

Article (refereed) - postprint

Winfield, Ian J.; van Rijn, Joey; Valley, Ray D. 2015. **Hydroacoustic quantification and assessment of spawning grounds of a lake salmonid in a eutrophicated water body.**

© 2015 Elsevier B.V.

This manuscript version is made available under the CC-BY-NC-ND 4.0 license <http://creativecommons.org/licenses/by-nc-nd/4.0/>



This version available <http://nora.nerc.ac.uk/509137/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

NOTICE: this is the author's version of a work that was accepted for publication in *Ecological Informatics*. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in *Ecological Informatics* (2015), 30. 235-240. [10.1016/j.ecoinf.2015.05.009](https://doi.org/10.1016/j.ecoinf.2015.05.009)

www.elsevier.com/

Contact CEH NORA team at
noraceh@ceh.ac.uk

Hydroacoustic quantification and assessment of spawning grounds of a lake salmonid in a eutrophicated water body

Ian J Winfield^{a,*}, Joey van Rijn^b, Ray D. Valley^c

^a Lake Ecosystems Group, Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, U.K.

^b HAS Den Bosch, University of Applied Sciences, Postbus 90108, 5200 MA, 's-Hertogenbosch, The Netherlands

^c Navico Inc. 1229 Tyler St. NE #120, Minneapolis, MN USA, 55413

* Corresponding author e-mail address: ijw@ceh.ac.uk (Ian J. Winfield)

Abstract

Accurate information on the location and condition of spawning grounds of environmentally-demanding lithophilic fish species, which may use only a very small area of their habitat for spawning, is critical to their conservation and fisheries management but is frequently lacking. Here, the new hydroacoustic system BioBase, which enables the rapid characterisation of features including lake bottom hardness (with soft, medium hard and hard bottoms represented by values of 0 to 0.25, 0.25 to 0.40, and 0.40 to 0.50, respectively), was applied to known spawning grounds of Arctic charr (*Salvelinus alpinus*) in the north basin of the eutrophicated lake of Windermere, U.K. The output of BioBase was successfully ground-truthed using an independent video-based system ($r^2 = 0.48$, $F = 17.705$, $p < 0.001$) and depth and bottom hardness descriptive statistics were produced for six spawning grounds. Average depth ranged from 9.4 m (North Thompson Holme) to 38.5 m (Balla Wray), while average bottom hardness ranged from 0.254 (Low Wray Bay) to 0.303 (North Thompson Holme). Detailed visual outputs were also produced for contrasting shallow (North Thompson Holme) and deep (Holbeck Point) spawning grounds, both of which showed high within-site spatial variation in bottom hardness and thus in suitability for spawning. Findings were consistent with earlier, less quantitative, interpretations of the possible effects of eutrophication and associated increased deposition of fine sediments on local Arctic charr reproduction.

Keywords: Arctic charr, bottom typing, *Salvelinus alpinus*, sedimentation, spatial distribution, Windermere

1. Introduction

Fish are highly mobile and highly selective in their use of habitat, especially in their use of spawning grounds in lakes (Winfield, 2004). Lithophilic species such as members of the widespread genera *Coregonus*, *Salmo* and *Salvelinus* require gravel or other hard substrates for spawning and as a result may use only a fraction of the total habitat for such purposes, even within the littoral zone where erosive processes often dominate (Low *et al.*, 2011). Furthermore, the quality of such limited spawning areas is particularly sensitive to the local deposition of fine sediments and as a result the

widespread environmental problem of eutrophication has frequently led to declines in recruitment and even to the local extinction of a number of lithophilic species (e.g. Maitland *et al.*, 2007; Winfield *et al.*, 2012; Winfield *et al.*, 2013).

Accurate information on the location and condition of spawning grounds of such environmentally-demanding fish species is critical to their conservation and fisheries management. In lakes where significant commercial or sport fisheries occur, valuable background information may be derived from the fishing community. However, such information rarely extends to a knowledge of the condition of the spawning grounds and is usually entirely absent in the absence of such fisheries. In such cases, appropriate knowledge usually depends on the use of laborious direct underwater observations by divers or remotely-deployed cameras (e.g. Coyle & Adams, 2011), subjective or qualitative measures that are difficult to verify or repeat (e.g. Ray & Burgman, 2006), or the use of indirect indicators such as using the spraints of opportunistic piscivores such as otters (*Lutra lutra*) to reveal the locations of inshore spawning aggregations (Hewitt & Winfield, 2013).

