night (Marjomäki & Huolila 2001, Axenrot & Degerman 2016, Jurvelius et al. 2016). In addition, dense vendace populations may force these species to use mainly littoral and benthic habitats (Beier 2001, Valkeajärvi & Marjomäki 2013). Hence, these species do not usually seriously hamper vendace density estimates in Finnish vendace lakes.

5.5 Fish density and biomass

While the focus of the present study was in evaluating the applicability of hydroacoustics and in developing analysis methods, results may also enable rough comparison of the pelagic fish density and biomass levels between studied lake types. One should keep in mind, that the estimates represent only the pelagic fish community while the total fish density or biomass of the lakes remain unknown. The species-specific pelagic fish density and biomass estimates, however, are of great value when exploring the structure and dynamics of pelagic food-webs. The confidence limits for density and biomass estimates are not presented for most southern lakes, because in most cases the estimates are averages over only two surveys. However, seven-year data (2004-2010) from L. Tuusulanjärvi enabled the computation of confidence limits. In this lake, the 95% confidence limits based on normal distribution were 12600-34900 ind./ha and 79-196 kg/ha. Confidence limits for density estimates from a single survey in each northern lake were relatively narrow (**V**).

Both the pelagic fish density and biomass were much higher in southern than in northern study lakes (Fig. 20). The density varied from 10 to 1800 ind./ha and biomass from almost 0 to 13 kg/ha in northern lakes, whereas respective ranges were 5000 to 24000 ind./ha and 25 to 138 kg/ha in southern lakes. Higher fish density and biomass in southern lakes are somewhat self-evident due to higher productivity and longer growing season. In northern lakes, pelagic densities were significantly higher in lakes with polymorphic whitefish than in lakes with monomorphic whitefish suggesting that polymorphic whitefish lakes may support more abundant predatory fish populations. The availability of pelagic prey fishes is especially important for the most abundant piscivore, brown trout (Næsje et al. 1998, Jensen et al. 2008, Thomas et al. 2017) and it appears that the carrying capacity of a lake with monomorphic whitefish can be easily exceeded with the intensive stocking programmes of brown trout.

In those southern lakes where smelt dominated strongly the pelagic fish assemblage, biomasses were relatively low. The most pronounced example of this was L. Hiidenvesi, where pelagic fish density was > 10000 ind./ha but biomass only 25 kg/ha. The most eutrophic and turbid lakes of the present study (L. Tuusulanjärvi and L. Rehtijärvi) had diverse pelagic fish assemblages with many cyprinid fish species and very high biomasses compared with other study lakes. In these lakes, the area of pelagic is small, which obviously contributes to the high pelagic biomass of cyprinid species. In addition, their migrations between littoral and pelagic areas are evidently the reason behind the high variation in the pelagic fish biomass estimates of L. Tuusulanjärvi (Malinen 2017). Based on a cohort analysis, the biomass of cyprinids per hectare must have been higher in the shallow areas outside the acoustic sampling, and the biomass (per the whole lake area) of three dominant cyprinid species alone may occasionally exceed 200 kg/ha (Malinen et al. 2017). Such high biomasses are typical for highly eutrophic lakes dominated by cyprinids (Horppila & Peltonen 1994, Sarvala et al. 2000).

One might expect that the fish density and biomass of vendace-dominated lakes in central Finland fall between those observed in the southern and northern lakes of the present study. This comparison is difficult, because usually only vendace densities and biomasses have been reported, though other species, especially smelt, inhabit the pelagic of these lakes. The other confusing factor is the high interannual variability of vendace populations (Jurvelius 1991, Marjomäki et al. 2004, Axenrot & Degerman 2016). In oligotrophic Lake Paasivesi, the density in August varied from 200 to 1000 ind./ha averaging about 500 ind./ha (Jurvelius 1991) and in oligotrophic Lake Puulavesi, from 20 to 4000 ind./ha averaging >1000 ind./ha (Marjomäki et al. 2014). In the two largest lakes of Sweden, the vendace density in September varied from almost 0 to ca. 1000 ind./ha averaging 200-500 ind./ha (Nyberg et al. 2001, Axenrot & Degerman 2016). The biomasses of vendace have been less frequently reported. The biomass appears to be generally < 20 kg/ha in Finnish lakes (Sarvala et al. 1998, Jurvelius et al. 2005 and 2011, Marjomäki et al. 2014). While the smelt density may exceed vendace