The technique of hydroacoustics is commonly used in lake studies of the abundance and distribution of fish (e.g. Winfield *et al.*, 2007a; Jones *et al.*, 2008), but it also has further value for investigations of lake habitats (Godlewska *et al.*, 2004). Its ability to produce rapid and highly accurate lake bathymetries and distribution maps of macrophytes has been exploited for some time (e.g. Valley *et al.*, 2005; Winfield *et al.*, 2007b; Spears *et al.*, 2009; Abukawa *et al.*, 2013), but more recent advances in hardware and particularly in software mean that hydroacoustic systems can now also generate information on the nature of the bottom substrate. For instance, Miller *et al.* (2015) recently used hydroacoustics in a multi-technique revisit to the spawning grounds of the salmonid Arctic charr (*Salvelinus alpinus*) in the lake of Windermere in north-west England, U.K. These spawning grounds were first described in qualitative detail on the basis of netting, limited observations by divers and local knowledge by Frost (1965) and are remarkable because they include both shallow inshore sites in the littoral zone and much deeper areas in offshore locations. The quantitative ability of the hydroacoustic and other systems deployed by Miller *et al.* (2015) facilitated the documentation of the impacts of several decades of eutrophication on the condition of the spawning grounds. However, although the elaborate SIMRAD Kongsberg EM3002D dual head hydroacoustic system used by Miller *et al.* (2015) was able to give 100% coverage of lake areas deeper than 5 m, it could not be deployed in the extreme inshore areas of the known inshore spawning grounds. This limitation was due to technical reasons, including the system's requirement for deployment from a relatively large vessel with associated substantial draft. In the context of studies of fish spawning grounds there is clearly a need for hydroacoustic systems which can be deployed from small vessels operating in the vitally important but shallow and logistically challenging littoral zone, ideally with a minimum of operating complexity in the field and at low cost.

Benefitting from a remarkable recent advance in consumer hydroacoustic systems developed primarily for the recreational fishing market as 'echo sounders' and from the ubiquitous advance in internet and mobile technologies, new tools have recently been developed that automate the processing and creation of aquatic habitat maps using 'off-the-shelf' echo-sounder systems with internal GPS and cloud-based software. In particular, the BioBase system (Navico Inc., 2014) has an ability to produce bathymetries and assessments of macrophytes and lake bottom characteristics from hydroacoustic data files recorded by consumer echo sounders. This has opened up new

opportunities for the crowd-sourcing of spatially-referenced environmental data at an unprecedented scale (Valley *et al.*, 2015). The ease of the field operation of the system's portable, low-cost hardware component coupled with its extremely shallow draft allows it to be used effectively wherever a shallow-draft vessel can be deployed.

In this study, we deploy the BioBase system on the known spawning grounds of Arctic charr in the north basin of Windermere in order to allow us to extend the observations of Miller *et al.* (2015) to make more effective use of hydroacoustic data to assess bottom conditions and to encompass the entire spawning grounds up to the approximately 1 m depth contour. In addition, we use an independent visual assessment of spawning ground condition to ground-truth these hydroacoustic observations and so for the first time produce comprehensive assessments of the current conditions of the spawning grounds with respect to eutrophication-associated impacts from sedimentation.

2. Methods

2.1 Study site

Windermere is situated (54°22'N, 2°56'W; altitude 39 m) in the English Lake District, U.K. It comprises a mesotrophic north basin (surface area 8.1 km², maximum depth 64 m) and a eutrophic south basin (surface area 6.7 km², maximum depth 44 m). The lake level is partially controlled by a weir at the southern end which over-rides natural drainage patterns, although these effects are limited. The first detailed observations of Arctic charr spawning in the lake were made by Frost (1965) who concluded that shallow spawning grounds ranged from 1 to 3 m depth, while deeper spawning grounds ranged from 15 to 20 m depth. The spawning substrate for shallow-water sites was described as always hard with a range of particle sizes from sand through to large stones or small boulders up to 0.25 m in diameter, with some areas also having some silt or a few macrophytes in the form of *Littorella* sp. Deep-water sites were characterised as having a stony bottom. The lake has subsequently experienced significant cultural eutrophication and while increased nutrient levels have been most pronounced in its south basin, some effects are also evident in the north basin (Winfield *et al.*, 2008). Nevertheless, a recent review of historic and contemporary evidence from netting spawning surveys collated by Miller *et al.* (2015) recorded Arctic charr at the four locations of Holbeck Point, Low Wray Bay, North Thompson Holme and Red Nab of the original six demonstrated or putative spawning grounds described in the north basin by Frost (1965). No evidence was found for contemporary use of the remaining two locations of Balla Wray and Meregarth, although spawning individuals were recorded from a site just west of the latter location.