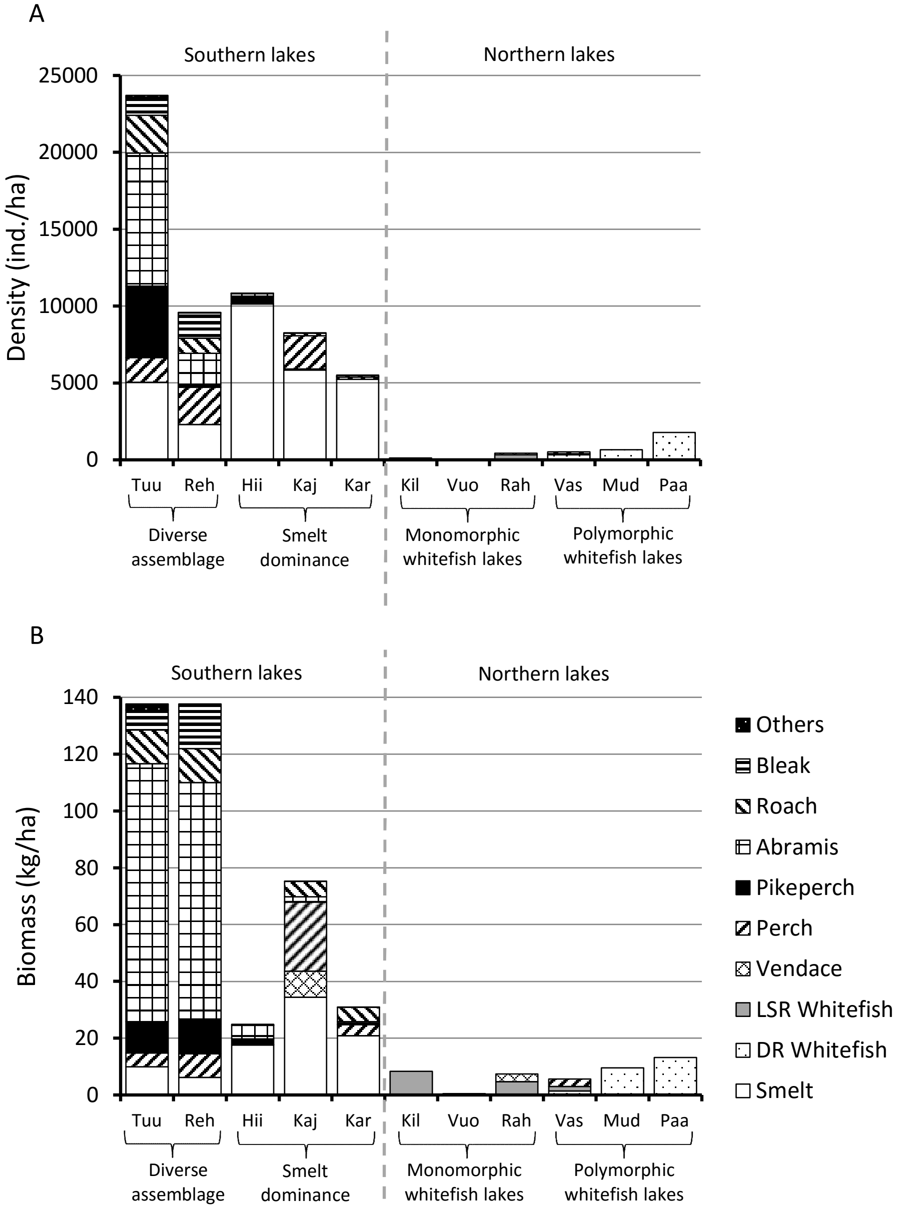

*Fig. 20. Species-specific density (A) and biomass (B) estimates for all study lakes as a sum of hydroacoustic estimate and trawling esitimate for the surface blind zone. In northern lakes, estimates are from night-time surveys in September while in southern lakes estimates are averaged over daytime surveys in August and October-November. In L. Tuusulanjärvi, estimates are averages over 2004-2010 while in other lakes estimates are based surveys conducted one year only (L. Hiidenvesi in 2007 when the species distribution was determined most completely). Very small-sized nine-spined sticklebacks have been excluded from estimates for northern lakes. Due to the difficulties of identification of small bream and white bream, they are presented as Abramis (**extra results and V**). Abbreviations for lake names are given in Table 1.*