2.2 The BioBase system

2.2.1 Overview

BioBase (www.cibiobase.com) is a cloud-based GIS software system that analyses hydroacoustic and GPS signals from Lowrance™ High Definition System (HDS®) consumer echo sounders (www.lowrance.com) to produce data on depth, macrophyte presence/absence, macrophyte height and bottom hardness.

The specific echo sounder used in this study was a Lowrance Gen 2 HDS-5, operating at a sound frequency of 200 kHz with a beam angle of 20°. Pulse rates are user-defined and typically vary between 10 and 20 pulses s^{-1} , with 15 pulses s^{-1} used in the present study. Pulse width is not user-controlled but is dynamic and varies depending on depth. BioBase algorithms are optimised at user settings of 3200 bytes s^{-1} and a range window set to 'Auto' which maximises the resolution of the acoustic envelope at the full range of depths sampled. GPS signals were European Geostationary Navigation Overlay Service (EGNOS)-corrected. In the field, hydroacoustic and GPS signals were logged to data storage cards (.sl2 format and subsequently uploaded post-survey to centralised servers of the BioBase system for analysis using the January 2014 release of BioBase.

GPS position is typically recorded every 1 s and bottom features from pulses that elapse between positional reports are averaged for each coordinate/data point. Therefore, the attribute value (i.e. depth, macrophyte presence/absence, macrophyte height and bottom hardness) of each data point along a travelled path comprises a summary of 5 to 30 pulses. Each pulse is subjected to a quality test to determine whether features can be extracted and, if so, it is sent on to feature detection algorithms. Those failing quality assurance tests are removed from the set used for subsequent analysis and the production of summary statistics.

2.2.2 Bottom hardness

Bottom hardness is determined by the amplitude of the second bottom echo. Relative bottom hardness values vary continuously with harder bottoms (rock, sand, gravel or hard clay) generating higher second echo amplitudes than soft bottoms (mud, silt) from which a second echo may in fact not be generated due to rapid signal attenuation. BioBase bottom hardness values are on a relative scale ranging with values of 0 to 0.25 representing soft bottoms, 0.25 to 0.40 medium hardness bottoms, and 0.40 to 0.50 representing hard bottoms. Minimum depth for bottom hardness detection was 0.73 m below the transducer face.

2.2.3 Map creation

Processed values for depth, macrophyte presence/absence, macrophyte height and bottom hardness were automatically sent to an ordinary point kriging algorithm in BioBase that predicted values in unsampled locations based on the geostatistical relationship of the input points. The kriging algorithm was an 'exact' interpolator in locations where sample points were close in proximity (approximately 1 to 5 m) and did not vary widely. Kriging smoothed bottom feature values where the variability of neighbourhood points was high.

2.2. Assessment of system performance

The ability of the bottom hardness algorithm of BioBase in terms of its ability to identify areas of lake bottom offering suitable spawning habitat for Arctic charr was ground-truthed by comparing its hydroacoustically derived hardness values with visually derived suitability values. The latter were generated by a technique developed by Coyle & Adams (2011) for the assessment of underwater

video recordings in the context of vendace (*Coregonus albula*) spawning habitat requirements, which are similar to those of Arctic charr. This assessment procedure is based on the presence of hard substrate types such as gravels, pebbles, cobbles and boulders, but also takes into account the presence of fine sediments which are unsuitable for spawning. Such analysis was applied to 22 spot underwater video recordings collected simultaneously with corresponding stationary hydroacoustic recordings made using a Lowrance Gen 2 HDS-5 echo sounder (Lowrance, www.lowrance.com) in conjunction with BioBase during daylight on and near the inshore spawning ground of North Thompson Holme in the lake's north basin. The video recordings were made using an underwater video camera deployed near the lake bottom at depths from 1.2 to 13.4 m for periods of 3 minutes at each location within the overall site, during which the camera was rotated through 360° in every minute of observation. Note that macrophytes were effectively absent from the study site at the time of the assessment. Further details are given in van Rijn (2013), although note that this earlier study used a beta version of the current bottom hardness algorithm which is now improved in performance (RDV, unpublished data).

2.3 Assessment of spawning grounds

A series of hydroacoustic surveys was performed at all Arctic charr spawning grounds in the north basin of Windermere (i.e. Balla Wray, Holbeck Point, Low Wray Bay, Meregarth, North Thompson Holme and Red Nab; for further details see Miller *et al.* (2015)) during daylight in the spring of 2013 using the same Lowrance and BioBase system described above. Full methodological details are provided in van Rijn (2013), but essentially the system was deployed with a transducer depth of 0.5 m at a speed of 8 km h⁻¹ over the spawning grounds and adjacent areas. At each location, a series of parallel and perpendicular transects with respect to the nearest shoreline was conducted up to the minimum safe operating depth of the vessel of approximately 1 m. Bottom hardness values were generated at horizontal spacings of approximately every 2 m and interpolated via a simple kriging model in BioBase. Summary data are presented for all spawning grounds, but detailed visual outputs are presented here only for the shallow spawning ground of North Thompson Holme and the deep spawning ground of Holbeck Point. Both locations continue to be used by spawning Arctic charr (Miller *et al.*, 2015). Note that, as for during the assessment of system performance, macrophytes were effectively absent from the study site at the time of the surveys and so are not considered further here.

3. Results

3.1 Assessment of system performance

A significant ($r^2 = 0.48$, $F = 17.705$, $p < 0.001$) simple linear regression was observed between hydroacoustically derived bottom hardness values and visually derived spawning suitability values as shown in Fig. 1. Data points spanned almost all of the possible ranges of each measure, with no outliers from the observed relationship.

3.2 Assessment of spawning grounds

Depth and bottom hardness descriptive statistics for the six spawning grounds of the north basin of Windermere originally described by Frost (1965) are given in Table 1. Average depth ranged from 9.4 m (North Thompson Holme) to 38.5 m (Balla Wray), while average bottom hardness ranged from 0.254 (Low Wray Bay) to 0.303 (North Thompson Holme).

Detailed visual outputs for the bathymetrically-contrasting spawning grounds of North Thompson Holme and Holbeck Point are shown in Figs 2 and 3, respectively. The previously known gently shelving and relatively shallow bathymetry of North Thompson Holme is clearly illustrated, but within-site variation in bottom hardness and thus in suitability for spawning is revealed for the first time. North Thompson Holme exhibited the highest average bottom hardness value of all spawning grounds, yet only 7% of even this area had individual gridded point values greater than 0.40 representing hard bottom conditions. Relatively hard bottom is present in both the deepest and the shallowest areas of the spawning ground originally defined by Frost (1965), but the hardest bottom area which corresponds to optimal lithophilic spawning conditions under the visual assessment of Coyle & Adams (2011) is localised to the south-east part of the ground. In contrast, bathymetry at Holbeck Point is much steeper and relatively hard areas are limited to the south-east area of this spawning ground. Although the original description of this site by Frost (1965) refers to localised suitable spawning conditions at depth, there is no indication of such within the present hydroacoustic derived measures of bottom hardness with no individual gridded point values greater than 0.40.

4. Discussion

4.1 Assessment of system performance

Hydroacoustic data analysis using the BioBase system proved to be extremely rapid and needed a minimum of user involvement, with no requirement for repeated 'tuning' of algorithms commonly required by other approaches involving more sophisticated systems (e.g. Winfield *et al.* 2007b; Abukawa *et al.*, 2013). As such, it rapidly generated highly objective results independent of potential observer bias.

The strength and simplicity of the positive relationship empirically observed between hydroacoustically derived bottom hardness values and visually derived suitability values was remarkable. Despite substantial heterogeneity in bottom conditions within the study area, no outliers from the overall relationship were observed. Such agreement is particularly encouraging given the heterogeneity in bottom hardness observed inshore, the substantial range of depth values (1.2 to 13.4 m) over which the relationship was observed, and the fact that changing bottom contours can potentially complicate the analysis of hydroacoustic data (Simmonds & MacLennan, 2005). Evidently, the bottom hardness algorithm of BioBase was robust against all such complications under the environmental conditions of this study.