density, the biomass of this small-sized fish remains generally below 10 kg/ha in oligotrophic Fennoscandian lakes (Nyberg 2001, Jurvelius et al. 2005). These values, and those for the northern lakes of the present study, suggest that northern DR whitefish lakes can reach almost as high fish density and biomass as vendace lakes at lower latitudes. However, this comparison is confused by differing fishing pressure: the DR whitefish populations are almost unfished but vendace populations are heavily exploited. The total biomass level of unfished vendace and smelt stocks remains unknown.

6. Future research

6.1 Southern lakes

In the southern eutrophic lakes, hydroacoustics and trawling proved to be an applicable assessment method for smelt. It is highly valuable, when one wants to monitor the food-web effects of lake restoration, such as biomanipulation and hypolimnetical oxygenation, in smelt-dominated lakes. This kind of monitoring is under way in the Enonselkä basin of L. Vesijärvi, where the effects of 8-year-lasting hypolimnetical aeration are studied extensively. The hydroacoustics has already revealed very unexpected responses of smelt population to the disappearance of the cool-water hypolimnion (Malinen & Vinni 2016). The acoustic data together with diet analyses of fish and versatile data from other trophic levels (Kuoppamäki 2016) makes it possible to study the dynamics of the pelagic food-web and its responses to restoration measures.

Hydroacoustics has proved to be valuable also in the monitoring of L. Tuusulanjärvi, where several restoration measures are carried out (Hietala 2017). Although in this lake, the acoustic estimation of total fish biomass is not possible due to a large proportion of shallow areas, it gives valuable information on the composition of the pelagic fish community. Long time series enables investigation concerning the dynamics of smelt population, such as the factors determining year-class strength. Interestingly, hydroacoustics appears to be an applicable method also for estimating the density of young-of-the-year pikeperch and hence the strength of a year-class in this lake. This would be a novel approach. Furthermore, acoustic data may also give a new insights into interactions between smelt and pikeperch.

6.2 Northern lakes

Although the present study revealed the superiority of autumn over mid-summer, the optimal timing and the duration of the sampling window remains still unclear. The most accurate estimates of the fish density and biomass (of the whole lake) are achieved at the moment when the pelagic occurrence of whitefish population has its maximum. It would be informative to study the succession of pelagic whitefish density with frequent surveys during August-October. To determine the ultimate factors behind pelagic occurrence, acoustics should be complemented by monitoring of temperature, light, zooplankton succession and the diet of whitefish. The study should be preferably carried out in at least two lakes, one with a monomorphic whitefish population, and the other with polymorphic populations. The hypothesis is that zooplankton succession has stronger effect in monomorphic lakes, because there are better possibilities to use alternative prey resources than in polymorphic lakes, where benthic habitats are burdened with the competition of other whitefish morphs. This kind of study would highly improve understanding about the possibilities and restrictions of hydroacoustics in whitefish population estimation. For populations having a narrow sampling window and strong dependence on fluctuating zooplankton, the applicability is considerably lower than for populations which have more stabile pelagic occurrence.

Echo-surveys in some northern lakes revealed that very small-sized nine-spined stickleback may be abundant even though is only occasionally caught by a trawl, and hardly ever by gill-nets. While this species has been known to inhabit littoral areas of northern lakes (Kainulainen-Immonen 1980), hydroacoustic surveys showed that it also utilizes the pelagic zone at least during dark autumn nights. So far, the presence of nine-spined stickleback in pelagic of large lakes have not been reported in Fennoscandia but there are some observations from North American lakes (Nelson 1968, Griswold & Smith 1973). The abundance of nine-spined stickleback suggests that its role in the pelagic food web of northern Fennoscandian lakes should be explored. The present study suggests that hydroacoustics is a suitable estimation method for nine-spined stickleback and the data already collected from the northern lakes should enable the estimation of its pelagic density. One forthcoming study will focus on the estimation of density of nine-spined stickleback and exploring its possible effects on higher (brown trout) and lower (zooplankton) trophic levels.