4.2 Assessment of spawning grounds

The present study successfully used ground-truthed hydroacoustics to extend the observations of Miller *et al.* (2015) to encompass the entire spawning grounds of Arctic charr in the north basin of

Windermere. While qualitative comparisons between these two studies show that results are similar for common surveyed areas, the new observations are more quantitative in terms of bottom hardness and very importantly extend up to the approximately 1 m depth contour. For the first time, accurate statistics were produced on the depths and bottom hardness values of each of the six spawning grounds first described by Frost (1965). Bottom hardness values have no historical precedent and so such comparisons cannot be made, but it is clear that depth characteristics of the spawning grounds are more complex than originally described by Frost (1965) who was undoubtedly working with relatively simple equipment and techniques. Although such physical complexity can be usefully summarised into the simple statistics of averages, minima and maxima, it is far better and more usefully described by detailed three-dimensional maps as presented here for the shallow spawning ground of North Thompson Holme and the deep spawning ground of Holbeck Point.

In both locations, areas of hard bottom were very localised and in each comprised only 7% or less of the spawning grounds' entire areas as defined by Frost (1965). Such relatively limited distributions of hard bottom areas may be a purely natural feature of lake habitats, a possibility which can only be determined by further such surveys at pristine lakes. Alternatively, they may reflect the impacts of sedimentation associated with eutrophication during recent decades at Windermere as described by Winfield *et al.* (2008). Such postulated temporal changes cannot be addressed in detail due to a lack of historical data, but the failure of the present survey to detect suitable spawning conditions at depth at Holbeck Point despite earlier direct observations of such by divers up to the mid-1960s reported by Frost (1965) suggests that local sedimentation has indeed occurred. The dangers of eutrophication-associated sedimentation have been highlighted in general terms for Arctic charr by Low *et al.* (2011) and such impacts were concluded to have contributed to a decline of this species observed in Windermere in recent years by Miller *et al.* (2015). Although Frost (1965) reported fish spawning on a gravel tongue at depths of between 9.8 and 28.0 m, more recent biological surveys have notably only found fish spawning at 10.0 m (Miller *et al.*, 2015) which approximately equates to the maximum depth of hard bottom areas observed in the present study. The fact that in Windermere such deep spawning Arctic charr are the rarer spring-spawning sub-populations (Corrigan *et al.*, 2011) amplifies the conservation implications of any such deteriorations in spawning ground conditions.

4.3 Next steps

The present study has clearly demonstrated the technical feasibility and scientific robustness of the BioBase system for the rapid hydroacoustic assessment of lake bottom conditions with respect to the demanding environmental requirements of lithophilic spawners. As such, it meets the pressing need for a hydroacoustic system which can be deployed from a small vessel operating in the vitally important but shallow and logistically challenging littoral zone. High maneuverability in shallow areas allows for greater coverage of patchy habitats and thus more precise delineation (and thus potentially protection) of suitable sites. Moreover, the system's minimal operating complexity in the field, the low cost of 'off-the-shelf' echo sounders and automated cloud data processing mean that that it is eminently suitable for use in citizen science research and monitoring programmes which are now making major contributions to environmental management on a global basis (Silvertown, 2009). For freshwater habitats, an outstanding example of such work is the 1974-onwards voluntary measurement of lake water clarity throughout Michigan, U.S.A., which has developed into an

invaluable extensive and long-term dataset (Bruhn & Soranno, 2005). Although BioBase was initially developed to map macrophytes, its more recently developed capacity to extract bottom hardness information from the same data files means that, for example, such macrophyte monitoring programmes can also contribute to assessing local sedimentation associated with eutrophication or simply locating potential fish spawning habitat. As for macrophytes, the ability of BioBase to use opportunistically collected data for bottom analyses greatly increases its utility in the citizen science arena. In the future, the approach would benefit from the development of standardised survey protocols to increase further the comparability and thus value of results. Such standardisation is now commonplace within hydroacoustic studies of fish populations (e.g. Bean, 2003; Hateley *et al.*, 2013) and ensures direct comparability over time and space such that results can now be robustly compared at national (e.g. Winfield *et al.*, 2013) and international (e.g. Emmrich *et al.*, 2012) scales.

5. Conclusion

This study has shown that hydroacoustics can be used very effectively, efficiently and rapidly to describe, assess and monitor the characteristics of lake bottoms even in the previously intractable shallow areas of the littoral zone. Furthermore, such observations can be performed to very high spatial resolutions and produce highly visual outputs which are readily presentable to non-specialists. The technique can also make effective use of the great potential of citizen science which is playing an increasingly important role in environmental and fisheries management around the world.

6. Acknowledgements

We thank our colleagues Ben James and Janice Fletcher for their assistance in the field and Helen Miller of the University of Southampton for allowing the present use of her polygons of the spawning grounds. JvR was funded in part through the Erasmus programme of the European Union.

References

- Abukawa, K., Yamamuro, M., Kikvidze, Z., Asada, A., Xu, C. & Sugimoto, K. (2013). Assessing the biomass and distribution of submerged aquatic vegetation using multibeam echo sounding in Lake Towada, Japan. *Limnology* **14**, 39-42.
- Bean, C.W. (2003). A standardised survey and monitoring protocol for the assessment of Arctic charr, *Salvelinus alpinus* L., populations in the UK. *Scottish Natural Heritage Research, Survey and Monitoring Report*. Scottish Natural Heritage, Edinburgh, U.K.
- Bruhn, I.C. & Soranno P.A. (2005). Long term (1974-2001) volunteer monitoring of water clarity trends in Michigan lakes and their relation to ecoregion and land use/cover. *Lake and Reservoir Management* **21**, 10-23.
- Corrigan, L.J., Lucas, M.C., Winfield, I.J. & Hoelzel, R.A. (2011). Environmental factors associated with genetic and phenotypic divergence among sympatric populations of Arctic charr (*Salvelinus alpinus*). *Journal of Evolutionary Biology* **24**, 1906-1917.

Coyle, S. & Adams, C.E. (2011). Development of a methodology for the assessment of the quality of vendace spawning substrate and its application to sites in Scotland and northern England. *Scottish Natural Heritage Commissioned Report No. 308*.

Emmrich, M., Winfield, I. J., Guillard, J., Rustadbakken, A., Vergés, C., Volta, P., Jeppesen, E., Lauridsen, T. L., Brucet, S., Holmgren, K., Argillier, A. & Mehner, T. (2012). Strong correspondence between gillnet catch per unit effort and hydroacoustically derived fish biomass in stratified lakes. *Freshwater Biology* **57**, 2436-2448.

Frost, W. E. (1965). Breeding habits of Windermere charr, *Salvelinus willughbii* (Günther) and their bearing on speciation of these fish. *Proceedings of the Royal Society, Series B* **163**, 232–284.

Godlewska, M., Swierzowski, A. & Winfield, I. J. (2004). Hydroacoustics as a tool for studies of fish and their habitat. *Ecohydrology & Hydrobiology* **4**, 417-427.

Hateley, J., Clabburn, P., Drastik, V., Godlewska, M., Guillard, J., Kubecka, J., Morrissey, E., Thackeray, S. J. & Winfield, I. J. (2013). Standardisation of hydroacoustic techniques for fish in fresh waters. In: Papadakis, J. S. & Bjørnø, L. (editors) *Proceedings of the First Underwater Acoustics Conference*. FORTH Institute of Applied & Computational Mathematics. Heraklion, Greece. pp. 1595-1600.

Hewitt, S. M. & Winfield, I. J. (2013). Location of whitefish (*Coregonus lavaretus*) spawning grounds using Eurasian otter (*Lutra lutra*) spraints and prey remains. *Advances in Limnology* **64**, 333-343.

Jones, I. D., Winfield, I. J. & Carse, F. (2008). Assessment of long-term changes in habitat availability for Arctic charr (*Salvelinus alpinus*) in a temperate lake using oxygen profiles and hydroacoustic surveys. *Freshwater Biology* **53**, 393-402.

Low, J. J., Igoe, F., Davenport, J. & Harrison, S. S. C. (2011). Littoral spawning habitats of three southern Arctic charr (*Salvelinus alpinus* L.) populations. *Ecology of Freshwater Fish* **20**, 537–547.

Maitland, P. S., Winfield, I. J., McCarthy, I. D. & Igoe, F. (2007). The status of Arctic charr *Salvelinus alpinus* in Britain and Ireland. *Ecology of Freshwater Fish* **16**, 6-19.

Miller, H., Winfield, I. J., Fletcher, J. M., James, J. B., van Rijn, J., Bull, J. M. & Cotterill, C. J. (2015). Distribution, characteristics and condition of Arctic charr (*Salvelinus alpinus*) spawning grounds in a differentially eutrophicated twin-basin lake. *Ecology of Freshwater Fish* **24**, 32-43. DOI: 10.1111/eff.12122.

Navico Inc. (2014). BioBase User Reference Guide. *Minneapolis, MN, USA*.

Ray, N. & Burgam, M. A. (2006). Subjective uncertainties in habitat suitability maps. *Ecological Modelling* **195**, 172-186.

Silvertown, J. (2009). A new dawn for citizen science. *Trends in Ecology & Evolution* **24**, 467-471.