7. Conclusions

The present study revealed that there are many fundamental differences in the hydroacoustic fish stock assessment between southern smelt lakes and northern whitefish lakes (Table 3). Remarkable differences exist in suitable seasons and diel periods for a survey and in the most serious sources of bias. In this respect, both lake groups differ considerably from the lake type most intensively studied in Finland, vendace-dominated large lakes. The results stress that knowledge of seasonal and diel movements of target species and prior knowledge of the structure of pelagic food-web are very important prerequisites for a valid hydroacoustic survey.

In southern smelt lakes, comparable population estimates can be achieved by daytime or night-time surveys during late July-October. In turbid lakes, the acoustic sampling should always be supported by surface trawling in order to estimate approximately the fish density of the surface blind zone. If one wants to assess also young-of-the-year smelt, trawling should be extended to shallow areas outside the acoustic sampling. The existence of phantom midge larvae should be explored. In cases of abundant phantom midge population, the reverberation by larvae should be eliminated either by thresholding (low densities) or by equation 5 (high densities). Situations may also exist when elimination is not possible with the present methods. The unbiased fish sampling is important, because many other species, especially cyprinids may inhabit the pelagic zone. Fish sampling should be made with a pelagic trawl, because gill-nets produce seriously biased species distributions due to the low catchability of smelt. Night sampling may require extensive trawl sampling because the vertical distributions of young-of-the-year and older smelt are overlapping and cover the whole water column.

In northern whitefish lakes, autumn nights are the only possible timing for an acoustic survey aiming at population estimation. In lakes with polymorphic whitefish, hydroacoustics is a promising method for DR whitefish estimation but poor for LSR or SSR whitefish estimation. In lakes with monomorphic LSR whitefish, the applicability of hydroacoustics varies from good to poor depending on the pelagic occurrence of whitefish. The most relevant bias sources appeared to be the occurrence of fish in the bottom dead zone of the echosounder and in shallow areas outside the acoustic sampling. The possible contribution of very small-sized nine-spined stickleback on detected targets should be considered even if they occurred only occasionally in the catches. The conclusions about the applicability of hydroacoustics in population estimation should be treated with caution, because it was not possible to evaluate the duration of suitable time window for survey or its interannual variation with the present data. A narrow window with high year-to-year variation would seriously reduce the applicability of hydroacoustics. It would be useful to explore this topic with repeated surveys during the summer and autumn.

Table 3. Summary of differences between the three common lake groups found in Finland relative to hydroacoustic assessment.

	Southern smelt lakes	Northern whitefish lakes	Vendace lakes
Pelagic fish density	High	Low	Average
Pelagic fish biomass	Average	Low	Average
Suitability for vertical echo sounding	Average	Low-High[1]	High
Suitable diel period for survey	Day or night	Night	Night
Suitable season for survey	July-September	September	August-September (May)
Duration of sampling window	Long	Short	Long
Interannual variability in sampling window	Low	Possibly high	Low
Suitable analysis method	Echo integration, mean σ from trawl catch	Echo counting or echo integration, mean σ from TS-distribution	Echo counting or echo integration, mean σ from TS-distribution
Relevant bias sources by fish inaccessbilty[2]	Surface blind zone, shallow areas for 0+ fish	Bottom dead zone, shallow areas	-
Other bias sources			
Chaoborus reverberation	Serious	Negligible	Not reported[3]
Confusion by other species	Relevant	Relevant	Relevant
Typical confusing species	Cyprinids	Nine-spined stickleback, perch	Smelt

[1] Depending on the pelagic occurrence of whitefish population
[2] During the suitable sampling window
[3] Needs clarification in humic vendace lakes

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List of abbreviations

0+	young-of-yhe-year
CPUE	catch per unit effort
DR	densely rakered
DVM	diurnal vertical migration
ind./h	individuals per hour
ind./ha	individuals per hectare
LSR	large sparsely rakered
s_a	total area scattering coefficient (m^2/ha)
$s_a(f)$	total area scattering coefficient from fish (m^2/ha)
SSR	small sparsely rakered
thr(a)	s_v-threshold applied in computing $s_a(f)$ in the reverberation elimination method
TS	target strength (dB)
σ_{sp}	spherical cross-section (m^2)
σ_{bs}	backscattering cross-section (m^2)