Simmonds, J. & MacLennan, D. N. (2005). Fisheries Acoustics: Theory and Practice, 2nd Edition. Wiley-Blackwell, Oxford, UK.

Spears, B. M., Gunn, I. D. M., Carvalho, L., Winfield, I. J., Dudley, B., Murphy, K. & May, L. (2009). An evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven, Scotland. *Aquatic Botany* **91**, 75-81.

Valley, R. D., Drake, M. T. & Anderson, C. S. (2005). Evaluation of alternative interpolation techniques for the mapping of remotely-sensed submersed vegetation abundance. *Aquatic Botany* **81**, 13–25.

Valley, R. D., Johnson, M. B., Dustin, D. L., Jones, K. D., Lauenstein, M. R., & Nawrocki, J. (2015). Combining hydroacoustic and point-intercept survey methods to assess aquatic plant species abundance patterns and community dominance. *Journal of Aquatic Plant Management* **53**, 121-129.

van Rijn, J. (2013). The state of spawning grounds: assessment of the Arctic charr (*Salvelinus alpinus*) spawning grounds in Windermere, U.K. *Unpublished undergraduate research project*. 's-Hertogenbosch, The Netherlands: HAS Den Bosch, University of Applied Sciences. 41 pp.

Winfield, I. J. (2004). Fish in the littoral zone: ecology, threats and management. *Limnologia* **34**, 124-131.

Winfield, I. J., Fletcher, J. M. & James, J. B. (2007a). Seasonal variability in the abundance of Arctic charr (*Salvelinus alpinus* (L.)) recorded using hydroacoustics in Windermere, UK and its implications for survey design. *Ecology of Freshwater Fish* **16**, 64-69.

Winfield, I. J., Yallop, M. L., Onoufriou, C., O'Connell, M. J., Godlewska, M. Ward, R. M. & Brown, A. F. (2007b). Assessment in two shallow lakes of a hydroacoustic system for surveying aquatic macrophytes. *Hydrobiologia* **584**, 111-119.

Winfield, I. J., Fletcher, J. M. & James, J. B. (2008). The Arctic charr (*Salvelinus alpinus*) populations of Windermere, U.K.: population trends associated with eutrophication, climate change and increased abundance of roach (*Rutilus rutilus*). *Environmental Biology of Fishes* **83**, 25-35.

Winfield, I. J., Adams, C. E., Bean, C. W., Durie, N. C. Fletcher, J. M., Gowans, A. R., Harrod, C., James, J. B., Lyle, A. A., Maitland, P. S., Thompson, C. & Verspoor, E. (2012). Conservation of the vendace (*Coregonus albula*), the U.K.'s rarest freshwater fish. *Advances in Limnology* **63**, 547-559.

Winfield, I. J., Bean, C. W., Gorst, J., Gowans, A. R. D., Robinson, M. & Thomas, R. (2013). Assessment and conservation of whitefish (*Coregonus lavaretus*) in the U.K. *Advances in Limnology* **64**, 305-321.

Table 1: Average, minimum and maximum depths and bottom hardness values recorded at the spawning grounds of the north basin of Windermere originally described by Frost (1965).

Spawning ground	Depth (m)			Bottom hardness value		
	Average	Minimum	Maximum	Average	Minimum	Maximum
Balla Wray	38.5	8.9	59.3	0.255	0.232	0.342
Holbeck Point	18.5	0.6	49.0	0.267	0.225	0.388
Low Wray Bay	11.5,	0.5	32.0	0.254	0.101	0.410
Meregarth	29.5	19.7	41.3	0.267	0.242	0.297
North Thompson Holme	9.4	1.4	20.1	0.303	0.104	0.478
Red Nab	19.5	0.6	46.2	0.274	0.222	0.421

Figure 1: Comparison of hydroacoustically derived bottom hardness values with visually derived spawning suitability values for 22 sites on and near the inshore spawning ground of North Thompson Holme, including a fitted simple linear regression ($r^2 = 0.48$, $F = 17.705$, $p < 0.001$).

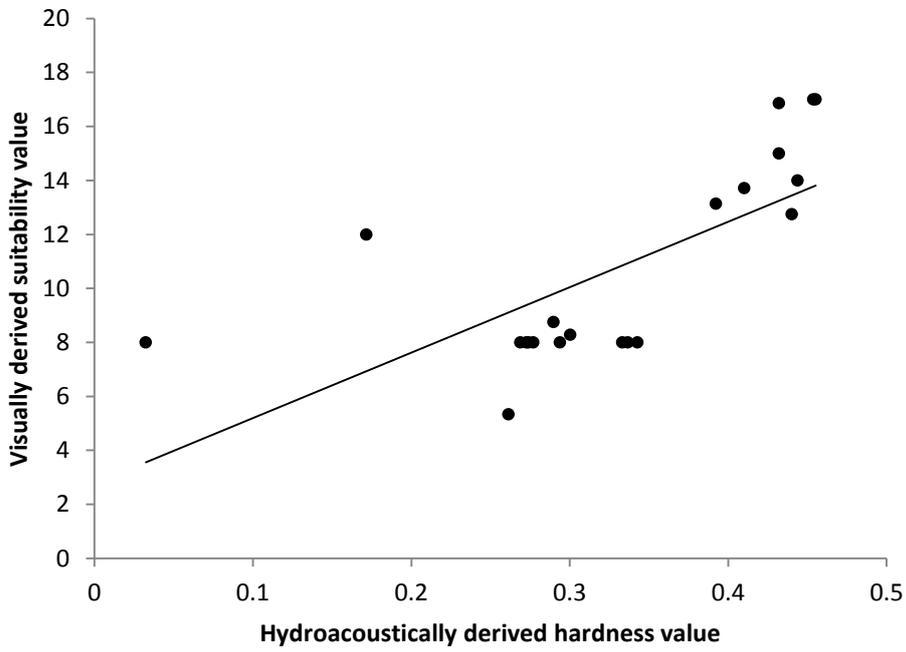


Figure 2: Three-dimensional map of bottom hardness overlain on bathymetry at and near the shallow spawning ground of North Thompson Holme. Bottom hardness varies from 0.00 (very soft, represented by dark blue) to 0.50 (very hard, represented by dark orange). X and Y axes represent Transverse Mercator projections (British National Grid Datum). The specific area of the spawning ground as originally described by Frost (1965) is shown enclosed within a continuous line.

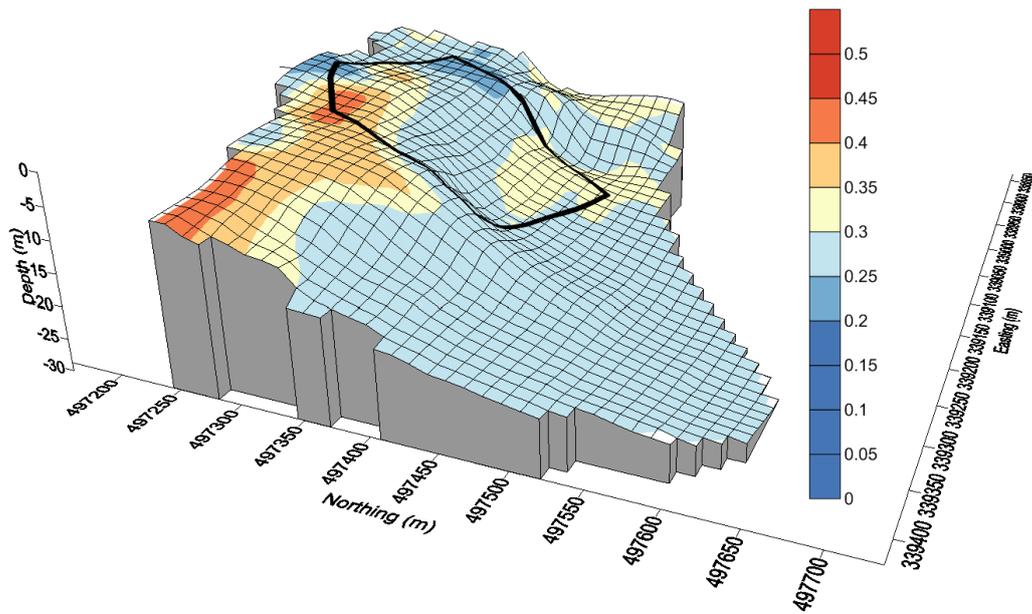


Figure 3: Three-dimensional map of bottom hardness overlain on bathymetry at and near the deep spawning ground of Holbeck Point. Bottom hardness varies from 0.00 (very soft, represented by dark blue) to 0.50 (very hard, represented by dark orange). X and Y axes represent Transverse Mercator projections (British National Grid Datum). The specific area of the spawning ground as originally described by Frost (1965) is shown enclosed within a continuous line.

